Atlantic White Cedar Restoration Ecology and Management

Proceedings of a Symposium
Christopher Newport University
May 31 - June 2, 2000

Editors
Robert B. Atkinson
Robert T. Belcher
David A. Brown
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ATLANTIC WHITE CEDAR
RESTORATION ECOLOGY AND MANAGEMENT

Proceedings of a symposium held
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Biography
Education: B.A. Brooklyn College, M.A. Columbia University (Microbial Genetics), Ph.D. State University of NY at Binghamton (Ecology and Limnology).
Current Position: Director of the Swamp Research Center in Woods Hole, MA, Laderman conducts research at the Woods Hole Marine Biological Laboratory and is a faculty affiliate at the Yale Peabody Museum. From 1990-2002 she was research affiliate and lecturer in wetland ecology and restoration at the School of Forestry & Environmental Studies, Yale University.

Dr. Laderman's teaching and professional consulting focuses on wetland ecology, natural resource management, and environmental restoration. Her research at the Woods Hole Marine Biological Laboratory and Yale University has centered on the structure, function, and management of acid freshwater wetlands. She has authored three books on Atlantic white cedar (AWC) and other coastal forests; has organized and chaired several cedar-related international and national conferences, and serves as advisor on freshwater wetland and landuse issues to federal, state and local government and private agencies. Selected publications can be found in the Bibliography within this volume.

Laderman directs the AWC Network, conducting a 13-state all-taxon biodiversity survey of AWC wetlands rangewide. The Network is currently creating interactive digital libraries and websites of the system's higher plants, protists and field sites. Recent work included the cloning of a gene from a protozoan-algal symbiont isolated from field collections.

She most recently has served as a director of the New Haven Land Trust, as a member of the Cranberry Bog Subcommittee (advisory to Falmouth Township, MA), the Environmental Advisory Commission for the City of New Haven, CT. and the scientific advisory boards of the Atlantic White Cedar Alliance and the Audubon Coastal Center (Milford, CT). Affiliations include: Society of Wetland Scientists, Society for Environmental Restoration, Assoc. of State Wetland Managers, Massachusetts Assoc. of Wetland Scientists.

Personal Statement by Dr. Laderman

I first fell under the spell of Atlantic white cedar swamps while hunting for rotifers – a varied group of microscopic multicellular animalcules known to inhabit acid waters. These early studies led to a lifelong fascination with the unique freshwater wetland forests dominated by the fragrant brooding *Chamaecyparis thyoides*. My first (and highly valued) field and lab assistants were my husband and our children. With the three children still in grade school, I made a list of research topics that might eventually emerge from the goldmine of the cedar swamps. This list, honed, modified and amplified, has guided my research ever since. My doctoral thesis explored the ecology and evolution of cedar swamp algae. I was fortunate to be able to do my first post-doctoral work in the Department of Botany at the Smithsonian in Washington DC, intending to continue the thesis studies. However, distracted by the wealth of the National Herbarium and Library, I started work on what became the Checklist (and later, the website) of Atlantic White Cedar Flora. The need for more data led me to convene the first Atlantic White Cedar Wetlands Symposium at the Marine Biological Labs in Woods Hole, MA (1984), and international symposia on coastally restricted forests in Yokohama, Japan (INTECOL 1990) and at the Yale University School of Forestry and Environmental Studies in New Haven CT (1991). Various publications (listed below) grew from each conference. Our seven grandchildren now share in the continuing adventure of cedar swamp exploration. Aside from the cedar wetland work, my most satisfying professional endeavor has been directing the distinguished lecturer series “The Restoration Agenda” (1994-2001) at the Yale School of Forestry and Environmental Studies.

With warm gratitude, I credit all my colleagues in the very special world of Atlantic white cedar studies who provide the fabric and base for our continuing efforts in the field.

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WHY DOES THE FRESHWATER GENUS *CHAMAECYPARIS* HUG MARINE COASTS?

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Abstract: Chamaecyparis is a catastrophe-dependent, stress-adapted, extremophilic keystone species. A few conifers in the Northern Hemisphere are found in nature no more than 250 km from continental margins. More than half of these trees are the seven species of the genus *Chamaecyparis.* The issues addressed here are: What enables this genus to grow in challenging habitats? Why don't these species naturalize inland? What characteristics allow them to succeed only near salt water? Which are the stresses and catastrophes apparently critical to and favored by each species? What environmental factors limit and draw these and other coastally restricted forests to marine rims? Though they differ in maximum height, girth and age, in form, habitat, environmental range and forest structure, they share many similar features. Despite their maritime locations, none of the species thrive in saline waters and soils. A strange combination of qualities is seen: the trees are catastrophe-dependent, stress-tolerant with broad niche potential, but are poor competitors in high-nutrient "easy" sites. Paradoxically, they all possess moisture-conserving features usually associated with arid lands. The high humidity, frequent salt-laden fogs and precipitation, giant heat-sink effects and violent storms are coastal phenomena that favor *Chamaecyparis*. It is probable that mineral-rich aerosols are the key to the genus' survival. The trees are endemics, poor dispersers, poor competitors restricted to dominance in increasingly fragmented islands. Their strategy is success through failure. They survive where, and only where, others cannot. And only when the mature trees fail – when windthrow, fire or harvest create canopy openings – are conditions suitable for their reproductive success.

Key Words: coastally restricted, catastrophe dependent, conifer, ecological apoptosis, extremophilic, forest, stress-tolerant, keystone species

INTRODUCTION

This study is an outgrowth of an investigation into the unusual ecology and biogeography of the wetland conifer *Chamaecyparis thyoides*, commonly known as Atlantic white cedar (AWC) or coast cedar. There are six close relatives of AWC (all in the coniferous genus *Chamaecyparis)* which are found in nature no more than 250 km from the east or west rims of the temperate northern Pacific Ocean. *Chamaecyparis thyoides*, sole representative of the genus bordering the Atlantic Ocean, is native only to a similar band along the United States coast (figure 1; tables 1 and 2). Members of the genus *Chamaecyparis* are quite similar morphologically (figure 2), but they are found in such a variety of habitats (tables 1, 2, and 3; box 1), it is hard to see commonalties of habitat, other than proximity to seacoasts. Soils, altitude and temperature range, and associated vegetation differ widely. The primary objective of this article is to explore the factors that may account for the peculiar and restricted geographic distribution of this genus. A more extended treatment of this subject, dealing with coastally restricted forest types of the Northern Hemisphere, is presented in *Freshwater Forests of Continental Margins* (Laderman 1998a). This paper is divided into three parts. Part I compares physical and biological properties of the species studied. Part II is a comparison of *Chamaecyparis* forest environments, including implications for species selection. Part III is a synthesis of the species-environment overviews.

Figure 1. Geographic Distribution of *Chamaecyparis* Forests. Black ink indicates the region within which each species is native. **A:** *Chamaecyparis formosensis* **B**: *C. taiwanensis* **C:** *C. lawsoniana* **D:** *C. nootkatensis* **E:** *C. obtusa* **F:** *C. pisifera* **G:** *C. thyoides* (Original map by J. Cook and F. Heide, modified by J.J. Donnette.) (Adapted from Laderman 1998a.)

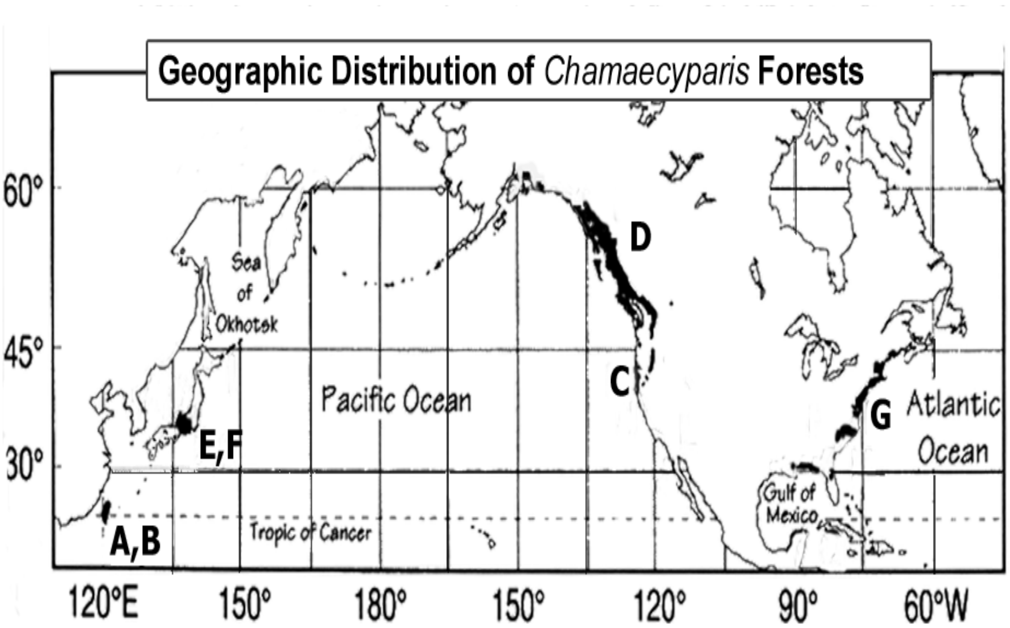

Table 1. *Chamaecyparis* forests: Site descriptions (Adapted from Laderman 1998)

Species	Country	Site Description[a]	Information Sources[b]
C. formosensis Taiwan cypress	Taiwan	Montane, moderately moist coniferous forests (often pure stands, in clouds)	Li 1963; Zobel 1998
C. taiwanensis Taiwan red cypress	Taiwan	Higher montane, well-drained coniferous forests (often pure stands, in clouds)	Li 1963; Zobel 1998
C. lawsoniana Port-Orford-cedar	USA (W)	Dry and wet, often poor soils, sand dunes, stream margins, bogs; fog common	FNA 1993; Greenup 1998; Zobel 1998
C. nootkatensis Yellow-cypress	Canada (W), USA (W)	Poor soils, bogs, disturbed sites; subalpine (S) to sea level (Alaska); high humidity	Dunsworth 1998; FNA 1993; Hennon 1998; Russell 1998; Zobel 1998
C. obtusa Hinoki cypress	Japan	Xeric sites, middle to upper slopes, ridges; soil: podzol, serpentine; warm temperate to subalpine	Yamamoto 1998; Zobel 1998
C. pisifera *Sawara cypress*	Japan	Wet or mesic sites, lower montane slopes, rocky depressions; thin, dry soils on ridges	Yamamoto 1998; Zobel 1998
C. thyoides Atlantic white cedar	USA (E)	Low-elevation acid bogs; fluctuating high water table; peat over sand soils	Eckert 1998; Laderman 1987, 1989, 1998; Stoltzfus 1998

Table 2. *Chamaecyparis* forests: Distribution[c]

	°N Latitude		Altitude (m)				
Species	Min-Max	Total Range	Min-Max	Total Range	Distance from Coast (km) Min-Max	Restricted to Coast? (<250 km)	Discontinuous Distribution[d]
C. formosensis	22°28’ - 24°49’	2°21’	850-2900	2050	8-75	Y	Y
C. taiwanensis	22°55’ - 24°46’	1°51’	1200-2800	1600	12-75	Y	Y
C. lawsoniana	40°50’ - 43°35’	2°45’	0-1950	1950	0-209	Y	Y
C. nootkatensis	41°25’ - 61°07’	19°42’	AK: 0-100	1000			
			BC: 0-1600				
			OR, WA: 600-2300		Outliers 425		
C. obtusa	30°15’ -37°10’	6°55’	10-2200 (2500 rare)	2190	0-150	Y	Y
C. pisifera	32°48’ - 39°32’	6°44’	110-2590	2480	0-150	Y	Y
C. thyoides	29°14’ - 44°20’	15°6’	0-457 avg. < 50	457	0-200 (250) avg. < 50	Y	Y

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[a] *Site description; distribution.* All entries refer to the natural condition in the native range, not to protected or horticultural situations. Most of the species will grow in a broad range of conditions if protected from competition.

[b] *Information sources.* Climatic data was also obtained from Great Britain Meteorological Office (1980) and NOAA (1992).

Notes for Table 2: Y = Yes. N = No. Avg. = Average. Blank = Information not available.

[c] *Distribution.* All entries refer to the natural condition in the native range, not to protected or horticultural situations.

[d] *Discontinuous Distribution.* “Y” indicates the species is absent from many apparently suitable habitats situated between extant stands.

Figure 2. *Chamaecyparis* morphology

(1) *C. formosensis* Branches, cones, seeds, flowers. From H.L. Li 1963.

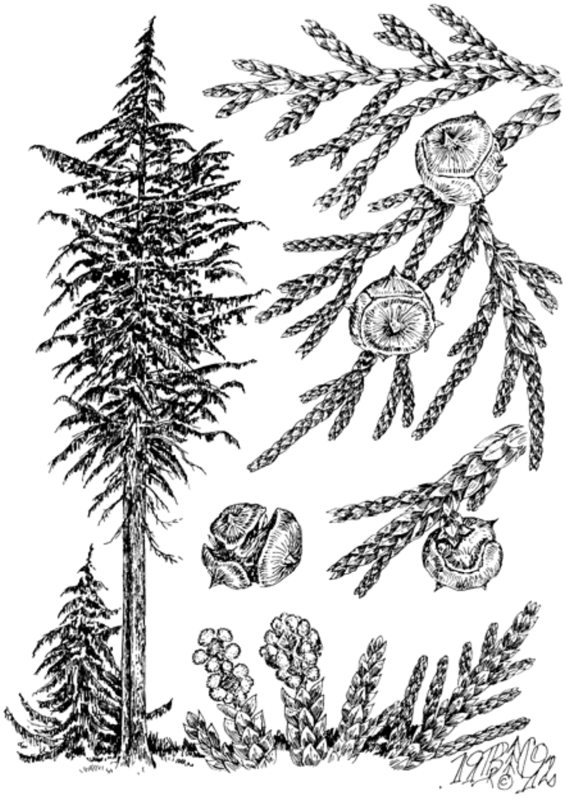
(2)a *C. taiwanensis* Tree above clouds. Original photo courtesy Paul Meyers.

(Figure 2 continued)
(2)b C. *taiwanensis* Cloud forest, trees above cloud level. (Original photo courtesy Paul Meyers.)

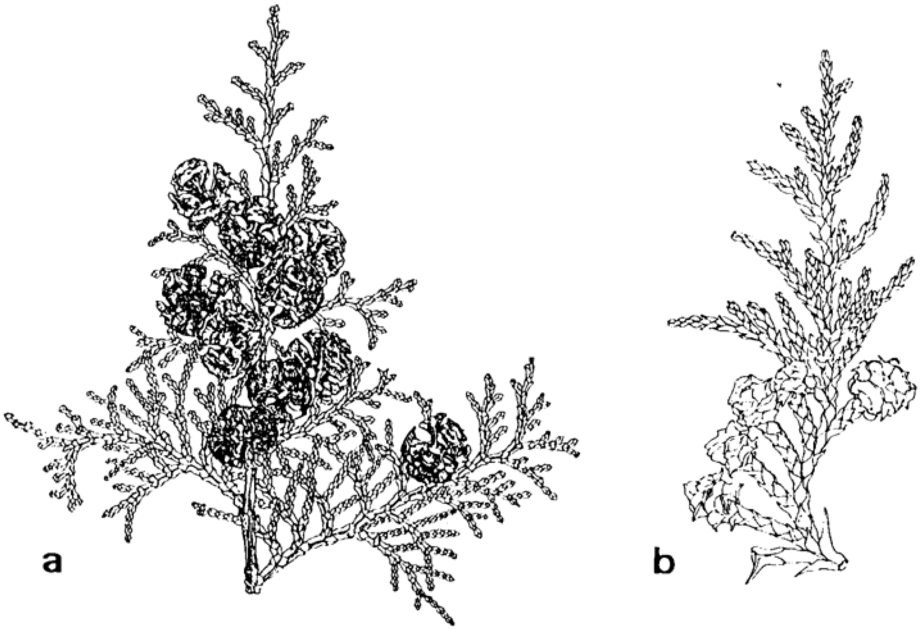
(3) *C. lawsoniana* Branch with cones. From Abrams 1923.

(Figure 2 continued)

(4) *C. nootkatensis* Mature tree, twigs, cones. From Dunsworth 1998. (Original illustration by B.L. Cunningham)



(5) Branches with cones. From Yatoh (1964) in Yamamoto 1998.
a. *C. obtusa* b. *C. pisifera*



(Figure 2 continued)
(6) *C. thyoides* a. Mature wetland forest with abnormally high water that killed all the trees within the year after this photograph was taken. Typical straight trunks, irregular conical crowns reflected in dark humic water. (Original photo courtesy A. E. Bye Associates)

(7) *C. thyoides* a. First-year seedling b. Branch with flowers c. Branch with cones Adapted from C.S. Sargent (1896) by Sheffield *et al*. 1998.

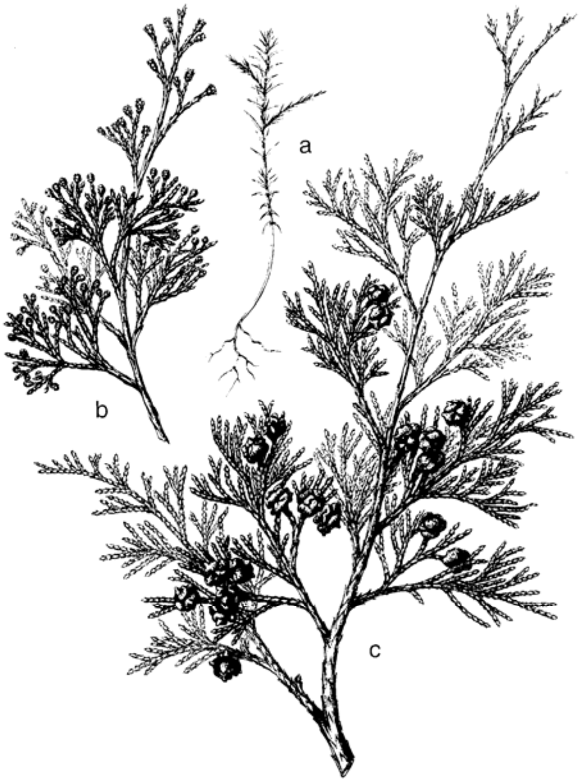


Table 3. *Chamaecyparis* forests: Physical features of the ecosystem

				Water		Regional Climate			
		Soil[a]						Temperature Mean (°C)[b]	
Species	Soil Type	Nutrient	Saturated	F = Flowing S = Standing	pH	Rainfall (mm/yr)	Relative Humidity	Minimum	Maximum
C. formosensis	shallow to moderately deep, moist mineral soils			none	N.R.	3000-4800	72-96% local clouds		
C. taiwanensis	shallow, often well-drained mineral soils		N	none	N.R.	3000-4800	72-96% local clouds		
C. lawsonianan	L, M, P, S, Se varies widely	all	N/Y	F, S, or none	4.2-7	1000-2400 1275 avg.	high at night; foggy; 77-89%	[-3]	33
C. nootkatensis	P, Po	poor neutral-acidic	N/Y	occasional or none		1300-3000		AK*: [-29]-[-17] [-9]-3.5 BC*:[-26.7] WA*:[-24.4]-[-28.9] CA*:[-18.9]	29-32 15-18 33.3 32.9 43.9
C. obtusa	Mo, Po, Se	poor	N	none	N.R.	1400-4100; most in growing season		[-9.2]	30
C. pisifera	M, P		N (sometimes Y)	none	N.R.	1400-4100		[-9.2]	30
C. thyoides	P over S	poor	Y	F, S	3.1-7	1186	53-86%	[-27.8]	41.7

Notes: Y = Yes. N = no. Avg. = Average. N.R. = Not relevant. Blank = information not available. * = Extreme temperature reported from any year at weather stations nearest the species' range.

[a] *Soil type.* L = loam, M = mineral, P = peat, Po = podzol, S = sand, Se = serpentine, and V= volcanic.

[b] *Temperature.* Average mean daily temperatures (except as noted) at weather stations in species' region. There are generally no weather stations at the colder high-altitude locations; no reliable data are available on conditions within the stands. Brackets [ ] denote negative numbers.

PART I. PROPERTIES OF THE DOMINANT TREES

This section compares the morphological, physiological, and ecological properties of the seven *Chamaecyparis* species. Separating the properties common to all the coastally restricted freshwater trees from those that they do not share allows the emergence of the key adaptations that restrict them – or fit them – to marine shores (Laderman 1998a). To ascertain the key adaptations that determine the ecological perimeters of *Chamaecyparis* species, I examine their distribution, longevity, reproduction and growth habit, morphology, ecological strategies, and evolutionary patterns.

Characteristics common to all coastally restricted non-deciduous forests of the Northern temperate zone are listed in box 2. These adaptations are most probably essential to success in coastal freshwater forests, and are selected for by coastal conditions. There are some characteristics common to all *Chamaecyparis*, but not to *all* coastally restricted species (box 3), and therefore not necessarily related to the coastal situation. Characteristics where the *Chamaecyparis* species vary widely from each other are those that are most probably not adaptive for the coastal environment (box 4).

Box 1 Environmental Diversity: Divergent Factors – Varying characteristics of the native habitats of coastally restricted forests

1. Environment type (e.g., montane vs. sea level; flat vs. hilly; or saturated vs. mesic soil)
2. Expressed niche breadth of native habitat
   (a) latitudinal range
   (b) temperature range
   (c) altitudinal range
3. Soil type (e.g., sand, peat, podzol, or serpentine)
4. Soil hydration (dry, saturated, or submerged)
5. pH of standing water, if and when it is present
6. Soil nutrient status

Box 2 Properties Common to Coastally Restricted Nondeciduous Trees[a]

1. Native only to within 250 km of a marine coast (by definition)
2. Sensitivity to saline groundwater and salt-laden winds
3. High aerial moisture requirement
4. Broad-niche potential (wide ecological amplitude; capacity to thrive in a great range of environments)
5. Poor competitive ability
   (a) outside the favored niche
   (b) in favorable or "easy" environments
   (c) in much of its potential range
6. Become dominants in special circumstances wherein they are better adapted to one or more restrictive factors
7. Discontinuous distribution and therefore contain the genetic and evolutionary effects found in ecological islands
   (a) founder effect
   (b) high susceptibility to change in the environment
   (c) greater variation between stands than from tree to tree within stands, due to reproductive isolation
8. Often, but not exclusively, monotypic stands
9. Do best in protected sites; do not thrive in exposed windy sites
10. Moisture-conserving features (sclerophylly)
    (a) waxy cuticle
    (b) needles
    (c) thick bark
11. Bark deeply fissured
12. Those in saturated soil have shallow roots, no tap root
13. Thrive in protected plantations or amenity plantings far from the natural range and under very different conditions
14. Wind pollinated
15. Seed transported by wind
16. Paleoendemic

[a] These properties refer to temperate zone trees in the northern hemisphere. Coastal deciduous species and non-evergreens in the temperate zone (*A. japonica, T distichuni, and N. aquatica)* and southern hemisphere (Weigand et al. 1992) and tropical trees (Olmsted and Durán García 1998) differ significantly in many properties from those compared here.

Biogeography

All *Chamaecyparis* species have a markedly discontinuous distribution: they are absent in many apparently suitable habitats situated between extant stands (tables 1, 2, and 3). Many of these species appear in a paleoendemic pattern indicating that their environments have changed greatly, or that the populations have been separated for long periods. Using detailed comparative morphological analysis, Edwards (1992) determined that the closest living relative of *C. nootkatensis* (yellow-cypress), a native of western North America, is *C. obtusa* (Hinoki cypress*)* in Japan. The closest relatives of Atlantic coastal *C. thyoides* grow thousands of kilometers away near the Pacific shore. Some characteristics of the southern variant, *C. thyoides* var. *henryae*, appear to be more similar to those of West Coast *Chamaecyparis* species than of *C. thyoides* itself *(*personal communication Angus Gholson 1980, Clewell and Ward 1987, see "Evolution" later in this essay for further discussion). Plate tectonics, paleobotany, and genetics may provide clues to the significance of the great distances between related species.

Box 3 Properties Common to all *Chamaecyparis* Species[a]

1. Stomata small, with thick "lips"
2. Needles very small
3. "Drip tip" features
4. Distinct assemblage in each type of environment
5. Possess secondary chemicals and therefore
   (a) resist decay
   (b) one or more parts toxic to some animal species
6. High seed production

[a] For properties common to all coastally restricted nondeciduous trees, see Box 2

Box 4 Properties Not Shared by Most *Chamaecyparis* Species

1. Longevity
2. Pace of initial seedling growth
3. Shade tolerance of seedlings and saplings
4. Capacity for vegetative reproduction
5. Height, girth at maturity
6. Epiphytes
7. One dominant family in associated species

Longevity, Reproduction, and Growth (tables 4 and 5)

The maximum age of the trees varies widely, from the relatively short-lived *C. thyoides* with a maximum current lifespan of less than 300 years (Clewell and Ward 1987), to the Methusalahs of the forest, *C. lawsoniana* (Port-Orford cedar) and *C. nootkatensis,* which may live longer than 3,000 years (Zobel 1998). All the species are monoecious (possess separate male and female flowers on the same tree). All are wind-pollinated, and seeds of all the species are transported by wind; some are also water-borne.

Dependence on vegetative reproduction in nature varies widely: *C. thyoides* and *C. obtusa* rarely resprout even after being repeatedly browsed, whereas *C. lawsoniana*, *C. nootkatensis* and *C. pisifera* (Sawara cypress) often reproduce vegetatively. Initial seedling growth also varies widely from species to species, and generally responds to edaphic (soil), nutrient, and surface conditions, the water and light regimen, weather, and competition from other trees and shrubs. There is no discernable common pattern among the species' responses to each of these factors. However, all the species seem capable of colonizing open sites.

The maximum size at maturity varies greatly among these species, ranging from *C. thyoides'* modest 28-36 m to *C. formosensis* (Taiwan cypress) and *C. lawsoniana*, which grow to nearly 60-70 m.

Table 4. *Chamaecyparis* species: Reproduction and growth

Species	Monoecious	Pollination	Seed Transport	Vegetative Reproduction[a]	Seedling		
					Init. Growth	Colonize Open Sites	Shade Tolerant
C. formosensis	Y	wind	wind	N?		Y	N
C. taiwanensis	Y	wind	wind	N?		Y	Y
C. lawsoniana	Y	wind	wind, water	Y	slow	Y	Y
C. nootkatensis	Y	wind	wind	Y	slow-moderate	Y	N(varies)
C. obtusa	Y	wind	wind	N	slow	Y	Y
C. pisifera	Y	wind	wind	Y	slower than *C. obtusa*	Y	Y
C. thyoides	Y	wind	wind, water	N	varies	Y, fast	N

Table 5. *Chamaecyparis* species: Morphology and other properties

Species	Size at Maturity			Bark	Leaf				
	Height (m) Average	Height (m) Maxi-mum	DBH (m) Max.	Furrowed Fissured	Needle	Ever-green	Epiphytes	Mychorrhizae	Resists Decay
C. formosensis		60-65	5.8-7	Y	Y	Y			Y
C. taiwanensis		40	3	Y	Y	Y			Y
C. lawsoniana	45	65-73	3.8-4.8	Y	Y	Y	Y	Y	Y
C. nootkatensis	25-35	40-50	2-3.7	Y	Y	Y	Y	Y	Y
C. obtusa		40-52	1.5-2	Y	Y	Y	N	Y	Y
C. pisifera		46-50	1.5-2	Y	Y	Y	N		Y
C. thyoides	28	36	1.2-2.1	Y	Y	Y	Y	N	Y

Notes: Y = Yes. N == No. Blank = Information not available. ? = Information contradictory.
[a] *Vegetative reproduction.* "Y" indicates that this is a common strategy in nature; it does not refer to the success of rooted cuttings or greenhouse layering.
Notes for Table 5: Y = Yes. N = No. Blank = Information not available. ? = Information contradictory.

Morphology: Leaves, Drip-tip, and Bark (box 3)

All the species have narrow evergreen needles with waxy surfaces and sunken stomata, and six-sided woody cones. All evergreens have a "drip-tip" feature: the needle, branchlet, and stem arrangements promote collection, condensation, and retention of ambient moisture, allowing for maximal absorption of both fluid and nutrient along the stems. Water gathers at the outer branch-tips and drips off, providing moisture to the root zone even when there is no precipitation.

Fissured or furrowed thick bark is another feature common to all the species. The crenelation slows and channels moisture, maximizing absorption during throughflow. Thick, insulating bark also protects mature trees from the heat of brief fires.

This cluster of morphological aspects presents a picture of species well-adapted to conserving both nutrients and water.

Dominance and Competition

The canopy is generally co-dominated by conifers in the higher-latitude forests, but at lower latitudes and altitudes, deciduous and coniferous species often share the canopy. Conifer dominance may be correlated with temperature, soils, and other variables not dependent on a marine coast. The shrub layer, like the canopy, tends to be dominated by plants with water-conserving features.

Zobel (1998) suggests that the success of *Chamaecyparis* in its restricted environments is probably dictated by interactions with other regional dominants. Conditions that stress other regionally dominant trees appear to favor this genus. Thus, while *Chamaecyparis* species are poor competitors in favorable or easy environments, they become the dominants in special circumstances where they are better adapted to one or more restrictive factors. Specific adaptations are discussed below.

Ecological Strategies and Properties. Mutualism and properties such as evergreenness, sclerophylly, and the synthesis of secondary chemicals (materials not necessary to basic metabolism), are trophic strategies of plants living in nutrient-deficient environments (Specht 1979). Other hallmarks of species dominant in stressful habitats are expressed in their competitive capacity, their specialist/generalist qualities, and their role as ecological determinants. Their existence in ecological islands and remnant patches contributes to the rarity of both the dominants and their associated species.

<u>Mutualism</u> (table 5). Most *Chamaecyparis* species are reported to harbor either mycorrhizae (fungi intertwined in their roots) or epiphytes (plants growing upon them). (This information is not presently available for the two Taiwanese species.) Mycorrhizal fungi transfer nutrients to their plant hosts, as, for instance, noted by Molina (1994) in the redwood forests. Such a handy movement of materials is of obvious benefit in nutrient-poor situations. Ectomycorrhizal (EM) fungi appear to play an important role in enabling host plants to tolerate the particular constraints of difficult soils. These EM fungi may also direct and limit the composition of associated species by inhibiting the growth of plants associated with other classes of mycorrhizae (e.g. arbuscular fungi) (Read 2002). Epiphytes (plants physically supported by, but not metabolically interdependent with, other vegetation), which are often abundant in moist forests, may also benefit their hosts. For example, it has been found that *Lobaria organa*, a lichen of the old-growth temperate coastal rainforest canopy,

contributes up to 50% of nitrogen added to the rainforest soil (Pike et al. 1977, Denison personal communication 1995).

Evergreenness. As previously noted, all *Chamaecyparis* are evergreen (table 5), and are often (but not exclusively) found on infertile soils. It is thought that evergreenness may be an effective adaptation to nutrient deficiency (Monk 1966, Small 1972, reviewed in Chabot and Hicks 1982, Jonasson 1989). The reasoning is that when all leaves are not lost each year, each molecule of photosynthesized carbon is retained longer, so that nutrients are more efficiently used (Specht 1979). The major contributing factors are thought to be: the long life span of each leaf, the reabsorption of leaf nutrients from aging leaves, and the translocation of nutrients directly from aging to newly expanding young leaves (Shaver 1981, Jonasson and Chapin 1985).

In a much-quoted study, Small (1972) found that evergreen species reabsorbed a higher percentage of leaf nutrients than deciduous species in the same environment. Jonasson (1989) observed that abundant nutrients favored fast-growing deciduous plants; a moderately reduced supply favored evergreens with short-lived leaves; and severe nutrient deprivation favored those with long-lived evergreen leaves.

The picture is extremely complex, for the rates and ratios of nutrient removal and translocation vary from species to species (Chapin 1980, Schulze and Chapin 1987, Chapin and Shaver 1989, Jonasson 1989). Further variation in plant biochemistry is observed when the same species grows in different environments (Whigham and Richardson 1988). Further research is required to clarify the correlation between soil nutrient availability, the evergreen habit, and coastal restriction.

Desert-like Sclerophylly: A Paradox in Humid Environs. Vegetation of dry regions is often evergreen and typically sclerophyllous, having thick, leathery, tough leaves with recessed stomata (pores through which gases move). These qualities are also characteristic of all *Chamaecyparis* (box 3). Sclerophylly prevents desiccation, providing a great advantage in desert-like environments, but it is a very strange feature for plants living in areas of high humidity. Why would plants possess water-conserving strategies in water-logged, foggy, or rainy environments? Are these actually techniques for maintaining a physiological balance of salts and water in an environment with frequently salt-laden air? Or for conserving nutrients in oligotrophic situations? These are expensive strategies, and may partially explain the poor competitive ability of *Chamaecyparis* species outside their zones of greatest adaptation.

The apparent anomaly may be more readily understood if one adopts the assumption suggested repeatedly in *Forested Wetlands* (Lugo et al. 1990a): in stressful sites, it is not the average situation, but the rare, erratically occurring catastrophe that determines the vegetational profile.

The paradox of water-conserving properties in wetland plants has intrigued scientists for decades. Ironically, an internal water debt may be created by one property that allows many species to survive in a low-nutrient environment: evergreenness. Evergreens continue to photosynthesize and respire at low temperatures. In very cold weather, water uptake is low or non-existent, but water is still lost via cuticular transpiration even when stomata are closed. Hence, water tends to be lost by evergreens in cold weather. This does not, however, explain sclerophylly in frost-free areas (Brown 1990, Lugo et al. 1990b).

Physiological drought may also be induced by a peat substrate, which, even when wet, does not readily release water. For example, Lugo et al. (1990b) observed that plants that do not wilt in sand until saturation is reduced to between 1.5 and 7.8%, will wilt in peat at 50% saturation. Water conservation may also be of advantage when there are toxic levels of humic or other acids (as in peat and podzol), or of aluminum (as in serpentines). *Chamaecyparis* species grow in each of these toxic soils (table 2). Soils are discussed in more detail under “Properties of the Environment.”

Water Stress Due to Root Inadequacy. The root pattern of trees growing in a normally high-moisture environment may be another key to the utility of conservation strategies. Such trees would be expected to be shallow-rooted for two reasons. First, in saturated soils with no water-flow, anoxia and chemically toxic conditions develop, killing deeper roots. Second, in unsaturated soils, the abundance of moisture in the air generally encourages surface root development. During the rare but recurring drought periods, these plants adopt a strategy of tolerance. They cannot adapt by allocating sufficient energy for rapid root growth when water tables drop below the shallow rhizosphere (root zone): their water-conserving properties allow them to tolerate the stress.

These characteristics and processes are significant at three levels. At the individual and species levels, water stress lethal to their competitors allows the survival of adapted species. At the ecosystem level, water loss is minimized during drought.

Competitive Capacity and Niche. All *Chamaecyparis* species normally fill only a limited subset of the environments in which they can grow. They have the capacity to thrive in a variety of situations (i.e., they are all broad-niche forms), but they do not compete well in much of their potential range. Zobel (1998) observed that, in nature, all the *Chamaecyparis* species occur in unusual forest communities, often limited to particular topo-edaphic conditions within a range of climatically controlled regional forest types.

Specialists and Generalists. Generalists (known as "r-selected species") are defined as forms that are phenotypically plastic or adaptable: they can change to fit different environments. For example, *C. nootkatensis* has an indeterminate growth pattern, for it does not form shoot buds (Russell 1993). Growth ceases if there is a severe drought or unusually cold weather during the growing season, and growth resumes without damage when warmer or wetter conditions return. In other words, it is a generalist for these traits. It has been shown that forms with a preponderance of r-selected traits tend to resist extinction (Laurance 1991).

Species that are good dispersers (are r-selected for dispersal ability) may be good survivors, because the demographic and genetic contributions of immigrants can bolster small populations and provide a buffer against extinction (Laurance 1991). All the coastal trees studied are poor dispersers, and lack this buffer.

Specialists (called “K-selected species”) are forms with a narrow capacity to use habitats or resources. An example is again *C. nootkatensis*, which has subpopulations with differing seedling morphology and physiology, with each subpopulation being classed as a specialist in these traits (Russell 1993). Laurance (1991) theorizes that a preponderance of K-selected, specialist traits is a significant predictor of extinction proneness. All the coastal trees have many specialist traits.

It appears that many *Chamaecyparis* species may follow the pattern of *C. nootkatensis*, in that it is a specialist in some characteristics, and a generalist in others. Russell (1993, 1998) examined this problem in detail.

Few researchers have systematically explored the ecological implications of the genetics of *Chamaecyparis* forests. Pioneers in this area include Eckert (1998), Edwards (1992), Russell (1998), and Zobel (1998).

Ecological Determinants

Many *Chamaecyparis* trees appear to create conditions that dictate, dominate, or determine their associates by shaping their environment. The associated species, not surprisingly, frequently possess many of the same ecological characteristics as the dominant: wide ecological amplitude, acid tolerance, and water-conserving features. Although many of these “constant companions” (in phytosociological parlance) are competent competitors in a broad range of situations, others, like their dominant tree, do not compete well outside their native habitat.

Secondary Chemicals. The restrictive nature of coastal sites appears to encourage the production of secondary chemicals, which are substances not essential to self-maintenance. All conifers contain resins, secondary chemicals occurring in canals in the bark and elsewhere (Prance and Prance 1993). All *Chamaecyparis* trees resist decay (table 5), a property resulting from the production of secondary chemicals. Some conifer needles also harbor symbiotic endophytic fungi that produce insect-repelling alkaloids (Carroll 1988 and 1991, Barbosa et al. 1991). Such chemicals are often toxic, and possess pharmaceutical or antibiotic properties that may be useful in medicine, agriculture, and industry.

Evolution

Paleoendemism and Neoendemism (box 2). It is postulated that plants growing in a restrictive environment probably have evolved in one of two ways (Stebbins 1942, Terrill 1951, Kruckeberg 1954, Brooks 1987), resulting in paleoendemic and neoendemic population types.

The paleoendemic, relict, or depleted population type is the remnant of species that were once highly successful. These plants currently have a widespread but disjunct distribution, and are confined to isolated stands. As the environment changed, paleoendemics failed to adapt. Descendants of the original species were restricted to progressively smaller, more remote populations. Their closest relatives may now be geographically far removed. The greater the environmental change, and the longer the population units remain separated, the more probable it is that they will be separated by greater distances. At the same time, the subpopulations become more distinct.

The other type (termed a neoendemic island population) was derived relatively recently from seeds of plants growing in neighboring, more moderate habitats. When some of the moderate-habitat plants were able to germinate and survive in the harsh environment, their “tolerant” genes were progressively selected for, and “intolerant” genes were weeded out of the population. The restrictive environment forced rapid evolution, ultimately producing a new biotype capable of thriving under harsh conditions. Their closest relatives are generally found nearby. The speed with which the biotype may evolve is related to the generation time of the plant: some herbaceous species can evolve quite rapidly under harsh conditions. For example, grass strains tolerant to mine wastes can develop within 30 years (Antonovics et al. 1971). Tolerant and intolerant biotypes can coexist in the moderate environment, with the neoendemic plants superficially bearing a close resemblance to their relatives lacking the capacity to thrive in the harsher habitat.

Evidence presented by all authors contributing to *Coastally Restricted Forests* (Laderman 1998b) indicates that *Chamaecyparis* species, like other evergreen coastal trees in the Northern Hemisphere, are paleoendemic species.

Remnant Patches, Rarity, and Extinction

Although the tree species here are all dominants or co-dominants (by definition locally abundant), they are in great danger of extinction because their habitats are so specialized and are distributed as islands over the landscape. Tilman et al. (1994) developed a model describing how even moderate destruction of habitat patches can lead to the extinction of the dominant competitor. They predict that associated species will be lost as habitat loss increases, with the best competitors going first. Furthermore, they expect that the more fragmented the ecological islands, the greater the extinctions that additional destruction will cause. This phenomenon first affects those best adapted to the specialized environment, the endemics, for these tend to be rare outside that habitat. The poor dispersal ability exhibited by many *Chamaecyparis* species exacerbates the situation.

Extinction may be a delayed effect, particularly among species with a long lifespan. Tilman et al. (1994) describe this as an extinction debt, a future ecological cost of current habitat destruction. As these authors suggest for all systems, fieldwork is required to determine if the extinction debt model is applicable to *Chamaecyparis* systems, and to ascertain the spatial and temporal scales to which it applies.

Habitat-restricted species are almost by definition rare or absent in most environments, although they may be abundant in their native sites. From a conservation viewpoint, the existence of *Chamaecyparis* forests in ecological islands is highly significant. The preservation of “sample” or representative stands will not save the taxonomic or genetic diversity of these systems.

Catastrophe Dependence. Dependence on catastrophic events appears to be an opportunistic strategy for the use of limited resources. Four types of catastrophes encountered in *Chamaecyparis* forests are discussed below: fire, harvest, hurricane, and drought.

<u>Fire</u>. Organisms use two basic strategies to successfully survive stress: avoidance and accommodation. Both strategies may be illustrated by the mature *C. lawsoniana* (Greenup 1998, Zobel 1998). Thick fire-resistant bark allows the tree to “avoid” and hence survive most forest fires, and its seed “accommodates” by sprouting vigorously in newly cleared gaps in the canopy. Another example of accommodation: *C. thyoides* is killed by hot fires, but only about one third of any year's seed-crop germinates each year. The rest of the seed, protected in the forest floor, remains to germinate opportunistically after a devastating fire (figure 3). The seed bank benefits from the fertilized, cleared, sunlit seedbed created by the conflagration.

<u>Harvest</u>. Under certain circumstances, clearcut harvest may have an effect similar to a hot fire for some species. Pure stands can regenerate if the forest floor is left in a state that encourages seed germination, or if conditions promote stump-sprouting for those species capable of it. Of course, restoration of biodiversity depends on many factors, and is often impossible to replicate. In old-growth forests, the complex interactive living web that requires decades or centuries to develop will be destroyed even when an apparently healthy stand replaces the cut forest.

<u>Hurricane</u>. As with other catastrophic disturbance, hurricanes present opportunities as well as problems. The effect on biodiversity and productivity can appear more like renewal than disaster for species capable of adapting in some way to the rare, erratically occurring major storm. Conner (1998) discusses what little is known of this process, and describes research efforts underway. In

Atlantic white cedar wetlands, the effect of high winds depends on the available seed sources (figure 4).

Figure 3a. Effects of fire during high water in Atlantic White Cedar wetlands. From Laderman 1989. (Original illustration by Tamar Laderman)

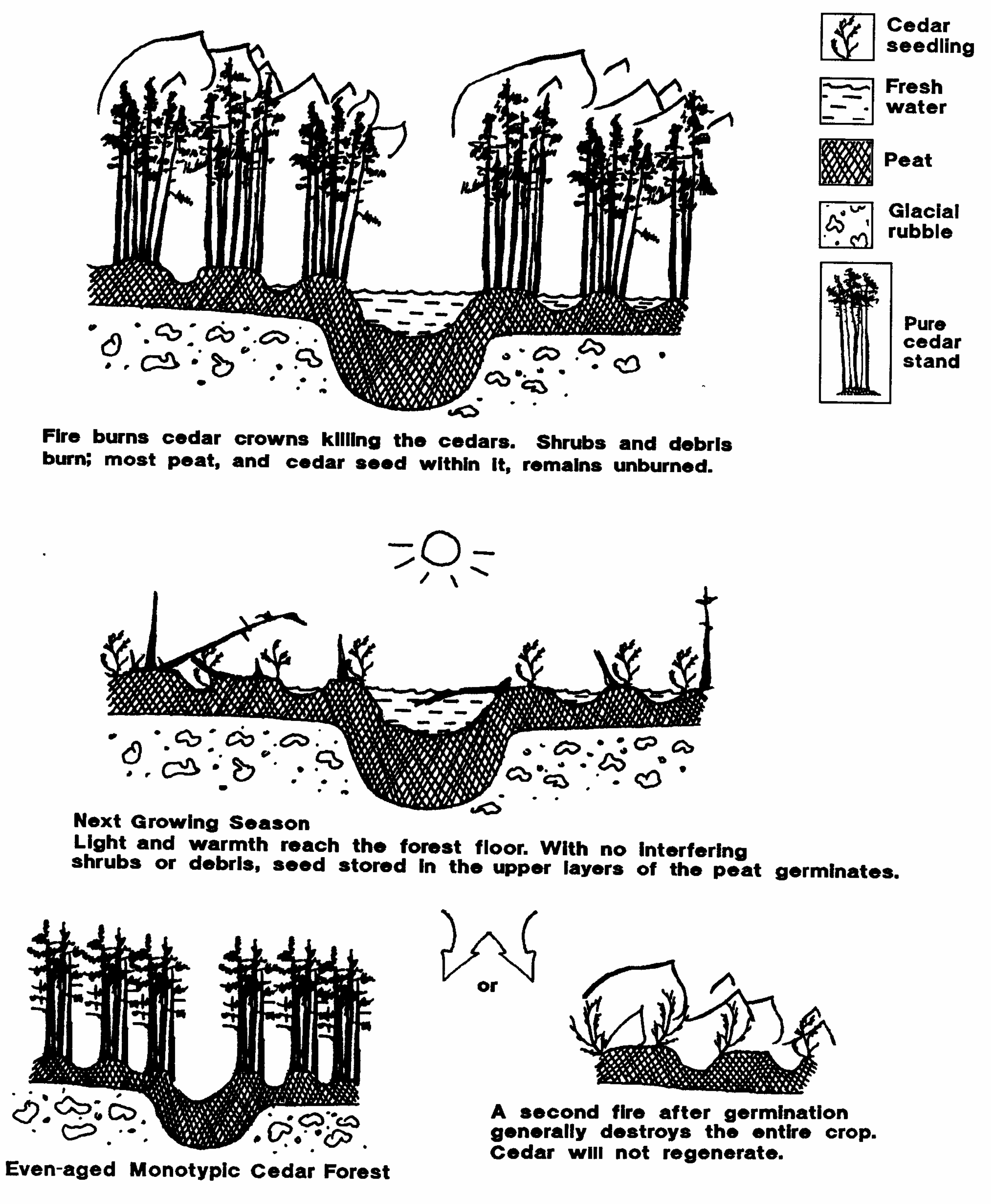


Figure 3b. Effects of fire during low water in Atlantic White Cedar wetlands. From Laderman 1989. (Original illustration by Tamar Laderman)

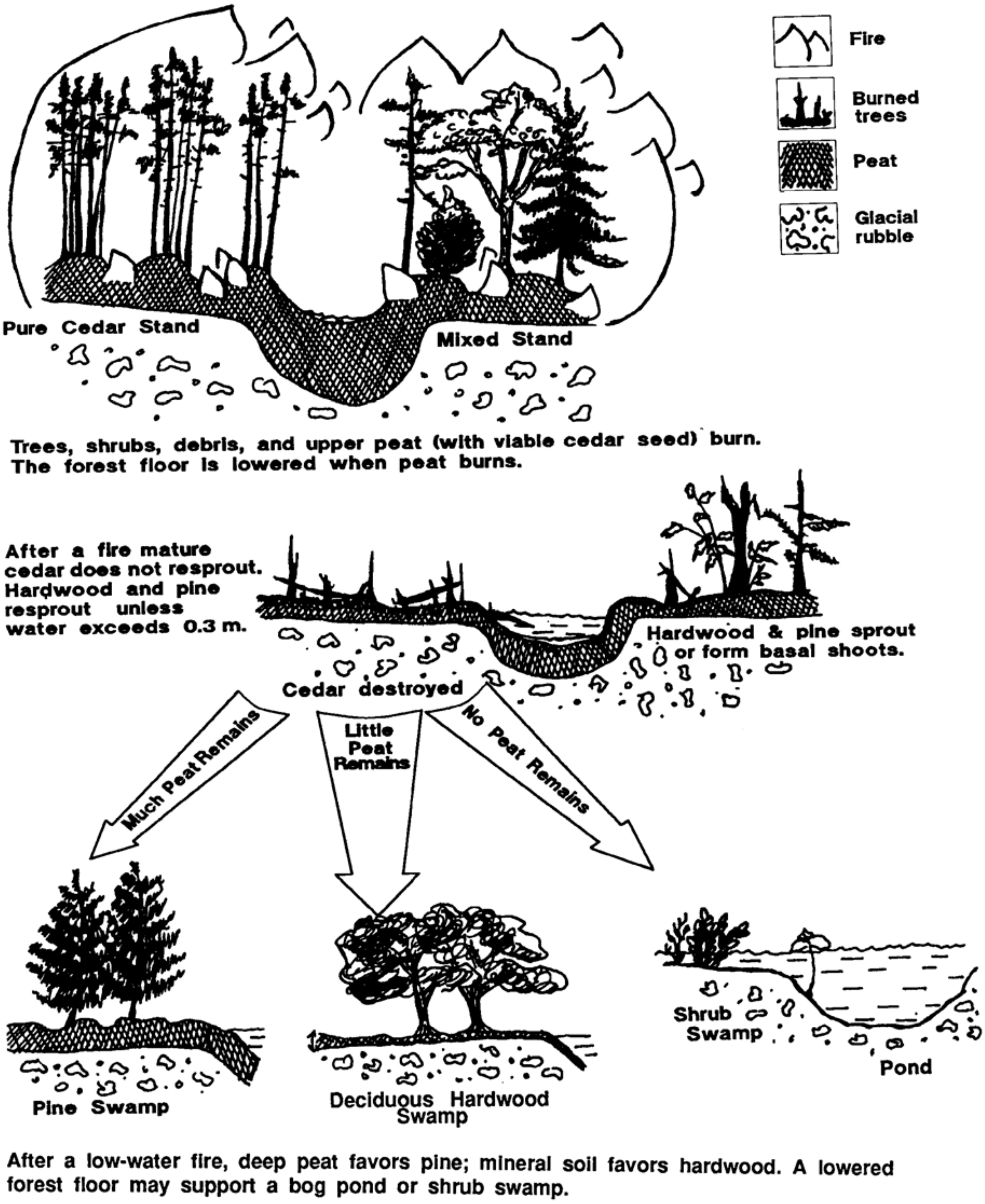
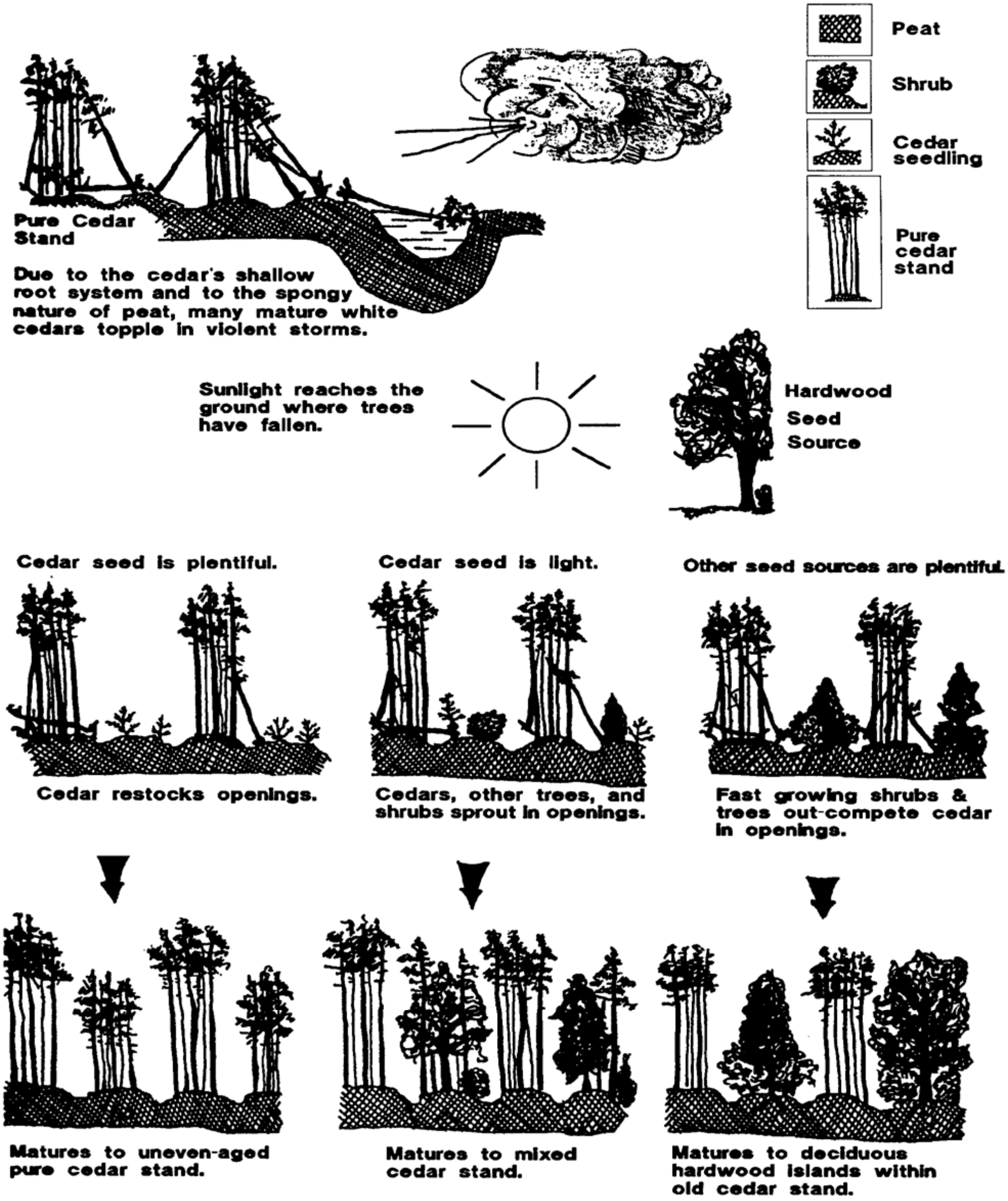


Figure 4. Effects of high winds in Atlantic White Cedar wetlands. From Laderman 1989. (Original illustration by Tamar Laderman)



Drought. In riverine forests, or those well-supplied by adequate flow, water is seldom limiting due to the continual inflow to the root zone. Therefore, there is little selection for water conservation (Lugo et al. 1990b). However, isolated basin wetlands, with no inflow, rely primarily on precipitation for their water. They are therefore dependent on the vagaries of the weather. Water stress may not occur often, but it is the extreme condition, not the average, that determines the plant community. Data available on transpiration rates of forested wetlands indicate that transpiration is lower in basin wetlands than in riverine wetlands even when standing water is present (Brown 1981, Blanken and Rouse 1996, Oren et al. 2001). This supports the hypothesis that where water stress is a recurring (but possibly rare) challenge, the trees that dominate such sites are those that have been selected to survive that challenge.

PART II. PROPERTIES OF THE ENVIRONMENT

Introduction

This section examines the environmental parameters of *Chamaecyparis* coastal forest habitats. The environments are compared, and the implications of common factors are explored. In segregating the habitat qualities that are common to all the forests from those they do not share, the key environmental factors that select for coastal species should emerge. Characteristics of *Chamaecyparis* forests are summarized in tables 1 and 3. Properties shared by all the ecosystems are listed in box 5; properties that vary among the systems are listed in box 1.

Biogeography (tables 1, 2 and 3; figure 1). Although all the systems considered here are native only to a narrow coastal band, it is evident that each dominant tree species occupies a wide range of environments (see Dunsworth 1998, Eckert 1998, Greenup 1998, Hennon et al. 1998, McWilliams et al. 1998, Russell 1998, and Zobel 1998). The wide environmental range is expressed by some in north-south geographic extent, by others in altitude, soil type, nutrient status, or atmospheric temperature range. In other words, the specific expressed niche breadths vary greatly among *Chamaecyparis* species.

Range. Geographic factors, especially latitude and altitude, influence the native ranges of *Chamaecyparis* species (tables 1 and 2; figure 1).

Latitude. *Chamaecyparis nootkatensis* has the greatest latitudinal range in the genus, extending 19.4 degrees from Alaska to northern Oregon (Dunsworth 1998, Hennon et al. 1998, Zobel 1998). In contrast, the Taiwanian species *C. taiwanensis* (Taiwan red cypress) and *C. formosensis* (Li 1963, Zobel 1998) and the North American *C. lawsoniana* (FNA 1993, Zobel 1998) range over only 1.51 and 2.45 degrees latitude, respectively. There is a nearly 20-fold difference between species with the greatest and smallest north-south range.

Altitude. The two Japanese species, *C. pisifera* and *C. obtusa*, have the greatest vertical range, extending 2,480 and 2,190 m respectively (Yamamoto 1998, Zobel 1998). In contrast, *C. thyoides* has a vertical range of only 457 m. There is nearly a 3,000-fold difference between species with greatest and least altitudinal range breadth.

Although the natural range of *Chamaecyparis* trees is geographically very limited, many of these species can thrive under cultivation far from their natural range and under quite varied conditions.

Climate. The range of climatic parameters varies widely, reflecting the longitudinal and altitudinal perimeters of the species being studied. Moreover, information on temperature, precipitation, and humidity is difficult to quantify and reliably evaluate at present, for localized conditions frequently differ markedly from those of the nearest weather station. Accurate multi-year weather records have been maintained for relatively small portions of the local habitats of each of these species.

Precipitation. Precise rainfall data are generally unavailable for determining the microclimate affecting a particular species. However, many *Chamaecyparis* species occur in regions of high rainfall, as for example all those species classified as coastal temperate rainforest (CTRF): *C. lawsoniana* and *C. nootkatensis* in the American northwest, and *C. obtusa* and *C. pisifera* of Japan (Weigand et al. 1992). It appears that Taiwan's *C. taiwanensis* and *C. formosensis* also fall within the CTRF zone, according to the criteria of Weigand et al. (1992).

The coastal temperate rainforest belt by definition has a precipitation minimum of 2,000 mm (Weigand et al. 1992). Some coastal species not in the temperate rainforest are subject to regular seasonal drought (Libby et al. 1968, Ornduff 1998). This apparent anomaly may be offset by high humidity in the immediate microclimate of individual stands. A common requirement of all *Chamaecyparis* species is an ample supply of water, either in the substrate or in the atmosphere as rainfall, fog, or clouds.

Soils (table 3). The soils supporting *Chamaecyparis* trees vary widely, including rich loam, sand, organic peat, podzol, and serpentine. They range from saturated to well-drained, and may be eutrophic, mesotrophic, or dystrophic (i.e., from rich to impoverished). Where there is standing water, soil pH ranges from 3.1 to 7.0. Many of these soils, especially pure peat, podzol, and serpentine, are recognized as difficult or impossible habitat for most other regional vegetation.

Four of the seven *Chamaecyparis* species may be found on peats: *C. lawsoniana, C. nootkatensis, C. pisifera* and *C. thyoides*. Peat soils consist of organic matter in various states of structural breakdown ranging from fibrous to mucky (Moore and Bellamy 1974, Allaby 1992). Pure peat contains few nutrients available to plants, due to its high cation exchange capacity (CEC), the near absence of oxygen in its waters, and the binding of nutrients within undecomposed organic compounds (Bear 1968, Moore and Bellamy 1974). Cation exchange results in acidification and the removal of available nutrients from the surrounding water and soil. Available phosphorus, potassium, and nitrogen are often extremely low or entirely absent. In acid peat there is virtually no nitrification (conversion of ammonia to nitrate) due to the absence of the necessary aerobic (oxygen-requiring) bacteria (Moore and Bellamy 1974). The lack of oxygen also effectively prevents the bacterial breakdown of organic matter into forms usable by plants.

Most often, peat is mixed with components such as clay, muck, and other mineral matter containing varying amounts of nutrients available to plants. Hence, the soil's nutrient status cannot be inferred solely from the identification of peat on a site. However, as peat reflects a saturated or periodically submerged substrate, particular site qualities and capacities of the plant population may be inferred from its presence.

Chamaecyparis nootkatensis and *C. obtusa* tolerate acidic infertile podzols, soils composed of an ashlike upper layer depleted of colloids, iron and aluminum, and a dark lower layer where these substances accumulate in toxic concentrations.

Chamaecyparis lawsoniana and *C. obtusa* tolerate a serpentine substrate. Serpentine soils, weathered from ultramafic rocks, are composed primarily of silicates high in magnesium, iron, and aluminum (Bear 1968). Where *C. lawsoniana* grows over ultramafic rock, the rock has weathered to produce a dense layer of fine clay, creating a perched water table with consistent seepage (Zobel

1998). Serpentines hold a suite of plants differing from their surrounding habitats in both species composition and superficial aspect. The plants are a xeromorphic (desert-like) group with marked vegetational discontinuities, impoverished in both species and numbers of individuals (Brooks 1987).

Implications of Environmental Factors

Influence of Oceans on Nearby Land (box 6). Oceans influence continental and island margins in many ways. The sea functions as a giant heat sink (in other words, it stores heat) due to the high latent heat of water. It moderates the extremes of temperature in summer and winter, and produces a longer fall and a later spring than is found further inland. The sea also strongly influences wind and storm patterns, which in turn will limit and shape animal communities and vegetation.

As hurricanes often sweep through many coastal areas, they are a recurring, and therefore a possibly determining aspect of coastal forest development (discussed in detail by Conner 1998). Materials produced in a system tend to accumulate at the boundary zone (ecotone) and are frequently transformed there as well. The land-water ecotone especially is recognized as a principal route for the transport of nutrients across landscapes via physical and biological means. High intensity winds produce salt-spray aerosols, which form as air bubbles burst and force droplets to spray up from the sea surface (Boyce 1951 and1954, Kientzler et al. 1954). The transfer of gases and aerosols from oceans restores biogeochemical components to the land in the form of gases, precipitation, and windborne materials. This forms a major source of inorganic nutrients for coastal habitats (Art et al. 1974). In any ecosystem, the degree of the influence of meteorologic components depends on local weather and the distance from the sources of airborne materials (Gorham 1958, Gambell and Fisher 1966), in this case, the sea. Applying the nutrient cycling model of Bormann and Likens (1967) to systems restricted to ocean borders, Henry Art (1971, 1976) suggested that the sea itself may not only directly affect, but actually control the function and structure of coastland ecosystems.

Relatively little is known of the role of the sea in controlling the distribution and development of coastal ecosystems, beyond the toxic effects of salt spray on vegetation (Conner and Day 1998). The major portion of the available data concerns the mineral content of coastal precipitation, fogs, and dusts. The nearer a system is to the sea, the higher the concentration of chemicals in precipitation, for example, magnesium, sodium, chloride, sulfate, and often calcium and potassium (Boyce 1951, Lovett and Lindberg 1993, Lajtha et al. 1995, Bowen and Valiela 2000).

The forests most strongly influenced by atmospheric nutrients are probably those with minimal geological and biological inputs (Art et al. 1974). Such circumstances are found where surface water inflow is low or absent, and where the parent rock is resistant to weathering. When biodegradation is inhibited by toxins, low temperature, or the lack of oxygen, atmospheric contributions are important components of the mineral supply.

The accumulation and transfer of materials in this complex fashion provides multiple benefits to adapted species. It acts both as a stressor eliminating competitors, and as a source of wealth available to the surviving *Chamaecyparis* trees.

Influence of Fog. All the *Chamaecyparis* species share one environmental feature: they thrive in very humid environments. All the species are affected by frequent fogs or shrouding by clouds (Paul Meyer, personal communication 1993, Dunsworth 1998, Greenup 1998, Hennon et al. 1998, Laderman 1998a, Russell 1998, Yamamoto 1998, and Zobel 1998). The *Chamaecyparis* found in the region with least rainfall, *C. thyoides*, grows in nature only in or immediately adjacent to wetlands.

Fog-drip, in many cases prevalent in all seasons, and sometimes localized as low clouds, makes rainfall data in the coastal region extremely difficult to interpret relative to tree requirements.

Some striking examples of the correlation between coastal species and fog come from the eastern shore of the Pacific Ocean: Libby et al. (1968) observed mildly foggy days on Cedros Island, off Baja California, when each *Pinus radiata* (Monterey pine) was covered by a separate cloud, while the desert between the pine groves was exposed to clear sky. The presence of localized fog seems critical for the growth of pines on Cedros and Guadalupe Islands. Ornduff (1998) reports that *Sequoia sempervirens* (coast redwood) fog-drip may add more than 25 cm to the effective summer precipitation at the root zone.

Catastrophe as a Controlling Element. Catastrophic events play an important role in determining the characteristics of *Chamaecyparis* ecosystems. These events include abrupt yet often impermanent changes in hydrology and geomorphology such as those caused by drought, storm, fire, beaver, or harvest. These disasters can be seen as essential agents favoring the ecosystems' characteristic biota.

Effects of Stress. In humid environments, stresses that permanently affect the hydrological regime, such as draining, diking, damming, and road or levee construction, tend to have a more severe adverse permanent impact on the vegetation than lumbering or most natural disasters (Lugo et al. 1990b). The canopy dominants native to the regions under study are adapted to survive or regenerate after fire, violent storms, temporary floods, and certain types of harvest. They appear to compete best under conditions that eliminate their competitors. Such occasional catastrophes may determine the vegetational structure of *Chamaecyparis* systems. Again, it is the extreme condition, not the average, that determines the plant community.

<u>Drought in Wet Sites</u>. Lack of water is a major environmental stress in any environment. In normally humid or wet regions, drought has peculiar evolutionary, ecological, and physiological implications. As noted earlier, only those wetland species capable of surviving severe dry periods will survive

<u>Regeneration after Disturbance</u>. Both in nature and under management, some *Chamaecyparis* species are known to regenerate successfully and rapidly into monotypic stands after catastrophic events that completely kill the standing mature trees. For example, under certain conditions *C. thyoides* successfully colonizes from seed after clearcut harvest, fire, or prolonged flooding (Little 1950, Laderman 1989). Such forests may be classed as perturbation-dependent ecosystems (Vogl 1980). In his study of hurricanes, Conner (1998) concludes that natural disasters are vital to the ecosystem dynamics of coastal systems.

<u>Selection by Fire</u>. Fire, a strong agent for species selection, functions as an erratic but recurring stress, affecting ecosystems in a way similar to drought (see Catastrophe Dependence, Part I). Fire is an important thinning agent (Schlesinger 1978) that increases landscape diversity (McKinley and Day 1979, Christensen et al. 1981) and hence maintains and helps determine species diversity. It reduces the importance of some species and enhances the dominance of others (Ewel and Mitsch 1978, Motzkin et al. 1993).

Although there are still many gaps in our understanding of the role of fire in forest systems, several effects are recognized. Fire clears the surface of most vegetation and debris, provides nutrients, exposes the forest floor to sunlight and warmth, and scarifies the surface. These multiple actions provide an ideal seedbed for the germination of some species. In wetlands, due to local variations in the wetness of the upper layers of the forest floor, fire resculpts the surface into crenelated hummocks and hollows. Hollows quickly fill with water. Burning also forms an impermeable skin on peat, creating or increasing poor drainage (Tallis 1983:322). This situation perpetuates and amplifies saturation of the soil, giving further advantage to wetland-adapted species.

Global Climate Change. There are climatic considerations at a different scale that should be factored into this analysis. Global climate change, which influences the distribution of all vegetation, affects coastal species most directly via alterations in sea level (Conner and Day 1998). This form of disturbance either regionally extirpates the *Chamaecyparis*, or it induces inland shifts of entire forests as oceans rise. The success of a system in surviving such large-scale change depends on (1) the capacity of all ecosystem components to "travel" fast enough to keep pace with the encroachment of salt water and (2) the existence of suitable terrain at the landward margin. A major factor now limiting the successful translocation of ecosystems with such stringent environmental parameters is the heavy development of so many coastal areas, which has already eliminated many potential habitats.

In the scenario of a rising sealevel, a variety of species mixes would develop, reflecting the variations in the capacities of each species existing in a specific overwashed area to migrate, colonize, and thrive in the precise conditions of adjacent inland sites. This variety is indeed what is now seen in many ecological island habitats dominated by *Chamaecyparis* trees.

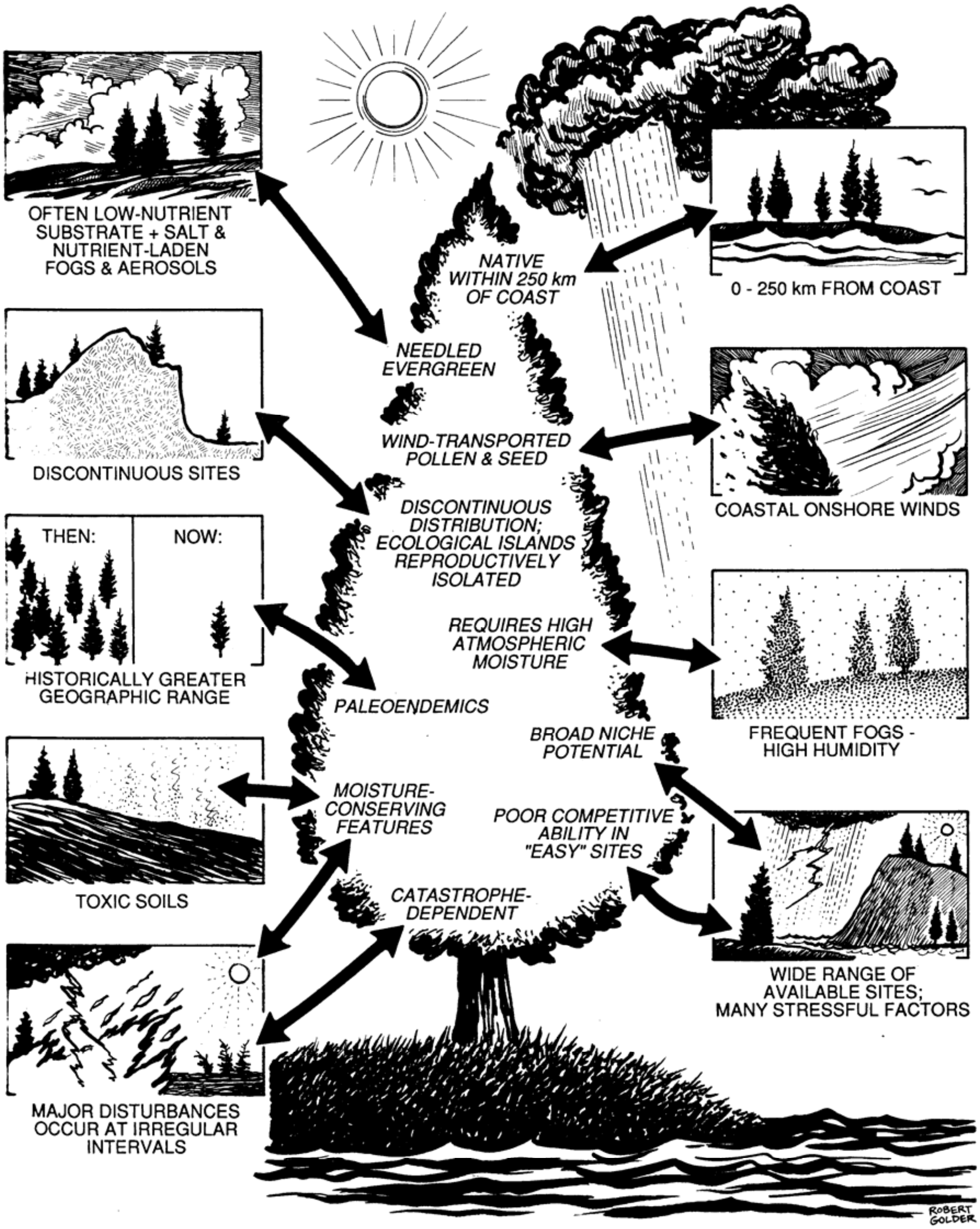
PART III. CORRELATIONS BETWEEN PROPERTIES OF THE TREES AND THEIR ENVIRONMENTS

We can now attempt to relate the capacities of *Chamaecyparis* species to the limitations of the habitats they dominate (figure 5). The next step is to devise experimental and analytical procedures to test the validity of the suggested relationships.

It may be fruitful to explore the following connected hypotheses. The factors that appear most closely tied to each other (as indicated in figure 5) are the key aspects that limit these species to the marine coastal environment. They are those properties shared by all the species, and in turn by all the habitats.

Coastal ecosystems have been shaped by the co-occurrence of the multiple factors resulting from the atmospheric conditions of a marine coast. The high humidity, salt-laden fogs and aerosols, giant heat sink effects, and violent storms combine to encourage the growth of species that are poor competitors in more moderate environs. The keys to their survival and dominance in isolated areas along the world's coasts are their mechanisms to withstand or to take advantage of stress.

Figure 5. Correlations between *Chamaecyparis* species and their habitats. (Original illustration by Robert Golder) (Adapted from Laderman 1998a)



Success through Failure

The strategy of *Chamaecyparis* species is that of outlasting others, a tortoise strategy, not in duration, but spatially, in niche breadth. *Chamaecyparis* trees occupy those parts of the sites where it is hardest to subsist. Most of their ancestors were repeatedly wiped out with all other species when successive disasters struck. Environmental stress selected for those characteristics that allowed survival of each successive disaster by progressively eliminating all those individuals unable to cope. Eventually progeny appeared with suites of genes adapted to multiple stressors. Similar characteristics may have also entered the genome of other species, but these traits would have been swamped by all those that gave species an advantage on more moderate sites, preventing the development of multi-resistance genomes. It is their very failure, their inability to compete on nonstressful sites, that provides an advantage to *Chamaecyparis* species. The quality of persistence under adversity encourages the selection of traits useful in a variety of disastrous situations.

A related hypothesis is worth further study. The combination of a high moisture requirement with sclerophylly may be a major factor in the development of *Chamaecyparis* species. Prime candidates to explain the apparent paradox of species possessing desertlike properties in a humid environment are: (1) the accumulation of toxic conditions in the soil combined with (2) saline aerosols and (3) the erratic recurrence of drought and other disasters. The salt-laden coastal atmosphere would provide the additional nutrients required to support trees withstanding such multiple stressors.

Ecological Apoptosis. In an exhaustive study comparing all the species of the genus, Zobel (1998) concluded that "*Chamaecyparis* seems limited to situations that reduce the importance of the major dominant trees." Catastrophic events can favor the success of *Chamaecyparis* by eliminating competition.

In nature, the concept of survival through failure may not be as unusual as it appears. This seemingly paradoxical requirement for successful stand regeneration may be analogous to the genetically programmed cell death known as apoptosis. Apoptosis, a process wherein all but selected body cells are pre-programmed to self-destruct, is now understood to be an essential (and possibly universal) tool for the proper development and survival of living organisms.

CONCLUSION

In summary: these species are endemics, poor dispersers, poor competitors restricted to becoming dominants in increasingly fragmented, specialized ecological islands. Each of these properties indicates that *Chamaecyparis* species are prime candidates for local extirpation. As each habitat island is destroyed, the environmental debt (Bormann 1990, 1994) and the extinction debt become greater (Tilman et al. 1994). Certain catastrophic events favor the survival of each *Chamaecyparis* species.

Quite frequently, the stringent site requirements cannot be fulfilled, and a coastal forest ecosystem is locally extirpated. This may help to explain the presence of numerous range gaps and relict stands, as well as macrofossil evidence of *Chamaecyparis* species in sites where they do not currently grow. Such stresses eliminate competition from canopy co-dominants and actually stimulate renewal of the species with adaptations that can create advantage from disaster.

The genus *Chamaecyparis* depends on a series of paradoxes for survival. It is a freshwater genus found only under the influence of large bodies of salt water. It lives only where humidity or soil moisture is high, but has many physiological traits that are of greatest benefit in a desert. It is a poor competitor under the best growing conditions, yet in a mixed forest will only thrive and dominate under adversity. *Chamaecyparis* is catastrophe dependent and exists often in remnant patches under threat of extinction. It is extremophilic not so much in the sense of requiring extreme conditions– rather, it is an extreme-tolerant taxon thriving on its own failure and that of its neighbors. To regenerate, the trees require major environmental disturbance such that the species' survival is dependent on recurring disasters.

All these factors emphasize the global uniqueness of *Chamaecyparis* as a genus. *Chamaecyparis thyoides* is doubly unique in that it is the sole Northern Hemisphere forest canopy species that is not only restricted to a marine margin, but to the freshwater wetlands of the coast.

The ecology and properties of each of the *Chamaecyparis* species may be better understood and their inherent values better appreciated when their unique features are identified. The gathering and assessment of existing data is a vital precursor and stimulant to relevant research; it is also a salient requirement for recognition, protection, and conservation of the unusual habitats that harbor these trees. This study assembles information on the widely dispersed *Chamaecyparis* forest systems to achieve these ends.

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LITERATURE CITED

Abrams, L. 1923. Flora of the Pacific States. Vol. 1:74. Stanford University Press, Stanford, CA.

Allaby, M., ed. 1992. The Concise Oxford Dictionary of Botany. Oxford University Press, New York.

Antonovics, J., A.D. Bradshaw, and R.G. Turner. 1971. Heavy metal tolerance in plants. Advances in Ecological Research 7:1-85.

Art, H.W. 1971. Atmospheric salts in the functioning of a maritime forest ecosystem. Dissertation. Yale University, New Haven.

Art, H.W. 1976. Ecological studies of the Sunken Forest, Fire Island National Seashore, New York. National Park Service Scientific Monographs. Series #7.

Art, H.W., F.H. Bormann, G.K. Voigt, and G.M. Woodwell. 1974. Barrier island forest ecosystem: role of meteorologic nutrient inputs. Science 184:60-62.

Barbosa, P., V.A. Krischik, and C.G. Jones, eds. 1991. Microbial mediation of plant-herbivore interactions. Wiley Interscience, New York.

Bear, F.E., ed. 1968. Chemistry of the Soil. Reinhold, New York.

Blanken, P.D. and W.R. Rouse. 1996. Evidence of water conservation mechanisms in several subarctic wetland species. Journal of Applied Ecology 33(4):842-850.

Bormann, F.H. 1990. The global environmental deficit. BioScience 40:74.

Bormann, F.H. 1994. Landscape restoration and ecosystem health. A series of talks at Yale School of Forestry and Environmental Studies, New Haven. Unpublished.

Bormann. F.H., and G.E. Likens. 1967. Nutrient cycling. Science 155:424-429.

Bowen, J. and I.Valiela. 2000. Historical changes in atmospheric nitrogen deposition to Cape Cod, Massachusetts, USA. Atmospheric Environment 35:1039-1051.

Boyce, S.G. 1951. Source of atmospheric salts. Science 113:620-621.

Boyce, S.G. 1954. The salt spray community. Ecological Monographs 24:29-67.

Brooks, R.R. 1987. Serpentine and its vegetation. Dioscorides Press, Portland, OR.

Brown, S. 1981. A comparison of the structure, primary productivity and transpiration of cypress ecosystems in Florida. Ecological Monographs 51:403-427.

Brown, S. 1990. Structure and dynamics of basin forested wetlands in North America. Pages 171-199 *in* A.E. Lugo *et al*., editors. Forested Wetlands. Ecosystems of the World, Vol. 15. Elsevier, New York.

Carroll, G.C. 1988. Fungal endophytes in stems and leaves: from latent pathogen to mutualistic symbiont. Ecology 69:2-9.

Carroll, G. 1991. Fungal associates of woody plants as insect antagonists in leaves and stems. Pages 253- 271 *in* P. Barbosa *et al*., editors. Microbial Mediation of Plant-Herbivore Interactions. Wiley Interscience, New York.

Chabot, B.F., and D.J. Hicks. 1982. The ecology of leaf life spans. Annual Review of Ecology and Systematics 13:229-259.

Chapin, F.S. III. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11:233-260.

Chapin, F.S., and G.R. Shaver. 1989. Differences in growth and nutrient use among arctic plant growth forms. Functional Ecology 3:73-80

Christensen, N., R.B. Burchell, A. Liggett, and E.L. Simms. 1981. The structure and development of pocosin vegetation. Pages 43-61 *in* C.J. Richardson, ed. Pocosin Wetlands. Hutchinson Ross, Stroudsburg.

Clewell, A.F., and D.B. Ward. 1987. White cedar in Florida and along the northern Gulf Coast. Pages 69-82 in A.D. Laderman, ed. Atlantic White Cedar Wetlands. Westview Press, Boulder.

Conner, W.H. 1998. Impacts of hurricanes on forests of the Atlantic and Gulf coasts, USA. Pages 271-277 in A. D. Laderman, ed. Coastally Restricted Forests. Oxford University Press, New York.

Conner, W.H., and Day, J.W. 1998. The effect of sea level rise on coastal wetland forests: the Mississippi Delta, USA, as a model. Pages 278-292 in A. D. Laderman, ed., Coastally Restricted Forests. Oxford University Press, New York.

Dunsworth, G.B. 1998. Problems and research needs for *Chamaecyparis nootkatensis* forest management in coastal British Columbia, Canada. Pages 70-81 in A. D. Laderman, ed. Coastally Restricted Forests. Oxford University Press, New York.

Eckert, R.T. 1998. Population genetic analysis of *Chamaecyparis thyoides* in New Hampshire and Maine, USA. Pages 171-184 in A. D. Laderman, ed. Coastally Restricted Forests. Oxford University Press, New York.

Edwards, S. 1992. Foliar morphology of *Chamaecyparis* and *Thuja*. Four Seasons 9:4-29.

Ewel, K.C., and W.J. Mitsch. 1978. The effects of fire on species composition in cypress dome ecosystems. Florida Science 41:25-31.

Flora of North America Editorial Committee (FNA). 1993. Flora of North America North of Mexico, Vol. 2. Pteridophytes and Gymnosperms. Oxford University Press, New York.

FNA. See: Flora of North America Editorial Committee.

Gambell, A.W., and D.W. Fisher. 1966. Chemical composition of rainfall, eastern North Carolina and southeastern Virginia. U.S. Geological Survey Water Supply Paper 1535-K.

Gorham, E. 1958. The influence and importance of daily weather conditions in the supply of chloride, sulphate, and other ions to fresh waters from atmospheric precipitation. Royal Society of London Philosophical Transactions Ser. B241:147-178.

Great Britain, Meteorological Office. 1980. Tables of temperature, relative humidity, precipitation, and sunshine for the world. Part 1: North America and Greenland. Part 5. Asia. Her Majesty's Stationery Office, London.

Greenup, M. 1998. Managing *Chamaecyparis lawsoniana* (Port-Orford-cedar) to control the root disease caused by *Phytophthora lateralis* in the Pacific northwest, USA. Pages 93-100 *in* A. D. Laderman, ed., Coastally Restricted Forests. Oxford University Press, New York.

Hennon, P.H., C.G. Shaw III, and E.M. Hansen. 1998. Reproduction and forest decline of *Chamaecyparis nootkatensis* (yellow-cedar) in southeast Alaska, USA. Pages 54-69 *in* A. D. Laderman, ed. Coastally Restricted Forests. Oxford University Press, New York.

Jonasson, S. 1989. Implications of leaf longevity, leaf nutrient reabsorption and translocation for the resource economy of five evergreen plant species. Oikos 56:121-131.

Jonasson S., and F.S. Chapin, III. 1985. Significance of sequential leaf development for nutrient balance in the cottonsedge, *Eriophorum vaginatum* L. Oecologia (Berlin) 67: 511-518.

Kientzler, C.F., A.B. Arons, D.C. Blanchard, and A.H. Woodcock. 1954. Photographic investigation of the projection of droplets by bubbles bursting at the water surface. Tellus 6:1-7.

Kruckeberg, A.R. 1954. The ecology of serpentine soils. III. Plant species in relation to serpentine soils. Ecology 35:267-274.

Laderman, A.D., ed. 1987. Atlantic White Cedar Wetlands. Westview Press, Boulder and London.

Laderman, A.D. 1989. The Ecology of Atlantic White Cedar Wetlands: a Community Profile. U.S. Fish and Wildlife Service Biological Report 85(7.21).

Laderman, A.D. 1998a. Freshwater forests of coastal margins. Pages 1-35 in *in* A.D. Laderman, ed. Coastally Restricted Forests. Oxford University Press, New York.

Laderman, A.D., ed. 1998b. Coastally Restricted Forests. Oxford University Press. New York, Oxford. 334 pp.

Lajtha, K., B. Seely, and I. Valiela. 1995. Retention and leaching losses of atmospherically-derived nitrogen in the aggrading coastal watershed of Waquoit Bay, MA. Biogeochemistry 28 (1):33-54.

Laurance, W.F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology 5:79-87.

Li, H.L. 1963. Woody Flora of Taiwan. Morris Arboretum. Livingston Publishing, Narberth, PA.

Libby, W.J., M.H. Bannister, and Y.B. Linhart. 1968. The pines of Cedros and Guadalupe Islands. Journal of Forestry 66:846-853.

Little, S. 1950. Ecology and silviculture of white cedar and associated hardwoods in southern New Jersey. Yale University School of Forestry Bulletin 56:103 pp.

Lovett, G.M., and S.E. Lindberg. 1993. Atmospheric deposition and canopy interactions of nitrogen in forests. Canadian Journal of Forestry Research 23:1603-1616.

Lugo, A.E., S. Brown, and M.M. Brinson, eds. 1990a. Forested Wetlands. Ecosystems of the World, Vol. 15. Elsevier, New York.

Lugo, A.E., S. Brown, and M.M. Brinson. 1990b. Concepts in wetland ecology. Pages 53-85 *in* A.E. Lugo et al., editors. Forested Wetlands. Ecosystems of the World, Vol. 15. Elsevier, New York.

McKinley, C.E., and F.P. Day. 1979. Herbaceous production in cut-burned, uncut-burned, and control areas of a *Chamaecyparis thyoides* (L.) BSP. *(Cupressaceae)* stand in the Great Dismal Swamp. Bulletin of the Torrey Botanical Club 106:20-28.

McWilliams, W.H., J.B. Tansey. T.W. Birch, and M.H. Hansen. 1998. Taxodium – Nyssa (cypress – tupelo) forests along the coast of the southern United States. Pages 257-270 *in* A. D. Laderman, ed. Coastally Restricted Forests. Oxford University Press, New York.

Molina, R. 1994. The role of mycorrhizal symbioses in the health of giant redwoods and other forest ecosystems. Pages 78-81 *in* P. S. Aune, coordinator. Proceedings of the Symposium on Giant Sequoias. U.S. Department of Agriculture General Technical Report PSW- GTR-151. Forest Service, Pacific Southwestern Research Station, Albany, CA.

Monk, C.D. 1966. An ecological significance of evergreeness. Ecology 47:504-505.

Moore, P.D., and D.J. Bellamy. 1974. The Peatlands. Springer-Verlag, New York.

Motzkin, G., W.A. Patterson III, and N.E.R. Drake. 1993. Fire history and vegetation dynamics of a *Chamaecyparis thyoides* wetland on Cape Cod, Massachusetts. Journal of Ecology 81:391-402.

NOAA (National Oceanic and Atmospheric Administration). Meteorological Data for 1992. US Dept. of Commerce, National Climatic Data Center, Asheville, NC.

Olmsted, I., and R. Duran Garcia. 1998. Distribution and ecology of low freshwater coastal forests of the Yucatan Peninsula, Mexico. Pages 237-256 *in* A.D. Laderman, ed. Coastally Restricted Forests. Oxford University Press, NY.

Oren, R., J. Sperry, B. Ewers, D. Pataki, N. Phillips, and J. Megonigal. 2001. Sensitivity of mean canopy stomatal conductance to vapor pressure deficit in a flooded *Taxodium distichum* L. forest: hydraulic and non-hydraulic effects. Oecologia 126(1):21-29

Ornduff, R. 1998. The *Sequoia sempervirens* (coast redwood) forest of the Pacific coast, USA. Pages 221-236 *in* A. D. Laderman, ed. Coastally Restricted Forests. Oxford University Press, New York.

Pike, L.H., R.A. Rydell, and W.C. Denison. 1977. A 400 year old Douglas fir tree and its epiphytes: biomass, surface area, and their distributions. Canadian Journal of Forest Research 7:680-699.

Prance, G.T., and A.E. Prance. 1993. Bark. Timber Press, Portland, OR.

Read, D.J. 2002. Towards ecological relevance – Progress and pitfalls in the path towards an understanding of mycorrhizal functions in nature. Pages 3-29 *in* Mycorrhizal Ecology. M.G.A. van der Heijden and I.R. Sanders, editors. Ecological Studies v. 157. Springer Verlag, Berlin, Heidelberg, New York.

Russell, J.H. 1993. Genetic architecture, genecology and phenotypic plasticity in seed and seedling traits of yellow-cedar *(Chamaecyparis nootkatensis* [D. Don] Spach). Dissertation. University of British Columbia, Canada.

Russell, J.H. 1998. Genecology of *Chamaecyparis nootkatensis*. Pages 82-92 *in* A. D. Laderman, ed., Coastally Restricted Forests. Oxford University Press, New York.

Schlesinger, W. 1978. Community structure, dynamics and nutrient cycling in the Okefenokee Cypress Swamp forest. Ecological Monographs 48:43-65.

Schulze, E.D., and F.S. Chapin III. 1987. Plant specialization to environments of different resource availability. Pages 120-148 *in* E.D. Schulze and H. Zwolfer, editors. Potentials and Limitations of Ecosystem Analysis. Springer-Verlag, Berlin.

Shaver, G.R. 1981. Mineral nutrition and leaf longevity in an evergreen shrub, *Ledum palustre* ssp. *decumbens*. Oecologia (Berl.) 49:362-365.

Sheffield, R.M., T.W. Birch, W.H. McWilliams and J. B. Tansey. 1998. *Chamaecyparis thyoides* (Atlantic white cedar) in the United States: Extent and characterization using broad-scale inventory data. Pages 111-123 *in* A. D. Laderman, ed., Coastally Restricted Forests. Oxford University Press, New York.

Small, E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. Canadian Journal of Botany 50:2227-2233.

Specht, R.L., ed. 1979. Heathlands and Related Shrublands of the World. Ecosystems of the World, Vol. 9A. Elsevier, Amsterdam.

Stebbins, G.L. 1942. The genetic approach to rare and endemic species. Madrono 6:241-272.

Stephens, R.R. 1991. Regeneration and management of coast redwoods (*Sequoia sempervirens*). Abstract in Symposium: Coastally Restricted Forests (April 9 - 11, 1991), New Haven. Unpublished.

Stoltzfus, D.L., and R.E. Good. 1998. Plant community structure in *Chamaecyparis thyoides* swamps in the New Jersey Pinelands Biosphere Reserve, USA. Pages 142-155 in *in* A.D. Laderman, ed., Coastally Restricted Forests. Oxford University Press, New York.

Tallis, J. H. 1983. Changes in wetland communities. Pages 311-347 *in* A.J.P. Gore, ed. Mires: Swamp, Bog, Fen, and Moor. Ecosystems of the World, Vol. 4A. Elsevier, Amsterdam.

Terrill, W.B. 1951. Some problems of plant range and distribution. Journal of Ecology 39:205-227.

Tilman, D., R.M. May, C.L. Lehman, and M.A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65.

Vogl, R.J. 1980. The ecological factors that produce perturbation dependent ecosystems. Pages 63-94 *in* J. Cairns, Jr., ed. The Recovery Process in Damaged Ecosystems. Ann Arbor Scientific Publisher, Ann Arbor.

Weigand, J., P.B. Alaback, A. Mitchell, and D. Morgan. 1992. Coastal temperate rain forests. Ecotrust, Portland, OR. Unpublished report.

Whigham, D.F., and C.J. Richardson. 1988. Soil and plant chemistry of an Atlantic white cedar wetland on the Inner Coastal Plain of Maryland. Canadian Journal of Botany 66:569-576.

Yamamoto, S.I. 1998. Regeneration ecology of *Chamaecyparis obtusa* and *C. pisifera* (Hinoki and Sawara cypress), Japan. Pages 101-110 *in* A.D. Laderman, ed. Coastally Restricted Forests. Oxford University Press, New York.

Zobel, D.B. 1998. *Chamaecyparis* forests: a comparative analysis. Pages 39-53 *in* A. D. Laderman, ed. Coastally Restricted Forests. Oxford University Press, New York.

REPAIRING THE COUNTRY’S ECOLOGICAL INFRASTRUCTURE: THE CUMULATIVE IMPACT OF SMALL DECISIONS

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Key Words: ecological infrastructure, sustainable development, sustainability, biotic impoverishment, environmentally benign decisions

INTRODUCTION

Aggregate small decisions exert a tyranny on the personal lives of individuals. Large numbers of people decide to drive on a particular highway at a particular time, and the result is a traffic jam. A hurricane, ice storm, or snowstorm is predicted and stores are depleted of flashlight batteries, foodstuffs, and the like. On a global scale, aggregate small decisions on the use of fossil fuels (particularly petroleum) substantially increases greenhouse gases (particularly carbon dioxide). Aggregate driving decisions, each insignificant on its own and generally localized, cause smog problems in Los Angeles and respiratory problems in Mexico City. Practically no attention is given to the serendipitous, beneficial effects of large numbers of environmentally benign decisions, which collectively might well result in a sustainable world and, at worst, will leave a more habitable planet for future generations.

Many citizens, even many biologists, are not particularly knowledgeable about the Atlantic white cedar. Even those well acquainted with the Atlantic white cedar may justifiably wonder if their efforts to restore it to some semblance of its former range and to improve management practices in its existing range will have a lasting, beneficial effect upon the bioregion in which it occurs and contribute significantly to the quest for global sustainable use of the planet and the desire to leave a more habitable planet for future generations. The answer to both questions is a resounding “yes” – if large numbers of similar groups concerned with the preservation and enhancement of ecological integrity of a wide variety of species and ecosystems contribute to an aggregate bioregional improvement and if sufficient aggregate bioregional improvements occur throughout the planet. The obstacles are unquestionably daunting because achieving such goals requires an enormous paradigm shift in human society’s relationship with natural systems, which constitute human society’s life support system and provide such services as maintaining the atmospheric gas balance. The consequences of a failure of the ecological life support system are appalling. For example, the Great Dismal Swamp is a unique and valuable ecosystem; failure to protect and enhance its ecological integrity in combination with large numbers of similar decisions elsewhere will have unfortunate, arguably catastrophic, effects on future generations of humans and millions of other species.

THE ATLANTIC WHITE CEDAR

If each generation accepts an additional amount of environmental degradation and loss of natural capital beyond the inherited state, the world will soon be biologically impoverished and inhospitable, and the biospheric life support system will cease to function adequately! Before the Civil War in the United States, the Atlantic white cedar (cedar) was a favorite choice for roofing shingles, and boat builders were very fond of it because of its light weight and resistance to decay. At present, commercial uses are limited to specialty wood products, possibly because of short supply. One central issue then becomes: should society cease to protect a species because its commercial value has declined, because no immediate commercial use is foreseeable in the future, or because the biodiversity of species in the planet's ecological life support system is not appreciated as it should be? The cedar requires nearly full sun and saturated soils. Ecological perturbations, such as catastrophic canopy fire and stress from saturated peat, are thought to be requirements for regeneration. Although clear-cutting does partially mimic natural environmental perturbations and allows some degree of regeneration, the ecological similarities between catastrophic fire and clear-cutting are minimal. No species should be considered in isolation from the ecosystem it inhabits, and while commercial value is assessed one species at a time, this approach is not sound for ecosystems because they have value both as a source of natural capital and as a provider of ecosystem services. While individual species may provide identifiable ecosystem services, the interdependent web of life is responsible for the particularly valuable services such as maintenance of atmospheric gas balance and transformation of nonhazardous wastes into additional natural capital. Ecosystem services are best considered by looking at the system that the cedar inhabits – swamps. One of the important ecosystem services that cedar swamps provide is storage of carbon as peat. Other services are discussed in more detail elsewhere in this symposium through the three prime focuses: (1) what strategies should be employed to ensure the continuation of the ecosystem services that are the basis of the planet's ecological life support system? (2) if each generation accepts the amount of ecological destruction that present generations are accepting, how long will the planet remain habitable and the quality of life acceptable? and (3) does human society have an ethical responsibility toward the other species on the planet beyond treating them as commodities and respecting them only for their commercial value?

THE SERENDIPITY OF ENVIRONMENTALLY BENIGN DECISIONS

The late William T. Odum (1982) of the University of Virginia produced a world-class paper entitled "Environmental Degradation and the Tyranny of Small Decisions." It was inspired by a paper from economist Alfred E. Kahn (1966) based on the economic impact of aggregate, small decisions. Both of their observations are based on the same phenomenon – the aggregate impact of seemingly insignificant, small decisions. Collectively, these small decisions (taken in the aggregate) tyrannize people by stealing time, fraying nerves, and disrupting schedules. Road rage merely increases the tyranny and the personal risks resulting from aggregate small decisions. Similarly, it is possible to drive a species to extinction one tree at a time. Should society become upset about the loss of one cedar? Becoming enraged is a difficult position to justify if only one particular tree is considered rather than the aggregate loss caused by large numbers of similar decisions to ignore the loss of one tree.

A flip side exists to the tyranny of small decisions – there is a serendipity of aggregate, environmentally benign decisions, each seemingly trivial and unimportant on its own, but in sufficient numbers the collective ecological protection and improved integrity of natural systems can be enormous. Society must keep this viewpoint constantly in mind when confronted with seemingly unmanageable environmental problems such as global warming. The collective impact of numerous, environmentally benign decisions at a particular place and time can reverse seemingly irreversible trends. This consequence is particularly evident in the case histories discussed in the National Research Council's (1992) book *Restoration of Aquatic Ecosystems: Science, Technology, and Public Policy*. When large numbers of people support environmental protection and ecological restoration, they usually are successful, even against seemingly overwhelming odds and obstacles. This support is being successful elsewhere in the world as well. The Chinese are revegetating the upper drainage basin of the Yangtze River, which will reduce erosion of soils and increase the life expectancy of the Three Gorges Reservoir by reducing the silt load being deposited behind the dam. The densely populated Netherlands has restored an ecosystem, including reintroduction of large mammals, in an area quite close to sizable population centers. Mass marketing revolutionized the industrial world, and mass concern about the fate of natural systems will revolutionize human society's relationship with them. At symposia such as this one, we must never lose sight of this possibility.

CONNECTIONS

People who consider themselves environmentalists are fond of affirming their "respect for the interdependent web of life" of which they are a part. This step is the first one on the long path toward environmental literacy – only a first step, not the final destination! The use of the word *respect* implies that the decision is optional. However, if humans are part of the interdependent web of life, then damage to the web threatens and impairs an individual's well being, ultimately even survival. Respect in this context is a weak, unsuitable word! If humans are part of the interdependent web of life, then they are dependent upon it! In short, there is no technological substitute for the biospheric/ecological life support system. If there is no technological substitute for the planet's ecological life support system, and if lives depend upon its functional well being, why not come directly to the point and acknowledge dependence upon it? Human activities are causing extinction of species, damaging the interdependent web of life, and threatening the life support systems by producing persistent toxic chemicals that disrupt endocrine systems and have a multitude of other deleterious effects. Anthropogenic artifacts (shopping malls, highways, etc.) are also displacing natural systems at an unsustainable rate.

Connections are the key factor in the interdependent web of life and the quest for sustainable use of the planet requires that human society examine these connections and become increasingly literate about them. Of course, absolute literacy is far beyond the capabilities of an individual, nation, or even of most organizations. For the Atlantic White Cedar Restoration Ecology and Management Symposium, establishing as many of these connections as possible has another component – it will draw in people who were unaware that their special interests are interlocked with cedar management. The downside is that it will inevitably be attacked by those who perceive their interests are threatened by cedar management. The overriding factor is that anything that threatens the integrity of the planet's ecological life support system threatens everyone, regardless of their special economic or other interests. None of these considerations seemed important during the frontier society or eras when vast unexplored territories existed in the United States. Then, the planet seemed infinite. At present, however, anyone who has failed to find a parking space realizes all too vividly that a finite planet with finite resources and a finite ecological life support system is being damaged or destroyed at a rate unprecedented in human history.

Almost certainly, critical connections of the cedar, Great Dismal Swamp, etc. to other parts of the bioregion will be disclosed at this symposium. A few illustrative examples follow.

Connections to Other Parts of the Americas

Many species of birds, particularly migratory birds, have enormous routes from their summer nesting grounds to their wintering grounds with stopovers in between. Twice annual migratory flights are especially stressful, not only with regard to the distance involved but also the hazards encountered en route. The elimination or degradation of habitat at any component of this system, including the beginning and the end, vastly increases the already hazardous journey. Bird watchers are particularly sensitive to migratory route damage, and it would be enlightening and educational for those interested in cedar management to develop ties with citizens of other components of the migratory route of at least one representative bird species. This connection would be a particularly valuable experience for students at all levels of the educational system.

Water and Air Sheds

Air and water pay no attention to political boundaries. The extensive, deliberately set fires of the last few years in Indonesia have adversely affected not only their own country but areas such as Thailand, well beyond its borders. Water management practices on the Colorado River have seriously diminished both the quantity and quality of the water reaching the Sea of Cortes. According to the British Broadcasting Corporation (BBC), land management practices in Mozambique have exacerbated the flooding problems, as have similar bad practices in the neighboring countries of Zimbabwe and Zaire from which water flows into Mozambique. If Sudan decided to dam the Blue and White Nile Rivers to provide water for irrigation to supply additional arable land and the consequent agricultural products for a growing population, Egypt would be deprived of water badly needed for its agricultural irrigation and the nutritional needs of an ever-growing population. The likelihood of war will be vastly increased if this scenario develops; war would increase the refugee problem in Africa and elsewhere. Food shortages will produce environmental refugees if the food supply does not keep pace with the population growth. Distant as these places are, Virginia is connected to them and the fate of its residents is linked to theirs, and all the connected human fates are linked to the fate of the environmental life support system.

HUMAN POPULATION SIZE AND PER CAPITA ECOLOGICAL FOOTPRINTS

The United Nations estimates that the population of the planet will double in the next 40 years. During my lifetime (77 years), the population of the world has more than doubled. Exponential growth simply cannot continue on a finite planet! Odum (1996) asks a key question: “Does human population growth spur economic development or strain it?” One might reasonably assert that rapid population growth has no economic or other benefit because social and environmental problems are created faster than they can be solved. Odum (1996) uses Egypt as a Malthusian microcosm in which the promise of technology (such as dams, high-yielding cultivars, and the like) simply discourages any attempts to limit population growth. Biwas (1993) notes that, between 1900 and 1990, arable land in Egypt increased from 5.5 to 7.5 million acres as a consequence of the construction of the Aswan dam, which permitted irrigation of dry land. However, during the same period, Egypt's population increased from 10 million to 50 million; thus, per capita arable land decreased from 0.5 to 0.1 acres. Even though increased yield, which provided more food per acre, was a factor, Egypt still has to import food to provide its people with even the barest essential diet. Exponential growth "won" over technological advances, as it usually does. In fact, on a finite planet, it is difficult to visualize ways in which exponential growth can ever be ignored or beaten in the long term.

Arguably, simple population size is less important than the size of the per capita "ecological footprint." Wackernegel and Rees (1996) have developed a method of calculating the environmental impact of an individual (or country) in terms of consumption of energy, material goods, and the like. For example, the United States, with a fraction of the world's total population, uses approximately 25% of the energy and material resources of the planet. The U.S. per capita ecological imprint is very large indeed, as is that of Canada and, to a lesser extent, developed countries in Europe and Asia, such as Japan. One might think that the size of the ecological footprint is directly correlated with the quality of life, but this is simply not true. The state of Kerala in India has a tiny per capita ecological footprint compared to the per capita footprint in the United States and Canada, yet the life expectancy is only slightly below that of the U.S. and the literacy rate is fractionally higher. A very important point exists in these statistics. When the world resource crises begin to be severe, it will be easy to denigrate the importance of preserving the integrity of the cedar ecosystem. One can almost write the statements: "Of course I support the preservation of the cedar in principle, but is it as important as __________?" Fill in the blank: economic development, creation of X number of new jobs, providing a site for a new industry, a new shopping mall, etc. However, the cedar ecosystems are an integral part of Virginia's ecological heritage. They are "umbrella species" whose protection inadvertently protects a host of less visible but essential species that inhabit the same ecosystem. Sacrificing an ecosystem to provide a simple way to address short-term emergencies is simply bad management. It requires little or no administrative skills and is unquestionably a zero sum game where there are always winners and losers. Skilled management requires more effort, multidimensional management skills, and, ideally, leads to a win-win situation in which both natural systems and human society benefit. Make no mistake; the cedar ecosystem will be repeatedly threatened by single-dimensional, one-objective managers who are becoming increasingly obsolete in a multidimensional global society. This situation will persist until a paradigm shift occurs in which natural capital is acknowledged as the primary source of human society's wealth without which technological development would not be possible (Diamond 1997).

RESTORING THE NATION'S ECOLOGICAL INFRASTRUCTURE: AIR, LAND, WATER, AND WILDLIFE

Most individuals take the delivery of potable drinking water for granted, as they do the ability to move from one spot to the other without paying tolls or enduring interminable delays. The American society expects enormous quantities of solid wastes to be removed from households (where it would soon constitute a health and space problem) and placed in some remote spot, preferably "not in my backyard" and more preferably far distant from the household. American society also expects a wide variety of food to be delivered in fresh condition, even in densely packed cities thousands of miles from where the food was produced. These and many other services are the result of having a very extensive series of pipes, transportation systems, etc., which collectively are termed *infrastructure.* This system is, in a sense, a technological infrastructure because much of it depends on engineer-designed and operated facilities. Former President George Bush, when he signed a national transportation bill, focused attention on the need to repair the country's crumbling infrastructure. At the end of the last century and the beginning of the present century, Virginia's legislative system has focused much attention on the need to repair and maintain the public highway system. However, preserving, maintaining, and restoring the state's and country's ecological infrastructure has not received comparable attention. This neglect has happened despite the fact that the well being of human society, particularly in the United States, has been based upon *natural capital*, namely the natural resource infrastructure that provides life-sustaining ecosystem services (such as maintaining a breathable atmosphere, nutrient cycling, waste transformation, water purification, solar energy capture, materials for bioengineering, and production of food, fiber and other raw materials so essential to the economy). Natural ecosystems have been providing such services free since the beginning of human history and, as a result, the ecological infrastructure is less noticed and less appreciated than the technological infrastructure, although both represent human society's life-support systems. Although much has been made about the declining birth rate in many countries (e.g., Eberstadt 2000), the world's population continues to grow (in 1999, it passed 6 billion) and will continue to rise until the middle of the present century for complex demographic reasons. Even a particular state or country with a birth rate well below replacement rate will probably not see a marked population decline because of increased human longevity, immigration, decreased infant and other mortalities, and the like. The United States, for example, is particularly accessible to inhabitants of countries with birth rates far higher than replacement rates, and the longevity of American citizens has increased dramatically over the last century.

A growing population, for whatever reasons, means less ecosystem services per capita unless ecosystems are better repaired and maintained than they are today. Furthermore, as Hawken et al. (1999) have shown, natural capitalism is the basis for the new emerging sustainable economy and practically all future economic growth, which they describe as the next industrial revolution. Fortunately, most industry, engineering, and many business persons are taking sustainable use of the planet seriously. For example, Hawken's (1993) book *The Ecology of Commerce* shows how environmental sensitivity can be coupled with substantial profits. The National Research Council (1996), which is the operating arm of the US National Academy of Sciences and the US National Academy of Engineering, has linked science and technology to society's environmental goals. *Time* (2000) magazine published a special edition commemorating Earth Day 2000 in which Ford Motor Company's advertisements focus on explicit environmental issues such as going solar, air quality, making parts for cars from soybeans, environmental consciousness, and the like. In addition, Nattrass and Altomare (1999) provide a persuasive discussion of how profit can go hand-in-hand with sustainable development. And last, but far from least, Anderson's (1998) book provides superb leadership in persuading the business community to operate more sustainably. Courageous books such as Common's (1995) show the limits to conventional economics in considerable detail, and books such as Luhrs' (1997) are increasingly popular on college campuses and among a significant minority of the general population. Raffensperger and Tickner (1999) have extensive discussions of the idea that when an activity raises threats of harm to human health and/or the environment, precautionary measures should be taken even if some cause-and-effect relationships are not fully established scientifically. Stated simply, the precautionary principle challenges human society to use reason and intelligence to act wisely and well when the consequences of not doing so may be catastrophic for human society, even though scientific "proof" as interpreted in courts of law is not robust. In a very real sense the precautionary principle shifts the burden of the proof to those making profits by exploiting the common grounds to prove that they are doing no harm rather than requiring persons who question their actions to do so. As is often the case in major paradigm shifts, adopting the precautionary principle has been difficult, arguably negligible, despite an increasing body of rhetoric showing justification for it. Some governments, particularly in Europe, and the United Nations have adopted the precautionary principle in principle but have not implemented it in any significant way.

Natural systems do not care if humans live or die, and natural systems do not seek to make a connection with them. Humans must take the responsibility of making a connection with their life support system because the consequences of not doing so will, at best, cause much human suffering and at worst result in a horrendous reduction of human numbers, even extinction of the species. Some discussions (*Time* 2000) provide a general status report on various components of the environment showing, for example, that the situation for freshwater is grim, while the impetus in other cases for remedial action is strong but somewhat less than urgent. Nevertheless, it is foolish to choose a part of the environment that is in dire need of attention and neglect the rest because the parts are all interconnected. Water quality and quantity is, in large part, a reflection of the surrounding land use management, and disruption of the hydrologic cycle by means of human artifacts, such as dams, canals, transfer pipelines and the like, can produce many unintended and largely unforeseen deleterious effects.

The big question is whether human society can facilitate a paradigm shift without first suffering horrendous consequences. Birth rates are falling over much of the developed world, but, even so, the world’s population will keep growing until at least mid-century, possibly beyond. Many of the world’s peoples, arguably as many as half, are living on such marginal incomes that getting to the next day, let alone getting to the next decade, is their primary focus. In affluent societies, materialism is dominant, although sustainable use of the planet is receiving increasing support. Human health and ecosystem health are closely coupled. Human society is dependent on ecological support systems and will suffer if they are not in robust condition.

Ultimately, the health of the country’s ecological infrastructure will depend on a huge number of local and regional decisions. The future of the cedar is a prime example of the “small” decisions, which in the aggregate will determine whether human society can develop a sustainable, harmonious relationship with the planet’s ecological life support system. A biologically impoverished world with an unhealthy ecological life support system will be neither sustainable nor desirable. However, not taking local and regional responsibility for the cedar and its counterparts elsewhere could produce such a world.

GLOBAL BIOTIC IMPOVERISHMENT

Worldwide biological systems are in decline, which is clearly the result of the aggregate effects of a vast multitude of small regional and local decisions. In mid-year 2000, Mayor Giuliani of New York City was reported by the news media as advocating use of pesticides to control mosquitoes that transmit the West Nile virus, which has proven fatal to some humans. His statement reportedly included the admission that he values humans above fish, worms, and other creatures. However, some of the species that will almost certainly be adversely affected by applications of pesticides will be ones that prey on mosquitoes and reduce their numbers substantially. Without the natural biological controls that will be eliminated by the pesticides, even more pesticide control for mosquitoes will be necessary.

People regularly express empathy for their fellow humans, even if the expression of this empathy results in the destruction of other creatures. Willingness to destroy biological components of the environment is just another part of a multitude of actions resulting in biotic impoverishment and which are generally justified either in terms of progress, economic development, empathy for other humans, or all of these together.

THE INDEPENDENCE FROM NATURE MODEL

All humans and all societies behave as they do because they have a certain mental model about how one should act and how things should be. In its simplest form, the most dangerous mental model is that humans are independent from natural systems and that they can domesticate or dominate the parts of nature that are important to them. Domination is certainly not true for the many disease-causing organisms that are becoming ever more resistant to antibiotics; AIDS; the gypsy moth in eastern United States; the Asian clam throughout the United States and many other parts of the world; the zebra mussel; cockroaches, house flies; mice; rats; fruit flies; and a long, long list of other organisms.

White-tailed deer were not a serious problem in the eastern United States in the middle of the 20th century and were, in fact, unknown in some areas where they are now considered pests. However, human society eliminated their predators, and they are now a problem on highways and are eating vegetation at Gettysburg National Memorial Park and in most suburban areas. Human society creates pests by reducing or eliminating their biological controls and by providing habitats that enhance the well being of the pests. Unlike human society, “pest societies” do not have unemployment. Human dominance and control are an illusion, which is why the pesticide manufacturers flourish, but the pests do not disappear.

A dangerous component of this mental model is that, because of creativity, technology, and ingenuity, humans no longer depend on nature’s services. Preliminary estimates of the monetary value of ecosystem services (such as a breathable atmosphere, etc.) are in the trillions of dollars (e.g., Costanza et al. 1997). However, attempts to convert ecosystem services into conventional economic valuing and terminology miss the primary point: there are no substitutes for most of these services and how does one truly value something that is irreplaceable? The misconception is that nature’s services will continue to human society at no cost, no matter what humans do to natural systems.

The mental model of an independence from nature is difficult to disprove. On a global scale, an ecological threshold would have to be crossed that would result in ecological disequilibrium and disruption of ecosystem services which, in turn, would cause enormous human suffering as well as suffering of other life forms. McNeill (2000) discusses in considerable detail the giant, uncontrolled experiment on planet Earth that the human race has undertaken in the 20th century. During the 20th century, environmental transformations have occurred at both a rate and a scale unprecedented in human history. One or more crucial environmental thresholds may have already been crossed that are placing ecosystems into disequilibrium and disrupting the delivery and reliability of ecosystem services. Many of the effects of human society upon natural systems are nonlinear, and, additionally, many thresholds and breakpoints exist. The likelihood of crossing one or more thresholds under these conditions is quite high and will require close observation to reduce the number of surprises. Since both individual and institutional behaviors are resistant to change, remedial action will probably be tardy, reluctant, and often fiercely resisted. Every area of the planet has one or more symbolic species, such as cedar, and, if society's empathy for symbolic species is heightened, the consequences of crossing an ecological threshold will almost certainly be significantly reduced. There are three sets of conditions that are likely to produce unexpected crossings of critical thresholds.

Discontinuities

Humans can drastically alter nature, but less well recognized is that nature can disrupt human society. Cairns and Bidwell (1996a,b) discuss some abrupt shifts (discontinuity) in previously stable states in which nature has adverse effects on human society. The abruptness will not necessarily be apparent on scales to which humans are accustomed but rather may be on geological, evolutionary, or other quite different and larger scales that apply to natural systems.

Sometimes discontinuity appears to be extremely abrupt, such as the rapidity with which many disease-causing organisms develop resistance to antibiotics. The AIDS epidemic has made behaviors once regarded as acceptable (at least in some human societies) as now life threatening and is causing major demographic discontinuities in Africa. The scale of the discontinuities may also vary from a worldwide climate shift resulting from anthropogenic greenhouse gases to a regional increase in pollution levels that threatens cedar.

Synergistic Effects

Environmental toxicologists have known for many decades that interactions of heavy metals and other toxicants can produce an effect significantly greater than their individual additive toxicities. However, these synergistic effects are not limited to toxicants. For example, increasing the temperature of the tundra may cause additional release of methane, which is a much more powerful greenhouse gas than carbon dioxide. This release could increase the greenhouse effect, leading to even greater release of methane and further increasing the temperature. Synergistic effects are particularly difficult to cope with because they are difficult to predict until they are observed. Once they occur, conditions that were "safe" in isolation from other conditions often have severe consequences synergistically.

Undetected or Unnoticed Trends

Most natural systems are both cyclic and highly variable, thus making early detection of a new trend difficult. As a consequence, early warning systems designed to detect changes from normal condition are likely to produce both false positives (indicating a change is occurring when it is not) or false negatives (indicating no change is occurring when in fact one is). Experience reduces but does not eliminate the number of false positives and false negatives. A limited number of false positives are beneficial because, like fire drills, they discover imperfections in the drill. However, if their frequency is too great, a signal of danger may not produce action because it is viewed as another false alarm. The old folktale of the boy who cried wolf so frequently that the villagers ignored his cry and, thus, were unprepared when the real wolf appeared remarks on this danger. False negatives are arguably far worse than false positives because they signal that everything is normal when it is not.

EXTERMINATING OUR RELATIVES

Various groups of indigenous peoples the world over refer to other species as their relatives. This conceptual model is an appropriate one because it demonstrates an empathy for other species separate from economic calculations of species as commodities or, to use the more common term, natural resources. Expressed in terms possibly more appropriate to the present, it is acceptable to use ecosystems in a sustainable way but not to abuse them in a non-sustainable way. The three most basic human needs are food, warmth (in the form of shelter or clothing or both), and water. Restrained harvesting for food and warmth on a sustainable basis is acceptable, but overharvesting that leads to extermination of species is not. Similarly, destroying habitat that leads to the extermination of a species has the same consequences as directly exterminating a species. Last, but not least, as Cousteau (2000) states, “There is only one body of water on our planet Earth, constantly traveling from one river, to one lake, to one ocean . . . The sea is a bonus to us all, soothing climates, washing beaches, feeding animals and people, connecting nations together, pregnant with resources of all kinds, but still sensitive and vulnerable.” Water ecosystems are not just fluids; they are living systems that can be impaired, injured, and transformed into debits rather than assets. Cousteau (2000) notes that convincing people to protect the environment by reasoning alone is essential but not sufficient: “... but now we need a more active army of people who love the sea, who understand that there is no life without water. And that we have to put all our efforts in saving whatever we can for future generations.”

The quality of life is not determined by material possessions once the basic needs have been satisfied. Destroying other creatures to accumulate material wealth, if done by everyone on the planet, will leave future generations with an inadequate ecological life support system and a quality of life dramatically diminished from the present one. What is needed is a paradigm shift that respects and honors the cedar and the habitat it requires. Replacing it and its habitat with human artifacts, if done for other species and habitats on a worldwide basis, will eliminate any realistic chance for sustainable use of the planet and for a quality life for future generations. In a worst possible case scenario, the ecological life support system could be placed in such a degree of disequilibrium that the planet becomes inhospitable to humans.

CONCLUDING STATEMENT

Just as an inappropriate conceptual model of the relationship between human society and nature can lead to numerous individual acts that are seemingly insignificant in isolation from others but will collectively still further damage natural living systems, a series of different individual acts, seemingly insignificant in isolation from others, can in the aggregate preserve natural systems and the integrity of the biospheric life support system. This conceptual model will give the current and future generations an opportunity to develop a sustainable relationship with natural systems.

There will almost certainly never be a court trial for the crimes of human society against the biosphere, but the consequences of the actions of human society will be more severe than any court judgment could be. Empathy for natural systems begins with those habitats that are best known, such as the habitat of cedar. With good fortune, the empathy will extend to habitats worldwide with the hope that the human societies associated with them will develop a strong empathy to protect their integrity and condition. Respect and esteem for habitats worldwide will result in sustainable use of the planet. Disrespect and disregard for habitat integrity and well being will likely result in an inhospitable planet and will definitely lower quality of life for present and future generations.

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LITERATURE CITED

Anderson, R. C. 1998. Mid-Course Correction: Toward a Sustainable Enterprise: The Interface Model. Chelsea Green Publishing Co., White River Junction, VT, USA. 204 pp.

Biwas, A. K. 1993. Land resources for sustainable agricultural development in Egypt. Ambio 22:556-580.

Cairns, J., Jr. and Bidwell, J. R.. 1996a. Discontinuities in technological and natural systems caused by exotic species. Biodiversity Conservation 5: 1085-1094.

Cairns, J., Jr. and Bidwell, J. R. 1996b. The modification of human society by natural systems: Discontinuities caused by the exploitation of endemic species and the introduction of exotics. Environmental Health Perspectives 104 (11): 1142-1145.

Common, M. 1995. Sustainability and Policy: Limits of Economics. Cambridge University Press, Cambridge, United Kingdom. 384 pp.

Costanza, R., d'Arge, R., de Groot, R., Faber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V. & Paruelo, J. 1997. The value of the world's ecosystem services and natural capital. Nature 387:253-260.

Cousteau, J-Y. 2000. Quote on cover. Calypso Log June issue.

Diamond, J. 1997. Guns, Germs and Steel: The Fates of Human Societies. W. W. Norton Company, New York, NY, USA.

Eberstadt, N. 2000. World depopulation: last one out turn off the lights. The Milken Institute Review First Quarter:37-48.

Hawken, P. 1993. The Ecology of Commerce. HarperCollins Publishers, New York, NY, USA.

Hawken, P., Lovins, A. & Lovins, H. 1999. Natural Capitalism: Creating the Next Industrial Revolution. Little, Brown, and Company Publishers, New York, NY, USA. 378 pp.

Kahn, A. E. 1966. The tyranny of small decisions: Market failures, imperfections, and the limits of economies. Kylos 19:23-41.

Luhrs, J. 1997. The Simple Living Guide. Broadway Books, New York, NY, USA. 444 pp.

McNeill, J. R. 2000. Something New Under the Sun: An Environmental History of the Twentieth-Century World. W. W. Norton and Co., New York, NY, USA. 421 pp.

National Research Council. 1992. Restoration of Aquatic Ecosystems: Science, Technology, and Public Policy. National Academy Press, Washington, DC, USA.

National Research Council. 1996. Linking Science and Technology to Society's Environmental Goals. National Academy Press, Washington, DC, USA. 530 pp.

Nattrass, B. and Altomare, M. 1999. The Natural Step for Business: Wealth, Ecology and the Evolutionary Corporation. New Society Publishers, Gabriola Island, British Columbia, Canada. 222 pp.

Odum, E. P. 1996. Ecology: A Bridge Between Science and Society. Sinauer Associates, Inc., Sunderland, MD, USA. 330 pp.

Odum, W. E. 1982. Environmental degradation and the tyranny of small decisions. BioScience 32(9):728-729.

Raffensperger, C. and Tickner, J. 1999. Protecting Public Health and the Environment: Implementing the Precautionary Principle. Island Press, Covelo, CA, USA. 385 pp.

Time (Special Edition for Earth Day). 2000. How to Save the Earth. 155(17):96 pp.

Wackernagel, M. and Rees, W. 1996. Our Ecological Footprint: Reducing Human Impact on the Earth. New Society Publishers, Gabriola Island, British Columbia, Canada. 160 pp.

THE ROLE OF HISTORICAL INQUIRY IN THE RESTORATION OF ATLANTIC WHITE CEDAR SWAMPS

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Abstract: An historical perspective is implicit in the restoration of damaged ecosystems, however explicit use is seldom made of available historical data. Practical reasons include the concern that historical data is not quantifiable and that temporal information gaps preclude interpretation of historical sources. A more insidious cause for omissions of historical information in restoration efforts is the long-standing divisions among disciplines that have placed history in the humanities and restoration ecology in the sciences. First described as endangered in 1748, cedar swamps now provide a unique opportunity to explore the role that historic data might play in landscape-level ecosystem restoration, and thus provide a strong incentive to transcend traditional disciplinary boundaries. The largest expanses of swamps dominated by cedar occur within 200 km of the first permanent English settlement in the New World. Historical data can be used to provide both a cultural and economic context for site selection and goal establishment in cedar swamp restoration. We also explore the role of historical sources in understanding hydrology, a driving variable in the decline of cedar swamps. Finally, we describe information needs for which historical knowledge has yet to be obtained.

Key Words: Alligator River, archaeology, carbon sequestration, ditches, goal setting, Great Dismal Swamp, hydrology, landscape-level, natural regeneration, tree rings, succession

INTRODUCTION

In the late 1950s and early 1960s, the English scientist and writer C. P. Snow, pondering a problem which had long bothered him, delivered lectures and wrote essays in which he took to task his scientific and humanistic colleagues in the Western intellectual world for their deliberate ignoring of each other. He was particularly harsh on humanists, for they consistently looked down upon scientists, claiming that they could neither think nor write. Citing himself as a counter-example to the image that humanists had created, he called for a bridging of the “Two Cultures” as he called them (Snow 1963). Since Snow's plea, there has been crossover between the two general areas of research and writing in the intervening four decades, but a sizeable chasm still exists between them. It is in the interest of bridging that gap, in at least a small way, that this partnership between biology and history was undertaken.

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), is an obligate wetland species (Reed 1988) that often occurs in dense, nearly monotypic stands in the outer coastal plain from Maine to Mississippi. Approximately 98% of the area once populated by cedar has disappeared since European colonization (Noss et al. 1995). The ecosystem cedar now dominates is considered globally threatened by the Nature Conservancy (Maryland Department of Natural Heritage 1994) and critically endangered by Noss et al. (1995). A long history of silvicultural exploitation has contributed to the decline, but hydrologic alteration is also thought to be a major factor (Laderman 1985). Drainage for agriculture and silviculture has increased over the last 200 years and Lilly (1981) suggested that up to 50% of the peat, which provides refugia for seeds and facilitates self-maintenance (regeneration after fire), has been lost to oxidation. There were immense stands of cedar atop accumulated peat, especially in the outer coastal plain of Virginia and North Carolina, and it is these areas where restoration may be possible.

Restoration is defined as returning an ecosystem to a close approximation of the original condition (NAS 1992), but the structure and function of long-damaged ecosystems may not be known. Since cedar was first described as endangered in 1748, the remaining stands have undergone some degree of hydrologic alteration, have been logged, and/or have experienced other anthropogenic disturbance. Thus, traditional scientific research may not provide adequate guidance for restoration of cedar swamps. Historical information, such as interviews (e.g., Brown and Atkinson This Volume, and Zimmermann and Mylecraine This Volume); corporate records (e.g., Brown and Atkinson This Volume); writings of colonists such as Byrd, Kalm, Lawson, and Ruffin; tree rings and radiocarbon dating (Zimmermann and Mylecraine This Volume); pollen analysis (Whitehead and Oaks 1979); and other sources may fill a variety of information gaps that currently limit restoration of this ecosystem. We will focus on the original extent of cedar, historical uses, and hydrologic conditions of stands in order to help characterize the ecosystem and the requirements for self-maintenance.

RESULTS AND DISCUSSION

ECONOMIC AND CULTURAL CONTEXT

1500s. Cedar has long been used by humans living on or near the east coast of the modern United States, but surprisingly few mentions of the tree appear in standard accounts of colonial technology. The tree was often mentioned in colonial travel accounts and other documentary sources from the early period.

Colonial era observers noted, too, how dependent parts of the colonies were on cedar. Contact era Indians and European colonists did use the tree, colonials, especially, harvested it extensively in the Delaware River Valley. Presumably Indians showed Europeans where the tree existed and their own uses of it. Indians of eastern North America used cedar for many purposes; ethnohistorians have shown over the last 30 years how much Europeans learned from American natives, but they have not mentioned extensive use of cedar (Lawson 1967, Axtell 1992). Many illustrations of Contact era Indian culture suggested the use of the tree and written sources clearly showed that eastern Indians made extensive usage of various cedar species.

1600s. The European invasion, which began in North America in earnest in the early 17th century, devastated Indian populations. Pandemic Eurasian and African diseases killed millions of American Indians (North, Central, and South) during the colonial era (from 1492 until 1783) in North America. But natives in many areas along North America's east coast taught Europeans the basics of survival on the continent, including uses of cedar.

Cedar was vital to the economy of southeastern Virginia and northeastern North Carolina until ditching, aided by the advent of steam technology, altered land use patterns. Natural resource extraction formed the economic base from the colonial period to present, as described by Ward (1989), in some regions where commerce is less viable. Kirby (1995) suggested that the region south of the James River in Virginia, including the Great Dismal Swamp (GDS) and continuing south around Albemarle Sound, was economically and culturally dependent on cedar and related forest products. Few historians seem to have picked up its importance to the colonial economy, but documentation comes from a variety of sources including personal property inventories and shipping logs.

1700s. John Lawson and Pehr (Peter) Kalm, two European naturalists, commented extensively on the uses to which Europeans put the tree by 1750. Lawson made a horseshoe-shaped overland expedition through the Carolinas in the early 1700s during which he wrote that many settlers in the Carolinas built and sold boats of cedar to the West Indies, especially Curaçao. The profits from the sales enabled them to procure imports from England and other colonial regions. He listed cedar's uses, including yards, top-masts, booms, and bowsprits for ship building; shingles for houses, roofs and siding; and cooperage, including pails and other buckets (Lawson 1967).

Peter Kalm, a student of Linnaeus who was acting on behalf of the Swedish Royal Society, toured North America between 1748 and 1750. His trip took him through the Delaware and Hudson River Valleys and into French Canada. He kept meticulous records, including a daily meteorological register. Several sections of his travel account discuss cedar and its importance to the burgeoning colonial economy of the Delaware Valley. He referred to the ongoing discussion over the proper scientific name for the tree, settling himself on *Cupressus thyoides* L. and stating that the English called it white cedar while his fellow Swedes referred to it as white juniper. *Cupressus thyoides* was later changed to *Chamaecyparis thyoides* by Britton, Stearns, and Pogenburg. Most importantly, Kalm called attention to the clearing of the tree from its local swamps in the valley, commenting: "Swamps and morasses formerly were full of them, but for the present these trees are for the greatest part cut down and no attempt as yet has been made to plant new ones." He continued by describing the tree, calling it very light and resistant to rot. In the form of shingles, cedar had become the standard roofing material in the Delaware Valley during the first century of European settlement there. Later in the travel account, he returned to the tree, analyzing its usefulness to the settlers and commenting that they "are not only lessening the number of these trees, but are even extirpating them entirely. People are here (and in many other places) in regard to wood bent only upon their own present advantage, utterly regardless of posterity." To demonstrate the problem created by the over-harvesting of the tree, he did dendrochronology on some of the recently-cut trees, finding that it took about 100 years for a cedar to reach about 41 cm (16 in) diameter. He concluded from his measurements that it would take about 80 years from germination for a tree to reach useful size (Kalm 1966), which is in contrast to estimates of 50 to 70 years in the most recent literature summary (Laderman 1989).

By 1750 the tree was being used for roof shingles, interior and exterior siding, cooperage, shipbuilding, and fencing. Fencing probably took the most trees, especially thinner ones of 30-38 cm (12-15 in), for fences were ubiquitous in European colonies by then. So much cedar had been harvested for fencing by 1750 that Benjamin Franklin and other Delaware River Valley naturalists were scrambling to find either other materials or new methods for fencing (Labaree 1961). Whether logging methods used for cutting and removing cedar encouraged or discouraged natural regeneration is not yet known.

As Kalm made his environmental and ecological appraisal of cedar, specifically, and what Europeans were doing to the North American environment and climate generally, plans began in colonial Virginia for significant exploitation of GDS. This huge swamp, straddling the modern Virginia-North Carolina border and containing Lake Drummond, is one of the great ecological features of southeastern Virginia-northeastern North Carolina. It contained extensive quantities of cedar (how much remains for further research) and is still an occasional supplier of the tree.

William Byrd II, one of the wealthiest tobacco planters in early to mid-18th century Virginia, proposed draining GDS in the aftermath of his work as one of the party charged with surveying the Virginia-North Carolina border in the late 1720s. His proposal, contained in his "Description of the Dismal Swamp and a Proposal to Drain the Swamp," was written sometime between 1728 and 1737. In it, he suggested the creation of stock company for the purpose of supplying labor and materials for digging drainage ditches to empty the swamp of water. As ditches were dug and portions of the swamp drained, the laborers (slaves provided by the stockholders) would then begin to clear lands for pasturage, then planting, according to the plan Byrd set forth. Hemp, necessary for ship's rope and bagging of grains, flour, and other commodities, could be grown on the cleared land. The plan fit well into the prevalent mercantilistic thought of mid-century, and it seems to have received support in England. However, it was not until the 1760s and 1770s that a company dedicated to the project was assembled. Then the American Revolutionary War intervened. Not until the 1780s and 1790s was work actually begun on the construction of ditches to drain GDS. For the next century, the Dismal Swamp Land Company, the company founded out of Byrd's plan and the activities of promoters like George Washington, worked to clear and farm the swamp lands, with only limited success.

1800s. Within the context of William Byrd's plan, cedar was central. The tree, of which large stands existed in the swamp, was heavily logged in the late 18th and 19th centuries. Suffolk, Virginia was founded in the mid-18th century and became a principal export center for cedar and other lumber products harvested in GDS. The town, located on the edge of the swamp in the 18th century, remained an important center of lumbering and was also the host of a small tourist trade of people who wanted to see the swamp and Lake Drummond at its center. Names for many of the city's roads reflect the significance of cedar: Juniper Landing, Cedar Mill Road, etc.

The Dismal Swamp Land Company met annually in Suffolk during the 19th century. That company exploited the shingle industry, employing about a half dozen vessels constantly in carrying shingles to northern markets. Literally, hundreds of laborers were employed in that industry alone, along with several hundred workers preparing other lumber products for markets. Captain Mills Riddick, a member of the Company, was one of the primary lumbermen engaged in exploiting the shingles, which were produced primarily from cedar, but also from other trees in the swamp as well, including bald cypress, *Taxodium distichum* (L.) Rich (Norfleet 1974). The business records of the Company and the Riddick family lumbering company should reveal much about the methods, products, markets, and transportation of cedar from the swamp to its final destinations.

1900s. The economic dependence on natural resources that began as subsistence farming with free roaming swine and timber harvest in the 17th century (Byrd 1728) became somewhat more commercial in the 20th century. Between the 1890s and 1920s, no less than 18 lumber and wood product companies were incorporated in Elizabeth City and heavy boat traffic in the Dismal Swamp Canal transported cedar and cedar wood products. Most cedar stands harvested during this period were not replanted (Lilly 1981), and did not regenerate to cedar (Phillips et al. 1998). New technology available after the civil war not only facilitated access to remote cedar stands, but also increased drainage throughout the peatlands of southeastern Virginia and northeastern North Carolina.

Additional work is needed to discern the quantity of cedar harvested, the locations and dates where harvesting occurred, and to estimate the value and extent of cedar products. After this analysis is done, then the full extent of human dependence on this ecosystem will be characterized. With this historical context, the value of a sustainable cedar harvest could be estimated which may provide an economic incentive for cedar restoration on privately held former cedar swamps. With so many landscapes in need of restoration, one factor used in prioritizing restoration efforts is the current or historic role of the ecosystem from the perspective of associated human populations (Cairns This Volume).

The Role of History in Cedar Swamp Restoration: Hydrology, Fire, and Peat

Selection of Sites and Goals for Restoration. Implicit in the term restoration is the notion that the ecosystem existed on the site at some point in the past. Reports of where cedar was harvested and descriptions of cedar swamps provide insights into the location, as well as the structure, of the ecosystem and thus provide targets for restoration.

Pollen analysis by Whitehead and Oaks (1979) suggests that cedar was a significant component of GDS for the last 3,000 years and several early authors reported that cedar was a dominant species in GDS (Kearney 1901, Korstian and Brush 1931). Maps generated since the late 1500s suggest that the original extent of GDS was far greater than at present. Lilly (1981) reviewed some of the estimates of the original extent of GDS in Virginia and North Carolina, and the largest estimate was 569,804 ha (Shaler 1890). The current extent of GDS has been estimated at between

194,251 ha and 103,601 ha, thus perhaps 20% of the original acreage remains (Lilly 1981). Of that, only a small portion presently consists of remnant cedar stands.

Given the length of time that portions of GDS have been drained and the effect of drainage on organic content of histosols (Lilly 1981), it is likely that either a mineral soil or histic epipedon remains in many areas. The diminished organic matter content and the resulting loss of effective water holding capacity represent important impediments to restoration in such sites, primarily through increased competition and greater risk of seed loss during fire.

Succession in Cedar Swamps. In addition to those lands where cedar was observed, cedar may have occurred elsewhere and was replaced, perhaps cyclically, by other ecosystems via natural succession. Because cedar is shade intolerant (Belcher and Atkinson This Volume, Korstian and Brush 1931, Little 1950, Pinchot 1900), shade tolerant hardwood species such as black gum (*Nyssa sylvatica*) and red maple (*Acer rubrum*) may replace cedar after 100-300 years, if no fire occurs (Buell and Cain 1943).

Several authors have concluded that cedar requires fire to regenerate and historical sources provide some support for this notion. Succession in ecosystems may be autogenic (result from factors strongly influenced by the ecosystem). Conversely, allogenic succession requires external factors, such as fire, flood, insect outbreaks, etc. for a particular sere. Evidence that cedar swamps exhibit allogenic succession, requiring severe canopy fires, can be found in corporate memos from GDS. Willis Riddick, the Dismal Swamp Land Company’s managing agent, reported extensive regeneration of cedar following an extensive fire in 1865.

Fire may be required for natural succession of cedar swamps; however, there is an important autogenic component to cedar succession. The peat substrate modifies the water table and provides a critical refuge for seeds during fire, which Korstian (1924) suggested was a strategy for cedar reestablishment. It is likely that cedar stands formed and were replaced in cycles that were repeated for thousands of years and throughout the peatlands of cedar’s range.

Cedar Swamp Ontogeny and Self-Maintenance

Once a site is selected and structural goals are determined, restoration requires replacement of functional processes that allow the ecosystem to persist through time and require minimal management effort, i.e., are self-maintaining. Examples of short-term maintenance mechanisms include seed pool establishment and vegetative regeneration (e.g. coppice regrowth), and these have been readily observed and measured in a variety of ecosystems. However, longer-term changes in ecosystem structure (succession) influence self-maintenance potential and are not be well documented, which increases the need for historical information regarding succession.

Cedar swamps tend to accumulate peat and require peat for self-maintenance in our range. Pollen analysis (Whitehead and Oaks 1979) suggested that GDS is 10,000 years old, accumulated peat at a rate of 30 cm per 1,000 years, and that cedar appeared 3,000 y.b.p. Peat, when saturated with water, provides a fire resistant seed reservoir that facilitates reestablishment after canopy fires. Short-term hydrology is important because the depth to water table at the time of a fire influences the depth to which a fire will burn into the peat, and thus whether seeds will be consumed by fire (Korstian 1924). Competition may also limit cedar regeneration if low water tables allow less flood tolerant species to invade (Shacochis et al. This Volume). Longer-term hydrology is also important for seed protection since seed burial follows peat accumulation. Longer term depth to water table influences the rates of primary productivity and decomposition, and thus determine peat accumulation rate. Therefore, regeneration, succession, and self-maintenance of cedar appear dependent on peat, fire, and both short- and long-term hydrologic regimes.

Role of Ditching

Contemporary writing on the decline of cedar lists both over-harvesting and drainage as primary causes (Laderman 1989, Levy and Walker 1979). The timing of the disappearance of most cedar stands is unclear, but lies at the heart of restoration strategies. If cedar declined prior to the Civil War, likely causes include over-harvesting or succession. However, if the decline followed the Civil War, more effective drainage, associated with advent of the steam engine, may be implicated. In this section, we explore the history of ditching in this region and its effect on ecosystem processes.

Since the late-glacial period, conditions at GDS favored accumulation of peat, which occurs when organic matter production exceeds loss. Hydrophytes maintain high primary production rates as saturated soils tend to slow microbial oxidation of organic matter, thus peat accumulates (Gambrell and Patrick 1978). As previously stated, the peat provides hydrologic modification and seed refugia that favor cedar swamp establishment. However, ditches drain the soil, which lowers water tables and reduces saturation periods. Lower water tables halt peat accumulation through rapid oxidation (mineralization), expose seed pools to fire, and eventually alter the vegetative composition of swamps. Furthermore, peatlands are a significant reservoir of carbon and drainage of peatlands has global greenhouse implications. Peatland drainage has also been cited as sources of nitrogen and mercury. Thus, an important role of an historic record is to refine estimates of the timing and extent of ditching.

How Indians and colonials gained access into the freshwater swamps in which cedar grew is not yet clear. Aerial photography in the Dare County Bombing Range of northeastern North Carolina indicated that the stands may have been harvested originally by water, which might have been learned from native Indians. Nineteenth and twentieth century methods of entry require ditching, railroading, or road building to enter the swamps. If Indians used hydrological techniques, such as ditching for drainage and log floating purposes, no evidence has been found to support such an idea for eastern natives. However, archaeologists have shown that many pre-Contact Indian Desert Southwestern cultures used a variety of irrigation techniques to water their maize, bean, and pepper crops, their principal foodstuffs (Cordell and Smith 1996). These techniques were used long prior to contact on the east coast; thus, it is possible that such techniques made their way from the Southwest to the east coast or that indigenous ditching developments were made in order to serve Indian purposes in exploiting swamps where water access is limited, such as GDS.

Sometime in the first millennium Common Era (CE), the peoples living in the Four Corners area of the modern United States known as the Anasazi began hydraulic engineering of their homelands to secure sufficient water for producing their crops. They, ancestors of the Pueblo peoples of today, constructed irrigation canals from rivers such as the Gila and built dams and dikes around low spots to impound water until needed. The land is still dotted with these hydraulic footprints visible today. The Anasazi even used declivities in rocks and boulders to catch a gallon or two of rainwater. Neither archaeological nor historical evidence has yet surfaced to prove that eastern Indians used hydraulic techniques, but the eastern regions of North America are and were generally humid with lots of rainfall. In the late 16th and early 17th centuries, however, two very serious droughts occurred along the mid-Atlantic coastline, and droughts of this severity typically only happen about every 500 to 1,000 years in this region (Kehoe 1981, Sauer 1971, Stahle et al. 1998). If eastern natives used hydraulic techniques for irrigation purposes, periods of such drought would have been the most likely times. Since eastern natives did use cedar for cabin and canoe construction, they might have also used hydraulic techniques to float logs out of the swamps in which the tree grows. Further historical investigation should reveal something on that question.

Washington Ditch is the first known ditch into GDS. The actual date of the ditch is difficult to establish, but the *Virginia Gazette* advertised land for sale adjacent to Washington Ditch on November 19, 1772. Other ditches extant prior to 1910 included Jericho Ditch (1810), Riddick Ditch (1816), Cross Canal/Hamberg Ditch (possibly a.k.a. Orapeake, mentioned in Kearney (1816)), Feeder Ditch (1812), Portsmouth Ditch (1890s), 5-Mile Ditch (NA), Big Entry Ditch (NA), and Tributary Ditch (NA). Dimensions of Washington Ditch were given as 3 to 4 m (10 to 12 ft) wide x 1 m (3 ft) deep for 8 km (5 mi) east to west in 1760s compared to the current 5 to 6 m (15 to 20 ft) wide and 3 m (10 ft) deep. In 1837, Edmund Ruffin reported that Jericho Ditch was 4 m (12 ft) wide and 1 m (4 ft) deep for 16 km (10 mi) running NW from Lake Drummond to Shingle Creek of Nansemond River, and was used for shingle export. Currently there are 51 major ditches in GDS with a combined length 315 km (196 mi), not including the Dismal Swamp Canal (Virginia Canals and Navigations Society, ND).

Ditching aided timber harvest and allowed conversion to agriculture in many portions of southeastern Virginia and northeastern North Carolina. Burrington, governor of NC, stated in 1734 that plantable land along navigable streams had already been taken up, and ditches provided a means of bringing shallow swamplands into production (Lilly 1981). Deeper swamps were also ditched, but drainage for agriculture was only feasible throughout the shallower margins. A means for lowering GDS water levels was provided by the construction of the Dismal Swamp Canal and its Feeder Ditch in the late 18th century through 1812. The Canal was completed in 1805, but was only deep enough to permit the passage of, ironically, shingle flats and lumber rafts of cedar and bald cypress. By 1814 a 20-ton decked boat made the passage (Brown 1981). Kearney (1816) studied the canal and found it too shallow for most vessels of the day and suggested that “steam machinery” be used to either improve the Dismal Swamp Canal or construct a new canal. His estimates placed the level of Lake Drummond at 7 m (24 ft) above the high tide mark in Nansemond River, Virginia and the level of the Dismal Swamp Canal at the Feeder Ditch as 1.5 m (6 ft) below the Lake (Kearney 1816). Similarly, Lilly (1981) estimated that with the locks in place by 1812, 6 m (19 ft) of lift were in the canal, thus solving the problem of heavier boat passage.

Surface elevations begin to change as soon as ditches begin to remove water from swamps. The surface elevation over several acres of swampland associated with Shirley Plantation on the James River dropped 46 cm (18 in) just 8 years after ditching (Kirby 1995). Kearney (1816) reported that four years after completion of the Dismal Swamp Canal, the soil in GDS had “shrunk” 0.3 m (12 in). East of the canal, Ruffin (1861) reported extensive ditching for agricultural development in the years following canal construction. Such chronic loss of peat is only exceeded by acute losses due to fire, which can burn deeply if the water table is lowered, such as by drainage. Several authors report deep peat fires in GDS (Chickering 1873), which may be followed by an open water habitat when/if water tables are restored.

The Dismal Swamp Canal would ultimately increase access for even more remote regions to the south. Northeastern North Carolina had always lacked a deep waterway for commercial export of forestry and agricultural products. Spurred by the Dismal Swamp Canal and several other factors, agricultural activities began to exploit the vast peatlands through drainage. Perhaps the earliest of these efforts was led by Josiah Collins and a group of businessmen from Edenton, North Carolina beginning in 1780s. Hundreds of slaves worked to dig ditches and a canal from Lake Phelps to the Scuppernong River (Lilly 1981). Writing in 1861, Edmund Ruffin reported that 0.9 m (3 ft) of peat had been lost in the roughly 20 years since his last visit to Collins plantation. Agricultural use of peatlands was generally profitable. The oxidation of peat released the phosphorus and potassium, that along with nitrogen fixed by peas that were inter-planted with corn, supplied the nutrients that crops required in this age before fertilizers were commercially available (Lilly 1981). Ditches lowered water tables even in the most remote peatlands, relegating peat and cedar swamps to the lowest landscape positions, where hydrologic gradients were too low for drainage so that agriculture could not take hold. It is in these areas that cedar persists today.

After the Civil War, the emphasis shifted from agriculture to forestry. Lilly (1981) suggested that harvestable cedar was largely timbered out in GDS and that the effort was concentrated in eastern North Carolina, where 95% of North Carolina’s wetlands are located (Wilson 1962). The more remote forests atop deeper peats were harvested last, so by the start of the 1900s, the counties of Dare, Hyde, Tyrell, and Washington on the Albemarle Peninsula were beginning a 50 to 60-year period of intense timber harvest. Pratt (1909 and 1912) in Lilly (1981) described the establishment of drainage districts in more than 230,000 ha (700,000 ac) following a 1909 act of the North Carolina state legislature. Later, more extensive ditching was conducted through the mid-1900s by paper companies that were establishing pine plantations.

Lilly (1981) stated that all the swampland in North Carolina has been logged at least once and has had some drainage imposed for agriculture or forestry. Most of the swamp development was limited to the margins until the 1800s, but drainage by ditches was adequate to convert 1,000s of ha of histosols to mineral soils.

FUTURE RESEARCH NEEDS

The Great Dismal Swamp and adjacent swamps in northeastern North Carolina represent the largest stands of cedar within its historic range, and some production of cedar products continues there. Availability of records in this region may yield additional insights. Examination of business records of lumber companies and canal and shipping records, may help estimate how much cedar was harvested annually or decadally. Important insights can also be gained through study of changes in wood use, evolution of harvesting methods, how the products were transported to market, and how rapidly cleared areas either returned to cedar or transitioned to red maple and black gum. Several recent reestablishment efforts have failed and the ecological requirements of cedar are not fully understood. Approximately 90% of the original acreage has disappeared, thus, one objective should be the generation of a map contrasting current and historical stands of cedar, which would provide clues to requisite environmental conditions.

There is a lack of data on historic water table depth, rates of subsidence caused by oxidation, and the structure of cedar swamps before, during and after the extensive hydrologic alterations of the last 400 years. Tree rings of standing and buried cedar may provide important corroboration of historical sources, including an indication of cedar swamp structure, tree growth response to water tables, etc.

Recovery of this ecosystem will require a multidisciplinary approach that includes historical, archaeological, and sociological as well as biological and ecological disciplines. Much of the former stands are under marginal agricultural cultivation and face development pressure due to their proximity to the coast. It is hoped that history, ecology and other disciplines can provide the technical information to support the restoration of some of these lands.

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LITERATURE CITED

Axtell, J. 1992. Beyond 1492: Encounters in Colonial North America. Oxford University Press, New York.

Belcher, R.T. and R.B. Atkinson. This Volume. Structural and ecophysiological responses of Atlantic white cedar across a range of shade intensities.

Betts, E.M. 1999. Thomas Jefferson's Garden Book: 1766-1824. Thomas Jefferson Memorial Foundation, Inc. Charlottesville, VA. 704 pages.

Brown, A.C. 1981. Juniper waterway: A history of the Albemarle and Chesapeake Canal. University Press of Virginia, Charlottesville, VA. 255 pp.

Brown, D.A. and R.B. Atkinson. This Volume. Interpretation of twenty-five years of Atlantic white cedar clearcutting in North Carolina

Byrd, W. 1967. Histories of the dividing line betwixt Virginia and North Carolina. Dover Publications, Inc. New York, NY.

Cairns, J. Jr. This Volume. Repairing the country's ecological infrastructure: The cumulative impact of small decisions.

Chickering, J.W. 1873. The flora of the Dismal Swamp. The American Midland Naturalist 7(9): 521-524.

Cordell, L.S. and B.D. Smith. 1996. Indigenous Farmers, pp. 220-221-2, 258 IN B.G. Trigger and W.E. Washburn (eds.). The Cambridge History of the Native Peoples of the Americas. Vol. I, North America, Part 1. Cambridge University Press, Cambridge, England.

Gambrell, R.P. and W.H. Patrick, Jr. 1978. Chemical and microbiological properties of anaerobic soils and sediments. p. 375-423. IN D.D. Hook and R.M.M. Crawford (eds.) Plant Life in Anaerobic Environments. Ann Arbor Science Publications, Inc., Ann Arbor, MI, USA.

Kalm, P. 1966. The America of 1750: Peter (sic) Kalm's Travels in North America, the English Version of 1770. Revised from the original Swedish and edited by Adolph B. Swenson. With a translation of new material from Kalm's Diary Notes. 2 Volumes. Reprint of the 1937 edition. Dover Publications, Inc., New York.

Kearney, T.H. 1901. Report on a Botanical Survey of the Dismal Swamp Region. Contrib. U.S. Natl. Herb., 5: 321-550.

Kehoe, A.B. North American Indians: A Comprehensive Account. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Labaree, L.W. 1961. The Papers of Benjamin Franklin, Volumes 3 and 4. Yale University Press, New Haven, Connecticut.

Laderman, A.D. 1989. The ecology of Atlantic white cedar wetlands: a community profile. USFWS Biological Report 85 (7.21).

Lawson, J. 1967. A New Voyage to Carolina. Edited with an Introduction by Hugh T. Lefler. University of North Carolina Press, Chapel Hill, North Carolina.

Lilly, J.P. 1981. A history of swampland development in North Carolina. Pp 20-39 IN C.J. Richardson (Ed.) Pocosin Wetlands. Hutchinson Ross Publ. Co., Stroudsburg, PA.

Maryland Department of Natural Heritage. 1994. Rare, threatened and endangered plants of Maryland.

Noss, R.F., E.T. LaRoe, and J.M. Scott. 1995. Endangered Ecosystems in the United States: A preliminary assessment of loss and degradation. National Biological Service, Biological Report 28:58.

Norfleet, F. Suffolk in Virginia, c. 1795-1840: A Record of Lots, Lives, and Likenesses. Whittet and Shepperson, Richmond, Virginia.

Osbon, C.C. 1919. Peat in the Dismal Swamp, Virginia and North Carolina. USGS, USGPO, Washington, DC.

Palik, B.J., P.C. Goebel, L.K. Kirkman, and L. West. 2000. Using landscape hierarchies to guide restoration of disturbed ecosystems. Ecological Applications 10(1): 189-202.

Phipps, R.L., D.L. Ierley, and C.P. Baker. 1978. Tree rings as indicators of hydrologic change in the Great Dismal Swamp, Virginia and North Carolina. USGS, Reston, VA

Pinchot, G. 1900. Silvicultural notes on white cedar. N.J. Geol. Surv. Ann. Rept., 1899: 131-135.

Ruffin, E. 1837. Observations made during an excursion to the Dismal Swamp. Farmers Register 4(9): 513-521.

Sauer, C.O. Sixteenth Century North America: The Land and the People as Seen by the Europeans. University of California Press, Berkeley, CA.

Shacochis, K.M., J.W. DeBerry, D.T. Loomis, R.T. Belcher, and R.B. Atkinson. This Volume. Vegetation importance values and weighted averages of Atlantic white cedar stands in Great Dismal Swamp and Alligator River National Wildlife Refuges.

Snow, C.P. 1963. The Two Cultures and the Scientific Revolution: The Rede Lecture for 1959. Cambridge University Press, New York.

Stahle, D.W., M.K. Cleaveland, D.B. Blanton, M.D. Therrell, and D.A. Gay. 1998. The Lost Colony and Jamestown drought. Science 280: 564-567.

Virginia Canals and Navigations Society. No Date. Great Dismal Atlas, Lexington, VA.

Whitehead, D.R. and R.Q. Oaks. 1979. Developmental history of the Dismal Swamp. Pp 25 to 43 IN Kirk, P.W. (Ed.) The Great Dismal Swamp. University of Virginia Press, Charlottesville, VA

Wilson, K.A. 1962. North Carolina wetlands: Their distribution and management. N.C. Wildlife Resources Commission, Raleigh, NC.

Zimmermann, G.L. and K.A. Mylecraine. This Volume. Reconstruction of an old growth Atlantic white cedar stand in the Hackensack Meadowlands of New Jersey: Preliminary results.

REMOTE SENSING INTERPRETATION OF TWENTY-FIVE YEARS OF ATLANTIC WHITE CEDAR CLEARCUTTING IN NORTH CAROLINA

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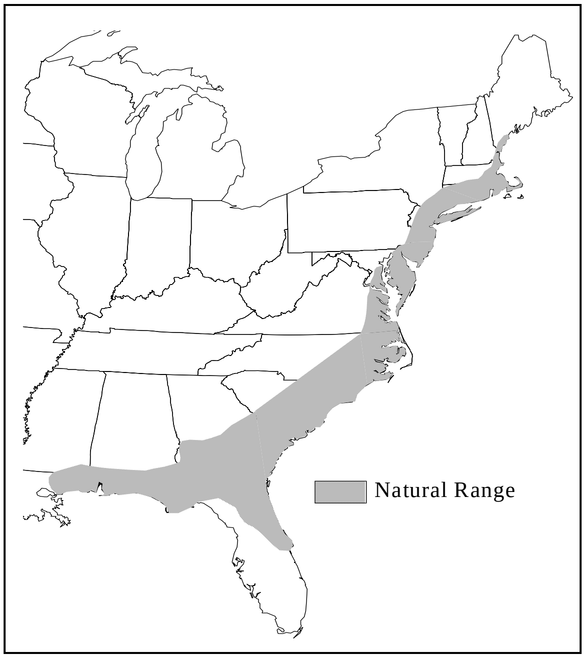
Abstract: The purpose of this study was to conduct a trend analysis using existing satellite imagery, available aerial photography, and logging records to determine the rate and acreage of Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), harvested since 1973 in northeastern North Carolina. MapInfo geographic information system (GIS) software was used to develop a GIS which combines digital baseline environmental data provided by the US Fish and Wildlife Service Alligator River National Wildlife Refuge, 1996 digital orthophotographic coverage obtained from Dare County in North Carolina, and 25 years of remote sensing multispectral satellite imagery, obtained from the US Geological Survey. Commercial extraction records were used to recreate the sequence of timber removal from the study area. The imagery was collected in late winter and early spring in approximately 5-year intervals starting with 1972. Spectral bands covered included visible light and the near-infrared band, which is known to show landscape changes in vegetation patterns. The functional GIS shows the progress of cedar clearcutting over time. Contrary to some reports in the literature, many of the clearcuts have regenerated naturally. Approximately 74.5% of the clearcut area within the area (547 ha) currently contains naturally regenerating cedar at varying growth stages. Average cedar stocking levels are 10,652 trees per ha. Future research includes investigation of biotic and abiotic factors influencing revegetation success of cedar.

Key Words: Chamaecyparis thyoides, geographic information system, remote sensing, digital orthophotography, MapInfo, multispectral satellite imagery

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), is a coastally restricted tree that is sensitive to salt intrusion and does not generally compete well with other species (Laderman 1989, 1998). Cedar is also susceptible to drought and flood conditions in the early growth stages (Akerman 1923, Trew 1957, Ehrenfeld 1995) and becomes shade-intolerant after establishment (Little 1950, Moore 1994). The range of the species is very narrow—from Maine to South Carolina along the Atlantic coast, through northern Florida, and across the Gulf coast to Mississippi (figure 1) (Korstian and Brush 1931).

Figure 1. Historic range of Atlantic white cedar (Korstian and Brush 1931).



The wood of cedar has been valued commercially, both for its characteristically uniform growth and its delightful aroma (Korstian and Brush 1931, Hanlon 1970). The species, more often than not, grows in dense monocultures, which has made commercial extraction at maturity very profitable. Hence, larger cedar stands of any commercial value have been systematically harvested throughout the range of the species (Little 1950, Laderman 1989).

Logging, and to a lesser degree agriculture, together have accounted for a total loss of approximately 90% of the cedar swamps in Virginia and North Carolina since the colonial era (Little 1950, Hughes 1995). Labor intensive methods to promote post-logging regeneration of the species have not been economically feasible to date (Brown and Atkinson 1999, personal communication Hughes 1995). However, some cedar stands in North Carolina have regenerated naturally after logging efforts. Laderman (1998) has indicated that logging may emulate the catastrophic disturbance required for successful cedar regeneration. Marginal success has previously been achieved through the use of fire as well (Baines N.D.).

Although the average cedar life span is approximately 150 years (Akerman 1923, Brownlie 1995), the cedar ecosystem naturally senesces to pond pine pocosin and maple/gum swamps in the absence of catastrophic natural or anthropogenic disturbances in this region (Richardson et al. 1981, Levy 1987, Laderman 1989). In fact, soil cores recently taken from the study area evidence the occurrence of mature cedar remnants approximately 3 m beneath an existing pond pine pocosin (Trettin personal communication 1998). From both the conservation and economic perspective, therefore, harvesting the mature cedar seems entirely feasible, if the cedar ecosystem can be successfully and economically regenerated after such a disturbance.

In North Carolina, Dare County Air Force Bombing Range and its neighbor US Fish and Wildlife Service (USFWS) Alligator River National Wildlife Refuge (ARNWR) together manage one of the largest remaining cedar inventories in the southeast range of the species (figure 2) (Davis 1998, personal communication Scott Smith 1996). The two agencies have cooperated over the past several years to reestablish cedar wherever feasible and to undertake studies that identify, protect, and enhance cedar ecosystems. After several studies that contributed considerably to cedar conservation and management (Bianchetti et al. 1995, Bonner 1995, Greenwood and Kellison 1995, Hinesley 1995, Johnson 1995, Jull et al. 1995, Lilly 1995, Phillips et al. 1991, L. Smith 1995, S. Smith 1995, Summerville 1995, Summerville and Hinesley 1995, Wicker 1995), an area jointly managed by both agencies was identified where cedar loss to timber harvest and its subsequent degree of natural regeneration might be evaluated (figure 3).

The analysis which follows, combines historical data and timber extraction records with satellite imagery, orthophotography, and personal interviews to determine the rate and acreage of cedar harvested from the area since 1973. In addition, the study addresses cedar regeneration in the areas harvested using transect data provided by USFWS ARNWR.

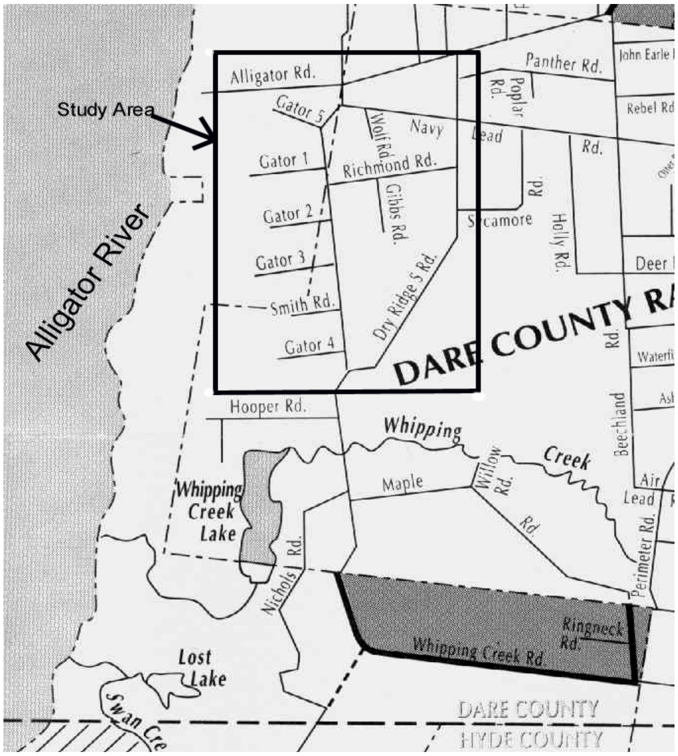
Figure 2. Location of Dare County Air Force Bombing Range and Alligator River National Wildlife Refuge, North Carolina (USFWS ARNWR 1997).

METHODS

Logging Records

WestVaCo intra-company memoranda describing logging operations and treatments dating from 1953 to 1978 were synthesized. Each record was carefully reviewed to determine whether the activity or event defined in the record occurred within the study area. On occasion, the activity described was pertinent even though it may not have occurred entirely within the study area (hurricanes, wildfires, and so on). Records were databased chronologically so that the sequence of timber removal and other relevant events could be determined.

Figure 3. Location map of the Five Gators Study Area (study area) (USFWS ARNWR 1997).



Personal Interviews

Local landowners, foresters, and lifetime residents who have witnessed the actual timber removal in Dare County over the years were also consulted. Area lumber mill operators were contacted to evaluate current and past uses of cedar. The most relevant information was recorded from interviews with former WestVaCo and Atlantic Forest Products employees. Tape-recorded interviews and oral histories from a number of individuals were also transcribed.

Henderson (personal interview 1998) stated that methods for logging cedar did not change between 1960 and 1995. All logging in the area was done using tracked feller-bunchers and skidders. Slash was left on site without windrowing, removal or burning. Associated species, such as loblolly bay, were cut but not removed.

Mapping Analysis

Geographic Information Systems software used for this study included MapInfo Professional™ and ArcView® GIS. MapInfo Professional™ was originally used to record and manage stand inventory data. ArcView® GIS was used to manipulate and classify processed satellite imagery. ArcView® was also used to calculate acreage of timber harvested.

Satellite Image Processing and Filtering

Multispectral LANDSAT imagery was obtained from the USGS EROS data center in April 1998. The images were selected based on the occurrence of timber harvests within the study area since 1973. The images were delivered on compact disc in binary format and then processed using Environment for Visualizing Images® (ENVI) software. Image files were converted to the desired wavelength combination for this analysis, bands 4, 2 and 1 (red, green and blue respectively), to simulate near-infrared imagery for remote sensing and visual inspection of vegetative patterns (ENVI 1997).

Each selected band of the satellite imagery was resized from 3913 samples and 3720 lines to 400 samples and 400 lines, which adequately represented the area. The image was deskewed using the scene-center longitude location as a reference to place the region of interest in a visual interface that appeared perpendicular to the analyst. Aspect ratio correction was used to account for oversampling in the scan direction. For older satellite imagery, gains and offsets in the binary data were calibrated based on azimuth and radiance using the information supplied in the header files which accompanied the USGS EROS Data Center satellite imagery.

To further enhance image quality for interpretation and classification, a number of filters were applied. The red, green and blue histograms for each processed image were simultaneously manipulated to increase variability between cover classes. Decorrelation adjustment of bland color composites produced mean and variance texture occurrences. The texture occurrence method was used for regions characterized by variations in brightness (ENVI 1997). Processed and filtered images were converted to grids which were then referenced to the USFWS ARNWR baseline road theme using Avenue, an Arc/Info® script.

Global Positioning System Survey

Beginning in 1995, a Trimble GPS (Global Positioning System) Pathfinder™ Pro XR system was used to develop the baseline road theme with decimeter accuracy. The Pro XR was accompanied by a backpack beacon receiver for real-time differential correction. Continuous center line points were taken along all roads and then projected in MapInfo Professional™ for GIS database development. Accuracy of GPS data points was confirmed by overlaying the baseline road theme on a 1987 SPOT satellite image with the same projection.

Stand Inventory

In a separate study beginning in 1995, cedar stands throughout the study area were systematically inventoried, using fixed-area 0.0008-ha circular plots installed 32 m apart along transects 63 m apart and perpendicular to access roads (Eagle 1999). Plot data included depth to water table, depth of peat, soil pH, and vegetation classes. All woody vegetation types were sampled in height classes, including naturally regenerated cedar.

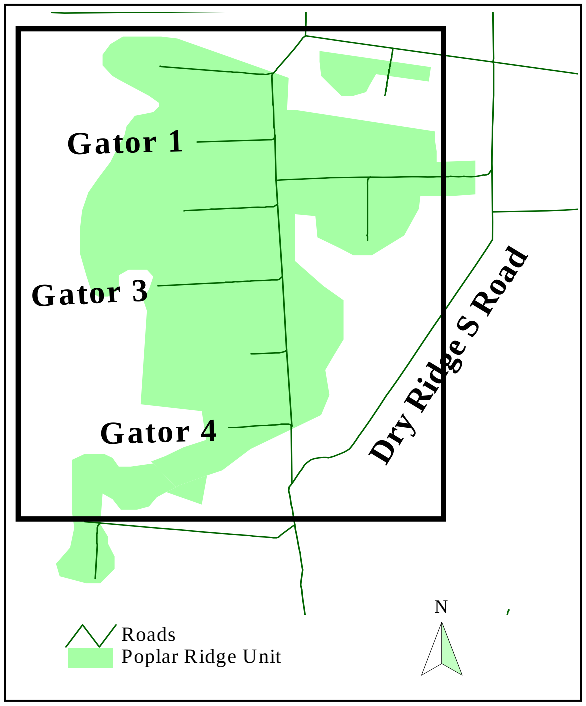
RESULTS

Logging Records

The stratified inventory was based solely on the occurrence of cedar. The Poplar Ridge Unit (1,170 ha) was mapped in 1978 and its location falls within the study area (figure 4). Information about when stands were harvested, and to what extent, was not available in the logging records. General information, such as date of harvest, was obtained through personal contact with foresters who have actively worked at or in the vicinity of the area since 1978, when Atlantic Forest Products, Inc. bought the timber rights to the area (personal interview Henderson 1998, personal interview Landino 1998). Ambrose (personal interview 1998) stated that, prior to logging access roads, networks of railways went throughout the swamp and the area was accessed year round.

George Henderson (personal interview 1998) indicated that none of the stands within in the study area were harvested in the winter between 1973 and 1987. According to Henderson, fewer roads were initially built on the west side of Dare County, including the area, because the area was so wet. Atlantic Forest Products conducted winter harvests mostly in Tyrell County because the county's road network, which was state-maintained, allowed access during the wet season. Dare County was initially logged mainly during the summer and late fall when the logging roads, which consisted primarily of clay, were dry and more accessible.

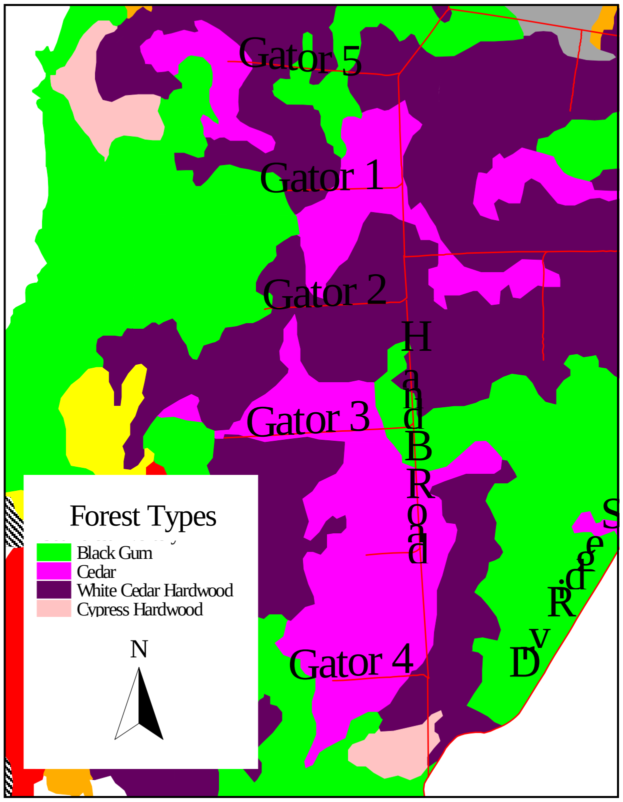
Figure 4. Poplar Ridge Unit (1,170 ha) in relation to the study area (outlined in bold).



Mapping Analysis

The 1960 Forest Type Map indicated that there were ha of the white cedar/hardwood type at the area in 1960. Pure stands of cedar comprised 332 ha. Black gum, which comprised 826 ha, generally occurred adjacent to cedar and cedar/hardwood types and extended beyond the study area boundaries (figure 5). The 1960 Forest Type Map was fairly useful in identifying age and size classes. The map showed that there were naturally regenerated stands of all sizes within the study area, indicating previous regeneration success (table 1). Stands as old as 110 years occurred in the southernmost part of the area and scattered 10-year old stands were also common at that time.

Figure 5. Cedar and cedar/hardwood associations in 1960 Forest Type Map.



Satellite Image Processing and Filtering

Processed images depicted larger community types but were not adequate for individual species classification at the given pixel resolution, which ranged from 50 to 80 m. The vegetative signatures for mature cedar and black gum stands were readily classified from the processed imagery (figure 6). However, it was not possible to separate the large pocosin-type areas into categories that would adequately define the composition of medium height cedar versus evergreen shrubs such as wax myrtle and gallberry. Also, quantification of communities along the Alligator River shoreline was not possible due to changes in shoreline outline. However, the satellite imagery was effective in illustrating the development of road networks and identification of harvested areas, which were confirmed as cedar stands (figure 7).

Table 1. Summarized forest inventory based on 1960 forest type map.

TYPE	AGE/VOLUME	HECTARES
Cedar	50 years old	148
Cedar	40 years old	180
Cedar	10 years old	4
Cedar / Hardwood	Class 1*	310
Cedar / Hardwood	Class 2	70
Cedar / Hardwood	Class 3	512
Black Gum	Class 1	826
Cypress Hardwood	Class 2	45
Hardwood	Class 2	53
Open	60 years old	53
Pond Pine	Class 1	134
Pond Pine Hardwood		88
Total		2423**

* Class 1: < 16.9cm^3/hectare; Class 2: 17.5 – 28.6cm^3/ha; Class 3: 29.1 – 57.7cm^3/ha.

** Atlantic white cedar and Atlantic white cedar/hardwood (1223 ha) includes 765 ha harvested in the study area plus 458 ha in adjacent stands which have not been harvested.

Figure 6. Comparison of cedar mapped units (left) and satellite image signature. The mapped cedar forest type in bright fuscia corresponds to the dark reddish-brown cedar signature from the 1973 satellite image. The satellite image has been filtered using an equalization stretch to enhance vegetative signatures.

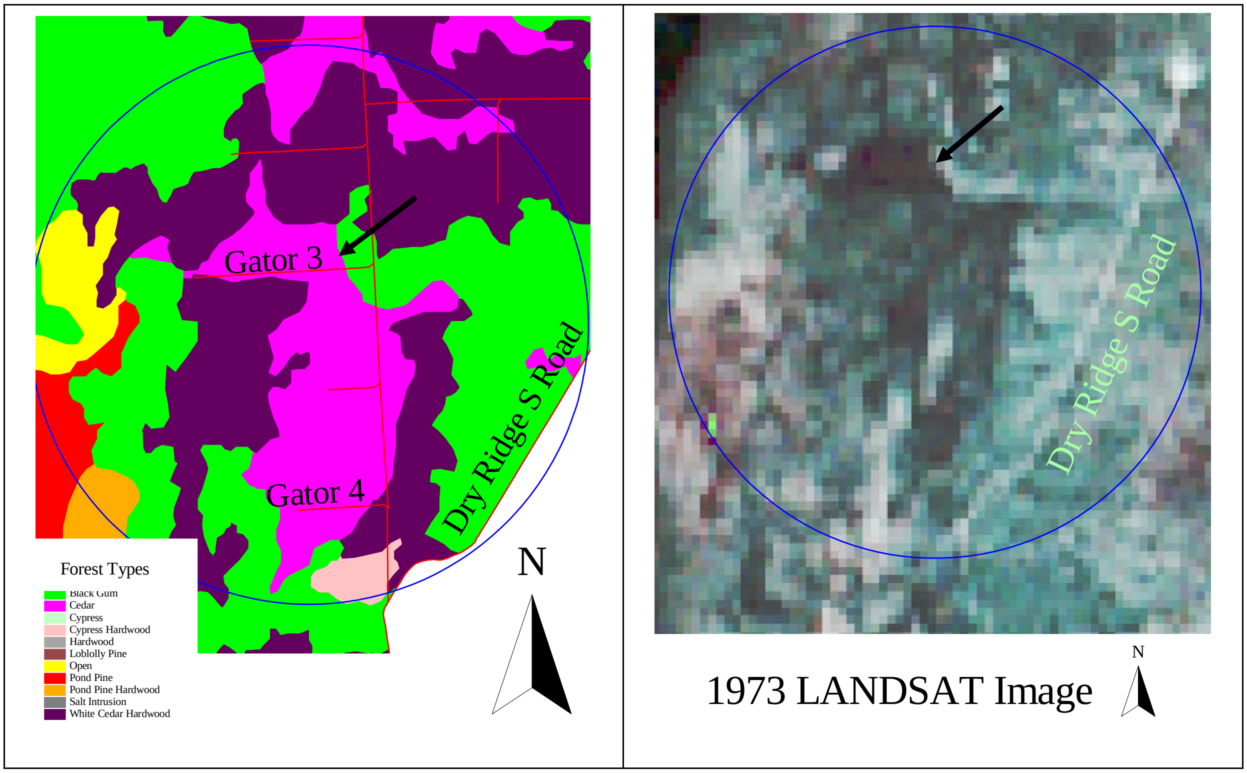
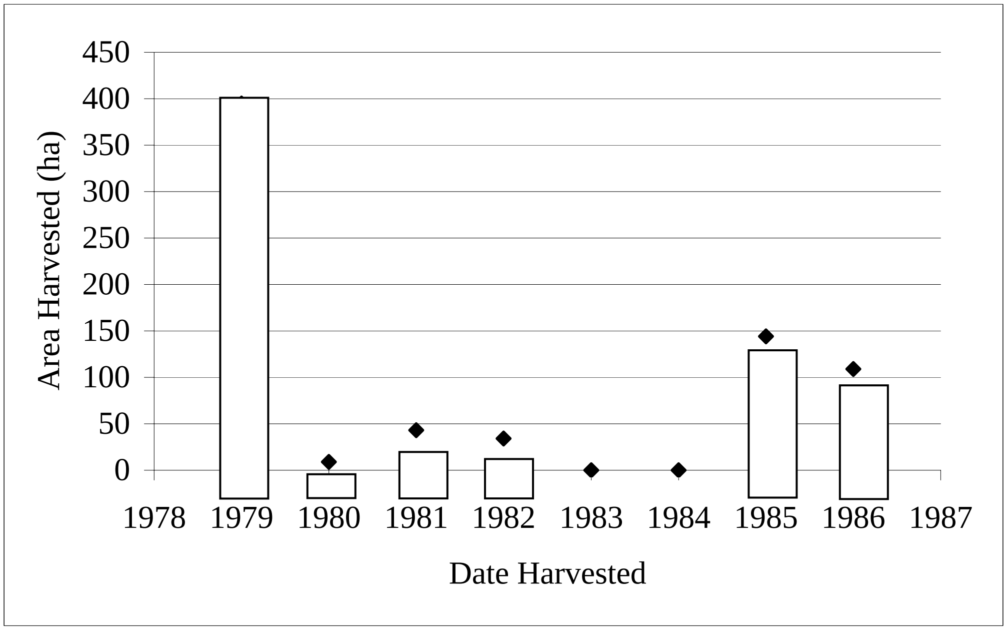
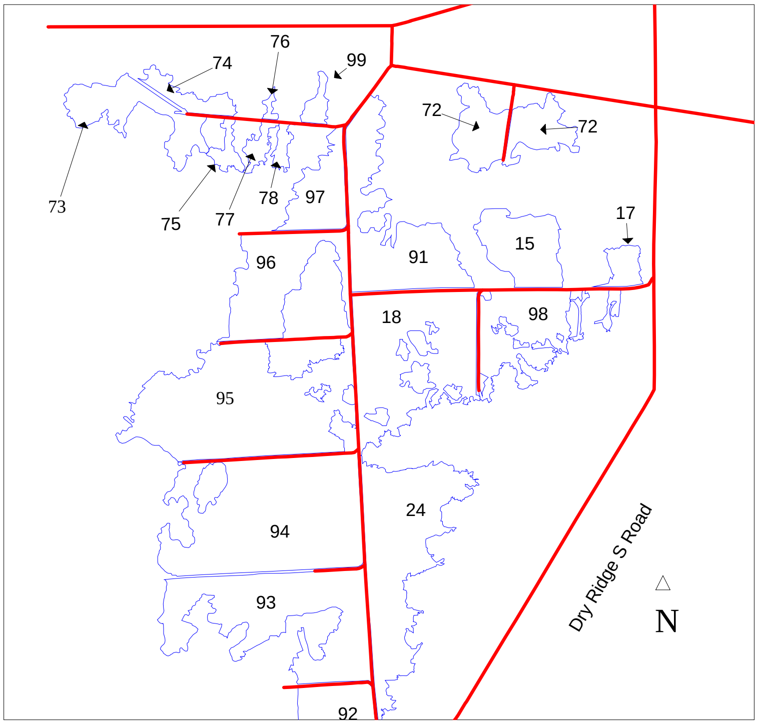


Figure 7. Date of mature cedar harvested in the study area.



By 1986, the clearcutting of mature cedar had been mostly completed. In 1995, ARNWR began evaluating the 21 clearcut cedar stands comprising 765 ha within the area for natural regeneration (figure 8) (Eagle 1999). After Atlantic Forest Products, Inc. left the area in 1986, there was a continued effort to harvest cedar from the remaining stands which, at that point, were only partially timbered. Satellite image classification indicated that cedar was actually harvested from the area through 1991, particularly in the southwest portion of the area.

Figure 8. Inventory of regenerated cedar stands (ARNWR 1998).
*Cedar stands were partially harvested in 1979 and again in the period from 1986 to 1991. The acreage estimate represents total harvested cedar.



Harvest Date	Stand	Ha
1979	18	71*
1979	91	54*
1979	94	106*
1979	95	103*
1979	96	40
1979	97	21
1980	17	7
1980	19	2
1981	73	25
1981	74	9
1981	76	1
1981	77	4
1981	99	4
1982	15	27
1982	75	4
1982	78	3
1985	72	31
1985	92	38
1985	93	75
1986	24	73
1986	98	36

Based on the results from the ARNWR cedar regeneration inventory, approximately 74.5% of the clearcut area within the area (547 ha) currently contains some component of naturally regenerating cedar at some growth stage. The average cedar stocking level is 10,652 trees per ha. In a very young naturally regenerated stand, the stocking level can exceed 247,000 trees per hectare (Korstian and Brush 1931). In a mature stand, there is currently no published number that quantifies healthy stocking levels, although 2,224 to 3,212 trees per ha has been reported (Little 1950). Overmature stands, in contrast, may only have 185 trees per ha (personal interview Henderson 1998).

One critical result of the ARNWR inventory was the identification of cedar in varying growth stages (Eagle 1999). The height growth interval greater than 2 m comprised 34.1% of the total naturally regenerating cedar. The only height growth interval that approached that percentage was the interval less than 30 cm (25.2%). Even stands that were harvested in 1979 had a considerable cedar component that was less than 30 cm.

DISCUSSION

According to the intra-company memoranda that were reviewed during this study, WestVaCo planted several hundred ha of cedar from 1953 to 1959 (Trew 1957, Earle 1958$^{a\text{-}d}$, Ehlen 1959$^{a\text{-}b}$). In Report NC-5 "Experimental Plantings 1953 through 1955" Trew acknowledged that hurricanes were responsible for destroying many of the cedar plantations (Trew 1957). Conner (1998) suggests that, in addition to salt flooding associated with coastal hurricane tidal surges, there is substantial organic export when the flood water subsides. During the course of the experimental plantings, descriptions of vegetative community associations and height growth increments were recorded. The mound-and-pool topography typically depicting cedar wetlands was also characterized (Trew 1957, Ehrenfeld 1995).

Landino (personal interview 1998) stated that cedar will not grow as quickly in the swamp as on an agricultural field. Brown and Atkinson (1999) have also confirmed this assertion. However, suppressed growth cannot account for the sheer volume of cedar which occurred in the less than 30 cm height interval throughout the area. If average growth rates were used (Akerman 1923), these small cedar might be aged to three years at the most. This implies that the study area either has a viable seed source for natural regeneration and that natural regeneration may occur, or that trees greater than 2 m may be mature enough to re-seed the area. The seed source could also be buried in the loose peat (Korstian and Brush 1931) or broadcast from nearby mature stands (Moore 1994).

Apparently, rabbit browse was a problem in WestVaCo's experimental plantings. Landino (personal interview 1998) indicated that the rabbit population was so large because of frequent wildfires. Even though sufficient animal browse could cause negative height increments to occur in cedar (Trew 1957), browse did not appear to be a critical factor in the ARNWR inventory and wildfires have been infrequent (personal communication Scott Smith 1998).

Satellite imagery was critical in the interpretation of the study area. However, use of collateral data such as personal interviews, old records, and maps was also essential given the size of the study area (1,170 ha) and the resolution of the imagery (30 m per pixel) (Fiorella and Ripple 1993, Evans and Hill 1990, Baumann 1990). The imagery was most useful in identifying large areas of cedar and following the progression of clearcuts over the study period (1973 to present). When combined with stand inventories, archive maps, and other information, remote sensing of satellite imagery proved to be a valuable analytical tool.

Recommendations for Further Study

Large-scale plantings will almost certainly never be an option within the study area due to access and costs. However, K.O. Summerville (personal communication 1997) stated that aerial broadcast of cones or seeds might successfully restock cedar areas. Continued collection of hydrologic data should help determine the effects of existing controls, ditches, and impoundments. Continued study and documentation of winter versus summer harvests is also recommended.

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The personnel and staff at Seymour Johnson Air Force Base, Headquarters Air Combat Command Operations, and Dare County Bombing Range were extremely helpful in the research effort. Scott Smith, Bryan Henderson, Jim Sabo and Emmett Carawan, in particular, are acknowledged for their continued efforts to find successful ways of restoring cedar to its original range and establish long-term silviculture of the species where feasible. Special thanks also are extended to the US EPA which is assisting with long-term ecological analysis of the study area, along with other cedar chronosequences. Without the assistance of former West Virginia Pulp and Paper Company foresters, George Henderson and Joe Landino, this report could not have been properly completed. Mr. Henderson and Mr. Landino provided crucial documents leading to the chronological sequencing of events that define the study area since 1972 and prior. Mr. Hubert Ambrose, a native of the Dare County peninsula, provided a rich oral history that filled in the activities prior to WestVaCo's ownership of the property dating back to the days when Dare Lumber Company owned much of the land in the study area. US Fish and Wildlife Service Alligator River National Wildlife Refuge employees were extremely helpful and provided valuable data which corroborates the history of the study area. In particular, Tom Eagle's assistance in both field interpretation and computer mapping was critical. Dare County, North Carolina provided orthophotography which was used as the baseline data for integration of all subsequent mapping layers. Without this baseline information, the research effort would have been significantly hindered. Christopher Newport University provided laboratory space and Geographic Information System workstation equipment.

LITERATURE CITED

Akerman, A. 1923. The white cedar of the Dismal Swamp. Va. For. Publ. 30:1-21.

Ambrose, H. July 14, 1998. Personal Interview with D. A. Brown regarding the history of cedar logging in Dare County. Manns Harbor, NC.

Baines, R. A. ND. Prospects for white-cedar: a North Carolina assessment. Duke University Forum, Durham, NC.

Baumann, P.R. 1990. Attempting to detect and record brushland in the northeastern United States using MSS data Schoharie County, N.Y., as a case study. Photogrammetric Engineering and Remote Sensing, vol. 56, March 1990, p. 387-391.

Bianchetti, A., R. C. Kellison, and K. O. Summerville. 1995. Seed dormancy and germination of Atlantic white-cedar (*Chamaecyparis thyoides*). In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Bonner, F. 1995. Seed conditioning and seed quality of Atlantic white cedar. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Brown, D. A. and R. B. Atkinson. (1999). Assessing the survivability and growth of Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P., in the Great Dismal Swamp National Wildlife Refuge. Department of Biology, Chemistry, and Environmental Science, CNU. U.S. Forest Service Southeastern Forest Research Publication.

Brownlie, D. J. 1995. Atlantic white-cedar (*Chamaecyparis thyoides*) natural regeneration at the Great Dismal Swamp National Wildlife Refuge, Suffolk, VA. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Conner, W.H. 1998. Impact of hurricanes on forests of the Atlantic and Gulf Coasts, USA. In Laderman, A. D. (ed.) 1998. Coastally restricted forests. Oxford University Press. New York, New York.

Davis, K. and S.M. Daniels. 1998. Inventory of Atlantic white cedar remnant stands in North Carolina. Seymour Johnson Air Force Base. Goldsboro, NC. 226 pp.

Eagle, Thomas R. Jr. 1999. Atlantic white cedar ecosystem restoration on Alligator River National Wildlife Refuge and United States Air Force Dar County Range. In 1997 Atlantic White Cedar Symposium Proceedings, Christopher Newport University, Virginia. USFS Southeast Forested Research Station Publication. Asheville, NC.

Earle, John D. 1958[a]. Personal Communication to William Ernst Jr. Regarding Estimate of 1959 Planting Season Requirements. North Carolina Woodlands. Manteo, NC.

Earle, John D. 1958[b]. North Carolina Woodlands Planting Report: 1958 Timber Management.

Earle, John D. 1958[c]. Memorandum To William Ernst Concerning Cypress Plantations at North Carolina Woodlands. Manteo, NC.

Earle, John D. 1958[d]. Personal Communication to William Ernst Jr. Regarding the 1959 Planting Season.

Ehlen, Rae R. 1959[a]. Personal Communication to W. J. Crumpacker Regarding Direct Seeding of Cypress. West Virginia Pulp and Paper Company. North Carolina Woodlands. Manteo, NC.

Ehlen, Rae R. 1959[b]. Personal Communication to W. J. Crumpacker Regarding Year Summary of Direct Seeding Study. West Virginia Pulp and Paper Company. North Carolina Woodlands. Manteo, NC.

Ehrenfeld, J. G. 1995. Microsite differences in surface substrate characteristics in *Chamaecyparis* swamps of the New Jersey pinelands. *WETLANDS*, Vol. 15, No. 2, June 1995, pp. 183-189.

ENVI Version 3.0. December 1997. Environment for Visualizing Images. Better Solutions Consulting Limited Liability Company. Lafayette, CO.

Evans, D.L. and J.M. Hill. 1990. LANDSAT TM versus MSS data for forest type identification. Geocarto International. 5: 13-20.

Fiorella, M and W.J. Ripple. 1993. Determining successional stage of temperate coniferous forests with LANDSAT satellite data. PE&RS - Photogrammetric Engineering and Remote Sensing. 59(2): 239-246.

Greenwood, L. L. and R. C. Kellison. 1995. Greenhouse production of Atlantic white cedar seedlings. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Hanlon, H. A. 1970. The bull hunchers. McClain Publishing Co., Parson, WV, 352 pp.

Henderson, G.C. 1998. Personal correspondence to Brown regarding “juniper” harvested in Dare County, North Carolina. Fairfield, NC.

Hinesley, E. 1995. Rooting Atlantic white cedar stem cuttings outdoors. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Hughes, J. H. 1995. Weyerhaeuser Company is helping with the effort to restore Atlantic white cedar in Coastal North Carolina. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Johnson, J. C. 1995. Alligator River National Wildlife Refuge’s approach to Atlantic white-cedar management. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Jull, L., F. A. Blazich, and L. E. Hinesley. 1995. Initial seedling growth of Atlantic white cedar as influenced by temperature and photoperiod. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Korstian, C. F., and W. D. Brush. 1931. Southern white cedar. US Dep. Agric. Tech. Bull. 251. 75 pp.

Laderman, A. D. (ed.) 1998. Coastally restricted forests. Oxford University Press. New York, NY.

Laderman, A. D. 1989. The ecology of the Atlantic white cedar wetlands: a community profile. US Fish Wildl. Serv. Biol. Rep. 85(7.21). 114 pp.

Landino, J. July 13, 1998. Personal interview with D. A. Brown regarding the history of Atlantic white cedar harvests in Dare County. Columbia, NC.

Levy, G.F. 1987. Atlantic white cedar in the Great Dismal Swamp and the Carolinas. In A. D. Laderman, (ed). Atlantic white cedar wetlands. Boulder, CO: Westview Press.

Lilly, J. P. 1995. Atlantic white cedar site adaptation and historical perspective. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Little, S. Jr. 1950. Ecology and silviculture of whitecedar and associated hardwoods in southern New Jersey. Yale Univ. Sch. For. Bull. 56. 103 pp.

Moore, S. E. 1994. Natural regeneration of Atlantic white cedar in the Great Dismal Swamp: A review of two studies. Paper submitted to the Great Dismal Swamp National Wildlife Refuge.

Phillips, R. W., W. E. Gardner, F. M. White and J. H. Hughes. 1991. Forestation with Atlantic white-cedar (*Chamaecyparis thyoides*) rooted cuttings and bare root seedlings. Paper presented to the Conference on Coastal Forests and Forested Wetlands, Yale University, New Haven, CN.

Richardson, C. J., R. Evans, and D. Carr. 1981. Pocosins: An ecosystem in transition. In C. J. Richardson (ed). Pocosin Wetlands. Hutchinson Ross Publ. Co., Stroudsburg, PA.

Smith, L. E. 1995. Regeneration of Atlantic white cedar at the Alligator River National Wildlife Refuge and Dare County Air Force Bombing Range. Master of Science Degree thesis submitted to North Carolina State University, Raleigh, NC.

Smith, S. B. 1995. Atlantic white cedar ecosystem restoration Dare County Air Force Range. In Proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Summerville, K. O. 1995. Atlantic white-cedar cone production area. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Summerville, K. O. and E. Hinesley. 1995. Provenance study trees rooted cuttings. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Trettin, C. 1998. Personal communication regarding the evidence of occurrence of Atlantic white cedar in Dare County, North Carolina pocosins. Charleston, SC.

Trew, I.F. February 1957. Experimental Plantings 1953 Through 1955 On North Carolina Woodlands. Report NC-5. West Virginia Pulp and Paper Company. North Carolina Research Project. Manteo, NC.

Trew, I.F. June 13, 1958. Memorandum to William Ernst Regarding Cypress Plantations at North Carolina Woodlands. NC.

Wicker, M. 1995. Atlantic white cedar wetland project. In proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

COMPARISON OF ABOVEGROUND STRUCTURE OF FOUR ATLANTIC WHITE CEDAR SWAMPS

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Abstract: Extensive logging, fire suppression and agricultural conversion of cedar stands have led to a dramatic decline in acreage and the designation as a globally threatened ecosystem by the Nature Conservancy. Consequently, quantifiable structural parameters are needed to set goals and monitoring criteria for cedar restoration. In this study, intermediate (20-35 years) and mature (60-70 years) stands from Great Dismal Swamp National Wildlife Refuge (GDSNWR) and Alligator River National Wildlife Refuge (ARNWR) were selected for structural comparison. Diameter at breast height (dbh), basal area, stem density, aboveground biomass and groundwater hydrology were measured in plots within each stand located along parallel transects during the growing seasons of 1998 and 1999. Total aboveground biomass ranged from 207,650 kg/ha for GDSNWR mature to 96,411 kg/ha for GDSNWR Intermediate. Average cedar dbh was larger at both GDSNWR sites than at the ARNWR sites. Live stem density was higher for ARNWR sites, particularly in ARNWR Intermediate, which was 15 times greater than GDSNWR Intermediate. ARNWR sites were wetter based upon annual twice daily depth to groundwater table readings. Several factors may be responsible for the structural differences among these naturally regenerating sites including site hydrologic history, site establishment conditions, and site age. Close agreement between the structural parameter results of this study and other previous cedar studies suggests that a high planting density of cedar in combination with an elevated groundwater table may be necessary to ensure the success of cedar restoration activities by providing adequate density at maturity and by emulating natural environmental conditions of the ecosystem.

Key Words: Atlantic white cedar, aboveground biomass, assessment, reference sites

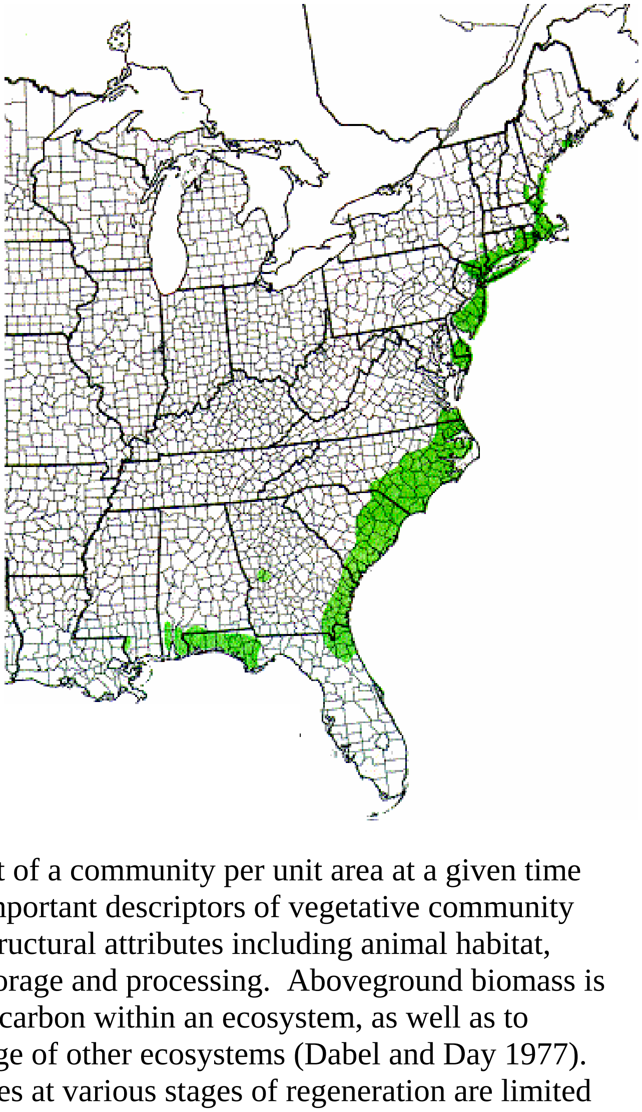
INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), historically occurred in isolated, even aged stands along the outer coastal plain from Maine, south to Florida and west to Mississippi along the Gulf coast states (Korstian and Brush 1931). While a few populations have been documented in southern Maine (Laderman et al. 1989) and to the west in Mississippi (Eleuterius and Jones 1972), vast cedar forests occurred in the outer coastal plain of the mid-Atlantic states including North Carolina, Virginia and New Jersey (figure 1). However, extensive logging for lumber (Akerman 1923), fire suppression (Korstian and Brush 1931), hydrologic modification (Frost 1987) and agricultural conversion (Whitehead 1972) of cedar stands have led to a decline in acreage of >98% across its entire range. The loss has been reported at 98-99% in the Great Dismal Swamp of Virginia and in North Carolina, and the ecosystem is currently listed as critically endangered (Noss et al. 1995).

Documentation of forested wetland structure is particularly important when the ecosystem that encompasses the forest type is in serious jeopardy of decline. Cedar vegetative community structure is important for the performance of various wetland functions and for establishing targets for restoration (NRC 1992). Aboveground vegetative structure has been utilized to characterize and compare many different ecosystems (Westlake 1963) and a variety of forested communities (Whittaker 1961, 1963, 1966, Grier and Logan 1977).

Southern deepwater swamps have received much attention due to the importance of lumber resources as well as the alarming loss rates (Conner and Day 1976, Day and Dabel 1978, Conner et al. 1981, Conner and Day 1982, Brown et al. 1997). Several researchers have described aboveground structure of wetland conifer species including Bald cypress *(Taxodium distichum* (L.)Richard) (Brown 1981, Schlesinger 1978, Mitsch and Ewel 1979) and Northern white cedar *(Thuja occidentalis* L.) (Reiners 1972). However, very few studies have quantified aboveground vegetative structure of cedar communities (Dabel and Day 1977).

Figure 1. Range of cedar. Adapted from Little (1971).



Aboveground biomass, measured as the weight of a community per unit area at a given time (Westlake 1963), and plant species composition are important descriptors of vegetative community structure. Several functions are influenced by these structural attributes including animal habitat, plant diversity, enhanced water quality and nutrient storage and processing. Aboveground biomass is also necessary to model the storage and processing of carbon within an ecosystem, as well as to provide a coarse means of comparison for a broad range of other ecosystems (Dabel and Day 1977). Studies that quantify aboveground structural differences at various stages of regeneration are limited for cedar ecosystems.

The present study sought to characterize and contrast aboveground structural parameters among two intermediate (20-35 years) and two mature (60-70 years) age classes of naturally regenerating cedar forests with an emphasis on the implications for ecosystem restoration. Results from this study, in combination with the published results of Dabel and Day (1977), and other similar wetland communities will aid in the selection and establishment of goals and monitoring criteria that may indicate success for cedar restoration activities at maturity.

METHODS

Study Stands

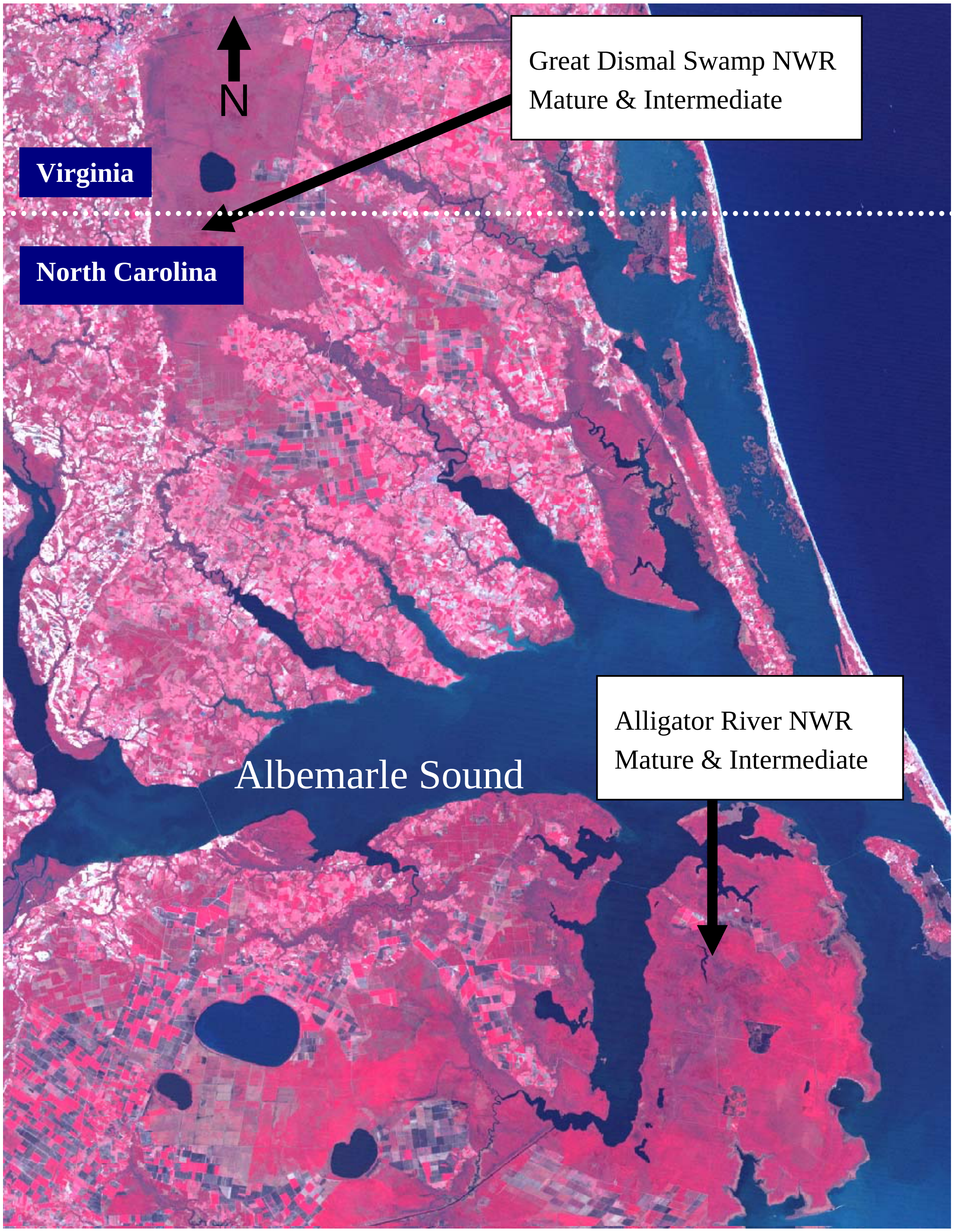
Two sites representing intermediate (25 - 35 years old) and mature (60 – 70 years old) cedar stands were chosen for study in GDSNWR using aerial photography, site age, site size, canopy dominance by cedar, site accessibility and local knowledge (personal communication GDSNWR refuge staff). Of the selection criteria listed above, emphasis was placed upon age, accessibility and canopy dominance by cedar in order to facilitate the objectives of the many research projects involved. The sites were located on the south side (North Carolina side) of Corapeake Ditch Road approximately 8.05 km from the western border of the refuge (figure 2). The mature and intermediate stands at GDSNWR were contiguous, and the difference in the ages of the two stands was believed to be the result of offset lumber harvesting schedules. Stands were surrounded by a mixed hardwood / cedar community dominated by red maple (*Acer rubrum* L.). The mature stand was characterized by a dense tree canopy almost exclusively formed by cedar and a thick under growth of shrubs, dominated by fetterbush (*Lyonia lucida* (Lam.) K. Koch) and sweet pepperbush (*Clethra alnifolia* L.). The intermediate stand was approximately 1.5 km south of Corapeake Ditch Road and was characterized by a mixed canopy of cedar and *A. rubrum* with a sparse shrub layer and large amounts of downed woody material.

Both a mature (60 – 70 years old) and an intermediate (15 – 25 years old) stand were selected for study in ARNWR located on the Albemarle Peninsula of North Carolina using similar selection criteria as for the GDSNWR sites. The mature site was located approximately 0.50 km from the northwest terminus of Sandy Ridge North Road, located in the central section of the refuge. The site was characterized by a closed, predominantly cedar canopy with a few pond pine (*Pinus serotina* Michaux) and loblolly bay (*Gordonia lasianthus* (L.) Ellis) present. This site had a sub-canopy of black gum (*Nyssa biflora* Walt.) and sweet bay (*Magnolia virginiana* L.) and a thick understory of shrubs including *L. lucida*, gallberry (*Ilex glabra* (L.) Gray) and large gallberry (*Ilex coriacea* (Pursh) Chapman). The intermediate site was located approximately one kilometer south of the mature site and adjacent to Sandy Ridge North Road. The intermediate site was characterized by very thick stands of pure cedar with infrequent, small open water areas typically referred to as “swales.” The open areas of these swales were dominated by *Sphagnum* spp. and waterlilies (*Nymphaea odorata* Aiton), while the outer edges often had a mixture of cedar, cypress, pond pine and *A. rubrum*.

Vegetative Structure

In September of 1998, preliminary information for aboveground structure of mature and intermediate age classes was gathered in nine 100-m^2 plots situated at 100-m intervals along established transects at each of the four forested sites for a total of 36 plots. In the 1999 vegetation

Figure 2. Location of Great Dismal Swamp NWR and Alligator River NWR.



survey, the number of plots was increased to eighteen 100-m^2 plots for each site to increase sampling area; however, other methods were unaltered.

Vegetation was identified to species using the *Manual of the Vascular Flora of the Carolinas* (Radford et al. 1964) and classified within one of three strata including trees ($\geq$ 2.54 cm in dbh or > 305.0 cm tall), shrubs (< 2.54 cm dbh, but $\geq$ 33.0 cm tall) and herbs (< 2.54 cm dbh and < 33.0 cm tall) following Oosting (1942) and Dabel and Day (1977).

Trees occurring in each 100-m^2 plot were identified to species and dbh were measured. A notable exception was ARNWR Intermediate, in which the tree stratum was sampled in 16-m^2 plots due to its considerably greater stem density. Least squares regression equations (table 1) developed for a cedar community in GDSNWR by Dabel and Day (1977) were used to calculate aboveground tree biomass based on dbh as the independent variable (Whittaker and Woodwell 1968). Baskerville (1972) reported that the use of logarithmic equations to evaluate biomass led to a 10-20% underestimation of the actual value; however, the simple allometric equation remains the most frequently used mechanism to determine biomass (Stanek and State 1978). Structural parameters including aboveground biomass, mean dbh, basal area and stem density were calculated using information gathered from the vegetation plots. Other equations have been generated using a combination of dbh and height or dbh and crown width (Peterson et al. 1970, Campbell et al. 1985). Campbell et. al (1985) suggested that measurement of dbh and height can contribute to total overall accuracy of aboveground biomass estimates. However, due to the large amount of time and data necessary to generate new equations, we chose to use the regression equations generated by Dabel and Day (1977). In addition, tree heights can be extremely difficult to measure in cedar stands.

Shrubs were identified to species and diameter at soil base, height, and two width measurements were recorded for each plant within a 16-m^2 nested plot located within each 100-m^2 plot. Shrub stratum dry weights were calculated using the regression equation (table 1). Stem densities were calculated using information from vegetation plots.

Table 1. Regression equations used to determine dry mass (kg) of vegetation of the form $\log_{10} Y = a + b (\log_{10} X)$, where (Y = dry mass in kg) and (X= diameter at breast height in cm). Equations developed by Dabel and Day (1977).

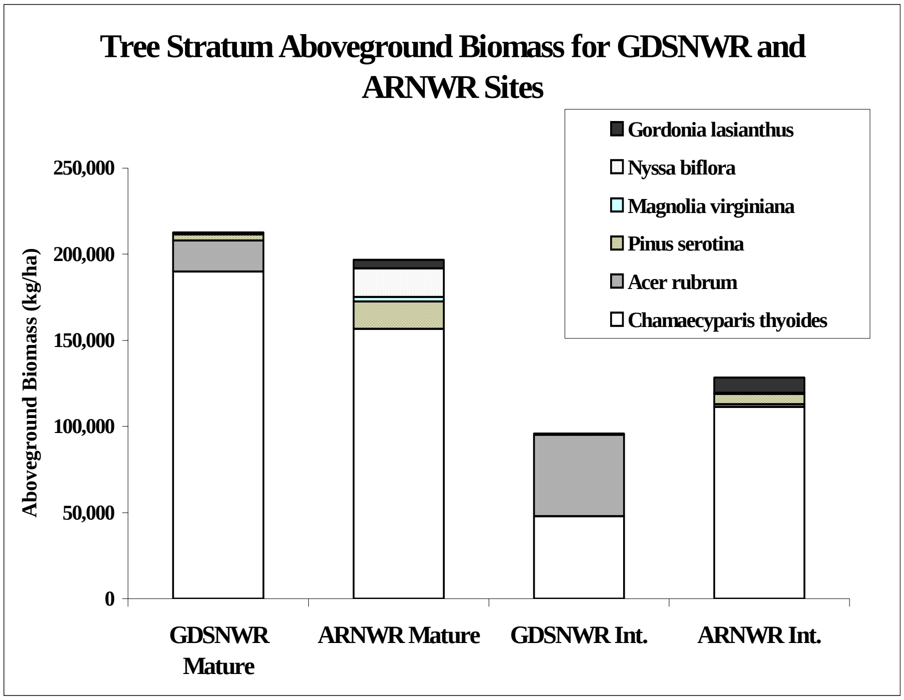
Species	Plant Component (kg)	A	B	r
Cedar	Leaves	-1.9419	2.1352	0.90
	Branches	-2.2978	2.5237	0.96
	Stems	-0.7600	2.0553	0.97
Hardwood Trees	Leaves	-2.1381	2.1516	0.90
	Branches	-1.4297	2.1880	0.90
	Stems	-1.0665	2.4064	0.99
Shrubs	Leaves	-1.8789	2.1716	0.96
	Stems	-1.3620	2.7172	0.98

Three 0.25-m^2 nested clip-plots were harvested at random locations in each 100-m^2 plot to estimate biomass of herbaceous vegetation in 1998. However, herbaceous growth was sparse, with a relative biomass less than 0.001% of the total aboveground biomass for all strata; thus, the herb stratum was not re-sampled in 1999. Vine species were not tallied for biomass due to the variable growth form as well as a lack of applicable biomass equations.

Hydrology

A groundwater table monitoring well was established adjacent to each of the nine pairs of vegetation sampling points in the spring of 1998. A centrally located well at each site was fitted with one Remote Data Systems (RDS) continuous recording well. Each schedule 40 PVC well with machined 0.025-cm slotting was inserted approximately 1 m into the soil and back filled with industrial grade sand to prevent clogging. The RDS continuous recording well for each site was programmed to record groundwater table depths twice daily and the information was downloaded to personal computer periodically from January 1999 to April 2000. The locations of each well are indicated in figures 3 and 4 for each site, blacked out sampling plots indicate each RDS well. In addition, groundwater table depths for each of the eight remaining wells per site were hand-monitored upon each field visit. Elevations within vegetation plots were measured in January of 1998 using a Topcon© Theodolite and were related to their respective groundwater monitoring wells. This relationship was used to establish a mean groundwater table depth for each vegetation plot (Atkinson et al. This Volume).

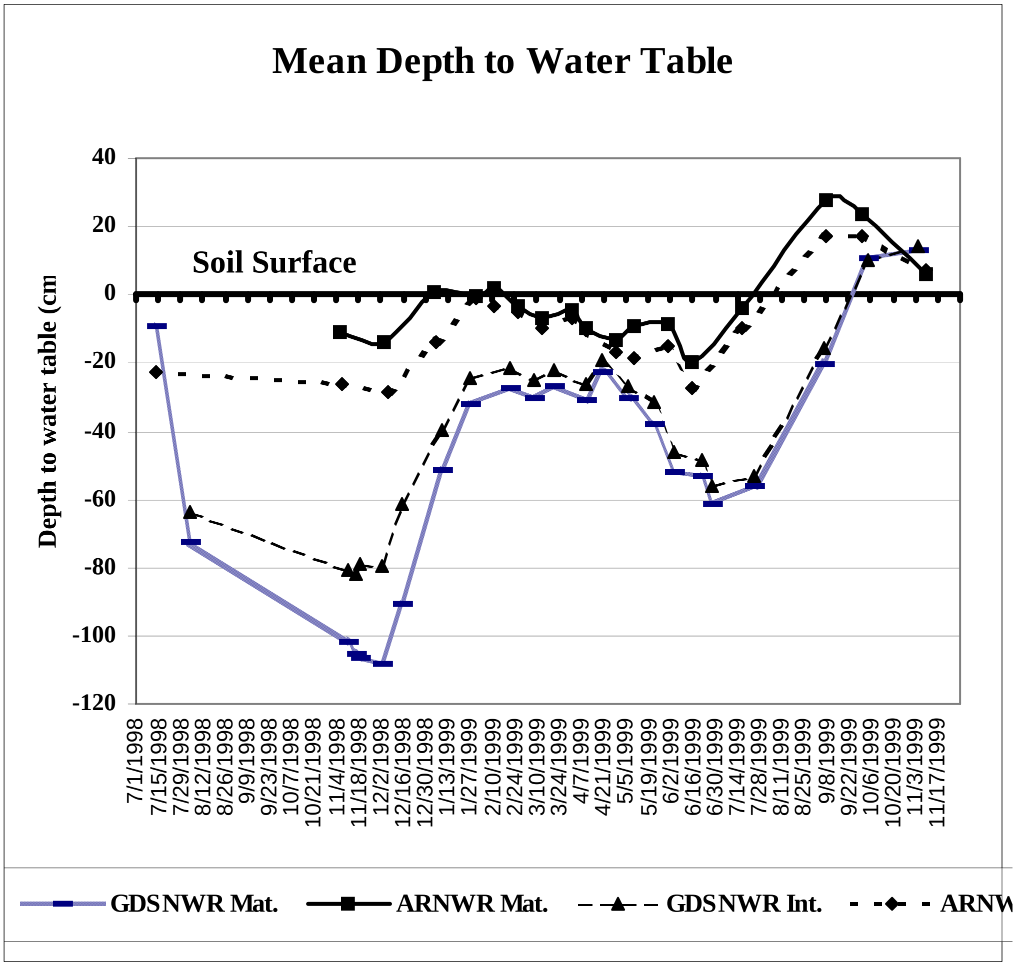
Figure 3. Aboveground tree stratum biomass for each species in GDSNWR and ARNWR Mature and Intermediate sites based upon a total sample area of 1800 m^2 per site for 1999 data. Letters (a, b and c) denote significant differences.



Statistical Analysis

The statistical package SIGMA STAT 2.03™ was used for all hypothesis testing. Tests for normality were run for each data set and means were compared using a student's t-test where the data were normally distributed. Where there were non-normal data, a Mann-Whitney rank sum test was employed. When more than two means were compared, Kruskal-Wallace One Way ANOVA on Ranks in combination with a Tukey Test or Dunn's Method multiple comparison tests were utilized

Figure 4. Mean depth to groundwater table for Mature and Intermediate-aged cedar swamps based upon manual hand-well readings.



(Zar 1996). A significance level of P<0.05 was used for all hypothesis testing. Where means were calculated for comparison, the standard error of the mean (SE) was listed. Unless otherwise indicated, means were based upon a sample size of eighteen plots for each site (n=18).

RESULTS

Mature Sites

Cedar exhibited the greatest relative biomass and relative basal area at GDSNWR Mature, 86.63% and 90.82% respectively, but these values were not statistically different from those calculated at ARNWR Mature (table 2). Despite comparable total cedar aboveground biomass measurements between the two mature sites, mean dbh at GDSNWR Mature (25.36 cm, SE 0.52, n=180) was greater than at ARNWR Mature (16.28 cm, SE 0.33, n=226), but stem density at GDSNWR Mature was approximately half that at ARNWR Mature (table 2). This trend of greater stem density, but smaller mean dbh at ARNWR Mature was even more pronounced among the intermediate sites.

Table 2. Structural attribute table ranked in order of aboveground biomass contribution for tree (≥ 2.54 cm dbh, >305 cm) and shrub (< 2.54 cm, but ≥ 33.0 cm tall) strata for Great Dismal Swamp NWR and Alligator River NWR Mature sites.

Structural Attributes of GDSNWR Mature Site

Tree Species	Basal Area (m^2 / ha)	Relative % Basal Area	Number (stems/ ha)	Biomass (kg/ha)	Relative % Biomass	Mean dbh (cm)
Cedar	55.08	90.82	1,006	179,886	86.63	25.36
Acer rubrum	3.88	6.39	211	18,136	8.73	13.35
Pinus serotina	0.61	1.00	17	3,534	1.70	13.57
Persea borbonia	0.40	0.65	156	1,723	0.83	3.60
Magnolia virginiana	0.27	0.45	67	949	0.46	6.43
Pinus taeda	0.18	0.30	6	854	0.41	20.40
Vaccinium corymbosum	0.13	0.21	150	323	0.16	3.19
Nyssa biflora	0.04	0.06	22	106	0.05	4.60
Other tree species	0.07	0.12	117	90	0.04	
Tree Stratum Total	60.64	100.00	1,750	205,602	99.01	
Shrub Stratum Total			19,965	2,047	0.99	
Total Aboveground			21,715	207,649	100.00	

Structural Attributes of ARNWR Mature Site

Tree Species	Basal Area (m^2 / ha)	Relative % Basal Area	Number stems/ ha	Biomass (kg/ha)	Relative % Biomass	Mean dbh (cm)
Cedar	49.91	82.43	2,083	156,715	78.42	16.28
Nyssa biflora	5.23	8.63	1,733	16,727	8.37	5.92
Pinus serotina	3.00	4.96	50	15,947	7.98	27.26
Gordonia lasianthus	1.12	1.86	161	4,864	2.43	7.18
Magnolia virginiana	0.73	1.20	183	2,471	1.24	6.64
Other tree species	0.56	0.93	772	1,650	0.83	
Tree Stratum Total	60.55	100.00	4,983	198,374	99.27	
Shrub Stratum Total			20,694	1,468	0.73	
Total Aboveground			25,677	199,841	100.00	

A difference in species composition in the tree stratum (Shacochis et al. This Volume) was reflected in the aboveground biomass measurements (figure 3). Of the major biomass contributors, only two tree species occurred in both mature sites, *P. serotina* and *M. virginiana*. Both are common wetland tree species with a wetland indicator status of facultative wetland (FACW) (USFWS 1988). *Gordonia lasianthus* was ranked fourth in aboveground biomass at ARNWR Mature; however, the geographic range of this wetland species is limited south of Virginia and therefore is not a component of GDSNWR sites.

Total aboveground tree biomass accounted for greater than 99% of the total aboveground biomass for each site, but was not different between GDSNWR Mature (207,650 kg/ha, SE 22,134) and ARNWR Mature (199,374 kg/ha, SE 11,770). However, both live and dead tree stem density was greater for ARNWR Mature than in GDSNWR Mature ($P<0.05$). *Acer rubrum* (18,136 kg/ha) was second only to cedar in terms of biomass contribution at GDSNWR Mature, while *N. biflora* (16,727 kg/ha) ranked second at ARNWR Mature. *Pinus serotina* ranked third in aboveground biomass (15,947 kg/ha), but exhibited the greatest mean dbh (27.26 cm) for any species at any site (table 2). Several shrub species occurred in both sites including *L. lucida*, *C. alnifolia*, *I. glabra*, *I. coriacea* and *Vaccinium corymbosum* L. (highbush blueberry) as well as saplings of all the trees listed in table 2 except for cedar. Shrub stratum biomass was greater for GDSNWR Mature (2048 kg/ha, SE 288) than ARNWR Mature (1468 kg/ha, SE 332). However, total shrub stratum stem density was not different between the two sites ($P<0.05$).

Intermediate Sites

Greater mean aboveground biomass ($P<0.002$), tree stem density ($P<0.001$), and mean shrub biomass ($P<0.005$) were recorded at ARNWR Intermediate, despite an estimated age of 10 years younger than GDSNWR Intermediate. Mean cedar dbh at GDSNWR Intermediate was 11.67 cm (SE 0.25, n=226) and 3.60 cm (SE 0.06, n=909) at ARNWR Intermediate, but the stem density of both tree (2,761 stems/ha) and shrub (361 stems/ha) strata was extremely low at GDSNWR Intermediate, even in comparison to the stem density of the mature sites (table 2). *Acer rubrum* was a co-dominant tree species at GDSNWR Intermediate contributing 49.04% relative total biomass as well as 41.36% relative basal area (table 3). In fact, cedar and *A. rubrum* together comprised 98.85% of the total aboveground biomass and 99.14% of the relative basal area at this site. In contrast, seven tree species were tallied to equal 98.16% of the relative biomass at ARNWR Intermediate (table 3). Relative total aboveground biomass at ARNWR Intermediate for cedar was 82.91%, comparable to the mature sites, and a mere 1.21% for *A. rubrum*. Furthermore, ARNWR Intermediate total stem density was over 15 times greater than that recorded at GDSNWR Intermediate, resulting in a total aboveground biomass that was 36,832.25 kg/ha, or 27.6% greater.

Hydrology

Both ARNWR Mature and Intermediate sites were far wetter than the GDSNWR sites based upon twice-daily depth to groundwater table readings taken by a Remote Data Systems (RDS) continuous recording well at each site ($P<0.001$, n=451). The annual depth to groundwater table means for ARNWR Mature (0.67 cm, SE 0.25) and for GDSNWR Mature (-43.93 cm, SE 0.66) reflect the large difference in mean groundwater tables. Mean depths to groundwater table based upon hand-well readings (figure 4) represent the groundwater table trends for each site where differences only exist between ARNWR and GDSNWR sites. Groundwater tables for all sites were raised to above the soil surface in late summer of 2000 in response to the effects of hurricanes Dennis and Floyd. Hurricane Dennis arrived at the coast of North Carolina on August 30th, 2000 and up to 48.25 cm of rain fell in some areas of the state. Shortly after, between September 15-17, 2000, hurricane Floyd reached the coast of North Carolina and 38.0 - 50.0 cm of precipitation was reported in many areas where soils were saturated or inundated from hurricane Dennis (figure 4) (Disaster Center 2000).

Table 3. Structural attribute tables ranked in order of aboveground biomass contribution for tree (≥ 2.54 cm dbh, >305 cm) and shrub (< 2.54 cm) strata for Great Dismal Swamp NWR and Alligator River NWR Intermediate sites.

Structural Attributes of GDSNWR Intermediate Site

Tree Species	Basal Area (m^2 / ha)	Relative % Basal Area	Number stems/ ha	Biomass (kg/ha)	Relative % Biomass	Mean dbh (cm)
Cedar	15.93	57.78	1,361	48,027	49.81	11.62
Acer rubrum	11.41	41.36	1,278	47,284	49.04	9.21
Magnolia virginiana	0.17	0.63	50	568	0.59	6.37
Ilex coriacea	0.03	0.11	39	77	0.08	2.93
Ilex opaca	0.03	0.09	22	69	0.07	3.73
Vaccinium corymbosum	0.01	0.02	11	16	0.02	2.80
Tree Stratum Total	27.58	100.00	2,761	96,040	99.62	
Shrub Stratum Total			361	370	0.38	
Total Aboveground			3,122	96,411	100.00	

Structural Attributes of ARNWR Intermediate Site

Tree Species	Basal Area (m^2 / ha)	Relative % Basal Area	Number (stems/ ha)	Biomass (kg/ha)	Relative % Biomass	Mean dbh (cm)
Cedar	40.43	85.15	31,563	111,372	82.91	3.61
Gordonia lasianthus	2.69	5.67	1,007	8,895	6.62	5.06
Pinus serotina	1.61	3.39	243	5,948	4.43	8.64
Persea borbonia	0.63	1.32	313	1,896	1.41	8.00
Acer rubrum	0.62	1.30	868	1,621	1.21	6.80
Lyonia lucida	0.49	1.04	3,090	956	0.71	1.37
Ilex coreacea	0.30	0.63	69	623	0.46	5.80
Nyssa biflora	0.18	0.39	1,181	553	0.41	1.71
Other tree species	0.53	1.12	1,389	1,378	1.03	
Tree Stratum Total	47.48	100.00	39,722	133,243	99.19	
Shrub Stratum Total			8,507	1,0823	0.81	
Total Aboveground			48,229	134,326	100.00	

DISCUSSION

Total aboveground biomass values generated in the present study rank near the middle of values for cedar and other swamp types previously reported (table 4). These published aboveground structural parameters including tree density, basal area and aboveground biomass values, may serve as a gross comparison of these ecosystems. Total aboveground biomass for both mature cedar sites in this study were slightly greater than the value reported by Dabel and Day (1977) for a mature, cedar dominated forest in the Great Dismal Swamp (table 4). However, aboveground biomass estimates were nearly equal for mature cedar sites. Preliminary height information results from this study suggest that there is no difference in tree height between GDSNWR and ARNWR Mature sites. Hence, biomass appears to be related to dbh and number of trees present, not tree height. This may be due to the fact that these stands were all harvested and managed to some degree for timber regeneration, resulting in an even-aged structure. *Taxodium distichum* ecosystems have the greatest reported aboveground biomass among swamp types, which is most likely related to greater age. Due to difficulty in wood harvest many southern deepwater cypress areas have not been clear-cut. In contrast, all of the cedar sites listed in table 4 have been harvested within the last century. While still difficult, lumber harvesters have developed machinery (e.g. fellerbunchers) and methodology (e.g. corduroy roads) to circumvent problems associated with the periodically flooded conditions present in most cedar swamps.

Table 4. Published estimates of tree stem density, basal area and aboveground biomass for cedar and other forested wetland communities ranked in order of decreasing biomass.

Community Type	Density (# stems/ha)	Basal Area (m^2/ha)	Biomass (kg/ha)	Source
Cypress-tupelo-gum swamp (Illinois)	325	62.80	455,000	Anderson & White 1970
Cypress (Virginia)	1,560	59.30	345,300	Dabel & Day 1979
Cypress forest (Georgia)	1,465	52.00	307,000	Schlesinger 1978
Mature Cypress dome (Florida)	3,951	70.80	266,000	Brown 1981
Cedar (Virginia)	2,000	55.80	220,500	Dabel & Day 1977
Mature cedar (GDSNWR)	1,750	60.64	207,650	This study
Mature cedar (ARNWR)	4,983	60.55	199,840	This study
Maple-black gum (Virginia)	2,080	39.00	195,700	Dabel & Day 1978
Northern white cedar (Minnesota)	2,755	42.20	159,600	Reiners 1972
Cedar* (ARNWR)	39,722	47.48	134,325	This study
Cedar* (GDSNWR)	2,761	27.58	96,410	This study
Cedar Rhode Island	1,100	20.03	N/A	Lowry 1984
Cedar Rhode Island	1,000	37.23	N/A	Lowry 1984
Cedar Rhode Island	2,633	49.24	N/A	Lowry 1984
Cedar Rhode Island	1,117	34.44	N/A	Lowry 1984

The shrub stratum of each site was dominated by shade tolerant species of the Ericaceae and Aquifoliaceae families, common associates of cedar swamps located in the mid-Atlantic region (Laderman 1989). Future research into the practical estimation of vine species biomass in the field, particularly *Smilax laurifolia* L., *Smilax rotundifolia* L., *Toxicodendron radicans* L., *Parthenocissus quinquefolia* (L.) Planchon and *Gelsemium sempervirens* (L.) Aiton is needed, as they may contribute to understory and sub-canopy structure. ARNWR Mature was the only site at which a significant sub-canopy was present. It consisted of small (5.92 cm, SE, n=312) *Nyssa biflora* Walt. trees that were suspected to have germinated after a non-catastrophic fire event, of which there was physical evidence observed within the site (e.g. burned wood and trees).

Based upon our sampling for each site, groundwater hydrology may be considered a major variable contributing to the structural differences among the four studied sites. The smaller mean dbh of trees at ARNWR Mature may be in response to lower productivity due to continued saturation of the soil surface (Megonigal 1992). However, the greater ARNWR tree densities and to some degree the lower aboveground biomass per stem were likely related to a combination of stand stocking density, post logging treatments, site quality and hydrologic regime. The herb stratum was almost non-existent at all sites most likely in response to intense shading, prolonged seasonal anoxic conditions and the nutrient limitations that are typical of cedar swamps (Laderman 1989). A notable exception was ARNWR Intermediate, which contained several standing water areas. These areas were artifacts of previous timber harvesting efforts and contained floating *Sphagnum* spp. bog mats, a feature only present in cedar swamps where disturbance allows enough light to penetrate the canopy and groundwater tables are consistently high (Laderman 1989). In addition to *Sphagnum* spp., there were other aquatic species including *Nymphea odorata* and *Utricularia* spp. (Loomis et al. This Volume), which supports our assertion that almost constant soil saturation was present at the ARNWR sites (figure 4). Other reasons to believe that our hydrologic assessment is correct (that the ARNWR sites exhibit much higher water tables than found in our GDSNWR sites) include vegetation composition (Shacochis et al. This Volume) and carbon quality of litter (Duttry et al. This Volume).

The number of species contributing to tree and shrub biomass was low at the GDSNWR sites, which is similar to values reported by Dabel and Day (1977) and slightly greater than the number of species at ARNWR. Increasing number of species for ARNWR to the south may be a response to a latitudinal gradient (Stevens 1989, Wilson 1999) in which temperature may be a controlling environmental variable for some species of plants. While this is not suspected to be a prominent effect, at least one species identified in this study, *G. lasianthus*, is known to be confined south of GDSNWR primarily due to temperature. In fact, ARNWR is the approximate northern limit for this wetland tree species which does not tolerate temperatures lower than –11.1ºC (USDA and NRCS 1999). *Gordonia lasianthus* was an important aboveground biomass contributor at ARNWR Mature; thus, it represents a significant component of the aboveground structure of that site.

Assessment of biomass structure is absolutely necessary in order to perform process studies of the cedar ecosystem (Dabel and Day 1977). Furthermore, vegetative structure has been used as a surrogate to assess function in created wetlands in Virginia by Atkinson et al. (1993). Due to the relative ease with which most structural data can be obtained, several methods have been developed or are currently in development that use structural parameters to estimate function, including the Hydrogeomorphic (HGM) Approach (Smith et al. 1995). Development and support of such functional assessment methodologies indicate that structural criteria are valuable for determining wetland restoration success. Restoration criteria should be based upon the structure of natural cedar communities in order to determine the success of a restoration activity at maturity. Structural data for studies of cedar vary depending upon site age or location, among other factors; however, these data may suggest a range for natural cedar swamps that can be targeted for restoration. Furthermore, the close agreement of structural parameter results of this study and of Dabel and Day (1977), including total aboveground biomass, basal area and density, suggest that these represent reasonable structural criteria to evaluate the success of cedar restoration activities that are conducted in the mid-Atlantic region.

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LITERATURE CITED

Akerman, A. 1923. The white cedar of the Dismal Swamp. Virginia Forestry Publication 30:1-21.

Atkinson, R. B., J. E. Perry, E. Smith, and J. Cairns. 1993. Use of created wetland delineation and weighted averages as a component of assessment. Wetlands 13:185-193.

Atkinson, R. B., J. W. DeBerry, D. T. Loomis, E.R. Crawford and R.T. Belcher. This Volume. Water tables in Atlantic white cedar swamps: implications for restoration

Baskerville, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. Canadian Journal of Forest Research 2:49-53.

Bormann, B. T. 1990. Diameter-based regression models ignore large sapwood-related variation in Sitka spruce. Canadian Journal of Forest Research 20:1098-1104.

Brown, S. L. 1981. A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida. Ecological Monographs 51:403-427.

Brown, S., P. Schroeder, and R. Birdsey. 1997. Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. Forest Ecology and Management 96:37-47.

Campbell, J. S., V. J. Lieffers and E. C. Pielou. 1985. Regression equations for estimating single tree biomass of trembling aspen: assessing their applicability to more than one population. Forest Ecology Management 11:283-295.

Conner, W. H. and J. W. Day, Jr. 1976. Productivity and composition of a bald cypress-water tupelo site and a bottomland hardwood site in a Louisiana swamp. American Journal of Botany 63:1354-1364.

Conner, W. H. and J. W. Day, Jr. 1982. The ecology of forested wetlands in the southeastern United States. p. 69-87. *In* B. Gopal (ed.) Wetlands: Ecology and Management National Institute of Ecology and International Scientific Publications, Jaipur, India.

Conner, W. H., J. G. Gosselink, and R. T. Parrondo. 1981. Comparison of the vegetation of three Louisiana swamp sites with different flooding regimes. American Journal of Botany 68:320-331.

Dabel, C. V. and Jr. F.P. Day. 1977. Structural comparisons of four plant communities in the Great Dismal Swamp, Virginia. Bulletin of the Torrey Botanical Club 104:352-360.

Day, F. P. and C. V. Dabel. 1978. Phytomass budgets for the Dismal Swamp ecosystem. Virginia Journal of Science 29:220-224.

Duttry, P. M., R.B. Atkinson, G. J. Whiting, R. T. Belcher, M. G. Kalnins and G. S. Thompson. This Volume. Soil respiration response to drainage and inundation of laboratory cores of soils from Atlantic white cedar peatlands and compensation sites in Virginia and North Carolina.

Eleuterius, L. N. and S. B. Jones. 1972. A phytosociological study of white-cedar in Mississippi. Castanea 37:67-74.

Frost, C. C. 1987. Historical overview of Atlantic white cedar in the Carolinas. P. 257-264. *In* A. D. Laderman (ed.) Atlantic White Cedar. Westview Press, Boulder, CO, USA.

Grier, C. G. and R. S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. Ecological Monographs 47:373-400.

Korstian, C. F. and W.D. Brush. 1931. Southern white cedar. U. S. Department of Agriculture Technical Bulletin 251.

Laderman, A. D. 1989. The ecology of the Atlantic white cedar wetlands: A community profile. U. S. Fish and Wildlife Service Biological Report 85 :7.21.

Little, E. L. 1971. Atlas of United Sates Trees. Vol. 1. Conifers and Important Hardwoods. Misc. Publ. No. 1146. U.S.D.A. Forest Service, Wash., DC 20402.

Loomis, D. T., R. T. Belcher, J. W. DeBerry, K. M. Shacochis and R. B. Atkinson. This Volume. A vascular flora of eight Atlantic white cedar communities.

Lowry, D.J. 1984. Water regimes and vegetation of Rhode Island forested wetlands. Thesis accepted by University of Rhode Island, USA.

Megonigal, P. T. and Jr. F. P. Day. 1988. Organic matter dynamics in four seasonally flooded communities of the Dismal Swamp. American Journal of Botany 75:1334-1343.

Megonigal, P. T. and Jr. F. P. Day. 1992. Effects of flooding on root and shoot production in bald cypress in large experimental enclosures. Ecology 73:1182-1193.

Mitsch, W. J. and K. C. Ewel. 1979. Comparative biomass and growth of Cypress in the Florida wetlands. The American Midland Naturalist 101:417-427.

Noss, R. F., E. T. LaRoe, and J. M. Scott. 1995. Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. Biological Report 28. US Department of the Interior, National Biological Services, Washington DC, USA.

National Research Council. 1992. Restoration of Aquatic Ecosystems. National Academy Press, Washington D.C.

Oosting, J. 1942. Plant communities of the piedmont, North Carolina. American Midland Naturalist 28:1-126.

Peterson, E. B., Y. B. Chan, and J. B. Cragg. 1970. Aboveground standing crop, leaf area and caloric value in an aspen clone near Calgary, Alberta. Canadian Journal of Botany 48:1459-69.

Radford, A. E., H. E. Ahles, and C. R. Bell. 1964. Manual of the Vascular Flora of the Carolinas. University of North Carolina Press, Chapel Hill, NC, USA.

Reiners, W. A. 1972. Structure and energetics of three Minnesota forests. Ecological Monographs 42:71-94.

Schlesinger, W. H. 1978. Community structure, dynamics and nutrient cycling in the Okefenokee Cypress swamp forest. Ecological Monographs 48:43-65.

Shacochis, K. M., R. T. Belcher, J. W. DeBerry, D. T. Loomis and R. B. Atkinson. This Volume. Vegetation importance values and prevalence index values of Atlantic white cedar swamps in the Great Dismal Swamp and Alligator River Nation Wildlife Refuges.

Smith, D. R., A. Ammann, C. Bartoldus, and M.M. Brinson. 1995. An approach for assessing wetland functions using hydrogeomorphic classification, reference wetlands, and functional indices. Wetlands Research Program. Technical Report WRP-DE-9.

Stanek, W. and D. State. 1978. Equations predicting primary productivity (biomass) of trees, shrubs and lesser vegetation based on current literature. Canadian Forestry Service, Pacific Forest Research Center BC-X-183.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: How so many species coexist in the Tropics. American Naturalist 133:240-256.

Westlake, D. F. 1963. Comparisons of plant productivity. Biological Review 38:385-425.

Whitehead, R. D. 1972. Developmental and environmental history of the Dismal Swamp. Ecological Monographs 42:301-315.

Whittaker, R. H. 1961. Estimation of net primary production of forest and shrub communities. Ecology 42:177-180.

Whittaker, R. H. 1963. Net production of heath balds and forest heaths in the Great Smoky Mountains. Ecology 44:176-182.

Whittaker, R. H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology 47:103-121.

Whittaker, R. H. and G. M. Woodwell. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. Journal of Ecology 56:1-25.

Wilson, E. O. 1999. The Diversity of Life. W. W. Norton and Company, New York, NY, USA.

USDA, NRCS. 1999. The PLANTS database (http://plants.usda.gov/plants). National Plant Data Center, Baton Rouge, LA, USA.

US Fish and Wildlife Service. 1988. National list of vascular plant species that occur in wetlands. US Fish & Wildlife Service Biological Report 88:24.

COMPARISON OF BIRD SPECIES RICHNESS IN ATLANTIC WHITE CEDAR AND HARDWOOD/PINE FORESTS

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Abstract: Atlantic white cedar swamps were first described as endangered in 1748 and little information on bird utilization of these forests is available. We studied breeding landbird populations in three age classes of cedar, and a mature hardwood/pine (HP) forest in southeastern Virginia and northeastern North Carolina. Birds were surveyed using the point count method during May and June, 1998. Sample points were established in large, contiguous forests, at least 100 m from any adjacent habitat type. Total number of species per habitat type included: cedar-young (15), cedar-intermediate (16), and cedar-mature (20) forests, and HP (31) forests. Bird species richness was significantly greater ($P < 0.001$) in HP versus all cedar age classes and in cedar-mature versus cedar-young. The highest Pearson Correlation Coefficients in the breeding bird communities were between cedar -intermediate and -mature (0.824). The HP community was more highly correlated with cedar-intermediate (0.70) than with cedar-mature (0.55). The most frequently observed species in the HP included ovenbird (see Appendix for scientific names), Carolina wren, tufted titmouse, prothonotary warbler, and acadian flycatcher. Prairie warbler, ovenbird, acadian flycatcher, worm-eating warbler, and Carolina wren were most abundant in the cedar-mature. Twelve species were surveyed in HP that were not surveyed in cedar-mature and two species were found in cedar-mature and not in HP forests.

Key Words: breeding birds, breeding bird species richness, Atlantic white cedar fauna, Great Dismal Swamp

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), swamps were once common along the mid-Atlantic outer coastal plain. Within this nontidal freshwater forest type, cedar, an obligate wetland tree species (Reed 1988), is typically dominant and often occurs in monotypic stands (Laderman 1987). Cedar is geographically restricted to freshwater wetlands in a narrow band along the eastern coastal United States ranging from Maine to Mississippi (Laderman 1989). The dramatic decline of this species and ecosystem is attributed to harvest without replanting, fire suppression, hydrologic alteration, and extensive development of coastal areas. Since the time of European colonization, loss of cedar swamps exceeds 90% for the Carolinas, and perhaps 98% in Virginia. Valued for the longevity, aroma, and growth form of its wood, research has focused on regrowing trees rather than rehabilitation or restoration of this once prevalent wetland ecosystem.

Few investigations of bird life in cedar forests have been published, perhaps due to the scarcity of this forest type. Studies by Terwilliger (1981 and 1987) and Miller et al. (1987) focused on a comparison of breeding landbirds in cedar and between cedar and other mature forest types. We could find no studies that compared the breeding bird community between chronosequences of cedar.

Bird population dynamics in forested habitats have been a subject of scientific research throughout the twentieth century. During the past 50 years, studies have been conducted in an attempt to determine habitat-related features that influence bird species diversity within a given area (MacArthur and MacArthur 1961, MacArthur 1964, Karr and Roth 1971, Willson 1974, Balda 1975, Rotenberry et al. 1979, Noon et al. 1980, Terwilliger 1987, Ornelas et al. 1993). Similar studies have addressed bird density, richness, and/or evenness (Odum 1950, Swift 1980, Swift et al. 1984, Bilcke 1982, DeGraaf and Chadwick 1987, James and Wamer 1982, Robbins et al. 1989, Wenny et al. 1993, Loiselle and Blake 1994, Annand and Thompson 1997).

In a paper on bird species diversity (BSD), MacArthur and MacArthur (1961) characterized the bird community of a given area by incorporating both the number of species and the number of individuals within each species, which they demonstrated to be largely a result of the structure of the horizontal vegetative layers within a habitat. The authors next characterized the floristic structure of bird habitat by measuring the horizontal vegetative layers within a habitat. More recent studies have confirmed these findings while demonstrating the influence of other factors (Terwilliger 1987, Karr and Roth 1971, Willson 1974, Roth 1976, MacArthur 1964). In this study, bird composition of a chronosequence of cedar was used to evaluate avifaunal habitat in natural and restored sites.

METHODS

Study areas were located in southeastern Virginia on Great Dismal Swamp National Wildlife Refuge and northeastern North Carolina on Alligator River National Wildlife Refuge, in young, intermediate, and mature cedar forests, and HP forests (table 1). At each site, two transects were established containing five sample points at 100-m intervals (Swift et al. 1984).

The vegetative community was assessed by determining the importance values (dominance, frequency, and stem density) of plant species adjacent to each sampling point. Vegetation community data from the cedar stands was reported in Shacochis et al. (This Volume).

Table 1. Successional stage and stand age for each cedar and HP study site.

Forest Type	Successional Stage	Stand Age
HP	mature	> 70 years
Cedar	mature	60-70 years
Cedar	intermediate	30 years
Cedar	young	< 5 years

Bird Survey Methods

Two transects were established within each forest type. Transects contained five sample points and each transect sampled 3.9 ha (9.7 ac). Two transects were surveyed per day and sampling order of all transects and points was randomized across visits.

Birds were surveyed using the point count method (Hamel et al. 1996) during late-May through June 1991. Bird surveying was conducted between 0600 and 1030 hours and each sample point was surveyed a minimum of 4 times for 10 minutes during each census (Verner 1998). Birds within 50 m of each sample point were identified by sight and/or sound following Hamel et al. (1996). Birds that were noted flying over or through the study area, but not perched, were recorded as “flyovers” and were not included in data analysis.

Data Analysis

Pointwise species richness was calculated as the number of species surveyed on each point within each habitat type. With the exception of flyovers, we assumed that all bird species seen or heard during point counts were breeding (Hamel et al. 1996). One-way analysis of variance and Tukey Test were used to calculate pointwise species richness among sites. Pearson Correlation Coefficients were used to contrast species composition among sites.

RESULTS

Greatest importance values for habitats surveyed included baldcypress (*Taxodium distichum*), red maple (*Acer rubrum*), and sweet gum (*Liquidambar styraciflua*) in the HP study sites and cedar, black gum (*Nyssa sylvatica*), and red maple in the cedar-mature sites. Greatest importance values included red maple, cedar and American holly (*Ilex opaca*) in the cedar-intermediate forest and the cedar-young site importance values were highest for dog-fennel (*Eupatorium capillifolium*), broomsedge (*Andropogon virginica*), and flat topped goldenrod (*Euthamia tenuifolia*).

A total of 946 observations of 49 species of birds were recorded during this study. The number of species at any one sample point was lowest at an cedar-young sample point (3) and highest at an HP sample point (16) in Great Dismal Swamp National Wildlife Refuge. The ovenbird, prairie warbler, acadian flycatcher, and Carolina wren were the most abundant species observed in all habitat types. Birds present in three of the four forest types included, in order of abundance, ovenbird (200 observations), acadian flycatcher (80 observations), Carolina wren (62 observations), common yellowthroat (59 observations), eastern towhee (41 observations), red-eyed vireo (35 observations), hooded warbler (28 observations), brown-headed cowbird (15 observations), and Carolina chickadee (11 observations) (table 2). The prairie warbler was the second most abundant species observed with

Table 2. Bird observations by habitat type.

		Habitat Types			
Species	Total Observations	Cedar-yng.	Cedar-inter.	Cedar-mat.	HP
ovenbird	200	0	77	52	71
prairie warbler	110	0	43	67	0
acadian flycatcher	80	0	36	26	18
Carolina wren	62	0	16	15	31
common yellowthroat	59	41	7	8	3
prothonotary warbler	43	0	2	22	19
eastern towhee	41	0	23	8	10
red-eyed vireo	35	0	30	1	4
tufted titmouse	30	0	3	2	25
hooded warbler	28	0	7	10	11
worm-eating warbler	24	0	3	18	3
common grackle	21	21	0	0	0
red-winged blackbird	21	21	0	0	0
eastern meadowlark	20	20	0	0	0
great crested flycatcher	19	0	0	13	16
yellow-billed cuckoo	17	0	0	3	14
brown-headed cowbird	15	0	7	5	3
Carolina chickadee	11	0	2	1	8
gray catbird	10	0	10	0	0
white-breasted nuthatch	10	0	0	0	10
pine warbler	8	0	0	1	7
grasshopper sparrow	7	7	0	0	0
red-bellied woodpecker	7	0	0	0	7
blue-gray gnatcatcher	6	0	1	0	5
downy woodpecker	6	0	0	0	6
northern cardinal	6	0	0	2	4
white-eyed vireo	6	0	0	4	2
northern bobwhite	5	5	0	0	0
eastern wood- pewee	5	0	0	0	5
black-and-white warbler	3	0	0	1	2
blue grosbeak	3	3	0	0	0
blue jay	3	0	0	0	3
mallard	3	3	0	0	0
Virginia rail	3	3	0	0	0
wood thrush	3	0	0	0	3
northern flicker	2	0	0	0	2
pileated woodpecker	2	0	0	0	2
black-throated green warbler	1	0	0	1	0
American bittern	1	1	0	0	0
common snipe	1	1	0	0	0
hermit thrush	1	0	1	0	0
Louisiana waterthrush	1	0	0	0	1
northern parula	1	0	0	0	1
red-shouldered hawk	1	0	0	0	1
American redstart	1	0	0	0	1
ruby-throated hummingbird	1	0	0	0	1
sora	1	1	0	0	0
American woodcock	1	1	0	0	0
wood duck	1	1	0	0	0

110 observations, but it was only observed in cedar-mature and cedar-intermediate forests. Total number of species per transect was lowest in cedar-young (11) and greatest in HP (27) (table 3).

Table 3. Total number of breeding bird species by site.

Transect	Cedar-yng. 1	Cedar-yng. 2	Cedar-inter. 1	Cedar-inter. 2	Cedar-mat. 1	Cedar-mat. 2	H/P 1	H/P 2
SR per point [†]	5.0	5.8	10.1	8.0	10.3	6.0	14.9	12.8
SR per site[‡]	11	13	15	12	17	11	23	27

[†] Species richness as the mean number of species recorded at each point

[‡] Species richness as the total number of species recorded at each site.

Twelve species were surveyed in HP that were not surveyed in cedar-mature including blue jay, downy woodpecker, northern flicker, blue-gray gnatcatcher, Louisiana waterthrush, northern parula, eastern wood-pewee, pileated woodpecker, red-bellied woodpecker, American redstart, red-shouldered hawk, and white-breasted nuthatch. Two species were surveyed in cedar-mature and not in HP forests including black-throated green warbler and prairie warbler.

Total number of breeding bird species was greatest in HP (31 species) followed by cedar-mature (20 species), cedar-intermediate (16 species), and cedar-young (15 species) (table 4). Mean number of species per sample point (table 5) was highest in HP (13.9) and lowest at cedar-young (5.4). Pointwise species richness was significantly greater in HP than cedar-mature habitat types ($P < 0.001$), and significantly greater in HP, cedar-mature, and cedar-intermediate, than in cedar-young ($P < 0.001$) (table 5). Pointwise species richness was not significantly different between cedar-mature and cedar-intermediate ($P > 0.69$).

Table 4. Total number of breeding bird species by habitat type.

Forest Type	Successional Stage	# of Species Observed
HP	mature	31
Cedar	mature	20
Cedar	intermediate	16
Cedar	young	15

Table 5. Total and mean number of species per sample point for each habitat type.

Point #	Forest Type			
	Cedar-young	Cedar-intermediate	Cedar-mature	HP
1	3	12	11	15
2	5	10	11	15
3	5	11	9	14
4	3	7	11	16
5	5	11	10	14
6	7	9	8	12
7	4	9	6	14
8	7	7	5	11
9	4	7	6	15
10	4	8	5	13
Mean	5.4	9.1	8.2	13.9

Pearson Correlation Coefficient results detected significant correlations among breeding bird communities: cedar-intermediate/-mature (0.824), cedar-intermediate/HP (0.700), and cedar-mature/HP (0.553) ($P < 0.05$).

DISCUSSION

Species totals in our study were within the range reported in other studies. Total number of breeding bird species was greatest in HP (27) and totaled from 20 to 15 in cedar stands. Terwilliger (1981) found 16 and 23 species in two mature cedar forests on Great Dismal Swamp National Wildlife Refuge. In forests other than cedar, Swift et al. (1984) reported a mean of 19.6 species in hardwood forests in western Massachusetts. Kendeigh and Fawver (1981) identified 23 species in a mature pine/oak forest, 26 species in a mixed hemlock-deciduous mature forest, and 14 species in an intermediate pine forest in the Great Smoky Mountains of Tennessee and North Carolina. Weller (1988) found 12 breeding bird species in a buttonbush-waterelm shrub swamp in Anderson County in eastern Texas.

Our results indicated a greater total number of breeding bird species in HP and number of species generally decreased with decreasing stand age within cedar stands, which may have been influenced by differences in vegetative strata of each site. MacArthur and MacArthur (1961) found that bird species diversity was directly correlated with foliage height diversity and was a function of the number of layers of vegetation and the evenness of foliage apportionment among the layers. Swift et al. (1984) found a positive correlation between bird species richness and small shrub density. Bilcke (1982) found a significant correlation between species richness and complexity of the vegetation structure. Also working in cedar forests, Terwilliger (1987) found higher breeding bird species richness in sites with a well developed midstory. Cedar-young and cedar-intermediate study sites in the present study contained only one and two vegetation strata respectively, whereas the HP site contained four layers including an herb, shrub, midstory, and canopy layer. The cedar-mature 1 stand contained herb, shrub, and canopy layer, but a poorly developed midstory (DeBerry 2000, Shacochis et al. This Volume). Therefore, structural discrepancies between the study sites may at least partially explain the difference in pointwise species richness between habitat types.

Regarding total breeding bird species between cedar-mature forests, cedar-mature 1 had a greater number and density of breeding bird species than did the cedar-mature 2 site. The cedar-mature 1 site had a greater mean dbh (25.36 vs. 16.28 cm), relative and total biomass, and shrub biomass than the cedar-mature 2 site (DeBerry 2000, DeBerry et al. This Volume). Thus, our findings seem to support the notion that FHD is a good predictor of bird diversity and abundance. Mean depth to the water table during the growing season at the cedar-mature 1 site was much greater (>30 cm) than that at the cedar-mature 2 site (2.1 cm) (Atkinson et al. This Volume). However, this finding contrasts with some studies that were not conducted in cedar swamps. Swift et al. (1984) who found a direct relationship between percent surface wetness and depth of muck to species richness and avian density in forested wetlands in Massachusetts. Grover and Baldesarre (1995), working in New York beaver ponds, also found greater spring bird species richness in wetter areas.

When viewed on a landscape level, the mature and intermediate cedar forests occurred in relatively small habitat patches in a virtual sea of HP. The number of species found in these cedar stands may have been reduced by the distance between, and relatively small size of, cedar forests throughout southeastern Virginia and northeastern North Carolina. The number of species in cedar stands may have been greater when this habitat type was more abundant and less isolated in this region.

In this study, prairie warblers were the most abundant bird species observed in cedar-mature and the second most abundant in cedar-intermediate forests, but were not observed in the HP forest. In her 1980 and 1981 breeding bird study in the Great Dismal Swamp, Terwilliger (1981) reported that prairie warblers were the most abundant species in 70 and 100 year-old cedar forests in Great Dismal Swamp, but were not observed in a mature maple-gum forest. The habitat of the prairie warbler was described by Dunn and Garrett (1997) as old fields, pastures, clear-cuts, power line rights-of-way, abandoned orchards, and reclaimed strip mine sites. This is in stark contrast to the habitat at our study sites. The high abundance of prairie warblers may be associated with the fairly well developed shrub and midstory communities in these cedar forests, but reasons for the abundance of this species were not clear.

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LITERATURE CITED

Annand, E.M. and F.R. Thompson. 1997. Forest bird response to regeneration practices in central hardwood forests. J. Wildl. Manage. 61(1):159-171.

Atkinson, R.B., J. DeBerry, D.T. Loomis, E.R. Crawford, and R.T. Blecher. This Volume. Water tables in Atlantic white cedar swamps: implications for restoration.

Balda, R.P. 1975. Vegetation structure and breeding bird diversity. Pp. 59- 80 in Proceedings of the symposium on management of forest and range habitats for nongame birds (D.R. Smith, Tech. Coord.). USDA For. Serv. Gen. Tech. Rpt. WO-1, Washington, D.C.

Bilcke, G. 1982. Breeding songbird community structure: influences of plot size and vegetation structure. Acta Oecol. 3:511-521.

DeBerry, J.W. 2000. A comparison of aboveground structure in four Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P., swamps. Christopher Newport Univ. M.S. Thesis. 82 pp.

DeBerry, J.W., R.T. Belcher, D.T. Loomis, and R.B. Atkinson. This Volume. Comparison of aboveground structure of four Atlantic white cedar swamps.

DeGraaf, R.M. and N.L. Chadwick. 1987. Forest type, timber size class, and New England breeding birds. J. Wildl. Manage. 51(1):212-217.

Dunn, J.L. and K.L. Garrett. 1997. A field guide to warblers of North America. Houghton Mifflin Co. New York, NY. 660 pp.

Grover, A.M. and G. Baldassarre. 1995. Bird species richness within beaver ponds in south-central New York. Wetlands. 15(2):108-118.

Hamel, P.B., W. Smith, D. Tweldt, J. Woehr, E. Morris, R. Hamilton, and R. Cooper. 1996. A land manager's guide to point counts of birds in the Southeast. USDA, Forest Service Tech. Rpt. SO-120. 39 pp.

Hamel, P.B. and N.O. Wamer. 1982. Relationships between temperate forest bird communities and vegetation structure. Ecology 63(l):159-171.

Karr, J.R. and R.R. Roth. 1971. Vegetation structure and avian diversity in several New World areas. Am. Nat. 105:423-435.

Laderman, A.D. 1987. Atlantic white cedar wetlands. Westview Press, Boulder, CO. 401 pp.

Loiselle, B.A. and John G. Blake. 1994. Annual variation in birds and plants of a tropical second-growth woodland. Condor. 96:368-380.

MacArthur, R.H., and J.W. MacArthur. 1961. On bird species diversity. Ecology 42(3):594-598.

MacArthur, R.H. 1964. Environmental factors affecting bird species diversity. Am. Nat. 98:387-397.

Miller, D., L. Gradischer, J. Orzel, W. Leak, and E. Miller. 1987. Changes in vegetation and breeding bird use in an Atlantic white cedar swamp from 1951 to 1984. pages 229-230 in A.D. Laderman, ed. Atlantic white cedar wetlands. Westview Press, Boulder, CO.

Noon, B.R., D.K. Dawson, S.B. Inkley, C.S. Robbins, and S.H. Anderson. 1980. Consistency in habitat preference of forest bird species. Trans. North Am. Wildl. Nat. Resour. Conf. 45:226-244.

Odum, E.P. 1950. Bird populations of the highlands (North Carolina) plateau in relation to plant succession and avian invasion. Ecology. 31(4):587-605.

Ornelas, J.F., M.C. Arizmendi, L. Marquez-Valdelmar, and H.A. Berlanga. 1993. Variability profiles for line transect bird censuses in a tropical dry forest in Mexico. Condor. 95:422-441.

Robbins, C.S., D.K. Dawson, and B.A. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildl. Monogr. 53(3). 34 pp.

Roth, R.R. 1976. Spatial heterogeneity and bird species diversity. Ecology 57:773-782.

Rotenberry, J.T., R.E. Fitzner, and W.H. Rickard. 1979. Seasonal variation in avian community structure: differences in mechanisms regulating diversity. Auk. 96:499

Shacochis, K.M., J.W. DeBerry, D.T. Loomis, R.T. Belcher and R.B. Atkinson. This Volume. Vegetation importance values and prevalence index values of Atlantic white cedar stands in Great Dismal Swamp and Alligator River National Wildlife Refuges.

Swift, B.L. 1980. Breeding bird habitats in forested wetlands of west-central Massachusetts. M.S. thesis, Univ. Massachusetts, Amherst.

Swift, B.L., J.S. Larson, and R.M. DeGraaf. 1984. Relationship of breeding bird density and diversity to habitat variables in forested wetlands. Wilson Bull. 96(1):48-59.

Terwilliger, K. 1987. Breeding birds of two Atlantic white cedar stands in the Great Dismal Swamp. pages 215-227 in A.D. Laderman, ed. Atlantic white cedar wetlands. Westview Press, Boulder, CO.

Terwilliger, K. 1981. Breeding bird census in Atlantic white cedar stand. Master's thesis. Old Dominion University, Norfolk, VA.

Verner, J. 1988. Optimizing the duration of point counts for monitoring trends in bird populations. Res. Note PSW-395. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture. 4 pp.

Weller, M.W. 1988. Bird use of an east Texas shrub wetland. Wetlands. 8:145-158.

Wenny, D.G. R. Clawson, J. Faaborg, and S. Sheriff. 1993. Population density, habitat selection and minimum area requirements of three forest-interior warblers in central Missouri. Condor. 95:968-979.

Willson, M.F. 1974. Avian community organization and habitat structure. Ecology 55:1017-1029.

APPENDIX: Common and scientific names of birds.

Family and common name		Scientific name
Ardeidae		
	American bittern	*Botaurus lentiginosus*
Anatidae		
	wood duck	*Aix sponsa*
	mallard	*Anas platyrhynchos*
Accipitridae		
	red-shouldered hawk	*Buteo lineatus*
Phasianidae		
	northern bobwhite	*Colinus virginianus*
Rallidae		
	Virginia rail	*Rallus limicola*
	sora	*Porzana carolina*
Scolopacidae		
	common snipe	*Gallinago gallinago*
	American woodcock	*Scolopax minor*
Cuculidae		
	yellow-billed cuckoo	*Coccyzus americanus*
Trochilidae		
	ruby-throated hummingbird	*Archilochus colubris*
Picidae		
	red-bellied woodpecker	*Melanerpes carolinus*
	downy woodpecker	*Picoides pubescens*
	northern flicker	*Colaptes auratus*
	pileated woodpecker	*Dryocopus pileatus*
Tyrannidae		
	eastern wood-pewee	*Contopus virens*
	acadian flycatcher	*Empidonax virescens*
	great crested flycatcher	*Myiarchus crinitus*
Corvidae		
	blue jay	*Cyanocitta cristata*
Paridae		
	Carolina chickadee	*Poecile carolinensis*
	tufted titmouse	*Baeolophus bicolor*
Sittidae		
	white-breasted nuthatch	*Sitta carolinensis*
Troglodytidae		
	Carolina wren	*Thryothorus ludovicianus*

Sylviidae		
	blue-gray gnatcatcher	*Polioptila caerulea*
Turdidae		
	hermit thrush	*Catharus guttatus*
	wood thrush	*Hylocichla mustelina*
Mimidae		
	gray catbird	*Dumetella carolinensis*
Vireonidae		
	white-eyed vireo	*Vireo griseus*
	red-eyed vireo	*Vireo olivaceus*
Parulidae		
	northern parula	*Parula americana*
	black-throated green warbler	*Dendroica virens*
	pine warbler	*Dendroica pinus*
	prairie warbler	*Dendroica discolor*
	black-and-white warbler	*Mniotilta varia*
	American redstart	*Setophaga ruticilla*
	prothonotary warbler	*Protonotaria citrea*
	worm-eating warbler	*Helmitheros vermivorus*
	ovenbird	*Seiurus aurocapillus*
	Louisiana waterthrush	*Seiurus motacilla*
	common yellowthroat	*Geothlypis trichas*
	hooded warbler	*Wilsonia citrina*
Emberizidae		
	eastern towhee	*Pipilo erythrophthalmus*
	grasshopper sparrow	*Ammodramus savannarum*
Cardinalidae		
	northern cardinal	*Cardinalis cardinalis*
	blue grosbeak	*Guiraca caerulea*
Icteridae		
	red-winged blackbird	*Agelaius phoeniceus*
	eastern meadowlark	*Sturnella magna*
	common grackle	*Quiscalus quiscula*
	brown-headed cowbird	*Molothrus ater*

FLORISTIC DIVERSITY OF EIGHT ATLANTIC WHITE CEDAR SITES IN SOUTHEASTERN VIRGINIA AND NORTHEASTERN NORTH CAROLINA

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Abstract: Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P., is an evergreen wetland species that typically grows in acidic peat soils from Maine to Florida. The trees often form dense, monotypic stands but shrubs, herbs, and bryophytes co-occur in certain portions of the range and at various stages in stand development. Floristic surveys were conducted in five naturally occurring stands and three restoration sites representing three age classes in northeastern North Carolina and southeastern Virginia. Species diversity was calculated for each site using the Shannon-Weiner function. Sites were also compared based on life history characteristics of the associated species. Compared to restored sites, naturally occurring stands had a lower species richness and lower diversity, but had a higher percentage of perennials.

Key Words: monotypic, associated species, floristic survey, evenness, wetland restoration

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), occurs coastally from Maine to Florida and west to Mississippi (Korstian and Brush 1931). Long valued for its timber, cedar has been reduced to less than 2% of its original range. Forming dense, monotypic stands it is often associated with its own distinctive biota (Laderman 1989).

Surveys of vascular flora have been conducted over most of the range including Lousiana (Conner et al. 1981), Florida (Clewell and Ward 1989), South Carolina (Pittman 1978), North Carolina (Kologiski 1977, Christensen et al. 1981), Tennessee (Quaterman 1950), Virginia (Chickering 1873), Maryland (Hull and Whigham 1987), New Jersey (Little 1951, Niering 1953), and New York (Lynn 1981, Torrey 1843). The purpose of this study was to contrast the floristic composition of cedar swamps that differ by management and age class.

METHODS

A floristic survey was conducted at five natural regenerating stands and three cedar restoration sites representing three different age classes: mature (~70 years), intermediate (~30 years), and young (<10 years). Naturally regenerated mature and intermediate stands and a young clear cut cedar stand were located in the Great Dismal Swamp National Wildlife Refuge (DS). Two of the sites were planted cedar compensation sites, which were restored agriculture fields adjacent to DS. Two sites were located at Alligator River National Wildlife Refuge (AR) including a naturally regenerated mature and intermediate site. The fourth young, planted cedar restoration site was located in Pocosin Lakes National Wildlife Refuge (PL).

Sampling at all eight sites was conducted in August of 1998 and 1999. Permanent transects were established at each site and sampling points were designated every 100 m for a total of nine points per site.

At the forested sites, two plots were associated with each point for a total of 18 plots per site. Within each plot, tree were sampled in 10-m^2 plots, shrubs in a nested 4-m^2 subplot, and herbs in three 1-m^2 subplots. Young site sampling was conducted in five 1-m^2 plots associated with each point, following Oosting (1942) and Dabel and Day (1977).

All plants were identified using "*Manual of the Vascular Flora of the Carolinas*" (Radford et al. 1964) and "*Manual of Vascular Plants of Northeastern United States and Adjacent Canada*" (Gleason and Cronquist 1991). Nomenclature followed Kartesz (1994).

Diversity was calculated for each stratum in each site using the Shannon-Wiener function (Krebs 1989). Species cover was used for all diversity calculations. Diversity measurements (H) are associated with a maximum diversity calculation (Hmax). Evenness, a measure equability, was also calculated for each stratum. The closer an evenness measure is to 1, the more the species' distribution within a site is proportionately equal (Zar 1984).

RESULTS

There were 94 taxa in 52 genera and 44 families (table 1). Six (6%) of the taxa were introduced species, all of which occurred in the cedar compensation sites (table 2). The flora of the cedar reference sites was typically less species rich (36 species) than compensation sites (71 species).

Compensation sites had several annuals (17, 24%) while no annuals were collected in reference sites. Compensation sites had more obligate upland species (6) and more obligate wetland species (18) than reference sites (2 and 5, respectively), which may reflect the greater range of elevations of these compensation sites.

Species diversity was greatest in the compensation sites, which was predictable for old-field succession (comp1 and comp2) and secondary succession (PL) areas (table 3). Diversity in the natural cedar sites was performed for each stratum. Sites showed a general trend of being most diverse in their herb strata and diversity was lowest in the tree strata.

Table 1. List of plants species. Nomenclature follows Gleason and Cronquist (1991). Key: LH=life history (H=herbaceous, S=shrub, V=vine, T=tree), IS=wetland indicator status (Reed 1988), C1=, C2=, ARM=Alligator River Mature, ARI=Alligator River Intermediate, DSY=Dismal Swamp Young, DSI=Dismal Swamp Intermediate, DSM=Dismal Swamp Mature, PL=Pocosin Lakes (young), C1=Compensation site 1, C2=Compensation site 2.

PTERIDOPHYTA		LH	IS	C1	C2	ARM	ARI	DSY	DSI	DSM	PL
Aspleniaceae	*Asplenium platyneuron* (L.) B.S.P.	H	FACU		X				X		
Blechnaceae	*Woodwardia areolata* (L..) T. Moore	H	OBL	X		X			X	X	X
Dennstaedtiaceae	*Pteridium aqualinum* (L.) Kuhn	H	FACU								X
Osmundaceae	*Osmunda cinnamomea* L.	H	FACW+			X		X	X	X	
Thelypteridaceae	*Thelypteris palustris* Schott	H					X				X
GYMNOSPERMAE											
Cupressaceae	*Chamaecyparis thyoides* (L.) B.S.P.	T	OBL	X	X	X	X	X	X	X	X
Pinaceae	*Pinus serotina* Michx.	T	FACW+			X	X		X	X	
	P. taeda L.	T	FAC							X	
Taxodiaceae	*Taxodium distichum* (L.) L.C. Rich.	T	OBL			X	X	X			
ANGIOSPERMAE: MONOCOTYLEDONEAE											
Cyperaceae	*Carex albolutescens* Schwein.	H	FAC+	X							X
	C. jorrii Bailey	H									X
	Cyperus odoratus L.	H	FACW	X	X						X
	C. strigosus L.	H	FACW	X							
	Scirpus cyperinus (L.) Kunth	H	OBL	X	X						X
Juncaceae	*Juncus acuminatus* Michx.	H	OBL								
	J. effusus L.	H	FACW+	X	X						X
	J. marginatus Rostk.	H	FACW	X	X						X
	J. repens Michx.	H	OBL	X							
	J. scirpoides Lam.	H	FACW+	X	X						
Poaceae	*Andropogon glomeratus* (Walt.) B.S.P.	H	FACW+	X							
	A. virginicus L.	H	FAC-	X	X						
	Arundinaria gigantea (Walt.) Muhl.	H	FACW	X							
	Digitaria sanguinalis (L.) Scop.	H	FAC-								
	Panicum dichotomiflorum Michx.	H	FACW	X							X
	Saccharum gigantea (Walt.) Pers.	H	FACW	X							
	Setaria viridus (L.) Beauv.	H		X	X						X
Smilacaceae	*Smilax bona-nox* L.	V	FAC								

	S. laurifolia L.	V	FACW+			X	X	X	X	X	X
	S. rotundifolia L.	V	FAC					X	X		
Typhaceae	*Typha latifolia* L.	H	OBL		X						
ANGIOSPERMAE: DICOTYLEDONEAE											
Aceraceae	*Acer rubrum* L.	T	FAC	X	X	X	X	X	X	X	
Amaranthaceae	*Amaranthus* sp.	H		X							
Anacardiaceae	*Rhus copallinum* L.	T/S							X		
	Toxicodendron radicans (L.) Kuntze	V/S	FAC			X	X	X	X	X	
Apocynaceae	*Apocynum cannabinum* L.	H	FACU	X	X						
Aquifoliaceae	*Ilex glabra* (L.) Gray	S	FACW-			X	X			X	
	I. coriacea (Pursh) Chapman	T/S	FACW			X	X		X	X	X
	I. opaca Ait.	T/S	FACU+				X	X	X	X	
	I. verticillata (L.) Gray	T/S	FACW+			X					
Araliaceae	*Aralia spinosa* L.	T/S	FAC							X	
Asteraceae	*Ambrosia artemesifolia* L.	H	FACU	X	X						
	Aster dumosus L.										
	Baccharis halimifolia L.	T/S	FAC								
	Bidens frondosa L.	H	FACW	X	X						
	Cirsium horridulum Michx.	H	FAC+								X
	Erechtites hieraciifolia (L.) Raf. ex DC.	H	FAC-	X	X						X
	Erigeron canadensis L.	H	UPL	X	X						
	E. strigosus Muhl. ex Willd.	H	FAC								X
	Eupatorium capillifolium (Lam.) Small	H	FACU	X	X						X
	E. perfoliatum L.	H	FACW+	X	X						
	E. serotinum Michx.	H	FAC	X							
	Euthamia tenuifolia (Pursh) Nutt.	H	FAC	X	X						X
	Gnaphalium obtusiflolium L.	H			X						X
	Senecio smallii Britt.	H									X
	Solidago fistulosa P. Mill.	H	FAC+	X	X						X
	S. rugosa P. Mill.	H	FAC	X	X						X
	Taraxacum officinale G.H. Weber ex Wiggers	H	FACU								X
	Vernonia noveboracensis (L.) Michx.	H	FAC+	X							
	Xanthium strumarium L.	H	FAC	X							
Chenopodiaceae	*Chenopodium album* L.	H	FAC-	X							
Clethraceae	*Clethra alnifolia* L.	S	FACW			X	X	X	X	X	
Convolvulaceae	*Ipomoea hederacea* Jacq	V	FACU	X	X						
	I. purpurea (L.) Roth	V	UPL	X	X						
Ericaceae	*Leucothoe racemosa* (L.) Gray	S	FACW			X	X				
	Lyonia lucida (Lam.) K. Koch	S	FACW			X	X	X	X	X	
	Rhododendron viscosum (L.) Torr.	S	FACW+			X					
	Spiraea tomentosa L.	S	FACW	X							
	Vaccinium corymbosum L.	S	FACW			X	X	X	X	X	
Fagaceae	*Quercus lyrata* Walt.	T	OBL			X					

Grossulariaceae	*Itea virginica* L.	S	OBL				X			X	
Haloragaceae	*Proserpinaca palustris* L.	H	OBL		X						
Hamamelidaceae	*Liquidambar styraciflua* L.	T	FAC+						X		
Hypericaceae	*Hypericum hypericoides* (L.) Crantz	H	FAC	X							
	H. sp.	H		X	X						
Lauraceae	*Persea borbonia* (L.) Spreng.	T	FACW			X	X	X	X	X	X
	P. palustris (Raf.) Sarg.	T				X	X		X	X	
	Sassafrass albidum (Nutt.) Nees	T	FACU								
Lentibulariaceae	*Utricularia gibba* L.	H	OBL		X		X				
Loganiaceae	*Gelsemium sempervirens* (L.) St. Hil.	V	FAC	X			X		X	X	
Magnoliaceae	*Magnolia virginiana* L.	T	FACW+			X	X		X	X	
Melastomataceae	*Rhexia mariana* L.	H	FACW+	X							X
	R. virginica L.	H	FACW+	X							
Myricaceae	*Myrica cerifera* (L.) Small	S	FAC+			X	X				X
Nyssaceae	*Nyssa sylvatica* Marsh.	T	OBL	X		X	X		X	X	
Onagraceae	*Ludwigia alternifolia* L.	H	OBL	X	X						
	L. decurrens Walt.	H	OBL	X							
	L. linearis Walt.	H	OBL	X	X						
	L. palustris (L.) Ell.	H	OBL	X	X						
Phytolaccaceae	*Phytolacca americana* L.	H	FACU+	X							
Polygonaceae	*Polygonum lapathifolium* L.	H	FACW	X							
	P. persicaria L.	H	FACW								
	P. sp.	H		X	X						
Rosaceae	*Rubus argutus* Link	S	FACU+	X	X	X			X	X	X
	R. hispidus L.	S	FACW		X			X			
Rubiaceae	*Mitchella repens* L.	H	FACU+						X		
Salicaceae	*Salix* sp.	T									X
Scrophulariaceae	*Lindernia dubia* (L.) Pennell	H			X						
	Veronica sp.	H		X							
Solanaceae	*Solanum carolinense* L.	H	FACU								X
Theaceae	*Gordonia lasianthus* (L.) Ellis	T	FACW			X	X				
Vitaceae	*Parthenocissus quinquefolia* (L.) Planch.	V	FAC			X	X	X	X	X	
	Vitis rotundifolia Michx.	V	FAC			X		X	X		

Table 2. Floristic composition of four young and four forested sites. 1 = Introduced species, 2 = Perennial life history, 3 = Annual life history.

Site	Native	Intro.[1]	Per.[2]	Ann.[3]	Herb	Shrub	Tree	Vine
Comp 1	45	5	39	12	43	4	3	1
Comp 2	34	5	29	10	35	2	2	0
PL	28	2	24	6	23	4	2	1
DS-Y	16	0	16	0	2	7	5	2
AR-I	22	0	22	0	2	9	7	4
DS-I	23	0	23	0	4	8	6	5
AR-M	22	0	22	0	2	10	8	2
DS-M	20	0	20	0	2	7	7	4

Table 3. Diversity measures, Hmax and evenness for all sites and strata

Trees	# of Species	Hmax	H	J
DS-Y	5	2.58	2.41	0.93
DS-I	6	3.17	1.77	0.56
DS-M	7	3.32	1.91	0.58
AR-I	7	3.70	2.30	0.62
AR-M	8	3.70	2.51	0.68
Shrubs				
DS-Y	7	3.58	2.96	0.82
DS-I	8	3.00	2.26	0.75
DS-M	7	3.70	2.53	0.68
AR-I	9	3.58	2.73	0.76
AR-M	10	3.81	2.44	0.64
Herbs				
Comp 1	50	5.67	4.72	0.83
Comp 2	39	5.29	4.45	0.84
PL	28	4.95	3.68	0.74
DS-Y	2	4.09	2.99	0.73
DS-I	4	4.09	3.49	0.85
DS-M	2	4.00	3.09	0.77
AR-I	2	4.09	3.33	0.82
AR-M	2	4.09	2.94	0.72

DISCUSSION

Dismal Young

Dismal young is a natural regenerating site that was harvested in 1995. The site was vegetated mostly by shrubs, coppiced trees and extensive growths of lianas including *Smilax* spp. and *Toxicodendron radicans*. Considerable slash was left on site after harvest, which appeared to limit light penetration. Large amounts of slash are known to negatively impact the successful regeneration of cedar (Akerman 1923, Korstian and Brush 1931, Little 1950). In areas that slash cover was not as extensive, a variety of shrubs persisted through the harvest including *Persea borbonia*, *Vaccinium corymbosum*, and *Clethra alnifolia*. Seedling recruitment was mostly *Acer rubrum*, but also included cedar and *Pinus taeda*. Numerous seed trees of cedar and *Taxodium distichum* had been left to aid in restocking but all had been blown over or were snapped off by the end of the second year. Logging slash was mostly covered by *Smilax laurifolia* and *Toxicodendron radicans*. The herbaceous layer was sparse and was composed of *Andropogon virginicus* and *Osmunda cinnamomea*. Species richness was the lowest for all the sites, but diversity calculation was high due to the high frequency of each species found. Species richness is likely to increase over time due to more seedling recruitment from *Liquidambar styraciflua, Ilex opaca, Nyssa biflora,* and other plants in adjacent forests. Some of the wetter areas, which are commonly flooded, have shown no recruitment. These areas have higher levels of water above the soil surface as compared to adjacent sites (Atkinson et al. This Volume) and may become dominated by sphagnum.

Pocosin Lakes

PL restoration site was planted with cedar after an intense fire destroyed the previous vegetative community. As a site undergoing secondary succession, herbaceous communities dominated it. Because of its early successional sere PL was species rich with more species (29) than all but the compensation sites. *Pteridium aqualinum*, which commonly occurs after a fire, was found throughout the site. Also common was *Eupatorium capillifolium*, *Cirsium horridulum*, *Erechtites heiracifolia* and *Solidago* spp. Ditching throughout the area contributed to extended periods of draw down at the site (Atkinson et al. This Volume). Shrub species recruited at the site included *Persea borbonia*, *Morella cerifera,* and *Baccharis halimifolia*. Wetter areas and areas near the ditches support *Juncus, Scirpus* and *Cyperus* spp.. The diversity calculations for this site exceeded all but compensation sites 1 and 2.

Alligator River Intermediate

Alligator River intermediate is characterized by a high density of cedar, approx 39,722 stems per ha (DeBerry et al. This Volume). The tree stratum was overwhelmingly dominated by cedar, but also included *Gordonia lasianthus*, *Taxodium distichum, Pinus serotina, Acer rubrum* and *Nyssa biflora*. The tree stratum at this site and the adjacent mature site were equally species rich, but diversity was lower in the intermediate site due to the very high relative frequency of cedar (DeBerry et al. This Volume). Compared to Dismal intermediate, AR intermediate had a higher species richness and a higher diversity calculation. The flora of AR intermediate differed from the other natural cedar sites mainly in the herbaceous stratum, which contained two aquatic species, *Nymphaea odorata* and *Utricularia gibba*, which grew in swales dominated by sphagnum. Also, the herbaceous layer did not contain *Osmunda cinnamomea* or *Woodwardia areolata*, two species found at all other natural cedar sites in this study.

The mature site at AR is adjacent to the intermediate site. Diversity in the tree stratum was similar to the intermediate site. The mature site contained *Quercus lyrata*, which was not found in the intermediate site. The shrub layer at AR mature was the most species rich of all the sites with 10 species.

Dismal Swamp

DS intermediate tree stratum had low diversity and the two most dominant trees were cedar and *Acer rubrum*. Other species included *Liquidambar styraciflua*, *Magnolia virginiana*, *Pinus serotina*, and *Nyssa sylvatica*. The only other natural site with lower tree species richness was DS young, which had recently been harvested. Diversity measures for the shrub stratum were also the lowest amongst the natural sites (H 2.26). The herb stratum at DS intermediate site was the most species rich with four species.

Mature Sites

Species richness among AR and DS mature sites was among the highest. The higher diversity in AR is attributed to the number of herb stratum species and low dominance of cedar. Also the presence of Loblolly bay (*Gordonia lasianthus*), which reaches its northern most limit in ARNWR, contributed to the higher tree stratum species richness. The shrub stratum in AR was more species rich than that of DS with (10 and 7 species, respectively). The diversity in the herb stratum was higher in Dismal because of a greater cover.

Compensation Sites 1 & 2

Compensation sites 1 and 2 showed high levels of diversity. Being prior converted ag land the site was undergoing old-field succession. Also contributing to the diversity was a variable topography due to the field crown in the middle of each 100 X 450 m block that caused variable water regimes. Heterogeneous environments (microtopographic variability) are often characterized by a greater variety of species in larger abundances than for a homogeneous environment (Vivian-Smith 1997). Center areas were little influenced by a varying water table and contained most of the upland species (Shacochis et al. This Volume). These areas supported a variety upland species such as *Eupatorium capillifolium*, *Cardamine hirsuta*, *Andropogon virginicus*, *Setaria glauca*, *Panicum dichotomoflorum* and *Euthamia tenuifolia*. Wet areas were often covered by *Juncus tenuis*, *Typha latifolia*, *Ludwigia alternifolia*, *Scirpus cyperinus* and *Saccharum giganteum*. This area also supported populations of upland plants due to the highly variable nature of the water table (Atkinson et al. This Volume), which often leaves wet areas dry for an extended period of time. Toward the edge of each block, near the ditches were open water areas that during periods of a high water table (winter, spring (Atkinson et al. This Volume)) supported a variety of water fowl and shore birds and were typically dominated by aquatic species like *Proserpinaca palustris* and *Utricularia gibba*. During dry times some areas were mudflats. Throughout the site were tree seedlings of a variety of volunteer species including *Pinus taeda*, *Liquidambar styraciflua*, *Liriodendron tulipifera* and *Acer rubrum*. The diverse habitat also contributed to the highest species richness of all the sites (54 species). Old-field succession is often associated with higher numbers of annuals and this site had

12, the highest number of all the sites. The compensation sites also had the highest number of non-native plants (5) with *Polygonum persicaria*, *Erechtites hieraciifolia*, *Ipomoea hederacea*, *Ipomoea purpurea* and *Setaria viridis*. Of the 54 species, 43 were herbaceous, 4 shrub and 6 tree species. The family Asteraceae was the most represented family at these sites with 13 species in 10 genera. Of the natural cedar sites only DS young had a member of the Asteraceae (*Erechtites heiraciifolia).* The Poaceae family was also a well represented with 7 species in 6 genera. The Poaceae family was only represented at one natural cedar stand, DS young (*Andropogon virginicus*).

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LITERATURE CITED

Atkinson, R.B., J.W. DeBerry, D.T. Loomis, E.R. Crawford, and R.T. Belcher. This Volume. Water tables in Atlantic white cedar swamps: implications for restoration.

Chickering, J.W. 1873. The flora of the Dismal Swamp. The American Midland Naturalist 7(9): 521-524.

Christensen, N.L., R.B. Burchell, A. Liggett, E.L. Simms, and others. 1981. The structure and development of pocosin vegetation. P. 43-61 IN Richardson, C.J. ed. Pocosin Wetlands. Hutchinson Ross Publ. Co., Stroudsburg, PA.

Clewell A.F. and D.B. Ward. 1989. White Cedar in Florida and along the northern Gulf Coast. P. 69-81 IN A.D. Laderman ed. Atlantic White Cedar Wetlands. Westview Press, Boulder, CO.

Conner, W.H., J.G. Gosselink, and R.T. Parrondo. 1981. Comparison of the vegetation of three Louisiana swamp sites with different flooding regimes. American Journal of Botany 68: 320-331.

Dabel C.V. and F.P. Day. 1977. Structural comparison of four plant communities in the Great Dismal Swamp, Virginia. Bulletin of the Torrey Botanical Club 104: 352-360.

DeBerry, J.W., R.T. Belcher, D.T. Loomis, and R.B. Atkinson. This Volume. Comparison of aboveground structure of four Atlantic white cedar swamps.

Hull, J.C. and D.F. Whigham. 1987. Vegetation patterns in 6 bogs and adjacent forested wetlands in the inner Coastal Plain of Maryland. p. 143-173 IN A.D. Laderman ed. Atlantic White Cedar Wetlands. Westview Press, Boulder, CO.

Kologiski, R.L. 1977. The phytosociology of the Green Swamp, North Carolina. N.C. Agric. Exp. Sta. Tech. Bull. 250. 101 p.

Korstian, C.F. and W.D. Brush. 1931. Southern white cedar. USDA Technical Bulletin 251. 75 pp.

Laderman, A.D. and D.B. Ward. 1987. Species associated with *Chamaecyparis thyoides*: a checklist with common synonyms. P. 385-397 In A.D. Laderman ed. Atlantic white cedar wetlands. Westview Press, Boulder, CO.

Little S. Jr. 1951. Observations on the minor vegetation of the Pine Barren swamps in southern New Jersey. Bulletin of the Torrey Botanical Club 78(2): 153-160.

Lynn, LM. 1981. The vegetation of Little Cedar Bog, southeastern New York. Bulletin of the Torrey Botanical Club 111(1): 90-95.

Niering, W.A. 1953. The past and present vegetation of High Point State Park, New Jersey. Ecological Monographs 23(2): 127-148.

Pittman, A.B., Jr. 1978. Survey of the vascular flora of Shealy's pond, a southern cedar bog. Univ. South Carolina, Columbia, SC.

Oosting, H.J. 1942. Plant communities of the piedmont, North Carolina. American Midland Naturalist 28: 1-126.

Quaterman, E. 1950. Ecology of cedar glades. I. Distribution of glade flora in Tennessee. Bulletin of the Torrey Botanical Club 77: 1-9.

Radford, A.E., H.A. Ahles and C.R. Bell. 1968. Manual of the Vascular Flora of the Carolinas. The University of North Carolina Press, Chapel Hill. 1183 p.

Shacochis, K.M., J.W. DeBerry, D.T. Loomis, R.T. Belcher and R.B. Atkinson. This Volume. Vegetation importance values and prevalence index values of Atlantic white cedar stands in Great Dismal Swamp and Alligator River National Wildlife Refuges.

Torrey, J., F.L.S. 1843. A Flora of the State of New York. Albany, New York, Carroll and Cook, Printers to the Assembly.

Vivian-Smith, G. 1997. Microtopographic heterogeneity and floristic diversity in experimental wetland communities. Journal of Ecology 85: 71-82.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

A RARE PLANT SURVEY OF ATLANTIC WHITE CEDAR HABITATS OF THE GEORGIA WESTCENTRAL FALL LINE SANDHILLS

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Abstract: The Georgia Westcentral Fall Line Sandhills are known for their local occurrences of rare and disjunct plant populations. Isolated stands of cedar along clear, cool, sand- bottomed, spring-fed creeks associate with longleaf pine uplands. Together these two keystone species form the nucleus of a unique ecosystem in westcentral Georgia. During 1998 and 1999 a rare plant survey of cedar habitats was performed. Typical rare plant species found with cedar include *Carex collinsii*, *Carex venusta*, *Fothergilla gardenii*, *Helenium brevifolium*, *Kalmia carolina*, *Myriophyllum laxum*, *Pinguicula primuliflora*, *Sarracenia rubra*, and *Schoenoplectus etuberculatus*. Noteworthy discoveries included *Utricularia floridana*, which has only been reported from Georgia in the Lake Seminole region, and a range extension for *Macbridea caroliniana*. The discovery of *Chamaecyparis thyoides* on a tributary formerly containing a population of *Sarracenia oreophila* in 1859 represents a previously unrecognized plant association for this federally endangered pitcher plant species. New drainages containing *Chamaecyparis thyoides* were discovered on tributaries of Patsiliga, Beaver, and Horse creeks in Taylor County, Beaver Creek in Crawford County, Black Creek in Talbot County, and Shoal Creek in Marion County. Taken together these discoveries represent significant additions to the distributional knowledge of cedar in westcentral Georgia.

Key Words: pitcher plants, rare plants, sand hills, *Sarracenia*, Atlantic white cedar

INTRODUCTION

The Georgia Westcentral Fall Line Sandhills are known for their local occurrences of rare and disjunct plant populations (Lane 1976; Sheridan et al. 1997, 1999; Wharton 1978). Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), communities along clear, cool, sand-bottomed, spring-fed creeks associate with longleaf pine uplands. The association of longleaf pine and cedar communities forms a unique ecosystem in westcentral Georgia. The significance of this ecosystem is underscored by the disjunction and isolation of the cedar community in the Georgia Westcentral Fall Line Sandhills. The nearest cedar communities are 175 km to the east in Richmond County, Georgia and 225 km to the south in the panhandle of Florida.

As population pressure and associated development continue to increase in westcentral Georgia, concerns have been raised about the fate of the rare cedar ecosystem. Cedar ecosystems are unusually vulnerable to the hydrological, chemical, and mechanical insults attendant with development. In particular, alterations in stream flow and sediment loading caused by both point and non-point sources can be especially devastating (Ehrenfeld and Schneider 1991, 1993). This project was therefore initiated to search for additional rare plants and significant natural areas in the Georgia Westcentral Fall Line Sandhills as part of phase 1 of the Fall Line Sandhills Conservation Plan (Cammack et al. 2000).

METHODS

The geographic area of this survey was confined to the Fall Line Sandhills of Westcentral Georgia including Bibb, Crawford, Macon, Marion, Peach, Schley, Talbot, Taylor and Twiggs counties. Priority habitats for investigation were longleaf pine sandhills, cedar swamps, clearwater ponds, sand springs, and riparian and hillside seepage communities.

Sites for investigation were determined by consulting the literature, helicopter flights (June 1998 and March 1999), personal reports, and USGS 7.5' topographic maps. An effort was made to find new sites with intact natural communities and rare plants rather than revisit sites previously identified by Sheridan et al. (1997, 1999). Field research was conducted from May 17 - August 13, 1998 and March 9 - 13, 1999. Potential rare plant occurrences for the region were determined by consulting Patrick et al. (1995). The local newspaper (Butler Herald) was also used to inform citizens of the survey, rare plants being sought, and to ask the public to report any sightings of such rare plants.

Rare plants were documented by voucher specimens provided the population size warranted a collection. All sites visited were located on USGS 7.5-minute topographic maps, populations of rare plants mapped, and a special plant data sheet prepared. In addition, each collection site received an alphanumeric identifier and a natural features data form was initiated. Past studies (Sheridan et al. 1997, 1999) were consulted and used similar data collecting procedures. Data forms from all field surveys are on file with the Georgia Natural Heritage Program, Social Circle, Georgia. Vouchers will be deposited at the University of Georgia Herbarium, Athens.

RESULTS

At least 89 sites have been investigated in the Fall Line Sandhills of Westcentral Georgia for rare plant occurrences by the senior author. This tally represents a conservative number of total sites visited since many botanically unproductive areas were not assigned an alphanumeric identifier during fieldwork in the late 1980s and early 1990s. Previous discoveries have been discussed elsewhere (Sheridan et al. 1997, 1999). Forty-four sites were found in this survey, which contained rare, threatened, or endangered plant species (table 1). The association of rare plant species found was rather predictable within the context of the upper reaches of Whitewater Creek in Taylor County and Juniper Creek in Marion County consisting of *Carex collinsii* Nuttall, *Carex venusta* Dewey var. *venusta*, *Chamaecyparis thyoides* (L.) B.S.P., *Helenium brevifolium* (Nutt.) Wood, *Pinguicula primuliflora* Wood and Godfrey, *Sarracenia rubra* Walt.and *Schoenoplectus etuberculatus* (Steudel) J. Sojak. Depending on site quality and geographic setting, these were the typical rare plant occurrences found within the cedar ecosystem of westcentral Georgia.

Table 1. TNC rarity ranks for selected Georgia Fall Line Sandhills plants*

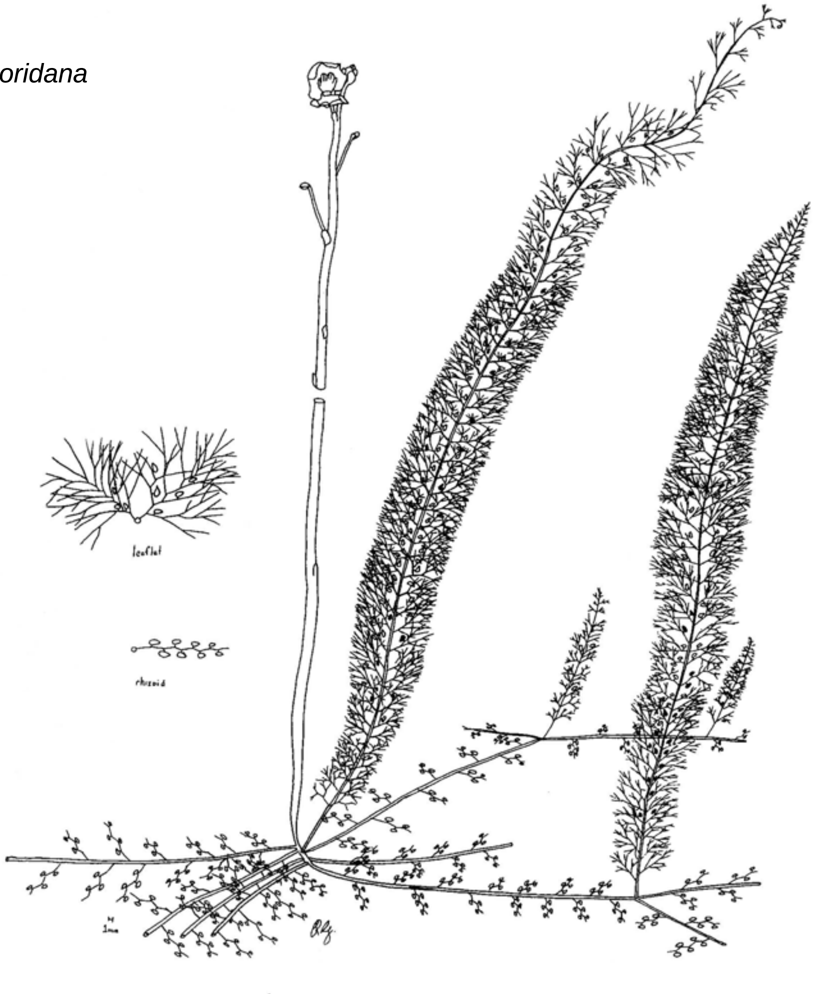
Species	Common Name	State Status	Global Rank	Georgia Rank
Carex collinsii	Narrow-fruit Swamp Sedge	N	G4	S2
Carex venusta	Dark Green Sedge	N	G4	S2?
Chamaecyparis thyoides	Cedar	N	G4	S2
Eriophorum virginicum	Tawny Cotton-grass	N	G5	S1
Fothergilla gardenii	Dwarf Witch-alder	N	G3G4	S2
Helenium brevifolium	Bog Sneezeweed	N	G3G4	S1
Kalmia carolina	Carolina Bog Myrtle	N	G4	S1
Macbridea caroliniana	Carolina Bog Mint	N	G2G3	S1
Myriophyllum laxum	Lax Water-milfoil	T	G3	S2
Pinguicula primuliflora	Clearwater Butterwort	T	G3G4	S1
Sarracenia oreophila	Green Pitcher Plant	E	G2	S1
Sarracenia rubra	Sweet Pitcher Plant	E	G3	S2
Schoenoplectus etuberculatus	Canby's Club-rush	N	G3G4	S1S2
Utricularia floridana	Florida Bladderwort	N	G3G5	S2S3

*Based on July 2001 rarity rankings. State Status: N = none, E = state endangered in Georgia, T = state threatened in Georgia. Global rank: G2 = globally imperiled, 6-20 populations; G3 = very rare and local throughout its range or found locally in a restricted range, or because of other factors vulnerable to extinction, 21-100 populations; G4 = apparently secure globally although it may be rare in parts of its range, 100-1000 populations; G5 = demonstrably secure globally, though it may be quite rare in parts of its range, 1000+ populations.
? = rank is uncertain. State rank: S1 = critically imperiled in the state, 1-5 populations; S2 = imperiled in the state, 6-20 populations; S3 = rare or uncommon in the state, 21-100 populations.

Both *Fothergilla gardenii* Murray and *Kalmia carolina* Small are strictly local in westcentral Georgia. *Kalmia carolina* is only found on the upper reaches of the Whitewater Creek drainage. All other sites are in the bog habitats of the Blue Ridge Mountains in northeast Georgia. A historical site was rediscovered for *Fothergilla gardenii* (GATAYL034) while no new sites were found for *Kalmia carolina* despite extensive field investigation. A range extension was recorded for *Macbridea caroliniana* (Walter) Blake on Juniper Creek in Marion County (GAMARI007). This species is recorded as G2G3S1 (i.e., globally rare and known in Georgia from less than five stations) by the

Georgia Natural Heritage program and represents a significant westward range extension into the Chattahoochee River watershed. A noteworthy discovery was Nash (figure 1). This bladderwort species has only been reported from extreme southwest Georgia in the Lake Seminole region. The documentation of this species as a disjunct in numerous sites in the Fall Line Sandhills further demonstrates the unique ecology of this region. Although the senior author has made an intense effort over the past ten years to find the federally endangered green pitcher plant, *Sarracenia oreophila* (Kearney) Wherry, no populations were discovered. A possible former occurrence for this species (GATAYL039) was recorded on the piedmont/fall line interface during this survey, based on interviews of local residents.

Figure 1.
Utricularia floridana



Utricularia floridana

4 to 9 yellow flowers, very like U. gibba, on swollen, reddish scapes. Extensive network of firmly-anchored rhizomes with stolons 1 to 3cm long bearing up to 8 bladders, alternate, on 1 to 1.5mm stalks. Large bladders to 2mm long × 1.5mm high. Plume-like leaves, red or green, to 90cm tall; much divided leaflets with bladders. Uncurling growing points. Species first noted because of detached scapes and leaves washed up on the lake edge; the majority of these continued growing. This included much divided leaves emerging from scales on the still-flowering scapes.
Central western Georgia, May 1998. Plant shown life size, with a slightly enlarged sample of a rhizoid and leaflet, both bearing traps.

A number of new drainages containing cedar were discovered through both ground and aerial surveys. Of particular significance were occurrences on tributaries of Patsiliga, Beaver, and Horse Creeks in Taylor County, Beaver Creek in Crawford County, Black Creek in Talbot County, and

Shoal Creek in Marion County (figure 2). Taken together these discoveries represent significant additions to the distributional knowledge of cedar in western Georgia. The discovery of cedar (GATAYL028) on Beaver Creek in Taylor County (figure 3) represents a previously unrecognized plant association between cedar and the green pitcher plant, *Sarracenia oreophila*. *Sarracenia oreophila* is principally a plant of the Cumberland Plateau, Blue Ridge, and Ridge and Valley provinces and the documentation of this plants occurrence on watersheds abundantly stocked with cedar clearly demonstrate a new rare plant associate for cedar ecosystems in westcentral Georgia. Additional investigation of these new cedar sites may expand the extent of rare plant occurrences in westcentral Georgia.

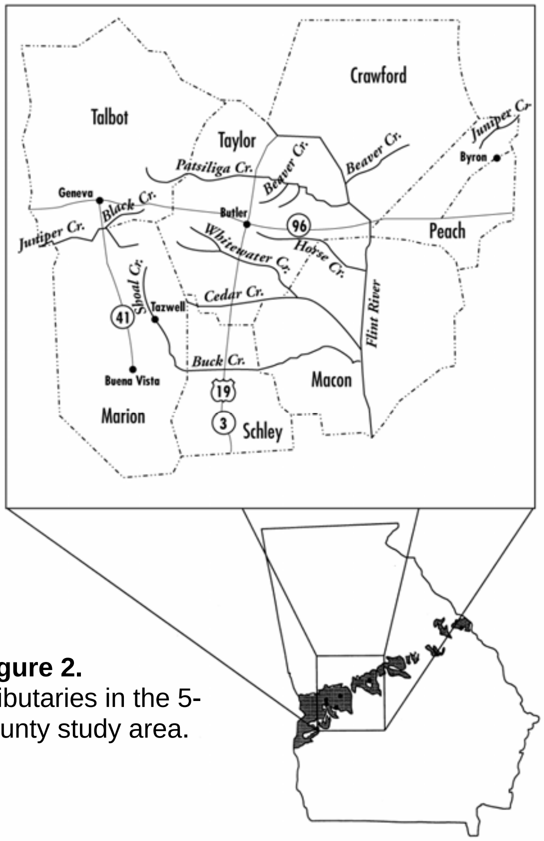


Figure 2.
Tributaries in the 5-county study area.

DISCUSSION

Physiogeographic Limitations of the Fall Line Sandhills Vegetation

The Westcentral Georgia Fall Line Sandhills are chiefly confined to Crawford, Marion, Talbot, and Taylor Counties (figure 2). Fragments of sandhills and sandhill vegetation are found in Bibb and Peach County but the sand is not as extensive, or as deep, and kaolin and sandy clay deposits are closer to the surface altering the vegetative composition. Extensive searches have been conducted east of the sandhills in Jones, Twiggs, and Wilkinson Counties, but these efforts failed to locate the same suite of rare plant species that are routinely found in the sandhills to the west. This suggests an underlying geological reason for the restriction of the rare plant species in the westcentral Georgia sandhills. Further work, however, is warranted along the Boggy Branch drainage in Bibb County (BIBB001) to rediscover *Sarracenia oreophila* and *S. rubra* previously reported for this degraded longleaf pine sandhill area (Troup and McDaniel 1980, Sheridan 1998).

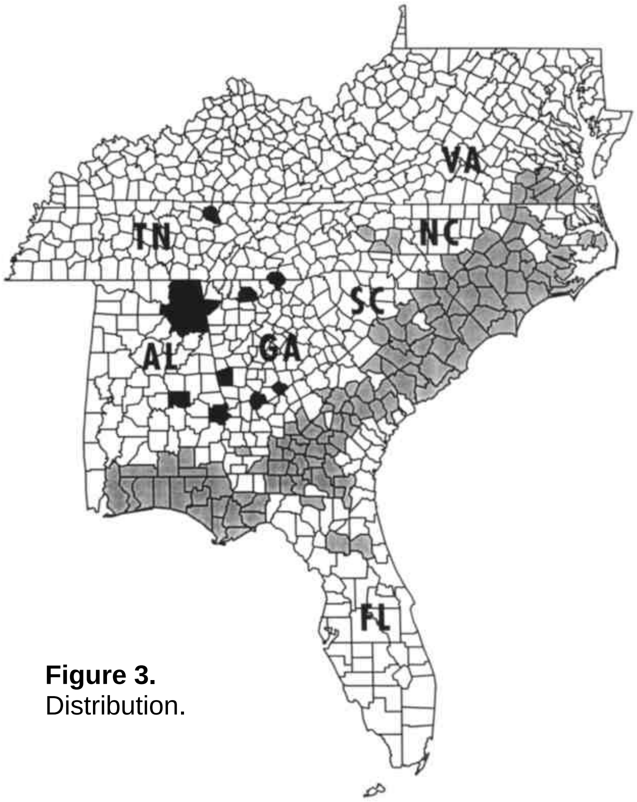


Figure 3.
Distribution.

The sandhills are limited to the south in Macon and Schley counties by the emergence of the Red Hills soils and to the west in Muscogee and Chattahoochee Counties by the dissected terrain associated with the Chattahoochee River. Investigations were conducted in August 1998 along tributaries feeding the Red Hills region including Trip Up Branch and Coon, Usry, Camp, Buck, and Little Muckalee Creeks. The rare plant species found in the sandhills were not found in these tributaries of the Red Hills. One of the best indications of both vegetative and edaphic changes was the disappearance of *Utricularia floridana* from aquatic habitats. *Utricularia floridana* seems to require the spring-fed, slightly tannic, clearwater ponds that are found in the sandhills. Ponds in the Red Hills apparently have more clay and sediments suspended in the water with a subsequent change in water chemistry.

Distribution of Cedar

Prior to this survey only four drainages (figure 2) were known to contain cedar in the westcentral Georgia sandhills: Juniper Creek in Marion County, Whitewater Creek in Taylor County, Cedar Creek in Schley and Taylor Counties, and Juniper Creek in Peach County (Sheridan et al. 1999). Additions to this known distribution were made by the discovery of several drainages containing cedar north and east of Butler in Taylor County, along Beaver Creek in Crawford County, the headwaters of Black Creek in Talbot County, along Whitewater Creek in Macon County, and on Shoal Creek in Marion County.

The Crawford County cedar population (GACRAW006) fills a gap in the range between the Peach County occurrence at Camp Benjamin Hawkins (GAPEAC001) and the Taylor County populations. Although this millpond site contains only a few individuals of cedar, it does suggest that winter aerial surveys in this region may be able to detect additional small cedar populations. The discovery of new cedar populations in this area may then reveal additional populations of rare plants. The previous discovery of *Sarracenia rubra* and other rare plant associates in Crawford County (Sheridan et al. 1997) implied the presence of cedar to the senior author. The subsequent discovery of a nearby population of cedar in Crawford County further highlights the strong plant associations within the cedar community in westcentral Georgia.

The cedar stands discovered on Patsiliga, Beaver, and Horse Creeks have several implications. The Patsiliga Creek site (GATAYL031) was reported by a logger who called the branch this site is located on Juniper Branch. He also reported that cedar he had cut from this site was different from other cedar he had harvested in the area and he called it Red Juniper. Apparently mature trees from this stand have a unique coloration to the heartwood which may prove worthy of investigation. This site is rather difficult to traverse due to its location adjacent to Patsiliga Creek and swamp. Aerial surveys found this site to harbor an extensive colony of mature cedar. The exact position and acreage of this stand within the Patsiliga Creek drainage remains to be determined.

The Horse Creek (GATAYL027) cedar population appears to be particularly robust and contains several associated rare plant species. In addition, some very large diameter wetland longleaf pines (*Pinus palustris* Miller) were also found in this community in the March 1999 survey. The cedar population occurs along approximately 2 km of this watershed.

The March 1999 aerial survey resulted in the discovery of cedar on Shoal Creek in Marion County, Black Creek in Talbot County, and into Macon County on Whitewater Creek. The Shoal Creek record is particularly important due to the association with *Taxodium distichum* (L.) Richard. Although cedar may be sympatric with *Taxodium* elsewhere in its range, this is the only site in westcentral Georgia where this association has been recorded. *Taxodium* tends to be very local in the westcentral fall line sandhills and further exploration of the Shoal Creek drainage may uncover additional, significant floristic records in this unusual association.

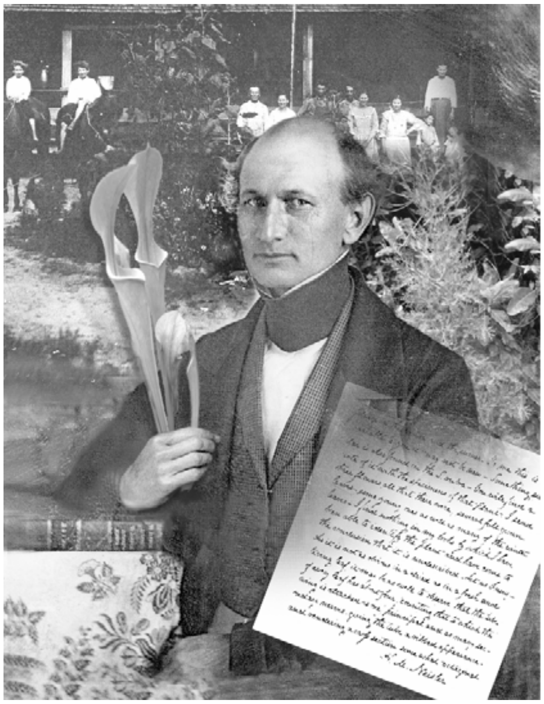
Search for *Sarracenia oreophila*

Despite a decade of work by the senior author, and additional field work by other investigators (Troup and McDaniel 1980), there is no extant fall line sandhills site for the federally endangered green pitcher plant, *Sarracenia oreophila*. Principally a plant of the Cumberland Plateau, Blue Ridge, and Ridge and Valley provinces, *S. oreophila* has only been documented from a maximum of five sites (four counties) within the fall line of Alabama and Georgia (figure 4)(Troup and McDaniel 1980, Sheridan 1998). All of these stations were small and in some cases consisted of a single plant (personal communication Randy Troup). What was the nature of the Taylor County population of *S. oreophila* and can any inferences be made about an association with cedar?

The discovery of cedar on a tributary of Beaver Creek (GATAYL028) is particularly significant since this is the reputed drainage for Neisler's (Figure 4) 1859 Taylor County, Georgia collection of *Sarracenia oreophila* (Troup and McDaniel 1980). The original specimen of *S. oreophila* collected by Dr. Neisler is at the Gray Herbarium and has been verified by several botanists, including the senior author, as *S. oreophila*. The association of cedar and *S. oreophila* has not previously been documented and the occurrence of both these species on the same watershed in close proximity demonstrate an association. In addition, a colony of cedar was also found nearby on Beaver Creek at Suggs Millpond with *Sarracenia rubra*. The association of both of these pitcher plants with cedar may therefore need to be considered in future botanical work in the fall line sandhills of Georgia.

Dr. Hugh Neisler was a physician in Taylor County, Georgia and had extensive communication with the noted botanist Asa Gray. Dr. Neisler had settled along Beaver Creek near Butler in Taylor County soon after the eviction of the local American Indians (mostly Muscogee Creeks). His writings provide a first-hand account of his discovery of *S. oreophila* and *S. rubra* at European settlement. Dr. Neisler's communications with Asa Gray have never been published and contain significant information about these threatened and endangered pitcher plants. These writings may provide insight for further investigation of cedar systems in westcentral Georgia.

Figure 4. Dr. Hugh Neisler



Dr. Neisler's Observations

On June 10, 1857 Neisler wrote about finding *Sarracenia rubra* on his property.

> "I am again sometimes pestered by finding peculiarities in plants unnoticed in the books, as for instance the leaf of a *Sarracenia* which I enclose, which is a young leaf of *S. rubra* – I found them growing in tufts on a spot of ground that had been burned over early in the spring. I was much

> puzzled in determining to what species it belonged, indeed I never should have found out if chance had not showed me a tuft – in which the fire had spared the central part consisting of a few last years leaves and the scape in flower – these were surronded at base by numerous young leaves of this form – which I never could have thought would change so much in becoming grown".

On June 27, 1857 he further commented "The trouble with me about the leaf of the *Sarracenia* was the very small tube and the broad lanceolate appendage in the full grown leaf you know, the appendage is very narrow and linear changing its form altogether, I have a dried specimen, in flower with both forms of leaves growing from it. I will try and save it for you."

On June 2, 1858 Neisler wrote about his recent discovery of an unidentified pitcher plant

> "Since writing last I have come up with a *Sarracenia* that I have not before seen – I found only the leaves. I am inclined to believe that it has not yet flowered. The leaves are small and slender till near the summit it enlarges to two or more inches in diameter wing linear, narrow; lamina much compressed below, sides reflected and arched over the opening of the tube – it and the throat internally streaked with purple – it is neither the *rubra*, *purpurea*, nor *flava* if the recollections of the last species are correct; some of the leaves are twenty five inches long – There is the same marked difference between the young and full grown leaves as in the *rubra* – in the latter you no doubt remember I mentioned this great difference to you and sent a young leaf that you might see for yourself – I have put up some half dozen leaves for you and will get the flowers if I can. I omitted to mention that the leaves of the *Sarracenia* above mentioned are so strongly nerved that a transverse section forms a polygon rather than a circle."

There are several significant aspects to Neisler's June 2nd letter. First, he comments that the throat of the unknown pitcher plant is streaked with purple and unlike *S. flava* that he was familiar with. Typically *S. flava* in Georgia either lacks purple pigment in the throat or has a disctinctive purple splotch in that area. In contrast, *S. oreophila* can have a throat streaked with purple as Neisler described. Also of significance is the presence of both *S. rubra* and the unidentified (*S. oreophila*) pitcher plant in the same general collecting area. *Sarracenia oreophila* rarely occurs within the range of any other pitcher plant species. The one documented co-occurrence was in the extirpated colony in the fall line of Alabama in Elmore County with *S. rubra* ssp. *alabamensis* and potentially in Bibb County, Georgia also within the range of *S. rubra*. Second, he comments on the distinctive strong nerving on the leaf of the pitcher plant which is also suggestive of *S. oreophila*.

He then wrote on June 18, 1858 (dots indicate where part of letter cut off)

> "I went out this morning to look up my *Sarracenia* that I told you .… a while since. It is a little singular that I can find … but in the one spot and there, nine feet square will …. the whole space occupied by them and six or eight …includes the whole number of plants. I can yet find … trace of a scape, either past, present or to come. Yet in searching for it, I have found something much more curious to me than the young leaves of the *S. rubra*, which I sent you a year or more ago. Around the bases of the phyllodia there are clusters of young leaves, that bear no trace or resemblance to them that I can see. And if they are ever changed into the … Nature does it by some hocus pocus that I cannot comprehend, as yet at least. I send you some of them. Also a young and tender phyllodium, scarcely longer than one of the strange leaves. Also another fully grown but dwarfed by disease or accident. It will give you an idea of the coloration and pubescence of the throat and lamina. Remember though that the perfect and fully grown phyllodia are entirely straight, two feet or more high, slender, enlarging gradually upwards, until near the summit they abruptly enlarge so that the throat may be often

three or four inches across – the nerves too, are much more decidedly and equally developed. Can you form an idea which of the species, it will, most likely, prove to be? I would observe lest - I forget – that the specimen may not give an exactly correct idea of the lamina in the phyllodia of the *Sarracenia*, its sides are reflected below and it is arched completely over the throat."

The "strange leaves" that Neisler refers to are the flattened, non-pitchered leaves produced by *S. flava*, *S. oreophila*, and *S. leucophylla*. Ironically these flattened leaves are now called phyllodia while the "phyllodia" that Neisler referred to are actually the pitchered leaves.

On July 22, 1858 he writes

"Since I wrote last, I have found the *Sarracenia* so often spoken of, in another spot, five or six plants, and an old scape with a rotten seed vessel, I think, of last year. This years flowers were probably destroyed by a late frost we had in April. The phyllodia are now all decaying and young leaves are springing up from the roots, these I now think will by winter be transformed into phyllodia, which surviving the period of flowering and fruiting next season will in their turn wither and be succeeded by others. If I am correct in my conjecture the difference between the young and full grown phyllodia in this plant is very remarkable and will form an interesting chapter in its history. I enclose another leaf to let you see the gradual change that has taken place since the one I sent you in my case, was gathered – You see that the thickened, concave margin of the leaf has changed its form somewhat and that the minute point at its extremity has bent over assuming very exactly the position of the future lamina! I also enclose a young phyllodium of *S. rubra* in which the lamina is well developed as also the tube a little more than half way down – but the remainder is precisely in the condition of the whole concave margin of the other leaf! What begins to look a little like a demonstration I think. I fear the *Sarracenia* may become a bore, so we will drop it for a time at least."

On August 18, 1858 he wrote

"No change in *Sarracenia* since my last visit. In the *S. rubra* I find tube and lamina fully formed in the bud! Still I sometimes find a leaf several inches long, without either. In the undetermined species – in the bud, as yet, leaves but no phyllodia! I now, know not what to make of it."

On April 28, 1859 he wrote

"These are the leaves and flowers of the *Sarracenia* I have so often mentioned to you. I discovered it twelve months since and have been able to find but two clusters of plants, as yet, a few hundred yards apart. One cluster on the edge of a swamp – the other on tussocks in a swamp – all together not a dozen plants. This year the leaves began to spring from the ground about the middle of March. At first the hood is erect and folded together and the mouth of the tube is closed. When they have arrived at their full height the hood slowly expands and the mouth of the tube opens and in the end the hood becomes beautifully arched over it. The scape appears when the leaves are up to some height – but the latter are fullygrown before the flowers unfold. The flowers are of a pale greenish yellow entirely without odor.

The large tubular leaves wither and die in the fall but in the mean while those small leaves come forth and are persistent during the winter, towards spring they begin to die – and at this time (28 April) scarcely one perfect one is to be found – the upper part of all of them to a greater or lesser degree being withered and dead – Thus the plant has an altogether different foliage in the winter and the summer. To me this is remarkable, to you it may not be new –

> Something similar is also found in the *S. rubra* – You will find a note of it with the specimens of that plant. I send three flowers, all that there were, several full grown leaves – some young ones as well as many of the winter leaves – I find nothing in my books by which I have been able to identify the plants and have come to the conclusion that it is undescribed – Let us know – As it is not as obvious in a dried as in a fresh and living leaf it may be as well to observe that the tube of every leaf has about four (counting that to which the wing is attached as one) principal and as many secondary nerves giving the tube a ribbed appearance and rendering a cross section somewhat octagonal."

In his April 28, 1859 letter Neisler recognizes that he has an undescribed species of pitcher plant. Another 74 years would pass before *Sarracenia oreophila* was officially described as a new species (Wherry 1933). Neisler also mentions the lack of flower odor and full development of the pitchers before the flowers open in his undescribed species, morphological traits which are unique to *S. oreophila*. His herbarium specimen to Asa Gray included the flattened, non-pitchered "strange leaves", now known as phyllodia. These leaves are diagnostic for *S. oreophila* since they are short, recurved and ensiform. Clearly Dr. Hugh Neisler was the first botanist to recognize the unique traits of *S. oreophila* and documented its occurrence in the fall line sand hills of westcentral Georgia. That this species occurred near his home in the sand hills along Beaver Creek is supported by his June 18, 1858 letter where he states "I went out this morning to look up my *Sarracenia…*". For Dr. Neisler to go out in the morning and collect leaves for herbarium specimens means that the plant had to grow within a relatively short distance, since transportation at that time was by horse or on foot.

In November 1859 he wrote

> "The *Sarracenia flava* does not grow with us as far as I yet know. I have been familiar with it in the low country of the Carolinas – years ago – and my recollection of it differs from the plant I have talked so much about. But your knowledge of and familiarity with the matter of course enables you to determine with little difficulty. Still it seems to me strange that the angular outline of a transverse section of the phyllodia so different from anything seen in the *purpurea* the *rubra* or *variolaris*, which I have frequent opportunities of seeing in their season, should be entirely overlooked in all the descriptions I have met with. If you wish it I can send you roots of this plant any day – as well as those of any other of our plants and shrubs – that you would like to add to your collection of living plants – it is much easier to me than to gather seed which is a much more difficult matter than I anticipated."

Of significance in the November correspondence is that Neisler indicates "frequent opportunities" of seeing *S. purpurea* and *S. variolaris* (now *S. minor*). *Sarracenia purpurea* is extremely rare in Georgia (having been extirpated from the few sites in southwest Georgia) and has never been documented from the west central fall line sandhills of Georgia. Did Neisler know of stations for this rare pitcher plant in western Georgia? Perhaps not, based on his earlier residence in the "low country of the Carolinas" where *S. purpurea*, *S. minor* and *S. flava* are still to be found (McDaniel 1971, Radford et al. 1968).

Neisler's descriptions of *S. oreophila* provide a unique look at the population biology of this federally endangered pitcher plant species at European settlement. The population was small, extremely localized, and sparse in reproductive events. A possible inference is that the clearing activities and burning that Dr. Neisler performed in 1858 may have helped expose this population along a shrubby swamp edge. The reference to the clump on tussocks also infers that the plants were migrating locally via water to new sites for establishment. Interestingly, Dr. Neisler's home was along Beaver Creek, which implies beaver activity along this stream system. Was beaver disturbance, including associated successional events, important to the dispersal of *S. oreophila* in

Taylor County, Georgia? Tussocks in beaver ponds are actively colonized by *S. rubra* today in Taylor County. An extensive colony (200 stems) of young pitcher plants occurs among clumps of various grasses and sedges (*Andropogon glomeratus*, *Rhynchospora* spp., *Carex* spp.) in an abandoned beaver pond along Black Creek. This site occupies nearly an acre and has recently been shown by the junior author to contain an additional rarity, namely tawny cotton-grass (*Eriophorum virginicum*). Curiously, the closest occurrence of *Eriophorum* may be with *S. oreophila* at one of its few Blue Ridge sites in Clay Co., North Carolina! A similar colonization strategy could have been exercised by *S. oreophila* in Taylor County and argues for further exploration of these habitats today for *S. oreophila*.

Intensive field work has resulted in the discovery of numerous *S. rubra* populations in the fall line sand hills of west central Georgia. What is the problem in locating an extant *S. oreophila* fall line population? Conceivably *S. oreophila* has gone extinct in the fall line and a restoration effort will be needed to reintroduce this species. Given the limited historical population size of *S. oreophila* in the fall line an extinction vortex may have occurred through the combined effects of inbreeding depression (Sheridan and Karowe 2000) and land use changes. In an extinction vortex the negative fitness effects of limited effective population size are amplified by negative land use changes (e.g. lack of fire) to the point that a species is driven to extinction.

Another possibility is that searches for *S. oreophila* in the fall line sandhills are mis-directed and should be focused more on the piedmont/fall line transition zone. *Sarracenia oreophila* was very local in the fall line sandhills of Georgia and Alabama and only reported, but not collected, from the Piedmont Province of Georgia (Wherry 1933, Troup and McDaniel 1980). Perhaps this species occurred locally in a narrow band in the transition zone between the piedmont and coastal plains. Some support for this hypothesis is offered by the location of historical records and personal reports (GATAYL039).

The occurrence of *S. rubra* as the only extant pitcher plant in seepage wetlands of the Georgia Westcentral Fall Line Sandhills is also rather remarkable. Although *Sarracenia* pitcher plants are known to occur as only a single species in a physiogeographic province (e.g. *S. alata* in Texas) the occurrence of *S. rubra* without the association of another pitcher plant species in an ecosystem is rare. Perhaps there is a subtle habitat difference on the piedmont/inner coastal plain transition that meets the habitat requirements of fall line *S. oreophila*. Further field work in this transition zone is necessary to test this hypothesis and to search for any remaining colonies of *S. oreophila*.

CONCLUSION

Our botanical surveys of rare plant occurrences within the cedar ecosystem of westcentral Georgia have demonstrated the biological significance of this region. Additional investigations will undoubtedly add more significant elements to this flora and provide insights for biogeographers to consider. However, over the past ten years we have slowly seen the land start to be developed and suffer degradation. This trend has accelerated and may only get worse with the completion of several high-speed roads through the region. One of the greatest dangers to the cedar community is the siltation of streams caused by clearing of land on adjacent slopes and the increased velocity and temperature of stormwater. Excessive siltation within the cedar ecosystems in westcentral Georgia may have catastrophic effects on the riparian rare plant communities. Increased stream flows influence water quality. Removal of forested buffers increases silt deposition. The rare plant community (especially *Myriophyllum*, *Pinguicula*, *Sarracenia*, *Utricularia*) is not tolerant of this kind of disturbance and can be lost as a result of such drastic habitat alterations. Effective long-term protection of this ecosystem will require an integrated ecosystem approach that successfully addresses the social, political, and environmental challenges of modern conservation biology.

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LITERATURE CITED

Cammack, S., E. Van De Genachte, and T. Patrick. 2000. Fall line sandhills conservation plan final report. Georgia Dept. of Natural Resources, Georgia Natural Heritage Program, Social Circle. 36pp.

Ehrenfeld, J. and J. Schneider. 1991. *Chamaecyparis thyoides* wetlands and suburbanization: effects of nonpoint source water pollution on hydrology and plant community structure. Journal of Applied Ecology 28: 467-490.

Ehrenfeld, J. and J. Schneider. 1993. Responses of forested wetland vegetation to perturbations of water chemistry and hydrology. Wetlands 13: 122-129.

Lane, R.L. 1976. The vascular flora of the west-central upper coastal plain of Georgia. Unpublished Ph.D. dissertation, University of Georgia, Athens. 132. pp.

McDaniel, S.T. 1971. The genus *Sarracenia* (Sarraceniaceae). Bulletin No. 9. Tall Timbers Research Station, Tallahassee, FL. 36 pp.

Patrick, T.S., J.R. Allison, and G.A. Krakow. 1995. Protected plants of Georgia.Georgia Dept. of Natural Resources, Georgia Natural Heritage Program, Social Circle. 246 pp.

Radford, A.E., H.E. Ahles, and C. R. Bell. 1968. Manual of the Vascular Flora of the Carolinas. The University of North Carolina Press, Chapel Hill. 1183 pp.

Sheridan, P. 1998. Red letter days of a Pennsylvania botanist. Carnivorous Plant Newsletter 27: 123-125.

Sheridan, P. and D. Karowe. 2000. Inbreeding, outbreeding, and heterosis in *Sarracenia flava* (Sarraceniaceae) in Virginia. American Journal of Botany 87: 1628-1633.

Sheridan, P., S. Orzell, and E. Bridges. 1997. Powerline easements as refugia for state rare seepage and pineland plant taxa. In: Williams, J.R., J.W. Goodrich-Mahoney, J.R. Wisniewski, J. Wisniewski, eds. The 6th international symposium on environmental concerns in rights-of-way management. Oxford: Elsevier Science: 451-460.

Sheridan, P., S. Orzell, and E. Bridges. 1999. Some noteworthy vascular plant records from Atlantic white-cedar, *Chamaecyparis thyoides* (L.) B.S.P., habitats of western Georgia. In: Shear, Theodore H.; Summerville, K.O., eds. Atlantic white-cedar ecology and management symposium; 1997 August 6-7; Newport News, Va. Gen. Tech. Rep. SRS-27. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. 82 pp.

Troup, R., and S. McDaniel. 1980. Current status report on *Sarracenia oreophila*. U.S. Fish and Wildlife Service, Jackson Field Office, Jackson, MS. 60 pp.

Wharton, C.H. 1978. The natural environments of Georgia. Publication No. B-114. Georgia Dept. of Natural Resources, Georgia Geologic Survey, Atlanta. 227 pp.

Wherry, E.T. 1933. The Appalachian relative of *Sarracenia flava*. Bartonia 15: 7-8.

SOIL BIOCHEMISTRY IN VIRGINIA AND NORTH CAROLINA ATLANTIC WHITE CEDAR SWAMPS

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Abstract: Atlantic white cedar wetlands are widely distributed along the Atlantic coastal plain on highly acidic organic soils. Site characterization is becoming increasingly important for restoration as stand acreage has greatly declined and cedar reestablishment has proven difficult. Soil substrate quality was determined at six naturally occurring cedar sites in Virginia and North Carolina representing three age classes (young, intermediate, and mature). Nine 10-cm sample soil cores were collected at each of the six sites during summer 1999. Soil nutrients (P, N, Fe, Mg, Zn, Ca, Cu, Al, Mn, and K) and physical properties (pH, volumetric water content, bulk density, organic matter content, and carbon content) were measured. Groundwater samples were also collected and analyzed for levels of total N, NO_3-N, NH_4–N, and PO_4-P. Total carbon was the only soil physical property that was not different among sites. Total carbon site medians were between 47.0% and 49.8%. The largest difference in site mean values among soil physical properties was in bulk density, ranging from 0.084 ± 0.021 g/cm^3 to 0.244 ± 0.027 g/cm^3. Aluminum was the only nutrient parameter for which concentrations were not found to be different among sites. Total N (percent dry weight) means ranged from 1.39 ± 0.20% to 1.76 ± 0.15%, while NH_4–N levels ranged from 1.4 ppm to 212.9 ppm. There was variation in soil physical properties and nutrient concentrations among the three age classes, however differences were likely influenced by confounded variables including landscape position, geology, and hydrology rather than age. Ditching was present in all sites but effectiveness differed, which may help explain some differences in nutrient and soil properties among sites. Generally these results for cedar stands were within the range of values reported for stands along the eastern coastal range. The organic matter, NO_3-N, and Ca values tended to be high and pH values were low compared to other sites.

Key Words: Atlantic white cedar, soil nutrients, biochemistry, Pocosin Lakes, soil, Great Dismal Swamp, Alligator River

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P (cedar), occurs along the Atlantic coast. These wetlands have been converted to other ecosystems as logging, ditching and drainage, road construction, suburbanization, and agriculture have occurred, reducing the acreage of cedar considerably (Noss et al. 1995) and altering the soil substrate in remaining stands.

An alteration that greatly influences site conditions of cedar stands in North Carolina and Virginia are the ditches and canals dug in the remaining wetlands. Draining these cedar swamps for agricultural and silvicultural purposes has occurred over varying lengths of time and, by lowering the water table, impacted microbial activity; peat dynamics; soil physical properties; and nutrient mobility, mineralization and availability.

Few studies have quantified aspects of the physical or biochemical characteristics of cedar swamps (Day and Dabel 1978, Day 1982, Gomez and Day 1982, Lowry 1984, Bandle and Day 1985, Whigham and Richardson 1988, Ehrenfeld and Schneider 1991, Zhu and Ehrenfeld 1999). In this study, soil physical properties and nutrient concentrations were assessed in order to (1) characterize the physical and biochemical status of both existing and recently restored cedar stands, (2) suggest factors that may have affected nutrient content such as site history, hydrologic conditions and landscape position, and (3) identify conditions necessary for cedar regeneration and establishment.

METHODS

Study Sites

The Great Dismal Swamp National Wildlife Refuge (GDS) is located on the coastal plain in North Carolina and Virginia. The soils consisted of highly acidic peat layers with Typic Medisaprists as the most common soil type (Soil Conservation Service 1974). An extensive network of ditches has significantly lowered the water table (Atkinson et al. This Volume[a]). The three sites sampled in the GDS were along the North Carolina and Virginia border, close to the Corapeake Ditch, and included three age classes of cedar: young (2 yrs), intermediate (25-35 yrs), and mature (60-70 yrs). The Alligator River National Wildlife Refuge (AR) is located mostly in Dare County, NC. Organic soils predominate and cedar most frequently occurred on Dare and Pungo Series soils. Drainage ditches were also found throughout the refuge but the area was inundated for long periods during most growing seasons (Atkinson et al. This Volume[a]). Two stands were studied at AR including an intermediate (25-35 yrs) and a mature site (60-70 yrs). The eighth study site was located in Washington County, NC on Pocosin Lakes National Wildlife Refuge (PL). This site was burned within the past ten years and was on acidic organic soils that were ombrotrophic. The organic soils were highly decomposed resulting in a mucky peat. The soils were classified as Typic Haplosaprist, Cumulic Humaquept, and Mollic Endoaqualf by the National Soil Survey Center (2000). This site was planted in 1998 and was classified in a young age class represented this site and cedar was planted in 1998. The eight sites (three in GDS, two in AR, and one in PL) included a range of age classes (table 1) and sites differed in their history of harvest, ditching and recent management strategies (Atkinson et al. This Volume[b]).

Sampling

Soil and groundwater samples were collected in July 1999 from each of nine points along transects at each of the six sites. Cores for soil physical properties were collected using a bulb planter at a 10-cm depth. A stainless steel boring auger was used to collect soil samples for nutrient analysis. Groundwater samples were collected from wells dug at transect points during the time of sampling. Well depths varied according to water table accessibility. Groundwater samples were collected in 0.5-L bottles with 2 ml concentrated sulfuric acid per L for preservation and stored on ice during transportation to the laboratory for analysis.

Soil Physical Property Analysis

Soil cores were measured for bulk density, volumetric water content, saturation, pH, percent organic matter (by mass), and total carbon. Samples were weighed before and after oven drying for 24 h at 105°C. Bulk density was calculated as dry weight/core volume. Volumetric water content was calculated as the water weight/core volume. Saturation was calculated as water weight/pore space. Soil pH was determined using a 1:1 soil to water volume ratio. Percent organic matter was determined by ashing 2 g of dried soil at 550°C for 16 h and was calculated as ((dry weight – ash weight)/dry weight) X 100 (Karam 1993).

Soil Nutrient Analysis

Soil concentrations of Al, Ca, Cu, Fe, Mg, Mn, K, and Zn were determined using a Mehlich 1 extractant and measured on a Spectroflame, model FTMOA85D, inductively coupled plasma atomic emission spectrometer (ICP-AES) (Donohoe and Heckindorn 1996). Soil cores were analyzed for NH_4-N, NO_3-N, total N and total C using a Carlo Erba nitrogen-carbon analyzer (Miller 1997, Method S-9.3, 3.5, 1.0 to 1.7). Total P was measured colorimetrically using the reagents of Murphy and Riley (1962) on a Shimadzu UV-VIS spectrophotometer after sulfuric acid digestion (Diamond 1995). Sodium hydroxide was used to extract moderately labile P, comprised of extractable inorganic and organic P. Total extractable P was then measured on the ICP-AES. Extractable inorganic P was measured colorimetrically, while extractable organic P was calculated as the difference between inorganic and total extractable P (Beck 1993).

Groundwater Nutrient Analysis

Water samples were analyzed for total Kjeldahl nitrogen, NO_3-N, and NH_4-N (USEPA 1979, Method 351.2, 353.2, and 350.1). Total P was measured using an ICP-AES and PO_4-P determined following the ascorbic acid reduction method of Murphy and Riley (1962).

Normality was assessed using the Kolmogorov-Smirnov Normality Test and, when non-normal, the Kruskal-Wallis one way analysis of variance on ranks was used for determining differences for each parameter among sites at the $P < 0.05$ level. Multiple pairwise comparison analyses (Tukey Test) were used to determine differences between sites at the $P < 0.05$ level. Variability was reported as ± 1 standard deviation, unless otherwise indicated.

RESULTS

Soil Physical Properties

Mean soil pH was lowest in the GDS mature (GDS$_{mat}$) site (3.3). The PL site had the highest mean soil pH at 4.0. The soil bulk density at PL was higher than all other sites (range of means 0.084 ± 0.021 to 0.244 ± 0.027 g/cm^3). Soil volumetric water content was highest at the AR intermediate (AR$_{\text{int}}$) site (47.3 ± 10.1%). Soil saturation at AR$_{\text{int}}$ was 87.1%, which was more than twice the average of the remaining study sites in North Carolina and Virginia. The GDS intermediate (GDS$_{\text{int}}$) site had the lowest average value for water content at 18.4 ± 2.6%. Organic matter was very high at all sites ranging from 93.0 to 97.5%. All three sites in the GDS had organic matter values of 93.0%. Total carbon median values ranged from 46.3 to 49.8%, and this was the only soil physical property variable not different among sites (P = 0.08)(table 1).

Table 1. Summary of soil physical properties for July 1999 on six cedar sites expressed as mean (std. dev.) or median values (n = 9) to a depth of 10 cm. Comparable data (age classes unknown) are shown where applicable. Sites with different letters are significantly different (p < 0.05, Tukey Test) for a given property.

Site or Source	Age Class	pH	Bulk Density (g/cm^3)	Water Content (%)	Saturation (%)	Organic Matter (%)	Total Carbon (% dry weight)
This Study: Alligator River	intermediate	3.5 ab	0.084 (0.021) a	47.3 (10.1) a	87.1 a	97.5 a	47.0 a
	mature	3.6 ac	0.097 (0.012) a	32.6 (8.5) b	54.4 ac	97.0 a	46.3 a
This Study: Great Dismal	intermediate	3.6 ac	0.117 (0.022) a	18.4 (2.6) c	23.9 b	93.0 b	46.3 a
	mature	3.3 b	0.163 (0.034) b	31.1 (6.5) b	47.0 ab	93.0 b	47.9 a
	young	3.4 ab	0.163 (0.027) b	23.4 (7.9) bc	34.8 bc	93.0 b	48.1 a
This Study: Pocosin Lakes	young	4 c	0.244 (0.027) c	32.0 (7.8) b	43.6 ab	95.0 b	49.8 a
NC, Great Dismal Swamp (Bandle & Day 1985)	-	3.4	-	-	-	84.6 (2.4)	-
Rhode Island (Golet & Lowry 1987)	-	4.95, 4.26 (groundwater)	-	-	-	-	-
Maryland (Whigham & Richardson 1988)	-	5.34 (0.11)	-	-	83.3 (1.2)	59.4 (5.0)	-
New Jersey (Zhu & Ehrenfeld 1999)	-	3.55 (0.04) - 4.01 (0.04)	0.05 (0.01) - 0.07 (0.01)	-	-	-	-
Mississippi (Eleuterius & Jones 1972)	-	4.8 - 5.0	-	-	-	-	-
Florida (Collins et al. 1964)	-	6.6 - 7.5	-	-	-	-	-
NC, Washington County (Dolman and Buol 1967)	-	-	-	-	-	56.9	-
New Jersey (Ehrenfeld 1995)	-	-	0.08 (0.04)	-	-	-	-
Florida (Clewell and Ward 1987)	-	6.6 - 7.5	-	-	-	-	-

Soil Nutrients

Nitrogen and Phosphorus. Soil N and P parameters are shown in table 2. The mean total N value from all sites combined was 1.57 ± 0.07% (range of site means 1.39 ± 0.20 - 1.77 ± 0.16%). Soil NO_3-N and NH_4-N values per site varied greatly. Pocosin Lakes had the lowest NO_3-N concentration at 2.9 ppm and the highest NO_3-N concentration (71.5 ppm) was found in the GDS_{mat} site. Ammonia concentrations ranged from 1.4 ppm at PL to 212.9 ppm at GDS_{int}. Carbon to nitrogen ratios ranged from 25.77 at GDS_{int} and 38.53 at PL.

Table 2. Summary of soil nitrogen and phosphorus for July 1999 on six cedar sites expressed as mean (std. dev.) or median values (n = 9) to a depth of 10 cm. Comparable data (age classes unknown) are shown where applicable. Sites with different letters are significantly different ($p < 0.05$, Tukey Test) for a given property.

Site or Source	Age Class	Total Nitrogen (% dry weight)	Nitrate (ppm)	Ammonia (ppm)	C:N	Total Phosphorus (% dry weight)	Extractable Total Phosphorus (ppm)	N:P
Alligator River	intermediate	1.44 (0.23) b	4.7 b	80.1 bc	34.77 a	0.046 b	331.2 a	31.05 a
	mature	1.40 (0.25) b	4.6 b	129.4 ac	30.41 a	0.043 b	247.2 b	34.11 a
Great Dismal	intermediate	1.77 (0.16) a	19.4 ab	212.9 a	25.77 b	0.352 a	311.4 ab	5.37 b
	mature	1.76 (0.15) a	71.5 a	71.3 ab	26.63 ab	0.327 a	264.3 ab	5.22 b
	young	1.64 (0.18) ab	42.8 a	94.4 ac	28.68 ab	0.045 b	253.2 ab	38.56 a
Pocosin Lakes	young	1.39 (0.20) ab	2.9 b	1.4 b	38.53 ab	0.022 b	150.6 ab	58.26 a
NC Coastal Plain (Ralston & Richter 1980)	-	-	-	13.4 (1.4) mg/ 1000 cc	-	-	3.62 (0.24) mg/ 1000 cc	-
Maryland (Whigham & Richardson 1988)	-	1.59 (0.13)	0.76 (0.05) ug/g	66.7 (13.7)	-	0.07 (0.01)	-	-
NC, Great Dismal Swamp (Day 1982)	-	1.22	-	-	42	0.08	-	-
New Jersey (Zhu & Ehrenfeld 1999)	-	16.2 (0.9) - 23.6 (0.9) g/kg	0.1 (0.0) - 3.0 (2.8) mg/kg	6.1 (2.5) - 26.5 (10.1) mg/kg	-	-	-	-
Great Dismal Swamp (Bandle & Day 1985)	-	-	-	-	-	-	1.68 (0.31) mg/g	-
NC, Washington County (Dolman & Buol 1967)	-	1.40	-	-	35.02	5 ppm	-	-

Total P concentrations were comparatively low except for values determined at GDS_{int} and GDS_{mat}. Values at these two sites were higher (0.35% and 0.33%, respectively) than in the remaining sites, which ranged from 0.02% at PL to 0.05% at AR_{int} ($P < 0.05$). The high P concentrations at GDS_{int} and GDS_{mat} resulted in N:P ratios being lower than the other sites, which ranged from 31.05 to 58.26 ($P < 0.05$).

Macronutrients. Soil macronutrients (Ca, Mg, K) are shown in table 3. Calcium concentrations ranged from 809.7 *u*g/g at AR_{int} to 4,572.6 *u*g/g at PL. Magnesium concentrations ranged from 315.8 *u*g/g at GDS_{yng} to 925.6 *u*g/g at AL_{mat}. Potassium levels were highest at the AR sites, averaging 372.8 ± 50.9 *u*g/g, and lowest at PL (81.5 *u*g/g), which was different ($P < 0.05$).

Table 3. Summary of soil nutrients for July 1999 on six cedar sites expressed as mean (std. dev.) or median values (n = 9) to a depth of 10 cm. Comparable data (age classes unknown) are shown where applicable. Sites with different letters are significantly different ($p < 0.05$, Tukey Test) for a given property.

Site or Source	Age Class	Ca (ug/g)	Mg (ug/g)	Fe (ug/g)	Zn (ug/g)	Mn (ug/g)	Al (ug/g)	K (ug/g)	Cu (ug/g)
Alligator River	intermediate	809.7 a	676.7 ac	80.9 ac	18.0 a	7.4 a	191.1 a	423.7 a	1.3 a
	mature	1,234.4 ac	925.6 ac	143.7 a	16.6 a	9.8 a	267.5 a	321.9 a	1.0 a
Great Dismal	intermediate	4,463.4 b	692.4 ac	55.8 bc	26.0 a	39.6 b	270.2 a	194.7 ab	0.6 ab
	mature	3,208.0 bc	332.2 b	36.1 b	12.6 ab	12.2 ab	241.8 a	116.8 b	0.4 b
	young	3,349.7 bc	315.8 b	41.1 bc	15.2 ab	18.5 ab	285.2 a	87.4 b	0.4 b
Pocosin Lakes	young	4,572.6 b	509.7 bc	48.6 ab	3.4 b	3.3 a	335.8 a	81.5 b	0.5 ab
NC, Great Dismal Swamp (Bandle & Day 1985)	-	8.95 (0.34) meq/100g	0.91 (0.04) meq/100g	-	-	-	-	0.32 (0.06) meq/100g	-
Maryland (Whigham & Richardson 1988)	-	1,808 (317)	1418 (182)	6.29 (0.78) mg/g	-	-	8.0 (1.2) mg/g	-	
Florida (Collins et al. 1964)	-	791 - 2,144	115 - 404	-	-	-	-	12 - 38	-
NC, Great Dismal Swamp (Day 1982)	-	1.99%	0.15%	-	-	-	-	-	-
NC, Washington County (Dolman & Buol 1967)	-	1.60 mg/100g	0.75 mg/100g	-	-	-	-	0.12 mg/100g	-
NC, Great Dismal Swamp (US FWS 1992)	-	-	302	4,200	15	20	8640	-	6.2

Micronutrients and Heavy Metals. Micronutrients and heavy metals (Al, Cu, Fe, Mn, and Zn) were measured at all eight sites (table 3). No differences were found for Al concentrations among all study sites. The highest Al concentration in the GDS was 285.2 *u*g/g at the GDS_{yng} site. The highest concentrations of Fe and Cu found at the GDS were 55.8 *u*g/g for Fe and 0.6 *u*g/g for Cu. The range of Zn and Mn concentrations were 3.4 to 26.0 *u*g/g for Zn and 3.3 to 39.6 *u*g/g for Mn.

Groundwater Nutrients

Nitrogen and Phosphorus. Groundwater parameters were measured at seven of the eight sites (table 4). Total P concentrations at the AR sites and NH_4-N concentrations at AR_{mat} were undetectable. The mean Total P concentration was 0.68 ± 0.02 ppm and there were no differences among concentrations in the GDS sites ($P < 0.05$). Mean inorganic P concentrations were higher ($P < 0.05$)

at the GDS sites than those at the AR sites. Nitrate and NH_4-N levels were also comparatively low at the AR sites. The highest NO_3-N concentration at the AR sites was 6.7 ppm, compared to 369.6 ppm at the GDS_{mat} site. The average groundwater NH_4-N concentration was 2.66 ± 0.94 ppm. Because of the low water table during sampling, groundwater samples were not taken at PL.

Table 4. Summary of groundwater nutrients for July 1999 on six cedar sites expressed as mean (std. dev.) or median value to a depth of 10 cm. Comparable data (age classes unknown) are shown where applicable. Sites with different letters are significantly different ($p < 0.05$, Tukey Test) for a given property.

Site or Source	Age Class	Total Phosphorus (ppm)	Inorganic Phosphorus (ppm)	Organic Phosphorus (ppm)	Nitrate (ppm)	Ammonia (ppm)
Alligator River	intermediate	-	0.03 (0.04) a	-	6.7 b	0.7 (0.0) n=2 b
	mature	-	0.04 (0.07) n=7 a	-	5.7 a	-
Great Dismal	intermediate	0.69 (0.35) n=7 a	0.47 (0.32) n=8 b	0.38 (0.20) n=7 a	257.6 b	2.17 (0.82) b
	mature	0.65 (0.11) n=7 a	0.44 (0.19) n=8 b	0.35 (0.07) n=7 a	369.6 b	2.56 (0.71) b
	young	0.70 (0.27) n=8 a	0.43 (0.27) n=8 b	0.45 (0.21) n=8 a	168.4 b	5.22 (1.93) a
Pocosin Lakes	young	-	-	-	-	-
New Jersey (Ehrenfeld & Schneider 1991)	-	14.4 (3.9) ug/L	-	-	-	39 (2.7) ug/L
NC Pocosins (Walbridge & Richardson 1991)	-	-	-	-	0 - 22 ueq/L	0 - 90 ueq/L
NC, North Central Coastal Plain (Brinson et al. 1981)	-	0.57 mg/L	-	-	-	0.18 mg/L

DISCUSSION

Soil Physical Properties

The range of pH values measured in our sites (3.3 to 4.0) was close to the pH of 3.4 that Bandle and Day (1985) found in the GDS, but generally lower than most other studies, especially 5.3 in Maryland (Whigham and Richardson 1988), 4.8 to 5.0 in Mississippi (Eleuterius and Jones 1972), and 6.6 to 7.5 in Florida (Collins et al. 1964). Golet and Lowry (1987) found that cedar maximum growth rates in Rhode Island were higher at sites with a pH above 4.0. When pH is lowered, P complexes into forms unavailable to plants (Day 1982). Aluminum and iron become more soluble and therefore limit phosphorus availability (Lucas and Davis 1961). Lower pH can also lead to decreased microbial activity, which can effect decomposition rates (Lucas and Davis 1961). Thus, growth of cedar in Virginia and North Carolina may be inhibited by low soil pH.

Mean soil organic matter content was 93.0% in GDS, while Bandle and Day (1985), also working in GDS, reported a mean organic matter content of 84.6%. These values are somewhat higher than the 59.4% organic matter content that Whigham and Richardson (1988) reported for cedar stands in Maryland. Soil organic matter content did not appear to influence soil bulk density among study sites. While organic matter content only ranged from 93.0 to 97.5%, mean soil bulk densities ranged from 0.08 to 0.244 g/cm^3. Zhu and Ehrenfeld (1999) found slightly lower bulk density mean values ranging from 0.05 to 0.07 g/cm^3 in cedar stands in New Jersey.

Saturated soils are common in cedar swamps, which typically occur on deep peats that are saturated to the surface for long durations during the growing season (Atkinson et al. This Volume[a]). The mean soil saturation level at all sites was 48.5 ± 8.8%. The AR_{int} site had the highest soil saturation level of 87.1%, similar to a cedar stand in Maryland (83.3 ± 1.2%) (Whigham and Richardson 1988). Saturated or waterlogged soils result in a reduced uptake of soil nutrients by trees because root systems are confined to a shallower absorption zone (Ralston and Richter 1980). Poor soil aeration also restricts root respiratory processes thereby reducing the rate of nutrient uptake, thus the uptake of nutrients may be inhibited at the AR sites.

Soil Nutrients

Nitrogen and Phosphorus. Concentrations were highest at GDS_{int} for both total N (1.77 ± 0.16%) and total P (0.352%). Total N concentrations ranged from 1.39 ± 0.20% to 1.76 ± 0.15% and total P concentrations ranged from 0.022% to 0.327% at the remaining sites. Day (1982) reported that N and P accumulate in the soils of most GDS communities. Wharton et al. (1982) suggest that N and P are mobilized when pH rises, which supports why the lowest N and P concentrations were found at the site where pH was highest. Acidic conditions lead to a low level of P availability (Bollard and Butler 1966). The average extractable P from all the study sites was 259.7 ppm, falling within the range found in soils of the same region. Extractable P values found elsewhere in the coastal plain of North Carolina varied somewhat, from 1.68 mg/g to 3.62 mg/1,000 cm^3 (Dolman and Buol 1967, Ralston and Richter 1980). Total P was 0.08% in Maryland cedar stands (Whigham and Richardson 1988), which was about half of the average total P determined in this study (0.16%). Brinson et al. (1981), in a study of N and P in riverine wetland forests of the north central coastal plain of North Carolina, found the groundwater had a total P value of 0.57 mg/L, compared to the 0.68 ppm average at GDS. Phosphorus availability typically limits plant growth in pocosin soils (Woodwell 1958, MacCarthy and Davey 1976, Wilbur and Christensen 1983, Simms 1987). Gomez and Day (1982) suggested that compared to upland forests, all GDS communities appeared to be nutrient-poor. However, P concentrations found at GDS are much higher than P concentrations at PL and AR, suggesting that P could be deficient and a limiting nutrient at GDS sites.

The total N concentration trend among the three refuges was GDS>AR>PL. The mean total N value from all sites combined was 1.577% (range 1.39% to 1.77%), which is comparable to the 1.59% mean found in Maryland cedar stands (Whigham and Richardson 1988). The range of total N values determined is only slightly lower than the 16.2 to 23.6 g/kg range found by Zhu and Ehrenfeld (1999) in cedar sites in New Jersey. North Carolina (Washington County) and Virginia (GDS) sites in close proximity to the study sites had total N values of 1.22% (Day 1982) and 1.40% (Dolman and Buol 1967), respectively.

High water tables and high soil saturation levels, such as those measured in AR sites, can reduce extractable N in peat soils (Gore and Urquhart 1966). However soil saturation at PL was about half that of AR and the lowest total N, NO_3-N, and NH_4-N concentrations were at PL. Ralston and Richter (1980) reported that pocosin soils of the North Carolina coastal plain exhibited a mean NH_4-N concentration of only 13.4 mg/1000 cm^3, while other cedar stands had NH_4-N levels ranging from 6.1 mg/kg (Zhu and Ehrenfeld 1999) to 66.7 *u*g/g (Whigham and Richardson 1988). Pocosin Lakes had the lowest soil NO_3-N concentration at 2.9 ppm, however this value was similar to cedar soil NO_3-N values ranging from 0.1 to 3.0 mg/kg reported in New Jersey (Zhu and Ehrenfeld 1999).

The leaching of both organic and inorganic N is increased by drainage (Paavilainen and Paivanen 1995). The PL site burned in the last 10 years, which can cause reduced nutrient availability after the first growing season (Wilbur and Christensen 1983, Walbridge 1989). Gomez and Day (1982) noted that the nutrient content of leaf fall indicated possible lower levels of N in cedar stands.

Other Macronutrients. The Mg concentration range in this study was 315.8 - 925.6 *u*g/g. A slightly lower Mg concentration range (115 - 404 ppm) was found in a Florida cedar stand (Collins et al. 1964), while a higher range (1,418 ± 182 *u*g/g) was found in a Maryland cedar site (Whigham and Richardson 1988). Another recorded Mg concentration in the GDS was 302 ppm (USFWS 1992), just below the 315.8 *u*g/g measured at GDS_{yng}. Pocosin Lakes had the highest pH of all sites, and also had the lowest K concentration. The cedar sites in this study had much higher concentrations of K than other wetlands studied in the region (Bandle and Day 1985, Collins et al. 1964, Dolman and Buol 1967). Gomez and Day (1982) also found differences between cedar and the other communities for K in litter fall of the GDS.

Calcium concentrations among this study ranged from 809.7 *u*g/g at AR_{int} to 4,572.6 *u*g/g at PL. A cedar stand in Florida had a similar soil Ca range, from 791 to 2,144 ppm (Collins et al. 1964), despite having several other substrate conditions that were very different from those found in our stands. Available Ca is deficient in highly acidic soils (Bollard and Butler 1966, Kramer and Kozloski 1979, Maas 1969, Sutcliff 1962), however in the presence of high pH estuarine water, as in the cedar stands of Maryland, Whigham and Richardson (1988) determined that cedar tissues were accumulating comparatively high levels of Ca. In a litter nutrient study in the GDS, Gomez and Day (1982) found that deposition of Ca in leaf fall was below that reported in the Okefenokee Swamp, and Bandle and Day (1985) noted that Ca is not readily available in soils of the GDS.

Micronutrients and Heavy Metals. Little comparable data in the literature was found for concentrations of micronutrients and heavy metals in cedar swamps. The highest concentrations of Fe found at the GDS were 55.8 *u*g/g. Whigham and Richardson (1988) found the soil Fe concentration of a cedar stand to be 6.29 ± 0.78 mg/g. There was no difference in the concentrations of Al among all study sites. The highest Al concentration in the GDS was 285.2 *u*g/g (GDS_{yng}). Zinc and Mn concentrations in a survey of contaminants in the GDS (15 and 20 ppm respectively) were almost exactly in the middle of the ranges determined in this study (3.4 - 26.0 *u*g/g [Zn] and 3.3 - 39.6 *u*g/g [Mn]) (USFWS 1992). However, because of the distance involved (> 8 km), it is unlikely that the results in this study were affected by any possible contaminant source referenced in the survey.

Groundwater Nutrients

Nitrate values in this study ranged from 5.7 ppm to 369.6 ppm. Mean groundwater NH_4-N concentrations ranged from 0.7 ± 0.0 ppm to 5.22 ± 1.93 ppm. Other groundwater NH_4-N concentrations from the region were 0.18 mg/L (Brinson et al. 1981) and 0 to 90 *u*eq/L (Walbridge and Richardson 1991). Mean groundwater total P concentrations ranged from 0.65 ± 0.11 ppm to 0.70 ± 0.27 ppm. Groundwater total P in cedar stands of New Jersey was found to be 14.4 ± 3.9 ug/L (Ehrenfeld and Schneider 1991), while riverine wetland forests of the North Carolina coastal plain had a total P concentration of 0.57 mg/L (Brinson et al. 1981).

Hydrologic Impacts

Both the GDS and AR sites contained ditches and canals for drainage purposes, which allowed comparison of hydrologic influences on substrate quality (tables 1 through 4). The AR sites generally were higher in soil moisture, percent saturation, and organic matter content, while the GDS sites had higher soil bulk densities, which supported the notion that GDS stands were drained more effectively than AR stands.

In drained sites, the organic matter in the soil becomes oxidized. (Lilly) 1981 reported that ditched peatlands in eastern North Carolina had been oxidized to the point that the soil was reclassified as mineral soil. Organic matter in GDS sites was slightly lower than in AR sites, probably due in part to the suspected higher decomposition rates. Nutrients are also leached by drainage, especially N (Paavilainen and Paivanen 1995). As nutrients are leached, they become less available to plants or may be exported from sites through ditches and canals.

Despite these factors favoring nutrient losses, the GDS averaged higher concentrations of soil total N, total P, Ca, Mn, and groundwater NO_3-N. The GDS is located immediately east of the Suffolk scarp and receives surface runoff from adjacent upland forests, agricultural lands, and from adjacent swamps, including Pocosin, Cypress, Moss, Adam’s, Taylor, Duke, Corapeake, and Folly Swamps. This surface inflow into the GDS may provide nutrients that offset nutrient losses resulting from the ditches and canals. The AR is located further east in the coastal plain than the GDS and does not receive significant surface runoff. It receives surface flow from the Albemarle Sound during times of high water via the Alligator River (Atkinson et al. This Volume[a]).

CONCLUSION

Few regional generalizations were evident concerning the soil biochemistry of cedar swamps. Variation existed among the six study sites in North Carolina and Virginia, as 27 of the 29 parameters measured were different. The greatest differences were detected for pH, calcium, nitrate, and organic matter content, and were due in part to landscape position and the effectiveness of ditches and canals, which greatly influence hydrology. Soil saturation and the low soil pH were might also influence biochemical processes and nutrient availability. Most data fell within published ranges from cedar stands in other states. Physical property and nutrient content values among all cedar stands with available data reveal that cedar can successfully tolerate a wide range of substrate types.

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LITERATURE CITED

Atkinson, R. B., J. W. DeBerry, D. T. Loomis, E.R. Crawford, and R. T. Belcher. This Volume[a]. Water tables in Atlantic white cedar swamps: implications for restoration.

Atkinson, R.B., T.E. Morgan, D.A. Brown, and R.T. Belcher. This Volume[b]. The role of historical inquiry in the restoration of Atlantic white cedar swamps.

Bandle, B. J. and F. P. Day. 1985. Influences of species, season and soil on foliar macronutrients in the Great Dismal Swamp. Bulletin of the Torrey Botanical Club 112(2):146-157.

Beck, M. A. 1993. Sequential extraction of inorganic and organic phosphorus pools. (unpublished).

Bollard, E. G. and G. W. Butler. 1966. Mineral nutrition of plants. Ann. Rev. Plant Physiology 17: 77-112.

Brinson, M. M., H. D. Bradshaw, and E. S. Kane. 1981. Nitrogen cycling and assimilative capacity of nitrogen and phosphorus by riverine wetland forests. Water Resources Research Institute of the University of North Carolina.

Collins, E. A., C. D. Monk, and R. H. Spielman. 1964. White-cedar stands in northern Florida. Quarterly Journal of the Florida Academy of Science 27(2):107-110.

Clewell, A. F. and D. B. Ward. 1987. White cedar in Florida and along the northern gulf coast. Pages 69-82. *In* A. D. Laderman, ed. Atlantic white cedar wetlands. Westview Press, Boulder, CO.

Day, F. P. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63(3):670-678.

Day, F. P. and C. V. Dabel. 1978. Phytomass budgets for the Dismal Swamp Ecosystem. Virginia Journal of Science 29:220-224.

Diamond, D. 1995. Orthophosphate in soils. Lachat Instruments. QuickChem method 10-115-01-1-A.

Dolman, J. D. and S. W. Buol. 1967. A study of organic soils (Histosols) in the tidewater region of North Carolina. North Carolina Agricultural Experiment Station. Tech Bul. No. 181.

Donohoe, S. J. and S. E. Heckindorn. 1996. Laboratory procedures: Virginia Tech soil testing and plant analysis laboratory. Publication 452-881.

Ehrenfeld, J. G. and J. P. Schneider. 1991. *Chamaecyparis thyoides* wetlands and suburbanization: effects on hydrology, water quality and plant community composition. Journal of Applied Ecology 28:467-490.

Eleuterius, L. N. and S. B. Jones. 1972. A Phytosociological study of white-cedar in Mississippi. Castanea 37:67-74.

Golet, F. C. and D. J. Lowry. 1987. Water regimes and tree growth in Rhode Island Atlantic white cedar swamps. Pages 91-110. *In* A. D. Laderman, ed. Atlantic white cedar wetlands. Westview Press, Boulder, CO.

Gomez, M. M. and F. P. Day. 1982. Litter nutrient content and production in the Great Dismal Swamp. American Journal of Botany 69:1314-1321.

Gore, A. J. P. and C. Urquhart. 1966. The effects of waterlogging on the growth of *Molina caerulea* and *Eriphorum vaginatum*. Journal of Ecology 54: 617-634.

Karam, A. 1993. Chemical properties of organic soils. Pages 461-463. *In* M. R. Carter, ed. Soil Sampling and Methods of Analysis. Canadian Society of Soil Science, Lewis Publishers.

Kramer, P. J. and T. T. Koslowski. 1979. Physiology of woody plants. Academic Press, New York.

Laderman, A. D. (ed.) 1987. Atlantic white cedar wetlands. Westview Press, Boulder, CO.

Loach, K. 1968. Relations between soil nutrients and vegetation in wet-heaths. Journal of Ecology 56: 117-127.

Lowry, D. 1984. Water regimes and vegetation of Rhode Island forested wetlands. Master’s Thesis. University of Rhode Island, Kingston.

Maas, E. V. 1969. Calcium uptake by excised roots and interactions with alkali cations. Plant Physiology 44: 985-989.

MacCarthy, R. and C. B. Davey. 1976. Nutritional problems of *Pinus taeda* L. (Loblolly Pine) growing on pososin soil. Soil Science Society America Journal 40: 582-585.

Miller, Robert O. 1997. Lab proficiency testing program. Version 4. Western States.

Murphy, J. and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27: 31-36.

National Soil Survey Center. 2000. Primary characterization data for Washington County, NC. USDA Natural Resources Conservation Service, Soil Survey Laboratory. http://vmhost.cdp.state.ne.us/~nslsoil/soil.html

Noss, R. F., E. T. LaRoe, and J. M. Scott. 1995. Endangered ecosystems in the United States: A preliminary assessment of loss and degradation. National Biological Service, Biological report 28:58.

Ralston, C. W. and D. D. Richter. 1980. Identification of lower coastal plain sites of low soil fertility. Southern Journal of Applied Forestry 4:84-88.

Schlesinger, W. H. 1978. Community structure, dynamics and nutrient cycling in the Okefenokee cypress swamp-forest. Ecological Monographs 48: 46-65.

Simms, E. L. 1987. The effect of nitrogen and phosphorus addition on the growth, reproduction, and nutrient dynamics of two ericaceous shrubs. Oecologia 71: 541-547.

Soil Conservation Service. 1974. Great Dismal Swamp and Dismal Swamp Canal study: report on ascertainment of soil types and agricultural information. Northeast Technical Service Center, Upper Darby, Pennsylvania.

Sutcliff, J. F. 1962. Mineral salts absorption in plants. Pergamon Press, New York.

Terry, T. A. and J. H. Hughes. 1975. The effects of intensive management on planted loblolly pine (*Pinus taeda* L.) growth on poorly drained soils of the Atlantic coastal plain. Pages 351-378. *In* B. Bernier and C.H. Wegnet, ed. Forest soils and forest land management. Proceedings of the North American Forest Soils Conference 4th, 1973.

U. S. Environmental Protection Agency. 1979. Methods of chemical analysis of water and wastes. Environmental Protection Agency, Cincinnati, OH, USA.

U. S. Fish and Wildlife Service. 1992. A survey of contaminants in the Great Dismal Swamp National Wildlife Refuge, Virginia. Environmental Contaminants Branch, U. S. Fish and Wildlife Service, White Marsh, VA.

Walbridge, M.R. 1989. Increased P availability to in situ anion-exchange resins following fire in North Carolina coastal plain pocosin. Poster presented at Tenth Annual Meeting, Society of Wetland Scientists, May 30-June 2, 1989, Orlando, FL.

Walbridge, M. R. and C. J. Richardson. 1991. Water quality of pocosins and associated wetlands of the Carolina Coastal Plain. Wetlands 11: 417-439.

Western States 1997. Method S-9.3. Method S-1.0 to 1.7.

Wharton, C. H., W. M. Kitchens, E. C. Pendleton, and T. W. Sipe. 1982. The ecology of bottomland hardwood swamps of the Southeast: a community profile. U. S. Fish and Wildlife Service, Biological Services Program, Washington, D.C. FWS/OBS-81/37.

Whigham, D. F. and C. J. Richardson. 1988. Soil and plant chemistry of an Atlantic white cedar wetland on the Inner Coastal Plain of Maryland. Canadian Journal of Botany 66:568-576.

Wilbur, R. B. and N. L. Christensen. 1983. Effect of fire on nutrient availability in a North Carolina coastal plain pocosin. American Naturalist 110: 54-61.

Woodwell, G. M. 1958. Factors controlling growth of pond pine seedlings in organic soils of the Carolinas. Ecological Monographs 28: 219-236.

Zhu, W. X. and J. G. Ehrenfeld. 1999. Nitrogen mineralization and nitrification in suburban and undeveloped Atlantic white cedar wetlands. Journal of Environmental Quality 28:523-52

RECONSTRUCTION OF AN OLD GROWTH ATLANTIC WHITE CEDAR STAND IN THE HACKENSACK MEADOWLANDS OF NEW JERSEY: PRELIMINARY RESULTS

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Abstract: A portion of an ancient old growth Atlantic white cedar stand cut and buried years ago, was unearthed in 1998 on a mitigation site near Mill Creek in the Hackensack Meadowlands of New Jersey. During 1999, before the site was flooded, a 1.7 ha study area in the 10.9 ha stump field was sampled and mapped. The position, size, and condition of 625 stumps and 20 downed logs were measured. Sections of 20 stumps and logs were cut and 3 sections of the most recent growth from two stumps and a downed log were radiocarbon dated. Preliminary results show an average stump diameter of 55.26 cm with a diameter distribution suggesting an even-aged stand with disjunct higher diameter groupings in the 140 - 150 and 150 - 160 cm classes. While detailed dendrochronological and cross-dating analyses are yet to be done, initial aging of the cross-sections showed the six completely intact (pith, all rings and outer bark present) sections range in age from 215 to 505 years old. The 505-year-old section was removed from a 1.5 m long intact downed log retrieved from dredging a deep channel around the stump field. The other 5 complete sections varied from 215 to 294 years old. The remaining 14 cross-sections had various degrees of intactness ranging from near complete to significant sections rotted or missing and those sections ranged in age from 151 to 329 years old. Radiocarbon dating shows that the oldest cedar arrived in this area of the Meadowlands sometime between the 8th and 10th centuries, much earlier than the previous literature had suggested. The date that the trees were cut is more uncertain and requires further study. Spatial analyses and use of the Stand Visualization System were also applied to the data to study and reconstruct the stand. From the data collected, a picture emerges of an old growth cedar stand probably harvested when the trees averaged 257 years old with some larger (probably dead) individuals from a previous stand which were more than 500 years in age.

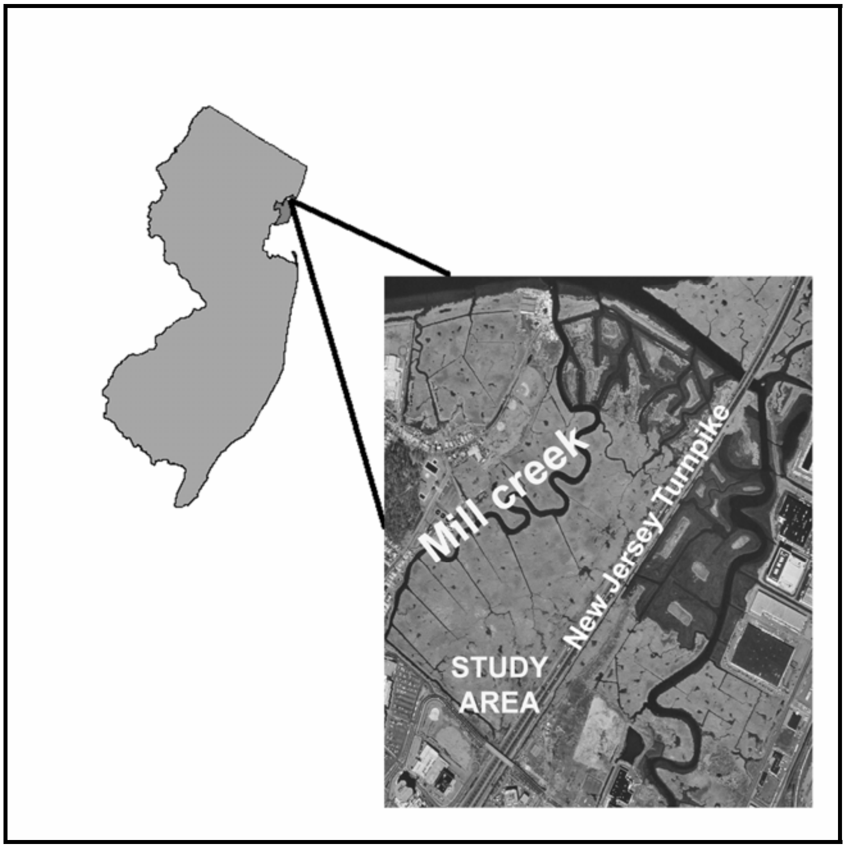
Key Words: old growth, radiocarbon dating, stand reconstruction, dendrochronology, diameter distribution

INTRODUCTION

The exploitation of Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), since European settlement has caused extirpation or serious reduction in acreage throughout its range. For centuries, exploitation has left virtually no cedar forest standing beyond their rotation age. Consequently only a few scattered individuals have been reported that show the potential upper age limit of the species. Gifford (1895) relates an 1868 report from Dennisville, New Jersey that a Dr. Beesley found a 1.8 m diameter cedar stump possessing 1080 rings, and another stump under it from the previous forest that was aged to be 500 years old. Heusser (1949a) counted 304 rings on a stump encountered in the same area studied here from digging in 1947-48 construction of the New Jersey Turnpike. No stand of cedar showing its potential to become old growth has been previously measured.

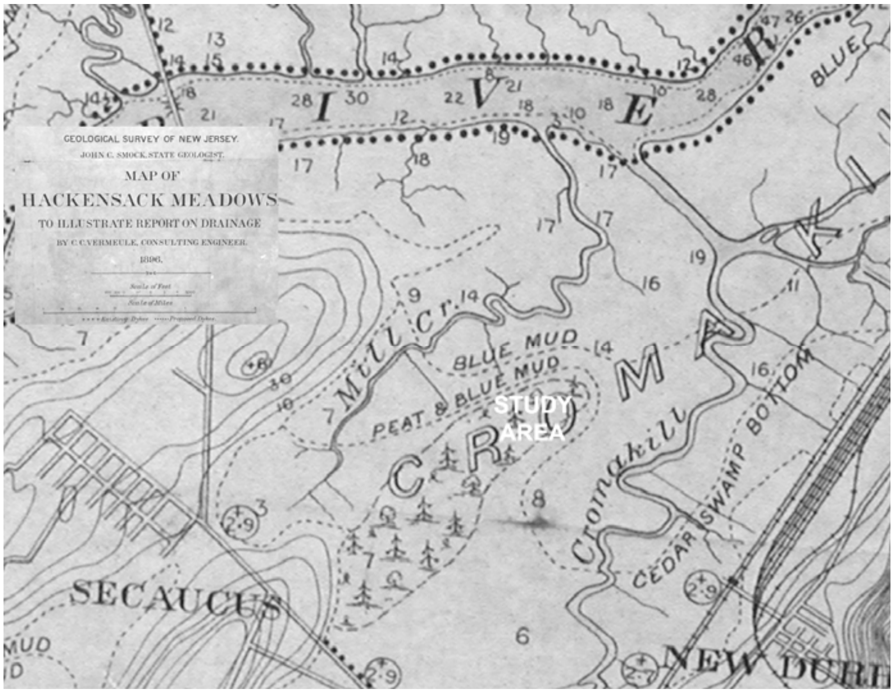
The Hackensack Meadowlands District consists of about 7086 ha. The 1.7 ha study area is part of a 46.1 ha wetlands mitigation site project initiated by the Hackensack Meadowlands Development Commission (HMDC). The study area is located next to the eastern spur of the New Jersey Turnpike (figure 1). This area is a part of the much larger historic New Durham swamp. Pleistocene ice retreated 8,000 - 10,000 years ago in this area and the postglacial fresh water Lake Hackensack eventually drained. Basal ligneous peat formation started above varved clays of old Lake Hackensack about 2610 years ago (Carmichael 1980).

Figure 1. Location of the study area in New Jersey. Inset is a 1995 aerial photo with the study area showing Mill Creek and New Jersey Turnpike (New Jersey Department of Environmental Protection).



Heusser (1963) found the deepest peat in the Secaucus swamp formed 2025 years ago BP (± 300 years). Using pollen analysis and macrofossils, Heusser (1949b) determined from peat deposits the probable vegetation succession in the Secaucus area after Lake Hackensack drained. Heusser found black ash (*Fraxinus nigra*), alder (*Alnus* sp.), and birch (*Betula* sp.) to be among the first tree species, although he speculates fir (*Abies* sp.) forests could have preceded, but peat-forming conditions weren't present. Black spruce (*Picea mariana*) and tamarack (*Larix laricina*) followed and persisted from the 1st century to the late 19th century. Cedar presence is difficult to determine since its pollen is thin-walled and apertulate (Rue and Traverse 1997). In peat cores taken by Rue and Traverse (1997) in the Hackensack Meadowlands, *Cupressaecae* pollen was detected but in such extremely low frequencies that statistical testing was not performed. Heusser (1949a) found cedar macrofossils only at or near the surface at Secaucus and he suggested cedar only became numerous in the 1400s. Cedar may have occupied as much as one-third of the Hackensack Meadowlands before rising sea level, fire, peat subsidence, diking, ditching, and severe cutting dwindled its numbers (Sipple 1971-72). The Mill Creek cedar were often referred to as part of the New Durham Swamp. Torrey et al. (1819) reported a number of species he found unique to the New Durham Swamp. According to Torrey's measurements, the New Durham Swamp was then between 22.05 and 33.1 ha. Vermeule's (1896) map (figure 2) shows live cedar and "cedar bottom" in our study area and that the swamp extended far beyond the area excavated and exposed during the mitigation. Vermeule estimated live cedar present in 6% of the Meadowlands (511 ha) in the last years of the nineteenth century; while cedar bottom occupied 21% (1653 ha). Neither Torrey nor Vermeule commented on the size of the cedar or whether there was cutting prior to their surveys. Waksman (1942) hypothesized that peat subsidence due to ditching was more than a meter in the 1800s, thus exacerbating flooding and salt-water intrusion that helped to create the cedar bottoms mapped by Vermeule. Heusser reports in 1949 that the last cedar in Secaucus died in 1935. Attempts to reintroduce cedar to the Meadowlands have all failed due to muskrat herbivory and salt-water intrusion (Pierson 1999).

Figure 2. Section of 1896 Vermeule map showing the New Durham swamp. Our study area seems to be in a northern area mapped as being live cedar and cedar bottom forest. Photo of Vermeule map by Brett Bragin.



The stump forest in this study was uncovered in 1998 while workers were dredging the site for a 46.1 ha tidal marshland mitigation project (figure 3). The objectives of this preliminary study were to study the spatial, diameter, and age structures of this ancient cedar stand and to estimate when the trees lived using radiocarbon dating.

METHODS

Figure 3. Photo showing part of the cedar stump field exposed at the beginning of the mitigation process. Photograph by Robert Williams

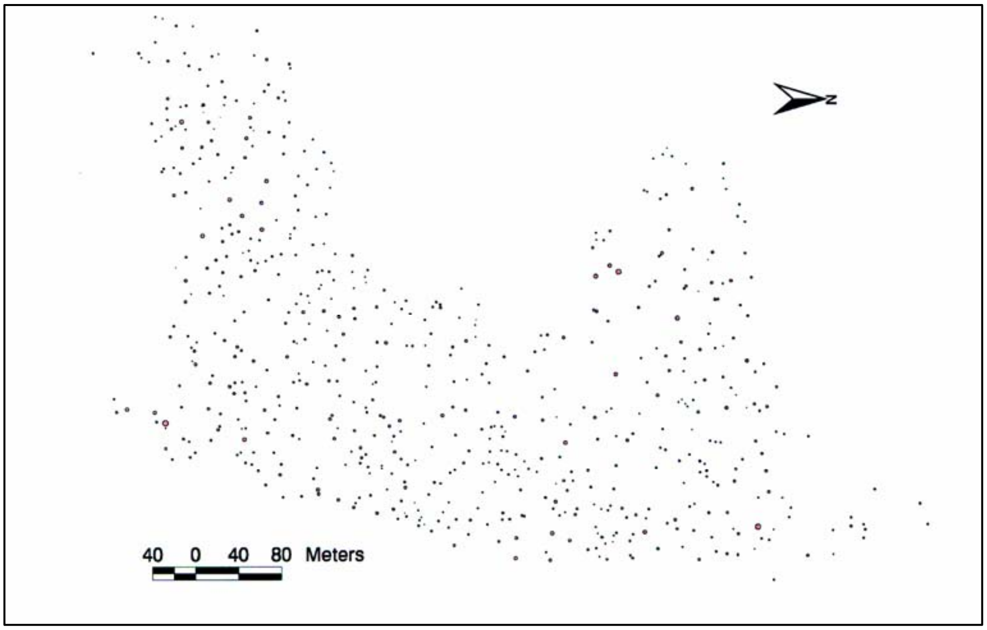
The study area was sampled during the late summer and fall of 1999, while work was proceeding with impoundment construction and other mitigation work. A theodolite was established at a fixed point along the edge of the exposed stump field. All cedar stumps within a 1.7 ha area were cleaned of soil and vegetation with wire brushes. The small and long axis diameters of each stump and exposed log was measured and the general condition (presence of rot, missing sections, fire scars, etc.) of stumps was recorded. A surveying rod was then placed over the estimated center of the stump and polar coordinates taken (angle, stadia and center rod measurements). Twenty cross-sections approximately 6 cm thick were taken from stumps and logs in the mapped and surrounding stump field, and edges of the excavated channel, which surrounded the stump field and was excavated to a depth of 1.65 m below sea level.

The cross-sections were brought back to the lab where they were cleaned, dried, and sanded to 600 grit. Three or four independent observers aged each cross-section, but the presence of false rings prevented precise age determinations. Six cross-sections were complete, possessing both a pith and intact outer bark with no wood missing in between. All other sections were missing some parts (though another six cross sections were nearly complete lacking probably no more than 10 rings based on previous intact growth). Three pieces (containing an average of 30 rings to meet minimum weight requirements) from two stumps and one downed log were radiocarbon dated by Beta Analytic (Beta Analytic 2000) and cellulose extraction was performed on the downed log sample. The downed log was 1 of 90 logs and 110 stumps taken from channel excavation during the present mitigation (Geo-Con 2000).

Data from the stump position survey were converted into Cartesian coordinates using an EXCEL (Microsoft 2000) program. The data were then input into ARCVIEW (ESRI 2000) along with average stump diameters to produce a scaled map of the stumps in the study area. The Stand Visualization System was used to produce a visual representation of how the stand looked when it was alive. Spatial statistics were performed on the data to quantitatively determine if spatial patterns existed. The spatial distribution of all stumps was analyzed calculating Ripley’s K(d) for 100 random simulations. Ripley’s K(d) can be used to test for overall pattern departures from a Poisson process and has been used to look for spatial patterns in forests (Moeur 1993). Spatial analyses were done using CrimeStat (Levine 2000), and ARCVIEW scripts. All other data analyses used SAS (SAS Institute 2000).

RESULTS

Figure 4. Scaled map of stump field surveyed showing relative position and size of stumps. A total of 625 stumps were found and measured within the area.

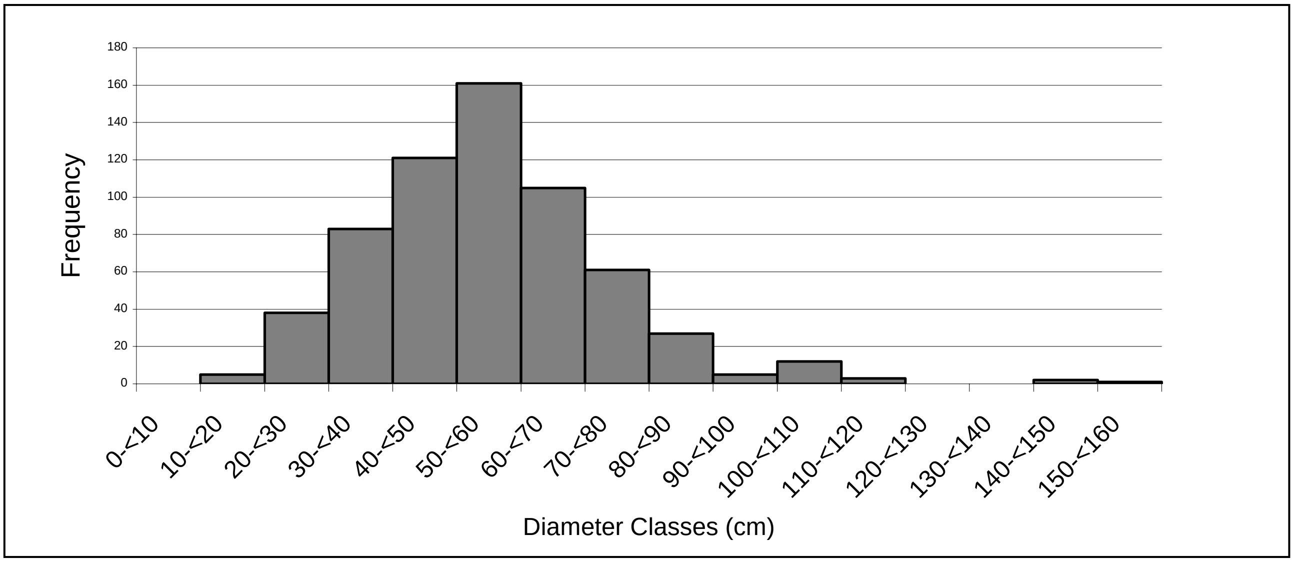


We surveyed 1.7 ha of the approximately 10.9 ha stump field (figure 4). During mitigation, the site elevation was lowered from approximately 0.90m above mean sea level to present sea level (where the stand was found). Vermeule's (1896) map lacked elevations and tide information for the study area but noted that the immediate surrounding area was about 0.87 m (2.9 ft) above sea level. Vermeule's map legend stated mean high tides of 0.72 m (2.4 ft) and mean low tides of 0.72 m (2.4 ft) below sea level; therefore, average high tide at Mill Creek cedar bog was exposed by about 0.15 m (0.5 ft). In our study area, Vermeule's map estimated about 2.1 meters (7 ft) of "mud below the natural meadow surface".

The height and uniformity of the stumps, as well as the scarcity of logs, strongly suggested that most of the trees were cut. A total of 625 stumps and 20 downed logs, all of which were cedar, were measured and their positions recorded in our surveyed area (figure 5). Cedar density was 367.6 stems per ha, assuming all stumps were live but excluding downed logs. The mode for stump diameters was 50 - 60 cm (figure 6). No fire scars were found on any stumps in the field or any log cross-sections.

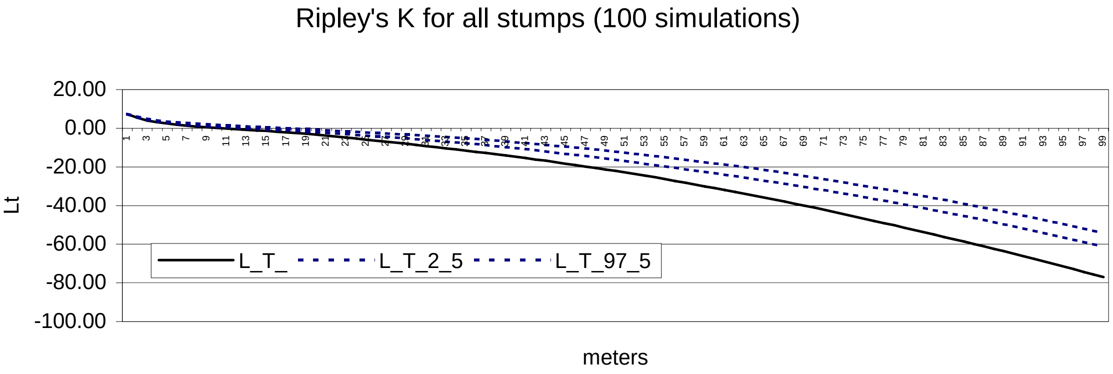
Figure 5. Aerial photograph showing most of the stump field portion of the finished mitigation area as of 2000. The study area that was mapped is outlined and the channel is below and to the left.

Figure 6. Frequency distribution of sampled stump diameter classes (n=625).



The Ripley analysis detected negative values across all distances and suggested a non-random distribution that tended towards a regular (or 'repulsing') pattern (figure 7). The grand mean nearest neighbor distance was 2.98 m for all stumps. Only six trees or logs had all rings intact and the average diameter growth for these sections was 0.266 cm per year for an average of 257.8 years. One of the largest trees, number 226, exhibited a diameter growth of 0.320 cm per year for 237+ years (table 1).

Figure 7. Ripley's K simulation for all stumps. A 95% confidence limit (dotted lines) for a random distribution of stumps is represented by the LT2.5 and LT 97.5 lines. The solid line (LT) represents the stump field data.



Radiocarbon dating estimated that the oldest log, which was excavated from the channel, was 630 ± 40 years BP (table 2). A stand map was generated based on data from Korstian and Brush (1931) and measurements of live trees (with site index assumed to be 50) using Stand Visualization System (version 3.31, 1999, by Robert McGaughey, US Forest Service Pacific Northwest Experiment Station) (figure 8).

Table 1. Ages of sampled sections (not cross-dated).

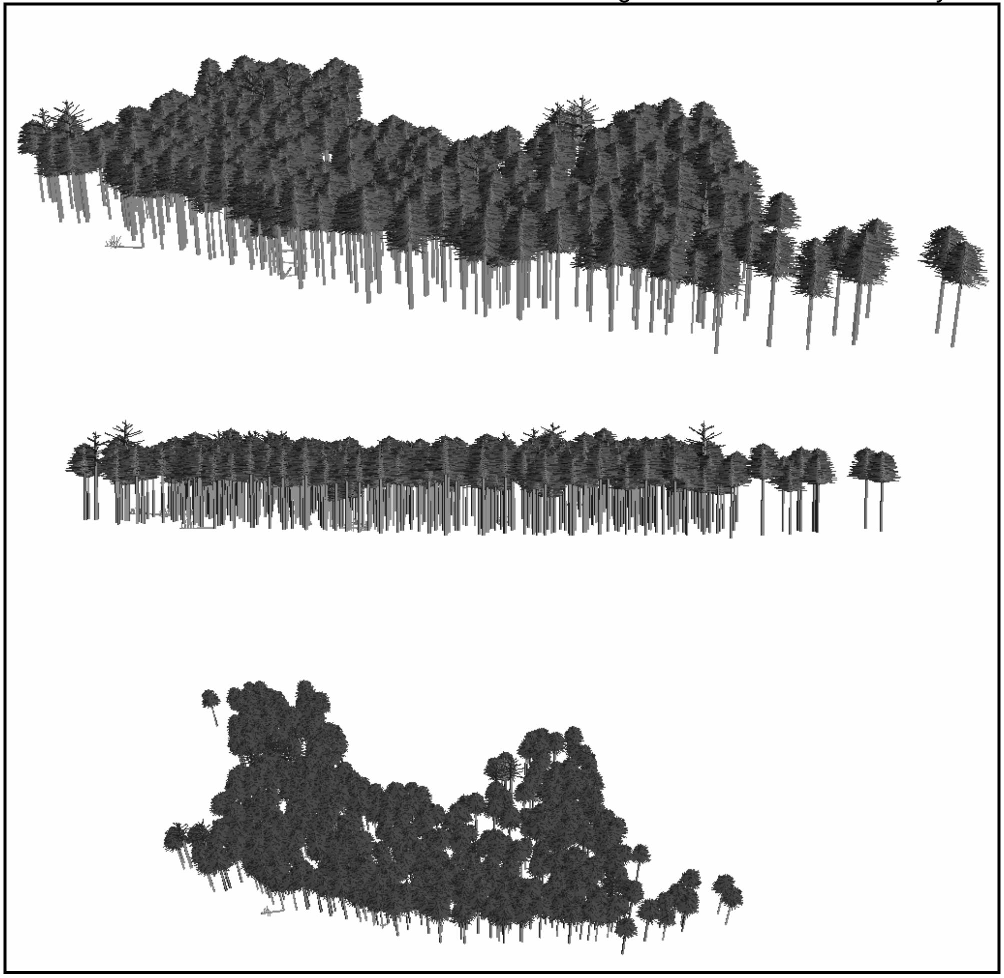
Description/condition	Average diameter (cm)	Rings counted	Average diameter growth (cm/year)
sample from stump field, intact (all rings present)	61.3	294	0.208
sample from stump field, intact	91	290	0.314
sample from stump field, intact	71	220	0.323
sample number 503 from mapped stump field, intact	102.8	270	0.381
sample number 100 from mapped stump field, intact	43.8	215	0.204
downed log dredged from channel, section from 0.3m above roots, log was 1.5 m long, intact	86.5	505	0.171
downed log from channel, section was 1. 22 m above root collar, log was 12.19 m long, pith but no outer bark	67.6	267	0.253**
sample number 34 from mapped stump field, nearly intact: few pith rings missing	74.9	248+	0.294 **
sample number 121 from mapped stump field, nearly intact: few pith rings missing	114.5	285+	0.402**
sample number 46 from mapped stump field, nearly intact: few pith rings missing	49.53	281+	0.175**
sample number 93 from mapped stump field, nearly intact: few pith rings missing	44.4	252+	0.144**
sample number 140 from mapped stump field, nearly intact: few pith rings missing	46.2	237+	0.195**
sample from stump field, pith but no outer bark	56.2	327+	0.295**
sample from stump field, pith and outer bark missing	40.5	329+	0.123**
sample number 397 from mapped stump field: pith missing	45.1	161+	0.280**
sample from stump field, pith and outer bark missing	29.4	151+	0.195 **
sample from stump field, pith and outer bark missing	61.8	181+	0.341**
sample number 96 from mapped stump field, center section missing, outer bark intact	102.8	218	0.244**
sample number 149 from mapped stump field: center and outer bark missing	86.6	206+	0.204**
sample number 226 from mapped stump field: large center missing but small outer bark area intact.	149.8	237+	0.320**

** Sample growth estimated using surviving wood

Table 2. Description of material sampled and results from radiocarbon dating. All samples were of wood from behind intact bark. Samples from mapped stump 503 and downed log are about 0.3 m above ground or root level. The sample used from stump 226 was about 0.2 m above ground level.

Description	Age (uncalibrated) estimate	95% probability calibrated
stump 503, looked cut and similar to most stumps in the field	240 ± 50 years BP	1510 to 1595 AD (Cal BP 435 to 360), 1615 to 1680 AD (Cal BP 330 to 265), 1740 to 1805 AD (Cal BP 215 to 140), or 1930 to 1950 AD (Cal BP 25 to 0)
stump 226, only outer section intact, more disintegrated than other stumps	430 ± 50 years BP	1415 to 1520 AD (Cal BP 535 to 430) or 1575 to 1625 AD (Cal BP 375 to 325)
downed 1.52 m log dredged from channel; cellulose extraction method used on sample	630 ± 40 years BP	1290 to 1410 AD (Cal BP 660 to 540)

Figure 8. Three views of the reconstructed Mill Creek stand using the Stand Visualization System (SVS).



The diameter distribution was similar to those for even-aged forest stands except there were no trees in the 120- to <140-cm class (figure 6). One of those three largest stumps was number 226 (149.8 cm). Not much of this tree remained, although it was in the best condition of the 3 largest trees. Though approximately half the stump section was missing, 237 rings were counted, suggesting that the tree was considerably older. The root section possessed 184 rings but was also incomplete. Using the ages of the five intact stump field cross-sections, we estimated that the average stump age was 257 years at the time the trees were cut. Using the average growth rate of those intact trees (0.266 cm/yr) we estimated the age of the missing section of tree 226 and thus its total age to be about 514 years old.

DISCUSSION

Based on the Ripley's K analysis, the spatial pattern of all the stumps was fairly evenly distributed, which is common among old growth stands resulting from intra- and interspecific competition (Ford and Diggle 1981, Kenkel 1988, Moeur 1993). The density we calculated was a minimum estimate since some stumps were so badly damaged that we could have missed a few when mapping the area. The unusual shape or perimeter of the sample area is due, on all but one side (south), to the line of sight from the theodolite, which was impeded by the dyke system and/or New Jersey Turnpike (figure 5).

Based on radiocarbon dating, the downed log from the channel (which had the most accurate radiocarbon dating) was the earliest to die (between 1290 and 1410 AD, 95% probability). This coupled with its age of 505 years indicated that cedar occurred in the Meadowlands between 785 and 905 AD, which is centuries sooner than Heusser (1949b) had estimated. As for the other two samples, their times of death were more recent and hence the accuracy was reduced. Tree 226 may have also existed at that early date and died roughly in the same time period as the downed log (1415 to 1520 AD). Alternatively, tree 226 may have died over a century later, between 1575 and 1625 AD.

Tree 503 had 4 possible time periods it was cut, but given the timing of exploitation of cedar by Europeans, and the maps by Torrey and Vermeule, it is improbable that the stand was cut before the 1700s. Yet another interpretation is that the stand was at least partially cut between 1740 and 1805 and regrew prior to the work of Torrey (1819) and Vermeule (1897). Based on the Vermuele map, it appears that our study area was on the northwestern edge of the New Durham Swamp and had both live and dead cedar during the 1890s, so it is also possible that this section of the cedar stand never regenerated after cutting or was dying because of salt-water intrusion. It is very doubtful that the 1930 - 1950 estimated date for tree 503 is accurate since Harshberger and Burns (1919) spoke of only a few cedar remaining in the Meadowlands near Newark. Also Heusser (1949b) reported the last of the cedar in Secaucus died in the 1930s long after the primary exploitation and changing environment had reduced cedar to a few isolated groups or individuals. Therefore, we concluded the site was a more than 250 year old, old growth cedar stand that was cut in the 18th or 19th century. We further conclude that the stand contained individual trees that were more than 500 years old, which persisted as dead or living remnants of an earlier stand.

We hope to further resolve these timing issues with data being collected by Ms. Nicole Davi who works in the Tree-ring Laboratory of Lamont-Doherty Earth Observatory of Columbia University. Ms Davi is sampling large living cedar (over two centuries old) in New Jersey and New York that may yield information on cedar response to the environment. Her data may facilitate cross-dating and establishment of a larger chronology for our Mill Creek data. We continue to sift through historical documents for further narratives on the New Durham Swamp.

Work continues with the data and more recent samples. A Velmex tree ring machine is being used to measure tree ring widths on all sections. We are using J2X software with additional dendrochronological software (i.e., COFECHA). We hope future dendrochronological and statistical analyses of the sections will yield more accurate ages and insights into the environmental conditions and dynamics of the stand and environs.

CONCLUSION

There is much left to the imagination that we will never know concerning this old growth stand. But what is obvious is that stands of cedar can reach ages far in excess of what humans have allowed or documented since their discovery and utilization of this resource. There were probably at least one and possibly two or more old growth stands that contained cedar that lived and died on the Mill Creek site prior to its cutting.

The cedar at Hackensack Meadowlands completely disappeared a few decades ago though our data suggests that it initially occurred between the eighth and tenth centuries. A number of attempts have been made to restore cedar to the Hackensack Meadowlands, however rising sea level, muskrats, and the effects of years of human impact have prevented return of the species. It is hoped that information generated at this site will aid in that effort.

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LITERATURE CITED

Beta Analytic, Inc. 2000. 4985 S.W. 74th Court Miami, FL, USA 33155

Carmichael, D. P. 1980. A record of environmental change during recent millennia in the Hackensack tidal marsh, New Jersey. Bull. Torrey Botan. Club 107(4): 514-524.

Diggle, P.J. 1983. Statistical Analysis of Spatial Point Patterns. Academic Press. London. 148 pages.

ESRI. 2000. ARCVIEW. 380 New York Street. Redlands, CA 92373-8100.

Ford, E.D. and P.J. Diggle. 1981. Competition for light in a plant monoculture modeled as a spatial stochastic process. Ann. Bot. 48:481-500.

Geo-Con. 2000. Information obtained from Geo-Con records who did the mitigation. Geo-Con Northeastern Office. 116 Burrs Road, Suite A. Westampton, NJ 08060.

Gifford, J. 1895. A Preliminary Report on the Forest Conditions of South Jersey. In: Annual Report of the State Geologist for the Year 1894. John L. Murphy Publishing Company. Trenton, New Jersey.

Harshberger, J.W. and V.G. Burns. 1919. The vegetation of the Hackensack Meadowlands: a typical American fen. Trans. Wagner Free Inst. Science. Phil.: 9. Part I.

Heusser, C.J. 1949a. A note on buried cedar logs at Seacacus, New Jersey. Torreya, Bull. Torrey Bot. Club 76: 305-306.

Heusser, C.J. 1949b. History of an estuarine bog at Seacacus, New Jersey. Torreya, Bull. Torrey Bot. Club 76:385-406.

Kenkel, N.C. 1988. Pattern of self-thinning in Jack pine: Testing the random mortality hypothesis. Ecology 69: 1017-1024.

Korstian C.F. and W.D. Brush. 1931. Southern white cedar. USDA Forest Service Technical Bulletin 251. Washington, D.C. 75pp.

Levine, N. CrimeStat: A Spatial Statistics Program for the Analysis of Crime Incident Location. Ned Levine & Associates, Houston, TX, and the National Institute of Justice, Washington, DC. May 2000.

EXCEL. 2000. Software. Microsoft Corporation. Washington. USA.

Moeur, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. Forest Science 39(4): 756-775.

Pierson, G. 2000. Retired State forester for New Jersey. Interview.

Rue, D. J. and A. Traverse. 1997. Pollen analysis of the Hackensack, New Jersey Meadowlands tidal marsh. Northeastern Geol. and Environ. Sci. 19 (3): 211-215.

SAS Institute Inc. 2000. SAS Campus Drive, Cary, North Carolina 27513, USA.

Sipple, W.S. 1971-72. The past and present flora and vegetation of the Hackensack Meadows. Bartonia 41: 4-56.

Torrey, J.C., W. Eddy, and D.V. Knevels. 1819. A catalogue of plants growing spontaneously within thirty miles of the City of New York. Albany.

Waksman, S.A. 1942. The peats of New Jersey and their utilization. Part I. Bull. 55A Geol. Ser. N.J. Dept. Conserv. & Dev.

Vermeule, C.C. 1896. Map of the Hackensack Meadowlands to Illustrate Report on Drainage. In The Annual Report to the State Geologist for the Year 1896. MacCrellish and Quigley, Trenton, New Jersey.

WATER TABLES IN ATLANTIC WHITE CEDAR SWAMPS: IMPLICATIONS FOR RESTORATION

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Abstract: In Atlantic white cedar (cedar) swamps, hydrology may influence critical components of swamp restoration and management including regeneration and growth of cedar, primary production, decomposition, as well as peat accumulation and global carbon storage. However, very few studies have characterized water table dynamics of cedar swamps. In this study we seek to quantify various aspects of hydrology for comparison with other cedar stands and for future evaluation of cedar regeneration and carbon dynamics. Study sites included young wetland compensation sites (two sites) and two replicates of three age classes of cedar (mature, intermediate and young) in national wildlife refuges including Alligator River (AR), Great Dismal Swamp (DS), and Pocosin Lakes (PL) in southeastern Virginia and northeastern North Carolina. Nine wells, including one continuously recording well, were installed along permanently established transects at each of the eight sites in summer 1998. Depth to water table was measured twice daily in continuously recording wells and twice monthly in manually read wells, which were regressed to yield continuous depth to water table estimates for all wells. Mean 1999 growing season depth to water table, ranked from shallowest to deepest, were AR-Mature, AR-Intermediate, DS-Young, DS-Mature, compensation site 2, compensation site 1, DS-Intermediate, and PL-Young. Water table variability was lowest in the AR sites, but precipitation influenced depth to water table at all sites. Palmer Drought Severity Index was positively correlated with depth to water table in all sites and was more strongly correlated with depth to water table than was potential evapotransporation. Although only one year of data is presented, the compensation sites, DS-I, DS-M, and PL-Y exhibited a mean depth to water table deeper for the given climatic conditions than that reported for most cedar stands.

Key Words: water table, cedar establishment, compensation, hydrophyte, climate, carbon storage, precipitation, evapotransporation

INTRODUCTION

Hydrology has been identified as the single most important factor influencing forested wetland processes including primary production and decomposition (Conner et al. 1981, Wharton et al. 1982, Brinson et al. 1984). Day and Megonigal (2000) summarized several years of primary production and decomposition studies in the DS and reported that hydrology, primarily depth to water table, could be used to distinguish between Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), swamps and three other major forest community types.

The depth to water table in cedar swamps is thought to influence critical components of restoration, including cedar regeneration (Korstian 1924, Harrison et al. This Volume), cedar growth (Harrison et al. This Volume), and carbon storage functions (Whitehead and Oaks 1979). Natural regeneration and growth of cedar are important for management of stands in national wildlife refuges and compensation sites where self-maintenance (cedar establishment after fire or harvest) is preferred over replanting and herbicide applications. Carbon storage is important for natural stand self-maintenance because cedar swamps require peat for hydrologic modulation (Whitehead and Oaks 1979) and for protection of the seed bank during fire (Korstian 1924). Carbon storage is also relevant to global greenhouse gas concerns since cedar swamp productivity and decomposition are influenced by water tables that may change cedar swamps from a carbon sink to a source (Whitehead and Oaks 1979). Pre-colonial era peat accumulation rates in the DS were approximately 33.3 cm per 1,000 yr, but ditching reversed the trend (Whitehead and Oaks 1979).

Cedar occupies a fairly narrow range of hydrologic conditions and the life cycle exhibits an interaction with peat. Although it is an obligate wetland species (Reed 1988), cedar is physiologically intolerant of prolonged inundation, at least during the seedling stage (Akerman 1923, Brown and Atkinson 1999). When water tables rise, often as a result of damming by roads (Van Druten and Eagle 2000) or deep peat burns (Akerman 1923, Korstian 1924), cedar stands may revert to high or low pocosin (Schafale and Weakley 1990, Sharitz and Gibbons 1982). Conversely, deeper water tables, which may result from ditching, favor aggressive competitors such as red maple (*Acer rubrum* L.), which is known to invade cedar stands and is the most commonly associated tree in New Jersey (Laderman 1989, Stoltzfus and Good 1990) and Virginia (Kearney 1901, Laderman 1989, Shacochis et al. This Volume, Loomis et al. This Volume).

Carbon storage in cedar swamps and other peatlands occurs when primary production rates exceed respiration rates. Ponding and shallow water tables slow decomposition, thus lowering respiration rates and favoring peat accumulation, which further increases water-holding capacity and modulates water table fluctuations (Whitehead and Oaks 1979). Wetland hydrology may be altered by ditching associated with various activities such as road construction, suburbanization (Ehrenfeld and Schneider 1991), and with silviculture and agriculture (Osbon 1919, Lilly 1981[a]). Where effective ditching has occurred, water tables drop and duration of saturation is shortened. As a result, peat oxidation is facilitated and Whitehead and Oaks (1979) suggested that approximately 1 m has been lost to oxidation in 125 years since construction of Dismal Swamp Canal (DSC). In time, oxidation in drained peatlands may proceed until a mineral soil results (Lilly 1981[b]). Furthermore, the risk of rapid peat loss by fire is increased.

Climate data including Palmer Drought Severity Index (PDSI) and potential evapotransporation (PET, a maximum estimate of water loss that assumes that soil moisture is never limited) may be correlated with the depth to water table and may improve predictions of cedar swamp hydrology. In this study, PDSI and PET data were compared to continuously recorded depth to water tables at eight ditched cedar stands in northeastern North Carolina and southeastern Virginia. The purpose of this paper is to contribute to the database regarding the range of depths to water table that support cedar swamps.

SITE DESCRIPTION

Cedar swamps in North Carolina and Virginia are primarily located on the Pamlico Terrace east of the Suffolk Scarp. Of the eight sites in this study, three are in the Great Dismal Swamp National Wildlife Refuge (DS) and two are wetland compensation sites (Comp 1 and Comp 2) that are adjacent to the refuge and within the historic acreage of DS. Drainage from the DS flows to both Chesapeake Bay and to Albemarle Sound. Sites in the current study lie in the southern half of DS and once may have drained south to Albemarle Sound. The flow of all five sites is currently channeled to the DSC, which is known to exhibit alternating northerly and southerly flow, influenced primarily by locks at Deep Creek, Virginia on the Southern Branch of the Elizabeth River and South Mills, North Carolina on the Pasquotank River.

The DSC and Lake Drummond appear to be a significant component of DS hydrology. Chartered in 1787 by the Commonwealth of Virginia and in 1790 by the State of North Carolina, the 35 km-long DSC was completed in 1805. A 5 km-long canal called the Feeder Ditch connects Lake Drummond to DSC. Prior to 1977, the water level in Lake Drummond was allowed to drop to a low level as water was released through a spillway on the Feeder Ditch in order to maintain proper navigable depths in the DSC. The importance of Lake Drummond to DS hydrology was noted in a report by Norfolk District, US Army Corps of Engineers (1986), which stated that the lake is the focal point for management and control of water in the refuge. With federal passage of Public Law 93-402 in August 1974, management of water levels in Lake Drummond was required to place the highest priority on refuge ecology. In order to meet the Congressional mandate, spillway gates were closed whenever the lake level dropped from 5.2 m to 4.8 m.

The three remaining sites were in national wildlife refuges within the Albemarle Sound watershed including Alligator River (AR) and Pocosin Lakes (PL). Two sites were in AR in Dare County, which was bounded by the Alligator River to the west, Albemarle Sound and Croatan Sound to the north and east, and Pamlico Sound and Hyde County to the south. One site was within PL in Tyrell County, 3 km south of Pocosin Lake.

Ditches were within 200 to 300 m of all wells in the current study. Duever (1988) stated that canals (and presumably ditches) can lower water tables and increase outflow rates following rain events. Ditches at the DS sites were connected to Lake Drummond and, via the Feeder Ditch, to the DSC and Albemarle Sound, North Carolina. In contrast, the hydrologic gradient at AR sites appeared to be reversible, at times bringing water into the site from the Alligator River.

The eight sites primarily occurred on histosols (table 1) and consisted of four young sites including the two compensation sites, a 2-yr old salvage clearcut in DS, and a 4-yr post-fire site at

Table 1. Soil organic matter for the 8 study sites. Estimates based on 9 samples taken at a depth of 10 cm in July 1999 (from Thompson et al. This Volume).

	AR-I	AR-M	Comp 1	Comp 2	DS-Y	DS-I	DS-M	PL-Y
OM (%)	97.51	97.01	32.12	20.17	92.96	93.03	92.96	94.95

PL. The compensation sites and the burned site at PL were formerly cedar swamps that had been drained for agriculture in the 1900s and were planted in cedar in 1996. The salvage clearcut in DS occurred in 1996 and was allowed to regenerate naturally. The four remaining sites represented two more age classes including an intermediate (22 - 35 years) stand and a mature (65 – 75 years) stand in both AR and DS. All four sites had been commercially logged and allowed to regenerate naturally. Vegetation relative importance values (RIV) were calculated as the sum of relative dominance, relative density, and relative frequency (divided by 3) by Shacochis et al. (This Volume). Cedar had the highest RIV in DS-M (61.3), while the lowest RIV occurred in DS-I (41.0). The intermediate and mature sites at both refuges occurred on Pungo Muck with Belhaven inclusions (Tant 1992, Moore 1996). The wetland compensation sites were described as “made land” in the Norfolk County Soil Survey (Francis 1959).

METHODS

Multiple permanent transects were established at each site and nine wells were placed at 100-m intervals (wells were positioned at random and arranged as dictated by site dimensions). Wells were constructed of schedule 40 PVC with machined 0.025 cm slotting and were inserted to a soil depth of approximately 1.0 m and were back-filled with industrial grade sand to prevent clogging (U.S. Army Corps of Engineers 1993). A remote data system (RDS) continuous recording well was inserted in a central point at each site, and a manually read well was inserted in all eight remaining points per site. The RDS wells recorded depth to water table twice daily and data were downloaded to PC. Data were recorded from September 1997 to April 2000, but only 1999 data, which were most complete, were used in this study. Elevations were estimated with a laser level and stadium rods at each well and within the adjacent vegetation sampling plots, including 3 estimates per 1.0-m^2 plot in young sites and 6 estimates per 10.0-m^2 plot in intermediate and mature sites. Topography is relevant in this study because it interacts with water tables to influence actual soil moisture at each site.

Estimated starting and ending dates for the growing season were based on 10.2 ^{o}C (28 ^{o}F) air temperature thresholds at a frequency of 5 years in 10 and were obtained from NRCS county soil survey reports for Dare County, North Carolina and the City of Suffolk, Virginia. Precipitation data used in this study were obtained from USGS Station Lake Drummond in Great Dismal Swamp, VA [Number 02043600, Latitude 36^{o}35’42”N and Longitude 76^{o}26’23”W]. Climate data including Palmer Drought Severity Index (PDSI) and potential evapotransporation (PET) were obtained from Climate Prediction Center, NCEP, NWS, NOAA 2001.

RESULTS

Climatic Data

Long-term (more than 50 years) average annual precipitation ranged from 109.0 cm (43.3 in) at Norfolk (Francis 1959) to 133.6 cm (52.6 in) in New Holland, North Carolina obtained from Dare County Soil Survey (Tant 1992). Other estimates of average annual precipitation near the sites included 130.0 cm (51.2 in) at Wallaceton (Francis 1959) and 121.9 cm (48.0 in) at Holland, VA (Reber et al. 1981).

According to the Wallaceton-Drummond Climatological Station, since 1930, median annual precipitation was 126.0 cm (SD 24.1) per year and ranged from a high of 191.3 cm in 1982 to a low of 69.9 cm in 1965. The total for 1999 was 140.7 cm, slightly above the median (figure 1). Monthly precipitation in 1999 was below normal prior to June and above normal after June (figure 2). Precipitation during the period from February through June totaled 37.8 cm, which was 12.5 cm below the long-term average for this 5-month period (50.3 cm). Hurricanes struck the study area in September (Floyd) and October (Irene). Precipitation totaled 25.7 cm in September and 22.4 cm in October and the two-month total precipitation (47.5 cm) was the 10th highest two-month total since 1930. In our study area, the total precipitation from June through October (82.3 cm) was 33.5 cm above the mean for this 5-month period (48.8 cm) (figure 2).

The Palmer Drought Severity Index (PDSI) (Heddinghause and Sabol 1991) was used to characterize precipitation conditions during the study period. The lowest PDSI during the 1999 growing season was –2.8 (mild drought), which was recorded for the week ending July 3. The mild drought persisted for approximately 1 month, from the weeks ending June 5 to July 3. The highest PDSI, 4.7 (extreme moist spell, which is the wettest category), was recorded for the week ending October 23. PET is based on temperature, solar declination angle, and division constants such as mean latitude. The lowest PET was 0.3 and occurred on October 30. The highest, 1.7, was recorded for July 10 (Climate Prediction Center, NCEP, NWS, NOAA 2001). Both PDSI and PET were significantly correlated with depth to water table (table 2).

Figure 1. Annual precipitation totals from 1930 to 1999 from the Wallaceton-Drummond Climatological Station

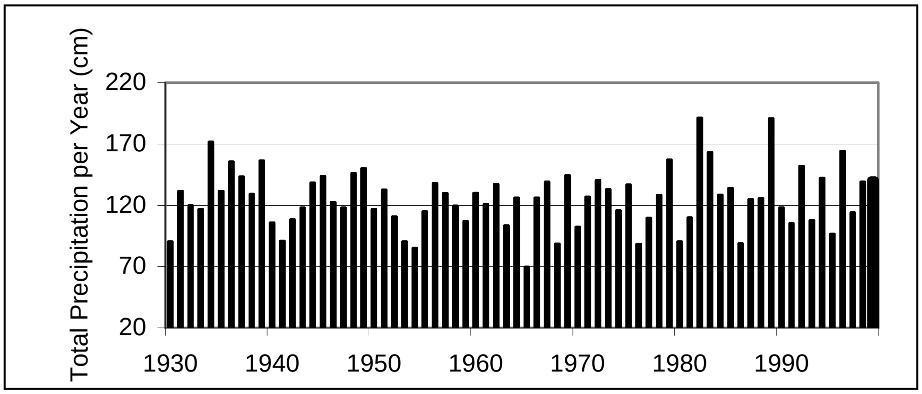

Figure 2. Monthly precipitation during 1999 and over the 70-yr period from 1930 through 1999 from Wallaceton-Drummond Climatological Station

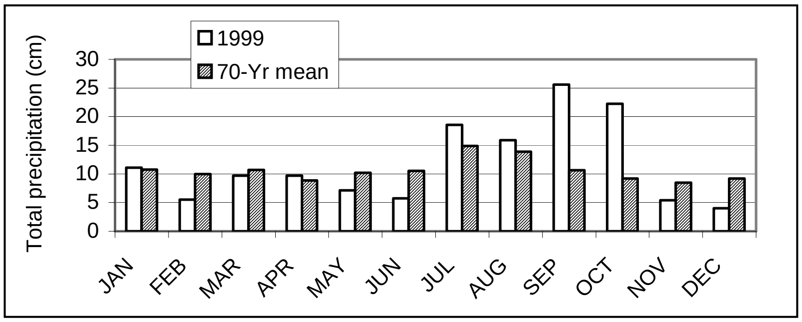

Table 2. Simple linear regressions of Palmer Drought Severity Index (PDSI) and potential evapotranspiration (PET) with depth to water table in each of the eight sites for the 1999 growing season. N = number of dates on which PDSI and PET data were available from NOAA Climate Division 1. Note that all regressions were significant, except PET at AR-I.

		AR-I	AR-M	Comp 1	Comp 2	DS-Y	DS-I	DS-M	PL-Y
PDSI	R^2	0.41	0.57	0.61	0.52	0.81	0.89	0.90	0.51
	P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	n	32	30	32	32	30	32	32	21
PET	R^2	0.03	0.28	0.50	0.40	0.64	0.59	0.58	0.52
	P	0.34	0.005	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	N	32	30	32	32	30	32	32	21

AR-I = Alligator River Intermediate, AR-M = Alligator River Mature, Comp 1 = Compensation site 1, Comp 2 = Compensation site 2, DS-Y = Dismal Swamp Young, DS-I = Dismal Swamp Intermediate, DS-M = Dismal Swamp Mature, and PL-Y = Pocosin Lakes Young.

Growing season length for Dare County is 257 d, continuing from March 13 to November 25 (Tant 1992). Growing season for Suffolk, VA is 223 d and continues from March 29 to November 7 (Reber et al. 1981). Unless stated otherwise, Suffolk growing season dates were used throughout this paper, however soil temperatures remained above 5.0 ^{o}C throughout 1999-2000 winter months (personal communication Dr. Gary Whiting).

Depth to Water Table

Median depth to water table during the 1999 growing season differed across sites (Kruskal-Wallis One-Way ANOVA on Ranks, $P < 0.001$, $n = 224$). Water table depth exceeded 30 cm for DS-I, DS-M, PL-Y (figure 3a), Comp 1, and Comp 2 (figure 3b). However, median depth to water tables for AR-I and AR-M were –3.8 and 2.1 cm, respectively (figure 3c).

The AR sites exhibited much shallower water tables and less fluctuation than the remaining sites. Depth to water table as a percentage of the growing season was calculated for all sites (table 3). The standard deviation of water table averaged 7.9 cm in the AR sites, compared to 25.2 cm for the remaining sites (figure 4).

The two compensation sites exhibited a unique topography, which resulted from their preparation for agriculture in the 1960s. Field crowns and swales, which were adjacent to ditches, were present at these two sites. RDS wells were positioned near the crown, thus actual inundation rates for most of each site were generally longer than indicated by figure 4. Inundation rate was 37.5% (SD 20.0) for Comp 1 and 41.1% (SD 27.7) for Comp 2.

Topography among the sites was influenced somewhat by recent land uses. In sites exposed to silvicultural practices (AR and DS), mound and pool topography with a range of 22 to 36 cm repeats in 4 - 6 m intervals (table 4). However, sites Comp 1, Comp 2, and PL-Y were converted to agriculture and graded, and mean range of relative elevation across field crowns were 38.4 cm (13.0), 62.1 cm (8.1), and 19.7 cm (5.2), respectively. Tire ruts were a small but persistent feature of the two compensation sites and were arranged parallel to the field crowns and were more pronounced at lower elevations. These features caused localized ponding that affected vegetation within 1.0-m^2 plots in these sites. The PL-Y site was burned by August 1997.

Figure 3a. Water levels for Pocosin Lakes and Dismal Swamp young, intermediate and mature sites and precipitation from the Wallaceton-Drummond Climatological Station.

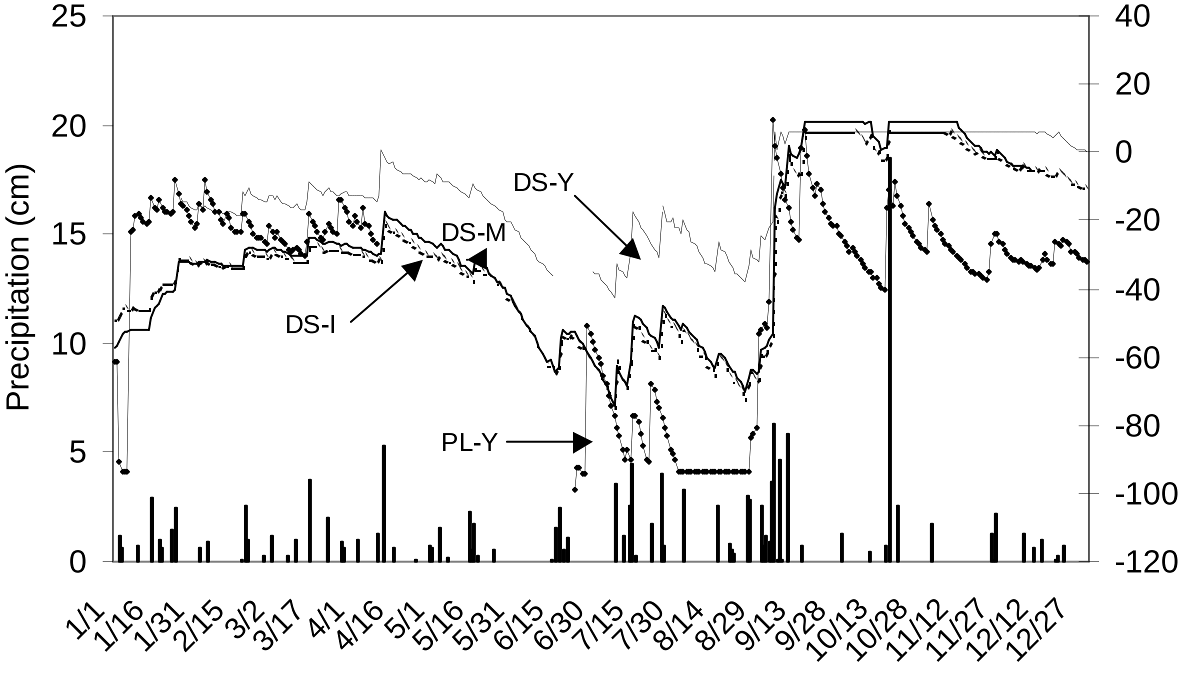

Figure 3b. Water levels for two compensation sites and precipitation from the Wallaceton-Drummond Climatological Station.

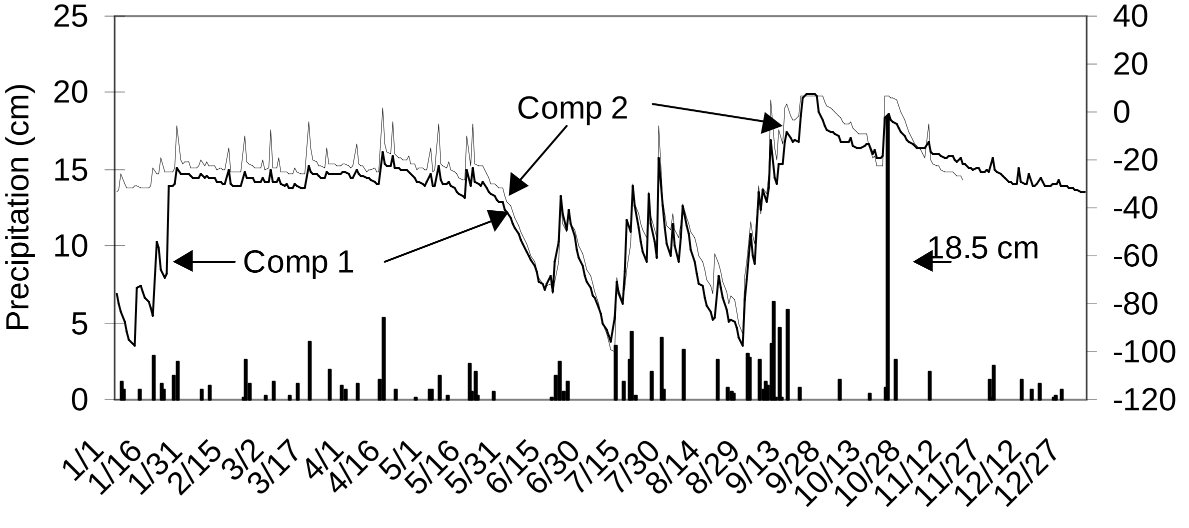

Figure 3c. Water levels for Alligator River intermediate and mature sites and precipitation from the Wallaceton-Drummond Climatological Station.

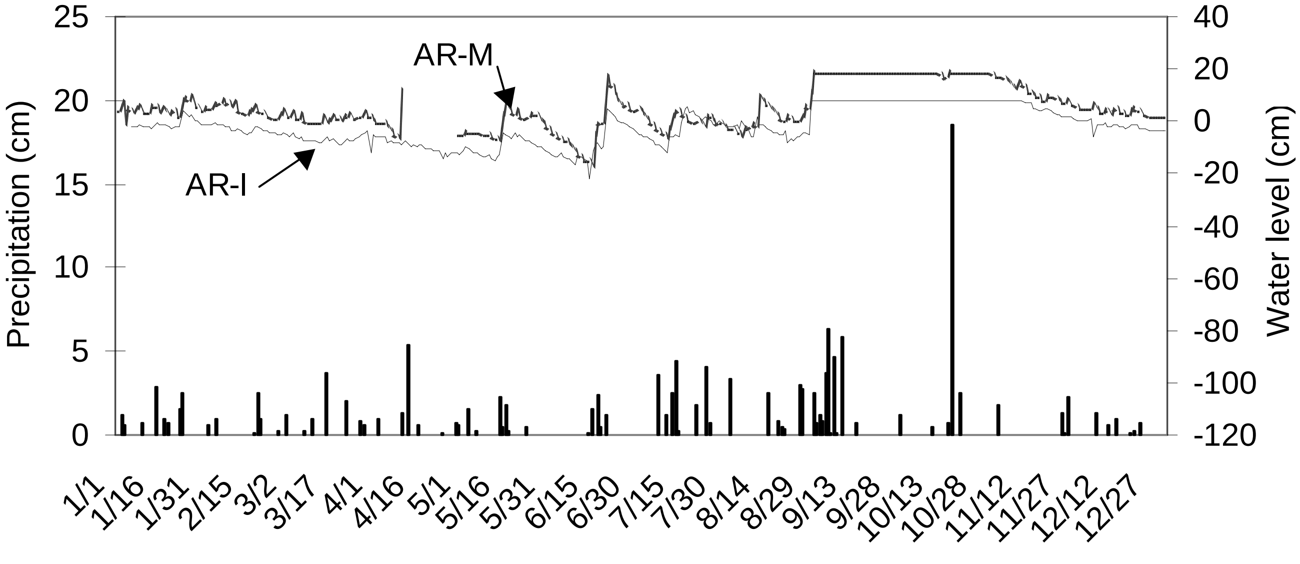

Table 3. Percentage of 1999 growing season (March 29- November 7) with water table above or below selected datum points for eight cedar swamps. Calculations based on remote data systems continuous recording wells.

	AR-I	AR-M	Comp 1[a]	Comp 2[a]	DS-Y	DS-I	DS-M	PL-Y
Inundated	37.9	62.1	2.7	10.3	31.0	21.4	24.6	2.6
WT 10 cm or farther below surface	21.4	3.9	90.2	77.7	55.7	73.7	72.8	93.4
WT 20 cm or farther below surface	0.4	0.0	71.4	68.3	38.1	71.9	68.8	80.1

[a] RDS wells were located near the highest point on each field crown. As a result, inundation rates for plots exhibit longer inundation rates than wells.

WT = depth to water table.

Figure 4. Mean depth to water table during the 1999 growing season, March 29 to November 7 (Error bars = 1 SD)

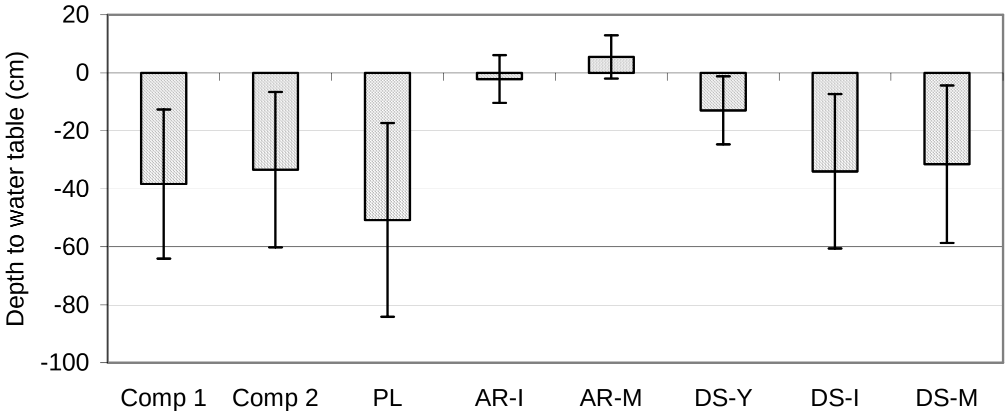

Table 4. Water table and topographic parameters for the eight sites including results of RDS and manually read well linear regressions, measures of topographic variability, and water table ranges among wells and plots. All units are cm unless otherwise indicated.

	AR-I	AR-M	Comp 1	Comp 2	DS-Y	DS-I	DS-M	PL-Y
RDS/ Manual well (R^2)	0.95	0.92	0.99	0.99	0.98	0.99	0.99	0.98
TV (deviation)[†]	12.8	7.8	na	na	na	11.3	13.8	na
TR (range of elevations)[‡]	34.1 (14.3)	23.3 (3.8)	< 3.0[§]	< 3.0[§]	21.2 (5.4)	29.3 (13.1)	36.4 (20.6)	< 3.0[§]
WT range (9 wells)[¬]	16.7	14.6	18	18.4	10.8	20.3	12.4	na
WT range (9 plots)[Π]	33.9	13.9	68.9	79.6	na	15.2	15.5	na

[†] Topographic variation measures as grand mean standard deviation for 6 estimates in each of 9 plots per site.

[‡] Topographic range measured as the highest minus the lowest elevation for each plot averaged over the 9 plots per site.

[§] plot area limited to 1-m^2

[¬] Water table range among wells is the average daily difference (maximum - minimum) in depth to water table among the 9 wells per site.

[Π] Water table range among plots is the average daily difference (maximum - minimum) in depth to water table among all plots per site.

DISCUSSION

Depth to Water Table

Seasonal trends for hydrographs in the current study were similar to those reported for cedar swamps (Golet and Lowry 1987, Laderman 1989, Reynolds et al. 1981), and were also similar to those reported for cypress swamps (Duever et al. 1975, Duever 1988) and red maple swamps. Cedar swamp water regimes are classified as seasonally flooded, which Cowardin et al. (1979) defined as “Surface water [that] is present for extended period especially early in the growing season, but is absent by the end of the season in most years. When surface water is absent, the water table is often near the land surface." However, inundation during the early growing season was only detected in the AR and DS-Y sites. The remaining sites only exhibited inundation during and after the hurricanes.

A shallow water table, similar to that measured in the AR sites, has been reported for cedar swamps. Golet and Lowry (1987) compared hydrologic signatures and precipitation among six cedar swamps for seven consecutive years in Rhode Island. They reported that surface water was present during the growing season for an average of 18% for the seven sites during the driest year (1981) and 76% in the wettest year (1979). In our study, the AR sites had the highest inundation rates (AR-I = 37.9% and AR-M = 62.1%) and the remaining sites were only inundated after the hurricanes. Water tables were almost never deeper than 20 cm below the surface at the AR sites. In contrast, the water table was below 20 cm for about 70% of the growing season in the remaining sites (except DS-Y).

Though the Rhode Island hydrology study is the most extensive, several authors have also reported shallow water tables for cedar swamps. Cedar swamps typically exhibit a mound and pool topography and Korstian (1924) reported that water ordinarily stands in pools for several consecutive months during the winter and spring. Little (1950) indicated that the water table in cedar stands ranged from 2.5 cm above the surface to a depth of 20.3 cm. In a cedar swamp in New Jersey, Reynolds et al. (1981) reported that water tables averaged 10 cm beneath the surface, and never exceeded a depth of 30 cm, including during a drought. During the mild drought in early summer of our study, water tables dropped to no more than 15 cm beneath the surface in the AR sites; however, water tables in most other sites were as deep as 100 cm during the drought.

Caution must be taken in interpreting these findings. Only one year (1999) of nearly continuous water table data and cedar swamp hydrology can vary considerably among years (Golet and Lowry 1987). However, our study of these sites continued from 1997 through 2000 and field observations of water tables generally support our findings.

Another limitation that must be considered is the general lack of information on natural cedar swamp hydrology. Few hydrologic studies have been conducted in cedar swamps and none of those studies preceded the wave of cedar swamp alteration that began in the colonial period (Lilly 1981[a], Atkinson et al. This Volume). Cedar swamp hydrology has been altered by roads, ditches, timber harvest, harvest of buried logs, and conversion to other land uses. Future studies should attempt to use tree rings to establish pre-colonial relationships between tree rings, water tables, and climate.

Indicators of Water Table Depth

PDSI were significantly correlated with water tables at all eight sites (R^2 range = 0.41 – 0.90, $p < 0.001$). Depth to water table and PDSI tended to be less correlated with wetter sites (AR, R^2 ranged from 0.41 to 0.57) than with drier sites (DS, R^2 was 0.81 and 0.90), perhaps because water tables were already shallow at AR when several of the precipitation events occurred at the end of the growing season. Thus, absolute predictions of water tables may require more data. The PET (R^2 ranged from 0.35 to 0.74) and was also correlated significantly with depth to water tables at all sites except AR-I ($R^2 = 0.03$, $p = 0.34$), however, the correlations between water table and PDSI were higher.

Implications for Vegetation Dynamics

Red maple is the most common co-dominant tree with cedar and may outcompete cedar under certain hydrologic conditions. Red maple swamps are usually drier than cedar swamps, however drainage of vast expanses of the outer coastal plain has altered hydroperiods (Lilly 1981[a]). Frost (1987) and Schafale and Weakley (1990) reported that cedar occupied a narrow hydrologic position toward the dry end of the moisture gradient and intermediate between that of deciduous swamp forests and evergreen pocosins. Lowry (1984) compared Rhode Island cedar and that State's wettest red maple swamps and found that cedar swamps had significantly shallower water tables and that surface water was present in cedar swamps for nearly twice as much of the growing season. Reynolds et al. (1981) compared water tables for a cedar swamp with that of a red maple swamp from April 1980 through May 1981, including a drought in 1980. Mean depth to water table in the cedar swamp was approximately 5 cm to 70 cm above that of the red maple swamp. Without hydrologic restoration, it appears likely that the study sites at DS and PL and portions of Comp 1 and 2 will come to be dominated by species other than cedar, including red maple.

Several authors have noted a microtopographic feature in cedar swamps (Levy and Walker 1974, Lowry 1984, Ehrenfeld 1995, Brown and Atkinson 1999). Hummock-hollow microtopography was well developed at all sites where there was no history of agricultural land use. Elevations of hummocks ranged from 21 to 36 cm above the hollow bottoms, which is similar to the average of 35 cm that Ehrenfeld (1995) reported for cedar in Lebanon State Forest, New Jersey. In that study, substrate differences were primarily correlated with ground cover, which consisted of either *Sphagnum* spp. or bare litter, and moisture content of the peat was more closely associated with Sphagnum cover than with elevation.

Field crowns and swales at compensation sites in this study exceeded the normal topographic range of cedar swamp mound and pool topography. Mylecraine et al. (This Volume) found that elevation was closely correlated with depth to water table in a planted site that was similar to Comp 1 and Comp 2. Where field crowns and swales remain, the water table depths may include a range that exceeds the ability of young cedar to survive (Mylecraine et al. This Volume, Harrison et al. This Volume).

Implications for Carbon Dynamics

The peat substrate of natural cedar swamps may exert some degree of autogenic control of water tables, resulting in shallower water tables with less fluctuation (Whitehead and Oaks 1979). Ditches tend to channel flow and conduct water through peatlands (Daniel 1981) and ditches and canals have caused the most change in hydrology in DS (Lichtler and Walker 1974). Organic matter decomposition rates are lower during long periods of saturation when compared to alternating hydroperiods, which tend to optimize decomposition (Reddy and Patrick 1975, Brinson et al. 1981). Lilly (1981[b]) worked extensively with drained peatland soils in North Carolina and has suggested that oxidation will, in time, convert any organic soil to a mineral soil.

In the current study, only AR-I and AR-M exhibited a water table shallow enough to cause saturation to the surface for most or all of the growing season. The greatest water table fluctuations were detected at the compensation sites (mean SD = 21 cm), which had the lowest organic matter content, and the lowest fluctuation was at the AR sites (mean SD = 6.0). Fluctuating water tables (SD 16.8) were also reported in the DS in 1999 (Brown and Atkinson 1999) and in 1978 (Phipps et al. 1978). Furthermore, low water tables, which are now common in portions of DS, PL, and portions of both compensation sites, could result in catastrophic peat loss during fire. Oaks and Coch (1973) reported a loss of 2 m (6 feet) of peat in a fire within DS in 1930.

The DS lies on the Atlantic Coastal Plain in Virginia and North Carolina. It is bounded on the west by the Suffolk Scarp, which has an altitude of between 18 m and 21 m (60 and 70 feet). At present, the eastern border of DS is actually within the Deep Creek Swale, which was the site of construction of the DSC around 1800. There is a west to east dip of approximately 2 cm per 100 m (1 foot per mile) across the DS, ranging from an elevation of 7.6 m (25 feet) at the toe of the Suffolk Scarp to 4.6 m (15 feet) at the Deep Creek Swale. The DS-I and DS-M sites were far more effectively drained than the AR sites, which range from 0 to 3 m above sea level; however, many other variables influence the effectiveness of ditches (Lilly 1981[b]) and cause changes in water table depth within peatlands (Daniel 1981).

It is important to state that some portions of DS have actually become wetter over time, often as a result of impounding via ditch castings (Shaler 1890, Whitehead and Oaks 1979). The complex network of ditches in DS may necessitate a stand by stand management approach.

Conclusion

Hydrology is a driving factor in wetlands in general and in important processes within cedar swamps. The three hydrologic conditions that exert the greatest influence on successful cedar regeneration may be (1) depth to water table at time of fire, (2) mean depth to water table during the growing season, and (3) fluctuation in depth to water table. In this study, only two sites (AR-I and AR-M) exhibited hydrologic conditions that are clearly similar to naturally occurring cedar swamps, based on the available literature.

Water table depth is of critical importance to cedar regeneration (Akerman 1923, Frost 1987, Korstian 1924, and Little 1950) and to oxidation of organic carbon (Lilly 1981[b]), which is globally significant given the extent of peatlands in southeastern Virginia and Northeastern North Carolina (Richardson 1981). Ditches can facilitate discharge of water from peatlands, resulting in lower water tables. Management of both regeneration of cedar and accumulation of peat should consider modification of ditches in some portions of DS, PL, and the compensation sites. Field crowns should be graded down in future restoration efforts on agricultural lands.

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LITERATURE CITED

Akerman, A. 1923. The white cedar of the Dismal Swamp. VA. For. Publ. 30:1-21.

Atkinson, R.B., T. E. Morgan, D.A. Brown, and R.T. Belcher. This Volume. The role of historical inquiry in the restoration of Atlantic white cedar swamps.

Bridgham, S., Faulkner, S. and C.J. Richardson. 1991. Steel rod oxidation as a hydrologic Indicator in wetland soils. Soil. Sci. Soc. Am. J., 55:856-861.

Brinson, M.M., A.E. Lugo, and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Annual Rev. Ecol. Systematics,12:123-161.

Brinson, M.M., H.D. Bradshaw, and E.S. Kane. 1984. Nutrient assimilative capacity of an alluvial floodplain swamp. Journal of Applied Ecology, 21: 1041-1057.

Brown, D.A. and R.B. Atkinson. 1999. Assessing the survivability and growth of Atlantic white cedar [*Chamaecyparis thyoides* (L.) B.S.P.] in the Great Dismal Swamp National Wildlife Refuge. pp 1-7 IN T. Shear and K.O. Summerville (Eds.) Atlantic White Cedar: Ecology and Management Symposium. USDA Forest Service GTR SRS-27.

Conner, W.H., J.G. Gosselink, R.T. Parrondo. 1981. Comparison of the vegetation of three Louisiana swamps sites with different flooding regimes. American Journal of Botany, 68: 320-331.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Service, Washington, D.C., USA.

Daniel, C.C. 1981. Hydrology, geology, and soils of pocosins. Pp. 69-108 IN (C.J. Richardson ed.) Pocosin Wetlands: An Integrated Analysis of Coastal Plain Freshwater Bogs in North Carolina. Hutchinson Ross Publ. Co., Stroudsburg, PA.

Day, F.P. and J.P. Megonigal. 2000. Plant organic matter dynamics in the Dismal Swamp. PP. 51-57 IN R.K. Rose (Ed.) The Natural History of the Great Dismal Swamp. Omni Press, Madison, WI.

Duever, M.J. 1988. Hydrologic processes for model of freshwater wetlands, IN Mitsch, W.J., M. Straskraba, and S.E. Jorgensen (eds.) Wetland Modeling. Elsevier, New York.

Duever, J.J., J.E. Carlson, and L.S. Riopelle. 1975. Ecosystem analysis at Corkscrew Swamp. pp 627-725 IN H.T. Odum, K.C. Ewel, J.W. Ordway, and M.K. Johnston (eds.) Cypress Wetlands for Water Mangaement, Recycling, and Conservation. Second Annual Report to National Science Foundation and Rockefeller Foundation. Center for Wetlands, University of Florida, Gainesville, FL.

Ehrenfeld, J.G. 1995. Microsite differences in surface substrate characteristics in Chamaecyparis swamps of the New Jersey Pinelands. Wetlands, 15:183-189.

Ehrenfeld, J.G. and J.P. Schneider. 1991. *Chamaecyparis thyoides* wetlands and suburbanization: effects on hydrology, water quality and plant community composition. J. Applied Ecology, 28:467-490.

Francis, H.E. 1959. Soil Survey for Norfolk County, Virginia. US Dept of Agriculture, Soil Conservation Service.

Frost, C.C. 1987. Historical overview of Atlantic white cedar in the Carolinas. Pp 257-264 in A.D. Laderman (ed.) Atlantic white cedar wetlands. Westview Press, Boulder, CO.

Golet, F.C. and D.J. Lowry. 1987. Water regimes and tree growth in Rhode Island Atlantic white cedar swamps IN A. Laderman (ed.) Atlantic White Cedar Wetlands. Westview Press, Boulder CO. (out of press)

Harrison, J. and R.B. Atkinson. This Volume. Effects of water table on the survival of and growth in two young, planted Atlantic white cedar sites.

Heddinghause, T.R. and P. Sabol. 1991. A review of the Palmer drought severity index and where do we go from here? Proceedings of the Seventh Conference on Applied Climatology. American Meteorological Society, Boston, Massachusetts.

Kearney, T. H. 1901. Report on a botanical survey of the Dismal Swamp region. Contrib. U.S. Natl. Herb., 5:321-550.

Korstian, C.F. 1924. Natural regeneration of southern white cedar. Ecology, 5:188-191.

Laderman, A.D. 1989. The ecology of Atlantic white cedar wetlands: a community profile. USFWS Biological Report 85 (7.21).

Levy, G.F. and S.W. Walker. 1974. Forest dynamics in the Dismal Swamp of Virginia. Pp 101-126 IN Kirk, P.W. (Ed.) The Great Dismal Swamp. University of Virginia Press, Charlottesville, VA.

Lichtler, W.F. and P.N. Walker. 1974. Hydrology of the Dismal Swamp: Virginia and North Carolina. U.S.G.S. 200 West Grace Street, Richmond, VA

Lilly, J.P. 1981[a]. A history of swampland development in North Carolina. Pp 20-39 IN C.J. Richardson (ed.) Pocosin Wetlands. Hutchinson Ross Publ. Co., Stroudsburg, PA. 1981.

Lilly, J.P. 1981[b]. The blackland soils of North Carolina: Their characteristics and management. Technical Bulletin No. 270. North Carolina Agricultural Research Service. Raleigh, NC.

Little, S. Jr. 1950. Ecology and silviculture of whitecedar and associated hardwoods in southern New Jersey. Yale University School of Forestry Bulletin 56:1-103.

Loomis, D.T., K.M. Shacochis, J.W. DeBerry, R.T. Belcher and R.B. Atkinson. This Volume. Flora of Atlantic white cedar stands in Great Dismal Swamp and Alligator River National Wildlife Refuges.

Lowry, D. J. 1984. Water regimes and vegetation of Rhode Island forested wetlands. Masters Thesis, University of Rhode Island, Kingston.

Moore, S.E. 1996. Natural Regeneration of Atlantic white cedar in the Great Dismal Swamp. North Carolina State University, Raleigh, NC.

Mylecraine, K.A., Zimmermann, G.L., Kuser, J.E. This volume. The effects of water table depth and soil moisture on the survival and growth of Atlantic white cedar.

Norfolk District, US Army Corps of Engineers. 1986. Situation Report and Environmental Assessment: Dismal Swamp Canal, Virginia and North Carolina. September 1986.

Oaks, R.Q. and N.K. Coch. 1973. Post-Miocene stratigraphy and morphology, southeatern Virginia. Virginia Division of Mineral Resources Bulletin 82.

Osbon, C.C. 1919. Peat in the Dismal Swamp, Virginia and North Carolina. USGS, USGPO, Washington, DC.

Phipps, R.L., D.L. Ierley and C.P. Baker. 1978. Tree rings as indicators of hydrologic change in the Great Dismal Swamp, Virginia and North Carolina. USGS, Reston, VA

Reber, E.J., A.B.Moulton, P.J. Swecker, J.S. Quesenberry, and D. Bradshaw. 1981. Soil Survey of City of Suffolk, Virginia. USDA, SCS, andVPI&SU.

Reddy, K.R. and W.H. Patrick, Jr. 1975. Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil. Soil Bio. Biochem., 7: 87-94.

Reed, P.B., Jr. 1988. National List of Plant Species That Occur in Wetlands: National Summary. U.S. Fish and Wildlife Service, Washington, DC, USA. Biological Report 88(24).

Reynolds, P.E., W.R. Parrott, J.R. Maurer, and D.C. Hain. 1981. Computer mapping of seasonal groundwater fluctuations for two differing southern New Jersey swamp forests pp 771-783 IN T.B. Brann and H.G. Lund (eds.) Proceedings of a National Workshop on In-Place Resource Inventories: Principles and Practices. Society of American Foresters.

Richardson, C.J. 1981. Pocosins: Ecosystem processes and the influence of man on system response. Pp. 135-151 IN (C.J. Richardson ed.) Pocosin Wetlands: An Integrated Analysis of Coastal Plain Freshwater Bogs in North Carolina. Hutchinson Ross Publ. Co., Stroudsburg, PA.

Schafale, M.P. and A.S. Weakley. 1990. Classification of the natural communities of North Carolina; third approximation. N.C. Natural Heritage Program. N.C. Dept. of Environment, Health and Natural Resources, Raleigh, N.C. 325 p.

Shacochis, K.M., J.W. DeBerry, D.T. Loomis, R.T. Belcher and R.B. Atkinson. This Volume. Vegetation importance values and weighted averages of Atlantic white cedar stands in Great Dismal Swamp and Alligator River National Wildlife Refuges.

Shaler, N.S. 1890. General account of the freshwater morasses of the United States, with a description of the Dismal Swamp district of Virginia and North Carolina. U.S. Geological Survey, Annual Report 10:255-339.

Sharitz, R.R. and J.W. Gibbons. 1982. The ecology of southeastern shrub bogs (pocosins) and Carolina bays: a community profile. U.S. Fish and Wildlife Serv. Div. of Biol. Serv. Washington, DC. FWS/OBS-82/04. 93 pp.

Stoltzfus, D.L. and R.E. Good. 1990. Plant community structure in *Chamaecyparis thyoides* swamps in the New Jersey Pinelands Biosphere Reserve, USA. IN Pp. 142-155 IN A.D. Laderman (Ed). Coastally Restricted Forests. Oxford University Press, New York.

Thompson, G., R.T. Belcher and R.B. Atkinson. This Volume. Biogeochemical properties of Atlantic white cedar wetlands: Implications for restoration compensation.

Tant, P.L. 1992. Soil County Survey of Dare County, North Carolina. US Dept of Agriculture, Soil Conservation Service.

U.S. Army Corps of Engineers. 1993. Installing monitoring wells/piezometers in wetlands. WRP Technical Note. HY-IA-3.1.

Van Druten, B. and T.R. Eagle. 2000. Comprehensive survey of 3,000 acres of Atlantic white cedar [*Chamaecyparis thyoides* (L.) B.S.P.] clearcut tracts on the Dare County Peninsula, North Carolina. 145 pp. In R.T. Belcher, D.A. Brown and R.B. Atkinson (eds.) Restoration of Atlantic White Cedar Ecosystems at Dare County Bombing Range, North Carolina: A Compendium of Research.

Wharton CH, W.M. Kitchens, E.C. Pendleton, T.W. Sipe. 1982. The ecology of bottomland hardwood swamps of the southeast: a community profile. Washington, DC, USA, U.S. Fish and Wildlife Service, Biological Services Program.

Whitehead, D.R. and R.Q. Oaks. 1979. Developmental history of the Dismal Swamp. Pp. 24 to 43 IN Kirk, P.W. (ed.) The Great Dismal Swamp. University of Virginia Press, Charlottesville, VA.

INFLUENCE OF ENVIRONMENTAL GRADIENTS ON ATLANTIC WHITE CEDAR WETLANDS IN SOUTHEASTERN VIRGINIA

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Abstract: Various agencies and organizations are attempting to reestablish Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), wetlands throughout the historic range of the species, which has been logged from many areas without replacement. In this two-year study that began in February 1996, 257 bare-root cedar cuttings were planted in an abandoned agricultural field in Chesapeake, Virginia, and 241 rooted cuttings were planted in the Great Dismal Swamp National Wildlife Refuge. The purpose of the study was to examine the effects of environmental variables (soil pH, water table elevation, soil moisture and bulk density) on the establishment of cedar and other species. The agricultural field was prepared in 1996 by clipping herbaceous materials to a uniform height of 20 cm. The swamp was prepared in 1991 using tracked machinery to clear a 2.8-ha area dominated by mature hardwoods with a lesser component of poorly performing cedar. In 1996, the swamp held standing water, was inundated to a depth of more than 30 cm in troughs and there was very little naturally regenerated cedar present on adjacent mounds. Canonical correspondence analysis (CCA) indicated that the two sites were sharply different, primarily due to longer hydroperiods at the swamp and higher soil pH at the agricultural field. CCA also detected a significant effect of water table elevation, which covaried with hydroperiod. At the agricultural field, analyses of variance between four water table elevation ranges (quartiles) showed a significant influence of elevation on bulk density, soil moisture and weighted average (i.e., average percent cover of all vegetation per plot, weighted according to predicted occurance in wetlands). Similar vegetative responses occurred at the swamp site, where growth, soil moisture, pH, and species composition also appeared to correspond to microsite elevation differences.

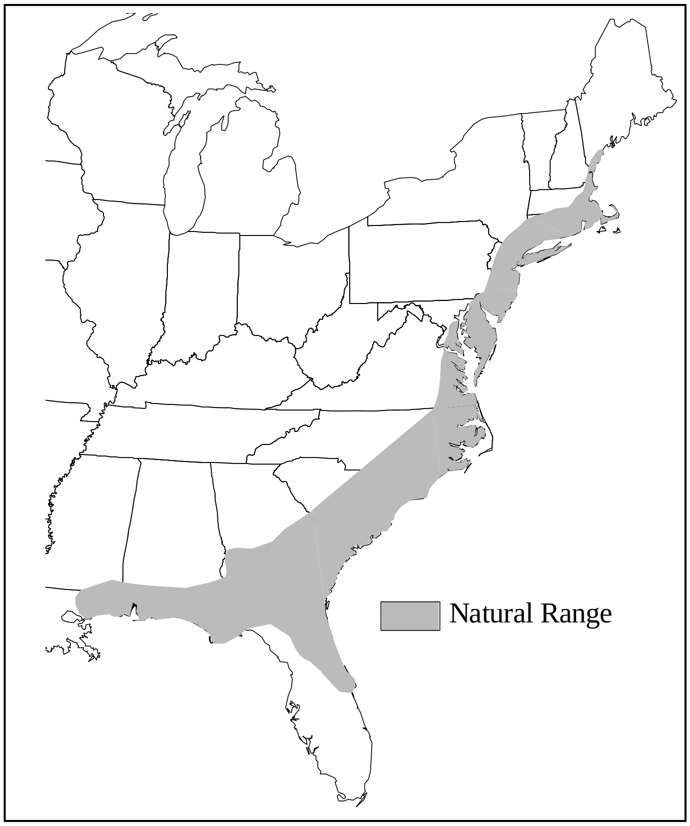
Key Words: water table elevation, Great Dismal Swamp, soil moisture, canonical correspondence analysis, soil pH, *Chamaecyparis thyoides*

INTRODUCTION

The efficiency of harvesting Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), in the eastern United States improved dramatically with the advent of steam technology after the Civil War (Moore 1939, Stewart 1979, Frost 1987, Atkinson et al. This Volume). Much of the cedar in the southeast was summarily removed during the "cedar boom" from 1893 to 1947 (Hanlon 1970, personal communication Henderson 1998). By 1950, studies from North Carolina to New Jersey were initiated to determine why cedar, which had recovered from at least two prior 70-year rotation harvests, was no longer regenerating naturally (Akerman 1923, Little 1950, Hanlon 1970). Attempts are currently underway to restore cedar habitat across the natural range of the species (figure 1).

Among several factors influencing growth and survivorship of cedar are competition, soil characteristics, and hydrology. Baines (ND) noted that dense regeneration of cedar led to less undergrowth competition. Little (1950) maintained that only dense, pure stands were expected to produce adequate seed for post-harvest restocking. Moore (unpubl.) concluded that competition from sweet pepperbush (*Clethra alnifolia*) also negatively impacted cedar regeneration. Logging slash also reduces cedar growth and survivorship (Korstian and Brush 1931, Moore 1939, Little 1950). Furthermore, Buell and Cain (1943) noted that cedar was not productive in the shade of other vegetation or among dense weedy growth.

Figure 1. Historic range of cedar habitat (Korstian and Brush 1931).



Survival can also be influenced by soil characteristics. Korstian and Brush (1924) found considerable variability in the soil characteristics of cedar habitat. Day (1982) studied four community types in the Great Dismal Swamp and determined that the cedar community had the lowest soil pH. Phillips, Gardner, and Summerville (1992) found that cedar performed better on deep organic, low pH soils in North Carolina. Ruffin (1861) and later Korstian (1924) stated that cedar occurs on areas of swamp peat overlying a sandy soil. Over the years, the relationship between cedar growth and soil pH has been examined carefully (Collins and others 1964, Eleuterius and Jones 1972, Levy and Walker 1979, Smith 1995).

Laderman (1989) contended that hydrology was a controlling factor in cedar wetlands. The degree to which successful cedar regeneration occurs after wildfires and prescribed burning efforts has also been attributed to hydrologic conditions (Akerman 1923, Korstian 1924, Buell and Cain 1943). Closely associated with hydrology, microrelief has also been examined in some detail. Hughes (personal communication 1996) has stated that microrelief may lessen the effects of competition and microsite drainage. Frost (1987) noted that cedar occupied a narrow elevation niche between the swamp forest and the pocosin bog, and that disturbance of basic wetland hydrology can influence cedar growth and survivorship. According to Little (1950) the average range in depth, from mean elevation to water table, was between -2.5 cm (inundation) and 20.3 cm for the cedar swamp. Mean water table elevation differences have had a measurable influence on species composition in wetlands (Ehrenfeld 1995a). In cedar wetlands, that elevation gradient also covaries with soil pH, bulk density and soil moisture (Brown and Atkinson 1999, Laderman 1998).

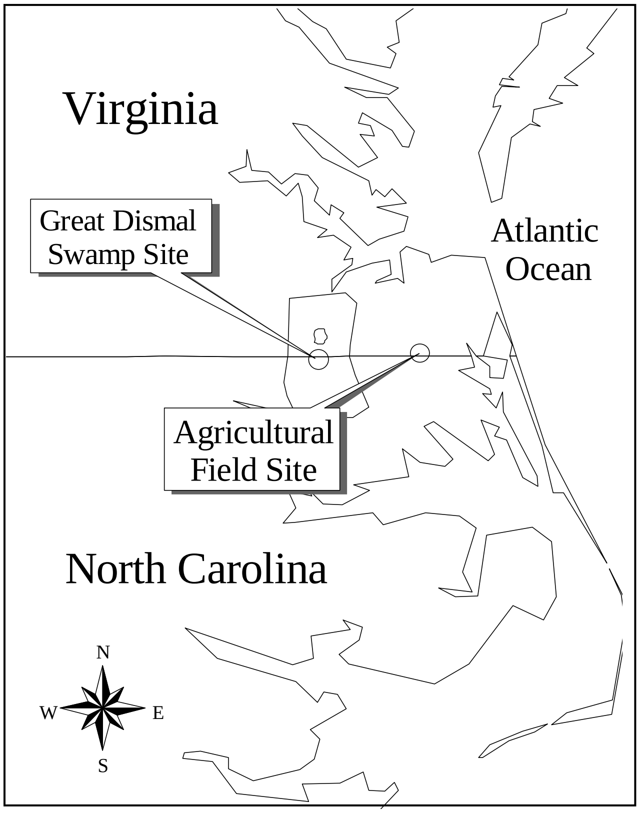
In this study, 257 rooted cedar cuttings were planted in six transects along an elevation gradient to study the effects of soil pH, bulk density and soil moisture on response variables (growth, percent cover, species richness) in an abandoned agricultural field in Chesapeake, Virginia. Weighted average was also closely examined (Atkinson et al. 1993). Another 243 rooted cuttings, following the same planting design, were placed in a 2.8-ha cutout in the Great Dismal Swamp. Plotwise statistical tests at both sites included analysis of variance (ANOVA), linear regression, Anderson-Darling normality tests, two-sample T-tests, and canonical correspondence analysis, using an alpha level of 0.05 unless otherwise mentioned (Minitab 1995, Clarke 1994, Sokal and Rohlf 1995, Ter Braak 1987).

Site Description

The recently abandoned agricultural field is located in Chesapeake, Virginia within the historic reaches of the Great Dismal Swamp (figure 2). The agricultural field is bounded by a paved road on the east side and a dirt road on the south. The north end is flanked by a remnant water control structure and the west side grades into the mature forested watershed of the Northwest River. Hydric soil types identified on the agricultural field (USDA 1982) include Tomotley and Acredale loams.

The swamp site is located at the corner of Forest Line and Corapeake Ditches at the Virginia state line in an open, relatively flat 2.8-ha clearing in the Great Dismal Swamp (figure 2) where cedar still occurs naturally (USFWS 1986, personal observation 1996). The soil type at the swamp site, that was cleared in 1991 to examine natural cedar regeneration (Brownlie 1995), was Pungo muck (hydric) (Tant 1982, Tant 1995). By 1996, the swamp had been heavily recolonized by sweet pepperbush (*Clethra alnifolia*) and, to a much lesser extent, other wetland shrub and graminoid species.

Figure 2. Location of agricultural field and swamp sites.



METHODS

Experimental Design

The agricultural field was prepared in 1996 by hand-clearing the herbaceous layer to about 20 cm high. The study plot was established at the agricultural field by placing six parallel transects every 1.5 m, following the natural elevation contour. The same general design was used to establish transects in the swamp study plot, which was originally cleared in 1991. Though the swamp site was relatively flat compared to the agricultural field, microtopography at the swamp varied considerably along each transect.

Planting Density

One year-old rooted cuttings were obtained in 1996 from the Weyerhaeuser Nursery in Washington, North Carolina. The rooted cuttings were coated in kaolin clay to prevent drying and were packaged in groups of 100 individuals, the initial height of which ranged from 12 to 20 cm. In 1996, rooted cuttings were planted on 1.5-m spacings in the first four transects and 0.75-m spacing in the last two transects at both sites.

Morphometric Measurements, Percent Cover and Weighted Averages

Rooted cuttings were measured initially, and for two consecutive field seasons, to record growth increments. Morphometric parameters included circumference, height, volume, and percent cover. Circumference was measured by circling the broadest width (diameter) of the rooted cutting canopy with a fiberglass metric tape. Heights were recorded by measuring from the root collar to the topmost growth of each rooted cutting. A conical shape was assumed to approximate cedar canopy volume (V). Canopy volume estimates (modified from Comeau et al. 1993, Shirazi et al. 1998, Brown and Atkinson 1999) were based on height (h) and circumference (c) to provide the volume of a cone ($V=[c*h]/3$). Percent cover per meter-square was estimated for each rooted cutting and for all other species in each plot following Mueller-Dombois and Ellenberg (1974). Species were identified from Radford et al. (1968) for weighted average calculation within each 1.0-m^2 plot (plotwise) (Atkinson et al. 1993). Species richness and relative frequencies were also determined (Mueller-Dombois and Ellenberg 1974).

Soil Sampling

Soils were collected within a 10-cm radius of each rooted cutting using a 300-mL cylinder. Plotwise soil samples were analyzed to determine soil pH, bulk density, and soil moisture to a depth of 10 cm (Foth 1990, Carter 1993). Soil pH was determined by mixing one part soil with two parts distilled water and measuring the pH of the suspended mixture. Bulk density was determined as the soil dry weight (oven dried at 105^{o}C for 10 days) divided by the volume of soil collected (300 mL). Soil moisture content was derived by calculating mass of water per unit mass of dry soil. Additionally, soil cores were taken along a transect at seven representative points adjacent to each site to evaluate organic content and observe qualitative differences in soil texture and color. Subsamples from the representative cores were analyzed for chemical composition and particle size (Foth 1990).

Elevation and Well Data

Plotwise elevation measurements were recorded at both sites using a standard survey level and rod. The elevation measurements were relative to four reference benchmarks and four permanent Remote Data Systems RDS WL-40 continuous water monitoring wells (WL40s) installed at the sites.

A total of four WL40s were installed, one near each end of the study area between the third and fourth transects at both research sites, following standard installation procedures (U.S. Army Corps of Engineers 1993), and modified procedures for swamp conditions (Gregory 1996 personal communication). Water table depths were recorded (Remote Data Systems ND, Hewlett-Packard Company 1993) and mean growing season water table depth at both sites was determined. The mean growing season water table depth was subtracted from plotwise elevations at both sites to provide plotwise mean water table elevations (Wells 1942, Little 1950, Ehrenfeld 1995b).

To assess possible effects of water table elevation at the agricultural field, the site was divided into four ranges (first, second, third and fourth quartiles). Water table elevations at the swamp were also divided into four microtopographic zones (Brown and Atkinson 1999).

RESULTS AND DISCUSSION

Experimental Design

The experimental design at both sites was identical, but due to differences in between-site species and environmental variables, CCA was able to assign a large portion of between-site variability to the primary axes across which the data were distributed (figure 3). The plotwise ordination of environmental data from both sites indicated that environmental variables (soil pH, bulk density) were positively correlated with response variables among agricultural field plots and inversely correlated with response variables among swamp plots (eigenvalue = 0.88). Species followed the same general distribution pattern as plots (figure 4). Species in the agricultural field were widely dispersed across the environmental gradient. Species occurring in the swamp had indicator statuses of FAC or wetter (Reed 1988) and were highly correlated with soil moisture and water table elevations in CCA. The fit of the ten dominant species between sites was illustrated in CCA (figure 5). *Clethra alnifolia*, cedar, and *Ilex glabra* were correlated with soil moisture and water table elevation. *Smilax laurifolia* and *Acer rubrum* were correlated primarily with soil moisture, while *Andropogon glomera*tus and *Xyris caroliniana* were strongly correlated with water table elevation. *Hypericum mutilium*, *Bidens aristosa*, *Campsis radicans*, and *Juncus tenuis* were strongly correlated with soil pH and bulk density in the agricultural field.

Plotwise relative cover and frequency of all species occurring within and between sites were used to calculate between and within-site importance values (IV) and dominance (table 1). *Clethra alnifolia* was the most important species in the swamp plots (IV=59.6), while cedar was the second most important species (IV=44.2). Cedar was the only important species occurring at both sites (IV=25.5). *Acer rubrum* occurred at both sites but was not an important species in the agricultural field at the time of the study. The agricultural field had a higher species richness overall ($p<0.01$), averaging 11.8 species per plot.

The influence of sharp environmental gradients resulted in height, circumference and volume increments in cedar growth that were higher at the agricultural field ($p<0.01$ for all variables). Mean soil pH at the agricultural field (5.3) was higher than for the swamp (3.9) ($p<0.01$). Bulk density was also much higher at the agricultural field (0.73 g/cm^3) than in the swamp (0.12 g/cm^3) ($p<0.01$). Soil moisture content was lower ($p<0.01$) in the agricultural field loam (30%) than in the swamp muck (344%). Soil moisture differences were largely predicted by water table elevations (correlation $R^2=0.72$)(figure 6).

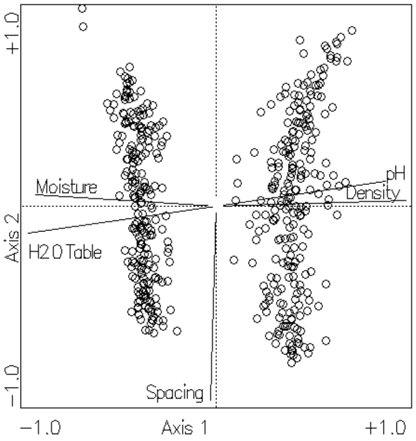


Figure 3. Distribution of plots across the environmental gradient. Separation at the origin indicates a break in the gradient between swamp water table elevations left of the origin and agricultural field water table elevations to the right.

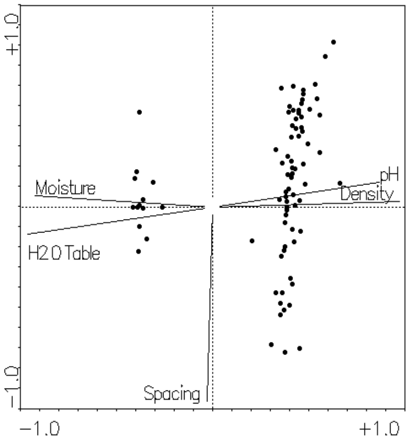


Figure 4. Distribution of species between environmental gradients. Numerically important species are spatially separated by the environmental gradient. See table 1 for list of species' importance values.

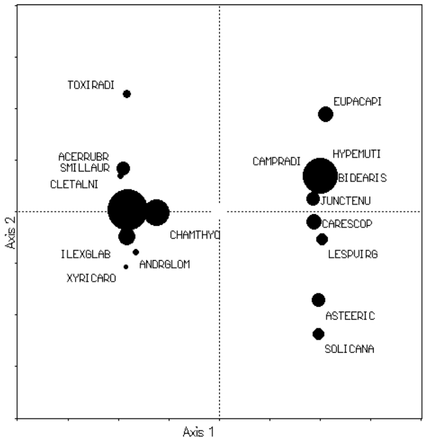


Figure 5. Fit of species across environmental gradient based on between- and within-site importance values. Primary axis eigenvalue (0.88) is significant at $p<0.01$. Species located left of origin have wetland indicator statuses of FAC, FACW, or OBL (Reed 1988).

Table 1. Relative cover, frequency, among- and within-site importance values (IV) for dominant between-site species.

Species/ CANOCO Nomenclature	Among-Site Relative Cover	Among-Site Relative Frequency	Among-Site Importance Value	Within-Site Importance Value (Ag. Field)	Within-Site Importance Value (Swamp)
Clethra alnifolia L/ CLETALNI	5.5	20.1	25.6	Not present	59.6
Chamaecyparis thyoides (L.) B.S.P./ CHAMTHYO	11.9	13.6	25.5	12.7	44.2
Bidens aristosa (Michx.) Britt./ BIDEARIS	5.2	13.0	18.2	33.8	Not present
Ilex glabra (L.) Gray/ ILEXGLAB	3.2	7.5	10.8	Not present	26.7
Carex scoparia Schkuhr ex Willd./ CARESCOP	4.7	4.3	9.0	15.3	Not present
Acer rubrum L./ ACERRUBR	3.9	3.4	7.3	Unimportant	20.5
Vaccinium corymbosum L./ VACCCORY	1.7	4.4	6.0	Not present	14.7
Juncus tenuis Willd./ JUNCTENU	4.3	1.7	6.0	9.4	Not present
Lespedeza virginica / LESPVIRG	3.2	1.7	5.0	7.9	Not present
Hypericum mutilum L./ HYPEMUTI	3.6	1.2	4.8	7.4	Not present

Planting Density

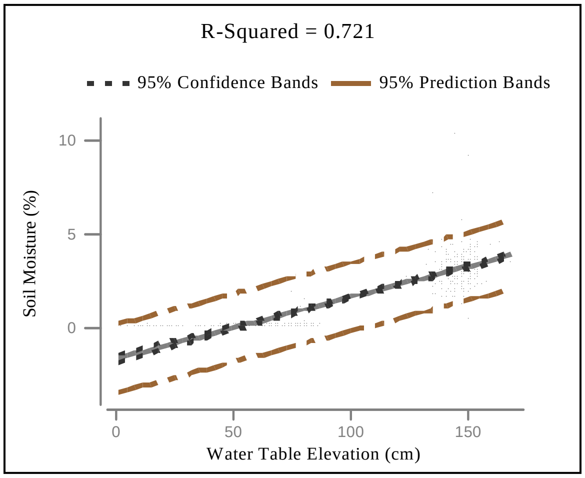


Figure 6. Fitted line plot of soil moisture regressed with water table elevations.

At the agricultural field, species richness was higher in densely spaced transects in the highest water table elevation (first quartile) ($p<0.03$). Planting density was not related to species richness in the three lower water table elevation ranges ($p>0.05$). Weighted averages were higher in the highest water table elevation (first quartile) at the agricultural field ($p<0.02$); however denser cedar plantings in the middle two water table elevation ranges (second and third quartiles) appeared to have no effect on the weighted average. Planting density was related to weighted average in the lowest water table elevation range (fourth quartile) ($p<0.01$). Cedar height differences between planting density treatments were negligible ($p<0.2$). However, mean cedar circumference and canopy volume were higher in the denser plantings ($p<0.01$, $p<0.04$, respectively) even though only one planted cedar was measured in each 1.0-m^2 plot.

In the swamp, planting density did not effect species richness ($p=0.6$). Brown and Atkinson (1999) determined that higher planting densities increased percent cover of rooted cuttings ($p<0.01$). However, the effect of higher planting densities did not seem to influence growth parameters between water table elevation ranges in the swamp. Water table elevations as a single treatment influenced cedar growth in the two middle water table elevation ranges ($p<0.04$, second quartile; $p<0.02$, third quartile respectively).

Morphometric Measurements, Percent Cover and Weighted Averages

Rooted cuttings were measured immediately following planting in February 1996. First and second year morphometric measurements and survivorship were recorded in January 1997 and March 1998 respectively. At the agricultural field, 252 out of 257 (98 %) trees survived the first year while 235 (91.4 %) trees remained in the second year. Each successive year since planting, all measured growth parameters increased at the agricultural field (table 2 and figure 7) ($p<0.01$).

Table 2. Height growth increments of rooted cuttings at the agricultural field after first (1997) and second (1998) year growing seasons (cm).

			1997 Height			1998 Height	
Transect	n	Min	Max	Mean	Min	Max	Mean
AFS1	30	28	90	57.3	45	152	81.1
AFS2	28	15	117	56.4	35	162	79.1
AFS3	29	27	101	60.0	44	136	79.1
AFS4	31	30	77	60.6	35	110	80.0
AFD5	57	18	94	61.0	30	143	82.0
AFD6	60	17	92	56.7	21	126	76.7
Grand Mean				58.7			79.7

Planted cedar cover was included in the plotwise weighted averages at the agricultural field site. To determine whether the obligate wetland species (Reed 1988) would alter the mean weighted average when planted at a drier site, weighted averages were also calculated omitting cedar cover. Mean weighted averages, with and without cedar cover in the plots, did not differ (p>0.3).

Weighted averages were different between the two site (p<0.01). The mean weighted average at the agricultural field was 2.5, while that of the swamp was only 1.8, indicating that the indicator statuses of species in the swamp were primarily FACW and OBL.

Species richness at the agricultural field was high (mean=11.8 species per meter square). As previously discussed, relative frequency and cover of each species were calculated to determine importance values. Table 3 listed the 20 most frequently occurring species in the agricultural field. Most of those twenty species were in the herb stratum and included *Bidens aristosa*, *Carex scoparia*, *Juncus tenuis*, and *Hypericum mutilum*.

Relative percent cover of *Bidens aristosa* was highest (26.7%), followed by *Carex scoparia* (8.9%), *Aster ericoides* (6.4%), and *Eupatorium capillifolium* (5.3%). Relative percent cover of planted cedar in the agricultural field (4.5%) was lower (p<0.01) than cedar relative percent cover in the swamp (22.4%), where cedar also occurred naturally in the plots.

Figure 7. Between-year log-normal growth comparisons of height, circumference and volume at the agricultural field (cm).

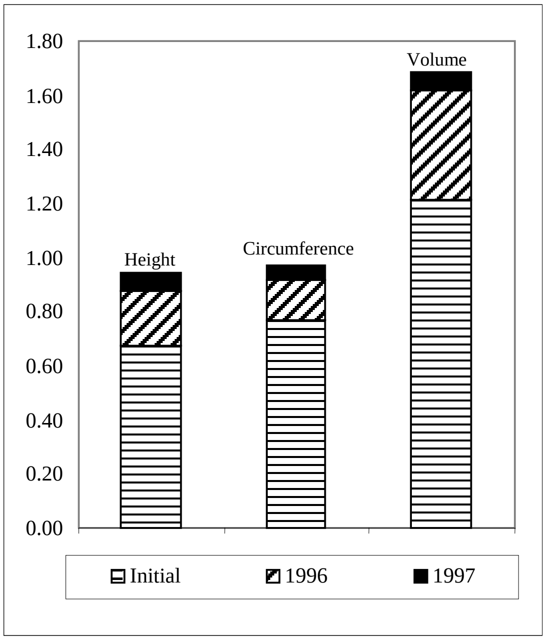


Table 3. Relative frequencies of twenty most frequently occurring species in the agricultural field.

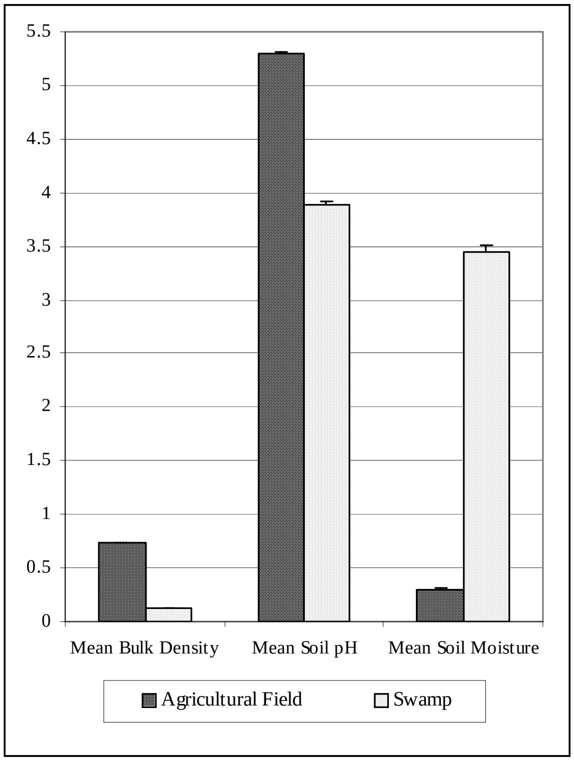
Species	**Relative Frequency**
Chamaecyparis thyoides (L.) B.S.P.	0.82
Bidens aristosa (Michx.) Britt.	0.71
Carex scoparia Schkuhr ex Willd.	0.64
Juncus tenuis Willd.	0.59
Hypericum mutilum L.	0.50
Lespedeza virginica (L.) Britt.	0.44
Solanum carolinense L.	0.41
Campsis radicans (L.) Seem. ex Bureau	0.40
Ludwigia alternifolia L.	0.31
Liquidambar styraciflua L.	0.26
Eupatorium capillifolium (Lam.) Small	0.25
Lobelia siphilitica L.	0.23
Allium vineale L.	0.22
Carex vulpinoidea Michx.	0.22
Aster ericoides L.	0.22
Aster lateriflorus var. *lateriflorus* (L.) Britt.	0.21
Aster lateriflorus (L.) Britt.	0.21
Andropogon virginicus L.	0.20
Rhexia mariana L.	0.19
Panicum dichotomiflorum Michx.	0.18

Soil Sampling

Soil samples from both sites were collected to a depth of 10 cm using a 300-mL cylinder. The samples were immediately weighed, and then oven dried for two weeks at 105^{o}C. Soil moisture and bulk density were derived from the wet and dry weights prior to testing the samples for soil pH (Foth 1990, Carter 1993). Soil pH (Carter 1993) ranged from 4.2 to 6.1 (mean = 5.57) in the agricultural field. This was different (p<0.01) from soil pH in the swamp (mean = 3.9). Mean bulk density at the agricultural field site was 0.73g/cm^3. Mean soil moisture was

30.3%. Linear regression detected that soil moisture was negatively related to bulk density at the agricultural field site ($R^2 = 0.26$) and in the swamp ($R^2 = 0.18$). Mean bulk density in the swamp was 0.12 g/cm^3 and mean soil moisture was 344.7% (figure 8).

Figure 8. Between-site comparison of soil characteristics, bulk density (g/cm^3), soil pH and moisture content (1/100th %).



Water Table

Plotwise weighted averages at the agricultural field varied between the first and second water table elevation ranges ($p<0.01$) and between the second and third water table elevation ranges ($p<0.03$), but not between the third and fourth elevation ranges ($p>0.2$). No morphometric differences were noted between the water table elevation ranges. Likewise, plotwise species richness at the agricultural field was not influenced by water table elevation. Soil moisture ($p<0.01$) and bulk density ($p<0.01$) varied, but only at the highest water table elevation range at the agricultural field. Water table elevation appeared to have no influence on pH between ranges.

Continuous well data were recorded throughout the study period. At the agricultural field, the mean growing season depth to the water table was 84 cm and the mean growing season depth to the water table in the swamp was 18 cm. Water was rarely observed at the surface during the growing season at the agricultural field, whereas standing water was fairly common in the swamp.

CONCLUSIONS

Environmental Variables

Water table differences among sites may have led to the observed differences in environmental variables. Nowhere was this more apparent than in CCA, which illustrated the sharp discontinuity for the water table gradient. Ehrenfeld (1995b) maintains that species distributions overlap along an elevation gradient, but the absence of intermediate water table depths continuous, CCA output may have differed.

Weighted averages were also influenced by water tables. Weighted averages between sites showed that the swamp site was limited to species with wetland indicator status of facultative, facultative wetland, or obligate wetland. At the agricultural field, facultative upland and upland indicator statuses were also represented.

Planting Density

Baines (ND) stated that cedar seedlings may be more densely planted than other tree species and that this may lead to less undergrowth competition. Cedar have only been planted for two years, and the relative frequency of planted cedar in the agricultural field was only slightly higher than for colonizing species in the study area. The effect of planting density on species richness (which was not significant) may not manifest itself for several growing seasons.

Morphometric Measurements, Percent Cover and Weighted Averages

According to Brownlie (1996 personal communication), survivorship over 50% may be acceptable for cedar plantings. The high level of survivorship at the agricultural field site (91.4 %) was encouraging, but may have been influenced by the unique site conditions present in a recently abandoned agricultural field, including the absence of measurable competition from shrubs or other woody species. Growth increments were similar to those found in the literature (Akerman 1923, Korstian 1924). Growth in the agricultural field was higher than in the swamp, which may have resulted from site conditions at the agricultural field that resulted in cedar receiving nearly full sunlight (Comeau et al. 1993, Barnes et al. 1990, Buell and Cain 1943, Eleuterius and Jones 1972). Growth in the agriculture field may have also been enhanced by limited shrub or herb competition. In addition, soil in the agricultural field was rarely saturated to the surface. Inundation was observed on several occasions at the swamp site, the stress from which may have led to lower growth rates (Korstian 1924, Little 1950, Wallace et al. 1996).

Soil Sampling

Based on this analysis, soil and hydrologic characteristics seemed to have the greatest overall influence between sites. According to Wallace et al. (1996), soil nutrients may be limited in anaerobic conditions. The proximity of the water table to the surface at the swamp site resulted in flood conditions on many occasions and may also have limited the available of nutrients for cedar growth at the swamp site. At the agricultural field, soil pH was higher than at the swamp, providing a less acid substrate for plant establishment (Carter 1993). Bulk density was also higher at the agricultural field site and may be partially attributed to compaction (Carter 1993). Compaction did not appear to influence bulk density of soils in the swamp, where mean soil moisture was 344% (Wallace et al. 1996).

Water Table

This study detected a correlation between soil moisture, bulk density and water table elevation, which differs from results reported by Ehrenfeld (1995a). Pittman (1978) found a correlation between water table elevation and vegetation zones. Brown and Atkinson (1999) also found differences in vegetative growth among zones in the swamp. Growth differences occurred in height, circumference, and volume between cedar planted in the agricultural field versus cedar planted in the swamp($p<0.01$), suggesting that growth was influenced by the elevation gradient.

In summary, cedar growth and survival may be vegetative competition, soil characteristics, and water table proximity to the soil surface. The need for careful planting and frequent monitoring is critical to successful rangewide habitat restoration efforts. This study points to water table elevation as a potential indicator of site performance. Little (1950) determined that, in a New Jersey cedar swamp, the average depth to the water table of a cedar swamp was between –3 and 20 cm. In this study, depth to the mean growing season water table in the agricultural field (84 cm) was more than 4-fold deeper than that of the swamp (18 cm).

RECOMMENDATIONS

Site selection and design are critical for habitat restoration. The proximity thewater table to the soil surface should be considered when restoring cedar. If merely increasing survival and growth for a single generation without restoring the historic ecosystem function is desired, then planting in moderately well drained agricultural fields may advance that goal. However, it is uncertain whether characteristics such as soil moisture and bulk density can ever be successfully restored without duplicating the effects of inundation and microsite relief so often associated with cedar wetlands. In our study, every measure of cedar growth was more vigorous on agricultural fields than in the native habitat. A complete functional evaluation of both site types could be conducted to confirm that agricultural fields may be restored to cedar wetlands.

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LITERATURE CITED

Akerman, A. 1923. The white cedar of the Dismal Swamp. Va. For. Publ. 30:1-21.

Atkinson, R.B., T.E. Morgan, D.A. Brown, and R.T. Belcher. This Volume. The role of historic inquiry in the restoration of Atlantic white cedar swamps.

Atkinson, R.B., J.E. Perry, E. Smith, J. Cairns, Jr. 1993. Use of created wetland delineation and weighted averages as a component of assessment. Wetlands 13:185-193.

Barnes, P.W., W. Beyschlag, R. Ryel, S.D. Flint, and M.M. Caldwell. 1990. Plant competition for light analyzed with a multi-species canopy model. Oecologia. 82:560-566.

Brown, D.A. and R.B. Atkinson. 1999. Assessing the survivability and growth of Atlantic White Cedar (*Chamaecyparis thyoides* (L.) B.S.P.) in the Great Dismal Swamp National Wildlife Refuge. p. 1-7 In Shear, T. and K.O. Summerville(eds). Atlantic White Cedar: Ecology and Management Symposium. 6-7 Aug. 1997. Newport News, VA. USDA For. Serv., Southern Res. Sta. Gen. Tech. Rep. SRS-27.

Buell, M.F. and R.L. Cain. 1943. The successional role of southern white cedar, *Chamaecyparis thyoides*, in southeastern North Carolina. Ecology. 24:85-93.

Carter, M.R. (ed.). 1993. Soil sampling and methods of analysis. Canadian Society of Soil Science. Lewis Publishers. Boca Raton, FL.

Clarke, G.M. 1994. Statistics and experimental design: an introduction for biologists and biochemists. Wiley & Sons, Inc., New York, NY.

Collins, E.A., C.D. Monk, and R.H. Sherman. 1964. White cedar stands in northern Florida. Quart. Jour. Florida Acad. Sci. 27:107-110.

Comeau, P. G., T. F. Braumandl, and C. Y. Xie. 1993. Effects of overtopping vegetation on light availability and growth of Engleman spruce seedlings. Can. J. For. Res.23:2044-48.

Day, F.P. Jr. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology. 63:670-678.

Ehrenfeld, J. G. 1995a. Microsite differences in surface substrate characteristics in *Chamaecyparis* swamps of the New Jersey pinelands. Wetlands 15:183-189.

Ehrenfeld, J.G. 1995b. Microtopography and vegetation in Atlantic white cedar swamps: the effects of natural disturbances. Can. J. Bot. 73:474-484.

Eleuterius, L.N. and S.B. Jones. 1972. A phytosociological study of white-cedar in Mississippi. Castanea. 37:67-74.

Frost, C.C. 1987. Historical overview of Atlantic white cedar in the Carolinas. In A. D. Laderman, (ed). Atlantic White Cedar. Boulder, CO: Westview Press. p. 257-264.

Foth, H. D. 1990. Fundamentals of soil science, 8th edition. John Wiley and Sons. New York, N.Y. 360 p.

Hanlon, H. A. 1970. The bull hunchers. McClain Publishing Co., Parson, WV, 352 p.

Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R., (eds). 1987. Data analysis in community and landscape ecology. Pudoc, Wageningen, Netherlands. 284 p.

Korstian, C.F. 1924. Natural regeneration of southern white cedar. Ecology. 5:188-191.

Korstian, C. F. and W. D. Brush. 1931. Southern white cedar. U. S. Dep. Agric. Tech. Bull. 251. 75 p.

Laderman, A. D. 1989. The ecology of the Atlantic white cedar wetlands: a community profile. U. S. Fish Wildl. Serv. Biol. Rep. 85(7.21). 114 p.

Laderman, Aimlee D. (ed.) 1998. Coastally Restricted Forests. Freshwater Forests of Continental Margins: Overview and Synthesis. Oxford Univ. Press. New York, N.Y.

Levy, G.F. and S.W. Walker 1979. Forest Dynamics in the Dismal Swamp of Virginia. In Kirk, P. W. Jr., (ed.). The Great Dismal Swamp. Charlottesville, VA: Univ. Press of Virginia.

Little, S. Jr. 1950. Ecology and silviculture of whitecedar and associated hardwoods in southern New Jersey. Yale Univ. Sch. For. Bull. 56. 103 p.

Maryland Heritage & Biodiversity Conservation Programs Department of Natural Resources. 1994. Rare, threatened and endangered plants of Maryland. Internet <ftp://ftp.heritage.tnc.org /pub/nhp/us/md/mdplant.html>.

Moore, E.B. 1939. Forest management in New Jersey. N.J. Dept. of Conserv. Dev. 55.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 p.

Phillips, R. W., W. E. Gardner, and K. O. Summerville. 1992. Plantability of Atlantic white cedar rooted cuttings and bare root seedlings. Paper presented at 7th Biennial Southern Silvicultural Research Conference, Mobile, AL.

Pittman, A.B.Jr. 1978. Survey of the vascular flora of Shealy's pond, a southern cedar bog. MS Thesis. Univ. South Carolina, Columbia. 87 p.

Radford, A. E., H. E. Ahles, and C. R. Bell. 1968. Manual of the Vascular Flora of the Carolinas. The Univ. of North Carolina Press. Chapel Hill, NC. 1166p.

Reed, P. B., Jr. 1988. National list of plant species that occur in wetlands: Northeast (Region1). U. S. Fish Wildl. Serv. Biol. Rep. 88(26.1). 111 p.

Remote Data Systems. ND. WL40 series operation manual. Remote Data Systems Business Development Ctr. Whiteville, NC.

Ruffin, E. 1861. The origin and manner of geological formation of the great swamps of the Atlantic Coast. p.155-249. In Agricultural, geological and descriptive sketches of lower North Carolina and the similar adjacent lands. N.C. Agric. and Geol. Survey, Raleigh. Printed at the Institution for the Deaf & Dumb & the Blind, Raleigh. (Hill F259.R8—Special Collections)

Shirazi, M.A., P.K. Haggerty, C.W. Hendricks, and M. Reporter. 1998. The role of thermal regime in tundra plant community restoration. Restoration Ecology 6: 111-117.

Smith, L.E. 1995. Regeneration of Atlantic white cedar at the Alligator River National Wildlife Refuge and Dare County Air Force Bombing Range. Ph.D. Dissertation. North Carolina State Univ. Raleigh.

Stewart, P.C. 1979. Man and the swamp: the historical dimension. In Kirk, P. W. Jr., (ed.). The Great Dismal Swamp. Charlottesville, VA: Univ. Press of Virginia. p. 57-73.

Sokal, R.R. and J.F. Rohlf. 1995. Biometry: The principles and practice of statistics in biological research. W. H. Freeman and Company, New York, NY.

Tant, P.L. 1995. U. S. D. A. Natural Resources Conservation Service Soil Survey of Camden County, North Carolina. U. S. Government Printing Office: 1995-386-441/00025.

Tant, P.L. 1982. U. S. D. A. Soil Conservation Service Soil Survey of Currituck County, North Carolina. U. S. Government Printing Office: 1982 O - 352-621 : QL 3.

Ter Braak, C.J.F. 1987-1992. CANOCO - a FORTRAN program for Canonical Community Ordination. Microcomputer Power, Ithaca, New York, USA.

U.S. Army Corps of Engineers. 1993. Installing monitoring wells/piezometers in wetlands. WRP Technical Note HY-IA-3.1.

U.S.D.A. Soil Conservation Service. 1982. Soil Survey Report for Naval Security Group Activity Northwest. Soil Conservation Service, Chesapeake, VA.

U.S. Fish and Wildlife Service, Region 5. Draft Environmental Impact Statement: Master Plan Great Dismal Swamp National Wildlife Refuge. 1986.

Wallace, P.M., D. M. Kent, and D. R. Rich. 1996. Responses of wetland tree species to hydrology and soils. Restoration Ecology. 4:33-41.

Wells, B.W. 1942. Ecological problems of the southeastern United States Coastal Plain. Bot. Rev. 8:533-561.

SOIL RESPIRATION RESPONSE TO WATER LEVELS OF SOILS FROM ATLANTIC WHITE CEDAR PEATLANDS IN VIRGINIA AND NORTH CAROLINA

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Abstract: Atlantic white cedar (cedar) stands often occur in peatlands. Organic matter accumulates when the production rate exceeds the decomposition rate, which is typically associated with a positive water balance. As peat accumulates, the swamp exhibits autogenic control of hydrology and the moist peat provides a seed refugium that is essential for cedar self-maintenance. Hydrologic alteration for agriculture and silviculture has contributed to the decline in acreage, and restoration requires reestablishment of appropriate water levels and organic matter accumulation rates. Soil respiration was measured under laboratory conditions to examine how water level affects decomposition at six sites in North Carolina and Virginia. Two of the sites were mature (>60 years) cedar stands; two were cedar stands of intermediate age (20-30 years); and two were young (< 8 years) sites. Six cores were collected from each site and allowed to equilibrate to field capacity. Carbon dioxide flux rates were measured by capping the laboratory columns and collecting gas samples from the headspace, then analyzing via gas chromatography. Three cores from each site remained drained and three were saturated. Saturated cores from the three Great Dismal Swamp (GDS) sites exhibited lower CO_2 flux rates than saturated cores from the two Alligator River (AR) sites ($P < 0.05$). Pocosin Lakes (PL) was the only site for which the CO_2 flux rate was not significantly lower during the concurrent drained treatment when compared to the initial drained treatment, probably due to loss of labile carbon resulting from a recent fire. Mean CO_2 flux upon drawdown was positively related with the number of days during the mid 50 days of the growing season that field hydrology was within 15 cm of ground surface ($r^2 = 0.73$). The relationship also held for mean annual water table levels ($r^2 = 0.71$). These results suggest that management of peatlands to maintain shallow water table levels for longer periods of time will reduce carbon and organic matter loss via aerobic soil respiration and maintain or enhance peat deposits that are so important to cedar ecosystem self-maintenance. Based on these results, reducing or minimizing artificial drainage in GDS would help preserve peatmass; however, peatmass at AR can be preserved by maintaining current water table levels.

Key Words: Atlantic white cedar, soil respiration, temperate peatlands, hydrology, self-maintenance, organic matter accumulation

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), swamp ecosystems services and self-maintenance in Virginia and North Carolina are dependent upon the persistence of a peat substrate. As peatlands form, swamps gain autogenic control over hydrology and subsequent peat dynamics (Bridgham et al. 1996, Moore and Bellamy 1974). Peatlands develop when there is a positive water balance and vegetative production is greater than decomposition by microorganisms. Decomposition, or mineralization, leads to the development of chemically complex humic substances (e.g. humic and fulvic acids) that are resistant to oxidation. Constraints on decomposition include anaerobic conditions associated with long duration of saturation, carbon quality of litter, nutrient availability, and pH (Bridgham et al. 1996).

National wildlife refuges at Alligator River, Great Dismal Swamp, and Pocosin Lakes and parties required to compensate for wetland loss are undertaking restoration of cedar swamps. Much of the impact to cedar swamps in the mid-Atlantic region has resulted from drainage (Atkinson et al. This Volume[a]). Peat drainage speeds oxidation, and both litter and soil organic matter tend toward more recalcitrant (i.e. lower quality) carbon compounds as they decompose (Bosatta and Agren 1991). Oxidation can be expected to increase initially under aerobic conditions but the long-term effect of drainage leads to eventual decline in the rate of oxidation as high quality carbon compounds are rapidly decomposed and recalcitrant carbon and mineral compounds form a greater fraction of the remaining soil (Lilly 1981). Bridgham and Richardson (1992) found that the most likely cause of differences in soil respiration in North Carolina peatlands were initial litter quality (chemical and nutrient composition and suitability for decomposer organisms) and carbon quality of the peat.

Measurement of gaseous carbon loss from litter and soil provides a comparable measure of decomposition among different sites as well as integrating carbon loss from a variety of soil substrates within individual sites (Heal et al. 1981). The objectives of this study were: (1) to compare the effects of hydrology on the peat mass using mid-growing season water table levels at Great Dismal Swamp and Alligator River, (2) to determine which sites have been, or are likely to be, negatively impacted by hydrologic alteration, and (3) to determine if the Great Dismal Swamp sites have been more effectively drained than the Alligator River sites and evaluate the influence of substrate on organic mineralization rates.

METHODS AND MATERIALS

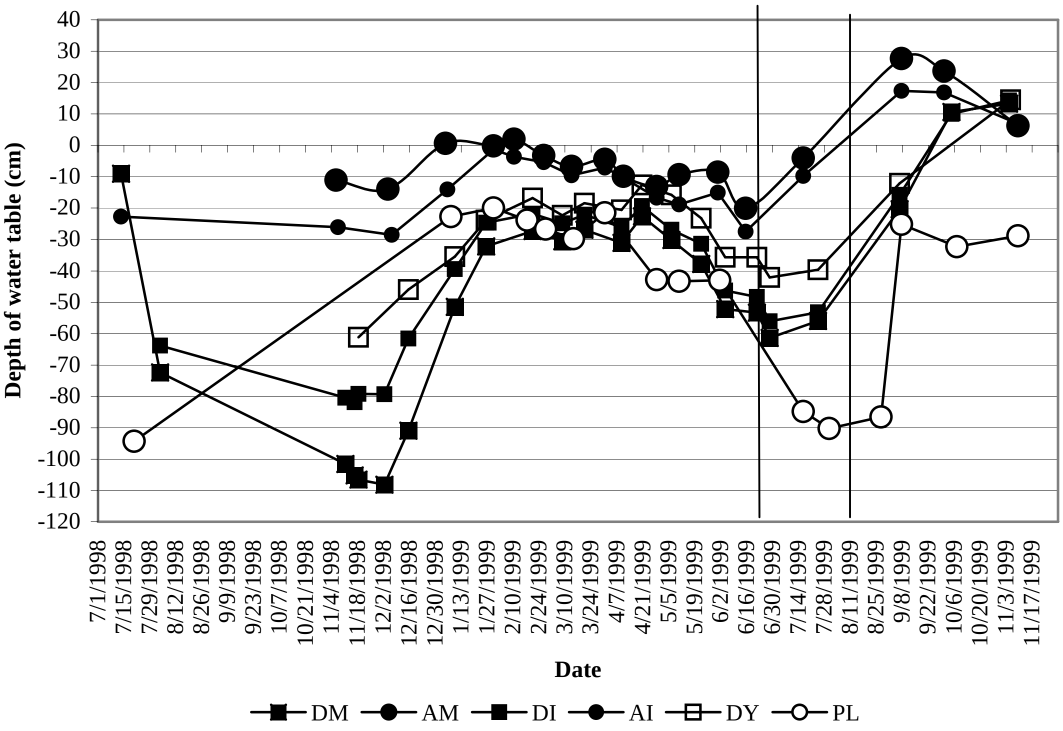
Site Description

The six study sites have all undergone hydrologic alteration in some form. Three sites were located in the Great Dismal Swamp (GDS), which was first ditched in the late 1700s but was effectively drained by the early 1900s (Atkinson et al. This Volume[a]). Two other sites located on the peninsula formed by the Alligator River (AR) were also ditched, but these sites exhibit a much higher water table than do the GDS sites (Atkinson et al. This Volume[b]). The site at Pocosin Lakes (PL) exhibits water table characteristics similar to GDS despite a severe fire that oxidized considerable surficial peat. Sites represented a chronosequence of cedar stands and are further described in Atkinson et al. (This Volume[b]).

Field Hydrology Conditions

Hydrology was monitored at all sites from summer 1998 to autumn 2000 using an array of nine wells including one RDS well that recorded water level two times per day. Hydrologic monitoring indicated that water levels in AR mature and intermediate-aged sites ranged from surface flooding to 20 cm below ground surface during the mid growing season. All other sites showed a pattern of late spring drawdown followed by a fluctuation in water levels that did not rise to within 30 cm of ground surface throughout the growing season (Atkinson et al. This Volume[b]). The 50 days during the middle of the growing season (June 24 through August 12) at the two mature sites were chosen to reflect peak seasonal soil respiration. Mean depth to water table for that period was 4 cm below ground surface for AR mature site and 56 cm below surface for the GDS mature site, and these conditions were used as laboratory treatments (figure 1).

Figure 1. Mean water table depths for six cedar stands. The mid 50 days of the growing season are indicated by vertical lines.



Great Dismal Swamp mature (DM), GDS intermediate (DI), GDS young (DY), Alligator River mature (AM), AR intermediate (AI), and Pocosin Lakes (PL)

Peat Core Collection and Preparation

Between January 11 and 18, 2000, six soil cores were collected in the vicinity of a continuous recording well located on each of the six sites. Cores of the top 30 cm of peat were collected directly into 10.2-cm internal diameter polyvinyl chloride columns that were 60 cm in length. Compression was minimized by precutting roots to the same depth for all cores to facilitate core extraction. The columns were capped both top and bottom during field collection, returned to the laboratory the same day and held at 4-8 °C. Cores were drained by removing tops and replacing the bottom caps with a layer of spun polyester fiber and fiberglass screen which were immersed in reservoirs of distilled water to allow the initially saturated cores to drain freely to field capacity. After six to eight days, the bottoms of cores were again capped prior to beginning the treatment regime.

Treatments

In the initial drained treatment, all six cores from the six sites were allowed to remain drained to 30 cm below the soil surface. Beginning after a 7-day equilibration period, sampling was conducted weekly over a 40-day period. On the 41st day, concurrent drained and saturated treatments began. Three of the six cores from the six sites were randomly selected and saturated with distilled water to 4 cm below the soil surface, while the remaining three cores from each site were maintained in the drained condition. Thus, for the initial drained treatment, there were six replicate cores for each site on each sampling date; whereas for the concurrent drained and saturated treatments, there were three replicate cores per treatment for each site on each sampling date.

For sampling, each column was capped and sealed against air loss. The headspace gas was made uniform by drawing and expelling gas via a syringe. Three 8-ml samples of gas were drawn into syringes and 4 ml was injected into a gas chromatograph equipped with a thermal conductivity detector for analysis.

Carbon dioxide emission rate was calculated as the linear change in concentration over time from the first to the third sample for every core on each sampling date. Mean CO_2 emission rates were calculated for each treatment at each site. One-way analysis of variance (ANOVA) was used to determine significant differences among sites and between drained and saturated treatment. Student's t-test and linear regression were used to determine if parameters describing field hydrology conditions were predictors of CO_2 flux rates from organic soils.

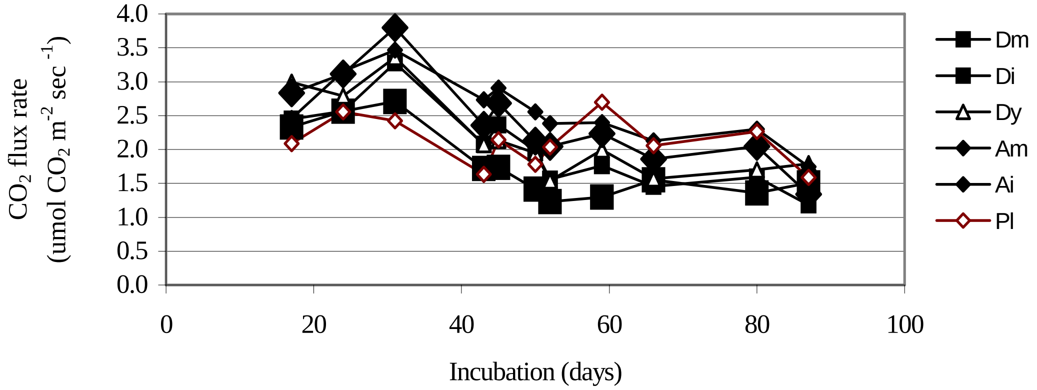
RESULTS

The CO_2 flux rate from all drained cores first rose, then declined over time during incubation days 30 through 87 (figure 2a). Emission rates generally peaked during the third sampling date (after 31 days incubation) and the minimum rate was recorded at the end of incubation (incubation day 87).

Initial Drained Treatment

The peak CO_2 flux rate for any site in the drained treatment was 3.8 µmol CO_2 m^{-2} sec^{-1} and occurred in cores from the AR mature site. There was no significant difference between GDS, AR, and PL in the initial drained treatment ($P > 0.05$).

Figure 2a. Carbon dioxide flux rates for drained cores over the incubation period of both the initial and concurrent drained treatments.



Concurrent Treatments

The cores having the lowest emission rates under a drained condition were from the GDS mature site (1.0 µmol CO_2 m^{-2} sec^{-1}). The CO_2 flux rate from the saturated cores declined initially then became generally stable over time from incubation days 45 through 87. Peak CO_2 flux rate for the saturated condition occurred in the AR mature cores and was 2.1 µmol CO_2 m^{-2} sec^{-1}. The minimum emission rate under the saturated condition was for a GDS mature site core at 0.4 µmol CO_2 m^{-2} sec^{-1}. The saturated treatment resulted in CO_2 flux rates significantly lower for the combined GDS sites (mature, intermediate and young, 1.19 µmol CO_2 m^{-2} sec^{-1}) than for the combined AR sites (mature and intermediate, 1.64 µmol CO_2 m^{-2} sec^{-1}) ($P < 0.05$). During the concurrent treatments, saturated cores exhibited lower mean CO_2 flux rates than the drained treatment ($P < 0.05$). Differences between drained and saturated cores were found at the AR intermediate site, GDS intermediate site and PL (young) (figure 2b). PL is the only site for which CO_2 flux was not lower during the concurrent drained treatment than it was in the initial drained treatment.

Initial and Concurrently Drained Treatments Combined

The grand mean CO_2 flux rate for drained cores (initially and concurrently drained treatments) from all of the GDS sites was 1.87 µmol CO_2 m^{-2} sec^{-1}, which was lower than from AR cores (2.27 µmol CO_2 m^{-2} sec^{-1}) ($P < 0.005$). For the total experimental period, differences were not detected within age classes, but the grand mean CO_2 flux rate for GDS was less than for AR ($P < 0.05$) (figure 2a).

Saturated Treatment

The grand mean for all GDS cores was 1.59 µmol CO_2 m^{-2} sec^{-1}, which was significantly lower than for all AR cores (2.16 µmol CO_2 m^{-2} sec^{-1}) ($P < 0.001$). Among saturated cores within age classes, GDS mature (0.98 µmol CO_2 m^{-2} sec^{-1}) was lower than AR mature (1.65 µmol CO_2 m^{-2} sec^{-1}) ($P < 0.05$) (figure 2c).

Figure 2b. Comparison of mean CO_2 flux rates within (a, b and c represent significant differences, $P < 0.05$) and between sites for initial drained and concurrent treatments. Error bars are standard error.

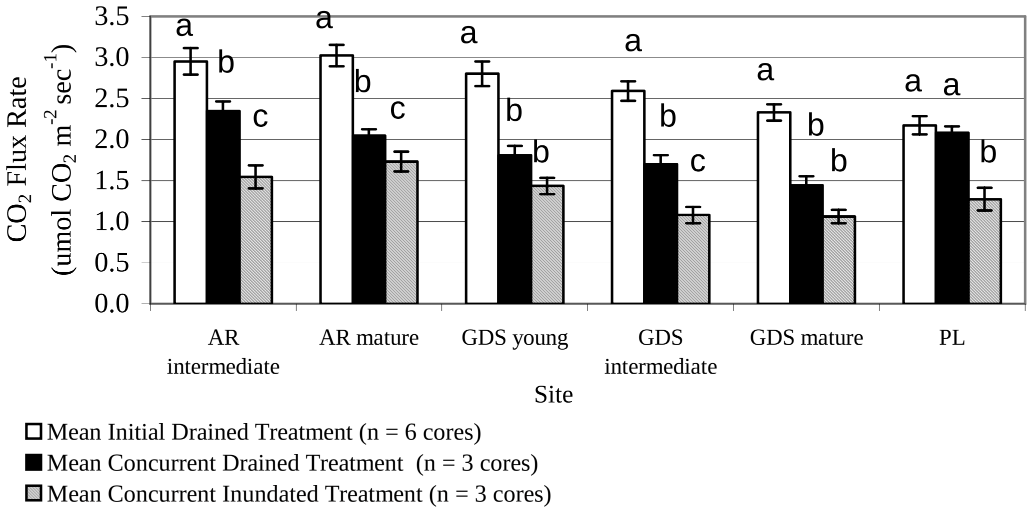
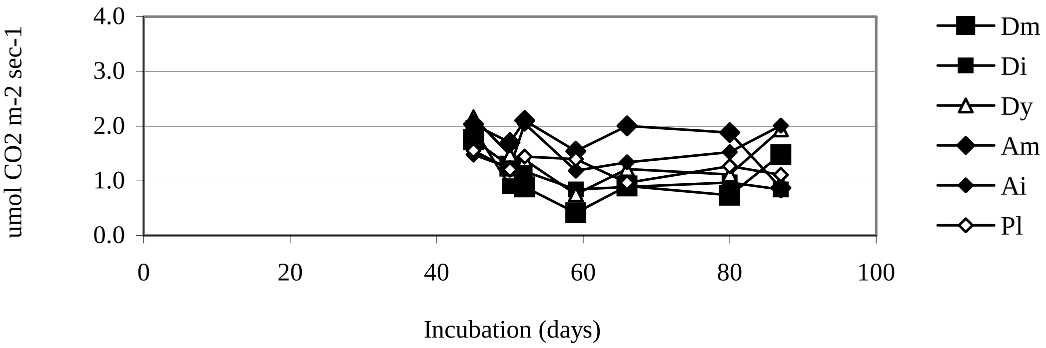


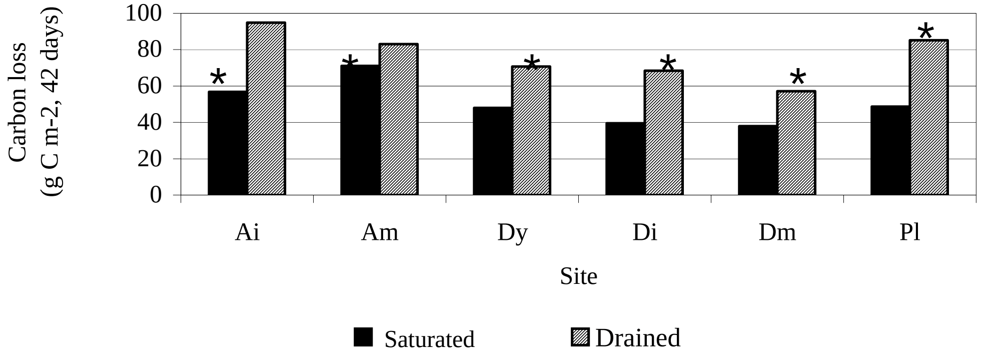
Figure 2c. Carbon dioxide flux rates for the saturated treatment of cores over time.



Cumulative Carbon Loss

Total carbon loss as CO_2 over the period of concurrent treatments (figure 3) was estimated by integrating the CO_2 flux rates over time (42 days of concurrent treatments) based on water table levels that were measured in the field (figure 1). When exposed to normal field conditions, (i.e. GDS cores were drained and AR cores were saturated), the carbon loss from GDS cores was not different from the AR cores. However, when cores were exposed to reciprocal field conditions (i.e. GDS cores were saturated and AR cores were drained), the carbon emission rates differed greatly: emission rates for saturated GDS cores were 37.95 and 39.44 g C m^{-2} for the mature and intermediate sites,

Figure 3. Mass of carbon lost as CO_2 over the 42-day concurrent treatments comparing the usual field hydrology condition during the growing season (*) and the alternate (reciprocal) condition.



respectively. For the drained AR cores, rates were 83.10 and 94.83 g C m^{-2} for the mature and intermediate sites, respectively. This corresponded to a 38.4% decrease in flux rate in GDS cores and a 39% increase in AR cores.

Flux Rates and Field Hydrology

In both AR sites, the water table was within 15 cm of the ground surface for >250 days per year and for all 50 days of the mid-growing season; but for the remaining sites, the water table was within 15 cm of the ground surface for only 6 to 99 days per year and 0 days within the mid-growing season period. The CO_2 flux rates for AR sites were higher than those of the other sites ($P < 0.05$) and field hydrology data from the mid 50 days of the growing season was a good predictor of CO_2 emissions from drained cores ($n = 6$, $r^2 = 0.73$, $P < 0.001$) (table 1). The relationship was similar using yearly data for the sites ($n = 6$, $r^2 = 0.71$, $P < 0.001$).

Table 1. Carbon dioxide flux rates from Alligator River mature and intermediate sites were significantly higher than those of all other sites ($p < 0.05$). The relationship between the number of days (of the 50 mid growing season days) that the seasonal water table is within 15 cm of the ground surface was also predictive of the mean CO_2 flux rates of cores when drained ($r^2 = 0.73$).

Sites	Number of days seasonal water table is within 15 cm of ground surface		Mean CO_2 flux rates of cores when drained
	Mid 50 days of growing season	Yearly	µmol CO_2 m^{-2} sec^{-1}
Am	50	326	2.37
Ai	50	251	2.55
Dy	0	99	2.11
Pl	0	18	2.05
Dm	0	10	1.71
Di	0	6	2.03

Alligator River mature (Am), AR intermediate (Ai), Great Dismal Swamp young (Dy), GDS mature (Dm), GDS intermediate (Di), and Pocosin Lakes (Pl)

DISCUSSION

Drained Condition

Under both the saturated and drained treatments, CO_2 flux rates at GDS sites were lower than in the AR sites, which suggests that there was less labile carbon in the soil at GDS than at AR. Carbon dioxide flux rates measured in this study were similar to potential aerobic respiration measured by Bridgham and Richardson (1992) working in short pocosin and tall pocosin, two other peatlands communities in eastern North Carolina.

Gradually, as the drained cores also lost water via evaporation, a moisture deficit may have inhibited microbial respiration and contributed to decreasing CO_2 flux rates. The addition of water to the drained cores prior to the last two sampling dates resulted in an increase in flux rate for the GDS mature site. The flux rates in the other sites remained either approximately steady or decreased slightly. In addition, the trend of declining CO_2 emission rates over time suggested that labile carbon sources were declining in all cores over the course of this study.

Saturated Condition

For all sites, saturated cores exhibited lower CO_2 emission rates than drained cores. Anoxic conditions associated with saturated soil conditions have been widely reported to limit decomposer efficiency and thus lower rates of CO_2 emission (Bridgham and Richardson 1992, Moore and Knowles 1989, Moore and Dalva 1997, Hogg et al. 1992).

Field Hydrology and Soil Respiration

The CO_2 flux rate of the cores when drained may have reflected the duration within mid-growing season or annually of the seasonal water table position being within a critical depth from the surface. Under both the saturated and drained treatments, the CO_2 flux rates at GDS sites were lower than for the AR sites.

Over the 42-day period of concurrent drained or saturated treatments, when the summer field conditions were considered (i.e. drained condition for GDS sites and saturated condition for AR sites), estimated total carbon losses from the drained GDS cores and saturated AR cores (mature and intermediate) were not different. Bridgham and Richardson (1992) concluded that the most likely cause of differences in soil respiration (CO_2 and CH_4 production) between plant communities of North Carolina peatlands was low carbon quality of the peat, as opposed to other factors studied such as nutrient concentration, pH, and aerobic/anaerobic condition. Similarly, in a study designed to predict the effect of global warming and climate change, Hogg et al. (1992) found that peat exposed to long periods of aerobic conditions were highly decay resistant. In the present study, the number of days during the middle of the growing season in which water tables were within 15 cm of the surface was found to be a good predictor of mean and peak CO_2 flux. The extended shallow water table preserves labile carbon that can then be more rapidly lost as CO_2 if the water table is depressed.

The GDS intermediate age site had greater carbon loss in the 42-day treatment than the AR intermediate site. One explanation may be a higher litterfall of *Acer rubrum* L. (red maple) in GDS than in AR (DeBerry et al. This Volume), and red maple decomposes faster than cedar (Gomez and Day 1982).

The PL site was the only site for which flux rates did not decrease from initial to concurrent drained treatments. Hogg et al. (1992) found that, although peat fires remove the more labile surface organic matter and may expose formerly buried peat to aerobic conditions, the respiration rate may not be higher because the exposed peat is recalcitrant. Ash from the burned peat does not necessarily promote higher respiration rates, probably due to variability in microbial populations. PL underwent a fire and also has a deep seasonal water table similar to those of the GDS sites. PL drained treatment flux rates did not differ over time which suggests that peat strata were increasingly recalcitrant with depth (Bridgham and Richardson 1992, Hogg et al. 1992).

Some inferences may be drawn regarding altered water tables at these sites. According to the findings of Hogg et al. (1992) the greatest loss of dry mass occurs from the top 10 cm under warm, drained conditions, such as present in our sites at GDS. Shallow water tables are currently more prevalent at AR. The AR sites would be more susceptible to large CO_2 loss in a global warming scenario in which rising temperature co-occurred with lower water tables. Efficient drainage would have a similar effect since Hogg et al. (1992) found aeration to be more important than higher temperatures. GDS, having undergone extended periods of drawdown, is less susceptible to increased temperatures and further drawdown than AR since peat is already recalcitrant. However, deeper peats were not sampled in this study and the effects of a lower water table on these deeper layers cannot be predicted from our results.

Another limitation of our study is the duration of incubation. Megonigal et al. (1996) found that the microbially active season extends throughout the entire year in North Carolina and throughout the southeastern United States. Therefore, to fully represent soil respiration and carbon loss, one would have to consider the conditions during an entire year.

Management Implications

The results of this experiment are applicable to the management of hydrology for the preservation of the peat associated with cedar wetlands of the mid-Atlantic coast. Although field measurement of CO_2 emissions does not appreciably differ between the Great Dismal Swamp and Alligator River NWR sites, (Kalnins personal observation), the flux rates within each site appear to be under hydrologic control. The results from cores in the present study suggest that the lower CO_2 emission rates from GDS cores under both hydrologic treatments were the result of poor substrate quality (carbon quality) following historically higher emission rates under more than 100 years of artificially drained conditions. To maintain stores and to decrease the loss of annual carbon input in these sites, it would be necessary to extend the number of days per year that a site is saturated with water at depths shallower than 15 cm below ground surface. It is also important to note that the deep seasonal water table at these GDS sites makes them susceptible to deep peat fires, while the AR sites are susceptible to rapid decomposition of organic matter should they be efficiently drained.

In conclusion, the promotion and maintenance of a peat-based cedar ecosystem is dependent upon maintenance of a hydrologic regime that allows sufficient organic matter (and carbon) to be sequestered. A hydrologic regime with a persistent shallow water table is required to limit the biochemical oxidation of peat, protect against deep fires, and promote carbon sequestration.

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LITERATURE CITED

Atkinson, R. B., T. E. Morgan, R. T. Belcher, and D. A. Brown. This Volume[a]. The role of historical inquiry in the restoration of Atlantic white cedar.

Atkinson, R. B., J. W. DeBerry, D. T. Loomis, E. R. Crawford, and R. T. Belcher. This Volume[b]. Water tables in Atlantic white cedar swamps: implications for restoration.

Bosatta, E. and G. Ågren. 1991. Dynamics of carbon and nitrogen in the organic matter of the soil: a generic theory. The American Naturalist 138 (1):227-245.

Bridgham, S. D., C. J. Richardson, E. Maltby, and S. P. Faulkner. 1991. Cellulose decay in natural and disturbed peatlands in North Carolina. Journal of Environmental Quality 20:695-701.

Bridgham, S. D. and C. J. Richardson. 1992. Mechanisms controlling soil respiration (CO_2 and CH_4) in Southern peatlands. Soil Biology and Biochemistry 24(11): 1089-1099.

DeBerry, J.W., R.T. Belcher, D. T. Loomis, and R. B. Atkinson. This Volume. Aboveground biomass structure of four managed Atlantic white cedar swamps in North Carolina.

Dolman, J. D. and S. W. Buol. 1967. A study of organic soils (Histosols) in the Tidewater region of North Carolina. Technical Bulletin no. 181. North Carolina Agricultural Experiment Station. North Carolina State University at Raleigh. 51 pp.

Gomez, M. M. and F. P. Day, Jr. 1982. Litter nutrient content and production in the Great Dismal Swamp. American Journal of Botany 69(8): 1314-1321.

Heal, D. W., P. W. Flanagan, D. D. French, and S. F. Maclean, Jr. 1981. Decomposition and accumulation of organic matter In: Bliss, O. C., O. W. Heal, and J. J. Moore, editors. Tundra ecosystems: a comparative analysis. Cambridge University Press, Cambridge, New York pp. 587-633.

Hogg, E. H., V. J. Lieffers, and R. W. Wein. 1992. Potential carbon losses from peat profiles: Effects of temperature, drought cycles and fire. Ecological Applications 2:298-306.

Kalnins, M. 2000. Personnal communication.

Korstian, C. F. 1924. Natural regeneration of Southern White Cedar. Ecology 5(2):188-194.

Lilly, J. P. 1981. The blackland soils of North Carolina: Their characteristics and management for agriculture. North Carolina Agricultural Research Service Technical Bulletin no. 270. 70 pp.

Megonigal, J. P., S. P. Faulkner, and W. H. Patrick. 1996. The microbial activity season in Southeastern hydric soils. Soil Science Society of America Journal 60:1263-1266.

Moore, P. D. and D. J. Bellamy. 1973. Peatlands. Paul Elek. London. 221 pp.

Moore, T. R. and R. Knowles. 1989. The influence of water table levels on methane and carbon dioxide emissions from peatland soils. Canadian Journal of Soil Science 69: 33-38.

Moore, T. R. and M. Dalva. 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. Soil biology and biochemistry 29 (8):1157-1164

Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. Conservation Biology 10 (4):1163-1174.

A COMPARISON OF CH_4 AND CO_2 PRODUCTION IN RESTORED AND NATURAL ATLANTIC WHITE CEDAR SWAMPS

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Abstract: Most wetlands act as a sink for carbon and store it in peat soils. This carbon sink functions to buffer atmospheric carbon dioxide increases. Carbon mineralization still occurs within the soil profile, which generates both CO_2 and CH_4 under anaerobic conditions. The carbon sink is a necessary process for the successful establishment of restored sites. We compared the rates of methane and carbon dioxide production in proposed restored and natural cedar swamp soils. Eight different sites were examined in southeastern Virginia and northeastern North Carolina. Three of these sites are restoration sites that have been either logged or farmed in recent years. The other five sites are natural cedar swamps which range in age from recently logged (a young regeneration site), intermediate (20 to 30 years), to mature (+65 years) sites. Three soil cores (30 cm deep), collected from each site, were sampled every ten-centimeter depth interval, placed in a stoppered flask, flushed with nitrogen and incubated at 24.5C. Flask headspace was sampled every other day for two weeks. Gases were analyzed on a GC equipped with FID and TCD detectors. Methanogenic activity was apparent in two natural cedar stands located in North Carolina (Alligator River National Wildlife Refuge). Only the two restoration farm sites had significant levels of activity producing 20% of the activity level as the ARNWR sites. Carbon dioxide production was elevated in the natural sites as compared to the restored sites. Within each site, higher levels of CO_2 production were associated with the surface depths (0 to 10 cm) as compared to the lower soil depths. This higher activity may be related to the greater density of live roots located within this surface soil.

Key Words: carbon sink, methanogenic activity, wetland compensation

INTRODUCTION

Many wetlands act as a sink for carbon and store it in peat soils (Gorham 1991). This carbon sink functions to buffer atmospheric carbon dioxide increases, however carbon mineralization still occurs within the soil profile, which releases both CO_2 and CH_4 to the atmosphere (Aselmann and Crutzen 1989, Cicerone and Oremland 1988). Under anaerobic conditions biological methanogenesis serves as the terminal step in carbon flow in many wetland habitats (Zindler 1993). These gases can also serve as carbon and energy sources for microbial populations prior to emission to the atmosphere (Zindler 1993).

Depending on the location and position within the landscape, many wetlands act as carbon sinks, building up peat soils over long time periods (Aselmann and Crutzen 1989). In wetland types characterized with peat soils, the carbon sink into wetlands should be considered as a necessary functional property of a successfully restored site. As an indicator of this functional aspect, our goal was to examine the potential of soils to produce methane and carbon dioxide in both natural cedar forested wetlands and proposed restored sites within the Southeast Virginia and northeast North Carolina regions.

METHODS

Eight wetland sites were examined in Southeastern Virginia and Northeastern North Carolina. Three of these sites are located in the Great Dismal Swamp National Wildlife Refuge and are within 1 km of each other. These are all natural cedar stands that range in age from a young site (logged) which is two years old (DY), to a intermediate site which is 20-30 years old (DI), and to a mature site which is approximately 65 years old (DM). Two other sites were located within the Alligator River National Wildlife Refuge in North Carolina. These sites are also natural cedar swamps that have an age range from intermediate (AI) to mature (AM). Two other sites located at a compensation site (C1-8 yrs old & C2-6 yrs old) were created wetlands that were planted with cedar on land that was recently farmed. This site is located on the eastern side of the Great Dismal Swamp. A site was also located at Pocosin Lakes National Wildlife Refuge (PL), which is a restoration site that was recently burned and planted with cedar.

Three soil cores were extracted to 30 cm depths from each site using a stainless steel coring tube (8-cm diameter). The intact soil cores were transferred to PVC carrying tubes, flushed with N_2 gas (to maintain anaerobic conditions) and transported back to lab for further processing.

The cores were extracted from the PVC tubes under an N_2 atmosphere in a glovebox, and subdivided into 10cm depth intervals. Each depth was hand-homogenized, and a small subsample (ca. 1 gdw) was placed into a flask. The flasks were stoppered, sealed, and 10 ml of water was added to produce a peat-soil slurry. Each flask was evacuated and flushed with nitrogen three times on a manifold to assure anaerobic conditions within the flasks. Each flask was pressurized to 1.5 atmospheres to allow for multiple headspace sampling. Samples were incubated at 24.5C over the course of the experimental sampling. This temperature is close to the maximum ambient soil temperature measured in the field and would produce maximum activity levels.

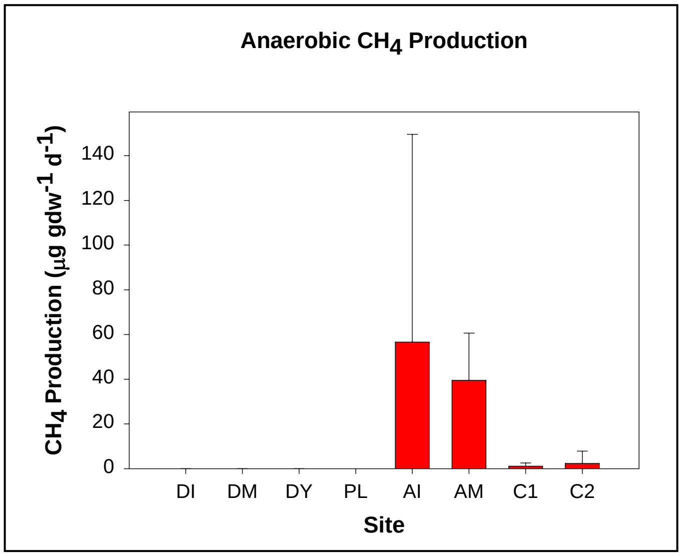
Each flask headspace was sampled every 48 hours over 14 days. Samples were immediately analyzed on a gas chromatograph equipped with thermal conductivity and flame ionization detectors to measure carbon dioxide and methane, respectively.

Rates of CO_2 and CH_4 production were calculated by linear regression. Statistical comparisons among sites and depths were conducted with two-way analysis of variance using Sigma Stat® (SPSS Inc., Chicago, Illinois).

RESULTS

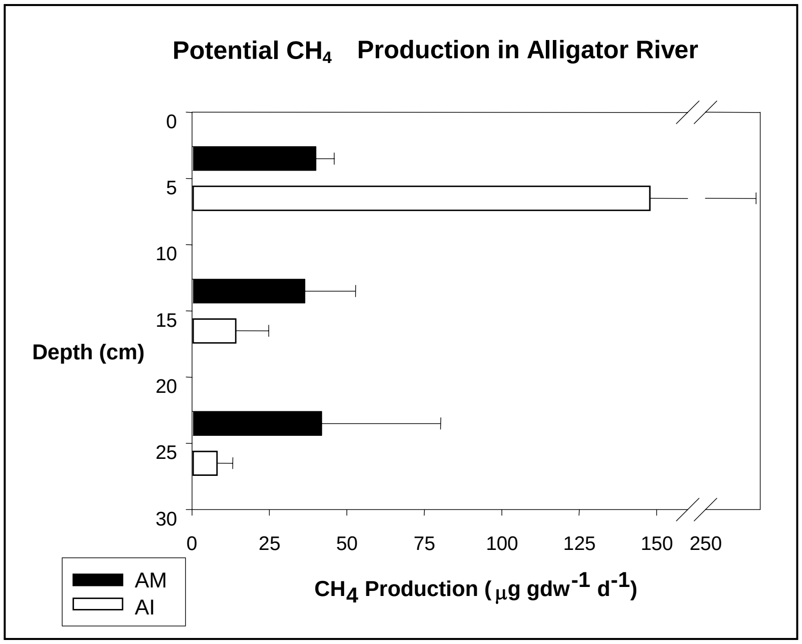
Methane production was only observed in the Alligator River sites (AM, AI) and the Compensation sites (C1, C2; figure 1). Methane production at all other sites was found to be statistically insignificant. AM and AI had the greatest production with rates up to 58 gCH_4 m^2 h^{-1}. Statistically greater amounts of CH_4 were produced in AI (ANOVA, p=0.050).

Figure 1. Potential anaerobic methane production in all sites. Methane production was only observed in Alligator River and Compensation sites.



Within the four sites that did produce CH_4, production was examined at each depth interval. In most cases, there was greatest production near the surface (0 to 10 cm) and lower production with depth. The surface depths (0 to 10 cm) were statistically different then the other two depths, but the two lower depths were not statistically different to each other in most all sites. AI showed this decreasing production profile (figure 2). However, in contrast, AM site was located only 500 m distance from AI, had CH_4 evenly produced over all depth intervals (figure 2). This pattern of greatest production near the surface was also apparent at the compensation sites (figure 3).

Figure 2. Potential anaerobic methane production at each depth in both Alligator River sites. At Alligator Intermediate (AI), production was greatest near the surface. The Alligator Mature (AM) site showed no change with depth.



Carbon dioxide production was observed in all sites (table 1) with greatest production rates measured in the natural sites (AI, AM, and DM). AM and AI were statistically greater than DM (ANOVA, p = 0.05). All sites showed a profile with depth having higher rates near the surface and lower rates with depth (table 1). The surface depths were significantly different than the two lower depths (ANOVA, p=0.05). The two lower depths were not significantly different from each other within each site.

Figure 3. Potential anaerobic methane production at each depth for the compensation sites. Production was greatest at the surface for both sites.

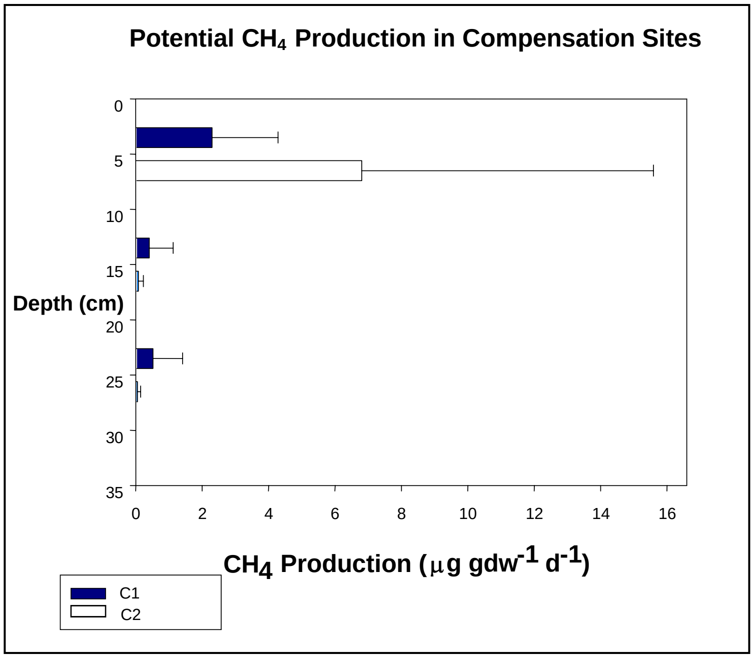


Table 1. Potential anaerobic carbon dioxide production at each depth for each site. All sites had decreasing production with depth, except AM, which was similar to emissions of methane, which had no profile.

Site	CO_2 Production (μg CO_2 gdw^{-1} d^{-1})		
	Depth		
	5 cm	15 cm	25 cm
DI	164.1	141.4	101.5
DM	238.6	125.2	124.4
DY	171.5	104.4	83.4
PL	83.2	108.0	96.8
AM	237.3	198.1	193.8
AI	345.4	202.6	163.3
C1	35.1	31.1	25.4
C2	27.9	20.0	22.7

DISCUSSION

The differences in methane production found within these sites may be due to soil moisture effects. The CH_4 production observed in the Alligator River sites and the compensation sites are associated with higher water tables in these sites as compared to the other sites (Moore and Dalva 1993). Moore and Dalva (1993) examined CH_4 and CO_2 production in a subarctic fen, a temperate bog and a temperate swamp. They found much higher CH_4 production with elevated water tables. The higher water table in the Alligator and Compensation sites can promote the anaerobic condition in which methanogens proliferate.

The greater CH_4 production associated with AM and AI soils could also be due to a higher density of roots in these sites. The higher density of roots will provide more substrates for microbes, thus producing more CH_4 (Phelps and Zeikus 1984, Harvey et al. 1989, Yavitt and Lang 1990).

Methane production with depth was also observed. In the AM site, CH_4 was similar throughout the soil profile. This was probably because the roots are distributed evenly throughout the 30 cm profile in the AM site (Rodgers and Day, Abstract presented at this symposium). In the Alligator Intermediate site, greater CH_4 production was measured closer to the surface. We suggest that this profile is due to a greater concentration of roots near the surface. This profile of higher CH_4 production near the surface was also observed within the compensation soils and most likely is also related to live root profile.

All sites produced CO_2 from soil respiration. The Alligator River sites were found to be statistically greater than all the other sites. This was probably due to an increased organic matter content and substrate production in these sites (Bridgham and Richardson 1992). Bridgham and Richardson (1992) found that the amount of organic matter is highly correlated with CO_2 production and N mineralization in Minnesota peatlands. Root exudation and turnover could also explain the increased amount of organic matter within AM and AI sites. The compensation sites were significantly lower than other sites for CO_2 production. The compensation sites also had significantly lower organic matter content (unpubl. data, Whiting, Garda, Kalnins, and Kessler).

Production of CO_2 with depth indicated that the DM and DY sites as well as the AI site all had higher rates near the surface and decreasing rates with depth. This near surface production is most likely related to the greater root concentration near the surface. The AM site did not show a profile with depth, as with the CH_4. Again, this is most likely related to an even distribution of roots within this mature cedar site.

From the non-production of methane within sites that are typically considered functional wetlands (Dismal Swamp NWR), we suggest that CH_4 production should not be used to indicate that an important functional aspect of a wetland has become established. Production of CO_2 (a measure of the total microbial activity within these soils) may also be very difficult to utilize as a measurement indicator since many processes (rooting depth, previous moisture history) can vary widely from site to site, and even within a site.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Aselmann, I. and P.J. Crutzen. 1989. Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. Journal of Atmospheric Chemistry 8: 307-358.

Bridgham, S. D. and C. J. Richardson. 1992. Mechanisms controlling soil respiration (CO_2 and CH_4) in southern peatlands. Soil Biology. 24: 1089-1099.

Cicerone, R.J. and R. Oremland. 1988. Biogeochemical aspects of atmospheric methane. Global Biogeochemical Cycles 2: 299-327.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecological Applications 1(2): 182-195.

Harvey H. R., R. D. Fallon, and J. S. Patton. 1989. Methanogenesis and microbial lipid synthesis in anoxic salt marsh sediments. Biogeochemistry 7: 111-129.

Moore, T. R. and M. Dalva. 1993. The influence of temperature and water table position on methane and carbon dioxide emissions from laboratory columns of peatland soils. Journal of Soil Science. 44: 651-64.

Phelps T. J. and J.G. Zeikus. 1984. Influence of pH on terminal carbon metabolism in anoxic sediments from a mildly acidic lake. Applied and Environmental Microbiology 48, 1088-1095.

Yavitt J. B. and G. E. Lang. 1990. Methane production in contrasting wetland sites: response to organic-chemical components of peat and to sulfate reduction. Geomicrobiology Journal 8, 27-46.

Zindler, S.H. 1993. Methanogenesis. Chapman and Hall: New York.

EFFECTS OF WATER TABLE ON SURVIVAL AND GROWTH OF ATLANTIC WHITE CEDAR IN TWO YOUNG PLANTED SITES

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Abstract: Atlantic white cedar (cedar) is an obligate hydrophyte with a narrow range of hydrologic tolerance. The species is in decline due to logging, drainage, and development. High mortality has been reported for many plantings and the exact hydrologic conditions necessary for successful cedar restoration are poorly understood. In 1995, approximately 15,000 rooted cuttings were planted in a 12-ha wetland compensation site consisting of prior converted cropland in Chesapeake, VA (Site 1). A second, adjacent site of similar size was planted in 1996 (Site 2). In winter 1999-2000, we quantified survivorship and growth of cedar in ninety 8 x 5.5-m plots. Plot elevation and well data were used to calculate mean water table depth (MWTD) at each plot. Mortality was estimated at 73% and 65%, respectively. Cedar mortality was related to MWTD at Site 2 ($r^2=0.46$, $P<0.001$, $n=45$) and lowest mortality occurred when the mean water table was between –5 and –40 cm. Growth, measured as change in height, was inversely correlated with MWTD at both sites ($r^2=0.44$, $P<0.001$, $n=45$ at Site 1; $r^2=0.37$, $P<0.001$, $n=33$ at Site 2), indicating better growth in dryer plots.

Key Words: agriculture, growth, wetland compensation, water table, wetland restoration, *Chamaecyparis thyoides*

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.)B.S.P. (cedar), forests have been in decline since prior to the 1740s due to logging, drainage, and development (Laderman 1989 and Atkinson et al. This Volume [a]). Little quantitative data is available to explain the specific conditions required for successful tree establishment (Laderman 1989). Hydrology has been cited as a controlling factor in root zone aeration, nutrient availability and transport, soil temperature, and moisture availability (Laderman 1989). Depending on the flood tolerance of plant species, the anaerobic conditions resulting from inundation may lead to leaf chlorosis, leaf senescence, inhibition of growth, partial injury, or death (Pezeshki 1994). Restoration attempts have increased in recent years, but tree establishment has often been unsuccessful. Cedar is an obligate hydrophyte (occurring in wetlands 99% of the time) (Reed 1988). However, many authors report that newly planted seedlings are particularly susceptible to water stress (Akerman 1923, Little 1950, Clewell and Lea 1990, and Brown and Atkinson 1999). Eagle (2001) cites persistent inundation as the main reason for limited regeneration in planted cedar at a restoration site on Alligator River National Wildlife Refuge. Golet and Lowry (1987) note that few quantitative descriptions of water regimes exist for most wetland types, including cedar.

In this paper, we report the relationship between hydrology and survivorship and growth of cedar at two wetland compensation sites. These results will help define the conditions necessary for successful cedar wetland restoration.

SITE DESCRIPTION

Each of the two 12-ha sites was prior converted cropland in Chesapeake, VA. Each site was divided into three 100 m X 400 m sections by approximately 1 m deep ditches. Field crowns were a prominent feature and were up to 1 m higher in elevation than the edges of ditches (figure 1a).

In January 1995, 1-yr old rooted cedar cuttings were planted on 2.75-m (9 foot) spacing at one Site 1. Site 2, located 400 m southwest of Site 1, was planted in May 1996 with the same spacing, which totaled approximately 1320 trees/ha. Both sites were part of a mitigation bank, and restoration efforts also included raising the water table, installing an electric fence, and mowing and applying herbicide in the first years to reduce competition (personal communication Steve Martin).

Soil at the sites was “Portsmouth mucky loam”, which is an acidic, poorly drained soil with high organic matter in the surface layer (Henry et al. 1958). Small inclusions of the Othello series soil, also strongly acidic and poorly drained, were documented in one section of Site 1 (personal communication Steve Martin). Both soils are found on the hydric soils list (U.S. Department of Agriculture 1985), but were altered by ditches and cultivation. Colonizing vegetation was dominated by *Panicum dichotomiflorum* Michx. and *Juncus effusus* L. at Site 1, and *Eupatorium capillifolium* (Lam.) Small, *Andropogon virginicus* L., *Ludwigia palustris* (L.) Ell., and *Euthamia tenuifolia* (Pursh) Nutt. at Site 2 (Shacochis et al. This Volume). Average temperatures at the sites ranged from 3.9° C (39.1° F) in January and 25.8° C (78.5° F) in July. The growing season was 269 days, from March 8 to December 1. Mean annual precipitation was 113.4 cm, with a monthly low of 7.2 cm in November, and a high of 12.9 cm in July (Natural Resources Conservation Service 2002).

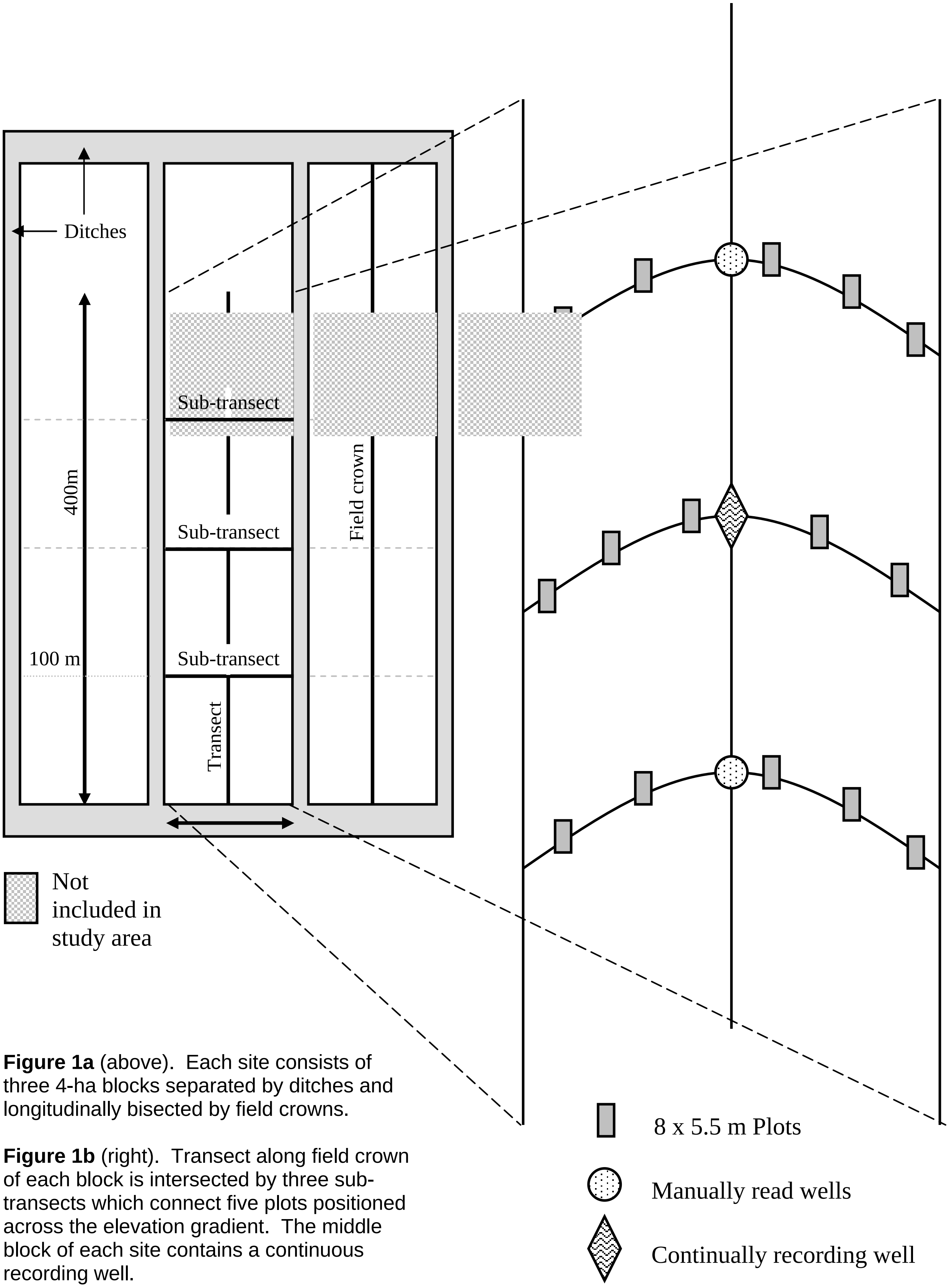


Figure 1a (above). Each site consists of three 4-ha blocks separated by ditches and longitudinally bisected by field crowns.

Figure 1b (right). Transect along field crown of each block is intersected by three sub-transects which connect five plots positioned across the elevation gradient. The middle block of each site contains a continuous recording well.

METHODS

Transects were established down the center (along the field crown) in each of three sections at each site. Three sub-transects, spaced 100 m apart, were perpendicular to each main transect along an elevation gradient (figure 1b). Five 8 x 5.5-m plots were established across field crowns on each sub-transect, for a total of 45 plots at each site. Survivorship and growth were quantified for each tree in all plots using height, width of crown at widest point, basal diameter, color, and posture of tree (upright, bent over more than 30^0, fallen) in January 2000. Trees were considered dead if no green foliage was visible or if no tree was present at a spot where the linear arrangement of surviving trees suggested a tree had been planted.

Elevation was measured at each plot and used in the calculation of mean water table depth (MWTD) at each plot. A Remote Data Systems (RDS) continually recording well was located at the center of each site and eight manually read wells were positioned as shown in figure 1b. Water table depth was measured twice daily using RDS wells, and monthly at the manually read wells, from August 1998 to January 2000.

RDS readings and manually read well readings showed a strong, positive relationship ($r^2 > 0.95$) (Atkinson et al. This Volume[b]). Daily water table depth was calculated for each plot by using this correlation and the relative elevation at each well and plot. Based on these data, several hydrology parameters were calculated for each plot and were used for regression comparisons with growth and mortality measurements within each plot.

We used an abridged version of the 1999 growing season data (March – August) because of the unusually high precipitation at the sites in September and October resulting from two consecutive hurricanes (figures 2 and 3).

Figure 2. Average precipitation for the five growing seasons since the cedar were planted, the adjusted 1999 growing season we used for analysis, and a mean of all five growing seasons.

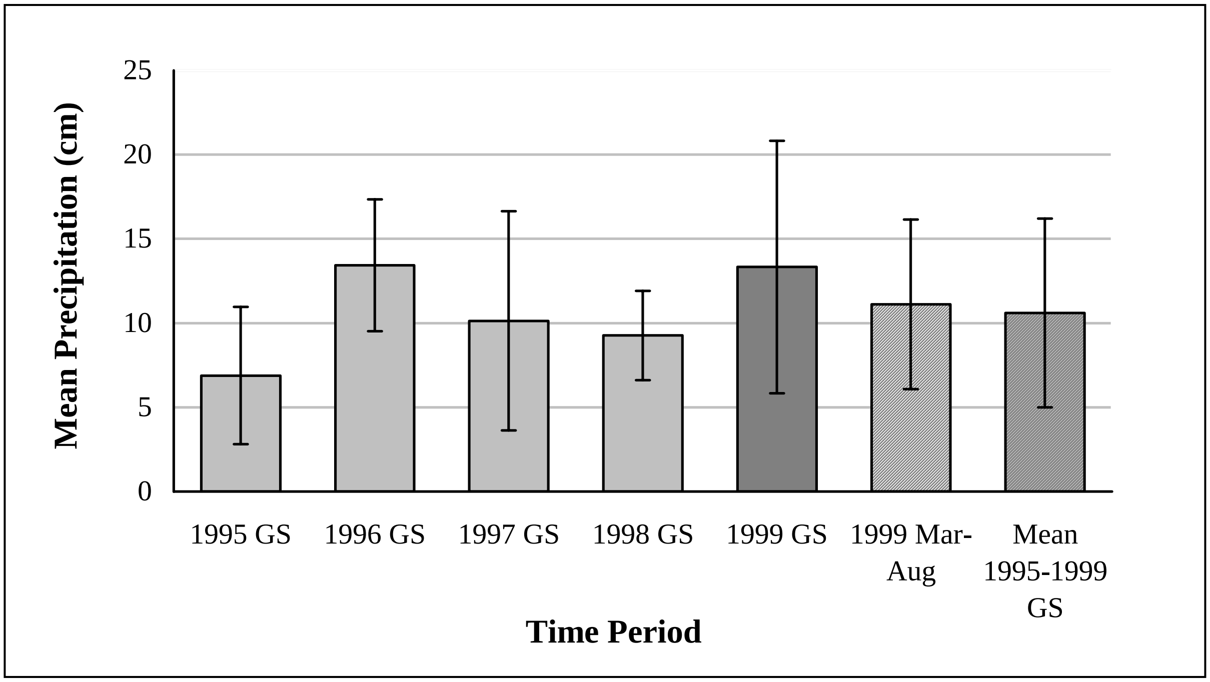
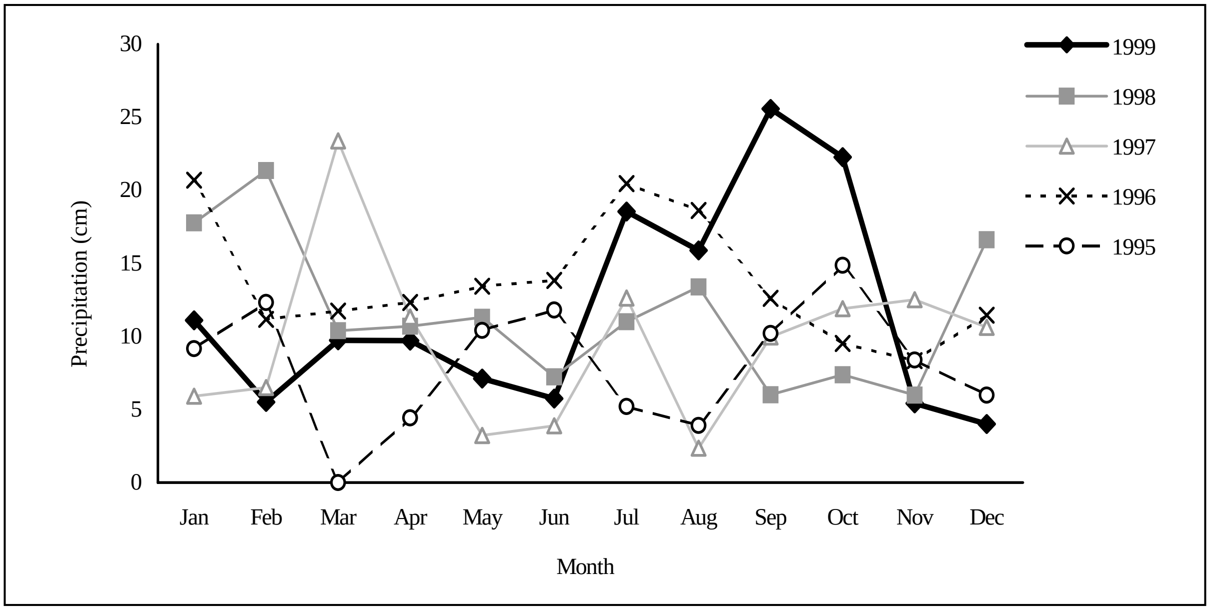


Figure 3. Total precipitation per month over the five years since cedar were planted. Hurricanes Dennis and Floyd in September 1999 resulted in an unusually high water table at both sites for the remainder of the growing season.



Survivorship and growth were compared to several parameters based on water table data gathered from March 1, 2000 to August 31, 2000 for each plot, including:

Mean water table depth (MWTD): Mean calculated depth to water table (positive values indicate inundation).
Duration of inundation (DI): Percent of days during the abridged growing season that a plot was inundated.
Duration of saturation (DS): Variation of DI, percent of days that water table was below –15 cm (-6 in).
Frequency of inundation (FI): Number of times a plot became inundated within the abridged growing season.
Frequency of saturation (FS): Variation of FI, number of times water table rose above –15 cm.
Longest continuous inundation (LCI): Longest number of days in a row within the abridged growing season that a plot was inundated.
Longest continuous saturation (LCS): Longest days in a row the water table was above –15 cm.
Average inundation (AI): The average depth of water above the surface.

DS, FS, and LCS were also calculated relative to -30 cm (-12 in) and -46 cm (-18 in).

Cedar survivorship and growth were compared to these parameters at each plot using linear or polynomial regressions to evaluate the relationship with water tables and to identify the hydrologic conditions that were most conducive to minimum mortality and maximum growth. Mann Whitney

Rank Sum tests were also used to compare site-wise means of several parameters. A P-value of less than 0.05 was used to determine significance. SigmaStat (Access Softek 1995) was used for all statistical analyses.

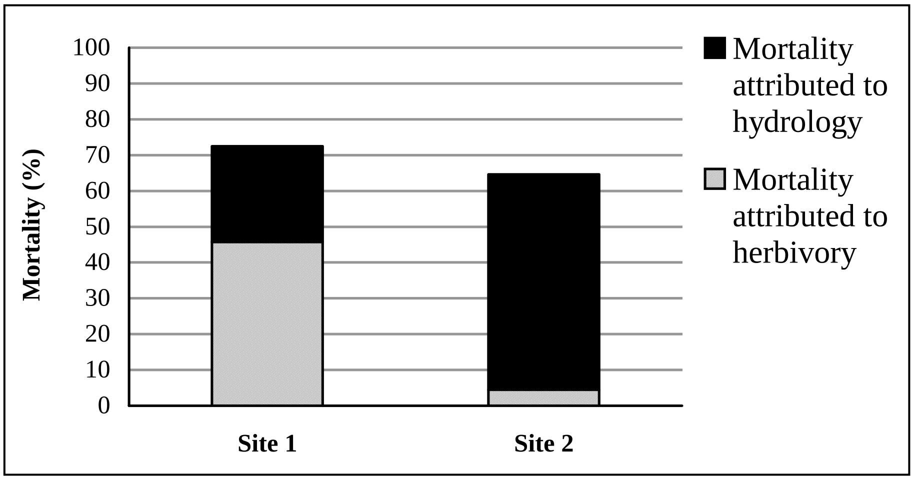
Girdling, defined as chewing through the cambium around the entire circumference of the tree, was prevalent in many portions of the study area. We excluded any completely girdled trees from these analyses, however, many trees were partially girdled and survived, and were included in analyses.

RESULTS

Between-Site Differences

Mortality at Site 1 was 72.5% and 64.6% at Site 2, which was significantly different (Mann Whitney Rank Sum Test, P<0.001). Girdling of trees by small mammals appeared to cause approximately 70% of all mortality at Site 1, while less than 10% of all mortality at Site 2 was caused by herbivory (figure 4). Mortality attributed to hydrology was significantly higher at Site 2. A large portion of the mortality due to hydrology at the wettest plots appeared to have occurred in the first few years.

Figure 4. Total cedar mortality and mortality attributed to hydrology and herbivory at the two sites.



Site 2 was significantly wetter than Site 1, based on AI (Mann Whitney Rank Sum Test, P=0.002). Site averages of MWTD, DI, and LCI were also higher (wetter) at Site 2 (table 1), though not significantly (P>0.05). The distribution of water table depths among plots at Site 2 (Mean=-15.0 cm, SD=22.1 cm) was more even than at Site 1 (Mean=-20.3 cm, SD=13.6 cm), and a larger percentage of plots in Site 1 exhibited a MWTD in an intermediate range (figure 5).

We calculated average growth per year based on height of planted cuttings (30 cm) and the number of growing seasons since planting and estimated average growth as 38 cm/yr at Site 1 and 35 cm/yr at Site 2, which was not significantly different (P=0.199).

Mortality / Attributed to Hydrology

At Site 2, MWTD and mortality were curvilinearly related (r^2=0.46, P<0.001, n=45). The resulting curve predicts that minimum mortality (50% or less) from hydrology may occur when the water table is approximately –30 cm (figure 6). The lowest average mortality (40%) occurred between –11 cm and –37 cm. Alternatively, 11 of 13 plots with mean water tables above the surface experienced 100% mortality.

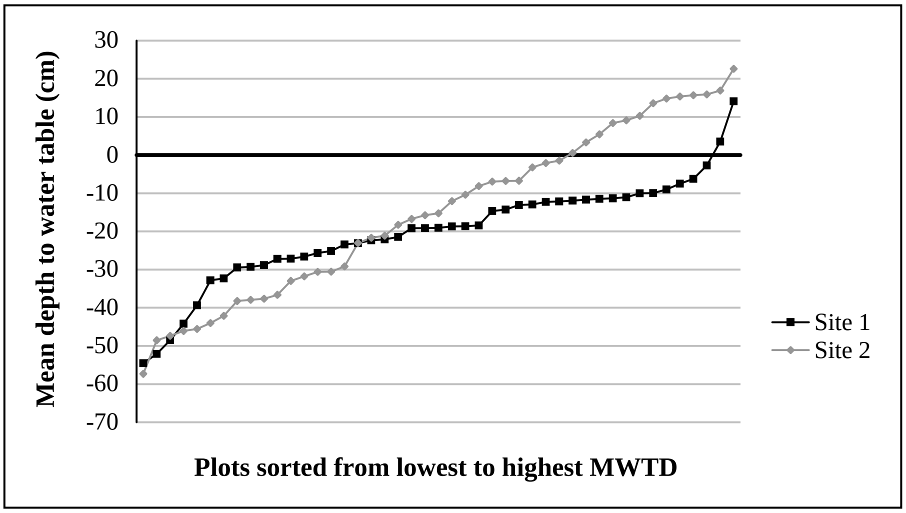
Table 1. Summary of site-wise means of five hydrologic parameters measured from March through August 1999. Plot maximums and minimums at each site are also listed

	Site 1	Site 2
Mean Water Table Depth (cm)	-20.3	-15.0
maximum plot mean depth	14.1	22.6
minimum plot mean depth	-54.6	-57.3
Average Duration of Inundation (%)	23.1	33.4
maximum duration at plot	72.8	79.6
minimum duration at plot	0	0
Average Frequency of Inundation (# times in 6mo)	6	7
maximum frequency at plot	14	19
minimum frequency at plot	0	0
Average Longest Continual Inundation (days)	34	48
maximum longest continual inundation	98	100
minimum longest continual inundation	0	0
Average Inundation (cm)	4.2	10.4
maximum average inundation at plot	25.4	31.5
minimum average inundation at plot	0	0

We also found a significant relationship between DI and mortality at Site 2 ($r^2=0.47$, $P<0.001$, $n=45$). Mortality was highest when DI was greater than 50% (figure 7). The average mortality of those plots with a DI of 50% or less was 45%, whereas the average mortality of those plots with a DI greater than 50% was 88%.

The most variability in growth or mortality at both sites was explained by either inundation or saturation above-15 cm, so the saturation above -30 cm and -46 cm parameters are not referenced again.

Figure 5. Distribution of water table levels of plots at the two sites.



LCI also showed a significant relationship with mortality at Site 2 (r^2 =0.47, P<0.001, n=45, figure 8). Those plots with a LCI of 23 days or less had an average mortality of 47%, whereas the plots with a LCI of 88 days of more had an average mortality of 78%.

However, it was impossible to pinpoint a more specific critical point for this parameter because this data set has no LCI values between 23 and 88 days. Eleven of the thirteen plots with an LCI of 91 days or more exhibited 100% mortality.

Mortality at Site 1 was not significantly related to any hydrology parameters (r^2 < 0.07, P>0.10). FI and FS were not significantly related to mortality at either Site 1 or Site 2 (table 2).

Growth

Site 1. MWTD exhibited a significant, inverse relationship with both cedar height (r^2=0.44, P<0.001, n=45) and width (r^2=0.40, P<0.001, n=45) (figures 9a and 9b). The average height of living trees at Site 1 was 223 cm, with individual trees ranging from 60 to 400 cm. The average width of living trees at Site 1 was 113 cm, with individual trees ranging from 30 to 200 cm.

DS better explained variability in growth parameters than DI (table 3). DS was related significantly to both height (r^2=0.45, P<0.001, n=45) and width (r^2=0.40, P<0.001, n=45). Trees grew taller and wider when water table was only briefly within –15 cm (figures 10a and 10b) or inundated.

Variability in growth parameters was also better explained by LCS than LCI (table 3). LCS was inversely and significantly related to both height (r^2=0.38, P<0.001, n=45) and width (r^2=0.38 P<0.001, n=45) (figures 11a and 11b).

Figure 6. The relationship between mortality and MWTD at Site 2. Higher positive numbers indicate wetter plots.

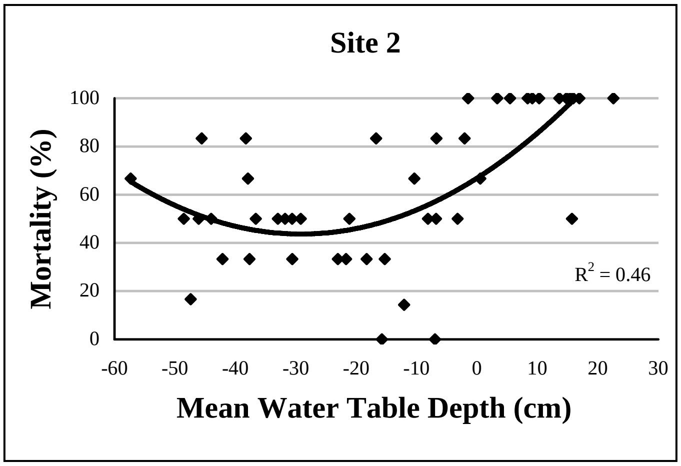


Figure 7. The relationship between mortality and FI at Site 2.

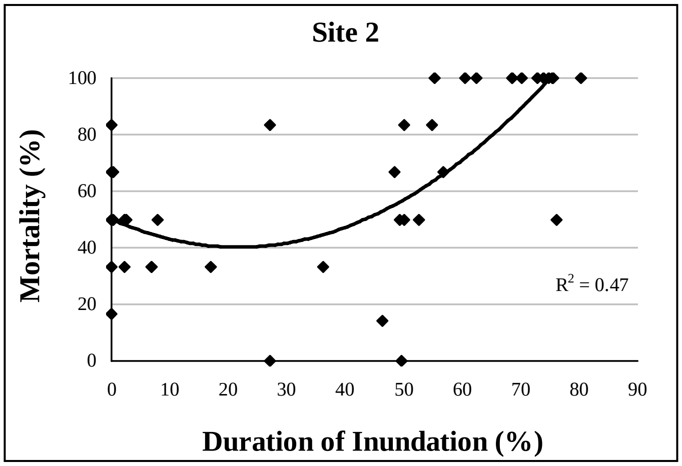


Figure 8. The relationship between mortality and LCI at Site 2.

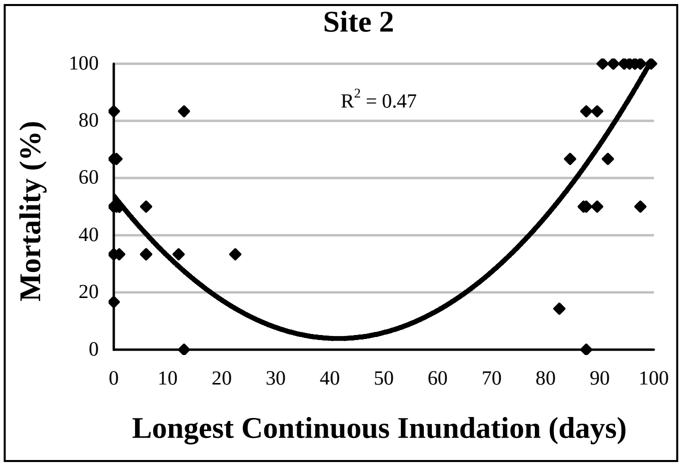


Table 2. Results of polynomial regressions of mortality with listed hydrology parameters at Sites 1 and 2.

	MORTALITY			
	Site 1 (n=45)		Site 2 (n=45)	
	r^2	P	r^2	P
Mean Water Table Depth	0.05	0.323	0.46	<0.001
Duration of Inundation	0.07	0.291	0.47	<0.001
Duration of Saturation (>-15 cm)	0.03	0.398	0.43	<0.001
Frequency of Inundation	0.03	0.433	0.06	0.258
Frequency of Saturation (>-15 cm)	0.01	0.665	0.16	0.056
Longest Continuous Inundation	0.06	0.243	0.47	<0.001
Longest Continuous Saturation (>-15 cm)	0.01	0.727	0.21	0.022
Average Inundation	0.04	0.355	0.47	<0.001

Figure 9a. Relationship between average tree height and mean water table depth at Site 1.

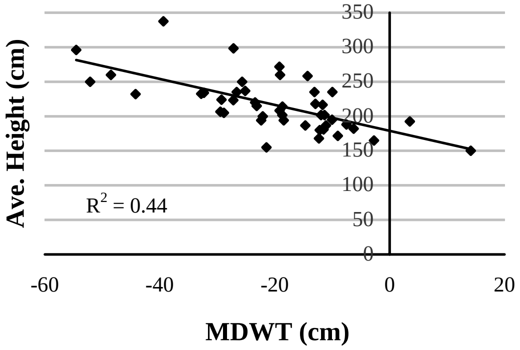


Figure 9b. Relationship between average tree width and mean water table depth at Site 1.

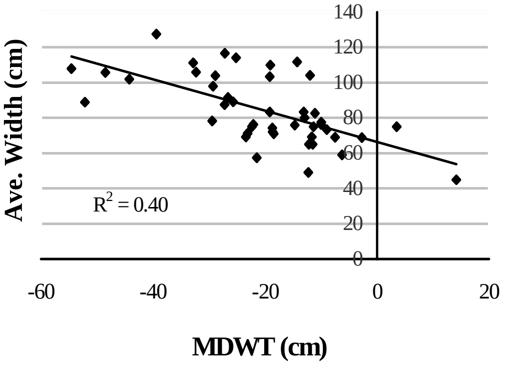


Table 3. Results of linear regressions of height and width with listed hydrology parameters at Site 1. A polynomial regression was used to compare frequency to height and width.

	GROWTH SITE 1			
	Tree Height (n=45)		Tree Width (n=45)	
	r^2	P	r^2	P
Mean Water Table Depth	0.44	<0.001	0.40	<0.001
Duration of Inundation	0.30	<0.001	0.31	<0.001
Duration of Saturation (>-15 cm)	0.44	<0.001	0.40	<0.001
Frequency of Inundation	0.31	0.004	0.40	<0.001
Frequency of Saturation (>-15 cm)	0.18	0.038	0.13	0.087
Longest Continuous Inundation	0.30	<0.001	0.30	<0.001
Longest Continuous Saturation (>-15 cm)	0.37	<0.001	0.38	<0.001
Average Inundation	0.35	0.002	0.39	<0.001

Figure 10a. Relationship between average tree height and frequency of saturation at Site 1.

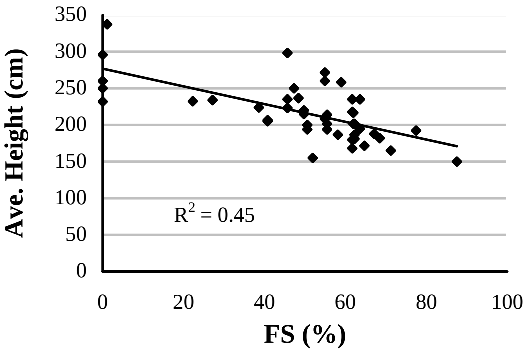


Figure 10b. Relationship between average tree width and frequency of saturation at Site 1

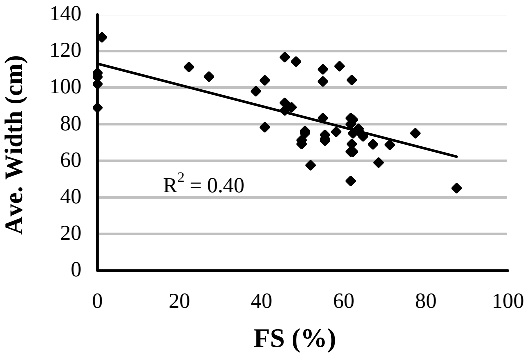


Figure 11a. Relationship between average tree height and longest continuous saturation.

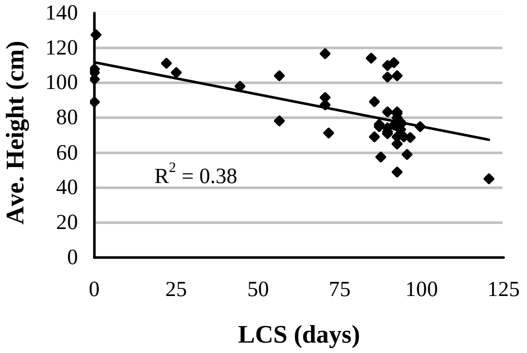
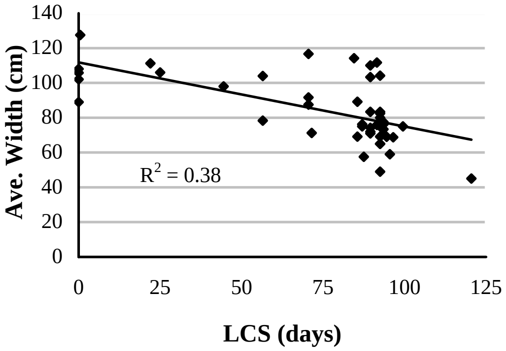


Figure 11b. Relationship between average tree width and longest continuous saturation.



Alternatively, FI better explained the variability in growth parameters than FS (table 3). Height and width showed a significant curvilinear relationship to frequency (r^2=0.31, P=0.004, n=45; r^2=0.40, P<0.001, n=45, respectively).

Site 2. Height and width measurements were taken at Site 2 shortly after an extensive deer browse event in which deer gnawed lateral branches, but not tops, of trees in our plots. This event confounded the relationship between width and hydrology parameters (table 4), so we only address height at Site 2.

Table 4. Results of linear regression of height and width with listed hydrology parameters at Site 2. A polynomial regression was used to compare frequency to height and width.

	GROWTH SITE 2			
	Tree Height (n=33)		Tree Width (n=33)	
	r^2	P	r^2	P
Mean Water Table Depth	0.37	<0.001	0.28	0.002
Duration of Inundation	0.27	0.002	0.17	0.073
Duration of Saturation (>-15 cm)	0.46	<0.001	0.28	0.018
Frequency of Inundation	0.34	0.004	0.28	0.022
Frequency of Saturation (>-15 cm)	0.01	0.825	0.02	0.638
Longest Continuous Inundation	0.24	0.004	0.15	0.029
Longest Continuous Saturation (>-15 cm)	0.50	<0.001	0.26	0.022
Average Inundation	0.42	0.002	0.29	0.019

Height was significantly related to MWTD (r^2=0.37, P<0.001, n=33) at Site 2. Results suggest that trees grow taller in dryer areas within this range of water table levels and under these conditions (figure 12). The average height of living trees at Site 1 was 167 cm, with individual trees ranging from 30 to 280 cm.

DS better explained height variability than DI (table 4) at Site 2 (r^2=0.46, P<0.001, n=33). Average live tree height was greater the less duration the plot was saturated over 15 cm below the surface (figure 13).

Longest continuous saturation above -15 cm could explain approximately half of the variability in height at Site 2 (r^2=0.50, P<0.001, n=33). Far less was explained by LCI (table 3.4). Average live tree height was negatively related to period of continuous time the plot was saturated more than 15 cm below the surface (figure 14).

FI was significantly related to tree height (r^2=0.34, P=0.004, n=33).

DISCUSSION

Cedar establishment requires a narrow range of water table depths. Akerman (1923) reported that cedar seedlings are susceptible to death by drought and drowning through their first growing season, and continue to be susceptible to drowning through their second year. The lowest average mortality rate at our site (40%) was achieved when the MWTD was between –11 cm and –37 cm. Mortality rates exceeded 93% in the 13 plots that had MWTD greater than 0 (inundated). Mortality was also slightly elevated at the dryer plots. Mylecraine et al. (This Volume), in New Jersey, planted cedar stecklings in rows across an elevation gradient and found the highest survivorship (96%) after one year in the rows with a MWTD of –9 and –29 cm (the two rows with the shallowest water table in their study). Thus, minimum mortality could be predicted to occur between –5 and –40 cm.

Figure 12. Relationship between average height and MWTD at Site 2.

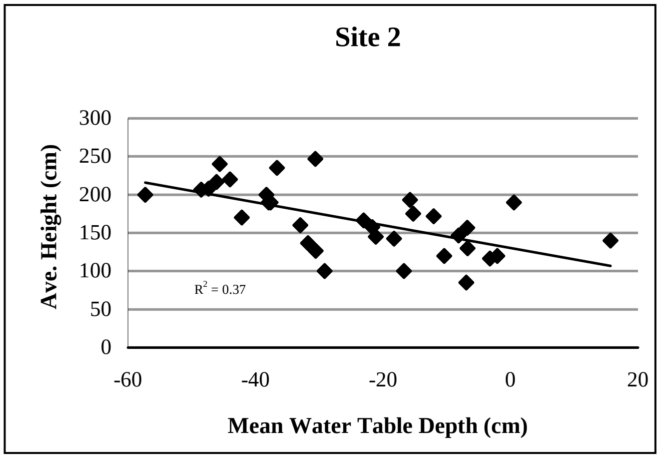


Figure 13. Relationship between average height and DS at Site 2.

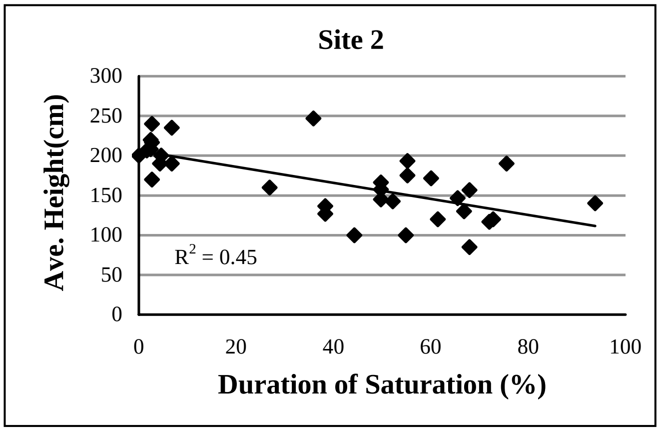
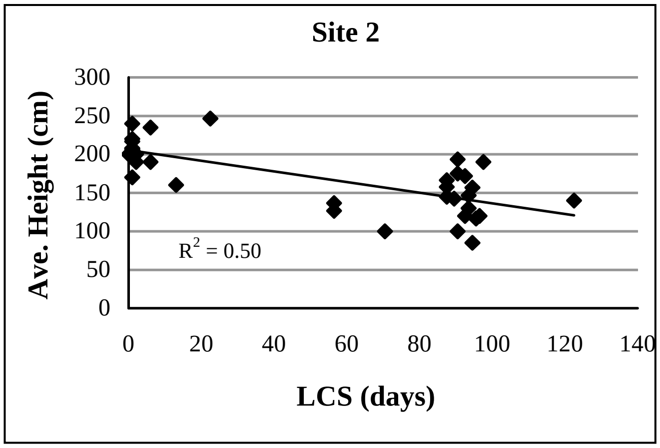


Figure 14. Relationship between average height and longest continuous saturation at Site 2.



Our results indicated that growth (measured as height and width) was significantly related to water table depth at both sites. Growth increased as the water table became deeper (figure 12), the maximum depth recorded at –57 cm. Similarly, Mylecraine et al. (This Volume) found that the best growth was achieved at water tables between –21 and –40 cm. Both our study and Mylecraine et al. (This Volume) seem to suggest that maximum growth occurs when water tables are approximately 10 cm or more lower than depths that encourage maximum survivorship.

Alternatively, Brown and Atkinson (1999), in their study of first year naturally regenerating cedar, reported that maximum growth occurred in plots with a water table between 6 and –3 cm. While significantly shallower than the optima reported in the current study, we must note that theirs was an historic natural cedar site and the soil was predominantly peat.

Percent continuous inundation is used to identify wetland types in the Fish and Wildlife Service classification system (Cowardin et al. 1979). Laderman (1989) cites a New Jersey study in which long, continuous flooding resulted in the death of cedar. LCI was significantly related to mortality at Site 2 and LCS was significantly related to growth at Sites 1 and 2. This is important for management because LCI is visually assessable and could be adjusted with water control structures. These results suggest that targeting an appropriate MWTD could still be ineffective in minimizing mortality and maximizing growth in young cedar if the water table remained above, at, or immediately beneath the surface for too long. However, these findings must be evaluated carefully since we are reporting actual continuous days saturated or inundated within a six-month period.

Saturation of the root zone is cited as important for growth and mortality of vegetation (Environmental Laboratory 1987 and Pezeshki 1994). When regressed with mortality, DI and LCI had higher r^2 values than either DS or LCS. Laderman (1987) and Little (1950) indicate that cedar is severely stressed when their boles are submerged, but not when water tables are slightly below the soil surface. In our study, growth was more closely related to saturation (DS and LCS) than inundation (DI and LCI). After the first two growing seasons, when cedar appear more intolerant of submergence, it is reasonable to assume that low nutrient availability associated with a saturated root zone could limit growth more directly than inundation.

MWTD at our sites were deeper than reported for mature cedar in the literature. Both Baines (no date) and Little (1950) reported that cedar sites had relatively dry surfaces, but that water table averaged deeper than –10 to –12 cm. While MWTD at our sites were –20 and –15 cm MWTD inplots ranged from –57 to 23 cm and approximately 30% of plots at Site 2 had MWTD of 0.0 or higher (inundated). This is more topographic variability than reported for mound and pool topography usually associated with cedar forests (Atkinson et al. This Volume[b]). In their Rhode Island study of six cedar forests aging from 46 to 105 years, Golet and Lowry (1987) reported that annual mean depth to water table ranged from 13 to –11 cm. While mature cedar can survive in inundated conditions, a deeper water table may be necessary initially to reduce mortality.

Mean growth rates for cedar were similar to those reported in the literature. When rooted cuttings were planted at Site 1 in January 1995 and at Site 2 in May 1996, average height was approximately 30 cm. Little and Garrett (1990), provide a detailed description of cedar and indicated that on favorable open sites, cedar usually grow 20-30 cm in height during the second year, and about 30 cm/year for several years thereafter. Akerman (1923) suggests that cedar grow approximately 46 cm/year until 10 years old. Taking both estimates into account, we might expect young cedar to grow approximately 38 cm/year for their first several years. After five growing seasons the height of trees at Site 1 averaged 223 cm, which is similar to the expected 220 cm. After almost four growing seasons, the height of trees at Site 2 averaged 167 cm, which is also similar to the expected 174 cm.

One factor that should be considered in interpreting our results is water table manipulation at the sites. We used six months of the 1999 growing season as a surrogate for water tables between 1995 and 1999, therefore the absolute depths we report may be slightly shallower or deeper than optimum. Hydrologic manipulation at Site 1 may explain the failure to detect a significant relationship with mortality. Our various hydrology parameters are closely related to each other and we recommend caution in asserting the significance of one parameter in contrast to another. As a whole, however, hydrology accounted for approximately 35% to 50% of the variability in growth and mortality at our sites, which is comparable to a study by Golet and Lowry (1987) in which six linearly regressed hydrology parameters explained approximately 50% of the variability in growth at the sites they studied.

Management Recommendations

- Higher survivorship may result from planting young cedar on a relatively level surface (not varying more than 35 cm) and carefully managing the water level until cedar are a few years old, as opposed to purposefully moving earth to create macro/microtopography.
- To reduce mortality, planted cedar should not be exposed to inundation for more than three continuous weeks, or for more than a total of 50% of the growing season in their first several years.
- Higher survivorship may result from initially targeting a MWTD of -5 to –40, and while better growth occurred at dryer plots in our study, we do not recommend subsequently lowering the water table, if self-maintenance of the site is the goal, since mature natural cedar forests typically have higher water tables (15 to -15 cm).
- More research is needed to determine the effect of establishing cedar at these suggested low water tables and then raising water tables to levels typical of natural stands.
- Planting cedar at higher densities, and emulating naturally regenerating stands, could help offset the high mortality reported in sites of varying topography where intermediate water levels drown some seedlings and desiccate others.

CONCLUSIONS

Hydrology, soil characteristics, and plant composition vary between different cedar restoration sites, and it is unclear whether specific conditions correlated with survivorship at one site are directly applicable to another. However, we believe our study may help define the conditions necessary for successful cedar wetland restoration by identifying a range of water table depths to reduce mortality.

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LITERATURE CITED

Akerman, A. 1923. The White Cedar of the Dismal Swamp. Virginia Forestry Publication 30:1-21.

Atkinson, R. B., T. E. Morgan, D. A. Brown, and R. T. Belcher. This Volume[a]. The role of historical inquiry in the restoration of Atlantic white cedar swamps.

Atkinson, R. B., D. T. Loomis, J. W. DeBerry, E.R. Crawford, and R. T. Belcher. This Volume[b]. Water tables in Atlantic white cedar swamps: implications for restoration.

Baines, R. A. ND. Prospects for white cedar: a North Carolina assessment. FOREM. School if Forestry and Environmental Studies. Duke University, NC. p. 8-11.

Brown, D. A. and R. B. Atkinson. 1999. Assessing the survivability and growth of Atlantic white cedar [*Chamaecyparis thyoides* (L.)B.S.P.] in the Great Dismal Swamp National Wildlife Refuge. Department of Biology, Chemistry, and Environmental Science, CNU. U.S. Forest Service Southeastern Forest Research Publication.

Clewell A. F. and R. Lea. 1990. Creation and restoration of forested wetland vegetation in the southeastern United States. *In* Kusler, J. A. and M. E. Kentula. Wetland creation and restoration: the status of the science. Regional review. 195-231. Washington, DC, Island Press.

Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wildlife Service, Washington, D.C., USA.

Eagle, Jr., T. 2001. Atlantic white cedar ecosystem restoration on Alligator River National Wildlife Refuge and United States Air Force Dare County Bombing Range. *In* Belcher, R.T., R.B. Atkinson, and D.A. Brown (eds.) Restoration of Atlantic white cedar ecosystems at Dare County Bombing Range, NC: A compendium of research. Newport News, VA.

Environmental Laboratory. 1987. Corps of Engineers Wetland Delineation Manual. Technical Report Y-87-1, Army Engineers Waterway Experiment Station, Vicksburg, MS.

Golet, F. C. and D. J. Lowry. 1987. Water regimes and tree growth in Rhode Island Atlantic white cedar swamps. p. 91-110. *In* A. D. Laderman (ed.) Atlantic white cedar wetlands. Westview Press, Boulder, CO.

Henry, E. F., J. Chudoba, and H. C. Porter. 1958. Soil Survey, Norfolk County, Virginia. Government Printing Office, Washington D.C.

Laderman, A. D. 1989. The ecology of Atlantic white cedar wetlands: a community profile. U. S. Fish and Wildlife Service Biological Report 85(7.21). Washingotn, D.C.

Levy, G. F. 1987. Atlantic white cedar in thre Great Dismal Swamp and the Carolinas. p. 57-67. *In* A. D. Laderman (ed.) Atlantic white cedar wetlands. Westview Press, Boulder, CO.

Little, S. 1950. Ecology and silviculture of whitecedar and associated hardwoods in southern New Jersey. Yale University School of Forestry Bulletin. 56.

Little, S. and P. W. Garrett. 1990. *Chamaecyparis thyoides* (L.)B.S.P., Atlantic White Cedar. In R. M. Burns and B. H. Honkala (eds.), Silvics of North America, Vol. 1, Conifers, U.S.D.A. For. Serv. Agric. Handbk. 654, Washington D.C.

Martin, S. 2000. Personal communication. U.S. Army Corps of Engineers, Norfolk District.

Mitsch, W. J. and J. G. Gosselink. 1993. Wetlands. Van Nostrand Reinhold, New York, New York.

Mylecraine, K. A., G. L. Zimmerman, and J. E. Kuser. This Volume. The effects of water table depth and soil moisture on the survival and growth of Atlantic white cedar.

Natural Resources Conservation Service. 2002. U.S. Department of Agriculture. http://www.nrcs.usda.gov/

Pezeshki, S. R. 1994. Plant response to flooding. In R. E. Wilkinson (ed.) Plant-Environment Interactions, Marcel Dekker, Inc., New York, pp. 289-321.

Reed, P. B., Jr. 1988. National list of plant species that occur in wetlands: Northeast (Region 1). U.S. Fish and Wildlife Service Biological Report 88(26.1).

Shacochis, K. M., J. W. DeBerry, D. T. Loomis, R. T. Belcher, and R. B. Atkinson. This Volume. Vegetation importance values and prevalence index values of Atlantic white cedar stands in Great Dismal Swamp and Alligator River National Wildlife Refuges.

U.S. Department of Agriculture. 1985. Hydric Soils of the United States. U.S. Department of Agriculture, Soil Survey Division.

THE EFFECTS OF WATER TABLE DEPTH AND SOIL MOISTURE ON THE SURVIVAL AND GROWTH OF ATLANTIC WHITE CEDAR

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Abstract: Atlantic white cedar (cedar) is considered an obligate wetland species, although its exact hydrologic requirements are not completely understood. This study provides quantitative data on the effects of water table depth and soil moisture on the survival and growth of cedar. We planted rooted cuttings during fall 1998, in successive rows along water table gradients at three sites within the Clayton Sand Company property in Lakehurst, New Jersey. We installed a series of test wells at each site and measured water table levels every two to four weeks from fall 1998 to fall 1999. Percent soil moisture was measured gravimetrically several times during the growing season. Here we present first year data for two of the three sites. Water table measurements ranged from above to greater than 140 cm below the ground surface. For site 1, we found significant differences between rows (representing different water table levels) of stecklings for height growth, but not survival. At site 2 we found significant differences in survival but not height growth. Despite these different responses, the water table depths at which we found greatest performance were similar for both sites. Height growth at site 1 was greatest with an estimated mean water table between –21.41 and –40.85 cm, with a maximum of 8.89 cm and a minimum of –60.78. For site 2, we found the highest survival rates with an estimated mean water table between –9.36 and –29.00 cm, with a maximum of 6.83 and a minimum of –53.85. Corresponding values for mean soil moisture content at Site 1 ranged from 10.33% to 18.12% at the surface, and 17.71% to 22.77% at 20 cm depth. At Site 2, these values ranged from 13.40% to 21.00% at the surface, and 10.90% to 21.90% at 20 cm depth. This is part of an ongoing study that will continue for additional seasons. The results should be helpful in identifying suitable sites for restoration projects based on knowledge of water table levels.

Key Words: cedar, restoration, *Chamaecyparis thyoides,* Cupressaceae

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), is restricted to freshwater wetlands along the Atlantic and Gulf coasts. It is found within a narrow belt 80 to 160 km wide, from southern Maine to central Florida and westward to southeastern Mississippi. Within this belt, the distribution is very patchy, depending on the occurrence of suitable sites (Little 1950). It is a valued species for several reasons, and has been called the most important timber tree of the pine region of southern New Jersey (Moore and Waldron 1938). Its wood is durable, light weight, aromatic, and usually has an even, straight grain, and is used for a variety of timber products (Korstian and Brush 1931, Little 1950). Cedar ecosystems also provide many ecological benefits (Kuser and Zimmermann 1995).

Over the past two centuries, there has been a significant decline in the area occupied by cedar in New Jersey (Mylecraine and Zimmermann 2000, New Jersey Forest Service, unpublished data), as well as throughout its range (Kuser and Zimmermann 1995). Reasons for this decline include white-tailed deer herbivory, wildfire, past harvesting procedures, hydrologic change, development, and competition with other species (Mylecraine and Zimmermann 2000). Recently, there has been considerable interest in restoring cedar on suitable sites, to increase the overall acreage occupied by this species. Suitable habitat must be identified, and information about the specific requirements of cedar will be needed.

Hydrologic conditions are very important in determining wetland structure and function. Hydrology may be the single most important determinant of the establishment and maintenance of wetland types and wetland processes. (Mitsch and Gosselink 2000). Hydrology primarily affects the chemical and physical aspects of a wetland, which in turn affect the biotic components of the system. In cedar wetlands, several variables are controlled by hydrology, including aeration of the root zone, availability and movement of nutrients, soil temperature regime, and the availability of moisture (Laderman 1989).

The occurrence of cedar may be limited by unfavorable moisture conditions (Little 1950). It is often considered an obligate wetland species, and is considered New Jersey’s only obligate wetland tree species (Reed 1988). However, Moore and Waldron (1940) suggest that it may have also historically occupied a considerable portion of the intermediate zones between upland and lowland sites, characterized by poorly drained sands, but “the combination of cutting and frequent fires that have occurred since settlement has tended to reduce the area in cedar to the wetter portions it now occupies.” Quantitative and functional aspects of water regimes, as well as the moisture conditions that limit cedar’s distribution have not been well defined (Little 1950, Laderman 1989).

Hydrologic regimes vary considerably among cedar stands, as well as seasonally and annually (Lowry 1984, Laderman 1989). Water table depths are generally highest in late winter and early spring, and lowest in autumn (Laderman 1989). In a typical cedar stand, depressions may contain standing water for several months, although the water table may fall as much as 60 to 90 cm below the surface during dry autumns (Korstian 1924). Golet and Lowry (1987) examined several cedar stands in Rhode Island, and found the mean annual water level over 7 years to range from 13 cm above to 11 cm below the ground. However, water table levels varied significantly between years, primarily in response to variations in annual precipitation. Their results indicated that water regimes may be partially responsible for the relative distributions of cedar and red maple, one of cedar's main competitors (Golet and Lowry 1987).

In the New Jersey Pinelands, Epstein (1995, 1997) identified six hydrogeologic freshwater wetland types which may support cedar: (1) ponded, (2) perched, (3) stream flood, (4) tidal flood,

(5) unconfined groundwater discharge, and (6) confined groundwater discharge wetlands. Each of these wetland types has different characteristics and susceptibilities (Espstein 1993), and hydrologic conditions may vary significantly among individual cedar swamps.

Moisture is considered one of the critical factors for cedar regeneration (Little 1950, Zimmermann 1997). Either too much or too little water can be detrimental. Pinchot (1899) observed that generally there is more complete reproduction in dry swamps than in wet swamps with standing water, possibly because the standing water prevents the germination of cedar seeds (Harshberger 1916). On the other hand, relatively dry swamps may provide too little moisture for adequate germination of cedar seed and growth of seedlings (Little 1950), making reproduction on such sites problematic (Zimmermann 1997). Zimmermann (1997) suggests that drier sites can be regenerated "provided planted cedar seedlings are large and their roots dipped in an antidessicant before outplanting" and if appropriate measures are taken to control white-tailed deer browsing and competition from hardwood species.

Little (1950) suggested that cedar may be able to compete better with hardwoods on higher water tables. However, relatively poor growth is attained on extremely wet sites, probably because of inadequate aeration (Little 1950). Observations by Korstian and Brush (1931) suggest that growth is also reduced on upland soils. Microtopography may play an important role in many swamps, providing a range of moisture conditions. Akerman (1923) concluded that seedlings originating midway between the top and base of hummocks had the best survival. Ehrenfeld (1995), found that cedar, as well as its associated species, tends to avoid the lower microsites. Little (1950) suggests that best growth is achieved in swamps with a relatively dry surface, but with the water table at a depth no greater than 10 to 13 cm below the surface. Variation within and between years, as well as the duration of flooding or soil saturation (hydroperiod) may also be important factors.

Quantitative studies on the effects of hydrologic variables on cedar growth are very limited. Golet and Lowry (1987) attempted to relate annual radial growth with water regimes at six wetlands in Rhode Island. Although they found significant relationships between radial growth and single hydrologic variables, no consistent relationship was found across sites. Using multivariate models with six measures of water regime, they accounted for 50% of the total variation in radial growth. However, when other site variables were added (including groundwater pH, crown closure, specific conductance of soil, and tree density), the model accounted for 85% of the total variation.

For this study, we focused on two groundwater discharge wetlands at the Clayton Sand Company property in Jackson, New Jersey. Because of the nature of these sites, we were able to eliminate many confounding factors and focus on hydrologic variables. Specific objectives were: (1) to characterize the hydrology at these sites, using water table depth and soil moisture, and (2) to assess the survival and growth of planted cedar rooted cuttings in relationship to these hydrologic variables.

METHODS

Site Descriptions

This study was conducted at the Clayton Sand Company property, located in Jackson Township, Ocean County, New Jersey (40°4'N, 74°23'W). We chose three sites within the property, two of which are presented here. These sites are both groundwater discharge wetlands with significant elevational and water table gradients over relatively short distances.

Both sites have been highly disturbed in the past and are relatively free of vegetation. Site 1 is adjacent to a sand mining operation, with a slope leading down to a large body of water. It is approximately 0.33 ha, measuring 46 m parallel to the slope and 73 m perpendicular to the slope. The site is completely free of vegetation, with the exception of cedar seedlings planted for a previous experiment (Haas and Kuser 1999). Site 2 is located in an area previously used for cranberry production, with a steep slope leading to a body of water. It is approximately 0.04 ha, measuring 44 m parallel to the slope and 8 m perpendicular to the slope. Some vegetation has begun to invade the slope, including: mosses, herbaceous plants, red maple, winged sumac (*Rhus copallina* L.), and cedar. All competing vegetation was manually removed at the time of planting. Both sites are located within a surrounding matrix of little or no vegetative cover, thus eliminating shading from outside.

Soils on both sites are mostly sand, with a small amount of gravel at depths of about 1.2 to 1.5 m below the surface. Site 1 has a bare sand surface, while Site 2 has a very thin (2-3cm) layer of mulch and litter at the surface. The soil within each site is relatively homogenous.

Experimental Design

We planted cedar stecklings (rooted cuttings) in fall, 1998, along the water table gradients at each site. Stecklings were rooted in March 1998 at the New Jersey State Nursery in Jackson, NJ, and ranged from 6.4 to 27.9 cm in height (mean=15.4, se=0.2) at planting. The number of parent trees used to root the cuttings is unknown. At Site 1 we planted 366 total stecklings, in 16 rows, at 1.8 m spacing within rows, and 3.7 to 10-m spacing between rows. At Site 2 we planted a total of 125 stecklings, in 5 rows, at 1.8-m spacing within rows, and 1 to 2-m spacing between rows. For both sites, stecklings in each row represent replicates at the same position along the water table gradient. To avoid any differences in initial heights between rows, we randomly assigned stecklings to rows.

To measure steckling performance along the water table gradients, we monitored both survival and growth of all stecklings through the first growing season. We calculated growth by measuring total stem heights at the time of planting and again at the end of the season.

To monitor water table depth, we established a series of test wells at each site. The wells were made from PVC piping, 1.5 m in length and 2.5 cm in diameter. To allow water to flow into the pipe yet prevent clogging, several small holes were made in the lower half of the pipe and covered with a screen. At Site 1, 29 wells were installed prior to the study, and an additional 7 wells were installed during the spring of 1999. At Site 2, 14 wells were installed prior to the study. All wells were located within the areas of planted stecklings. We manually measured the depth to the water table at each well approximately once every two (growing season) to four (non-growing season) weeks from fall, 1998 to fall, 1999.

We mapped and calculated relative elevations for all rows of stecklings and test wells, using an optical transit. For each steckling row, three elevations were taken (beginning, middle, and end of row) and averaged to estimate the elevation for that row.

We collected soil samples to determine soil moisture content, both at the surface and at 20 cm depth. Samples were taken from the center of each row of stecklings on six occasions throughout the growing season for Site 1 and on five occasions for Site 2. Soil moisture content was determined gravimetrically, and expressed as the percentage of oven dry weight of the soil.

Data Analysis

We analyzed cedar survival and growth response to hydrologic conditions at both sites. We conducted all data analyses using SAS (The Statistical Analysis System). We used the well data to establish the relationships between elevation and mean, minimum, and maximum water table depth for each site. We used these relationships to calculate mean, minimum and maximum water table depths for each row of cedar plantings. We averaged soil moisture measurements over the growing season by row, and plotted soil moisture (at the surface and 20 cm below the surface) by water table depth to examine the relationship between these variables.

We used chi-square analyses to test for differences in steckling survival among rows. We calculated height growth for all stecklings by subtracting the initial height from the height at the end of the 1999 growing season. We also calculated relative growth rates (RGR) as: (height growth/initial height)*100. We tested these growth data for normality, and found that they did not meet the assumptions of conventional analysis of variance (ANOVA). Therefore, we used the Kruskal-Wallis test, analysis of variance by ranks, to test for differences in growth rate among rows (representing different water table levels) of stecklings. If the Kruskal-Wallis test was significant, we performed nonparametric multiple comparisons (Zar 1996) to further investigate the differences among rows.

RESULTS

Site 1

Elevation, mean, maximum, and minimum water table depths for each test well are shown in table 1. Mean water table depths at site 1 ranged from –139 cm to –28 cm below the ground surface, with a maximum of 0 cm and minimum of –141 cm. The test wells were 152 cm in total length, with up to 141 cm below the ground surface. However, on some occasions, the water table depth reached below the depth of the test wells for some of the higher elevation wells; therefore, the minimum measurement of –141 cm is probably an underestimation of the actual minimum at this site.

The relationships between elevation and mean, maximum and minimum water table levels are shown in figure 1. These relationships were significant (r^2=0.93, 0.86, and 0.89 for mean, maximum and minimum water table depth, respectively).

We present steckling survival and growth data in table 2, along with elevation, percent soil moisture (at the surface and at 20 cm below the surface) and estimated values for mean, maximum and minimum water table depths, by row. Figure 2 graphically displays average elevation (m) and the mean water table depth (cm) for each row of cedar stecklings. Mean, maximum and minimum water table depths for each row were calculated using the elevation of the row and the relationships between elevation and these water table variables, established from the well data.

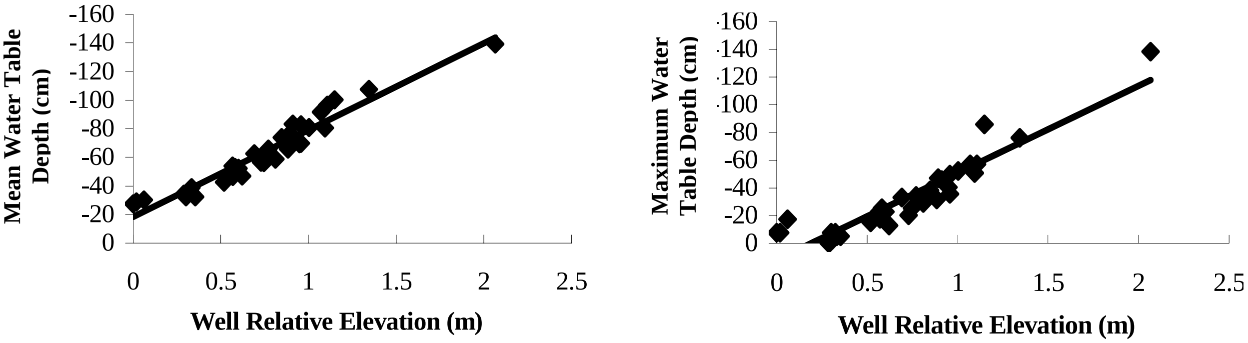
Mean surface soil moisture ranged from 18.12% for row 3 to 0.49% for row 15. At 20 cm depth, soil moisture ranged from 22.77% for row 3 to 2.1% for row 16. We found a significant relationship between water table depth and soil moisture, both at the surface (r^2=0.94, $p<0.001$) and at 20cm depth (r^2=0.90, $p<0.001$) for rows with mean water table depths of ≤ 60 cm below the surface. For rows where mean water table depths were > 60 cm below the surface, we did not find a significant relationship between the two variables (figure 3).

Table 1. Relative elevation and water table data for each test well at Site 1, including elevation, the number of water table measurements (n), mean, maximum, and minimum water table, and coefficient of variation. We measured relative elevation using an optical transit. We calculated mean, minimum, and maximum water table values from a series of measurements [approximately every two (growing season) to four (non-growing season)] between fall 1998 and fall 1999. Missing data are represented by ".".

Well ID	Elevation (m)	n	Mean WT (cm)	Minimum WT (cm)	Maximum WT (cm)	Coefficient of Variation
K1	1.11	21	-96.44	-109.47	-57.15	-14.46
K2	0.91	21	-83.11	-102.62	-45.72	-17.25
K3	0.69	21	-62.52	-78.99	-33.02	-21.16
K4	0.57	21	-53.87	-68.33	-22.86	-24.30
K5	0.29	21	-34.14	-53.59	0.00	-46.28
K6	0.00	7	-27.50	-38.86	-7.62	-37.51
L1	1.07	21	-91.46	-107.95	-57.15	-15.72
L2	0.96	21	-82.81	-101.60	-49.53	-17.50
L3	0.85	21	-73.85	-97.54	-38.10	-20.90
L4	0.58	21	-52.79	-68.07	-25.40	-24.74
L5	0.31	21	-35.20	-56.64	-2.54	-43.32
L6	0.06	8	-30.16	-42.67	-17.53	-31.18
M-1	.	8	-137.32	-137.41	-137.16	-0.26
M0	1.15	8	-100.11	-108.59	-85.85	-9.17
M1	1.00	21	-80.84	-101.60	-52.07	-17.28
M2	0.89	21	-76.46	-98.81	-46.99	-18.42
M3	0.77	21	-65.67	-86.61	-34.29	-22.73
M4	0.60	21	-52.20	-64.77	-22.86	-23.22
M5	0.33	21	-38.70	-62.48	-5.08	-42.93
N1	0.96	21	-69.66	-88.90	-35.56	-20.25
N2	0.81	21	-58.79	-83.82	-29.21	-22.81
N3	0.62	21	-46.88	-61.98	-12.70	-29.40
N4	0.52	21	-42.61	-55.63	-15.24	-29.35
N5	0.32	21	-37.13	-76.96	-7.62	-46.56
N6	0.02	7	-28.96	-49.02	-7.62	-43.98
O-1	2.07	7	-139.23	-140.72	-138.43	-0.52
O0	.	8	-109.06	-112.52	-101.85	-4.22
O1	1.09	21	-80.47	-97.79	-50.80	-17.54
O2	0.95	21	-69.46	-86.11	-40.64	-20.45
O3	0.75	21	-56.24	-73.41	-25.40	-24.53
O4	0.57	21	-46.51	-66.29	-17.78	-29.31
O5	0.30	21	-32.41	-52.83	-7.62	-40.82
P1	1.34	20	-107.50	-125.22	-76.20	-13.73
P2	0.88	20	-65.63	-80.26	-31.75	-21.68
P3	0.73	20	-56.64	-75.18	-20.32	-26.14
P4	0.35	21	-32.45	-55.37	-5.08	-40.44

Figure 1. Relationship between elevation and mean, maximum, and minimum water table depths for Site 1.

$y = -60.740x - 18.375$; $r^2 = 0.9378$, $p<0.0001$ $y=-62.830x + 12.029$; $r^2 = 0.8608$, $p<0.0001$



$y=-55.061x - 40.404$; $r^2 = 0.8912$, $p<0.0001$

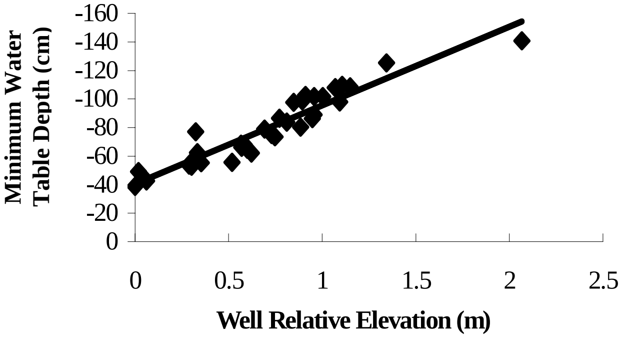


Table 2. Results for Site 1, including number of stecklings (n), relative elevation (elev), mean, maximum and minimum water table depths (95% confidence interval), mean soil moisture (surface and 20 cm depth), % survival, height growth, and relative growth rate (RGR) by row. Elevation values were calculated as the average of three measurements for each row. Water table values were calculated using the relationships between elevation and these variables, established from test well data. The Kruskal-Wallis test indicates significant ($p < 0.0001$) differences in relative growth rate between rows. Superscripts indicate groupings based on nonparametric multiple comparisons.

Row	n	Elev (m)	Mean Water Table (cm)[1]	Maximum Water Table (cm)[2]	Minimum Water Table (cm)[3]	Mean Surface Soil Moisture (%)	Mean Soil Moisture 20 cm. (%)	Survival (%)	Ht Growth Mean	Ht Growth SE	RGR Mean	RGR SE
1	24	0.05	-21.41 (±4.43)	8.89 (±7.15)	-43.16 (±5.44)	15.47	21.05	100	4.70	0.68	30.38^{ab}	5.19
2	23	0.20	-30.52 (±3.73)	-0.54 (±6.03)	-51.42 (±4.59)	13.65	22.47	91.3	5.51	0.53	39.75^{a}	5.92
3	23	0.11	-25.06 (±4.14)	5.12 (±6.68)	-46.46 (±5.09)	18.12	22.77	95.65	3.87	0.52	26.89^{abc}	4.48
4	10	0.24	-32.95 (±3.56)	-3.05 (±5.75)	-53.62 (±4.38)	15.03	20.62	100	4.57	0.87	33.74^{abc}	6.56
5	11	0.37	-40.85 (±3.05)	-11.22 (±4.92)	-60.78 (±3.75)	10.33	17.71	100	2.23	0.62	17.72^{abcd}	6.23
6	11	0.59	-54.21 (±2.42)	-25.04 (±3.91)	-72.89 (±2.98)	4.28	11.28	100	1.37	0.35	10.22^{bcd}	2.64
7	11	0.52	-49.96 (±2.58)	-20.64 (±4.17)	-69.04 (±3.17)	6.46	15.17	100	0.80	0.14	4.84^{d}	0.83
8	41	0.58	-53.60 (±2.44)	-24.41 (±3.94)	-72.34 (±3.00)	2.89	8.39	97.56	1.00	0.28	11.50^{d}	4.77
9	29	0.65	-57.86 (±2.34)	-28.81 (±3.79)	-76.19 (±2.88)	0.75	5.84	100	1.37	0.17	9.04^{cd}	1.19
10	29	0.73	-62.72 (±2.31)	-33.84 (±3.74)	-80.60 (±2.85)	2.18	4.53	89.66	1.06	0.18	7.35^{d}	1.46
11	30	0.80	-66.97 (±2.36)	-38.24 (±3.82)	-84.45 (±2.91)	0.6	5.48	82.76	1.02	0.16	7.83^{d}	1.29
12	40	0.91	-73.65 (±2.56)	-45.15 (±4.13)	-90.51 (±3.14)	0.88	3.32	89.74	0.61	0.18	3.48^{d}	1.36
13	22	1.01	-79.72 (±2.86)	-51.43 (±4.61)	-96.02 (±3.51)	2.75	5.72	86.36	0.41	0.49	2.17^{d}	3.16
14	23	1.11	-85.80 (±3.19)	-57.71 (±5.15)	-101.52 (±3.92)	1.2	4.84	90.91	1.45	1.05	5.27^{d}	3.42
15	21	1.33	-99.16 (±4.14)	-71.53 (±6.69)	-113.64 (±5.10)	0.49	4.11	100	0.22	0.54	1.43^{d}	3.07
16	18	2.06	-143.50 (±7.93)	-117.40 (±12.81)	-153.83 (±9.75)		2.1	77.78	0.56	0.63	4.09^{cd}	5.113

[1] Calculated based on water table levels at 36 test wells, using the equation: mean water table = -60.740(elevation) –18.375 (r^2 = 0.9378)

[2] Calculated based on water table levels at 36 test wells, using the equation: maximum water table = -62.830(elevation) +12.029 (r^2 = 0.8608)

[3] Calculated based on water table levels at 36 test wells, using the equation: minimum water table = -55.061(elevation) –40.404 (r^2 = 0.8912)

Figure 2. Average elevation and average water table depth during the study period for 16 rows of Atlantic white cedar stecklings planted at Site 1 within the Clayton Sand and Gravel property in Lakehurst, New Jersey.

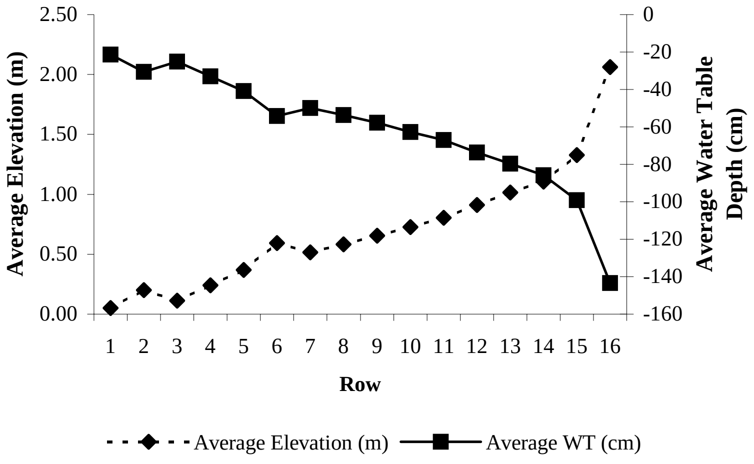
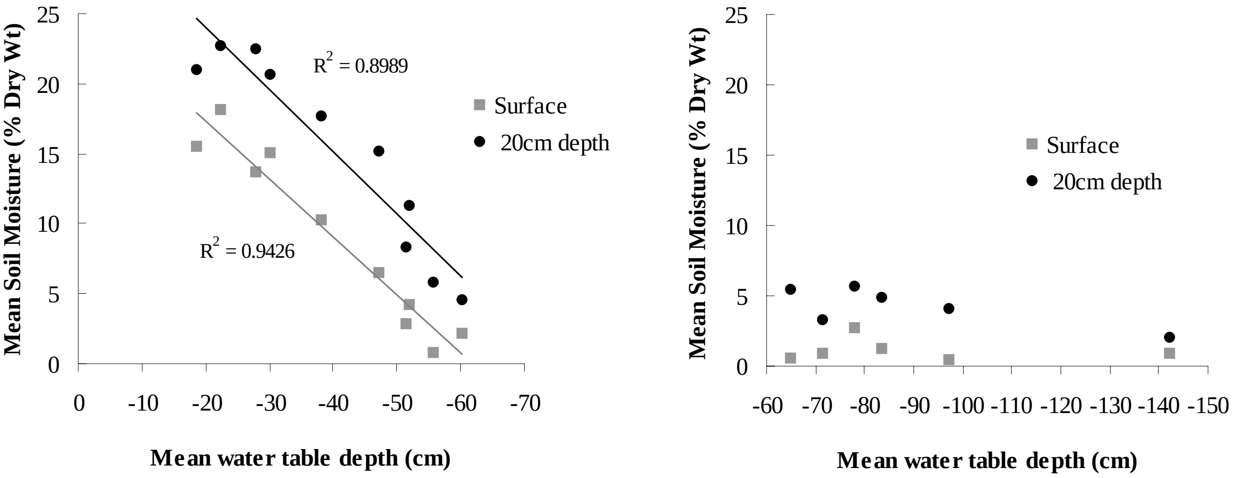
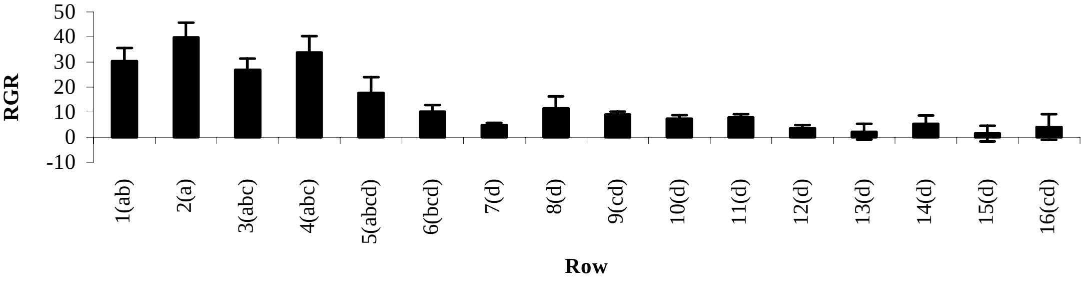


Figure 3. Average soil moisture (surface and 20 cm depth) by water table depth for Site 1. There is a significant relationship between these variable for water table depths no greater than –60 cm (60 cm below the surface), but not for water table depths greater than –60 cm.



We found that survival was independent of row number (chi-square, α=0.05), indicating no significant differences in survival among rows during the first season. However, row 16 was the driest row and also had the lowest survival rate (77.78%). We did find significant differences among rows for relative growth rate (figure 4). The Kruskal-Wallis test indicated significant (p<0.0001) differences in height growth between rows, with groupings based on nonparametric multiple comparisons displayed in table 1 and figure 4. The first five rows (group a) of stecklings exhibited the greatest relative growth rate. Mean water table depths for these rows were –21.41, -30.52, -25.06, –32.95, and –40.85 cm, respectively, with a maximum of 8.89 cm and a minimum of –60.78 cm. Mean surface soil moisture content for these rows was 15.47%, 13.65%, 18.12%, 15.03%, and 10.33%. At a depth of 20 cm, soil moisture averaged 21.05%, 22.47%, 22.77%, 20.62%, and 17.71%.

Figure 4. Relative Growth Rate (RGR) for Site 1 by row. The Kruskal-Wallis test indicated significant differences in height growth between rows. Groupings based on nonparametric multiple comparisons are indicated in parentheses.



Site 2

In table 3, we display elevation, mean, maximum, and minimum water table depths for each test well. Mean water table depths ranged from –131 to –6 cm, with a maximum of 6.35 and a minimum of –139 cm. As in Site 1, the water table depth reached below the well depth for the highest elevation wells, and the minimum measurements for these wells probably underestimate the actual minimum.

Table 3. Relative elevation and water table data for each test well at Site 2. Mean, minimum, and maximum water table values were calculated from a series of measurements between the fall of 1998 and fall of 1999. All wells were measured manually approximately every two (growing season) to four (non-growing season) weeks during this period. These values were used to establish the relationship between elevation and water table variables.

Well ID	n	Elevation (m)	Mean WT (cm)	Minimum WT (cm)	Maximum WT (cm)	Coefficient of Variation
AA1	19	1.30	-119.82	-126.37	-114.30	-2.33
AA2	19	1.33	-131.50	-139.07	-116.84	-5.36
F1	20	0.60	-63.91	-73.98	-50.17	-11.53
F2	20	0.33	-32.32	-63.50	-2.54	-40.65
F3	20	0.02	-6.08	-26.67	2.54	-112.69
G1	20	0.62	-68.34	-91.44	-50.80	-14.53
G2	20	0.22	-10.65	-26.99	6.35	-99.11
G3	20	0.00	-5.64	-19.05	5.715	-113.77
H1	20	0.70	-77.29	-102.87	-60.33	-14.70
H2	20	0.21	-24.97	-49.53	-8.26	-43.16
H3	20	0.06	-10.90	-82.87	5.08	-166.87
I1	20	0.98	-88.77	-109.22	-66.68	-15.37
I2	20	0.26	-24.84	-37.47	-7.62	-36.25
I3	20	0.11	-9.61	-28.89	3.175	-86.63

The relationships between elevation and mean, maximum and minimum water table levels are shown in figure 5. There is a significant relationship (r^2=0.93, 0.92, and 0.77 for mean, maximum and minimum water table depth, respectively) between elevation and these water table variables.

Figure 6 shows the average elevation and the estimated mean water table depth for each row of cedar stecklings. Table 4 displays steckling survival and growth data, along with elevation, percent soil moisture and estimated values for mean, maximum and minimum water table depths, by row. Mean soil moisture ranged from 21.00% for row 1 to 6.15% for row 5 at the surface, and from 21.90% for row 1 to 2.65% for row 5 at a depth of 20 cm. The relationship between elevation and soil moisture at this site was not as clear as that for site 1 (figure 7). There is a significant relationship between mean water table depth and mean soil moisture at 20 cm depth (r^2=0.80, p=0.04), but not mean surface soil moisture.

Percent survival ranged from 96%, for rows 1 and 2, to only 12% for row 5 (figure 8). Chi-square analysis found that survival was not independent of row (α=0.05), indicating that survival was not the same across all rows. The rows with the highest survival rate had estimated mean water table values of –9.36 and –29.00 cm, with an estimated maximum water table of 6.83 cm and minimum of –53.85. Values for mean soil moisture content were 21.0% and 13.4% at the surface, and 21.9% and 10.9% at 20 cm depth. For this site, we did not find a significant relationship (p=0.063) between relative growth rate and row number.

Figure 5. Relationship between elevation and average water table depth for Site 2.

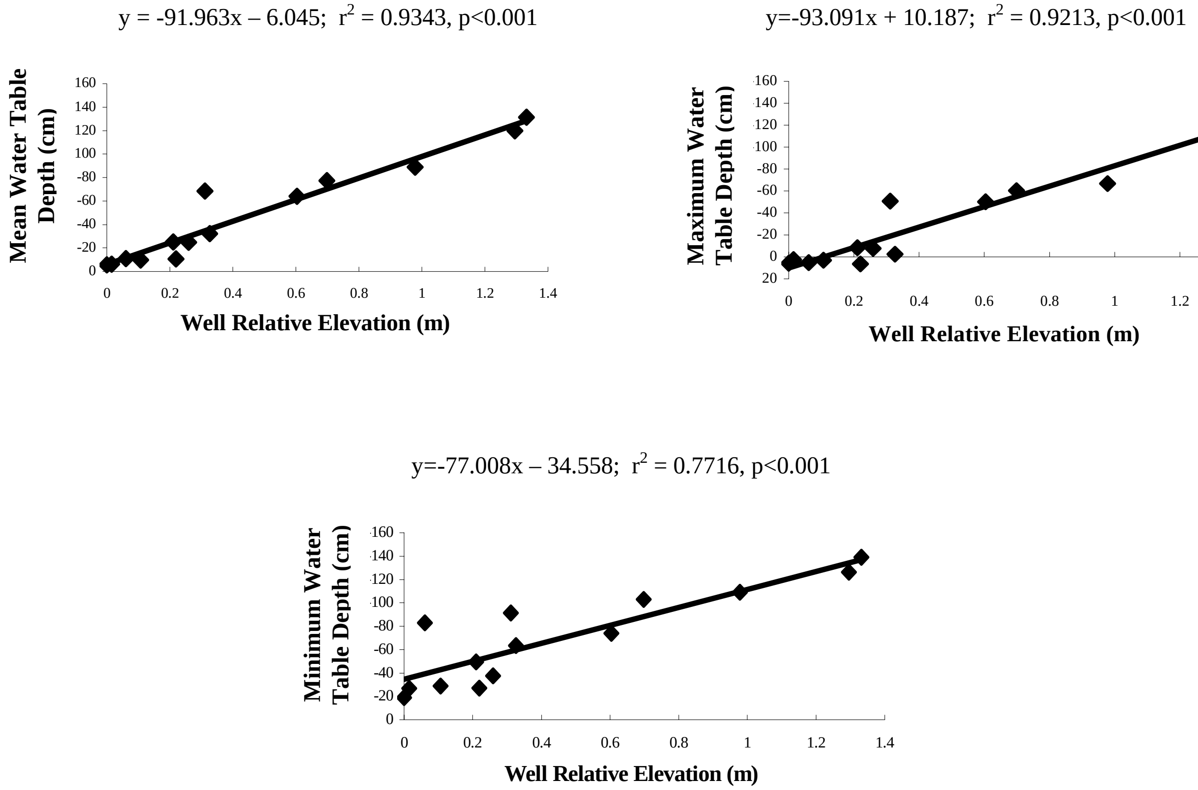


Figure 6. Average elevation and average water table depth for 5 rows of cedar stecklings at Site 2 within the Clayton Sand and Gravel property in Lakehurst, New Jersey.

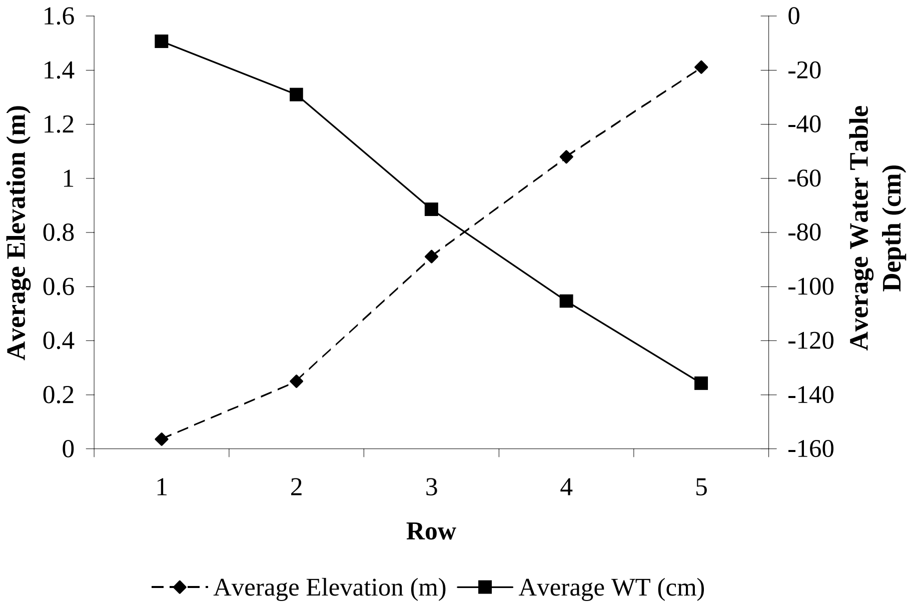


Table 4. Results for Site 2, including relative elevation (elev), mean, maximum, and minimum water table depths (95% confidence interval), mean soil moisture (surface and 20 cm depth), number of stecklings (n), % survival, and height growth, by row. Analysis of variance indicates no significant difference in height growth between rows.

Row		Elev (m)	Mean Water Table (cm)[1]	Maximum Water Table (cm)[2]	Minimum Water Table (cm)[3]	Mean Surface Soil Moisture (%)	Mean Soil Moisture 20 cm (%)	Survival (%)	Ht Growth Mean (cm)	Ht Growth SE	RGR Mean	RGR SE
1	25	0.04	-9.36 (±9.34)	6.83 (±10.42)	-37.34 (±16.05)	21.00	21.90	96	1.12	0.50	6.05	2.79
2	25	0.25	-29.00 (±7.54)	-13.08 (±8.31)	-53.85 (±12.81)	13.40	10.90	96	1.93	0.29	13.00	1.98
3	25	0.71	-71.40 (±7.77)	-55.88 (±8.67)	-89.41 (±13.35)	12.00	6.87	60	0.41	0.89	3.44	5.44
4	25	1.08	-105.00 (±11.68)	-90.42 (±13.02)	-117.60 (±20.06)	11.75	5.46	64	3.21	1.02	22.10	6.91
5	25	1.41	-136.00 (±16.09)	-121.16 (±17.95)	-143.26 (±27.65)	6.15	2.65	12	0.77	0.23	4.28	1.32

[1] Calculated based on water table levels at 14 test wells, using the equation: mean water table = -91.963(elevation) –6.0447 (r^2 = 0.9343)

[2] Calculated based on water table levels at 14 test wells, using the equation: maximum water table = -93.091(elevation) +10.187 (r^2 = 0.9213)

[3] Calculated based on water table levels at 14 test wells, using the equation: minimum water table = -77.008(elevation) –34.558 (r^2 = 0.7716)

Figure 7. Average soil moisture (surface and 20 cm depth) by water table depth for Site 2. There is a significant relationship between soil moisture at 20 cm depth and water table depth, but between surface soil moisture and water table depth.

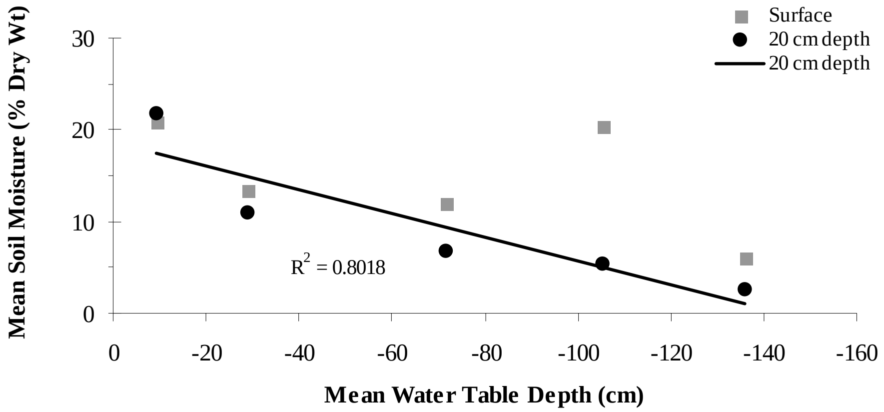
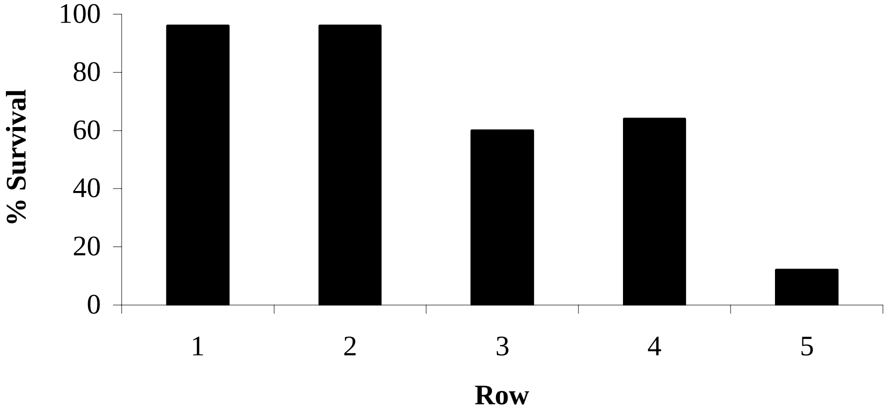


Figure 8. Percent survival of cedar stecklings by row for Site 2.



DISCUSSION/CONCLUSION

We have presented first-year data on the effects of water table depth and soil moisture on the survival and growth of cedar stecklings at two study sites at the Clayton Sand property in Jackson, New Jersey. The response to water table depths varied between the two sites. For Site 1, we found a significant relationship between row number (each row representing a different position along a hydrologic gradient) and cedar relative growth rate, but not survival. For Site 2, we found a significant relationship between row number and cedar survival, but not height growth. For Site 1, best growth was achieved with the mean water table estimated at –21.41 to –40.85 cm, with a maximum of 8.89 cm and a minimum of –60.78. For Site 2, the highest survival rates were achieved with the mean water table estimated at –9.36 to –29.00 cm, with a maximum of 6.83 cm and a minimum of –53.85 cm. Corresponding values for mean soil moisture content at Site 1 ranged from 10.33% to 18.12% at the surface, and 17.71% to 22.77% at 20 cm depth. At Site 2, these values ranged from 13.40% to 21.00% at the surface, and 10.90% to 21.90% at 20 cm depth.

There are many possible causes for cedar's varied response to water table depth between the two sites. Although both sites are located on sandy soil, differences in soil texture, chemistry or other variables, may have affected growth rates. At Site 2, the large percentage of mortality for some rows may have prevented us from finding a relationship between relative growth rate and row. The nature of the hydrologic gradient and number of rows at each site may also be important. Site 1 had a more continuous water table gradient and a total of 16 rows. Site 2 had a steeper gradient with only 5 rows. These variations may help to account for the different responses between sites.

Despite the differences between sites, the results support earlier observations on cedar's moisture requirements. Little (1950) stated that best growth is achieved in swamps with a relatively dry surface, but with the water table depth no greater than -10 to -13 cm (4 to 5 in), but did not specify the amount of seasonal variation or the length of time at that depth. Korstian (1924) observed that the water table in cedar swamps may fall to as much as –61 to –91.44 cm during dry autumns. Our data from Site 1 indicate that best growth was achieved with a mean water table depth of –21.41 to –40.85 cm (maximum 8.89 cm and minimum –60.78). Both Little (1950) and Korstian and Brush (1931) have suggested that growth is slower on drier sites. This is supported by the reduction in relative growth rate at higher elevations at Site 1.

Our data indicate some surface flooding at lower elevations of both sites. Golet and Lowry (1987) found that surface flooding in several cedar swamps in Rhode Island ranged from 18-76% of the growing season. However, several authors have suggested that too much surface flooding may be detrimental to cedar regeneration. Harshberger (1916) suggests that standing water prevents the germination of cedar seed, and Allison and Ehrenfeld (1999) found reduced growth of cedar seedlings under inundated conditions when compared with moist, well-drained conditions. We did not find reduced survival or growth at higher water table depths, probably because neither site experienced substantial surface flooding during the first season. New Jersey experienced a severe drought during this season, so water table depths may have been lower than normal.

The results of this study will help in identifying suitable sites for future cedar restoration sites, based on knowledge of water table levels. However, these sites are both groundwater discharge wetlands on sandy soils, and the results may not be directly applicable to other wetland or soil types. The differential response to hydrology between the two sites also has implications for restoration. There may be other factors, such as soil texture or soil chemistry, that will affect cedar performance at a particular site and should be considered.

This study focused solely on survival and height growth in response to hydrologic conditions. In New Jersey, height growth is an important factor, due to the large population of white-tailed deer. Deer browsing is a critical factor, often hindering cedar regeneration throughout the state (Little and Somes 1965, Zimmermann 1997). Seedlings or stecklings that can grow faster may be able to reach heights unattainable by deer more quickly, thus reducing the amount of time and cost involved in deer protection (electric fencing, individual tree shelters). In addition to height growth, future studies may benefit by including other response variables, such as biomass and diameter growth, to better assess cedar’s response to water table depth.

These data represent first year data from an ongoing study. Due to severe drought conditions during 1999, the water table levels measured are probably not typical of a “normal” year. Water table levels may vary significantly between years, therefore several more seasons will be required to account for some of this variation and assess the long term response to these gradients.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Akerman, A. 1923. The white cedar of the Dismal Swamp. Virginia Forestry Publication 30:1-21.

Allison, S. K. and J. G. Ehrenfeld. 1999. The influence of microhabitat variation on seedling recruitment of *Chamaecyparis thyoides* and *Acer rubrum*. Wetlands 19(2):383-393.

Ehrenfeld, J. G. 1995. Microtopography and vegetation in Atlantic white-cedar swamps: the effects of natural disturbances. Canadian Journal of Botany 73:474-484.

Epstein, C. M. 1993. Hydrogeology of the Atlantic white-cedar regeneration sites in the New Jersey Pinelands. In G. Zimmermann. Continuation of the Atlantic white-cedar regeneration experiments. Richard Stockton College of New Jersey, Pomona, NJ.

Epstein, C. M. 1995. Hydrologic classification of New Jersey Coastal Plain Wetlands. In K. L. Campbell (ed.) Proceedings, Versatility of wetlands in the agricultural landscape, Sept. 17-20, 1995. American Society of Agricultural Engineers.

Epstein, C. M. 1997. A field based hydrologic classification for smaller wetlands. Wetland Journal 9(3):8-11.

Golet, F. C. and D. J. Lowry. 1987. Water regimes and tree growth in Rhode Island Atlantic white cedar swamps. Pages 91-110 In A. D. Laderman (ed.) Atlantic White Cedar Wetlands. Westview Press, Inc. Boulder, CO.

Haas, M. J. and J. E. Kuser. 1999. Effects of propagule type, geographic origin, and fertilization on first year performance of Atlantic white-cedar (*Chamaecyparis thyoides*) in New Jersey. Pages 22-26 In T. H. Shear and K. O. Summerville (eds.) Atlantic white-cedar: ecology and management symposium; 1997 August 6-7; Newport News, VA. Gen. Tech. Rep. SRS-27. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 82pp.

Harshberger, J. W. 1916. The Vegetation of the New Jersey Pine-Barrens. Christopher Sower Company, Philadelphia, PA.

Lowry, D. J. 1984. Water regimes and vegetation of Rhode Island forested wetlands. M.S. thesis, University of Rhode Island, Kingston. 174pp.

Korstian, C. F. 1924. Natural regeneration of southern white cedar. Ecology 5:188-191.

Korstian, C. F. and W. D Brush. 1931. Southern white cedar. Technical Bulletin 251. USDA Forest Service. Washington, DC, USA.

Kuser, J. E. and G. L. Zimmermann. 1995. Restoring Atlantic white-cedar swamps: Techniques for propagation and establishment. Tree Planters' Notes 46(3):78-85.

Laderman, A. D. 1989. The ecology of the Atlantic white cedar wetlands: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.21), Washington, D.C. 114pp.

Little, S. 1950. Ecology and silviculture of white cedar and associated hardwoods in southern New Jersey. Yale University School of Forestry Bulletin 56:1-103.

Little, S. and S. A. Somes. 1965. Atlantic white-cedar being eliminated by excessive animal damage in south Jersey. Research Note NE-33. USDA Forest Service, Northeastern Forest Experiment Station, Delaware, OH. 3pp.

Mitsch, W. J. and J. G. Gosselink. 2000. Wetlands. 3rd Ed. John Wiley, New York, NY.

Moore, E. B. and A. F. Waldron. 1938. Southern white cedar. NJ Department of Conservation and Development, Division of Forests and Parks Technical Note 3. 4pp.

Moore, E. B. and A. F. Waldron. 1940. Growth studies of southern white cedar in New Jersey. Journal of Forestry 38:568-72.

Mylecraine, K. A. and G. L. Zimmermann. 2000. Atlantic white-cedar: Ecology and Best Management Practices Manual. NJDEP, Division of Parks and Forestry, New Jersey Forest Service.

Pinchot, G. 1899. A study of forest fires and wood production in southern New Jersey. Appendix to Annual Report of the State Geologist for 1898.

Reed, P. B. 1988. National list of plant species that occur in wetlands: Northeast (Region 1). US Department of the Interior, Fish and Wildlife Service. Washington, DC.

Sheffield, R. M., T. W. Birch, W. H. McWilliams, and J. B. Tansey. 1998. *Chamaecyparis thyoides* (Atlantic white-cedar) in the United States. Pages 111-123 In AD Laderman (ed.) Coastally Restricted Forests. Oxford University Press. New York.

Zar, J. H. 1996. Biostatistical Analysis. 3rd Ed. Prentice Hall. Upper Saddle River, New Jersey.

Zimmermann, G. L. 1997. The Atlantic white-cedar (*Chamaecyparis thyoides*) regeneration experiments: Final Report. Richard Stockton College of NJ, Pomona, NJ.

RESTORING ATLANTIC WHITE CEDAR ON AN ABANDONED BLUEBERRY FIELD AND CRANBERRY BOG IN LEBANON STATE FOREST, NEW JERSEY

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Abstract: The acreage of cedar has declined drastically over the past two centuries in New Jersey and throughout its range. Recent interest has focused on restoring former cedar sites that have been converted to other wetland types and land uses. For successful restoration projects, we need to identify optimal site conditions and management techniques for this species. Here we examine several factors affecting cedar restoration of 20.2 ha (50 acres) of abandoned blueberry fields and cranberry bogs in Lebanon State Forest, Ocean County, New Jersey. We conducted three separate experiments. The first experiment tested the effects of site preparation treatment (single vs. double drum chopping), water table depth, elevation, and deer browsing on planted cedar stecklings (rooted cuttings). Deer browsing was severe, despite electric fencing around the entire site. Survival was high, averaging 92% after the 1998 growing season, and 88% after the 1999 season. We estimated that approximately 4557 cedar stecklings per hectare (1844 per acre) survived throughout the 15.4 ha (38 acres) of abandoned blueberry fields. Water table depths observed seem to be suitable, averaging –40.7 cm below the ground surface, with a range of –117.1 to +33.02 cm. The second experiment tested the effectiveness of two fertilizer treatments (Osmocote and Bio-pak) on survival and growth of stecklings. Despite heavy deer browsing, the treated stecklings performed significantly better than controls on all except one block, with no significant difference between fertilizers. The third experiment monitored the effectiveness of natural seeding on the 4.8 ha (12 acre) abandoned cranberry bog. Regeneration in this area averaged 30,568 seedlings per ha (12,370 per acre) after the first year, but was patchy due to limited seed availability. Supplemental planting may be required to stock some areas lacking regeneration. Overall, we believe that the restoration of cedar on this site has been successful, although it will take many years to ultimately assess long-term success. This site may be used as a model for future restoration projects, particularly on other agricultural or shrub dominated sites.

Key Words: cedar, fertilization, site preparation, wetland restoration, *Chamaecyparis thyoides*

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), is a wetland tree species found in freshwater swamps and bogs along the Atlantic and Gulf Coasts of the United States, usually within a coastal belt 80 to 160 km wide (Little 1959). It is an important species ecologically, aesthetically, and economically. Cedar is an important timber species because of its fragrant, light weight, straight-grained, decay and insect resistant wood (Korstian and Brush 1931, Little 1950). The economic value of its wood is generally greater than that of its hardwood associates (Little 1950), and is used for a variety of timber products including: boats, tanks, siding, fencing, shingles, poles, posts, boxes and crates (Korstian and Brush 1931, Ward 1989).

At the time of European settlement, cedar may have occupied 46,538 ha in New Jersey (New Jersey Forest Service 1997). By 1974, there were fewer than 20,234 ha, and by 1986, the New Jersey Forest Service estimated there were 16,871 ha, with 10,577 ha containing greater than 50% cedar (New Jersey Forest Service, unpublished data). Reasons for this decline include: white-tailed deer herbivory, wildfire, past harvesting procedures, conversion to agriculture, conversion to other wetland types, hydrologic change, and development (Mylecraine and Zimmermann 2000).

The majority of cedar in New Jersey is found within the Pinelands (Laderman 1989), where it occupies approximately two percent of this 445,000-ha region (Roman and Good 1983). Nearly half of New Jersey’s cedar acreage is found on state lands, including parks, forests, and wildlife management areas (Zampella 1987). Recent interest has focused on the maintenance of current cedar stands in the state, as well as restoration of suitable areas which may have contained cedar in the past, particularly in the Pinelands region (Zampella 1987, Zimmermann 1997, Mylecraine and Zimmermann 2000). As a result of this interest, the New Jersey Forest Service formed an Atlantic White Cedar Initiative steering committee in 1995, with several goals and objectives related to cedar management, restoration, research, and sustainability (New Jersey Forest Service 1997).

Potential sites for restoration in the state include: hardwood or pitch pine lowlands, mixed hardwood/pine/cedar wetlands, barren sites (i.e. mined sites), wildfire sites, shrub dominated sites, and former agricultural wetlands (Mylecraine and Zimmermann 2000). Although there has been some interest in converting mature hardwood or pine stands to cedar, the removal of the current overstory will be very time consuming and expensive, making this type of restoration difficult. Shrub dominated sites and recent agricultural wetlands may require less site preparation, making restoration on these sites more feasible. In the Mullica River basin, the conversion of mature cedar stands to shrub dominated wetlands has been a dominant trend over the past 61 years (Zampella and Lathrop 1997). Restoration of cedar on these sites would be desirable.

In order to successfully restore cedar in New Jersey, we need to determine the optimal site conditions and techniques for restoration. Choosing an appropriate site may be the most important factor in determining success of a restoration. Soil and soil moisture may be the chief factors limiting the occurrence of cedar. This species is generally confined to areas of organic peat overlying sandy subsoil (Korstian and Brush 1931), but can also be found on wet mineral soils. Moisture is considered one of the critical factors for natural regeneration of cedar. Both too much and too little water can be detrimental to cedar regeneration (Korstian and Brush 1931, Little 1950, Zimmermann 1997). At this time, the specific water table requirements for cedar plantings are not entirely clear.

Appropriate restoration techniques for cedar must also be chosen. Factors to be considered include site preparation, introduction method (plantings, seed, natural regeneration), competition control, deer protection, and the potential use of fertilization. Some of the major obstacles include white-tailed deer browsing and competing vegetation. Deer browsing is considered the primary factor preventing natural regeneration in the state. For this reason, electric fencing, tree shelters, and other methods have been employed (Kuser and Zimmermann 1995, Zimmermann 1997).

Competing hardwood and shrub vegetation, primarily red maple, *Acer rubrum* L., also have a negative effect on regeneration (Moore 1996, Kuser and Zimmermann 1995). In New Jersey, the wetlands approved herbicide, Arsenal®, is commonly used to control red maple and other hardwood species without burning the cedar foliage (Kuser and Zimmermann 1995).

Previous studies in New Jersey (i.e. Zimmermann 1997, Haas and Kuser 1999) have provided some information on techniques for natural regeneration and plantings, although many questions remain unanswered. The objectives of this present study are to (1) determine whether restoration on this type of site is successful, and (2) identify site factors and techniques that allow optimal survival and growth of cedar. Specifically, we examine the effects of abiotic and biotic influences on survival and growth of cedar, including elevation, water table depth and white-tailed deer browsing, as well as restoration techniques for establishment, including site preparation (single vs. double drum chopping), planting, natural seeding, and fertilization. This information will be useful for planning future restoration efforts on former agricultural wetlands or other shrub dominated sites.

METHODS

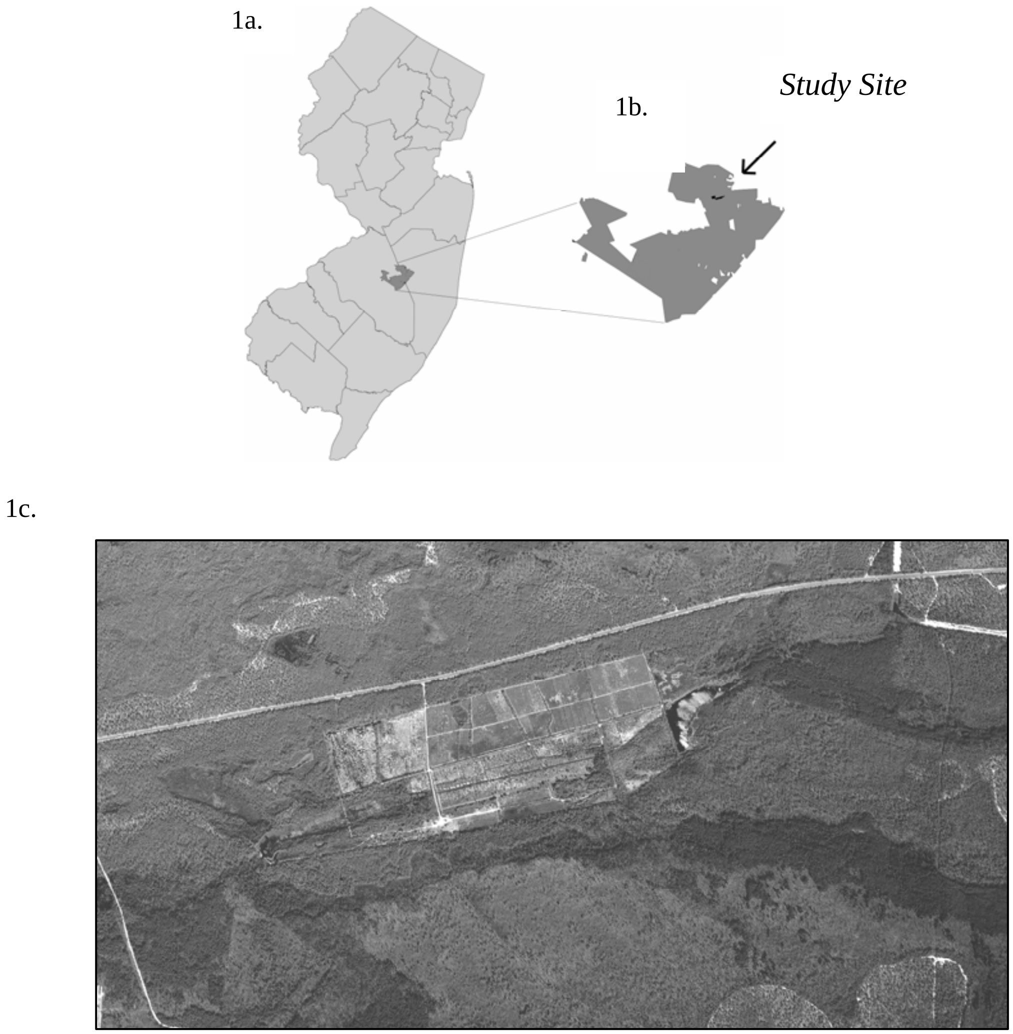
Site Description and History

The study area is located in Lebanon State Forest (39°56’ N, 74°28’ W), in the eastern portion of Manchester Township, Ocean County, New Jersey (figure 1). The area is a 20.2 ha (50 acre) wetland mitigation site, consisting of 15.4 ha (38 acres) of abandoned blueberry fields and a 4.8 ha (12 acre) abandoned cranberry bog. The goals of the mitigation project were “to reestablish an Atlantic white cedar wetlands forest on a site that had been converted to agricultural use” as well as “to allow for some scientific experimentation to utilize and apply various techniques” (Williams 1995).

The soil type was identified as Atsion sand. Atsion soils are described as poorly drained, sandy, siliceous, mesic Aeric Haplaquods (USDA SCS 1980). The New Jersey Forest Service does not include Atsion soils in their definition of the Ecological Land Type (ELT) for cedar, although a significant portion of the current cedar acreage was found on non-ELT Atsion soils (unpublished data New Jersey Forest Service).

Aerial photos of the site showed the presence of cedar upstream from the study site, as well as in other surrounding areas, indicating that this species probably occupied the site prior to disturbance (figure 1). Approximately 60 years ago, the site was cleared for blueberry and cranberry production, and an extensive internal road and ditch system was constructed. All ditches and roads are still functioning, although recent agricultural use has been limited. Prior to this mitigation, the site was mostly shrub dominated, with early tree succession beginning in some areas (Williams 1995).

Figure 1. Location of study site. 1a. Location of Lebanon State Forest in New Jersey. 1b. Location of study site within Lebanon State Forest. 1c. 1995 CIR Aerial Photograph showing study site (cleared area) and surroundings. The areas of dark vegetation are cedar stands.



Cedar Restoration on this Site

The blueberry fields were cleared of all vegetation and brush hogged in the spring of 1995. Blueberry stands quickly resprouted, and additional site preparation was necessary. During the spring of 1996, these areas were drum-chopped, which created a great deal of microtopography throughout the site, including numerous depressions and elevated ridges. Herbicide was applied in June 1997 to control grasses, followed by an aerial application of Arsenal® during the fall of 1997.

During the spring of 1996, approximately 5200 stecklings and 1000 wildlings were planted throughout the abandoned blueberry areas. The following spring, an additional 40,000 stecklings were planted with ~ 1.8 m by 1.8 m spacing. The New Jersey Forest Service planted approximately 1,400 stecklings in October 1997, and an additional 40,000 were planted during the spring of 1998.

A total of 87,600 individuals were planted on the 15.4 ha of blueberry fields between the spring of 1996 and spring of 1998.

The abandoned cranberry bog was mechanically cleared during the summer of 1997, and the resulting slash was not removed. The slash was not evenly distributed over the entire area, but was very clumped, with areas covered with slash, adjacent to slash-free areas. This site was aerially sprayed with Arsenal® during the fall of 1997. Restoration on this area was through natural seeding. There was an existing cedar stand to the northeast of this area, which provided only a limited seed source, because of the prevailing northwesterly winds during the months of seed dispersal. In addition, a small amount of advanced cedar regeneration, present prior to site clearing, was left uncut and also provided a limited seed source.

The entire 20.2 ha site (including both blueberry field and cranberry bog) was enclosed by a five strand, solar powered electric fence to minimize the effects of deer browsing. After heavy deer browsing the first winter, individual tree shelters were also installed around some of the stecklings in May 1998.

Experimental Design

Experiment 1. We conducted three separate experiments to monitor the success of this mitigation. The first experiment was conducted on a 10.1 ha (25 acre) portion of blueberry field (figure 2) to examine the effects of site preparation, elevation, and water table depth on the growth and survival of planted cedar stecklings. There were two treatments, single and double drum chopped, which we further divided into four blocks per treatment. Within each block, we randomly selected 25 cuttings during the fall of 1997 (cohort 1), and an additional 25 in the spring of 1998, from those planted in May 1998 (cohort 2). Height and basal diameter growth of these cuttings were measured for two full growing seasons. To examine the effect of deer browse, we visually estimated the percentage of the total foliage lost each winter, and for 1999 calculated the height loss by comparing spring height with the previous fall height.

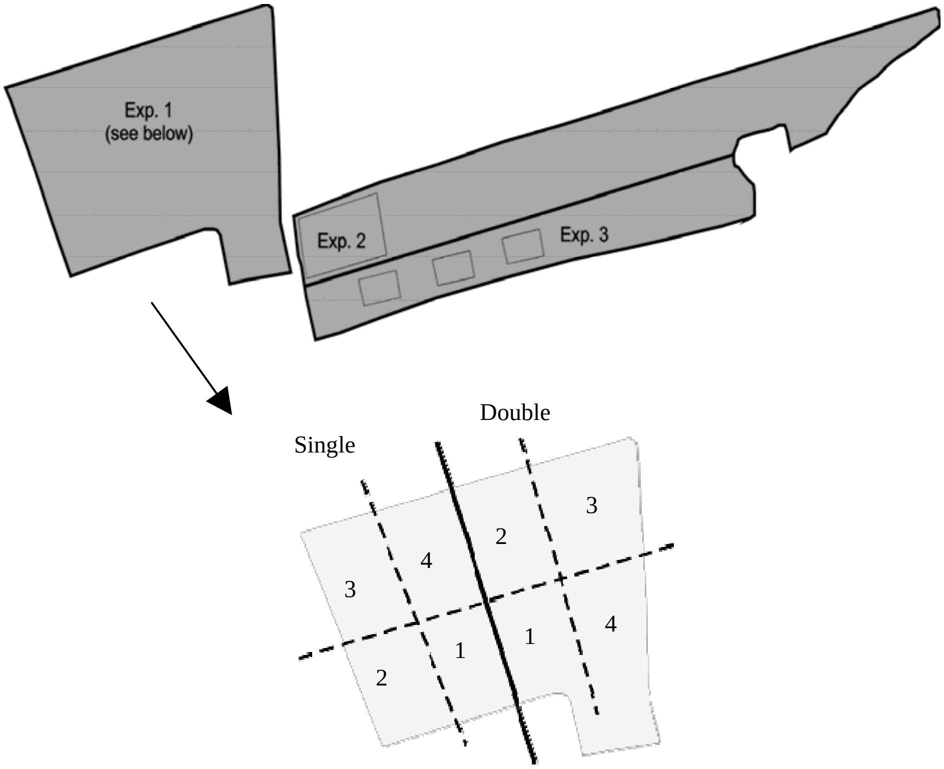
For each individual cutting, we determined the exact elevation and location using an optical transit. We assigned the steckling with the lowest elevation as 0, and then calculated relative elevation for all other sample trees.

To measure water table depth, we installed a series of 12 test wells throughout the study area. Each well consists of PVC piping with holes and screening, to allow water flow into the well. We manually measured water table levels at each well approximately every two to four weeks during the study period.

Experiment 2. A second experiment was conducted on another portion of blueberry field to examine the effects of two different fertilizers on the survival and growth of planted cedar stecklings. We planted a total of 216 stecklings in October 1997, with 72 stecklings in each of the following three treatments:

1. Osmocote – a 12-14 month slow release fertilizer, with the formulation 17:7:12 (N:P:K). The application rate was 14.4g per steckling, placed at bottom of the planting hole.
2. Bio-pak – a slow release fertilizer, with the formulation 16:6:8. The suggested application rate was one Bio-pak for each 30 cm of height. We used one Bio-pak for each steckling, placed at the bottom of the planting hole, regardless of height.
3. Control – no fertilizer applied.

Figure 2. Locations and experimental designs for three experiments to study the restoration of cedar on a former agricultural site in the New Jersey Pinelands. Experiments 1 and 2 were located on abandoned blueberry fields, while Experiment 3 was located on an abandoned cranberry bog. Experiment 1 tested the effects of site preparation treatment (single *vs.* double drum chopping), deer browsing, elevation, and water table depth on the survival and growth of planted stecklings. Within each treatment, 4 blocks were delineated. Within each block, 25 stecklings were chosen from each cohort (cohort 1 was planted prior to Fall 1997, cohort 2 was planted in Spring 1998), for a total of 50 stecklings per block. Experiment 2 tested the effectiveness of two fertilizer treatments on the survival and growth of cedar stecklings. Experiment 3 tested the effectiveness of natural regeneration from scattered seed trees and a limited outside seed source. Three blocks were delineated, and 12 plots were measured in each.



Stecklings were planted using a variation of a randomized block design. The area was divided into 6 blocks. Each block consisted of 6 plots (2 per treatment), each with 6 stecklings, and separated by a row of stecklings with no fertilizer as a buffer between treatments.

We monitored survival, height and basal diameter growth, and deer browse twice yearly during the study period. We placed four test wells in the area, to monitor water table depths, and measured the elevation for each individual steckling, using an optical transit.

Experiment 3. We conducted a third experiment to monitor cedar regeneration from natural seeding on the abandoned cranberry bog area. Three blocks were randomly selected within this area and twelve 1m^2 plots were established within each block to observe cedar regeneration.

RESULTS

Experiment 1

Overall survival averaged 92% after the 1998 season, and 88% after 1999 (table 1). Assuming similar survival rates in the year prior to the study began, and similar survival rates throughout the entire 15.4 ha (including areas not studied), we estimate that approximately 4557 stecklings per ha (1844 per acre) have survived through the 1999 growing season.

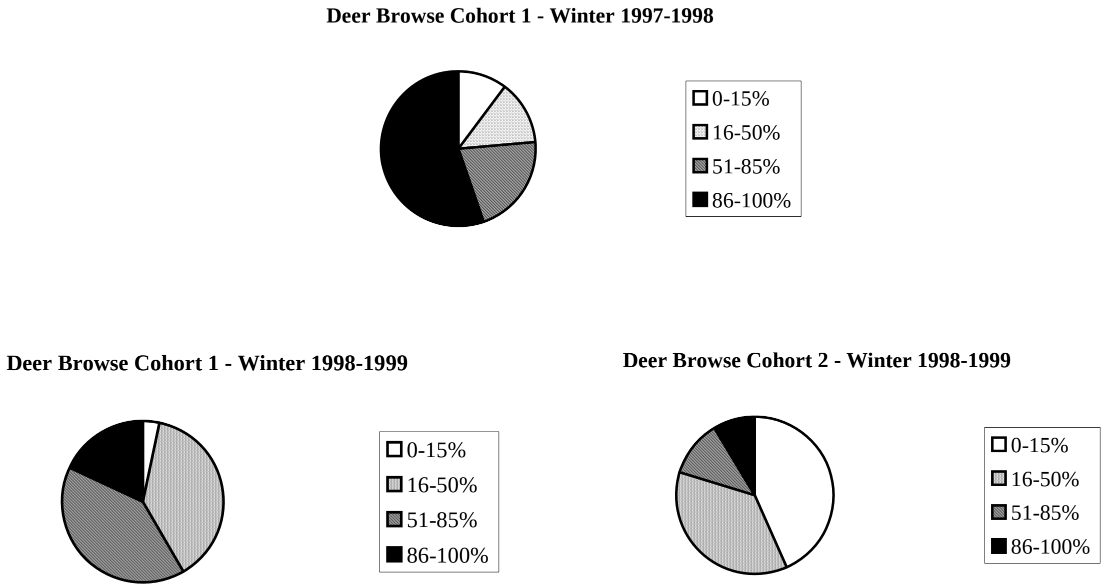
Table 1. Results for Experiment 1. Percent survival, height and diameter growth (standard error) by treatment and cohort, averaged across blocks. For the 1998 growing season, only net height and diameter growth was calculated (fall 1998 – fall 1997). Net height growth does not take into account height loss due to winter deer browse. For the 1999 growing season, actual height growth was also calculated (height fall 1999 – height spring 1999), to take into account deer browse and reflect the actual growth added by the plant.

	Single Drum Chopped		Double Drum Chopped	
	Cohort 1	Cohort 2	Cohort 1	Cohort 2
1998 Growing Season				
% Survival	95.00 (1.91)	96.00 (0)	91.00 (3.79)	85.00 (6.61)
Net Ht. Growth (cm)	36.06 (1.82)	10.11 (1.07)	31.34 (1.69)	8.89 (0.99)
Net Diam. Growth (cm)	0.45 (0.02)	0.14 (0.02)	0.43 (0.02)	0.12 (0.01)
1999 Growing Season				
% Survival	92.00 (2.58)	94.00 (1.15)	88.75 (2.93)	79.75 (4.25)
Net Ht. Growth (cm)	24.24 (1.49)	25.11 (1.52)	23.65 (1.58)	25.48 (1.76)
Actual Ht. Growth (cm)	36.20 (1.33)	32.49 (1.85)	33.63 (1.69)	27.84 (1.89)
Net Diam. Growth (cm)	0.60 (0.03)	0.34 (0.02)	0.52 (0.04)	0.32 (0.02)

Despite electrical fencing, white-tailed deer browsing has been the largest problem at this site (figure 3). Although steckling survival was not significantly affected by level of deer browse, significant losses in height growth and total amount of foliage occurred. After the first winter, 55% of all cohort 1 stecklings had an estimated 86-100% of their total foliage browsed, 21% were 51-85% browsed, 13% were 16-50% browsed, and only 10% were browsed 15% or less. Browse levels were slightly less severe during the second winter, with 18% of cohort 1 stecklings browsed 86-100%, 40% browsed 51-85%, 38% browsed 16-50%, and 3% browsed 15% or less. Individual tree shelters installed on cohort 2 trees during the fall of 1998 resulted in a reduction, but not elimination, of browse, as a number of these stecklings were browsed prior to installation (figure 3). During the winter of 1998-1999 we report an average height loss of 20% for cohort 1 and 15% for cohort 2 due to deer browsing.

Averaged across all treatments, net height growth (fall 1997 to fall 1998) was 22 cm in 1998, and 24 cm in 1999, despite significant height losses each year due to deer browsing. Actual height growth for 1999 (spring 1999 to fall 1999) averaged 33 cm. Basal diameter growth averaged 0.28 cm in 1998 and 0.45 cm in 1999. Table 1 shows growth, broken down by treatment, cohort and block. We plotted heights throughout the study period in figure 4, by treatment, cohort and block. Repeated measures analysis of variance, conducted on steckling height over the study period, indicate the following factors to be significant (α=0.05): time, interaction between time and site preparation treatment, interaction between time and block, within treatment, and interaction between time and cohort. Conducted on steckling basal diameter over the study period, the following factors were

Figure 3. Estimated deer browse for experiment 1. We estimated the percentage of total foliage browsed for each steckling, at the end of each winter season, and categorized each steckling as 0-15% , 16-50%, 51-85%, or 86-100% browsed. These charts show the proportion of stecklings in each browse category, by cohort and year. During the fall of 1998, tree shelters were installed on all cohort 2 stecklings. This reduced the amount of severe deer browse, although some stecklings were browsed before the tree shelters were put in place.



Deer Browse Cohort 1 - Winter 1997-1998

Deer Browse Cohort 1 - Winter 1998-1999

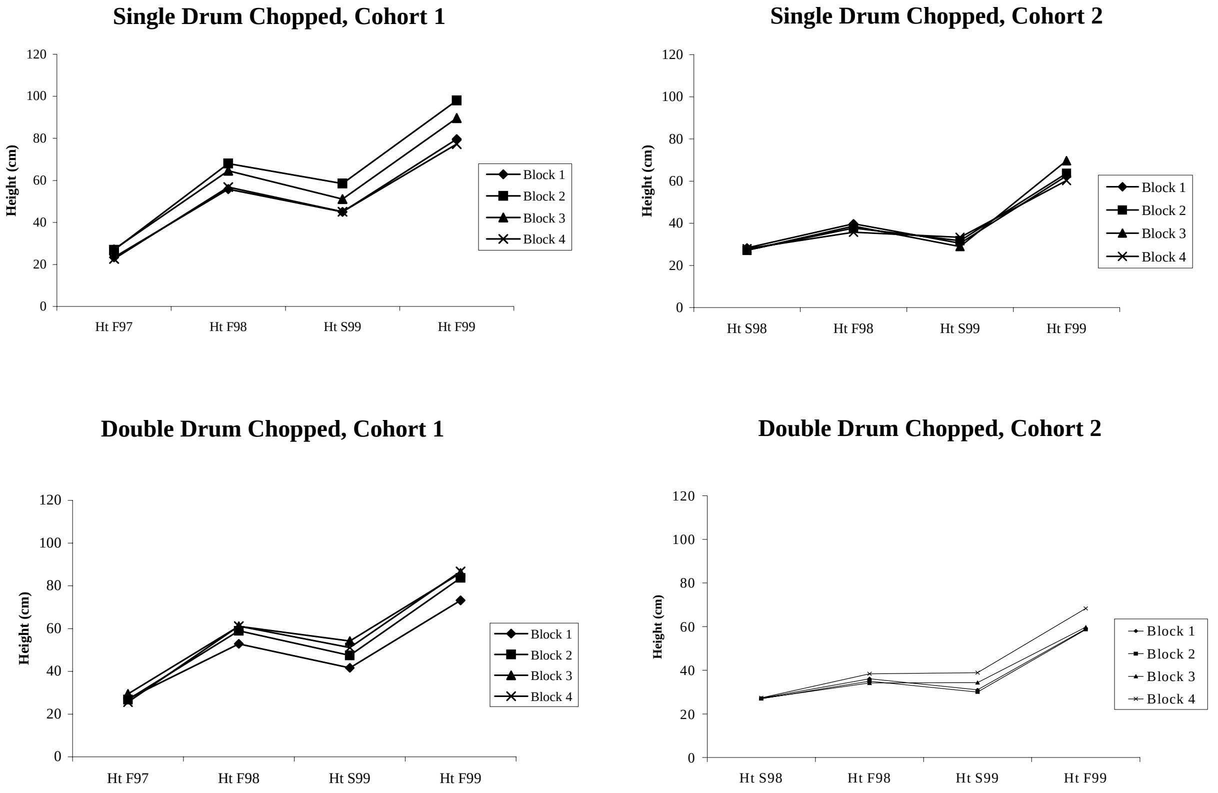
Deer Browse Cohort 2 - Winter 1998-1999

significant: time, interaction between time and block, within treatment, and interaction between time and cohort.

The significant cohort effect, for both height and diameter, was not surprising, given the different planting times. The newly established cohort 2 grew only 9.55 cm in net height and 0.13 cm in diameter in 1998, compared with 33.36 cm and 0.44 cm for cohort 1. In 1999, net height growth for the two cohorts was comparable (23.89 cm for cohort 1 and 25.27 cm for cohort 2) while differences in diameter growth were still evident (0.56 cm for cohort 1 and 0.33 cm for cohort 2). Site preparation treatment (single vs. double drum chopping) was significant for height, but not for diameter. Stecklings in the single drum chopped treatment performed slightly better than those in the double drum chopped area. Although the severe deer browsing that occurred makes it difficult to draw conclusions about treatment effects on height growth, it appears that double drum chopping did not improve steckling performance.

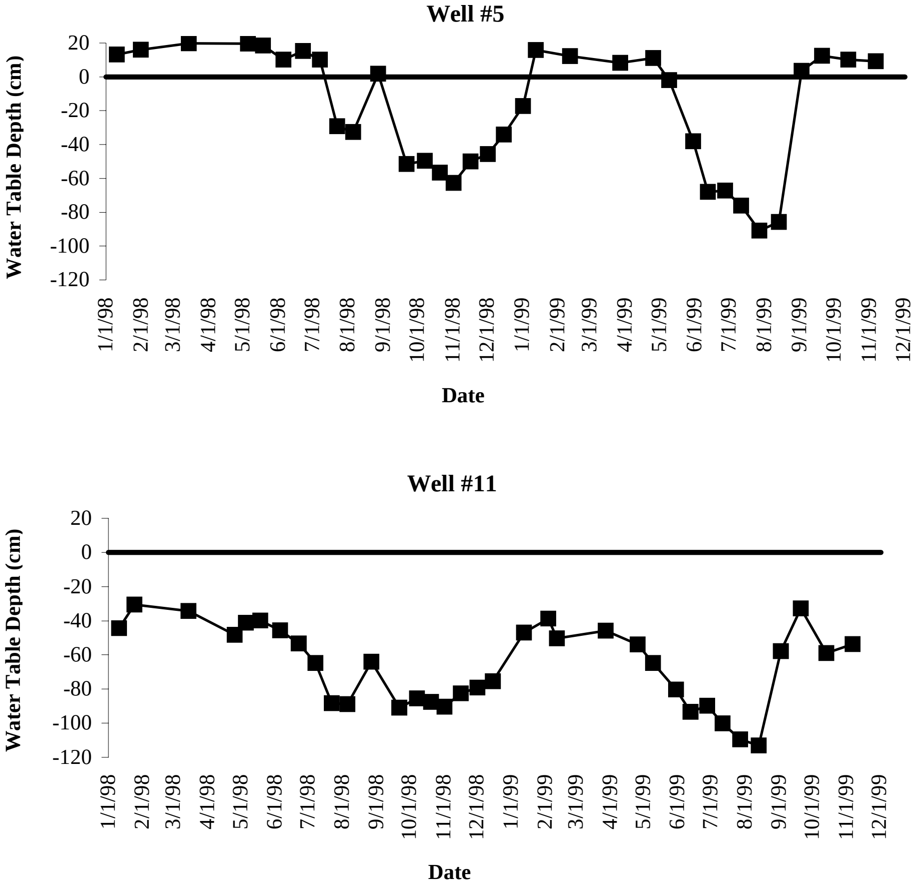
Relative elevation of stecklings ranged from 0 to 125.3 cm, with an average elevation of 8.5 cm. We did not find a significant relationship between relative elevation and either height or diameter growth. This probably indicates that the full range of elevations at the site were suitable for cedar growth.

Figure 4. Heights (Ht) of cedar stecklings planted on an abandoned blueberry field, by cohort and site preparation treatment. Cohort 1 includes stecklings planted prior to Fall 1997 (F97). Cohort 2 includes stecklings planted in Spring 1998 (S98). Repeated measures analysis of variance indicates the following factors to be significant (∝=0.05): time, interaction between time and site preparation treatment, interaction between time and block (within treatment), and interaction between time and cohort. The interaction between time and block (within treatment), along with the severe deer browsing that occurred, made it difficult to draw conclusions about site preparation treatment effects. However, there was a significant cohort effect.



The average water table throughout the study period was -40.7 cm below the ground surface, with a range from greater than –117.1 to +33.02. To show the amount of variation in water table depths, we show data from the wells with the highest and lowest values in figure 5. Seasonal variation in water table was apparent, as well as variation between years. New Jersey experienced drought conditions during the summer of 1999, and this was apparent from these data. Despite variation in water table depths across the site, we were unable to test the effects of these variations on individual steckling performance. There was no direct relationship between relative elevation and water table depth, therefore we could not determine the exact water table values for each steckling. The entire range of water table depths observed seem to be very suitable for the establishment, survival and growth of cedar plantings.

Figure 5. Water table levels for two selected test wells. Well #5 has had the highest water table throughout the study period, while well #11 the lowest.



Experiment 2

Here we were interested in the effects of fertilizer treatment on the survival and growth of planted stecklings (table 2). Survival through the second season was significantly higher for the control treatment, compared with the fertilizer treatments (chi-square p=0.03). For the Bio-pak, Osmocote, and control treatments, respectively, net height growth averaged 26.1 cm, 24.1 cm, and 13.46 cm during 1998, and 14.53 cm, 15.35 cm, and 8.64 cm during 1999. Actual height growth during 1999 averaged 25.43 cm, 27.18 cm, and 18.84 cm (table 2). Results of repeated measures analysis of variance found time, interaction between time and treatment, and interaction between time and block, within treatment, to be significant ($\propto = 0.05$). Heights over the study period by treatment and block are given in figure 6. For all blocks except block 4, average heights for both fertilizer treatments are greater than the control. We didn't find any overall difference in height growth between the Bio-pak and Osmocote treatments, with Osmocote treated stecklings performing best on some blocks, and Bio-pak treated stecklings performing best on others. Fertilized stecklings did not experience higher levels of deer browsing than controls.

Table 2. Results for Experiment 2. Percent survival, height and diameter growth (standard deviation) and deer browse by treatment, averaged across blocks. For the 1998 growing season, only net height and diameter growth were calculated (fall 1999-fall 1998). For the 1999 season, actual height growth was also calculated (height fall 1999-height spring 1999). Deer browse was determined by visually estimating the percentage of total foliage lost during the previous winter. It is presented as the total number of trees that experienced four levels of browse (0-15%, 16-50%, 51-85%, or 86-100% foliage lost).

	Osmocote	Bio-pak	Control
1998 Growing Season			
% Survival	90.5 (4.96)	94.7 (1.69)	100 (0.00)
Net Ht. Growth (cm)	24.11 (1.72)	26.21 (1.64)	13.46 (1.63)
Net Diam. Growth (cm)	0.44 (0.03)	0.46 (0.02)	0.25 (0.02)
Browse 1 (0-15%)	48	41	40
Browse 2 (16-50%)	18	16	15
Browse 3 (51-85%)	4	7	8
Browse 4 (86-100%)	2	8	8
1999 Growing Season			
% Survival	85.2 (6.53)	85.8 (4.03)	96.83 (2.01)
Net Ht. Growth (cm)	15.35 (1.14)	14.53 (1.82)	8.64 (1.25)
Actual Ht. Growth (cm)	27.18 (1.34)	25.43 (1.35)	18.84 (1.16)
Net Diam. Growth (cm)	0.33 (0.07)	0.34 (0.03)	0.22 (0.02)
Browse 1 (0-15%)	10	9	15
Browse 2 (16-50%)	30	35	39
Browse 3 (51-85%)	15	14	9
Browse 4 (86-100%)	2	1	3

Water table depths were slightly lower in this area than Experiment 1, averaging –47.7 cm (range from greater than –103.124 cm to –5.08 cm). Water table levels showed similar seasonal and yearly patterns, and were approximately equal across the study area.

Experiment 3

In this part of the study we monitored natural regeneration on a portion of the abandoned cranberry bog. After the first growing season we identified all woody species within thirty-six 1m^2 plots (table 3). Cedar seedling densities from natural seeding averaged 31,111 seedlings per ha (12,590 per acre); however, regeneration was very patchy, being concentrated mostly around individual seed trees, and 58% of all plots contained no cedar at all. We believe the patchiness of regeneration results from limited seed availability, rather than unsuitable site conditions.

Figure 6. Results of Experiment 2. Heights of planted cedar stecklings over the study period, by fertilizer treatment and block. Results of a repeated measures analysis of variance show the following factors to be significant; time, interaction between time and treatment, and interaction between time and block, within treatment. This indicates that the height response differed over time across treatments, but that the treatment effect varied by block. The treatment effect cannot be interpreted without looking at the response by individual blocks.

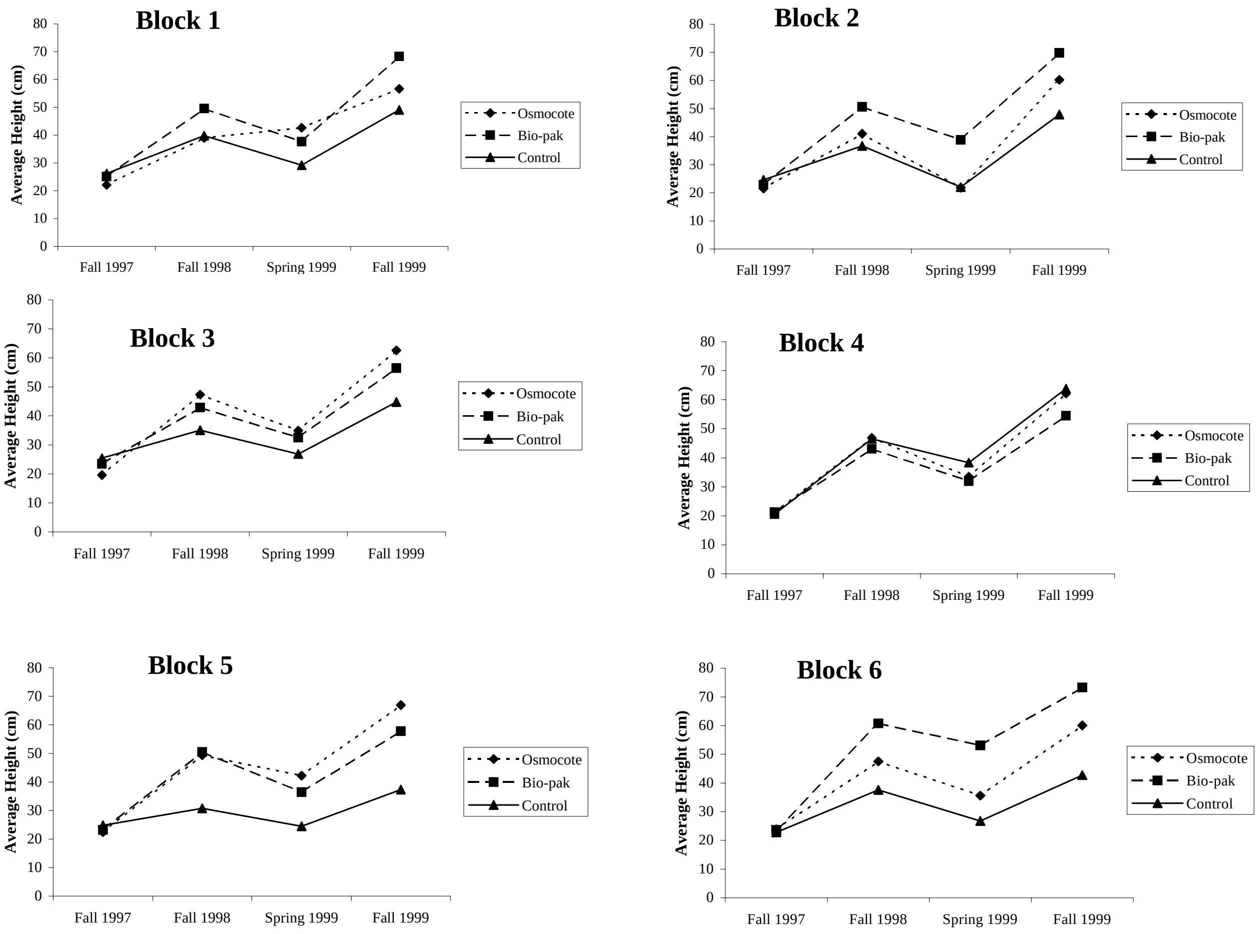


Table 3. Results for experiment 3. The purpose of this part of the study was to monitor natural cedar regeneration on a portion of the abandoned cranberry bog. All woody vegetation within 36 1 m^2 plots was identified. For each species we display mean densities, standard errors, and the percentage of plots that species was found in.

	Mean density (# per ha)	Standard error	Percentage of plots identified (%)
Chamaecyparis thyoides	31,111.11	12,622.59	41.67
Acer rubrum L.	555.56	555.56	2.78
Vaccinium corymbosum L.	277.78	277.78	2.78
Ilex glabra (L.) A.Gray	4,722.22	3321.08	8.33
Kalmia angustifolia L.	14,444.44	7,404.89	19.44
Chamaedaphne calyculata (L.) Moench	4,722.22	2,439.30	13.88
	Mean percent cover (%)	Standard error	Percentage of plots identified
Rubus sp.	10.97	3.03	58.33
Vaccinium macrocarpon Aiton	1.81	1.11	19.44

DISCUSSION/CONCLUSION

We examined several factors affecting cedar restoration on an abandoned blueberry field and cranberry bog in New Jersey. Site conditions seem to be appropriate for cedar establishment and survival. We believe soil series (Atsion sand) and moisture (average water table depth –40.7 cm for Experiment 1, and –47.7 cm for Experiment 2) conditions were suitable. The relationship between water table depth and relative elevation was not clear, so we were not able to test the effects of water table variation across the site on steckling performance. However, the lack of a relationship between elevation and steckling performance indicates that the entire range of elevations was suitable.

We believe that the restoration techniques used (drum-chopping, herbicide, and planting) were also appropriate. We feel that the combination of drum chopping and Arsenal® application was successful in reducing competition, as we did not observe competing vegetation prohibiting cedar survival or growth. Double drum chopping did not increase steckling performance, compared with single drum chopping.

Planting of cedar stecklings was also successful. We estimate that 4557 cedar have survived per ha on the 15.4 ha abandoned blueberry field. Data on seedling numbers required to produce a fully stocked cedar stand are lacking. If long-term survival rates are high, however, we believe this number should be adequate to fully stock the site.

The largest problem encountered was deer browsing, despite electric fencing. Electric fencing has been successful in reducing or eliminating browsing on other sites in New Jersey (Zimmermann 1997). We believe the larger area enclosed (50 acres) for this present study may have resulted in the observed increase in browse. Hinesley et al. (This Volume) suggest that the larger the enclosure, the more likely it is for deer to breach the fence. This should be taken into account when planning future restoration projects.

Natural seeding on the 4.8 ha abandoned cranberry bog has produced patchy regeneration. We believe this results from the limited availability of seed, rather than unsuitable site conditions for regeneration. If competing vegetation were controlled over the next several years, the gaps in regeneration would probably fill in. However, to achieve a rapid result, supplemental planting may be required to fill in these gaps.

Overall, site conditions have been suitable for the establishment, survival and growth of cedar. We believe that this site can be used as a model for future restoration projects, particularly on agricultural or shrub dominated sites.

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LITERATURE CITED

Haas, M. J. and J. E. Kuser. 1999. Effects of propagule type, geographic origin, and fertilization on first year performance of Atlantic white-cedar (*Chamaecyparis thyoides*) in New Jersey. Pages 22-26 In Shear TH, and KO Summerville (eds.) Atlantic white-cedar: ecology and management symposium; 1997 August 6-7; Newport News, VA. Gen. Tech. Rep. SRS-27. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 82 pp.

Hinesley, L. E., S. A. Smith, and M. A. Wicker. This Volume. Protecting newly established Atlantic white cedar and baldcypress with electric fences, tree shelter tubes, wire cages and total exclusion plots.

Korstian, C. F. and W. D. Brush. 1931. Southern white cedar. USDA Forest Service Technical Bulletin 251. Washington, DC. 75pp.

Kuser, J. E and G. L Zimmermann. 1995. Restoring Atlantic white-cedar swamps: Techniques for propagation and establishment. Tree Planters’ Notes 46(3):78-85.

Laderman, A. D. 1989. The ecology of the Atlantic white cedar wetlands: a community profile. US Fish and Wildlife Service Biological Report 85(7.21). 114pp.

Little, S. 1950. Ecology and silviculture of white cedar and associated hardwoods in southern New Jersey. Yale University School of Forestry Bulletin 56:1-103.

Little, S. 1959. Silvical characteristics of Atlantic white-cedar. USDA Forest Service, Northeastern Forest Experiment Station Paper No. 188. 16pp.

Moore, S. E. 1996. Natural Regeneration of Atlantic white cedar in the Great Dismal Swamp. PhD. dissertation. North Carolina State University, Raleigh, NC.

Mylecraine, K. A. and G. L. Zimmermann. 2000. Atlantic white-cedar: Ecology and Best Management Practices Manual. NJDEP, Division of Parks and Forestry, New Jersey Forest Service. 84pp.

New Jersey Forest Service. 1997. Forest health action update: Atlantic white-cedar decline. NJDEP, Division of Parks and Forestry, New Jersey Forest Service. 1p.

Roman, C. T. and R. E. Good. 1983. Wetlands of the New Jersey Pinelands: values, functions, impacts and a proposed buffer delineation model. Center for Coastal and Environmental Studies, Rutgers, The State University, New Brunswick, NJ.

United States Department of Agriculture, Soil Conservation Service. 1980. Soil Survey of Ocean County, New Jersey.

Ward, D. B. 1989. Commercial utilization of Atlantic white-cedar (*Chamaecyparis thyoides*, CUPRESSACEAE). Economic Botany 43(3):386-415.

Zampella, R. A. 1987. Atlantic white cedar management in the New Jersey Pinelands. Pages 295-311 In AD Laderman (ed.) Atlantic White Cedar Wetlands. Westview Press, Inc. Boulder, CO.

Zampella, R. A. and R. G. Lathrop. 1997. Landscape changes in Atlantic white-cedar (*Chamaecyparis thyoides*) wetlands of the New Jersey Pinelands. Landscape Ecology 12:397-408.

Zimmermann, G. 1997. The Atlantic white-cedar (*Chamaecyparis thyoides*) regeneration experiments: Final Report. Submitted to the NJDEP and USDA Forest Service. Richard Stockton College of NJ, Pomona, NJ. 190pp.

VEGETATION IMPORTANCE VALUES AND PREVALENCE INDEX VALUES OF ATLANTIC WHITE CEDAR STANDS IN GREAT DISMAL SWAMP AND ALLIGATOR RIVER NATIONAL WILDLIFE REFUGES

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Abstract: Since the 1700s, Atlantic white cedar (cedar), an obligate wetland species, declined by over 90% in Virginia and North Carolina due to anthropomorphic alterations in the natural perturbation regime of fire and hydrology. Naturally occurring cedar stands provide reference sites and aid in selecting goals for restoration. To quantify vegetative composition within each stratum, importance values (IV) were calculated for all species within tree, sapling/shrub, and herbaceous strata for three age classes [young (<8 years), intermediate (~30 years), and mature (<70 years)] of cedar swamp stands from both Great Dismal Swamp (GDS) and Alligator River (AR) National Wildlife Refuges. Since hydrologic changes are considered to be a major factor contributing to cedar decline, prevalence index values (PIV), a continuous variable that gauges plant community response to hydrology, were calculated for nested plots within each stratum. PIV for all strata in all sites ranged from 1.00 to 4.00 with a mean (μ) of 2.35. The tree stratum generally had a lower PIV (μ = 1.33) than the sapling/shrub (μ = 2.10) or herb stratum (μ = 2.64). The lowest PIV was found in the tree stratum of AR-mature (μ = 1.06), whereas GDS-intermediate had the highest tree PIV (μ = 2.14). The PIV tended to be higher when importance values were high for red maple, loblolly pine, and sweet pepperbush. Failure to reestablish the necessary hydrologic regime within cedar sites may result in replacement by mesophytic species.

Key Words: Atlantic white cedar, Great Dismal Swamp, hydrology, hydrophytic vegetation, importance values, prevalence index value, wetland restoration, *Chamaecyparis thyoides*

INTRODUCTION

Restoration of altered lands, especially the restoration of appropriate hydrology, is crucial to regaining healthy Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P (cedar), forests (Laderman 1989). Wetland vegetation structure is primarily influenced by high water tables and resultant anaerobic soil conditions (Tiner 1993). The frequency and duration of flooding affect plant species composition in wetlands as well as the growth form of some species (Young et al. 1993). However, cedar swamps are also affected by substrate characteristics (Thompson et al. This Volume).

Naturally regenerating cedar forests with lower water tables may be replaced by more mesic communities such as bottomland hardwood forests (Levy 1987, Penfound 1952). Conner (1988) found that two facultative species, *Acer rubrum* L. (red maple) and *Liquidambar styraciflua* L. (sweetgum), which sometimes replace cedar, grew best in sites that were intermittently flooded. These wetlands are defined as areas with substrate that is usually exposed, but surface water is present for variable periods without detectable seasonal periodicity. Thus the interval between inundations could be weeks, months, or years (Cowardin et al. 1979).

Cedar-associated species have been listed by a number of authors (Loomis et al. This Volume, Laderman 1987, Musselman et al. 1977, Little 1950, Korstian and Brush 1931, Kearney 1901), but little quantitative data is available (Laderman 1987). Prior to the 1900s, cedar communities were characterized as dense monotypic stands with a very sparse shrub layer (Little 1950, Korstian and Brush 1931, Kearney 1901). Kearney (1901) stated that juniper lights, dense monotyic stands of cedar, were rapidly being replaced by a hardwood association within the interior of the GDS.

The calculation of prevalence index values (PIV), also known as weighted averages (Wentworth et al. 1988, Curtis and Mcintosh 1951, Whittaker 1951, Ellenberg 1948), has been used in wetland delineation (Scott et al. 1989, Carter et al. 1988, Wentworth et al. 1988, Environmental Laboratory 1987) and monitoring of created wetlands (Atkinson et al. 1993). PIV is a continuous variable that combines the indicator status and dominance of each species to estimate the plant community response to hydrology within individual sampling plots. The purpose of this paper is to contrast vegetation within four stands at GDS and AR and to provide a baseline PIV for future cedar restoration efforts from these natural stands.

METHODS

Fieldwork was conducted during the 1998-1999 growing seasons. Sites were selected to represent a chronosequence based on time since last harvest and consisted of two mature (>70 years), two intermediate (~30 years), and one young (<8 years) sites and were further described in Atkinson et al. (This Volume)

Eighteen 100-m^2 quadrats were established along transects at each site to evaluate the tree, sapling/shrub, and herbaceous layer dominance following Dabel and Day (1977). Vegetation greater than 3.0 m tall and greater or equal to 2.54 cm dbh were recorded as part of the canopy stratum. The sapling/shrub stratum included all vegetation less than 3.0 m tall, as well as plants that were greater than 0.3 m tall and less than 2.54 cm dbh. Saplings/shrub canopy cover was measured in eighteen 16-m^2 nested quadrats. Percent cover of the herbaceous stratum, all vegetation less than 0.3 m tall or less than 2.54 cm dbh, was measured in fifty-four 1-m^2 nested quadrats.

Prevalence indicator values were calculated using the following formula (Jongman et al. 1987):

$$PIV= (y_1u_1+y_2u_2+\ldots+y_mu_m)/100$$

where $y_1,y_2,\ldots,y_m$ are the relative dominance estimates for each species in the plot, and u_1,u_2,u_m are the regional indicator values of each species.

Indicator categories range from 1 to 5, PIV does also (table 1). Thus, a plot composed of all OBL wetland species would have a PIV of 1, and a plot of all UPL species would have a PIV of 5 (Jongman et al. 1987). Indicator status was obtained from the *National List of Plant Species that Occur in Wetlands Southeast, Region 2* (Reed 1988). Cedar that had been planted was eliminated from PIV calculations since the species was directly established rather than naturally occurring.

Table 1. Wetland indictor categories of plant species under natural conditions (Reed 1988).

Wetland Indicator Category	Estimated Probability of Occurrence in Wetlands	Assigned Indicator Status
Obligate Wetland (OBL)	Greater than 99%	1
Facultative Wetland (FACW)	67 to 99%	2
Facultative (FAC)	34 to 66%	3
Facultative Upland (FACU)	1 to 33%	4
Obligate Upland	Less than 1%	5

SIGMA STAT 2.03™ version 2 (SPSS Inc. 1992) was used for all hypothesis testing. Statistical tests for plots at all sites included analysis of variance (ANOVA) of water table depth and linear regression of water table depth and prevalence index values. Normality was tested using the Kolmogorov-Smirnov test, and means were compared using a Student's t-test for normally distributed data. A Mann-Whitney rank sum test was employed for non-normal data. When more than two means were compared, Kruskal-Wallace One Way ANOVA on Ranks in combination with Dunn's Multiple Comparison test was utilized. A significance level of $p < 0.05$ was used for all hypothesis testing. Variability was reported as the standard deviation of the mean (σ). Vegetative means (μ) were based upon a sample size of 18 plots for tree and shrub/sapling strata in intermediate and mature sites ($n = 18$), and 45 plots for the herbaceous stratum in GDS-young site ($n = 45$) and 54 plots for herbaceous strata in intermediate and mature sites. Unlike the herbaceous stratum for GDS-young, the intermediate and mature herbaceous strata were sparse, therefore a higher number of plots was used.

RESULTS

In addition to cedar, tree species with high RIV included *Acer rubrum* and *Nyssa biflora* (table 2). The sapling/shrub stratus was more species rich and species with high RIV included *Acer rubrum, Clethra alnifolia, Ilex coriacea, Lyonia lucida, Persea borbonea, and Vaccinium corymbosum* (table 3).

There was no difference in the tree stratum PIV for AR- intermediate ($\mu = 1.26$, $\sigma = 0.25$), AR-mature site ($\mu = 1.07$, $\sigma = 0.08$) and GDS-mature site ($\mu = 1.25$, $\sigma = 0.33$) ($p>0.05$, $n = 18$)

(figure 1). The tree stratum of GDS-intermediate had a higher PIV ($\mu = 2.15$, $\sigma = 0.51$, $p < 0.05$) than either GDS-mature ($\mu = 1.20$, $\sigma = 0.32$) or AR-mature ($\mu = 1.07$, $\sigma = 0.08$).

Table 2. Species relative importance values in the tree stratum for AR and GDS sites.

Species	North*	South*	GDS**	AR-I	AR-M	GDS-I	GDS-M
Acer rubrum L.	16.2	14.6	15.1	9.0	1.7	50.0	13.9
Chamaecyparis thyoides (L.) B.S.P.	42.8	18.7	58.2	67.4	53.4	45.0	65.3
Gordonia lasianthus L. Ellis	-----	-----	-----	13.1	7.45	-----	----
Liquidambar styraciflua L.	2.2	-----	-----	-----	-----	0.9	-----
Magnolia virginiana L.	2.0	5.0	8.9	-----	6.9	3.1	5.9
Nyssa aquatica L.	-----	4.0	-----	-----	-----	-----	-----
Nyssa biflora Walt.	4.9	25.3	12.7	0.81	23.9	-----	1.8
Persea borbonia (L.) Spreng.	-----	6.2	1.3	5.49	2.6	-----	11.4
Pinus serotina Michx.	-----	3.2	------	2.92	3.4	0.98	0.5
Pinus taeda L.	1.6	7.6	------	-----	-----	-----	1.65
Taxodium distichum (L.) L.C. Rich	-----	6.4	2.9	1.34	0.64	-----	-----
Other species	30.3	4.4	0.9	-----	-----	-----	-----

*Sheffield et al. 1998: described all habitat types for northern and southern cedar range
**Levy and Walker 1979: described cedar stands in GDS

Table 3. Species relative importance values in the sapling/shrub stratum for AR and GDS sites.

SPECIES	ARI	ARM	GDSY	GDSI	GDSM
Acer rubrum L.	10.79	2.32	4.42	37.92	1.37
Aralia spinosa L.	------	------	------	------	0.79
Asimina triloba (L.) Dunal	------	------	1.49	------	------
Chamaecyparis thyoides (L.) B.S.P.	2.62	-----	10.30	------	-------
Clethra alnifolia L.	6.53	2.29	22.61	8.97	27.52
Gordonia lasianthus L. Ellis	3.40	2.39	-------	------	-----
Ilex coriacea (Pursh) Chapman	9.34	29.09	1.06	3.39	0.49
Ilex glabra (L.) Gray	1.02	5.15	-----	------	0.70
Ilex opaca Aiton	0.73	------	1.88	1.66	2.65
Itea virginica (L.)	------	-------	1.06	-----	2.62
Lyonia lucida (Lam.) K. Koch	28.81	38.78	13.78	9.21	29.88
Magnolia virginica L.	------	0.60	------	1.65	1.92
Myrica cerifera (L.) Small	------	0.56	------	------	-------
Nyssa biflora Walt	1.91	0.54	------	------	------
Persea borbonea (L.) Spreng	3.86	13.90	24.50	32.41	21.54
Pinus taeda L.	------	------	10.68	-----	------
Quercus lyrata Walt.	-----	0.54	-----	------	------
Rhododendron viscosum (L.) Torr.	0.73	0.79	------	------	-----
Rubus argutus Link.	------	0.59	1.84	4.79	0.47
Rubus hispidus L.	-----	------	1.16	-----	-----
Toxicodendron radicans (L.) Kuntz	----	------	------	------	0.70
Vaccinium corymbosum L.	30.24	2.47	6.29	-----	9.34

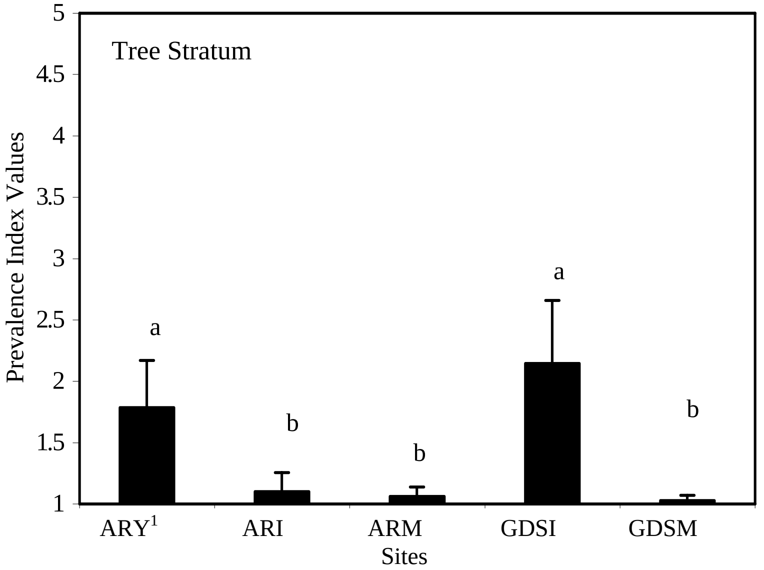
There was a higher PIV for the sapling/shrub strata at GDS sites ($\mu = 2.43$, $\sigma = 0.40$) than at AR sites ($\mu = 2.02$, $\sigma = 0.28$) ($p < 0.05$, $n = 18$) (figure 2). The PIV for GDS- intermediate and GDS-young PIV did not differ ($p > 0.05$). For the herb stratum, the AR sites ($\mu = 2.17$, $\sigma = 0.36$) had lower PIV than GDS sites ($\mu = 2.87$, $\sigma = 0.47$) ($p < 0.05$) (figure 3). There was no difference in PIV among the GDS sites or among the AR sites ($p > 0.05$).

DISCUSSION

Prevalence index values provide an indication of the effect that water tables have on vegetation distribution. High correlations were obtained between depth to water table and plant distribution for compensation sites (Shacochis 2001). High PIV at GDS-intermediate and mature sites indicated that low water tables that were recorded for 1999 in GDS may have persisted for some time. These data suggest that water tables in similar stands at GDS may favor invasion by red maple and that fire may be more likely to eliminate cedar from the seed reservoir as well as the canopy.

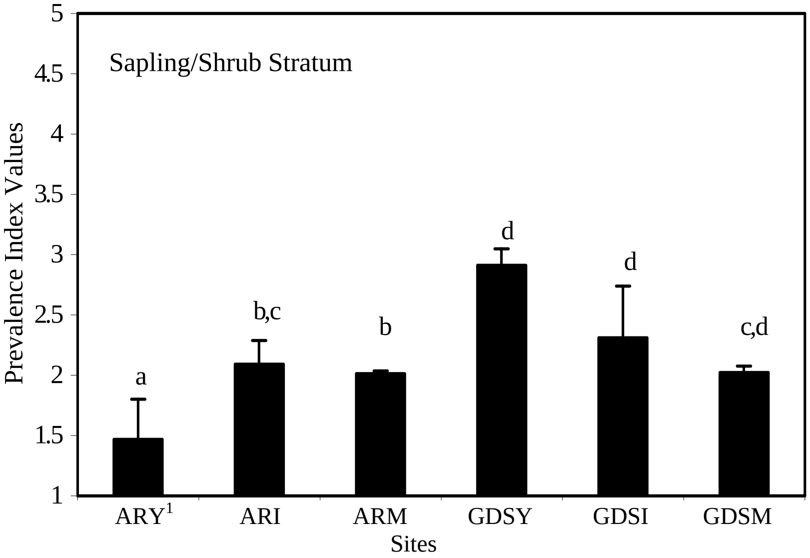
GDS-intermediate was the only site that exhibited a sparse shrub layer and a high RIV for red maple in the sapling/shrub stratum. FACW shrub species, especially fetterbush and redbay, had a total RIV of up to 99% in most sites; however, the RIV for these species totaled only 17% in GDS-intermediate. FAC species totaled 81% of sapling/shrub RIV at GDS-intermediate. The most important species within the GDS-intermediate sapling/shrub stratum was red maple (RIV = 37.9%). Shrubs provide some indication of hydrology, but are

Figure 1. Tree prevalence index values for the intermediate and mature sites as well as for a young site in AR that was studied by Smith (1995). Prevalence index values greater than or equal to 3.0 are characteristic of upland sites. Means with the same letter are not significantly different ($p>0.05$).



[1]Smith 1995

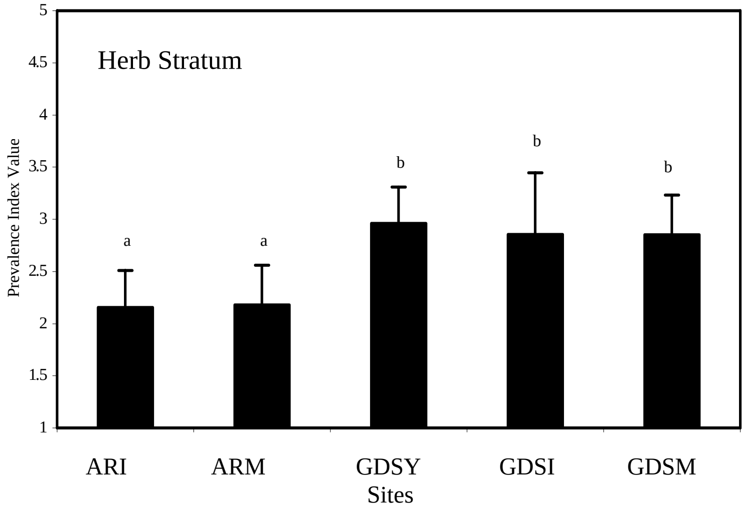
Figure 2. Sapling/shrub stratum prevalence index values for all five sites as well as for a young site in AR that was studied by Smith (1995). Means with the same letter are not significantly different ($p>0.05$).



[1]Smith 1995

unlikely to replace cedar in the canopy. Because of the high density of red maple saplings at the GDS sites, this species is likely to have an increasing RIV in the tree stratum. Black gum has a high importance at AR-mature and, like red maple, may replace cedar. However, black gum is an OBL species and its presence, along with generally low PIV values at the AR sites, suggest that cedar may have a competitive advantage if a fire regime is in place in this region.

Figure 3. Herb stratum prevalence index values for the AR and GDS sites. Mean with the same letter are not significantly different (p>0.05).



The drier sites found at GDS had much higher PIV. Other species with high importance values were typically FAC with the most important facultative species being red maple. The prevalence indicators for trees, shrubs, and herbs may reflect temporal differences in water levels. The most sensitive stage to inundation in most vascular plant life cycles is seed germination and establishment (Carter 1986). Herbaceous strata were usually sparse in the mature cedar stands. Herb and sapling/shrub strata typically had a higher PIV than tree strata. The higher PIV for herbs could be due to low cover and vegetation being present on hummocks but not in hollows. The lower PIV for the tree stratum at AR could be a result of high water tables that were present at the time of regeneration. However, well data from these sites suggest that AR sites are wetter than sites in GDS throughout most of the growing season (Atkinson et al. This Volume).

Fire or clearcutting these sites at the GDS could change vegetative composition to more mesophytic species due to the recent changes in hydrology (Lichtler et al. 1979). For example, in the GDS-young site that was previously dominated by a dense stand cedar (452 trees per ha), FAC and FACU species, including red maple and loblolly pine, exhibited a higher importance at the time of this study. Therefore, we suggest that a higher water table be established at similar sites prior to, or concurrent with, restoration efforts.

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LITERATURE CITED

Atkinson, R.B., J.E. Perry, E. P. Smith, and J. Cairns. 1993. Use of created wetland delineation and weighted averages as a component of assessment. Wetlands 13:185-193.

Atkinson, R.B., J.W. DeBerry, D.T. Loomis, E.R Crawford, and R.T. Belcher. This Volume. Water tables in Atlantic white cedar swamps: Implications for restoration.

Carter, V. 1986. An overview of hydrologic concerns related to wetlands of the U.S. Canadian Journal of Botany 64: 365-374.

Carter, V., M.K. Garrett, and P.T. Gammon. 1988. Wetland boundary determination in the Great Dismal Swamp using weighted averages. Water Resources Bulletin 24: 297-306.

Conner, W.H. 1988. Response to coastal wetland forests to human and natural changes in the environment with emphasis on hydrology. In Hook D. and L. Russ (eds.). The Forested Wetlands of the Southern U.S. Forest Service Southeastern Forest Experimental Station. Asheville, N.C.

Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRoe. 1979. Classification of Wetlands and Deepwater Habitats of the United States, FWS/OBS-79/31, U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC.

Curtis, J.T. 1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison, WI.

Curtis, J.T. and R.P. McIntosh. 1951. An upland forest continuum in the prairie forest border region of Wisconsin. Ecology 32: 476-496.

Dabel, C.V. and F.P. Day, Jr. 1977. Structural comparisons of four plant communities in the Great Dismal Swamp, Virginia. Bulletin of the Torrey Botanical Club 104 (4): 352-360.

Environmental Laboratory. 1987. Corps of Engineers Wetlands Delineation Manual. Final Report. Y-87-1. Vicksburg, MS: United States Department of the Army.

Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R. (eds.) 1987. Data analysis in community and landscape ecology. Pudoc, Wagenigen, Netherlands.

Kearney, T.H. 1901. Report on a botanical survey of the Dismal Swamp region. Contributions to the U.S. Natural Herbarium 5:321-550.

Korstian, C.F. and W.D. Brush. 1931. Southern white cedar. U.S. Department of Agriculture Technical Bulletin. 251.

Laderman, A.D. 1987. Atlantic White Cedar Wetlands. Westview Press. Boulder, CO.

Laderman, A.D. 1989. The ecology of Atlantic white cedar wetlands: a community profile. U.S. Fish Wildlife Service Biological Report 85 (7.21).

Lichtler, W.F., P.N. Walker and P.W. Kirk Jr., (ed.). 1979. Great Dismal Swamp. University Press of Virginia. Charlottesville, VA.

Little, S. Jr. 1950. Ecology and Silviculture of Whitecedar and Associated Hardwoods In Southern New Jersey. Yale University School of Forestry Bulletin; 56.

Loomis, D.T., R.T. Belcher, J.W. DeBerry, K.M. Shacochis, and R.B. Atkinson. This Volume. A vascular flora of eight Atlantic white cedar communities.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons. New York, N.Y.

Musselman, L.J., D.L. Nickrent, and G.F. Levy. 1977. A contribution toward a vascular flora of the Great Dismal Swamp. Rhodora. (79): 240-268.

Penfound, W.T. 1952. Southern swamps and marshes. Botanical Review. 18:413-446.

Reed, P.B., Jr. 1988. National List of Plant Species That Occur in Wetlands: Southeast (Region 2). U.S. Fish and Wildlife Service, Washington, DC, USA. Biological Report. 88 (24).

Shacochis K.M. 2001. Evaluation of Vegetation Community Structure in Atlantic White Cedar *Chamaecyparis thyoides* (L.) B.S.P. in Restoration Sites. Master Thesis. Christopher Newport University. Newport News, VA.

Smith, L. E. 1995. Regeneration of Atlantic White Cedar at the Alligator River National Wildlife Refuge and Dare County Air Force Bombing Range. Masters Thesis. North Carolina State University. Raleigh, N.C.

SPSS, Inc. SigmaStat For Windows. Version 2.03, copyright 1992.

Tiner, R.W. 1993. Field Guide to Coastal Wetland Plants of the Southeastern United States. Amherst, Massachusetts: The University of Massachusetts Press, Boston, MA.

Wentworth, T.R., G.P. Johnson, and R.L. Kologiski. 1988. Designation of wetlands by weighted averages of vegetation data: a preliminary evaluation. Water Resources Bulletin 24: 389-396.

Young, P.J., J.P. Megonigal, R.R. Shartz, and F.P. Day. 1993. False ring formation in baldcypress (*Taxodium distichum*) saplings under two flooding regimes. Wetlands 13: 293-298.

AN ANALYSIS OF STRUCTURAL AND ECOPHYSIOLOGICAL RESPONSES OF ATLANTIC WHITE CEDAR ACROSS A RANGE OF SHADE INTENSITIES

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Abstract: *Chamaecyparis thyoides* (cedar) is a tree long prized for its lightweight, extremely durable and decay resistant wood has been logged extensively since European colonization. Cedar was once more common throughout its range, but populations have declined due to over harvesting and other anthropogenic effects. Most restoration attempts have been largely unsuccessful, with practitioners citing fire control, ditching, draining, and reduced light intensities resulting from shading by competitors and logging slash. Light intensity has been recognized as an important factor in the growth, survival, and competitive success in restoration projects involving cedar. However, there is no consensus regarding light requirements of the species. In this study, 60 two-yr-old bare root cedar cuttings were grown in peat filled mesocosms under six shade treatments. The treatments consisted of 100, 45, 37, 27, 15, and 5 % of full sun. Individual tree height and basal diameter were recorded monthly April through November. Above and belowground biomass, leaf area and volume, and canopy cover were calculated at the end of the growing season. Photosynthetic response curves were used to evaluate photosynthetic rates at eight PAR levels. These results suggest that two-yr-old cedar cuttings can survive up to 95 % shading, but low growth rates affecting height, basal diameter, above and belowground biomass, and leaf area reduce chances for competitive success.

Key Words: Atlantic white cedar, biomass, ecophysiology, shade, structure

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), is an obligate wetland (Reed 1988), evergreen conifer which frequently occurs in dense stands in freshwater swamps, pocosins, bogs, bays, lake shores and along stream banks. The natural range of cedar is from sea level to 150 m (492 ft) in the outer Atlantic coastal plain from Maine to Florida, and west to Mississippi (Korstian and Brush 1931).

The requirements for growth and reproduction of cedar vary across its range, but the species is generally associated with saturated, acidic (pH 3.2-5.5) soils high in peat content and low in silt, clay and minerals (Laderman 1982).

Hydrologic and fire regimes are critical influences on cedar ability to naturally regenerate, grow and produce the dense, even-aged monotypic stands reported in North Carolina and Virginia. Cedar requirements for fire and water appear paradoxical: cedar stands are destroyed by fire, but fire also clears competition from the substrate surface, permitting seeds of cedar to germinate and grow. During times of low water, a very hot fire burns peat and destroys the seed pool, which results in lower elevations and more inundation. Persistent inundation can drown cedar seedlings, whereas mature trees may tolerate these conditions. Where conditions remain unaltered, cedar may regenerate when fire and moist peat facilitate germination and growth, while restricting competition (Laderman 1987, Little 1950).

Attempts to restore or establish cedar forests have generally been unsuccessful because of inappropriate fire control, ditching, draining, and shading (Dabel and Day 1977, Frost 1987, Ehrenfeld and Schneider 1991, Laderman 1989). Shading produced by logging slash or competing vegetation may allow other plant communities to become established, and cedar co-occurs with aggressive and fast growing wetland species including *Acer rubrum* L. (red maple), *Nyssa sylvatica* var. *biflora* (Wal.) Sargent (swamp black gum), *Clethra alnifolia* L. (sweet pepper bush.), *Lyonia lucida* (Lam.) K. Koch (fetterbush), *Vaccinium corymbosum* L. (highbush blueberry), and several vine and herbaceous species (Loomis et al. This Volume).

Selected harvesting and regeneration of cedar stands with various site preparations including mechanical, controlled burns, and herbicides have been attempted by natural resource managers and foresters. The primary goal of these treatments has been to decrease competition, thereby increasing the amount of light that reaches the seedlings.

Light intensity has been recognized as an important factor in the survival and competitive growth of cedar seedlings (Akerman 1923, Korstian and Brush 1931, Laderman 1989, Little 1950). However, there is no consensus regarding light requirements. Numerous researchers suggest cedar is shade intolerant (Ash et al. 1983, Buell and Cain 1943, Fowells 1965, Laderman 1989, Motkin et al. 1993, Noyes 1939, Pinchot 1899) and others report the species is shade tolerant (Akerman 1923, Baker 1922, Eleuterius and Jones 1972, Little 1950, Moore 1939), even out competing *A. rubrum* under low light conditions (Hickman and Neuhauser 1978). Yet another possibility is that cedar is shade tolerant in its early years and becomes less tolerant with age (Korstian and Brush 1931).

In a greenhouse study, Little (1950) determined that initial growth of cedar was comparable to that of *A. rubrum* and *Magnolia virginiana* L. (sweet bay) only under light shade and with a high water table. Under these conditions, the coniferous seedlings were taller than those of sweet bay and approached the height of *A. rubrum* seedlings. With increasing shade, differences due to the water table tended to decrease among all species, especially cedar. Little (1950) concluded that cedar requires open, moist conditions for adequate growth.

In a recent study in the Great Dismal Swamp, Moore (1996) reported no differences in the growth of four-year-old cedar saplings between full sun and 45% of full sun. However, Summerville et al. (1999) found differences between growth of cedar seedlings between full sun and 45% of full sun.

Zimmerman and Mylecraine (1999) measured photosynthetic rates of cedar seedlings from three different sources and grown under four different light treatments. Photosynthetic rates ranged from -0.02 to 13.7 μmol m^{-2} s^{-1} and averaged 4.20 μmol m^{-2} s^{-1}. Differences were reported between light treatments and between sources. The current study was designed to discern the structural and ecophysiological response of cedar cuttings to a range of shade intensities in order to predict optimal and tolerable shading levels.

METHODS

Site Description

The Great Dismal Swamp National Wildlife Refuge (GDSNWR) is located in southeastern Virginia and northeastern North Carolina. The refuge contains most of the remnant populations of cedar in southeastern Virginia. The study site was located in a fallow agriculture field adjacent to the Great Dismal Swamp and east of State Route 604.

Study Design

To eliminate natural shading, a 0.40-ha (0.98-acre) site was cleared of all woody and herbaceous vegetation, and mowed weekly throughout the study. Twelve mesocosms consisting of plastic pools with a diameter of 1.42 m (4.7 ft) and 0.28 m (11.0 in) deep were installed with the rim set flush with the soil surface. The pools were then filled with peat moss (Southland Importers, Inc., Greensboro, NC) to a uniform depth of 28 cm (11.0 in). A hole was placed in each mesocosm wall 10.2 cm (4 in) below soil surface to allow drainage.

Six sunlight treatments were arranged in a complete randomized block design and included 45, 37, 27, 15, 5 % of ambient sunlight and a control (full ambient sunlight). Shade house frames were constructed of 3.8-cm (1.5-in) PVC pipe above 10 of the mesocosms to support shade cloth (PAK Inc., Norcross, GA). The resulting shade intensity within each mesocosm was calibrated at the start, after 15 weeks, and at the end of the study. Shade intensity was measured using a Li-Cor PAR button and was found to be within $\pm$ 1 % of its labeled shade intensity.

Two-year-old bare root cedar cuttings of uniform height of 35.8 cm (14.0 in) s.d. 4.7 cm were obtained from Weyerhaeuser Nursery, Washington, NC. After roots were pruned 15.25 cm (6.0 in) below root collar, five trees were randomly selected and planted in each mesocosm on March 3, 1998. A threshold for statistical significance of $p < 0.05$ was used throughout this study.

Morphometry

Tree height and basal diameter were measured monthly throughout the 1998-growing season (April through November). Heights to the nearest 1.0 mm (0.04 in) were estimated as the distance from root collar to maximum vertical growth of each rooted cutting. Basal diameter for each tree was measured with dial calipers to the nearest 0.1 mm at the soil surface.

Canopy cover was estimated by measuring the maximum diameter, based on distance from the end of one branch to the end of another. The distance (or diameter) across the tree canopy was used to calculate the area by the equation: area = π (diameter/2)^2.

Rooted cuttings were harvested in November 1998 and aboveground portion of each was physically separated into leaves or woody stems, sealed in plastic bags and stored at 4ºC. The belowground (root) portion of the trees was washed thoroughly to remove soil.

Leaf volume for each tree was estimated by displacement within a 250-ml graduated cylinder. A flat bed scanner connected to a personal computer and Corel Draw 8 (Corel Corporation, Ottawa, Ontario, Canada) was calibrated and used to estimate leaf area (personal communication Dr. Mark Gray 1998).

Leaves, woody stems, and roots were dried at 60º C to a constant weight. Six dry biomass parameters were measured including total, aboveground, belowground, stem, and leaf biomass, and shoot (aboveground biomass) to root (belowground biomass) ratio.

Ecophysiological

A portable, climate controlled, closed-system phytochamber was used to estimate CO_2 fluxes for eight trees for each light treatment. The phytochamber consisted of four major parts including a rectangular chamber, a soil respiration exclusion plate, a climate control system, and a sensor system (Bartlett et al. 1990, Whiting et al. 1992). A LI-COR model 6200 portable photosynthesis system (LI-COR, Inc., Lincoln, Nebraska, USA) measured chamber air temperature, relative humidity, photosynthetically active radiation (PAR), and CO_2 concentration. Three sides of the 0.35-m^3 (0.46-yd^3) chamber were covered with transparent (~90% PAR transmission) Teflon film with the remaining side and top composed of a clear polycarbonate sheet. The chamber was placed on top of a soil respiration exclusion plate during sampling and sealed with a closed-cell foam gasket and clamps prior to sampling.

Temperature within the phytochamber was maintained within 1°C of ambient temperature by the climate control system. The chamber's climate control system consisted of an ice water reservoir with pump, a heat exchanger and mixing fans and temperature was controlled by adjusting a flow-value, which restricted the flow of cold water from the reservoir to the heat exchanger. The air was mixed in the chamber with 2 fans that circulated the air at a velocity of 4.9 km hr^{-1} (3.1 mi hr^{-1}), which was comparable to velocities measured at the study site.

The chamber was deployed between 700 to 1600 PAR to utilize maximum light levels in defining light response curves. Net CO_2 exchange was calculated from changes in CO_2 concentration within ~ 10 ppm of local ambient. Net aboveground exchange response to light was measured during natural light reduction from clouds and by using screens placed over the chamber to provide incremental reduction in PAR intensity. Total aboveground plant respiration was measured by placing a blackout shroud over the chamber.

The CO_2 exchange measured in the chamber equaled the net exchange of CO_2 or net aboveground exchange (NAE) for the stem and foliage. NAE is the uptake or release of CO_2 in the chamber resulting from the difference between CO_2 added to the atmosphere by way of stem respiration and CO_2 taken up the plant during photosynthesis (Whiting et al. 1992). The convention of CO_2 uptake from the atmosphere being a positive sign (+) and release to the atmosphere a negative (-) will be used in this paper.

Empirical Modeling

NAE data was related to PAR empirically with a model based on the equation for a rectangular hyperbola:

$$NAE = \frac{(\alpha * \mathrm{PAR} * \mathrm{GP}_{\max})}{(\alpha * \mathrm{PAR}) + \mathrm{GP}_{\max}} - R_A$$

where α is the initial slope of NAE versus PAR, PAR is measured in microEinsteins $m^{-2} s^{-1}$ (1 Einstein = 1 mole of photons), GP_{max} is the empirically derived gross photosynthetic exchange of CO_2, and R_A is aboveground respiration term determined from dark condition measurements (Johnson and Thornley 1984, Whiting 1994). The slope and GP_{max} were derived for each tree using a nonlinear parameter estimation routine (TableCurve, Jandel Scientific, Corte Madera, California).

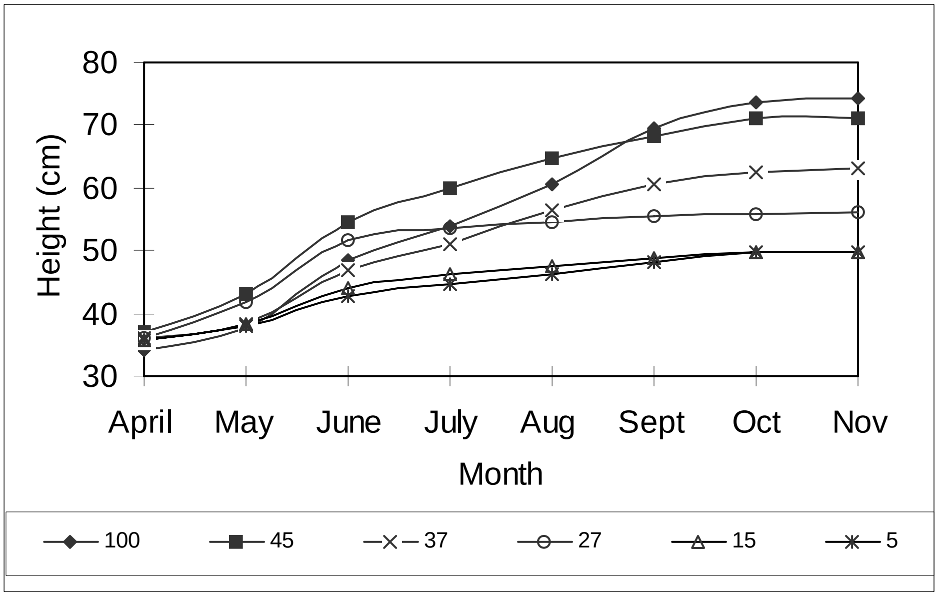
RESULTS

Survivorship

Survivorship of rooted cuttings during this study exceeded 98%. At the conclusion of the study in November 1998, only 1 of the 60 rooted cuttings had died, and that plant had been exposed to15% of full sun.

Morphometry

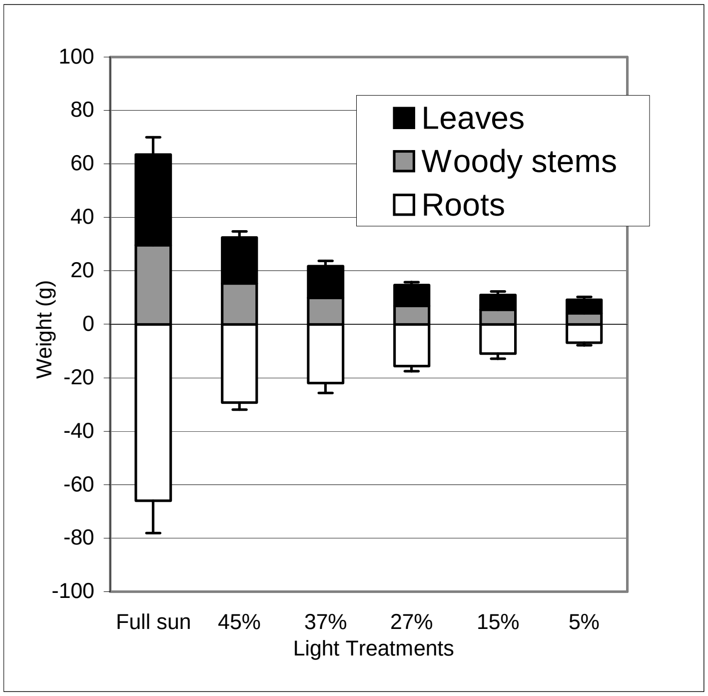
Figure 1. Mean cedar total height across light treatments. Light treatments are expressed as percent of full sun.



From May to the end of August, cuttings in the 45% of full sun treatment were taller than any other treatment including full sun. From September to November cuttings in the full sun treatment out grew the other cuttings. At the conclusion of the growing season mean tree height was: Full Sun > 45% > 37% > 27% > 15% > 5% (figure 1).

In May and June, cutting height was not different among light treatments ($p > 0.05$). Cuttings in the 5% of full

Figure 2. Cedar biomass as effected by light treatments.



sun treatment began to show less growth than control cuttings in July ($p < 0.05$). In August, cuttings in the 15% of full sun treatment also showed less monthly growth than the control ($p < 0.05$). During September, October, and November, cuttings in the 27, 15 and 5% treatments were shorter than those growing in full sun ($p < 0.05$).

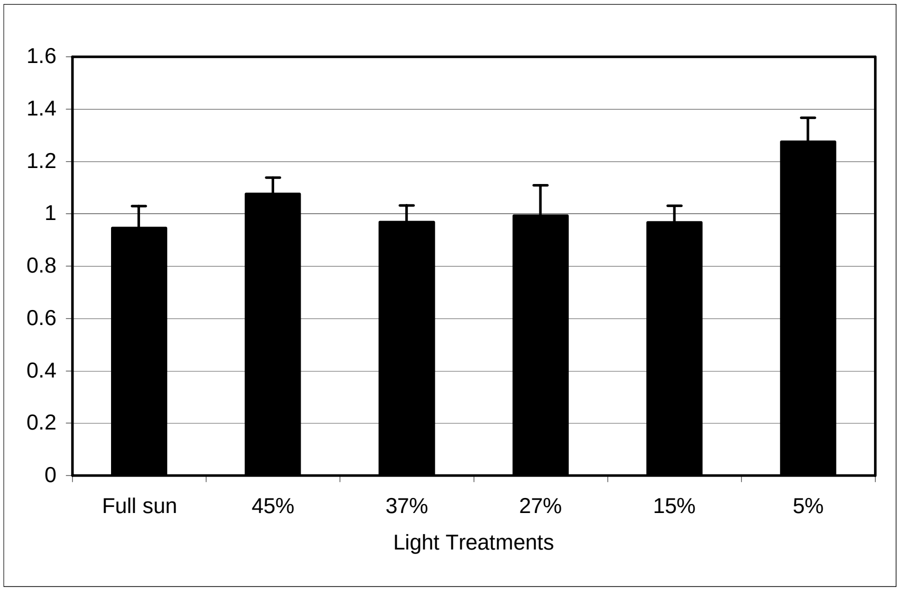
Basal diameter growth trend was similar to tree height, with cuttings in the 5% treatment showing less growth in July ($p < 0.05$), followed by the 15% in August ($p < 0.05$). In October and November, cuttings in the 37, 27, 15, and 5% of full sun treatments all showed less growth than the control cuttings ($p < 0.05$).

Total plant, aboveground, and belowground production during this experiment showed less growth in the 27, 15 and 5% treatments than in the control ($p < 0.05$). Final leaf, woody and belowground biomass also showed less growth in the 27, 15 and 5% treatments than in the control ($p < 0.05$) (figure 2). Analysis of shoot to root ratios revealed no differences at any light level ($p < 0.05$) (figure 3).

Leaf volume and leaf area showed less growth in the 27, 15 and 5% treatments than in the control ($p < 0.05$) (figure 4). Leaf volume and leaf area were found to be positively correlated (Pearson Correlation) ($r^2 = 0.977$). Canopy cover showed less growth in the 15 and 5% treatments than in the control ($p < 0.05$).

Ecophysiology

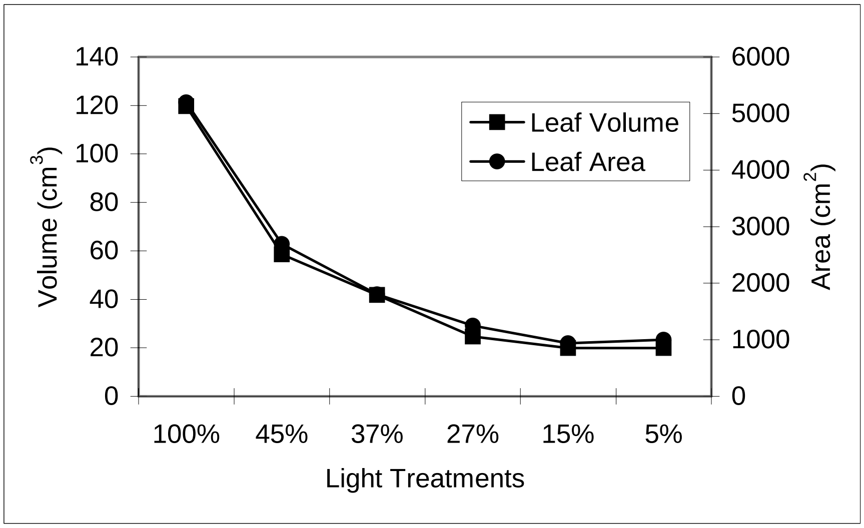
Figure 3. Cedar shoot-to-root ratios as effected by light treatments.



The empirical modeling coefficients for each tree were derived by using a nonlinear parameter estimation routine (table 1). Light response curves were generated using the empirical modeling coefficients for each tree. Predicted NAEs were evaluated for PAR levels of 20, 100, 300, 600, 900,1200, 1500 and 1800 μmol m^{-2} s^{-1} for each of eight trees per light treatment. Empirical modeling detected ed no differences in predicted

NAE between light treatments for PAR levels of 20 and 100 μmol m^{-2} s^{-1}($p < 0.05$). At a PAR value of 300 μmol $m^{-2}s^{-1}$, predicted NAE of the plants in the 5% of full sun treatment was less when compared to the control plants ($p < 0.05$). At PAR levels of 600, 900, 1200, 1500 and 1800 μmol m^{-2} s^{-1}, predicted NAE of the 27, 15 and 5% of full sun plants were less than that of the control plants ($p < 0.05$) (table 2).

Figure 4. Cedar leaf volume and leaf area as effected by light treatments.



DISCUSSION

Growth Experiments

Bjorkman (1981) studied and reported that photosynthesis, which provides nearly all of the carbon and chemical energy needed for autotrophic plant growth, is dramatically influenced by light intensity. The present study found that the growth of two-yr-old cedar cuttings was reduced by light intensities less than or equal to 27% of full sun for most parameters (table 3). The effect of shading on cedar in this study supports the findings of Little (1950), Moore (1996), and Summerville et al. (1999).

In a greenhouse study, Little (1950) determined that initial growth of cedar was comparable to that of *A. rubrum* and *M. virginiana* only under light treatments of 65 -70% of full sunlight and with a water table between 0.64 - 7.6 cm (0.25 - 3.0 in). Under these conditions, the cedar seedlings were taller than those of *M. virginiana* and approached the height of *A. rubrum* seedlings. With lower light levels, differences due to the water table tended to decrease among all species, especially cedar. Little (1950) was unable to identify a specific shade intensity threshold but concluded that cedar requires open, moist conditions for adequate growth.

In the Great Dismal Swamp, Moore (1996) compared growth of four-yr-old cedar saplings between full sun, 45% of full sun treatment via shade cloth and natural competition. Moore (1996) reported the height growth of the five tallest trees per plot were full sun > 45% of full sun > natural competition. No significant differences in cedar growth in full sun and 45% of full sun were found. Natural competition limited growth, but no light readings were reported (Moore 1996).

The results of the present study suggest that a moderate shading of 55% between June and August may increase cedar growth. The extreme heat can trigger stomata to close in plants exposed to full sun, thereby stopping photosynthesis for long periods of time (Bjokman 1981). Summerville et al. (1999) found similar results, while conducting seed germination studies. A 50% shade treatment was applied to the seedbeds immediately after sowing seeds and the remaining beds were exposed to full sun. Summerville et al. (1999) reported significantly lower growth between newly germinated cedar seedlings in full sun than in 45% of full sun, but these plants were younger than those in the current study.

Table 1. Nonlinear parameter estimates from equation in empirical modeling section.

Date	Treatment	Tree #	α (μmol CO2 / μE)	GP_{max} (μmol CO2 m^{-2} s^{-1})	R_A (μmol CO2 m^{-2} s^{-1})	T_{AIR} °C	R^2
Oct 30	Full sun	1001	0.008 (0.0004)	15.34 (1.45)	0.26 (0.064)	19.2	0.99
Nov 28	Full sun	1002	0.013 (0.0008)	9.36 (0.44)	0.24 (0.063)	16.5	0.99
Nov 12	Full sun	1003	0.008 (0.0004)	18.92 (1.71)	0.27 (0.056)	37.0	0.99
Nov 28	Full sun	1004	0.017 (0.0011)	6.32 (0.21)	0.16 (0.058)	13.7	0.99
Nov 2	Full sun	2001	0.004 (0.0003)	7.35 (2.30)	0.15 (0.027)	22.4	0.97
Nov 23	Full sun	2002	0.006 (0.0005)	5.99 (0.54)	0.18 (0.046)	21.9	0.98
Nov 12	Full sun	2003	0.003 (0.0003)	1.48 (0.12)	0.03 (0.024)	19.8	0.96
Nov 23	Full sun	2004	0.005 (0.0003)	3.29 (0.14)	0.07 (0.024)	20.0	0.99
Oct 31	45%	1551	0.005 (0.0005)	1.21 (0.04)	0.09 (0.020)	19.2	0.98
Nov 22	45%	1552	0.010 (0.0010)	2.15 (0.08)	0.10 (0.032)	11.8	0.98
Nov 17	45%	1553	0.011 (0.0009)	3.35 (0.12)	0.12 (0.038)	21.8	0.98
Nov 22	45%	1554	0.014 (0.0018)	1.19 (0.04)	0.04 (0.023)	10.7	0.97
Nov 6	45%	2551	0.012 (0.0008)	3.95 (0.11)	0.06 (0.047)	10.1	0.98
Nov 28	45%	2552	0.003 (0.0007)	0.37 (0.02)	0.07 (0.014)	22.5	0.91
Nov 12	45%	2553	0.007 (0.0006)	1.64 (0.57)	0.11 (0.022)	15.1	0.98
Nov 24	45%	2554	0.014 (0.0024)	1.96 (0.09)	0.18 (0.042)	21.8	0.97
Nov 1	37%	1631	0.003 (0.0002)	3.02 (0.17)	0.14 (0.024)	25.0	0.99
Nov 28	37%	1632	0.006 (0.0005)	2.65 (0.14)	0.07 (0.029)	22.3	0.98
Nov 18	37%	1633	0.010 (0.0007)	3.02 (0.09)	0.06 (0.031)	14.9	0.99
Nov 28	37%	1634	0.010 (0.0009)	3.02 (0.13)	0.17 (0.039)	21.1	0.98
Nov 2	37%	2631	0.011 (0.0015)	1.47 (0.06)	0.17 (0.037)	19.8	0.95
Nov 23	37%	2632	0.001 (0.0003)	0.64 (0.08)	0.03 (0.018)	16.3	0.93
Nov 19	37%	2633	0.007 (0.0011)	0.67 (0.02)	0.02 (0.015)	20.5	0.97
Nov 23	37%	2634	0.004 (0.0010)	0.51 (0.03)	0.04 (0.023)	14.1	0.92
Nov 1	27%	1731	0.009 (0.0010)	1.29 (0.04)	0.10 (0.022)	15.9	0.98
Nov21	27%	1732	0.010 (0.0017)	1.66 (0.08)	0.25 (0.047)	19.4	0.96
Nov 18	27%	1733	0.006 (0.0008)	1.14 (0.05)	0.02 (0.021)	12.6	0.97
Nov 24	27%	1734	0.002 (0.0008)	0.61 (0.04)	0.02 (0.028)	17.9	0.90
Nov 5	27%	2731	0.003 (0.0007)	0.43 (0.03)	0.07 (0.020)	15.4	0.92
Nov 25	27%	2732	0.007 (0.0023)	0.58 (0.05)	0.12 (0.038)	17.8	0.86
Nov 16	27%	2733	0.006 (0.0009)	0.67 (0.03)	0.02 (0.016)	21.4	0.96
Nov 25	27%	2734	0.006 (0.0009)	1.08 (0.06)	0.02 (0.027)	18.0	0.95
Oct 31	15%	1851	0.003 (0.0006)	0.49 (0.03)	0.03 (0.017)	16.9	0.91
Nov 22	15%	1852	0.002 (0.0004)	0.57 (0.06)	0.07 (0.023)	18.0	0.88
Nov 17	15%	1853	0.002 (0.0006)	0.44 (0.04)	0.06 (0.023)	25.1	0.89
Nov 22	15%	1854	0.002 (0.0004)	0.31 (0.02)	0.01 (0.012)	14.7	0.95
Nov 5	15%	2851	0.012 (0.0012)	1.88 (0.05)	0.13 (0.031)	17.2	0.98
Nov 24	15%	2852	0.007 (0.0008)	1.09 (0.04)	0.07 (0.019)	22.5	0.98
Nov 16	15%	2853	0.004 (0.0004)	1.42 (0.06)	0.04 (0.018)	24.9	0.98
Nov 24	15%	2854	0.015 (0.0034)	1.53 (0.09)	0.23 (0.056)	20.9	0.92
Nov 18	5%	1951	0.003 (0.0007)	0.26 (0.02)	0.13 (0.010)	16.6	0.92
Nov 23	5%	1952	0.007 (0.0021)	0.24 (0.02)	0.04 (0.014)	21.3	0.89
Nov 18	5%	1953	0.013 (0.0039)	0.27 (0.02)	0.11 (0.017)	16.1	0.88
Nov 22	5%	1954	0.032 (0.0125)	0.26 (0.02)	0.04 (0.015)	16.1	0.91
Nov 6	5%	2951	0.013 (0.0025)	1.55 (0.08)	0.16 (0.050)	11.8	0.93
Nov 25	5%	2952	0.008 (0.0019)	0.61 (0.03)	0.004 (0.023)	15.6	0.93
Nov 16	5%	2953	0.013 (0.0026)	0.80 (0.04)	0.01 (0.026)	14.7	0.94
Nov 25	5%	2954	0.021 (0.0032)	0.82 (0.03)	0.08 (0.019)	14.5	0.97

Coefficients for CO_2 exchange and light relationships derived from non-linear parameter estimation ($\pm$ SE) of the hyperbolic model. T_{AIR} is the temperature of the chamber headspace during measurements.

Table 2. Predicted NAE (μmol CO_2 $m^{-2}s^{-1}$) for selected PAR (μE $m^{-2}s^{-1}$) values.

		PAR							
Treatment	Tree #	20	100	300	600	900	1200	1500	1800
Full sun	1001	-0.103	0.507	1.838	3.433	4.685	5.694	6.524	7.219
Full sun	1002	0.018	0.932	2.574	4.088	5.032	5.678	6.148	6.504
Full sun	1003	-0.110	0.514	1.907	3.637	5.043	6.207	7.189	8.026
Full sun	1004	0.152	1.153	2.625	3.706	4.280	4.636	4.879	5.054
Full sun	2001	-0.075	0.196	0.792	1.517	2.095	2.566	2.957	3.288
Full sun	2002	-0.065	0.364	1.203	2.069	2.661	3.091	3.418	3.674
Full sun	2003	0.018	0.191	0.484	0.733	0.879	0.975	1.043	1.094
Full sun	2004	0.022	0.348	0.930	1.464	1.796	2.022	2.186	2.310
45%	1551	-0.005	0.247	0.560	0.755	0.849	0.905	0.941	0.967
45%	1552	0.092	0.603	1.174	1.500	1.649	1.735	1.790	1.829
45%	1553	0.092	0.725	1.565	2.123	2.401	2.567	2.678	2.757
45%	1554	0.191	0.612	0.893	1.006	1.050	1.073	1.088	1.098
45%	2551	0.165	0.850	1.807	2.476	2.819	3.029	3.169	3.271
45%	2552	-0.021	0.093	0.189	0.233	0.252	0.262	0.268	0.272
45%	2553	0.010	0.364	0.792	1.053	1.177	1.250	1.298	1.331
45%	2554	0.063	0.632	1.151	1.405	1.512	1.571	1.609	1.635
37%	1631	-0.083	0.128	0.545	0.978	1.275	1.492	1.657	1.787
37%	1632	0.040	0.412	0.993	1.448	1.699	1.859	1.969	2.050
37%	1633	0.121	0.676	1.424	1.929	2.183	2.336	2.438	2.511
37%	1634	0.015	0.577	1.329	1.832	2.085	2.236	2.337	2.410
37%	2631	0.018	0.447	0.836	1.025	1.105	1.149	1.177	1.196
37%	2632	-0.003	0.083	0.220	0.330	0.392	0.432	0.460	0.480
37%	2633	0.100	0.326	0.490	0.558	0.585	0.600	0.609	0.615
37%	2634	0.032	0.189	0.324	0.386	0.412	0.427	0.435	0.442
27%	1731	0.065	0.445	0.786	0.951	1.020	1.058	1.083	1.099
27%	1732	-0.069	0.381	0.827	1.057	1.158	1.215	1.251	1.276
27%	1733	0.093	0.380	0.685	0.851	0.926	0.968	0.995	1.014
27%	1734	0.021	0.135	0.288	0.390	0.441	0.472	0.492	0.507
27%	2731	-0.022	0.092	0.207	0.268	0.295	0.310	0.319	0.326
27%	2732	-0.006	0.202	0.339	0.393	0.414	0.425	0.432	0.436
27%	2733	0.075	0.285	0.460	0.540	0.574	0.592	0.603	0.611
27%	2734	0.076	0.342	0.630	0.790	0.863	0.904	0.931	0.949
15%	1851	0.012	0.134	0.265	0.336	0.369	0.387	0.399	0.407
15%	1852	-0.033	0.070	0.211	0.308	0.357	0.387	0.407	0.421
15%	1853	-0.024	0.082	0.200	0.267	0.298	0.316	0.327	0.335
15%	1854	0.021	0.106	0.189	0.231	0.249	0.260	0.266	0.271
15%	2851	0.085	0.610	1.112	1.365	1.474	1.535	1.574	1.601
15%	2852	0.053	0.353	0.644	0.792	0.856	0.892	0.914	0.930
15%	2853	0.040	0.284	0.627	0.867	0.991	1.066	1.117	1.154
15%	2854	0.017	0.522	0.908	1.076	1.144	1.180	1.203	1.219
5%	1951	-0.085	0.004	0.070	0.098	0.109	0.115	0.119	0.121
5%	1952	0.044	0.133	0.170	0.182	0.186	0.188	0.190	0.191
5%	1953	0.019	0.110	0.139	0.148	0.151	0.152	0.153	0.154
5%	1954	0.142	0.196	0.209	0.212	0.213	0.214	0.214	0.214
5%	2951	0.061	0.548	0.949	1.131	1.206	1.247	1.273	1.290
5%	2952	0.125	0.347	0.487	0.542	0.563	0.574	0.581	0.585
5%	2953	0.179	0.477	0.646	0.708	0.731	0.743	0.751	0.756
5%	2954	0.206	0.518	0.653	0.696	0.712	0.720	0.725	0.729

Table 3. Summary of structural and ecophysiological results.

	FS-45%	FS-37%	FS-27%	FS-15%	FS-5%
Height	-	-	*	*	*
Basal diameter	-	*	*	*	*
Total Biomass	-	-	*	*	*
Aboveground biomass	-	-	*	*	*
Belowground biomass	-	-	*	*	*
Leaf Biomass	-	-	*	*	*
Stem Biomass	-	-	*	*	*
Shoot: Root Biomass	-	-	-	-	-
Leaf Area	-	-	*	*	*
Leaf Volume	-	-	*	*	*
NAE at PAR of 20	-	-	-	-	-
NAE at PAR of 100	-	-	-	-	-
NAE at PAR of 300	-	-	-	-	*
NAE at PAR of 600	-	-	*	*	*
NAE at PAR of 900	-	-	*	*	*
NAE at PAR of 1200	-	-	*	*	*
NAE at PAR of 1500	-	-	*	*	*
NAE at PAR of 1800	-	-	*	*	*

* indicates significantly less when compared to full sun ($\alpha = 0.05$). - indicates no significant difference detected when compared to full sun ($\alpha = 0.05$).

Many other studies have shown how shading can inhibit tree growth (Knowe 1994, Comeau et al. 1993, Wagner et al. 1989). Knowe (1994) found that removal of all competition resulted in exponential height growth in young Douglas fir (*Pseudotsuga menziesii*) plantations while partial removal resulted in linear height growth.

Many species respond to light stress by increasing the proportion of shoot growth in contrast to roots (McDermott 1954). The lack of significant difference in shoot-to-root ratios across treatments in this study suggests that light intensity does not effect cedar carbon allocation between aboveground and belowground structures.

Photosynthesis Experiments

In the present study, PAR values at or above 600 μmol m^{-2} s^{-1} significantly reduced the predicted NAE of the plants in 27, 15 and 5% treatments when compared to the control plants (table 3) ($p < 0.05$). Zimmerman and Mylecraine (1999) measured photosynthetic rates of cedar seedlings from three different sources that were treated with four different light intensities. Photosynthetic rates ranged from -0.02 to 13.7 μmol m^{-2} s^{-1} and averaged 4.20 μmol m^{-2} s^{-1}. Significant differences were reported between light treatments and between sources. No minimum light requirements were suggested (Zimmerman and Mylecraine 1999). Havranek and Benecke (1978) reported similar photosynthetic rates in three other conifer species.

Implications for Self-Maintenance

This study supports the view expressed in Laderman (1989), that light and fire are important for cedar self-maintenance. Fire serves as the perturbation that removes competition, allowing sufficient light to reach the soil surface to stimulate seed germination and growth. It is axiomatic that cedar swamps could be reestablished if the relation between fire frequency, water table and light could be restored to pre-European colonization conditions.

Active Management

With most of the remaining cedar swamps occurring in areas that have been highly impacted by draining, logging activity, and fire suppression, typically some form of active-management or rehabilitation is necessary to regenerate this species. This study provides resource managers with information on the response of two-yr-old cedar to various light regimes. At two years post fire or timber harvest, growth from competitors such as *A. rubrum*, *N. sylvatica* and various vines may cause lethal shading of cedar cuttings. This study suggests that a threshold exists at 27% shade, which resource managers can use to determine when and if a regeneration site needs to be treated with an herbicide, hand-cleared, or otherwise released from competition.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Akerman, A. 1923. The white cedar of the Dismal Swamp. *Va. For. Publ*. 30:1-21.

Ash, A. N., C. B. McDonald, E. S. Kane, and C. A. Pories. 1983. Natural and modified pocosins: literature synthesis and management options for fish and wildlife. U.S. Fish Wildl. Serv. FWS/OBS-83/04. 156 pp.

Baker, W.M., 1922 Forestry for Profit. N.J. Department of Conservation and Development. 85 pp

Barlett, D.S., G.J. Whiting, and J.M. Hartman. 1990. Use of vegetation indices to estimate intercepted solar radiation and net carbon dioxide exchange of a grass canopy. Remote Sens. Environ. 30:115-128.

Bjorkman, O. 1973. Comparitive studies on photosynthesis in higher plants. In: Giese, A. (ed) Current topics in photobiology, photochemistry and photophysiology, Vol. 8 Academic Press, New York, 1-63.

Bjorkman, O. 1981. Response to different quantum flux densities. In O.L. Lange, P.S. Nobel, C.B. Osmond, H. Ziegl, eds. Physiological Plant Ecology I: Responses to the Physical Environment. Springer-Verlag, New York. Pp 57-107.

Buell, M. F., and R. L. Cain. 1943. The successional role of southern white cedar, *Chamaecyparis thyoides*, in southeastern North Carolina. *Ecology* 24:85-93.

Comeau, P.G., T.F. Braumandl, and C.Y. Xie. 1993. Effects of overtopping vegetation on the light availability and growth on Englemann spruce (*Picea engelmannii*) seedlings. Can. J. For. Res. 23:2044-2048

Dabel, C. V. and F. P. Day. 1977. Structural Comparisons of plant communities in the Great Dismal Swamp, Virginia, USA. *Bull. of the Torrey Bot Club* 104:352-360.

Ehrenfeld, J. G. and J. P. Schneider. 1991. *Chamaecyparis thyoides* wetlands and suburbanization: effects on hydrology, water quality and plant community composition. *J. of Appl. Eco*. 28:467-90.

Eleuterius, L. N., and S. B. Jones. 1972. A phytosociological study of white-cedar in Mississippi. *Castanea* 37:67-74

Fowells, H. A. 1965. Silvics of forest trees of the United States. U.S. Dep. Agric., Agric. Handb. 271. 762 pp.

Frost, C. C. 1987. Historical overview of Atlantic white cedar in the Carolinas. Pages 257-264 in A.D. Laderman, ed. *Atlantic White Cedar Wetlands*. Westview Press, Boulder, CO.

Gray, M.S. 1998. Personal communication, Department of Biology, Chemistry and Environmental Science, Christopher Newport University.

Hickman, J.C. and J.A. Newhauser. 1978. Growth patterns and relative distribution of *Chamaecyparis thyoides* and *Acer rubrum* in Lebanon State Forest, New Jersey. Bartonia 45:30-36.

Johnson, I.R. and J.H. Thornley. 1984 A model of instantaneous and daily canopy photosynthesis. Journal of Theoretical Biology. 107:531-545.

Knowe, S. A. 1994. Effect of competition control treatments on height-age and height diameter relationships in young Douglas-fir plantations. For. Ecol. mgt.(67):101-11.

Korstian, C. F., and W. D. Brush. 1931. Southern white cedar. U.S. Dep. Agric. Tech. Bull. 251. 75 pp.

Laderman, A. D. 1982. Comparative community structure of *Chamaecyparis thyoides* bog forests: canopy diversity. *Wetlands* 2:216-230.

Laderman, A. D. 1989. The Ecology of Atlantic White Cedar Wetlands: A community profile. U.S. Fish Wildl.Serv. Biol. Rep. 85(7.21). 114pp.

Little, S. 1950. Ecology and silviculture of white cedar and associated hardwoods in southern New Jersey. Yale Univ. Sch. For. Bull. 56. 103 pp.

Loomis, D.T., R.T. Belcher, J.W. DeBerry, K.M. Shacochis, and R.B. Atkinson. This Volume. A vascular flora of eight Atlantic white cedar communities.

McDermott, R.E. 1954. Effects of saturated soils on seedling growth of some bottomland hardwood species. Ecology 35:36-41

Moore, E. B. 1939. Forest management in New Jersey. N.J. Department of Conservation and Development. 55 pp.

Moore, S. E. 1996. *Natural Regeneration of Atlantic White-Cedar in the Great Dismal Swamp.* North Carolina State University, Raleigh, NC.

Motzkin, G. Patterson, III, W. A. Drake, N. E. R. 1993. Fire history and vegetation dynamics of a *Chamaecyparis thyoides* wetland on Cape Cod, Massachusetts. *J. of Ecology*. 81, 391-402.

Noyes, J.H. 1939. Silvicultural management of southern white cedar in Connecticut. Master's Thesis. Yale University, New Haven, CT. 31 pp.

Pinchot, G. 1899. A study of forest fires and wood production in southern New Jersey. Appendix to Annual report of the State Geologist for 1898. 102pp.

Reed, P. B. 1988. Wetland plant list: Northeast region; Southeast region. National Wetlands Inventory, U.S. Fish Wildl. Serv., St. Petersburg, FL Unpaginated.

Summerville, K.O., W.E. Gardner, L.E. Hinesly, and R.E. Bardon. 1999. Atlantic white cedar plant production. In Shear, T.H., and K.O. Summerville (eds) Atlantic white cedar: ecology and management symposium; 1997 August 6-7; Newport News, VA. Gen Tech Rep. SRS-27. Asheville, NC: US Department of Agriculture, Forest Service, Southern research Station. 82 pp.

Wagner, R.T., T.D. Petersen, D.W. Ross and S.R. Radosevich. 1989. Competition thresholds for the survival and growth of Ponderosa pine seedlings associated with woody and herbaceous vegetation. *New. For.* 3:151-170

Whiting, G.J., D.S. Barlett, M. Fan, P. Bakwin, and S. Wofsy. 1992. Biosphere / atmosphere CO_2 exchange in tundra ecosystems: Community characteristics and relationship with multispectual surface reflectance. *J. Geophysical Research* 97:16,671-16,680.

Whiting, G.J. 1994. CO_2 exchange in the Hudson Bay lowlands: Community characteristics and multispectral reflectance properties. *J. Geophysical Research* 99:1519-1528.

Zimmermann, G.L., K.A. Mylecraine, 1999. Preliminary study of photosynthetic rates of Atlantic white cedar sources from New Jersey. In Shear, T.H., and K.O. Summerville (eds) Atlantic white cedar: ecology and management symposium; 1997 August 6-7; Newport News, VA. Gen Tech Rep. SRS-27. Asheville, NC: US Department of Agriculture, Forest Service, Southern research Station. 82 pp.

DEVELOPMENT OF ATLANTIC WHITE CEDAR GROWTH AND YIELD MODELS FROM SUPPLEMENTAL INVENTORY DATA COLLECTED AT DARE COUNTY BOMBING RANGE

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Abstract: Several biometric models have been developed from supplemental cedar inventory data collected at Dare County Bombing Range, North Carolina. The method presented demonstrates how height, diameter, and volume growth equations can be developed from inventory data collected at a single point in time, as opposed to the traditional approach requiring multiple measurements of established plots over a period of time. Multiple ring counts and width measurements were taken on each of 215 trees. These diameter growth rates, when coupled with height growth estimates from site index curves, yielded single stem volume growth models. The multiple increment periods measured indicated whether growth was increasing or decreasing from one period to the next. Combining the single stem models with stand data from the inventory produced stand level growth models. The resulting models were used to develop long term sustainable harvest plans for the installation. Predicted versus observed values are presented. The model forecasts compare favorably with historical data and implications are drawn from management.

Key Words: *Dare County Bombing Range, site index, radial growth, growth and yield, rotation age, inventory*

INTRODUCTION

This report discusses a variety of growth and yield equations for Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), based on data collected at Dare County Bombing Range (Range) in North Carolina. Forecasting models were needed in the development and documentation of a Forest Management Plan for the installation. Equations, and conclusions based on them, are compared to findings in Korstian and Brush (1931). Similarities and differences are discussed.

Most forecasting models are based on repeated measures of sample plots over time (continuous forest inventory, or CFI plots). This paper describes how data collected from standing trees at a single point in time can be used to capture time changes. Measurements were taken from standing trees. The exact model parameters may or may not be valid outside the Dare County region, but it is believed the technique may be of universal use.

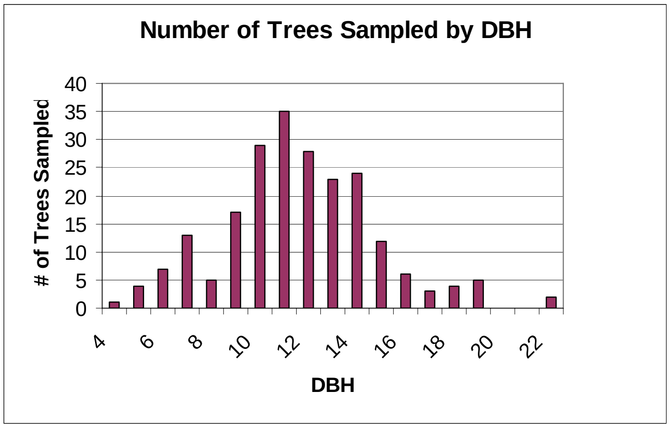
METHODS

The growth data was collected 1997 and 1998 as part of a cedar forest inventory. The inventory sampled approximately 5% of the pure stands. Forest stands were considered to be cedar stands if their total basal area consisted of at least 50% cedar.

In the field, standard forest inventory data was collected with a 10 basal area factor prism. This data enabled the calculation of trees per acre, volumes, and diameter distributions. In addition to this stand and stock data, increment cores were taken on selected dominant and co-dominant trees on the odd- numbered plots. The measurements that are critical to this study include the current age, the number of years required to grow the last radial inch, the width of the last 10 rings, and height. Total height and age are used to determine site index and to quantify height growth. A total of 215 cores were taken and used in the final analysis.

By selecting dominant or co-dominant trees closest to plot center, bias was generally avoided and the trees sampled should be representative of the stands in which they were found. Obviously, intermediate and suppressed trees are underrepresented in the data. However, these trees contain a relatively small amount of the stand volume and, in many cases, should not be expected to survive for the rotation. Given these considerations, the sizes of trees cored can be expected to represent the general range of tree sizes in the respective stands. The average age of the trees sampled was 57 years. The average diameter and height are 12 inches and 56 feet, respectively. The average estimated site index is 58, base 50. The total number of trees cored was summarized by diameter class (figure 1).

Figure 1. Number of trees sampled by diameter breast height.



Site Index and Height Growth

Height growth is typically modeled as a function of tree or stand age and site index. Very little height or site index data is available for cedar. Korstian and Brush (1931) published some general relationships representing averages for the entire range of cedar. Carmean and others (1989) fitted the Korstian and Brush (1931) data to a site index function. While this function and the resulting curves are for the entire natural range of cedar, they are the only known curves in existence for the species and so were chosen for use in this study. Application of these equations to the Range data has resulted in apparently accurate estimates of volume. Site index in this study was determined using base age 50.

Site index was determined for each tree sampled, and then the trees in a given stand were averaged. The site index equation was used instead of the printed site index curves. This approach allowed for a more precise estimate of site index than is possible when interpolating between the lines of a printed graph. Additionally, Carmean and others (1989) manipulated the site index equation into an equation that estimates height based on site index and age. Using this equation is analogous to reading heights off of a site curve for a given site index across a range of ages. By holding site index constant and substituting past or future ages, the equation can be used to determine past or future height. As mentioned, the equation is more precise than estimating values interpolated between curves. Small differences in the age-site index relationship could have significant impacts on the height estimated. The equation was used to determine past heights of sampled trees as part of the overall process of determining their volume growth. The site index and height equations are shown as equations 1 and 2 respectively.

$$S = BH + c_1H^{c2}(1-e^{c3A})^{c4H\hat{}c5} \qquad (1)$$

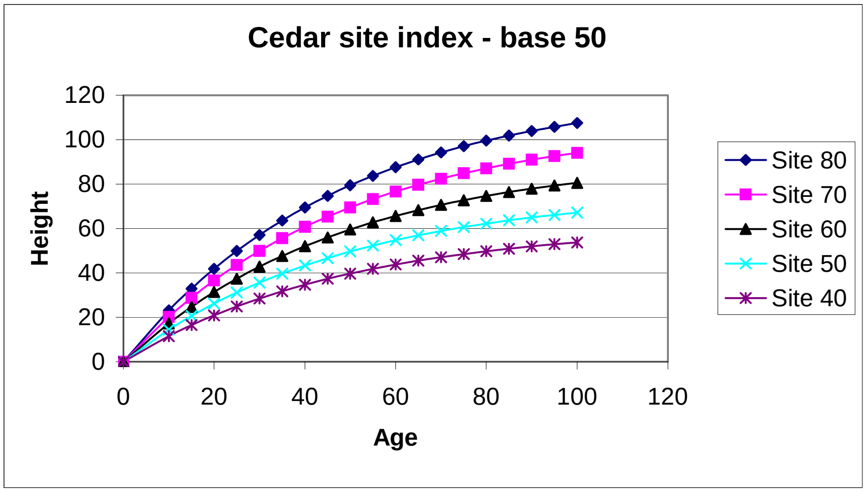
$$H = BH + b_1S^{b2}(1-e^{b3A})^{b4S\hat{}b5} \qquad (2)$$

where S = site index, H = total height, BH = 0 when A = total age and 4.5 when A = dbh age, S = site index, e = base of the natural logarithms, bi's and ci's are regression coefficients given below.

	b1,c1	b2,c2	b3,c3	b4,c4	b5,c5
S	0.6528	1.0000	-0.0213	-1.0243	-0.0046
H	1.5341	1.0013	-0.0208	0.9986	-0.0012.

Site index curves have been generated with equations 1 and 2 (figure 2). Curves are provided for site indices ranging from 40 to 80. As mentioned, these curves can be thought of as height growth curves. Once the site index is determined for a tree or stand, the future or past heights can be closely approximated by holding site index constant and reading the height corresponding to the past or future.

Figure 2. Cedar site index curves, base 50.



It should be noted that the curves and equations are probably not suitable at very young tree ages. Early seedling and sapling growth is highly affected by competition and is too variable to be predicted precisely. After age 20-25 the heights tend to become more uniform as the trees form a single-layered closed canopy.

Diameter Growth

Height and diameter are the two components of a tree's growth. Generally, the volume of a geometric solid, such as a tree, is a function of the height and the diameter squared. Diameter simply has a greater impact on tree volume than does height. Because of this greater importance, greater effort has been spent analyzing and documenting diameter growth. As previously mentioned, two measurements were made of diameter growth. The width of the last 10 rings was measured, and the number of rings in the last inch of radial growth was counted. In a few cases there would be exactly 10 rings in the last inch of radial growth and these two measures would be identical.

In most cases however, this approach resulted in measurements of tree diameter at two different past ages. The width of the last 10 rings always yielded the diameter 10 years ago. The number of rings in the last inch would sometimes be less than 10 and sometimes greater. If there were more than 10 rings in the last inch of growth then an age more than 10 years in the past resulted. For less than 10 rings an age less than 10 years into the past resulted. These two measures of past tree size, coupled with the current tree size, yield three age-size pairs for a given tree. For discussion, these three ages can be described as young, mid-aged, and current. The current age is understood to mean the age at the time of the inventory. The height at each of these three ages was determined using the approach described in the site index section.

Diameter Growth Model

The early, mid, and current diameter measurements for each of 215 trees yielded a total of 627 usable observations from which to develop a diameter growth model. Most trees yielded 3 measurements. Trees where the early and mid measurements were the same yielded only 2 distinct measurements. Various equations were fitted to this data to find one that could adequately predict diameter growth. Possible models were tested by inserting values for the early or mid period into the equation and forecasting the tree size into a later age period. For example, tree sizes from the early period were forecasted into the mid and current ages and then compared with the actual measured values. Mid-aged trees were forecasted into the current period. A flexible model was desired that would not only be accurate through various time periods, but would also be suitable for individual tree volumes and for overall stand volumes.

The final model that best represented that data was one that followed the general form suggested by Beck and Della-Bianca (1972):

$$\ln dbh_2 = 1.11096(A_1/A_2)(\ln dbh_1) + 2.645291(1-A_1/A_2) + 0.004587(1-A_1/A_2)(S) - 0.18273 \quad (3)$$

where ln = natural logarithm, $dbh_{1,2}$ = diameter breast height at times 1 and 2 (in years), and S = site index, base age 50.

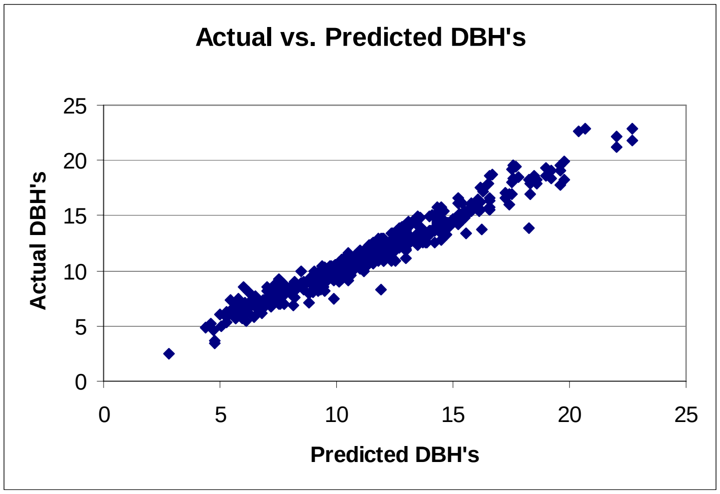
Comparison of the actual values to the predicted values shows very close agreement. The average difference was 0.024 inches. The average absolute difference (ignoring sign) was 0.57 inches. The average length of the prediction interval was 8.7 years, the maximum was 48 years.

The average absolute difference of 0.57 inches indicates a high degree of precision in the model selected. This would be the average amount over or under the true diameter that would be expected when the model is used to predict a large sample of trees.

It should be noted that the overestimates and the underestimates will largely cancel out each other as indicated by the average difference of 0.024 inches (sign considered). In any event, the roughly half inch difference would make even less difference when the trees are recorded in whole inch or 2-inch classes as in an inventory. The model incorporated trees of a wide range of ages, stocking levels, and site indices. Even greater predictive ability is possible when individual trees and stands are considered in isolation.

Figure 3 shows a comparison of the actual and predicted values. The graph shows a high degree of correlation between the two.

Figure 3. Comparison of the predicted and actual diameters for the diameter growth model (in inches).



Tree Volume

This study used total volume growth above a 1-foot stump as the basis for determining growth rates. It is a reasonable assumption that merchantable volume increases at roughly the same rate as does total volume. While this assumption will not always hold at the point where large pulpwood trees grow into small sawtimber, it will also not hold where increases in merchantable volume are limited by defects such as forks, conks, etc. In both cases the calculations will result in the correct amount of total growth, but in the first case, it will underestimate the amount of sawtimber growth. In the second case, the amount of sawtimber in certain trees will be overestimated as the merchantable growth lags total growth. When applied to a sufficiently large number of trees, these two situations will tend to cancel the effect of each other. It will be shown that the results from this analysis are very close to those more general results of Korstian and Brush (1931). This close agreement tends to support the above contention about merchantable growth.

The volume of a given tree was determined using a volume equation form developed by Kozak (1969) and the equation is shown in a general form (equation 4). The a,b, and c coefficients were derived from a taper equation fitted to data from the Range (Daniels 1998). The integral of the taper equation is the volume equation presented. The equation yields cubic feet from a 1-foot stump to the tip. Cubic feet were chosen as the unit of measure because they are more precisely estimated than are board feet or cords.

$$V = 0.005454dbh^2\ [(a*(H-1))+((b*(H^2-1))/2H)+((c*(H^3-1))/3H^2)] \qquad (4)$$

where H = total height, dbh = diameter breast height, a, b and c are the following regression coefficients estimated from data. a = 1.2179, b = -2.60576, and c = 1.42255.

Using the three ages (young, mid, and current discussed above) and their respective heights and diameters, this equation was used to determine three volumes for each tree (a volume for each time period). These three volumes and the ages at which they occurred were used to calculate the tree's growth in terms of annual compound percentage rates. The three ages produced two distinct periods of growth: one from young to mid-aged, and the other from mid-aged to current age. These periods were usually, though not always, of different lengths. The percentage growth rate was determined for the young to mid time period as follows: $V_{mid} = V_{young}(1+r)^n$, where V_{young} = volume at the youngest age, V_{mid} = volume at the mid age, r = percentage compound growth rate, and n = the number of years in the interval from young to mid. In instances where the “10 years ago” age was the same as the “1 inch ago” age, no time interval existed. Thus, no rate for this period could be calculated. The compound growth rate from the mid age to the present age (i.e. at the time of the inventory), was calculated from the equation $V_{current} = V_{mid}\,(1+r)^n$ was used, where $V_{current}$ = volume at the current age and other variables are as before.

Because the more recent period of growth is more indicative of its future growth (at least in the short term), the more recent period was used in determining the annual growth.

Volume Growth Model

The procedures described above for predicting height growth and predicting diameter growth can be combined to predict volume growth. The future diameter and the future height are independently predicted for the age in question, then equation 4 or other suitable volume equation can be used to determine the future volume. An alternative is to predict future volumes directly from present volumes without needing the diameters and heights. The diameters and heights are used in model development but are not needed in the final equation. The same data set that yielded 627 diameter measurements also yielded 627 volume estimates at various ages. These points were used to develop the model presented as equation 5. The model structure follows Beck and Della-Bianca (1972) as before.

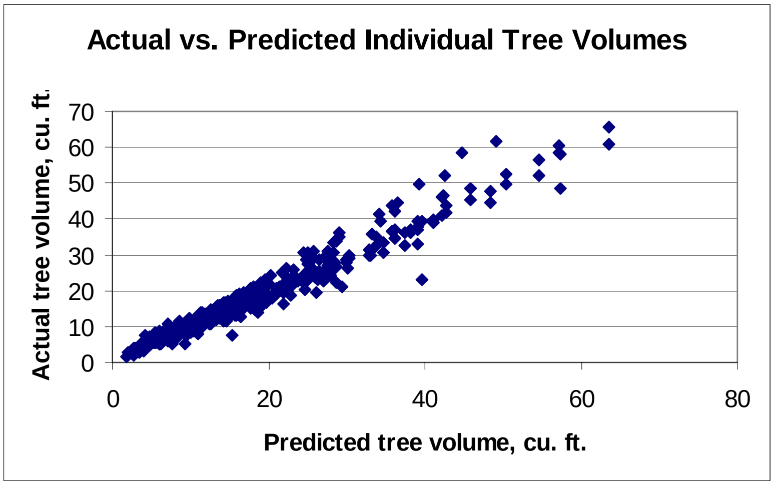
$$\ln V_2 = 1.126689(A_1/A_2)(\ln V_1) + 3.588006(1-A_1/A_2) + 0.010867(1-A_1/A_2)(S) - 0.17685 \qquad (5)$$

where ln = natural logarithm, $V_{1,2}$ = volume per tree (cu. ft.) at times 1 and 2 (in years), and S = site index, base age 50.

Note that this equation differs from equation 4 in a number of ways. Equation 5 predicts future volume based on current (or past volume). Current or past volume is determined from equation 4 and then entered as an independent variable into equation 5. Equation 5 does not require height and dbh, whereas these parameters would be used in equation 4. Thus, equation 5 is essentially a shortcut that bypasses the need to perform individual height and diameter calculations. Results predicted from this equation and results predicted from a combination of equations 2 (height), 3 (diameter), and 4 (volume) will vary slightly. The choice of model or model system depends on the application and affords some flexibility in the forecasting approach. The high degree of accuracy in the second approach (equation 5) suggests that it might be the most appropriate for the overall stand level forecasting needed for management planning. Figure 4 shows the close agreement between predicted and actual volumes.

Stand Level Growth Model

Figure 4. Actual vs. predicted individual tree volumes.



The final modeling objective was to combine all the relevant data (historical and that recently acquired at Dare County Range) into a single model that was suitable for predicting growth on a stand level. The rate of growth of the stands should follow very nearly the rate of growth of the individual trees as determined above. As previously discussed, there is little or no data collected from fixed plots over long periods of time. Few growth trends have been observed by tracking a given stand through time. The approach described above is as comprehensive as any discovered in the literature, and yet the conclusions concerning growth rate have been developed by taking a current stand and studying its past rather than studying it into the future. As discussed above in the diameter section, the average length of the forecast period was 8.7 years. This is fairly close to the planning horizon of 10 years, but it tells us little of what the stand will do beyond this interval. Korstian and Brush (1931) do provide data pertaining to stands older, younger, and on a wider array of site indices than are found on the Range. Their data was collected in a variety of states on stands grown under a wide range of conditions. They did not track the growth of individual stands via permanent plots over time, but do nonetheless provide data on older and younger stands from which general trends can be estimated. Stands on the Range generally contain less volume than would be predicted based on the Korstian and Brush (1931) data.

The present author believes this is due to the fact that Korstian and Brush (1931) based their conclusions on the concept of a stand being “well stocked.” Of the 63 plots they measured, 16 (roughly 25%) were discarded as not being “well stocked plots mathematically” (p.56). They considered these discarded plots to be insufficiently stocked for their analysis. These plots however, were probably typical of the stands in which they were measured. Natural stands are not homogeneous and it is common to measure plots that contain much lower volumes than the rest of the stand. These “gaps” or “patches” are common and are due to irregularities in reforestation, disturbances, or other microsite variations. Discarding low volume plots will raise the overall volumes calculated (i.e. the low plots are removed and the higher plots are averaged together). There is no way to know the volumes of the discarded plots from the data published in the report. It can only be surmised that their inclusion would lower the reported values.

Another possible reason for the discrepancy is that Korstian and Brush (1931) included volumes for 8 and 9-inch trees in their tables. These were recorded as pulpwood in the Range data. For comparison however, the 8 and 9-inch trees in the Range data were converted to their sawtimber equivalent and added to the sawtimber volume. This lessened the discrepancy, but only slightly in most stands.

A third possible reason for the difference is that Korstian and Brush (1931) reported their volumes on the International 1/8-inch log rule. The International 1/4-inch rule (now the standard) was used for the Range data. This would factor alone would account for 9.5% of the discrepancy (which averaged roughly 14%).

Despite these differences in absolute volumes, it was hoped that the Korstian and Brush (1931) data could be used to determine accurate *trends* in the life of cedar stands. When the above discrepancies were rectified to the extent possible, it can be shown that the Range growth data described in this report gives very nearly the same growth in percentage terms as does the Korstian and Brush (1931) data. This seems to be the first confirmation of the Korstian and Brush (1931) data, and, at the same time, would appear to support the findings of the present analysis.

What was needed then was a model incorporating the actual historic growth rate of Range stands, the observed current conditions of Range stands, the trends observed on Range stands, and the trends Korstian and Brush (1931) observed in older and younger stands. The following equation is presented as such a model.

$$\ln BF_2 = 0.91853(A_1/A_2)(\ln BF_1) + 7.308278(1-A_1/A_2) + 0.07141(1-A_1/A_2)(S) + 0.830277 \quad (6)$$

where ln = natural logarithm, $BF_{1,2}$ = volume per acre (bd. ft.) at times 1 and 2 (in years), and S = site index, base age 50.

This equation was developed for site indices 40 - 70, which include the vast majority (if not all) of the stands on the Range.

As mentioned, there is some discrepancy between the volumes found on the Range and those anticipated by Korstian and Brush (1931). The above equation attempts to synthesize the two findings and could be used as presented. It can however, be improved upon by calibrating it with each stand on a stand-by-stand basis prior to forecasting.

Growth Model Calibration

By setting Age 1 equal to Age 2 in the above equation a volume estimate for the present time can be achieved. This volume, ideally, would be the same as that actually found. This is not the case for a variety of reasons (see the preceding section) though the estimates are generally fairly close. To calibrate equation 6, simply divide the actual volume by the predicted volume when Age 1 is set equal to Age 2. This is the relative stocking as compared to Korstian and Brush's “well stocked” stands. It is impossible to capture this difference in equation 5 alone because the stands may well have started out at very different stocking levels, or experienced different levels of management. These differences alone could account for the present volume differences. It is assumed in this study that a stand will maintain this same relative stocking throughout its life. Alternative assumptions are that the stand continues to fall farther and farther behind the growth of a “well stocked” stand, or that it accelerates in growth to catch up to where it would have been under ideal conditions. These two extreme alternatives are not rational and have little if any empirical support for any species. Based on the discussion presented in Davis and Johnson (1987) the most likely trend is that the stand will continue to grow at or near the same level of relative stocking as it had in the past.

The model should show a general decrease in growth rate with age. Based on the Korstian and Brush (1931) data, a stand of cedar trees beyond the sapling stage will decrease in growth rate by roughly a third over the course of a decade. Obviously this varies with initial stocking, site index, and other variables, and is a broad average.

After the relative stocking is determined, the model (equation 6) is used to forecast future stand volumes throughout the length of the planning period (10 years). The forecasted values are then multiplied by the relative stocking to find the calibrated new volume. These future volumes form the basis for planning.

RESULTS

The fit of equation 6 is generally very good as is shown by table 1. Table 1 shows the Range measured growth rate and the growth rate predicted by the stand level equation. The values are ranked in order of the slowest growing to the fastest growing (based on Dare County). Stand numbers refer to the inventory of 1998 (Aerial Dimensions 1998).

Table 1. Comparison of Dare County measurements with model predictions.

Stand	DCR	Model
321	0.0232	0.02281
316	0.02876	0.025037
313	0.03436	0.038704
317	0.03651	0.034163
328	0.03784	0.033658
318	0.04235	0.029483
300	0.04515	0.038709
302	0.048509	0.063084
306	0.05432	0.048585
332	0.05432	0.048585
312	0.05466	0.052964
320	0.0556	0.0627
315	0.05621	0.082912
319	0.05705	0.068801
307	0.05846	0.094009
322	0.0592	0.088527
304	0.059756	0.065571
303	0.060295	0.076716
301	0.06139	0.050377
310	0.064775	0.040695
311	0.064775	0.062291
314	0.06774	0.0622
323	0.0875	0.087529
330	0.1793	0.177992

DISCUSSION

While there are some small differences from stand to stand, most are very close. The original Range data yielded an average growth rate of 6.06% for all the remnant stands in the forest. The model would forecast an average growth rate of 6.47% for the same stands. Figure 5 compares the predicted and observed percentage growth rates.

By the end of the third year the model forecasts an average rate of 6%. This appropriately shows a slowing growth. By the end of the decade, if left unmanaged, the model would predict an average growth rate of approximately 4.5%. This reduction in growth rate is roughly a decrease of one third, and is consistent with the findings of Korstian and Brush (1931). The overall growth rate decreases with age in both the Dare and Korstian and Brush data. Figure 6 below shows the nature of this decrease with the Range data and a rapid decrease in the growth rate beginning around age 40. This decrease is extremely steep by age 40, and has leveled off to between 2 and 3 by age 55-60.

Figure 5. Predicted vs. observed growth rates.

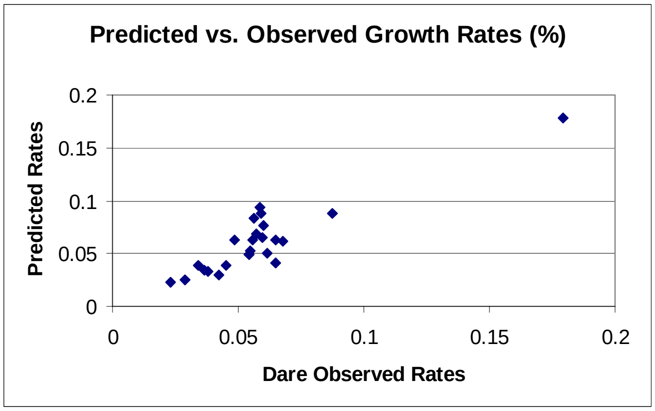
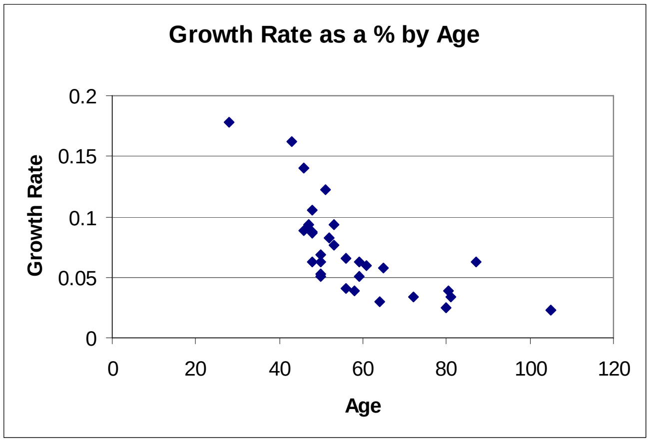


Figure 6. Percentage growth by age.



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LITERATURE CITED

Aerial Dimensions, 1998. Forest Inventory Dare County Bombing Range. 62p.

Beck, D.E., and L. Della-Bianca 1972. Growth and Yield of thinned yellow-poplar. U.S. Forest Serv., Southeastern For. Exp. Sta., Res. Pap. SE-101. 20 pp.

Carmean, Willard H., Jerold T. Hann and Rodney D. Jacobs. 1989**.** Site Index Curves for Forest Tree Species in the Eastern United States. General Technical Report 128. St. Paul, MN: USDA, Forest Service, North Central Forest Experiment Station. 142 pp.

Daniels, Stephen M. 1998. Evaluation of Existing Taper Equations to Predict Bole Diameters of Atlantic white cedar, in Shear, Theodore H.; Summerville, K.O., eds. 1999. Atlantic white cedar: ecology, and management symposium; 1997 August 6-7; Newport News, VA. Gen. Tech. Rep. SRS-27. Ashville, NC: US Department of Agriculture, Forest Service, Southern Research Station. 82.

Davis, Lawrence S. and K. Norman Johnson. 1987. Forest Management. McGraw-Hill. 790 pp.

Korstian, C. F., and W.D. Brush. 1931. Southern white cedar. U. S. Department of Agriculture Technical Bulletin 251.

PROTECTING NEWLY ESTABLISHED ATLANTIC WHITE CEDAR AND BALDCYPRESS WITH ELECTRIC FENCES, TREESHELTER TUBES, WIRE MESH CAGES, AND TALL FENCES

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Abstract: Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), (1-1 transplants = one year as a seedling and 1 year in a transplant bed) and baldcypress, *Taxodium distichum* (L.) Rich, (1-0 seedlings = 1 year in a seedbed) were hand planted on a drained Pungo soil in Washington County, N.C. Trees were protected from deer and rabbits by (1) electric fences, (2) Tubex Treeshelters, (3) hardware cloth cages, and (4) tall fences made of hardware cloth. In the following 3 years, cedar produced up to 1.8 m of new growth and bald cypress grew much slower. Protection devices, although effective, were judged to be too expensive to be feasible in large plantings on this site.

Key Words: herbivory, white-tailed deer, electric fences, exclusion devices

INTRODUCTION

Pocosin Lakes National Wildlife Refuge (PLNWR) was formed in 1990 by the union of Pungo National Wildlife Refuge and land formerly owned by First Colony Farms. It is centrally located on the Albemarle-Pamlico peninsula in eastern North Carolina, the site of the greatest pocosin acreage in the United States (Ingram and Otte 1981, Richardson et al. 1981). PLNWR has 7,900 ha in Washington Co., 22,800 ha in Tyrrell Co., and 14,600 ha in Hyde Co.

Much of the PLNWR property in Washington Co. was subjected to drainage and agriculture by corporations in the past 40 years, first by Atlantic Farms in the 1950s and 1960s, and then First Colony Farms in the 1970s and 1980s. There is a system of roads, canals, and ditches that divide it into 130-ha blocks. Ditches and canals have lowered the water table, thus accelerating the loss of peat by oxidation and subsidence. In the last 100 years, major fires have occurred about once every 9-11 years (personal communication Steve Barnes), resulting in extensive loss of peat. The PLNWR installed flashboard risers to restore wetland hydrology to 8,100 ha south of Lake Phelps and east of Pungo Lake that had been ditched and drained prior to U.S. F.W.S. acquisition (Hinesley and Wicker 1997). To date, 18 culverts with risers have been installed, as well as an additional 11 new culverts.

Because the area in question was mostly devoid of swamp forest, a major effort is underway to replant wetland tree species such as Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), cypress, and pond pine (*Pinus serotina* Michx.). To date, about 800 ha has been replanted. In 1995, the dominant vegetation was broomsedge (*Andropogan glomeratus* (Walt.) B.S.P.)**,** with smaller amounts of sedge (*Cyperus* spp.) and slender goldentop (*Euthamia tenuifolia* (Pursh) Nutt.), and scattered specimens of gallberry (*Ilex glabra* (L.) A. Gray), wax myrtle (*Myrica cerifera* L.), evergreen bayberry (*Myrica heterophylla* Raf.), red bay (*Persea borbonia* Spreng.), swamp bay

(*Persea palustris* Sarg.), sweet bay (*Magnolia virginiana* L.), pond pine (*Pinus serotina* Michx.), swamp titi (*Cyrillia racemiflora* L.), fetterbush lyonia (*Lyonia lucida* (Lam.) K. Koch), and occasional patches of canebreak (*Arundinaria gigantea* (Walt.) Muhlenb.).

Efforts to replant cedar and cypress on PLNWR have been hindered by severe damage from white-tailed deer and rabbits. Surveys (unpublished) on PLNWR have indicated deer populations as high as 100 deer per km^2. Observations in northeastern United States (Jones et al. 1993) indicate that herds exceeding 50 deer per km^2 can negatively impact species richness, abundance, and composition; and populations above 125 deer per km^2 can totally eliminate all ground vegetation in some systems, including threatened and endangered species. In unprotected plantings on PLNWR, extensive damage soon after planting has made it impossible to determine the early growth potential of cedar and cypress. One study used 1-1 transplants about 0.5 m tall, and there was a 30% net loss in height the first year (Hinesley et al. 1999). The first large planting at PLNWR enclosed 120 ha, and was surrounded with a Gallagher-style electric fence that proved to be relatively ineffective (Hinesley and Wicker 1997). More recently, damage has been minimal in several 1-ha plots near those described in the current study.

Given the need to find a workable method to establish cedar and cypress, we initiated an experiment to compare several methods of mechanical protection for newly planted trees.

METHODS

The planting site is nearly level, with a Pungo soil (dysic, thermic Medisaprist), and is located at Lat 35^o 16' N and Long 33^o 33' W. Depth of peat is 2.1 - 2.7 m, elevation above sea level = 4.6 m, and the water table ranges from 15-40 cm below the surface during the year. Twelve plots were installed in autumn 1996. Each plot was 15 x 15 m, and plots were separated by buffer areas about 30-m wide. Six treatments (two plots per treatment) were randomly assigned to the 12 plots: control (no protection), tall fence made of hardware cloth (total exclusion), low electric fence, high electric fence, Tubex Treeshelters, and wire mesh cages. Chemical repellents were not tested because local foresters (Weyerhaeuser Corp.) believed they lost effectiveness after several rains and they are expensive. Total exclusion plots were included in order to observe long-term changes in vegetation in the absence of browsing.

Each total exclusion plot consisted of a 3-m tall hardware cloth fence (two tiers of galvanized 12.5-gauge wire mesh, 1.5 m tall, 5 x 10 cm mesh) attached to 10-cm diameter steel pipes by stainless steel clamps. Pipes (length = 6.4 m) were pushed vertically into the soil using a tracked excavator.

Gallagher-style electric fences (Gallagher Power Fence Inc., San Antonio, TX 78270-8900) were installed, using white poly-tape (1.3 cm-wide) (Stafix Electric Fencing Ltd, Aukland, New Zealand) mounted on studded T-posts. Two plots had high fences (6-strand, 1.8 m tall; wires at 30-cm intervals) and two plots had low fences (2-strand, 0.9 m tall, wires at 0.5 and 0.9 m). All four plots had a one-strand lead wire [(height = 0.5 m, distance in front of the fence = 0.9 m). Each high fence was grounded on the 3rd and 5th strands, and strands 1, 2, 4, and 6 were charged. All wires were charged on the low fence. Fences were powered with a Stafix 3-fence charger, two 20-W solar panels (Solarex, Frederick, MD 21701) and a marine battery. Line voltage was pulsed at 6 to 7 kV.

Trees were hand-planted in February 1997. Each plot contained three rows of cedar and three rows of cypress, with 6 plants per row. Spacing was 2.4 m between rows and within rows. Cedar planting stock was bare-root 1-1 transplants grown in a sandy loam soil at the N.C. Forest Service nursery in Goldsboro, N.C., with initial height of 0.36 to 0.46 m. There is no established price for 1-1 plants, but 1-0 seedlings (1 year as a seedling) cost $120 per thousand. Cypress planting stock was 1-0 seedlings (average height = 0.7 m) from the same nursery. Purchase price for cypress was $12 for 100 plants.

Treeshelter tubes (Treessentials Co., Mendota Heights, MN 55120) were placed over plants in the designated plots, and supported by a steel rod (1 cm diameter) driven vertically into the peat soil. Each tube (1.5 m tall) had a built-in plastic cinch-tie near the top and bottom to attach it to the rod. Wire cages (1.5 m tall x 0.3 m diameter) were cut from 5 x 10-cm galvanized hardware cloth, placed over the trees, and supported by a steel rod secured to the cage either by ring clamps or wire. A 30-m roll of hardware cloth yielded 32 cages.

The materials cost (includes no labor or maintenance) for each method was as follows:

Treeshelter tube ($2.19; steel rod = $0.50).

Wire cage (14 gauge = $1.50; 12 gauge = $2.25; steel rod = $0.50).

Electric fence:
Fixed costs: $1400 (includes two 20-W solar panels)
Tall fence: ($1.57 per linear m); low fence ($1.05 per linear m).

The charger, solar panels, battery, wires, cages and tubes were checked regularly. Fence lines were sprayed twice each year with Roundup® to remove herbaceous vegetation that could ground the fence.

Initial height was measured on each plant. Survival and total height was measured during the winter following each of the first three growing seasons. Results are reported after 3 years of growth in the field. Survival percentages were transformed to arcsin values before analysis. Data were analyzed using SAS and GLM procedures (SAS Inc. 1994).

RESULTS

Survival after 3 years ranged from 94% to 100%, with no significant differences among species or protection methods (table 1). Non-protected cedar, despite heavy browsing, more than doubled in height during the first 3 years. Browsing injury in control plots was minimal during the first winter, but increased the 2nd and 3rd years. Protected cedar reached a height of about 2.0 m after 3 years, a 5-fold increase from the initial height. Treeshelters increased height growth of both species, but the effect was more dramatic with cypress. Cypress exhibited a strong "greenhouse effect" inside Treeshelters (table 1), reaching an average height of 1.7 m, compared to 1.0 to 1.1 m for other methods, including controls. Despite that, its very slow growth indicated that it was unsuitable for this site. For both species, there was no significant difference in the results for high or low electric fences (table 1), so nothing was gained by using a fence more than 1 m tall.

Table 1. Effect of various protection methods on survival and height of cedar and baldcypress (BC) 3 years after planting on a Pungo soil in Pocosin Lakes National Wildlife Refuge.

Protection Method	Survival of cedar (%)	Survival of BC (%)	Height of cedar (cm)	Height of BC (cm)
Total exclusion	97	97	210 bc	101 a
Wire mesh cages	100	100	201 b	105 a
Treeshelters	100	100	220 c	168 c
Low electric fence	94	94	199 b	114 b
High electric fence	94	91	199 b	106 ab
None (control)	94	97	146 a	99 a
Species	ns		**	
Method	ns		**	
S x M	ns		**	

Mean separation by least squares test of Ho: mean(i) = mean(j).
Significance: ** ($P \leq 0.01$); n = 36.
Initial height: cedar (36-46 cm); BC (70-74 cm).

DISCUSSION

Although exclusion devices reduced or eliminated deer browsing in the small plots used in our study (table 1), there were numerous problems, and no method appeared to be economically feasible beyond a small scale. The cost of tubes, cages, and support stakes was high -- $2.00 to $3.00 per plant, and labor and maintenance would further increase the costs. Stocking could range from 300 to 800 trees per acre for cedar, depending on objectives. Treeshelters and cages appear to be prohibitively expensive if costs are capitalized over a long forest rotation.

Electric fences require regular maintenance, including spraying with herbicides at least twice per year. The solar-powered system occasionally broke down, and poly-wire was prone to break. Strong, steady winds across this vast, open site pulled poly-wire back and forth in the plastic insulators, resulting in fraying and occasional breakage. Frayed wires also reduced the line voltage. Wind and UV deterioration stretched and further weakened the poly-wire strands. In addition, wires were occasionally broken, apparently the result of deer jumping into the wire, or becoming entangled. Owing to maintenance and expense of poly-wire, we suggest galvanized or aluminum wire. However, using poly-tape as the top strand might be beneficial because it is clearly visible, and also flutters in the wind, thus creating a sound that deer can hear. The same result could be obtained by tying flagging to the wires at given intervals to make the fence more visible.

The price of electric fences per unit area decreases with increasing size of enclosure. Earlier comparisons of costs associated with various methods of protection showed that electric fences became the most economical alternative when the planting area exceeded about 1.5 ha (Kays 1996). Similarly, at a stocking of 1,240 trees/ha (500 trees/acre), the economic threshold would be approximately 1 ha for electric fences to be most economical in our study.

Deer exclusion devices are rarely 100% effective, but complete effectiveness is not required to obtain satisfactory cedar regeneration (Zimmermann 1993). Based on our experiences on this site, there appears to be a scale factor in the effectiveness of electric fences; the larger the enclosure, the more likely it is for deer to breach the fence. We do not know the threshold size for reliability, but it would likely vary depending on deer movements, habits, alternate food sources, and topography in relation to the fence. In the present study, no damage occurred in the small plots (15 x 15 m) surrounded by electric fences (table 1). Little damage has occurred in 1-ha plots adjacent to the current experiment, but damage has been severe in a nearby130-ha enclosure (Hinesley and Wicker 1997). Other researchers have successfully used electric fences to exclude deer from cedar plots up to 4 ha in area (Zimmermann 1993).

The use of galvanized or aluminum wire, which costs about half as much as and poly-tape, would eliminate many problems associated with poly-tape. In addition, a public electrical source, if available, would eliminate the need for expensive solar panels and batteries, further reducing costs. The 40-W solar panel seemed to adequately charge the battery during the winter months when it was common to have 3 to 5 consecutive days of overcast weather.

On this site, Treeshelters prevented deer browsing, but had several disadvantages. Cedar, with its delicate, flimsy leader, tends to bind inside the tubes and is then unable to straighten, although it continues to grow and lignify. Later, a small branch or shoot becomes a leader lower on the stem; often, several leaders develop. At least half the trees emerged from the 1.5-m tubes with multiple leaders, and with serpentine, crooked stems inside the tubes, rather than straight stems. If single leaders are desired, most trees would require pruning to remove multiple leaders. This problem did not occur with cypress. The tendency to bind inside the tubes reduced average height by an unknown amount during the 3 years of measurement. Despite that, trees grown in Treeshelters were significantly taller, compared to most other treatments (table 1), particularly for cypress. Perhaps some of the problems with Treeshelters would be less pronounced with a shorter tube.

Wind caused many cedar leaders to be skinned and partly debarked by abrasion against the top edge of the plastic tube. Further, steady wind over a period of months and years caused some rods to slowly work downward into the peat, eventually slipping below the upper cinch-tie, which caused the tube to flop to the side. If not straightened, these trees would be ruined. This problem would probably not occur with wooden stakes.

Ultimate quality and performance are unknown for trees grown in Treeshelters. When a tree emerged from the tube, the stem was weak and barely able to stand upright without the tube. Even a mild wind could blow the plant over or cause it to lean. Presumably, as trees continue to enlarge, and are subjected to wind, the stems will gain sufficient strength to give adequate support. Treeshelters will eventually deteriorate under the influence of UV light.

In this study, support rods would have to be removed after several years in the field to prevent stems from eventually growing around them. Again, this would be unnecessary with wooden stakes. Steel rods were used in this study because they were cheaper and less bulky than wooden stakes of similar length, and could be reused through several cycles of tree planting.

Although wire mesh cages are effective, they must be removed after several years in the field, along with the supporting steel rod. Occasionally, a cage was mashed or pulled over, apparently because a deer got tangled in the mesh. Cages and rods can be re-used for several cycles of tree planting, thus decreasing the per-tree cost of a single cycle. For example, if a cage could be used five times, the materials cost for a single cycle would be 20% of the initial cost. However, the labor and time required for recycling would add to costs. Cages are bulky, and occupy a large volume, which increases the difficulty and costs of storage and transportation. On this site, deer browsing is minimal above a height of 1 m, suggesting that smaller cages, Treeshelters, and stakes could be used.

CONCLUSIONS

Various methods of protecting newly established cedar and cypress were effective in reducing damage from deer, but all were judged to be too expensive for large planting operations. However, it might be feasible to use such methods in small plantings, with the objective of eventually expanding the planting areas through natural regeneration. Electric fences would be the cheapest alternative with plot size of about 1 ha. All methods, especially electric fences and Treeshelter tubes, required considerable maintenance and labor, which further increased costs. Where damage from deer is severe, and where intense harvesting of deer is impractical, we believe it might be more feasible to use 2-year-old planting stock (1-1, 2-0, tubeling + 1) that could better withstand vegetative competition, and browsing by deer and rabbits. Such plants could be readily handled by planting contractors, and would require no further maintenance or labor following planting -- a tremendous advantage in large planting areas.

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LITERATURE CITED

Hinesley, L. E. and A. M. Wicker. 1997. Atlantic white cedar wetland restoration project: Pocosin Lakes National Wildlife Refuge. Rpt. for non-point source pollution demonstration project.

Hinesley, L. E., L. K. Snelling, G. A. Pierce, and A. M. Wicker. 1999. Effect of peat amendments, shade and seedling size on growth of Atlantic white cedar transplants. Southern J. Appl. Forestry 23: 5-10.

Ingram, R. L. and L. J. Otte. 1981. Peat in North Carolina wetlands. pp. 125-134. *In*: C. J. Richardson (ed.). Pocosin wetlands: an integrated analysis of coastal plain freshwater bogs in North Carolina. Hutchinson Ross Publishing Co., Stroudsburg, Pa.

Jones, S. B., D. deCalesta and S. E. Chunko. 1993. Whitetails are changing our woodlands. Am. Forests 99(11-12): 20-25.

Kays, J. S. 1996. Deer protection for small forest plantations: comparing costs of tree shelters, electric fencing and repellents. p. 5-12. *In*: Brissette, J. C. (ed). Proc. of the Tree Shelter Conf., 20-22 June 1995, Harrisburg, PA. Northeastern For. Expt. Sta. Gen. Tech. Rpt. 221.

Richardson, C. J., R. Evans, and D. Carr. 1981. Pocosins: an ecosystem in transition. p. 3-19. *In*: C. J. Richardson (ed). Pocosin wetlands: an integrated analysis of coastal plain freshwater bogs in North Carolina. Hutchinson Ross Publishing Co., Stroudsburg, Pa.

SAS Institute Inc. 1988. SAS/STAT Users Guide. Version 6, 4th ed. SAS Institute. Inc., Cary, N. C.

Zimmermann, G. L. 1993. Continuation of the Atlantic White-cedar regeneration experiments: Final report. Submitted to the N. J. Dept. of Environmental Protection, Office of Science and Research. Richard Stockton College, Pomona, N. J. 190 pp.

SURVIVAL AND GROWTH OF ATLANTIC WHITE CEDAR PLANTINGS IN LOUISIANA AND MISSISSIPPI

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Abstract: Atlantic white cedar (cedar) is a native forest dominant in isolated areas throughout the Atlantic Coastal Plain and in a portion of the Gulf of Mexico Coastal Plain. Although the range of this species extends west to southern Mississippi, stands are uncommon in this area. In addition, most of the existing Mississippi stands are privately owned and afforded little long-term protection. To examine the feasibility of planting cedar at the western edge of its range and to determine if the species is a viable replacement for pine in wet areas, one-year-old seedlings were planted at three pine plantation sites in Louisiana and wildings at two bay-head locations in Mississippi. Overall, survival was high (87%), especially in the Louisiana sites, and after 10 growing seasons the trees averaged 5.3 m in height and 6.1 cm in diameter. This growth rate compared favorably with cypress and slash pine of other studies. The results of this study have shown that cedar can be a viable choice for restoration efforts or forest product plantings.

Key Words: Atlantic white cedar, plantings, survival, growth

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), is a native of the Atlantic coast from Maine to Florida and of the Gulf of Mexico coast (Laderman 1989). Although the range of this species has been reported to extend into southeastern Louisiana (Mohr 1901, Korstian and Brush 1931), Eleuterius and Jones (1972) described two stands in southern Mississippi as the westernmost limit for the species. Herbarium specimens from the University of Louisiana, Monroe, show that cultivated specimens from throughout Louisiana are producing cones, although no natural or escaped stands have been reported west of the Pearl River. Brown (1945), however, suggested that the species was probably present in Louisiana, most likely along the Pearl River in St. Tammany Parish, based upon Mohr (1901).

Naturally occurring populations of cedar are sparse east of the Pearl River in Mississippi (Ward and Clewell 1989). Only two notable populations, one at Juniper Creek near Poplarville and one at Bluff Creek in VanCleave, are known to still exist. The Juniper Creek stand lies at the western most boundary of the species' range. Although about 80% of this stand is in private ownership, a portion owned by Weyerhaeuser Corporation has been designated as an area of their special interest and therefore afforded some level of protection (personal communication Tina Knoll, Weyerhaeuser Inc., 211 Armstrong Road, Columbia, MS 39429). The stand was heavily damaged by Hurricane Camille in 1969 and recovery seems to have been slow, as the remaining cedar trees are small, stunted, and appear to be highly stressed (personal communication Joseph Cruthirds, 6021 Vermillion blvd., New Orleans, LA 70122-4237). The Bluff Creek stand was described in detail by Eleuterius and Jones (1972) who found an extensive stand of cedar along an 11-km length of the creek. In most areas of this stand cedar was dominant with lesser amounts of slash pine (*Pinus elliottii*), swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walter) Sargent), and cypress (*Taxodium distichum* (L.) Rich). Stems of cedar ranged up to 70 cm in diameter and 30 m in height and were generally intermediate in elevation between the cypress/tupelo and the pines.

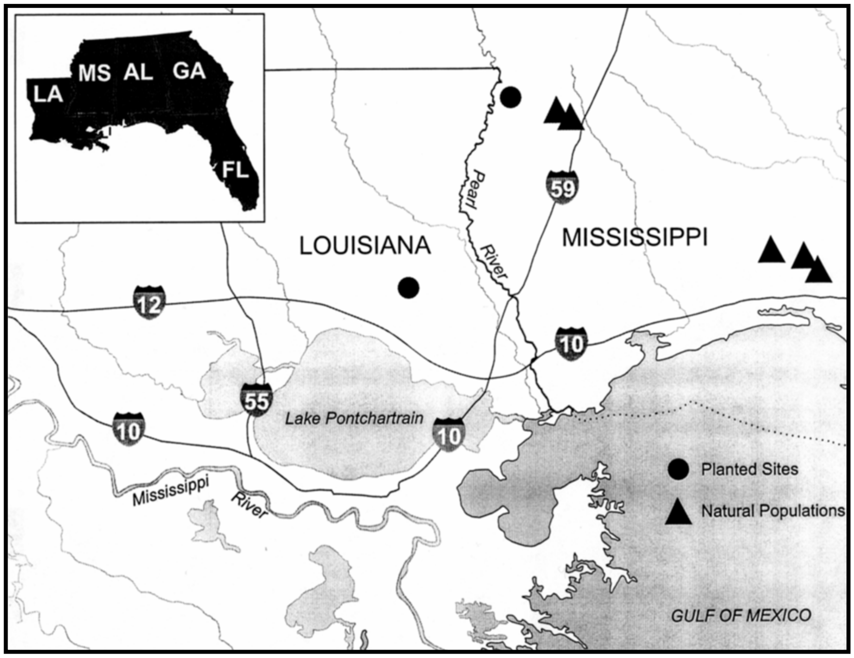
Concern for the loss of cedar in Mississippi and other areas along the Gulf of Mexico Coast is high because of urbanization, agriculture, and conversion to pine plantations (Ehrenfeld and Schneider 1991). Since logging, few large cedar remain (Ward and Clewell 1989), and urbanization is degrading the Bluff Creek stand at an increasingly rapid rate (personal communication Joseph Cruthirds). Development of restoration techniques for this species and community type are important for the future sustainability of cedar along the Gulf of Mexico Coast.

METHODS

Description of Study Sites

To examine the feasibility of planting cedar in wet areas, we planted 1-year-old seedlings at three sites on private land in eastern Louisiana in the lower Pearl River watershed and planted wildings at two bay-head areas (headwater areas characterized by sweet-bay, *Magnolia virginiana* L., see Laderman 1989) on the Bogue Chitto National Wildlife Refuge in Southern Mississippi (figure 1). Study sites in Louisiana include a plantation area (PINE) that was too wet to support slash pine, the edge of a cypress pond (POND), and a fertilized and bedded site within the pine plantation that had not been planted (FERT). The Mississippi site was within a woody area characterized by black gum (*Nyssa sylvatica* Marsh.) and sweet-bay (*Magnolia virginiana* L.). Cutting trees to provide an artificial opening in the forest canopy created gaps within this site. These two gap sites have been combined into one unit (WILD) because of their close proximity (< 50 m) and the overall low survival of cedar at this location (only 15 trees now remaining). A more detailed description of the study sites can be found in McCoy et al. (1999).

Figure 1. Louisiana and Mississippi study site locations and natural stands of cedar in Mississippi.



Soil types at the Louisiana sites are Myatt for the POND site and Stough for the PINE and FERT sites. These are typical soil types for the area, representing 32.2% of the land area of St. Tammany Parish. These soils are fine, sandy loams generally found on level ground and represent poorly drained to somewhat poorly drained flats or stream terraces. The Stough soil is slightly acidic with a pH of 5. Site indexes for loblolly pine at each site are 86-92 ft and 80-90 ft for Myatt and Stough, respectively (USDA 1990).

Soils at the Bogue Chitto NWR WILD site are of the Bibb type: nearly level, poorly drained soils with a pH between 4.5 and 5.5. These soils often flood several times a year (USDA 1983).

Field Methods

Thirty wildlings, natural 1- or 2-year-old seedlings, were collected in the Vancleave, Mississippi area and transplanted to the Bogue Chitto NWR site on January 6, 1989, and 290 1-year-old greenhouse seedlings were planted at the Louisiana sites on March 3, 1990. Heights were measured to the nearest centimeter at the time of planting and again during the late winter or early spring of 1990, 1991, and 1994. Heights were measured to the nearest decimeter at the FERT site in 1997 and at all sites in March 2000. Diameters were measured for all trees greater than 140 centimeters in height during the 1994, 1997, and 2000 measurement periods. Because measurements were only recorded at the FERT site in 1997, the data is not included in this analysis.

Three soil samples were collected at each site during the winter 2000 measurement period for determination of moisture content and particle size distribution. Samples were collected with a soil probe to a depth of approximately 20 cm. In addition, live seedlings of cedar were counted in 1-m^2 plots on the southwest corner of five individual trees.

Differences in diameter vs. height, vines vs. no vines, and height growth among the Louisiana sites were tested for significance with separate one-way analysis of variance procedure, using JMP (SAS Institute, Inc. 1988).

RESULTS AND DISCUSSION

Survival Rates

Survival was excellent for seedlings planted in Louisiana, with an average of 94% survival at the end of the 1994 growing season and 91% at the end of the 1999 growing season (table 1). Individual site survival was 94%, 82%, 98% for FERT, PINE, POND (Louisiana) respectively, and 56% for WILD (Mississippi) by the end of the 1999 growing season. These survival percentages are encouraging, especially considering the declining rainfall amounts (NCDC 2000) from 1993 to 1999 and the subsequent drought conditions in the area (figure 2).

The transplanted wildlings at the Mississippi bay-head had the lowest survival rates of all sites. These wildlings experienced early mortality, and survival continued to drop through the 1999 growing season. Low survival at this site may be related to a combination of stresses (Clewell and Ward 1987). The shock of removing these seedlings from their natural site of germination and then planting them a month later may have stressed many beyond their capacity to recover. Shading may have also added stress (Belcher et al. This Volume), as the canopy gaps created for these plantings were relatively small and did not provide abundant light to the forest floor. Laderman (1989) reported that cedar seedlings require open conditions for good survival. In addition, it appears that soil moisture and/or flooding may have also been a problem.

The WILD site had the highest soil moisture (25%) of all the sites, and this site is prone to intermittent flooding throughout the year (USDA 1983). Cedar can withstand very wet conditions,

Table 1. Height and diameter growth of the cedar at each of the sites for 1990, 1991, 1994, and 1999. Measurements in centimeters.

		------------Height------------			------------Diameter-----------		
Site	Year	N	Mean	STD	N	Mean	STD
FERT	1990	156	16.1	3.2	.	.	.
	1991	150	46.2	11.6	.	.	.
	1994	148	233.5	63.4	137	1.6	0.9
	1999	146	561	124	146	6.6	2.3
PINE	1990	89	19.1	3.4	.	.	.
	1991	81	32.5	5.8	.	.	.
	1994	80	91.2	34.8	.	.	.
	1999	73	452	83	72	4.9	1.7
POND	1990	44	16.8	3.7	.	.	.
	1991	44	39.2	8.3	.	.	.
	1994	43	158.4	49.2	27	0.7	0.5
	1999	43	534	98	43	6.1	1.9
WILD	1989	27	30.3	17.2	.	.	.
	1991	24	51.7	39.7	.	.	.
	1994	19	163.8	82.5	5	1.7	1.0
	1999	15	669	219	14	7.1	2.2
LA Sites Only	1991	275	41.0	11.4	.	.	.
	1994	271	179.7	83.1	236	1.4	1.0
	1999	262	526	119	261	6.0	2.2

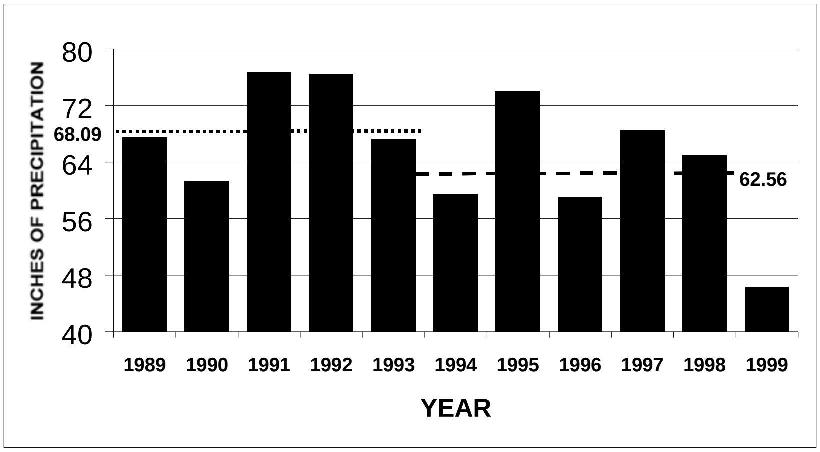
but the species usually grows on hummocks slightly elevated above the forest floor (Allison and Ehrenfeld 1999). The trees, and especially the seedlings, become stressed and do not thrive when the bole is under water (Laderman 1989, McKevlin and Hook 1995). One of the two canopy gaps created for these plantings was near a small stream, whereas the other gap was located on the stream. The stream gap had the lowest survival at only 27%. Away from the stream, survival was 75%. Although we do not have water level information for the period covering this study, the fact that survival was poorest at the gap situated on the small stream suggests that flooding may have had a negative effect.

Direct comparisons of survival and/or growth between the Louisiana seedling sites and the wildling sites in Mississippi must be made with caution. The wildings were planted a year earlier (1989) than the seedlings, and were planted to a site with very different environmental conditions. It is possible that all differences observed relate more to site conditions than any differences between the wildlings and nursery grown seedlings. We did not have any sites where both wildings and seedlings had been planted, so direct comparisons are not possible. In addition, the small sample size for the wildings would make any comparison problematic.

Height Growth

Following the 1999 growing season, significant differences in height growth among sites were noted (figure 3) in spite of high variation of height within sites (table 1). Trees at the WILD site achieved the greatest average height at 669 cm, but it must be remembered that the wildlings are 1 year older than the seedlings at the Louisiana sites. Examination of the average annual height growth from 1990 to 2000 revealed that the WILD site had consistently higher growth rates (64.6 cm / year) as compared with the other sites (54.4 cm, 43.3 cm, and 51.7 cm / year for FERT, PINE, and POND, respectively) (table 2).

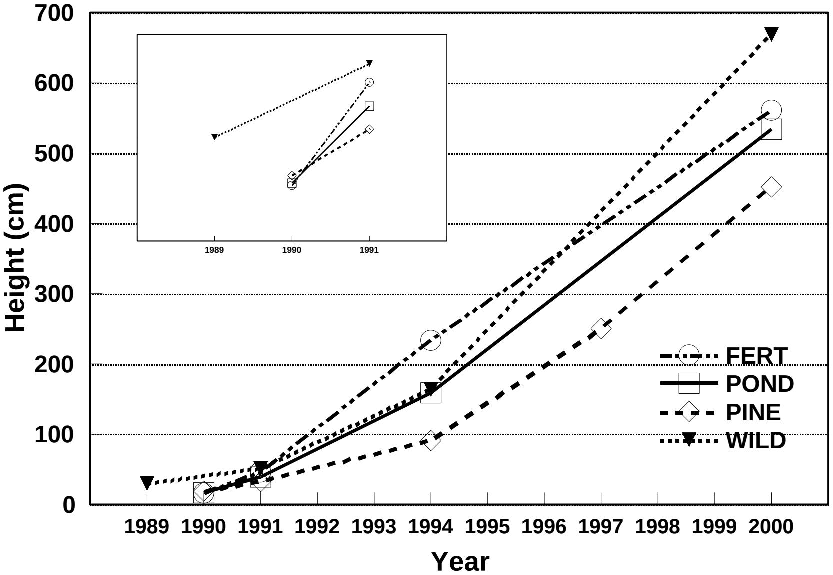
Figure 2. Mean annual rainfall 1989 – 1999 for St. Tammany Parish, Louisiana. Mean totals for years 1989 – 1993 and 1994 – 1999 are depicted as dashed lines above those years.



A factor that may be affecting growth at the Louisiana sites is a phosphorus deficiency in the Myatt and Stough soils (personal communication Paxton Tate, Weyerhaeuser Inc., 29159 Hwy 435, Abita Springs, LA). The FERT and POND site were aerially fertilized in 1990 with 280 kg/ha (250 lbs/acre) of diammonium phosphate (DAP) and had average annual growth of 46.7 cm and 30.0 cm, respectively, between 1991 and 1994. During this same period trees at the PINE site achieved only 14.7 cm growth per year. In 1995 the PINE site was fertilized and subsequently achieved 60.2 cm/year growth, which was similar to growth at the FERT and POND sites (54.4 cm and 62.5 cm, respectively) during the same time period (table 2). Haas et al. (2002) reported similar increases in growth of cedar seedlings with fertilization.

Height growth for the cedar at these sites has exceeded the growth projections based on 1997 data (McCoy et al. 1999) by about 100 cm. This places the potential growth of cedar in Louisiana between cypress (Keeland and Conner 1999) and slash pine (USFS 1976) yearly growth rates.

Figure 3. Cumulative height growth of cedar seedlings and wildlings at each of the four study sites. Inset shows early growth more clearly.



Diameter Growth

Prior to 1994 most trees were less than 1.4 m in height, and so no comparisons of diameters could be made among sites. By the end of the 1999

Table 2. Mean yearly height growth in centimeters for for years 1991-1994, 1994-2000 and 1990-2000. Sites with different letters are significantly different within a growth period for FERT, PINE, and POND only ($P < 0.0001$).

Site	1991-1994		1994-1999		1990-1999	
	Mean	STD	Mean	STD	Mean	STD
FERT	46.7^a	(14.1)	54.4^b	(13.6)	54.4^a	(12.4)
PINE	14.7^c	(8.1)	60.2^a	(11.3)	43.3^b	(8.3)
POND	30.0^b	(11.6)	62.5^a	(13.2)	51.7^a	(9.7)
WILD	41.4	(18.8)	71.1	(30.3)	64.0	(21.5)

growing season, however, only one tree was below 1.4 m. Overall, the average diameter-at-breast height (dbh) was 6.0 cm, with the greatest diameter growth at the WILD site (7.1 cm) and the least diameter growth at the PINE site (4.9 cm). Minimum and maximum diameter growth for the six growing seasons from 1994 through 1999 was 0.4 and 1.7 cm per year, respectively. These figures probably underestimate diameter growth, as many of the trees were less than 1.4 m in height at the 1994 measurement, especially at the PINE site. These data do indicate that the trees included in this study are growing at rates similar to cedar trees in the more northern extent of the range (0.79 – 1.79 cm per year; Golet and Lowry 1987). As expected, there was a strong correlation ($r^2 = 0.86$) between tree height and dbh for the 2000 measurements at all sites. Young trees often maintain a strong correlation between these variables, but the relationship could be expected to degrade as diameter growth continues after the trees have reached their maximum height.

Cones and Seedlings

Cones were observed on a few of the planted seedlings at the PINE site in 1997. By the end of the 1999 growing season, cones were observed on most of the planted trees at the FERT, PINE, and POND sites. The majority of cones still retained seeds when the saplings were measured in March 2000. The presence of an abundant cone production and the presence of cedar seedlings indicate that this stand has become successfully established and may be expanding. Seedling production was high under the parent trees with an average of 74 seedlings per square meter at the FERT site. Seedlings were also found at the PINE and POND sites, but densities at these sites were not measured and appeared to be considerably less in number than at the FERT site. Although most seedlings were small (< 25 cm) and were generally observed under the parent trees, a few seedlings up to 60 cm in height were found at least 8 m from the nearest potential parent tree.

Vegetative Competition and Animal Browsing

A potential problem for the cedar saplings at the Louisiana sites was the heavy growth of laurel greenbrier (*Smilax laurifolia* L.). This woody vine can compete with saplings by growing over them and providing excessive shade or by mechanically breaking the branches or boles during storms. In some cases the weight of vine cover alone is sufficient to damage a sapling or small tree. An analysis of height growth for cedar trees with more than a meter of this vine in its canopy compared with trees without the vine revealed no significant differences ($P > 0.55$; 27 with vines and 43 without vines). Continued growth of the vines, however, could result in future damage.

Although deer, rabbit, and rodent predation on seedlings has been shown to be high in some cedar stands along the east coast (Kuser and Zimmerman 1995), it is unknown what effect, if any, deer predation may have on the seedlings in our study. None of the original planting in our study, nor any of the new seedlings observed in 1999, showed any signs of browsing.

CONCLUSIONS

Cedar is native to southern Mississippi and has been specifically noted in both Jackson and Pearl River counties (Laderman 1989). Although the species has not been reported in any specific natural stands in Louisiana, the proximity of the Mississippi stands suggests that the current or past presence of this species is probable (Mohr 1901 and Brown 1964).

The number of individual trees and populations of cedar at the edge of its western range are small. Because most of the cedar stands along the Mississippi gulf coast are on private lands, they are unprotected and subject to disturbance through land conversion or indirect effects of development in the surrounding areas. This effect can be seen on the Bluff Creek population where urbanization continues to reduce the area occupied by cedar (personal communication Joe Cruthirds). Ehrenfeld and Schneider (1991) showed that as the level of urbanization increased, reproduction of cedar decreased significantly. Although cedar is a tree of high commercial value (Ward and Clewell 1989), the small volume available in Mississippi is not sufficient to generate a strong market.

Establishment of natural cedar stands is hindered by the sparse distribution and narrow range of habitats in which it will successfully grow, and by the limited ability of the species to disseminate seed. Coupled with continued land development, this will most likely further diminish the area occupied by cedar stands. The existing populations may constitute refugia for genes particular to this area (Kuser et al. 1997). It may be important to keep the current stands and to establish additional stands throughout the Gulf Coast to maintain a viable population. This can be done through a combination of protecting existing stands and with plantings in appropriate areas. This study has shown that cedar stands can be effectively established along the Gulf Coast through planting of either seedlings or wildlings. More research is needed to document the extent and composition of existing cedar stands and as well as habitat restoration, community dynamics, anthropogenic impacts, genetic diversity, and possible development of future forest products in the Gulf Coat area.

ACKNOWLEDGMENTS

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LITERATURE CITED

Allison, Stuart, K. and J.G. Ehrenfeld. 1999. The influence of microhabitat variation on seedling recruitment *of Chamaecyparis thyoides* and *Acer rubrum*. Wetlands 19(2):383-393.

Belcher, R.T., R.B. Atkinson, and G.J. Whiting. This Volume. Structural and ecophysiological responses of Atlantic white cedar across a range of shade intensities.

Brown, C.A. 1945. Louisiana trees and shrubs. Louisiana Forestry Commission, Baton Rouge, Louisiana. 115 p.

Brown, C.A. 1964. Commercial trees of Louisiana. Louisiana Forestry Commission, Baton Rouge, LA. 80 p.

Clewell, A.F. and Ward, D. B. 1987. Atlantic white-cedar wetlands, Atlantic white-cedar in Florida and along the northern gulf coast. P. 69-82. In Laderman, A. D. (ed.) Atlantic white-cedar Wetlands. Westview Press, Boulder, CO.

Ehrenfeld, J.G and J.P. Schneider. 1991. *Chamaecyparis thyoides* wetlands and suburbanization: effects on hydrology, water quality and plant community composition. Journal of Applied Ecology 28:467-490.

Eleuterius, L.N. and S.B. Jones. 1972. A phytosociological study of white-cedar in Mississippi. Castanea 37:67-74.

Golet, F.C. and D. J. Lowry. 1987. Water regimes and tree growth in Rhode Island Atlantic white-cedar swamps. P. 91-110 In A.D. Ladermand. (ed.) Atlantic white-cedar wetlands. Westview Press, Boulder, CO.

Haas, Michael J. and John E. Kuser. 2002. Establishment of *Chamaecyparis thyoides* on an extremely low-nutrient sandy site in the Atlantic Coastal Plain, U.S.A. Restoration Ecology. In Revision.

Keeland, B.D., and W.H. Conner. 1999. Natural regeneration and growth of *Taxodium distichum* (L.)Rich. in Lake Chicot, Louisiana, after 44 years of flooding. Wetlands 19(1):149-155.

Korstian, C.F. and W.D. Brush. 1931. Southern white cedar. U.S. Dept. Agric. Tech. Bull. 251. 75pp.

Kuser, J.E., T.R. Meagher, D.L. Sheely. and A. White. 1997. Allozyme frequencies in New Jersey and North Carolina populations of Atlantic white-cedar, *Chamaecyparis thyoides* (Cupressaceae). American Journal of Botany 84(11):1536-1541.

Kuser, J.W. and G.L. Zimmerman. 1995. Restoring Atlantic white-cedar swamps: a review of techniques for propagation and establisment. Tree Planters Notes 46:78-85

Laderman, A.D. 1989. The ecology of Atlantic white-cedar wetlands: a community profile. Biological Report 85(7.21). U.S. Department of the Interior, U.S. Fish and Wildlife Service. 115 p.

McCoy, J.W., B.D. Keeland, and J.A. Allen. 1999. Atlantic white-cedar plantings in St. Tammany Parish, Louisiana, and the Bouge Chitto National Wildlife Refuge, Mississippi. P. 36-41 In Shear, T.H. and K.O. Summerville (eds). Proceedings: Atlantic white-cedar Ecology and Management Symposium (1997 August 6-7) Newport News, VA. Gen. Tech. Rep. SRS-27. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

McKevlin, M.R. and D.D. Hook. 1995. Morphological and physiological differences between rooted cuttings of Atlantic white-cedar grown in contiuously flooded or moist peat. P. 311-319. In Edwards, M. B. (compiler) Proceedings of the Eighth Biennial Southern Silvicultural Research Conference. USDA Forest Service, Southern Research Station, Asheville, NC.

Mohr, C. 1901. Notes on the red cedar. U.S. Department Agric. Division of Forestry. Gov. Printing Office Bull. 31.

NCDC (National Climatic Data Center). 2000. Climate Division Drought Data. http://www.ncdc.noaa.gov/onlineprod/drought/main.html. Date accessed:5/16/2000.

SAS Institute Inc. 1988. SAS/STAT User's Guide, Release 6.03 edition.. SAS Institute Inc. Cary, NC. 1,028 p.

USDA (U.S. Department of Agriculture). 1990. Soil survey of St. Tammany Parish, Louisiana. Soil Conservation Service. 141 p.

USDA (U.S. Department of Agriculture). 1983. Soil survey of Pearl River County, Mississippi. Soil Conservation Service. 124 p.

USFS (U.S. Forest Service). 1976. Volume, yield, and stand tables for second growth southern pines. Misc. Publ. 50. U.S. Department of Agriculture, Forest Service.

Ward, D.B. and A.F. Clewell. 1989. Atlantic white-cedar (*Chamaecyparis thyoides*) in the southern states. Florida Scientist 52:8-47.

ALLOZYME VARIATION WITHIN AND AMONG SELECTED POPULATIONS OF ATLANTIC WHITE CEDAR

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Abstract: We present preliminary results of a rangewide genetic study of cedar, *Chamaecyparis thyoides* (L.) B.S.P. We examined the distribution of genetic variation within and among a set of 15 populations, using 11 allozyme loci. Averaged across all populations, 56.4% of loci were polymorphic, the effective number of alleles per locus (A_e) was 1.315, observed heterozygosity (H_o) was 0.171, and expected heterozygosity (H_e) was 0.172. We divided populations into six regions (1) northern – Maine and New Hampshire, (2) central – New Jersey and Delaware, (3) eastern Florida panhandle, (4) central Florida, (5) eastern Mississippi, and (6) western Florida panhandle. We used Analysis of Molecular Variance (AMOVA) to delineate the extent of geographic differentiation within and among regions and populations. We could ascribe an estimated 79.8% of the total variance to individuals within populations, 15.1% to regions, and 5.1% to populations within regions. We calculated genetic distances between pairs of populations, performed a UPGMA cluster analysis, examined the relationship between genetic and geographic distances between population pairs, and found regional patterns of variation that agreed with the AMOVA results. We also used AMOVA to examine differences between *C. thyoides* var. *henryae* and *C. thyoides* var. *thyoides*. The varietal distinction did (or did not) account for a significant portion of the total variation, depending on how the varieties are delineated, and whether all stands (or only southern stands) are included in the analysis. If the glacial refugia for cedar were in Florida, Alabama and/or Mississippi, and if the species then slowly migrated northward in post-Pleistocene times, we might expect a negative relationship between genetic diversity and latitude, but we found no relationship between expected heterozygosity or allelic richness and latitude in this study. The alternatives are that cedar spent the ice age east of the current Atlantic coastline, in more than one location, or had a means of long distance dispersal, following glacial melting.

Key Words: geographic variation, *Chamaecyparis thyoides*

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), is a wetland species of the Atlantic and Gulf Coastal states, occurring from southern Maine to central Florida, and west to Mississippi. It is typically found within a narrow coastal belt, 80 to 160 km wide. Within this belt, the distribution is patchy, depending on the occurrence of suitable sites (Little 1950). It is an important species ecologically and aesthetically, and is a valued timber species. However over the past two centuries there has been a rangewide decline, with many previous Cedar sites being converted to other wetland types and land uses. There has been much recent interest in the species, its management, and restoration. Genetic diversity within cedar should be taken into account when developing management, conservation, and restoration plans.

The cedar populations found along the Gulf Coast and surrounding areas have been considered by many as a separate taxon. Li (1962) described a new species, *Chamaecyparis henryae* Li, which included the populations in the western panhandle of Florida, southern Alabama and southeastern Mississippi. The new species was distinguished from *C. thyoides* by several characters, among them: mostly eglandular leaves, lighter, yellowish green foliage, and smoother bark (Li 1962). Little (1966) agreed that these populations were different, but viewed them as a mere geographical variety, *C. thyoides* var. *henryae* (Li)Little, and extended this designation to all stands in Florida and western Georgia as well. Ward and Clewell (1989) concluded that *C. thyoides* var. *henryae* was a valid taxonomic unit, and mapped its distribution, based on the presence/absence of a small median gland on the facial leaves, which is present on *C. thyoides* var. *thyoides*, but absent from *C. thyoides* var. *henryae*. Their mapped distribution for *C. thyoides* var. *henryae*, however, included only the western Florida panhandle and Alabama (Ward and Clewell 1989).

Genetic diversity allows any species to adapt to variable environments over space and time, reduces vulnerability to pests, and may be used for future breeding purposes (Ledig 1986). Geographic patterns of genetic diversity may reflect recent gene flow and dispersal patterns within and among populations, as well as historical processes that have led to these patterns. Knowledge of the diversity and distribution of genetic variation within and among forest tree populations is crucial to genetic management, making it possible to develop strategies to prevent gene depletion and ensure conservation (National Research Council 1991). This knowledge can also be used to choose stock materials for breeding purposes and restoration efforts. The distribution of genetic variation within and among cedar populations should be taken into account when developing management and restoration plans for the species.

Allozyme markers have been widely used to assess genetic diversity within tree species (Brown and Moran 1981, Hamrick et al. 1981, Li and Adams 1989, Berg and Hamrick 1997). Prior to this study, there have been two smaller studies of allozyme variation in cedar (Kuser et al. 1997, Eckert 1998). Kuser et al. (1997) examined allozyme variation among New Jersey and North Carolina populations, and found that 9% of the total allozyme variation was attributable to differences among populations, compared with 5% found in *Chamaecyparis lawsoniana* (Millar and Marshall 1991) and 14% in *C. nootkatensis* (Ritland et al. 2001). Eckert (1998) examined a number of New Hampshire and Maine cedar populations and found substantial differences among stands for certain loci. He found that these populations were not genetically depauperate, as might be expected of populations at the edge of the species' range, and concluded that these populations are probably relict from a time when the species was more widespread (Eckert 1998). The present study is the first to examine allozyme variation throughout cedar’s entire range.

These types of genetic data can be used to infer historical processes (Conkle 1992, Schnabel et al. 1993, Leonardi and Menozzi 1995). The glacial refugium and migration route of cedar, following the Pleistocene glaciation, is not completely understood. The last of the Wisconsin glaciations reached its peak about 18,000 years before present (BP) and there is evidence that the ice sheet began to melt perhaps as early as 15,000 yr. BP (Watts 1979). For eastern North American plant and animal species, there were two main regions that served as refugia during this time: (1) mid-latitude North America, south of the ice sheet, and (2) the Atlantic coastal plains, east of the ice sheet, now submerged to form the continental shelf. Sea level is estimated to have been at least 85 m below the present level, perhaps as much as 130 m (Pielou 1991). There is also evidence that populations of the same species migrated back from different refugia, subsequent to glacial melting and rising sea level (Morgenstern 1996).

For species that migrated slowly northward from a southern refugium, we might expect a negative relationship between genetic diversity and latitude. For example, a number of conifers of the western US, including *Pinus coulteri* (Ledig 1987) and *Sequoiadendron giganteum* (Fins and Libby 1994), exhibit higher variability in southern populations and a decrease in variability towards the northern portions of their ranges. Alternatively, for species that migrated from an off-shore refugium, we might expect to find a negative relationship between genetic diversity and distance from the Pleistocene shoreline.

Kuser et al. (1997) found no relationship between genetic similarity and geographic proximity among New Jersey and North Carolina populations of *C. thyoides*, and concluded that cedar must have had a means of long distance dispersal, as it migrated from a southern refugium to its present distribution. In North Carolina, Cupressaceae pollen grains are found in sediments at 25,000 yr BP, are absent during the glacial epoch, and then reappear about 10,000 yr BP (Whitehead 1981). At Helmetta Swamp, on the coastal plain of New Jersey, *Chamaecyparis* macrofossils indicate a presence as early as 10,000 yr BP (Watts 1979), possibly suggesting a continental shelf refugium.

Belling (1977), however, postulated that cedar recolonized the Northeast by first colonizing the Piedmont, between the coastal plain and the Appalachians, between 3770 to 6800 yr BP. She argued that Appalachian sites were colonized next, between 4020 and 5780 yr BP, followed by the coastal plain, between 380 and 3560 yr BP (Belling 1977). Although these results are based on macrofossil evidence from a small number of sites within only the northern portion of cedar's range, they do not support an off-shore glacial refugium. The clues are fragmentary, and the migration route of cedar is not completely understood.

We present here the preliminary results of a study that examines genetic variation throughout cedar's range. We report allozyme frequencies for 15 populations within 6 regions of the species range: (1) northern – Maine and New Hampshire, (2) central – New Jersey and Delaware, (3) eastern Florida panhandle, (4) central Florida, (5) eastern Mississippi, and (6) western Florida panhandle. The specific objectives of this study are to (1) examine the overall allozyme diversity within and among populations, (2) determine whether there are differences between *C. thyoides* var. *thyoides* and *C. thyoides* var. *henryae* populations, and (3) elucidate (if possible) cedar's recolonization route, following glaciation.

METHODS

Populations

We sampled 15 cedar populations between July 1999 and January 2000 (figure 1 and table 1), taking foliage samples from 40 individual trees per population, chosen to be at least 15 m apart, whenever possible. The foliage samples were kept on ice until they were brought back to the lab for electrophoretic processing.

Electrophoresis

We performed horizontal starch gel electrophoresis on foliage samples, ground in liquid nitrogen and prepared with the extraction buffer described by Mitton et al. (1979), as modified by Eckert (1998), and with the addition of 2-Mercaptoethanol. We used gel and electrode buffer systems, modified from Soltis et al. (1983) and Pasteur et al. (1988), and enzyme assays modified from Hebert and Beaton (1993) and Wendel and Weeden (1989). We scored fourteen allozyme loci: phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6-PGD-1, 6-PGD-2), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH-1, MDH-2), malic enzyme (ME), glucose-6-phosphate dehydrogenase (G-6-PDH), phosphoglucoisomerase (PGI-2), glycerate-2-dehydrogenase (G-2-DH), shikimate dehydrogenase (SKD), glutamate oxaloacetate transaminase (GOT-1, GOT-2), and fluorescent esterase (FE). We excluded loci (ME, GOT-1 and FE) from our analyses due to inconsistent results.

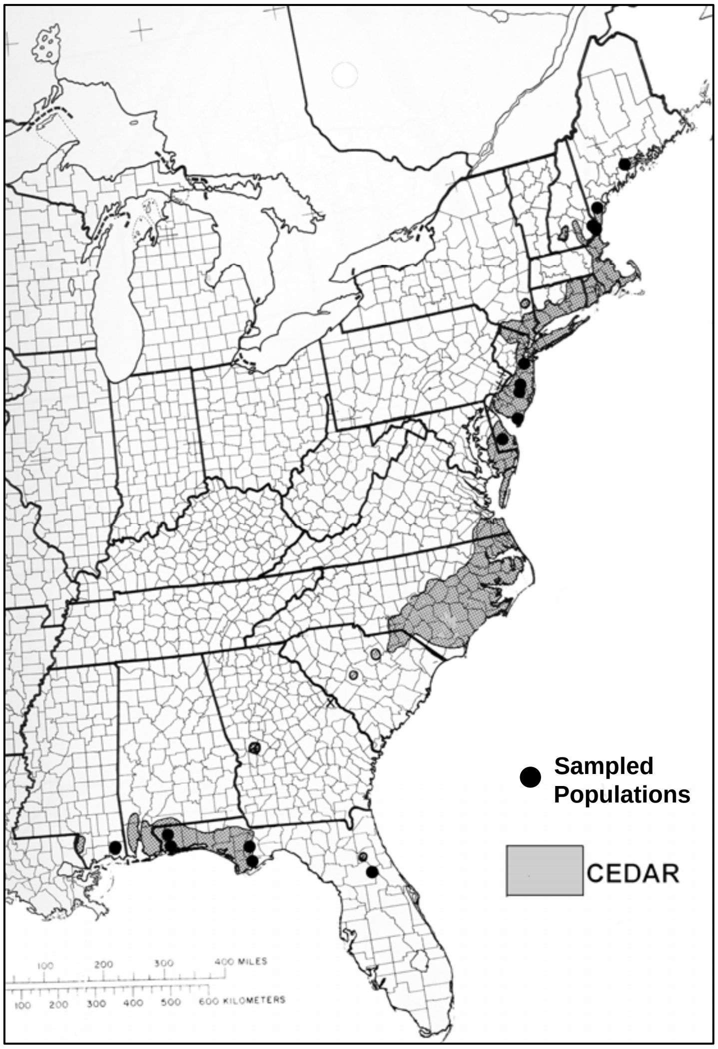
Data Analysis

Geographic patterns. Due to differences in sample sizes and missing data for some loci, we randomly selected 20 individuals from each population, for which a full set of allozyme assays were available, for data analysis. We determined allele frequencies for each of the 15 populations, and calculated the following standard measures of genetic diversity: proportion of polymorphic loci, with no criteria (P_{NC}), proportion of polymorphic loci, with the most common allele present at a frequency $\leq 95\%$ (P_{95}), number of alleles (A) and effective number of alleles (A_e) per locus, observed heterozygosity (H_o) and expected heterozygosity (H_e).

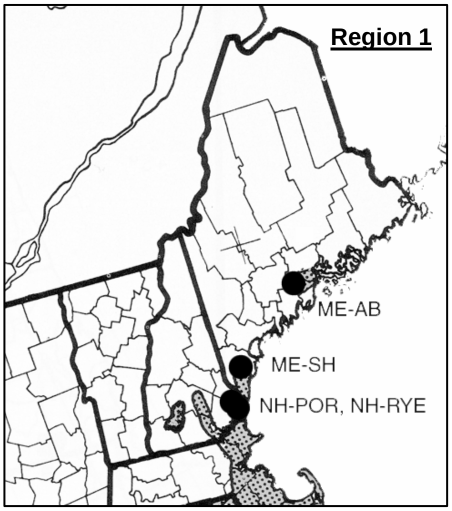
To delineate the extent of geographic differentiation within and among populations and regions, we employed analysis of molecular variance, AMOVA (Excoffier et al. 1992). This technique uses an analysis of variance format, derived from a matrix of codominant squared distances between pairs of individuals (Peakall et al. 1995). The analysis produces estimates of variance components and *F*-statistic analogs, designated as Φ - statistics. The correlation of random individuals within a region, relative to that of random pairs of individuals drawn from the whole species, is designated Φ_{RT}. The correlation of random individuals within populations, relative to that of random pairs of individuals drawn from the region, is designated Φ_{PR}, and the correlation of random individuals within populations, relative to that of random pairs drawn from the entire species, is designated Φ_{PT}. Formally, $(1- \Phi_{PT}) = (1- \Phi_{PR})(1- \Phi_{RT})$. The normality assumption for conventional analysis of variance is inappropriate for molecular data, so a permutational (data reuse) approach is used to test the significance of the variance components and Φ - statistics (Excoffier et al. 1992).

Figure 1. Range of cedar (adapted from Little 1971), showing locations of the 15 populations sampled (black circles). 1a. shows the locations relative to the entire range of the species. 1b. shows the populations included in Region 1. 1c. shows the populations included in Region 2. 1d. shows the populations included in Regions 3, 4, 5 and 6.

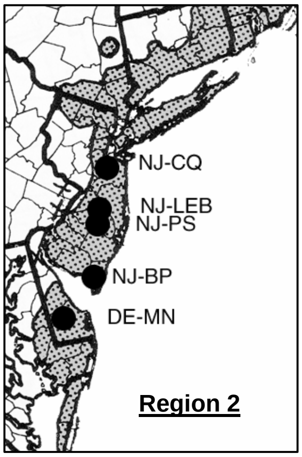
1a.



1b.



1c.



1d.

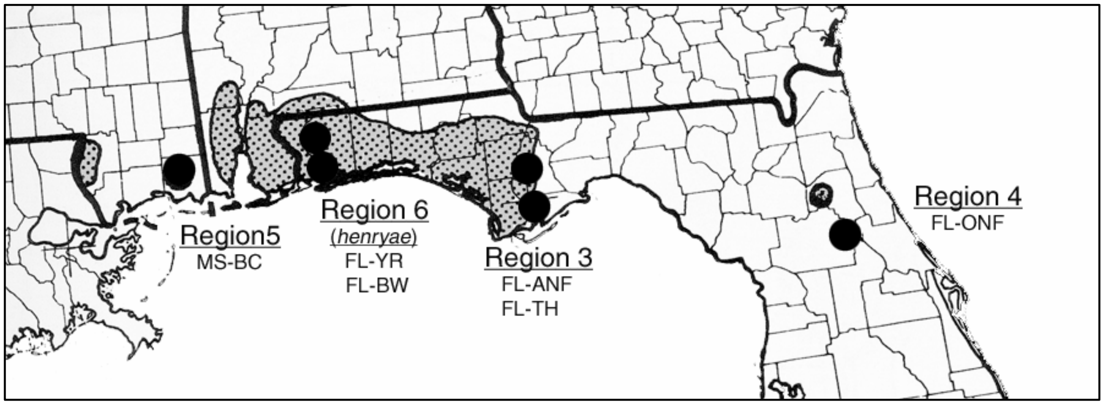


Table 1. Description of all populations sampled, including regional designation, abbreviation used throughout, location, and ownership.

Site	County, State	Latitude	Longitude	Ownership
Region 1				
Appleton Bog (ME-AB)	Knox County, ME	44°20’	69°16’	The Nature Conservancy, ME
Saco Heath Preserve (ME-SH)	York County, ME	43°33’	70°28’	The Nature Conservancy, ME
Portsmouth Cedar Stands (NH-POR)	Rockingham County, NH	43°1’	70°48’	unknown
Rye (NH-RYE)	Rockingham County, NH	42°59’	70°47’	The Nature Conservancy, NH
Region 2				
Lebanon State Forest (NJ-LEB)	Burlington/Ocean Counties, NJ	39°53’	74°30’	State of New Jersey
Cheesequake State Park (NJ-CQ)	Middlesex County, NJ	40°26’	74°16’	State of New Jersey
Penn Swamp, Wharton State Forest (NJ-PS)	Burlington County, NJ	39°41’	74°40’	State of New Jersey
Belleplain State Forest (NJ-BP)	Cape May County, NJ	39°11’	74°51’	State of New Jersey
Middleford North Preserve (DE-MN)	Sussex County, DE	38°40’	75°33’	The Nature Conservancy, DE
Region 3				
Apalachicola National Forest (FL-ANF)	Liberty County, FL	30°10’	84°53’	U.S. Forest Service
Tates Hell State Forest (FL-TH)	Franklin County, FL	29°55’	84°50’	State of Florida
Region 4				
Ocala National Forest (FL-ONF)	Marion County, FL	29°12’	81°39’	U.S. Forest Service
Region 5				
Bluff Creek (MS-BC)	Jackson County, MS	30°32’	88°42’	private
Region 6				
Yellow River (FL-YR)	Santa Rosa County, FL	30°33’	86°58’	State of Florida
Blackwater River State Forest (FL-BW)	Santa Rosa County, FL	30°51’	86°51’	State of Florida

We performed AMOVA to assess differences within and among geographic regions. We divided populations into six regions: (1) northern, (2) central, (3) eastern Florida panhandle, (4) central Florida, (5) eastern Mississippi, and (6) western Florida panhandle (see table 1 for regional designations). Because morphological and taxonomical differences have been suggested between the southern populations (Li 1962, Ward and Clewell 1989) they were divided into four different regions (regions 3 through 6). These additional divisions maximized the percentage of the total genetic variance that we could account for in the analysis. The northern and central regions were not divided further because such divisions did not increase the percentage of variance explained.

We also computed time-linearized pairwise genetic distances between all pairs of populations, based on Φ_{PT} values between each pair of populations, and conducted a cluster analysis of population groupings, using the unweighted pair group method algorithm (UPGMA) on these pairwise distances to assess overall similarities among populations.

Varietal Differences. To assess the divergence of *C. thyoides* var. *henryae* and *C. thyoides* var. *thyoides,* we performed five separate AMOVA analyses using three different separations of var. *henryae* from var. *thyoides*:

Analysis	*C. thyoides* var. *henryae* (reference)	*C. thyoides* var. *thyoides*
1	Regions 3-6: All FL and MS populations (Little 1966)	Regions 1,2
2	Region 6: W. FL panhandle (Ward and Clewell 1989)	Regions 1-5
3	Region 6: W. FL panhandle (Ward and Clewell 1989)	Regions 3-5
4	Regions 3,6: All of FL panhandle	Regions 1,2,4,5
5	Regions 3,6: All of FL panhandle	Regions 4,5

Glacial refugium. To test the idea that cedar spent the ice age in a southern refugium and moved slowly northward following glacial retreat, we plotted (H_e) and (A) against latitude to assess north-south patterns of diversity. We also used regression analysis to examine the relationship between genetic and geographic distances between population pairs. If this species migrated northward following glacial retreat, we would expect to see a negative relationship between genetic diversity and latitude, as well as a significant relationship between genetic and geographic distances.

RESULTS

All eleven loci were polymorphic in at least one population, although some loci (6-PGD-1, IDH, MDH-2, G-2-DH and GOT-2) were monomorphic in most populations. Three loci (6-PGD-1, IDH, and MDH-1) exhibited two alleles, five loci (6-PGD-2, MDH-1, G-6-PDH, G-2-DH, and GOT-2) exhibited three alleles, and three loci (PGM, PGI-2, and SKD) exhibited four alleles. We display allele frequencies for all fifteen populations in table 2. Allelic differences among populations are evident. For example, allele 1 at the G-2-DH locus is found only in the two New Hampshire populations. At the SKD locus, alleles 1 and 4 are found only in southern populations. At the PGM locus, allele 1 is absent in the two region 6 populations, but is present in all other populations.

Standard measures of genetic diversity are displayed in table 3. Averaged across all populations, 56.4% of loci were polymorphic with no criteria and 46.7% of loci were polymorphic with the most common allele at a frequency of 0.95 or less. The average number of alleles per locus (A) was 1.769, and the effective number of alleles per locus (A_e) was 1.315. Observed heterozygosity ($H_o = 0.171$) was very close to the expected value ($H_e = 0.172$), indicating local panmixia within populations. The expected heterozygosity was slightly higher than that found by Kuser et al. (1997) among New Jersey and North Carolina populations. Observed heterozygosity was also higher than that found by Eckert (1998) for New Hampshire and Maine populations ($H_o = 0.12$), and that found by Millar and Marshall (1991) for *C. lawsoniana* ($H_o = 0.13$), although different sample sizes and allozyme loci make it difficult to compare results directly across studies.

Geographic Patterns

We show the results of AMOVA, conducted among the six regions, and individually for each region, in table 4 and figure 2. The among-regions analysis was based on a distance matrix with 14 individuals per population, while the within-region AMOVAs were conducted with 20

Table 2a. Allele frequencies at the first 7 allozyme loci, for all 15 populations sampled.

	ME-AB	ME-SH	NH-POR	NH-RYE	NJ-LEB	NJ-CQ	NJ-PS	NJ-BP	DE-MN	FL-ANF	FL-TH	FL-ONF	MS-BC	FL-YR	FL-BW
PGM															
1	0.200	0.425	0.300	0.125	0.225	0.325	0.125	0.075	0.250	0.425	0.325	0.675	0.100	-	-
2	0.350	0.450	0.450	0.625	0.475	0.200	0.475	0.450	0.300	0.225	0.300	0.200	0.625	0.450	0.475
3	0.450	0.125	0.250	0.250	0.300	0.475	0.400	0.475	0.450	0.350	0.350	0.125	0.250	0.450	0.500
4	-	-	-	-	-	-	-	-	-	-	0.025	-	0.025	0.100	0.025
6-PGD-1															
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.975	1.000	1.000
3	-	-	-	-	-	-	-	-	-	-	-	-	0.025	-	-
6-PGD-2															
1	-	-	-	-	-	-	0.050	-	0.050	-	-	-	-	-	-
2	0.825	0.600	0.925	0.800	0.900	0.850	0.875	0.925	0.825	0.450	0.425	0.725	0.625	0.500	0.625
3	0.175	0.400	0.075	0.200	0.100	0.150	0.075	0.075	0.125	0.550	0.575	0.275	0.375	0.500	0.375
IDH															
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.900	0.975	1.000	1.000	1.000	1.000
3	-	-	-	-	-	-	-	-	-	0.100	0.025	-	-	-	-
MDH-1															
1	-	-	-	-	-	-	-	-	-	0.050	-	-	-	0.100	0.025
2	0.125	-	0.125	0.075	-	0.075	0.100	0.025	-	-	-	0.175	-	-	0.025
3	0.875	1.000	0.875	0.925	1.000	0.925	0.900	0.975	1.000	0.950	1.000	0.825	1.000	0.900	0.950
MDH-2															
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.975	0.900
3	-	-	-	-	-	-	-	-	-	-	-	-	-	0.025	0.100
G-6-PDH															
1	0.500	0.225	0.100	0.325	0.175	0.100	0.225	0.150	-	0.075	0.025	0.275	0.025	0.025	0.025
2	0.500	0.750	0.900	0.675	0.825	0.900	0.775	0.850	1.000	0.925	0.975	0.725	0.975	0.975	0.975
3	-	0.025	-	-	-	-	-	-	-	-	-	-	-	-	-

individuals per population. We were able to attribute 15.1% to regional differences, 5.1% to differences among populations within regions, and 79.8% to variation within populations. Overall $\Phi_{RT} = 0.151$, $\Phi_{PR} = 0.060$, and $\Phi_{PT} = 0.202$. The proportion of variance attributed to populations within regions varied by region; 9.0% for region 1, 4.9% for region 2, and 0% for regions 3 and 6. Regions 4 and 5 contained only one sampled population, so differentiation among populations could not be determined.

We used pairwise inter-population genetic distances (table 5) and cluster analyses (figure 3) to summarize the detailed pattern of population differences. Southern populations of clustered together, except for Ocala National Forest (central Florida), and are separated from northern and central populations. There appears to be no clear distinction between northern and central populations, although the two populations from Maine seem to be somewhat distinct from New Hampshire, New Jersey, and Delaware populations.

Table 2b. Allele frequencies at the final four allozyme loci, for all 15 populations sampled.

	ME-AB	ME-SH	NH-POR	NH-RYE	NJ-LEB	NJ-CQ	NJ-PS	NJ-BP	DE-MN	FL-ANF	FL-TH	FL-ONF	MI-BC	FL-YR	FL-BW
PGI-2															
1	0.200	0.450	0.250	0.350	0.150	0.150	0.275	0.225	0.050	-	-	-	0.025	-	-
2	-	-	0.025	-	-	-	0.125	-	0.025	0.125	0.075	-	0.025	0.125	0.100
3	0.600	0.550	0.650	0.650	0.825	0.775	0.600	0.775	0.925	0.875	0.900	1.000	0.950	0.875	0.900
4	0.200	-	0.075	-	0.025	0.075	-	-	-	-	0.025	-	-	-	-
G-2-DH															
1	-	-	0.025	0.025	-	-	-	-	-	-	-	-	-	-	-
2	1.000	1.000	0.975	0.975	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.850	1.000	1.000
3	-	-	-	-	-	-	-	-	-	-	-	-	0.150	-	-
SKD															
1	-	-	-	-	-	-	-	-	-	0.025	-	-	0.200	-	0.075
2	0.075	0.125	0.050	0.125	0.100	0.175	0.075	0.025	0.050	0.025	-	0.400	-	0.100	0.100
3	0.925	0.875	0.950	0.875	0.900	0.825	0.925	0.975	0.950	0.875	0.975	0.575	0.800	0.775	0.675
4	-	-	-	-	-	-	-	-	-	0.075	0.025	0.025	-	0.125	0.150
GOT-2															
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.850	0.900	0.925
3	-	-	-	-	-	-	-	-	-	-	-	-	0.150	0.100	0.075

Table 3. Measures of genetic diversity for all 15 populations sampled individually, and then averaged across populations to estimate species wide diversity. Measures include: Proportion of polymorphic loci using no criteria (**P_{NC}**), proportion of polymorphic loci with the most common allele found at a frequency of 95% or less (**P_{95}**), alleles per locus (A), effective number of alleles per locus (A_e), observed heterozygosity (H_o) and expected heterozygosity (H_e).

Population	P_{NC}	P_{95}	A	A_e	H_o	H_e
ME-AB	54.545	54.545	1.727	1.442	0.191	0.213
ME-SH	45.455	45.455	1.636	1.393	0.195	0.198
NH-POR	54.545	54.545	1.727	1.238	0.168	0.162
NH-RYE	63.636	54.545	1.727	1.338	0.177	0.196
NJ-LEB	45.455	45.455	1.636	1.272	0.155	0.144
NJ-CQ	54.545	54.545	1.727	1.310	0.168	0.169
NJ-PS	54.545	54.545	1.818	1.356	0.191	0.186
NJ-BP	54.545	36.363	1.636	1.222	0.132	0.128
DE-MN	36.363	36.363	1.636	1.229	0.091	0.107
FL-ANF	63.636	63.636	1.818	1.268	0.186	0.186
FL-TH	54.545	27.273	1.818	1.316	0.123	0.136
FL-ONF	45.455	45.455	1.636	1.339	0.195	0.189
MS-BC	72.727	54.545	2.000	1.309	0.195	0.184
FL-YR	72.727	54.545	1.909	1.348	0.218	0.194
FL-BW	72.727	63.636	2.091	1.342	0.182	0.194
SPECIES	56.363	49.697	1.769	1.315	0.171	0.172

Table 4. Summary of results from AMOVAs conducted on a matrix of codominant squared distances between pairs of individuals from 15 cedar populations.

Source	df	SS	MS	Est. Var.	% total	Φ	P
[1]***<u>All Regions</u>***							
Among Regions (1,…, 6)	5	78.491	15.698	0.369	15.08	$\Phi_{RT} = 0.151$	<0.001
Among Pops within Regions	9	33.286	3.698	0.125	5.08	$\Phi_{PR} = 0.060$	<0.001
Within Populations	195	381.429	1.956	1.956	79.84	$\Phi_{PT} = 0.202$	<0.001
[2]***<u>Region 1</u>***							
Among Pops within Regions	3	21.038	7.012	0.233	9.04	$\Phi_{PT} = 0.090$	<0.001
Within Populations	76	178.350	2.347	2.347	90.96		
[2]***<u>Region 2</u>***							
Among Pops within Regions	4	13.570	3.392	0.0860	4.89	$\Phi_{PT} = 0.049$	0.002
Within Populations	95	158.850	1.672	1.672	95.11		
[2]***<u>Region 3</u>***							
Among Pops within Regions	1	40.000	1.150	0.000^{*}	0	$\Phi_{PT} = 0.000^{*}$	0.6920
Within Populations	38	33.000	1.921	1.921	100		
[2]***<u>Region 6</u>***							
Among Pops within Regions	1	37.400	1.575	0.000^{*}	0	$\Phi_{PT} = 0.000^{*}$	0.6850
Within Populations	38	45.700	2.187	2.187	100		

[1]Performed using 14 individuals per population. [2]Performed using 20 individuals per population. *Negative values set to 0.

Figure 2. 2a. Proportion of the total variance attributed to differences among regions, among populations within regions, and within populations for 15 cedar populations (see table 1 for regional designations). 2b.-2e. Proportion of the total variance within each region attributed to differences among populations and within populations. Regions 4 and 5 are excluded because these regions contain only one population. Therefore the among population component cannot be determined for these populations. All estimated variance components were derived from AMOVA.

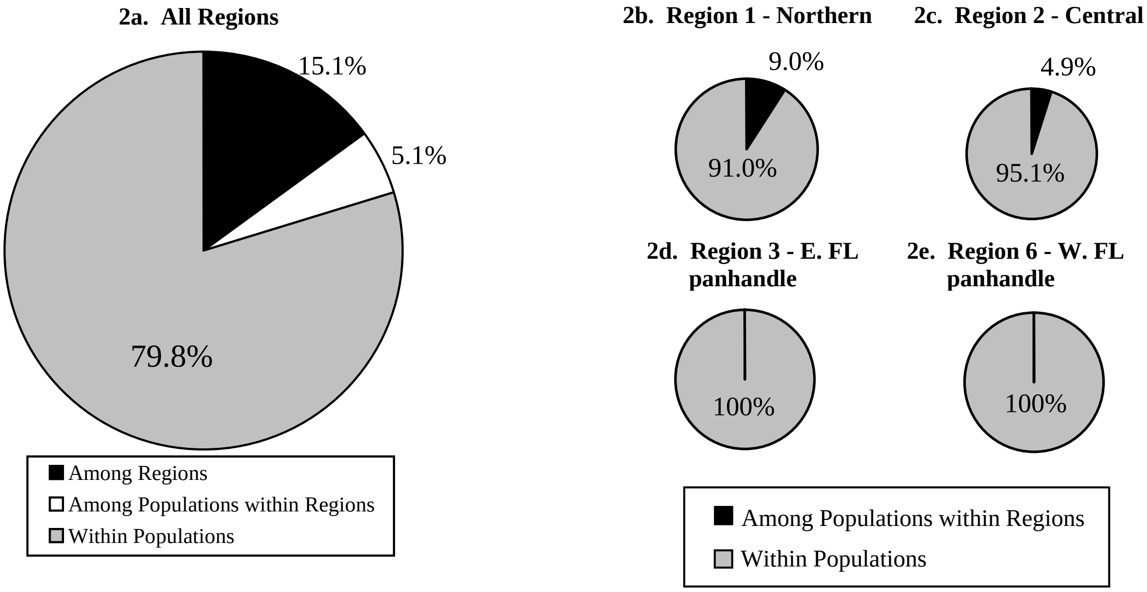
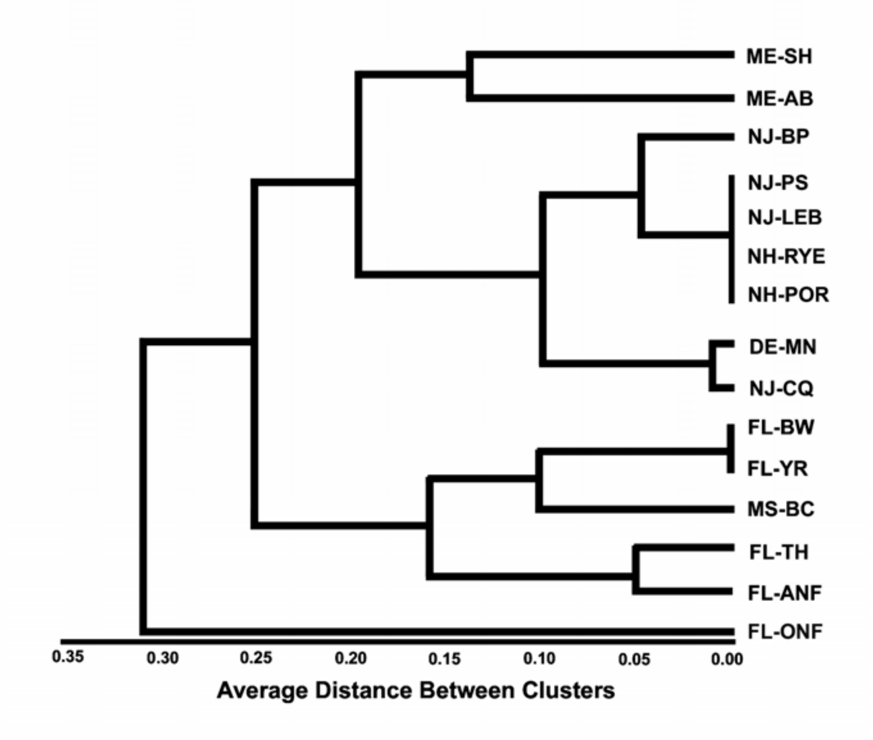


Table 5. Estimated genetic and geographic distances between pairs of cedar populations. Time-linearized genetic distances were derived from Φ_{PT} values between each pair, and are displayed below the diagonal. Geographic distances between populations (km) are displayed above the diagonal. Populations within each of the six regions are shaded.

	ME-AB	ME-SH	NH-POR	NH-RYE	NJ-LEB	NJ-CQ	NJ-PS	NJ-BP	**DE-MN**	**FL-ANF**	FL-TH	FL-ONF	MS-BC	FL-YR	FL-BW
ME-AB	-	129.8	191.6	193.6	657.0	597.6	683.2	736.8	819.3	2090.1	2109.7	2008.7	2293.1	2181.6	2149.0
ME-SH	0.14	-	65.2	68.1	527.9	468.0	554.2	608.3	690.4	1960.4	1980.0	1881.5	2164.1	2052.0	2019.5
NH-POR	0.09	0.16*	-	4.0	465.6	406.8	491.8	545.2	627.7	1900.0	1918.9	1817.5	2107.6	1993.7	1961.3
NH-RYE	0.09*	0.11*	0.00**	-	463.8	405.3	490.0	543.2	625.8	1898.0	1917.3	1815.3	2106.6	1992.4	1960.0
NJ-LEB	0.13*	0.14	0.00**	0.00**	-	64.4	26.4	83.5	162.8	1434.9	1453.8	1356.5	1654.7	1534.6	1502.9
NJ-CQ	0.20*	0.23*	0.03	0.14*	0.01	-	90.2	147.8	225.4	1492.8	1512.1	1419.3	1706.2	1588.7	1556.7
NJ-PS	0.04*	0.17*	0.00**	0.00**	0.00**	0.08*	-	57.8	136.4	1380.0	1427.9	1330.1	1630.4	1509.6	1478.0
NJ-BP	0.20*	0.34*	0.06	0.09*	0.01	0.08*	0.02	-	83.5	1358.4	1376.9	1274.3	1586.4	1462.9	1431.7
DE-MN	0.29*	0.36*	0.10	0.21*	0.06	0.01	0.12*	0.03	-	1274.9	1293.5	1193.9	1504.2	1379.9	1348.8
FL-ANF	0.38*	0.20*	0.33*	0.34*	0.28*	0.27*	0.32*	0.40*	0.28*	-	28.2	330.6	368.8	204.6	203.3
FL-TH	0.31*	0.22*	0.19*	0.20*	0.11*	0.15*	0.17*	0.16*	0.10*	0.05	-	318.3	378.1	216.9	219.7
FL-ONF	0.28*	0.25*	0.25*	0.30*	0.24*	0.23*	0.29*	0.44*	0.34*	0.28*	0.32*	-	696.3	534.6	533.6
MS-BC	0.37*	0.29*	0.19*	0.15*	0.12*	0.25*	0.18*	0.21*	0.25*	0.27*	0.12*	0.36*	-	166.2	180.5
FL-YR	0.39*	0.31*	0.28*	0.26*	0.21*	0.27*	0.22*	0.25*	0.25*	0.12*	0.01	0.40*	0.12*	-	35.2
FL-BW	0.34*	0.33*	0.20*	0.21*	0.14*	0.18*	0.15*	0.14*	0.17*	0.21*	0.07	0.33*	0.08	+0.00	-

* - statistically significant (∝ = 0.05)
** - negative distances set to 0

Figure 3. Phenogram for 15 cedar populations. Clusters were produced using the unweighted pair group method algorithm (UPGMA) based on genetic distance between pairs of populations.



Varietal Differences

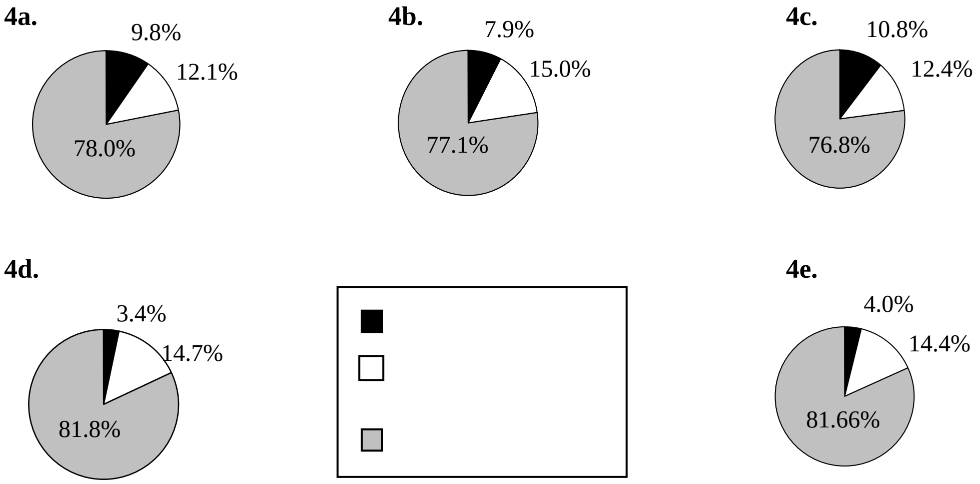
Here we examined genetic differentiation between *Chamaecyparis thyoides* var. *thyoides* and *C. thyoides* var. *henryae*. We show the results of AMOVAs comparing the two varieties in table 6 and figure 4. An estimated 9.83% of the total variance can be attributed to varietal differences, using Little's (1966) designation of *C. thyoides* var. *henryae*, where all Florida and Mississippi populations in this study are treated as var. *henryae* (regions 3-6). Using Ward and Clewell's (1989) designation, however, where only the western Florida panhandle populations (region 6) are treated as var. *henryae*, we can attribute 7.88% of the total variance to varietal differences, although this estimate is not quite statistically significant ($\alpha \geq 0.05$). Using an alternate definition of var. *henryae*, including both western and eastern panhandle populations (Regions 3 and 6), we can attribute 10.75% of the variation to varietal differences.

Table 6. Summary of results from five AMOVAs conducted to assess the divergence between *C. thyoides* var. *henryae* and typical *C. thyoides*. See Methods for detailed descriptions of comparisons.

Source	df	SS	MS	Est. Var.	% total	Φ	P
[1]*Henryae* (Little 1966) vs. *thyoides*							
Among Varieties (Reg. 1-2 vs. 3-6)	1	31.050	31.050	0.246	9.83	$\Phi_{RT} = 0.098$	0.001
Among Pops within Varieties	13	80.726	6.210	0.304	12.12	$\Phi_{PR} = 0.134$	<0.001
Within Populations	195	381.429	1.956	1.957	78.04	$\Phi_{PT} = 0.220$	<0.001
[1]*Henryae* (Ward & Clewell 1989) vs. *thyoides*							
Among Varieties (Reg. 1-5 vs. 6)	1	16.999	16.999	0.200	7.88	$\Phi_{RT} = 0.079$	0.066
Among Pops within Varieties	13	94.778	7.291	0.381	15.02	$\Phi_{PR} = 0.163$	<0.001
Within Populations	195	381.429	1.956	1.956	77.10	$\Phi_{PT} = 0.229$	<0.001
[2]*Henryae* (Ward & Clewell) vs. other southern *thyoide*s							
Among Varieties (Reg. 3-5 vs. 6)	1	14.042	14.042	0.086	3.42	$\Phi_{RT} = 0.034$	0.213
Among Pops within Varieties	4	37.825	9.456	0.370	14.72	$\Phi_{PR} = 0.152$	<0.001
Within Populations	114	234.600	2.058	2.058	81.86	$\Phi_{PT} = 0.181$	<0.001
[1]*Henryae* (alternate definition) vs. *thyoides*							
Among Varieties (Reg. 1,2,4,5 vs. 3,6)	1	28.861	28.861	0.274	10.75	$\Phi_{RT} = 0.108$	<0.001
Among Pops within Varieties	13	82.916	6.378	0.316	12.41	$\Phi_{PR} = 0.139$	<0.001
Within Populations	195	381.429	1.956	1.956	76.84	$\Phi_{PT} = 0.232$	<0.001
[2]*Henrya*e (alternate definition) vs. other southern *thyoides*							
Among Varieties (Reg. 4,5 vs. 3,6)	1	14.629	14.629	0.100	3.96	$\Phi_{RT} = 0.040$	0.130
Among Pops within Varieties	4	37.238	9.309	0.363	14.39	$\Phi_{PR} = 0.150$	<0.001
Within Populations	114	234.600	2.058	2.058	81.66	$\Phi_{PT} = 0.183$	<0.001

[1] Performed using 14 individuals per population. [2] Performed using 20 individuals per population.

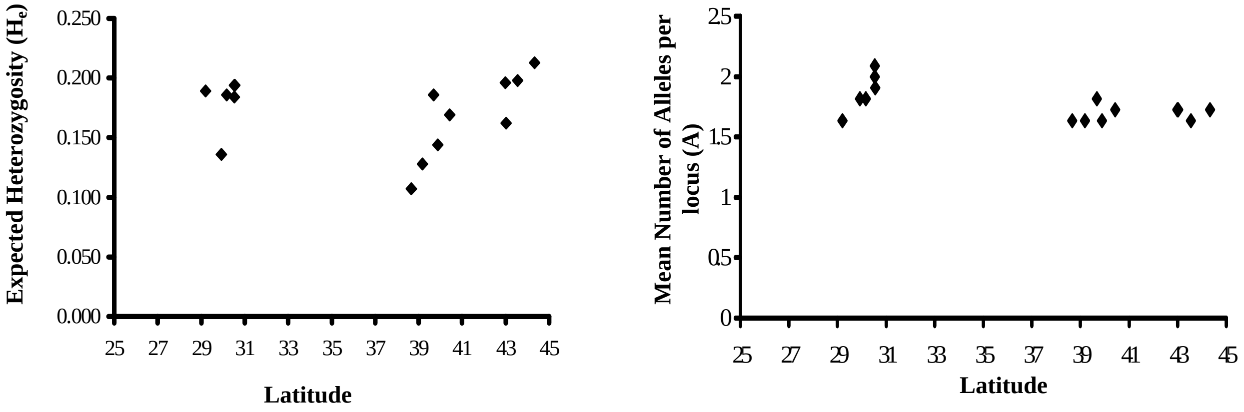
Figure 4. Proportion of total variance attributed to differences among varieties, among populations within varieties and within populations for 15 cedar populations. All variance components were derived from AMOVA. 4a. We considered all FL and MS populations (Regions 3-6) *C. thyoides* var. *henryae* (Little 1966), and compared them against all other populations (Regions 1 and 2). 4b. We considered the western FL panhandle populations (Region 6) *C. thyoides* var. *henryae,* as defined by Ward and Clewell (1989), and compared them against all others (Regions 1-5). 4c. We considered all FL panhandle populations (Regions 3 and 6) var. *henryae*, and compared them against all other populations (Regions 1,2,4,5) 4d. We compared the two western FL panhandle (Region 6) *C. thyoides* var. *henryae* populations (Ward and Clewell 1989) with only the remaining Florida and Mississippi populations (Regions 3,4,5). 4e. We considered all FL panhandle populations (Regions 3 and 6) var. *henryae*, and compared them against the remaining FL and MS populations (Regions 4 and 5).



To remove the confounding due to large latitudinal distances and focus on the varietal distinction, we compared *C. thyoides* var. *henryae* populations with other southern populations of *C. thyoides* var. *thyoides* (regions 3, 4 and 5). We conducted two analyses. For the first analysis, we used Ward and Clewell's (1989) definition of var. *henryae* (region 6). For the second analysis, we used the alternate definition (regions 3 and 6). For both analyses, the estimated between-group variance component (varietal contrast) was not statistically significant, indicating that neither of these definitions of *C. thyoides* var. *henryae* account for a significant portion of the variation found among these southern populations. At this time, the appropriate definition of var. *henryae* remains unclear.

Among the southern populations, *C. thyoides* var. *thyoides* (regions 3-5) clustered more closely with southern *C. thyoides* var. *henryae* populations (region 6) than with *C. thyoides* var. *thyoides* populations from the central (region 2) and northern (region 1) portions of the range (figure 5). Therefore, broad regional differentiation seems to be more apparent than varietal differentiation.

Figure 5. 5a. Expected heterozygosity (H_e) and 5b. mean number of alleles per locus (A) plotted by latitude.


5a.

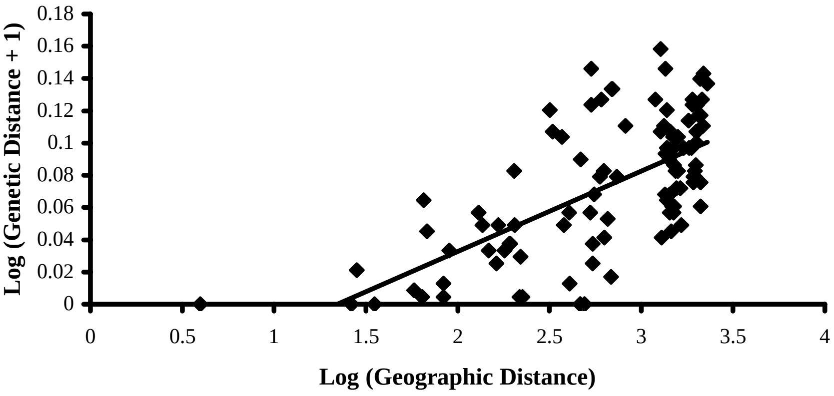
5b.

Glacial Refugium

If cedar spent the last ice age in a southern refugium and migrated northward following glacial retreat, we may expect to see a negative relationship between genetic diversity and latitude. However, there is no apparent relationship between expected heterozygosity or mean number of alleles per locus and latitude (see figure 5).

We may also expect to find a significant relationship between genetic and geographic distances, with closer populations being more genetically similar. Both genetic and geographic distances between population pairs are displayed in table 5. We plotted log (genetic distance + 1) by log (geographic distance) in figure 6, and found a significant relationship ($r^2 = 0.416$, $p<0.001$) between genetic and geographic distances.

Figure 6. Log (genetic distance +1) by log (geographic distance) plotted for all pairs of *Chamaecyparis thyoides* populations.



DISCUSSION

Geographic Patterns

The largest proportion (79.84%) of the total allozyme variation was that within populations, a fairly typical result for a wind-pollinated, outcrossing, long-lived tree species (Hamrick and Godt 1990). A significant amount of variation was also attributed to regional differences (15.08%) and differences among populations within regions (5.08%). The Φ_{PT} value of 0.202 is much greater than the comparable F_{ST} value of 0.094 calculated among New Jersey and North Carolina populations by Kuser et al. (1997), probably due to the wider geographic sampling of the present study and the naturally fragmented nature of cedar stands.

Varietal Differences

There do appear to be some differences between *C. thyoides* var. *henryae* and *C. thyoides* var. *thyoides*. For example, allele 1 for the PGM locus is absent from the two *C. thyoides* var. *henryae* populations (region 6, Ward and Clewell 1989), but is present in every *C. thyoides* var. *thyoides* population (regions 1-5). However, this varietal distinction does not account for a significant amount of the total variation, when compared either with (a) other Florida and Mississippi stands (regions 3-5), or (b) all other populations (regions 1-5). Using Little's (1966) more inclusive definition of *C. thyoides* var. *henryae* (regions 3-6), the varietal contrast accounts for 9.83% of the variation. An alternate definition of *C. thyoides* var. *henryae*, which includes both eastern and western Florida panhandle populations (regions 3 and 6) accounted for 10.75% of the total variation within the species. Of course, these two contrasts are confounded with latitudinal effects, representing differences between northern and southern *C. thyoides* populations, and regional variation within this species is known to be large.

Southern populations of *C. thyoides* var. *thyoides* (regions 3-5) clustered more closely with southern *C. thyoides* var. *henryae* populations (region 6) than with *C. thyoides* var. *thyoides* populations from the central (region 2) and northern (region 1) portions of the range. Based on these allozyme data, we conclude that *C. thyoides* var. *henryae* is divergent, but not more so than other regional populations. It is still not clear exactly how this variety should be defined, or if the varietal distinction should be recognized. More detailed analyses within the southern region, will be needed to better address this question.

Glacial Refugium

We found a slight relationship between genetic and geographic distances, but no relationship between expected heterozygosity and latitude, indicating that cedar probably did not migrate slowly northward from a southern refugium. There are at least three other possible scenarios (1) cedar had a means of rapid long distance dispersal, as it moved from a southern refugium to its current distribution, (2) cedar spent the ice age in unglaciated areas off of the Atlantic coast, which are now submerged, or (3) cedar had more than one glacial refugium. Additional sampling of populations throughout other portions of the species range may help to identify cedar's glacial refugium and migration path, following the Wisconsin glaciation.

CONCLUSION

We have presented preliminary allozyme data for 15 cedar populations from the northern, central and southern portions of the range. We found significant regional differentiation among populations. There appear to be slight differences between *C. thyoides* var. *henryae* and *C. thyoides* var. *thyoides*, although the degree of differentiation is not large compared to the degree of regional differentiation. At this time, the appropriate definition of var. *henryae* is not clear. We believe that additional sampling in other areas not included here (i.e. Maryland, North Carolina, South Carolina, Georgia, etc.) will be necessary to adequately assess genetic variation in this species and to possibly identify its glacial refugium and postglacial migration route.

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LITERATURE CITED

Belling, A. J. 1977. Postglacial migration of *Chamaecyparis thyoides* (L.) BSP (southern white cedar) in the northeastern United States. Ph.D. Dissertation. New York University, New York, NY, USA.

Berg, E. E. and J. L. Hamrick. 1997. Quantification of genetic diversity at allozyme loci. Canadian Journal of Forest Research 27:415-424.

Brown, A. H. D. and G. F. Moran. 1981. Isozymes and the genetic resources of forest trees. p. 1-10. *In* M. T. Conkle (technical coordinator) Proceedings of the Symposium on Isozymes of North American Forest Trees and Forest Insects, July 27, 1979, Berkeley, CA, USA. U.S. Forest Service General Technical Report PSW-48. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, USA.

Conkle, M. T. 1992. Genetic diversity – seeing the forest through the trees. New Forests 6:5-22.

Eckert, R. T. 1998. Population genetic analysis of *Chamaecyparis thyoides* in New Hampshire and Maine, USA. p. 171-184. *In* A. D. Laderman (ed.) Coastally Restricted Forests. Oxford University Press, New York, NY.

Excoffier, L., P. E. Smouse, and J. M. Quattro. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA restriction data. Genetics 131:479-491.

Fins, L. and W. J. Libby. 1994. Genetics of Giant Sequioa. p. 65-68. *In* P. S. Aune (technical coordinator) Proceedings of the symposium on Giant Sequoias: their place in the ecosystem and society, June 23-25, 1992, Visalia, CA, USA. U. S. Forest Service General Technical Report PSW-GTR-151. Pacific Southwest Research Station, Albany, CA, USA.

Hamrick, J. L., J. B. Mitton, and Y. B. Linhart. 1981. Levels of genetic variation in trees: influence of life history characteristics. p. 35-41. *In* M. T. Conkle (technical coordinator) Proceedings of the Symposium on Isozymes of North American Forest Trees and Forest Insects, July 27, 1979, Berkeley, CA, USA. U.S. Forest Service General Technical Report PSW-48. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.

Hamrick, J. L. and M. J. W. Godt. 1990. Allozyme diversity in plant species. p.43-63. *In* H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir (eds.) Plant Population Genetics, Breeding, and Genetic Resources. Sinauer Associates Inc. Sunderland, MA, USA.

Hebert, D. N. and M. J. Beaton. 1993. Methodologies for allozyme analysis using cellulose acetate electrophoresis. Helena Laboratories, Beaumont, Texas.

Kuser, J. E., T. R. Meagher, D. L. Sheely, and A. White. 1997. Allozyme frequencies in New Jersey and North Carolina populations of Atlantic white-cedar, *Chamaecyparis thyoides* (Cupressaceae). American Journal of Botany 84:1536-1541.

Ledig, F. T. 1986. Conservation strategies for forest gene resources. Forest Ecology and Management 14:77-90.

Ledig, F. T. 1987. Genetic structure and the conservation of California's endemic and near-endemic conifers. p. 587-594. *In* T. S. Elias (ed.) Conservation and Management of Rare and Endangered Plants. The California Native Plant Society, Sacramento, CA, USA.

Leonardi, S. and P. Menozzi. 1995. Genetic variability of *Fagus sylvatica* L. in Italy: the role of postglacial recolonization. Heredity 75:35-44.

Li, H-L. 1962. A new species of *Chamaecyparis*. Morris Arboretum Bulletin 13:43-46.

Li, P. and W. T. Adams. 1989. Range-wide patterns of allozyme variation in Douglas-fir (*Pseudotsuga menziesii*). Canadian Journal of Forest Research 19:149-161.

Little, E. L. 1966. Varietal transfers in *Cupressus* and *Chamaecyparis*. Madrono 18:161-192.

Little, E. L. 1971. Atlas of United States Trees: Vol. 1. Conifers and Important Hardwoods.USDA Forest Service Miscellaneous Publication No. 1146. Washington, D.C., USA.

Little, S. 1950. Ecology and silviculture of white cedar and associated hardwoods in southern New Jersey. Yale University School of Forestry Bulletin 56:1-103.

Millar, C. I., and K. A. Marshall. 1991. Allozyme variation of Port-Orford-Cedar (*Chamaecyparis lawsoniana*): Implications for genetic conservation. Forest Science 37:1060-1077.

Mitton, J. B., Y. B. Linhart, K. B. Sturgeon, and J. L. Hamrick. 1979. Allozyme polymorphisms detected in mature needle tissue of ponderosa pine. Journal of Heredity 70:86-89.

Morgenstern, E. K. 1996. Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture. UBC Press, Vancouver, Canada.

National Research Council. 1991. Managing Global Genetic Resources: Forest Trees. National Academy Press, Washington, D.C., USA.

Pasteur, N., G. Pasteur, F. Bonhomme, J. Catalan, and J. Britton-Davidian. 1988. Practical Isozyme Genetics. Ellis Horwood Limited, Unwin Brothers, Woking.

Peakall, R., P. E. Smouse, and D. R. Huff. 1995. Evolutionary implications of allozyme and RAPD variation in diploid populations of dioecious buffalograss *Buchloe dactyloides*. Molecular Ecology 4:135-147.

Pielou, E. C. 1991. After the Ice Age: The Return of Life to Glaciated North America. The University of Chicago Press, Chicago, IL, USA.

Ritland C., T. Pape, and K. Ritland. 2001. Genetic structure of yellow cedar (*Chamaecyparis nootkatensis*). Canadian Journal of Botany 79:822-828.

Schnabel, A., J. L. Hamrick, and P. V. Wells. 1993. Influence of Quaternary history on the population genetic structure of Douglas-fir (*Pseudotsuga menziesii*). Canadian Journal of Forest Research 23:1900-1906.

Soltis, D. E., C. H. Haufler, D. C. Darrow, and G. J. Gastony. 1983. Starch gel electrophoresis in ferns: A compilation of grinding buffers, gel and electrode buffers, and staining schedules. American Fern Journal 73:9-27.

Ward, D. B. and A. C. Clewell. 1989. Atlantic white-cedar (*Chamaecyparis thyoides*) in the southern states. Florida Scientist 52:8-47.

Watts, W. A. 1979. Late Quaternary vegetation of central Appalachia and the New Jersey coastal plain. Ecological Monographs 49:427-469.

Wendel, J. F. and N. F. Weeden. 1989. Visualization and interpretation of plant isozymes. p. 5-45. *In* D. E. Soltis and P. S. Soltis (eds.) Isozymes in Plant Biology. Dioscorides Press, Portland, OR.

Whitehead, D. R. 1981. Late-Pleistocene vegetational changes in northeastern North Carolina. Ecological Monographs 51:451-471.

SEED QUALITY AND COMPARISON OF PLANTING TECHNIQUES FOR ATLANTIC WHITE CEDAR AT ARLINGTON ECHO OUTDOOR EDUCATION CENTER, ANNE ARUNDEL COUNTY, MARYLAND

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Abstract: Cedar is a local tree on the Severn and Magothy Rivers in Maryland with a total of nine sites. Recruitment in cedar stands is effected by variation in germination rates due to poor seed quality, insect damage, and variation in embryo dormancy. Reforestation success may depend on the size of the seedling used and where planted within the wetland matrix. Our goal was twofold: 1) to compare the survival of rooted cuttings, seedlings, and freshly harvested cuttings stuck in the ground, and 2) to determine the cause for our low germination rate of 9% with 1997 cedar seed. Rooted cuttings, seedlings, and freshly collected stems were co-planted at thirty-nine plots across environmental gradients including cedar forested wetland, sedge hummocks in scrub-shrub wetland, and seepage slopes at fresh/tidal interfaces. Our greatest survival in planting across an environmental gradient was obtained in cedar forested wetland (62-68%), while the lowest survival occurred on seepage slopes at fresh/tidal interfaces (5-10%). None of the freshly harvested cuttings stuck in the ground survived. We found that 15% of seed produced was good quality while most seed was of poor quality (85%). One of the reasons for the high rate of poor quality seed was insect destruction of the megagametophyte and embryo. A possible source of the low germination rate observed in 1997 Arlington Echo seed may thus be due to insect parasitization.

Key Words: Atlantic white cedar, germination, Severn River

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), is a coastally restricted obligate wetland tree (Laderman 1987). Little (1950) reported the difficulty of regenerating stands of this tree due to variable seed germination rates, herbivore grazing, and competition. Recruitment in cedar stands is also effected by variation in germination rates due to poor seed quality, insect damage, and variation in embryo dormancy (USDA 1974, Laderman 1987).

Cedar is very local on the Severn and Magothy Rivers, Maryland with a total of nine sites (Sheridan et al. 1999). Sheridan et al. (1999) suggested the restoration of these cedar habitats be based on a sound ecological foundation. An essential component of cedar restoration in Maryland is an understanding of the factor(s) controlling fitness. The purpose of this research was to determine the quality of native cedar seed and the survival rate of cedar planted across an environmental gradient at Arlington Echo Outdoor Education Center in Anne Arundel County, Maryland.

METHODS

Site Description

Arlington Echo Outdoor Education Center is located along the Severn River near Annapolis, Maryland. A native stand of cedar occurs along a narrow, unnamed tributary of the Severn River that flows through the Arlington Echo property. Eighty-eight cedar trees have been counted at this site (Sheridan et al. 1999). The cedar occur as individuals or small clumps of trees amongst red maple, *Acer rubrum* L., swamp, in emergent shrub-scrub ecotones, and at the base of toe slope seeps at fresh/tidal interfaces.

Seed Quality

Arlington Echo was visited on October 3, 1998 and an extension pole was used to collect approximately 30 branches bearing cones from a total of seven trees. Boyle and Kuser (1994) found higher fitness of seeds from mature trees and we attempted to harvest from mature trees as much as possible. Cone bearing branches were also collected from four saplings in the marsh edge. Diameter and position of tree within the site were recorded as field notes and hand drawn maps. Branches bearing cones were then removed from trees and both tree and branch numbered for future reference. Cones were only collected from three large trees due to the difficulty of reaching cone-bearing branches, even with a 3-m extension pole. Cedar is self-pruning (personal communication Litton Musselman) and branches are sparse to non-existent in the lower reaches of mature trees.

Seven hundred forty one cones were removed from branches and each cone individually packaged in a labeled #1 coin envelope for drying. Envelopes were placed in the drying oven for 3 days for ease of seed removal following the methods of Boyle and Kuser (1994). Oven temperatures ranged between 35-44^{0}C. Once dried, seeds were manually extracted from cones, counted (5608 seeds), the envelope labeled with the number of seeds, and seeds returned to the envelope. Debris from seed extraction was then discarded.

Once all seeds were counted, one tenth of the seed containing envelopes were randomly selected for each tree (envelopes per tree ranged from 4-20 with a total of 74 envelopes selected) and set aside for seed quality analysis. Remaining seeds were used to determine average weight per seed per tree. Average seed mass was determined by dividing total seed mass by total number of seeds. Seed quality was determined by cutting the seeds open with a razor blade and examining the cross section. Healthy white gametophytic tissue was scored as good quality while brown or shrunken tissue, insect damaged or infested seed, or empty seeds, scored as poor quality. Healthy cross sections were placed in a 0.05% tetrazolium solution to determine viability through color change.

Survival Study

Three different treatments (seedlings, rooted cuttings, and fresh non-rooted cuttings) were used to measure the survival rate of cedar propagules across three environmental gradients at Arlington Echo (cedar forest, sedge hummocks in scrub-shrub wetland, and seepage slopes at the fresh/tidal interface). Cedar naturally grows in all three habitats at the site. All propagules were collected at Arlington Echo.

Propagule Preparation

Seedlings. In Oct. 1997, seed was collected from 17 trees and saplings and stored in envelopes using the methods described above. Seed from each tree was then sowed on the surface of a pre-moistened peat/sand mix in shallow trays measuring 50 cm long, 28 cm wide, and 5 cm deep. Seeds were allowed to stratify outside under a shelter for one month at the Meadowview Biological Research Station (MBRS). Soil moisture was maintained through careful surface watering. Trays were then brought into a greenhouse on 3/25/98 and percent germination measured on 5/11/98. Germinated seedlings were repotted on 6/27/98 into 6 cm pots and placed in bottom-watered beds in full sun. Seedlings were mulched in the fall with pine straw for winter protection and mulch removed the following spring.

Rooted Cuttings. There were 420 cuttings made from the same trees from which seed was collected and ranged in size from 7-15 cm. They were dipped in Rootone®, labeled by tree origin, and placed in moist peat/sand beds under benches in a greenhouse on 10/24/97. Greenhouse temperatures were maintained above freezing through occasional use of a wood stove. Cuttings were potted in late June and early July 1998 and the number of cuttings that rooted was recorded. Potted cuttings were then placed in bottom-watered tanks and placed in full sun. Plants were then mulched in the fall with pine straw for winter protection. Mulch was removed in the spring of 1999.

Fresh Cuttings. Ninty fresh cuttings were taken from a recently toppled cedar tree at Arlington Echo on 5/15/99. Cuttings averaged 28 cm in length and were wrapped in moist newspaper prior to planting on the same day.

Propagule Planting and Data Collection

Forty-five planting sites across the three environmental gradients were selected and flagged on 5/14/99. Seedlings and rooted cuttings were bare rooted on 5/14/99 and placed in a dilute Miracid solution. The average height of seedlings and rooted cuttings was 8 and 23 cm, respectively. Seedlings and cuttings were transported to Arlington Echo on 5/15/99. Each planting site received a total of six implants consisting of pairs of seedlings, rooted cuttings, and fresh cut cedar stems. Survival and growth data was then collected the following year on 3/26/00. Standard deviation was determined for average number of seeds per cone for cedar trees. The average seed mass was also determined.

RESULTS

Seed Quality

Oven drying of seeds was not an effective way to open cedar cones. Many cones had to be manually “cracked” to get all the seeds. There was also an unpredictable rise in oven temperature to 44^0C that could have compromised future seed germination experiments. The average number of seeds per cone ranged from 7 to 9 depending on the tree (table 1).

Tree diameter did not appear to effect the average number of seeds per cone. Average seed mass ranged from 0.597-1.438 mg with an overall average of 0.938 mg (table 2). We obtained a similar average seed mass of 9.4 mg on cedar seed from Arlington Echo in 1997.

Table 1. Average number of seeds per cone for cedar at Arlington Echo

	Tree Number							
	1	2	3	4	5	6	7	Total
Tree Diameter	43.7	44.9	41.3	6.4	1.9	5.0	4.4	
Total Seeds	734	1050	1281	926	277	473	867	5608
# Cones	85	129	198	125	39	60	105	741
Average	9	8	7	7	7	8	8	
Std. Dev.	3.1	3.4	3.4	2.8	2.3	3.1	3.3	

Table 2. Average seed mass for cedar at Arlington Echo

	Tree Number							
	1	2	3	4	5	6	7	Total
# Seeds	659	935	1136	847	252	431	777	5037
Mass (g)	0.481	0.857	0.777	1.046	0.244	0.620	0.464	4.489
Avg. mass (mg)	0.7298	0.9165	0.6839	1.2349	0.9682	1.4385	0.5971	0.9384

Good quality seed (ca. 3 mm in length) ranged from 1-62%, depending on the tree, with an overall average of 15.4% (table 3). There also seemed to be an association between smaller diameter trees and better quality seed. Most seed, however, was of poor quality with an overall average of 84.6%.

Some of the poor quality seeds were also very tiny (less than a millimeter). One of the reasons for the high rate of poor quality seed was possibly due to destruction of the megagametophyte and embryo by an observed larva (possibly the reported parasite of cedar, *Megatigmus thyoides*, personal communication K.O. Summerville). Many poor quality seed

Table 3. Seed quality of cedar at Arlington Echo

		Tree Number							
		1	2	3	4	5	6	7	Total
# Seeds		75	115	145	79	25	42	90	571
Good	#	1	14	8	27	11	26	1	88
Quality	(%)	1.3	12.2	5.5	34.2	44.0	62	1.1	15.4
Poor	#	74	101	137	52	14	16	89	483
Quality	(%)	98.7	87.8	94.5	65.8	56.0	38.0	98.9	84.6

contained tiny frass particles and in many cases the translucent larva was still present. Boyle and Kuser (1994) reported three categories for their poor quality seed (brown or deformed embryos, insect damage, empty). We found it difficult to make the first two distinctions. We were also not satisfied with the accuracy of the tetrazolium test because of the difficulty in properly slicing the seed to expose the embryo. Boyle and Kuser (1994) reported a similar difficulty with tetrazolium test interpretations and instead also relied on other visual aspects of seed quality.

Survival Study

Germination of the 1997 seed used for producing seedlings averaged 9% (range 4-14%) and average seed weight was 0.9 mg. There were 34% of cedar cuttings that rooted in the greenhouse (range 0-68%). When seedlings and rooted cuttings were planted back at Arlington Echo across the three environmental gradients the highest survival was obtained in the cedar forest. Survival was lower in both the scrub-shrub and seepage slopes at the fresh/tidal interface (table 4). None of the fresh cut cedar stems survived in any environmental gradient.

Table 4. Survival (%) of cedar planted at Arlington Echo

	Treatment		
Gradient	Rooted Cuttings	Seedlings	Fresh Cuttings
Cedar Forest (n=8)	62	68	0
Sedge hummocks in scrub-shrub (n=21)	40	42	0
Fresh/tidal interface (n=10)	10	5	0

DISCUSSION

Germination tests with 1997 seed from Arlington Echo involved 17 trees and resulted in an average germination rate of 9% (range 4-14%) and average seed weight of 0.9 mg. This experiment with 1998 seed from 7 trees resulted in the same overall average seed weight and a possible explanation for the low observed germination rate. We originally suspected a high level of inbreeding depression in Arlington Echo cedar because of the limited population size (88 trees). We thought that inbreeding depression was being expressed in seed quality (hence the low germination rate) and that examination of seed would disclose deformed embryos which would support this hypothesis. We did find some deformed seed that suggests a certain amount of inbreeding but do not think inbreeding is the major cause of low germination.

Megastigmus thyoides has been reported as a new pest of cedar (DeBarr personal communication with K.O. Summerville). *Megastigmus* lays its eggs in the seeds of cedar and destruction of seed can exceed 90% (personal communication K.O. Summerville). Potentially the larva observed in Arlington Echo cedar seed is *Megastigmus*. An effort should be made to confirm this identification and determine this species ecological interaction in the cedar ecosystem. No work has been done on the life cycle of *Megastigmus* (personal communication K.O. Summerville).

We think that the source of the low germination rate in 1997 Arlington Echo seed may be principally due to seed destruction by the parasite observed in this study. Although cedar seed can take up to 3 years to germinate (Laderman 1989) the low germination rate with 1997 seed (9%) can largely be explained as the result of poor quality seed (85%) found in this study. Presumably delayed germination phenomena would explain the rest of the difference. Addressing both parasitization and germination enhancement of cedar seed should therefore be a productive field for conservation biologists in the future.

The extreme localization of cedar stands on the western shore of Maryland, and at Arlington Echo in particular, has been an active topic of conversation among Maryland conservation biologists, land managers, and decision makers. Cedar at Arlington Echo survive best in habitats (e.g. cedar forest) where they are currently most abundant. In contrast, survival of cedar at Arlington Echo is lower in habitats where they occur at a lower frequency (e.g. scrub-shrub and seepage slopes at the fresh/tidal interface). Many of the cedar stands on the western shore of Maryland are in a similar landscape position and hydrogeological setting as Arlington Echo. While pollution and sedimentation have reduced the extent of habitat available for cedar on the western shore of Maryland this study demonstrates that their current localization may largely be due to limited appropriate habitat for survival.

LITERATURE CITED

Boyle, E.D. and J.E. Kuser. 1994. Atlantic white-cedar propagation by seed and cuttings in New Jersey. Tree Planters Notes45: 104-111.

Laderman, A.D. 1987. Atlantic white-cedar wetlands. Boulder, CO: West view Press. 401 p.

Laderman, A.D. 1989. The ecology of Atlantic white-cedar wetlands: A community profile. Bill. Rep. 85(7.21). Washington, US Fish and Wildlife Service, National Wetlands Research Center. 144p.

Little, S., Jr. 1950. Ecology and silviculture of whitecedar and associated hardwoods in southern New Jersey. Yale University School of Forestry Bulletin 56. 103 p.

Sheridan, P., R. Cole, J. Broemsera-Cole, R. Kibby, R. Muller, K. Underwood. 1999. A census of Atlantic white-cedar on the western shore of Maryland. Ed. by Theodore Shear and K. O. Summerville. Proceedings: Atlantic white-cedar: ecology and management symposium; 1997 August 6-7; Newport News, VA. Gen. Tech Rep. SRS-27. Asheville, NC: US Dept. of Agriculture, Forest Service, Southern Research Station. Pp. 61-65.

USDA. 1974. Seeds of woody plants in the United States. Ag. Hdbk. No. 450. Washington, DC: USDA Forest Service. 883 p.

ATLANTIC WHITE CEDAR ECOSYSTEM RESTORATION: DARE COUNTY BOMBING RANGE, NORTH CAROLINA

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Abstract: In 1992, the Department of Defense Legacy Resource Management Program provided initial funding to restore approximately 1,214 ha (3,000 ac) of Atlantic white cedar, *Chamaecyparis thyoides* (cedar), ecosystem. Prior to Air Force ownership of the timber rights for this area, the forest had been clearcut during a twenty-year period. Roads built to access the timber resource adversely impacted the hydrologic regime of the area, leaving it in a severely altered condition. The U.S. Air Force formed a collaborative partnership with the Alligator River National Wildlife Refuge, North Carolina Division of Forest Resources, and North Carolina State University. Representatives from these agencies organized a steering committee and developed a strategic plan to accomplish the following: inventory cutover areas and remnant stands, promote and enhance natural regeneration, develop seed and seedling sources, develop and implement artificial regeneration methods, restore previously high-graded stands, increase the presence of cedar on the installation, implement a geographic information system and differential global positioning system, and establish water control and management to restore a more natural hydrologic regime.

Key Words: conservation, sustainable yield, management, partnerships, restoration, enhancement, Legacy, establishment

INTRODUCTION

Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), is a minor but important component of forested wetlands in the coastal plain from Mississippi to Maine (Laderman 1989). The most extensive stands were once found in coastal counties from North Carolina to New Jersey (Laderman 1989). Cedar occurs in both pure stands and in various mixed associations that, depending on the region, include bald cypress, red maple, sweet gum, pond pine, loblolly pine, pitch pine, white pine, swamp black gum, laurel oak, water oak, yellow birch, hemlock, sweet bay, magnolia, loblolly bay, and red bay (Kuser and Zimmerman 1995).

Cedar was once one of the most valuable timber species in North America (Korstian and Brush 1931). The tree can grow to 26 m (85 ft) and greater than 51 cm (20 in) in diameter. The wood is light, strong, aromatic, and resistant to rot. Before the industrial revolution, and well into the twentieth century, cedar was used extensively as the basic raw material in boats, tank stock, posts, framing timbers, pilings, shingles, poles, and siding. Though the economic value for cedar in the manufacture of boats, shingles, and siding remains very high, cedar ecosystems have been reduced to less than 10% of their original distribution before European settlement (Frost 1987). Only scattered, disjunct stands and trees remain. In 1994, The Nature Conservancy listed cedar ecosystems as globally threatened: a reflection of concern for species survivorship, wildlife habitat loss, and wetland protection (Maryland Heritage & Biodiversity Conservation Programs Department of Natural Resources 1994).

The Dare County peninsula, which is bordered by Alligator River, Pamlico, and Croatan Sounds, has a long history of timber activity associated with cedar. Dare Lumber Company harvested cedar here from 1885 until 1930. West Virginia Pulp and Paper Company (WestVaCO) managed the forest resources on the peninsula from 1950 to 1975, establishing extensive road and canal systems. MacMillan Bloedell, Inc. harvested cedar in the area from 1975 to 1985. Alligator Timber Company continued harvesting cedar from 1985 to 1989 (Brown and Atkinson 1999).

CONSERVATION STRATEGIES

Acquisition and Management

At the height of lumbering activities in Dare County in 1964, the U.S. Air Force purchased 18,866 ha (46,620 ac) to establish Dare County Bombing Range, which provides bombing and gunnery training for fighter pilots in the Air Force, Navy, Marine Corps, and Air National Guard. Ordnance delivery and strafing are restricted to two targeted impact areas, which total 809 ha (2,000 ac). The remaining balance of 18,057 ha (44,620 ac) is managed for multiple-use and sustained yield of natural resources using an ecosystem approach. In 1981, the Air Force purchased all available timber rights on Dare County Bombing Range, including extensive tracts of cedar in various condition—a result of prior harvest, wildfire and drainage, coupled with poor natural regeneration.

In 1987, The Nature Conservancy entrusted over 60,703 ha (150,000 ac) of land on Dare County peninsula to the U.S. Fish and Wildlife Service, which created Alligator River National Wildlife Refuge. The refuge boundary completely surrounds Dare County Bombing Range. The resulting contiguous block of federally protected land now exceeds 80,371 ha (198,600 ac). Plant communities in the expanded area include swamp forests, pocosins, cedar and old-growth pond pine forests, fresh and saltwater marshes. Protected animal species include the red-cockaded woodpecker, red wolf, American alligator, and black bear.

Land acquisition and protection strategies of The Nature Conservancy on Dare County peninsula quickly sparked the interest of local researchers and managers, who began meeting in 1988 to share expertise. In 1992, the Department of Defense Legacy Resource Management Program provided multi-year funding authority to initiate a complex and challenging project: Restoration of the Degraded cedar Ecosystems at Dare County Bombing Range. The U.S. Air Force Air Combat Command provided additional funding from Conservation and Forestry programs.

Research Goals and Objectives

Through the Legacy program, the U.S. Air Force formed collaborative partnerships with the Alligator River National Wildlife Refuge, North Carolina Division of Forest Resources, and North Carolina State University. Agency representatives formed a steering committee chaired by the Dare County Bombing Range Forester. The basic premise of the committee was to promote only those activities that would result in cedar establishment. Primary goals of the strategic plan were to review available literature on cedar; to research the local area’s silvicultural history; to inventory cutover areas for natural regeneration; to inventory remnant cedar stands; to develop geographic information and differential global positioning systems; to promote and enhance natural regeneration; to develop seed and seedling sources; to develop and implement artificial regeneration methods; to establish water control and management to restore hydrology; to restore previously high-graded stands; and to establish partnerships for continued outreach and research. The current status of strategic plan goals is reflected in a number of case studies, which are summarized in the following section.

STRATEGIC PLAN HIGHLIGHTS

Inventories

Cutover Areas. Initial plans called for an inventory of 1,214 ha (3,000 ac) of nearly contiguous cutover tracts to determine success or failure of natural regeneration and the level of competing undesirable plant species. The area is almost equally divided by the shared boundary of Dare County Bombing Range and Alligator River National Wildlife Refuge. Bids received from prospective contractors ranged from $110,000 to $2,000,000. After reviewing the proposals, the steering committee decided to use Refuge personnel and interns to accomplish the inventory. Results of the cutover tract inventory indicated that nearly all of the 1,214 ha are suitable for release (Van Druten and Eagle 2000).

Remnant Cedar Stands. In a multi-year study of the growth of cedar on the Dare County Bombing Range, an inventory of remnant cedar stands was also conducted (Daniels 1999). The study determined the growth rate of individual stands on the Range as well as the overall annual growth of cedar on all stands. The data will be used to determine the annual allowable cut and to prepare a comprehensive management plan that will provide for sustained management of cedar on the installation.

Daniels (1999) also determined that the annual gross growth of cedar is approximately 1,433 m^3 of saw timber (607,000 bf) and 2,635 m^3 of pulpwood (727 cords). The total standing volume of cedar is 23,489 m^3 of saw timber (9,953,051 bf) and 39,226 m^3 of pulpwood (10,821 cords). There are 465 ha (1,148 ac) of cedar stands included in the analysis. Based on this hectarage and the volumes estimated, there are an average of 51 m^3 per ha of saw timber (8,670 bf per ac) and 85 m^3 per ha of pulpwood (9.4 cords per ac). There is, however, a wide range in these values between stands. This volume and the associated growth are distributed unevenly across the forest as different stands are growing at different rates and have different starting volumes.

Data Collection and Chronosequencing. In 1997, Christopher Newport University in Virginia began a remote sensing survey of 25 years of cedar clearcutting associated with an inventory of the 1,214 ha (3,000 ac) cutover study area. This survey provided an extensive review of the available literature on cedar. In order to accurately determine the chronological order of clearcuts, research of the local area's silvicultural history was also conducted. Timber inventory maps of Dare peninsula dating to the late 1800's were discovered in a barn in nearby Tyrell County as a result of the research effort and are now archived at the Outer Banks History Museum. Oral histories from surviving WestVaCO foresters were also recorded. The retired foresters reviewed the remote sensing survey for quality assurance of the data interpretation.

GIS and GPS Development. The Range and Refuge staffs are working together to develop a geographic information system (GIS). A global positioning system (GPS) base station has been established to provide accurate maps using differential correction software. GIS and GPS have augmented partnership opportunities through sharing digital databases, equipment, expertise, and volunteer services. A sizeable GIS database has been developed for the Range and Refuge that extends beyond the cedar coverage to include the locations of roads, culverts, and other important attributes. The Air Force provided training for Refuge staff so that both agencies developed their data consistently. Currently, the Air Force is working with the U.S. Geologic Survey to ensure that consistent data collection continues in subsequent inventories and essays.

Hydrologic Restoration

An ongoing hydrologic study involving the U.S. Geologic Survey is assimilating baseline data on water quality and water movement throughout and adjacent to the 1,214 ha (3,000 ac) study area. Long term monitoring will provide valuable information necessary for determining locations of water control structures to establish water management for the restoration of the altered hydrology and ameliorate disturbed wetland functions. The U.S. Army Corps of Engineers provided a Nationwide Permit Number 27 authorizing the installation of 10 culverts with water control structures; five will be installed during the year 2000. Also critical to restoring water controls, is the repair and maintenance of access roads throughout the range. These roads will be surveyed and inventoried for existing culverts, so that water can be effectively managed on a landscape level.

High-Graded Stand Restoration

The Air Force has hired a contractor to prepare a Forest Management Plan for Dare County. Elements of the plan include the following: determining a precise rotation age for cedar; growth data previously collected for cedar and loblolly pine species; determine sustainable harvesting and regeneration goals; and guidelines for restoration of previously high-graded stands.

Regeneration Techniques

Enhancement. North Carolina State University received Legacy funding to investigate interrelationships and effects of soil type, time of year harvest, and subsequent site conditions on natural regeneration. A study released in 1995 concluded that regeneration was more probable on Belhaven and Pungo mucks logged in the winter (Smith 1995). Soil acidity and percent base saturation were good predictors of cedar trees or saplings in both soil types. Hydrology appeared to be more critical to cedar success on Pungo muck soils, where different sediment deposits were found beneath the organic layer. General observations indicated that the presence of *Sphagnum* moss might be linked to the success of cedar. Microrelief also appeared to play an important role in cedar success (Smith 1995).

Cutover areas with a sufficient number of cedar seedlings 1,500 stems per ha (600 stems per ac) were recommended for herbicide treatment to release the seedlings from overtopping vegetation. Wax myrtle and gall berry shrubs are typically the most difficult of the competing plant species to control because of the waxy cuticle covering their leaves. Arsenal has proven to be an effective herbicide on these plants. Working with representatives from American Cyanamid, Dare County Bombing Range was one of three test sites in an effort to add "*release of cedar*" to the Arsenal label. The Environmental Protection Agency approved the new label in August 1995. Thus far, two spraying operations for release of cedar saplings have taken place. A total of 71 ha (175 ac) were sprayed in 1998. In 1999, 139 ha (343 ac) of cedar were released.

Natural Regeneration. Approximately 40 ha (100 ac) of mature (60 years old or more) cedar have been successfully naturally regenerated using clearcutting and seed tree regeneration techniques. Innovative logging methods have been tested in an effort to minimize soil disturbance during harvest operations. Placing the harvester on mats, using dual wheels with large rubber tires mounted on front and back axles of conventional rubber-tire skidders, and constructing corduroy skid trails from timber and logging slash have proven to be very effective in reducing soil disturbance and rutting. Some rutting has purposely been allowed, however, to replicate the microtopographic relief that enhances seed germination and establishment. Merchantable timber in the corduroy skid trails has been extracted upon completion of harvest operations.

Artificial Regeneration. Site preparation methods for artificial regeneration in organic soils that were evaluated included mowing, roller drum chopping, sheering and piling, herbicide applications, and a combination of herbicide and burning. Mowing was determined to be too costly. Physical limitations associated with heavy equipment pulling a roller drum chopper over saturated organic muck soil proved to be too difficult to overcome. Complications encountered while attempting to prescribe burn precluded adequate results for evaluation.

Seed and Seedling Source Development

In the beginning, the lack of available seedlings was the most limiting factor in the effort to restore previously high-graded timber stands. In the mid-to-late 1950s WestVaCO attempted production of cedar seedlings, but was unsuccessful.

The Legacy project funded several U.S. Forest Service Southern Forest Experiment Station research projects in 1993. Improved techniques were developed for extracting, cleaning, germinating, testing, and storing seeds. Soil seed bank tests indicated that cedar seed is viable for at least three years. Preliminary results from a tetrazolium test determined that trees with adequate cross-pollination could yield viable seed at six years of age (Bonner and Summerville 1999).

The Legacy project also supported North Carolina Division of Forest Resources research projects. The North Carolina Division of Forest Resources conducted two studies related to nursery production of cedar. One involved monitoring the effects of soil temperature and sunlight intensity to determine the best cultural practice and soil treatment to enhance seed germination and subsequent growth for bare-root seedling production. The other was a seedling standard evaluation study, which provided information to help guide decisions made by the nursery staff on what is considered to be an acceptable bare root-seedling for artificial regeneration.

In 1993, the North Carolina Division of Forest Resources established a provenance study plot at Dare County Bombing Range. This study helped determine genetic variation of growth, wood structure, and aromatic oil content of trees within local seed sources and between different soil types across the coastal plain of North Carolina. Seedlings were grown from seed extracted from five high quality trees that exhibited superior growth characteristics. The parent trees were found on Range property. Containerized seedlings were planted in peat soil. Other soil types included in the concurrent studies were wet mineral and stream flood plain. The North Carolina Division of Forest Resources began producing seedlings from seed in 1994. To date, 36 ha (90 ac) of cedar have been hand planted.

TECHNOLOGY TRANSFER

Partnerships

Interagency partnerships are dynamic by nature. They require formulating common goals and long range planning to address inherent differences in policies, procedures, and workloads. Regularly scheduled meetings have been effective in addressing issues related to contractual procedures, administrative charges, funding procedures, and fiscal schedules between federal and state governments. A continual, open dialogue has helped to minimize problems and mediate solutions.

The North Carolina Division of Forest Resources, North Carolina State Extension Forestry, U.S. Air Force, U.S. Fish and Wildlife Service, and forest products companies have jointly sponsored field trips and meetings in eastern North Carolina and Virginia to inform the citizens about current management of the cedar resource. The public has shown great appreciation for these forums, which highlighted management and restoration efforts by government agencies, forest industry, and non-industrial private landowners.

Workshops

In August 1995, 80 people attended a cedar Workshop in Washington, North Carolina sponsored by the N.C. Division of Forest Resources. The workshop featured brief presentations of over 24 research and demonstration projects throughout the eastern United States. The workshop culminated with the group committing to formally organize the various efforts of restoring and managing cedar. The North Carolina Division of Forest Resources formally addressed the group and stated that it was prepared to provide personnel and administrative support as a means to continue the efforts presented at the workshop (personal communication S. Adams 1995).

In November 1995, a follow-up planning session was held in Elizabeth City, North Carolina. Twenty-two participants from states along the Atlantic coast from North Carolina to Massachusetts represented universities, federal and state regulatory and resource management agencies, private non-industrial forest landowners, and forest industry. The group outlined a broad scope of management and research issues. There was unanimous agreement that a formal organization dedicated to the promotion of the restoration and management of cedar forest communities was imperative.

Professional Alliances

Soon after the 1995 meetings, the Atlantic White Cedar Alliance was formed. Education, outreach, and research were recognized as the primary missions of the Alliance. The Alliance focuses on both the species and the ecological communities in which it occurs. Both biological and economical facets are studied and promoted, including preservation, restoration, conservation, management, harvesting, and utilization. The organization will collect and disseminate information about the species, and serve as a clearinghouse from which professionals, landowners, and interested citizens can obtain the most current information. Membership is open to anyone interested, and no dues are currently assessed. The merits of organizing as an independent effort or attaching to an existing established organization will continue to be explored. A nine-member interim advisory group was formed to further develop and implement the organization.

Symposia and Conferences

In 1997 Christopher Newport University sponsored a symposium, "Atlantic White Cedar: Ecology and Management," in cooperation with the North Carolina Division of Forest Resources, North Carolina State University Forestry Department Extension and Outreach, and Richard Stockton University of New Jersey. The symposium highlighted opportunities to improve the information base on cedar and associated habitats, restoration, hydrology, soil and site relationships, regeneration, management, and potential for utilization. The U.S. Forest Service Southern Research Station published the proceedings from the symposium in General Technical Report SRS-27. The proceedings can be downloaded from the World Wide Web at http://www.srs.fs.fed.us/pubs/gtr/gtr_srs027.pdf. Richard Stockton University of New Jersey has established a web page to facilitate further dissemination of information related to cedar at http://www.stockton.edu/~wcedars/. Christopher Newport University is organizing a repository of information cedar research at http://www.cnu.edu/cedar/.

Christopher Newport University also produced a compendium, which represents the current body of knowledge associated with cedar restoration efforts on Dare County Bombing Range (Belcher et al. 2000). Research is ongoing and the status of cedar management will be updated regularly through the outreach mechanisms established early in the Legacy project (web sites, newsletters, and so on).

CONCLUSION

The Department of Defense Legacy Resource Management Program project has been a public relations success for the Air Force and all partners involved. New information is constantly being assembled to assist in the recovery and management of the cedar ecosystem. The restoration project has also provided an opportunity for the Air Force to take a proactive role in natural resources management that contributes to a greater cause. Genetic and species preservation, enhanced biological diversity, wetland restoration, and increased aesthetic considerations are just a few of the benefits expected from this innovative Legacy project.

The results of much of the research is currently being applied and the success of cedar restoration efforts on Dare County Bombing Range will depend largely on the continued partnering and exchange of information between all involved parties as new information is assembled and digested.

ACKNOWLEDGEMENTS

The Air Force wishes to thank those partners, researchers, and enthusiasts who contributed to this very innovative and complex project.

LITERATURE CITED

Belcher, R.T., D.A. Brown and R.B. Atkinson (Eds). 2000. Restoration of Atlantic White Cedar Ecosystems at Dare County Bombing Range, North Carolina: A Compendium of Research.

Bonner, F.T. and K.O. Summerville. 1999. Production and Quality of Atlantic White Cedar Seed in Coastal North Carolina.

Brown, D.A. and R.B. Atkinson. This Volume. Interpretation of twenty-five years of Atlantic white cedar clearcutting in North Carolina.

Daniels, S.M. 1999. Report of Findings for the Dare County Range – Atlantic White Cedar Growth Analysis

Frost, C.C. 1987. Historical view of Atlantic White Cedar in the Carolinas. pp. 257-264. in A.D. Laderman, ed. Atlantic White Cedar Wetlands. Westview Press, Boulder, CO.

Korstian, C.F. and W.D. Brush. 1931. Southern White Cedar. U.S. Dept. Agric. Tech. Bull. 2251.

Kuser J.E. and G. Zimmerman. 1995. Restoring Atlantic White Cedar Swamps. A Review of Techniques for Propagation and Establishment. Tree Planting Notes 46 (3):78-85.

Laderman, A.D. 1989. Atlantic White Cedar Wetlands. Westview Press, Boulder, CO.

Maryland Heritage & Biodiversity Conservation Programs Department of Natural Resources. 1994. Rare, Threatened and Endangered Plants of Maryland.

Smith, L.E. 1995. Regeneration of Atlantic White Cedar at the Alligator River National Wildlife Refuge and Dare County Air Force Bombing Range. In Proceedings of Current Developments with Atlantic White-Cedar Management (unpubl). Washington, NC.

Van Druten, B. and T.R. Eagle. 2000. Comprehensive Survey of 3,000 Acres of Atlantic White Cedar Clearcut Tracts on the Dare County Peninsula, North Carolina. IN Belcher, R.T., D.A. Brown and R.B. Atkinson (Eds). 2000. Restoration of Atlantic White Cedar Ecosystems at Dare County Bombing Range, North Carolina: A Compendium of Research

ABSTRACTS

Included here are presentations for which papers were not published in this volume.

EVALUATION OF AEROBIC CARBON DIOXIDE PRODUCTION IN PEAT SOILS OF RESTORED AND NATURALLY REGENERATED ATLANTIC WHITE CEDAR SWAMPS IN SOUTHEASTERN VIRGINIA AND NORTHEASTERN NORTH CAROLINA

BOYLES, STACEY L., Jennifer Garda, Mike D. Harrison, Mark G. Kalnins, Patricia M. Duttry, Robert B. Atkinson, and Gary J. Whiting.

Christopher Newport University.

A significant portion of the global carbon pool is stored in wetland peat soils. These wetland ecosystems act as a carbon sink, which can buffer atmospheric carbon dioxide increases. The restoration of these peat forming wetland ecosystems depends on these soils acting as a carbon sink. The purpose of this study was to evaluate the rate of peat oxidation of Atlantic white cedar (cedar) swamp soils and compare those potential oxidation rates of cedar stands under restoration to those that have naturally regenerated. The restored sites for this project include Pocosin Lakes (PL) located in Northeastern North Carolina and Edge Farm (EF) located in Southeastern Virginia. Naturally regenerated sites for this project include juvenile, intermediate, and mature cedar stands located in Dismal Swamp (DS) in Southeastern Virginia and mature and intermediate stands located in Alligator River National Wildlife Refuge (AR) in Northeastern North Carolina. Three soil cores (30 cm deep), collected from each site, were sampled every ten-centimeter depth interval, placed in a stoppered flask, flushed with air and incubated at 24.5C. Flask headspace was sampled every other day for two weeks. Gases were analyzed on a GC equipped a TCD detector. The carbon dioxide production rates of the mature and intermediate naturally regenerated sites (AR and DS) were significantly greater than (4-5 times) the restored sites (PL and EF). This difference may be related to greater root density and total soil organic content in the naturally regenerated sites as compared to the restores sites.

DECOMPOSITION DYNAMICS WITHIN RESTORED AND NATURALLY REGENERATING ATLANTIC WHITE CEDAR (*CHAMAECYPARIS THYOIDES*) WETLANDS OF THE MID-ATLANTIC COASTAL PLAIN.

CRAWFORD, EDWARD R. and Frank P. Day.

Old Dominion University.

Rates of organic matter accumulation are of paramount importance in Atlantic white cedar (cedar) ecosystem structure and function. A root and leaf litter decomposition study is currently in progress within naturally regenerating and restored cedar wetlands in southeastern Virginia and northeastern North Carolina. The objectives of this study are to evaluate how environmental and substrate quality factors influence above and belowground decay dynamics within cedar wetlands. Root decomposition rates were quantified using vertical litterbags 40 cm long (10 cm pockets) containing preweighed roots inserted into the soil in November 1998. After 150 days, percent mass remaining of native root material was determined within each of three treatments, restored, intermediate and mature. Across the vertical soil profile, percent mass remaining ranged from 75% to 83% in the restored sites and from 83% to 86% in the intermediate and mature sites. Leaf litterbags were deployed at each site in January 1999. After 90 days, percent mass remaining ranged from 87% in the restored sites to 84% in the intermediate sites. Soil pH was monitored monthly within each site. Soils were collected from 4 depth intervals (0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm). Three samples from each depth interval were measured with an Orion® 290 A portable pH meter. Soil pH was higher across the vertical profile in the restored sites (avg. 4.5) compared to the intermediate and mature sites (avg. 3.5). Depth of soil oxidation as measured by the steel rod technique was monitored monthly by placing six 81 cm long uncoated mild steel rods into the soil, retrieving them and recording depth of rust on each rod. The average depth of oxidation (± 1 standard error) was –12.0 cm ± 3.4 for the restored sites, -21.7 cm ± 2.5 for the intermediate aged sites and –22.2 cm ± 1.0 for the mature sites. Within the restored sites, pH was an order of magnitude higher at all depth intervals and depth of oxidation in the rooting zone was dramatically lower than compared to the intermediate and mature sites. In general, belowground mass loss within the restored sites was greater across all depth intervals and decreased with increasing depth. In contrast, leaf litter mass loss was similar across all treatments.

DYNAMICS OF A RARE TREE SPECIES: ATLANTIC WHITE CEDAR AT BROWN MILL POND, NEW HAMPSHIRE.

GENGARELLY, L.M.

University of New Hampshire.

Decline of Atlantic white cedar, *Chamaecyparis thyoides* (cedar), a rare, wetland tree of the eastern coastal United States, may be due to succession in which older cedar stands are replaced by more shade-tolerant trees. My objective was to assess natural cedar regeneration in stands at Brown Mill Pond, Rye, New Hampshire and project future changes in stand structure. Based on aerial photographs and ground reconnaissance, five communities were identified. Age- and size-structure of tree species were examined to infer successional trends. Depth to water table and moisture content were also measured. In all communities, except the pond edge, cedar occurred in even-aged stands (> 90 years old) and successful recruitment was lacking. Patch cuts (0.01 to 0.2 ha) made ca. 40 years ago allowed successful cedar regeneration. Proper establishment conditions at the pond edge community were most likely produced by hydrology. In three communities, arboreal associates will increase as cedar obtains maximum stand age and the canopy breaks up over the next 100 years. Eastern hemlock and red spruce will likely increase in the mixed conifer community, which has the lowest water table. Red maple will co-dominate with cedar in areas with a higher water table, such as the cedar-red maple community. Thus, cedar will not be completely replaced by arboreal associates, as cedar establishment is evident in small forest patch cuts and along the pond edge.

A NEW METHOD FOR REESTABLISHING ATLANTIC WHITE CEDAR SWAMPS: EARLY RESULTS FROM THE GREAT DISMAL SWAMP.

GRAINGER, KIRA N., Bryan Poovey, Jeffrey W. DeBerry, Robert T. Belcher and Robert B. Atkinson.

Christopher Newport University.

The historical range of Atlantic white cedar (cedar) included the eastern coastal plain region from maine to florida and west to Mississippi. As a result of ditching, Intensive harvesting and development, less than 10 % remains. Natural reestablishment of cedar is thought to require fire, and there is no consensus on harvesting methods that would facilitate regeneration, which may mimic this perturbation. The study site was a 2.4-ha cedar stand in the Great Dismal Swamp National Wildlife Refuge that was harvested and then cleared with a kg blade in 1991. We sampled 13 randomly selected 1m^2 plots in the stands during spring 2002. In each plot, the number of cedar seedlings and the height of each seedling were recorded. The stem density averaged 9.6 (sd 5.3) and the average height was 1.4m (sd 0.3). Saplings were taller when stem density was greater, but the trend was not significant ($p < 0.05$). Successful stocking densities for cedar range from 13,000 to 32,000 seedlings per ha, therefore, we conclude that the technique may be used to restore cedar swamps under conditions similar to those in this site. Additional sites should be tested in hopes that restoration of cedar may be achieved within its historic range.

THE EFFECTS OF GEOGRAPHIC ORIGIN, TYPE OF PROPAGULE, AND FERTILIZER APPLICATION ON THE RESTORATION OF ATLANTIC WHITE CEDAR.

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To define the variables affecting the restoration of Atlantic white cedar, *Chamaecyparis thyoides* (cedar), the impacts on growth of (1) geographic origin, (2) the age of the parent tree and the type of propagule, and (3) fertilizer amendment of poor soils, were investigated. Growth was measured as the increase in height and stem diameter during the first two years after planting. No differences were detected between trees from geographically dispersed sites in New Jersey and North Carolina. Seedlings and cuttings (stecklings) from mature parents (25-60 yr. old) grew comparably. From very old (>110 yr.) donor trees, stecklings showed poor vigor, growing the slowest of all trees studied. Although stecklings from juvenile trees grew best in the greenhouse, once outdoors seedlings and stecklings from mature parents, and seedlings from very old parents, grew best. Fresh and decomposed mulches either inhibited or only slightly improved growth and biomass production compared to no-treatment controls. Timed-release inorganic fertilizer increased growth and biomass two-fold over controls. Further stimulation, up to four-fold that without treatment, was achieved by combinations of mulch and fertilizer. Tissue nitrogen, phosphorus and potassium contents followed these trends. Application of these results should increase the probability of success in cedar restorations.

AEROBIC AND ANAEROBIC CO_2 AND CH_4 PRODUCTION POTENTIALS OF LEAF AND ROOT LITTER AT DIFFERENT STAGES OF DECOMPOSITION IN ATLANTIC WHITE CEDAR SWAMPS AND RESTORATION SITES.

HARRISON, MICHAEL D., Edward R. Crawford, Frank P. Day, and Gary J. Whiting.

Christopher Newport University.

Carbon deposition and storage in Atlantic white cedar (cedar) swamps is dependent on both input of carbon via primary production and output through decomposition of organic matter. As dead organic matter (DOM) ages, decomposition rates decrease as the remaining organic carbon becomes refractory. Our goal was to determine the level of microbial activity associated with the decomposition of DOM of different types and ages under controlled laboratory conditions. Field samples were obtained in two mature cedar stands, two intermediate cedar stands, and one cedar restoration site from surface litterbags, containing needles, and subsurface bags containing roots that had been placed in the field 2 months and 1-year prior to collection. Aboveground litter was incubated aerobically and roots were incubated under air and N_2 headspaces at 24°C. Two month-old litter showed three to four times higher rates of production than the year-old litter. Litter CO_2 production was five times greater than root CO_2 production in all sites. Methanogenic activity was only associated with 1-year old roots at the deeper soil depths of the Alligator River NWR sites. This may be related to the consistently higher water tables in these sites. The lack of methane production in the two-month old roots suggests that methanogenic bacteria require more than two months to establish populations large enough to produce detectable methanogenic activity. The different ages of sample materials and differing rates of methane and carbon dioxide production suggest that recent DOM can support a high level of microbial activity that possibly utilizes available non-structural carbohydrates. As decomposition proceeds, the initial microbial activity slows as substrate availability decreases with complex carbohydrates and lignin becoming a greater portion of the remaining DOM.

CONTRIBUTION OF ROOT RESPIRATION TO SURFACE CO_2 EMISSIONS WITHIN ATLANTIC WHITE CEDAR SWAMPS IN NORTH CAROLINA AND VIRGINIA.

KALNINS, MARK G., Melissa J. Kessler, & Gary J. Whiting.

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Significant carbon reservoirs exist within soils of Atlantic white cedar (cedar) forested wetlands. The transfer of carbon to this reservoir is tightly coupled to formation of above and below-ground litter. The transformation of litter carbon to dissolved organics and gaseous CO_2 is primarily microbially mediated. The direct *in situ* measurement of CO_2 loss from cedar peat soils is confounded by the addition of CO_2 originating from autotrophic root respiration. An *in situ* experiment was designed to detect both seasonal and diurnal heterotrophic (microbial communities) and autotrophic (roots) respiratory activity over a 1 year period within cedar swamps in Alligator River (ARNWR) and Great Dismal Swamp (GDSNWR) National Wildlife Refuges in North Carolina and Virginia. Live root respiration (RR) was eliminated from peat surface CO_2 emissions by establishing 9 m^2 trenched plots.

Surface emissions were measured monthly within RR-free trenched plots and adjacent non-trenched reference plots. RR-free plots in ARNWR, which were characterized by persistent inundation, consistently showed 25-40% lower surface emissions than adjacent reference plots. RR-free plots in DSNWR, with a lower water table position, showed less of a reduction in surface emissions as compared to reference plots. These results suggest that roots are responsible for 20-50% of total surface emissions in ARNWR and 0-15% in DSNWR. Estimates of root respiration provide a means of calculating carbon loss from the heterotrophic soil community, and are therefore necessary for construction of site-specific soil carbon budgets. We suggest that the development of a soil carbon budget should be considered when developing criteria for successful establishment of cedar swamps.

FACTORS INFLUENCING SEASONAL SOIL TEMPERATURE CHARACTERISTICS OF EIGHT *CHAMAECYPARIS THYOIDES* WETLAND SITES IN VIRGINIA AND NORTH CAROLINA.

KESSLER, MELISSA J., Mark G. Kalnins, and Gary J. Whiting.

Christopher Newport University.

Soil temperature affects many biological processes in forested wetland systems. Those especially important to carbon cycling include plant growth, soil respiration rates, and microbial processes. Many factors can influence soil temperature, such as vegetative cover, local climate, soil structure, and soil moisture. A disturbance (logging) can have a significant effect on these variables. We characterized soil temperature in a chronosequence of natural *Chamaecyparis thyoides* (L.) B.S.P. forested wetlands and mitigation bank sites. Temperature was related to site history, soil moisture, soil organic matter content, soil bulk density, and vegetative cover. Soil temperatures (10cm) were monitored by continuous data loggers for 18-months, beginning in September 1998. During that time, soil moisture and depth to water table was measured monthly. Soil temperature differences among sites were related to light energy received at soil surface; sites with lowest vegetative cover have highest average soil temperature. Average diurnal temperature range was also greater in these sites. Higher water tables and lower bulk densities were found to buffer soil temperature change. Mature stands demonstrated cooler soil temperatures, and appeared to be relatively insulated from temperature change due to unseasonably warm or cool days. We suggest that seasonal and daily variation of soil temperature may be used as an easily measured environmental indicator of recovery from disturbance.

COMPREHENSIVE SURVEY OF 3,000 ACRES OF ATLANTIC WHITE CEDAR, *CHAMAECYPARIS THYOIDES* (L.) B.S.P., CLEARCUT TRACTS ON THE DARE COUNTY PENINSULA, NORTH CAROLINA

VAN DRUTEN, B.M. and T.R. Eagle Jr.

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The purpose of this study was to perform extensive regeneration surveys on 3,000 acres of land held by the U.S. Air Force Dare County Bombing Range and Alligator River National Wildlife Refuge on the Dare County Peninsula. In 1992, a cooperative project was initiated by the Alligator River National Wildlife Refuge, U.S. Air Force Dare County Range, North Carolina State University, and North Carolina Division of Forest Resources to oversee the restoration of Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P. (cedar), in clearcut tracts that were at one time mature cedar stands. The status of natural regeneration occurring in the 3,000 acres of clearcut tracts identified for this project was evaluated from 1995 to 1997. Results show that there is tremendous variability within and between stands in relation to stocking levels of cedar seedlings and the amount of competition. There is an abundance of stands (35 stands, or 78%) that have adequate levels of natural regeneration, but there is severe growth inhibition in 34 of these 35 stands. A key inhibitor of the natural regeneration of cedar stands seems to be the high level of shrub competition that exists in these clearcut tracts. Chemical release of cedar from particularly high levels of shrub competition through the application of Arsenal7® may allow it to grow freely in stands with adequate natural regeneration levels. This must be incorporated with modifications of the hydrologic regime, which has been altered by the construction of roads**,** in order for the cedar to regenerate in pure stands.

POSTER ABSTRACTS

THE USE OF ATLANTIC WHITE CEDAR, *CHAMAECYPARIS THYOIDES* (L.) B.S.P., IN WETLAND BONSAI.

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Bonsai is a method of cultivating a plant by artificially restricting its growth. This limitation of growth results in an aesthetically pleasing miniature version of the organism. We were interested in expanding the horticultural use of Atlantic white cedar (cedar) and felt that bonsai offered that opportunity. We have observed natural cedar hummocks containing such desirable associate plants as *Sarracenia*, *Drosera*, *Utricularia*, and *Sphagnum* moss. In many cases these hummocks represented natural bonsai. We are successfully duplicating this environment and are testing the market response to this product.

FINE ROOT PRODUCTION AND TURNOVER IN NATURALLY-RECOVERING AND CREATED ATLANTIC WHITE CEDAR (*CHAMAECYPARIS THYOIDES*) WETLANDS.

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Ecologically-based management and restoration practices for Atlantic white cedar (cedar) wetlands have recently focused on peat accumulation and system-level carbon cycling as critical ecosystem functions in the maintenance of this threatened community type. Fine root dynamics play an important yet little-studied role in organic matter production in forested wetlands. Using minirhizotrons, fine root dynamics are being quantified for naturally-recovering stands (mature, intermediate, and young age classes) and for two mitigation sites with cedar plantings (4-6 years since planting) in Virginia and North Carolina, USA. Minirhizotrons are clear butyrate cylinders that are inserted into the soil in order to observe fine roots in situ. A microvideo camera is lowered into the minirhizotrons to record images of roots growing along the outer surface. Images of roots are digitized in order to catalog individual root length/width measurements as well as various attribute data (e.g., root color, presence of mycorrhizae). The ability to repeatedly observe roots in situ with minimal disturbance to roots and soil offers many advantages over other methods of root measurement. Indices of root production and mortality as well as rates of root elongation can be directly measured at the individual root level. In addition, tracking root cohorts allows for detailed insight into root phenologies in the field setting. Images of fine roots are sampled on 45-day intervals to a depth of 64 cm. Root length densities (RLD) changed little in mature and intermediate sites but fluctuated in young and mitigation sites during the initial 266-day sampling period. By April 1999, mean RLD was greatest in mature sites (5.2 mm/cm^2) and similar in intermediate, young and mitigation sites (3.7, 3.9, and 4.5 mm/cm^2, respectively). Differences were observed between mitigation and naturally-recovering sites in root length production and mortality. While production was highest in mitigation sites, mortality equaled production, suggesting differences in turnover rates

and fine root contributions to soil organic matter in mitigation sites. Fine root biomass obtained from cores is being used to assess the applicability of minirhizotrons to community-level root biomass estimation.

EFFECT OF DROUGHT CONDITIONS ON THE PHOTOSYNTHETIC RATE OF ATLANTIC WHITE CEDAR.

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The negative effect of drought conditions on restoration of Atlantic white cedar, *Chamaecyparis thyoides* (L.)B.S.P., has been documented. Through greenhouse experiments the effect of induced drought on white cedar photosynthetic rate was measured with a Ciras-1 portable photosynthesis system using an automated control system cuvette. Sixteen rooted white cedar cuttings were planted in a large plastic tub. Photosynthesis was measured prior to the outset of drought, and then at 8,15, 22, 29, and 35 days of drought (no water) conditions. At each time period photosynthesis was measured on 8 plants at three light levels: 50, 1000, and 2000 μmoles photons m^{-2} s^{-1}. Stomatal conductance and evapotranspiration were also measured. Leaf areas were estimated by tracing the leaf in the cuvette, and calculating from the scanned image. Multivariate analyses and data contrast transformation were used in data interpretation. In repeated time analysis, the Wilk's Lambda statistic was highly significant for the time effect (p=0.0001), but the interaction between time and light was not significant. Light effected photosynthetic rate when averaged over all time periods (p=0.001). The contrast transformation found mean photosynthetic rates after 22, 29, and 35 days of drought were significantly different (p=0.001) from the pre-drought (control) photosynthetic rate. Mean photosynthetic rates after 8 and 15 days of drought were not significantly different from the pre-drought level.

BIBLIOGRAPHY

Adams, J.M., H. Faure, L. Faure-Denard, J.M. McGlade, and F.I. Woodward. 1990. Increases in terrestrial carbon storage from the last glacial maximum to the present. Nature 348(20): 711-714.

Akerman, A. 1923. The white cedar of the Dismal Swamp. Virginia Forestry Publication 30: 1-21.

Amador, J.A. and R.D. Jones. 1995. Carbon mineralization in pristine and phosphorus-enriched peat soils of the Florida Everglades. Soil Science 159 (2): 129-141.

Amador, J.A. and R.D. Jones. 1997. Response of carbon mineralization to combined changes in soil moisture and carbon-phosphorous ratio in a low phosphorous histosol. Soil Science 162(4): 275-282.

Andrejko, M.J., F. Feine, and A.D. Cohen. 1983. Comparison of ashing techniques for determination of the inorganic contents of peats. p 5-20 IN P.M. Jarrett (Ed.). Testing of peats and organic soils. ASTM STP 820. American Society for Testing and Materials.

Armentano, T.V. and E.S. Menges. 1986. Patterns of change in the carbon balance of organic soil-wetlands of the temperate zone. Journal of Ecology. 74: 755-774.

Armstrong, W. 1967. The oxidizing activity of roots in waterlogged soils. Physiologica Plantarium 20: 920-926.

Arseneault, D. and S. Payette. 1997. Reconstruction of millennial forest dynamics from tree remains in a sub-arctic tree line peatland. Ecology 78(6): 1873-1883.

Ash, A.N., C.B. Mcdonald, E.S. Kane, and C.A. Pories. 1983. Natural and modified pocosins: literature synthesis and management options. 156. U.S. Fish and Wildlife Service, Division of Biological Services, Washington, D.C., U.S. Fish and Wildlife Service.

Ashe, W.W. 1894. The forests, forest lands, and forest products of eastern North Carolina. Raleigh, North Carolina, Josephus Daniels, state printer and binder, presses of E.M. Uzzell.

Ashton, R.E., Jr. 1981. Interpretation of pocosins in North Carolina: The state of the art. Richardson, C.J. (Ed.) Pocosin Wetlands. 183-195. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Atkinson, R.B. 2001. Final Report: Atlantic White Cedar Swamp Restoration: Monitoring Ecosystem Services and Self-Maintenance. Grant Number R825799, US EPA National Center for Environmental Research. Christopher Newport University, Newport News, Virginia 23606. Unpublished Final Report.

Atkinson R.B. and J. Cairns Jr. 1994. Possible use of wetlands in ecological restoration of surface mined lands. Journal of Aquatic Ecosystem Health 3: 139-144.

Atkinson, R.B. and J. Cairns, Jr. 2001. Plant decomposition and litter accumulation in depressional wetlands: Functional performance of two wetland age classes that were created via excavation. Wetlands 21(3): 354-362.

Atkinson, R.B., J.E. Perry, and J. Cairns, Jr. In Review. Vegetation communities of 20-year old created depressional wetlands.

Atkinson, R. B., W. L. Daniels, and J. Cairns, Jr. 1998. Hydric soil development in depressional wetlands: A case study from surface mined landscapes. p. 182-197. In S.K. Majumdar, E.W. Miller, and F.J. Brenner (Eds.) Ecology of Wetlands and Associated Habitats. Pennsylvania Academy of Science, Philadelphia, PA.

Atkinson, R.B., J.E. Perry, E.P. Smith, and J. Cairns, Jr. 1993. Use of constructed wetland delineation and weighted averages as a component of assessment. Wetlands 13(2): 185-193.

Baines, R.A. ND. Prospects for white cedar: a North Carolina assessment. FOREM. School of Forestry and Environmental Studies. Duke University. North Carolina 8-11.

Baines, R.A. ND. Silviculture of Atlantic white cedar (*Chamaecyparis thyoides*). Unpubl.

Bakker, S.A., C. Jasperse, and J.T.A. Verhoeven. 1997. Accumulation rates of organic matter associated with different successional stages from open water to carr forest in former tributaries. Plant Ecology 129: 113-120.

Baldwin, H.I. 1961. Further notes on *Chamaecyparis thyoides* in New Hampshire. Rhodora 63: 281-285.

Bandle, B.J. and F.P. Day, Jr. 1985. Influence of species, season, and soil on foliar macronutrients in the Great Dismal Swamp. Bul. of the Torrey Botanical Club 112: 146-157.

Barnes, J.S. 1981. Agricultural adaptability of wet soils of the North Carolina coastal plain. Richardson, C.J. (Ed.) Pocosin Wetlands. 225-237. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Barnes, P.W., W. Beyschlag, R. Ryel, S.D. Flint, and M.M. Caldwell. 1990. Plant competition for light analyzed with a multi-species canopy model. Oecologia 82: 560-566.

Barry, W.J., A.S. Garlo, and C.A. Wood. 1996. Duplicating the mound-and-pool microtopography of forested wetlands. Restoration and Management Notes 14: 15-21.

Bartlett, H.H. 1909. The submarine C*hamaecyparis* bog at Woods Hole, Massachusetts. The New England Botanical Club 11: 221-235.

Baskerville, G.L. 1972. Use of logarithmic regression in the estimation of plant biomass. Canadian Journal of Forest Research 2: 49-53.

Bay, R.R. 1967. Ground water and vegetation in two peat bogs in northern Minnesota. Ecology 48(2): 308-310.

Beck, AF, Garnett WJ. 1983. Distribution and notes on the Great Dismal Swamp population of *Mitoura hesseli* Rawson and Ziegler (Lycaenidae). Journal of the Lepidopterists Society 37: 289-300.

Belling, A.J. 1987. A comparison of morphological characteristics of *Chamaecyparis thyoides, Thuja occidentalis, and Juniperus virginiana.* Laderman, A. (Ed.) Atlantic White Cedar Wetlands.

Belling, A.J. 1987. Postglacial history of Atlantic white cedar in the northeastern United States (abstract). 191.

Benner, R.M., A. Moran, and R.E. Hodson. 1985. Effects of pH and plant source on lignocellulose biodegradation rates in two wetland ecosystems, the Okeefenokee Swamp and a Georgia salt marsh. Limnology and Oceanography 30: 498-499.

Benner, R., A.E. Maccubbin, and R.E. Hodson. 1984. Anaerobic biodegradation of the lignin and polysaccharide components of lignocellulose and synthetic lignin by sediment microflora. Applied and Environmental Microbiology. 47(5): 998-1004.

Berg, B. 2000. Litter decomposition and organic matter turnover in northern forest soils. Forest Ecology and Management 133: 13-22.

Berkeley, E. and D. Berkeley. 1976. Man and the Great Dismal. Virginia Journal of Science 27: 141-171.

Bianchetti, A., R.C. Kellison, and K.O. Summerville. N.D. Seed dormancy and germination of Atlantic white cedar (*Chamaecyparis thyoides*). Unpubl. abstract.

Bianchetti, A., R.C. Kellison, and K.O. Summerville. 1994. Substrate and temperature tests for germination of Atlantic white cedar seeds. Tree Planters Notes 45: 125-127.

Biondi, F. 1999. Comparing tree-ring chronologiesand repeated timber inventories as forest monitoring tools. Ecological Applications 9(1): 216-227.

Bloom, A.L. 1971. Glacial eustatic and isostatic controls of sea level since the last glaciation. *In* K.K. Turekian (Ed.) The late Cenozoic glacial ages. Yale University Press, New Haven, Connecticut, pp. 355-379.

Boelter, D.H. 1966. Hydrological characteristics of organic soils in lake states watersheds. Journal of Soil and Water Conservation. p 50-53.

Bonner, F. N.D. Seed conditioning and seed quality of Atlantic white cedar. Unpubl. abstract.

Bormann, B.T. 1990. Diameter-based regression models ignore large sapwood-related variation in Sitka spruce. Canadian Journal of Forest Research 20: 1098-1104.

Bosatta, E. and other. 1991. Dynamics of carbon and nitrogen in the organic matter of the soil: a general theory. The American Naturalist. 138(1): 227-245.

Boyle E.D. and J.E. Kuser. 1994. Atlantic white-cedar propagation by seed and cuttings in New Jersey. Tree Planters Notes 45: 104-111.

Braun-Blanquet J, Pavilliard J. 1930. Vocabulary of Plant Sociology. Cambridge, Massachusetts, Cambridge Botany School.

Bricker-Urso, S., S.W. Nixon, J.K. Cochran, D.J. Hirschberg, and C. Hunt. 1989. Accretion rates and sediment accumulation in Rhode Island salt marshes. Estuaries 12(4): 300-317.

Bridgham, S.D. 1991. Mechanisms controlling soil carbon cycling in North Carolina peatlands. Ph.D. dissertation. School of Forestry and Environmental Studies, Duke University. 230 pp.

Bridgham, S.D., C.J. Richardson, E. Maltby, and S.P. Faulkner. 1991. Cellulose decay in natural and disturbed peatlands in North Carolina. Journal of Environmental Quality 20: 695-701.

Bridgham, S.D. and C.J. Richardson. 1992. Mechanisms controlling soil respiration (CO_2 and CH_4) in Southern peatlands. Soil Biology and Biochemistry 24(11): 1089-1099.

Bridgham, S.D. and C.J. Richardson. 1993. Hydrology and nutrient gradients in North Carolina peatlands. Wetlands 13(3): 207-218.

Bridgham, S.D., J. Pastor, J.A. Janssens, C. Chapin, and T.J. Malterer. 1996. Multiple limiting gradients in peatlands: a call for a new paradigm. Wetlands 16(1): 45-65.

Brinson, M.M. 1991. Landscape properties of pocosins and associated wetlands. Wetlands 11: 441-465.

Brinson, M.M., A.E. Lugo, and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Annual Rev. Ecol. Syst. 12: 123-161

Brinson, M.M., H.D. Bradshaw, and E.S. Kane. 1984. Nutrient assimilative capacity of an alluvial floodplain swamp. Journal of Applied Ecology 21: 1041-1057.

Broadbent, F.E. 1960. Factors influencing the decomposition of organic soils of the California delta. Hilgardia 29(13): 587-612.

Brower D.J. and other. 1981. The formulation of a management plan for pocosins in coastal North Carolina. Richardson, C.J. (Ed.) Pocosin Wetlands. 318-333. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Brown, A., S.P. Mathur, T. Kauri, and D.J. Kushner. 1988. Measurement and significance of cellulose in peat soils. Canadian Journal of Soil Science 68: 681-685.

Brown, D.A. 1999. Analysis and restoration of Atlantic white cedar (*Chamaecyparis thyoides* (L.)B.S.P.) ecosystems in southeastern Virginia. Masters Thesis, Christopher Newport University.

Brown, D.A. and R.B. Atkinson. 1999. Assessing the survivability and growth of Atlantic white cedar (*Chamaecyparis thyoides* (L.) B.S.P.) in the Great Dismal Swamp National Wildlife Refuge. Atlantic white-cedar ecology and management symposium. Asheville, NC, U.S. Department of Agriculture, Forest Service, Southern Research Station.

Brown, J.K. 1976. Estimating shrub biomass from basal diameters. Canadian Journal of Forest Research 6: 153-158.

Brown S., P.Schroeder, and R. Birdsey. 1997. Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. Forest Ecology and Management 96: 37-47.

Brown, S.L. 1978. A comparison of cypress ecosystems in the landscape of Florida. Dissertation, University of Florida.

Brown, S.L. 1981. A comparison of the structure, primary productivity, and transpiration of cypress ecosystems in Florida. Ecological Monographs 51(4): 403-427.

Brownlie, D.J. ND. Atlantic White Cedar (*Chamaecyparis thyoides)* Natural Regeneration at the Great Dismal Swamp National Wildlife Refuge, Suffolk, VA. 2.

Bruce, J.P., M. Frome, E. Haites, H. Janzen, L.Pattan, and K. Paustian. 1999. Carbon sequestration in soils. Journal of Soil and Water Conservation 1999(1): 382-389.

Brush, W.D. 1947. Knowing your trees: Atlantic white cedar (L.) Britton, Sterns, and Poggenberg. Amer. For. 53(5): 218.

Buell, M.F. 1970. Time origin of New Jersey Pine Barrens bogs. Bull. of the Torrey Bot. Club 97(2): 105-108.

Buell, M.F. and R.L. Cain. 1943. The successional role of southern white cedar, *Chamaecyparis thyoides,* in southeastern North Carolina. Ecology 24, 85-93.

Cairns, J. Jr. and K.L. Dickson. 1972. An ecosystematic study of the South River, Virginia. Bulletin 54. Blacksburg, VA, VPISU.

Cameron, C.C., J.S. Esterle, and C.A. Palmer. 1989. The geology, botany and chemistry of selected peat-forming environments from temperate and tropical latitudes. International Journal of Coal Geology 12: 105-156.

Campbell, R.G. and J.H. Hughes. 1991. Impact of forestry operations on pocosins and associated wetlands. Wetlands 11: 467-479.

Campbell, J.S., V.J. Lieffers, E.C. Pielou. 1985. Regression equations for estimating single tree biomass of trembling aspen: assessing their applicability to more than one population. Forest Ecology Management 11: 283-295.

Campbell R.G. and J.H. Hughes. 1981. Forest management systems in North Carolina pocosins: Weyerhaeuser. Richardson, C.J. (Ed.) Pocosin Wetlands. 199-213. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Campbell, R.N. Jr. and C.J. Richardson. 1981. Pocosin Wetlands. 215-224. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Canfield, R.H. Application of the line interception method in sampling range vegetation. Journal of Forestry 388-394.

Carter A.R. 1987. Cedar restoration in the Dismal Swamp of Virginia and North Carolina. A. D. Laderman. Atlantic White Cedar. 323-325. Boulder, CO, Westview Press.

Carter, V. 1979. Remote sensing applications to the Dismal Swamp. Kirk, P.W. Jr. (Ed.) The Great Dismal Swamp. 80-100. Charlottesville, VA, University Press.

Carter, V. 1986. An overview of the hydrologic concerns related to wetlands in the United States. Canadian Journal of Botany 64: 364-374.

Chickering, J.W. 1873. The flora of the Dismal Swamp. The American Midland Naturalist 7(9): 521-524.

Christensen, N.L., R.B. Burchell, A. Liggett, E.L. Simms, and others. 1981. The structure and development of pocosin vegetation. P. 43-61 IN Richardson, C.J. (Ed.) Pocosin Wetlands. Hutchinson Ross Publ. Co., Stroudsburg, PA.

Clark, A., T. Cunia, V.J. LaBau, and E.H. Wharton. 1987. Estimating tree biomass regressions and their error. (abstract). NE-GTR-117.

Clark, M.K., D.S. Lee, and J.B. Funderburg, Jr. 1985. The mammal fauna of carolina bays, pocosins, and associated communities in North Carolina: an overview. Brimleyana 11: 1-38.

Clewell, A.F. and R. Lea. 1990. Creation and restoration of forested wetland vegetation in the southeastern United States. J.A. Kusler and M. E. Kentula (Eds.). Wetland creation and restoration: the status of the science. Regional review. 195-231. Washington, DC, Island Press.

Clewell, A.F. 1981. Natural setting and vegetation of the Florida panhandle: An account of the environments and plant communities of Northern Florida west of the Suwanee River. Mobile Alabama, U.S, Army Corps of Engineers.

Clewell, A.F. and D.B. Ward. 1989. White Cedar in Florida and along the northern Gulf Coast. 69-81. A. Laderman (Ed.). Atlantic White Cedar Wetlands. Westview Press, Boulder, CO.

Clymo, R.S. Ion exchange in *Sphagnum* and its relation to bog ecology. Annals of Botany, N.S. 27: 309-324.

Clymo, R.S. 1983. Peat. In: Goodall, D.W. (ed.). Ecosystems of the World Volume 4. Gore, A.J.P. (ed.). Mires: Swamp, bog, fen and moor-general structure. New York. Elsevier Scientific Publ. Co. p. 159-224.

Cocke, E.C., I.F. Lewis, and R. Patrick. 1934. A further study of Dismal Swamp peat. American Journal of Botany 21: 374-395.

Collins, E.A., C.D. Monk, and R.H. Sherman. 1964. White cedar stands in northern Florida. Quart. Jour. Florida Acad. Sci. 27: 107-110.

Collins, M.E., G.W. Schellentrager, J.A. Doolittle, and S.F. Shih. 1986. Using ground-penetrating radar to study changes in soil map unit composition in selected Histosols. Soil Science Society of America Journal 50:408-412.

Comeau, P.G., T.F. Braumandl, and C.Y. Xie. 1993. Effects of overtopping vegetation on light availability and growth of Engelmann spruce seedlings. Can. J. For. Res. (23): 2044-2048.

Conner, W.H. and J.W. Day. 1982. The ecology of forested wetlands in the southeastern United States. Gopal, B. et al. (Eds.) Wetlands: Ecology and Management. 69-87. Jaipur, India, National Institute of Ecology and International Scientific Publ..

Conner, W.H. and J.W. Day, Jr. 1976. Productivity and composition of a bald cypress-water tupelo site and a bottomland hardwood site in a Louisiana swamp. American Journal of Botany 63: 1354-1364.

Conner, W.H., J.G. Gosselink, and R.T. Parrondo. 1981. Comparison of the vegetation of three Louisiana swamp sites with different flooding regimes. American Journal of Botany 68: 320-331.

Cooper, A.W. 1981. A policy for pocosin preservation. Richardson, C.J. (Ed.) Pocosin Wetlands. 334-341. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Copeland, B.J., R.G. Hodson, S.R. Riggs, and J.E. Easley, Jr. The Ecology of Albemarle Sound, North Carolina: an estuarine profile. Washington, D.C.: U.S, Fish and Wildlife Service, Division of Biological Services.

Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRoe. 1979. Classification of wetland and deepwater habitats of the United States. U. S. Fish and Wildlife Service, FWS/OBS-79/31.

Craft, C.B. and C.J. Richardson. 1998. Recent and long-term organic soil accretion and nutrient accumulation in the Everglades. Soil Science Society of America Journal 62:834-843.

Craft, C.B., J. Reader, J.N. Sacco, and S.W. Broome. Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. Ecological Applications

Crawford, R.L. 1981. Lignin biodegradation and transformations. John Wiley and Sons, Inc. New York, 154 pp.

Dabel C.V. and F.P. Day, Jr. 1977. Structural comparisons of four plant communities in the Great Dismal Swamp, Virginia. Bulletin of the Torrey Botanical Club 104(4): 352-360.

Dana, S.T. (ed.) 1945. Cutting Practices for the Carolinas: Report of Cutting Practices Committee, Appalachian Section, Society of American Foresters. Journal of Forestry.

Daniel, III., C.C. 1981. Hydrology, geology, and soils of pocosins: A comparison of natural and altered systems. Richardson, C.J. (Ed.) Pocosin Wetlands. 69-108. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Davidson, E.A. and P.A. Lefebvre. 1993. Estimating regional carbon stocks and spatially covarying edaphic factors using soil maps at three scales.

Davis, K.N., S.M. Daniels. 1997. Inventory of Atlantic white-cedar remnant stands in North Carolina. Goldsboro, North Carolina: Seymour Johnson Air Force Base.

Day F.P. and C.V.Dabel. 1978. Phytomass budgets for the Dismal Swamp ecosystem. Virginia Journal of Science 29: 220-224.

Day, F.P. Jr. 1979. Litter accumulation in four plant communities in the Dismal Swamp, Virginia. American Midland Naturalist 102(2): 281-289.

Day, F.P. Jr. 1982. Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63(3): 670-678.

Day, F.P. Jr. 1987. Production and decay in a *Chamaecyparis thyoides* swamp in Southeastern Virginia. Laderman, A.D. (Ed.) Atlantic white cedar wetlands.

Dean, G.W. 1969. Forests and forestry in the Dismal Swamp. The Virginia Journal of Science 20: 166-173.

DeBerry J.W. 2000. A comparison of aboveground structure in four Atlantic white cedar, *Chamaecyparis thyoides* (L.) B.S.P., swamps. Masters Thesis, Christopher Newport University, Newport News, VA.

Deevey, E.S. 1949. Biogeography of the Pleistocene: Part I: Europe and North America. Bulletin of the Geological Society of America 60: 1316-1416.

Delcourt, P.A. and H.R. Delacourt. 1977. The Tunica Hills, Louisiana-Mississippi: Late glacial locality for spruce and deciduous forest species. Quaternary Research 7: 218-237.

DeLaune, R.D., J.H. Whitcomb, W.H. Patrick, Jr., J.H. Pardue, and S.R. Pezeshki. 1989. Accretion and canal impacts in a rapidly subsiding wetland. I. ^{137}Cs and ^{210}Pb techniques. Estuaries 12(4): 247-259.

Delcourt, P.A. and H.R. Delcourt. 1977. The Tunica Hills, Louisiana Mississippi: late glacial locality for spruce and deciduous forest species. Quaternary Research 7: 218-237.

Dickerman, J.A., A.J. Stewart, and R.G. Wetzel. 1986. Estimates of annual aboveground production: sensitivity to sampling frequency. Ecology 67(3): 650-659.

Dill and others. 1987. Atlantic white cedar on the Delmarva Peninsula., pp. 41-51.

Dolman, J.D. and S.W. Buol. 1967. A Study of organic soils (histosols) in the tidewater region of North Carolina. North Carolina: Agricultural Experiment Station.

Dolme. 1981. Primary production and seasonal aspects of emergent plants in a tidal freshwater marsh. Estuaries 4(2): 139-142.

Donnette, R.L. and A.D. Laderman. 1998. Coastal forest management and research. Pages 306-316 in A. Laderman (Ed.) Coastally Restricted Forests.

Drenner, R.W. and A. Mazumder. 1999. Microcosm experiments have limited relevance for community and ecosystem ecology: comment. Ecology 80: 1081-1085.

Dubensky, M.M., R.S. Berg, and W.S. Berry. 1993. Forest wetland area and distribution: A forest and paper industry policy. Journal of Forestry 20-24.

Dulohery, C.J., L.A. Morris, and R. Lowrance. 1996. Assessing forest soil disturbance through biogenic gas flux. Soil Science Society of America Journal 60: 291-298.

Dunn, W.J., L.N. Schwartz, and G.R. Best. 1987. Structure and water relations of the white cedar forests of North Central Florida (abstract). 111.

Earle, C.J. and M.P. Frankis. 1999. Geocities.com. Cuppressaceae.

Eastman, L.M. 1978. Rare and endangered vascular plant species in Maine. Unpublished.

Edwards, S.W. 1983. Cenozoic history of Alaskan and Port Orford *Chamaecyparis* cedars. PhD dissertation. University of California, Berkley. 271 pp.

Edwards, S.W. 1985. The remarkable range of Port-Orford-Cedar. Four Seasons 7(1): 4-16.

Ehrenfeld, J.G. 1995. Microsite differences in surface substrate characteristics in *Chamaecyparis* swamps of the New Jersey pinelands. Wetlands 15: 183-189.

Ehrenfeld, J.G. 1995. Microtopography and vegetation in Atlantic white cedar swamps: the effects of natural disturbances. Can. J. Bot. 73: 474-484.

Ehrenfeld, JG and J.P. Schneider. 1991. *Chamaecyparis thyoides* wetlands and suburbanization: effects on hydrology, water quality and plant community composition. J. of Appl. Eco. 28: 467-490.

Ehrenfeld, J.G. 1983. The effects of changes in Land-use on swamps of the New Jersey Pine Barrens. Biological Conservation 25: 353-375.

Ehrenfeld, J.G. and J.P. Schneider. 1990. The response of Atlantic white cedar wetlands to varying levels of disturbance from suburban development in the New Jersey pinelands. 63-78.

Eleuterius, L.N. and S.B. Jones. 1972. A phytosociological study of white-cedar in Mississippi. Castanea 37, 67-74.

Ferguson, R.H. and C.E. Mayer. 1974. The Timber Resources o fNew Jersey. Darby, PA, Northeastern Forest Experiment Station, Forest Service, U.S. Department of Agriculture.

Flanagan, P.W. and K. Van Cleve. 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Canadian Journal of Forestry Research. 13: 795-817.

Fritts, H.C. Tree Rings and Climate. 1976. New York, Academic Press.

Frost, C.C. 1987. Historical overview of Atlantic white cedar in the Carolinas. A. D. Laderman (Ed.) Atlantic White Cedar. 257-264. Boulder, CO, Westview Press.

Gaius, R.S. 1986. Woody stem production in Alaskan tundra shrubs. Ecology 67: 660-669.

Gale, M.R., J.W. McLaughlin, M.F. Jurgensen, C.C. Trettin, T. Soelsepp, P.O. Lydon, and others. 1998. Plant community responses to harvesting and post-harvest manipulations in a *Picea-Larix-Pinus* wetland with a mineral substrate. Wetlands 18(1): 150-159.

Gambrell, R.P. and W.H. Patrick, Jr. 1978. Chemical and microbiological properties of anaerobic soils and sediments. pp. 375-423 In: D.D. Hook and R.M.M. Crawford (Eds.) Plant Life in Anaerobic Environments. Ann Arbor Science Publishers, Inc. Ann Arbor, MI.

Gardner, W.E., K.O. Summerville, and J.P.Lilly. ND. Reintroduction of Atlantic white cedar in the Lower Coastal Plain (Unpubl abstract).

Garren, K.H. 1943. Effects of fire on vegetation of the southeastern USA. The Botanical Review 9: 617-654.

Gennadieyev, A. 1997. Rate of humus (organic carbon) accumulation in soils of different ecosystems. Soil Processes and the Carbon Cycle. 103-107, New York, CRC Press.

Gibson, D.J. and R.E. Good. 1986. Population structure and thinning in natural stands of Atlantic White Cedar (*Chamaecyparis thyoides* (L.) B.S.P.). Oecologia 69: 348-353.

Gilliam, J.W. 1991. Wet soils in the North Carolina lower coastal plain. Wetlands

11: 391-398.

Gilliam, J.W. and R.W. Skaggs. 1981. Drainage and agriculture development: effects on drainage waters. Richardson, C.J. (Ed.) Pocosin Wetlands. 109-124. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Glooschenko, V. 1990. Effect of peatland development on water quality, fish and wildlife habitat in Canada, a review. 85-93.

Goldberg, R. 1995. G.H. Weyerhaeuser nursery in 25th year of production. A(1): 1.. Plymouth, NC.

Golet, F.C. and D.J. Lowry. 1987. Water regimes and tree growth in Rhode Island Atlantic white cedar swamps, p. 91-110 In: A.D. Laderman (Ed.) Atlantic White Cedar Wetlands. Westview Press, Boulder, CO. 401 pp.

Gomez, M.M. and F.P. Day Jr. 1982. Litter nutrient content and production in the Great Dismal Swamp. American Journal of Botany 69: 1314-1321.

Good, R.E. 1987. Prospects and programs: Research needs, funding, and funding mechanisms (abstract). 365.

Gorham, E. 1987. The ecology and biogeochemistry of *Sphagnum* bogs in central and eastern North America. 3-15.

Greenwood, L.L. Greenhouse production of Atlantic white cedar seedlings. Synopsis of results from research toward requirements for Master's degree. Unpubl.

Grier, C.G. and R.S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: Biomass distribution and production budgets. Ecological Monographs 47: 373-400.

Hackney, C.T. and G.F. Yelverton. 1990. Effects of human activities and sea level rise on wetland ecosystems in the Cape Fear River Estuary, North Carolina, USA. 55-61.

Hanlon, H.A. 1970. The Bull-Hunchers: A saga of the three and a half centuries of harvesting the forest crops of the Tidewater Low Country. Parson, WV: McClain Publ. Co.

Harper, R.M. 1926. A middle Florida cedar swamp. Torreya 26: 81-84.

Harris, A.S. 1969. *Chamaecyparis Spach* (White Cedar). Seed Production. U.S. Dep. Agric. Handbk. 450: 316-320.

Harwood, H.J. and P.S. McMullan, Jr. 1981. Peat energy for North Carolina: an economic analysis. Richardson, C.J. (Ed.) Pocosin Wetlands. 255-269. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Havens, K. 1996. Plant adaptations to saturated soils and the formation of hypertrophied lenticels and adventitious roots in woody species. VIMS, Gloucester, VA.

Heal, O.W., P.W. Flanagan, D.D. French, and S.F. Maclean, Jr. 1981. Decomposition and accumulation of organic matter. In L.C. Bliss, O.W. Heal, and J.J. Moore (Ed.) Tundra Ecosystems: a comparative analysis. Cambridge University Press, Cambridge, NY p. 587-633.

Heath, M.S. Jr. Political economy of alternative management strategies for pocosins in North Carolina. 305-317. Richardson, C.J. (Ed.) Pocosin Wetlands. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Heath, R.C. 1975. Hydrology for the Albemarle-Pamlico Region, North Carolina: A Preliminary Report on the Impact of Agricultural Developments. U.S. Geological Survey.

Heinselman, M.L. 1963. Forest sites, bog processes, and peatland types in the glacial Lake Agassiz region, Minnesota. Ecological Monographs 33(4): 327-374.

Heinselman, M.L. 1970. Landscape evolution, peatland types, and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. Ecological Monographs 40(2): 235-261.

Heliotis, F.D. and C.B. DeWitt. 1987. Impact of domestic wastewater on *Thuja occidentalis* in a northern Michigan cedar swamp. 289-291.

Hemond, H. 1987. Hydrologic and biogeochemical problems in wetlands research: Some proposed approaches. 367-370.

Hemond, H., W. Nuttle, E. Nichols, D. Chen, K. Stolzenbach, M. Schaefer, and J. Knott. 1987. Hydrologic technology for freshwater wetlands. 113-121.

Hennon, P.E., C.G. Shaw III, E.M. Hansen, and others. 1987. Onset, spread, and community relationships of decline in *Chamaecyparis nootkatensis* in southeast Alaska. 331-337.

Henry, E.F. 1970. Soils of the Dismal Swamp of Virginia. Virginia Journal of Science 21(2): 41-45.

Hershey, R.R. and W.A. Befort. 1995. Aerial Photo Guide to New England Forest Cover Types, MAY. Radnor, PA, USDA Forest Service.

Heusser, C.J. 1963. Pollen diagrams from three former cedar bogs in the Hackensack tidal marsh, northeastern New Jersey. Bull. of the Torrey Bot. Club 90: 16-28.

Hillman, G.R. 1992. Some hydrological effects of peatland drainage in Alberta's boreal forest. Canadian Journal of Forest Research 22: 1588-1596.

Hinesley, E. ND. Production of Atlantic white cedar transplants. Current Developments with Atlantic White-Cedar Management. Unpubl.

Hinesley, E. Rooting Atlantic white cedar stem cuttings outdoors. Current Developments with Atlantic White-Cedar Management. Unpubl.

Hinesley E. ND. Site prep x species interactions. Current Developments with Atlantic White-Cedar Management. Unpubl.

Hinesley E. ND. Wetland restoration. Current Developments with Atlantic White-Cedar Management. Unpubl.

Hinesley, E. 1999. Pocosin Lakes National Wildlife Refuge Forest Habitat Management Plan. 80pp. Raleigh, N.C., North Carolina State University.

Hinesley, L., F.A. Blazich, and L.K. Snelling. 1994. Propagation of Atlantic white cedar by stem cuttings. Horticultural Science 29(3): 217-219.

Hobart, S.G., G.W. Dean, and E.E.Rodger. 1981. The History of the Virginia Division of Forestry. VPISU Library.

Hogg, E.H., V.J. Lieffers, and R.W. Wein. 1992. Potential carbon losses from peat profiles: effects of temperature, drought cycles and fire. Ecological Applications 2: 298-306.

Homann, P.S., P. Sollins, M. Fiorella, T. Thorson, and J.S. Kern. 1998. Regional soil organic carbon storage estimates for western Oregon by multiple approaches. Soil Science Society of America Journal 62: 789-796.

Houghton, R.A. 1993. Is carbon accumulating in the northern temperate zone? Global Biogeochemical Cycles 7(3): 611-617.

Houghton, R.A. Estimating changes in the carbon content of terrestrial ecosystems from historical data. p. 175-193.

Hughes, J.H. ND. Weyerhaeuser Company is helping with the effort to restore Atlantic white cedar in coastal North Carolina. Current Developments with Atlantic White-Cedar Management. Unpubl.

Hull, J.C. and D.F. Whigham. 1987. Vegetation patterns in 6 bogs and adjacent forested wetlands in the Inner Coastal Plain of Maryland. pp. 143-173. In: A.D. Laderman (Ed.) Atlantic White Cedar Wetlands. Westview Press. Boulder, CO.

Hungerford, R.D., W.H. Frandsen, and K.C. Ryan. 1996. Heat transfer into the duff and organic soil. Missoula, Montana, USDA Forest Service Intermountain Research Station Intermountain Fire Sciences Lab.

Hunt, F.A. 1986. National register of big trees. Am. For. 92: 21-52.

Hyvinen, R., I. Gren, and E. Bosatta. 1998. Predicting long-term soil carbon storage from short-term information. Soil Science Society of America Journal. 62: 1000-1005.

Ingram, R.L. and L.J. Otte. 1981.Peat in North Carolina wetlands. Richardson, Curtis J. Pocosin Wetlands. 125-134. Richardson, C.J. (Ed.) Pocosin Wetlands. Stroudsburg, PA, Hutchinson Ross Publ. Co.

IPPC. 1995. Technical Summary. Inter-governmental Panel on Climate Change, WMO. Geneva, Switzerland. 44p.

Johnson J.C. ND. Alligator River National Wildlife Refuge's approach to Atlantic white cedar management. Current Development with Atlantic White-Cedar Management. Unpubl.

Jain, T.B., R.T. Graham, and D.L. Adams. 1997. Carbon to organic matter ratios for soils in Rocky Mountain coniferous forests. Soil Science Society of America Journal 61: 1190-1195.

Johnson, J.W. 1980. Atlantic white cedar. Eyre, F.H. (Ed.) Forest Cover Types of the U.S. and Canada. 75. Soc. Amer. Foresters.

Jones, S.B. 1967. An accessible location for white cedar in Mississippi. Castanea 323: 118.

Jull, L.G., F.A. Blazich, and L.E. Hinesley. ND. Initial seedling growth of Atlantic white cedar as influenced by temperature and photoperiod. Current Developments with Atlantic White-Cedar Management. Unpubl.

Karam, A. 1993. Ash content and organic matter content (ASTM D2974 1988). Pp. 461-463 In: M.R. Carter (Ed.) Soil Sampling and Methods of Analysis. Canadian Soc. Soil Science. Lewis Publ. Boca Raton, FL.

Karlin, E.F. 1997. The drowned land’s last stand: an island Atlantic white cedar peat swamp in Orange County, N.Y., J. Torrey Botanical Society 124(1): 89-97.

Kern, J.S. 1994. Spatial patterns of soil organic carbon in the contiguous United States. Soil Science Society of America Journal 58: 439-455.

Klinger, L.F. 1990. Global patterns in community succession: 1. Bryophytes and forest decline. In: P.S. Mankiewicz (Ed.) The role of plants in landscape transformation. Memoirs of the Torrey Botanical Club 24(1): 50.

Knowe, S.A. 1994. Effect of competition control treatments on height-age and height diameter relationships in young Douglas-fir plantations. For. Ecol. Mgt. 101-111.

Kologoski, R.L. 1977. The Phytosociology of the Green Swamp, North Carolina. North Carolina, North Carolina Agricultural Experiment Station.

Korstian, C.F. 1924. Natural regeneration of southern white cedar. Ecology 5: 188-191.

Korstian, C.F. and W.D. Brush. 1931. Southern white cedar. U.S.D.A. Tech. Bull. 251 75 pp.

Kraus, J.W. 1988. A guide to ocean dune plants common to North Carolina. Chapel Hill, NC: The University of North Carolina Press.

Kuenzler, E.J., P.J. Mulholland, L.A. Yarbro, L.A. Smock. 1980. Distributions and budgets of C, P, Fe, and Mn in a floodplain swamp ecosystem. Universityof North Carolina, Chapel Hill, Water Resources Research Institute.

Kuser, J.E., T.R. Meagher, D.L. Sheely, and A. White. 1997. Allozyme frequencies in New Jersey and North Carolina populations of Atlantic white cedar, *Chamaecyparis thyoides* (Cupressaceae). American Journal of Botany 84(11): 1536-1541.

Kuser, J.E. ND. White-cedar genetics, propagation and establishment in New Jersey. Current Developments with Atlantic White-Cedar Management. Unpubl.

Laderman A.D. 1980. Algal ecology of a *Chamaecyparis thyoides*/Sphagnum bog: an in situ microcosm study. Dissertation, State University of New York at Binghamton. 208 pp.

Laderman A.D. 1987. Atlantic white cedar in the glaciated northeast (abstract).

Laderman, A.D. 1982. The Atlantic white cedar swamp: prime candidate for investigation. Wetlands 2: 61-74.

Laderman, A.D. Editor. 1987. Atlantic White Cedar Wetlands. Westview Press, Denver, CO. 401 pp. Based on a symposium, 9-11 Oct. 1984, Woods Hole MA. 401 pp.

Laderman, A.D. Editor. 1998. Coastally Restricted Forests. Oxford University Press, London, New York. Based on 2 symposia: Intecol Aug. 1990, Yokohama, Japan; New Haven CT, Apr. 1991. 350 pp.

Laderman, A.D. 1982. Comparative community structure of *Chamaecyparis thyoides* bog forests: canopy diversity. Wetlands 216-230.

Laderman, A.D. 1987. Taxonomic clustering of the algae in a *Chamaecyparis* glacial kettle. Pages 191-208 in Atlantic White Cedar Wetlands.

Laderman, A.D. 1989. The ecology of the Atlantic white cedar wetlands: a community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.21).

Laderman, A.D. 1998. Freshwater forests of continental margins: overview and synthesis. Pages 1-38 *in* Coastally Restricted Forests.

Laderman, A.D. 1975. Sediment deposition and growth irregularities in *Chamaecyparis thyoides* kettle bogs. Biol. Bull. 149: 434.

Laderman, A.D. 1987. Taxonomic clustering of the algae in a *Chamaecyparis thyoides* glacial kettle. 193-209. Laderman, A.D. (Ed.) Atlantic White Cedar Wetlands. Boulder, Colorado, Westview Press.

Laderman, A.D.and D.B. Ward. 1989. Flora associated with *Chamaecyparis thyoides*: a distribution checklist. Pages 91-107 in Ecology of Atlantic White Cedar Wetlands: a Community Profile.

Laderman, A.D. and D.B. Ward. 1987. Species associated with *Chamaecyparis thyoides*: a checklist with common synonyms. 385-397 Laderman, A.D. (Ed.) Atlantic white cedar wetlands. Boulder, CO, Westview Press.

Laderman, A.D., F.C. Golet, B.A. Sorrie and H.L. Woolsey. 1987. Atlantic white cedar in the glaciated Northeast. Pages 19-34 in Atlantic White Cedar Wetlands.

Laidig, K.J. and R.A. Zampella. 1999. Community attributes of Atlantic white cedar (*Chamaecyparis thyoides*) swamps in disturbed and undisturbed pinelands watersheds. Wetlands 19(1): 35-49.

Landers, J.L., D.H. Van Lear, and W.D. Boyer. 1995. The longleaf pine forests of the southeast: requiem or renaissance? Journal of Forestry 39-44.

Landin, M.C. 1993. Wetlands: Proceedings of the 13th Annual Conference of the Society of Wetland Scientists. South Central Chapter, Society of Wetland Scientists. 990 pp. Utica, MS, 9175-9351.

Larson, J.S. 1987. Federal, state, and foundation funding for wetland research: Sources and approaches. 375-379.

L'vesque, M.P. and H. Dinel. 1982. Some morphological and chemical aspects of peats applied to the characterization of Histosols. Soil Science. 133(3): 324-335.

L'vesque, M.P. and H. Dinel. 1982. Some morphological and chemical aspects of peats applied to the characterization of Histosols. Soil Science 133(3): 324-335.

L'vesque, M.P. and S.P. Mathur. 1979. A comparison of various means of measuring the degree of decomposition of virgin peat materials in the context of their relative biodegradability. Canadian Journal of Soil Science. 59: 397-400.

Levandowsky, M. 1987. Biochemical and physiological adaptations of plant cells to acid environments. 241-249.

Levy, G.F. 1987. Atlantic white cedar in the Great Dismal Swamp and the Carolinas. In: A.D. Laderman (Ed.). Atlantic white cedar wetlands. Boulder, CO, Westview Press.

Levy, G.F. and S.W. Walker. 1979. Forest dynamics in the Dismal Swamp of Virginia. IN Kirk P.W. Jr. (Ed.), The Great Dismal Swamp. University Press of Virginia, Charlottesville, VA.

Li, H-L. 1962. A new species of *Chamaecyparis*. Morris Arboretum Bulletin 13(3): 43-46.

Lichtler, W.F. and P.K. Walker. 1974. Hydrology of the Dismal Swamp, Virginia-North Carolina. U.S. Geological Survey. Richmond, VA.

Lide, R.F., V.G. Meentemeyer, J.E. Pinder, III, and L.M. Beatty. 1995. Hydrology of a Carolina bay located on the upper Coastal Plain of western South Carolina. Wetlands 15: 45-57.

Lilly, J.P. ND. Atlantic white cedar site adaptation and historical perspective. Current Developments with Atlantic White-Cedar Management. Unpubl.

Lilly, J.P. 1981. The blackland soils of North Carolina: Their characteristics and management for agriculture. NC Agricultural Research Service Technical Bulletin no. 270. 70 pp.

Lilly, J.P. 1981. A history of swamp land development in North Carolina. IN C.J. Richardson (Ed.) Pocosin Wetlands. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Lilly, J.P. Organic soils: Atlantic white cedar. Current Developments with Atlantic White-Cedar Management. Washington, NC. Unpubl.

Lindenmuth, W.D. and J.M. Vasievich. 1981. An economic analysis of intensive timber management of Pocosins. Richardson, C.J. (Ed.) Pocosin Wetlands. 270-282. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Little, E.T. 1966. Varietal transfers in *Cupressus* and *Chamaecyparis*. Madrono 18(6): 161-192.

Little, S. Jr. 1950. Ecology and silviculture of whitecedar and associated hardwoods in southern New Jersey. Yale Univ. Sch. For. Bull. 56.

Little, S. Jr. 1964. Fire ecology and forest management in the New Jersey pine region. Tall Timbers Fire Ecology Conference 3: 34-59.

Little, S. Jr. 1959. Silvical characteristics of Atlantic white cedar. U.S.D.A. For. Serv. NE Exp. Sta. Res. Pap. 119.

Little S. Jr. 1951. Observations on the minor vegetation of the Pine Barren swamps in southern New Jersey. Bulletin of the Torrey Botanical Club 78(2): 153-160.

Little, S. Jr. 1959. Silvical Characteristics of Pitch Pine (*Pinus rigida)*. Upper Darby, PA, Northestern Forest Experiment Station, USDA.

Little, S. Jr., J.P. Allen, and E.B. Moore. 1947. Controlled burning as a dual-purpose tool of forest management in New Jersey's pine region. Journal of Forestry 811-818.

Little, S. and P.W. Garrett. *Chamaecyparis thyoides* (L.)B.S.P., Atlantic White Cedar. 103-108. unpubl.

Little, S. Jr. 1952. Prescribed burning as a tool of forest management in the northeastern states. 496-500, Unpubl.

Lynn, W.C., W.E. McKinzie, and R.B. Grossman. 1974. Field laboratory tests for characterization of Histosols. In: Aandahl, A.R., et al. (Eds.). Histosols: Their Characteristics, Classification, and Use. SSSA Special Publ. no. 6. Soil Science Society of America. Madison, WI. p. 11-21.

Lynn, LM. 1981. The vegetation of Little Cedar Bog, southeastern New York. Bulletin of the Torrey Botanical Club 111(1): 90-95.

Lynn, L.M. and E.F. Karlin. 1985. The vegetation of the low-shrub bogs on northern New Jersey and adjacent New York: Ecosystems at their southern limit. Bulletin of the Torrey Botanical Club 112(4): 436-444.

Madgwick, H.A.I. and T. Satoo 1975. On estimating the aboveground weights of tree stands. Ecology 56: 1446-1450.

Magellan Systems Corporation. 1996. Magellan GPS NAV 5000DLX User Guide.

Maki, T.E. 1974. Factors affecting forest production on organic soils. In: Aandahl, A.R., et al., (Eds.). Histosols: Their Characteristics, Classification, and Use. SSSA Special Publ. no. 6. Soil Science Society of America. Madison, WI. p. 119-136.

Mallik, A.U. 1990. Microscale succession and vegetation management by fire in a freshwater marsh of Atlantic Canada. 19-29.

Mallik, A.U. 1990. Smoldering combustion, thermal decomposition and nutrient content following controlled burning of *Typha* dominated organic mat. 7-16.

Marburger, J.E. 1993. Biology and management of *Sagittaria latifolia* Willd. (Broad-leaf Arrow-head) for wetland restoration and creation. Restoration Ecology 1: 248-255.

Marburger, J.E. 1993. Biology and management of *Sagittaria latifolia* Willd. (Broad-leaf Arrow-head) for wetland restoration and creation. Restoration Ecology 1(4).

Mathur, S.P. and M. Lévesque. 1985. Negative effect of depth on saturated hydraulic conductivity of Histosols. Soil Science. 140(4): 462-466.

Mavor, J.W. Jr. and B.E. Dix. 1987. New England cedar wetlands in Native American ritual. 265-269. A.D. Laderman (Ed.) Atlantic White Cedar Wetlands. Westview Press, Boulder, CO.

McCarron, J.K., K.W. McLeod, and W.H. Conner. 1998. Flood and salinity stress of wetland woody species Buttonbush (*Cephalanthus occidentalis*) and Swamp Tupelo (*Nyssa sylvatica* var. *biflora*). Wetlands 18(2): 165-175.

McCarthy G. 1884. The August flora of the Dismal Swamp and vicinity. The American Naturalist 18(3): 288-290.

McIver, E.E. 1994. An early *Chamaecyparis* (Cuppressaceae) from the late Cretaceous of Vancouver Island, British Columbia, Canada. Canadian Journal of Botany 72: 1787-1796.

McKee, W.H. 1978. Rust on iron rods indicates depth of soil moisture. In W.W. Balmer (Ed.) Proceedings, Soil Moisture and Site Productivity Symposium. Myrtle Beach, SC, 1-3 Nov 1977. U.S.D.A., Forest Service.

McKinley, C.E. and F.P. Day, Jr. 1979. Herbaceous production in cut, burned and control areas of a *Chamaecyparis thyoides* Cupressaceae stand in the Great Dismal Swamp. Bull. Torrey Bot. Club 106: 20-28.

McMullan, P.S. Jr. ND. History of Development of the Albemarle-Pamlico Region with Emphasis on Dare, Hyde, and Tyrrell Counties. unpubl.

McWeeney, L. 1998. Reconstruction of the Mashantucket Pequot Cedar Swamp paleoenvironment using plant macrofossils, New England. In A.D. Laderman (Ed.) Coastally Restricted Forests. Oxford University Press, New York.

Meanley, B. 1979. An analysis of the birdlife of the Dismal Swamp. pp. 261-276 In: Kirk, P.W. Jr. (Ed.) The Great Dismal Swamp. Charlottesville, VA, University Press of VA.

Meanly, B. 1972. The Great Dismal Swamp. Audobon Naturalist Society, Washington D.C.

Megonigal, J.P., S.P. Faulkner, and W.H. Patrick. 1996. The microbial activity season in Southeastern hydric soils. Soil Science Society of America Journal. 60: 1263-1266.

Megonigal, P.T. and F.P. Day, Jr. 1992. Effects of flooding on root and shoot production in bald cypress in large experimental enclosures. Ecology 73: 1182-1193.

Megonigal, P.T., F.P.Day, Jr. 1988. Organic matter dynamics in four seasonally flooded communities of the Dismal Swamp. American Journal of Botany 75: 1334-1343.

Millar, C.I. and K.A. Marshall. 1991. Allozyme variation of Port Orford-Cedar (*Chamaecyparis lawsoniana)*: implications for genetic conservation. Forest Science 37(4): 1060-1077.

Miller D, L. Gradischer, J. Orzel, W. Leak, and E. Miller. 1987. Changes in vegetation and breeding bird use in an Atlantic white cedar swamp from 1951-1984. Laderman. A.D. (Ed.) Atlantic White Cedar Wetlands. Westview Press, Boulder, CO.

Miller, R.B. and F.G. Meyer. 1989. Identification of the Heath-leaved Cypress, *Chamaecyparis thyoides 'Ericoides' (Cupressaceae)*. Baileya 23(2): 57-67.

Mitsch, W.J. and K.C. Ewel. 1979. Comparative biomass and growth of Cypress in the Florida wetlands. The American Midland Naturalist 101: 417-427.

Mitsch, W.J. and Gosselink, J.G. Wetlands. 1993. Van Nostrand Reinhold, New York.

Mitsch, W.J. and W.G. Rust. 1984. Tree growth responses to flooding in a bottomland forest in northeastern Illinois. Forest Science 30: 499-510.

Monk, CD. 1966. An ecological study of hardwood swamps in north-central Florida. Ecology 47: 649-653.

Monschein, T.D. 1981. Values of pocosins to game and fish species in North Carolina. Richardson, C.J. (Ed.) Pocosin Wetlands. 155-170. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Moore, E.B. 1939. Forest management in New Jersey. N.J. Dept. of Conserv. Dev. 55.

Moore, E.B. and A.F. Waldron. 1940. Growth studies of southern white cedar in New Jersey. Journal of Forestry 568-572.

Moore, J.H. and J.H.Carter, III. 1987. Habitats of white cedar in North Carolina. pp. 177-189 IN A.D. Laderman (Ed.) Atlantic White Cedar Wetlands. Westview Press, Boulder, CO.

Moore, P.D. 1989. The ecology of peat forming processes. In: P.C. Lyons and B. Alpern (Eds.) Peat and Coal: Origin, Facies, and Depositional Models. International Journal of Coal Geology 12: 89-103.

Moore, P.D. and D.J. Bellamy. 1973. Peatlands. Paul Elek. London. 221 pp.

Moore, S.E. 1996. Natural regeneration of Atlantic white cedar in the Great Dismal Swamp. Raleigh, NC, North Carolina State University.

Moore, S.E. ND. Natural regeneration of Atlantic white cedar in the Great Dismal Swamp: a review of two studies. Paper presented to the U.S. Fish and Wildlife Service, Great Dismal Swamp National Wildlife Refuge 2 pp. Unpubl.

Moore, T.R. and R. Knowles. 1989. The influence of water table levels on methane and carbon dioxide emissions from peatland soils. Canadian Journal of Soil Science 69: 33-38.

Moore, T.R. and M. Dalva. 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. Journal of Soil Science 44: 651-664.

Moore, T.R. and M. Dalva. 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. Soil biology and biochemistry 29(8): 1157-1164.

Motzkin, G., W.A. Patterson, and E.R. Drake. 1993. Fire history and vegetation dynamics of a *Chamaecyparis thyoides* wetland on Cape Cod, Massachusetts. Journal of Ecology 81: 391-402.

Mowbray, T. and W.H. Schlesinger. 1988. The buffer capacity of organic soils of the Bluff Mountain Fen, North Carolina. Soil Science 146(2): 73-79.

Mueller-Dombois, D. and H.Ellenberg. 1974. Aims and Methods of Vegetation Ecology. Wiley, New York, NY.

Myers, R.S., G.P. Shaffer, and D.W. Llewellyn. 1995. Baldcypress (*Taxodium distichum* (L.) Rich.) restoration in southeast Louisiana: the relative effects of herbivory, flooding, competition and macronutrients. Wetlands 15: 141-148.

Needham, RN. 1982. *Chamaecyparis thyoides*: a unique plant community. Unpubl.

Neill, C., C. Cerri, J. Melillo, B. Feigl, P. Steudler, J. Moraes, and M. Piccolo. 1997. Stocks and dynamics of soil carbon following deforestation for pasture in Rondonia. Soil Processes and the Carbon Cycle. 9-28. CRC Press, New York.

Niering, W.A. 1953. The past and present vegetation of High Point State Park, New Jersey. Ecological Monographs 23(2): 127-148.

Noss, R.F., E.T. LaRoe, and J.M. Scott. 1995. Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. US Department of the Interior, National Biological Services, Washington D.C.

O'Brien, A.L. 1977. Hydrology of two small wetland basins in eastern Massachusetts. Water Resources Bulletin 13(2): 325-340.

O'Neill, J. 1987. The Army Corps of Engineers and Wetland Regulation. 347-349.

Oaks, R.Q. Jr. and D.R. Whitehead. 1979. Geologic setting and origin of the Dismal Swamp, southeastern Virginia and northeastern North Carolina. IN Kirk, P.D. Jr. (Ed.) The Great Dismal Swamp. The University Press of Virginia, Charlottesville. 427 pp.

Oaks, R.Q. and N.K. Coch. 1973. Post-Miocene stratigraphy and morphology, southeastern Virginia. Virginia Division of Mineral Resources Bulletin 82.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164: 262-270.

Olmstead, Frederick Law. 1984. The Cotton Kingdom. The Modern Library, New York, NY.

Oosting, J. 1942. Plant communities of the piedmont, North Carolina. American Midland Naturalist 28: 1-126.

Paratley, R.D. and T.H. Fahey. 1986. Vegetation-environment relations in a conifer swamp in central New York. Bulletin of the Torrey Botanical Club 113(4): 357-371.

Parent, L.E., J.A. Millette, and G.R. Mehuys. 1982. Subsidence and erosion of a Histosol. Soil Science Society of America Journal 46: 404-408.

Pearsall, W.H. and E. Gorham. 1956. Production ecology: Standing crops of natural vegetation. Oikos 7: 193-201.

Peterson, E.B., Y.B. Chan, and J.B. Cragg. 1970. Aboveground standing crop, leaf area and caloric value in an aspen clone near Calgary, Alberta. Canadian Journal of Botany 48: 1459-1469.

Phillips, R.W., W.E. Gardner, and K.O. Summerville. 1992. Plantability of Atlantic white cedar rooted cuttings and bare root seedlings. 7th Biennial Southern Silvicultural Research Conference.

Phillips, R.W. Forestation with Atlantic white Cedar (*Chamaecyparis thyoides*) rooted cuttings and bare root seedlings. unpubl.

Phipps, R.L., D.L. Ireley, C.P. Baker. 1979. Tree rings as indicators of hydrologic change in the Great Dismal Swamp, Virginia and North Carolina. U.S. Geological Survey, Report USGS/WRI-78-136 WRI-78-136.

Pittman, A.B., Jr. 1978. Survey of the vascular flora of Shealy's pond, a southern cedar bog. Columbia, SC, Univ. South Carolina.

Postel, S.L. 1980. The Economic Benefits of Pocosin Preservation. P. 283-301 IN Richardson, C.J. (Ed.) Pocosin Wetlands. Hutchinson Ross Publ. Co., Stroudsburg, PA,

Potzger, J.E. 1945. The Pine Barrens of New Jersey: a refugium during Pleistocene times. Butler University Botanical Studies 7:182-193.

Powell, S.W. and F.P. Day, Jr. 1991. Root production in four communities in the Great Dismal Swamp. American Journal of Botany 78(2): 288-297.

Pratt, J.H. 1999. Drainage of North Carolina Swamp Lands. Journal of the American Peat Society 2(3): 158-163.

Prokopovich, N.P. 1985. Subsidence of peat in California and Florida. Bulletin of the
Association of Engineering Geologists 22(4): 395-420.

Quaterman, E. 1950. Ecology of cedar glades. I. Distribution of glade flora in Tennessee. Bulletin of the Torrey Botanical Club 77: 1-9.

Radford, A.E., H.A. Ahles, and C.R. Bell. 1968. Manual of the Vascular Flora of the Carolinas. The University of North Carolina Press, Chapel Hill, N.C.

Ramsey, E.W., K.R. Hinkle, and L.E. Benander. 1970. Waters of the Dismal Swamp. The Virginia Journal of Science 21(3): 81-83.

Reader, R.J. and J.M. Stewart. 1972. The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. Ecology 53:

Reddy, K.R. and W.H. Patrick. 1975. Effect of alternate aerobic and anaerobic conditions on redox potential, organic matter decomposition and nitrogen loss in a flooded soil. Soil Bio. Biochem. 7: 87-94.

Reiners, W.A. 1972. Structure and energetics of three Minnesota forests. Ecological Monographs 42: 71-94.

Reynolds, P.E., W.R. Parrott, J.R. Maurer, and D.C. Hain. 1981. Computer mapping of seasonal groundwater fluctuations for two different southern New Jersey swamp forests. 772-783.

Richardson, C.J. and others. 1981. An integrated analysis of coastal plain freshwater bogs in North Carolina. IN C.J. Richardson (Ed.) Pocosin Wetlands: Hutchinson Ross Publ. Co., Stroudsburg, PA.

Richardson, CJ. 1985. Mechanisms controlling phosphorous retention capacity in freshwater wetlands. Science 228: 1424-1427.

Richardson, CJ. 1991. Pocosins: an ecological perspective. Wetlands 11: 335-354.

Richardson, C.J. (Ed.). 1981. Pocosin Wetlands. Hutchinson Ross Publ. Co., Stroudsburg, PA.

Richardson, CJ. 1981. Pocosins: Ecosystem processes and the influence of man on system response. P. 135-151 IN Richardson, C.J. (Ed.) Pocosin Wetlands. Hutchinson Ross Publ. Co., Stroudsburg, PA.

Richardson, C.J., R. Evans, and D. Carr. 1981. Pocosins: An ecosystem in transition. P. 3-19 IN Richardson, C.J. (Ed.) Pocosin Wetlands. Hutchinson Ross Publ. Co., Stroudsburg, PA.

Richardson, C.J. and E.J. McCarthy. 1994. Effect of land development and forest management on hydrologic response in Southeastern coastal wetlands: Areview. Wetlands 14(1): 56-71.

Richter, B.D., J.V. Baumgartner, J. Powell, and D.P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. Conservation Biology 10 (4): 1163-1174.

Richter, D.D., D. Markewitz, S.E. Trumbore, and C.G. Wells. 1999. Rapid accumulation and turnover of soil carbon in a re-establishing forest. Nature 400: 56-58.

Rigg, G.B. 1940. Comparisons of the development of some *Sphagnum* bogs of the Atlantic coast, the interior and the Pacific coast. Am. Journ. Botany 27: 1-14.

Robbins, C.S., D.K. Dawson, and BA Dowell. 1988. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monographs 103, 1-34.

Rojstaczer, S. and S.J. Deverel. 1995. Land subsidence in drained Histosols and highly organic mineral soils of California. Soil Science Society of America Journal 59: 1162-1167.

Roman, C.T., R.E. Good, and S. Little. 1987. Atlantic white cedar swamps of the New Jersey Pinelands. Pages 35-40 in A.D. Laderman (Ed.) Atlantic White Cedar Wetlands. Westview Press, Boulder, CO.

Roman, C.T., R.E. Good, and S. Little. 1990. Ecology of Atlantic white cedar swamps in the New Jersey pinelands. 163-173.

Sargent, C.S. 1880. A Catalogue of the Forest Trees of North America. Government Printing Office.,Washington, DC.

Satterlund, D.R. 1960. Some interrelationships between groundwater and swamp forests in the western upper peninsula of Michigan. Ann Arbor, Michigan, University of Michigan, University Microfilms, Inc.

Schlesinger, W.H. 1978. Community structure, dynamics and nutrient cycling in the Okefenokee Cypress swamp forest. Ecological Monographs 48: 43-65.

Schlesinger, W.H. 1986. Changes in soil carbon storage and associated properties with disturbance and recovery. p 194-220 *In* J.R. Trabalka and D.E. Reichle (Eds.), The Changing Carbon Cycle: A Global Analysis. Springer-Verlag, NY.

Schlesinger, W.H. 1990. Evidence from chronosequence studies for a low carbon storage potential of soils. Nature 348: 232-234.

Schmid, J.A. 1987. Atlantic white cedar in the Hackensack Meadowlands, New Jersey: Its historic extirpation and future reestablishment. Pages 317-321 IN A.D. Laderman (Ed.) Atlantic White Cedar Wetlands. Westview Press, Inc. Boulder, CO.

Schneider, J.P. and J.G. Ehrenfeld. 1987. Suburban development and cedar swamps: Effects on water quality, water quantity, and plant community composition. 271-287 IN A.D. Laderman (Ed.) Atlantic White Cedar Wetlands. Westview Press, Inc. Boulder, CO.

Seischab, F.K. 1987. Succession in a *Thuja occidentalis* wetland in western New York. 211-215.

Shafale, M.P. and A.S. Weakley. 1990. Classification of the Communities of North Carolina Third Approximation. North Carolina Natural Heritage Program Division of Parks and Recreation Department of Environment, Health and Natural Resources. Raleigh, NC.

Shaler, N.S. 1890. General Account of the Fresh-water Morasses of the United States, with a description of Virginia and North Carolina. U.S.G.S. 10th annual Report for 1888-1889, USGS. 253-339.

Shaw, C.G., III, A. Eglitis, T.H. Laurent, and P.E. Hennon. 1987. An overview of decline and mortality of *Chamaecyparis nootkatensis* in Southeast Alaska. 327-331.

Shear, T. and K.O. Summerville (Eds.). 1999. Proceedings: Atlantic White Cedar Ecology and Management Symposium. United States Department of Agriculture Forest Service. 82 pp.

Silberhorn, G.M. 1995. Atlantic white cedar (*Chamaecyparis thyoides* (L.) BSP). Wetlands Program, Wetland Flora Technical Report. Virginia Institute of Marine Science, Gloucester Point, VA.

Silins, U. and R.L. Rothwell. 1998. Forest peatland drainage and subsidence affect soil water retention and transport properties in an Alberta peatland. Soil Science Society of America Journal 62: 1048-1056.

Simpson, B. 1990. Juniper/Washington's Entry. Simpson, B. The Great Dismal: A Carolinian's Swamp Memoir. 23-60. The University of North Carolina Press. Chapel Hill, North Carolina

Sipple, W.S. and W.A. Klockner. 1980. A unique wetland in Maryland. Castanea 45: 60-69.

Smilauer, P. 1992. CANODRAW. Microcomputer Power, Ithaca, New York.

Smith, F.W. and S.C. Resh. 1999. Age-related changes in production and below-ground carbon allocation in *Pinus contorta* forests. Forest Science 45: 333-341.

Smith, L.E. 1995. Regeneration of Atlantic white cedar at the Alligator River National Wildlife Refuge and Dare County Air Force Bombing Range. North Carolina State University, Raleigh, NC.

Smith, S.B. ND. Atlantic white cedar ecosystem restoration Dare County Air Force Range. Current Developments with Atlantic White-Cedar Management. Unpubl.

Soil and Plant Analysis Council, Inc. 1992. Handbook on reference methods for soil analysis.

Sørenson, LH. 1974. Rate of decomposition of organic matter in soil as influenced by repeated air drying-rewetting and repeated additions of organic material. Soil Biology and Biochemistry 6: 287-292.

Sorrie, B.A. and H.L. Woolsey. 1987. The status and distribution of Atlantic white cedar in Massachusetts. 135-143.

Stanek, W. and D. State. 1978. Equations predicting primary productivity (biomass) of trees, shrubs and lesser vegetation based on current literature. Canadian Forestry Service, Pacific Forest Research Center BC-X-183: 1-58.

Stephens, J.C. 1974. Subsidence of organic soils in the Florida Everglades: a review and update. pp. 352-374. Environments of South Florida.

Stevens, G.C. 1989. The latitudinal gradient in geographical range: How so many species coexist in the Tropics. American Naturalist 133: 240-256.

Stewart, P.C. 1979. Man and the swamp: The historical dimension. pp. 57-73 In Kirk, P.W. Jr. (Ed.) The Great Dismal Swamp. University Press of Virginia, Charlottesville, VA.

Stockwell, K.D. 1999. Structure and history of the Atlantic white cedar stands at Appleton Bog, Knox County, Maine. Natural Areas Journal 19(1): 47-56.

Stokes, M.A. and T.L. Smiley. 1996. An Introduction to Tree-Ring Dating. The University of Arizona Press, Tucson, Arizona.

Stone, W. 1894. Summer birds of the Pine Barrens of New Jersey. The Auk 133-139.

Stoughton, S. 1996. Helping Hands: Volunteers take to the woods in a difficult project that foresters say may keep cedar off the endangered list by helping it propagate. Virginia.

Street, M.W. and J.D. McClees. 1981. North Carolina's coastal fishing industry and the influence of coastal alterations. P. 238-251 IN Richardson, C.J. (Ed.) Pocosin Wetlands. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Summerville, K.O. ND. Atlantic white cedar cone production area. Current Developments with Atlantic White-Cedar Management. Unpubl.

Summerville, KO. ND. Atlantic white cedar herbicide evaluation. Current Developments with Atlantic White-Cedar Management . Unpubl.

Summerville, KO. ND. Atlantic whtie cedar Provenance study in North Carolina. Current Developments with Atlantic White-Cedar Management. unpubl.

Summerville, KO. ND. Bare-root vs. container seedlings. Current Developments with Atlantic White-Cedar Management Unpubl.

Summerville, KO. ND. Nursery bed soil amendments effects on seedling production. Current Developments with Atlantic White-Cedar Management. Unpubl.

Summerville, K.O., B. Gardner, and T.Shear. ND. A call for the formation of an Atlantic whtie cedar alliance. Current Developments with Atlantic White-Cedar Management. unpubl.

Summerville, K.O. and E. Hinesley. ND. Atlantic white cedar bare-root seedling standard evaluation. Current Developments with Atlantic White-Cedar Management. Unpubl.

Summerville, K.O. and E. Hinesley. ND. Provenance study trees rooted cuttings. Current Developments with Atlantic White-Cedar Management. Unpubl.

Svenson, H.K. 1929. *Chamaecyparis thyoides* in New Hampshire. Rhodora 31: 96-98.

Soil and Plant Analysis Council, Inc. 1992. Handbook on reference methods for soil analysis. Council on Soil Testing and Plant Analysis. Athens, GA. 202 pp.

Swamson, D.K. and D.F. Grigal. 1989. Vegetation indicators of organic soil properties in Minnesota. Soil Science Society of America Journal 53: 491-495.

Swails, L.F. 1957. A study of mature stand of Atlantic white cedar in South Carolina. Univ. South Carolina, Columbia, SC.

Swindel, B.F., L.F. Conde, J.E. Smith, and C.A. Hollis. 1982. Green weights of major tree species in north Florida pine flatwoods. Southern Journal of Applied Forestry 3: 74-78.

Taggart, J.B. 1981. Pocosin natural areas in North Carolina. p. 171-182 IN Richardson, C.J. (Ed.) Pocosin Wetlands. Stroudsburg, PA, Hutchinson Ross Publ. Co.

ter Braak, Cajo J.F. 1988. CANOCO. Microcomputer Power, Ithaca, New York.

ter-Mikaelian, M.T. and M.D. Korzukhin. 1997. Biomass equations for sixty-five North American tree species. Forest Ecology and Management 97: 1-24.

Terry, R.E. 1986. Nitrogen transformation in Histosols. p. 57-70 IN Chen, Y. and Y. Avnimelech (Ed.). The role of organic matter in modern agriculture. Dordrecht, Netherlands. Martinus Nijhoff Publ.

Terwilliger, K. 1987. Breeding birds of two Atlantic white cedar (*Chamaecyparis thyoides*) stands in the Great Dismal Swamp. pp. 215-227 IN A.D. Laderman (Ed.) Atlantic White Cedar. Boulder, CO: Westview Press.

Thompson, G.S. 2001. Assessment of soil biochemistry in Mid-Atlantic regional white cedar swamps. MS Thesis, Christopher Newport University, Newport News, VA. 68 pp.

Tiner, R.W., Jr., W. Zinni and K. Drake. 1987. An update of the U.S. Fish and Wildlife Service's National Wetlands Inventory Project. 339-342.

Train, E. and F.P. Day, Jr. 1982. Population age structures of tree species in four plant communities in the Great Dismal Swamp, Virginia. Castanea 47(1): 1-16.

Torrey, J., F.L.S. 1843. A Flora of the State of New York. Albany, New York, Carroll and Cook, Printers to the Assembly.

Tripp, J.T.B. 1987. The Atlantic white cedar swamp: Prospects for regulatory protection 353-362.

Tritton, L.M. and J.W. Hornbeck. 1982. Biomass Equations for Major Tree Species of the Northeast. USDA Forest Service.

Turgeon, J.J., K. Kamijo, and G. DeBarr. 1997. A new species of *Megastigmus* Dalman (Hymenoptera: Torymidae) reared from seeds. Proceedings of the Entomological Society of Washington 99(4): 608-614.

Uchida, K., N. Tomaru, C. Tomaru, C. Yamamoto, and K. Ohba. 1997. Allozyme variation in natural populations of Hinoki, *Chamaecyparis obtusa* (Sieb. Et Zucca.) Endl. and its comparison with the plus-trees selected from artificial stands. Breeding Science 47: 7-14.

United States Department of Agriculture Soil Conservation Service. 1997. Keys to soil Taxonomy (7th edition). Pocahontas Press, Inc., Blacksburg, VA. 545 pp.

U.S. Fish and Wildlife Service R5. 1986. Draft Environmental Impact Statement: Master Plan Great Dismal Swamp National Wildlife Refuge.

Updegraff, K., J. Pastor, S.D. Bridgham, and C.A. Johnston. 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecological Applications 5(1): 151-163.

Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. The American Naturalist 119 (4): 553-572.

Vitt, D.H. and N.G. Slack. 1975. An analysis of the vegetation of *Sphagnum*-dominated kettle-hole bogs in relation to environmental gradients. Can. J. Bot. 53: 332-359.

Vivian-Smith, G. 1997. Microtopographic heterogeneity and floristic diversity in experimental wetland communities. Journal of Ecology 85: 71-82.

Wagner, R.T., T.D. Petersen, D.W. Ross, and S.R. Radosevich. 1989. Competition thresholds for the survival and growth of ponderosa pine seedlings associated with woody and herbaceous vegetation. New For. 151-170.

Walbridge, M.R. 1991. Phosphorous availability in acid organic soils of the lower North Carolina coastal plain. Ecology 72(6): 2083-2100.

Wallace, P.M., D.M. Kent, and D.R. Rich. 1996. Responses of wetland tree species to hydrology and soils. Restoration Ecology 4: 33-41.

Ward, D.B. 1963. Southeastern limit of *Chamaecyparis thyoides*. Rhodora 65: 359-363.

Wardwell, R.E., W.A. Charlie, and K.A. Doxtader. 1982. Test method for determining the potential for decomposition in organic soils. pp. 218-227 IN P.M. Jarrett (Ed.) ASTM Special Technical Publication 820: Testing of Peat and Organic Soils. American Society for Testing and Materials, Philadelphia, PA.

Watts, W.A. 1983. Vegetational history of the eastern United States 25,000 to 10,000 years ago. IN Porter S.C. (Ed.) The Late Pleistocene. University of Minnesota Press, Minneapolis, Minnesota.

Weiss, R., J. Alm, R. Laiho, and J. Laine. 1998. Modeling moisture retention in peat soils. Soil Science Society of America Journal 62: 305-313.

Wells, B.W. 1942. Ecological problems of the southeastern United States coastal plain. Bot. Rev. 8: 533-561.

Werner, A.K. and M.J. Apps. 1999. A 70-year analysis of carbon fluxes in the Canadian forest sector. Ecological Applications 9: 526-547.

Westlake, D.F. 1963. Comparisons of plant productivity. Biological Review 38: 385-425.

Wharton, C.H., W.M. Kitchens, E.C. Pendleton, and T.W. Sipe. 1982. The ecology of bottomland hardwood swamps of the southeast: A community profile. Washington, DC, USA, U.S. Fish and Wildlife Service, Biological Services Program.

Wheeler, M. 1996. The vertical forest. Discover 77-82.

Whigham, D.F. 1981. An outside perspective on the Pocosins Conference and suggestions for future work. 346-355 IN Richardson, C.J. (Ed.) Pocosin Wetlands. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Whigham, D.P. and C.J. Richardson. 1988. Soil and plant chemistry of an Atlantic white cedar wetland on the inner coastal plain of Maryland. Canadian Journal of Botany 66: 568-576.

Whitehead, R.D. 1972. Developmental and environmental history of the Dismal Swamp. Ecological Monographs 42: 301-315.

Whitehead, D.R. and R.Q. Oaks, Jr. 1979. Developmental history of the Dismal Swamp. IN Kirk, P.D. Jr. (Ed). The Great Dismal Swamp. The University Press of Virginia, Charlottesville, VA. 427 pp.

Whittaker, R.H. 1953. A consideration of climax theory: the climax as a population and pattern. Ecological Monographs 23: 41-78.

Whittaker, R.H. 1961. Estimation of net primary production of forest and shrub communities. Ecology 42: 177-180.

Whittaker, R.H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology 47: 103-121.

Whittaker, R.H. 1963. Net production of heath balds and forest heaths in the Great Smoky Mountains. Ecology 44: 176-182.

Whittaker, R.H., F.H. Bormann, G.E. Likens, and T.G. Siccama. 1974. The Hubbard Brook ecosystem study: Forest biomass and production. Ecological Monographs 44: 233-252.

Whittaker, R.H. and G.M. Woodwell. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. Journal of Ecology 56: 1-25.

Wicker, M. ND. Atlantic white cedar wetland project. Current Developments with Atlantic White-Cedar Management. Unpubl.

Wieder, R.K. and G.E. Lang. 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63: 1636-1642.

Wilbur, H.M. 1981. Pocosin Fauna. P. 63-68 IN Richardson, C.J. (Ed.) Pocosin Wetlands. Stroudsburg, PA, Hutchinson Ross Publ. Co.

Wilde, S.A., E.C. Steinbrenner, R.S. Pierce, R.C. Dosen, and D.T. Pronin. 1953. Influence of Forest cover on the state of the ground water table. Soil Science Society of America Proceedings 17: 65-67.

Wilder, H.B., T.M. Robison, and K.L. Lindskov. 1978. Water Resources of Northeast North Carolina. U.S. Geological Survey, Raleigh, NC.

Wilson, E.O. 1999. The Diversity of Life. W.W. Norton and Company. New York.

Wilson, K.A. 1962. North Carolina Wetlands: Their Distribution and Management (Dare and Washington). Game Division North Carolina Wildlife Resources Commission, Raleigh, NC.

Woodwell, G. 1958. Factors controlling growth of pond pine seedlings in organic soils for the Carolinas. Ecological Monographs 38: 129-236.

Yanoskey, T.M. and W.M. Kappel. 1997. Tree Ring Record 100 Years of Hydrologic Change within a Wetland. U.S.G.S.

Yanoskey, T.M. Evidence of Floods on the Potomac River from Anatomical Abnormalities in the Wood of flood-Plain Trees. US Government Printing Office. Washington D.C.

Yates, R.F. and F.P. Day. 1983. Decay rates and nutrient dynamics in confined and unconfined leaf litter in the Great Dismal Swamp. The American Midland Naturalist 110(1): 37-45.

Young, P.J., J.P. Megonigal, R.R. Sharitz, and F.P. Day. 1993. False ring formation in baldcypress (*Taxodium distichum*) saplings under two flooding regimes. Wetlands 13(4): 293-298.

Young, P.J., B.D. Keeland, and R.R. Sharitz. 1995. Growth response of baldcypress (*Taxodium distichum* (L.) Rich.) to an altered hydrologic regime. American Midland Naturalist 133: 206-212.

Zampella, R.A. and R.G. Lathrop. 1997. Landscape changes in Atlantic white cedar (*Chamaecyparis thyoides)* wetlands of the New Jersey Pinelands. Landscape Ecology 12: 397-408.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Zhu, W-X and J.G. Ehrenfeld. 1999. Nitrogen mineralization and nitrification in suburban and undeveloped Atlantic white cedar wetlands. Journal of Environmental Quality 28: 523-529.

Zimmermann, G. 1996. The Atlantic white cedar (*Chamaecyparis thyoides*) regeneration experiments: years three and four (final reports). Richard Stockton College of New Jersey, Stockton, N.J.

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