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THE INFLUENCE OF MICROHABITAT VARIATION ON SEEDLING RECRUITMENT OF *CHAMAECYPARIS THYOIDES* AND *ACER RUBRUM*

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Abstract: *Chamaecyparis thyoides* (Atlantic white-cedar) swamps are in decline in the New Jersey Pinelands, while *Acer rubrum* (red maple) swamps are increasing. One possible reason for this occurrence may be differences in seedling recruitment of the two species. Seedling establishment of different species is expected to vary with physical conditions and requirements for safe sites. This study examined differences in seedling recruitment for *C. thyoides* and *A. rubrum* in the New Jersey Pinelands. A field survey of six *C. thyoides* swamps found that *C. thyoides* seedlings occur most often under an open or *C. thyoides* canopy on peaty, cedar needle covered soils or on mats of *Sphagnum.* In contrast, *A. rubrum* seedlings were most often found under *A. rubrum* canopies on *Sphagnum* mats or grass-dominated bottom areas. A greenhouse experiment was conducted to determine whether differences in microhabitat occupation were related to differences in growth of *C. thyoides* and *A. rubrum* seedlings. Seedlings were grown in different soil types (*Sphagnum* or peat) and at different water levels (inundated, saturated, or moist soil) typical of those found in *C. thyoides* swamps within the New Jersey Pinelands. *Chamaecyparis thyoides* experienced the greatest increase in height in moist soils and the least increase in height in inundated soils. *Chamaecyparis thyoides* achieved greater biomass than *A. rubrum* in peat soil, while *A. rubrum* had greater biomass in *Sphagnum.* These results indicate that *C. thyoides* and *A. rubrum* differ in conditions that are best for their seedling growth and that different management schemes may favor one species over the other.

Key Words: New Jersey Pinelands, seedling establishment, safe sites, wetlands

INTRODUCTION

There has been a decrease in the extent of *Chamaecyparis thyoides* (L.) Britton, Sterns, and Poggenburg (Atlantic white-cedar) in the wetlands of the New Jersey Pinelands over the past several decades and a gradual increase in the extent of hardwood species, especially *Acer rubrum* L. (red maple)(Zampella 1987). *Chamaecyparis thyoides* historically has been the dominant tree species in these swamps (Little 1979, Zampella 1987). Decrease in the extent and dominance of *C. thyoides* has been a cause for concern because *C. thyoides* is a desirable species for historical, economic, silvicultural, and aesthetic reasons (Zampella 1987, Ehrenfeld and Schneider 1991). *Acer rubrum* and other hardwood swamp species are generally considered to be less desirable in Pinelands swamps (Zampella 1987).

The decline in *C. thyoides* has been associated with human-caused disturbances reducing the amount of *C. thyoides* and a lack of successful recruitment of *C. thyoides* seedlings (Zampella 1987). *Chamaecyparis thyoides* swamps located in the Pinelands, which have experienced repeated exposure to disturbance or constant, low-level disturbances such as suburban run-off and the presence of roads, generally have few *C. thyoides* seedlings and lack soil conditions conducive to growth of *C. thyoides* seedlings (Ehrenfeld and Schneider 1991). Ehrenfeld and Schneider (1991) suspect that lack of *C. thyoides* seedlings will lead to replacement of *C. thyoides* by hardwood swamps, which correlates well with Zampella's (1987) analysis of historical trends. *Chamaecyparis thyoides* seedlings also appear to be a preferred item in the diet of *Odocoileus virginianus* Zimmermann (white-tailed deer), and areas with large populations of deer suffer large reductions in the number of *C. thyoides* seedlings (Little 1950, Stoltzfus 1990). If grazing pressure greatly reduces *C. thyoides* seedling survival, only slightly higher survival by *A. rubrum* may be enough to allow *A. rubrum* to replace *C. thyoides* as the dominant species in Pineland's swamps. *Acer rubrum* has been reported to become a swamp dominant following disturbance to Illinois cypress swamps (Anderson and White 1970).

Successful establishment of plant seedlings depends upon the seeds reaching safe sites (Harper 1977, Bazzaz 1991, Schupp 1995) that have conditions conducive to germination and growth. Safe sites have sometimes been envisioned as a species-specific regeneration niche (Grubb 1977) or plant invasion/recruitment window (Johnstone 1986). Many factors such as variations in microtopography, soil moisture, light availability, nutrient availability, presence of potential competitors, and presence of potential herbivores interact to form the boundaries of the safe site for a particular species (Harper 1977, Johnstone 1986). Safe sites or regeneration niches should be viewed as areas with differing probabilities of successful establishment (Harper 1977, Schupp 1995), so that a good safe site has a high probability of successful recruitment and a poor safe site has a low probability of recruitment. A safe site then is a site where a seed can successfully germinate and grow, although some sites will be "safer" or have higher probability of establishment than others. Each species presumably has a unique set of conditions that form its safe site or regeneration niche (Grubb 1977, Harper 1977).

About 15–20% of the New Jersey Pinelands are lowland forests (McCormick 1979), which are typically dominated by *C. thyoides, A. rubrum, Nyssa sylvatica* Marshall (black gum), and *Pinus rigida* Miller (pitch pine). *Chamaecyparis thyoides* often occurs in dense stands that may have a few tall *P. rigida* extending into the canopy and an understory of *A. rubrum* and *N. sylvatica. Chamaecyparis thyoides* forests are often surrounded by or adjacent to broadleaf lowland forests dominated by *A. rubrum. Nyssa sylvatica* and *Magnolia virginiana* L. (swamp magnolia) commonly occur in the broadleaf lowland forests. The hydrology is usually similar in both kinds of lowland forests (McCormick 1979, Zampella 1987).

Chamaecyparis thyoides seedlings have their highest rates of establishment in areas with peaty soils where the water table remains at or near the soil surface (10–13 cm deep) during the summer (Little 1950). Little (1950) found that *C. thyoides* seedlings often grew best on raised hummocks within New Jersey Pinelands swamps. In contrast, *A. rubrum* seedlings may become established even in areas with standing water and frequently grow well in open areas following disturbance (Korstian 1924). Thus, the two species seem to differ in their requirements for successful establishment and may have different safe sites.

Ehrenfeld (1995a) examined the relationship between microtopography and vegetation in Pinelands *C. thyoides* swamps. High points (hummocks) and low points (hollows or bottoms) had an average mean height difference of 30–37 cm in undisturbed, burned, and *C. thyoides* blowdown swamp sites, although height differences could be greater than 100 cm at some sites. Seedlings of several tree species, including *C. thyoides* and *A. rubrum,* and seedlings and adults of the shrubs *Clethra alnifolia* L., *Eubotrys racemosa* (L.) Nutt., *Gaylussacia frondosa* (L.) Torrey and Gray, *Kalmia angustifolia* L., *Rhododendron viscosum* (L.) Torrey, and *Vaccinium corymbosum* L., were most common at intermediate heights above the bottoms. All species avoided the lowest elevations. The abundances of woody plants shifted from swamp to swamp as the availability of intermediate height sites changed due to disturbance.

In a related study, Ehrenfeld (1995b) measured physical microhabitat differences between hummocks and hollows covered by either dead litter or live *Sphagnum.* Ehrenfeld found that presence or absence of *Sphagnum* had a large influence on the physical characteristics of hummocks and hollows. In particular, litter-topped hummocks and hollows had much greater differences in soil moisture content than did *Sphagnum*-covered hummocks and hollows. Litter-topped sites typically had drier hummock soil than hollow soil, whereas *Sphagnum*-covered areas had only slight differences in soil moisture, probably because of the movement of water within the *Sphagnum.*

This study was designed to examine the conditions under which *C. thyoides* and *A. rubrum* seedlings were most likely to achieve successful establishment. Six swamps located within the New Jersey Pinelands were surveyed to determine which microhabitats had the largest number of *C. thyoides* and *A. rubrum* seedlings. Microhabitats varied in terms of topographic elevation as well as presence or absence of *Sphagnum.* We also determined whether the two species differed in microhabitats they occupied most often. A greenhouse experiment was conducted to test whether *C. thyoides* and *A. rubrum* seedlings experienced different growth rates in different soil types (peat soil versus *Sphagnum*) and different water-level/soil-moisture conditions.

Table 1. Location of cedar swamps surveyed in this study. Two of the swamps, Papoose and Plains Branch, had adjacent undisturbed and burned portions that were surveyed. Mean depth (cm) to the water table is given for each swamp; standard errors are in parentheses.

Name of Swamp	State Forest	Latitude	Longitude	Water Table Depth—cm (se)
Coopers Branch	Lebanon	39 52′ 20″	74 31′ 02″	12.2 (1.35)
Reeds Branch	Lebanon	39 50′ 49″	74 30′ 51″	17.5 (1.72)
Shinns Branch	Lebanon	39 53′ 06″	74 30′ 20″	8.4 (1.64)
South Branch Mt. Misery	Lebanon	39 52′ 57″	74 28′ 18″	10.0 (2.06)
Papoose Branch—Undisturbed	Penn	39 45′ 00″	74 26′ 36″	13.6 (0.84)
Papoose Branch—Burned	Penn	39 45′ 00″	74 26′ 36″	13.8 (2.21)
Plains Branch—Undisturbed	Penn	39 47′ 28″	74 25′ 14″	7.9 (1.03)
Plains Branch—Burned	Penn	39 47′ 28″	74 25′ 14″	1.4 (0.46)

MATERIALS AND METHODS

Study Area

This research was conducted during the summer of 1993 in *C. thyoides* swamps located within the New Jersey Pinelands. The Pinelands occupy an area of about 445,000 ha on the outer Coastal Plain of southern New Jersey. The area is characterized by relatively flat, low-lying, sandy, acidic, and nutrient-poor soils (Forman 1979). Upland areas are dominated by forests of *Pinus rigida* and *Quercus* sp. (*Q. alba* L., *Q. prinus* L., *Q. velutina* Lam.), while lowlands are dominated by stands of *P. rigida, C. thyoides,* and *A. rubrum.*

The six *C. thyoides* swamps (Table 1) surveyed in the study were located within the northeastern corner of the Pinelands to ensure relatively similar habitat characteristics. All but one of the swamps were surrounded by *P. rigida* lowlands. The swamp on the South Branch of Mt. Misery was surrounded by a mixed *Pinus* and *Quercus* woodland. All of the swamps were relatively old, with none having been logged within the past 60 years (Stoltzfus 1990). The swamps at Papoose Branch and Plains Branch had been partially burned by wildfires in 1982 and 1990, respectively. This allowed a comparison of seedling establishment between undisturbed and recently burned swamps.

Field Surveys

A single sample plot of 20 × 20 m was established in each swamp. Papoose Branch and Plains Branch had sample plots established in burned and unburned areas of each swamp. The plots were located at least 100 m away from roads to minimize potential impacts of edges on human disturbance of seedlings. On each sampling date, five 20-m transects were randomly placed extending perpendicularly away from a 20-m-long baseline. Twenty points were sampled at 1-m intervals along each transect so that 100 points were sampled per site during each sampling period. The swamps were sampled twice during the summer, in early June and late July. The samples were collected at these two times to include seedlings that germinated in the spring and seedlings that germinated in the summer. Any *C. thyoides* and *A. rubrum* plants smaller than 10 cm in height were counted as seedlings. Different transects were sampled each time so no sample points were counted twice.

Surface microhabitat type and canopy cover were recorded at each sample point. Eighteen different microhabitat types could be reliably distinguished in the field (Table 2). Microhabitat surveys were limited to sites that were not flooded during the period of the survey; thus, sites with only standing water were excluded from the survey. The microhabitat types were similar to those observed by Huenneke and Sharitz (1986) in a cypress-tupelo swamp in the Savannah River floodplain. The microhabitats were divided into groups as to whether they were in depressions (bottoms) such as swamp bottom muck, *Sphagnum* bottom, cedar needle bottom, grass bottom; on raised hummocks such as *Sphagnum* hummock, cedar needle hummock, burned soil hummock; on dead wood such as fallen log (> 2.5-cm diameter), fallen branch, stump, within 10 cm of dead wood; on live wood such as a trunk, within 10 cm of a trunk, shrub, within 10 cm of a shrub, on a root, within 10 cm of a root; and standing water. We felt that microhabitats within 10 cm of either large live or dead stem or roots were dominated by presence of the stem or root.

Canopy cover was measured using a simple periscope made of PVC pipe with crosshairs fixed to the top of the periscope. A plumb bob was used to ensure that the periscope was vertical when the observation was made. The periscope was held directly over the sample and whatever was observed at the intersection of the crosshairs was scored as the canopy at that point. One observation was made per sample point. One-hundred points were sampled per site per sam-

Table 2. Availability of microhabitat types and distribution of number of seedlings in each microhabitat type in undisturbed and burned swamps.

	All Swamps	Undisturbed Swamps			Burned Swamps		
Microhabitat type	% Sample Points	% Sample Points	*C. thyoides* count (%)	*A. rubrum* count (%)	% Sample Points	*C. thyoides* count (%)	*A. rubrum* count (%)
Sphagnum bottom	22.9	26.2	253 (25.4)	104 (34.4)	13.5	25 (17.5)	108 (18.6)
Sphagnum hummock	17.7	19.0	273 (27.4)	122 (40.4)	14.0	28 (19.6)	93 (16.0)
Cedar needle hummock	17.6	23.0	324 (32.6)	48 (15.9)	1.5	11 (7.7)	0 (0)
Swamp bottom muck	7.4	7.7	2 (.2)	11 (3.6)	6.5	0 (0)	0 (0)
Grass bottom	6.9	0	0 (0)	0 (0)	27.5	24 (16.8)	260 (44.7)
Cedar needle bottom	6.6	8.8	91 (9.1)	9 (3.0)	0.2	0 (0)	31 (.5)
Standing water	4.2	3.3	0 (0)	0 (0)	6.8	0 (0)	0 (0)
Near deadwood	4.0	3.1	15 (1.5)	5 (1.7)	6.8	4 (2.8)	39 (6.7)
Near shrub	2.8	0.8	9 (.9)	0 (0)	8.8	28 (19.6)	62 (10.7)
Fallen log	2.2	2.1	8 (.8)	0 (0)	2.5	6 (4.2)	5 (.9)
Stump	1.3	0.7	4 (.4)	0 (0)	3.0	1 (.7)	4 (.7)
Near trunk	1.5	2.0	5 (.5)	1 (.3)	0	0 (0)	0 (0)
Shrub	1.2	0.3	0 (0)	0 (0)	4.0	1 (.7)	7 (1.2)
Burned soil hummock	1.1	0	0 (0)	0 (0)	4.2	14 (9.8)	0 (0)
Fallen branch	0.9	1.1	10 (1.0)	0 (0)	0.5	0 (0)	0 (0)
Trunk	0.9	1.2	0 (0)	0 (0)	0	0 (0)	0 (0)
Roots	0.2	0.2	0 (0)	1 (.3)	0.2	1 (.7)	0 (0)
Near roots	0.1	0.2	1 (.1)	1 (.3)	0	0 (0)	0 (0)

pling period. The percentage of sample points occupied by a particular canopy type was recorded and used in subsequent data analysis. Seven canopy types were observed: open sky, *C. thyoides, A. rubrum, Nyssa sylvatica, Magnolia virginiana, Vaccinium corymbosum* (blueberry), and *Clethra alnifolia* (sweet pepperbush).

A 0.10 m^2 quadrat was placed at each sampling point. The number of *C. thyoides* and *A. rubrum* seedlings found within the quadrat was counted and recorded.

Wells to measure depth of the water table were permanently installed at the 4 corners of each sample plot. Wells were constructed of a 1.5 m long piece of 2.5-cm-diameter PVC pipe with perforations cut into the pipe every 2 cm. The wells were pushed into the soil so that only 10 cm of pipe remained above the soil surface. The well openings were covered with a PVC cap. Water-table depth was measured using a Solinst Water Level Meter.

Soil-moisture content was measured gravimetrically for each plot by collecting a 2 cm^3 plug of soil from the soil surface. Soil samples were collected during the last week of July, with one set of samples coming from each swamp. Samples were collected from the swamp bottom muck, *Sphagnum* bottom, *Sphagnum* hummock, cedar needle bottom, cedar needle hummock, and grass bottom microhabitats only. Soil samples were placed in plastic bags and taken to the laboratory to determine wet weight. The samples were then dried for 48 hours at 70°C and weighed again. Soil moisture was calculated as the percentage difference between dry and wet weights. Many of the soil samples were super-saturated with water when collected and thus contained much more water than 100% of their dry weight.

Greenhouse Experiments

Chamaecyparis thyoides and *A. rubrum* seedlings were obtained from the Arrowhead Nursery located in Malaga, New Jersey on June 25, 1993. Seedlings were all descended from stock native to the New Jersey Pinelands (J. Arensault pers. comm.). The seedlings were 2.5 to 5 cm tall at the time of purchase, and were in their first growing season since germination. At the time of purchase the seedlings were growing in greenhouse flats. Individual seedlings were transplanted into standard square plastic pots with a soil volume of 450 cm^3 upon return to the Rutgers Pinelands Field Station. Prior to transplanting, the seedlings were gently washed to remove the greenhouse soil from their roots. Seedlings were planted into one of two soil types collected from *C. thyoides* swamps: peat soil from South Branch Mt. Misery or live *Sphagnum* with a little sand from Coopers Branch. Both *C. thyoides* and *A. rubrum* seedlings had been observed growing on carpets of live *Sphagnum* in bottoms and hummocks in the field. The *Sphagnum* was collected from *Sphagnum* bottom microhabitat and the peat from cedar needle hummock microhabitat.

The seedlings were then placed in small plastic pools in the greenhouse at the Rutgers Pinelands Field Station. Seedlings were grown in a greenhouse to ensure uniform environmental conditions and to minimize the chance of disturbance by humans or animals.

Seedlings were randomly assigned to one of three water-level/soil-moisture treatments: 1) inundated in which the water level was maintained even with the soil surface, 2) saturated in which the water level was maintained 5 cm below the soil surface, 3) moist in which pots were thoroughly watered at least every other day, but the pots were allowed to drain. In the moist water treatment, the plastic pools had many perforations to allow drainage. Two pools were assigned randomly to each water-level/soil-moisture treatment. A total of 6 pools were used. Each pool contained 5 replicates of every possible combination of seedling species and soil type. Thus, each pool contained 5 *C. thyoides* seedlings growing in *Sphagnum,* 5 *C. thyoides* seedlings growing in peat, 5 *A. rubrum* seedlings growing in *Sphagnum,* and 5 *A. rubrum* seedlings growing in peat. Seedlings were randomly mixed together within each pool.

At the start of the experiment (June 25, 1993), each plant was individually marked and its starting height was measured. The seedlings were allowed to grow until August 16, 1993. The seedlings were checked at least every other day for mortality and any deaths recorded. At the end of the experiment, the seedlings were measured for final height above ground. The seedlings were then placed in a drying oven for 48 hours at 70°C. When dry, the seedlings were weighed to determine their root, shoot, and total biomass.

Soil moisture was analyzed gravimetrically at the end of the greenhouse experiment by randomly selecting 3 pots for each combination of seedling species, soil type, and water-level/soil-moisture treatment. A 2 cm^3 plug was collected from the top of each pot and analyzed as in the field study.

Data Analysis

Field Surveys. Chi-square tests were performed to compare the number of observed seedlings from a particular microhabitat type to the expected number of seedings based on the proportional occurrence of that microhabitat. Separate chi-square analyses were performed for *C. thyoides* and *A. rubrum* seedlings. Similar chi-square tests were performed to determine whether the number of seedlings observed differed from the number expected with respect to canopy type. The affinity of *C. thyoides* and *A. rubrum* seedlings for bottom habitats (low and wetter habitats) was compared to the affinity for hummock habitats (high and drier habitats) using unpaired, two-tailed t-tests. The microhabitat types compared were swamp bottom muck, *Sphagnum* bottom, cedar needle bottom, and grass bottom for low sites versus *Sphagnum* hummock, cedar needle hummock, and burned hummock for high sites. Affinity was calculated by dividing the number of seedlings found on either bottom or hummock habitat by the number of times we sampled bottom or hummock habitat in each transect. We also compared the affinity of *C. thyoides* and *A. rubrum* seedlings for *Sphagnum* vs. non-*Sphagnum* microhabitat types using unpaired, two-tailed t-tests. The microhabitat types compared were *Sphagnum* bottom and *Sphagnum* hummock versus swamp bottom muck, cedar needle bottom, cedar needle hummock, grass bottom, and burned hummock for non-*Sphagnum* microhabitat types. Affinity was calculated by dividing the number of seedlings found on either *Sphagnum* or non-*Sphagnum* habitat by the number of times we sampled *Sphagnum* or non-*Sphagnum* habitat in each transect. A repeated measures ANOVA was used when comparing water-table depth among the swamps so that average water-table depth on each sampling date could be included in the analysis.

Greenhouse Experiment. Seedling survival was compared among the plastic experimental pools by a one-way ANOVA, with pool as the independent variable and percentage of seedlings surviving until the end of the experiment as the dependent variable. There was no significant difference in survival among the pools ($F = 1.093$, $df = 5, 114$, $p = 0.3681$). Therefore, we combined data among pools with the same water-level/soil-moisture treatment when performing further data analyses.

Separate three-way ANOVAs were performed to compare change in height (growth) of the seedlings, shoot biomass, and soil-moisture content. In each three-way ANOVA, the independent variables were seedling species, water-level/soil-moisture treatment, and soil type. Homogeneity of the variances for all data was tested prior to the ANOVAs using Cochran's C Test. *Post hoc* Bonferroni/Dunn tests were performed to compare treatments following a significant ANOVA result.

RESULTS

Field Surveys

A total of 1138 *C. thyoides* seedlings and 883 *A. rubrum* seedlings were observed during this study. As

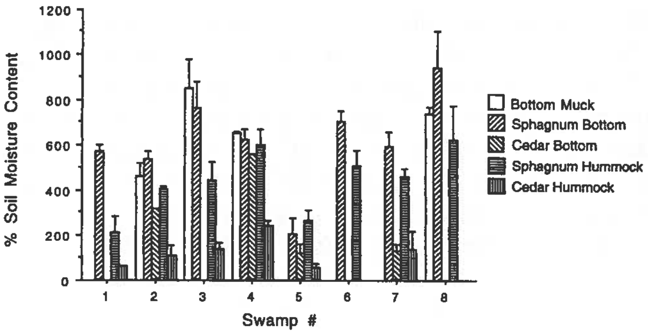

Figure 1. Mean soil-moisture content measured gravimetrically and expressed as a percentage of dry weight of soil. Soil samples were collected at random points in 5 different soil types located within 8 swamps. Three replicate samples were collected for each soil type in each swamp. Swamp #: 1 = Reeds Branch, 2 = Shinns Branch, 3 = Coopers Branch, 4 = South Branch Mt. Misery, 5 = Papoose Branch undisturbed portion, 6 = Papoose Branch burned portion, 7 = Plains Branch undisturbed portion, 8 = Plains Branch burned portion. Error bars show ±1 S.E.

will be shown below, *C. thyoides* and *A. rubrum* seedlings were not distributed randomly with respect to microhabitat or canopy cover, and the two species differed in their distribution patterns with respect to both microhabitat and canopy cover.

When all swamps are considered together (n = 1600 sample points because each swamp plot was sampled twice), the most prevalent microhabitat types are *Sphagnum* bottom, *Sphagnum* hummocks, and cedar needle hummocks (Table 2). Other fairly common microhabitats, those that occurred at greater than 5% of the sample points, were swamp bottom muck, grass bottom, and cedar needle bottom. The burned portions of Papoose Branch and Plains Branch differed in composition of microhabitats from the undisturbed swamps. The burned swamps were dominated by grass bottom, *Sphagnum* hummock, *Sphagnum* bottom, points within 10 cm of growing shrubs, and swamp bottom muck (Table 2).

Soil moisture content differed significantly among microhabitat types measured (swamp bottom muck, *Sphagnum* bottom, *Sphagnum* hummock, cedar needle bottom, cedar needle hummock, and grass bottom; F = 30.720, df = 5, 57, p <0.0001) and among swamps (F = 62.425, df = 7, 57, p < 0.0001). Both the swamp bottom muck and *Sphagnum* bottom soils were extremely moist, holding an average amount of water equal to 678% and 621% of their dry weights, respectively (Figure 1). The highest average soil-moisture content for a soil type was 942% for the *Sphagnum* bottom at Plains Branch, burned portion. The driest soil type was soil from cedar needle hummocks, which contained water equal to 125% of its dry weight. The unburned portion of Plains Branch had the highest average soil-moisture content for an entire swamp (617%), while the burned portion of Papoose Branch had the lowest average soil-moisture content (164%) (Figure 1).

Depth to the water table differed significantly among the swamps (repeated measures ANOVA, F = 3.055, df = 7, 96, p <0 .05). The burned portion of Plains Branch had the highest water table (closest to the surface) and Reeds Branch had the lowest water table (Table 1).

Chamaecyparis thyoides seedlings were not distributed at random with respect to microhabitat types in the undisturbed swamps (X^2 = 71.358, df = 16, p < 0.0001). *Chamaecyparis thyoides* seedlings were most often found on cedar needle hummocks, *Sphagnum* hummocks, *Sphagnum* bottoms, and cedar needle bottoms in the undisturbed swamps (Table 2). *Acer rubrum* seedlings were not distributed at random with respect to microhabitat type in undisturbed swamps either (X^2 = 197.485, df = 16, p < 0.0001). *Acer rubrum* seedlings occurred most often on *Sphagnum* bottoms, *Sphagnum* hummocks, and grass bottoms in the undisturbed swamps (Table 2).

Only 143 *C. thyoides* seedlings were found in the burned swamps (portion of Papoose Branch burned in 1982 and portion of Plains Branch burned in 1990), and they were not randomly distributed with respect to microhabitat type (X^2 = 27.986, df = 10, p <0 .01). Most of these *C. thyoides* seedlings were found in *Sphagnum* hummock, *Sphagnum* bottom, near shrub and grass bottom habitats (Table 2). Over half of the *A. rubrum* seedlings were found in burned swamps. They were not distributed at random with respect to microhabitats (X^2 = 43.173, df = 10, p < 0.0001). *Acer rubrum* seedlings most often occurred on either grass bottoms or *Sphagnum* bottoms (Table 2).

Chamaecyparis thyoides, which occupied 50.3% of the canopy, was the major component of the canopy when all swamps were considered together (Table 3). Open areas (26%) were also an important component of the canopy. The burned portions of the swamps differed in canopy composition from the undisturbed swamps. *Chamaecyparis thyoides* occupied 67.3% of the undisturbed canopy; open areas and *Nyssa sylvatica* were also fairly common. The burned portions of the swamps were dominated by open areas, while *A. rubrum* was also common (Table 3).

Chamaecyparis thyoides seedlings were found more often than expected in the open and underneath *C. thyoides* canopy in the undisturbed swamps and thus were not randomly distributed with respect to canopy (X^2 = 42.239, df = 6, p <0 .0001) (Table 3). *Acer rubrum* seedlings were distributed randomly with re-

Table 3. Availability of canopy types and distribution of number of seedlings in each canopy type in undisturbed and burned swamps.

	All Swamps	Undisturbed Swamps			Burned Swamps		
Canopy type	% Sample Points	% Sample Points	*C. thyoides* count (%)	*A. rubrum* count (%)	% Sample Points	*C. thyoides* count (%)	*A. rubrum* count (%)
Open	26.0	10.6	159 (16.0)	25 (8.3)	71.5	109 (76.2)	223 (38.4)
C. thyoides	50.3	67.3	709 (71.3)	206 (68.2)	0	0 (0)	0 (0)
A. rubrum	9.2	6.3	47 (4.7)	21 (7.0)	17.8	27 (18.9)	263 (45.3)
Nyssa sylvatica	11.5	11.9	55 (5.5)	38 (12.6)	10.0	7 (4.9)	83 (14.3)
Magnolia virginiana	0.4	0.5	3 (. 3)	2 (.7)	0	0 (0)	0 (0)
Vaccinium corymbosum	2.2	2.7	21 (2.1)	7 (2.3)	0.7	0 (0)	12 (2.0)
Clethra alnifolia	0.4	0.6	1 (.1)	3 (1.0)	0	0 (0)	0 (0)

spect to canopy in the undisturbed swamps (X^2 = 1.634, df = 6, p =0.95) (Table 3).

In the burned swamps, *C. thyoides* seedlings were distributed at random with respect to canopy cover (X^2 = 2.767, df = 3, p = 0.429). In contrast, *A. rubrum* seedlings were not distributed at random with respect to canopy cover (X^2 = 36.183, df = 3, p <0 .0001). *Acer rubrum* seedlings were most often found under an *A. rubrum* canopy and were not found in open areas in the burned swamps (Table 3).

Chamaecyparis thyoides seedlings did not differ in their occurrence on hummocks or bottoms (t = 1.85, df = 30, p= 0.074). There was no significant difference in the number of *A. rubrum* seedlings with respect to hummock versus bottom microhabitats (t = 0.71, df = 30, p = 0.48). There was also no significant difference in the frequency of occurrence of hummock and bottom microhabitat types among the swamps (t = 1.26, df = 30, p= 0.22).

There was no significant difference in the occurrence of *C. thyoides* seedlings with respect to presence or absence of *Sphagnum* in the microhabitat (t = 0.95, df = 30, p = 0.35). *Acer rubrum* seedlings also did not differ with respect to *Sphagnum* or non-*Sphagnum* microhabitat type (t = 1.17, df = 30, p = 0.25). There was no difference in the frequency of occurrence of *Sphagnum* versus non-*Sphagnum* microhabitat types among the swamps (t = 0.15, df = 30, p = 0.88).

Table 4. Number of seedlings observed in each swamp.

Swamp	*C. thyoides*	*A. rubrum*
Reeds Branch	57	72
Shinns Branch	128	43
Coopers Branch	63	56
South Branch Mt. Misery	254	64
Papoose Branch Unburned	232	25
Papoose Branch Burned	54	580
Plains Branch Unburned	261	42
Plains Branch Burned	89	1

Chamaecyparis thyoides seedlings were much more abundant in the undisturbed portions than in the burned portions of Papoose Branch (232 seedlings vs. 54) and Plains Branch (261 vs. 89) swamps (Table 4). *Acer rubrum* seedlings were less common than *C. thyoides* seedlings in all of the swamps except for Reeds Branch and the burned portion of Papoose Branch. Over half of the *A. rubrum* seedlings observed (580) were found in the burned portion of Papoose Branch. The burned swamp at Papoose Branch had a canopy with many *A. rubrum* trees and bottom areas dominated by grass and *Sphagnum.*

The numbers of seedlings observed in each transect in each swamp on each of two sampling dates were compared for burned versus unburned swamp areas. There was no significant difference in the abundance of *C. thyoides* seedlings in unburned portions of the swamps compared the burned portions of the swamps (t = −1.00, df = 14, p = 0.33). *Acer rubrum* seedlings were significantly more common in the burned portions than in the unburned portions of the swamps (t = 2.54, df = 14, p = 0.024). There was a significant difference in the abundance of microhabitat types between the unburned and burned portions of the swamps (F= 5.83, df= 34, 252, p< 0.001). This difference was largely due to the presence of grass bottom and burned hummock microhabitats in the burned swamps that did not occur in the unburned portions of the swamps.

Greenhouse Experiment

The soil moisture content of the moist soil treatment (602% ± 40.06) (mean ± standard error) was slightly less than the average soil-moisture contents measured in the field for swamp bottom muck (678% ± 52.93)

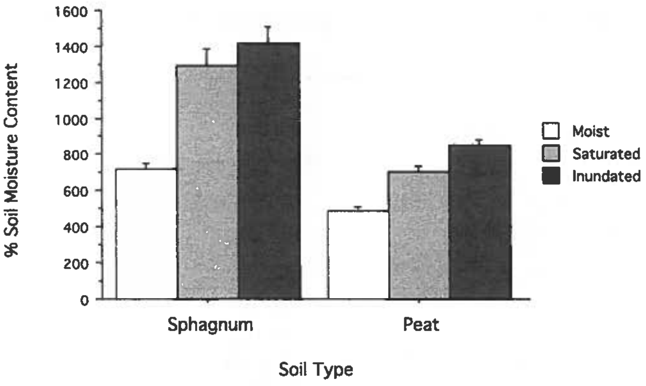

Figure 2. Mean soil-moisture content shown as percent of dry weight for sphagnum and peat soils exposed to different water-level/soil-moisture treatments. Error bars show ±1 S.E.

and *Sphagnum* bottom (621% ± 46.06) soils. The inundated soil treatment (1131% ± 97.98) and the saturated soil treatment (998% ± 98.84) both had soil-moisture contents higher than the highest average measured in the field (942% ± 161.49 in the *Sphagnum* bottom at Plains Branch, burned portion). Soil-moisture content differed significantly among water-level treatments (F = 58.620, df = 2, 24, p <0 .0001) (Figure 2).

Chamaecyparis thyoides seedlings experienced their greatest growth (measured as change in height from the start to the finish of the experiment) in the moist, drained soil conditions. Growth was least in the inundated soil conditions and intermediate in saturated soil. *Acer rubrum* seedlings had similar growth in all conditions (Figure 3). Thus, a significant species × water-level interaction was detected (Table 5). *Chamaecyparis thyoides* grew more than *A. rubrum* in the moist and saturated soil conditions. *Acer rubrum* and *C. thyoides* grew about the same in inundated soil conditions (Figure 3). Soil type did not have a significant effect on growth of either *C. thyoides* or *A. rubrum.*

Both *C. thyoides* and *A. rubrum* had significantly less shoot biomass in the inundated soil conditions than in other soil conditions (Table 5) (Figure 4). *Chamaecyparis thyoides* had its greatest shoot biomass in the moist soil and intermediate biomass in saturated soil. *Acer rubrum* had its greatest biomass in the saturated soil and intermediate biomass in the moist soil. *Chamaecyparis thyoides* had significantly greater shoot biomass in the moist soil than *A. rubrum,* while

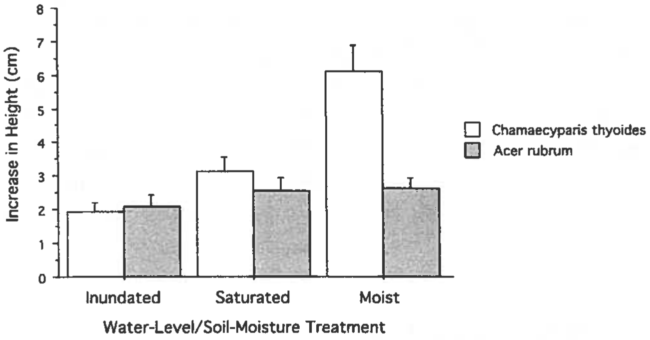

Figure 3. Mean increase in height (growth) (cm) of the *C. thyoides* and *A. rubrum* seedlings for the period of the study, June 25 to August 16, 1993. Means were calculated for all seedlings in specific water-level/soil-moisture treatments. Error bars show ±1 S.E.

Table 5. ANOVA tables for comparisons of change in height (growth) and shoot biomass for *C. thyoides* and *A. rubrum* seedlings in the greenhouse experiment. Sources of variation are Species (*C. thyoides* or *A. rubrum*); Water level (inundated, saturated, or moist); Soil (*Sphagnum* or peat).

Change in height (growth) of the seedlings

Source of variation	DF	F	p
Species	1	12.465	0.0007
Water level	2	13.531	<0.0001
Species × Water level	2	8.253	0.0005
Soil	1	0.388	0.5347
Species × Soil	1	0.206	0.6507
Water level × Soil	2	2.853	0.0629
Species × Water level × Soil	2	2.349	0.1013
Residual	90		

Shoot biomass of the seedlings

Source of variation	DF	F	p
Species	1	0.776	0.3806
Water level	2	4.343	0.0158
Species × Water level	2	3.489	0.0347
Soil	1	0.039	0.8438
Species × Soil	1	4.134	0.0450
Water level × Soil	2	2.595	0.0802
Species × Water level × Soil	2	0.869	0.4227
Residual	90		

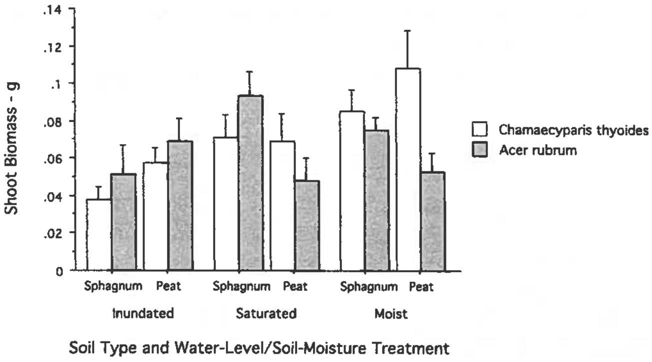

Figure 4. Mean shoot biomass (g) for *C. thyoides* and *A. rubrum* seedlings plotted for soil type and water-level/soil-moisture treatment at the end of the experiment. Error bars show ±1 S.E.

A. rubrum had significantly greater shoot biomass in the inundated soil. There was a significant interaction between soil type and species and a significant interaction between soil type and water level, and both influenced shoot biomass (Table 5). *Post hoc* Bonferroni/Dunn tests showed that *C. thyoides* achieved higher shoot biomass in peat soils than in *Sphagnum* soils and had greater shoot biomass than *A. rubrum* in moist and saturated peat soils. *Acer rubrum* achieved higher shoot biomasses in *Sphagnum* soils and had greater shoot biomass than *C. thyoides* in inundated and saturated *Sphagnum* soils (Figure 4).

DISCUSSION

Field Survey

Chamaecyparis thyoides and *A. rubrum* seedlings differed in the types of microhabitats they occupied and in the types of canopy under which they were found. In general, both species were most common in microhabitats that were not close to (within 10 cm) either live or dead plants. Both species were found in *Sphagnum* bottoms and hummocks, but *C. thyoides* was also commonly found on cedar needle bottoms and hummocks, and *A. rubrum* was commonly found on grass bottoms in disturbed swamps. Neither species was ever found growing in standing water.

Seedlings of different species of both woody and herbaceous plants have been observed to occur in different microhabitats in other studies of seedling establishment in temperate woody swamps and floodplain forests (Hardin and Wistendahl 1983, Huenneke and Sharitz 1986, 1990, Streng et al. 1989, Titus 1990). These other studies found a general trend for seedlings to grow in somewhat elevated areas and not in standing water. Standing water and soils saturated with water limit seedling survival and growth of most temperate woody species (Kozlowski 1984). The swamps observed in this study only had standing water in deep depressions or pools (at least 25 cm in depth) and stream meanders during the summer of 1993, a drought summer (J. Ehrenfeld pers. obsv.). Thus, the seedlings were able to germinate and grow even in shallow depressions and bottom microhabitats. In other, wetter years, seedlings probably would not have grown in the bottoms due to standing water. A critical issue is that seeds may germinate in sites that are not conducive to long-term survival. Seeds may be trapped close to adult plants and germinate there even though the chance for subsequent survival is low or the sites that provide the best location for germination may be subject to seed predation that prevents successful recruitment (Streng et al. 1989, Huenneke and Sharitz 1990). Although this study did not examine long-term survival of the seedlings, other studies have indicated that while most germination and initial establishment occurs on hummocks, long-term survival of the seedlings is strongly influenced by the presence or absence of deer grazing (Zampella 1987).

Chamaecyparis thyoides seedlings were most often found growing on hummocks (of *Sphagnum* or cedar needles) and bottoms dominated by *Sphagnum* or cedar needles in the undisturbed swamps. The cedar needle hummocks and bottoms were microhabitats in which a layer of cedar needles, usually 2 to 4 cm thick, lay on top of peaty soils (Ehrenfeld 1995b). *Chamaecyparis thyoides* seedlings have a long-standing reputation for preferring to establish on peaty soils (Korstian 1924, Little 1950). *Acer rubrum* seedlings were found most often on *Sphagnum* bottoms and hummocks and grass bottoms and in the past have been reported to grow more frequently in areas that lack peat soil (Korstian 1924). The two species seemed to occupy somewhat different microhabitats in the cedar swamps studied due to their differences in occurrence on cedar needle- or grass-dominated microhabitats.

Seed dispersal and establishment are often strongly influenced by the presence of parent plants (Harper 1977). *Chamaecyparis thyoides* seedlings were most common under an open canopy or a canopy of *C. thyoides* trees that probably served as a source for the seeds or a seed bank. *Chamaecyparis thyoides* seedlings can establish in full sun if a nearby source of seeds exists or if a seed bank survives a disturbance such as fire or logging. If fires are severe enough to destroy the peat layer, *C. thyoides* is limited in its ability to re-establish (Korstian 1924, Little 1979). *Acer rubrum* is often successful at invading open sites (Korstian 1924, Little 1979), and in this study, *A. rubrum* was most common under a canopy of young *A. rubrum* trees. The wind-borne samaras of *A. rubrum* allow it to easily invade open areas within a swamp or forest. The swamp located in the burned portion of Papoose Branch had many *A. rubrum* that probably became established after the fire in 1982, and these trees may have provided a source for the many *A. rubrum* seedlings observed there. In contrast, the burned portion of the swamp at Plains Branch lacked many *A. rubrum,* probably due to the relatively short time since the fire in 1990 (3 years at the time of the study).

Greenhouse Experiment

Chamaecyparis thyoides and *A. rubrum* seedlings differed in their response to the water-level/soil-moisture treatments. In general, *C. thyoides* achieved better growth than *A. rubrum* (in terms of height and biomass) in the moist but freely draining soil, while *A. rubrum* achieved better growth in the saturated soil.

Although both species had their poorest growth in the inundated soils, *A. rubrum* usually grew better than *C. thyoides* in the inundated soils and seemed better able to tolerate those conditions. Soil type (in terms of peat vs. *Sphagnum*) only influenced shoot biomass, with *C. thyoides* achieving higher shoot biomass in peat soils and *A. rubrum* achieving higher shoot biomass in *Sphagnum* soils.

The differences in growth fit past observations of *C. thyoides* seedlings growing well in peat soils and *A. rubrum* occurring in non-peat soils (Korstian 1924). Moizuk and Livingston (1966) reported that *A. rubrum* seedlings that grew on floating mats of live *Sphagnum* in upland Massachusetts bogs usually did not survive more than 1 to 2 years. Vedagiri and Ehrenfeld (1991) conducted a two-month microcosm experiment and observed that roots of *A. rubrum* seedlings in live *Sphagnum* grew "loosely" and rarely grew down into sediment underneath the *Sphagnum.* In this experiment, *A. rubrum* seedlings may not have survived if allowed to grow for a longer period of time. Also, using established seedlings rather than starting with seed (as in Vedagiri and Ehrenfeld (1991)) may have given *A. rubrum* seedlings a better chance to develop deeper growing roots. The *Sphagnum* carpets observed in the Pinelands swamps lay directly over peat or muck and are not floating mats. It is thus possible that given enough time, the roots of *A. rubrum* seedlings may grow through the *Sphagnum,* reach a more solid substrate, and become established plants.

The experimental conditions seem representative of those in nature. None of the field soil samples came from sites with standing water. Sites with standing water in a *Sphagnum* or cedar needle bottom would probably have soil-moisture contents as high as those in the inundated treatment. The experimental results indicate that *C. thyoides* can grow well (at least in comparison to *A. rubrum*) in any conditions measured in the field. However, *A. rubrum* may have an advantage in conditions that are wetter (such as during floods or runoff) than observed during the field survey. Korstian (1924) reported that *A. rubrum* seedlings can "sprout and come up through a foot or more of water (pg. 191)."

Similar results have been observed in other studies of woody swamp species. *Nyssa sylvatica* var. *biflora* (swamp tupelo) and *N. aquatica* (water tupelo) both grew poorly in conditions of deep, stagnant water, and water tupelo grew better in deep, moving water and shallow, moving water (Harms 1973). Swamp tupelo only grew well in shallow, moving water. The two species also differed in response to soil types, with water tupelo growing better in more nutrient-rich soil and swamp tupelo growing the same in nutrient-rich and nutrient-poor soils (Harms 1973). Herbaceous wetland species have also been shown to differ in their growth in different water levels (Grace and Wetzel 1981, Kirkman and Sharitz 1993).

CONCLUSIONS

The results of this study together with those of Ehrenfeld (1995a, 1995b) help to place bounds on the safe sites/regeneration niches for *C. thyoides* and *A. rubrum* in the Pinelands. While both species can become well-established on *Sphagnum*-covered ground and greenhouse pots, *C. thyoides* has better recruitment success in cedar needle/litter covered soil and *A. rubrum* has better success in disturbed areas where grass is the dominant ground cover. Greenhouse experiments showed a tendency for *C. thyoides* to grow better than *A. rubrum* in slightly drier conditions. Thus, the species do seem to differ in terms of safe site. However, of greater importance in terms of successful establishment in current Pinelands' conditions is the presence of a seed source. Both *C. thyoides* and *A. rubrum* had their largest number of seedlings in areas where there was a canopy of adult trees to supply seeds. This study found most *C. thyoides* under a *C. thyoides* canopy. Greenhouse growth experiments observed best growth of *C. thyoides* seedlings in peat soils. Microhabitats lacking in peat soils and a canopy lacking *C. thyoides* favored *A. rubrum.* Overall, successful *C. thyoides* reproduction and establishment of new stands of *C. thyoides* seems to be dependent upon both peat soils and a source of *C. thyoides* seeds.

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LITERATURE CITED

Anderson, R. C. and J. White. 1970. A cypress swamp outlier in southern Illinois. Illinois Academy of Science 63:6–13.

Bazzaz, F. A. 1991. Habitat selection in plants. American Naturalist 137:S116-S130.

Ehrenfeld, J. G. 1995a. Microtopography and vegetation in Atlantic white-cedar swamps: the effects of natural disturbances. Canadian Journal of Botany 73:474–484.

Ehrenfeld, J. G. 1995b. 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. Journal of Applied Ecology 28:467–490.

Forman, R. T. T. 1979. Pine Barrens: Ecosystem and Landscape. Academic Press, New York, NY, USA.

Grace, J. B. and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. American Naturalist 118:463–474.

Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biological Reviews 52:107–145.

Hardin, E. D. and W. A. Wistendahl. 1983. The effects of floodplain trees on herbaceous vegetation patterns, microtopography and litter. Bulletin of the Torrey Botanical Club 110:23–30.

Harms, W. R. 1973. Some effects of soil type and water regime on growth of tupelo seedlings. Ecology 54:188–193.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, New York, NY, USA.

Huenneke, L. F. and R. R. Sharitz. 1986. Microsite abundance and distribution of woody seedlings in a South Carolina cypress-tupelo swamp. American Midlands Naturalist 115:328–335.

Huenneke, L. F. and R. R. Sharitz. 1990. Substrate heterogeneity and regeneration of a swamp tree *Nyssa aquatica*. American Journal of Botany 77:413–419.

Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. Biological Reviews 61:369–394.

Kirkman, L. K. and R. R. Sharitz. 1993. Growth in controlled water regimes of three grasses common in freshwater wetlands of the southeastern U.S. Aquatic Botany 44:345–359.

Korstian, C. F. 1924. Natural regeneration of southern white-cedar. Ecology 2:188–191.

Kozlowski, T. T. 1984. Responses of woody plants to flooding. p. 129–163. *In* T. T. Kozlowski (ed.) Flooding and Plant Growth. Academic Press, New York, NY, 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.

Little, S. 1979. Fire and plant succession in the New Jersey Pine Barrens. p. 297–314. *In* R. T. T. Forman (ed.) Pine Barrens: Ecosystem and Landscape. Academic Press, New York, NY, USA.

McCormick, J. 1979. The vegetation of the New Jersey Pine Barrens. p. 229–243. *In* R. T. T. Forman (ed.) Pine Barrens: Ecosystem and Landscape. Academic Press, New York, NY, USA.

Moizuk, G. A. and R. B. Livingston. 1966. Ecology of red maple (*Acer rubrum* L.) in a Massachusetts upland bog. Ecology 47:942–950.

Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82: 399–409.

Stoltzfus, D. L. 1990. Development of community structure in relation to disturbance and ecosystem fragmentation in Atlantic white-cedar swamps in the Pinelands National Reserve, New Jersey. Ph.D. Dissertation. Rutgers University, New Brunswick, NJ, USA.

Streng, D. R., J. S. Glitzenstein, and P. A. Harcombe. 1989. Woody seedling dynamics in an East Texas floodplain forest. Ecological Monographs 59:177–204.

Titus, J. H. 1990. Microtopography and woody plant regeneration in hardwood floodplain swamp in Florida. Bulletin of the Torrey Botanical Club 117:429–437.

Vedagiri, U. and J. Ehrenfeld. 1991. Effects of *Sphagnum* moss and urban runoff on bioavailability of lead and zinc from acidic wetlands of the New Jersey Pinelands. Environmental Pollution 72: 317–330.

Zampella, R. A. 1987. Atlantic white-cedar management in the New Jersey Pinelands. p. 295–311. *In* A. D. Laderman (ed.) Atlantic White-cedar Wetlands. Westview Press, Boulder, CO, USA.

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