

Fire history and vegetation dynamics of a *Chamaecyparis thyoides* wetland on Cape Cod, Massachusetts

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Summary

1. Fire history and vegetation change over the past millennium and modern successional trends in a *Chamaecyparis thyoides* (Atlantic white cedar) wetland on Cape Cod, Massachusetts were investigated using fine-resolution pollen analysis and stand age-structure analyses

2. Before European settlement (c. 1650 AD) low cedar pollen percentages correspond with abundant charcoal, whereas cedar dominates when charcoal values are low. Five fires occurred at 100–200-year intervals in prehistoric time. Since settlement, fires have been rare and cedar dominates the pollen profile.

3. During the past two centuries timber cutting has become a significant factor in the vegetation dynamics of this system. In the nineteenth century intensive cutting resulted in the establishment of cedar. During the first half of the twentieth century, light timber thinnings favoured *Acer rubrum* (red maple) regeneration. In the past few decades, neither cedar nor its principal associate, red maple, have regenerated beneath the undisturbed cedar overstorey.

4. Our results indicate that, at this site, vegetation composition and successional trends have largely been controlled by allogenic factors in both pre- and post-settlement times. Vegetation changes resulting from autogenic factors are not evident during the 1000-year study period.

5. Age-structure analyses of modern stands in combination with fine-resolution pollen analyses are useful in comparing current vegetation dynamics with those of earlier times. In the 600–800 years before establishment of the current mature stand, cedar did not persist for more than 100–200 years without stand-regenerating fires. Thus the survival of the current stand much beyond its present age of c. 150 years would be atypical compared to the centuries prior to settlement. The present lack of cedar regeneration suggests that a management policy excluding disturbance would eventually lead to a decline in the importance of cedar.

6. Our results suggest that an understanding of processes that influence community composition and structure over long periods of time may indicate conservation objectives and management guidelines different from those directed at the preservation of communities that, at a given point in time, appear to be unique on the landscape.

Key-words charcoal community conservation, pollen analysis, succession

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Introduction

Recent attempts to conserve 'natural community diversity' have resulted in the creation of many nature reserves selected for their exemplary and

often unusual vegetation associations. An understanding of the ecological and historical processes that have allowed these unusual associations to develop is required in order to identify appropriate conservation objectives for these natural areas, and to develop management strategies for achieving these objectives. Frequently, such an understanding

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requires investigations at a variety of temporal scales in order to relate recent trends to longer-term dynamics. This is particularly true in regions with a history of intensive human settlement, and for communities dominated by long-lived tree species.

In this study we investigate long- and short-term vegetation dynamics in an Atlantic white cedar (*Chamaecyparis thyoides*) wetland on Cape Cod, Massachusetts. Although many cedar wetlands are now preserved as unique natural communities (Whigham 1987), developing conservation and management objectives for these wetlands has proved to be difficult, because previous investigations (Little 1950, Hickman & Neuhauser 1977) that have focused solely on modern vegetation dynamics have produced conflicting assertions about successional trends and life-history characteristics of the two tree species (Atlantic white cedar and red maple *Acer rubrum*) that dominate most cedar wetlands. Differences in land-use practices between presettlement Indian populations and postsettlement Europeans in eastern North America (Cronon 1983, Patterson & Sassaman 1988) suggest that it may not be possible to infer long-term processes from current vegetation patterns. Therefore we employed fine-resolution pollen analysis (Green 1983, Green & Dolman 1988) of peat sediments and age-structure analyses of existing trees to relate recent vegetation trends to processes occurring over longer time periods.

ATLANTIC WHITE CEDAR WETLANDS IN THE NORTH-EASTERN UNITED STATES

Throughout their distribution range in eastern North America, *Chamaecyparis thyoides* wetlands are uncommon, having decreased historically in areal extent and in biological diversity (Laderman 1989). Current estimates indicate that there are less than 5300 ha of *C. thyoides* wetlands remaining in the glaciated north-eastern United States (Motzkin 1991). Much of the historic decrease is attributable to human activity through conversion to agricultural, industrial, or commercial uses, and through selective logging of cedar. Flooding by beavers and sea level rise have been responsible for additional losses.

Natural autogenic successional processes, in which, in the absence of disturbance, *C. thyoides* is replaced by more shade-tolerant species, have been implicated in the loss of cedar wetlands by some investigators (Buell & Cain 1943, Little 1950). Little (1950) states that *C. thyoides* typically forms even-aged stands that establish after disturbances such as fire (especially under flooded conditions when seed reserves in the upper organic layers remain protected), windthrow, temporary flooding and salt-spray damage.

According to Little (1950) *C. thyoides* is less shade-tolerant than *Acer rubrum* which reproduces beneath established cedar canopies to form all-aged

populations that may replace cedar when overstories break up with increasing stand age. Little's model of autogenic succession in *C. thyoides* wetlands raises concerns about the loss of cedar dominance in sites protected from disturbance and has led to silvicultural practices that emphasize cutting and the use of prescribed fire (Korstian & Brush 1931, Noyes 1939, Little 1950, Johnson 1980). In the North-east, small clearcuts within existing stands are recommended for regenerating even-aged patches of cedar (Little 1950, Zampella 1987, Roman, Good & Little, in press).

Hickman & Neuhauser (1977) present a different interpretation of successional trends in cedar wetlands of New Jersey, however. They report no maple or cedar regeneration beneath undisturbed cedar canopies and state that during establishment cedar may be more shade-tolerant than maple. Contrary to Little (1950) Hickman & Neuhauser (1977, p. 35) assert that cedar should not be considered in any general way subclimax to maple. Resolution of this apparent conflict has important implications for the management of *C. thyoides* wetlands.

In this study we investigated successional trends in an old-growth stand at the Marconi Atlantic White Cedar Swamp (MAWCS), a 5-ha wetland at Cape Cod National Seashore. The MAWCS is currently protected from fire and timber cutting and is therefore potentially threatened by the successional trends identified by Little (1950). This study addresses the following questions:

- 1 How have autogenic and allogenic processes influenced successional trends at the Marconi Atlantic White Cedar Swamp during the past ~1000 years?
- 2 How have disturbance frequency and type changed since European settlement?
- 3 Is there evidence that either cedar or maple continuously establish beneath existing overstorey canopies?
- 4 Is Atlantic white cedar likely to persist at the site in the foreseeable future?
- 5 What conservation and management objectives emerge from an understanding of the long-term dynamics of this system?

Study site

The Marconi Atlantic White Cedar Swamp is located in South Wellfleet, Massachusetts (Fig. 1). It occupies a kettle depression in outwash sand and gravel deposits which support oak-pitch-pine (*Quercus* spp. – *Pinus rigida*) forests on the adjacent upland. Maximum depth of organic sediments in the Swamp, which has no surface inflow or outflow, is 7 m. The climate of the region is humid continental, with a maritime influence. Precipitation averages c. 103 cm year⁻¹ (Patterson *et al.* 1985).

Historical records suggest that Europeans settled Wellfleet c. AD 1640 (Altpeter 1937). By the late seventeenth century, forests on outer Cape Cod had

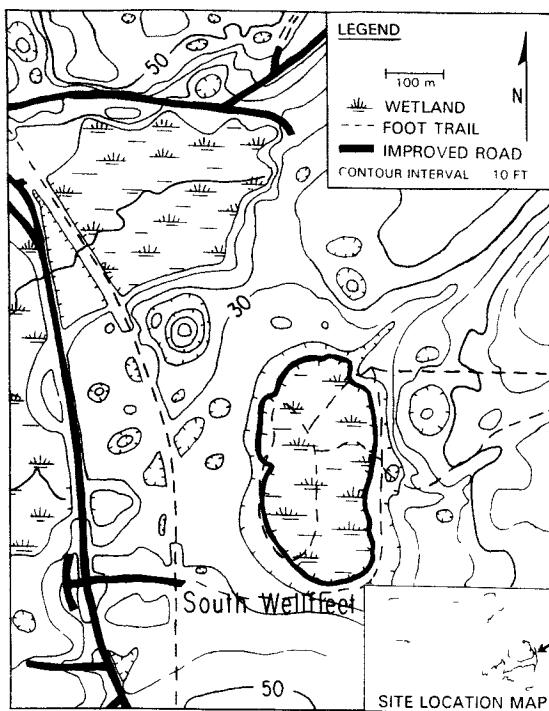


Fig 1 Location map for the Marconi Atlantic White Cedar Swamp (MAWCS) Cape Cod National Seashore South Wellfleet Massachusetts

been so heavily exploited that several towns adopted ordinances prohibiting the cutting of wood (Altpeter 1937, McCaffrey 1973). Agricultural activity peaked in 1860, with *c.* 30% of the land area being used for crop and pasture (Altpeter 1937). Pitch pine that now occurs on the upland surrounding the Marconi Swamp established following agricultural abandonment between the late nineteenth and mid-twentieth centuries.

Data from Belling (1977) indicate that *C. thyoides* occurred in Massachusetts as early as 6800 BP, but its distribution and relative abundance since that time are uncertain. Cedar first arrived at the Marconi site *c.* 3000 years ago. Within 500–1000 years of its arrival, cedar dominated the site and continued to do so until *c.* 1000 years ago when it declined in Belling's pollen profiles, and pitch pine and red maple increased. A charcoal layer coincides with these changes in pollen suggesting that a fire swept through the area, resulting in an increase in pitch pine in the uplands and a decrease in the relative importance of cedar in the Swamp. Cedar pollen percentages increased again in the profile at approximately the time of European settlement (Belling 1977).

Atlantic white cedar in Massachusetts was much valued for wood products (Emerson 1850), and it is likely that there was at least some removal of cedar from the Marconi site in the eighteenth and nineteenth centuries. Cedar has been the dominant tree species at the Swamp since at least the mid-19th century, however, and much of the current stand is

comprised of mature trees as old as 200 years. For the past 30 years, the Swamp has been protected except for limited cutting to build a boardwalk for public access.

Only three overstorey species currently occur in the Marconi Swamp, cedar dominates, red maple is common and pitch pine is present as scattered individuals. Understorey species include *Vaccinium corymbosum*, *Rhododendron viscosum*, *Clethra alifolia*, *Ilex verticillata*, *I. glabra*, *Leucothoe racemosa* and *Gaylussacia frondosa*. *Sphagnum* spp. dominate the ground cover with *Maianthemum canadense*, *Woodwardia virginica* and *Osmunda cinnamomea* also present.

Methods

VEGETATION CHARACTERIZATION

A 20-m × 20-m grid was established throughout the Swamp in 1988 and sampled for overstorey cover using variable-radius plots (Mueller-Dombois & Ellenberg 1974). All live and dead trees were tallied by species at each of 162 points on the grid. On 57 of the 400-m² grid cells (30% sample), the releve method (Mueller-Dombois & Ellenberg 1974) was used to estimate percentage cover for all vascular plant species, with stems grouped in height classes defined according to Kuchler's Physiognomic Classification system (Kuchler 1967). Species were assigned cover scores according to the Braun–Blanquet scale (Mueller-Dombois & Ellenberg 1974). Cover values were used to calculate importance values, as follows: For each species on each relevé, Braun–Blanquet cover values were summed for all the strata within which the species occurred. The number of strata within which the species occurred was then subtracted from the summation, with the value 1 added to the total (see Clark & Patterson 1985). This procedure results in a minimum value of 1 assigned to a species that occurs in only one stratum with a cover value of 1 (single occurrence, minimal cover). Because of the nonlinear nature of the Braun–Blanquet cover class values, this procedure emphasizes the occurrences of species within strata (more than their cover) and increases the importance of species that occur in multiple strata relative to those that occur in a single stratum.

Patterns of structural variability within the Marconi Swamp were also evaluated through interpretation of 1984 colour-infrared aerial photographs (scale 1:25 000). Nomenclature follows Seymour (1989).

AGE-STRUCTURE ANALYSIS

Ten sample plots were located in the three distinct stands identified by our vegetation characterization (see Results), and diameter at breast height (d.b.h.)

and crown classification (dominant, codominant, intermediate or suppressed) were recorded for all stems >5 cm d b h. Increment cores for age determination were taken within 30 cm of the ground from all trees >5 cm d b h. Sample plots were $20\text{ m} \times 20\text{ m}$ (five plots in stand I, two in stand II, and one in stand III), except in two plots in stand III which comprised dense stands of small stems where $10\text{ m} \times 10\text{ m}$ plots were employed (Fig 2).

Within each plot, height and basal diameter of all woody stems >3 cm tall but <5 cm d b h were sampled in 10–15 randomly located 4 m^2 subplots. The small size of tree stems in the understory subplots made coring for age determinations impractical. To determine the age distribution of stems <5 cm d b h, we cut, aged, and recorded the basal diameter of 55 maple and 24 cedar stems. Regression analyses revealed significant correlations between age and diameter for both species. Equations generated were used to estimate the ages of tree stems from the subplots.

PALEOECOLOGICAL INVESTIGATIONS

To reconstruct the history of vegetation previously occupying the site, we examined written accounts and maps on file at Cape Cod National Seashore and the Wellfleet Historical Society. We also obtained a

peat core 10 cm in diameter and 91 cm long from a point near the centre of the Swamp (Fig 2). The core was sampled at 1-cm intervals, and subsamples selected at 2–3-cm intervals were examined microscopically for pollen and charcoal content after preparation using a modification of the acetolysis technique (Faegri & Iversen 1975). Although we could not separate the pollen of *Chamaecyparis* from that of red cedar *Juniperus virginiana*, there is currently little *Juniperus* growing in the forests surrounding the Swamp. This fact, plus the occurrence of *Chamaecyparis* wood throughout the core, suggests that most of the Cupressaceae pollen occurring in the peat samples was derived from cedar growing in the Swamp itself.

Surface samples of organic material were obtained from the Swamp to evaluate the relationship between current vegetation and modern pollen rain. Samples were obtained from five locations for which we had overstorey basal area data (see Fig 2). We selected locations that ranged from nearly pure stands of dense, mature cedar to openings that contained up to one-third of their basal area as red maple.

The area of charcoal fragments on microscope slides was estimated using the point-count method of Clark (1982), with values expressed as the ratio of charcoal area to fossil pollen (Ch P).

Peat sections 5 cm long were removed at 33–38, 60–65, and 85–90 cm and dated by ^{14}C analysis at Beta Analytic, Inc., Miami, Florida. Pollen indicators [i.e. increases in *Ambrosia*, *Rumex*, *Plantago* and Gramineae for European settlement (c. AD 1650) and a decline in *Castanea* (c. AD 1910) (Clark & Patterson 1984)] were used to date peat from the upper portion of the core. Detrended correspondence analysis (Hill 1979, Gauch 1982) of pollen data was used to examine the relationship between fire occurrence and vegetation change.

Results

VEGETATION CHARACTERIZATION

Analysis of aerial photographs indicated the presence of three structurally distinct stands (Fig 3). The stand that occupies most of the wetland (stand I) consists of large, open-grown cedars as well as forest-grown cedars and maples of approximately the same height. A smaller stand (II) with cedar of greater density and smaller diameter occurs in the southwestern portion of the Swamp. In the southeastern portions of the Swamp are areas of dense but shorter cedar (stand III). Additional areas of dense (and apparently young) cedar were identified during field sampling. These areas are very small and are not recognizable as cedar on aerial photographs. They appear instead as canopy gaps or areas with low, dense vegetation (Fig 3). Two relevés

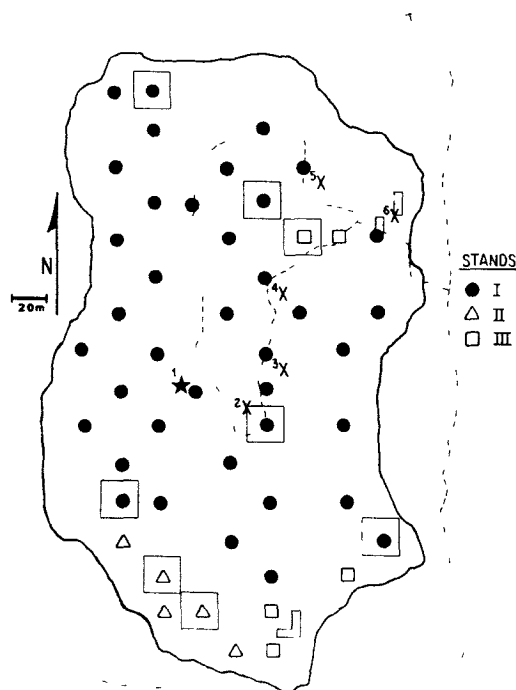


Fig 2 Sample locations in the MAWCS. Small circles, triangles and squares represent relevés categorized by stand (see Results and fig 3). Large, open polygons are intensive sample plots, and dashed lines represent trails. The sites from which the peat core (*) and surface samples (X) for pollen and charcoal analyses were extracted are also indicated.

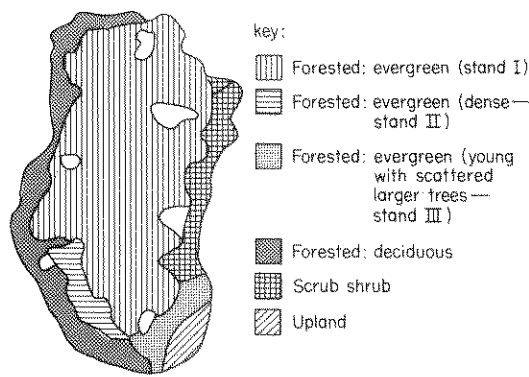


Fig. 3. Vegetation of the MAWCS based upon interpretation of 1984 colour-infrared aerial photographs. Unshaded areas represent canopy gaps with low, dense vegetation.

(one sampled intensively) were taken in such an area and are categorised as stand III in Fig. 2. Individuals in stands II and III lack the large, open-grown crowns typical of stems in stand I.

The three stands are similar with respect to total basal area and its distribution among species (Table 1). The ratio of cedar to red maple for the Swamp as a whole is 4.3:1. Maple is relatively more important at the edges of the wetland than in the centre, particularly along the western edge.

Table 2 summarizes the relevé data for stands defined by photointerpretation and ground reconnaissance and for vegetation strata defined during relevé sampling. The three stands are similar with respect to summed importance values for trees, mosses and herbaceous species. Stands I and III are similar with respect to shrub importance, with the summed importance values for stand II two-thirds those of stands I and III. The distribution of relevés categorized as representing stands I, II or III is shown in Fig. 2.

Stand I has the highest density of stems >20 cm d.b.h. and very few smaller stems. Stand II is dominated by stems 10–20 cm d.b.h., with few stems >25 cm d.b.h. Stand III is characterized by stems

Table 2. Average species importance values by stand

	Stand		
	I	II	III
Trees			
<i>Chamaecyparis thyoides</i>	9.0	10.2	11.2
<i>Acer rubrum</i>	8.8	8.4	7.8
<i>Pinus rigida</i>	0.1	0.6	0.0
Shrubs			
<i>Clethra alnifolia</i>	3.4	3.8	2.6
<i>Smilax</i> spp.	2.3	1.2	2.4
<i>Vaccinium corymbosum</i>	6.4	6.6	7.8
<i>Rhododendron viscosum</i>	4.5	4.6	4.8
<i>Leucothoe racemosa</i>	3.5	1.4	2.2
<i>Ilex glabra</i>	2.0	2.2	2.6
<i>Gaylussacia frondosa</i>	1.0	0.0	0.6
<i>Rhus radicans</i>	1.4	0.2	0.8
<i>Amelanchier</i> spp.	0.2	0.0	0.0
<i>Gaylussacia baccata</i>	2.1	0.0	1.0
<i>Ilex verticillata</i>	2.4	1.0	2.4
Unknown	0.8	0.6	0.6
<i>Aronia</i> spp.	1.1	0.0	1.2
<i>Kalmia angustifolia</i>	0.5	0.0	1.2
<i>Lyonia ligustrina</i>	0.0	0.0	0.2
<i>Nemopanthus mucronata</i>	0.1	0.0	0.0
<i>Decodon verticillatus</i>	0.0	0.4	0.0
Herbs			
<i>Trientalis borealis</i>	0.8	0.6	0.0
<i>Woodwardia virginica</i>	2.0	0.8	1.2
<i>Osmunda cinnamomea</i>	0.4	0.4	0.0
<i>Aralia nudicaulis</i>	0.1	0.0	0.0
<i>Carex</i> spp.	0.4	0.4	0.4
Grass spp.	0.1	0.0	0.0
<i>Bartonia virginica</i>	0.1	0.0	0.0
<i>Mitchella repens</i>	0.1	0.0	0.0
Mosses			
<i>Sphagnum</i> spp.	6.4	6.4	5.2
Other mosses	3.5	3.6	4.0
Sum of average importance values			
Trees	17.9	19.2	19.0
Shrubs	31.7	22.0	30.4
Herbs	4.0	2.2	1.6
Mosses	9.9	10.0	9.2
Total	63.5	53.4	60.2

Table 1. Average basal area for stands I, II and III at the Marconi Atlantic White Cedar Swamp

Species	Status	Basal area (m ² /ha)		
		stand I (n = 110)	stand II (n = 7)	stand III (n = 16)
<i>Chamaecyparis thyoides</i>	live	40.8	36.6	42.2
	dead	7.9	8.9	6.1
<i>Acer rubrum</i>	live	9.9	11.0	5.2
	dead	0.9	0.3	0.9
<i>Pinus rigida</i>	live	1.3	0.0	1.2
	dead	0.1	0.0	0.1
Other	live	0.2	0.0	0.6
Average Total Basal Area		61.6	56.8	56.3

5–10 cm d b h., with very few stems >20 cm d b h (Motzkin 1990)

Variable-radius-plot and releve data indicate that the vegetation of MAWCS is fairly homogeneous with respect to species composition. Although the three stands are structurally distinct (Fig. 3, Motzkin 1990), they are quite uniform floristically.

AGE-FREQUENCY DISTRIBUTIONS

Increment cores were obtained for 586 live cedar trees and 135 live maples. Regression analyses of age vs. d b h for stems with sound cores showed a significant positive correlation for both cedar ($R^2 = 0.68$, $P = 0.0001$) and maple ($R^2 = 0.43$, $P = 0.0001$). Regression equations (for cedar, $\text{age} = 17.8 + 3.79 \times \text{d b h}$, and for maple, $\text{age} = 29.5 + 3.28 \times \text{d b h}$) were used to estimate the ages of live stems for which sound cores could not be obtained. For small stems (<5 cm d b h.), age and basal diameter (BD) are positively correlated (for cedar, $\text{age} = 1.2 + 12.0BD$, $R^2 = 0.91$, $P = 0.0001$, for maple, $\text{age} = 2.34 + 6.84BD$, $R^2 = 0.80$, $P = 0.0001$).

Age-frequency distributions, in 10-year age classes, were developed for cedar and maple in each stand (Fig. 4). These graphs include overstorey stems for which ages from sound cores were obtained, estimates of ages of live stems for which no sound cores were obtained, and estimates of ages of understorey stems. Inclusion of ages estimated from regression equations does not appear to change the general pattern of the age-frequency distributions, but instead emphasizes trends evident from aged trees.

Stand I

This stand occupies most of the Swamp and is dominated by cedars 100–150 years old (Fig. 4a). Density of cedars older than 100 years is higher here than in the other stands, although for red maple older than 100 years density is much lower than for cedar (Fig. 4).

Age-frequency distributions for the five intensive sample plots in this mature stand reveal two distinct subtypes. Stand Ia has abundant cedar in the 100–150-year-old age classes but no cedar that has regenerated in the past 80–90 years (Table 3). The few maple stems that occur here are scattered throughout several age classes. Stand Ib includes areas with lower densities of cedar in the oldest age classes and some cedar in several of the younger age classes. The regeneration, 40–80 years ago, of maple stems in stand Ib appears to correspond with the regeneration of cedar (Table 3).

Stand II

The stand in the south-western portion of the Swamp

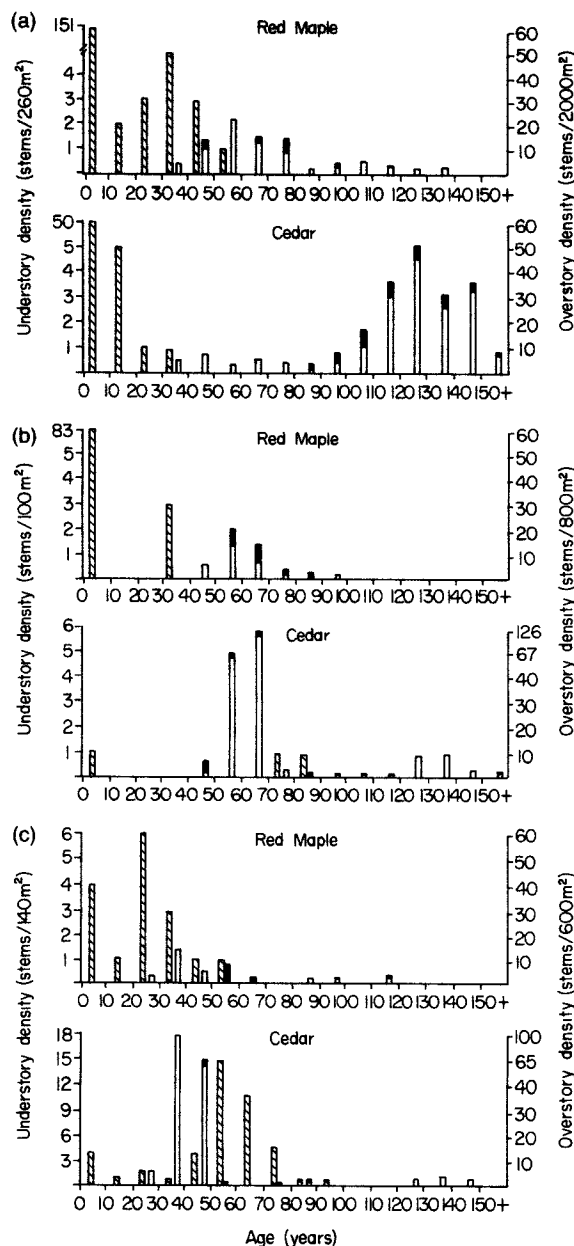


Fig. 4 Age-frequency distributions for cedar and red maple in (a) stand I, (b) stand II and (c) stand III. (□) overstorey ages from cored stems, (▨) estimated understorey ages, (■) estimated overstorey ages.

is dominated by cedars of intermediate age (50–70 years old) with a few maples of the same age. The density of cedar is approximately 5.5 times that of maple for these age classes (Table 3). There is no evidence of continuous recruitment of either species, but there are a few open-grown cedar stems that correspond in age to the 100–150-year-old stems observed in stand I. Remains of old, cut stumps are found throughout this stand.

Stand III

Trees in this stand are largely even-aged (Fig. 4c), with more cedar than maple in the 30–50-year age

Table 3 Cedar and red maple stem density (stems/ha) by age class for stands at the Marconi Atlantic White Cedar Swamp

Age class	Cedar				Maple			
	Ia	Ib	II	III	Ia	Ib	II	III
0–10 years	250	2667	125	222	5750	5833	8834	306
10–20 years	—	278	—	83	125	56	—	56
20–30 years	—	56	—	236	—	167	—	469
30–40 years	—	97	13	2050	125	256	292	369
40–50 years	—	67	88	2500	25	267	75	225
50–60 years	—	33	838	1233	25	231	263	175
60–70 years	—	50	1575	917	13	125	175	42
70–80 years	—	42	134	450	25	108	63	—
80–90 years	25	17	96	100	13	17	38	8
90–100 years	75	25	25	83	13	33	13	17
100–110 years	113	75	25	—	—	50	—	—
110–120 years	188	183	25	—	25	17	—	25
120–130 years	350	192	113	67	—	25	—	—
130–140 years	288	67	125	100	38	—	—	—
140–150 years	288	117	25	17	—	—	—	—
150+ years	63	42	13	—	—	—	—	—

classes. A few 100–150-year-old cedar are scattered throughout. Most understorey cedar stems were estimated to be about the same age as overstorey stems (Fig. 4c).

PALAEOECOLOGY OF THE SWAMP

Sediment dating by pollen indicators (i.e. the rise in agricultural indicators at ~ 28 cm = c. AD 1650) and by ^{14}C dating (c. AD 1500 at 35.5 cm, c. AD 1220 at 62.5 cm, and c. AD 860 at 87.5 cm) yields estimated peat accumulation rates of $0.079\text{--}0.09$ cm year $^{-1}$. Thus each 1-cm sample represents c. 12 years, with gaps of between about 12 and 24 years between samples. This resolution seems adequate for characterizing fluctuations in the abundance of cedar, which, in the absence of disturbance, can live to ages of 200–300 years or more.

Pollen stratigraphy shows that cedar has been present at the Marconi Swamp for the past 1100 years. Cupressaceae pollen percentages fluctuate from <5% to >80% prior to the increase in agricultural weed pollen at a depth of ~ 28 cm in the core (Fig. 5). The abundances of pine, oak, *Sphagnum* and several shrub and fern species also fluctuate widely in the lower two-thirds of the core. Charcoal pollen ratios vary from 0 to >26 000.

Shortly before the time of settlement (c. AD 1650), Cupressaceae percentages rise to levels that consistently exceed 80% during postsettlement time. Values for all other types except agricultural weeds have declined since settlement. Pollen percentages generally reflect the patterns of land-use outlined earlier. In contrast to the lower portion of the core, there is little charcoal in the upper 20 cm.

Cupressaceae pollen percentages for surface samples (Fig. 5) are uniformly high despite the fact

that cedar basal area at the locations from which the samples were taken vary (Table 4) as do distances from the edge of the Swamp (Fig. 2). Sample 6 (Fig. 2) for example, was taken from an opening (stand III) near the upland but has a cedar pollen percentage >70. This suggests that cedar pollen is over-represented in small openings in the otherwise cedar-dominated swamp and that low cedar percentages during prehistoric time represented swamp-wide declines in cedar and not simply small openings that might result from the destruction of one or a few overstorey trees.

Vegetation changes associated with presettlement fire occurrence and postsettlement fire suppression are evident in the results of detrended correspondence analysis of the pollen data (Fig. 6). Cedar pollen percentages decrease with increasing axis 1 values, whereas values for *Sphagnum* and fern allies increase. Most presettlement samples have values higher than 40 on axis 1. A subset of these samples (group B) has axis 1 values <100, with samples having generally higher cedar percentages and low-to-moderate *Sphagnum* and/or fern percentages compared to those farther to the right on axis one. Group C is represented by 10 samples that often comprise two or three adjacent samples (38/41, 47/50/53, 61/65/68) that are shifted far to the right on axis 1 compared to levels above and below them. These samples often have particularly large *Sphagnum* and Ch P values and low cedar pollen percentages, perhaps indicating open conditions associated with stand-replacing fires. Level 77, which is not associated with high Ch P values, occurs in the extreme lower right-hand corner of Fig. 6. Cedar and pine percentages for this sample are at their lowest presettlement levels in the profile, whereas *Sphagnum* percentages reach a maximum value of 82.5 indi-

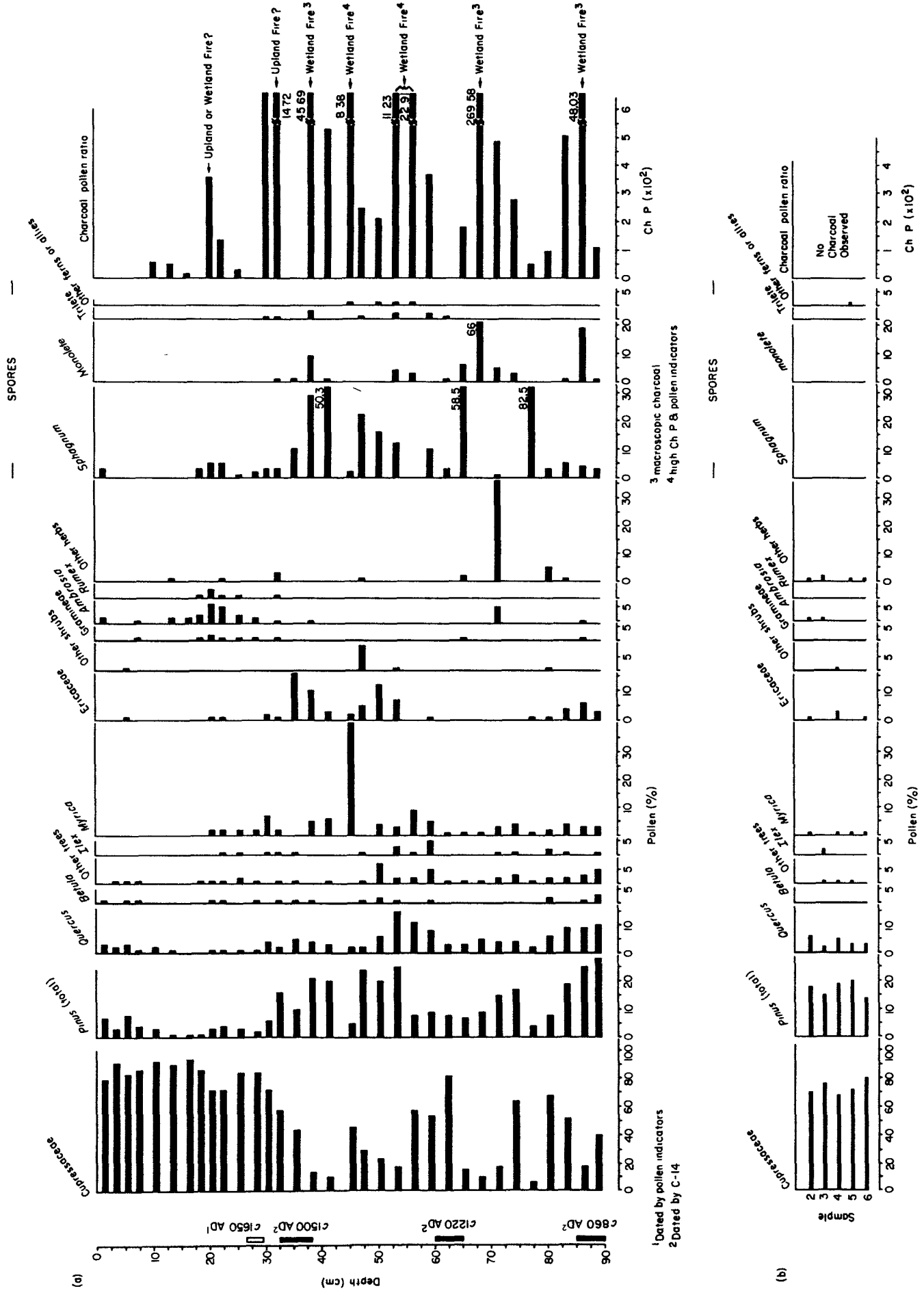


Fig 5 Pollen percentages and charcoal pollen ratios for samples from the top 90 cm of peat in (a) the MAWCS and (b) for surface samples

Table 4 Cedar and maple pollen percentages for modern surface samples from the Marconi Atlantic White Cedar Swamp with associated basal areas from variable radius plot sampling

Surface sample	Pollen (%)		Basal area (m ² /ha)	
	cedar	red maple	cedar	red maple
1 (top of core)	79.2	—	56.4	10.4
2	70.8	—	55.2	4.6
3	76.4	—	47.2	11.5
4	79.8	—	29.9	10.4
5	67.4	0.8	36.8	9.2
6	71.4	0.2	54.1	5.8

cating a sudden change in environmental conditions (Tallis 1964). This sample may represent a disturbance other than fire (e.g. a major windstorm).

High charcoal values at 30 and 32 cm occur after an increase in cedar pollen and just prior to the time that agricultural indicators increase, but they are not associated with a shift in the sample locations to the right on Figure 6. These values may represent a fire that occurred on the upland with little effect on the wetland itself. This interpretation is consistent with the fact that cedar pollen percentages continue to rise through the period represented by the fire and there are no other distinct changes in wetland species. Pine percentages decline sharply at this time, however, and *Myrica* (an upland shrub) percentages increase.

Postsettlement pollen spectra (group A, 0–30 cm plus the surface samples) are concentrated on the extreme left of axis 1. Only level 62 among the presettlement spectra is grouped with levels rep-

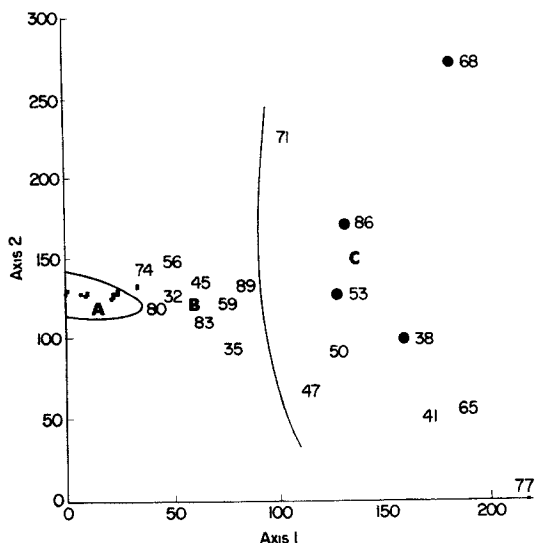


Fig. 6 Detrended correspondence analysis ordination of pollen percentage data for surface and stratigraphic samples from the MAWCS. Enclosed circles represent samples that have abundant charcoal and little Cupressaceae pollen. See text for descriptions of groups A, B and C.

resenting postsettlement time. All of these samples have abundant cedar pollen, little charcoal and few *Sphagnum*/fern spores.

Discussion

EVIDENCE FOR EPISODIC REGENERATION

Each of the stands identified by our analysis have age distributions that span only a few decades indicating that establishment of both cedar and maple is episodic rather than continuous. Stand I is dominated by even-aged, mature cedars. Even where cohorts of younger stems occur (stand Ib), the age structure of the cohorts indicates distinct episodes of establishment rather than continuous recruitment. These episodes probably correspond with disturbances — especially selective cutting. Periodic small blowdowns cannot be ruled out, but we saw little evidence in the form of downed stems to suggest that large, old trees were dying individually or in small groups to form these gaps. Stand Ib has lower densities of 100–150-year-old stems than stand Ia (Table 3) suggesting the removal by selective cutting of overstorey stems. The regeneration, 40-to-80 years ago, of maple in stand Ib corresponds with an increase in cedar stems, further suggesting that selective cutting during the first half of the twentieth century allowed both cedar and especially maple to become established. Selective cutting of only parts of the Swamp would be consistent with nineteenth- and twentieth-century ownership patterns which show the Swamp divided among as many as 12 different owners at various times.

The ability of red maple to sprout and grow quickly after a disturbance like cutting and the corresponding inability of cedar to reproduce vegetatively could result in a distribution of younger stems similar to that which occurs in stand Ib. Korstian & Brush (1931) describe the development after selective logging of two-aged stands similar to those encountered in portions of stand I. In contrast, abundant cut stumps and an absence of maple throughout stands II and III suggest that episodes of cedar rather than maple establishment followed brief periods of more intensive cutting in the area now occupied by these stands.

The relationship between disturbance events and episodes of cedar and maple regeneration supports Hickman & Neuhauser's (1977) observations that neither cedar nor maple successfully establish beneath closed canopies of mature cedar (e.g. as in stand Ia). Maple does not occur in all-aged populations in any of the stands we sampled. Disturbance in the form of selective cutting is a likely explanation for the occurrence of younger maple in some portions of stand Ib. The even-aged cohorts of maple that we have described at Marconi are not consistent with the all-aged populations that would be expected

from Little's (1950) explanation for cedar-maple interactions in New Jersey

FIRE AND THE PALEOECOLOGY OF CEDAR

The intent of our analysis was to characterize the vegetation and disturbance regime of the Swamp in the period immediately preceding the advent of European settlers. This period is often viewed by the National Park Service as a benchmark from which subsequent vegetation change can be measured. The results of our fine-resolution pollen analysis (Fig. 5) indicate a significant change in plant communities in response to changing disturbance regimes following European settlement. Fires were common prior to settlement. Most probably began in the highly flammable oak-pitch-pine forests on the upland and burned as intense surface or crown fires until they entered the Swamp. Cedar foliage is highly flammable, and wind-driven fires could have burned through the crowns of cedar despite the presence of standing water in the wetland. In addition, some fires may have burned at times when conditions were dry enough to allow the surface of the wetland to burn. A layer of charcoal 5 cm thick at 65 cm below the surface of the wetland indicates that one such fire burned c. AD 1170. Thinner layers of macroscopically visible charcoal at 38 and 87 cm (c. AD 1470 and AD 870, respectively) indicate other fires that almost certainly burned through the swamp. High Ch/P ratios and associated changes in pollen assemblages at 45 cm and 53–57 cm suggest that additional prehistoric fires burned in the Swamp c. AD 1390 and 1265.

Evidence that fires burned into the Swamp is strengthened by the fact that declines in cedar pollen percentages sometimes coincide with major charcoal peaks (especially at 45 and 57 cm). At other times, fires may have burned either through young cedar or other shrubby vegetation (e.g. at 38 cm). Despite the occurrence of at least five major fires in the Swamp during the last 1000 years, there is no evidence that cedar was completely extirpated from the wetland for even brief periods. Fire episodes were, in fact, often followed by the regeneration of a new cedar stand (e.g. at 38 and 86 cm). High presettlement pollen percentages for shrub species corresponding with low percentages for cedar suggest that the Swamp at times supported an open cedar stand quite different in structure and perhaps species composition from the one at the site today. High percentages for monolet fern spores (perhaps representing *Woodwardia virginica*, which is found in the Swamp today) coincide with high presettlement charcoal values. This provides additional evidence for the opening of the wetland surface to high light levels for at least a short time following prehistoric fires. No fern spores were found in any of the modern surface samples, whereas values in excess

of 60% coincide with the severe fire that burned into the Swamp c. AD 1170. At no time during the several hundred years prior to European settlement did cedar pollen percentages attain the consistently high levels (70–80%) found in surface samples.

High postsettlement cedar pollen percentages are accompanied by very low Ch/P values, which have never exceeded 500 during the past c. 200 years. Values do exceed 400 at 20 cm when pollen percentages for indicators of agricultural activity (*Ambrosia*, Gramineae, *Plantago* and *Rumex*) peak. This probably represents the period of maximum agricultural activity on Cape Cod (c. AD 1860). Upland pollen percentages show little response to this fire, but cedar declines about 10% and then recovers. A coincident rise in *Sphagnum* spores, which also fluctuate in response to fire in presettlement sediments, suggests that this postsettlement fire may have impacted at least a portion of the Swamp. The lack of macroscopically visible charcoal and of any response in fern spore percentages suggests a fire of different character than the ones that burned into the Swamp prior to settlement, however. The charcoal may represent the burning of slash from selective logging of cedar or a fire set near the Swamp to clear pastures of burn agricultural refuse.

Of particular interest in the interpretation of modern stand dynamics is the fact that pollen percentages for red maple never exceed 0.5% for any sample during the 1000-year record. Maples are insect-pollinated, and percentages are normally quite low, but we have observed values >5% for samples taken from Cape Cod swamps dominated by red maple. The very low values for the Marconi Swamp samples suggest that mature red maples have never, during the last 1000 years, been more important in the Swamp than they are today.

ALLOGENIC FACTORS AND THE DEVELOPMENT OF CEDAR

The results of our investigation of both current vegetation dynamics and vegetation trends over a 1000-year period indicate that allogenic factors have strongly influenced the vegetation of the Marconi Atlantic White Cedar Swamp. Age structure analyses of the modern vegetation suggest that cedar and maple establishment occurs only during distinct episodes following disturbance events. During the past 150 years, timber cutting has been the primary disturbance influencing the regeneration of both cedar and maple. Light thinnings apparently favoured red maple establishment over cedar in some areas, whereas more-intensive cutting resulted in the regeneration of even-aged stands dominated by cedar. Areas lacking evidence of cutting lack significant regeneration of either species. Prior to European settlement, fire rather than cutting influenced vegetation patterns at the Swamp. Fires burning

through the wetland destroyed existing cedar stands but allowed for subsequent cedar regeneration from seed stored in the upper organic soil horizon or from surviving mature trees. Presettlement fire frequency was apparently great enough to prevent dense stands of mature cedar (like the one that currently occupies much of the Swamp) from persisting for more than brief periods.

Previous studies of succession in Atlantic white cedar swamps have focused on the influence of auto-genic processes (Little 1950, Hickman & Neuhauser, 1977). The results of our investigation suggest that although disturbance regimes were different before and after European settlement, allogenic factors have been the dominant force influencing succession in the Marconi Atlantic White Cedar Swamp.

THE FUTURE COURSE OF VEGETATION DEVELOPMENT

Current National Park Service policies of wildfire suppression and preservation of natural vegetation rule out fire and timber cutting as factors likely to influence future vegetation development in the Marconi Atlantic White Cedar Swamp. Unlike wilderness areas in western North America, the Marconi Swamp is in an area where lightning fires are rare (Patterson *et al.* 1985). With no active prescribed burning program in place at the Seashore, only uncontrolled fires of human origin are likely to occur. With increasing fragmentation of the forest due to recreational and residential development in the area surrounding the Swamp, it is unlikely that fires will reach a size that could threaten the Swamp.

Never, during the past 1000 years, has the interval between fires exceeded the expected lifespan of cedar (200–300 years), and it is thus difficult to predict the course of future vegetation development. Factors other than fire that might influence vegetation development include windthrow and salt-spray damage associated with storm winds (Little 1950). Although these disturbances may occur, there are no studies of their influences on vegetation succession in cedar wetlands. A disturbance-free period of up to several hundred years is possible, however, and our discussion of future vegetation trends focuses on the effects of autogenic succession over such a time period.

In the absence of disturbance it is unlikely that significant amounts of cedar or maple will regenerate beneath the existing overstorey. As the mature, 100–150-year-old stand ages, individual trees may die creating small canopy gaps (Little 1950). Portions of the mature stand lacking young maple or cedar but with abundant shrubs will experience increases in shrub cover. Subsequent regeneration of either cedar or maple at these shrub-dominated sites will depend upon gap size and local site conditions. Elsewhere in the mature stand, past cutting has

allowed the establishment of younger cohorts of cedar and maple. In these areas established younger cedar and/or maple rather than shrubs will fill canopy gaps. Most areas have been thinned only lightly favouring the establishment of maple. Thus, maples will probably increase in importance relative to cedar throughout much of the present mature stand. Cedar appears to be longer-lived than red maple however. Cedars >150 years old are scattered throughout the Swamp, with the oldest cedar more than 200 years old. The oldest red maple that we aged was only 140 years. Thus, although red maple may increase in importance relative to cedar as existing mature stands break up, cedar may eventually again increase in relative importance as the young stems of both cedar and maple age and maples die at a younger age.

Stands II and III are currently 30–50 and 50–70 years old, respectively. These stands could survive for another 100–200 years before attaining the age where stand break-up might be expected. Unless disturbed by fire, windthrow cutting, or pathogens, these stands will probably remain intact during the time that the existing mature stand is breaking up. Thus, even if cedar dominance is greatly reduced through the break-up of the existing old stand (stand I), it is unlikely that cedar will become completely extirpated from the Marconi site within the next several centuries. It therefore seems reasonable to conclude that although modern disturbance regimes are quite unlike those of prehistoric times, cedar is not immediately threatened by a management strategy that favours protection over active manipulation of the vegetation. Cedar is likely to survive for a very long time at Marconi, but in a community that is different in structure and species abundances than the one existing at the site prior to settlement of New England by Europeans. A similar conclusion may apply to many natural areas preserved for the unique species or communities that they contain.

From ecological as well as management perspectives, an important observation that emerges from this investigation is that the vegetation of the Marconi Swamp has been extremely dynamic during the entire 1000-year period that we examined. This suggests that attempting to preserve the stand structure as it now occurs may not be an appropriate or practical conservation objective. Rather, priority should perhaps be placed on protecting a sufficient range of community types so that the disturbance of any particular site may be considered acceptable as a functional process in natural area preservation.

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