

HOLOCENE PALEOECOLOGY OF A FORESTED PEATLAND  
IN CENTRAL NEW ENGLAND, U.S.A.

A Thesis Presented By  
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## ABSTRACT

Biostratigraphic analyses of sediment from the Black Gum Swamp peatland, central Massachusetts, U.S.A., document a 13,000 year history of regional upland vegetation change as well as transitions in local wetland vegetation. Major changes in upland vegetation through the late-glacial and Holocene are broadly similar to those recorded at other New England pollen sites, although pollen evidence suggests that the transitional nature of central New England forests (indicated by intermediate values for *Acer saccharum*, *Fagus grandifolia*, *Quercus* and *Pinus strobus* compared to northern and southern sites) became established as early as 8000 yrs BP. Fluctuations in *Picea* pollen percentages between 11,000 and 10,000 yrs BP are attributed to the Younger Dryas climatic reversal.

Black Gum Swamp was originally the site of a glacial meltwater pond. Progressive shallowing resulting from the deposition of limnic sediment facilitated centripetal expansion of low shrubs (*Chamaedaphne*), sedges and *Sphagnum*. Closure of the basin by shrub vegetation is thought to have occurred by 8700 yrs BP. A transition from shrub vegetation to swamp forest becomes apparent after 8000 yrs BP. *Picea* (probably *P. mariana* and *P. rubens*) was one of the earliest and most important arboreal components in the peatland, demonstrating that peatlands may have served as refugia for the genus *Picea* during the hypsithermal. *Nyssa* becomes an important component of the swamp forest after 6000 yrs BP.

The distribution and abundance of modern vegetation at Black Gum Swamp appears to be associated with local variations in hydrological

regime. In the better-drained southern end of the swamp (near the outlet), trees (i.e. *Picea*, *Tsuga* and *Nyssa*) are more abundant whereas shrub densities are less. High species diversity may occur at basin margins due to microsite heterogeneity, minerotrophic, less-acid conditions, and proximity to upland propagule sources.

Stratigraphic evidence and radiocarbon-dated basal sediment provide the first documentation of areal expansion for a central New England peatland. Wetland surface area has more than doubled since the time of swamp-forest establishment at 8000 yrs BP. Hydrologic data from wells at Black Gum Swamp suggest that paludification may result from the ponding of upland seepage water at basin margins due to impeded drainage through peatland sediments with low transmissivity.

Swamp-forest vegetation has existed as a community type for the past 8000 years at Black Gum Swamp, despite long-term climatic change and short-term disturbance (fires, logging). The absence of depositional gaps in the pollen record or reversals in sediment stratigraphy suggest that the hydrological regime within the basin has never been dramatically altered, a factor that may explain the long-term stability of this forested peatland ecosystem.



# TABLE OF CONTENTS

	PAGE
ACKNOWLEDGEMENTS .....	i
LIST OF FIGURES .....	ii
LIST OF TABLES .....	iii
INTRODUCTION .....	1
SITE DESCRIPTION .....	6
METHODS .....	8
Paleoecology .....	8
Modern Vegetation .....	12
Surface-Water Chemistry .....	12
Hydrology .....	14
RESULTS .....	14
Basin Morphometry .....	14
Sediment Stratigraphy .....	16
Radiocarbon Dating and Sedimentation Rates .....	19
Loss-On-Ignition .....	21
Macrofossil Survey .....	21
Pollen Stratigraphy .....	28
Surface-Water Chemistry .....	32
Modern Vegetation .....	32
Hydrology .....	41
DISCUSSION .....	50
I. History of Upland Vegetation .....	51
II. History of Peatland Development .....	57
Directionality of Succession and Peatland Stability.....	65
Evidence for Peatland Expansion .....	66
Factors Influencing Peatland Expansion .....	68
III. Modern Wetland Vegetation .....	70
IV. Holocene History of <i>Nyssa</i> and <i>Picea</i> in New England .....	76
<i>Nyssa</i> .....	76
<i>Picea</i> .....	78
Evidence for the Younger Dryas Climatic Reversal.....	78
Wetlands as Mid-Holocene <i>Picea</i> Refugia.....	80
CONCLUSION .....	83
REFERENCES CITED .....	86
APPENDIX .....	94
1. List of Vascular and Non-Vascular Plant Species.....	94
2. Pollen Percentages for Taxa Not Appearing on Pollen Diagram	95

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## LIST OF FIGURES

FIGURE	PAGE
1. Topographic map showing the location of Black Gum Swamp and surrounding hills, streams and wetlands.....	7
2. Map showing basin morphometry and location of macrofossil, pollen and basal-sediment coring sites.....	9
3. Map showing the location of releve plots for vegetation sampling.....	13
4. Map showing location of wells used for relative water-level measurements in the peatland.....	15
5. Cross-section showing basin morphometry and the inferred location of the former lake level and sediment limit.....	17
6. Sediment stratigraphy at coring sites distributed throughout the wetland.....	18
7. Sedimentation curve for pollen-core sediment.....	20
8. Loss-on-ignition as determined for pollen-core sediment.....	22
9. Macrofossil diagrams for shallow-sediment cores.....	23
10. Macrofossil diagram for long core obtained at pollen-coring site.....	25
11. Temporal correlation between the radiocarbon-dated pollen core and the macrofossil core obtained at the T-1A coring site.....	26
12. Pollen diagram showing percentages for arboreal and non-arboreal taxa.....	29
13. Contour maps showing yearly and seasonal variations in surface-water acidity (pH).....	33
14. TWINSPLAN cluster diagram showing segregation of releve plots by vegetation community type.....	37
15. Comparison of basal area for canopy tree species at T-3, T-1A stand-reconstruction plots.....	42
16. Comparison of shrub basal area at T-3, T-1A stand-reconstruction plots.....	43
17. Least-squares linear regression of diameter versus age for <i>Picea</i> at the T-3 stand-reconstruction plot.....	44
18. Comparison of stand age-distribution for canopy species at the T-3 and T-1A stand-reconstruction plots.....	45
19. Least-squares linear regression of diameter versus age for <i>Picea</i> at the T-1A stand-reconstruction plot.....	47
20. Relative peatland water-level fluctuations at well locations.....	48
21. Cumulative precipitation for periods between water-level measurement at wells.....	49

## LIST OF TABLES

TABLE	PAGE
1. Radiocarbon dates from Black Gum Swamp sediment cores.....	11
2. Summary statistics for surface-water acidity (pH).....	34
3. Summary statistics for surface-water chemistry (cation concentrations).....	35
4. Chemical properties of waters from North American wetlands...	36
5. Mean cover values (%) for species in community types identified by TWINSPAN.....	38
6. Relative basal area for canopy tree species at T-3, T-1A stand-reconstruction plots.....	46
7. Pre-decline maxima and post-decline minima for <i>Tsuga</i> at Northeastern pollen sites.....	55
8. Vascular plant species primarily confined to wetland margins.	72

## INTRODUCTION

Studies of peatland development and succession have long been a focal point of wetland research. According to Gorham (1953), Boate (1652) and King (1685) provide early descriptions and classifications of peatlands in Great Britain and also provide some of the earliest observations regarding successional changes and developmental processes. In the early 19th century, DeLuc (1810), Aiton (1811) and Griffith (1811) were among the first to refer to the concept of an ordered sequence of vegetational change associated with lake in-fill (Gorham 1953). Clements (1916) later expanded upon this theme and popularized the terms "hydrosere" and "hydrarch succession" to refer to convergent patterns of wetland succession eventually leading to terrestrialization, i.e. the development of mesophytic forest vegetation. Successional theory was subsequently widely applied to northern peatlands by numerous researchers including Tansley (1939), Godwin (1934), Rigg (1940), Gates (1942) and Dansereau and Segadus-Vianna (1952). However, studies of northern peatland ecosystems by Heinselman (1963, 1970) and Sjörs (1961, 1980) suggest that development of mesophytic forest is not necessarily the final stage of succession, and that successional trends are not always unidirectional or convergent (Walker 1970, Zobel 1988). Instead, these authors contend that peatlands may develop individualistically in response to complex, site-specific interactions of changing allogenic and autogenic factors.

Zobel (1988) stresses the importance of spatial and temporal scale when addressing questions of vegetative change in peatlands. While succession on microforms (e.g. individual hummocks) may be observed over a period of years, community succession and the development of a bog-

complex may take centuries or millenia to complete. Determining the nature, rate and directionality of change therefore depends upon the time scale and scope of the investigation. Stratigraphic methods (surveys of sediment stratigraphy, radiometric dating of sediments, pollen and macrofossil analyses) may provide the ideal means for studying peatland development over an extended time scale, and appear to be most appropriate for resolving questions regarding the relative stability of peatland ecosystems and vegetation communities (cf. Foster et al. 1990).

Paleoecological research in central and southern New England has focused primarily on major vegetation transitions occurring on the upland. Consequently, information on the Holocene evolution of peatlands is largely absent from the published literature. Although several papers describe floristics and functional aspects of New England peatland ecosystems (e.g. Moizuk and Livingston 1966, Baldwin 1961, 1978, Damman and French 1987, Dunlop 1987, Fosberg and Blunt 1970, Paratley and Fahey 1986, Swan and Gill 1970), few researchers have attempted to analyze existing peatland vegetation as the most recent stage of a long-term developmental sequence driven by both allogenic and autogenic factors. Furthermore, little is known about the Holocene history of arboreal species such as *Picea* and *Nyssa sylvatica*, taxa that are generally uncommon in central and southern New England peatlands, but which may have played important roles in local peatland development.

Davis (1958) provides some pertinent information regarding the development of peatlands as part of a larger paper describing vegetation response to climate in central Massachusetts. In a palynological analysis of sediment from Goulds Bog, Davis invokes the presence of

habitat-indicator types in the pollen record (e.g. *Myrica*, *Picea*, *Typha*) to infer stages of hydrarch succession. The presence of recurrence surfaces (i.e. horizons separating older, more decomposed peat from younger, less-decomposed peat, usually indicating a period of slow peat accumulation and faster decomposition) and varying degrees of peat humification were utilized to infer the occurrence of climatic change affecting both the timing and direction of successional stages.

Although occurring well outside of New England, paleoecological research conducted at peatlands in the northern Midwest may provide generalized concepts of Holocene peatland development crucial to interpretations of biological and stratigraphic data generated at sites in the northeast. Some examples of relevant studies are outlined below.

After carrying out an exhaustive palynological analysis of sediments from a present-day *Typha* marsh in Minnesota, Janssen (1967) was able to document a transition from eutrophic wetland conditions (indicated by *Salix* and *Typha*) to a more mesotrophic nutrient regime characterized by the development of a *Larix-Picea* forest. Anthropogenic factors (i.e. logging on the adjacent upland) initiated reversion back to a *Typha* marsh in the early 20th century. In a paleoecological study of the Myrtle Lake Peatland, Minnesota, Janssen (1968) described similar early stages of lake in-fill and inferred that the more recent (3000 yrs BP) development of raised bogs and poor fens resulted from a transition to a cooler, wetter climate. Miller and Futyma (1987) and Futyma and Miller (1986) utilized paleoecological techniques to describe developmental sequences in Michigan peatland vegetation resulting from changing hydrological conditions associated with paludification and peat accumulation. In a study of Wisconsin peatlands, Winkler (1988)

reiterates the conclusion that a change to a wetter climate during the past 3000 years has been a critical element in the development of peatlands in the northern Midwest.

The current study attempts to describe the development of the Black Gum Swamp peatland, located in the Harvard Forest, Petersham, Massachusetts. The time period of the study ranges from the late-glacial - early postglacial period (approximately 13,000 yrs BP) to the present. Among the central questions being asked are: 1) what long-term successional trends have occurred through the Holocene, and has there been directionality towards a particular stage of peatland development?; 2) what accompanying major transitions in upland vegetation occurred during the Holocene, and can climatic change possibly influencing peatland development be inferred from these transitions?; 3) what autogenic and allogenic processes have determined patterns of vegetation succession at this central New England peatland, and do similar or different processes continue to influence vegetation distribution and abundance today?; 4) while peatland expansion through paludification of upland habitat has been inferred at peatlands in the northern Midwest, does this process occur in central New England, and are the mechanisms similar?

To answer these questions, detailed stratigraphic descriptions of basin sediments supplemented by pollen and macrofossil analyses and radiometric dating will be employed to record the progress of Holocene peatland development over the entire basin area. Environmental conditions and contemporary vegetation existing in the basin will also be described.



5

Results expected from biostratigraphic analyses include the following: 1) delineation of spatial and temporal variation in vegetation within the basin; 2) evaluation of the extent of horizontal expansion of the peatland throughout the Holocene; 3) documentation of the Holocene history of uncommon peatland taxa, e.g. *Nyssa* and *Picea*; and 4) estimation of the importance of allogenic disturbance processes (fire, drought, flooding) as factors influencing vegetation development at the community level.

Objectives associated with the study of modern vegetation and environmental conditions at Black Gum Swamp have been selected to complement information derived from paleoecological studies. Specific objectives include: 1) analysis of the spatial variations in vegetation in the context of environmental factors such as pH and nutrient status of surface water; 2) qualitative estimation of the extent of water and nutrient influx from upland sources and evaluation of the importance of these external inputs on vegetation; 3) characterization of patterns of internal water movement in the peatland; and 4) evaluation of the impact of past human land-use (e.g. logging) as a factor influencing contemporary patterns of vegetation distribution and abundance.

Results expected to be gained from this study should provide insight into the dynamic nature of peatland development and establish a temporal framework for transitions occurring within one particular peatland. It is also hoped that the application of research methods spanning a broad range of temporal and spatial scales will contribute toward an understanding of peatland ontogeny at Black Gum Swamp as a function of both long- and short-term ecological processes.

## SITE DESCRIPTION

The Harvard Forest, Petersham, Massachusetts, is located in the Central Uplands of Massachusetts, a moderately rugged physiographic region characterized by south-trending ridges and valleys (Motts and O'Brien 1981). Thin till deposits overlies acidic metamorphic and igneous bedrock (Zen 1983). Regional vegetation is predominantly the transition hardwood - hemlock - white pine type described by Westveld et al. (1956).

Black Gum Swamp is a 10-ha forested wetland occupying a till-floored basin flanked by hills to the north and northwest (Fig. 1). Site elevation is 366 meters (1200 ft) a.s.l. Upland soils surrounding the basin are stony fine sandy loams in the Brookfield series (Simmons 1941). Vegetation on the relatively dry western upland is dominated by young transition hardwoods whereas an extensive stand of hemlock (*Tsuga canadensis*) with lesser amounts of white pine (*Pinus strobus*), red spruce (*Picea rubens*), beech (*Fagus grandifolia*), red oak (*Quercus rubra*) and red maple (*Acer rubrum*) occurs on moist upland soils to the north and east. No active surface-water inlets occur at the site, but an intermittent outlet stream is located at the southwestern end of the swamp. Microtopography within the wetland consists of hummocks and hollows with a water table at or near the surface for most of the year. Qualitative observations indicate that hummock height and hollow surface area are greater in the wetter northern half of the swamp.

Relevé data obtained from 10-m radius plots indicate that red spruce is the most frequent canopy tree species, followed by red maple, hemlock, black gum (*Nyssa sylvatica*), yellow birch (*Betula alleghaniensis*) and white pine. Common shrubs include *Ilex*

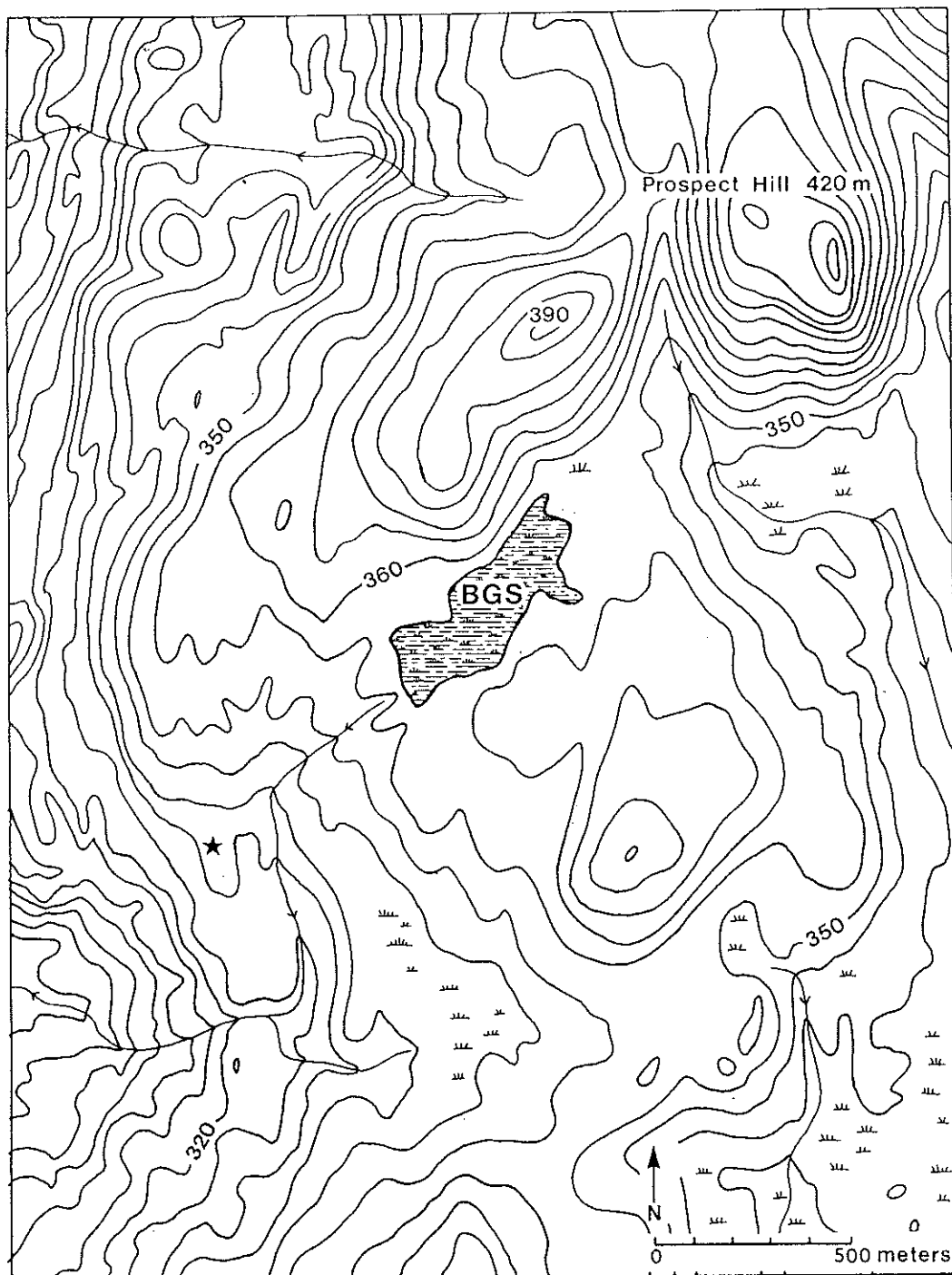


Fig. 1. Topographic map (5-m contour interval) showing the location of Black Gum Swamp (BGS) and surrounding hills, streams and wetlands. Harvard Forest headquarters is indicated by a star.

*verticillata*, *Nemopanthus mucronata*, *Vaccinium corymbosum* and *Viburnum cassinoides*. Woody vegetation is confined primarily to the tops and sides of hummocks, which also provide relatively dry microsites for herbaceous species more commonly associated with mesic uplands (e.g. *Aralia nudicaulis*, *Clintonia borealis*, *Trientalis borealis*, *Gaultheria procumbens* and *Mitchella repens*). *Sphagnum* spp., *Osmunda cinnamomea*, *Coptis groenlandica* and *Carex trisperma* typically line the bottoms and sides of hollows, occasionally in association with *Calla palustris* and *Smilacina trifolia* at the wettest sites. The swamp has been logged in the past, although apparently never clear-cut (Spurr 1956). A complete list of bryophytes and vascular plants is found in Appendix 1.

## METHODS

### Paleoecology

Wetland boundary delineation was accomplished with the use of color-infrared aerial photography (flight date September, 1985; scale 1:25,000) supplemented by pace-and-compass ground surveys. A series of seven transects were established across the swamp and permanently marked at 25-m intervals with PVC pipe. Basin morphometric data were obtained by sounding with thin steel rods at 10-m intervals across the transects and the sediment stratigraphy was examined at 25-m intervals. Sediment was extracted with a 50-cm Russian corer and described in the field. A 5-m core for pollen analysis was obtained from the deepest part of the basin on transect T-1A. Cores for macrofossil analysis were taken at the pollen-core site and from three other sites distributed throughout the swamp (Fig. 2). Sites for biostratigraphic analyses were located in areas with differing sediment depths and distances to shore to determine

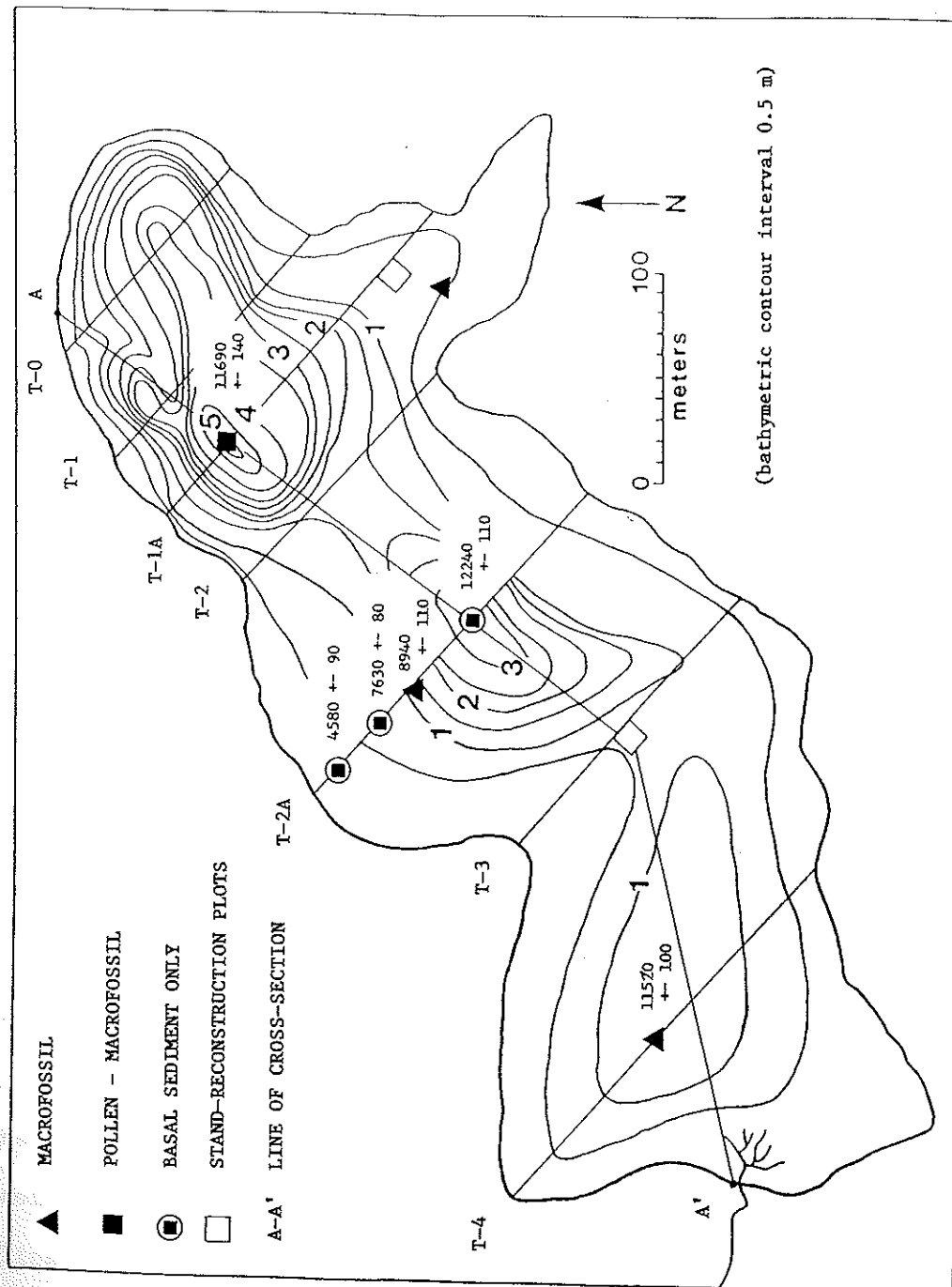


Fig. 2. Map showing basin morphometry, location of macrofossil, pollen and basal-sediment coring sites (dates indicate C-14 yrs BP), transect (T-#) locations, stand-reconstruction plots and the line of section for Fig. 5.

if these areas had different developmental histories. A series of four basal sediment cores for radiocarbon dating were obtained along the depth-gradient on transect T-2A, and an additional core was obtained from a location in the south-central portion of the swamp.

Core sub-sampling for pollen analysis was carried out by removing 0.5 cc of material from a narrow band of sediment ( $< 0.5$  cm) at measured stratigraphic intervals. Processing followed the acetolysis procedure of Faegri and Iversen (1975) as modified by Cushing (pers. comm.). Pollen analysis was performed with a Zeiss light microscope at 400x and 1000x (oil-immersion). A minimum of 300 arboreal pollen grains were counted at each level. During counting, the entire cover-slip area was examined with a series of equally-spaced traverses. The pollen percentage diagram for upland taxa is based on a sum excluding spores, aquatics and wetland taxa. Percentages for excluded taxa are based on the total pollen sum. Charcoal fragments larger than  $15\ \mu$  in longest dimension were counted using the point-intercept method (Clark 1982). Chronostratigraphy is based on seven radiocarbon dates (Table 1). Loss-on-ignition (organic-carbon content) was determined for sediment sub-samples obtained at 10-cm intervals using the methodology described by Dean (1974).

The four macrofossil cores were processed by washing 10-cm sections of sediment (80 cc) through #10 and #24 wire-mesh screens. For the macrofossil core obtained at the pollen-core site, material from two duplicate cores was pooled to obtain 160 cc samples. With the aid of a stereomicroscope, identifiable plant macrofossils were picked from the washing residue and preserved in a glycerin - water - alcohol solution (1:1:1). A visual estimate of the proportion of Lignosae, Herbaceae,

Table 1. Radiocarbon dates from Black Gum Swamp sediment cores.

Core Type	Location In Swamp	Depth Of Sample (cm)	Sediment Type	Sample Code	C-14 Age (yrs BP)
Pollen	T-1A 150 m	450 - 465	gyttja	Beta-31366	11690 +- 140
	"	370.5 - 377.5	gyttja	Beta-29919	9750 +- 450
	"	280 - 290	gyttja	Beta-31365	8910 +- 120
	"	240 - 250	shrub-sedge peat	Beta-31364	8680 +- 120
	"	202 - 208	shrub-sedge peat	Beta-29917	8560 +- 140
	"	160 - 170	swamp-forest peat	Beta-31363	7580 +- 90
	"	70.5 - 75.5	swamp-forest peat	Beta-29916	3340 +- 110
Basal Sediment	T-2A 90 m	400 - 410	gyttja-clay	Beta-42117	12240 +- 110
	T-2A 125 m	134 - 142	shallow-water sed.	Beta-42118	8940 +- 110
	T-2A 150 m	74 - 82	swamp-forest peat	Beta-43786	7630 +- 80
	T-2A 162 m	64 - 72	swamp-forest peat	Beta-42119	4580 +- 90
	T-4 125 m	117 - 125	swamp-forest peat	Beta-42120	11520 +- 100

Pteridophytae and Muscinae in the washing residue was made for each sample (Grosse-Brauckman 1986, Levesque et al. 1988). Wood macrofossils firm enough to be sectioned with a razor blade were identified on the basis of microscopic anatomical features observed with a light microscope at 100x and 400x (Panshin and DeZeeuw 1980, Hoadley 1990).

### Modern Vegetation

During the summers of 1988 and 1989, vegetation surveys (relevés) were carried out at 10-m radius plots located at 25-m intervals along transects (Fig. 3). Percent cover was estimated for all species in canopy, understory, herb layer, and ground layer height strata (Mueller-Dombois and Ellenberg 1974). Vegetation data were then subjected to two-way indicator species analysis (TWINSPAN; Hill 1979).

Reconstructions of stand histories were carried out in 25m x 25m plots (0.0625 ha) at locations on transects T-1A and T-3 (Fig. 2). These sites were selected to contrast patterns of revegetation in areas with differing hydrological regimes. The plot on T-3 is drier with less pronounced microtopography and is located in the interior of the swamp. The T-1A plot is near the swamp margin in an area with typically high surface-water levels and a relatively high hollow-hummock surface area ratio; this area also has a higher pH and is located near a seepage inlet. Increment cores were obtained from all trees occurring within the 25m x 25m plots. Cores were taken as low on the stem as possible, and diameters were measured at coring-height. Shrub stem diameters (dbh) were measured within one randomly-selected 10m x 10m subplot.

### Surface-Water Chemistry

Surface-water pH measurements were made with a Radiometer-Copenhagen portable pH meter at 25-m intervals along transects in May



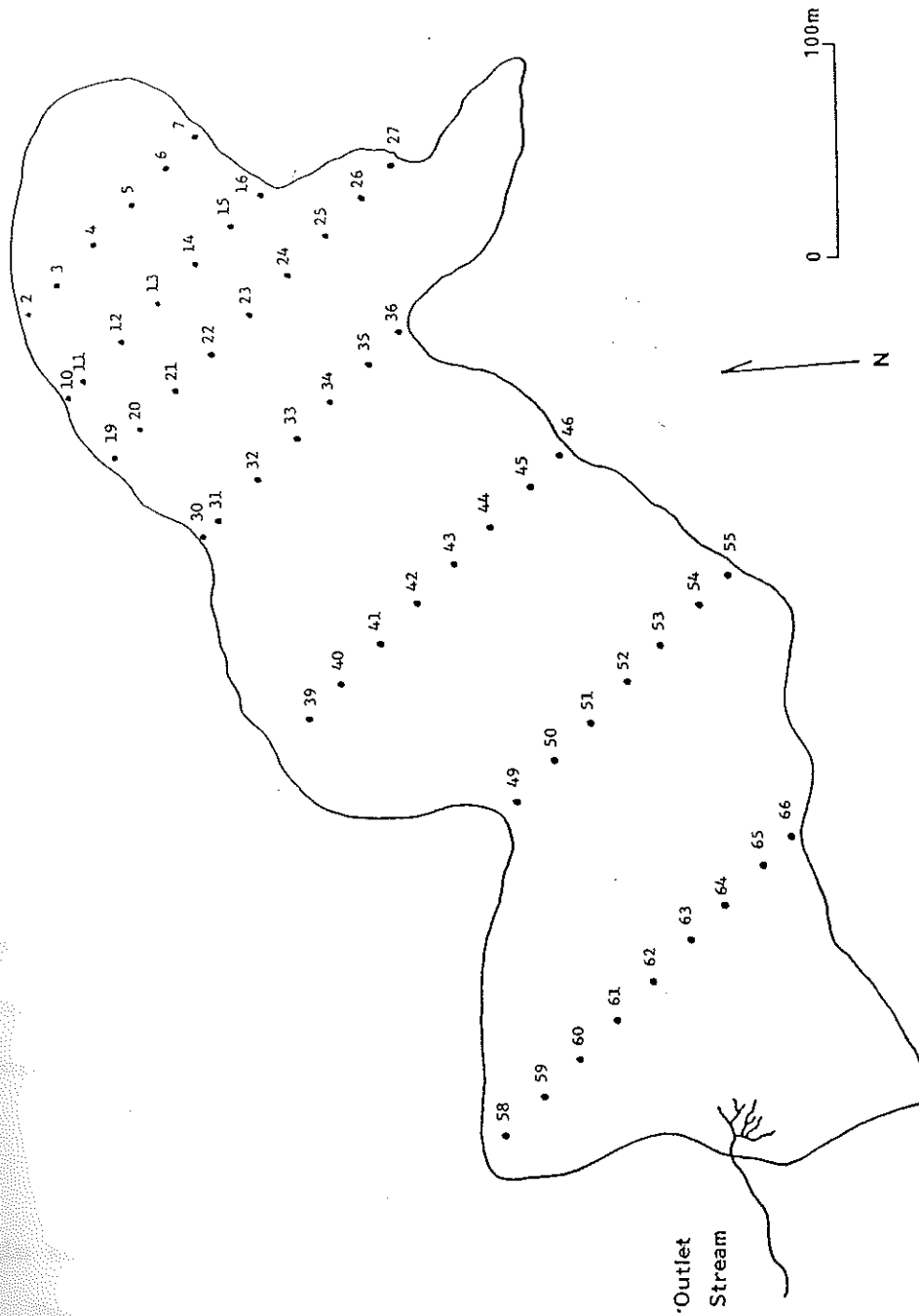


Fig. 3. Map showing the location of 10-m radius relevé plots for vegetation sampling.

and August of 1989 and 1990. In August 1990, surface-water samples for chemical analysis were obtained near the swamp margins and from interior locations along transects. Samples were frozen within four hours of collection and stored at 0 °C until analyzed. Concentrations of Ca<sup>++</sup>, Mg<sup>++</sup>, Na<sup>+</sup> and K<sup>+</sup> (mg/l) were determined by absorption spectrophotometry at the Center for Energy and Environmental Research, University of Puerto Rico (C. Asbury pers. comm.).

### Hydrology

A total of seven wells were established at margin and interior locations across the swamp (Fig. 4). Wells were constructed of 5-foot lengths of 5-inch diameter sewer pipe with 1/4-inch holes drilled into the lower two feet of the pipe-section. Wells were installed by excavating a hole in peat with a post-hole digger and lowering the pipe three feet into the hole or until basal till was contacted. A permanent reference level for relative water-depth measurements was established by stringing a taut nylon line between two adjoining trees over the top of each well. Depths to the top of the water table were obtained with a wooden dipstick. Observations were made on the average of once a week from May 1990 until winter freeze-up in late December. During a period of heavy rain in August, measurements were taken at two-day intervals. Precipitation data were compiled from Harvard Forest weather-station records (Harvard Forest Archives).

## RESULTS

### Basin Morphometry

Two discrete deep basins separated by a slightly shallower bench occupy the central and northern portions of Black Gum Swamp (Figs. 2 and

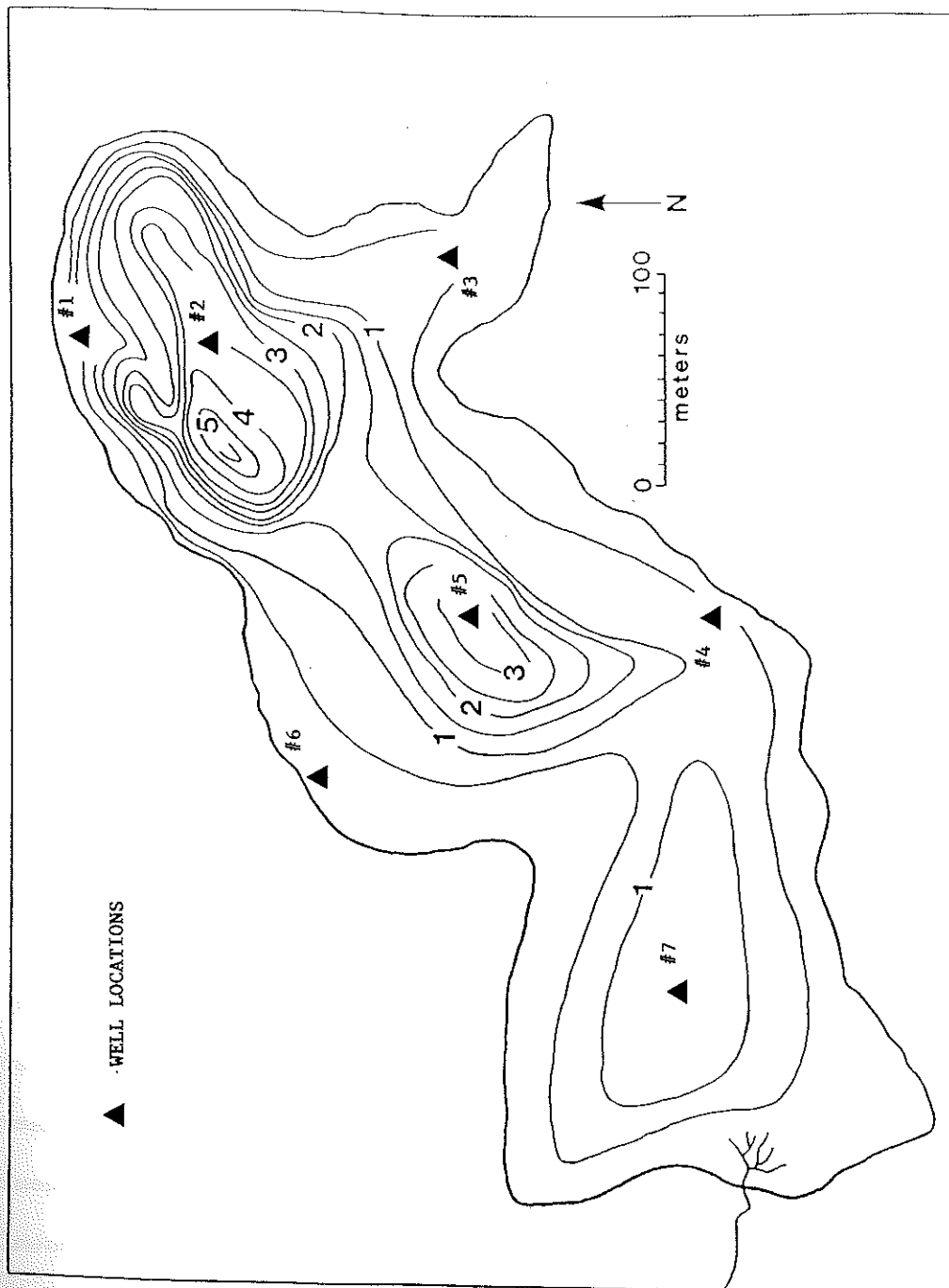


Fig. 4. Map showing the location of wells used for relative water-level measurements.

5). Both are irregularly elliptical with the northern basin being somewhat deeper (5 m) than the central basin (4.5 m), and are presumed to have formed as ice-block depressions in underlying till (Frederick Paillet, U.S. Geological Survey, pers. comm.). Shallow sediments (< 1.5 m) occur in a broad depression at the southern end of the swamp and at the eastern swamp projection. Although not portrayed in detail on the morphometric map, the floor of Black Gum Swamp has complicated local microtopography due to the presence of abundant boulders. The drainage threshold at the southern end of the swamp is broad and quite shallow.

#### Sediment Stratigraphy

Stratigraphic units at Black Gum Swamp are thickest over deep basin locations, thinning and truncating peripherally with decreasing basin depth. The deepest parts of the basin possess a series of well-defined sediment types in the following sequence (oldest listed first): 1) water-deposited glacial sand and clay, 2) algal gyttja, 3) shallow-water sediment, 4) shrub-sedge or shrub-fern-sedge peat grading to shrub peat, and 5) swamp-forest peat. Basal clay and overlying algal gyttja do not occur above the present 1.5 m depth contour, and shallow-water sediment and shrub peats are absent above 1 m. In shallow basin margins (< 1 m) and throughout most of the broad depression to the south, forest peat is deposited directly on mineral soil without intervening water-lain sediment. Local areas in the interior of the southern depression with sediment depths exceeding 1 m are underlain by basal shallow-water sediment over mineral soil. Detailed stratigraphic descriptions of sediment survey cores are provided in Fig. 6.

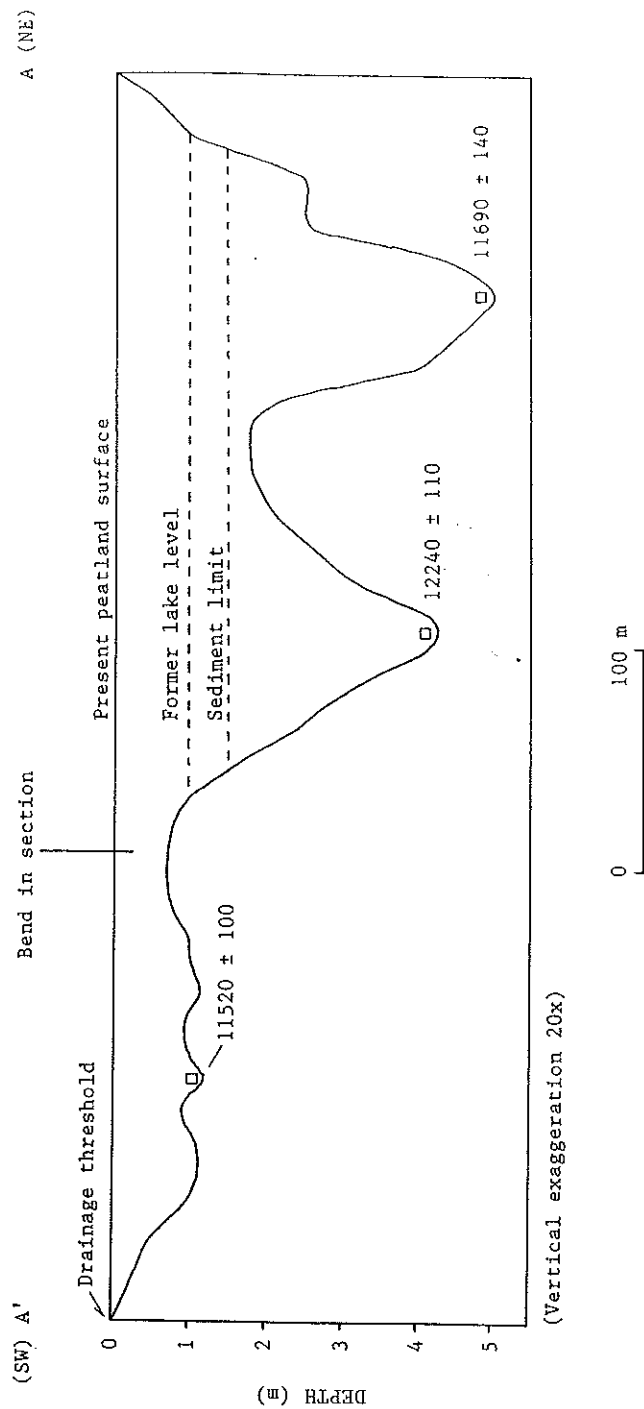


Fig. 5. Cross-section through line A-A' (see Fig. 2) showing basin morphometry and the inferred locations of the former lake level and sediment limit. Dates refer to the age (C-14 yrs BP) of basal sediment.

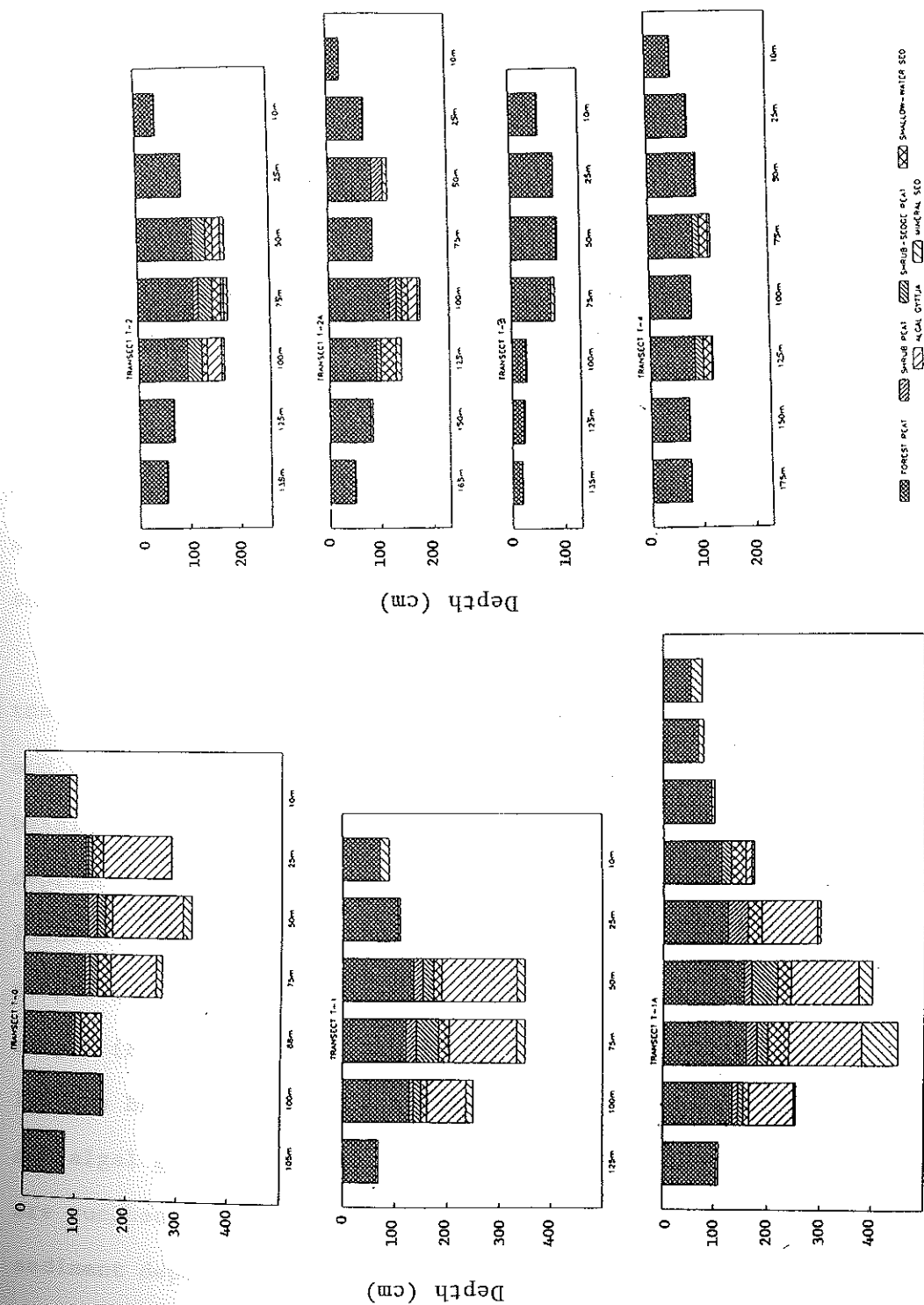


Fig. 6. Sediment stratigraphy at coring sites distributed throughout the wetland.

## Radiocarbon Dating and Sedimentation Rates

Linear interpolation between radiocarbon-dated horizons and a biostratigraphic marker horizon (hemlock decline, 4700 yrs BP; Davis 1981, Webb 1982) provide the basis for depth/age equivalents used to calculate sedimentation rates and for establishing the chronology of transitions in sediment biostratigraphy. Sedimentation rate changes with sediment type (Fig. 7). Algal gyttja was deposited at the rate of 0.046 cm/yr from 12,000 - 9750 yrs BP, increasing to 0.107 cm/yr from 9750 - 8800 yrs BP. From 8800 - 8700 yrs BP, shallow-water sediment was deposited at the rate of 0.173 cm/yr. Shrub peats were deposited from 8700 - 8100 yrs BP at the sharply increased rate of 0.333 cm/yr. After the transition from shrub peat to forest peat at 8100 yrs BP, sediment accumulation slows to 0.040 cm/yr. From 7600 to 200 yrs BP, forest peat accumulation remained slow, varying between 0.013 and 0.036 cm/yr, sharply increasing to 0.100 cm/yr after 200 yrs BP.

Radiocarbon dates from basal sediment (algal gyttja) obtained from the deepest portions of the central and northern basins (11,690  $\pm$  140 and 12,240  $\pm$  110 yrs BP, respectively) are roughly similar to the basal date obtained from the central portion of the shallow southern depression (11,520  $\pm$  100 yrs BP). Basal sediment dates from coring locations oriented along the depth gradient on transect T-2A are progressively younger from the basin interior to the present wetland margin (Fig. 2). At the 125-m coring site, the basal date of 8940  $\pm$  110 yrs BP is associated with a change in sediment stratigraphy: clay and algal gyttja pinch out at the present 1.5 m bathymetric contour and are succeeded at a slightly higher bathymetric level by shallow-water sediment deposited on mineral soil. At 150 m (basal age 7630  $\pm$  80 yrs

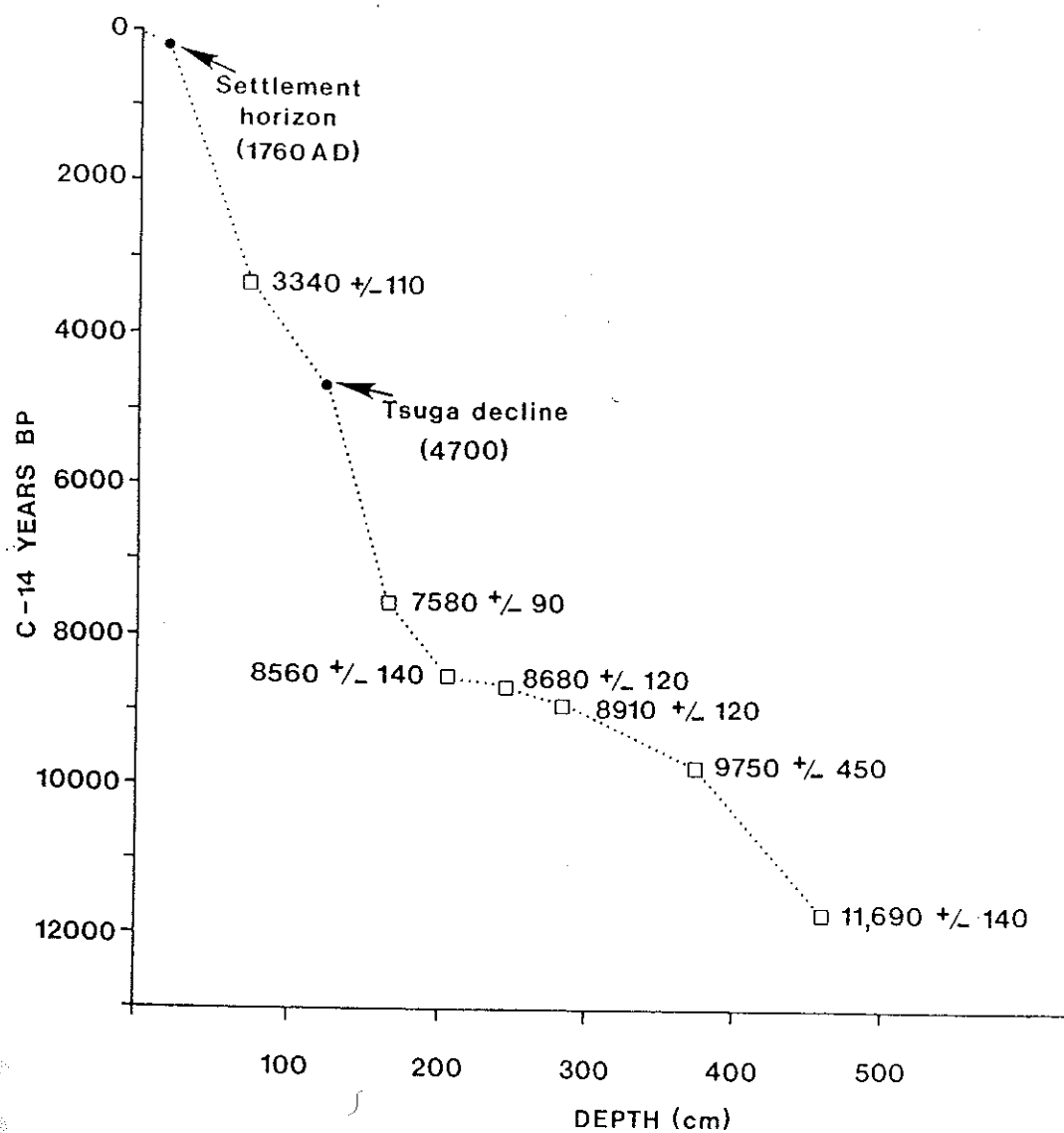


Fig. 7. Sedimentation curve for the pollen-core sediment based on radiocarbon dates (yrs BP) and biostratigraphic temporal markers (*Tsuga* decline and settlement horizon).



BP) and 162 m (basal age 4580  $\pm$  90 yrs BP), forest peat occurs over mineral soil at levels above the 1-m bathymetric contour.

#### Loss-On-Ignition

Percent loss-on-ignition (Fig. 8) shows an initial sharp increase in organic content (3% to 39%), indicating the transition from primarily minerogenic glacial sediment to gyttja. From 11,000 to 10,000 yrs BP, a leveling-off in organic content is noted, followed by a decrease to 22%. Organic content rises again to 30% at 9000 yrs BP, and then abruptly increases to 96% during the deposition of shallow-water sediment and shrub peat. After 8100 yrs BP, organic content remains consistently above 90% in swamp forest peat.

#### Macrofossil Survey

Highly-humified forest peat from the shallow eastern swamp lobe contains abundant undifferentiated Lignosae fragments distributed throughout the core. Herbacae, Muscinae and Pteridophytae remains are rare. *Picea* and *Tsuga* macrofossils are found in low numbers sporadically throughout, whereas seeds of *Nyssa sylvatica* occur only at the surface (Fig. 9).

Forest peat from the shallow southern depression (T-4, 125 m) also contains abundant undifferentiated Lignosae. Herbacae remains are low in volume but are distributed throughout the core. Pteridophyte roots are absent, and Muscinae debris (mostly *Sphagnum* spp.) occurs near the surface. *Larix* needles occur near the gradational forest peat - mineral soil contact, and *Pinus* needles occur at the surface. *Picea* needles occur just above the mineral soil contact and are abundant at the surface. *Tsuga* needles and *Acer rubrum* leaves are found only in uppermost sediments. *Sparganium* fruits in association with Cyperaceae

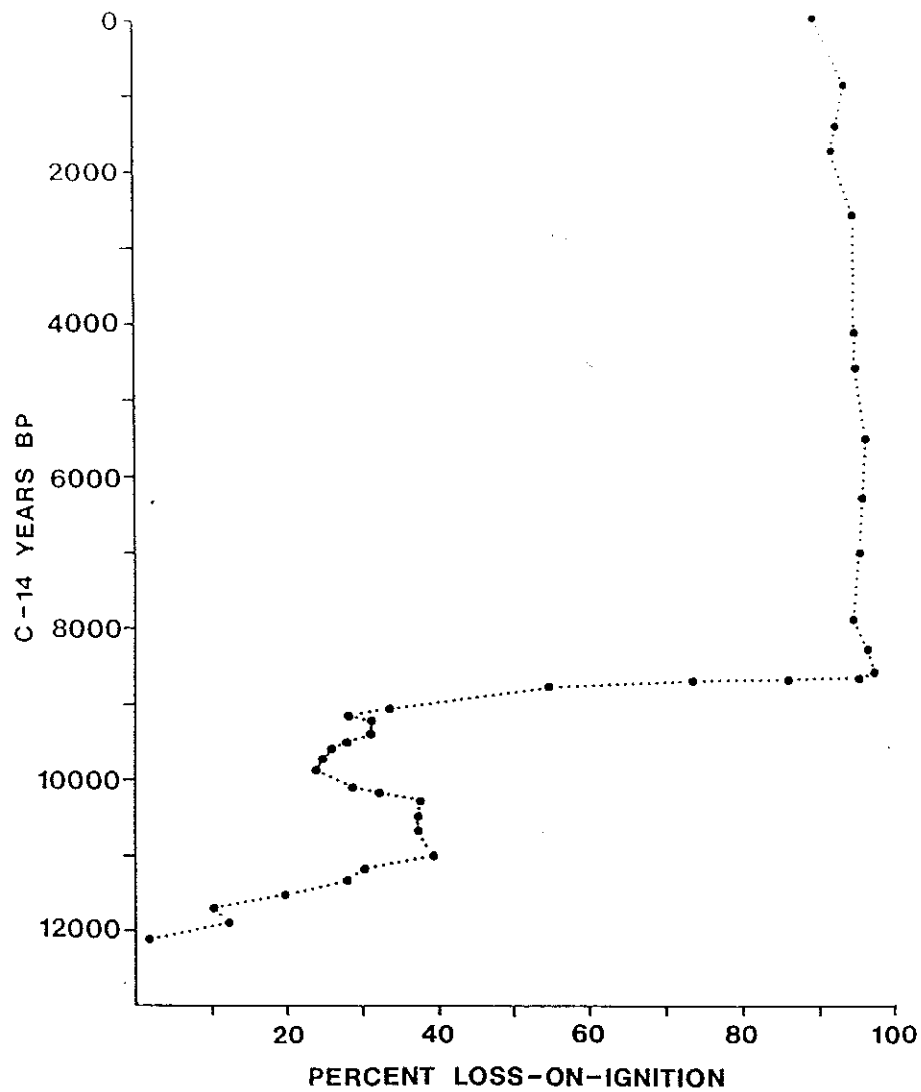


Fig. 8. Loss-on-ignition (organic content) for pollen-core sediment.

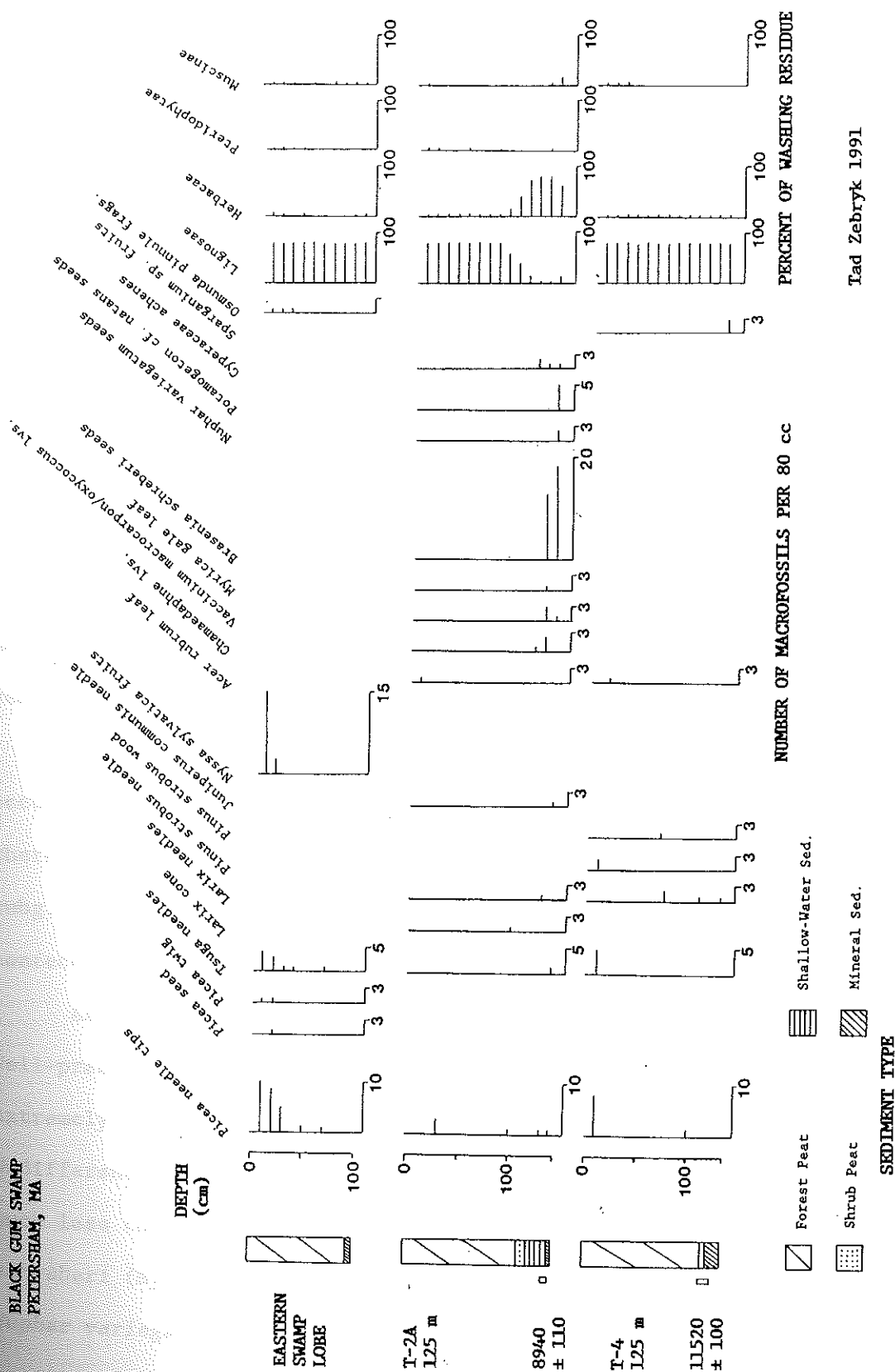


Fig. 9. Macrofossil diagrams for shallow sediment cores. Dates refer to the age (C-14 yrs BP) of basal sediment.

and Nymphaeaceae remains were found in primarily minerogenic basal sediments just below forest peat (basal radiocarbon date 11,520 +/- 100 yrs BP).

Distinct macrofossil assemblages are associated with a sequence of five sediment types recovered at the deep (5 m) coring site on transect T-1A, 150 m (Fig. 10). Radiocarbon dates obtained from pollen-core sediment obtained at the same site allow cross-dating of sediment-type transitions in the macrofossil core (Fig. 11).

**Assemblage I.** Basal glacial sediment; >12,000 yrs BP: Upland macrofossil taxa recovered include *Picea*, *Tsuga*, *Dryas integrifolia* and *Hypnum* (a bryophyte). Wetland and aquatic taxa present are *Salix*, *Brasenia schreberi*, *Ranunculus* subg. *Batrachium*, *Lamiaceae* cf. *Lycopus* sp., *Osmunda cinnamomea*, *Sphagnum* sp. and *Drepanocladus* sp. *Picea* needles are the most abundant identifiable macrofossil in washing residues dominated by mineral sediment.

**Assemblage II.** Algal gyttja; 12,000 - 9000 yrs BP: *Picea* needles occur throughout algal gyttja. *Sphagnum* stems occur sporadically and there is one occurrence of a single *Nuphar variegatum* seed. *Ranunculus* subg. *Batrachium* achenes and *Drepanocladus* stems are abundant near the contact with basal mineral sediment.

**Assemblage III.** Shallow-water sediment; 9000 - 8750 yrs BP: Well-preserved Herbaceae remains (mostly Nymphaeaceae and Cyperaceae) are extremely abundant, comprising 80% of the washing residue. Undifferentiated Lignosae (mostly fine roots) and Pteridophyte roots are much less common. Seeds of the floating aquatic species *Brasenia schreberi* (Nymphaeaceae) are frequent, occurring in association with *Nuphar variegatum* and *Potamogeton* spp. A diverse woody and herbaceous

Black Gum Swamp  
Petersham, MA

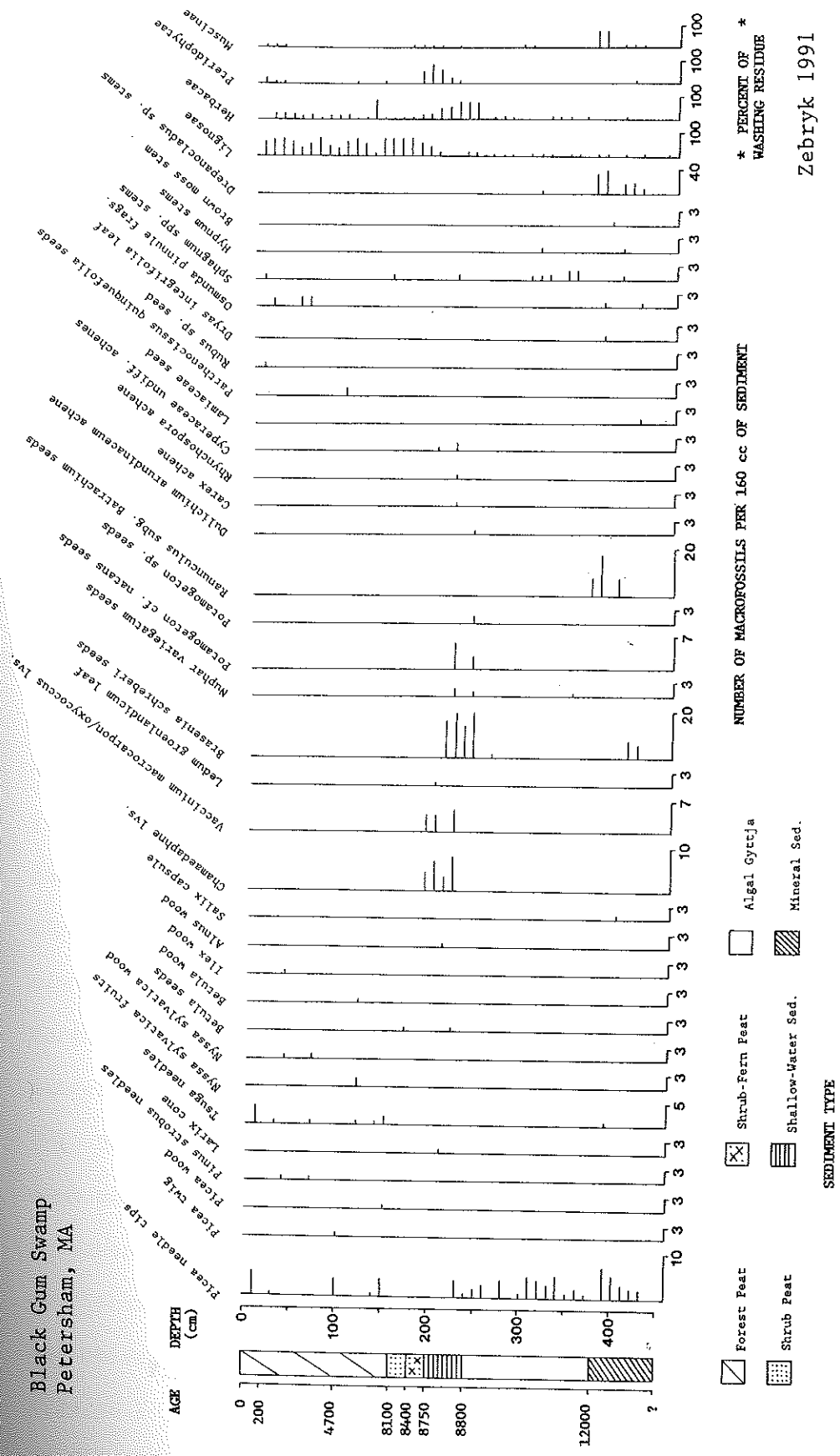


Fig. 10. Macrofossil diagram for sediment obtained at the T-1A (pollen core) site. Sediment ages are based on a stratigraphic correlation with the radiocarbon-dated pollen core.

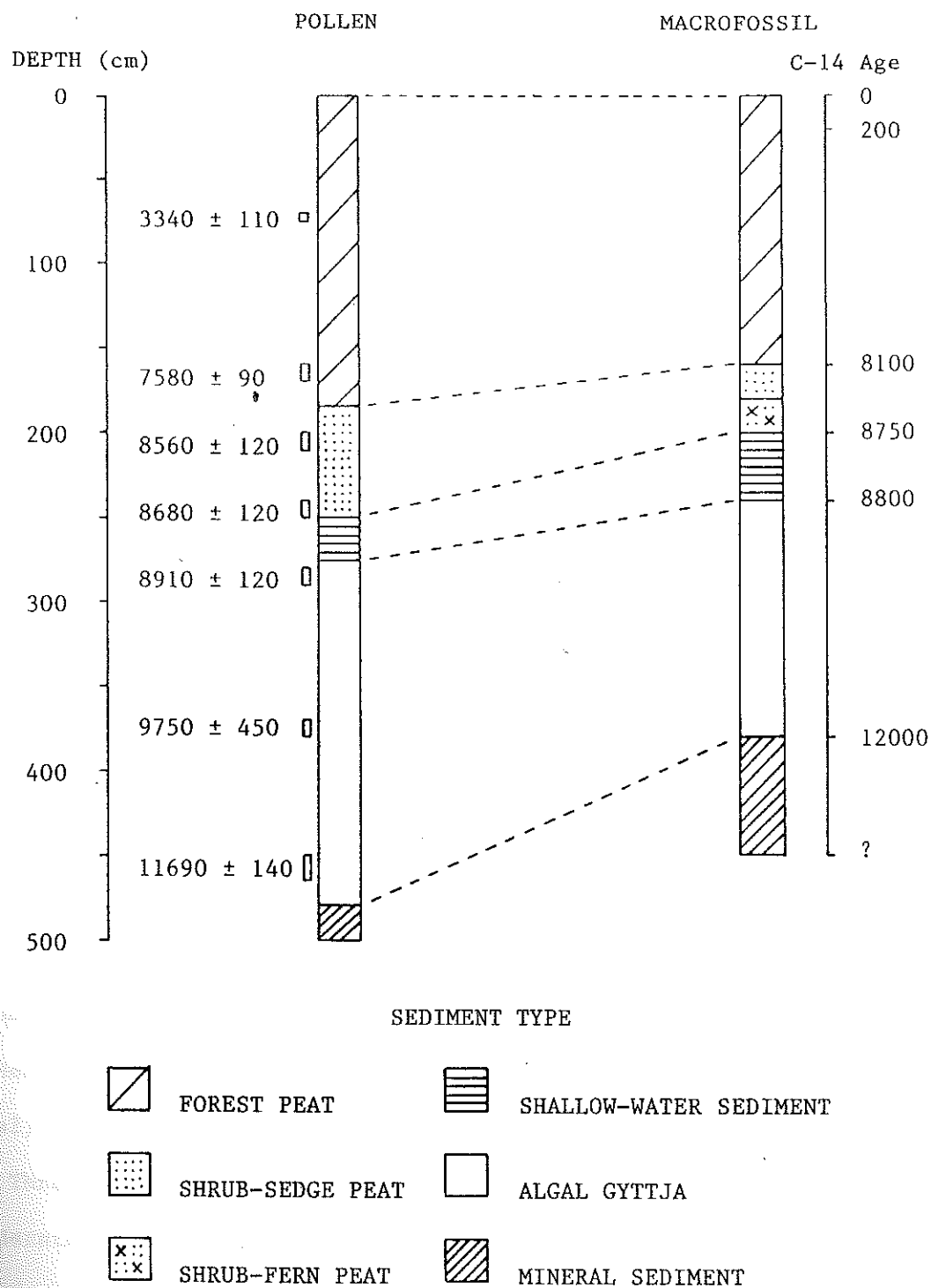


Fig. 11. Chronostratigraphic correlation between the radiocarbon-dated pollen core and the macrofossil core both obtained at the T-1A coring site.

macrofossil assemblage is also present, including *Picea* needles, a *Betula* sp. seed and *Larix* cone, *Alnus* wood, *Chamaedaphne calyculata* leaves, *Vaccinium macrocarpon/oxycoccus* leaves, *Sphagnum* stems, and achenes of *Dulichium arundinaceum*, *Carex* sp. and *Rhynchospora* sp.

Assemblage IV. Shrub-fern-sedge peat and shrub peat; 8750 - 8100 yrs BP: Pteridophyte roots and fine Lignosae roots are abundant, whereas Herbaceae remains are much less common. Specific macrofossils recovered include leaves of *Chamaedaphne*, *Vaccinium macrocarpon/oxycoccus* and *Ledum groenlandicum*.

Assemblage V. Swamp-forest peat; 8100 yrs BP - present: Large Lignosae fragments are abundantly distributed throughout this sediment type. Herbaceae debris is common while Pteridophyte roots and Muscinae (stems, leaves of *Sphagnum* spp.) are represented only in peat layers above 30 cm in depth. Macrofossils of woody taxa are frequent, including *Picea* (needles, wood, twig), *Pinus strobus* (needles), *Tsuga canadensis* (needles), *Nyssa sylvatica* (wood, fruits), *Betula* (wood) and *Ilex* (wood). Other taxa present are *Rubus* sp. (seed), *Osmunda cinnamomea* (pinnule fragments) and seeds of the upland species, *Parthenocissus quinquefolia* (apparently imported into the wetland by an animal).

Three stratigraphic units were observed in sediment retrieved from a moderately deep (1.5 m) coring site at 125 m on transect T-2A. The lowermost biogenic unit is shallow-water sediment occurring over mineral soil (basal radiocarbon date 8940 +/- 110 yrs BP). The macrofossil assemblage present is similar to that occurring in the same sediment type at T-1A, 150m. Herbaceae is abundant whereas Lignosae is uncommon; Pteridophytae and Muscinae are both rare. Seeds of aquatic species



(*Brasenia schreberi*, *Nuphar variegatum* and *Potamogeton* spp.) are frequent. Wetland shrub taxa include *Chamaedaphne*, *Vaccinium macrocarpon/oxycoccus* and *Myrica gale*. Arboreal macrofossils are rare; taxa present are *Picea*, *Larix* and *Tsuga*. One needle of *Juniperus communis* was recovered near the contact with mineral soil. Shrub-sedge peat consisting mostly of undifferentiated *Herbacae* and *Lignosae* debris occurs above shallow-water sediment. Forest peat overlies shrub-sedge peat. Undifferentiated *Lignosae* fragments are abundant throughout the core while *Muscinae* debris occurs only near the surface. Pteridophyte roots occur sporadically, but *Herbacae* remains are distributed throughout the core in low volume. Macrofossils of *Picea*, *Larix* and *Acer rubrum* are rare and sporadic.

#### Pollen Stratigraphy

Pollen percentage diagrams are subjectively divided into zones to facilitate the reporting of results (Fig. 12). Zones for the upland diagram correspond to major Holocene transitions in vegetation composition recognized at many northeastern pollen sites (Davis 1958, 1969, Gaudreau and Webb 1985). Pollen percentages for types not shown on the pollen diagrams are given in Appendix 2.

Zone 1 (12,500 - 11,800 yrs BP): Herbs are well represented in this zone, with grass and sedge comprising 40% of total pollen. Other herbaceous pollen types include *Saxifragaceae*, *Caryophyllaceae*, *Sanguisorba canadensis* and other *Rosaceae*, *Epilobium* and *Compositae*. Arboreal types present are *Picea*, diploxylon pine and *Populus*, while shrubs are represented by *Alnus*, *Salix*, *Betula*, *Shepherdia* and *Ericaceae*.



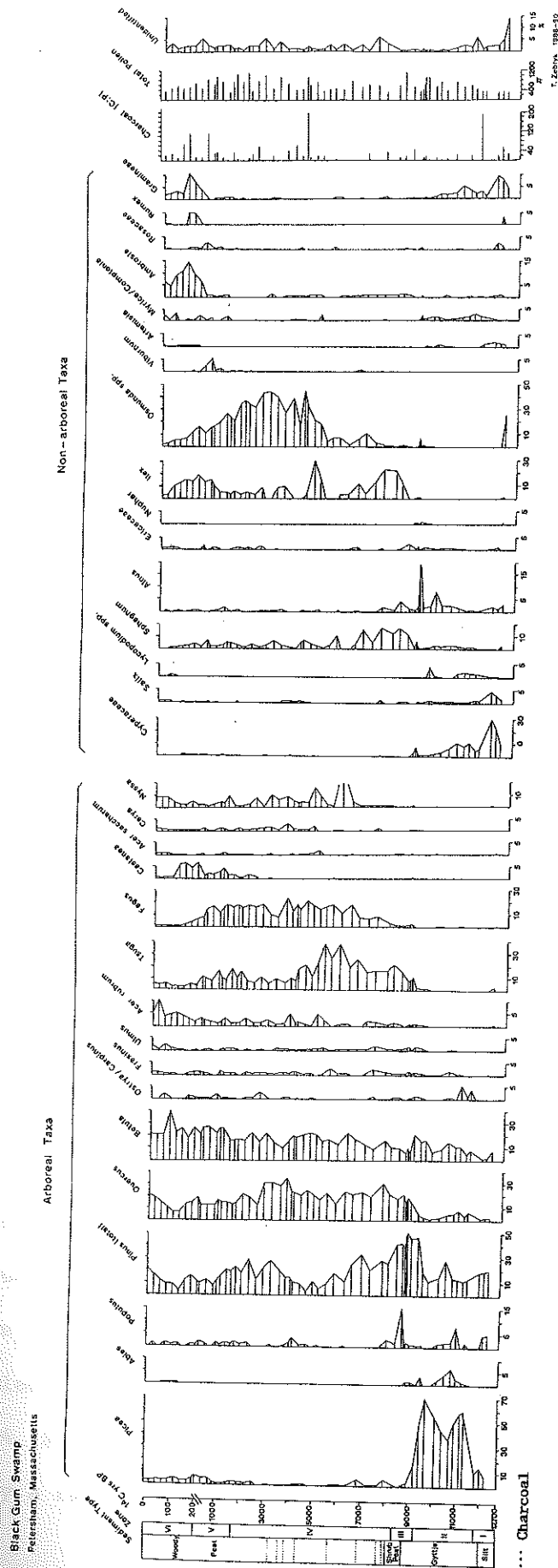


Fig. 12. Pollen diagram showing percentages for arboreal and non-arboreal taxa.

Zone 2 (11,800 - 9350 yrs BP): *Picea* is dominant during this period, reaching a maximum of 65% but declining to 16% at the end of the zone. The *Picea* profile has a double peak with an intervening decline to 37%. Diploxylon pine (mostly small-grained *Pinus banksiana*) increases to 50%. *Betula* percentages steadily increase, *Quercus* remains low, and *Abies* is low and variable. In the latter half of the zone, *Tsuga*, *Fagus*, *Acer rubrum* and *Ulmus* are present in low (< 2%) but continuous percentages. *Carya*, *Juglans* and *Nyssa* occur as scattered grains and *Populus* has sporadic low percentages. Wetland shrubs including *Alnus*, *Myrica/Comptonia*, *Salix* and *Ericaceae* are represented in low percentages, although *Alnus* later rises to 7%. Although initially high, graminoid percentages decline through the zone. Most other herbaceous species present in Zone 1 are absent in Zone 2. *Sphagnum* exhibits a small but steady increase from 1% to 3%.

Zone 3 (9350 - 8350 yrs BP): *Pinus* percentages reach a maximum value of 50% in this zone. The composition of *Pinus* species changes radically in mid-zone from nearly 100% diploxylon pine to mostly haploxylon pine (*Pinus strobus*) over a short stratigraphic interval representing a time span of 300 years. *Picea* falls rapidly but *Quercus* and *Tsuga* increase. *Fagus* and *Acer rubrum* maintain low percentages as *Betula* declines. *Alnus* continues to be important among wetland shrub taxa, reaching a peak of 19% in mid-zone. Values for *Ericaceae* reach a maximum, whereas sedge, *Osmunda* and *Sphagnum* later increase. Herbaceous species are rather rare, but grass maintains a low (<1%) percentage. *Nuphar* pollen appears in low percentages but is persistent in this zone.

Zone 4 (8350 - 2500 yrs BP): A large increase in *Tsuga* (to 38%) followed by a rapid decline to 7% is the major feature in this zone.

*Quercus* increases slowly, reaching peak percentages as *Tsuga* declines. Values for *Pinus* decrease gradually from 40% to 5%, but later increase to 20 - 30% by the end of the period. *Fagus* increases slowly and *Picea* is continuously present in low percentages. *Nyssa* is also continuously present, rising suddenly to 57% and remaining high but variable thereafter. *Ilex* is important throughout the zone, but percentages later become highly variable. *Alnus* is important early, but becomes sporadic, as do *Ericaceae* and *Myrica/Comptonia*. Percentages for *Osmunda* build gradually to a peak of 40%. *Sphagnum* is abundant early but gradually declines. *Acer rubrum* is continuously present in percentages < 5%.

Zone 5 (2500 - 200 yrs BP): *Picea*, *Castanea* and wetland shrub species (*Ilex*, *Alnus*, *Viburnum*, *Ericaceae*) increase during this period, and *Nyssa* experiences a moderate decrease. *Sphagnum* maintains lowered percentages as *Osmunda* declines rapidly. *Fagus* declines toward the end of the zone, but *Acer rubrum* remains steady.

Zone 6 (200 yrs BP - present): Agricultural indicators such as *Ambrosia*, *Rumex*, *Gramineae* and *Artemisia* increase as *Tsuga*, *Pinus* and *Quercus* decrease in the first half of the zone. *Castanea* percentages rise in conjunction with the decrease in *Tsuga*. Agricultural indicators and *Castanea* decline later in the zone as *Pinus* and *Quercus* recover. *Picea* suffers a moderate reduction early and does not return to former percentages. *Tsuga* remains depressed as *Ilex*, *Osmunda* and *Sphagnum* later decline. *Acer rubrum* increases steadily through the zone as *Nyssa* increases in the latter half.

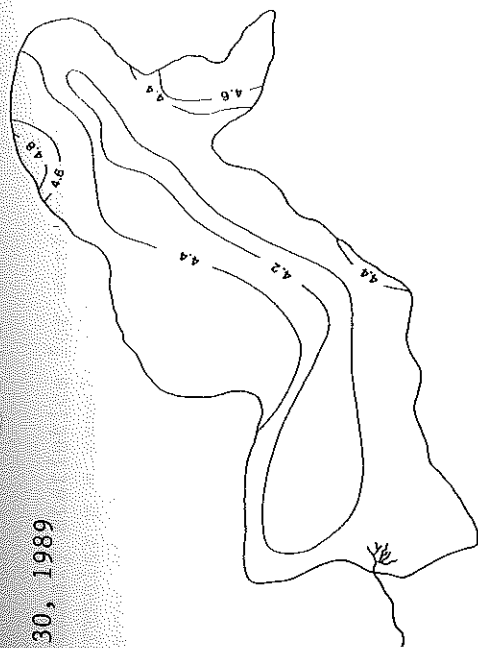
### Surface-Water Chemistry

Contour maps of pH indicate spatial, seasonal and yearly variation in surface-water acidity (Fig. 13). Values are uniformly lower in the basin interior compared to margin locations. Steep pH gradients were observed at the eastern swamp lobe and at a location on the northern margin. Seasonal and yearly variations in surface-water acidity expressed as pH were significant (Table 2). The mean pH for the swamp as a whole based on all four observations is  $4.10 \pm .37$ , indicating widespread, highly-acid conditions. (Note: pH rather than absolute  $H^+$  concentration is used as an index of surface-water acidity to ensure comparability of results with data from other wetland studies, e.g. Heinselman 1970, Jeglum 1971, Schwintzer and Williams 1974, Vitt and Slack 1975, Schwintzer 1978). Mean values for major cation concentrations are summarized in Table 3. A comparison of these values with chemical data from other North American wetlands suggests that Black Gum Swamp may be generally classified as a nutrient-impooverished wetland (Table 4; Tarnocai 1988).

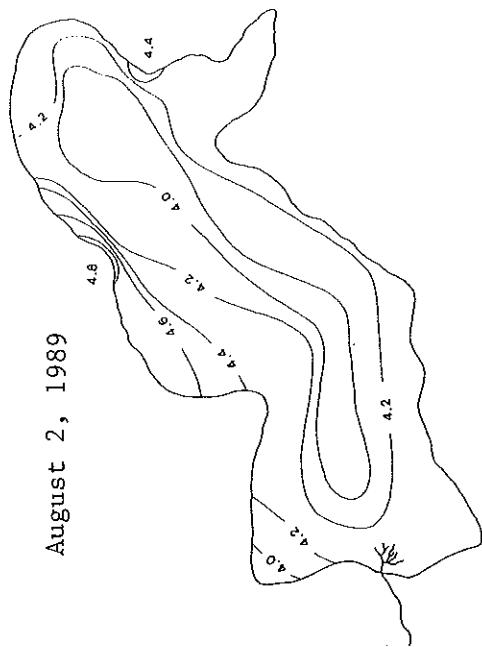
### Modern Vegetation

The results of two-way indicator species analysis indicates that the primary (level 1) dichotomy between plots is based on the relative frequency and abundance of *Picea* versus *Tsuga* (Fig. 14, Table 5). For plots dominated by *Picea*, level 2 subdivisions are based on the indicator species (cf. Hill 1979) *Ilex* spp./*Calla palustris* and *Aralia nudicaulis*. For plots dominated by *Tsuga*, level 2 subdivisions are based on the relative abundance of *Carex trisperma* and *Vaccinium corymbosum*. At the tertiary level, the *Ilex/Calla* subdivision of the *Picea*-dominated group is further divided into groups indicated by *Calla*

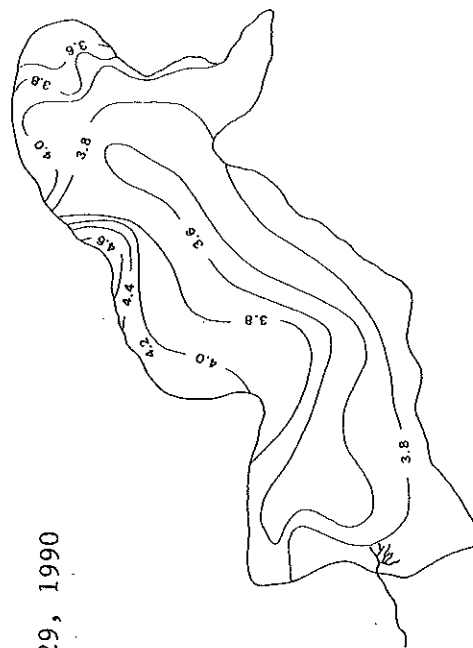
May 30, 1989



August 2, 1989



May 29, 1990



August 21, 1990

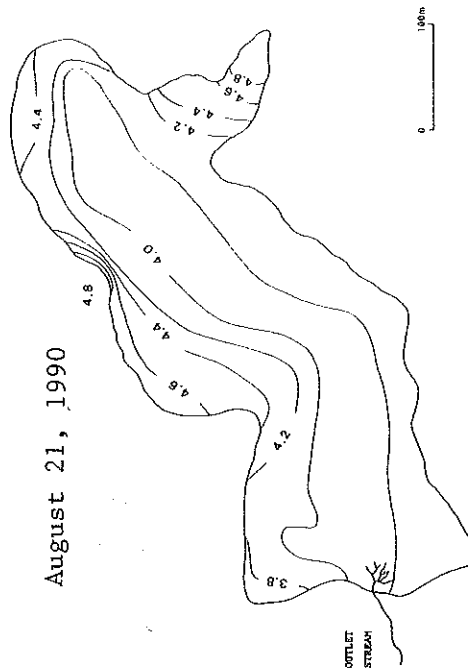


Fig. 13. Contour maps showing yearly and seasonal variations in surface-water acidity (pH).

Table 2. Summary statistics for surface-water acidity calculated on the basis of pH. (Statistical symbols: n = sample size,  $\bar{x}$  = mean, S = standard deviation of population, SEM = standard error of the mean, d.f. = degrees of freedom, d = confidence interval, t = t-statistic, p = probability)

Obs. Date	1. 5-30-89	2. 8-2-89	3. 5-29-90	4. 8-21-90	Mean pH
n	42	51	50	51	4
$\bar{x}$	4.35	4.166	3.79	4.10	4.10
S	0.154	0.238	0.195	0.231	0.232
SEM	0.023	0.033	0.027	0.032	0.116
d.f.	41	50	49	50	3
d	0.046	0.066	0.054	0.064	0.369

# Results Of Paired T-tests On Means Of pH Differences Between Observations

Obs. Pair	5/89-8/89	5/89-5/90	8/89-8/90	5/90-8/90
n	42	42	51	50
$\bar{x}$	0.2198	0.5721	0.06314	-0.3082
SEM	0.03166	0.0281	0.01915	0.01998
t	6.94	20.36	3.30	-15.43
d.f.	41	41	50	49
p	<0.00001	<0.00001	0.0018	<0.00001

Missing Cases:	9	9	0	1
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(NULL HYPOTHESIS: Mean of the differences between obs. is zero.)

Table 3. Summary statistics for surface-water chemistry (cation concentrations in mg/l).

	<u>CATION</u>			
	Ca++	Mg++	K+	Na+
n	24	24	24	24
$\bar{x}$	1.791	0.367	0.51	3.55
S	0.431	0.089	0.23	0.569
d.f.	23	23	23	23
SEM	0.088	0.018	0.047	0.116
d	+0.182	+0.37	+0.097	+0.240
Range	1.11-2.65	0.17-0.53	0.18-1.16	2.30-5.00

(Samples collected on 8-21-90.)



Table 4. Chemical properties of waters from North American wetlands (average values with range in brackets).

Wetland class	No. of samples	pH	Conductivity ( $\mu\text{S/cm}$ )	Exchangeable cations		Source
				Ca (mg/L)	Mg (mg/L)	
Bog	18	4.0 (3.7-4.4)	—	2.3 (1.2-3.7)	0.4 (0.2-0.9)	Schwintzer (1981)
	13	(4.6-5.1)	(35-62)	(0.2-0.8)	(0.1-0.2)	Gauthier (1980)
	10	(3.8-4.4)	31	0.2	0.1	Foster and King (1984)
Fen (poor)	193	(4.6-5.2)	(18-59)	(0.4-4.8)	(0.1-0.7)	Gauthier (1980)
	14	(4.7-5.5)	49	0.3	0.2	Foster and King (1984)
	1	5.0	—	2.4	0.4	Vitt <i>et al.</i> (1975)
Fen (moderately poor)	42	5.2	65	1.1	0.2	Gauthier (1980)
Fen (intermediate to rich)	9	7.2 (6.8-7.9)	281 (140-456)	28 (18-37)	11 (4-28)	Slack <i>et al.</i> (1980)
	21	6.1 (5.2-6.9)	59 (33-128)	10 (4-18)	—	Glaser <i>et al.</i> (1981)
	5	6.5 (5.4-7.1)	—	43 (7-124)	10 (2-15)	Schwintzer (1978)
Swamp (coniferous treed)	12	7.2 (6.9-7.8)	—	40 (22-52)	12 (8-17)	Schwintzer (1981)

(Source: Tarnocai 1988)



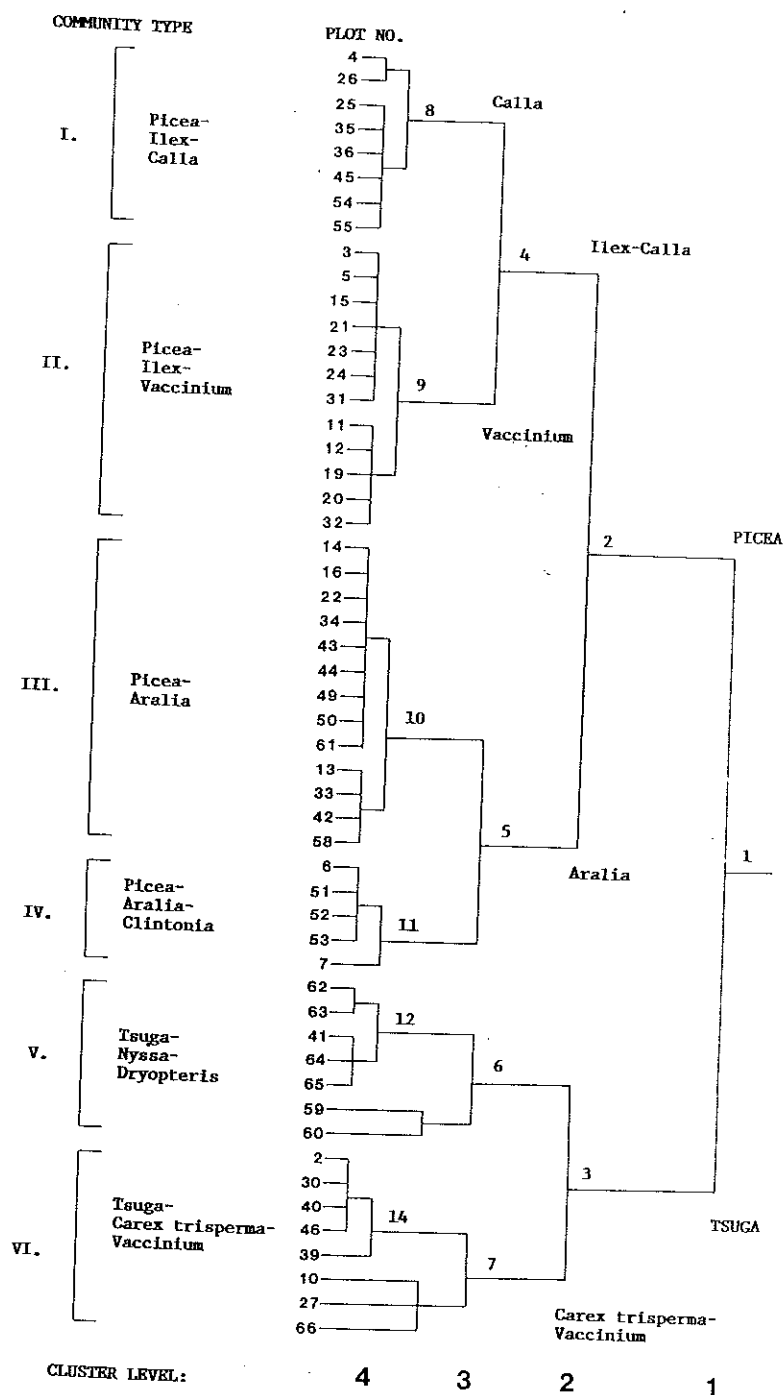


Fig. 14. TWINSPAN diagram showing segregation of relevé plots by vegetation community type. Numbers at nodes indicate divisions; plant names refer to indicator species.

Table 5. Mean cover values (%) for species in community types identified by TWINSpan.

Community Type	I. Picea- Ilex- Calla (n=8)	II. Picea- Ilex- Vaccinium (n=12)	III. Picea- Aralia (n=13)	IV. Picea- Aralia- Clintonia (n=5)	V. Tsuga- Nyssa- Dryopteris (n=7)	VI. Tsuga- Carex- Vaccinium (n=8)	
Mean pH	4.25 +-0.25	4.10 +- .12	4.05 +- .11	4.12 +- .28	3.93 +- .10	4.18 +- .32	
Site Conditions	Wet	Wet	Dry	Dry	Dry	Wet	
Distribution	East Margin	Northern End	Interior	Interior	Southern End	Margins	
TREES (%)							
						Overall Frequency (%) In Swamp:	
Picea rubens	24	38	36	49	15	10	94
Acer rubrum	15	19	25	15	11	14	91
Tsuga canadensis	20	11	7	9	35	50	72
Nyssa sylvatica	3	8	8	5	27	7	58
Pinus strobus	3	5	7	4	3	0	45
Betula alleghaniensis	7	6	5	0	6	15	45
Quercus rubra	0	1	0	0	0	0	4
Fraxinus nigra	0	0	0	0	0	<1	2
UNDERSTORY (%)							
Ilex spp.	54	31	3	7	11	16	81
Nemopanthus mucronata	9	18	26	15	15	7	79
Picea rubens	4	6	9	5	24	9	70
Vaccinium corymbosum	0	17	14	5	1	15	68
Betula alleghaniensis	4	4	6	<1	7	5	55
Tsuga canadensis	4	<1	1	1	14	13	43
Viburnum cassinoides	<1	3	4	<1	<1	7	41
Nyssa sylvatica	<1	2	1	2	14	6	36
Acer rubrum	<1	3	1	1	0	10	26
Rhododendron viscosum	1	0	0	0	2	<1	11
Kalmia latifolia	<1	0	2	<1	0	2	11
Rhus vernix	<1	<1	0	0	2	0	9
Hamamelis virginiana	0	0	<1	4	0	<1	7
Betula populifolia	0	0	1	0	0	2	6
Viburnum recognitum	5	0	0	0	0	<1	4
V. alnifolia	0	0	0	0	0	<1	2
Amelanchier sp.	0	0	0	0	0	<1	2
Fraxinus nigra	0	<1	0	0	0	0	2

Table 5. cont.

Community Type	I. Picea- Ilex- Calla (n=8)	II. Picea- Ilex- Vaccinium (n=12)	III. Picea- Aralia (n=13)	IV. Picea- Aralia- Clintonia (n=5)	V. Tsuga- Nyssa- Dryopteris (n=7)	VI. Tsuga- Carex- Vaccinium (n=8)	Overall Freq.
No. of Plots							
Mean pH	4.25 $\pm$ 0.25	4.10 $\pm$ 0.12	4.05 $\pm$ 0.11	4.12 $\pm$ 0.28	3.93 $\pm$ 0.10	4.18 $\pm$ 0.32	
Site Conditions	Wet	Wet	Dry	Dry	Dry	Wet	
Distribution	East Margin	Northern End	Interior	Interior	Southern End	Margins	
HERB LAYER (%)							
<i>Osmunda cinnamomea</i>	42	57	42	48	38	54	100
<i>Coptis groenlandica</i>	15	26	25	29	9	15	91
<i>Trientalis borealis</i>	2	2	4	8	1	2	81
<i>Acer rubrum</i>	2	<1	2	3	2	1	81
<i>Ilex</i> spp.	7	8	2	2	3	5	74
<i>Nyssa sylvatica</i>	<1	<1	3	2	6	2	72
<i>Carex trisperma</i>	5	5	<1	1	<1	1	68
<i>Maianthemum canadense</i>	2	6	1	4	3	3	62
<i>Aralia nudicaulis</i>	2	<1	5	10	1	1	58
<i>Viburnum cassinoides</i>	<1	3	4	<1	<1	7	57
<i>Cornus canadensis</i>	2	<1	<1	4	<1	3	49
<i>Nemopanthus mucronata</i>	2	3	2	5	<1	0	49
<i>Isuga canadensis</i>	1	<1	<1	3	<1	1	49
<i>Vaccinium corymbosum</i>	1	<1	1	1	<1	0	43
<i>Picea rubens</i>	<1	<1	<1	3	1	<1	40
<i>Rhododendron viscosum</i>	2	1	<1	0	<1	<1	36
<i>Betula alleghaniensis</i>	<1	<1	<1	1	<1	0	28
<i>Clintonia borealis</i>	0	<1	<1	2	<1	<1	26
<i>Calla palustris</i>	13	4	<1	0	<1	0	26
<i>Dryopteris simulata</i>	<1	0	1	0	5	2	17
<i>Aster simplex</i>	0	0	0	0	0	<1	13
<i>Vaccinium angustifolium</i>	<1	<1	<1	1	0	<1	11
<i>Medeola virginiana</i>	<1	0	0	5	<1	0	11
<i>Carex intumescens</i>	<1	0	<1	0	0	<1	11
<i>Smilacina trifolia</i>	0	<1	0	0	0	<1	7
<i>Viburnum alnifolia</i>	0	0	0	0	0	<1	7
<i>Quercus rubra</i>	<1	<1	0	<1	0	0	7
<i>Trillium undulatum</i>	0	<1	<1	<1	<1	0	7
<i>Gaultheria procumbens</i>	0	0	0	<1	0	<1	6
<i>Sorbus americana</i>	0	0	0	<1	<1	0	6
<i>Viburnum recognitum</i>	2	0	0	0	0	<1	4
<i>Rubus hispida</i>	0	0	0	<1	0	<1	4
<i>Arisaema atrorubens</i>	0	0	0	0	0	<1	4
<i>Uvularia sessilifolia</i>	0	0	0	0	0	<1	4
<i>Compositae</i> sp.	0	0	0	0	0	<1	4
<i>Fraxinus nigra</i>	0	<1	0	0	0	<1	4
<i>Chiogenes hispidula</i>	0	0	<1	0	0	0	2
<i>Kalmia angustifolia</i>	0	0	0	<1	0	0	2
<i>Pinus strobus</i>	0	0	0	0	0	0	2
<i>Dalibarda repens</i>	0	0	0	0	0	<1	2
<i>Leersia oryzoides</i>	0	0	0	0	0	<1	2
<i>Actaea</i> sp.	0	0	0	0	0	<1	2
<i>Aster acuminatus</i>	0	0	0	0	<1	<1	2
GROUND COVER (%)							
<i>Sphagnum</i> spp.	63	59	58	63	42	55	98
TOTAL SPECIES	42	42	42	42	41	52	

and *Vaccinium*. Indicator species are not associated with all other remaining level 3 dichotomies.

Level 4 divisions of the main *Picea* group indicate an association between site location and environmental conditions and vegetation composition and abundance. Plots associated with the wet east margin (division 8) are characterized by *Picea*, *Ilex* and *Calla*. *Vaccinium corymbosum* is absent from the understory. Wet interior and margin plots at the northern end of the swamp (division 9) are similar in composition but possess *Vaccinium* in the understory.

The *Aralia* subdivision of the main *Picea* group clusters relatively dry plots in the swamp interior. Plots in division 10 have infrequent *Ilex* and *Tsuga*, but high values for *Aralia* and *Nemopanthus*. Plots in division 11 are characterized by an abundance of *Picea* in the canopy and a variety of tree and shrub seedlings in the herb layer. In addition to *Aralia*, *Medeola virginiana* and *Clintonia borealis* are common in these plots.

Plots in the *Tsuga*-dominated group also demonstrate an association between site type and vegetation. Although *Picea* is distributed generally throughout the swamp, *Tsuga* appears to be most abundant at the southern end and at scattered locations on the swamp margin. Divisions 12 and 6 group plots from the southern end where *Tsuga* and *Nyssa* are relatively more abundant. *Dryopteris simulata* is frequent in these plots, but *Carex trisperma*, *Cornus canadensis* and *Maianthemum canadense* are uncommon. Divisions 14 and 7 cluster wet margin plots with abundant *Tsuga* and frequent *Vaccinium corymbosum*. These plots also have a wide variety of species normally associated with acid mesic uplands including *Viburnum alnifolium*, *Amelanchier* sp., *Dalibarda repens*, *Uvularia*

*sessilifolia* and *Arisaema atrorubens*. Wetland species rare elsewhere in the swamp are also present, including *Carex intumescens*, *Fraxinus nigra* and *Leersia oryzoides*.

Quantitative sampling at 0.0625-ha plots on transects T-3 and T-1A indicate substantial differences in species abundance (Fig. 15). *Picea* is clearly dominant among tree species on T-3, followed in abundance by *Acer rubrum*, *Tsuga*, *Nyssa* and *Pinus*. Shrubs are scarce (Fig. 16). A regression of stem diameter (dependent variable) versus age (independent variable) for *Picea* (Fig. 17) indicates that the two variables are significantly correlated ( $r^2 = 0.1$ ,  $p < .01$ ). While the correlation may be significant, the low  $r^2$  value suggests there is much unexplained variability in the data. The stand is primarily even-aged with most stems between 65 and 85 years of age (Fig. 18).

Although *Picea* is also the most abundant tree species at the plot on T1-A, *Acer rubrum* and *Tsuga* have higher relative basal area compared to the plot on T-3 (Table 6). *Pinus* is absent. Shrubs are abundant, with *Ilex* and *Nemopanthus* being the most common species. A regression of stem diameter vs. age for *Picea* (Fig. 19) indicates a similar significant correlation ( $r^2 = .4$ ,  $p < .01$ ), but again, the relatively low  $r^2$  value suggests there is unexplained variability in the data. The stand is uneven-aged with few stems older than 90 years (Fig. 18).

#### Hydrology

Water levels dropped at all wells from the period May 22 to July 30, 1990 (Fig. 20). After heavy rain (7.5 cm) during the period August 1 to August 8 (Fig. 21), water levels rose markedly at margin wells (# 1,3,4,6) and at an interior well (# 7) near the outlet stream. Water levels rose only slightly (2-5 cm) at other interior wells during this



Fig. 15. Comparison of basal area for canopy species at the T-3 and T-1A stand-reconstruction plots.



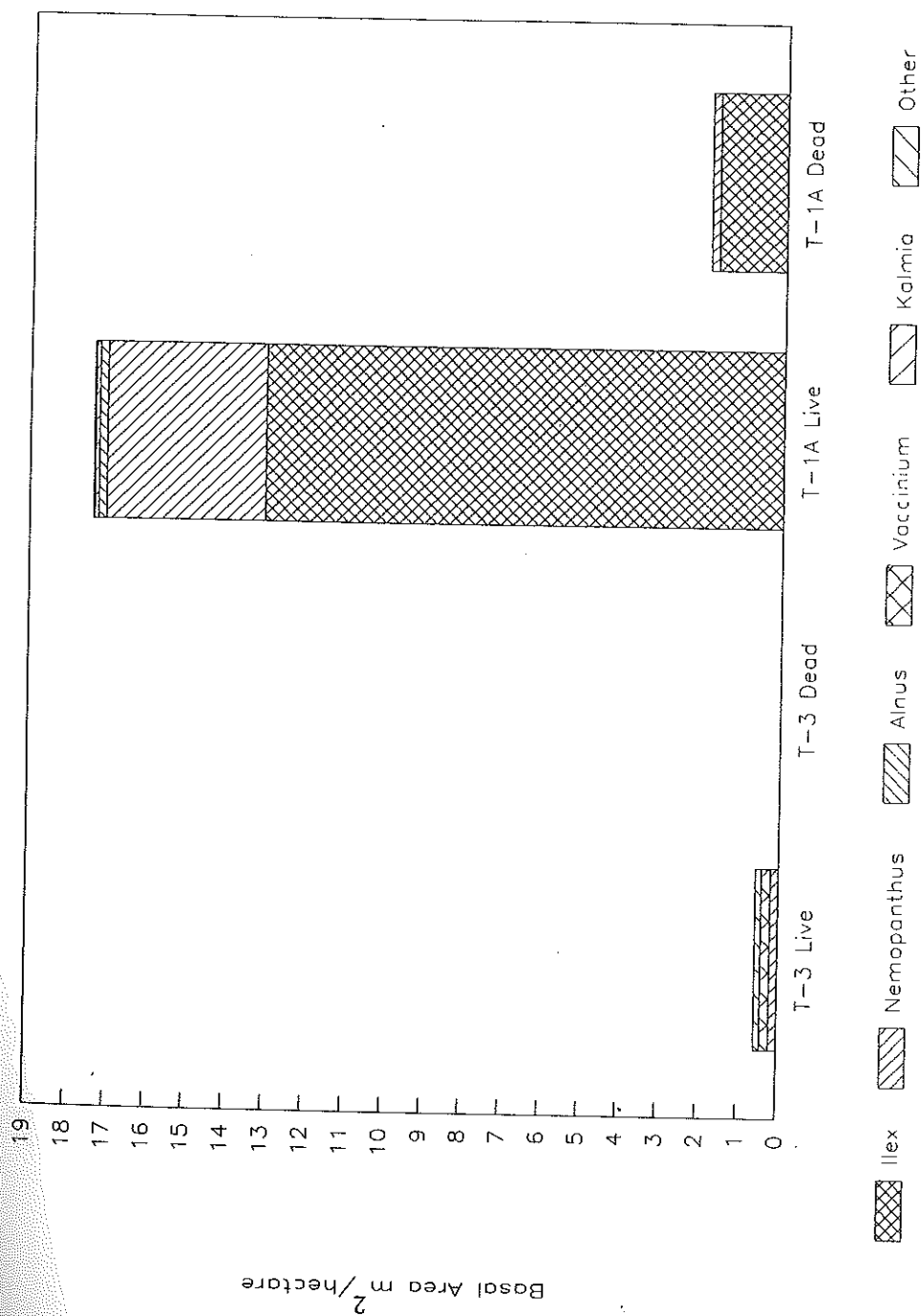


Fig. 16. Comparison of shrub basal area at the T-3 and T-1A stand-reconstruction plots.

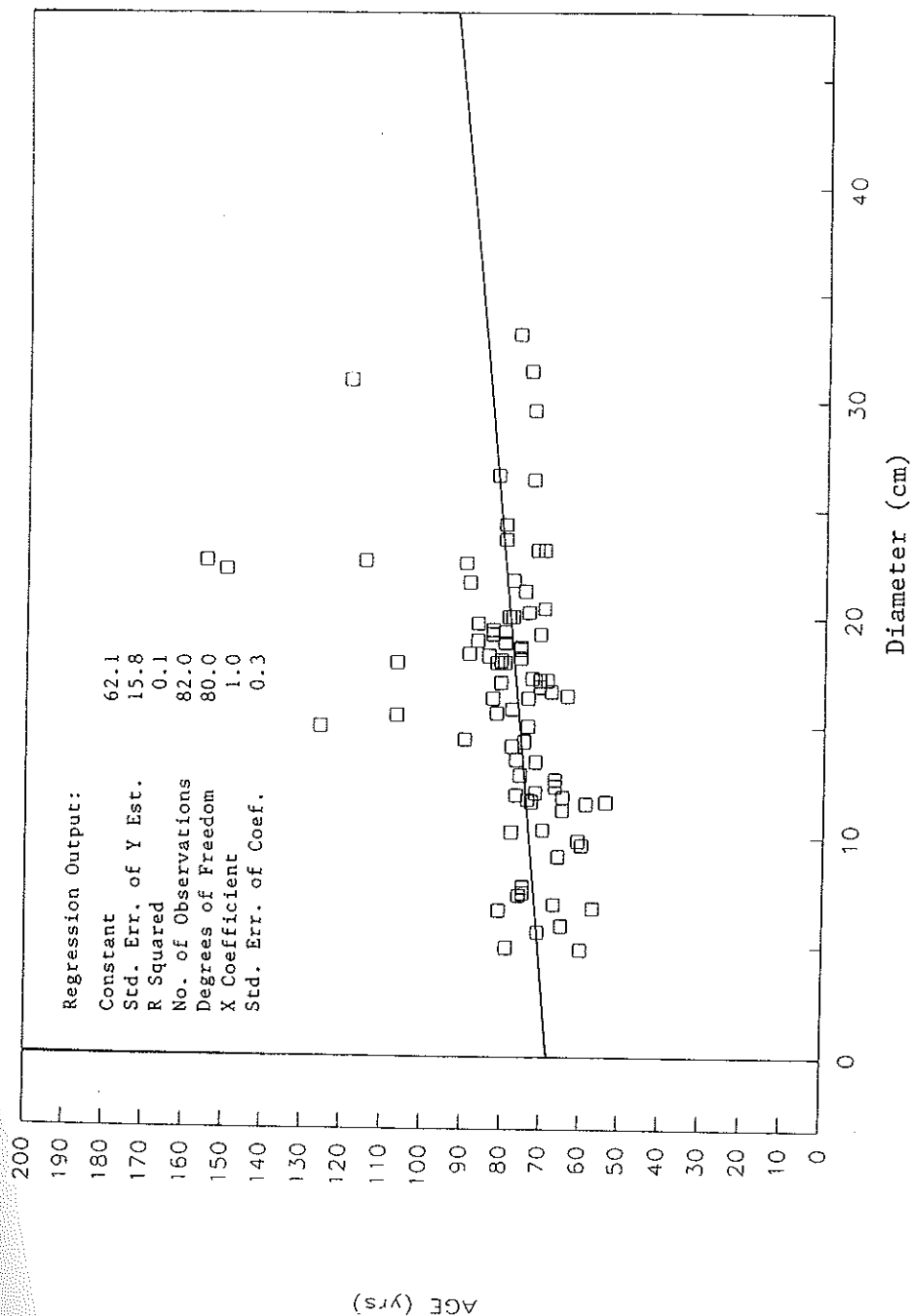


Fig. 17. Least-squares linear regression of diameter versus age for *Picea rubens* at the T-3 stand-reconstruction plot.



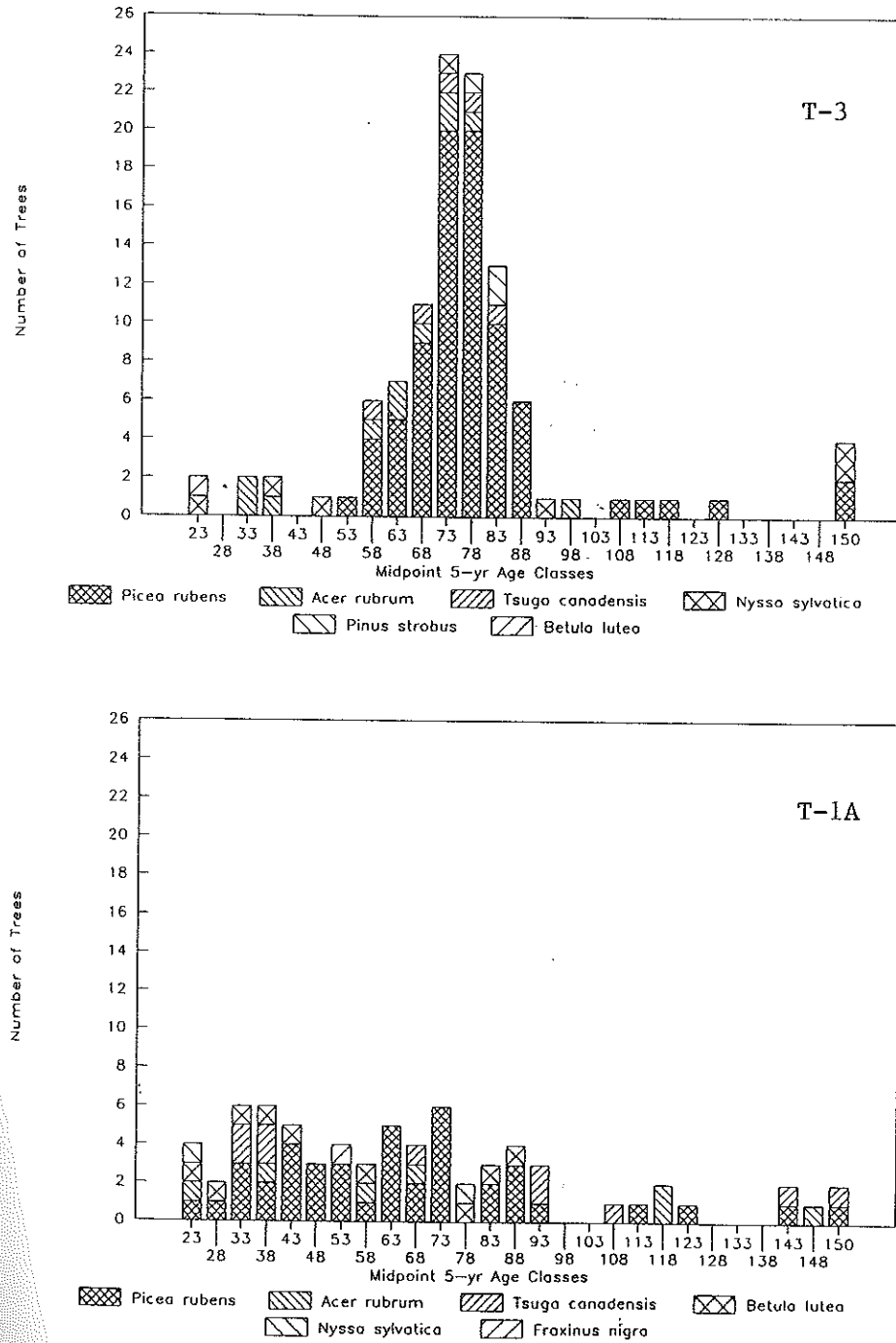


Fig. 18. Comparison of stand age-distribution for canopy species at the T-3 and T-1A stand-reconstruction plots.

Table 6. Relative basal area for canopy tree species (live and dead) at the T-3 and T-1A stand-reconstruction plots.

Live	T-3	T-1A
<i>Picea rubens</i>	72	49
<i>Acer rubrum</i>	8	21
<i>Nyssa sylvatica</i>	7	6
<i>Tsuga canadensis</i>	3	18
<i>Pinus strobus</i>	9	0
<i>Betula alleghaniensis</i>	1	6
<i>Fraxinus nigra</i>	0	1
Total	100%	100%
Dead		
<i>Picea rubens</i>	78	61
<i>Acer rubrum</i>	6	7
<i>Nyssa sylvatica</i>	0	0
<i>Tsuga canadensis</i>	0	8
<i>Pinus strobus</i>	16	0
<i>Betula alleghaniensis</i>	0	24
<i>Fraxinus nigra</i>	0	0
Total	100%	100%

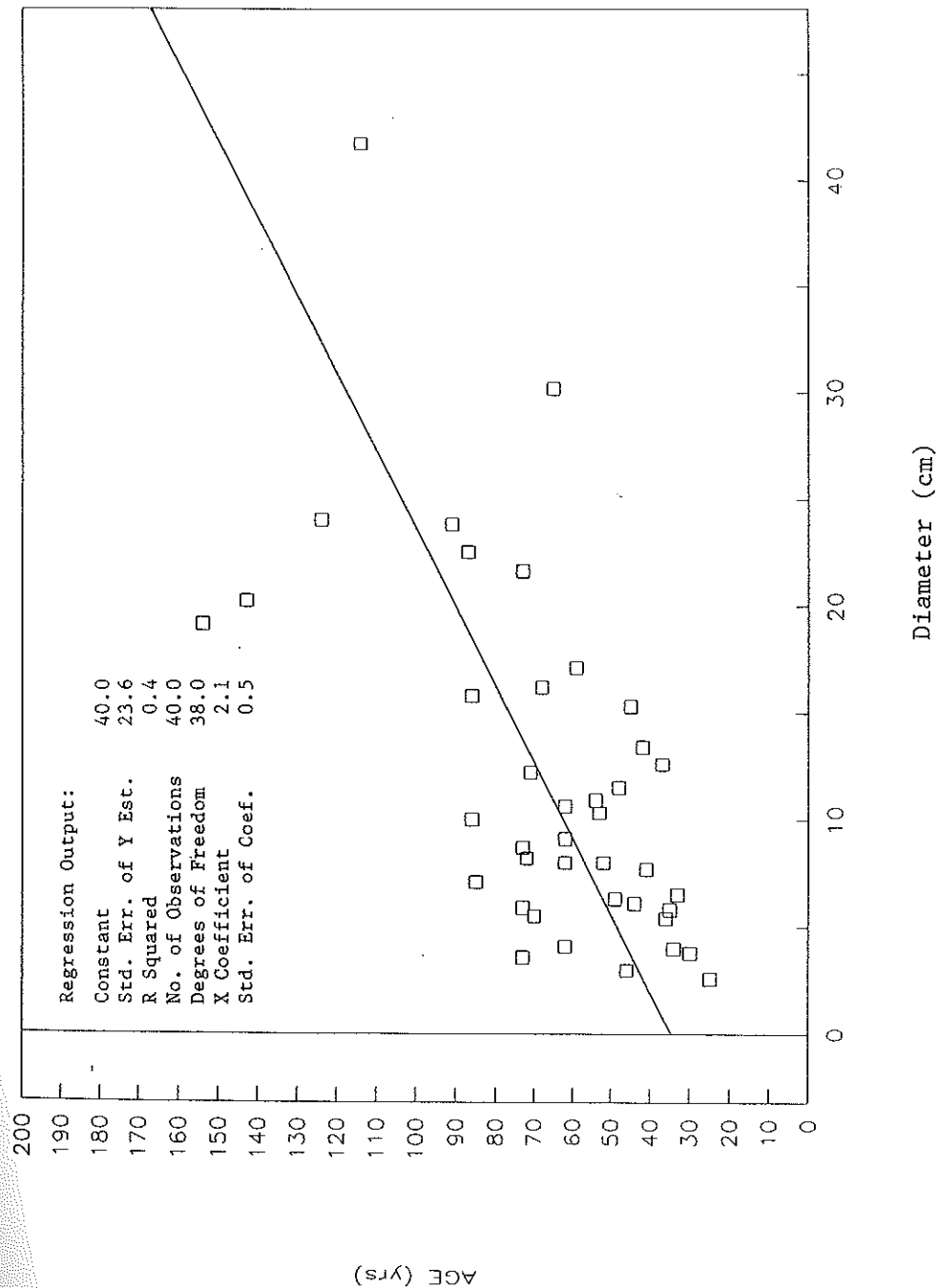
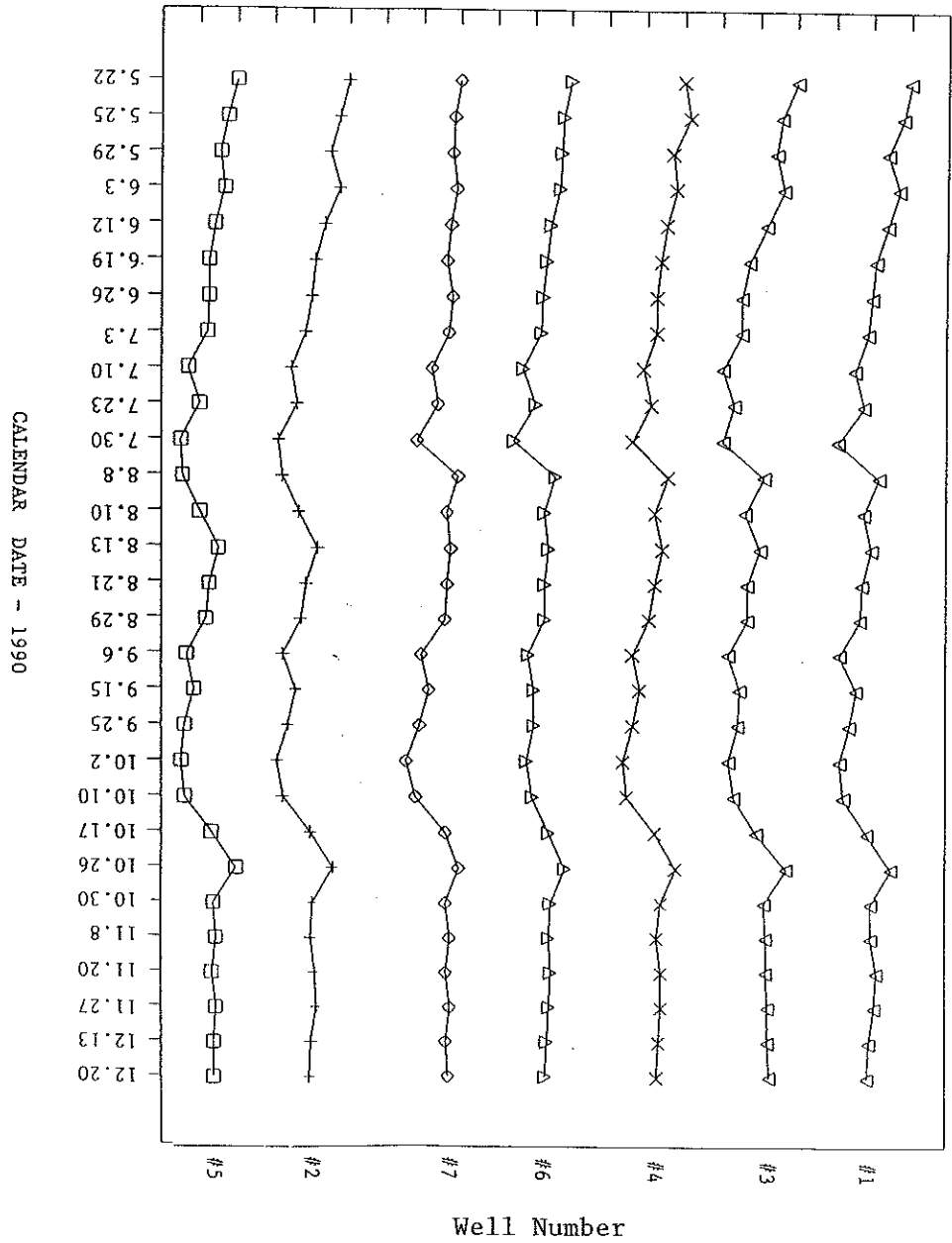


Fig. 19. Least-squares linear regression of diameter versus age for *Picea rubens* at the T-1A stand-reconstruction plot.

Relative Water-Level Change (cm)

Fig. 20. Relative wetland water-level fluctuations (cm) at well locations between indicated calendar dates. Note that the time scale along the x-axis is not linear. Tick marks on the left vertical axis represent 10-cm increments.



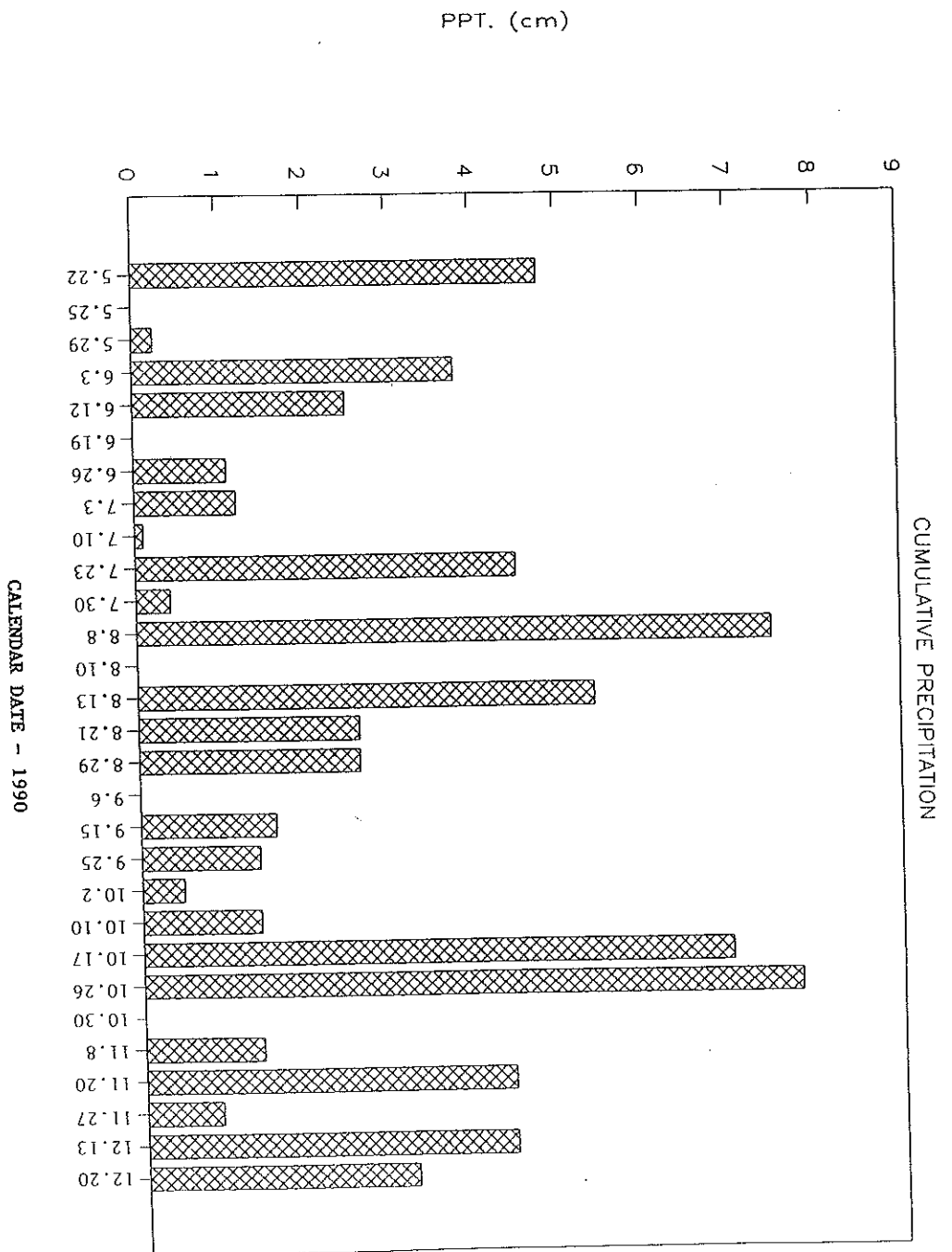


Fig. 21. Cumulative precipitation (cm) for periods between water-level measurements at wells. Note that the time scale along the x-axis is not linear.

period. Two days after rain ceased (Aug. 10), water levels dropped at margin wells and at the well near the outlet, but rose at interior wells. Weekly monitoring of water levels indicate a progressive decrease in level at all wells through the rest of the summer until a period of heavy rain (15 cm) during the interval October 17 - October 26 when water levels rose sharply. After a decline in water level during the period October 27 to October 30, water levels at all wells remained steady or declined slightly throughout the remainder of the measurement period which terminated on December 20.

#### DISCUSSION

The following discussion will cover four major subjects. Part one will provide an overview of the late-glacial and Holocene history of upland vegetation in the Black Gum Swamp watershed. Part two will synthesize pollen, macrofossil and stratigraphic evidence to provide a generalized community-level scenario of peatland development at Black Gum Swamp with emphasis placed on autogenic and allogenic factors influencing the rate and direction of development. In part three, modern peatland vegetation and environmental parameters will be described in order to demonstrate that similar autogenic and allogenic processes affecting vegetation development in the past continue to operate in the present. Part four will focus on the Holocene history of *Picea* and *Nyssa sylvatica*, wetland tree species with complete pollen records at Black Gum Swamp, but with missing or fragmentary mid-Holocene records elsewhere in New England.

## I. History of Upland Vegetation

Pollen assemblages in late-glacial sediments at Black Gum Swamp represent a transitional period when tundra vegetation co-existed with developing forest vegetation dominated by *Picea* and *Pinus banksiana*. *Populus* may have been locally present (Davis 1958), as low percentages associated with this poorly-preserved pollen type may belie its actual importance (Cushing 1967). *Betula*, *Alnus*, *Salix*, *Shepherdia* and ericaceous species probably occurred most abundantly along the moist shores of what was then a pond. Herbaceous species indicative of a tundra-like environment include abundant grasses and sedges and members of the Saxifragaceae, Caryophyllaceae and Rosaceae. *Picea* and NAP percentages in late-glacial sediments conform closely to values obtained from modern tundra or forest-tundra surface samples (Shane 1987, Davis and Webb 1975).

A warming period chronologically analogous to the northern European Allerød initiated the rapid *Picea* increase at 11,800 yrs BP. Although many herbaceous tundra species disappear, graminoids persist through the period, suggesting the existence of park-like conditions under a fairly open *Picea* canopy (Davis et al. 1975). Pine (probably *P. banksiana*) occurs with *Picea* during this period, but low- to moderate percentages (10 - 15%) for this typically over-represented pollen type suggest that pine was only a minor component of the *Picea* forest (Davis and Jacobson 1985). Similarly, relatively low values for *Betula* indicate that this species was of minor or local occurrence. Although appearing in low percentages, typically under-represented *Larix* and *Abies* may have been locally abundant around the margin of the pond. Rare arboreal types occurring as scattered grains include *Carya*, *Juglans* and *Nyssa*; pollen



grains from these species may have arrived via long-distance transport from the south. Low percentages for *Quercus* may represent input from rare local trees or extra-regional pollen rain. *Tsuga*, *Fagus*, *Acer rubrum*, *Fraxinus* and *Ulmus* become persistent in low percentages in the latter half of zone 2, indicating limited northward expansion of temperate forest species.

The rapid decrease in *Picea* and associated increases in *Pinus*, *Betula* and *Quercus* during the transition from Zone 2 to Zone 3 indicate major early-postglacial vegetational and climatic change (Ogden 1965). Similar changes are observed at nearby Tom Swamp (Davis 1958) and at other central and southern New England pollen sites such as Berry Pond, MA (Whitehead 1979), Rogers Lake, CT (Davis 1969) and Hawley Bog, MA (Patterson unpublished). Patterson (pers. comm.) has speculated that wildfires occurring in senescing *Picea* stands might have led to the quick establishment of early successional species like *Pinus* and *Betula* on exposed mineral soils.

*Pinus* is the most important arboreal species in Zone 3, and *Quercus* makes its first major increase. The sudden transition from diploxylon pine to haploxylon pine (*P. strobus*) is a feature that Black Gum Swamp shares with other pollen localities in both the Midwest and Northeast (Jacobson 1979, Whitehead 1979, Davis 1958). Jacobson (1979) describes a mechanism by which *Pinus strobus* invaded *Quercus* - *Pinus banksiana* forests in Minnesota, but no explanation for the rapid replacement of *Pinus banksiana* by *P. strobus* has yet been produced that may be applicable to the climate and vegetation of the northeast.

While *Pinus strobus* and *Quercus* are the principle components of the forest at this time, *Tsuga* makes a moderate increase. *Picea* is sharply



reduced but lingers in the pollen record. Both *Picea* and *Tsuga* probably persisted at the ecotone around the pond or in adjacent low-lying areas. *Ulmus*, *Acer rubrum* and *Fraxinus* may have occupied similar habitats.

*Pinus* decreases slowly after 8350 yrs BP (Zone 4) but *Quercus*, *Tsuga* and other temperate deciduous forest components continue to increase, signifying the initiation of the warm, dry hypsithermal interval. Among the minor tree taxa, *Ulmus* and *Fraxinus* remain persistent in low percentages, indicating the local presence of these species (Davis and Jacobson 1985). The degree to which conifers remain important through this period is consistent with the intermediate latitudinal location of Black Gum Swamp in New England. At Rogers Lake to the south, *Pinus* decreases at the same rapid rate that *Quercus* increases (Davis 1969). Maximum percentages for *Quercus* at this site are three times higher than at Black Gum Swamp, but *Tsuga* percentages are less than half as great. Pollen percentages for *Pinus*, *Tsuga* and *Quercus* more nearly approach values observed in analogous zones from northern sites such as Pownal Bog, VT (Whitehead and Bentley 1963) and Mirror Lake, NH (Likens and Davis 1975). The forests around Black Gum Swamp were different in some respects from the *Tsuga* - northern hardwood forest present during this period near Berry Pond and Hawley Bog in the western Berkshires of northern Massachusetts. *Acer saccharum* is a rare type at Black Gum Swamp, appearing only as scattered grains. Conversely, approximately 5% *Acer saccharum* is present at both Berry Pond and Hawley Bog. Percentages for *Fagus* are approximately 30% at Berry Pond and vary between 20 and 30% in the latter half of the zone at Hawley Bog, but percentages for *Fagus* only climb to a maximum of 17% late in the zone at Black Gum Swamp. *Quercus* is consistently less than

10% at Hawley Bog, but remain near 20% at Black Gum Swamp. These patterns seem to suggest that the transitional nature of forests in central Massachusetts became established as early as 8000 yrs BP.

*Tsuga* rises to a maximum of 38% by the end of the zone at Black Gum Swamp, signifying the existence of a *Tsuga*-dominated forest with lesser amounts of *Quercus*, *Betula* (probably *B. lenta* and *B. alleghaniensis*), *Fagus*, *Acer rubrum*, *Pinus*, *Fraxinus* and *Ulmus*. At about this time (5000 yrs BP), sites extending from north-central to northeastern North America all show maximum *Tsuga* percentages, although values attained by *Tsuga* at Black Gum Swamp seem to be higher than at many other New England sites (Table 7). The hemlock decline occurring at 4700 yrs BP greatly disturbed *Tsuga*-dominated forests throughout the northeast (Davis 1981). During the succeeding 1600 year interval, *Quercus*, *Betula*, *Fagus* and later, *Pinus*, are co-dominant with *Tsuga* throughout most of New England. However, relatively high post-decline percentages (10%) suggest that a large local population of *Tsuga* continued to exist near Black Gum Swamp.

Increased *Picea* percentages indicating a return to a cooler climate occur around 2600 yrs BP. The addition of *Castanea* as an important forest component occurs around 2300 yrs BP, roughly corresponding to regional arrival dates of 1600 yrs BP and 2000 yrs BP proposed by Whitehead (1979) and Davis (1969) for Berry Pond and Rogers Lake, respectively. As with other under-represented and/or poorly-dispersed pollen types (e.g. *Acer saccharum*), it is difficult to ascertain whether such an increase represents "arrival" or denotes a significant regional expansion of a pre-existing population (Gaudreau 1986). Also, reliance on a single site for an "arrival" date is probably injudicious.

Table 7. Pre-decline maxima and post-decline minima for *Tsuga* at Northeastern pollen sites.

Site	Lat.	Long.	Elev.	Max. %	Min % (after decline)	Author
Rogers Lake, CT	41°22'	72°7'	91 m	7	3	Davis 1969
Mohawk, CT	41°49'	73°17'	360 m	10	2	Gaudreau unpubl.
Duck Pond, MA	41°50'	70°0'	2 m	6	3	Winkler 1982
Belmont, NY	42°15'	77°55'	497 m	60	6	Spear & Miller 1976
Berry Pond, MA	42°30'	73°19'	600 m	15	5	Whitehead 1979
Black Gum Swamp, MA	42°32'	72°11'	366 m	37	11	Zebryk unpubl.
Hawley Bog, MA	42°34'	72°53'	549 m	30	10	Patterson unpubl.
Pownal Bog, VT	42°48'	73°11'	344 m	40	5	Whitehead & Bentley 1963
Mirror Lake, NH	43°57'	71°42'	200 m	35	5	Likens & Davis 1975
Brandreth, NY	43°55'	74°41'	583 m	50	10	Overpeck 1985
Deer Lake Bog, NH	44°2'	71°50'	1325 m	15	5	Spear 1989
Bugbee Bog, VT	44°22'	72°9'	398 m	60	15	McDowell <i>et al.</i> 1971
Moulton Pond, ME	44°38'	68°38'	143 m	40	5	R.B. Davis <i>et al.</i> 1975
Lac Dufresne, Quebec	45°51'	70°21'	650 m	10	2	Mott 1977

*Tsuga* increases with *Picea* during this period, indicating a similar positive response to inferred climatic cooling and perhaps increasing moisture. Curiously, *Fagus*, a northern hardwood species, does not show a positive response; instead, this species declines as *Tsuga* and *Castanea* increase. This trend seems to suggest that *Fagus* was perhaps unable to compete successfully against aggressive *Tsuga* and fast-growing *Castanea*, particularly in the somewhat warmer climate of central New England. Other sites that seem to demonstrate this interaction include Rogers Lake, CT (Davis 1969), Berry Pond, MA (Whitehead 1979), Bethany Bog, Highland Lake, Bingham Pond, and Mashpaug Pond, CT (Deevey 1943). Similar declines in *Fagus* at more northern sites may be associated with increases in *Picea*, *Tsuga* or *Pinus*; examples include Bugbee Bog, VT (McDowell et al. 1971), Pownal Bog, VT (Whitehead and Bentley 1963) and Mirror Lake, NH (Likens and Davis 1975).

Human impact on vegetation in the Black Gum Swamp watershed becomes evident after 200 yrs BP, with substantial increases in agricultural indicators such as *Ambrosia* and grass. Decreases in *Quercus*, *Tsuga* and *Fagus* during this period represent land-clearing activities associated with agriculture. Historical records (Raup and Carlson 1941) indicate that although the town of Petersham was incorporated in 1754 AD, preliminary settlement may have occurred as early as 1733 AD. *Castanea* increases substantially after settlement. Possible mechanisms accounting for this increase include a) release of understory *Castanea* after the cutting of *Tsuga* and hardwood overstory; b) increase in *Castanea* stems as a result of coppicing after land-clearing; c) increase in *Castanea* stems along hedgerows, stone walls, lot boundaries, etc. (Paillet 1988). In a description of land-use change inferred from

pollen indicators at Linsley Pond, CT, Brugam (1978) reports similar decreases in *Tsuga* and *Fagus* early in the settlement period with a corresponding increase in *Castanea*. Peak agricultural activity in the Harvard Forest area occurred around 1850 AD (Raup and Carlson 1941); maximum *Ambrosia* percentages may be associated with this date. Land abandonment was initiated after 1850 AD, resulting in reforestation of old fields first by *Betula populifolia* and later by *Pinus* and *Quercus*, which increase sharply after 1900 AD. A sharp decline in *Castanea* pollen percentages in near-surface sediments signals the occurrence of the chestnut blight. Kittredge (1913) reports the first incidence of blight in Petersham during the fall of 1910 AD. By 1912, virtually all *Castanea* trees in the area were severely affected.

In summary, major changes in upland vegetation throughout the Holocene are broadly similar to those recorded at other New England pollen sites. However, the pollen record at Black Gum Swamp suggests that the transitional nature of central New England forests (intermediate values for *Acer saccharum*, *Fagus*, *Quercus* and *Pinus* compared to southern and northern pollen sites) may have become established as early as 8000 yrs BP. Other distinctive aspects of the upland pollen record include evidence for a large pre- and post-decline *Tsuga* population in the watershed, and what may be a somewhat early date for the late-Holocene increase in *Castanea*. Additional details regarding the Holocene history of upland *Picea* populations in the Black Gum Swamp watershed will be brought out in part IV of the discussion.

## II. History of Peatland Development

Soon after regional deglaciation at 13,000 yrs BP, *Betula*, *Salix*, *Myrica*, *Alnus* and *Ericaceae* species grew along the littoral zone of what

was formerly a large meltwater pond. *Sphagnum* stems and leaves in late-glacial sediments indicate that wetlands may have been associated with basin margins (Futyma and Miller 1986). *Alnus*, and the aquatic taxa *Drepanocladus* sp., *Brasenia schreberi* and *Ranunculus* subg. *Batrachium* suggest that minerotrophic conditions occurred within the basin and at basin margins (Heinselman 1970, Janssen 1967, Futyma and Miller 1986, Jackson and Charles 1988). A leaf of the calcicole, *Dryas integrifolia*, recovered from near-basal sediments indicates there may have been an upland source of base-nutrients supplying the basin via surface run-off and sub-surface seepage. Miller (1989) describes an extensive macrofossil assemblage of other late-glacial tundra calcicoles deposited at nearby Tom Swamp in the Harvard Forest. Calcicoles later disappear with the major arrival of *Picea*, possibly as a result of soil-chemistry modification related to deposition of acidic litter and the progressive leaching of calcium from thin glacial soil over acidic bedrock. Increases in *Picea* pollen after 12,000 yrs BP indicate expanding regional populations, although a wood macrofossil recovered from basal sediment at the deepest part of the basin provides evidence spruce was on the local landscape well before this date, perhaps as early as 13,000 yrs BP.

Macrofossil and stratigraphic evidence indicates forest may have been present in the broad southern depression since the early postglacial. *Larix* needles recovered from radiocarbon-dated basal sediment (11,500 yrs BP) suggest this species was one of the earliest components of what was probably rich swamp forest (Heinselman 1970). Small ponds and hollows in this area appear to have supported minerotrophic shallow-water and fen vegetation as indicated by *Osmunda*



and *Sparganium* macrofossils associated with Cyperaceae and Nymphaeaceae remains. As sediments accumulated in the ponds and hollows, they were subsequently overspread by forest vegetation.

Early postglacial warming after 9750 yrs BP is inferred by the regional decline of *Picea* and the expansion of *Pinus*. Climatic amelioration is also reflected by the increased sedimentation rate of algal gyttja within the basin. Fringing shore-line vegetation (shrub carr) began to invade shallower waters by this time as indicated by increased *Alnus* and *Myrica* pollen percentages. Pollen diagrams from several northeastern sites (Davis 1969, Sirkin 1971, Likens and Davis 1975, Whitehead 1978) show similar increases in *Alnus* at this time, leading Nelson (1984) to conclude that these increases represent a regional phenomenon. Whitehead (1978) comments that high *Alnus* percentages may represent colonization of light gaps left by senescing upland *Picea*. An alternative explanation is that wetland *Alnus* populations (i.e. *Alnus rugosa*) expanded regionally in response to climatic warming along shores of what were formerly minerotrophic lakes. By 8950 yrs BP, aquatic species such as *Brasenia schreberi*, *Nuphar variegatum* and *Potamogeton* were established in open shallow water near the edge of the sediment limit at the present 1.5-m bathymetric contour. (This inference is based upon the finding that organic sediment containing abundant macrofossils of shallow-water aquatic taxa is deposited directly on mineral sediment (basal radiocarbon date 8940 yrs BP) just above the 1.5 m contour). Crow and Hellquist (1980, 1984) report that these species are often associated with mildly acidic or circumneutral waters in New England.

Shallowing associated with the deposition of limnic sediment enabled emergent and woody vegetation to spread to the basin interior by 8800 yrs BP. *Larix*, *Sphagnum* and diverse shrub species (*Chamaedaphne*, *Ledum*, *Myrica*, *Vaccinium oxycoccus/macrocarpon*, *Alnus*) associated with abundant Nymphaeaceae and Cyperaceae plant fragments and seeds indicate the proximity of centripetally-expanding shrub-mat vegetation to a central area of shallow open water. An abrupt transition from shallow-water sediment to shrub-sedge peat in the basin interior occurs at 8700 yrs BP. This change is accompanied by increases in *Sphagnum*, Cyperaceae and Ericaceae pollen, and deposition of abundant ericaceous macrofossils such as *Chamaedaphne* (leaves, roots, stems) and *Vaccinium oxycoccus/macrocarpon* (leaves). Ferns were locally abundant on the shrub mat, as peat recovered from the coring site on transect T-1A is largely composed of the wiry black roots typical of *Osmunda* spp. Complete closure of the basin by shrub vegetation apparently occurred at this time as evidenced by the absence of shallow-water pollen and macrofossil taxa.

The plant-indicator approach has been useful in relating nutrient regimes to wetland vegetation (e.g. Jeglum 1971, Dunlop 1987). At Black Gum Swamp, transitions in vegetation assemblages can be used to infer changes in nutrient status within the wetland. After 8700 yrs BP, the proliferation of ericaceous shrubs may indicate such a change, i.e. a transition from minerotrophic fen vegetation to an assemblage characteristic of oligotrophic bogs (Jeglum 1971, Heinzelman 1970, Vitt and Slack 1975). In a paleoecological study of the Lake Sixteen Peatland, northern Michigan, Futyma and Miller (1986) speculated that basin hydrology may be altered by the development of fringing vegetation



and subsequent peat accumulation, thus isolating interior basin waters and vegetation from the influence of minerotrophic seepage inputs. Such isolation may result in progressive nutrient depletion in all basin areas except at the narrow upland/wetland interface typically inhabited by the minerotrophic indicator species, *Alnus* (Heinselman 1970). The high cation-exchange capacity of *Sphagnum* associated with encroaching shrub mats may also lead to increased acidification (Clymo 1984). Because of its unique ability to profoundly modify the chemical environment, the invasion of *Sphagnum* is viewed by Zobel (1988) as a critical stage in autogenic bog succession.

Well-preserved macrofossils in shrub-sedge peat are indicative of below-water depositional processes associated with a floating shrub mat (Grosse-Brauckman 1986). Studying the development of shrub-mat vegetation at nearby Harvard Pond in Petersham, Swan and Gill (1970) describe a mechanism of shrub-mat growth in which ramifying *Chamaedaphne* branches sink under their own weight, thus contributing to the accumulation of below-water biomass and the eventual grounding of the shrub mat. Maximum thicknesses of shrub peat are generally located over the deepest parts of the basin in accordance with the model of shrub-mat development proposed by Kratz and DeWitt (1986) who demonstrated that ultimate shrub-peat thickness is a function of basin depth due to the potential distance between the lake bottom and the floating mat.

At 8100 yrs BP, increases in *Picea* pollen in stratigraphic association with *Picea* macrofossils (wood, needles) suggest that a transition from a shrub-dominated community to swamp forest was underway. This transition is contemporaneous with the onset of the warm, dry hypsithermal period (Deevey and Flint 1957), regionally

characterized in the Black Gum Swamp watershed by increases in temperate deciduous upland forest taxa such as *Tsuga*, *Fagus* and *Quercus*. Although no data are available, a drop in water level or grounding of the shrub mat may have facilitated expansion of spruce (most likely *Picea mariana*) on a relatively drier peatland substrate. Jeglum (1974) demonstrated that faster black spruce growth rates are directly related to increased aeration and decreased moisture regimes at a peatland in Ontario. However, continued high *Sphagnum* spore percentages suggest that the peatland surface was still very moist. A sharp increase in *Ilex/Nemopanthus* and *Alnus* pollen percentages and a drop in Ericaceae indicate that tall shrubs had succeeded the former ericaceous low-shrub community, and that tall shrubs were probably more abundant than arboreal vegetation during the early stages of this successional phase. *Acer rubrum* may have become more abundant on the peatland at this time, and low percentages of *Nyssa* pollen (2%) occurring between 8000 and 6000 yrs BP may reflect limited colonization of the peatland or population expansion in low-lying areas adjacent to the basin.

*Nyssa* becomes important on the peatland after 6000 yrs BP. The initial high pollen percentage spike may be indicative of a tree growing at the coring site (Patterson and O'Keefe unpubl.), demonstrating that *Nyssa* had spread into interior locations by this time. Although this is highly speculative, the apparent lag in the appearance of increased *Nyssa* percentages may possibly be attributed to the initial physical inadequacy of the peatland surface for colonization or expansion by this species. Although adapted to wetland conditions, some evidence exists that seeds of the southern congeneric species, *Nyssa aquatica*, are incapable of germinating while submerged (Shunk 1939), and that

germination success is much higher on emergent stable substrates in seasonally flooded southern swamp forests (Huenneke and Sharitz 1990). While little is known about the autecology of *Nyssa sylvatica* in the northeast, these same limitations may also apply. If so, the existence of stable dry-site microtopography may be a prerequisite for the initial colonization of northeastern peatlands by this species. After establishment, *Nyssa* populations may further expand by vegetative means. Excavation of a hummock occupied by *Nyssa* at a *Nyssa*-dominated peatland in nearby Orange, MA, revealed that this species is capable of cloning (root-suckering) in a wetland environment (Zebryk 1991). One clone was seen to arise from a main support root in the center of a water-filled hollow nearly 3 m from the parent stem. Similar evidence of cloning is also prevalent at Black Gum Swamp. These observations suggest that after establishment, *Nyssa* may be capable of aggressively colonizing seasonally-flooded habitats otherwise denied to species dependent upon seedling reproduction (e.g. *Acer rubrum*). Physiological adaptations to flooding (Keeley 1979), moderate shade tolerance (Fowells 1969), extreme longevity (Zebryk 1991) and the ability to reproduce vegetatively may give *Nyssa* a superior competitive advantage for long-term existence in a wetland environment.

During the period from 5000 to 2500 yrs BP, *Ilex* is variable while *Sphagnum* is reduced, perhaps reflecting a fluctuating hydrologic regime and a warmer, drier climate. *Osmunda* greatly increases after 5000 yrs BP, indicating well-lit conditions under what may have been a fairly open predominantly *Nyssa* - *Acer* canopy with frequent *Picea* and rare *Pinus* and *Tsuga*. Charcoal layers in forest peat are abundant between 4000 and 3000 yrs BP at the T-1A coring site, indicating that fires may

have spread from the upland to the peatland interior during periods of low water. Nearly all wetland taxa show temporary reductions in abundance around 4000 yrs BP, either declining or disappearing altogether. These changes are stratigraphically correlated with macroscopic charcoal layers and the highest C:P value observed, suggesting that peatland fire occurring after drought was the perturbing factor. Further recognition of specific fire-mediated vegetation changes within the wetland is impossible because of the coarse (200 - 300 yr) temporal resolution of the pollen and charcoal sampling intervals, and by the absence of well-correlated charcoal layers or similarly high C:P values in swamp-forest peat. However, the prevalence of charcoal in forest peat suggests that fire may have been a periodic, although infrequent, source of allogenic disturbance affecting peatland vegetation at the stand level throughout the Holocene.

An increase in *Picea* and a corresponding minor decrease in *Nyssa* after 2500 yrs BP may be a response to a transition to a cooler, moister regional climate. Accompanying increases in shrub species (*Ilex*, *Ericaceae* and *Viburnum*) suggest higher water levels within the peatland (Nelson 1984, Patterson and O'Keefe unpubl.). The steady decline in *Osmunda* may represent decreased insolation under a closing mixed coniferous and deciduous canopy.

Vegetation changes occurring after approximately 200 yrs BP are attributed to human intervention in the swamp after the arrival of European settlers. *Picea* was abundant at Black Gum Swamp at the time of settlement, affording a readily available source of this desirable and easily-worked timber species (Peattie 1950). Logging may have been carried out in winter while the peatland surface was frozen. A large

*Picea* stem (48.0 cm d.b.h., age 180 yrs) remaining in the southern portion of the swamp where *Picea* is abundant today provides some indication of the quality of virgin timber present at the time of settlement. A 68.0 cm diameter *Pinus strobus* stump in the same area demonstrates that this species also grew to large proportions in the swamp, although it was probably never common.

Moderate reductions in *Picea* pollen percentages from 200 - 100 yrs BP indicate periodic patch cuts rather than a single swamp-wide clear-cut. Left behind as undesirable species (Zebryk 1991), *Nyssa* and *Acer* may have increased in basal area, but higher pollen percentages may also indicate augmented pollen dispersal and magnified representation due to the removal of spruce. Increases in *Ilex*, *Viburnum*, *Ericaceae* and *Osmunda* may represent expansion of shrub and fern populations in light gaps produced by logging. These species later decline upon the return of *Picea*.

#### Directionality of Succession and Peatland Stability

Transitions in sediment type and changing pollen/macrofossil assemblages at Black Gum Swamp indicate that wetland development followed the classic pattern of linear hydrarch succession described by Clements (1916), Pearsall (1920) and Wilson (1935). As peatland forest has existed for the past 8000 yrs at this site, it might be argued that successional stages have been directed towards an extremely stable wetland community (Odum 1969). Stratigraphic uniformity within forest peat, what appears to be a fairly constant sedimentation rate, and relative continuity of swamp-forest vegetation in the pollen record all point towards long-term vegetation stability. Alterations in hydrologic regime, either by flooding or draining, can have dramatic consequences

on peatland vegetation as shown by Schwintzer (1974, 1978) and Jeglum (1974, 1975). However, because clearly - defined depositional gaps related to sharp drops in water-level (Webb and Lefkowitz 1988) and reversals in stratigraphy indicative of flooding are absent from the stratigraphic record at Black Gum Swamp, it can be inferred there has never been a dramatic long-term change in the hydrologic regime throughout the Holocene.

#### Evidence For Peatland Expansion

Decreasing radiocarbon ages for basal sediment along the depth gradient from the peatland interior to the present wetland edge provides evidence for gradual peatland expansion onto what was formerly upland, i.e. land area above the inferred former lake level at the present 1.0 m bathymetric contour. The location of the former lake level is estimated by the following stratigraphic criteria: a) algal gyttja and basal mineral sediment do not occur above the present 1.5 m bathymetric contour (interpreted as the sediment limit for the basin); b) other water-deposited sediment types (i.e. shallow-water sediment and shrub peats) do not occur above the present 1.0 m contour; and c), the maximum depth of forest peat deposited directly on mineral soil without intervening water-deposited sediment is approximately 1 m. Estimation of the location of the former lake level is rendered imprecise by the fact that lake level probably varied through time, and because vegetation producing forest peat may have occurred over a broad, possibly fluctuating ecotone. The mean horizontal rate of advance onto the low-lying upland area on the west side of the swamp is approximately 0.65 cm/yr. This rate may be an under-estimation: radiocarbon ages for basal sediment may be uniformly too old due to admixing of more recent



swamp-forest peat with older, pre-existing terrestrial organic sediments. Also, estimated rates of peatland expansion are highly dependent upon the topography of the fringing upland, with the fastest rates occurring in areas with little slope. Centrifugal peatland expansion may be a consequence of a progressive rise in the sub-surface peatland water table related to the steady accumulation of highly-humified forest peat with low hydraulic conductivity (Johnson et al. 1990, Boelter 1965). As downward and lateral movement of water is impeded by lower layers of impervious humified peat, water ponds at basin margins before slowly diffusing laterally into the peatland interior, causing swamping of the upland margin (Futyma and Miller 1986). This mechanism of expansion has been recognized in Michigan (Keough and Pippen 1984, Futyma and Miller 1986), Minnesota (Heinselman 1963, 1970), Sweden (Foster and Fritz 1987) and Canada (Foster and Glaser 1986). Hydrologic data from wells at Black Gum Swamp may provide some evidence for the operation of the same mechanism at a northeastern peatland.

Water-level fluctuations observed in late spring to midsummer of 1990 were closely tied to rainfall inputs. The general decrease in water level represents diminishing rainfall and increased rates of evapotranspiration. Upland soil profiles were probably not saturated during this period, and seepage inputs may have been minimal. After a week of heavy rainfall (7.5 cm) in August, water levels rose sharply at stations near the wetland margin but rose slowly at interior stations. Initial sharp increases at margin wells may represent peripheral ponding resulting from both precipitation input and entry of sub-surface seepage water from saturated upland soils, whereas concurrent slow increases at

interior wells are attributed primarily to direct precipitation input. When rainfall ceased, water levels dropped at the margin wells but continued to rise at interior stations, suggesting lateral diffusion of peripherally ponded water into the basin interior. Although the well in shallow sediments at the southern end of the swamp is an interior well, patterns of water-level fluctuations after the storm were quite similar to those at margin wells. The rapidity in response is attributed to water moving down-gradient towards the outlet. No such gradient may have existed within the peatland during earlier parts of Holocene: the outlet stream may have become active only after peat levels built up to the basin drainage threshold somewhere above the 0.5 m bathymetric contour.

At present, overland flow and seepage inputs may be most significant during the heavy rains of early spring when the subsoil is frozen. Typically, the outlet stream is only active during the early part of the growing season. During March 1990, incoming surface flow was observed at the eastern swamp projection after a period of heavy rain. Surface-water flow towards the outlet along the flooded basin periphery was also noted at this time, and may in fact be more important in terms of drainage rate and volume than slow subsurface lateral diffusion towards the outlet through the peatland interior.

#### Factors Influencing Peatland Expansion

Primary autogenic processes occurring within the Black Gum Swamp peatland (i.e. the growth, death and decomposition of vegetation) appear to be important factors responsible for the perpetuation and expansion of this wetland ecosystem. However, increased productivity of peatland vegetation and the accumulation of impervious, highly-humified peat are



autogenic processes leading to paludification (Futyma and Miller 1986) that may be mediated by a warm, dry climate (Gorham 1957). At Black Gum Swamp, the rate of paludification appears to have progressed faster during the hypsithermal interval (0.98 cm yr from 7630 to 4580 yrs BP) than during the moister, cooler post-hypsithermal period (0.32 cm yr from 4580 yrs BP to the present). However, it must be pointed out that available radiocarbon dates from basal sediment provide poor temporal resolution of changes in the rate of paludification. Additional basal sediment dates are necessary from sites bracketing the coring location where the 4580 yr BP date was obtained to substantiate or reject speculative theories regarding the influence of allogenic factors such as a warm climate on the rate of paludification. It may be that other processes operating independently of climate (for example, initiation of drainage through the outlet stream) may have been more important in controlling the paludification rate. At present, it seems likely that drainage via the outlet stream may constrain the rate of continued expansion unless outflow is obstructed at the drainage threshold.

To summarize, stratigraphic and radiometric data obtained at Black Gum Swamp provide the first evidence for horizontal expansion of a central New England peatland. Hydrologic data seem to suggest that the mechanism driving peatland expansion (i.e. peripheral ponding of water resulting from impeded drainage through highly-humified peats with low transmissivity) is similar to processes occurring at northern peatlands. Although the mean rate of expansion through the Holocene has been extremely slow (0.65 cm/yr), the amount of wetland area has more than doubled. The original peatland area enclosed by the 1-m bathymetric contour (the former lake level) is 4 ha, whereas the present total

peatland area is approximately 10 ha. However, because there may be considerable variation in hydrologic conditions at northeastern peatlands (Damman and French 1987), it may be unwise to make generalizations as to whether expansion has occurred at other peatlands in the region, or to assume that other peatlands may have had similar developmental histories.

### III. Modern Wetland Vegetation

Black Gum Swamp is currently dominated by a limited number of woody and herbaceous species occurring with greater than 80% frequency in plots throughout the swamp. Highly represented species with high cover values include *Picea rubens*, *Acer rubrum*, *Ilex* spp. (mostly *Ilex verticillata* with rare *I. laevigata*), *Nemopanthus mucronata*, *Osmunda cinnamomea*, *Sphagnum* spp., *Coptis groenlandica* and *Trientalis borealis*. Less frequent species with lower cover values include *Tsuga canadensis*, *Nyssa sylvatica* and *Vaccinium corymbosum*. Most other herbaceous and understory species are rare and local in occurrence (Table 5). The vegetation assemblage at Black Gum Swamp appears to be transitional between the *Carex trisperma* - *Picea mariana* forest community of northern peatlands and *Acer* - tall shrub communities associated with peatlands in the Appalachian Oak Zone (Damman and French 1987).

Because of the widespread nature of forest vegetation at Black Gum Swamp, there is little indication of distinct and easily discerned vegetation communities similar to those described for concentrically-zoned kettle-hole bogs. However, two-way indicator species analysis (TWINSPAN; Hill 1979) of releve data demonstrates that variations in species abundance and distribution are associated with specific locations within the peatland largely distinguished by differing

hydrological regimes. Generally wetter site conditions prevailing at basin margins and at the northern end of the swamp are indicated by the greater abundance of obligate and facultative wetland species such as *Calla palustris*, *Ilex* spp., *Smilacina trifolia* and *Carex trisperma* (Reed 1988). Wet conditions at the northern end of the swamp may be a consequence of increased upland seepage water input determined by watershed physiography (high ground to the north) and by impaired drainage related to distance from the outlet stream. As previously discussed, basin margins are typically wet due to the presence of ponded water.

A large number of plant species are exclusively associated with margins (31% of total species), or are more abundant at margins (Table 8). Margin environments are particularly favorable for high species diversity as a result of a) less-acid conditions and minerotrophic seepage water inputs; b) microsite heterogeneity; c) proximity to the upland.

Rare nutrient-demanding wetland species such as *Fraxinus nigra*, *Alnus rugosa*, *Carex intumescens* and *Leersia oryzoides* are primarily confined to less-acid, weakly minerotrophic basin margins. *Alnus rugosa* was found only at the eastern swamp lobe where a steep pH gradient indicates dilution of peatland acids by inflow of seepage water (Fig. 13). Heinselman (1970) documents the association of *Alnus* and *Fraxinus* in rich swamp forests experiencing minerotrophic seepage inflow at the Lake Agassiz peatland in Minnesota, and Bubier (1989) has noted the occurrence of *Alnus* at the margins of a minerotrophic stream passing through a peatland in Vermont. The persistence of *Alnus* pollen in the stratigraphic record suggests that relatively nutrient-enriched

Table 8. Vascular plant species primarily confined to wetland margins at Black Gum Swamp.

Upland species	Wetland Species (facultative and obligate)
<i>Amelanchier</i> sp.	<i>Alnus rugosa</i>
<i>Arisaema atrorubens</i>	<i>Aster simplex</i>
<i>Betula populifolia</i>	<i>Calla palustris</i>
<i>Dalibarda repens</i>	<i>Carex intumescens</i>
<i>Hamamelis virginiana</i>	<i>Fraxinus nigra</i>
<i>Quercus rubra</i>	<i>Leersia oryzoides</i>
<i>Uvularia sessilifolia</i>	<i>Viburnum recognitum</i>
<i>Viburnum alnifolium</i>	<i>Rubus hispidus</i>
Number of species .....	16
Total vascular species in swamp.....	51

conditions may have existed at basin margins during the entire developmental history of Black Gum Swamp.

At a forested wetland in central New York, Paratley and Fahey (1986) demonstrated that hummock-hollow microtopography can support a large number of wet- and dry-site plant species arrayed along an abrupt moisture gradient from the wet hollow bottom to the dry hummock top. Microsite heterogeneity within plots explains the co-occurrence of obligate wetland species and species usually associated with uplands at Black Gum Swamp.

Increased diversity at swamp margins may also be related to nearness of the upland. The probability that species typically associated with adjacent acidic mesic upland environments will occur at margin plots is enhanced by the proximity of propagule sources and by the availability of dry microsites (hummock tops) offering environmental conditions similar to those on the upland. Upland species found at swamp margins include *Quercus rubra*, *Kalmia angustifolia*, *Kalmia latifolia*, *Hamamelis virginiana*, *Gaultheria procumbens*, *Viburnum alnifolium*, *Amelanchier* sp., *Dalibarda repens* and *Uvularia sessilifolia*. The frequent occurrence of *Tsuga* at margin plots may also be a result of seeding-in from upland populations.

The relatively dry central swamp interior is characterized by fairly flat microtopography and lacks the large water-filled hollows found in the northern half of the swamp. Plots in this area have a high diversity of mesophytic herbaceous species and woody-plant seedlings due to the wide availability of relatively dry microsites. Although *Picea* is ubiquitous throughout the swamp, it is particularly abundant in the central interior, perhaps reflecting conditions of increased aeration

and drainage. *Tsuga* is also more abundant and frequent at the southern end of the swamp compared to northern interior locations. Studying vegetation at a dammed peatland in Ontario, Jeglum (1974) observed that growth rates of *Picea mariana* were enhanced by improved aeration and moisture regimes in the drained portion of peatland below the dam, whereas Paratley and Fahey (1986) noted the occurrence of *Tsuga* forest in areas of a wetland with lowest mean water table depths. Drier site conditions and associated high conifer abundance may be a consequence of improved drainage due to the nearness of the outlet stream. Although external nutrient-inputs from seepage water or groundwater may be minimal in this area, flow towards the outlet may provide improved conditions for tree growth. Work by Ingram (1967) has demonstrated that moving water increases ion transport and subsequent absorption by vegetation.

In addition to site factors, allogenic change brought about by human land-use may account for the abundance of *Picea* in the central portion of the swamp traversed by transect T-3. Plots 51-53 in division 11 (Fig. 14) occur within an area identified as second-growth *Picea* resulting from a patch-cut at the turn of the century (Harvard Forest Archives #1913-23). A reconstruction of the history of this *Picea*-dominated stand shows that it is even-aged, with most stems between 70 and 90 years of age. Hall (1912) reports that approximately 15 years after logging, stem densities of regenerating *Picea* were very high (1782 stems/hectare) and that shrub densities (*Ilex*, *Nemopanthus* and *Viburnum*) were also high. Despite intense intra- and interspecific competition, favorable site conditions and a high degree of shade tolerance may have enabled spruce to out-compete shrubs in this area. The ability of *Picea*

to remain alive while suppressed is reflected by the presence of numerous old but small trees (Fig. 17). Low shrub densities currently reflect the high degree of shading underneath the dense *Picea* canopy.

A similar reconstruction carried out in the more open, wetter shrub-dominated portion of the swamp on transect T-1A indicates that most trees in this area also originated after a cutting around the turn of the century. However, this stand is not overwhelmingly dominated by *Picea*, nor is it even-aged. Recruitment of *Picea*, *Tsuga* and deciduous trees appears to have been continuous but slow since disturbance. Hydrologic site conditions apparently have a major influence on the nature and rate of revegetation. Although the prevalence of moss-covered stumps indicates high tree densities before cutting, conifers were probably never as abundant as in the southern portion of the swamp. Sub-optimal conditions resulting from perennially high water levels and a relative lack of suitable dry microsites probably limited tree regeneration despite relatively high pH conditions and proximity to minerotrophic seepage water. Shrubs are particularly abundant, and probably flourished after the completion of cutting operations. Cross-sections cut through several moss-covered hummocks presently colonized by *Osmunda* and shrubs suggest that tree stumps have in some cases provided a nucleus (i.e. a microtopographic high) for subsequent hummock formation and colonization by vegetation. Although *Picea* basal area is lower (10.6 sq.m/ha) in this stand compared to the stand on transect T-3 (31.7 sq.m/ha), the presence of old but small trees (Fig. 19) may represent slow growth associated with sub-optimal hydrological conditions and interspecific competition with other woody species (i.e. shrubs and deciduous trees) rather than suppression related to intraspecific competition.



#### IV. Holocene History of *Nyssa* and *Picea* in New England

##### *Nyssa*

*Nyssa sylvatica* is presently an infrequent tree species throughout its range in New England, particularly at inland locations. Occurring throughout Massachusetts, Connecticut and Rhode Island, *Nyssa* has a northern range extension along the Maine coast, is disjunct in the Champlain Valley lowlands of Vermont and extends northward into southern Vermont and New Hampshire via the Connecticut River Valley (Little 1971). Although it occurs sparingly on mesic upland sites in transition-hardwood or oak-hickory forests in New England, *Nyssa* is more typically associated with the black ash - American elm - red maple forest type occurring in basin swamps and low-lying swales (Fowells 1965). *Nyssa* also occurs in acidic peatlands (pH range 3.6 - 5.6) in association with *Picea rubens*, *Acer rubrum*, *Tsuga canadensis* and *Betula alleghaniensis* at several sites in central New England (Zebryk unpublished). *Nyssa* becomes increasingly common south of New England in a variety of habitats, including both poorly-drained lowlands and mesic uplands.

*Nyssa* is rarely or poorly-represented on pollen diagrams from sites in the northeast. Consequently, little is known about the Holocene history of *Nyssa* within this region. With the exception of Black Gum Swamp in central New England, only coastal sites in southern New England provide a complete Holocene record of *Nyssa*. Ogden (1959) notes the occurrence of *Nyssa* pollen in gyttja at the Duarte Cranberry Bog, Martha's Vineyard, MA. Although the sediments are undated, *Nyssa* occurs in low (< 5%) percentages during the early postglacial pine increase or around 10,000 yrs BP (see Davis 1969). Dunwiddie (1990) also reports



the appearance of *Nyssa* in low percentages at 9500 yrs BP on Nantucket (No Bottom Pond), presumably representing long-distance transport from coastal mainland populations. The appearance of a local population on the island is indicated by a sharp increase in pollen percentage around 5000 yrs BP. The first appearance of *Nyssa* pollen on Block Island also occurs around 9500 yrs BP (long-distance transport) with the establishment of a local population by 7500 yrs BP. Low *Nyssa* percentages in southern coastal Connecticut were recorded by Deevey (1939) in early- to mid-pine zone sediments (9500 - 9000 yrs BP) at Linsley Pond and Job's Pond Kettle, where percentages increase at the time of the *Quercus* maximum during the warm, dry hypsithermal. Additional evidence of the occurrence of *Nyssa* in southern Connecticut is provided by Pierce and Tiffney (1986) who recovered *Nyssa* seeds from riverine sediments at New Haven radiocarbon-dated at 2800 yrs BP. Nelson (1984) records the appearance of *Nyssa* at 10,000 yrs BP in southeastern Massachusetts, and Patterson and O'Keefe (1980) document the local presence of *Nyssa* at 7000 yrs BP on Cape Cod.

Pollen data from Black Gum Swamp indicate that *Nyssa* was present in central New England at least by 8100 yrs BP. Estimations of earliest regional arrival dates based on pollen data from one site are risky, but it seems reasonable to assume *Nyssa* arrived later in central New England than in southern coastal New England. Despite being an entomophilous species (Eyde 1966), *Nyssa* pollen appears to be capable of extra-regional to long-distance transport. Wodehouse (1934) describes collecting airborne pollen 150 m from a source tree, and Dunwiddie reports *Nyssa* pollen in coastal island pond sediments at a time when *Nyssa* did not occur on the local landscape. Therefore, it seems

reasonable to infer from this information that if *Nyssa* was present on the regional landscape, pollen should be detected in large collecting-basins. However, the general absence of *Nyssa* pollen from central and northern New England sites throughout the Holocene may be an indication of the relative rarity and local occurrence of *Nyssa* in areas north of southern coastal New England, a distributional pattern that continues today. Perhaps only large local populations (as at Black Gum Swamp) or widespread regional populations produce sufficient pollen capable of being detected in the pollen record. Estimates of *Nyssa* arrival dates and determination of regional or local presence in central and northern New England may therefore depend fortuitously on the site selected for pollen analysis. Pollen analysis at wetland sites where *Nyssa* occurs now would increase the likelihood of obtaining additional details on the Holocene history of *Nyssa*.

### *Picea*

#### Evidence for the Younger Dryas Climatic Reversal

Early post-glacial *Picea* pollen abundances at Black Gum Swamp are indicative of an extensive *Picea* forest persisting for nearly 2500 years. However, a significant change in *Picea* abundance is apparently indicated by two distinct percentage peaks occurring through the period. Gaudreau and Webb (1985) mention similar double peaks at Tom Swamp, MA (Gaudreau unpublished), Rogers Lake, CT (Davis 1969) and Winneconnet Pond, MA (Suter unpublished). Shane (1987) reports the occurrence of double *Picea* peaks from sites on the Till Plains region south of the Great Lakes.

The earliest *Picea* peak for Midwestern and southern New England sites may be correlated with the northern European Allerod, a warming

period lasting from 12,500 - 11,000 yrs BP. In southern coastal New England (Rogers Lake, Winneconnet Pond) early *Picea* peaks observed at 13,000 years BP possibly indicate that climatic warming was initiated earlier than in Europe. The warming effect (or the *Picea* response) may have been time-transgressive within the New England area, as inland sites (Black Gum Swamp and Tom Swamp, both in Harvard Forest) exhibit *Picea* peaks at 11,500 and 12,000 yrs BP respectively. A general decline in *Picea* pollen following the initial peak suggests progressive warming eventually resulting in a climate unfavorable for *Picea*. A sharp increase in the minerogenic fraction of lake sediment at this time (Fig. 8) may represent accelerated erosion in the watershed associated with vegetation instability (Likens and Davis 1975) and wildfire, indicated by the high C:P ratio observed at 11,000 yrs BP. The resurgence in *Picea* pollen and attainment of second peaks at 11,000 years BP for southern coastal sites and at 10,000 yrs BP for inland sites implies the occurrence of a cooling period in New England, possibly correlated with the European Younger Dryas (11,000 - 10,200 yrs BP). As cited by Ruddiman (1987), Rind et al. (1986) concluded that a cooling event in New England can be explained by the presumed diversion of continental glacial meltwater into the North Atlantic rather than into the Gulf of Mexico, and therefore does not represent ice-sheet growth or reversal. At Black Gum Swamp, further evidence supporting the occurrence of a climatic reversal includes a decrease in the organic fraction of lake sediment possibly associated with a reduction in algal productivity (Shane 1987), and what appear to be slightly depressed values for *Pinus* and *Quercus* during the second *Picea* maximum. Inferring the occurrence of a climatic reversal from pollen evidence is problematic, however.

Except for the dramatic *Picea* pollen increase between 11,000 and 10,000 yrs BP, other equally-compelling evidence for a cooling trend is absent from the pollen record at Black Gum Swamp. The *Picea* response itself is ambiguous because *Picea* pollen grains were not identified to the species level during counting. (For a discussion of the difficulties associated with identifying *Picea* pollen grains, refer to Birks and Peglar 1980 and Hanson and Engstrom 1985.) However, species distinctions may be crucially important in providing a clearer interpretation of the *Picea* response to inferred climatic changes like the Younger Dryas. For example, if northern *Picea* species (i.e. *P. glauca* and *P. mariana*) increased from 11,000 to 10,000 yrs BP, this would provide additional evidence for the occurrence of a climatic reversal. Alternatively, an increase in *P. rubens* (a species with currently a more southern range distribution) relative to other *Picea* species could possibly indicate the continuation of warming during the early-postglacial period, thereby temporarily enabling *P. rubens* to outcompete and replace colder-climate *Picea* species. While this explanation conflicts with Shane's (1987) conclusions regarding the possible occurrence of the Younger Dryas, the absence of rigorous pollen and macrofossil evidence for associated vegetation responses makes such alternative explanations difficult to refute.

#### Wetlands as Mid-Holocene *Picea* Refugia

*Picea* is represented throughout the pollen record at several sites in northern New England including Moulton Pond, ME (Davis et al. 1975), Bugbee Bog, VT (McDowell et al. 1971), and Plissey Pond, Caribou Lake, Alder Lake and Goulds Lake, ME (Deevey 1951), but generally disappears from southern and central New England pollen sites by the mid-Holocene.

As the climate warmed, *Pinus*, then *Quercus* and *Tsuga* supplanted *Picea* from upland sites in southern and central New England. During the warmest part of the Holocene, large contiguous *Picea* populations probably remained viable only in the cooler, perhaps moister climate of northern New England (Gaudreau and Webb 1985). Although *Picea* probably disappeared from southern and central New England uplands by the beginning of the hypsithermal period, *Picea* species such as *P. mariana* and *P. rubens* may have continued to persist in low-lying swales or acidic peatland environments with an appropriate cool microclimate.

The long-term persistence of *Picea* pollen in Black Gum Swamp sediments lends strong support to the refugia theory. Low but steady *Picea* percentages averaging between 1% and 3% are recorded after the major *Picea* decline. The magnitude of these percentages indicates the presence of a local population (Davis and Webb 1975, Bradshaw and Webb 1985) occurring perhaps in the broad, shallow depression at the southern end of Black Gum Swamp or in adjacent low-lying swales. Small peaks in *Picea* pollen abundance beginning around 8000 yrs BP signal the development of swamp forest. Given the possible existence of a pre-existing local population, propagule availability may have facilitated rapid colonization of the peatland. Wood fragments identified as *Picea* sp. (R. Bruce Hoadley, pers. comm.) obtained near the base of swamp forest peat help to support the conclusion that *Picea* was perhaps the earliest and most abundant arboreal species colonizing the bog mat. Mid-Holocene *Picea* peaks at other wetland sites such as Totoket Bog and Bugbee Bog may represent a similar expansion of local *Picea* populations onto recently-grounded bog mats.

Increases in *Picea* percentages at northeastern pollen sites since 2000 yrs BP is indicative of the southward expansion of upland *Picea* populations in response to climatic cooling (Gaudreau 1986). The magnitude of percentage increases may be roughly correlated with latitude: northern sites nearest the center of the population distribution (i.e. sites located in spruce-fir or spruce-northern hardwood forests) have higher percentages than sites to the south in oak or transition-hardwood forests. Examples of northern sites with high (>5%) *Picea* percentages include Lac Dufresne, Quebec, Moulton Pond, ME and Brandreth Bog, NY; southern sites with low percentages (1% - 3%) include Mohawk Pond, CT, Duck Pond, MA, and Rogers Lake, CT. In a study of paired sites in central New England, Gaudreau (1986) identified topography as an important factor governing *Picea* abundance. A highland site (Berry Pond, MA, elev. 600 m) showed consistently higher *Picea* percentages (indicative of larger nearby populations) relative to a lowland site (Burden Lake, NY, elev. 192 m). Although occurring at an intermediate elevation (366 m) in the transition-hardwood area of central New England, Black Gum Swamp exhibits late-Holocene *Picea* pollen percentages comparable to high elevation sites like Berry Pond or more northern locations. The increase in *Picea* at Black Gum Swamp occurs at 2600 yrs BP. The timing of this increase is similar to some northern sites, and is somewhat earlier than at southern and other central New England sites. Both the earliness and magnitude of the *Picea* increase in the Black Gum Swamp watershed apparently reflect the rapid response of a small local *Picea* population to climatic change, analogous to increases observed for upland *Picea* at sites nearer the center of the population distribution. The later *Picea* "arrival" date at 2000 yrs BP

for most central and southern New England sites may reflect a) the absence of pre-existing local populations, and b), migration lag related to distance from northern population centers and discontinuities in habitat suitable for colonization.

The biostratigraphic record at Black Gum Swamp is unique in that it provides a detailed Holocene history for *Nyssa sylvatica* and *Picea*, taxa that are generally rare in peatlands throughout New England but which are locally common at Black Gum Swamp. This study provides the first documentation of the Holocene history of *Nyssa* at an inland site near its present northern range limit, and documents and describes in detail the history of *Picea* at a site near its present southern range limit in New England. This information may be of interest to paleoecologists and biogeographers pursuing questions related to the long-term survival of postglacial relict species (e.g. *Nyssa*) and the response of specific taxa to climatic change.

#### CONCLUSION

Results of paleoecological research at Black Gum Swamp demonstrate that early Holocene transitions in wetland vegetation communities followed the classic pattern of hydrarch succession. However, since the establishment of peatland vegetation, evidence for paludification and subsequent wetland expansion suggests that peatland development may be an open-ended, self-perpetuating process. The 8000-year record of swamp-forest vegetation at Black Gum Swamp furnishes tangible proof of the longevity and stability of this ecosystem. Similarities between northern peatlands and Black Gum Swamp in central New England indicate that analogous allogenic and autogenic processes may result in the

evolution of hydrological conditions leading to peatland permanence and subsequent expansion. Although long-term climatic change and short-term disturbance related to fire and human intervention have affected the abundance and composition of swamp-forest vegetation since 8000 yrs BP, the community itself has proven to be largely intractable. Substantive and rapid community-level changes appear to have occurred only during the early stages of hydrarch succession. Environmental stability within the Black Gum Swamp peatland may provide an explanation for the persistence of the northern genus *Picea* during an unfavorably warm climatic period (the hypsithermal), and may account for the continued long-term existence of the more southern species, *Nyssa*, despite the initiation of climatic cooling after 3000 yrs BP.

Although the amount of area presently occupied by peatlands in central and southern New England is small compared to northern New England (i.e. Maine) and the northern Midwest and Canada, these areas nevertheless furnish valuable wildlife habitat, serve as refugia for rare and endangered plant and animal species, act as water recharge/discharge areas and are aesthetically important as unique natural areas of great beauty. Furthermore, peatlands are extremely important repositories of climatic and biological information extending from the late-glacial period to the present.

Despite apparent stability and evidence for areal expansion, the slow growth rate of peat determines that peatlands are a non-renewable resource when viewed on the scale of a human lifetime. Peatlands are therefore highly sensitive to damage and exploitation. Peatlands in central and southern New England are currently being threatened by urban/suburban development and environmental degradation, while the



large northern peatlands in Maine and eastern Canada have been regarded as commercially exploitable sources of fuel and horticultural peat (Damman and French 1987). In a world threatened by the diminishment of carbon sinks and beset by global resource exploitation and loss of biological diversity, conservation and protection of peatland habitats should receive high priority in consideration of their high cultural, ecological and scientific value.

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Appendix 1. List of vascular and non-vascular plant species at  
Black Gum Swamp.

## TREES

*Acer rubrum*  
*Amelanchier* sp.  
*Betula alleghaniensis*  
*B. populifolia*  
*Fraxinus nigra*  
*Nyssa sylvatica*  
*Picea rubens*  
*Pinus strobus*  
*Quercus rubra*  
*Rhus vernix*  
*Sorbus americana*  
*Tsuga canadensis*

## SHRUBS

*Alnus rugosa*  
*Hamamelis virginiana*  
*Ilex laevigata*  
*I. verticillata*  
*Kalmia latifolia*  
*Lyonia ligustrina*  
*Nemopanthus mucronata*  
*Pyrus melanocarpa*  
*Rhododendron viscosum*  
*Vaccinium corymbosum*  
*Viburnum alnifolium*  
*V. cassinoides*  
*V. recognitum*

## PTERIDOPHYTES

*Dryopteris simulata*  
*Osmunda cinnamomea*

## HERBS

*Actaea* sp.  
*Aralia nudicaulis*  
*Arisaema atrorubens*  
*Aster acuminatus*  
*A. simplex*  
*Calla palustris*  
*Carex brunnescens*  
*C. intumescens*  
*C. trisperma*  
*Chiogenes hispidula*  
*Clintonia borealis*  
*Compositae* sp.  
*Coptis groenlandica*  
*Cornus canadensis*  
*Dalibarda repens*  
*Gaultheria procumbens*  
*Leersia oryzoides*  
*Maianthemum canadense*  
*Medeola virginiana*  
*Mitchella repens*  
*Rubus hispidus*  
*Smilacina trifolia*  
*Trientalis borealis*  
*Trillium undulatum*  
*Uvularia sessilifolia*  
*Vaccinium angustifolium*

## BRYOPHYTES\*

*Bazzania trilobata*  
*Dicranum undulatum*  
*Drepanocladus aduncus*  
*Sphagnum girgensohnii*  
*S. palustre*

\* (Nicolai, L.S. 1988)

Vascular species total ..... 51

Non-vascular species total ..... 7

Appendix 2. Pollen percentages for taxa not appearing on the pollen diagram.

Pollen Type	Depth (cm)/ C-14 Age									
	1 0	3 25	5 50	7 75	10 100	13 125	15 150	17 175	20 200	22 300
Cupressaceae	0.61	0.51	2.12	0.28	0.52	1.46	0	0.88	2.04	1.87
Tilia	0	0.51	0	0	0	0	0	0	0	0.15
Juglans cinerea	0.61	0	0	0.28	0.78	0	0.71	0	0	0
Platanus	0	0	0	0.57	0.52	0.83	0	0	0	0.15
Celtis	0.3	0	0	0	0	0	0	0	0	0
Liquidambar	0	0	0	0.28	0	0	0	0	0	0.15
Shepherdia	0	0	0	0	0	0	0	0	0	0
Corylus	0	1.03	0.57	0.85	0.78	1.46	0.27	0.88	1.97	0.78
Clethra	0	0	0	0	0	0	0	0	0	0
Cornus stolonifera	0	0	0	0	0	0	0	0	0	0
Sambucus pubens	0	0	0	0	0	0	0	0	0	0
Hamamelis	0	0	0	0	0	0	0	0	0	0
Galium sp.	0	0	0	0	0	0	0	0	0	0
Hypericum sp.	0	0	0	0	0	0	0	0	0	0.15
Cornus canadensis	0	0	0	0	0	0	0	0	0	0
Epilobium lobata	0	0	0	0	0	0	0	0	0	0
Actaea rubrum	0	0	0	0.28	0	0	0	0	0	0
Ranunculus sp.	0	0	0	0	0	0	0	0	0	0
Plantago spp.	0.92	0.77	0.96	0.28	0	0	0	0.17	0	0
Chenopodiaceae	0	0	0.19	0.28	0.26	0	0.21	0	0	0
Lamiaceae	0.3	0.51	0	0	0	0	0	0	0	0
Menyanthes	0	0	0	0	0	0	0	0	0	0
Caryophyllaceae	0	0	0	0	0	0	0	0	0	0
Sanguisorba canadensis	0	0	0	0	0	0	0	0	0	0
Saxifragus sp.	0	0	0	0	0	0	0	0	0	0
Viola sp.	0.3	0	0	0	0	0	0	0	0	0
Thalictrum	0	0.25	0	0	0	0	0	0	0	0.15
Mitchella repens	0	0.25	0	0	0	0	0	0	0	0
Sparganium sp.	0	0	0	0	0.55	0	0	0	0	0
Potamogeton sp.	0	0	0	0	0	0	0	0	0	0
Typha	0	0	0	0	0	0.28	0	0	0	0
Equisetum	0	0	0	0	0	0	0	0.11	0	0
Dryopteris	0	0	0	0	0	0	0	0	0	0
Pteridium	0	0	0.17	0.43	0.37	0.14	0	1.06	1.04	0.73
Dennstaedtia	0	0	0	0	0	0	0	0	0	0
Monolete spores	0	0.64	0	0.21	0.18	0.28	0	0.11	0	0.15

## Appendix 2, cont.

Pollen Type	26 550	30 850	33 990	37 1130	40 1400	42 1575	45 1750	47 2000	53.5 2300	60 2600
Cupressaceae	0.39	0	0	0.62	0.63	0.81	0	0.23	0	0.22
Tilia	0	0	0.21	0.31	0	0.32	0	0.69	0.26	0
Juglans cinerea	0	0	0	0	0.22	0	0	0	0	0
Platanus	0	0	0.21	0	0	0	0	0.23	0.23	0
Celtis	0	0	0	0	0	0	0	0	0	0
Liquidambar	0	0	0	0	0	0	0	0.23	0	0
Shepherdia	0	0	0	0	0	0	0	0	0	0
Corylus	0.59	2.8	0.21	0.31	0	0.16	0	0.46	0.17	0
Clethra	0	0	0	0	0	0	0	0	0	0
Cornus stolonifera	0	0	0	0	0	0	0	0	0	0
Sambucus pubens	0	0	0	0	0	0	0	0	0	0
Hamamelis	0	0	0	0	0	0	0	0	0	0
Galium sp.	0	0	0	0	0	0	0	0	0	0
Hypericum sp.	0	0	0	0	0	0	0	0	0	0
Cornus canadensis	0	0	0	0	0	0	0	0	0	0
Epilobium lobata	0	0	0	0	0	0	0	0	0	0.42
Actaea rubrum	0	0	0	0	0	0	0	0	0	0
Ranunculus sp.	0	0	0	0	0	0	0	0	0	0
Plantago spp.	0	0	0.81	0	0	0.32	0	0	0	0
Chenopodiaceae	0	0	0	0	0	0	0	0	0	0
Lamiaceae	0	0	0	0	0	0	0	0	0	0
Menyanthes	0	0	0	0	0	0	0	0	0	0
Caryophyllaceae	0	0	0	0	0	0	0	0	0	0
Sanguisorba canadensis	0	0	0	0	0	0	0	0	0	0
Saxifragus sp.	0	0	0	0	0	0	0	0	0	0
Viola sp.	0	0	0	0	0	0	0	0.23	0	0
Thalictrum	0	0	0	0	0	0	0	0	0	0
Mitchella repens	0	0	0.21	0	0	0.16	0	0	0	0
Sparganium sp.	0	0	0	0	0	0	0	0	0	0
Potamogeton sp.	0	0	0	0	0	0	0	0	0	0
Typha	0	0	0	0	0	0	0	0	0	0
Equisetum	0	0	0	0	0	0	0	0	0.09	0
Dryopteris	0	0	0	0	0	0	0	0	0	0
Pteridium	0.4	0	0	0.28	0.13	0.08	0.54	0.39	0.48	0
Dennstaedtia	0	0	0	0	0	0	0	0	0	0
Monolete spores	0.13	0	0.13	0.19	0	0.08	0	0.13	0	0

## Appendix 2, cont.

Pollen Type	65 2900	70 3200	80 3550	90 3800	95 4000	98 4100	110 4400	120 4650	125 4900	130 5150	134 5440
Cupressaceae	0	0.21	0	0.25	0.24	1.23	0	0	0	0	0
Tilia	0.29	0	0	0.27	0	0	0	0	0.52	0	0.99
Juglans cinerea	0	0	0	0.27	0.49	0	0	1.06	0	0	0.33
Platanus	0	0	0	0	0	0	0	0	0	0	0.99
Celtis	0	0	0	0	0	0	0	0.53	0	0	0
Liquidambar	0	0	0	0.25	0.24	0	0	0	0	0	0
Shepherdia	0	0	0	0	0	0	0	0	0	0	0
Corylus	0	0.21	0.36	0	0.24	0.28	0.19	2.89	0.23	0	0.3
Clethra	0	0	0	0	0	0	0	0	0	0	0
Cornus stolonifera	0.19	0	0	0	0	0	0	0	0	0	0
Sambucus pubens	0	0	0	0	0	0	0	0	0	0	0
Hamamelis	0	0	0	0	0	0	0	0	0	0	0
Galium sp.	0	0	0	0	0	0	0	0	0	0	0
Hypericum sp.	0	0	0	0	0	0	0	0	0	0	0
Cornus canadensis	0	0	0	0	0	0	0	0	0	0	0.61
Epilobium lobata	0	0	0	0	0	0	0	0	0	0	0
Actaea rubrum	0	0	0	0	0	0	0	0	0	0	0
Ranunculus sp.	0	0	0	0	0	0	0	0	0	0	0
Plantago spp.	0.39	0	0	0.25	0	0	0	0	0	0	0
Chenopodiaceae	0	0	0	0	0	0	0	0	0	0	0
Lamiaceae	0	0	0	0	0	0	0	0	0	0.47	0
Menyanthes	0	0	0	0	0	0	0	0	0	0.23	0
Caryophyllaceae	0	0	0	0	0	0	0	0	0	0	0
Sanguisorba canadensis	0	0	0	0	0	0	0	0	0	0	0
Saxifragus sp.	0	0	0	0	0	0	0	0	0	0	0
Viola sp.	0	0	0	0	0	0	0.19	0	0	0.23	0
Thalictrum	0	0	0	0	0	0	0	0	0	0	0
Mitchella repens	0	0	0	0	0	0	0	0	0.23	0.23	0
Sparganium sp.	0	0	0	0	0	0	0	0	0	0	0
Potamogeton sp.	0	0	0	0	0	0	0	0	0	0	0
Typha	0	0	0	0	0	0	0	0	0	0	0
Equisetum	0	0	0	0	0	0	0	0	0	0	0
Dryopteris	0	0	0	0	0	0	0	0	0	0	0
Pteridium	0.2	0	0	0	0.21	0.49	0.28	0	0	0.21	0.23
Dennstaedtia	0.2	0	0	0	0	0	0	0	0	0	0
Monolete spores	0.41	0	0	0	0.32	0	0	0	0	0	0

## Appendix 2, cont.

Pollen Type	139 5800	143.5 6200	147 6500	154 6900	160 7250	170 7750	180 8000	195 8350	220 8600	240 8700	260 8750
Cupressaceae	0	0	0	0	0	0	0	0	0	0.55	0
Tilia	0.33	0	0	0	0	0	0.14	0	0	0	0
Juglans cinerea	0	0.87	0	0	0	0	0	0	0.29	0	0.29
Platanus	0	0	0	0	0	0	0	0	0	0	0
Celtis	0	0	0	0	0	0	0	0	0	0	0
Liquidambar	0	0	0	0	0	0	0	0	0	0	0
Shepherdia	0	0	0	0	0	0	0	0	0	0	0
Corylus	0.13	0	0.22	0.19	1.48	0	0.84	1.68	0.29	0	0.98
Clethra	0	0	0	0	0	0	0	0	0	0	0
Cornus stolonifera	0	0	0	0	0	0	0	0	0	0	0
Sambucus pubens	0	0	0	0	0	0	0	0	0	0.82	0
Hamamelis	0	0.22	0	0	0	0	0	0	0	0	0
Galium sp.	0	0	0	0	0	0	0	0	0	0	0
Hypericum sp.	0	0	0	0	0	0	0	0	0	0	0
Cornus canadensis	0	0.45	0	0	0	0	0	0	0	0	0
Epilobium lobata	0	0	0	0	0	0	0	0	0	0	0
Actaea rubrum	0	0	0	0	0	0	0	0	0	0	0
Ranunculus sp.	0	0	0	0	0	0	0	0	0	0	0
Plantago spp.	0	0.45	0	0	0	0	0	0	0	0	0
Chenopodiaceae	0	0	0.22	0	0	0	0	0	0	0	0
Lamiaceae	0	0	0	0	0	0.19	0	0	0	0	0
Menyanthes	0	0	0	0	0	0	0	0	0	0	0
Caryophyllaceae	0	0	0	0	0	0	0	0	0	0	0
Sanguisorba canadensis	0	0	0	0	0	0	0	0	0	0	0
Saxifragus sp.	0	0	0	0	0	0	0	0	0	0	0
Viola sp.	0.13	0	0	0	0	0	0	0	0	0	0
Thalictrum	0	0	0	0	0.29	0	0	0	0	0	0.15
Mitchella repens	0.13	0	0	0	0	0	0	0	0	0	0
Sparganium sp.	0	0	0	0	0	0	0	0	0	0	0
Potamogeton sp.	0	0	0	0	0	0	0	0	0	0	0
Typha	0	0	0	0	0	0	0	0	0	0	0
Equisetum	0	0	0	0	0	0	0.7	0	0.28	1.85	0.15
Dryopteris	0	0	0	0	0	0	0	0	0	0	0
Pteridium	0.13	0.19	0	0.49	0	0	0	0	0	0	0
Dennstaedtia	0	0	0	0	0	0	0	0	0	0	0
Monolete spores	0	0.19	0	0.16	0	0	0	0	0	0	0

## Appendix 2, cont.

Pollen Type	275 8800	290 8950	320 9250	345 9450	370 9700	390 10100	405 10400	420 10700	429 10900	440 11150	447 11300
Cupressaceae	0.54	0	0	0.29	0	0	0	0.76	1.3	2.33	0
Tilia	0	0	0	0	0	0	0	0	0	0	0
Juglans cinerea	0.82	0.11	0	0	0	0.15	0	0.19	0	0	0.33
Platanus	0	0	0	0	0	0	0	0	0	0	0
Celtis	0	0	0	0	0	0	0	0	0	0	0
Liquidambar	0	0	0	0	0	0	0	0	0	0	0
Shepherdia	0	0	0	0	0	0	0	0	0	0	0
Corylus	0.13	0.23	0	0	0	0	0.21	0	0	0.84	0.27
Clethra	0	0.56	0	0	0	0	0	0	0	0	0
Cornus stolonifera	0	0	0	0	0	0	0	0	0	0	0
Sambucus pubens	0	0	0	0	0	0	0	0	0	0	0
Hamamelis	0	0	0	0	0	0	0	0	0.25	0	0
Galium sp.	0	0	0	0	0	0	0.21	0	0	0	0.27
Hypericum sp.	0	0	0	0	0	0	0	0	0	0	0
Cornus canadensis	0	0	0	0	0	0	0	0	0.51	0	0.82
Epilobium lobata	0	0	0	0	0	0	0	0	0	0.28	0
Actaea rubrum	0	0	0	0	0	0	0	0	0	0	0
Ranunculus sp.	0	0	0	0	0	0	0	0	0	0	0
Plantago spp.	0	0	0	0	0	0	0	0	1.02	0	0
Chenopodiaceae	0	0	0	0	0	0	0	0	0	0	0
Lamiaceae	0	0	0	0	0	0	0	0	0	0	0
Menyanthes	0	0	0	0	0	0	0	0	0	0	0
Caryophyllaceae	0	0	0	0	0	0	0.21	0	0	0	0
Sanguisorba canadensis	0	0	0	0	0	0	0	0	0	0	0
Saxifragus sp.	0	0	0	0	0	0	0	0	0	0	0
Viola sp.	0	0	0	0	0	0	0	0	0	0	0
Thalictrum	0	0	0	0	0	0	0	0	0	0	0
Mitchella repens	0	0	0	0	0	0	0	0	0	0	0
Sparganium sp.	0	0.22	0	0.25	0	0.69	0	0.18	0	0	0
Potamogeton sp.	0	0	0	0	0	0	0.65	0	1.27	0	2.17
Typha	0	0.22	0	0	0	0	0	0.18	0.22	0	0
Equisetum	0.1	0	0	0.12	0	0.27	0	0	0	0.28	0
Dryopteris	0	0	0	0	0	0.41	0	0.36	0	0	0
Pteridium	0	0	0	0	0	0	0.19	0	0.45	0	0.27
Dennstaedtia	0	0	0	0	0	0	0	0	0	0	0
Monolete spores	0	0	0	0	0	0	0.39	0	0.67	0	0.27

## Appendix 2, cont.

Pollen Type	470	480	490
	11800	12000	12200
Cupressaceae	1.36	0	9.09
Tilia	0	0	0.43
Juglans cinerea	0.34	0	0
Platanus	0	0	0
Celtis	0	0	0
Liquidambar	0	0	0
Shepherdia	0	1.28	0.86
Corylus	0	0	0
Clethra	0	0	0
Cornus stolonifera	0	0	0
Sambucus pubens	0	0	0
Hamamelis	0	0	0
Galium sp.	0	0	0
Hypericum sp.	0	0	0
Cornus canadensis	0	0	0
Epilobium lobata	0	0	0
Actaea rubrum	0	0	0
Ranunculus sp.	2.72	0	0
Plantago spp.	0	1.28	0.43
Chenopodiaceae	0	0	0
Lamiaceae	0	0	0
Menyanthes	0	0	0
Caryophyllaceae	0	0.32	0
Sanguisorba canadensis	0.68	0	0
Saxifragus sp.	0.34	0	0
Viola sp.	0	0	0
Thalictrum	0.68	0	0
Mitchella repens	0	0	0
Sparganium sp.	0	0	0
Potamogeton sp.	0	0	0
Typha	0.34	0.96	0
Equisetum	0	0	0
Dryopteris	0	0	0
Pteridium	0	0	0
Dennstaedtia	0	0	0
Monolete spores	0	0	0