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Vegetation ecology of tidal freshwater swamps of the lower Chesapeake Bay, United States of America

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Vegetation ecology of tidal freshwater swamps of the lower Chesapeake Bay, USA

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VEGETATION ECOLOGY OF TIDAL FRESHWATER SWAMPS OF THE LOWER CHESAPEAKE BAY, USA

A Dissertation

Presented to

The Faculty of the School of Marine Science

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In Partial Fulfillment

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Doctor of Philosophy

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by

Richard D. Rheinhardt

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APPROVAL SHEET

This dissertation is submitted in partial fulfillment of the requirements for the degree of

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DEDICATION

To those who strive to preserve biodiversity and the natural ecosystems of planet Earth.

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Without the support, encouragement, and comradery of the VIMS community, this work would never have been possible. I regret not being able to recognize everyone who assisted in this endeavor and I apologize if I have forgotten anyone.

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ABSTRACT

Woody and herbaceous vegetation were sampled in 23 tidal swamps along a tidal freshwater tributary of lower Chesapeake Bay. Four vegetative categories were ordinated with Detrended Correspondence Analysis (DECORANA). Species distribution patterns of each strata were compared with respect to edaphic factors, a wetness index, and mean water table depth.

Woody species are restricted to hummocks (topographic highs). Hummocks drain as quickly as the tide drops and so are partially inundated for only short periods each day. Although low in canopy diversity, tidal swamps are floristically rich in herbaceous and woody understory species, ranking them among the most speciose in temperate North America.

Canopy composition is related to the wetness of a site as determined by the percent of the forest floor covered by hollows (low inter-hummock depressions) and by mean water table depth. _Fraxinus_ spp. and _Nyssa_ _biflora_ dominated swamps are best developed in wetter sites, which contain higher calcium (Ca) and organic matter (Om) levels and where the mean water table depth is about -17 cm. In contrast, _Acer rubrum_-_Liquidambar_ _styraciflua_-_Nyssa_ _biflora_ dominated swamps occur at less wet sites where mean water table depth is deeper than 20 cm.

Although DECORANA separated canopy and herbaceous strata similarly, the woody subcanopy (shrubs and small understory tree species) did not separate into the same two communities. To determine whether this pattern might be indicative of forests in general, distributional data of canopy and subcanopy species were also compared using similarly collected data from a southern Appalachian forest. Sapling (juvenile canopy species) distribution patterns were also compared in both systems. Separate ordinations were performed on canopy, sapling, and subcanopy species.

Canopy trees and saplings showed a similar pattern of distribution, suggesting that resource requirements of saplings and canopy-statured adults are similar. In contrast, the subcanopy species of neither ecosystem showed any discernable distributional relationship to the canopy or sapling layers, suggesting that subcanopy life-forms may partition different resources than canopy species in temperate forests. If so, the common practise of combining sapling and subcanopy species in structural analyses may hinder our understanding of subcanopy structural patterns in forests.

VEGETATION ECOLOGY OF TIDAL FRESHWATER SWAMPS OF THE LOWER CHESAPEAKE BAY, USA

PREFACE

Wetlands are an important biospheric link between aquatic and terrestrial ecosystems and much recent scientific work has been devoted toward understanding the importance of wetlands to the integrity of both systems. Of special interest to estuarine ecologists is the flow of energy and nutrients between tidal wetlands and the estuary proper and the importance of wetlands to estuarine ecosystem dynamics.

Vegetation research in temperate estuarine wetlands over the past 25 years has focused primarily on the ecology of tidal salt marshes. Marsh ecologists have only recently expanded their investigations further up estuarine rivers into the tidal reaches that support oligohaline and freshwater marshes. In some rivers, tidal swamps (wetlands dominated by trees) occur upriver from, and sometimes behind, tidal freshwater marshes, but relatively little scientific work has been focused on their ecology or on their relationship to the rivers with which they are linked.

Prior to studying the dynamics of any ecosystem, one must first understand the structure and distribution of primary producers in that system. At present, very little is known about the compositional range of the vegetational assemblages associated with tidal swamps. A vital first step is to quantitatively characterize the tidal swamp vegetation of an entire tidal freshwater river and to determine the gradients and discontinuities present in the vegetative patterns.

An examination of National Wetland Inventory maps (NWI: U.S. Fish

Fish and Wildlife Service 1990), indicates that there are approximately 3,500 ha of tidal swamps within the lower Chesapeake Bay estuarine system, most of which are concentrated along three rivers: the Pamunkey, the Mattaponi, and the Chickahominy. The tidal swamps of these three rivers are classified on the NWI maps as tidal, seasonally flooded forested wetlands (Cowardin et al. 1979), suggesting that they are tidally flooded only on a seasonal basis (presumably during the spring thaw when river flow is maximal). However, hydrologic data are lacking for these ecosystems and so their true hydrodynamic regime is unknown.

Anadromous fishes, including white perch (Morone americana), American shad (Alosa sapidissima), and the commercially important striped bass (Morone saxatilis) spawn along the same tidal freshwater reaches where tidal swamps occur. Large flocks of migrating waterfowl also use the tidal freshwater areas as overwintering habitat and as foraging stops during migration.

Since European colonization of North America, environmental degradations following the wake of human population expansion have drastically reduced the amount of nontidal wetlands and tidal marshes that once thrived in the United States; now human population pressures are threatening the few remaining remnants of tidal swamps as well. In order to effectively preserve and manage our remaining wetland resources, it is vital for scientists to gain a better understanding of tidal swamp ecology and how these ecosystems are related to the ecology of the subestuarine rivers to which they are linked.

The Pamunkey River of Virginia is probably the most pristine tidal freshwater river in the Chesapeake Bay system. It also harbors 64% (2,236 ha) of the total remaining tidal swamp forests of the lower Chesapeake Bay. Thus, not only are the tidal swamps of the Pamunkey an important natural resource about which biological information is lacking, they also provide an ideal place to study natural vegetative distributions along environmental gradients.

Chapter 1 presents quantitative information on the vegetation of the swamp forests that occur along the tidal portion of the Pamunkey River. Swamps along the entire tidal portion (40 km) of the Pamunkey were sampled in order to try to understand how vegetation responds to the range in hydrologic regimes provided by the river. Seven vegetative categories of four stratal life-forms were sampled:
1) canopy trees, 2) saplings of canopy species, 3) seedlings of canopy species, 4) mature subcanopy species, 5) subcanopy seedlings, 6) vines, and 7) herbaceous plants. The subcanopy life-form is comprised of shade tolerant shrub and small tree species that are genetically adapted to exploit the low light conditions generally present under the canopy; subcanopy species almost never reach the canopy.

Data on the composition of the vegetative communities was subjected to Detrended Correspondence Analysis (DECORANA: Hill 1979, Hill and Gauch 1980) using the CANOCO package developed by Ter Braak (1988). DECORANA is an indirect ordination technique which graphically places samples (forest stands) in multivariate space (on ordination diagrams) based solely upon their compositional attributes. Various measured environmental parameters were statistically examined in relation to the ordination axes in order to determine the possible environmental parameters of importance in the distribution of species and communities. In addition, the directions and strengths of environmental gradients not aligned with the axes were examined using environmental biplot scores (Ter Braak 1986a, 1988). The goal was to infer some of the parameters that might be controlling community structure and species distribution patterns in tidal freshwater swamps.

The results of the vegetation study not only provide phytosociological information currently lacking about tidal swamp vegetation, but suggest which of the measured factors are most likely to be affected by anthropogenic influences and which are most ammenable to management to minimize or ameliorate anthropogenic impacts. Such data also establish quantitative baseline information so that any changes found in the distribution patterns of the vegetation or in the environmental factors might alert future resource managers of possible environmental changes taking place in the ecosystem.

A combined Bitterlich plotless and density field sampling method was employed to quantitatively sample the woody vegetation. This method wAs introduced by Lindsey et al. (1958) as an extremely efficient forest sampling method and later suggested for use in Virginia by Levy and Walker (1971) in order to standardize forest sampling methods there. This combined sampling method has been used successfully in Piedmont, Coastal Plain, and montane forest ecosystems. Special sampling tools (see Appendix 1) were designed and constructed by the author to enable an unaccompanied worker to efficiently sample vegetation under the difficult field conditions often encountered in swamps. These tools and methods can be advantageously applied in any forest ecosystem.

Chapter 2 presents the results of a study of groundwater fluctuations in tidal swamps and the relationship of flooding to community distribution patterns. Groundwater dynamics are rarely examined in wetlands, although it has been recently recognized that below-ground hydrodynamics is probably the most important parameter affecting nutrient cycling characteristics and vegetation patterns.

Groundwater wells were established in five of the sampled forests stands in order to determine the range of hydrologic conditions present within the Pamunkey River tidal swamp complex, to clarify the degree of coupling between tides and below-ground hydrodynamics, and to relate hydrologic differences between sites to compositional differences in vegetation patterns.

Chapter 3 is a comparative study of the relationship between canopy and subcanopy distribution patterns of two temperate forest ecosystems. Most forest ecology studies, including those of forested wetlands, only superficially examine the subcanopy stratum; that is, studies usually present only lists of the most common understory species even when the canopy and herbaceous strata have been quantified. The distribution of subcanopy species has usually been assumed to follow the same pattern as that established by the canopy and herb strata, but no evidence has ever been presented to substantiate such an assumption. Thus, in the course of sampling the tidal swamps, data on the subcanopy species were collected separately from that of the similarly sized saplings of canopy species. Comparisons of distribution patterns were made with identically collected data from southern Appalachian forests.

Chapter 1

A MULTIVARIATE ANALYSIS OF VEGETATION PATTERNS IN TIDAL FRESHWATER SWAMPS OF LOWER CHESAPEAKE BAY, USA

ABSTRACT

The woody and herbaceous vegetation of 23 tidal freshwater swamps were sampled along the Pamunkey River, a tributary of the York River (a subestuary of Chesapeake Bay). Tidally driven water level fluctuations were monitored and recorded in selected swamps. Four vegetative life-forms were examined and ordinated with Detrended Correspondence Analysis: trees (canopy and sapling sized), woody subcanopy (shrubs and understory trees), vines, and herbs. Species distribution patterns were compared in relation to edaphic factors, a flooding index, and duration of flooding in the root zone.

On the basis of the canopy composition, two tidal swamp communities were found, both subjected to a tidally forced hydroperiod regime within the upper 15 cm of their root zones, the approximate height of the hummocks. Nyssa biflora - Fraxinus spp. dominated swamps are best developed toward the more downriver reaches in the wetter sites, which contain more hollows, a higher organic matter content, and higher calcium levels. In contrast, Acer rubrum-Liquidambar styraciflua-Nyssa biflora dominated swamps are more common throughout the mid- to upriver reaches at less wet sites with lower organic matter and calcium levels. Taxodium distichum was found to co-dominate in two swamps that may represent relic conditions for the wetter sites.

Although low in canopy diversity, the tidal swamps are floristically rich in herbaceous and subcanopy species, ranking them among the most speciose in temperate North America. The microtopographic complexity (the hummocks vs. hollows pattern) appeared to be strongly related to species distribution patterns in the canopy, vine, and herbaceous strata. Although the ordinations segregated canopy and herbaceous strata similarly, the woody subcanopy did not segregate into the same two communities established by the canopy and herb strata, suggesting that the canopy may be partitioning different resources than the woody subcanopy.

INTRODUCTION

Little is known or has been published on tidal freshwater swamps, an ecosystem restricted to the upper freshwater reaches of some tidal tributaries. Few woody species are flood-tolerant and there are no temperate latitude salt-tolerant canopy trees. Thus, temperate latitude tidal swamps develop in areas that possess a wide tidal range, a voluminous river flow and low coastal plain relief, factors that appear to rarely occur together. In the Virginia part of Chesapeake Bay, tidal swamps are almost entirely restricted to three freshwater tidal rivers of the lower bay. Areal calculations of tidal swamps obtained from National Wetland Inventory maps (United States Fish and Wildlife Service 1990) of the lower bay revealed that the Pamunkey River contains 2,236 ha (64%), the Chickahominy River 674 ha (19%), and the Mattaponi River 592 ha (17%).

The paucity of published literature on tidal swamp forests may reflect their rarity. In their treatments of eastern North American forests, Braun (1950) and Barbour and Billings (1988) made no mention of tidal swamp forests, nor did Mitch and Gosselink (1986) in their exhaustive review of wetlands. Lugo et al. (1990) briefly mentioned the exitence of irregularly flooded (wind-driven) tidal swamps, but no further information was provided. In fact, only two published ecological studies have focused on tidal freshwater swamps (Doumlele et al. 1985, Brinson et al. 1985).

The Doumlele et al. (1985) study characterized the canopy and herbaceous vegetation of only one tidal swamp along the lower reaches of the Pamunkey River. In an unpublished study of tidal swamps, Fowler (1987) examined the seasonal production of the canopy and herbaceous strata of a tidal swamp located 2 km downriver from the Doumlele et al. (1985) site. The vegetation of both sites were dominated by ashes (Fraxinus spp.) and swamp blackgum (Nyssa biflora). None of the tidal swamp sites that occur along the remaining 38 km of the river were quantitatively examined, nor had any detailed environmental measurements been obtained.

Brinson et al. (1985) examined the relationships between primary production, nutrient cycling, and vegetational structure in four tidal swamp stands located along two tributaries of Pamlico Sound, a lagoonal estuary in North Carolina. However, the Pamlico Sound tidal swamps and those of the Pamunkey River differ markedly from one another in their physiognomy and hydrologic regime, thus rendering comparisons between the two difficult. The swamp stands on the Pamlico Sound tributaries are extremely limited in area (less than 0.1 ha) and consist primarily of narrow, fringing swamps, while those along the Pamunkey River commonly encompass areas larger than 50 ha. Further, the salinity of the farthest downriver section of the Pamunkey where tidal swamps terminate remains fresh (0.05 ppt) in contrast to some swamps along the Pamlico Sound tributaries (Brinson et al. 1985) which experience salinities in excess of 13 ppt at 25 cm depth (salinity levels in the upper 15 cm of the root zone are unknown). Also, the tidal range in Pamlico Sound is slight and irregular because of a hydroperiod influenced primarily by wind and river flow rather than by tidal forcing. In contrast, the hydroperiod of Pamunkey River tidal swamps is dominated by lunar tides (0.75-1.5 m range) exhibiting a mixed semi-diurnal inequality.

Flooding is important in tidal swamps because hydroperiod controls soil structure and nutrient availability in these as well as other wetlands. Flooding also creates an anaerobic stress for most plants; however, those species that can tolerate anoxic conditions in their upper root zones (flood-tolerant species) have a competitive advantage in flood-prone areas. Because wetland plant species differ in their tolerance to the saturation of their roots, differ in their nutrient requirements, and respond differently to soil structure, hydroperiod regime is recognized as being the most influential environmental factor controlling the vegetative structure of freshwater wetland communities in general and of swamp vegetation in particular. Although Brinson et al. (1985) measured both hydroperiod and salinity in the tidal swamps they studied in North Carolina, they were unable to totally separate the effects of the two factors. The relationship between hydroperiod and vegetation should be more easily clarified by studying swamps along the Pamunkey River because flooding waters there are fresh.

This study was initiated to quantitatively assess the vegetation of the tidal swamps along all of the Pamunkey River in Virginia to (1) determine the full compositional range of tidal swamps, (2) relate the tidally forced groundwater fluctuations in the upper root zone to plant community structure, and (3) relate selected edaphic factors to species distribution patterns.

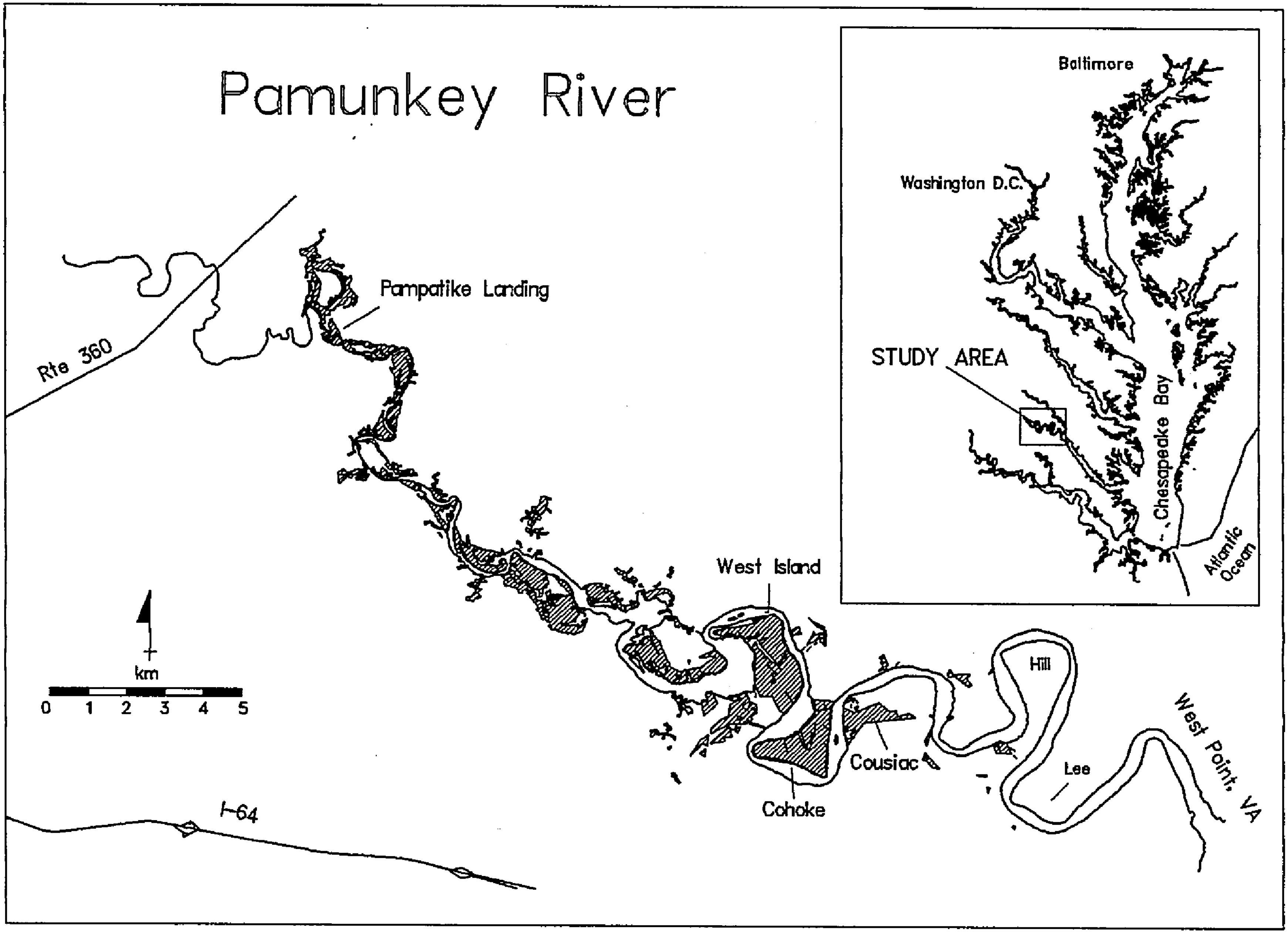
Study Area

This study was conducted along the Pamunkey River in parts of King William, New Kent, and Hanover counties in Virginia, within the northern range of the southern mixed hardwood forest region (Ware 1970, sensu Quarterman and Keever 1962). The Pamunkey is a meandering, low gradient coastal plain river flowing between Ashland and West Point, Virginia. From the U.S. Route 360 bridge to West Point, the river is tidal (Fig. 1.1). At West Point the Pamunkey merges with the Mattaponi River to form the York River, a major subestuarine river of lower Chesapeake Bay. The lower end of the Pamunkey, below Cousiac, supports tidal freshwater and oligohaline marshes. At this lower end, salinity generally ranges between 10 and 0.5 ppt, with higher salinity occurring during drought periods and toward the more downriver oligohaline reaches.

From the most downriver tidal swamp (Cousiac) to 40 km in river distance upriver (Fig. 1.1), the river is fresh and tidal; swamps dominate the wetland landscape, although tidal freshwater marshes are scattered throughout as well. Upriver of Cousiac, however, tidal marshes are usually restricted to the smaller islands and the shoreward fringes of some swamps in contrast to those marshes located downriver of Cousiac that encompass the entire inside bends of the river (from 300-400 ha in area). Where tidal swamps occur, the salinity rarely rises above 0.05 ppt except at the extreme downriver reach near Cousiac and then probably only during severe droughts.

Tidal swamp soils consist of a thick peat layer and alluvium deposits (Mixon et al. 1989) comprised of euic Ferric Medisaprists of the Mattan series (Hodges et al. 1988). The thick (40-128 cm) organic layer is composed of a mixture of herbaceous and woody plant remnants, including many logs and limbs. The alluvium deposits are primarily

Figure 1.1. Location of Pamunkey River tidal swamps. Tidal swamps occur from Cousiac marsh to just upriver from Pampatike Landing (green hatched areas). There are approximately 41.5 km (river distance) between the most upriver and the most downriver sites. Map drawn using ARC-INFO (ESRI 1989).


Pamunkey River
Pampatike Landing
Rte 360
West Island
Cohoke
Cousiac
Hill
Lee
West Point, VA
I-64
km
0 1 2 3 4 5
Baltimore
Washington D.C.
STUDY AREA
Chesapeake Bay
Atlantic Ocean

Holocene in origin, but include some low-lying Pleistocene terrace deposits as well (Mixon et al. 1989).

Normal average air temperatures near the study area at Walkerton, Virginia range from 2.4 C in January to 25.2 C in July (NOAA 1990, 1991). The frost-free season lasts for approximately 230 days (early April to early November). Normal annual precipitation is 113 cm and is fairly evenly distributed throughout the year; precipitation for 1989 was 140.7 cm and 114.6 cm for 1990 at Walkerton, Virginia (near the middle of the study area).

The distribution patterns of plant species in relation to the environmental factors they exploit can be best investigated by studying fully developed, mature ecosystems. The Pamunkey River is an ideal place to study the factors which influence species distribution patterns because tidal swamps along the Pamunkey are well developed, are relatively undisturbed, and flourish along a 40 km stretch of river. Thus, a wide range of potential habitat conditions are represented there.

METHODS

Field Data Collection

Potential vegetation sampling sites were marked on USGS 1:24,000 series quadrangle maps along the river course and at various distances from the river bank in an attempt to encompass the entire range of Pamunkey River tidal swamps. Sites marked on the quad maps were visited and then quantitatively sampled if they lacked evidence of recent disturbance.

A total of 23 stands were considered suitable for sampling. Seven vegetative categories of four strata were sampled, but data from only four categories are presented here: 1) canopy trees, 2) mature subcanopy shrubs and understory trees, 4) vines, and 4) herbaceous plants. Taxonomic nomenclature follows that of Harvill et al. (1986) and Radford et al. (1968).

Sampling plots for woody species were located along compass transects at least 30 m apart to avoid any overlap of plots. A species area curve analysis was used to determine the number of points needed to adequately sample a stand (usually three to four points). The combined rangefinder-Bitterlich plotless method (Lindsey et al. 1958, Levy and Walker 1971) was used to obtain the basal area (m^2/ha cross sectional area at 1.5 m above ground) of canopy trees (Grosenbaugh 1952). Tree densities (stems/ha) of canopy species were obtained from counts of all trees greater than 10 cm dbh (diameter at 1.5 m above ground) within a 10 m radius circlular plot centered at each sample point.

Stem densities of both subcanopy species and climbing vines (if taller than 1.5 m) were calculated from counts from within 5 m radius circular plots. The subcanopy stratum is comprised of shrub and understory tree species that are genetically adapted to exploit the understory. Shrubs are generally less than 2.5 m tall (e.g., Leucothoe racemosa, Vaccinium corymbosum); understory trees are generally less than 7.5 m tall (e.g., Ilex opaca, Carpinus caroliniana). Subcanopy species rarely reach the canopy, except under unusual circumstances. Therefore, the subcanopy species were treated as a life-form distinct from similarly sized saplings of canopy species because the two categories of species have evolved to exploit very different niches at maturity: the overstory and the subcanopy.

Although not presented here, the densities of three additional strata (saplings of canopy species and seedlings of both canopy and subcanopy species) were also calculated from the 5 m radius circular plots. Detailed compositional data by stands and stratum, sapling and seedling data, and environmental data can be obtained by consulting Appendix 5.

The herbaceous stratum of each of the 23 sites was sampled within a 10 day temporal window (12-21 July 1989) in order that any vegetational differences found between sites could be attributed primarily to environmental differences or to competitive interactions between species rather than to temporal differences. In each stand, 1 m^2 quadrats were placed at 10 m intervals along the canopy sampling transect and the percent coverage of each herb species within the quadrat was estimated as falling into one of seven coverage classifications (1-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-100%, 100%) derived from a method devised by Daubenmire (1968). An estimate of the area covered by hollows was also determined within each herbaceous species quadrat. Ten one square meter plots were sampled along each transect.

From each stand, at least 2 l of soil were collected from the upper root zone (top 15 cm) from several points along the sample transects and homogenized. Approximately 0.5 l of soil from each stand was sent to the Plant Analysis and Soil Testing Lab of the Virginia Polytechnic Institute and State University for soil pH determinations and mineral analyses. Soil mineral content in parts per million was determined using an inductively coupled plasma spectrometer (ICP) for phosphorus, potassium, calcium, soluble salts, and iron following procedures outlined in Donohue and Gettier (1988). Also, the distance by river from the mouth of the Pamunkey River to each site was calculated.

In 1990, two additional soil samples were collected from each site for organic matter determination: from hummock microsites and from hollows (interhummock areas) when present (40 samples total). Each sample consisted of cores 10 cm in diameter by 15 cm deep taken from four to five places from within each microsite type and then mixed in a 20 l bucket until homogenized. Approximately 0.75 l of soil was extracted from the homogenate to obtain organic matter content by combustion.

In 1989 and 1990, a 10 cm diameter polyvinyl chloride groundwater well, approximately 2 m in length (half of which was inserted vertically below ground), was established in each of six swamps. Water levels were measured relative to ground level every six minutes and recorded by a data logger. Indundation periods (percent time a swamp was flooded) were calculated from the data recorded by the data logger.

One well was established in a swamp directly across the river from a Virginia Institute of Marine Science (VIMS) tide gauge station at

Elsing Green (approx. midway between the most upriver and the most downriver sites). All wells were established within a hollow microsite when such sites were available in the swamps examined. In 1990, an additional well was established on a hummock adjacent to the well already in place within the hollow at the Elsing Green swamp site. In this swamp, water level fluctuations were concurrently monitored in both microsites to determine whether hydroperiods differ between microsite-types in the same stand.

Data Analysis

Importance values for canopy trees were calculated by averaging relative dominance (basal area) and relative density values. Only relative densities were determined for vines and species of the subcanopy stratum. Importance values for all herbaceous species in each stand were calculated by averaging the relative coverages (obtained from the midpoints of the coverage classifications) and relative frequencies following methods of Stephenson and Clovis (1983).

Herbaceous and woody species data were analysed with the indirect ordination algorithm Detrended Correspondence Analysis (Hill 1979, Hill and Gauch 1980), using the CANOCO software package developed by Ter Braak (1988). The measured environmental factors were tested for correlation with each other and with the first two ordination axes to assess relationships between environmental factors and relationships between the measured environmental factors and the vegetation patterns associated with the axes. All correlation coefficients were determined by the CANOCO program. Because 9 environmental variables were tested for correlation with the ordination axes, a restrictive significance level of 0.005 (approx. 0.05/9) was used to determine significance (see Chatfield 1989 for a discussion of the interpretation of correlagrams).

Contour enclosures of importance values of the most common and abundant species of each stratum were drawn on their associated ordinations. Environmental biplot scores (Ter Braak 1988) were obtained to depict the directions and relative strengths of underlying environmental gradients. Biplots of only the strongest variables (longest arrows) were plotted on the ordinations. Biplot scores are useful for representing strong environmental gradients that may not necessarily be significantly correlated with either of the ordination axes, although significance values cannot be attributed to these biplots. Each set of biplots (each ordination has its own set) was reduced by a constant value in order to fit it onto the ordination; hence the lengths of biplot arrows can be compared within an ordination diagram, but not between ordinations.

A paired-sample t-test (Minitab 1989, Ryan et al. 1976) comparing the organic matter content of hummocks with that of hollows failed to determine a significant difference in the proportion of organic matter present between the two microsite types and so microsite organic matter values were pooled for each stand.

RESULTS

Vegetation

Of the 20 canopy species encountered within sampled transects, five species accounted for over 95% of the total basal area (Table 1.1): *Fraxinus* spp. (ashes: primarily *F. pennsylvanica*, but may also include *F. profunda* and *F. caroliniana*), *Nyssa biflora* (swamp blackgum), *Acer rubrum* (red maple), *Taxodium distichum* (in 2 stands only), and *Liquidambar stryraciflua* (sweetgum). In contrast to the species poor canopy stratum, the understory is extremely rich. Twenty-one subcanopy species were found, ten of which occur in more than 50% of the stands sampled.

As is the case for the subcanopy stratum, the herb stratum is also extremely rich (69 species). Because a high seasonal turnover of herbaceous species appears to be characteristic of these swamps and because herbaceous sampling in this study was restricted to a 10 day period, it is likely that many more species occur in these tidal swamps on an annual basis than are herein recorded. Because forty-six county records were found in sampled plots visited over a two week period, it is likely that many more unmapped species (Harvill et al. 1986) are present as well.

An inspection of the canopy and herbaceous species compositions of the 23 sampled swamp stands, in concert with an examination of the ordination results, indicated the presence of two distinguishable tidal swamp community-types (Table 1.1) and two upriver, seasonally tidal

Table 1.1. Vegetative community structure of tidal freshwater swamps. Community-types are based upon canopy compositions. The Taxodium distichum (bald cypress) forest is possibly a relic ash-blackgum community, based on the close structural affinity of the canopy and herbaceous strata to the other ash-blackgum swamps. BA=basal area (dbh).

	Community-types		
	Ash-blackgum (n=12)	Ash-blackgum (Bald cypress subtype) (n=2)	Maple-sweetgum (n=6)
CANOPY			
Mean BA (m^2/ha)	35.6	31.1	31.7
Importance Value:			
Fraxinus spp.	41.5	19.7	13.2
Nyssa biflora	35.5	22.6	19.7
Acer rubrum	20.2	30.9	36.5
Liquidambar styraciflua	0.4	3.0	21.6
Taxodium distichum	0.1	21.2	-
Other species (n)	3.0 (8)	2.6 (2)	9.0 (11)
SUBCANOPY			
Mean Density (#/ha)	3,283	4,350	3,055
Relative Density:			
Lindera benzoin	22.3	21.2	3.6
Ilex verticillata	19.7	7.6	11.2
Carpinus caroliniana	11.0	6.8	9.0
Viburnum dentatum	7.3	2.5	8.2
Alnus serrulata	10.0	0.9	5.6
Ilex opaca	7.8	13.6	22.0
Magnolia virginiana	1.7	9.0	8.7
Other species (n)	20.2 (14)	38.4 (7)	31.7 (11)
VINES			
Mean Density (#/ha)	3,332	2,418	2,090
Relative Density:			
Smilax rotundifolia	47.6	42.9	76.2
Rhus radicans	18.7	10.3	6.5
Apios americana	11.5	7.9	0.3
Dioscorea villosa	7.1	19.3	7.6
Bignonia capreolata	5.4	11.5	6.2
Other species (n)	9.7 (7)	8.1 (2)	3.2 (5)

(Table 1.1 cont.)

Herbaceous composition of tidal swamps.

HERBS	Ash-blackgum (n=12)	Ash-blackgum (Bald cypress subtype) (n=2)	Maple-sweetgum (n=6)
Importance Value:			
Polygonum arifolium	20.9	14.9	2.5
Carex bromoides	8.9	13.2	8.0
Peltandra virginica	6.9	2.8	3.8
Saururus cernuus	5.9	7.3	10.9
Murdannia keisak	5.1	1.2	0.2
Uniola latifolium	3.1	-	-
Cinna arundinacea	3.1	3.2	1.3
Carex tribuloides	2.2	2.7	0.6
Carex intumescens	1.8	-	15.3
Boehmeria cylindrica	1.7	4.8	3.3
Solidago rugosa	1.6	1.2	2.9
Mitchella repens	1.4	4.1	5.1
Carex crinita	1.1	1.8	2.9
Other species (n)	36.3 (43)	43.6 (24)	43.2 (30)

swamps that differ compositionally from the true (diurnally flooded) tidal swamps and from each other. The two tidal swamp-types will be referred to hereafter as ash-blackgum or as maple-sweetgum swamps.

Ash-blackgum Swamps

One swamp type (Table 1.1) is dominated in the canopy by Fraxinus spp., Nyssa biflora, and Acer rubrum. The Pamunkey River swamps sampled by Doumlele et al. (1985) and Fowler (1986) are typical of these diurnally flooded ash-blackgum swamps. Taxodium distichum can also share canopy dominance in ash-blackgum swamps; yet only two cypress dominated swamps were located on the Pamunkey even after an extensive aerial reconnaisance. Numerous large (>75 cm dbh) bald cypress trees occur in the two swamps sampled.

Lindera benzoin (spicebush) and Ilex verticillata (common winterberry holly) are the most important subcanopy components of ash-blackgum swamps and were found in 11 of the 15 ash-blackgum swamps sampled (Table 1.1). Other less important, but locally abundant subcanopy species (IV>20) include Alnus serrulata (smooth alder), Ilex opaca (american holly), Viburnum dentatum (southern arrowwood), Leucothoe racemosa (fetter-bush), and Cornus foemina (swamp dogwood).

Climbing vines are usually extremely dense in ash-blackgum tidal swamps (greater than 3,100 stems per ha). Smilax rotundifolia (common greenbriar) and Rhus radicans (poison ivy) predominate, but Apios americana (american potato bean), Dioscorea villosa (wild yam), Bignonia capreolata (cross vine), and Smilax laurifolia (laurel greenbriar) are also locally abundant.

Ash-blackgum swamps are rich in herbaceous species: 56 herbaceous species were sampled in the plots of 14 sites (Table 1.1). The most important herbaceous species in ash-blackgum swamps are Polygonum arifolium, Peltandra virginica, Saururus cernuus, Carex bromoides, and Uniola latifolia. Other widespread and locally abundant herbs (IV>10) include Murdannia keisak, Cinna arundinaceae, Impatiens capensis, Cicuta maculata, Aster spp., Senecio aureus, Carex tribuloides, and Commelina virginica.

Maple-sweetgum Swamps

Maple-sweetgum swamps are dominated in the canopy by Acer rubrum, Nyssa biflora, Liquidambar styraciflua, and Fraxinus spp. (Table 1.1). Maple-sweetgum swamps differ in composition from ash-blackgum swamps primarily in that Liquidambar is an important canopy component of maple-sweetgum swamps, but is of low importance in ash-blackgum swamps. Also, although Acer rubrum is found in both swamp-types, it attains its highest importance in maple-sweetgum sites and was in fact the leading dominant in four of the five maple-sweetgum swamps sampled.

The subcanopy layer of maple-sweetgum swamps is dominated by Ilex opaca and Ilex verticillata. Other locally important subcanopy species (IV>20) include Magnolia virginiana (sweetbay magnolia), Alnus serrulata, Carpinus caroliniana (ironwood), Ilex decidua (deciduous holly), Asimina triloba (pawpaw), and Leucothoe racemosa.

Vines in maple-sweetgum swamps are dense (2,150 stems/ha) with Smilax rotundifolia overwhelmingly dominating (IV>55) the stratum. Other less important, but locally dense vines include Rhus radicans, Dioscorea villosa, Apios americana, and Bignonia capreolata.

The herbaceous stratum of maple-sweetgum tidal swamps harbors fewer herbaceous species than ash-blackgum swamps (42 vs. 56 species, Table 1.1). The most important species are Carex intumescens, C. bromoides and Saururus cernuus. Other locally important species (IV>15) include Leersia spp. (including L. oryzoides and L. lenticularis), Mitchella repens, Peltandra virginica, Rhus radicans, and Impatiens capensis.

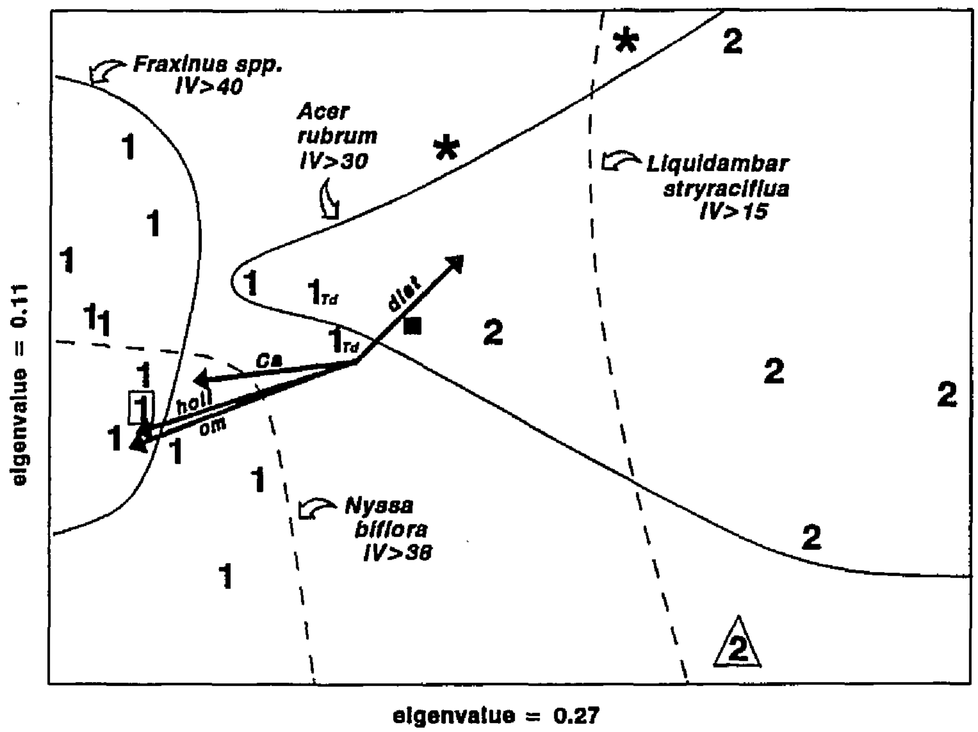
Ordinations

Separate ordinations of four life-forms (canopy, subcanopy, vines, and herbs) from 23 sampled stands are presented (Fig. 1.2a-d). Ash-blackgum (#1) and maple-sweetgum (#2) tidal swamps (Fig. 1.2a) were determined on the basis of the relative importance of Liquidambar styraciflua in them, i.e., maple-sweetgum swamps contain much more sweetgum. Note that the community-type (#1 or #2) to which a stand is affiliated is determined by its canopy composition for all four of the ordinations (Fig. 1.2a-d). Thus, a #1 in Fig. 1.2d (herbaceous ordination) means that the stand has an ash-blackgum canopy.

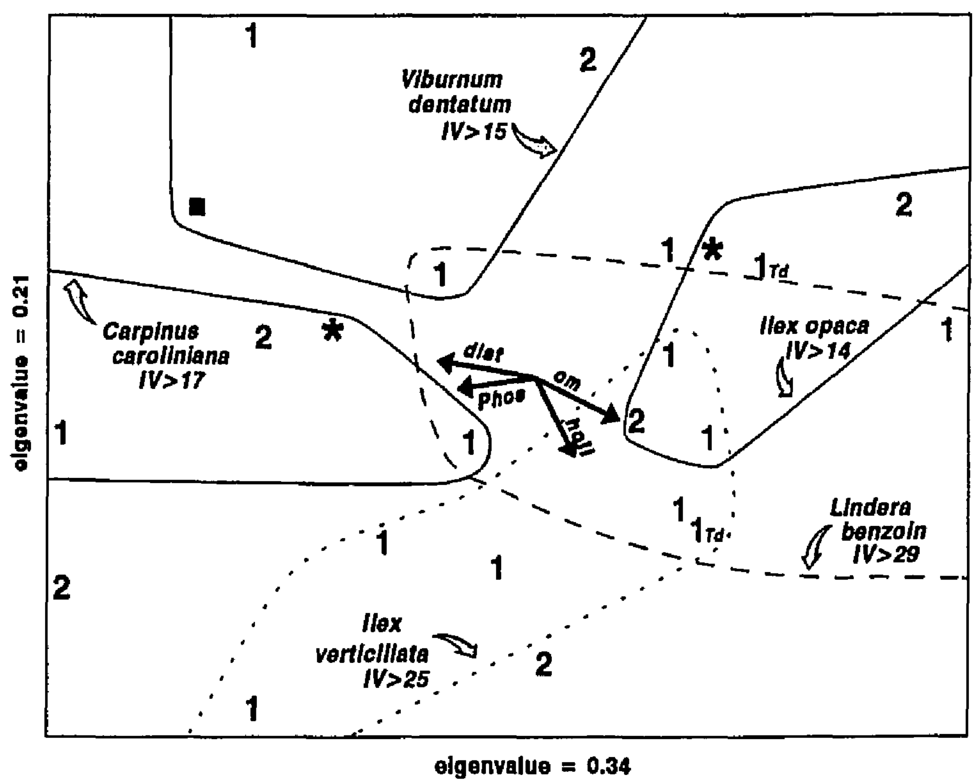
Two upriver stands were so different vegetatively from the other stands (and from each other) that they became partial disjuncts (sensu Gauch et al. 1977) on the initial ordination diagrams on all four ordinations. Both stands appeared to be little affected by tidal fluctuations (except seasonally). These two disjunct stands were thus given low (0.01) weights prior to the iteration procedure of DECORANA and were then reinserted into the ordination diagram at the end of the procedure (this capability is an option in the interactive DECORANA program of CANOCO). The two ash-blackgum stands (1_{Td}) in which Taxodium distichum is important (IV>17) occur near one another on the ordination. Other than being dominated by bald cypress, these two stands are structurally and physiognomically allied with the other ash-blackgum swamps (Table 1.1 and Fig. 1.2d). Also, the canopy composition of one stand (denoted by a square near the middle of the diagram) was

Figure 1.2. Ordination of four stratal life-forms of freshwater tidal swamps using DECORANA: a) canopy vegetation, b) subcanopy vegetation, c) vines, and d) herbaceous vegetation. The ash-blackgum stands are denoted by "1", the Bald cypress (ash-blackgum) subtype by "1_{Td}", maple-sweetgum stands by "2". The 2 seasonally flooded swamps are denoted by an (*), the intermediate stand by the solid square. Contours enclose stands if the importance values (IV) of the indicated species exceed the indicated values. For example, the solid contour line on the right of the canopy ordination (2a) encloses those stands in which the IV of Acer rubrum exceeds 30 (primarily maple-sweetgum swamps). A Nyssa biflora inlier (IV=29) in Fig. 1.2a is enclosed by the small box, an outlier (IV=43) is enclosed by a triangle. Exceptions (inliers) to the enclosures in Fig. 1.2d are enclosed by small boxes: Saururus cernuus (1 stand), Peltandra virginica (2 stands). Biplots are superimposed on the ordination and provide the relative strengths and directions of major measured gradients. Abbreviations for environmental variables are provided in Table 1.2. Significant correlations of environmental parameters with the ordination axes are as follows: canopy axis 1: % organic matter ($r=-0.64$, $P<0.005$) and % hollow ($r=-0.62$, $P<0.005$); subcanopy axes: no variables were significant; vine axis 1: % organic matter ($r=-0.64$, $P<0.005$) and % hollow ($r=-0.57$, $P<0.005$); herb axis 1: % hollow ($r=-0.85$, $P<0.001$).

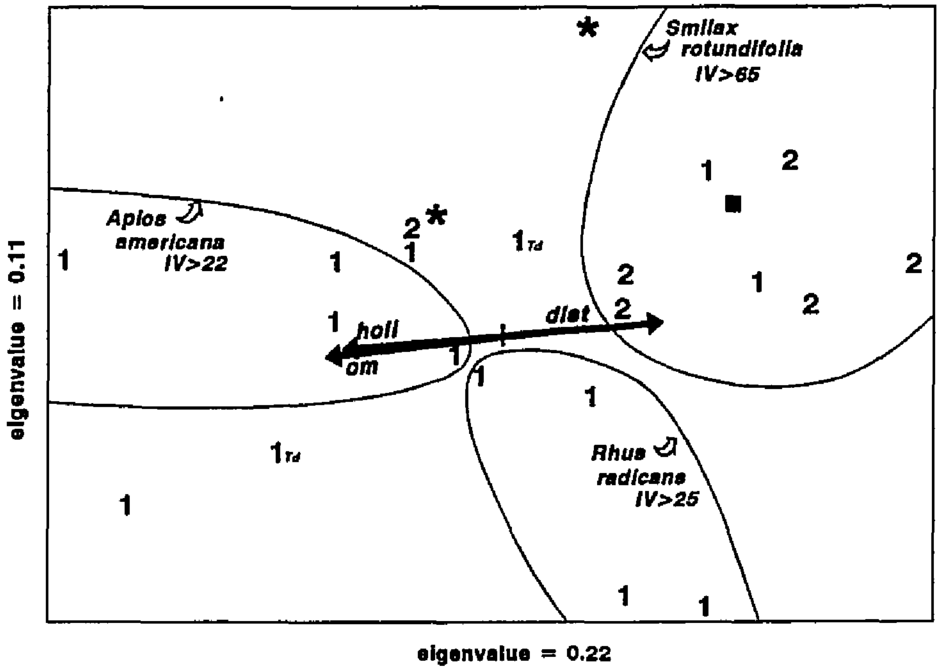
a) Canopy ordination of tidal swamps



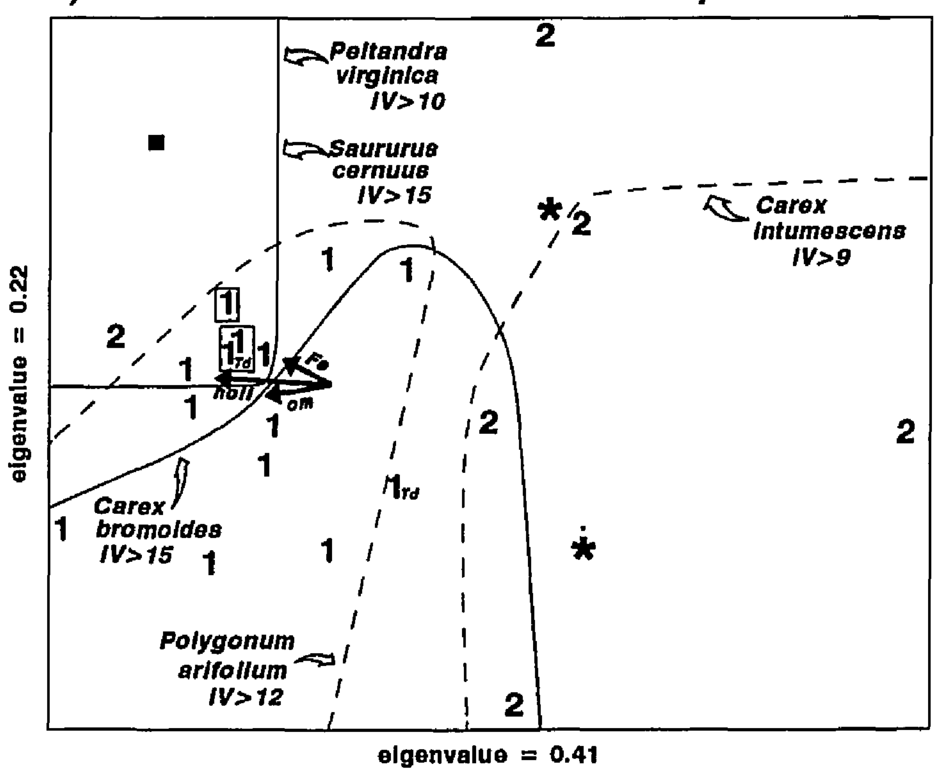
b) Subcanopy ordination of tidal swamps



c) Vine ordination of tidal swamps



d) Herbaceous ordination of tidal swamps



intermediate between that of the ash-blackgum and maple-sweetgum swamps. Thus, there were 14 ash-blackgum swamps (including 2 bald cypress co-dominated stands), 6 maple-sweetgum swamps, 2 upriver seasonal tidal swamps, and 1 intermediate swamp (23 sampled stands total).

A plot of species importance values on the canopy ordination (Fig. 1.2a) shows that Acer rubrum and Liquidambar styraciflua have their highest IVs in maple-sweetgum stands (IV>30 and IV>15, respectively) while Fraxinus spp. (IV>40) and Nyssa biflora (IV>38) are concentrated in ash-blackgum stands. According to the most important environmental biplots (those with the longest arrows) plotted on the ordination, a higher percentage of hollow microsites (holl) and higher organic matter levels (om) occur to the left of the ordination where the ash-blackgum stands are concentrated. These two variables were also found to significantly correlate with axis 1 of the ordination (holl: $r=-0.61$, $P<0.005$; om: $r=-0.62$, $P<0.005$), a further indication of the possible importance of these two parameters in segregating vegetation. Calcium levels also appear to be higher in the ash-blackgum stands, according to the biplot arrow. Axis 2 did not significantly correlate with any variables, although the distance upriver biplot arrow suggests that Nyssa is more important at the more downriver sites.

The ordination of the subcanopy stratum is presented in Fig. 1.2b. None of the environmental parameters show a significant correlation with either of the ordination axes. The biplot arrows, however, suggest that Lindera benzoin and Ilex opaca separate from Carpinus caroliniana along an upriver-downriver and phosphorus gradient with Carpinus being more prevalent upriver (possibly under a more shaded subcanopy) and in sites with higher phosphorus concentrations (Fig. 1.2b). Likewise, Viburnum dentatum and Ilex verticillata appear to separate along a wetness gradient (inferred from the biplot gradient of the % hollow and organic matter parameters) with *Ilex verticillata* being more prevalent in the wetter sites.

Note that the maple-sweetgum stands are intermingled with the ash-blackgum stands on the subcanopy ordination (Fig. 1.2b), i.e., there is no separation into the same ash-blackgum and maple-sweetgum community-types as separated by the canopy ordination (Fig. 1.2a). However, with the exception of *Lindera benzoin* and *Alnus serrulata*, most of the more prevalent subcanopy species appear to segregate rather distinctly with respect to where they are most important. *Lindera* shares dominance with each of the other major subcanopy species in at least one site, while *Alnus serrulata* does not separate into a distinct distributional pattern on the ordination (no contour enclosures could be drawn for *Alnus*).

All the major subcanopy species depicted on the ordination are broadly mixed in their presence (not dominance) across stands. In the 23 sampled stands, *Ilex verticillata* occurs in 20 stands, *Ilex opaca* in 18, *Lindera benzoin* in 15, and *Carpinus caroliniana*, *Viburnum dentatum*, and *Alnus serrulata* in 14 stands each. The remaining 17 subcanopy species are also widespread across stands, but are of lower importance and frequency.

As is the case for the subcanopy stratum, the vine stratum (Fig. 1.2c) also failed to separate into the same community-types established by the canopy (Fig. 1.2a). However, as was the case for the canopy ordination, axis 1 of the vine ordination was found to be significantly correlated with the percent organic matter ($r=-0.64$, $P<0.005$) and the percent hollow coverage ($r=-0.058$, $P<0.005$), with none of the measured environmental factors significantly correlating with axis 2. Although distance upriver (dist) was not significantly correlated with axis 1, its biplot arrow suggests that it is negatively associated with both organic matter content and percent hollow. These results suggest that Smilax rotundifolia occurs more upriver, in stands with less organic matter, and with less hollow coverage while Apios americana occurs at the other end of these gradients. Also, Rhus radicans appears to be more important in stands where Smilax rotundifolia and Apios americana are less important.

Unlike the subcanopy and the vine ordinations, however, the herbaceous ordination (Fig. 1.2d) did separate stands in a manner similar to that of the canopy ordination, i.e., ash-blackgum swamps (toward the left) separated from maple-sweetgum swamps (toward the right). The one exception was an herbaceous site that possesses an ash-blackgum herb layer (#2, located on the left of the ordination), but a maple-sweetgum canopy. The longest environmental biplot arrows are for the percent hollow and organic matter content. In addition, the percent hollow parameter significantly correlated with axis 1 ($r=-0.83$, $P<0.001$). Both parameters (holl and om) appear to separate ash-blackgum swamps from the less wet maple-sweetgum swamps.

Carex intumescens is most important (IV>9) in maple-sweetgum stands to the right while C. bromoides is more important (IV>15) in ash-blackgum swamps in the lower left of the ordination. Peltandra virginica (IV>10) and Saururus cernuus (IV>15) are most important in stands located in the upper left of the ordination. Peltandra has two lower values and Saururus one within the contour enclosure in Fig. 1.2d (delineated by boxes). Both Peltandra and Saururus were more often found in hollow microsites (found to occur 7.1 and 8.4 times more often in hollows than on hummocks, respectively) and so it is not surprising that both species are more important in ash-blackgum swamps where hollows are more prevalent. Polygonum arifolium (IV>12) is also an important species of primarily ash-blackgum sites where it too was found most often in hollow microsites (it was found to occur in hollows 7.6 times more often than on hummocks). The distribution of P. arifolium across stands (dashed line) overlaps that of Carex bromoides, Peltandra, and Saururus.

A comparison of means between environmental parameters of the two swamp types was calculated using a Welch's approximate t-statistic (Table 1.2). The results show that ash-blackgum swamps contain significantly more hollow area (hence they are wetter, P=0.02) than maple-sweetgum swamps, significantly higher calcium concentrations (P=0.004), and higher organic matter levels (P=0.02). These results are consistent with the correlation and biplot results for the canopy and herbaceous ordinations, on which the distinction between community-types was primarily based.

Hydrographic Regime

The Pamunkey River is narrow (20-30 m across) at the most upriver reach of tidal excursion. Small natural levees, some only 40 cm above mean high water, line the river banks in this tidal upriver section. Poorly drained depressions are scattered throughout the less elevated areas behind the levees. Although the tidal range of the river is approximately 1 m in this upriver section, surface flooding of the swamps behind the levees was never observed even during periods of high tides. Throughout most of the lower tidal reaches of the Pamunkey River, however, the tidal affect is so pronounced that tidal fluctuations occur daily within the upper root zone. A labyrinth of meandering and branching tidal creeks alternately flow backward into the

Table 1.2. Environmental differences between two tidal swamp communities. The probability that the means are different was determined using the Welch's approximate t-test. Significant differences (P<0.05) are underlined. Percent hollow was derived from cover estimates obtained coincident with the herbaceous strata survey. Abbreviations: holl (hollow), Phos (phosphorus), K (potassium), Ca (calcium), ss (soluble salts), Iron (Fe), Om (organic matter), dist (distance upriver from most downriver swamp stand in km), and SD (standard deviation).

Swamp type		%holl	pH	Phos	K	Ca	Mg	ss	Fe	Al	Cu	%Om	dist (km)
						Edaphic factors (ppm)							
Ash-blackgum	$\bar{X}$	65.5	4.8	10.8	67.5	806	118	508	57.3	38.5	0.66	40.5	22.6
(n=14)	SD	15.6	0.4	14.2	28.9	203	9	300	26.2	6.2	0.29	9.7	13.4
Maple-sweetgum	$\bar{X}$	25.0	4.9	8.0	66.5	578	119	239	47.9	42.1	0.64	25.2	27.8
(n=6)	SD	30.0	0.4	2.2	18.5	103	2	160	10.5	16.0	0.60	7.1	11.2
Probability		<u>0.02</u>	0.45	0.47	0.93	<u>0.004</u>	0.6	0.17	0.26	0.62	0.96	<u>0.02</u>	0.38

swamps during semi-diurnal flood tides and then drain during the following ebb tide.

The interiors of the low-lying diurnally flooded tidal swamps are composed of a patchwork of hummocks and hollows (low depressions between hummocks). The hummocks are elevated, relatively steep sided, flat-topped mounds generally 1-10 m^2 in area, the tops of which lie 14-16 cm above the adjacent low-lying hollows. The tops of all the hummock patches appear to be at about the same elevation and are composed of a shallow, dense, interwoven network of large roots and minute rootlets. Although levees appear to be absent along the tidal creeks throughout the interior of the swamps, the land immediately adjacent to the main stem of the river appears to be slightly higher in elevation than the interior areas.

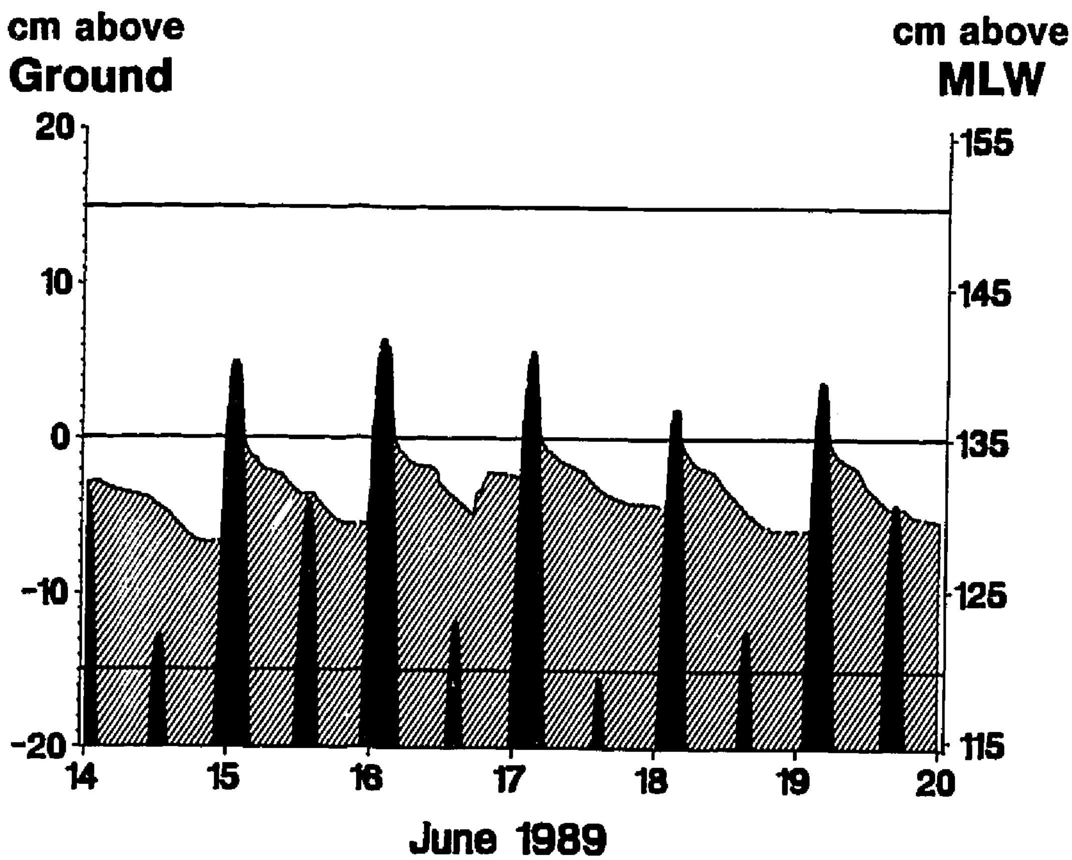
Figure 1.3 presents a hydroperiod regime typical of an ash-blackgum swamp in relation to river level changes over several days. River level fluctuations were measured by a VIMS tide gauge located across the river from the swamp (Fig. 1.1). Note how the hydroperiod of this swamp is tightly coupled to a mixed semi-diurnal tidal forcing. After flooding, the water level in the swamp falls with the tide until ground level is reached; the drawdown then slows until recharged by the following high tide. If the lower high tide is sufficiently high, the drawdown can be halted or reversed. During spring tide conditions, the hollows often become flooded twice daily and most of the upper root zone (top 15 cm) may remain flooded for several days. During neap periods, especially during apogeal conditions, neither high tide may breach ground level and the hollows sometimes remain unflooded for several days.

Throughout the course of the growing season, the upper 15 cm of the hummocks is flooded from 5-20% of the time while the upper 15 cm of the

Figure 1.3. Tidal swamp groundwater fluctuations for 14-20 June 1989. This site is located across the river from a VIMS tide gauge station at Elsing Green on the Pamunkey River. Lag time between water level changes in the swamp and the river (0.7 hr) has been subtracted. Solid fill represents the tidal pulse in the river (top of the tide curve). Hatched fill represents groundwater heights in the swamp. The "0" is ground level (at the surface of the hollow). MLW = mean low water. The two horizontal lines bracket the location of the hummocks (0 to +15 cm) in relation to the surface of the hollows. Note that tidal swamps occupy a very narrow region in the upper part of the tidal range. Data points were collected every 6 minutes. Graphics prepared using Statistical Analysis System Institute (1985) software .

Tidal Swamp Groundwater Fluctuations

Elsing Swamp, Pamunkey River



hollows is flooded 20-100% of the time. This is true even though the amplitude of the groundwater fluctuations, presumably in response to the adjacent tidal amplitude of the river, varies between sites. Measured amplitudes in groundwater fluctuations varied 22, 32, and 58 cm in the three ash-blackgum stands from which groundwater fluctuations were measured and 10 and 86 cm in the two maple-sweetgum stands measured (Appendix 2, Table A7).

Although hummock coverage is a useful indicator of the amount of high ground in a swamp, the hummocks themselves do not appear to affect groundwater dynamics. In the ash-blackgum stand across the river from the Elsing Green tide station, where water level fluctuations were simultaneously measured in the two adjacent microsites (hummocks and hollows), the fluctuations in the two microsites precisely coincided both temporally and physically, i.e., the hummock groundwater fluctuations occurred at a depth that equaled the difference in relative height between that of the hummock and that of the hollows (Appendix 2, Table A8). Thus, hummocks appear to be drier microsites than hollows because their surfaces occur 15-20 cm above the hollows.

During the course of three growing seasons (July 1988 through October 1990) the tops of the hummocks were never observed to be inundated nor did they ever show evidence (flotsam, water marks, etc.) of having been recently covered with water. Groundwell data indicated that only one of the downriver sites (Cohoke) experienced flooding above the hummocks, but for less than 0.06% of the time (Appendix 2, Table A7). In contrast, the hollows were almost always flooded during high tides, particularly during the higher of the two mixed semi-diurnal tides.

DISCUSSION

Pamunkey River tidal swamps appear to be of two types: ash-blackgum and maple-sweetgum swamps. The environmental differences between these two community-types appears to be related to their flooding regimes. Swamps with a higher coverage of hollows were found to be flooded for longer periods in the upper root zone and were found to support more ash and blackgum. The soils of such sites are probably anoxic for longer periods, which would tend to inhibit the decomposition of plant biomass and contribute to the accummulation of organic matter (peat). Thus, peat content and the amount of hollow coverage appear to be good indicators of the relative wetness of a tidal swamp. In fact, peat content may be a useful indicator of the degree of flooding in other swamp ecosystems as well.

The fact that one or both of these parameters (hollow and organic matter) were usually found to significantly correlate with axis 1 of the canopy, vine, and herbaceous ordinations and were gradients along which the species of these life-forms appeared to segregate indicates that wetness and flooding regime are probably the most important factors affecting canopy, vine, and herbaceous species distribution patterns in tidal swamps. The fact that the subcanopy failed to show any pattern of distribution with any of the measured environmental parameters (even hollow or organic matter content) or show any association with the species distribution patterns of the other strata suggests that the subcanopy may be partitioning different resources than the other strata.

The hollow coverage measurement obtained in this study may be a good indice of both the relative wetness of a site and the openess of its canopy. Although hydrographic measurements support the positive relationship between wetness and hollow coverage, measurements of canopy closure were not made and so there is no quantitative support for the latter relationship. However, the canopies of sites with higher ratios of hummock to hollow coverage appear to be more open. This phenomenon appears to be related to two factors; 1) trees, which are restricted to hummocks, are further apart on average because less space is available to support them and 2) in the wetter environments, trees also appear to be more stressed and their canopies less fully developed.

Unlike the diurnally flooded tidal swamps of the mid- to upriver reaches, flooding of the most upriver swamps appears to be episodic, perhaps vernal; flotsam is common at the bases of trees, and bare ground is prevalent (presumably resulting from scouring during floods). Standing water remaining in the depressions may be derived from rain water runoff or from intermittant floods that may occasionally breach the low levees. Groundwater fluctuations are tidally influenced, but occur 25-60 cm below ground. Because inundation of the upper root zone in these swamps is not intimately coupled to tidal forcing, except perhaps when the river is flooding from upriver inflow, such swamps should be more aptly characterized as seasonally flooded tidal swamps, due to the sporadic nature of tidal influence on them, rather than as true tidal swamps which flood on a daily basis. Only two of the seasonally flooded tidal swamps were sampled, primarily because additional, mature stands could not be found. Both stands were rich in canopy species, but contained a relatively depauperate understory.

Of the two true tidal swamp communities (ash-blackgum and maple-sweetgum swamps), neither is rich in canopy species (only five species account for over 95% of the total basal area) and, except for bald cypress, all are restricted to the hummocks in tidal swamps. Such low canopy diversity probably occurs because few trees can withstand the intensity of flooding that occurs in tidal wetlands. In light of such intense flooding, it is suprising that bald cypress was found in only three tidal swamps (in the canopy of two and in the sapling layer of one).

The Chickahominy River (a tidal tributary of the James River subestuary just south of the Pamunkey) and tidal swamps in northeastern Florida (Wharton et al. 1982) harbor extensive tracts of bald cypress, although published quantitative data are lacking for both areas. This suggests that either the environment of tidal swamps along the Pamunkey River somehow differs from those of other areas or bald cypress was eliminated from most swamps along the Pamukey River. Support for the later hypothesis is based primarily upon the fact that the canopies of the 12 ash-blackgum swamps which lack bald cypress are otherwise structurally similar to the two ash-blackgum swamps with bald cypress (Fig. 1.2a and Table 1.1) and that the herbaceous stratum of the 12 ash-blackgum swamps is structurally indistinguishable from that of the two bald cypress swamps (Fig. 1.2d and Table 1.1). Perhaps the two bald cypress swamps found in this study represent a relic condition for the other swamps where now only ash and blackgum share dominance. There was a conspicuous absence, however, of cypress stumps in the sites visited in this study.

Although the canopies of tidal swamp communities contain few species, tidal swamps are floristically rich in subcanopy (n=25) and herbaceous (n=69) species. This pattern is in contrast to that of nearby bottomland hardwood forests where the canopy is more closed (pers. obs.) and richer in species (Parsons and Ware 1982), but much less rich in herbaceous and subcanopy species. In fact, the subcanopy of tidal swamps appears to be the most speciose among temperate swamp ecosystems thus far described in the literature, and may rank among the richest in temperate North America, rivaling the mesic forests of southern east Texas described by Harcombe and Marks (1977) and other mesic southeastern U.S. coastal plain forests (Marks and Harcombe 1975). In herbaceous species richness, these tidal swamps rival those of the southern Appalachian cove forests and the mixed-mesophytic forests of the Cumberland Plateau, both considered to be the most floristically rich forests of the temperate zone (Braun 1950, Whittaker 1956, Rheinhardt 1981).

Perhaps the relative degree of openess of the canopies of tidal swamps provides a wider range of light conditions than would occur under a more closed canopy. The interplay of light and flooding may provide many heterogeneous habitat conditions over small spatial scales. Such heterogeneity may control understory structure and contribute to species richness by providing a variety of niches within a small area. Thus, Pamunkey River tidal swamps may be rich in understory species because the understory is shared by obligate and facultative wetland species, shade tolerant bottomland hardwood swamp species, shade intolerant tidal marsh species, and shade generalists, all within close proximity to one another and with their distributions regulated by variances in tidal flooding height of only a few centimeters. In fact, tidal swamps occupy such a narrow zone (15-20 cm, the height of the hummocks) in the upper portion of the tidal range (0.8-1.2m, based upon tide range data from stations 2505, 2507, 2509, 2511, National Ocean Service 1989), that any abrupt changes in the average water level or an increased rate in sea level rise might likely affect the distribution and character of this ecosystem.

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Chapter 2

THE RELATIONSHIP OF BELOWGROUND HYDROLOGY TO CANOPY COMPOSITION IN TIDAL FRESHWATER SWAMPS

ABSTRACT

Long-term groundwater fluctuations were examined to determine how hydroperiod regime relates to canopy composition in tidal freshwater swamps. Groundwater heights were monitored every six minutes in five representative freshwater tidal swamps, chosen from among 21 tidal swamps sampled. For one of the five monitored swamps, tide gauge data were compared with groundwater fluctuations in order to assess the role of tides in driving the hydrologic regime. The hydroperiods of the five swamps were also examined with respect to their canopy compositions to determine how differences in hydroperiod relate to structural differences in the canopy.

Flooding in tidal swamps is closely associated with high tides, but drainage between successive high tides is so slow that tidal swamps rarely become completely dry; thus, tidal swamps are restricted to the extreme wet end of the flooding gradient. Although the duration of above-ground flooding showed no relationship with canopy structure, the composition of the canopy was found to be related to root zone flooding as determined by the mean water table depth (MWT), the depth at which the soil is flooded 50% of the time. _Fraxinus_ spp. and _Nyssa biflora_ dominated swamps occur in the wetter sites (MWT = -17 cm), whereas _Acer rubrum_ and _Liquidambar styraciflua_ dominated swamps occur in the less wet sites (MWT = -22 to -28 cm).

Trees are restricted to topographic highs (hummocks) which are probably formed and maintained by the accumulation of logs and roots. Hummocks drain as quickly as the tide drops and so are partially inundated for only short periods each day, thus providing canopy trees substrate critical to their survival. It is hypothesized that with an increased rate in sea level rise as has been predicted for Chesapeake Bay (in response to natural and anthropogenic effects), biomass may not accumulate at a pace sufficient to maintain tidal swamps at their present locations, particularly if biomass is periodically removed by timbering.

INTRODUCTION

Common to all vegetated wetlands is the overriding influence of hydrology in creating the reduced conditions characteristic of wetland soils (Hook and Crawford 1980, Mitch and Gosselink 1986). Because flooded soils become quickly depleted of oxygen, most minerals and nutrients either become unavailable for uptake by plants or accumulate to toxic levels in the soil (Whitlow and Harris 1979). Thus, nutrient cycling dynamics of freshwater wetlands are usually attributed to flooding regimes (Brinson 1977, Patrick and Khalid 1974, Wharton and Brinson 1979, Wharton et al. 1982). Because plants respond differentially to the level of nutrients available to them and to the degree of anaerobiosis present in the soil, flooding has also been recognized as being the primary factor controlling freshwater wetland plant distribution patterns (Conner et al. 1981, Mitch and Gosselink 1986, Parsons and Ware 1982, Wharton et al. 1982) and ecosystem dynamics (Brinson et al. 1981, Day et al. 1988). However, little information is available in the peer reviewed literature concerning the short and long-term dynamics of groundwater fluctuations in the root zone of freshwater wetlands and how community structure is related to such fluctuations (Carter 1986).

The conditions present at the time of germination and early growth of a plant may be as critical to its success as the average hydrologic conditions encountered throughout its life-time (Gill 1970, Whitlow and Harris 1979, Tiner 1991). For example, bald cypress (<u>Taxodium</u>

distichum) is much more prone to death from prolonged flooding as a seedling than as an adult (Demaree 1932, Dubarry 1963). Thus, in order for bald cypress to establish itself in swamps, periodic unflooded conditions are essential.

The herbaceous plant communities of some freshwater marshes have been observed to change abruptly in composition in response to the effects of extreme hydrologic events on recruitment. For example, relatively abrupt changes in plant composition have been observed in the marshes of Okefenokee Swamp in response to drought and periodic fires (Gerritsen and Greening 1989, Greening and Gerritsen 1987, Duever 1982). Likewise, a rapid recovery after drought has been observed for prairie marshes (van der Valk and Davis 1978). Fairly rapid changes in community structure are common for marshes because many appear to harbor large seed banks composed of species of varying tolerances to drought and flooding (Kadlec, 1962, van der Valk and Davis 1978, Parker and Leck 1985). Also, most herbaceous marsh species possess a relatively long period (4-5 yr) of seed viability (Keddy and Reznicek 1982) and are capable of germinating and rapidly reaching their reproductive state, usually within one growing season, when conditions are suitable.

Although marshes may sometimes change radically in structure within short time scales in response to hydrographically mediated disturbances (particularly if annuals comprise an important component of the plant community), the composition of wetland forests (swamps) is unlikely to change so quickly in response to such changes. This is because trees may be better able to weather short-term hydrologic changes than herbaceous plants. Also, in response to major disturbances, trees generally take longer than herbs to reach maturity and so recovery to forest takes longer. In addition, canopy communities generally undergo long periods of succession after major disruptions. Lastly, tree seeds may not remain viable for long under flooded conditions and the seed bank composition may be depauperate in comparison to the composition of the canopy (Schneider and Sharitz 1986), making rapid recovery from unusual conditions less likely. Thus, the canopy structure of mature swamps probably reflects an integration of hydrologic conditions experienced by the community over time, encompassing both average conditions and rare, short-term hydrologic events (i.e., droughts or extremes in flooding duration). In order to separate the relative contribution of rare events affecting recruitment and survival of trees from the more normal hydrologic conditions in swamps, long-term hydrologic data would have to be compared with concurrently collected recruitment data; this has not yet been done.

In a study of bottomland hardwood swamps in the Virginia coastal plain, Parsons and Ware (1982) concluded that although they could find no relationship between soil moisture and the depth, frequency, or duration of flooding (obtained from bimonthly visits over one year), soil moisture and soil chemistry appeared to be related to forest structural patterns. Perhaps longer-term or more frequent measurements of below-ground fluctuations might have provided additional insight into the relationship of hydroperiod to species distribution patterns. Also, groundwater fluctuations below 16 cm were not measured and so the hydrodynamics in the root zone below 16 cm are unknown. In fact, except for two studies, quantitative data on root zone flooding in relation to structural patterns in forested wetlands are almost completely lacking in the literature.

In one of those two studies, Brinson et al. (1985) examined the relationships between primary production, nutrient cycling, and vegetation structure of four nontidal swamps whose flooding regime is driven by winds (located off Pamlico Sound, a lagoonal estuary in North Carolina). Because of the confounding affect of high salinity (>13 ppt) on plant survival, they were unable to totally separate the influences of hydroperiod and salinity on community dynamics. In the other study, Day et al. (1988) examined the influence of root zone hydrodynamics in relation to both above-ground and below-ground processes (production and decomposition rates) and species compositions of four stands located in the Great Dismal Swamp, a large depression swamp located on the coastal plain of southeastern Virginia and northeastern North Carolina. In comparing the above-ground and below-ground hydrodynamics of the four swamp sites, they determined that the duration of soil saturation below ground could not always be predicted by the duration of above-ground flooding and that some process rates appeared to be influenced more by subsurface hydrodynamics, where most of the large fluctuations in groundwater hydrodynamics were found to occur. Their results led them to caution that "erroneous interpretations of hydrologic relationships may result from observations of surface flooding dynamics alone". Thus, based upon the evidence from these studies, it seems that any study of community distribution patterns or ecosystem processes in swamps should incorporate information on below-ground hydrodynamics.

Most swamp systems experience wide ranges in hydrologic conditions within the course of several growing seasons. Thus, droughts and severe floods are an important part of the ecology of most swamps and may strongly influences recruitment patterns. Ideally, the effects of hydroperiod on canopy composition patterns could be examined in systems where extremes in hydrologic fluctuations are minimal or relatively unimportant. Freshwater tidal swamps might be the closest natural ecosystem to approach this condition. This is because flooding in tidal swamps may be so closely linked to tidal fluctuations that they are relatively little affected by severe floods and droughts. This is not to suggest that meteorological events are unlikely to influence the hydrographic regime of tidal swamps, but such effects may be relatively unimportant in comparison to those produced by the tides, particularly in areas where the tidal range is wide (>0.5 m).

Because the tidal influence overwhelms groundwater fluctuations caused by meteorological events, the overall variability of the hydroperiod of tidal swamps might be relatively small and an accurate hydroperiod signature might be obtained within a short time (within a few months or a few years). Also, the confounding factor of periodic drawdowns (dry conditions) probably rarely or never occur in tidal swamps and so drought stress can be eliminated as a factor that might confound canopy structural patterns. Thus, should tidal swamps be found to differ from one another with respect to their hydrographic regimes, and if canopy species distributions are found to differ, then an analysis of hydroperiod in relation to canopy compositions could provide insight into the importance of hydroperiod to the distribution of the canopy communities of tidal swamps.

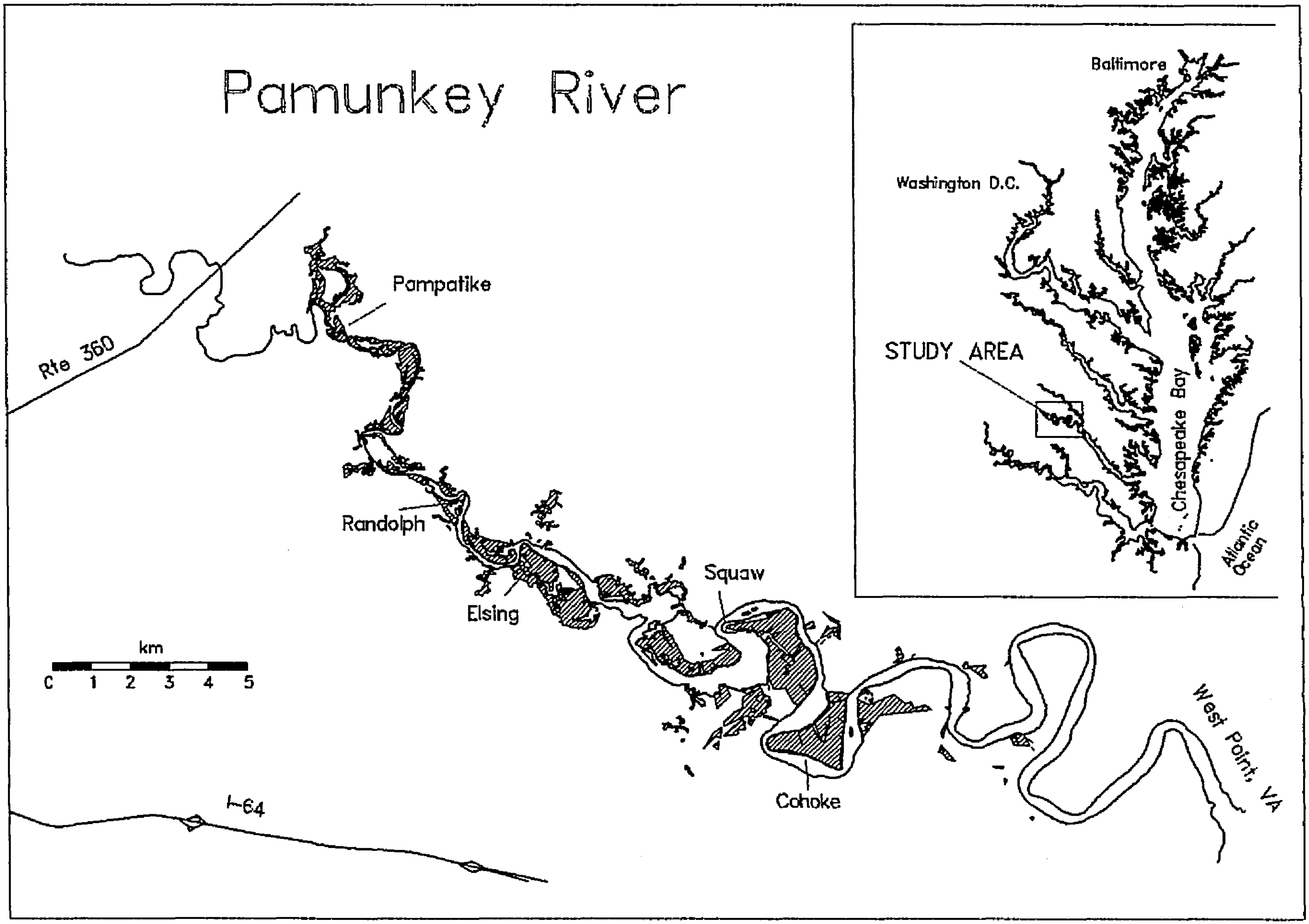
In order to determine how canopy communities are related to below-ground hydroperiods, this study was designed to 1) quantitatively determine the pattern of groundwater hydrology and the role and importance of tides in driving the hydrologic regime, 2) determine how compositional differences in the canopy stratum between sites are related to differences in the hydroperiod, and 3) develop an hypothesis addressing the development and maintenance of tidal swamps in relation to relative sea level changes and proposed anthropogenic alteration of the river's salinity distribution.

Study Area

The study was conducted along the Pamunkey River (Fig. 2.1), a meandering, low gradient coastal plain river which flows into the York River, a subestuary of Chesapeake Bay. Although the lower 65 km of the Pamunkey River is tidal, only the upper 40 km of the tidal section is fresh enough (<0.05 ppt) to support swamps. Tidal ranges vary (0.5 to 1.5 m) along the length of the river due to variations in the river's morphology. The soils of tidal swamps consist of a thick layer of peat and alluvium (Mixon et al. 1989) comprised of euic Ferric Medisaprists of the Mattan series (Hodges et al. 1988). Organic matter content of the upper 15 cm of soil varies between 9.0 and 63.8 % (Appendix 2, Table A2). Normal average air temperatures near the study area range from 2.4 C in January to 25.2 C in July (NOAA 1990). The frost-free season generally occurs from early April to early November. Normal annual precipitation is 113 cm, evenly distributed throughout the year. Precipitation for the two years of the study was 140.7 cm for 1989 and 114.6 cm for 1990 at Walkerton, Virginia (near the middle of the study area).

The substrate of freshwater tidal swamps is composed of an interdigitating network of topographically high and low areas (hummocks and hollows, respectively). Although the difference in topographic positions between hummocks and hollows is usually only about 15-20 cm, this seemingly small difference is biologically significant: trees are only found on the hummocks.

Figure 2.1. Location of study area and the five groundwell sites. Green hatched areas are the locations of tidal freshwater swamps. The map was drawn using ARC-INFO (ESRI 1989).


Pamunkey River
Rte 360
Pampatike
Randolph
Elsing
Squaw
Cohoke
West Point, VA
I-64
km
C 1 2 3 4 5
Baltimore
Washington D.C.
STUDY AREA
Chesapeake Bay
Atlantic Ocean

METHODS

Vegetation Sampling

At the point where each groundwater well was installed, canopy trees were sampled using the combined rangefinder-Bitterlich plotless method (Lindsey et al. 1958, Levy and Walker 1971). Importance values for canopy trees were obtained by averaging basal area (m^2/ha cross sectional area at 1.5 m above ground) and densities (trees/ha) of all trees greater than 10 cm dbh (diameter at 1.5 m above ground) within a 10 m radius circlular plot centered at each Bitterlich point. Taxonomic nomenclature follows Harvill et al. (1986) and Radford et al (1968).

Groundwater well Construction

Three groundwater wells were constructed of 10 cm diameter polyvinyl chloride pipe approximately 2 m in length, half of which was inserted vertically below ground. The below-ground section of each pipe was slotted to allow groundwater infiltration and wrapped in a #10 nitex plankton net to prevent the filling of the well by fine sediment. A customized differential float and pulley ten-turn 5k ohm potentiometer-type tide gauge, described by Fausak (1970), was mounted atop each well and covered with a battery case to prevent filling of the well by rainwater. The potentiometer was connected to a Campbell Scientific CR-10 digital data logger programmed to read the resistance of the potentiometer, convert the measured resistance to the height (in cm) of the float relative to ground level, and record the results.

All wells were established within a hollow microsite, except in one swamp (Randolph) which lacked hollows. The height of the nearest hummock to the hollow in which the well was placed was measured using a hand level. All canopy species grew upon the hummocks. This suggests that none of the canopy species encountered in this study can withstand the intensity of flooding, and the environmental conditions associated with such flooding, that occurs in the hollows.

Measurements were taken and recorded every six minutes from Spring through Autumn of 1989 and 1990 in synchrony with a Virginia Institute of Marine Science (VIMS) tide gauge station located at Elsing Green on the Pamunkey River. One well was established in the swamp (Elsing swamp) directly across the river from the VIMS tide gauge at Elsing Green (approx. midway between the most upriver and most downriver tidal swamp).

Groundwater wells were also established in two additional swamps during the second year of data collection, enabling the collection of data from a total of 5 tidal swamps over the two year study period. In 1990, an additional well was established on a hummock adjacent to the well already established at the Elsing swamp site. Water level fluctuations within the hummock and the adjacent hollow at this site were concurrently monitored by the same data logger to determine whether hydroperiods differ between adjacent microsite-types.

Data Analysis

Flooding data were adjusted to flooding height relative to the closest hummock surface because hummock heights differ somewhat between sites and the parameter of interest was flooding with respect to the microsite on which canopy species grow. Such an adjustment appeared justified because an assessment of the hydrologic data collected concurrently for the hollow and adjacent hummock at Elsing swamp showed that the two microsites possess identical groundwater dynamics. The only difference is that because the hummock surface is about 15 cm above that of the hollow, groundwater fluctuations relative to the surface of the hummock occur lower (by the magnitude of the hummock height) than groundwater fluctuations relative to the surface of the hollow. Inundation periods (percent of time flooded) were determined throughout the zone of groundwater fluctuations using a PASCAL program.

RESULTS

Vegetation

The composition of the canopy vegetation at the five groundwell sites is presented in Table 2.1. Cohoke, Elsing, and Pampatike swamps are dominated by ash (*Fraxinus spp*.: primarily *F. pennsylvanica*, but may also include *F. profunda* and *F. caroliniana*), swamp blackgum (*Nyssa biflora*), and red maple (*Acer rubrum*) in the canopy while Squaw and Randolph swamps are dominated by red maple and sweetgum (*Liquidambar styraciflua*) along with either ash or swamp blackgum. The primary difference between the two groups is that sweetgum codominates in the two maple-sweetgum swamps, whereas it is absent in the three ash-blackgum swamps. Also, ash is of much less relative importance in the maple-sweetgum swamps than in the ash-blackgum swamps. These five stands appear to represent the general range of canopy compositions measured in 16 other stands sampled as part of a detailed phytosociological study of the tidal swamps located along 40 km of the Pamunkey River (Appendix 4, Table A12.

Hydrographic Regime

Tidal swamps along the Pamunkey River are subjected to a mixed semidiurnal tidal regime; that is, there are two tidal cycles each day with successive tides being of different amplitudes (Fig. 2.2). Usually, the higher of the two tides floods the hollows while the lower of the two does not, although the lower tide does generally hinder the rate of drop in groundwater levels between the alternating higher high tides.

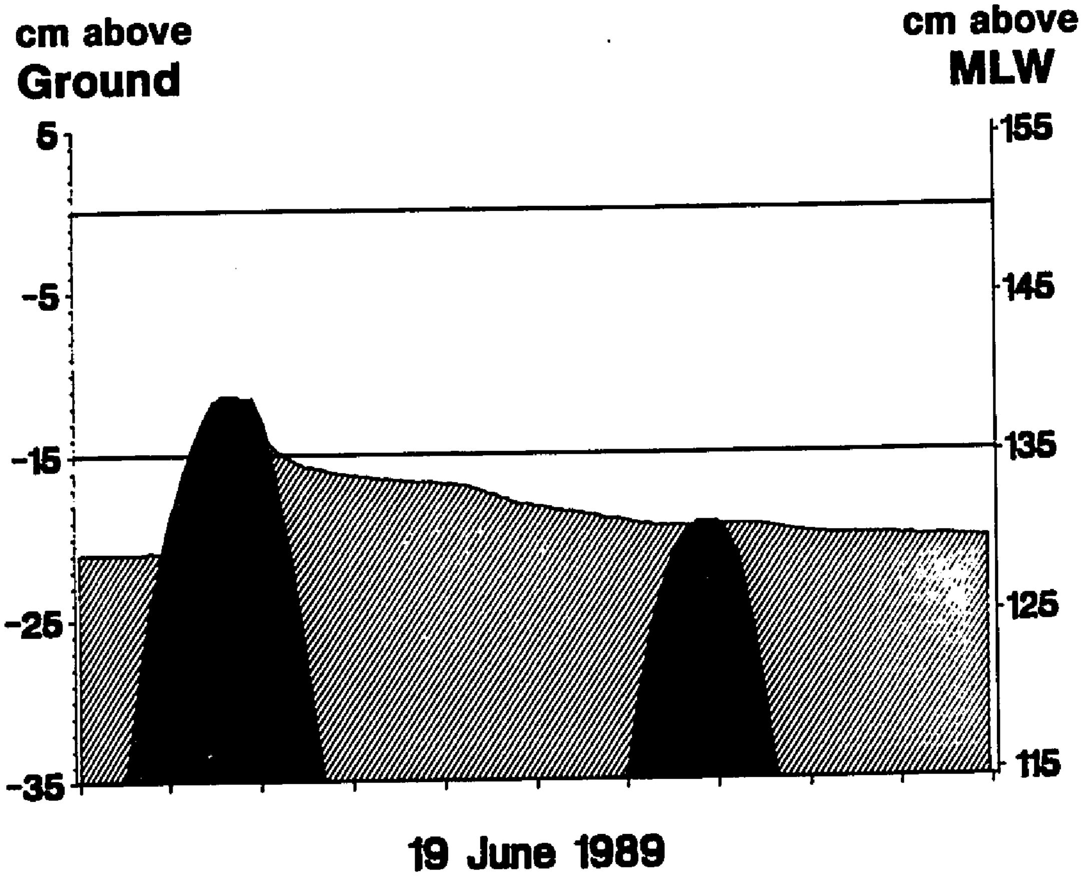
Table 2.1. Canopy composition of the five sites where groundwater wells were installed. Note that the two tidal swamp communities differ primarily in whether Liquidambar styraciflua (sweetgum) is present and by the relative importance of Fraxinus spp. (ashes).

	Ash-blackgum			Maple-sweetgum	
CANOPY	Cohoke	Elsing	Pampatike	Squaw	Randolph
Basal Area (m^2/ha)	20.0	44.0	42.0	36.0	26.0
Importance Value:					
Fraxinus spp.	43.1	56.8	30.8	18.0	18.2
Nyssa biflora	30.6	20.6	40.7	28.6	12.9
Acer rubrum	10.1	22.4	24.5	29.1	20.8
Liquidambar styraciflua	-	-	-	24.1	15.6
Liriodendron tulipifera	8.7	-	-	-	-
Quercus phellos	5.9	-	-	-	32.4
Quercus laurifolia	1.4	-	-	-	-
Quercus pogodaefolia	-	-	2.4	-	-

Figure 2.2. Typical daily hydrographic regime for a freshwater tidal swamp. The solid fill depicts the tidal pulse of the river, the hatching depicts the height of groundwater inundation. The top horizontal line represents the level of the hummock on which canopy species grow; the bottom line is the surface height of the hollow. Note the diurnal inequality of the tide and the slow rate of drainage after the receding water drops to below the height of the hollow. Groundwater fluctuations in the interior of the swamp lag 0.7 hr behind the tide and so all tide data times were adjusted accordingly. Graphics prepared using Statistical Analysis System (1985) software.

Tidal Swamp Groundwater Fluctuations

Elsing Swamp, Pamunkey River



Exceptions to a strict semi-diurnal condition sometimes occur during the bimonthly spring and rarer apogeal tides.

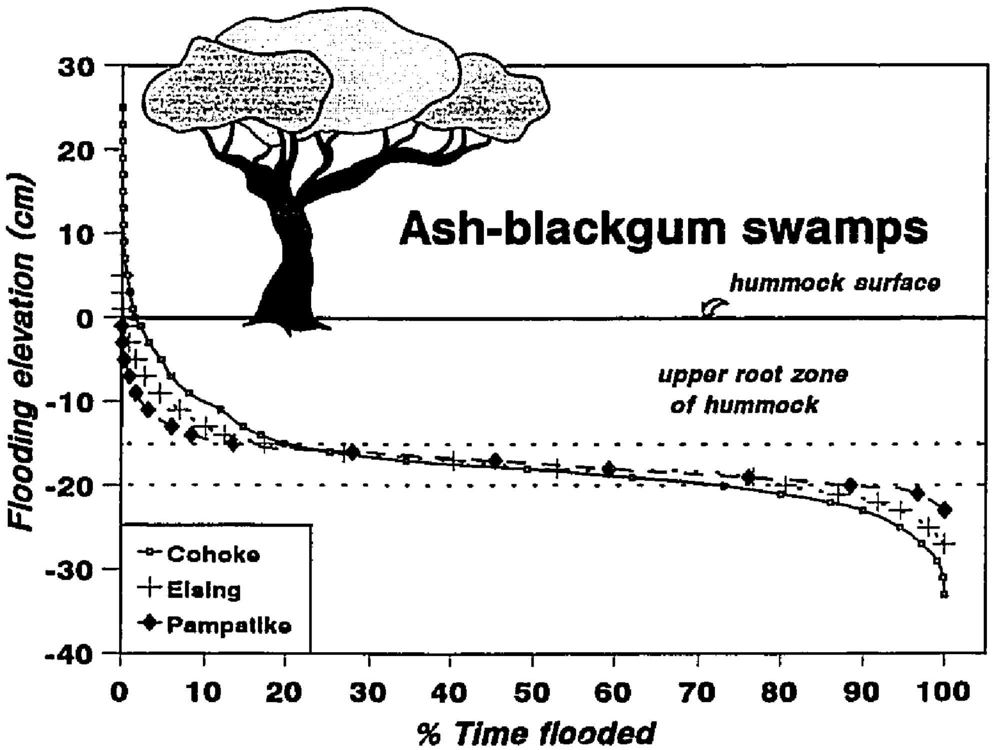
Major precipitation events do not appear to noticeably affect the flooding of tidal swamps. Even the maximum one day rainfall that occurred during the present study (7.2 cm) failed to cause any noticeable rise in the level of the river or in the groundwater depth at Elsing Green (such events would be extremely short-term). Likewise, low tides appear to have very little influence on inundation periods because water levels drop slowly once the tide height drops below the surface elevation of the hollows. Also, the next high tide (12.5 hr later) recharges the system before groundwater levels have dropped much (Fig. 2.2).

It appears that the composition of the substrate located below the elevation of the hollow surface slows the drainage of water during the ebb tide, but does not hinder the recharge rate brought upon by flood tide conditions. In contrast, the substrate of the hummocks does not appear to slow the rate of discharge that occurs during an ebbing tide (i.e., the water level drops at about the same rate as the falling tide until the elevation of the hollow is reached). The quick drainage through the hummocks may occur because the hummocks possess very little soil or peat; instead, the substrate appears to be composed primarily of a dense system of living roots, which may be poor at inhibiting drainage rates. An exception to the fast drainage pattern of hummocks seems to occur in Randolph swamp where hollow microsites are absent and mineral soil predominates. Living roots are much less dense in these kinds of swamps than in those which possess an interdigitating network of hummocks and hollows. In swamps without hollows, both the discharge (ebbing) and recharge (flooding) rates appear to be slowed by the character of the mineral substrate. Rises and drops in water levels are gradual and cycle through one rise and fall per day in apparent response to the higher of the two diurnal tides.

The hydroperiod regime for the five swamps in which hydrographic data were collected is presented in Fig. 2.3. Note that the duration of above-ground flooding (i.e., above the level of the hummock) varies between swamps. For example the ash-blackgum dominated Cohoke swamp (Fig. 2.3a) is more similar to the maple-sweetgum dominated Squaw swamp (Fig. 2.3b in duration of above-ground flooding than to the other two ash-blackgum dominated communities (Fig. 2.3a. However, the percentage of time that the soil is flooded between 15 and 20 cm depth in the upper root zone of the hummocks is more similar for the three ash-blackgum swamps examined (Fig. 2.3a) regardless of the amplitude of flooding (presumably determined by the upper range of the tidal amplitude of the river).

The portion of the inundation curve where the rate of change in the percent time flooded per unit elevation is greatest (delimited by dotted lines) occurs in the same region of the root zone (15-20 cm depth) in all three ash-blackgum swamps examined. In other words, for all three ash-blackgum swamps this 15-20 cm depth zone occurs in the portion of the root zone where minute differences in elevation (range=5 cm) correspond to large differences in the percent of time flooded (20-80%).

In contrast, although the hydroperiod regime of Randolph and Squaw swamps (both maple-sweetgum swamps) are dissimilar to one another in the shape of their inundation curves and in the duration of above-ground flooding (Fig. 2.3b), the region in which the greatest rate of change in flooding per unit elevation occurs is similar (within the 15-35 cm depth range for both, again delimited by dotted lines). Interestingly, as is


Ash-blackgum swamps
hummock surface
upper root zone
of hummock
Flooding elevation (cm)
30
20
10
0
-10
-20
-30
-40
Cohoke
Elsing
Pampatike
0
10
20
30
40
50
60
70
80
90
100
% Time flooded

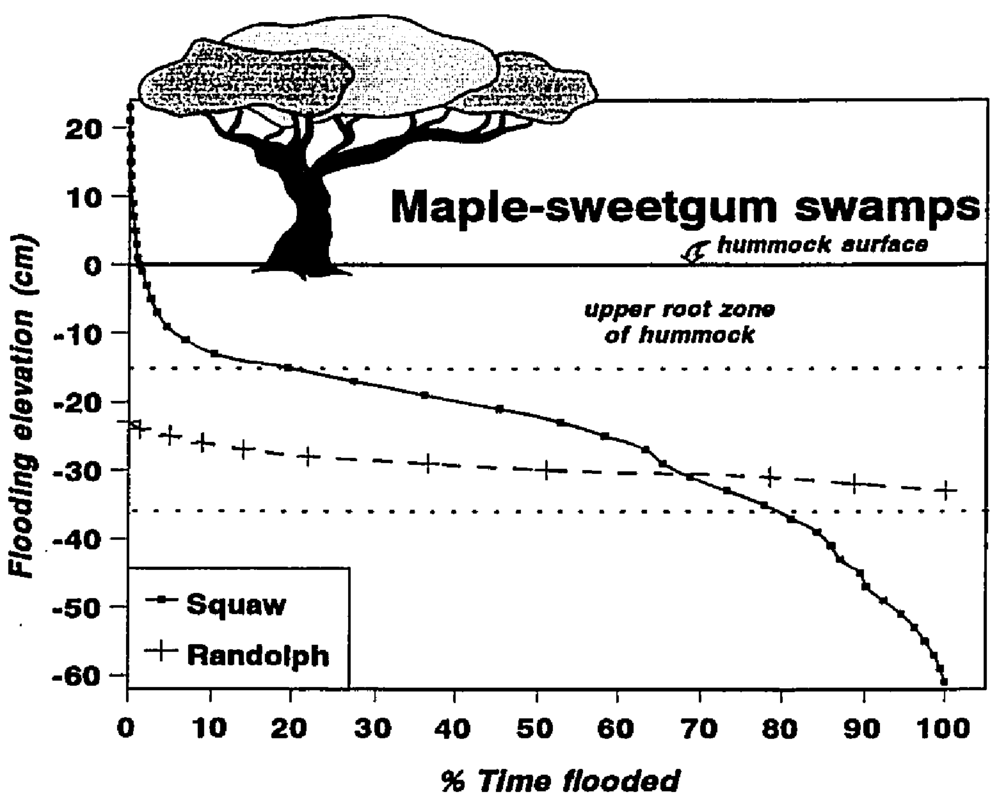

Maple-sweetgum swamps
hummock surface
upper root zone
of hummock
Flooding elevation (cm)
20
10
0
-10
-20
-30
-40
-50
-60
Squaw
Randolph
0
10
20
30
40
50
60
70
80
90
100
% Time flooded

Figure 2.3. Inundation curves for freshwater tidal swamps, percent time flooded vs. flooding elevation. The region of the inundation curve where the rate of change in the percent time flooded per unit elevation is greatest is delimited by dotted lines. Randolph swamp lacks hollows. The surface of the hollows occur at approximately 15 cm below that of the hummock surfaces for the other 4 swamps. Number of days of data collection: Cohoke 330d, Elsing 221d, Pampatike 80d, Squaw 86d, Randolph 57d. Note that the total tidal range of the river varies along its course, and so the range in water table fluctuations differs in swamps along the river (Cohoke: 58cm, Elsing: 32 cm, Pampatike 22 cm, Squaw: 86 cm, Randolph: 10 cm). Graphics prepared using Statistical Analysis System Institute (1985) software.

true for ash-blackgum swamps, the region of greatest change in flooding per unit elevation (at the 15-35 cm depth) in the maple-sweetgum swamps is also the depth at which the roots are flooded from 20-80% of the time (note Squaw swamp). Thus, a major difference in the hydroperiod regime between the two swamp-types is that the depth at which flooding occurs from 20 to 80% of the time is located over a wider range and at a lower depth in maple-sweetgum swamps than in ash-blackgum swamps (15-35 vs. 15-20 cm depths, respectively).

Perhaps an equally relevant way to compare the relative wetness of tidal swamps is to compare the depth at which the groundwater is floods the soil 50% of the time (mean water table depth). Maple-sweetgum swamps were found to possess a lower mean water table depth (-22 and -28 cm) than the ash-blackgum swamps examined (-17 cm for all three swamps). This indicates that ash-blackgum swamps are wetter than maple-sweetgum swamps and that of the two maple-sweetgum swamps examined, Squaw swamp is the wetter of the two (Fig. 2.3b).

Note that the inundation curve for Randolph swamp (Fig. 2.3b) differs in shape from that of the other swamps examined. This is probably because Randolph swamp was devoid of hollows and possessed the lowest organic matter content (9.0 %) of any of the 21 tidal swamps examined (Appendix 2, Table A2). Presumably, the relatively low organic matter content means that it possesses a higher mineral content. Certainly, roots are much less dense in Randolph swamp than in any of the other swamps examined. It appears that the substrate of Randolph swamp inhibits the full affects of tidal forcing and although its flooding amplitude is narrow (10 cm), the mean water table depth occurs sufficiently deep in the root zone to enable sweetgum and _Quercus phellos_ (rare in other tidal swamps) to codominate the canopy.

DISCUSSION

Tidal swamps may be the least confounding systems in which to examine the relationship of hydroperiod to vegetation patterns, because tidal swamps are rarely, if ever, subjected to dry conditions and major rainstorms appear to have little effect on river volume and hence, the flooding regimes of the swamps. Tides primarily drive the hydrologic regime of tidal swamps by recharging the system twice daily with fresh water. The intervals between recharges are so short that the water level drops very little between high tides. Although the maximum height of flooding due to the high tides may vary as much as 35 cm over a lunar cycle, the height of the water table in the root zone (below the hummocks) is much less variable.

The hollows of tidal swamps are usually flooded once per day and portions of the upper root zone of the hollows are almost continually saturated. Trees avoid this stressful zone by exploiting only the hummocks, which drain as quickly as the falling tide. Because completely dry conditions probably never occur in tidal swamps, it seems intuitive that the degree of wetness might be an important determinant of canopy species distributions in such swamps. However, the results of this study indicate that the duration of above-ground flooding is not necessarily related to below-ground hydrodynamics nor to the canopy structure of the forest. Instead, our results suggest that the mean water table depth of the root zone is a more biologically appropriate quantitative measure of wetness in tidal swamps because canopy structure appears to be related to this parameter, rather than to the duration of above-ground flooding or to the total range in the height of flooding. Thus, the more flood tolerant canopy species are more important in swamps where the mean water table depth is higher in elevation (nearer to the surface).

The parameter, mean water table depth, could perhaps be useful as an indicator of relative wetness in other swamp ecosystems as well; it is easily quantified if groundwater data of sufficient duration are obtained. One should be cautious, however, in the interpretation of short-term (1-3 yr) hydrologic data from nontidal swamps because such data may be insufficient to determine mean water table depth and the impact of root zone flooding on vegetative compositions, especially if extreme or rare hydrologic conditions are important in determining community structure by influencing recruitment.

Because a difference in mean water table depth of only a few cm is clearly related to the canopy composition of tidal swamp communities, even slight changes in the mean elevation of flooding could lead to profound structural changes in the composition of tidal swamps. The whole Chesapeake Bay region, including the Pamunkey River, is experiencing an average sea level rise of approximately 10 cm per century (Holdahl and Morrison 1974). Along the lower Pamunkey River, the ground is also subsiding, perhaps in response to groundwater withdrawal by a nearby paper mill, thus accelerating local sea level rise. A further increase in the rate of sea level rise may result from global climatic warming (in response to melting of the polar ice caps and thermal expansion of the oceans). As relative sea level rises, the mean water table depth in the upper root zone will also rise. In order for the swamps to maintain themselves, the hummocks will also have to rise at the same pace as the sea level.

Hummocks appear to be formed by the accumulation of fallen trees. Downed trees provide substratum for plants that are intolerant of a continual inundation of their roots. It seems that tidal swamp forests will prevail as long as biomass is added to the forest floor at a rate sufficient to keep pace with sea level rise. If these tidal forests are periodically harvested and if the biomass necessary for the maintenance and formation of hummocks is removed, it is probable, under the scenario of a relative rising sea level, that tidal marshes will eventually replace tidal swamps because marsh plants are more tolerant of inundation than are trees.

Even if left unharvested, the wetter ash-blackgum swamps will likely replace the less wet maple-sweetgum swamps as sea level rises, if biomass accumulation in the swamps can pace the quickening rate of relative sea level rise. In addition, the most downriver ash-blackgum forests will likely be replaced by freshwater marshes in response to the increase over time in the average salinity levels in the lower reaches of the river as sea level rises. Under this scenario, the entire tidal ecosystem will advance upriver as more land becomes flooded by the sea. However, the upriver portions of the Pamunkey River are being increasingly encroached upon by agricultural activities and urbanization. Thus, the natural, landward advance of the estuarine ecosystems will conflict with human-influenced systems.

Any large scale withdrawals of fresh water from the Pamunkey, as sometimes proposed, could also lead to an intrusion of salt water further upriver. This could result in an upriver displacement of the distributional ranges of tidal freshwater swamps and marshes.

The key to the survival of tidal swamps is whether they can accumulate biomass at a pace sufficient to outpace relative sea level rise. Tidal swamps are unlikely to persist if their biomass is periodically removed by commercial timbering.

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Chapter 3

DISPARATE DISTRIBUTION PATTERNS BETWEEN CANOPY AND SUBCANOPY LIFE-FORMS IN TWO TEMPERATE NORTH AMERICAN FORESTS

ABSTRACT

Quantitative vegetational data of canopy and woody subcanopy species (two life-forms adapted to occupy different strata at maturity) were compared with data collected in two temperate forests ecosystems to determine whether they exhibit a similar pattern of distribution. Tidal freshwater swamps (21 stands) and southern Appalachian forests (19 stands) were examined from data obtained using identical sampling methods. Separate structural analyses of the canopy, sapling, and subcanopy species were compared using the indirect ordination algorithm Detrended Correspondence Analysis. Environmental measurements collected in each stand were assessed for their relationship to the distribution of stands depicted by the ordination diagrams.

Canopy trees and saplings showed a similar pattern of distribution, suggesting that the resource requirements of saplings and canopy-statured adults are similar. In contrast, the subcanopy species (species genetically adapted to an understory existence, i.e., shrubs and small understory trees) of neither ecosystem showed any discernable distributional relationship to the canopy or sapling layers. In tidal swamps, there was no clear way to segregate subcanopy stands into communities. Also, environmental gradients associated with the subcanopy ordinations differed from those of the canopy and sapling strata in both forest systems, suggesting that subcanopy species partition different resources than do canopy species.

If a lack of similarity in distribution patterns between canopy and subcanopy species is universal in temperate forests, then the common practise of combining sapling and subcanopy species in structural analyses may hinder our understanding of subcanopy structural patterns in forests.

INTRODUCTION

Most natural forest ecosystems are composed of plant species morphologically and physiologically specialized to exploit a particular horizontal stratum at maturity (e.g., canopy, woody understory, and herbaceous layers). A partitioning of the vertical space in forests may have evolved among forest plants to gain competitive advantage within some restricted range of the vertical light gradient (Braun 1950, Grime 1977, Terbough 1985, Smith and Huston 1989). Such evolutionary specialization, however, has lead to a restriction in their genetic plasticity. For example, shrubs and small understory trees (both hereafter referred to as subcanopy species) are incapable of reaching canopy stature even when growing in full sunlight. Thus, plants of the canopy and understory appear to have evolved a different strategy for obtaining light. Perhaps they have acquired different needs with respect to other resources as well.

A review of the literature showed that in most North American phytosociological studies, canopy and subcanopy species are lumped together (often, all stems greater than 10 cm dbh are lumped together in vegetational analyses). This means that understory trees and shrubs are often included in structural and gradient analyses of forests. In studies that focus upon understory distribution patterns, woody understory stems of equivalent stature are often combined in community structural analyses: the saplings of canopy trees and mature subcanopy species. Potential differences between these two life-forms (canopy and subcanopy species) are usually neglected.

The lumping of canopy and subcanopy species in the study of vegetation patterns is likely to mask the distribution patterns of both if the environmental factors responsible for those distribution patterns differ. Thus, the mixing of canopy and subcanopy species in forest community structural analyses makes it difficult, if not impossible, to determine whether or what resources are being partitioned among or between these two life-forms, how the structural organization of forests is related to different resource partitioning strategies, and what factors are truely associated with the distribution of individual species. Because species of the subcanopy never reach canopy stature, combining canopy and subcanopy species also makes it more difficult to predict the future composition of forests.

One method of comparing the compositional affinities of samples from large data sets is to subject the quantitative data to multivariate analyses (i.e., ordination, cluster analysis, etc.) and then examine environmental factors that might be related to the observed patterns. By comparing differences and similarities in the distribution patterns of different life-forms on separate ordination diagrams in concert with their relationships to environmental measurements, it may be possible to detect differences in the underlying gradients of importance.

In one such study, Bratton (1975) examined differences in the vegetation patterns of the herbaceous layers and the overlying canopies of forests in the Great Smoky Mountains. Samples of canopy and herbaceous vegetation were both subjected to a Principle Components Analysis (PCA) and the positions of the samples on the ordination were compared along the first axis. Both strata appeared to associated with the same environmental gradients (moisture and elevation) and although spacing between groups differed, the ordering and grouping of stands along the axis was similar for both strata.

Other multivariate comparisons of canopy and herbaceous species distribution patterns and environmental relationships have been examined for southern Appalachian forests (Rheinhardt and Ware 1984) and for tidal swamp forests (this study, Chapter 1). In both systems, the distribution of the canopy and herbaceous samples appeared to be related to similar environmental gradients (a duration of soil saturation gradient in the tidal swamps and a moisture-fertility gradient in the mountain forests). The similar pattern of distribution exhibited by herbaceous and canopy species of these two disparate temperate forests suggests that they may both be responding to similar environmental gradients, although the precise nature of the gradients involved may differ among forest ecosystems.

In contrast to studies suggesting that species distribution patterns of the the canopy and herbaceous strata are similar to one another, there is some indication in the literature that the structural complexity (richness) of the subcanopy may be unrelated or negatively related to the complexity of the canopy. Harcombe and Marks (1977) found a sharp contrast between the high subcanopy species richness (20 species) of mesic southern mixed hardwood forests and the relatively low canopy richness (7 species) of those forests. They attributed the high subcanopy species richness to favorable (relatively high) light levels in the understory, although differences in light levels were not used to evaluate species distribution patterns in the subcanopy. In a study of five New Jersey pine barren swamps, Ehrenfeld and Gulick (1981) attributed the high shrub biomass they found there ($\bar{x}$=5,837, range=1,993-12,322 kg/ha) to high light penetration into the subcanopy of the swamps. No contrast was found, however, between the species richness of trees and shrubs (both life-forms contained few species).

Differences found between the structural complexity of the subcanopy and the canopy of these two forest systems, pine barren swamps and mesic coastal plain forests, suggest that perhaps canopy and subcanopy species partition different resources or different portions of the same resource. If this is true, then an examination of separate ordinations of the subcanopy and canopy, along with an examination of associated environmental gradients in relation to the ordination positions of the stands, might detect differences between canopy and subcanopy life-forms with respect to the distribution patterns of the samples and the factors responsible for any such differences. A similar comparison of ordinations and environmental gradients between subcanopy and sapling communities of the same size-class might suggest how closely these communities allied in the distribution of their component species.

It is unlikely that compositional comparisons between the canopy and seedling strata can provide much insight into the distribution patterns exhibited by the species of the canopy and subcanopy. This is because the relative number of seeds that germinate each year and the mortality rate of seedlings, generally those stems less than 1.5 m tall, often vary tremendously between species, between years, and between microsites (Daubenmire 1968, Grubb 1977, Huenneke and Sharitz 1986, Titus 1990), especially those of canopy species (Good and Good 1972, Streng et al. 1989). However, larger individuals of the understory (those >1.5m tall) are more likely to survive to maturity than are seedlings.

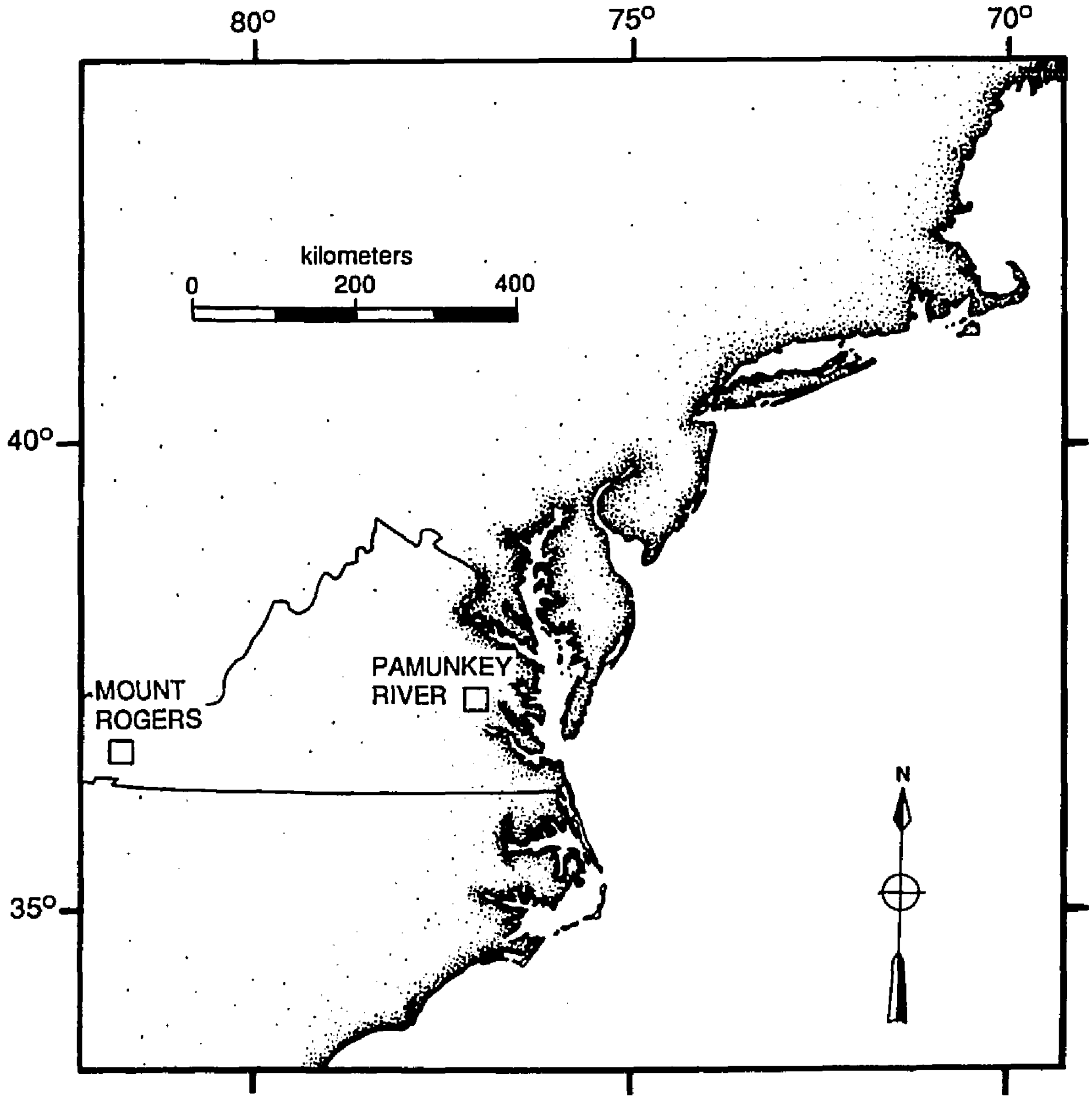
If the sapling and canopy compositions are indeed similar in mature, self-reproducing forests, then separate ordinations of the two life-forms may show similar distribution patterns. If subcanopy species follow the pattern established by the canopy, stands should segregate in the same manner, even though the species composition of the communities would differ. If, however, subcanopy species are distributed independently from that of the overlying canopy (and perhaps also from the sapling strata as well), such differences should be detectable by comparing ordinations of the three strata. Differences and similarities might also be illuminated by the relationship between species distribution patterns and the environmental gradients that appear to be associated with the patterns.

This study was initiated to determine whether the common practice of combining subcanopy species and saplings in vegetation analysis is justified. Multivariate analyses were applied to two very different temperate forest ecosystems, to which identical sampling techniques had been applied, to determine whether there is evidence that the subcanopy and canopy species in a forest partition the same resources and whether canopy species partition the same resources as adults and saplings. Such an examination has not been previously attempted.

Study sites

The two kinds of forests examined in this study, tidal swamps and mountain forests, are located at approximately the same latitude (between 36 and 38 N latitude). Approximately 440 km separates the two areas (Fig. 3.1). The tidal swamps are located along the Pamunkey River, a meandering, low gradient coastal plain river flowing into the York River, a subestuary of lower Chesapeake Bay. Tidal swamps occur along 40 km of the Pamunkey, which harbors the most extensive tidal swamp system on Chesapeake Bay (some exceed 300 ha).

Figure 3.1. Location of the temperate North American forests compared in this study. The tidal swamps are located on the Pamunkey River, a coastal plain tributary of Chesapeake Bay. The Mount Rogers-Whitetop complex are a part of the southern Blue Ridge physiographic province.



80°
75°
70°
kilometers
0
200
400
40°
35°
MOUNT
ROGERS
PAMUNKEY
RIVER
N

The mountain forests examined in this study are located on the summits, slopes, and adjacent ridges of Mount Rogers and Whitetop mountains in southwest Virginia. These mountains, located in the northern section of the southern Blue Ridge physiographic province, comprise the highest two peaks in Virginia. Extensive, natural tracts of spruce-fir and northern hardwood forests occur there as do open slope mesic forests. Thus, these mountains contain a wide variety of elevation and topographic-moisture regimes, which in turn support numerous vegetational community-types.

METHODS

The southern Appalachian forests of Mount Rogers were sampled in 1980. Basal area (dominance) of canopy stems were obtained from 69 stands, but only 19 of those stands are examined in this study (i.e., those in which densities of canopy, sapling, and subcanopy strata were also obtained). Data from these 19 mountain stands were compared with twenty-one tidal swamps sampled in 1988-1989.

Sampling methods for the collection of canopy, subcanopy, and sapling data were identical in both studies. Importance values for canopy species were obtained by averaging basal areas and relative densities for stems greater than 10 cm dbh (diameter at 1.5 m). Relative density values only were obtained for subcanopy species and saplings. Saplings (juvenile canopy species) were counted if less than 10 cm dbh and greater than 1.5 m tall; subcanopy species were counted if taller than 1.5 m regardless of diameter (subcanopy species were generally less than 10 cm dbh).

Subcanopy species were considered to be those woody species which do not normally reach the canopy under natural conditions in forests. These species include shrubs and small understory trees. There is no clear-cut way to ecologically separate shrubs from understory trees since they overlap considerably in size and both are evolutionarily adapted to the low light environment of the understory. Clearly, although saplings of canopy trees are similar in size to that of subcanopy species, they differ radically in stature at maturity.

The American chestnut was once an important canopy tree in the southern Appalachian forests, but is now relegated to the understory as root sprouts. However, because chestnut rarely reaches reproductive age in the subcanopy, it does not meet the definition of a subcanopy species.

Nine environmental parameters were examined in the tidal swamps, 10 in the southern Appalachian stands; some were identical for both ecosystems (pH, phosphorus, potassium, calcium, and organic matter) and some were unique to one or the other of the two systems (swamps: iron, distance upriver from the most downriver swamp, % hollow, soluble salts, and in mountain forests: elevation, aspect (sensu Beers et al. 1966), nitrate nitrogen, soil moisture, magnesium). More detailed descriptions of the vegetation sampling methods and of environmental data collection methods can be found in Rheinhardt (1981: mountain forests, Chapter 1 and Appendix 2: tidal swamp forests) and in Rheinhardt and Ware (1984). Taxonomic nomenclature follows that of Harvill et al. (1986) and Radford et al. (1968).

Subcanopy, canopy, and saplings of canopy species were independently subjected to Detrended Correspondence Analysis (Hill 1979, Hill and Gauch 1980), an indirect ordination algorithm, using the CANOCO package developed by Ter Braak (1988). The environmental factors were tested for correlation with the first two ordination axes to assess possible relationships between the environmental factors and the variance in vegetation patterns accounted for by the axes. Regression coefficients and environmental biplot scores were determined as part of the CANOCO output. Although significance values cannot be attributed to biplot scores, they are useful for representing strong environmental gradients that may not necessarily be significantly correlated with either of the ordination axes.

RESULTS

Plant communities

Two distinguishable community-types (based only upon their canopy compositions) occur in tidal swamps: an ash-blackgum and a maple-sweetgum type. Ash-blackgum communities are dominated in the canopy by various ash species (Fraxinus spp.), and swamp blackgum (Nyssa biflora), while maple-sweetgum swamps are dominated by red maple (Acer rubrum), sweetgum (Liquidambar styraciflua), and swamp blackgum (Nyssa biflora). Bald cypress (Taxodium distichum) codominates in two stands that appear to be structurally similar to ash-blackgum communities in all other respects. The canopy of both swamp communities is low in species richness; although 20 canopy species occur in tidal swamps, the 5 above mentioned species account for over 95% of the total basal area of trees in all stands sampled (Chapter I and Appendix 5).

In contrast to the low canopy richness of any one stand, the subcanopy of tidal swamps harbors a total of 22 subcanopy species, 10 of which occur in more than 50% of the stands sampled. The mean number of subcanopy species encountered per stand is 8.5 (sd= 2.2, n=21). The most abundant and widespread subcanopy species occurring in the tidal swamps include spicebush (Lindera benzoin), common winterberry holly (Ilex verticillata), American holly (Ilex opaca), southern arrowwood (Viburnum dentatum), and ironwood (Carpinus caroliniana).

The canopy of southern Appalachian forests of the Mount Rogers area supports seven discernable community-types, based upon canopy basal area data from 67 stands (Rheinhardt and Ware 1984). The spruce-fir community, located on the summit of Mount Rogers, is dominated by Fraser fir (Abies fraseri), red spruce (Picea rubens), and yellow birch (Betula lutea); the summit of neighboring Whitetop Mountain is similar in composition, but lacks fir and so is dominated by spruce and yellow birch (spruce community). The leading dominant of yellow birch communities is yellow birch with various associates depending on elevation, aspect, and topographic position. For the ravine subtype, codominants include hemlock (Tsuga canadensis), Fraser magnolia (Magnolia fraseri), and spruce; for the boulder field subtype, codominants may include spruce, sugar maple (Acer saccharum), or sweet buckeye (Aesculus octandra). Northern hardwood communities are dominated primarily by beech and sugar maple, with an appreciable amount of yellow birch. Mixed mesophytic communities are diverse and variable in composition with numerous mesic hardwoods dominating the canopy, including white basswood (Tilia heterophylla), sugar maple, beech, white ash (Fraxinus americana), yellow birch, sweet buckeye, northern red oak (Quercus rubra), and red maple. In mesophytic-oak communities, the leading dominant is northern red oak, but mesic and submesic species share dominance as well, including beech, sugar maple, yellow birch, buckeye, and red maple. Northern red oak communities are dominated, as the designation suggests, by northern red oak. Codominants include red maple, chestnut oak (Quercus prinus), and sweet pignut hickory (Carya ovalis) at drier sites and sugar maple and basswood at more mesic sites.

Both the canopy and subcanopy vary considerably in species richness depending on topographic position and affiliated soil moisture regimes. In all, there are 28 canopy species and 23 subcanopy species (excluding chestnut, Castanea dentata, which is a canopy species relegated to understory status by the chestnut blight, Endothia parasitica). The most widespread and important subcanopy species in the Mount Rogers-Whitetop complex include moosewood (Acer pensylvanicum), witch-hazel (Hammamelis virginiana), mountain maple (Acer spicatum), alternate-leaf dogwood (Cornus alternifolia), hobblebush (Viburnum alnifolium), and mountain holly (Ilex montana). The mean species richness of the subcanopy community is 5.3 (sd=2.7, n=19), one third lower than tidal swamps.

Ordinations

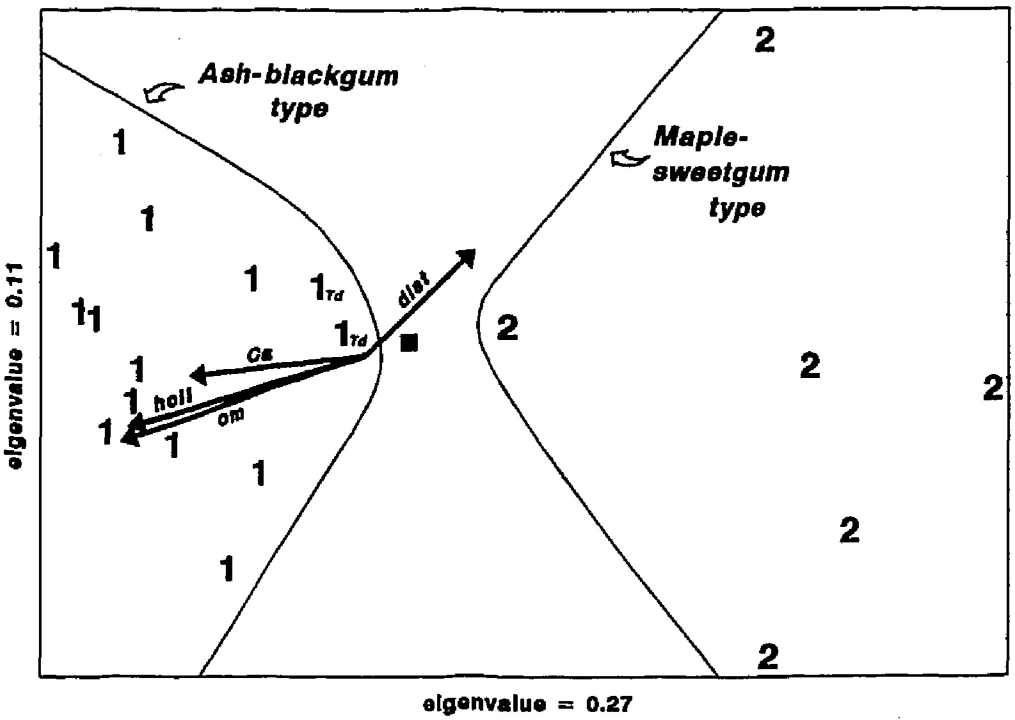
Tidal swamps

The two tidal swamp communities segregated without overlap on the ordination diagram on the basis of their canopy compositions (Fig. 3.2a). Note that the numbers designate the community to which the canopy of the stand is affiliated. A comparison of this ordination diagram with that of the sapling ordination (Fig. 3.3a) indicates that the sapling stratum follows the same pattern as that exhibited by the overstory. There are only two exceptions: one maple-sweetgum (canopy-categorized) stand is within the group of ash-blackgum stands and one ash-blackgum stand is nestled among the maple-sweetgum stands on the ordination (Fig. 3.3a).

Similar environmental gradients also appear to separate the canopy and sapling strata of the two swamp-types: distance upriver from the most downriver site, the amount of the forest floor covered with hollows (interhummock depressions) and organic matter content. The percentage of the forest floor covered by hollows is an indirect measure of the wetness of a stand. Organic matter content and calcium tend to covary with wetness and so show similar patterns in both strata. In other

Figure 3.2. Canopy ordinations of a) tidal swamp forests and b) southern Appalachian forests of the Mount Rogers-Whitetop complex using DECORANA. Community-types are enclosed by solid lines. The numbers refer to community-types (i.e., #1 in Fig. 3.2a = ash-blackgum tidal swamps, #1 in Fig. 3.2b = Northern Hardwoods community, #2 in Fig. 3.2b = Mixed Mesophytic Community, etc.) In the tidal swamp ordination, the bald cypress subtype (1_{Td}), is possibly a relic ash-blackgum community, based on the close structural affinity of the canopy and herbaceous strata to the other ash-blackgum swamps. A compositionally intermediate tidal swamp stand is indicated by the solid square. Abbreviations for environmental variables are as follows: holl (hollow), Ca (calcium), Moist (moisture), iron (Fe), om (organic matter), dist (distance upriver from most downriver swamp stand in km), elev (elevation), NNO3 (nitrate nitrogen), pH (pH). Significant correlations of environmental parameters with the ordination axes are as follows: for tidal swamps, axis 1: % organic matter ($r=-0.64$, $P<0.005$), calcium ($r=-0.46$, $P<0.05$), and % hollow ($r=-0.62$, $P<0.005$) and for axis 2: distance upriver ($r=0.47$, $P<0.05$). For the southern Appalachian forests, axis 1: pH ($r=-0.55$, $P<0.01$) and elevation ($r=0.50$, $P<0.05$) and axis 2: % organic matter ($r=-0.53$, $P<0.01$).

a) Canopy ordination of tidal swamps



b) Canopy ordination of southern Appalachian forests

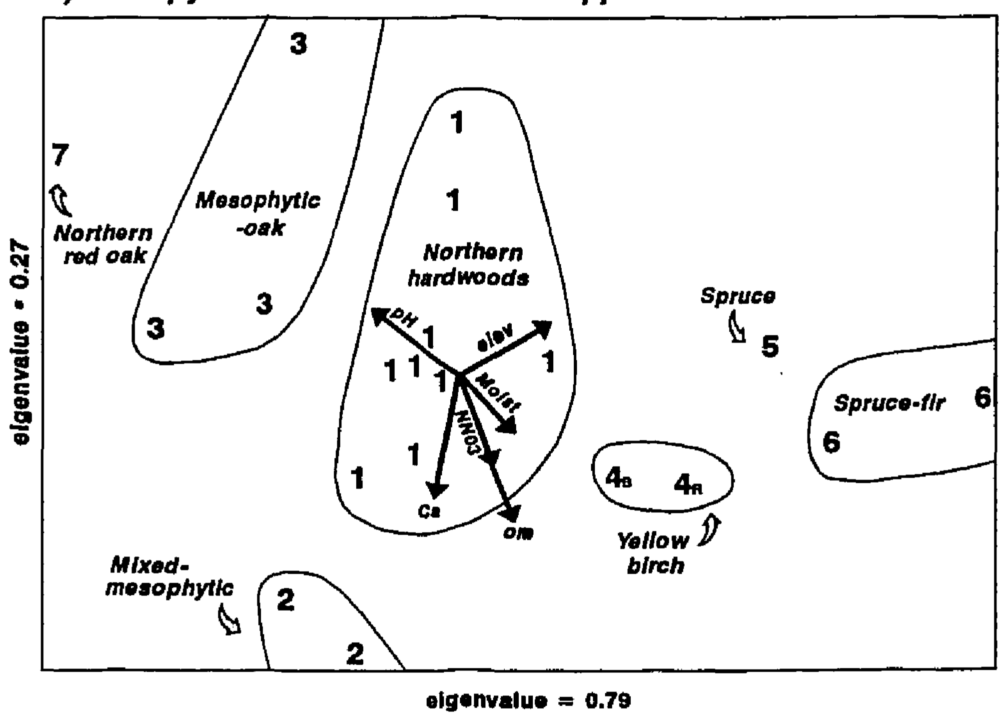
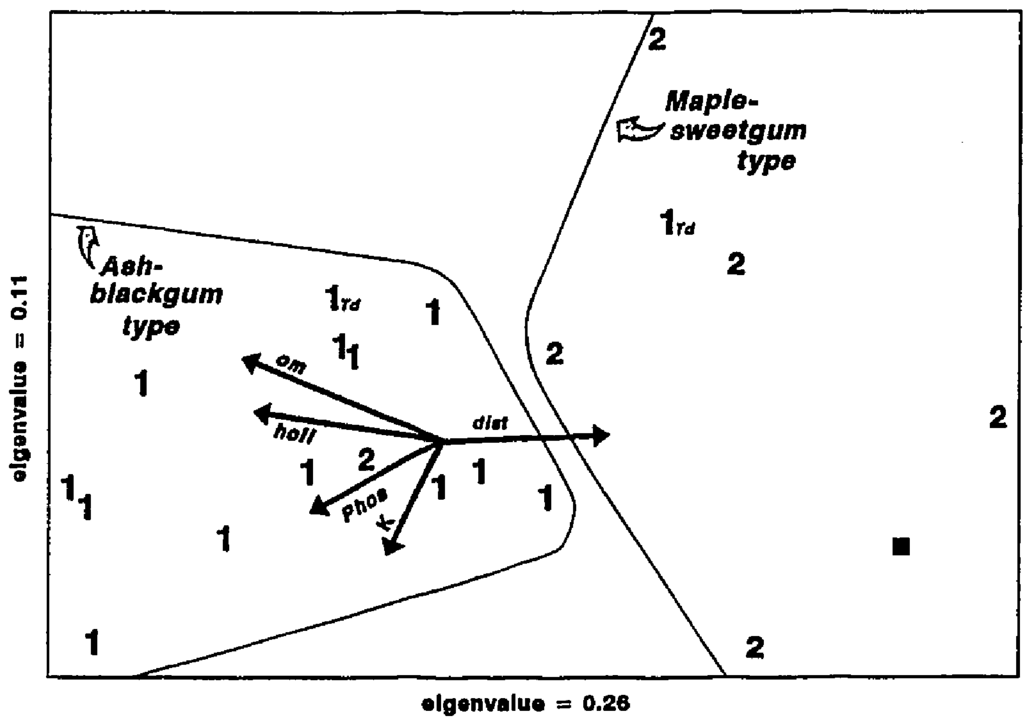
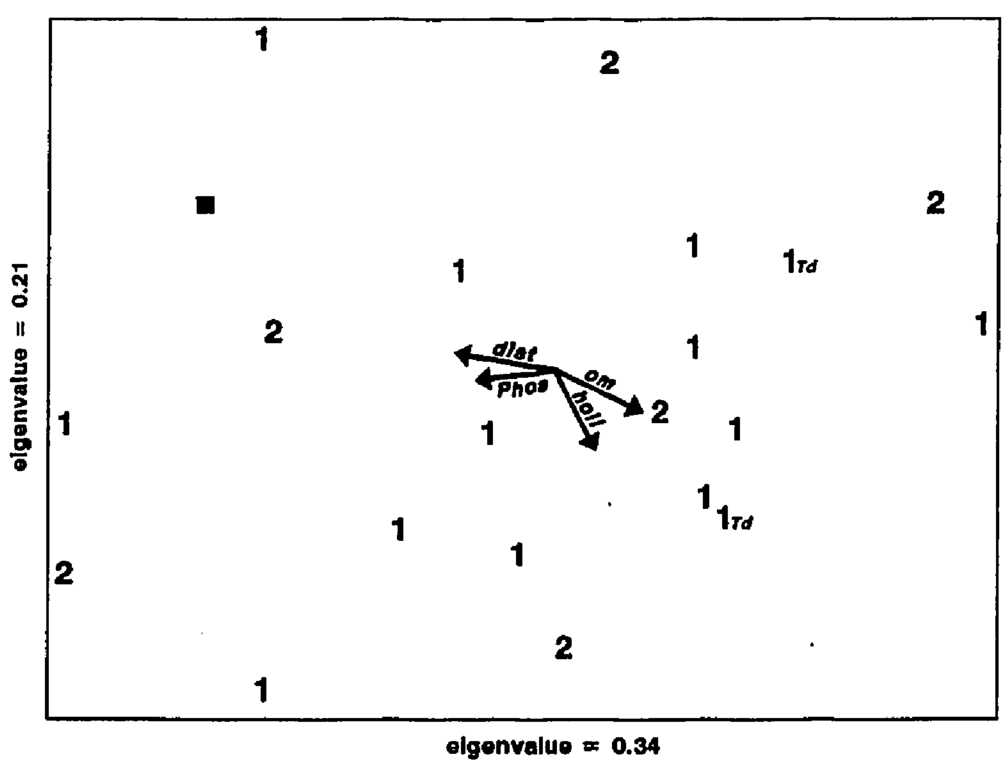


Figure 3.3. Ordinations of tidal swamp a) sapling and b) subcanopy strata. Community-types (numbers) are based on the canopy compositions as shown in Fig. 3.2a. Abbreviations for community-types and environmental variables follow those in Fig. 3.2, plus phos (phosphorus) and K (potassium). Significant correlations of environmental parameters with the sapling ordination axes are as follows, axis 1: % organic matter ($r=-0.47$, $P<0.05$), % hollow ($r=-0.46$, $P<0.05$), and distance upriver ($r=0.45$, $P<0.05$) and axis 2: potassium ($r=-0.66$, $P<0.005$), pH ($r=-0.57$, $P<0.005$), and phosporus ($r=-0.44$, $P<0.05$). No variables were significant with either subcanopy ordination axis.

a) Sapling ordination of tidal swamps



b) Subcanopy ordination of tidal swamps



words, the wetter the site, the higher the peat (organic matter) content and the calcium concentration (note biplot arrows in Figs. 2a and 3a).

An evaluation of the subcanopy stratum (Fig. 3.3b) shows that the maple-sweetgum stands (#2) are interspersed among the ash-blackgum stands (#1). Thus, although their canopies segregate into the two distinct communities, there is no clear way to segregate the subcanopies into the same two communities. Also, when relative densities of subcanopy species are plotted on the ordination (Chapter 1), individual species segregate with respect to where they are important on the ordination, but the distribution patterns are such that groups of stands with similar subcanopy composition (subcanopy communities) do not emerge. The most important environmental gradients measured in the subcanopy appear to be wetness, distance upriver, phosphorus, and organic matter content, although none of these are significantly correlated with either of the ordination axes.

Southern Appalachian forests

Seven mountain forest communities segregate on the canopy ordination of southern Appalachian forests (Fig. 3.2b). The spruce stand is similar to the spruce-fir stands, except for the lack of fir. The yellow birch stands are similar to the spruce stands, except that they lack appreciable amounts of spruce.

The sapling understory segregates in a manner similar to that of the canopy. For most of the stands (13 out of 17), the composition of the canopy and sapling strata are of the same type: seven of the eight northern hardwood stands, the spruce stand, both spruce-fir stands, one of two mixed-mesophytic stands (stand #2, top enclosure), one of three mesophytic-oak stands (stand #3, bottom), and the northern red oak stand (left). In fact, the ordering of stands along axis 1 of the ordination is almost identical for both ordinations. There are only three exceptions, all northern hardwood stands (Fig. 3.4a: the one stand in the spruce-fir enclosure and 2 others which are located at different positions within the array of northern hardwood points).

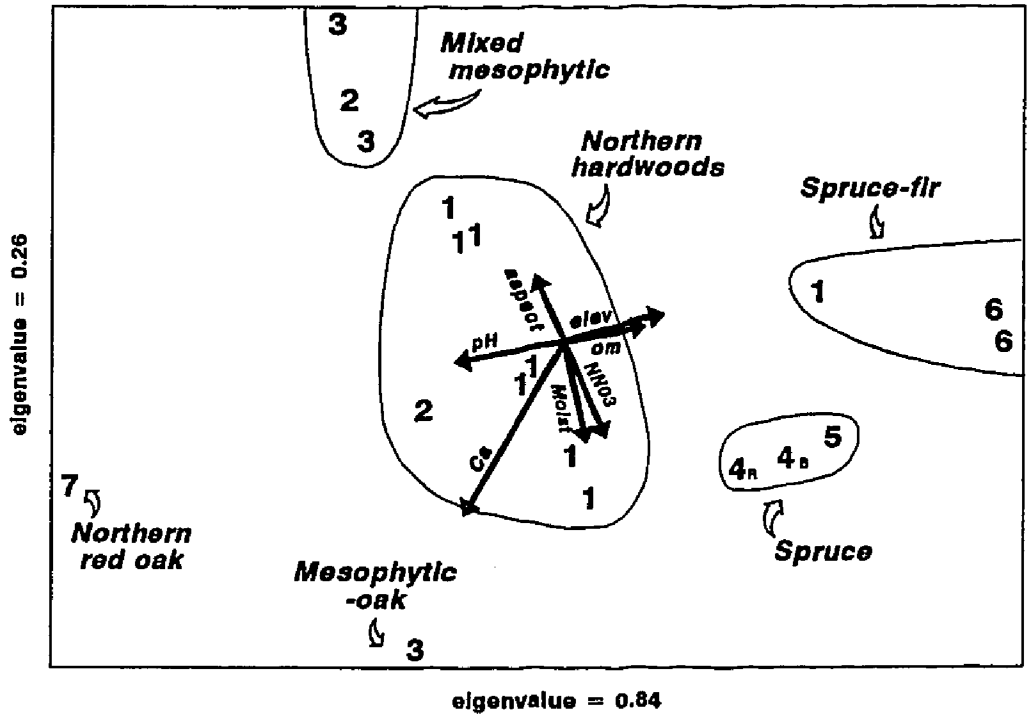
The few exceptions to the pattern are all cases in which higher elevation communities are extending their ranges downslope. One of the mixed-mesophytic stands has beech increasing in importance in the sapling strata (#2 within the northern hardwoods enclosure). Spruce and fir are reproducing well in one of the northern hardwoods stands, which caused it to move into the spruce-fir enclosure far right. Spruce is reproducing abundantly in the two yellow birch communities, making their sapling compositions very similar to that of the spruce stand. Also, two of the three mesophytic-oak stands (#3) have mixed-mesophytic saplings gaining in relative abundance (note top enclosure, Fig. 3.4a).

Consistent relationships between environmental gradients and community distribution patterns of the different strata are less distinct for southern Appalachian forests than for tidal swamps, but the patterns are still fairly consistent. The canopies of the Mount Rogers-Whitetop forests seem to separate along an elevation and fertility-moisture gradient, a pattern recognized by others working in southern Appalachian forests (Braun 1950, Bratton 1975, Whittaker 1956). In both the canopy and sapling strata, yellow birch, spruce, and spruce-fir appear to separate from the other communities along an elevation gradient. The soils of these higher elevation communities also tend to contain higher levels of organic matter and are more acidic (Fig. 3.2b and 3.3a).

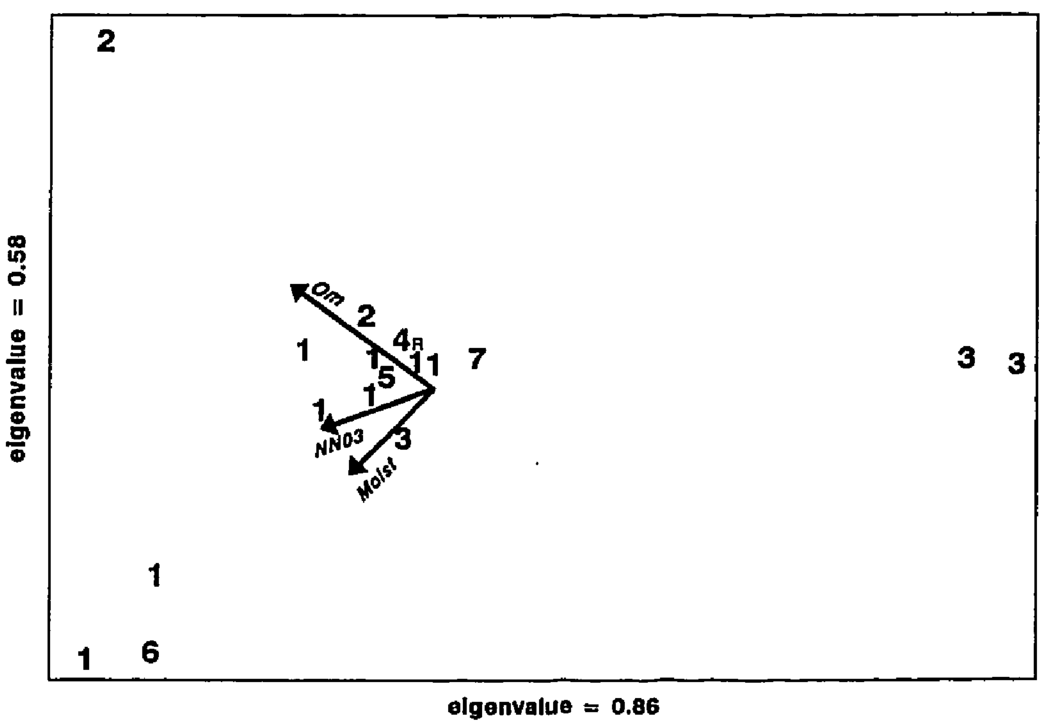
An examination of the distribution of stands based upon their subcanopy compositions (Fig. 3.4b) shows a phenomenon similar to that

Figure 3.4. Ordinations of southern Appalachian forests a) sapling and b) subcanopy strata. Community-types (numbers) are based on the canopy compositions as shown in Fig. 2b. One northern hardwood stand lacked subcanopy individuals greater than 1.5m tall and one yellow birch stand was downweighted because it contained only one species in the subcanopy (thus n=17 for the subcanopy ordination). Abbreviations for community-types and environmental variables follow those in Figs. 3.2 and 3.3. In the sapling stratum, pH was significantly correlated with axis 1 ($r=-0.49$, $P<0.05$). No variables were significant with either subcanopy ordination axis.

a) Sapling ordination of southern Appalachian forests



b) Subcanopy ordination of southern Appalachian forests



exhibited by the tidal swamp forests, that is the subcanopy stratum differs in its community distribution patterns in comparison to that of the overlying canopy. The numbers denote the community-type to which those stands belong based upon their canopy compositions. As was true for the subcanopy ordination of tidal swamps, like numbers do not lie near one another, i.e., subcanopy does not segregate in the same manner as does the canopy. For example, *Acer pensylvanicum* dominates the subcanopy of at least one stand of all the community-types, except for spruce-fir. The eleven stands grouped together near the biplot arrows (Fig. 3.3b) all possess high relative densities of *A. pensylvanicum* (58-100%) in the subcanopy. In other words, none of the communities (as defined by the canopy structure) possess a subcanopy that can be considered to be typical of the community.

DISCUSSION

This study indicates that the canopy and sapling strata of two different temperate forests show a similar pattern in the way they segregate on vegetational ordinations. This means that the community structures of the canopy and sapling layers are similar in mature forests and support the conventional wisdom that mature forests are stable (self-reproducing). Note that in some of the southern Appalachian stands, species of higher elevations appear to be increasing in relative importance in the sapling stratum. This may portend the future composition of these stands. The ordinations also reveal that similar environmental gradients are associated with the distribution patterns of the canopy and sapling strata, suggesting that the resource requirements of saplings and canopy-statured adults are similar.

Observations by plant ecologists that the sapling and herb communities appear to show a close affiliation to the canopy community may have led many to assume that subcanopy species are likewise affiliated. This study shows that the compositions of the canopy and subcanopy (shrubs and small understory trees) of two different temperate forest ecosystems are unrelated to the compositions of their overlying canopies and that the environmental gradients associated with the ordinations of the two strata likewise lack a similarity of pattern. If this lack of similarity in distribution patterns between the canopy and subcanopy is universal throughout temperate forests, then the common practice of combining sapling and subcanopy species in structural analyses has likely hindered our understanding of the structural patterns and resource partitioning in forests.

Why, as this study appears to indicate, might subcanopy and canopy strata differ in their species distribution patterns? Tilman (1988) proposed that plants require two classes of resources, light and soil resources (including nutrients and water) and that the acquisition of these resources has led to different evolutionary and competitive strategies among plants. A plant's genetic make-up determines the potential range of its competitive ability (plasticity) to obtain resources. Plants that evolved to compete for high intensity light at maturity (i.e., canopy species) may be genetically adapted to allocate much more of their energy to the production of above ground biomass (woody support tissue) than species that evolved the capability to mature and reproduce in shade (i.e., subcanopy species). Perhaps the variation in community distribution patterns between the canopy and subcanopy strata found in this study reflect a differential requirement for resources in response to the differential allocation of biomass by the two life-forms.

More in depth sampling of all vegetative strata in other forest ecosystems is needed to determine whether differences in the distribution patterns between strata is true for forests in general. Rarely are all forest strata sampled in phytosociological studies and there are only a few instances provided in the literature where each stratal life-form has been subjected to its own ordination. Vegetation ecologists usually refrain from combining herbaceous plants and woody seedlings in structural analyses; perhaps we should likewise avoid combining subcanopy and canopy life-forms.

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OVERVIEW

The tidal freshwater swamp landscape is a microtopographic mosaic of hummocks and hollows, providing a complex array of patchily distributed microhabitats. The vegetation responds to this complexity; all the woody species, except for bald cypress, are restricted to the hummocks, while herbaceous species are distributed between both microsite-types depending on their tolerance to flooding. Because hummocks vary in size, they likewise vary in the number of trees that they can support. Also, the crowns of canopy trees are underdeveloped (probably in response to moisture stress). The combination of moisture stress and the pattern of hummock distribution provide a complex mosaic of light patterns in the understory. The interplay of light and flooding provides heterogeneous habitat conditions over small spatial scales and these factors likely combine to control community structure and species richness by providing a variety of niches within a small area. Overlying this localized complexity are broad environmental gradients of flooding and nutrient availability that encompass the entire wetland complex and to which tidal swamp species subtly respond.

Although environmental factors associated with tidal swamps are part of a continuum, the vegetation of tidal swamps could be compositionally segregated into two communities, one dominated in the canopy by ashes, swamp blackgum, red maple (and perhaps once by bald cypress) and the other dominated in the canopy by red maple, swamp blackgum, and sweetgum. The primary difference between the two community-types is the inversely related codominance of ash and sweetgum in the two community-types. Swamps which contain sweetgum as a codominant possess relatively more hummock area and possess a lower mean saturation depth (i.e., depth at which the soil is saturated 50% of the time). This implies that mean soil saturation depth may be an important environmental parameter to which tidal swamp trees respond.

The ash-blackgum community-type occurs along the entire geographic range of Pamunkey swamps, although this wetter swamp-type is more prevalent and extensive downriver where the river is wider and the meanders of the river are more pronounced. However, because hydroperiod appears to be the most important parameter affecting the community structure of tidal swamps and the distributions of community-types along the river (responses to edaphic factors are less easily detectable and probably are themselves controlled by hydroperiod), the wetter ash-blackgum swamps can be quite extensive upriver where conditions are suitable for their development.

The herbaceous stratum of tidal swamps appears to follow the same pattern as that expressed by the canopy stratum, i.e., the same two community-types are distinguishable whether determined by canopy or by herbaceous species compositions. Some of the herbaceous species growing in the hollows are those that also inhabit tidal freshwater marshes (presumably those that are shade-tolerant and less salt-tolerant). Such close floristic affinity between freshwater marshes and swamps is not surprising considering their proximity to one another and the similarity in their hydrologic conditions. Tidal swamps also harbor herbaceous species common to bottomland hardwood forests of the area. Thus, tidal swamps appear to lie along a portion of the environmental continuum between tidal marshes and bottomland hardwood swamps.

The subcanopy stratum, however, does not follow the pattern expressed by the canopy and herb layers. This difference in distribution patterns between canopy and subcanopy life-forms was also found to be true of southern Appalachian forests. Thus, it appears that canopy and subcanopy life-forms may partition different resources or different portions of the same resource gradient. More in-depth sampling of vegetation by life-form type in other forest ecosystems is needed to determine whether the differences found between canopy and subcanopy species distribution patterns in the two forests systems examined in this study are indicative of forests in general.

The subcanopy of tidal swamps is extremely rich is species: twenty-one subcanopy species were found, ten of which were found in more than 50% of the stands sampled. If seasonally flooded upriver tidal swamps are included, 25 subcanopy species were found. Cove forests of the southern Appalachians and mixed-mesophytic forests of the Cumberland Plateau are considered to be the most floristically rich forests in temperate North America (Braun 1950), yet these associations harbor many fewer subcanopy species at the community level (Whittaker 1956, Rheinhardt 1981) than do the tidal swamps sampled in this study. For example, Braun (1950) listed 21 subcanopy species for the Cumberland Plateau, but this included a variety of communities from exposed ridges to deep ravines.

Harcombe and Marks (1977) described mesic forests of the Big Thicket area of southern east Texas and other mesic southeastern U.S. coastal plain forests (Marks and Harcombe 1975) as being extremely rich in subcanopy species also (21 species). Thus, tidal swamp forests along the Pamunkey River appear to harbor one of the most diverse subcanopy assemblages in eastern North America and perhaps of temperate North

America. It is undoubtedly the richest subcanopy assemblage yet published for swamp communities.

It is unclear why tidal swamps harbor such a rich subcanopy. Perhaps the relatively sparse canopy allows more light penetration than is usual for swamp forests and the subcanopy species finely partition the unusually long light gradient. Perhaps the microtopographic complexity of the hummock-hollow pattern provides a long moisture-flooding gradient which is likewise partitioned. Perhaps periodic disturbance (flooding stress) prevents monopolization of resources by competitive dominants, thus preventing competitively superior species from eliminating weaker competitors. More detailed work needs to be done to determine the causes for such high diversity.

The herbaceous vegetation of tidal swamps is also extremely speciose and luxuriant. Again, perhaps the diversity of niches, a possible interplay of light and moisture, enables many herbaceous species to occur together. Sixty-nine species were found in 205 m^2 within a 10 day temporal window. Forty-six species were discovered which had not been recorded by botanical collectors as having occurred in the three counties of the study; a few of those species represented extensions of their recorded range, although most occurred within their previously recorded distributional range. This probably means that the three counties of the study have not received adequate attention from botanical collectors. Thus, it is likely that many more unmapped species are present in these tidal swamps as well, particularly if collections are made throughout an entire growing season.

Groundwater fluctuations in most of the Pamunkey River swamps are closely coupled to the mixed semidiurnal tidal regime. These are true tidal swamps; flooding occurs daily in the upper root zone (top 15 cm) in concert with high tides. Thus, these swamps should be more aptly classified as diurnally flooded forested wetlands on National Wetland Inventory maps, rather than as seasonally flooded systems as they are currently classified and inventoried (to accuratley classify these diurnally flooded tidal swamps, a new classification category will have to be devised). Some of the most upriver tidal swamps, however, may indeed be seasonally flooded because groundwater (measured in the summer) fluctuates with the tide at 40-60 cm below ground, at a much lower depth than in the mid- to downriver swamps. They also lack hollows and are so devoid of the hummock and hollow pattern.

Hummocks are rarely completely inundated; groundwell data collected over one to two growing seasons indicate that the water level exceeded +15 cm less than 1% of the time at downriver sites, 0.25 % of the time at midriver sites, and never (during the period examined) at the most upriver site. Thus, the upper 15 cm of hummock soil, where the roots of woody swamp species are concentrated, are rarely flooded above ground.

Because these hummocks are composed primarly of a dense network of roots and minute rootlets (with little in the way of mineral soil), the water table rises and falls with little resistence in the upper root zone (height of the hummock). This means that the hydrodynamics of this portion of the root zone closely follows that of the tidal regime. The peaty organic consistency of the soil from the elevation of the hollow and lower inhibits a fast downward movement of the water table so that the water level does not drop much before the next high tide. Thus, tidal swamps probably rarely, and perhaps never, experience drought conditions.

Because flooding occurs in such a regular and predictable pattern and extreme conditions of flooding or drought are rare or absent in tidal swamps, this system may provide an ideal natural laboratory for studying the effects of hydrology and competition on vegetation patterns. Many nontidal systems experience extreme conditions of drought and flooding events that may affect recruitment patterns. Such extreme hydrologic events would thus be a source of variation effecting community structure and so would mask the effects of physiological tolerances and competitive interactions. For example, bald cypress requires dry conditions in order to germinate and establish itself in the community. After establishment, bald cypress is one of the most flood-tolerant species of temperate latitude swamps. However, without an occasional period of dryness (even if once a decade), it would not be able to persist in the community.

The vegtative communities of the Pamunkey River tidal swamps are in delicate balance with the present hydrologic regime. A slight increase of only a few cm in the river's mean water height could severely limit the ability of woody species to survive or outcompete herbaceous species if such an increase occurs at a rate faster than woody species can keep pace. Regional landscape subsidence from massive withdrawals of groundwater or thermal expansion of the oceans could both increase the rate of local sea level rise, which could prove to be deleterious to the continued existence of tidal swamps in lower Chesapeake Bay and perhaps in other areas as well.

Woody species appear to owe their continued existence to the presence of hummocks, usually only 15-20 cm in height, and in fact, appear to maintain hummocks in the face of a rising sea level by contributing the biomass necessary for their development. Thus, tidal swamps are precariously balanced at the upper portion of the tidal range and must keep pace with a rising sea level or perish. Any abrupt changes in the rate of sea level rise or the periodic removal of timber would likely have a devastating impact on the present distribution of tidal swamp communities.

As the human population of the region continues to grow, pressures to exploit the resources of the Pamunkey watershed will undoubtedly increase. Increased resource exploitation could compromise the integrity of the Pamunkey River ecosystem, including that of tidal swamp communities. Changes in the community structure of the vegetation could in turn lead to changes in flooding frequency and duration and nutrient cycling dynamics between the swamps and the subestuary. These changes might ultimately lead to a reduction of water quality in the subestuary and to a further reduction of fishery yields in Chesapeake Bay.

Future research needs

It appears that tidal swamps of the lower Chesapeake Bay have not received adequate attention from botanical collectors. A floristic study of the three counties bordering the Pamunkey River (New Kent, Hanover, and King William counties) could provide much needed information on the flora of tidal swamps.

Although the Pamunkey River harbors the most extensive system of tidal swamp forests of the lower Chesapeake Bay, somewhat extensive tracts of tidal swamps also occur along the Mattaponi (to the north of the Pamunkey) and the Chickahominy (to the south). The Chickahominy, in particular, is known to possess some extensive tracts of bald cypress. A comparison of the herbaceous communities of some of those bald cypress stands with data collected in this study could perhaps provide an indication as to whether bald cypress might have been more extensive on the Pamunkey River (this study found the herbaceous structure of two bald cypress codominated stands to be almost identical to that of the ash-blackgum stands).

Another way to examine the possible past importance of bald cypress is to pursue a paleoecological examination of pollen in peat from cores taken from tidal swamps. Such a study might also provide information on the progressive changes in the composition of plant communities along the river in relation to past sea level changes. This could provide information needed to make reasonable predictions about potential future changes in tidal swamp communities in response to sea level rise.

In order to predict the fate of tidal swamps in response to various rates of sea level rise, estimates on the rate of biomass production (addition) to swamp floor and sediment accretion rates could be measured. This type of study could be particularly useful if made in conjunction with the above mentioned paleoecological study.

Finally, we do not know how the nutrient regimes of these tidal swamps are related to the river ecosystem or whether the two community-types differ in nutrient cycling dynamics. Perhaps nutrient cycling dynamics differ between swamp-types and perhaps nutrient cycling dynamics are closely related to tidal fluctuations. We do not even know if production is actually transported to the river or whether tidal swamps are nutrient sinks or transformers. Such studies could provide much needed information on the value of this resource to other trophic levels.

This study provides much needed preliminary information on the structure of the primary producers of the ecosystem and their distributions in relation to environmental parameters. Much more scientific work needs to be done before we can fully appreciate the function, ecology, and beauty of tidal swamp ecosystems.

APPENDIX 1

Sampling gear:

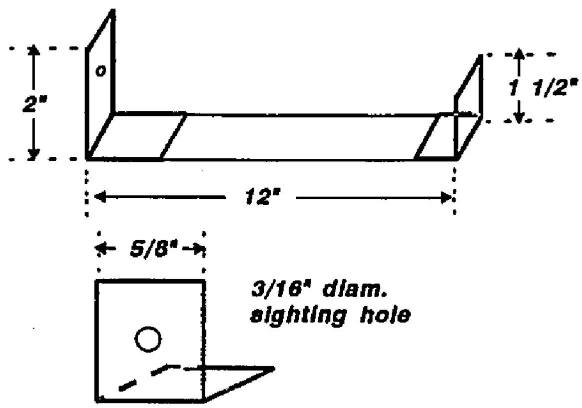
An angle gauge was used to sight a graduated pvc center rod to determine the edges of the 10 m diameter circles from within which densities were determined. The dimensions of the center stake and angle gauge are as follows (variations can be constructed).

a) Angle gauge construction: This can be constructed from a 1 foot wooden ruler (Fig. A1). Two different sized "L" braces should be bolted to each end of the ruler. Both "L" braces were 5/8" wide; one was 2" in length, the other was 1 1/2" in length. The flat edge of the ruler is turned vertically and the pvc rod is sighted through the hole in the larger "L" brace. The observer's position (at eye position) is considered to be within 10 m of the rod if the angle of sight subtended by the "L" brace at the opposite end of the ruler falls within the 10 m marks on the graduated center rod (see discussion of rod construction below).

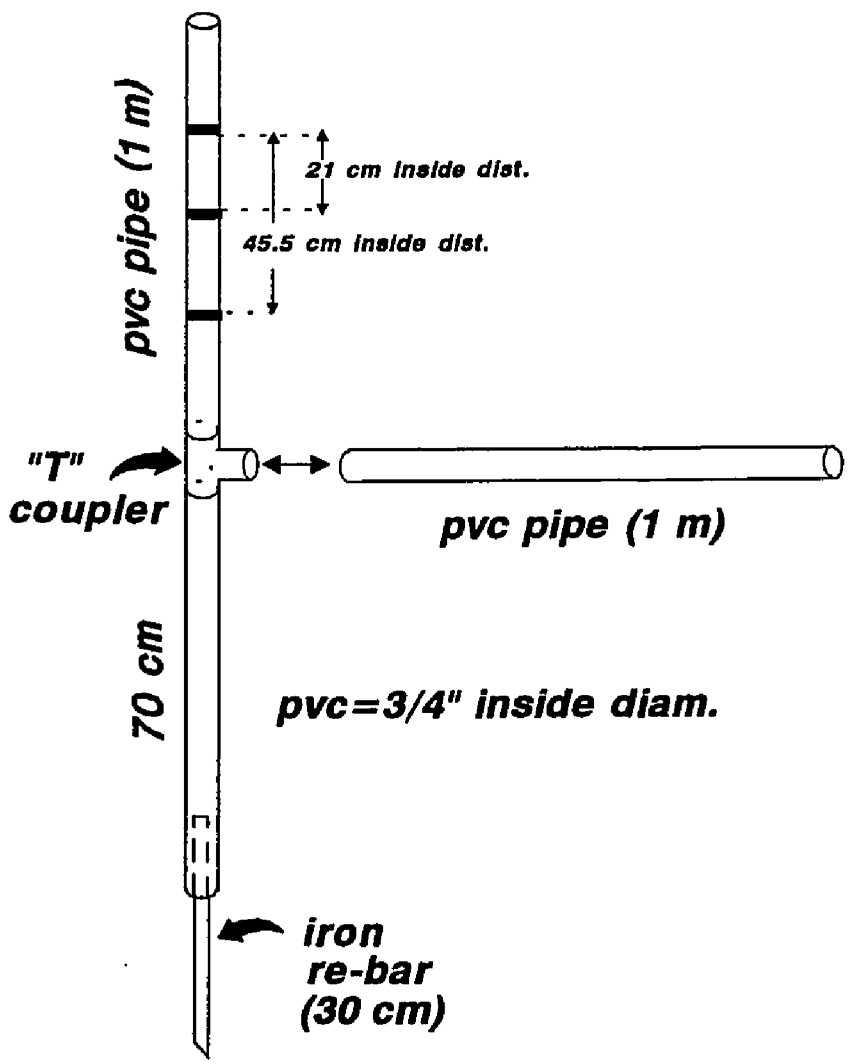
b) Sighting pole construction: Constructed from two 2 cm (3/4") inside diameter pvc pipes connected with a pvc "T"-coupler (Fig. A1b), the lower pipe section is 70 cm long and the upper one 1 m long. By imbedding a 30 cm long iron reinforcement bar (re-bar) of the approximate inside diameter of the lower pvc pipe, the iron rod (with pvc pipe atop it) can be easily driven vertically into the ground. The

Figure A1. Forest sampling gear constructed to measure 5 and 10 m radius circles. a) Angle gauge used to sight horizontal bands on the sighting pole located at the center of the circle. b) Sighting pole made of pvc pipe with horizontal bands. The sighting pole can be broken into 2 sections at the "T" coupler joint. Then the top piece and another 1 m long pvc pipe can be joined at right angles for two sides of a 1 m^2 sampling quadrat.

a) Angle Gauge



b) Sighting Pole & Quadrat Grid



upper pvc pipe should be wrapped with bands of black electrical tape (or painted in black bands) to serve as the sighting regions for the angle gauge. Place bands 21 cm apart for measuring 5 m diameter circles and 45.5 cm apart for measuring 10 m diameter circles (only applicable if the angle gauge is constructed with the above dimensions). The upper section of pvc pipe (of 1 m length) can be disconnected from the lower section at the junction with the with the "T"-coupler and joined to another pvc pipe of 1 m length to form two sides of a 1 m^2 vegetation sampling quadrat.

Groundwater well tape construction

A well tape was constructed to calibrate the data logger readings against the true groundwater water level fluctuations. The true depth to the water table from ground level was measured within tube-wells constructed of 2.5 cm (1") inside diameter slotted pvc tubes driven into the ground within 1 m of each of the data logger-monitored wells and capped with duct tape to prevent rainwater infiltration.

The well tape was constructed as follows. Speaker wire was attached with duct tape to a stainless steel rod one meter in length so as to extend slightly past one end of the rod; approximately 0.5 cm of wire was exposed at the overhanging end. A Micronta 8-range multitester was connected to the wire at the opposite (top) end. When the multitester set to K-ohms scale, the tester meter is deflected when the bare end of the speaker wires contact water. Thus, the rod can be lowered down the tube-well until a deflection is noted. The distance to the water table can then be calculated and the appropriate calibration entered into the data logger program.

Table A1. Data logger (Campbell CR-10) programs.

Program		(using 1 CR-10)	(using 2 CR-10s)
P04	01	1	2
	02	15	15
	03	1	1
	04	1	1
	05	5	5
	06	2500	2500
	07	1	1
	08	.12162	.12162
	09		
P86	01	10	10
P77	01	0110	0110
P70	01	1	2
	02	1	1
P72	01	1	1
	02	2	2

APPENDIX 2

Table A2. Environmental data collected from tidal swamp stands. Minerals are in parts per thousand, P=phosphorus, K=potassium, Ca=calcium, SS=soluble salts, Ntot=total nitrogen, Zn=zinc, Fe=iron, Al=aluminum, Cu=copper. Std=Stand #, holl=% Hollow coverage, pH=pH, %Om = % organic matter, Dist=distance in km from most downriver tidal swamp.

Std	Holl	pH	P	K	Ca	Mg	SS	Ntot	Zn	Fe	Al	Cu	%Om	Dist (km)
01	60.5	6.0	60	157	1200	120	576	-	6.1	14.0	39.55	0.18	52.5	2.10
02	88.7	5.5	21	91	1164	120	563	-	6.1	48.0	32.58	0.34	63.8	4.86
03	96.0	4.9	7	56	792	120	486	-	6.1	53.2	36.75	0.57	46.2	14.09
04	87.0	4.4	6	66	888	120	1152	-	6.1	72.1	39.97	0.49	57.1	0.00
05	55.2	4.3	7	63	936	120	1011	-	6.1	57.1	41.31	0.73	50.2	22.68
06	60.2	4.6	5	47	720	120	448	3	6.1	39.5	34.23	0.57	62.1	23.97
07	76.2	4.6	8	44	480	84	205	3	6.1	102.6	34.12	1.06	29.0	25.59
08	58.7	4.6	7	53	792	120	333	-	6.1	49.4	45.76	0.77	50.5	23.97
09	52.2	5.0	8	59	720	120	179	3	6.1	82.8	34.59	1.18	25.0	38.39
10	67.7	4.8	7	53	564	120	179	3	6.1	78.9	31.01	0.82	23.7	38.39
11	0.0	4.9	4	59	684	120	141	3	4.9	46.1	39.97	0.25	9.0	28.35
12	40.5	5.4	9	104	720	120	243	3	6.1	29.0	44.00	0.25	18.7	13.93
13	38.5	4.9	7	85	648	120	192	20	6.1	129.4	44.84	1.14	32.7	29.97
14	1.5	5.2	10	58	528	120	102	3	3.5	58.5	23.09	0.72	14.6	32.07
17	74.0	4.9	9	59	564	120	192	20	6.1	46.2	25.86	0.79	22.8	35.96
20	0.0	4.8	8	47	780	120	218	38	6.1	31.4	24.83	0.89	11.7	40.50
21	0.0	4.2	9	63	516	120	550	10	6.1	55.5	61.63	1.73	11.9	41.47
22	0.0	4.5	8	74	684	120	499	90	6.1	11.3	55.16	0.62	11.7	39.85
24	34.0	5.1	7	56	456	114	205	3	3.5	52.3	58.16	0.13	36.7	15.06
25	59.0	4.7	6	75	948	120	832	-	6.1	59.8	42.57	0.69	39.8	15.06
26	52.5	4.5	3	31	864	120	576	-	6.1	30.9	34.93	0.17	59.7	21.38
28	62.2	4.4	4	74	588	120	422	3	6.1	80.6	40.19	0.68	33.4	28.51
29	67.5	5.0	5	69	744	120	154	-	6.1	80.0	35.00	1.00	36.9	39.69

Table A3. Inter-correlation matrix for environmental variables measured in tidal swamps. Abbreviations follow those of Table 1, Appendix 2.

% holl	1.0000							
pH	.0339	1.0000						
ppt P	.0980	.7122	1.0000					
ppt K	.0555	.7100	.8331	1.0000				
ppt Ca	.4066	.3699	.5715	.5541	1.0000			
ppt SS	.3246	-.3418	.1138	.1289	.6058	1.0000		
ppt Fe	.1305	-.3359	-.4109	-.2613	-.4272	-.2121	1.0000	
% Om	.6445	-.0009	.2261	.0795	.6881	.6010	-.2415	1.0000
dist	-.4019	-.3570	-.4520	-.4648	-.6731	-.5850	.4127	-.6355
	% holl	pH	ppt P	ppt K	ppt Ca	ppt SS	ppt Fe	% Om

Table A4. Environmental data collected from montane forest stands of Whitetop and Mount Rogers, southwest Virginia. Minerals are in parts per thousand: P=phosphorus, K=potassium, Ca=calcium, SS=soluble salts, NNO3=nitrate nitrogen, Zn=zinc. Std=Stand #, elev=elevation, Asp=aspect, Slope= slope angle in degrees, pH=pH, %Om = % organic matter, %moist=%available moisture.

Std	elev	Asp	Slope	pH	P	K	Ca	Mg	%om	NNO3	Zn	Mn	%moist
1	1197	350	50.5	4.3	9	17	1020	50	22.4	75	6.1	16.1	68.8
2	1335	357	29.7	3.8	9	150	360	32	22.7	108	5.8	16.1	53.1
3	1433	205	3.8	3.5	15	55	132	15	21.1	53	2.0	16.1	53.7
4	1280	338	45.0	3.3	7	33	240	30	22.7	25	5.2	0.1	81.8
5	1494	4	40.5	3.6	13	91	156	20	21.6	83	4.9	16.1	84.2
6	1591	98	28.6	3.2	7	23	72	11	22.4	25	2.3	5.6	84.2
7	1585	125	21.6	4.0	4	28	192	12	17.0	28	4.6	16.1	69.7
8	1361	107	13.5	3.9	9	23	108	11	19.3	22	1.2	5.3	80.0
9	1439	92	34.2	4.1	60	25	216	24	14.5	20	1.5	5.3	78.4
10	1609	153	12.0	3.7	27	15	72	9	19.3	9	0.9	1.6	84.2
11	1426	205	38.3	4.6	10	26	600	43	17.9	21	2.4	3.8	84.2
12	1234	301	33.7	3.9	7	48	144	23	22.7	3	2.5	3.9	58.6
13	1209	272	37.4	4.8	8	36	516	38	14.7	9	1.7	4.9	58.6
14	1452	142	19.4	3.9	11	22	156	13	20.0	19	2.0	8.0	77.0
15	1487	260	30.6	3.3	60	33	192	13	15.1	16	1.2	8.0	71.5
16	1128	78	14.0	5.1	7	51	216	24	14.5	1	1.6	5.8	28.6
17	1285	182	34.7	4.3	14	42	420	29	17.0	17	2.4	8.0	64.1
18	1356	277	17.6	3.6	8	51	168	23	22.7	50	2.6	12.0	84.2
19	1311	350	32.4	4.3	13	15	432	9	16.1	4	1.4	7.0	84.2
20	1739	120	27.6	3.3	11	28	108	11	22.7	40	6.1	6.9	84.2
21	1209	260	6.3	4.7	9	125	120	26	19.3	1	2.6	3.1	36.2

Table A5. Inter-correlation matrix for environmental variables measured in southern Appalachian forests of Mount Rogers and Whitetop. Abbrevia-tions follow those of Table 1 (Appendix 2), plus Mg=magnesium, NN03= nitrate nitrogen. asp= slope aspect.

Elev	1.0000							
asp	-.0207	1.0000						
pH	-.6735	-.2497	1.0000					
ppt P	.2028	.1051	-.0375	1.0000				
ppt K	-.2591	.0399	.0852	-.1704	1.0000			
ppt Ca	-.4577	.0807	.4515	-.1183	-.1395	1.0000		
ppt Mg	-.5958	-.0645	.4808	-.0903	.1935	.8057	1.0000	
% Om	.2576	.2455	-.7258	-.3596	.2449	-.1117	-.0285	1.0000
ppt NN03	.1599	.3427	-.3817	-.0813	.4712	.2623	.2552	.5429
	Elev	pH	ppt P	ppt K	ppt Ca	ppt Mg	% Om	ppt NN03

Table A6. Organic matter concentrations for hummocks and hollows. Samples were were taken from various places within the stand and homogenized; hummock and hollow samples were taken separately. Samples were removed from the homogenate and dried at appr. 100 deg C. Three subsamples from each sample were combusted in a muffle oven at 500 deg. C for 6 hours. (Om= organic matter, Std=stand #, H=hummock, I=hollow, A, B, C= 3 subsamples).

Std	Tray wt	Soil+Tray	Soil+Tray-OM	%Om
1HA	1.392	7.210	4.165	0.523
1HB	1.585	7.142	4.247	0.520
1HC	1.595	7.202	4.226	0.530
1IA	1.315	10.470	5.641	0.527
1IB	1.306	11.643	6.254	0.521
1IC	1.305	9.609	5.192	0.531
2HA	1.305	7.625	3.959	0.580
2HB	1.303	7.320	3.839	0.578
2HC	1.307	7.708	3.992	0.580
2IA	1.310	6.400	2.921	0.683
2IB	1.306	3.478	1.934	0.710
2IC	1.308	4.440	2.262	0.695
3HA	1.311	8.592	4.234	0.598
3HB	1.306	7.634	3.878	0.593
3HC	1.309	6.819	3.524	0.598
3IA	1.388	11.465	8.196	0.324
3IB	1.560	8.116	5.881	0.340
3IC	1.541	8.494	6.229	0.325
4HA	1.386	8.510	4.391	0.578
4HB	1.552	6.974	3.936	0.560
4HC	1.563	8.244	4.487	0.562
4IA	1.298	7.677	3.991	0.577
4IB	1.304	8.252	4.258	0.574
4IC	1.298	8.600	4.378	0.578
5HA	1.300	7.235	4.269	0.499
5HB	1.291	6.826	4.003	0.510
5HC	1.285	6.839	4.042	0.503
5IA	1.285	6.341	3.843	0.494
5IB	1.295	5.438	3.419	0.487
5IC	1.293	5.679	3.414	0.516
6HA	1.295	8.799	3.379	0.722
6HB	1.298	10.509	4.304	0.673
6HC	1.308	6.452	2.599	0.749
6IA	1.307	6.924	3.954	0.528
6IB	1.307	6.195	3.646	0.521
6IC	1.303	8.125	4.476	0.534
7HA	1.304	11.539	8.712	0.276
7HB	1.310	13.185	9.816	0.283
7HC	1.318	10.955	8.207	0.285
7IA	1.317	12.320	9.088	0.293
7IB	1.317	12.126	8.947	0.294
7IC	1.322	14.623	10.50	0.310

Table A6 (cont.)

Std	Tray wt	Soil+Tray	Soil+Tray-OM	%Om
8HA	1.397	9.949	7.107	0.332
8HB	1.588	15.431	10.790	0.335
8HC	1.579	10.289	7.325	0.340
8IA	1.310	7.503	3.947	0.574
8IB	1.331	6.924	2.985	0.704
8IC	1.303	8.795	3.235	0.742
9HA	1.314	11.789	9.255	0.241
9HB	1.296	15.995	12.510	0.237
9HC	1.304	14.682	11.440	0.242
9IA	1.300	13.591	10.090	0.285
9IB	1.318	10.094	7.600	0.284
9IC	1.305	9.169	6.848	0.295
10HA	1.309	9.530	7.191	0.284
10HB	1.314	9.172	6.835	0.297
10HC	1.307	8.252	6.893	0.195
10IA	1.399	10.644	8.645	0.216
10IB	1.550	18.767	14.980	0.219
10IC	1.595	14.809	12.050	0.209
11HA	1.313	19.497	17.870	0.089
11HB	1.324	20.098	18.470	0.086
11HC	1.312	21.289	19.460	0.092
12HA	1.318	11.693	9.6470	0.197
12HB	1.324	14.354	11.830	0.193
12HC	1.293	13.100	10.680	0.205
12IA	1.555	14.658	12.390	0.173
12IB	1.577	12.106	10.270	0.174
12IC	1.570	16.250	13.630	0.178
13HA	1.303	8.333	6.308	0.288
13HB	1.297	11.851	8.674	0.301
13HC	1.318	7.380	5.453	0.317
13IA	1.308	15.438	10.400	0.356
13IB	1.304	13.644	9.301	0.351
13IC	1.309	14.763	10.080	0.348
14HA	1.287	18.254	16.620	0.096
14HB	1.284	19.874	18.150	0.092
14HC	1.284	14.561	11.320	0.244
14IA	1.1287	14.283	12.350	0.147
14IB	1.284	15.758	13.420	0.162
14IC	1.305	14.085	12.320	0.137
17HA	1.573	17.238	13.950	0.209
17HB	1.554	15.805	12.620	0.223
17HC	1.543	13.795	11.000	0.228
17IA	1.293	11.131	8.664	0.250
17IB	1.302	15.490	12.160	0.234
17IC	1.308	14.045	11.190	0.224
20HA	1.309	13.493	11.960	0.125
20HB	1.328	14.137	12.490	0.128
20HC	1.324	11.230	10.000	0.124
21HA	1.326	19.909	17.620	0.123
21HB	1.301	15.845	14.160	0.115
21HC	1.308	18.861	16.760	0.120

Table A6 (cont.)

Std	Tray wt	Soil+Tray	Soil+Tray-OM	%Om
22HA	1.312	16.973	14.640	0.148
22HB	1.324	15.515	13.430	0.147
22HC	1.327	21.644	18.770	0.142
24HA	1.561	11.937	9.242	0.259
24HB	1.541	13.777	10.950	0.231
24HC	1.540	13.432	10.660	0.233
24IA	1.556	12.859	6.832	0.533
24IB	1.550	11.322	6.188	0.525
24IC	1.569	10.671	5.942	0.519
25HA	1.559	10.451	7.074	0.379
25HB	1.575	13.890	9.080	0.390
25HC	1.300	10.525	6.884	0.394
25IA	1.330	11.314	7.109	0.421
25IB	1.320	8.326	5.523	0.400
25IC	1.326	12.182	7.846	0.399
26HA	1.578	8.300	4.680	0.538
26HB	1.577	10.054	5.703	0.513
26HC	1.579	8.102	4.590	0.538
26IA	1.313	4.494	2.379	0.664
26IB	1.313	5.288	2.636	0.667
26IC	1.315	4.721	2.497	0.652
28HA	1.565	14.500	11.070	0.265
28HB	1.546	15.635	11.730	0.277
28HC	1.546	12.636	9.530	0.280
28IA	1.325	6.416	4.398	0.396
28IB	1.320	10.025	6.500	0.404
28IC	1.316	6.703	4.603	0.389
29HA	1.324	10.653	7.833	0.302
29HB	1.322	11.326	8.425	0.289
29HC	1.308	10.972	8.124	0.294
29IA	1.302	8.925	5.516	0.447
29IB	1.298	7.792	4.961	0.435
29IC	1.300	7.826	4.898	0.448

Table A7. Inundation periods for five tidal swamps.

swamp-type		Ash-blackgum		Maple-sweetgum	
site	Cohoke	Elsing	Pampatike	Squaw	Randolph
area	365ha	65ha	5ha	35ha	5ha
river width	650m	525m	70m	425m	200m
# days of data	330d	221d	80d	86d	57d
distance upriver	2.1km	22.7km	38.4km	13.9km	28.3km
height (cm) above ground		Percent time inundated			
+25	0.00				
+23	0.01			0.00	
+21	0.03			0.03	
+19	0.05			0.07	
+17	0.06			0.11	
+15	0.07			0.13	
+13	0.14			0.15	
+11	0.18			0.17	
+ 9	0.25			0.37	
+ 7	0.34			0.49	
+ 5	0.65	0.00		0.66	
+ 3	0.95	0.06		0.81	
+ 1	1.34	0.17		1.02	
+ground-level	**1.55**	**0.25**		**1.26**	
-1	2.26	0.37	0.00	1.57	
-3	3.25	0.84	0.07	2.12	
-5	4.77	1.70	0.33	2.66	
-7	5.96	2.79	0.95	3.44	
-9	8.06	4.59	1.74	4.59	
-11	11.88	6.956	3.18	6.83	
-13	14.68	10.09	6.02	10.28	
---15	**19.78**	**17.35**	**13.47**	**19.45**	
-17	34.50	40.44	45.34	27.33	
-19	62.05	76.67	76.14	36.07	
-21	80.07	87.01	96.69	45.24	
-23	89.93	94.57	100.00	52.77	0.00
-25	94.54	98.04		58.35	5.04
-27	97.17	100.00		63.26	13.97
-29	99.14			65.35	36.61
-31	99.83			68.62	78.42
-33	100.00			73.08	100.00
-35				77.74	
-37				81.11	
-39				84.25	
-41				85.89	
-43				87.00	
-45				89.42	
-47				90.18	
-49				92.29	
-51				94.46	
-53				96.22	
-55				97.49	
-57				98.65	
-59				99.40	
-61				100.00	
total range	58cm	32cm	22cm	86cm	10cm

Table A7 (cont.)

Additional data points for the five swamps.

swamp-type	Ash-blackgum			Maple-sweetgum	
site	Cohoke	Elsing	Pampatike	Squaw	Randolph
-14	16.94	12.47	8.40	1.02	
-16	25.24	26.82	27.09	1.26	
-18	49.18	52.91	59.27	1.57	
-20	73.02	80.67	88.37	2.12	
-22	86.01	91.81		2.66	
-24				3.44	1.38
-26					8.88
-28					21.97
-30					50.99
-32					88.70

Table A8. Inundation data for the hummock site at Elsing Swamp.

	Elsing (hummock)
Area	65ha
River width	525m
# days of data	139d
Distance upriver	22.7km

Height (cm) above ground	Percent time inundated
++++++++++++++++++++++++top+of+hummock++++++++++++++++++++	
-1	
-3	
-5	
-7	
-9	0.00
-11	0.11
-13	0.41
-15	0.96
-17	1.78
-19	2.67
-21	4.27
-23	6.25
-25	15.92
-27	24.30
-29	41.35
-31	74.70
-33	88.10
-35	94.04
-37	98.30
-39	100.00

APPENDIX 3

Table A9. Partial floristic list of vascular plants found in freshwater tidal swamps along the Pamunkey River, Chesapeake Bay, USA. Includes only those species found within sampled plots in King William, New Kent, and Hanover Counties. Nomenclature follows Harvill et al. 1986).

PTERIDOPHYTA
OSMUNDACEAE
Osmunda regalis Linnaeus
POLYPODIACEA
Athyrium asplenioides (Michaux) Eaton
Sy = A. felix-femina var. aspenioides (Michaux) Farwell
Lorinseria areolata (Linneaus) Presl
Sy = Woodwardia aureolata (Linnaeus) T. Moore
Onoclea sensibilis Linnaeus
Thelypteris thelyperoides (Michaux) Holub
Sy = T. palustris Schott
GYMNOSPERMAE
CUPRESSACEAE
Juniperus virginiana Linnaeus
PINACEAE
Pinus taeda Linnaeus
TAXODIACEAE
Taxodium distichum (Linnaeus) L. C. Richard
ANGIOSPERMAE
ARACEAE
Arisaema triphyllum (Linnaeus) Schott
Peltandra virginica (Linnaeus) Schott
COMMELINACEAE
Commelina virginica Linnaeus
Murdannia keisak (Hasskarl) Hand.-Mazz.
Sy = Aneilema keisak Hasskarl
CYPERACEAE
Carex bromoides Willdenow
Carex crinata Lambert
C. debilis Michaux
C. gracillima Schweinitz
C. grayi Carey
C. intumescens Rudge
C. tribuloides Wahlenberg
DIOSCOREACEAE
Dioscorea villosa Linnaeus
IRIDACEAE
Iris sp. (prob. I. virginica Linnaeus)
JUNCACEAE
Juncus effusus Linnaeus
LILIACEAE
Melanthium virginicum Linnaeus
Smilax laurifolia Linnaeus
S. rotundifolia Linnaeus
Uvularia sessilifolia Linnaeus

Table A9 (cont.)

ORCHIDACEAE
- Habenaria clavellata (Michaux) Sprengel
  - Sy = Platanthera clavellata (Michaux) Leur

POACEAE
- Uniola latifolia Michaux
  - Sy = Chasmanthium latifolium (Michaux) Yates
- Cinna arundinacea Linnaeus
- Elymus virginicus Linnaeus
- Festuca obtusa Biehler
- Glyceria striata (Lambert) A. S. Hitchcock
- Leersia spp. Swartz (incl. L. lenticularis Michaux and L. oryzoides (Linnaeus) Swartz)
- Microstegium vimineum (Trinius) A. Camus
- Panicum clandestinum Linnaeus
- P. commutatum Schultes
- P. dichotomum Schultes

PONTEDERIACEAE
- Pontederia cordata Linnaeus
- Zizania aquatica Linneaus

ACERACEAE
- Acer negundo Linnaeus
- A. rubrum Linnaeus

ANACARDIACEAE
- Rhus radicans Linnaeus
  - Sy = Toxicodendron radicans (Linnaeus) Kuntze

ANNONACEAE
- Asimina triloba (Linnaeus) Dunal

APIACEAE
- Cicuta maculata Linnaeus
- Cryptotaenia canadensis (Linnaeus) A. P. de Candolle
- Oxypolis rigidior (Linnaeus) Rafinesque
- Sanicula canadensis Linnaeus

AQUIFOLIACEAE
- Ilex decidua Walter
- I. opaca Aiton
- I. verticillata (Linnaeus) Gray

ASTERACEAE
- Aster spp. Linnaeus (incl. A. novi-belgii Linnaeus, A. simplex Willdenow, and A. vimineus Lambert)
- Bidens coronata (Linnaeus) Britton
- B. tripartita Linnaeus
- Elephantopus carolinianus Raeusch
- Eupatoriadelphus dubius (Poiret) K. and R.
  - Sy = Eupatorium dubium Willdenow ex Poiret
- Rudbeckia laciniata Linnaeus
- Senecio aureus Linnaeus
- Solidago rugosa Miller

BALSAMINACEAE
- Impatiens capensis Meerburgh

BETULACEAE
- Alnus serrulata (Aiton) Willdenow
- Betula nigra Linnaeus
- Carpinus caroliniana Walter

Table A9 (cont.)

BIGNONIACEAE
    Bignonia capreolata Linnaeus
        Sy = Anistostichus capreolata (Linneaus) Bureau
    Campsis radicans (Linnaeus) Seemann
CAMPANULACEAE
    Lobelia cardinalis Linnaeus
CAPRIFOLIACEAE
    Lonicera japonica Thunberg
    Sambucus canadensis Linneaus
    Viburnum dentatum Linnaeus
    V. nudum Linnaeus
    V. prunifolium Linnaeus
CELASTRACEAE
    Euonymus americanus Linnaeus
CLETHRACEAE
    Clethra acuminta Michaux
CONVOLVULACEAE
    Cuscuta sp.
CORNACEAE
    Cornus foemina P. Miller
        Sy = C. stricta de Lambarck
EBENACEAE
    Diospyros virginiana Linnaeus
ERICACEAE
    Leucothoe racemosa (Linnaeus) Gray
    Lyonia ligustrina (Linnaeus) A. P. de Candolle
    Rhododendron atlanticum (Ashe) Rehder
    Vaccinium corymbosum Linnaeus
FABACEAE
    Amphicarpa bracteata (Linnaeus) Fernald
    Apios americana Medicus
    Desmodium laevigatum (Nuttall) A. P. de Candolle
FAGACEAE
    Fagus grandifolia Ehrhart
    Quercus lyrata Walter
    Q. laurifolia Michaux
    Q. michauxii Nuttall
    Q. phellos Linnaeus
    Q. pogoda Rafinesque
HAMMAELIDACEAE
    Liquidambar styraciflua Linnaeus
HYPERICACEAE
    Hypericum walteri
        Sy = Triandenum walteri (Gmelin) Gleason
JUGLANDACEAE
    Carya cordiformis (Wangenheim) K. Koch
LAMIACEAE
    Lycopus virginicus Linnaeus
LAURACEAE
    Lindera benzoin (Linnaeus) Blume
MAGNOLIACEAE
    Liriodendron tulipifera Linnaeus
    Magnolia virginiana Linnaeus

Table A9 (cont.)

MALVACEAE
Hibiscus moscheutos Linnaeus
MYRICACEAE
Myrica cerifera Linnaeus
NYSSACEAE
N. sylvatica var. biflora (Walter) Sargent
Nyssa syvatica var. sylvatica Marshall
OLEACEAE
Chionanthus virginicus Linnaeus
Fraxinus spp. Linnaeus (incl. F. profunda (Bush) Bush,
F.caroliniana P. Miller, and F. pennsylvanica Marshall)
ONAGRACEAE
Circaea lutetiana (Linnaeus)
Ludwigia alternifolia Linnaeus
L. palustris (Linnaeus) Elliott
PLATANACEAE
Platanus occidentalis Linnaeus
POLYGONACEAE
Polygonum arifolium Linnaeus
P. hydropiperoides Michaux
P. virginianum Linnaeus
Rumex verticillatus Linnaeus
RANUNCULACEAE
Thalictrum pubescens Pursh
Sy = T. polygamum Muhlenberg
ROSACEAE
Amelanchier arborea (Michaux f.) Fernald
Geum canadense Jacquin
Rosa palustris Marsh
Rubus spp. Linnaeus
RUBIACEAE
Galium obtusum Bigelow (prob. var. obtusum Bigelow)
Mitchella repens Linnaeus
SALICACEAE
Populus deltoides (Bartram) ex Marshall
SAURURACEAE
Saururus cernuus Linnaeus
SAXIFRAGACEAE
Itea virginica Linnaeus
SCROPHULARIACEAE
Chelone glabra Linnaeus
ULMACEAE
Celtis laevigata Willdenow
Ulmus americana Linnaeus
U. rubra Muhlenberg
URTICACEAE
Boehmeria cylindrica (Linnaeus) Schwartz
VIOLACEAE
Viola papilionacea Pursh
VITACEAE
Parthenocissus quinquefolia (Linnaeus) Planchon
Vitis sp. Adanson

Table A10. Alphabetical list of woody species.

Canopy

01 Acer rubrum
02 Betula nigra
03 Carya cordiformis
04 Celtis laevigata
05 Diosporum virginiana
06 Fagus grandifolia
07 Fraxinus spp.
08 Juniperus virginiana
09 Liriodendron tulipifera
10 Liquidambar styraciflua
11 Nyssa biflora
12 Nyssa sylvatica
13 Pinus taeda
14 Platanus occidentalis
15 Populus deltoides
16 Quercus laurifolia
17 Quercus lyrata
18 Quercus michauxii
19 Quercus phellos
20 Quercus pogoda
21 Taxodium ditichum
22 Ulmus americana
23 Ulmus rubra

Subcanopy

01 Alnus serrulata
02 Amelanchier arborea
03 Asimina triloba
04 Carpinus caroliniana
05 Chionanthus virginicus
06 Clethra acuminata
07 Cornus foemina
08 Diospyros virginiana
09 Euonymus americanus
10 Ilex decidua
11 Ilex opaca
12 Ilex verticillata
13 Itea virginica
14 Leucothoe racemosa
15 Lindera benzoin
16 Lyonia ligrustrina
17 Magnolia virginiana
18 Myrica cerifera
19 Rhododendron atlanticum
20 Rosa palustris
21 Sambucus canadensis
22 Vaccinium corymbosum
23 Viburnum dentatum
24 Viburnum nudum
25 Viburuum prunifolium

Vines

01 Apios americana
02 Bignonia capreolata
03 Campsis radicans
04 Cuscuta sp.
05 Dioscorea villosa
06 Lonicera japonica
07 Parthenocissus quinquefolia
08 Rhus radicans
09 Smilax laurifolia
10 Smilax rotundifolia
11 Vitus spp.

Table All. Alphabetical list of herbaceous species.

01 Arisaema triphyllum
02 Aster spp.
03 Athyrium asplenioides
04 Bidens coronata
05 Bidens tripartita
06 Boehmeria cylindrica
07 Carex bromoides
08 Carex crinita
09 Carex debilis
10 Carex gracillima
11 Carex grayi
12 Carex intumescens
13 Carex tribuloides
14 Chelone glabra
15 Cicuta maculata
16 Cinna arundinacea
17 Circaea lutetiana
18 Commelina virginica
19 Cryptotaenia canadensis
20 Desmodium laevigatum
21 Elephantopus carolinianus
22 Elymus virginicus
23 Eupatoriadelphus dubius
24 Festuca obtusa
25 Galium obtusum
26 Geum canadense
27 Glyceria striata
28 Habenaria clavellata
29 Hypericum walteri
30 Impatiens capensis
31 Iris virginica
32 Juncus effusus
33 Leersia spp.
34 Lobelia cardinalis
35 Lonicera japonica
36 Lorinseria areolata
37 Ludwigia alternifolia
38 Ludwigia palustris
39 Lycopus virginicus
40 Melanthium virginicum
41 Microstegium vimineum
42 Mitchella repens
43 Murdannia keisak
44 Onoclea sensibilis
45 Osmunda regalis
46 Oxypolis rigidior
47 Panicum clandestinum
48 Panicum commutatum
49 Panicum dichotomum
50 Peltandra virginica
51 Polygonum arifolium
52 Polygonum hydropiperoides
53 Polygonum virginianum
54 Pontedaria cordata
55 Rhus radicans
56 Rubus sp.
57 Rudbeckia laciniata
58 Rumex verticillatus
59 Saniculus canadensis
60 Saururus cernuus
61 Senecio aureus
62 Solidago rugosa
63 Thalictrum pubescens
64 Thelyteris thelyptroides
65 Uniola latifolia
66 Uvularia sessilifolia
67 Viola papilionacea
68 Zizania aquatica
69 Zizia aurea

APPENDIX 4

Table A12. Canopy composition of ash-blackgum tidal swamp communities.

	STANDS											
CANOPY	std06	std25	std07	std04	std03	std05	std02	std28	std01	std13	std09	std10
Basal Area (m^2/ha)	47.3	40.0	47.3	30.0	34.7	32.0	29.0	33.3	24.0	40.0	37.3	33.3
Importance value:												
Nyssa biflora	57.2	52.2	47.2	46.1	39.1	31.6	31.4	29.5	29.1	25.5	20.4	16.0
Fraxinus spp.	23.2	23.3	33.1	40.6	40.5	50.0	49.7	35.3	43.4	57.5	50.7	52.0
Acer rubrum	14.2	24.4	19.2	11.0	20.3	18.3	17.6	32.7	16.6	12.1	27.9	27.0
Taxodium distichum	1.4	-	-	-			-	-	-	-	-	-
Liquidambar styraciflua	1.4	-	-	1.7			1.2	-	-	-	-	-
Liriodendron tulipifera	2.6	-	-	-				-	6.7	-	-	-
Quercus phellos			0.6	-				0.7	3.2	2.1	-	-
Quercus michauxii				0.6				-	2.7		1.0	-
Diospyros virginiana								1.6	-		-	-
Quercus laurifolia									0.9		-	-
Quercus pogoda											0.9	1.7
Ulmus americana												2.3

Table A13. Subcanopy composition of ash-blackgum tidal swamp communities.

	STANDS											
	std06	std25	std07	std04	std03	std05	std02	std28	std01	std13	std09	std10
Density (#/ha)	2,376	1,825	2,376	3,946	2,928	5,331	3,469	4,583	276	4,753	1,953	5,559
Relative density:												
Lindera benzoin	29.6	41.9	51.8	-	13.0	32.8	33.0	32.4	13.6	19.6	-	-
Ilex verticillata	25.2	9.3	10.7	26.9	52.2	18.0	8.2	4.6	7.2	25.9	15.2	32.8
Ilex opaca	12.6	20.9	8.9	14.0	7.2	3.1	7.3	7.4	3.8	-	6.5	-
Alnus serrulata	3.0	16.3	-	8.6	20.2	15.6	-	4.6	4.2	40.2	-	6.9
Magnolia virginiana	9.6	-	8.9	1.1	-	-	1.8	-	-	-	-	-
Leucothoe racemosa	9.6	-	-	-	-	-	-	9.3	-	-	-	34.6
Viburnum nudum	0.7	-	-	-	4.3	5.5	13.7	-	0.4	-	-	-
Clethra acuminata	3.7	-	-	-	-	0.9	-	-	-	-	4.3	-
Vaccinium corymbosum		2.3	1.6	11.8	5.9	3.7	3.7	1.9	-	11.7	-	16.2
Viburnum dentatum		4.7	8.9	-	1.4	4.7	5.5	25.0	-	1.8	28.3	6.9
Chionanthus virginicus		2.3	3.6	-	-	-	-	-	-	-	-	-
Itea virginica		2.3	-	1.1	-	-	-	0.9	-	0.9	10.9	1.5
Viburnum prunifolium			5.4	-	-	-	-	3.7	-	-	6.5	-
Carpinus caroliniana			1.8	5.4	-	17.2	-	7.4	68.9	9.8	6.5	15.3
Myrica cerifera				9.7	-	-	-	-		-	-	-
Lyonia ligustrina				16.1	-	-	25.7	-		0.9	-	-
Amelanchier arborea				4.3	-	-	-	1.9		-	-	-
Cornus foemina				1.1	1.4	0.8	-	0.9		0.9	21.7	-
Ilex decidua						-	-					2.3
Sambucus canadensis						0.8	-					
Diospyros virginiana							1.9					

Table A14. Vine composition of ash-blackgum tidal swamp communities.

	STANDS											
	std06	std25	std07	std04	std03	std05	std02	std28	std01	std13	std09	std10
Density (# per ha)	3,140	3,267	3,734	1,655	3,119	4,540	3,480	3,819	3,766	5,092	2,801	1,570
Relative Density:												
Smilax rotundifolia	33.8	39.0	48.9	38.5	34.7	50.5	57.3	35.5	44.0	70.0	34.8	83.8
Apios americana	8.1	5.2	21.6	-	38.9	23.4	14.6	-	25.3	-	1.5	-
Bignonia capreolata	17.6	2.6	3.4	10.3	1.4	6.5	1.2	7.8	3.3	-	10.6	-
Dioscorea villosa	20.3	16.8	1.1	-	13.8	7.5	14.6	3.3	7.7	0.8	-	-
Rhus radicans	16.2	24.7	20.4	51.3	-	10.3	7.3	31.1	11.0	6.7	30.3	16.2
Parthenocissus quinquefolia	4.1	-	-		6.9	1.9	1.2	2.2	2.1	3.3	9.1	
Smilax laurifolia		10.4	4.5		1.4		2.4	18.9	2.2	18.3	-	
Campsis radicans		-			-		-	-	3.3		13.6	
Lonicera japonica		1.3			1.4		-	1.1	-			
Vitus sp.					-		1.2		1.1			
Cuscuta sp.					1.4							

Table A15. Herbaceous composition of ash-blackgum tidal swamp communities.

Importance value:	STANDS std01	std02	std03	std04	std05	std06	std07	std09	std10	std13	std25	std28
Uniola latifolium	2.9	-	0.8	1.9	4.1	2.0	4.7	3.7	2.3	14.2	-	-
Cinna arundinacea	5.8	1.8	0.8	1.5	2.5	4.1	4.7	9.9	2.3	2.8	-	0.9
Polygonum arifolium	16.6	21.4	22.2	25.9	16.4	12.8	30.1	25.4	17.0	21.4	21.2	20.8
Carex bromoides	25.4	8.5	0.8	16.6	-	18.0	-	-	12.2	5.4	2.5	17.8
Saururus cernuus	1.4	4.2	6.2	2.5	5.8	9.9	4.7	15.5	16.1	5.8	-	-
Rhus radicans	2.9	0.9	1.4	-	4.9	3.4	-	8.4	3.3	3.8	3.6	9.3
Peltandra virginica	2.7	6.7	14.9	-	5.8	4.8	5.8	11.1	16.2	4.7	0.9	9.0
Cicuta maculata	8.0	11.1	2.4	4.5	3.9	2.0	-	-	1.2	-	1.7	-
Solidago rugosa	5.0	2.7	1.6	1.9	4.1	-	-	2.3	-	-	5.3	-
Impatiens capensis	2.1	3.6	5.1	-	5.8	4.1	-	-	-	0.9	22.4	1.7
Aster spp.	-	-	1.6	-	1.6	2.7	1.1	3.4	15.7	4.2	-	6.0
Mitchella repens	1.4	0.9	-	-	1.6	4.5	-	2.5	-	1.9	3.5	-
Commelina virginica	2.2	-	0.8	-	13.4	-	1.7	-	1.1	3.6	-	1.6
Viola papilionacea	2.1	0.9	0.8	1.0	0.8	-	-	-	2.3	2.3	3.5	4.7
Oxypolis rigidior	0.7	-	0.8	1.9	0.8	-	-	-	-	0.9	1.7	2.3
Osmunda regalis	-	-	6.7	-	1.6	1.3	-	-	-	-	-	2.4
Boehmeria cylindrica	1.5	-	1.3	-	-	3.3	1.1	-	-	2.3	4.2	-
Thalictrum pubescens	-	1.8	-	1.0	0.8	1.3	-	-	-	0.9	0.9	2.6
Carex intumescens	3.6	0.9	3.2	-	3.3	0.7	-	-	-	5.6	3.4	0.9
Thelypteris thelyptroides	1.4	-	2.2	1.0	-	0.7	-	-	-	-	-	-
Galium obtusum	2.9	0.9	0.8	-	-	-	-	2.5	1.1	-	-	0.9
Panicum clandestinum	5.8	11.1	-	-	1.6	-	4.7	-	-	-	-	-
Lycopus virginicus	1.4	4.2	1.6	-	-	5.3	1.1	-	-	1.9	0.9	1.6
Sanicula canadensis	2.9	1.8	-	-	-	-	1.1	-	-	0.9	0.9	-
Senecio aureus	1.4	-	-	1.0	5.5	4.8	-	-	-	-	14.1	-
Carex crinita		-	4.1	-	0.8	2.0	2.8	1.2	2.3	-	-	-
Hypericum walteri		1.5	0.8	-	-	4.5	-	-	-	-	-	-
Murdannia keisak		7.2	11.7	7.8	-	3.8	16.1	-	-	11.1	-	2.9
Pontederia cordata		3.6	1.4		-	-		-	-	-	-	-
Arisaema triphyllum		2.4	-		0.8	0.7		-	1.1	1.4	-	0.9

Table A15. (cont.)

	STANDS											
	std01	std02	std03	std04	std05	std06	std07	std09	std10	std13	std25	std28
Melanthium virginicum		0.9	-	-	-	-	-	-	-	-	-	-
Rudbeckia laciniata		-	2.7	-	6.3	-	-	-	-	-	-	-
Elymus virginicus		-	-	-	0.8	-	-	1.2	-	-	-	-
Rubus sp.		-	-	-	-	-	-	2.3	-	-	-	-
Carex tribuloides		-	-	-	5.5	-	14.5	-	5.6	1.3	-	-
Carex gracillima		-	-	-	-	-	-	10.4		-	-	-
Eupatoriadelphus sp. (dubium or fistulosus)		-	0.8	-	0.8	-	-			-	-	-
Leersia sp. (lenticularis and oryzoides)		0.9	-	1.0		1.3	2.9			-	-	5.1
Geum canadense			2.4	-		0.7				-	-	0.9
Lobelia cardinalis				3.5		-				-	-	-
Glyceria striata				-		-				0.9	0.6	-
Habenaria clavellata				-		0.7				0.9	0.9	0.9
Zizania aquatica				20.1							-	-
Zizia aurea				-							-	-
Desmodium sp.(laevigatum?)				1.0							-	-
Microstigium vimineum											3.5	-
Iris virginica												0.9
Carex grayi												0.9
Uvularia sessilifolia												0.9

Table A16. Woody composition of bald cypress subtype of ash-blackgum tidal swamp communities.

	STANDS	
CANOPY	std08	std26
Basal Area (m^2/ha)	35.0	27.3
Importance value:		
Nyssa biflora	21.8	23.4
Fraxinus spp.	16.3	23.1
Acer rubrum	34.3	27.6
Taxodium distichum	24.9	17.6
Liquidambar styraciflua	-	6.1
Liriodendron tulipifera	2.6	-
Quercus lyrata		2.0
SUBCANOPY		
Density (#/ha)	4,328	4,371
Relative density:		
Lindera benzoin	38.6	3.9
Ilex verticillata	10.3	4.9
Ilex opaca	11.8	15.5
Alnus serrulata	-	1.9
Magnolia virginiana	1.5	16.5
Leucothoe racemosa	11.8	15.5
Viburnum nudum	-	-
Clethra acuminata	8.8	-
Viburnum dentatum	-	4.9
Chionanthus virginicus	-	4.9
Itea virginica	-	4.9
Viburnum prunifolium	1.5	-
Carpinus caroliniana	-	13.6
Cornus foemina	1.5	1.9
VINES		
Density (# per ha)	1,655	3,182
Relative Density:		
Smilax rotundifolia	19.2	66.6
Apios americana	3.8	12.0
Bignonia capreolata	23.1	-
Dioscorea villosa	34.6	4.0
Rhus radicans	15.4	5.3
Parthenocissus quinquefolia	7.7	6.7
Smilax laurifolia	-	5.3

Table A17. Herbaceous composition of the bald cypress subtype of ash-blackgum tidal swamp communities.

	STANDS	
	std 8	std26
Importance values:		
Peltandra virginica	4.8	0.8
Polygonum arifolium	20.2	9.6
Saururus cernuus	10.0	4.7
Carex bromoides	9.2	17.2
Murdannia keisak	1.7	0.8
Iris virginica	1.7	0.8
Mitchella repens	1.7	6.5
Senecio aureus	4.6	-
Osmunda regalis	2.8	-
Boehmeria cylindrica	6.1	3.3
Impatiens capensis	1.1	1.6
Rhus radicans	1.1	0.8
Bidens comosa	2.8	0.8
Lycopus virginicus	2.1	2.5
Cinna arundinacea	3.1	3.3
Glyceria striata	6.2	-
Polygonum sp. (prob. hydropiperoides)	2.2	0.8
Zizia aurea	1.1	-
Rubus	1.1	-
Chelone sp. (prob. glabra)	1.1	-
Aster sp.	2.8	1.6
Carex crinita	1.1	2.5
Thalictrum pubescens	1.1	-
Carex tribuloides	5.5	-
Hypericum walteri	1.7	3.3
Leersia sp. (lenticularis or oryzoides)	1.1	3.2
Lorinseria areolata		16.0
Panicum dichotum		1.6
Carex debilis		1.5
Cicuta maculata		2.5
Galium obtusum		1.6
Eupatoriadelphus sp. (dubius or fistulosum)		1.6
Saniculus canadensis		0.8
Thelypteris thelyptroides		1.6
Solidago rugosa		2.5
Oxypolis rigidior		0.8
Arisaema triphyllum		1.6
Pontederia cordata		1.6
Elephantopus caroliniana		1.6

Table A18. Woody composition of maple-sweetgum tidal swamp communities.

	STANDS					
	std12	std11	std14	std17	std21	std24
CANOPY						
Basal Area (m^2/ha)	32.0	28.0	34.7	34.7	26.0	35.0
Importance Value:						
Acer rubrum	46.7	37.6	32.9	30.1	46.1	26.0
Liquidambar styraciflua	24.9	21.1	12.7	31.5	16.5	23.1
Fraxinus spp.	10.7	10.0	29.6	5.3	23.6	-
Nyssa biflora	17.6	8.5	19.6	30.0	45.4	42.7
Quercus phellos		21.6	2.4	1.8	-	-
Ulmus rubra		-	-	0.6	5.3	1.3
Quercus michauxii		-	-	-	2.8	-
Quercus pogoda		-	-	-	2.8	-
Platanus occidentalis		1.2	-	-	-	-
Betula nigra			1.7	-	-	-
Fagus grandifolia			0.9	-	-	-
Pinus taeda				0.6	-	1.5
Celtis laevigata					2.8	-
Liriodendron tulipifera						2.8
Nyssa sylvatica						2.6
SUBCANOPY						
Density (#/ha)	4,031	2,801	2,376	6,238	1,485	1,400
Relative Density:						
Ilex verticillata	41.1	3.0	5.4	11.6	-	6.1
Magnolia virginiana	16.8	27.3	-	5.4	-	1.1
Ilex opaca	16.8	12.1	21.4	6.1	5.7	69.7
Alnus serrulata	9.5	9.1	-	15.0	-	-
Viburnum dentatum	4.2	39.4	-	5.4	-	-
Leucothoe racemosa	-	1.5	-	23.1	-	-
Vaccinium corymbosum	5.3	-	5.4	13.6	-	-
Carpinus caroliniana	-	1.5	42.9	4.1	5.7	-
Viburnum prunifolium	-	4.5	12.5	0.7	-	-
Itea virginica	3.2	-	-	0.7	-	6.1
Chionanthus virginicus	1.1	1.5	-	2.7	-	-
Cornus foemina	2.1		-	-	2.9	-
Lindera benzoin			8.9	0.7	2.9	9.1
Asimina triloba			-	-	51.4	-
Ilex decidua			3.6	-	31.2	-
Clethra acuminata				10.2		-
Euonymus americanus				0.7		-
Lyonia ligustrina						6.1

Table A18. (cont.)

	STANDS					
	std12	std11	std14	std17	std21	std24
VINES						
Density (#/ha)	3,013	721	2,503	4,201	1,146	955
Relative Density:						
Smilax rotundifolia	69.0	88.2	78.0	55.5	66.7	100.0
Rhus radicans	15.5	-	8.5	4.0	11.1	
Dioscorea villosa	11.3	-	5.1	29.3	-	
Lonicera japonica	1.4	-	-	-	-	
Smilax laurifolia	1.4	-	-	6.1	-	
Vitus sp.	1.4	-	-	-	3.7	
Bignonia capreolata		11.8	-	3.0	18.5	
Parthenocissus quinquefolia			8.5	-	-	
Apios americana				2.0	-	

Table A19. Herbaceous composition of maple-sweetgum tidal swamp communities.

	STANDS					
	std12	std11	std14	std17	std21	std24
Importance values:						
Carex intumescens	9.2	45.0	16.3	-	21.6	-
Sanicula canadensis	2.2	1.2	5.7	-	-	-
Commilina virginica	1.1	3.0	2.0	-	9.9	-
Solidago rugosa	3.5	14.1	-	-	-	-
Elephantopus caroliniana	1.1	3.1	-	-	-	-
Rubus sp.	3.1	4.8	-	-	-	2.9
Lorinseria areolata	1.1	1.2	-	-	-	5.9
Impatiens capensis	2.2	1.2	-	-	-	18.1
Carex bromoides	24.0	-	15.7	8.4	-	-
Saururus cernuus	10.0	-	2.0	30.9	16.2	6.2
Leersia spp.	1.1	-	20.8	-	-	-
Mitchella repens	3.5	-	10.0	2.1	-	15.4
Viola papilionacea	2.2	1.2	3.6	-	-	-
Glyceria striata	1.1	4.8	-	8.8	-	-
Galium obtusum	1.1	3.7	-	-	-	-
Rhus radicans	9.1	-	-	-	16.2	12.1
Boehmeria cylindrica	1.1	-	-	-	12.8	6.2
Onoclea sensibilis	3.1	-	-	-	-	12.2
Polygonum arifolium	3.1	-	4.0	2.1	-	5.8
Carex crinita	-	5.1	-	-	6.4	5.9
Athyrium asplenioides	-	7.2	-	-	-	2.9
Desmodium sp. (laevigatum?)	-	1.2	-	-	-	-
Juncus effusus	-	2.5	-	-	-	-
Panicum commutatum	-	1.2	-	-	-	-
Peltandra virginica	-		-	23.1	-	-
Microstigium vimineum	-		-	10.8	-	-
Aster spp.	-		4.0	-	6.4	-
Festuca obtusa	-		-	-	6.4	-
Carex tribuloides	-		-	-	3.5	-
Eupatoriadelphus dubius	1.1		-	-		-
Murdannia keisak	1.1		-	-		-
Thelypteris thelyptroides	8.2		-	-		-
Geum canadense	2.2		-	-		-
Senecio aureus	1.3		-	-		-
Polygonum virginiana	2.2		-	-		-
Panicun dichotum			-	-		-
Cinna arundinacea			7.7	-		-
Lycopus virginicus			7.7	-		2.9
Rumex verticillatus				2.1		-
Bidens comosa				3.9		-
Arisaema triphyllum				2.1		2.9
Uniola latifolium				-		
Polygonum hydropiperioides				5.4		

Table A20. Composition of Stand 29, a stand intermediate in composition between ash-blackgum and maple-sweetgum tidal swamp communities. This swamps is located near the head of a tidal tributary of the Pamunkey River to the east of and adjacent to "The Island" near Pampatike Landing.

CANOPY

Basal Area (m^2/ha)	31.3
Importance Value:	
Acer rubrum	30.8
Fraxinus spp.	29.4
Nyssa biflora	26.6
Quercus phellos	6.1
Quercus lyrata	4.1
Liquidambar styraciflua	1.9
Ulmus rubra	1.0

SUBCANOPY

Density (# per ha)	5,050
Relative Density:	
Cornus foemina	26.1
Ilex verticillata	21.0
Vaccinium corymbosum	16.2
Viburnum dentatum	15.1
Carpinus caroliniana	15.1
Alnus serrulata	7.6
Lyonia ligustrina	6.7
Amelanchier arborea	4.2
Ilex decidua	3.4
Itea virginica	0.8

VINES

Total Density (#/ha)	1,612
Relative Density:	
Smilax rotundifolia	86.8
Apios americana	5.3
Bignonia capreolata	2.6
Campsis radicans	2.6
Smilax laurifolia	2.6

HERBS

Importance Value:	
Saururus cernuus	26.6
Uniola latifolium	23.2
Peltandra virginica	11.7
Aster spp.	6.9
Carex tribuloides	6.9
Carex crinita	6.9
Rhus radicans	6.4
Boehmeria cylindrica	3.2
Circaea lutetiana	3.2
Panicum dichotum	1.6
Ludwigia palustris	1.6
Polygonum arifolium	1.6

Table A21. Woody composition of seasonally flooded tidal swamp communities.

	STANDS	
	std20	std22
CANOPY		
Basal Area (m^2/ha)	23.5	23.3
Importance Value:		
Fraxinus spp.	32.6	13.5
Acer rubrum	26.5	3.1
Fagus grandifolia	13.1	3.6
Liquidambar styraciflua	7.6	26.6
Nyssa sylvatica	2.1	2.8
Carya cordiformis	4.8	8.4
Ulmus americana	3.8	16.1
Quercus michauxii	-	10.5
Ulmus rubra	-	9.8
Quercus lyrata	5.5	-
Quercus pogoda	2.7	-
Quercus phellos	1.1	-
Populus deltoides	1.1	-
Platanus occidentalis		3.6
Pinus taeda		1.4
SUBCANOPY		
Total Density (#/ ha)	1,528	1,867
Relative Density:		
Ilex opaca	58.3	38.6
Asimina triloba	20.8	9.1
Carpinus caroliniana	12.5	29.5
Ilex decidua	4.2	15.9
Viburnum prunifolium	-	6.8
Lindera benzoin	4.2	
VINES		
Density (#/ha)	1,305	679
Relative Density:		
Smilax rotundifolia	56.1	56.2
Lonicera japonica	29.3	-
Bignonia capreolata	7.3	18.7
Vitus sp.	-	25.0
Parthenocissus quinquefolia	7.3	

Table A22. Herbaceous composition of seasonally flooded (upriver) tidal swamp communities.

	STANDS	
Importance Value:	std20	std22
Rhus radicans	30.7	7.2
Festuca obtusa	20.6	7.4
Carex debilis	8.1	38.1
Mitchella repens	7.4	11.7
Viola papilionacea	6.8	12.8
Carex intumescens	-	12.5
Geum canadense	-	8.7
Cryptotaenia canadensis	5.6	-
Chelone sp. (prob. glabra)	5.6	-
Aster spp.	2.5	1.4
Impatiens capensis	2.5	
Polygonum virginianum	2.5	
Elephantopus carolinianus	2.5	
Senecio aureus	2.5	
Lycopus virginicus	2.5	

APPENDIX 5

Table A23. Relative basal area, density, and Importance values (I.V.) for canopy species, by stand. Importance values are the averages of relative basal area and relative density of canopy species >10 cm dbh.

Stand 1
Total basal area: 24.0 m^2/ha
Total density: 1,218 stems/ha

	Relative Basal area	Relative Density	I.V.
Fraxinus spp.	41.6	45.2	43.4
Nyssa biflora	27.8	30.4	29.1
Acer rubrum	16.7	16.5	16.6
Liriodendron tulipifera	8.3	5.2	6.7
Quercus phellos	5.6	0.8	3.2
Quercus laurifolia	-	1.7	0.9

Stand 2
Total basal area: 29.0 m^2/ha
Total density: 1,012 stems/ha

	Relative Basal area	Relative Density	I.V.
Fraxinus spp.	46.6	52.9	49.7
Nyssa biflora	37.9	25.0	31.4
Acer rubrum	13.8	21.4	17.6
Liquidambar styraciflua	1.7	0.7	1.2

Stand 3
Total basal area: 34.2 m^2/ha
Total density: 922 stems/ha

	Relative Basal area	Relative Density	I.V.
Fraxinus spp.	40.5	31.0	40.5
Nyssa biflora	34.6	43.7	39.1
Acer rubrum	15.4	25.3	20.3

Table A23 (cont.)

Stand 4
Total basal area: 30.7 m^2/ha
Total density: 211 stems/ha

	Relative Basal area	Relative Density	I.V.
Nyssa biflora	44.4	-	46.1
Fraxinus spp.	40.0	60.0	40.6
Acer rubrum	13.3	20.0	11.0
Liquidambar styraciflua	2.2	20.0	1.7
Quercus michauxii	0.6	-	0.6

Stand 5
Total basal area: 32.0 m^2/ha
Total density: 827 stems/ha

	Relative Basal area	Relative Density	I.V.
Fraxinus spp.	50.0	50.0	50.0
Nyssa biflora	31.6	32.2	31.6
Acer rubrum	18.3	17.9	18.3

Stand 6
Total basal area: 47.3 m^2/ha
Total density: 806 stems/ha

	Relative Basal area	Relative Density	I.V.
Nyssa biflora	57.7	56.6	57.2
Fraxinus spp.	25.4	21.1	23.2
Acer rubrum	11.3	17.1	14.2
Liriodendron tulipifera	1.6	3.9	2.6
Taxodium distichum	1.4	1.3	1.4
Liquidambar styraciflua	2.8	-	1.4

Stand 7
Total basal area: 23.7 m^2/ha
Total density: 986 stems/ha

	Relative Basal area	Relative Density	I.V.
Nyssa biflora	53.5	40.9	47.2
Fraxinus spp.	25.4	40.9	33.1
Acer rubrum	21.1	17.2	19.2
Quercus phellos	-	1.2	0.6

Table A23 (cont.)

Stand 8
Total basal area: 35.0 m^2/ha
Total density: 715 stems/ha

	Relative Basal area	Relative Density	I.V.
Acer rubrum	31.4	37.2	34.3
Taxodium distichum	34.3	15.6	24.9
Nyssa biflora	25.7	17.8	21.8
Fraxinus spp.	5.7	26.7	16.3
Liriodendron tulipifera	2.0	2.2	2.6

Stand 9
Total basal area: 37.3 m^2/ha
Total density: 700 stems/ha

	Relative Basal area	Relative Density	I.V.
Fraxinus spp.	50.0	51.5	50.7
Acer rubrum	28.6	27.3	27.9
Nyssa biflora	19.6	21.2	20.4
Quercus pogoda	1.8	-	0.9

Stand 10
Total basal area: 33.3 m^2/ha
Total density: 795 stems/ha

	Relative Basal area	Relative Density	I.V.
Fraxinus spp.	56.0	48.0	52.0
Acer rubrum	26.0	28.0	27.0
Nyssa biflora	12.0	20.0	16.0
Ulmus americana	2.0	2.7	2.3
Quercus pogoda	2.0	1.3	1.7
Quercus michauxii	2.0	-	1.0

Stand 11
Total basal area: 28.0 m^2/ha
Total density: 562 stems/ha

	Relative Basal area	Relative Density	I.V.
Acer rubrum	35.7	39.6	37.6
Quercus phellos	26.2	17.0	21.6
Liquidambar styraciflua	21.4	20.8	21.1
Fraxinus spp.	4.8	15.1	10.0
Nyssa biflora	9.5	7.5	8.5
Platanus occidentalis	2.4	-	1.2

Table A23 (cont.)

Stand 12
Total basal area: 32.0 m^2/ha
Total density: 668 stems/ha

	Relative Basal area	Relative Density	I.V.
Acer rubrum	45.8	47.6	46.7
Liquidambar styraciflua	29.2	20.6	24.9
Nyssa biflora	14.6	20.6	17.6
Fraxinus spp.	10.4	11.1	10.7

Stand 13
Total basal area: 40.0 m^2/ha
Total density: 859 stems/ha

	Relative Basal area	Relative Density	I.V.
Fraxinus spp.	53.3	61.7	57.5
Nyssa biflora	35.0	16.0	25.5
Acer rubrum	8.3	16.0	12.1
Quercus michauxii	1.7	3.7	2.7
Quercus phellos	1.7	2.5	2.1

Stand 14
Total basal area: 34.7 m^2/ha
Total density: 711 stems/ha

	Relative Basal area	Relative Density	I.V.
Acer rubrum	40.4	25.4	32.9
Fraxinus spp.	25.0	34.3	29.6
Nyssa biflora	15.4	23.9	19.6
Liquidambar styraciflua	13.5	11.9	12.7
Quercus phellos	1.9	3.0	2.4
Betula nigra	1.9	1.5	1.7
Fagus grandifolia	1.9	-	0.9

Table A23 (cont.)

Stand 17
Total basal area: 34.7 m^2/ha
Total density: 891 stems/ha

	Relative Basal area	Relative Density	I.V.
Liquidambar styraciflua	25.0	38.1	31.5
Acer rubrum	36.5	23.8	30.1
Nyssa biflora	32.7	27.4	30.0
Fraxinus spp.	5.8	4.8	5.3
Quercus phellos	-	3.6	1.8
Ulmus rubra	-	1.2	0.6
Pinus taeda	-	1.2	0.6

Stand 20
Total basal area: 23.5 m^2/ha
Total density: 238 stems/ha

	Relative Basal area	Relative Density	I.V.
Fraxinus spp.	31.9	33.3	32.6
Acer rubrum	21.3	30.0	26.5
Fagus grandifolia	12.8	13.3	13.1
Liquidambar styraciflua	8.5	6.7	7.6
Quercus lyrata	4.3	6.7	5.5
Carya cordiformis	6.4	3.3	4.8
Ulmus americana	4.3	3.3	3.8
Quercus pogoda	2.1	3.3	2.7
Nyssa sylvatica	4.3	-	2.1
Quercus phellos	2.1	-	1.1
Populus deltoides	2.1	-	1.1

Stand 21
Total basal area: 26.0 m^2/ha
Total density: 350 stems/ha

	Relative Basal area	Relative Density	I.V.
Acer rubrum	43.6	48.5	46.1
Fraxinus spp.	23.1	24.2	23.6
Liquidambar styraciflua	17.9	15.2	16.5
Ulmus rubra	7.7	3.0	5.3
Quercus michauxii	2.6	3.0	2.8
Quercus pogoda	2.6	3.0	2.8
Celtis laevigata	2.6	3.0	2.8

Table A23 (cont.)

Stand 22
Total basal area: 23.3 m^2/ha
Total density: 254 stems/ha

	Relative Basal area	Relative Density	I.V.
Liquidambar styraciflua	26.6	33.3	26.6
Ulmus americana	16.1	8.3	16.1
Fraxinus spp.	13.5	4.2	13.5
Quercus michauxii	10.5	12.5	10.5
Ulmus rubra	9.8	8.3	9.8
Carya cordiformis	8.4	8.3	8.4
Fagus grandifolia	3.6	4.2	3.6
Platanus occidentalis	3.6	4.2	3.6
Acer rubrum	3.1	4.2	3.1
Nyssa sylvatica	2.8	-	2.8
Pinus taeda	1.4	-	1.4

Stand 24
Total basal area: 35.0 m^2/ha
Total density: 604 stems/ha

	Relative Basal area	Relative Density	I.V.
Nyssa biflora	48.5	36.8	42.7
Acer rubrum	25.7	26.3	26.0
Liquidambar styraciflua	20.0	26.3	23.1
Liriodendron tulipifera	2.9	2.6	2.8
Nyssa sylvatica	-	5.3	2.6
Pinus taeda	2.9	2.6	1.5
Ulmus rubra	-	2.6	1.3

Stand 25
Total basal area: 40.0 m^2/ha
Total density: 954 stems/ha

	Relative Basal area	Relative Density	I.V.
Nyssa biflora	63.3	41.1	52.2
Acer rubrum	20.0	28.9	24.4
Fraxinus spp.	23.2	30.0	23.3

Table A23 (cont.)

Stand 26
Total basal area: 27.3 m^2/ha
Total density: 636 stems/ha

	Relative Basal area	Relative Density	I.V.
Acer rubrum	19.5	33.3	27.6
Nyssa biflora	26.8	20.0	23.4
Fraxinus spp.	23.1	26.7	23.1
Taxodium distichum	22.0	13.3	17.6
Liquidambar styraciflua	7.3	5.0	6.1
Quercus lyrata	2.4	1.7	2.0

Stand 28
Total basal area: 33.3 m^2/ha
Total density: 753 stems/ha

	Relative Basal area	Relative Density	I.V.
Fraxinus spp.	16.0	28.1	35.3
Acer rubrum	16.1	49.3	32.7
Nyssa biflora	39.3	19.7	29.5
Diospyros virginiana	0.7	1.4	1.6
Quercus phellos	-	1.4	0.7

Stand 29
Total basal area: 31.3 m^2/ha
Total density: 541 stems/ha

	Relative Basal area	Relative Density	I.V.
Acer rubrum	36.2	25.5	30.8
Fraxinus spp.	25.6	33.3	29.4
Nyssa biflora	27.7	25.5	26.6
Quercus phellos	6.4	5.9	6.1
Quercus lyrata	4.3	3.9	4.1
Liquidambar styraciflua	-	3.9	1.9
Ulmus rubra	-	2.0	1.0

Table A24. Relative densities of saplings and seedlings of canopy species, by stand. Saplings are taller than 1.5 m and are less than 10 cm dbh. Seedlings are shorter than 1.5 m.

Stand 1
Total density (stems/ha):
Saplings 1,486
Seedlings 276

	Saplings	Seedlings
Fraxinus spp.	73.6	92.4
Nyssa biflora	15.0	-
Quercus laurifolia	10.7	-
Acer rubrum	0.7	-
Liriodendron tulipifera	-	7.5

Stand 2
Total density (stems/ha):
Saplings 955
Seedlings 319

	Saplings	Seedlings
Fraxinus spp.	73.3	90.0
Acer rubrum	20.0	10.0
Ulmus americana	6.7	-

Stand 3
Total density (stems/ha):
Saplings 3,355
Seedlings 1,994

	Saplings	Seedlings
Fraxinus spp.	91.1	93.6
Acer rubrum	5.1	-
Diosporos virginiana	2.5	-
Nyssa biflora	1.3	4.3
Juniperus virginiana	-	2.1

Table A24. (cont.)

Stand 4
Total density (stems/ha):
Saplings 2,419
Seedlings 211

	Saplings	Seedlings
Fraxinus spp.	45.6	60.0
Acer rubrum	42.1	20.0
Nyssa biflora	7.0	-
Liquidambar styraciflua	5.3	20.0

Stand 5
Total density (stems/ha):
Saplings 1,400
Seedlings 254

	Saplings	Seedlings
Fraxinus spp.	54.5	83.3
Acer rubrum	39.4	-
Nyssa biflora	6.1	16.7

Stand 6
Total density (stems/ha):
Saplings 1,825
Seedlings 297

	Saplings	Seedlings
Fraxinus spp.	55.8	57.1
Acer rubrum	34.9	14.2
Liquidambar styraciflua	4.6	14.2
Nyssa biflora	4.6	-
Juniperus virginiana	-	14.2

Stand 7
Total density (stems/ha):
Saplings 2,376
Seedlings 297

	Saplings	Seedlings
Fraxinus spp.	82.1	42.9
Nyssa biflora	10.7	28.6
Liquidambar styraciflua	7.1	14.3
Acer rubrum	-	14.3

Table A24. (Cont.)

Stand 8
Total density (stems/ha):
Saplings 1,273
Seedlings 445

	Saplings	Seedlings
Fraxinus spp.	50.0	57.1
Acer rubrum	40.0	-
Nyssa biflora	5.0	-
Juniperus virginiana	5.0	-
Taxodium distichum	-	42.8

Stand 9
Total density (stems/ha):
Saplings 1,060
Seedlings 2,376

	Saplings	Seedlings
Fraxinus spp.	73.3	80.3
Liquidambar styraciflua	10.6	3.6
Nyssa biflora	8.0	10.7
Acer rubrum	5.3	5.4
Quercus phellos	2.7	-

Stand 10
Total density (stems/ha):
Saplings 2,673
Seedlings 1,230

	Saplings	Seedlings
Fraxinus spp.	47.6	51.7
Nyssa biflora	25.4	13.7
Acer rubrum	14.3	-
Liquidambar styraciflua	7.9	24.1
Quercus pogoda	-	6.8
Ulmus americana	4.8	3.4

Stand 11
Total density (stems/ha):
Saplings 1,273
Seedlings 1,825

	Saplings	Seedlings
Liquidambar styraciflua	46.7	14.0
Fraxinus spp.	20.0	76.7
Nyssa biflora	16.7	4.6
Acer rubrum	6.7	-
Quercus phellos	6.7	2.3
Ulmus rubra	3.3	-
Juniperus virginiana	-	2.3

Table A24. (cont.)

Stand 12
Total density (stems/ha):
Saplings 4,328
Seedlings 1,867

	Saplings	Seedlings
Nyssa biflora	59.8	2.3
Fraxinus spp.	33.3	85.7
Liquidambar styraciflua	6.9	11.9

Stand 13
Total density (stems/ha):
Saplings 1,188
Seedlings 42

	Saplings	Seedlings
Fraxinus spp.	46.4	100.0
Nyssa biflora	21.4	
Acer rubrum	17.9	
Liquidambar styraciflua	7.1	
Quercus michauxii	3.6	
Fagus grandifolia	3.6	

Stand 14
Total density (stems/ha):
Saplings 1,570
Seedlings 424

	Saplings	Seedlings
Fraxinus spp.	70.3	50.0
Liquidambar styraciflua	13.5	30.0
Acer rubrum	8.1	10.0
Quercus phellos	2.7	10.0
Nyssa biflora	2.7	-
Ulmus rubra	2.7	-

Stand 17
Total density (stems/ha):
Saplings 2,291
Seedlings 636

	Saplings	Seedlings
Acer rubrum	46.3	46.7
Liquidambar styraciflua	22.2	20.0
Fraxinus spp.	18.5	6.7
Nyssa biflora	13.0	13.3
Quercus phellos	-	13.3

Table A24. (cont.)

Stand 20
Total density (stems/ha):
Saplings 159
Seedlings 255

	Saplings	Seedlings
Acer rubrum	60.0	-
Liquidambar styraciflua	20.0	-
Ulmus americana	20.0	12.5
Carya cordiformis	-	25.0
Fraxinus spp.	-	25.0
Nyssa biflora	-	12.5
Acer negunda	-	12.5
Fagus grandifolia	-	12.5

Stand 21
Total density (stems/ha):
Saplings 159
Seedlings 255

	Saplings	Seedlings
Acer rubrum	100.0	-
Fraxinus spp.		68.7
Ulmus americana		18.7
Liquidambar styraciflua		6.2
Celtis laevigata		6.2

Stand 22
Total density (stems/ha):
Saplings 255
Seedlings 6,577

	Saplings	Seedlings
Liquidambar styraciflua	33.3	1.3
Ulmus americana	33.3	1.3
Betula nigra	16.7	0.6
Populus deltoides	16.7	-
Quercus michauxii	-	78.7
Carya cordiformis	-	8.4
Fraxinus spp.	-	1.9
Acer rubrum	-	1.3

Stand 24
Total density (stems/ha):
Saplings 764
Seedlings 574

	Saplings	Seedlings
Fraxinus spp.	37.5	
Liquidambar styraciflua	25.0	77.7
Acer rubrum	12.5	-

Table A24. (cont.)

Stand 25
Total density (stems/ha):
Saplings 2,122
Seedlings 849

	Saplings	Seedlings
Fraxinus spp.	92.0	100.0
Acer rubrum	6.0	
Nyssa biflora	2.0	

Stand 26
Total density (stems/ha):
Saplings 1,570
Seedlings 1,400

	Saplings	Seedlings
Acer rubrum	59.5	42.4
Fraxinus spp.	21.2	18.9
Liquidambar styraciflua	10.8	27.3
Nyssa biflora	6.1	8.1
Quercus phellos	2.7	-
Ulmus americana	-	3.0

Stand 28
Total density (stems/ha):
Saplings 1,825
Seedlings 594

	Saplings	Seedlings
Fraxinus spp.	58.1	42.9
Nyssa biflora	18.6	14.3
Acer rubrum	14.0	7.1
Liquidambar styraciflua	9.3	7.1
Quercus laurifolia	-	21.4
Quercus phellos	-	7.1

Stand 29
Total density (stems/ha):
Saplings 1,103
Seedlings 296

	Saplings	Seedlings
Nyssa biflora	38.5	-
Acer rubrum	23.1	14.3
Fraxinus spp.	19.2	42.9
Ulmus rubra	7.7	
Liquidambar styraciflua	3.8	14.3
Quercus phellos	3.8	-
Quercus michauxii	3.8	
Quercus lyrata	-	28.6

Table A25. Relative densities of subcanopy adults and seedlings, by stand. Subcanopy adults are stems taller than 1.5 m, seedlings are shorter than 1.5 m.

Stand 1
Total density (stems/ha):
Adults 2,801
Seedlings 1,861

	Adults	Seedlings
Lindera benzoin	13.6	79.5
Carpinus caroliniana	68.9	2.3
Ilex verticillata	7.2	-
Alnus serrulata	4.2	2.3
Ilex opaca	3.8	2.3
Diospyros virginiana	1.9	-
Viburnum nudum	0.4	7.4
Viburnum dentatum		7.4
Myrica cerifera		2.8

Stand 2
Total density (stems/ha):
Adults 3,469
Seedlings 5,060

	Adults	Seedlings
Lindera benzoin	33.0	49.7
Lyonia ligrustrina	25.7	-
Viburnum nudum	13.7	11.9
Ilex verticillata	8.2	1.2
lex opaca	7.3	7.5
Viburnum dentatum	5.5	-
Vaccinium corymbosum	3.7	1.9
Magnolia virginiana	1.8	0.6
Clethra acuminata	0.9	7.5
Amelanchier arborea	-	0.6
Itea virginica	-	1.9

Stand 3
Total density (stems/ha):
Adults 979
Seedlings 2,291

	Adults	Seedlings
Ilex verticillata	52.2	14.8
Alnus serrulata	20.2	3.7
Lindera benzoin	13.0	66.7
Ilex opaca	7.2	1.8
Viburnum nudum	4.3	7.4
Viburnum dentatum	1.4	3.7
Cornus foemina	1.4	-
Rubus sp.	-	1.8

Table A25. (cont.)

Stand 4
Total density (stems/ha):
Adults 3,946
Seedlings 3,352

	Adults	Seedlings
Ilex verticillata	26.9	2.5
Lyonia ligrustrina	16.1	17.8
Ilex opaca	14.0	24.0
Vaccinium corymbosum	11.8	3.8
Myrica cerifera	9.7	20.2
Alnus serrulata	8.6	13.9
Amelanchier arborea	4.3	3.8
Carpinus caroliniana	5.4	-
Cornus foemina	1.1	2.5
Itea virginica	1.1	2.5
Magnolia virginiana	1.1	-
Lindera benzoin	-	7.6
Viburnum dentatum	-	1.3

Stand 5
Total density (stems/ha):
Adults 5,331
Seedlings 2,037

	Adults	Seedlings
Lindera benzoin	32.8	75.0
Ilex verticillata	18.0	4.2
Carpinus caroliniana	17.2	-
Alnus serrulata	15.6	8.3
Viburnum nudum	5.5	-
Viburnum dentatum	4.7	-
Ilex opaca	3.1	4.2
Vaccinium corymbosum	1.6	-
Cornus foemina	0.8	-
Sambucus canadensis	0.8	-
Chionanthus virginicus	-	6.2
Viburuum prunifolium	-	2.1

Table A25. (cont.)

Stand 6
Total density (stems/ha):
Adults 5,728
Seedlings 3,861

	Adults	Seedlings
Lindera benzoin	29.6	59.3
Ilex verticillata	25.2	4.4
Ilex opaca	12.6	4.4
Leucothoe racemosa	9.6	2.2
Magnolia virginiana	9.6	1.1
Vaccinium corymbosum	5.9	-
Clethra acuminata	3.7	-
Alnus serrulata	3.0	-
Viburnum nudum	0.7	6.6
Chionanthus virginicus	-	3.3
Cornus foemina	-	2.2
Carpinus caroliniana	-	1.1

Stand 7
Total density (stems/ha):
Adults 2,376
Seedlings 2,843

	Adults	Seedlings
Lindera benzoin	51.8	91.0
Ilex verticillata	10.7	-
Ilex opaca	8.9	3.0
Magnolia virginiana	8.9	-
Viburnum dentatum	8.9	1.5
Viburuum prunifolium	5.4	-
Chionanthus virginicus	3.6	-
Carpinus caroliniana	1.8	-
Viburnum nudum	-	4.5

Table A25. (cont.)

Stand 8
Total density (stems/ha):
Adults 4,328
Seedlings 5,919

	Adults	Seedlings
Lindera benzoin	36.8	44.1
Vaccinium corymbosum	16.2	1.1
Leucothoe racemosa	11.8	11.8
Ilex opaca	11.8	6.5
Ilex verticillata	10.3	6.5
Clethra acuminata	8.8	5.4
Cornus foemina	1.5	-
Magnolia virginiana	1.5	-
Viburuum prunifolium	1.5	2.2
Chionanthus virginicus	-	10.7
Viburnum nudum	-	8.6
Alnus serrulata	-	3.2

Stand 9
Total density (stems/ha):
Adults 1,952
Seedlings 2,291

	Adults	Seedlings
Viburnum dentatum	28.3	25.0
Cornus foemina	21.7	35.7
Ilex verticillata	15.2	1.8
Itea virginica	10.9	16.1
Carpinus caroliniana	6.5	3.6
Viburuum prunifolium	6.5	1.8
Ilex opaca	6.5	-
Clethra acuminata	4.3	-
Ilex decidua	-	8.9

Table A25. (cont.)

Stand 10
Total density (stems/ha):
Adults 5,559
Seedlings 5,342

	Adults	Seedlings
Leucothoe racemosa	34.6	39.7
Ilex verticillata	32.8	5.6
Carpinus caroliniana	15.3	5.6
Viburnum dentatum	6.9	15.9
Alnus serrulata	6.9	3.2
Ilex decidua	2.3	1.6
Itea virginica	1.5	17.5
Lindera benzoin	-	4.0
Rosa palustris	-	3.2
Clethra acuminata	-	1.6
Viburnum nudum	-	1.6
Ilex opaca	-	0.8

Stand 11
Total density (stems/ha):
Adults 2,801
Seedlings 6,789

	Adults	Seedlings
Viburnum dentatum	39.4	48.1
Magnolia virginiana	27.3	5.6
Ilex opaca	12.1	1.9
Alnus serrulata	9.1	4.4
Viburuum prunifolium	4.5	9.4
Ilex verticillata	3.0	3.1
Carpinus caroliniana	1.5	3.7
Chionanthus virginicus	1.5	-
Leucothoe racemosa	1.5	0.6
Viburnum nudum	-	17.5
Cornus foemina	-	1.2
Clethra acuminata	-	0.6
Lindera benzoin	-	0.6
Rhododendron atlanticum	-	0.6
Vaccinium corymbosum	-	0.6

Table A25 (cont.)

Stand 12
Total density (stems/ha):
Adults 4,031
Seedlings 3,395

	Adults	Seedlings
Ilex verticillata	41.1	27.5
Magnolia virginiana	16.8	5.0
Ilex opaca	16.8	2.5
Alnus serrulata	9.5	5.0
Vaccinium corymbosum	5.3	-
Viburnum dentatum	4.2	26.2
Itea virginica	3.2	17.5
Cornus foemina	2.1	-
Chionanthus virginicus	1.1	6.2
Lindera benzoin	-	2.5
Clethra acuminata	-	1.2
Unknown	-	1.2

Stand 13
Total density (stems/ha):
Adults 4,753
Seedlings 4,370

	Adults	Seedlings
Alnus serrulata	40.2	13.6
Ilex verticillata	25.9	28.2
Lindera benzoin	19.6	32.0
Carpinus caroliniana	9.8	1.0
Viburnum dentatum	1.8	1.0
Cornus foemina	0.9	-
Itea virginica	0.9	8.7
Lyonia ligrustrina	0.9	-
Viburnum nudum	-	12.6
Euonymus americanus	-	2.9

Table A25. (cont.)

Stand 14
Total density (stems/ha):
Adults 2,376
Seedlings 3,819

	Adults	Seedlings
Carpinus caroliniana	42.9	3.3
Ilex opaca	21.4	7.8
Viburuum prunifolium	12.5	8.9
Lindera benzoin	8.9	30.0
Ilex verticillata	5.4	7.8
Vaccinium corymbosum	5.4	-
Ilex decidua	3.6	5.5
Viburnum nudum	-	16.7
Viburnum dentatum	-	10.0
Itea virginica	-	8.9
Cornus foemina	-	1.1

Stand 17
Total density (stems/ha):
Adults 6,238
Seedlings 9,717

	Adults	Seedlings
Leucothoe racemosa	23.1	6.6
Alnus serrulata	15.0	2.2
Vaccinium corymbosum	13.6	4.8
Ilex verticillata	11.6	3.1
Clethra acuminata	10.2	68.1
Ilex opaca	6.1	0.9
Viburnum dentatum	5.4	5.7
Magnolia virginiana	5.4	-
Carpinus caroliniana	4.1	-
Chionanthus virginicus	2.7	-
Itea virginica	0.7	6.1
Euonymus americanus	0.7	0.4
Lindera benzoin	0.7	-
Viburuum prunifolium	0.7	-
Lyonia ligrustrina	-	1.3
Viburnum nudum	-	0.4

Table A25. (cont.)

Stand 20
Total density (stems/ha):
Adults 1,528
Seedlings 2,387

	Adults	Seedlings
Ilex opaca	58.3	5.3
Asimina triloba	20.8	77.3
Carpinus caroliniana	12.5	1.3
Lindera benzoin	4.2	6.7
Ilex decidua	4.2	1.3
Itea virginica	-	4.0
Amelanchier arborea	-	2.7
Euonymus americanus	-	1.3

Stand 21
Total density (stems/ha):
Adults 1,485
Seedlings 721

	Adults	Seedlings
Asimina triloba	51.4	76.5
Ilex decidua	31.2	11.8
Carpinus caroliniana	5.7	-
Ilex opaca	5.7	-
Lindera benzoin	2.9	11.8
Cornus foemina	2.9	-

Stand 22
Total density (stems/ha):
Adults 1,867
Seedlings 2,843

	Adults	Seedlings
Ilex opaca	38.6	13.4
Carpinus caroliniana	29.5	7.5
Ilex decidua	15.9	40.3
Asimina triloba	9.1	26.9
Viburuum prunifolium	6.8	10.4
Viburnum dentatum	-	1.5

Table A25. (cont.)

Stand 24
Total density (stems/ha):
Adults 2,100
Seedlings 2,164

	Adults	Seedlings
Ilex opaca	69.7	14.7
Lindera benzoin	9.1	26.4
Itea virginica	6.1	26.4
Ilex verticillata	6.1	11.8
Lyonia ligrustrina	6.1	2.9
Magnolia virginiana	1.1	14.7
Viburnum dentatum	-	2.9

Stand 25
Total density (stems/ha):
Adults 1,825
Seedlings 3,861

	Adults	Seedlings
Lindera benzoin	41.9	54.9
Ilex opaca	20.9	1.1
Alnus serrulata	16.3	3.3
Ilex verticillata	9.3	1.1
Viburnum dentatum	4.7	7.7
Chionanthus virginicus	2.3	27.8
Itea virginica	2.3	25.3
Vaccinium corymbosum	2.3	-
Magnolia virginiana	-	1.1
Cornus foemina	-	1.1

Stand 26
Total density (stems/ha):
Adults 4,371
Seedlings 4,031

	Adults	Seedlings
Magnolia virginiana	16.5	7.4
Ilex opaca	15.5	24.2
Leucothoe racemosa	15.5	-
Carpinus caroliniana	13.6	4.2
Vaccinium corymbosum	11.7	9.5
Chionanthus virginicus	4.9	10.5
Ilex verticillata	4.9	8.4
Viburnum dentatum	4.9	4.2
Itea virginica	4.9	-
Lindera benzoin	3.9	4.2
Alnus serrulata	1.9	3.1
Cornus foemina	1.9	4.2
Lyonia ligrustrina	-	15.8

Table A25. (cont.)

Stand 28
Total density (stems/ha):
Adults 4,583
Seedlings 4,837

	Adults	Seedlings
Lindera benzoin	32.4	44.7
Viburnum dentatum	25.0	10.5
Leucothoe racemosa	9.3	0.9
Ilex opaca	7.4	4.4
Carpinus caroliniana	7.4	1.8
Ilex verticillata	4.6	2.6
Alnus serrulata	4.6	1.8
Viburuum prunifolium	3.7	3.5
Amelanchier arborea	1.9	1.8
Vaccinium corymbosum	1.9	0.9
Itea virginica	0.9	25.4
Cornus foemina	0.9	0.9
Viburnum nudum	-	0.9

Stand 29
Total density (stems/ha):
Adults 5,050
Seedlings 2,037

	Adults	Seedlings
Cornus foemina	26.1	12.5
Ilex verticillata	21.0	52.1
Viburnum dentatum	15.1	2.1
Carpinus caroliniana	15.1	-
Alnus serrulata	7.6	16.7
Lyonia ligrustrina	6.7	4.2
Amelanchier arborea	4.2	2.1
Ilex decidua	3.4	2.1
Itea virginica	0.8	8.3

Table A26. Relative coverages, frequencies, maximum coverages, and importance values (I.V.) of herbaceous species, by stand.

Stand 1

	% Coverage	% Frequency	Maximum Coverage	I.V.
Carex bromoides	40.5	10.2	85.8	25.4
Polygonum arifolium	23.1	10.3	67.5	16.6
Cicuta maculata	8.0	8.0	15.0	8.0
Panicum clandestinum	4.7	6.8	15.0	5.8
Cinna arundinacea	4.7	6.8	15.0	5.8
Solidago rugosa	2.1	7.9	17.5	5.0
Carex intumescens	1.5	5.7	2.5	3.6
Galium obtusum	1.2	4.5	2.5	2.9
Rhus radicans	1.2	4.5	2.5	2.9
Uniola latifolia	2.4	3.4	15.0	2.9
Peltandra virginica	1.2	4.5	2.5	2.7
Commelina virginica	2.1	2.3	15.0	2.2
Impatiens capensis	0.9	3.4	2.5	2.1
Viola papilionacea	0.9	3.4	2.5	2.1
Boehmeria cylindrica	1.8	1.1	1.5	1.5
Mitchella repens	0.6	2.3	2.5	1.4
Saururus cernuus	0.6	2.3	2.5	1.4
Thelyteris thelyptroides	0.6	2.3	2.5	1.4
Oxypolis rigidior	0.3	1.1	2.5	0.7
Lycopus virginicus	0.6	2.3	2.5	0.6
Senecio aureus	0.6	2.3	2.5	0.6
Saniculus canadensis	1.2	1.5	2.5	0.4

Table A26. (cont.)

Stand 2

	% Coverage	% Frequency	Maximum Coverage	I.V.
Polygonum arifolium	28.9	14.1	67.5	21.4
Cicuta maculata	11.3	10.9	37.5	11.1
Panicum clandestinum	14.3	7.8	37.5	11.1
Carex bromoides	12.3	4.7	67.5	8.5
Murdannia keisak	9.8	4.7	67.5	7.2
Peltandra virginica	4.0	9.4	15.0	6.7
Lycopus virginicus	2.3	6.2	15.0	4.2
Saururus cernuus	0.5	3.1	37.5	4.2
Impatiens capensis	4.0	3.1	15.0	3.6
Pontedaria cordata	1.0	6.2	2.5	3.6
Solidago rugosa	0.7	4.7	2.5	2.7
Arisaema triphyllum	1.7	3.1	15.0	2.4
Cinna arundinacea	0.5	3.1	2.5	1.8
Saniculus canadensis	0.5	3.1	2.5	1.8
Thalictrum pubescens	0.5	3.1	2.5	1.8
Hypericum walteri	1.5	1.6	15.0	1.5
Carex intumescens	0.2	1.6	2.5	0.9
Galium obtusum	0.2	1.6	2.5	0.9
Leersia spp.	0.2	1.6	2.5	0.9
Melanthium virginicum	0.2	1.6	2.5	0.9
Mitchella repens	0.2	1.6	2.5	0.9
Rhus radicans	0.2	1.6	2.5	0.9
Viola papilionacea	0.2	1.6	2.5	0.9

Table A26. (cont.)

Stand 3	% Coverage	% Frequency	Maximum Coverage	I.V.
Polygonum arifolium	31.9	12.5	67.5	22.2
Peltandra virginica	17.3	12.5	67.5	14.9
Murdannia keisak	16.6	6.9	37.5	11.7
Osmunda regalis	7.8	5.6	67.5	6.7
Saururus cernuus	5.5	6.9	15.0	6.2
Impatiens capensis	3.3	6.9	15.0	5.1
Carex intumescens	0.9	5.6	2.5	3.2
Rudbeckia laciniata	2.7	2.8	15.0	2.7
Cicuta maculata	0.7	4.2	2.5	2.4
Geum canadense	0.7	4.2	2.5	2.4
Rhus radicans	1.3	1.4	15.0	2.3
Onoclea sensibilis	3.3	1.4	37.5	2.3
Thelyteris thelyptroides	1.6	2.8	15.0	2.2
Carex crinita	1.5	2.8	15.0	2.1
Solidago rugosa	0.4	2.8	2.5	1.6
Lycopus virginicus	0.4	2.8	2.5	1.6
Aster spp.	0.4	2.8	2.5	1.6
Boehmeria cylindrica	1.3	1.4	15.0	1.3
Carex bromoides	0.2	1.4	2.5	0.8
Cinna arundinacea	0.2	1.4	2.5	0.8
Commelina virginica	0.2	1.4	2.5	0.8
Eupatoriadelphus dubius	0.2	1.4	2.5	0.8
Galium obtusum	0.2	1.4	2.5	0.8
Oxypolis rigidior	0.2	1.4	2.5	0.8
Pontedaria cordata	0.2	1.4	2.5	0.8
Rubus sp.	0.2	1.4	2.5	0.8
Uniola latifolia	0.2	1.4	2.5	0.8
Viola papilionacea	0.2	1.4	2.5	0.8

Table A25 (cont.)

Stand 4	% Coverage	% Frequency	Maximum Coverage	I.V.
Polygonum arifolium	34.9	16.9	85.0	25.9
Zizania aquatica	25.0	15.3	97.5	20.1
Carex bromoides	19.7	13.6	67.5	16.6
Murdannia keisak	8.9	6.8	85.0	7.8
Cicuta maculata	2.2	6.8	15.0	4.5
Cicuta maculata	5.2	2.7	37.5	3.9
Lobelia cardinalis	1.9	5.1	15.0	3.5
Saururus cernuus	1.7	3.4	15.0	2.5
Osmunda regalis	0.5	3.4	2.5	1.9
Oxypolis rigidior	0.5	3.4	2.5	1.9
Peltandra virginica	0.5	3.4	2.5	1.9
Aster spp.	0.5	3.4	2.5	1.9
Solidago rugosa	0.5	3.4	2.5	1.9
Uniola latifolia	0.5	3.4	2.5	1.9
Cinna arundinacea	1.4	1.7	15.0	1.5
Desmodium laevigatum	0.2	1.7	2.5	1.0
Leersia spp.	0.2	1.7	2.5	1.0
Senecio aureus	0.2	1.7	2.5	1.0
Thalictrum pubescens	0.2	1.7	2.5	1.0
Thelyteris thelyptroides	0.2	1.7	2.5	1.0
Viola papilionacea	0.2	1.7	2.5	1.0

Table A25 (cont.)

Stand 5

	% Coverage	% Frequency	Maximum Coverage	I.V.
Polygonum arifolium	23.6	9.3	37.5	16.4
Commelina virginica	18.8	8.0	37.5	13.4
Rudbeckia laciniata	7.4	5.3	37.5	6.3
Impatiens capensis	3.6	8.0	15.0	5.8
Peltandra virginica	3.6	8.0	15.0	5.8
Saururus cernuus	4.9	6.7	15.0	5.8
Senecio aureus	7.1	4.0	37.5	5.5
Carex tribuloides	7.1	4.0	37.5	5.5
Rhus radicans	1.9	8.0	2.5	4.9
Solidago rugosa	1.6	6.7	2.5	4.1
Uniola latifolia	1.6	6.7	2.5	4.1
Carex intumescens	2.6	4.0	15.0	3.3
Cinna arundinacea	2.3	2.7	15.0	2.5
Aster spp.	0.6	2.7	2.5	1.6
Mitchella repens	0.6	2.7	2.5	1.6
Panicum clandestinum	0.6	2.7	2.5	1.6
Osmunda regalis	1.9	1.3	15.0	1.6
Arisaema triphyllum	0.3	1.3	2.5	0.8
Carex crinita	0.3	1.3	2.5	0.8
Elymus virginicus	0.3	1.3	2.5	0.8
Eupatoriadelphus dubius	0.3	1.3	2.5	0.8
Oxypolis rigidior	0.3	1.3	2.5	0.8
Thalictrum pubescens	0.3	1.3	2.5	0.8
Viola papilionacea	0.3	1.3	2.5	0.8

Table A26. (cont.)

Stand 6

	% Coverage	% Frequency	Maximum Coverage	I.V.
Carex bromoides	7.8	28.3	85.0	18.0
Polygonum arifolium	10.0	15.6	67.5	12.8
Saururus cernuus	5.6	14.3	67.5	9.9
Lycopus virginicus	4.4	6.2	15.0	5.3
Senecio aureus	7.8	1.8	2.5	4.8
Peltandra virginica	6.7	2.9	15.0	4.8
Mitchella repens	4.4	4.7	37.5	4.5
Hypericum walteri	3.3	5.7	37.5	4.5
Impatiens capensis	6.7	1.6	2.5	4.1
Cinna arundinacea	6.7	1.6	2.5	4.1
Murdannia keisak	3.3	4.4	37.5	3.8
Rhus radicans	5.6	1.3	2.5	3.4
Boehmeria cylindrica	3.3	3.4	15.0	3.3
Aster spp.	4.4	1.0	2.5	2.7
Carex crinita	2.2	1.8	15.0	2.0
Uniola latifolia	3.3	0.8	2.5	2.0
Cicuta maculata	3.3	0.8	2.5	2.0
Leersia spp.	2.2	0.5	2.5	1.3
Osmunda regalis	2.2	0.5	2.5	1.3
Thalictrum pubescens	2.2	0.5	2.5	1.3
Carex intumescens	1.1	0.3	2.5	0.7
Geum canadense	1.1	0.3	2.5	0.7
Habenaria clavellata	1.1	0.3	2.5	0.7
Thelyteris thelyptroides	1.1	0.3	2.5	0.7
Arisaema triphyllum	1.1	0.3	2.5	0.7

Stand 7

	% Coverage	% Frequency	Maximum Coverage	I.V.
Polygonum arifolium	43.3	17.0	67.5	30.1
Murdannia keisak	19.4	12.8	67.5	16.1
Carex tribuloides	16.2	12.8	67.5	14.5
Chelone glabra	3.2	8.5	15.0	5.8
Saururus cernuus	3.0	6.4	15.0	4.7
Uniola latifolia	3.0	6.4	15.0	4.7
Cinna arundinacea	0.9	8.5	2.5	4.7
Carex intumescens	3.0	6.4	15.0	4.7
Leersia spp.	1.6	4.3	15.0	2.9
Carex crinita	3.5	2.1	37.5	2.8
Commelina virginica	1.4	2.1	15.0	1.7
Aster spp.	0.2	2.1	2.5	1.1
Boehmeria cylindrica	0.2	2.1	2.5	1.1
Iris virginica	0.2	2.1	2.5	1.1
Lycopus virginicus	0.2	2.1	2.5	1.1
Rhus radicans	0.2	2.1	2.5	1.1
Saniculus canadensis	0.2	2.1	2.5	1.1

Table A26. (cont.)

Stand 8

	% Coverage	% Frequency	Maximum Coverage	I.V.
Polygonum arifolium	24.1	16.4	15.0	20.2
Saururus cernuus	11.0	1.1	67.5	10.0
Carex bromoides	11.2	7.3	85.0	9.2
Glyceria striata	8.8	3.6	67.5	6.2
Boehmeria cylindrica	4.8	7.5	37.5	6.1
Carex tribuloides	9.1	1.8	85.0	5.5
Peltandra virginica	2.4	7.3	15.0	4.8
Senecio aureus	5.6	3.6	37.5	4.6
Cinna arundinacea	0.8	5.4	2.5	3.1
Aster spp.	2.1	3.6	15.0	2.8
Osmunda regalis	1.9	3.6	15.0	2.8
Bidens coronata	1.9	3.6	15.0	2.8
Polygonum hydropiperoides	2,7	1.8	2,5	2.2
Lycopus virginicus	0.5	3.6	2.5	2.1
Hypericum walteri	1.6	1.8	15.0	1.7
Murdannia keisak	1.6	1.8	15.0	1.7
Iris virginica	1.6	1.8	15.0	1.7
Mitchella repens	1.6	1.8	15.0	1.7
Leersia spp.	0.3	1.8	2.5	1.1
Carex crinita	0.3	1.8	2.5	1.1
Impatiens capensis	0.3	1.8	2.5	1.1
Chelone glabra	0.3	1.8	2.5	1.1
Rhus radicans	0.3	1.8	2.5	1.1
Rubus sp.	0.3	1.8	2.5	1.1
Thalictrum pubescens	0.3	1.8	2.5	1.1
Zizia aurea	0.3	1.8	2.5	1.1

Stand 9

	% Coverage	% Frequency	Maximum Coverage	I.V.
Polygonum arifolium	32.2	18.7	67.5	25.4
Saururus cernuus	14.5	16.6	37.5	15.5
Peltandra virginica	9.8	12.5	37.5	11.1
Carex bromoides	12.5	8.3	37.5	10.4
Cinna arundinacea	15.7	4.2	85.0	9.9
Rhus radicans	4.3	12.5	2.5	8.4
Uniola latifolia	1.2	6.2	2.5	3.7
Aster spp.	2.7	4.2	15.0	3.4
Galium obtusum	0.8	4.2	2.5	2.5
Mitchella repens	0.8	4.2	2.5	2.5
Rubus sp.	2.4	2.1	15.0	2.3
Solidago rugosa	2.4	2.1	15.0	2.3
Carex crinita	0.4	2.1	2.5	1.2
Elymus virginicus	0.4	2.1	2.5	1.2

Table A26. (cont.)

Stand 10

	% Coverage	% Frequency	Maximum Coverage	I.V.
Polygonum arifolium	16.2	17.9	37.5	17.0
Peltandra virginica	17.4	15.1	37.5	16.2
Saururus cernuus	19.1	13.2	37.5	16.1
Aster spp.	18.3	13.2	37.5	15.7
Carex bromoides	17.0	7.5	67.5	12.2
Carex tribuloides	3.8	7.5	15.0	5.6
Rhus radicans	3.0	3.7	15.0	3.3
Carex crinita	0.9	3.7	2.5	2.3
Cinna arundinacea	0.8	3.8	2.5	2.3
Uniola latifolia	0.8	3.8	2.5	2.3
Viola papilionacea	0.9	3.7	2.5	2.3
Commelina virginica	0.4	1.9	2.5	1.1
Galium obtusum	0.4	1.9	2.5	1.1
Cicuta maculata	0.4	1.9	2.5	1.1
Arisaema triphyllum	0.4	1.9	2.5	1.1

Stand 11

	% Coverage	% Frequency	Maximum Coverage	I.V.
Carex intumescens	67.9	22.2	85.0	45.0
Solidago rugosa	10.4	17.8	37.5	14.1
Athyrium asplenioides	5.6	8.8	37.5	7.2
Carex crinita	3.6	6.7	15.0	5.1
Rubus sp.	2.0	6.7	15.0	4.8
Glyceria striata	2.0	6.7	15.0	4.8
Galium obtusum	0.8	6.7	2.5	3.7
Elephantopus carolinianus	1.8	4.4	15.0	3.1
Commelina virginica	3.8	2.2	37.5	3.0
Juncus effusus	0.6	4.4	2.5	2.5
Impatiens capensis	0.3	2.2	2.5	1.2
Desmodium laevigatum	0.3	2.2	2.5	1.2
Lorinseria areolata	0.3	2.2	2.5	1.2
Panicum commutatum	0.3	2.2	2.5	1.2
Saniculus canadensis	0.3	2.2	2.5	1.2
Viola papilionacea	0.3	2.2	2.5	1.2

Table A26. (cont.)

Stand 12

	% Coverage	% Frequency	Maximum Coverage	I.V.
Carex tribuloides	34.5	13.5	85.0	24.0
Saururus cernuus	14.2	5.8	67.5	10.0
Carex intumescens	5.0	13.2	37.5	9.1
Rhus radicans	12.4	5.8	67.5	9.1
Thelyteris thelyptroides	12.7	3.8	85.0	8.2
Mitchella repens	1.1	5.8	2.5	3.5
Solidago rugosa	1.1	5.8	2.5	3.5
Onoclea sensibilis	2.5	3.8	15.0	3.1
Rubus sp.	2.5	3.8	15.0	3.1
Polygonum arifolium	2.5	3.8	15.0	3.1
Polygonum virginianum	0.7	3.8	2.5	2.2
Geum canadense	0.7	3.8	2.5	2.2
Ludwigia alternifolia	0.7	3.8	2.5	2.2
Viola papilionacea	0.7	3.8	2.5	2.2
Impatiens capensis	0.7	3.8	2.5	2.2
Senecio aureus	0.7	1.9	2.5	1.3
Leersia spp.	0.4	1.9	2.5	1.1
Lorinseria areolata	0.4	1.9	2.5	1.1
Boehmeria cylindrica	0.4	1.9	2.5	1.1
Commelina virginica	0.4	1.9	2.5	1.1
Elephantopus carolinianus	0.4	1.9	2.5	1.1
Eupatoriadelphus dubius	0.4	1.9	2.5	1.1
Murdannia keisak	0.4	1.9	2.5	1.1
Glyceria striata	0.4	1.9	2.5	1.1
Galium obtusum	0.4	1.9	2.5	1.1

Table A26. (cont.)

Stand 13

	% Coverage	% Frequency	Maximum Coverage	I.V.
Polygonum arifolium	27.4	15.5	85.0	21.4
Uniola latifolia	23.3	5.2	15.0	14.2
Murdannia keisak	15.6	6.9	97.5	11.2
Saururus cernuus	6.4	5.2	37.5	5.8
Carex intumescens	4.3	6.9	15.0	5.6
Carex bromoides	7.5	3.4	67.5	5.4
Peltandra virginica	2.5	6.9	15.0	4.7
Aster spp.	1.6	6.9	15.0	4.2
Rhus radicans	0.7	6.9	2.5	3.8
Commelina virginica	3.8	3.4	37.5	3.6
Cinna arundinacea	0.5	5.2	2.5	2.8
Boehmeria cylindrica	1.3	3.4	15.0	2.3
Viola papilionacea	1.3	3.4	15.0	2.3
Lycopus virginicus	0.4	3.4	2.5	1.9
Mitchella repens	0.4	3.4	2.5	1.9
Arisaema triphyllum	1.1	1.7	15.0	1.4
Carex tribuloides	1.1	1.5	15.0	1.3
Saniculus canadensis	0.2	1.7	2.5	0.9
Thalictrum pubescens	0.2	1.7	2.5	0.9
Glyceria striata	0.2	1.7	2.5	0.9
Habenaria clavellata	0.2	1.7	2.5	0.9
Impatiens capensis	0.2	1.7	2.5	0.9

Stand 14

	% Coverage	% Frequency	Maximum Coverage	I.V.
Leersia spp.	31.7	10.0	97.5	20.8
Carex intumescens	19.3	13.3	37.5	16.3
Carex bromoides	21.4	10.0	37.5	15.7
Mitchella repens	3.4	16.7	2.5	10.0
Lycopus virginicus	5.5	10.0	15.0	7.7
Cinna arundinacea	5.5	10.0	15.0	7.7
Saniculus canadensis	4.8	6.7	15.0	5.7
Aster spp.	1.4	6.7	2.5	4.0
Polygonum arifolium	1.4	6.7	2.5	4.0
Viola papilionacea	4.1	3.3	15.0	3.6
Saururus cernuus	0.7	3.3	2.5	2.0
Commelina virginica	0.7	3.3	2.5	2.0

Table A26. (cont.)

Stand 17

	% Coverage	% Frequency	Maximum Coverage	I.V.
Saururus cernuus	39.7	22.2	37.5	30.9
Peltandra virginica	24.0	22.2	37.5	23.1
Microstegium vimineum	6.9	14.8	15.0	10.8
Glyceria striata	10.3	7.4	37.5	8.8
Carex bromoides	13.2	3.7	67.5	8.4
Polygonum hydropiperoides	3.4	7.4	15.0	5.4
Bidens tripartita	0.5	7.4	2.5	3.9
Mitchella repens	0.5	3.7	2.5	2.1
Polygonum arifolium	0.5	3.7	2.5	2.1
Arisaema triphyllum	0.5	3.7	2.5	2.1
Rumex verticillatus	0.5	3.7	2.5	2.1

Stand 20

	% Coverage	% Frequency	Maximum Coverage	I.V.
Rhus radicans	43.0	18.5	37.5	30.7
Festuca obtusa	19.0	22.2	15.0	20.6
Carex debilis	10.2	11.1	15.0	8.1
Mitchella repens	3.8	11.1	2.5	7.4
Viola papilionacea	2.5	11.1	2.5	6.8
Cryptotaenia canadensis	7.6	3.7	15.0	5.6
Chelone glabra	7.6	3.7	15.0	5.6
Impatiens capensis	1.3	3.7	2.5	2.5
Lycopus virginicus	1.3	3.7	2.5	2.5
Polygonum virginianum	1.3	3.7	2.5	2.5
Senecio aureus	1.3	3.7	2.5	2.5
Aster spp.	1.3	3.7	2.5	2.5
Elephantopus carolinianus	1.3	3.7	2.5	2.5

Stand 21

	% Coverage	% Frequency	Maximum Coverage	I.V.
Carex intumescens	25.6	17.6	37.5	21.6
Rhus radicans	14.9	17.6	15.0	16.2
Saururus cernuus	14.9	17.6	15.0	16.2
Boehmeria cylindrica	14.0	11.7	15.0	12.8
Commelina virginica	8.1	11.7	15.0	9.9
Carex crinita	7.0	5.9	15.0	6.4
Aster spp.	7.0	5.9	15.0	6.4
Festuca obtusa	7.0	5.9	15.0	6.4
Carex tribuloides	1.2	5.9	2.5	3.5

Table A26. (cont.)

Stand 22	% Coverage	% Frequency	Maximum Coverage	I.V.
Carex debilis	54.1	22.2	37.5	38.1
Viola papilionacea	5.7	20.0	2.5	12.8
Carex intumescens	5.0	20.0	2.5	12.5
Mitchella repens	10.1	13.3	15.0	11.7
Geum canadense	6.3	11.1	15.0	8.7
Festuca obtusa	8.2	6.7	15.0	7.4
Rhus radicans	10.1	4.4	37.5	7.2
Carex gracillima	0.6	2.2	2.5	1.4

Stand 24	% Coverage	% Frequency	Maximum Coverage	I.V.
Athyrium asplenioides	1.3	4.5	2.5	22.8
Impatiens capensis	22.6	13.6	2.5	18.1
Mitchella repens	17.3	6.5	15.0	15.4
Onoclea sensibilis	20.0	4.5	37.5	12.2
Rhus radicans	10.7	13.6	15.0	12.1
Saururus cernuus	8.0	4.5	15.0	6.2
Boehmeria cylindrica	19.5	4.5	15.0	6.2
Carex crinita	2.7	9.1	2.5	5.8
Polygonum arifolium	2.7	9.1	2.5	5.8
Lorinseria areolata	2.7	9.1	2.5	5.8
Lycopus virginicus	1.3	4.5	2.5	2.9
Rubus sp.	1.3	4.5	2.5	2.9
Arisaema triphyllum	1.3	4.5	2.5	2.7

Table A26. (cont.)

Stand 25

	% Coverage	% Frequency	Maximum Coverage	I.V.
Impatiens capensis	30.1	14.7	67.5	22.4
Polygonum arifolium	30.7	11.8	67.5	21.2
Senecio aureus	17.9	10.3	67.5	14.1
Saniculus canadensis	4.1	11.8	15.0	7.9
Solidago rugosa	1.9	8.8	2.5	5.3
Rhus radicans	1.3	5.9	2.5	3.6
Mitchella repens	1.3	5.9	2.5	3.5
Viola papilionacea	1.3	5.9	2.5	3.5
Microstegium vimineum	2.5	4.4	15.0	3.5
Carex intumescens	2.5	4.4	15.0	3.4
Carex bromoides	2.2	2.9	15.0	2.5
Oxypolis rigidior	0.6	2.9	2.5	1.7
Cicuta maculata	0.6	2.9	2.5	1.7
Geum canadense	0.3	1.5	2.5	0.9
Habenaria clavellata	0.3	1.5	2.5	0.9
Lycopus virginicus	0.3	1.5	2.5	0.9
Peltandra virginica	0.3	1.5	2.5	0.9
Thalictrum pubescens	0.3	1.5	2.5	0.9
Glyceria striata	0.3	1.5	2.5	0.6

Table A26. (cont.)

Stand 26	% Coverage	% Frequency	Maximum Coverage	I.V.
Carex bromoides	23.7	10.7	37.5	17.2
Lorinseria areolata	25.0	6.7	85.0	16.0
Polygonum arifolium	11.2	8.0	37.5	9.6
Mitchella repens	3.8	9.3	15.0	6.5
Saururus cernuus	6.7	2.7	15.0	4.7
Boehmeria cylindrica	2.6	4.0	15.0	3.3
Hypericum walteri	2.6	4.0	15.0	3.3
Cinna arundinacea	1.3	5.3	2.5	3.3
Leersia spp.	3.8	2.7	15.0	3.2
Carex crinita	1.0	4.0	2.5	2.5
Solidago rugosa	1.0	4.0	2.5	2.5
Lycopus virginicus	2.2	2.7	15.0	2.5
Arisaema triphyllum	1.9	1.3	15.0	1.6
Elephantopus carolinianus	0.6	2.7	2.5	1.6
Impatiens capensis	0.6	2.7	2.5	1.6
Eupatoriadelphus dubius	1.9	1.3	15.0	1.6
Saniculus canadensis	1.9	1.3	15.0	1.6
Thelyteris thelyptroides	1.9	1.3	15.0	1.6
Pontedaria cordata	1.9	1.3	15.0	1.6
Panicum dichotomum	0.6	2.7	2.5	1.6
Galium obtusum	0.6	2.7	2.5	1.6
Aster spp.	0.6	2.7	2.5	1.6
Carex debilis	0.3	2.7	2.5	1.5
Bidens coronata	0.3	1.3	2.5	0.8
Cicuta maculata	0.3	1.3	2.5	0.8
Iris virginica	0.3	1.3	2.5	0.8
Murdannia keisak	0.3	1.3	2.5	0.8
Oxypolis rigidior	0.3	1.3	2.5	0.8
Peltandra virginica	0.3	1.3	2.5	0.8
Polygonum hydropiperoides	0.3	1.3	2.5	0.8
Rhus radicans	0.3	1.3	2.5	0.8

Table A26. (cont.)

Stand 28

	% Coverage	% Frequency	Maximum Coverage	I.V.
Polygonum arifolium	29.8	11.8	85.0	20.8
Carex bromoides	25.4	10.3	85.0	17.8
Rhus radicans	11.3	7.4	37.5	9.3
Peltandra virginica	7.8	10.3	15.0	9.0
Aster spp.	3.2	8.8	15.0	6.0
Leersia spp.	2.9	7.4	15.0	5.1
Viola papilionacea	2.0	7.4	15.0	4.7
Boehmeria cylindrica	2.6	5.9	15.0	4.2
Murdannia keisak	4.3	1.5	37.5	2.9
Thalictrum pubescens	0.9	4.4	2.5	2.6
Osmunda regalis	2.0	2.9	15.0	2.4
Oxypolis rigidior	1.7	2.9	15.0	2.3
Impatiens capensis	0.6	2.9	2.5	1.7
Commelina virginica	1.7	1.5	15.0	1.6
Carex grayi	0.3	1.5	2.5	0.9
Carex intumescens	0.3	1.5	2.5	0.9
Cinna arundinacea	0.3	1.5	2.5	0.9
Galium obtusum	0.3	1.5	2.5	0.9
Geum canadense	0.3	1.5	2.5	0.9
Habenaria clavellata	0.3	1.5	2.5	0.9
Iris virginica	0.3	1.5	2.5	0.9
Lycopus virginicus	0.3	1.5	2.5	0.9
Uvularia sessilifolia	0.3	1.5	2.5	0.9
Arisaema triphyllum	0.3	1.5	2.5	0.9

Stand 29

	% Coverage	% Frequency	Maximum Coverage	I.V.
Saururus cernuus	43.2	19.0	37.5	26.6
Uniola latifolia	27.5	19.0	15.0	23.2
Peltandra virginica	9.2	14.3	2.5	11.7
Aster spp.	6.7	7.1	15.0	6.9
Carex crinita	6.7	7.1	15.0	6.9
Carex tribuloides	6.7	7.1	15.0	6.9
Rhus radicans	3.3	9.5	2.5	6.4
Boehmeria cylindrica	1.7	4.8	2.5	3.2
Circaea lutetiana	1.7	4.8	2.5	3.2
Ludwigia palustris	0.8	2.4	2.5	1.6
Panicum dichotomum	0.8	2.4	2.5	1.6
Polygonum arifolium	0.8	2.4	2.5	1.6

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