PRIMARY PRODUCTION AND TEMPORAL VARIATION IN THE MACROPHYTIC COMMUNITY OF A TIDAL FRESHWATER SWAMP

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ABSTRACT

Cohoke Swamp is a relatively undisturbed tidal freshwater wetland of the Chesapeake Bay drainage basin. A study of the vegetative community of this swamp was performed during 1984 to evaluate temporal variation and net primary production. The understory structure was discovered to vary considerably throughout the growing season. Net primary production of the macrophytic community was estimated to be 12,272 kg/ha during 1984, which is substantial compared to other forest and wetland ecosystems.

Trees and shrubs were sampled by the point-centered quarter method to ascertain species distributions and woody production. Data from litterfall collections were combined with measurements of woody production to determine total canopy production (7442 kg/ha/yr). Four species dominated the overstory: *Fraxinus pennsylvanica*, *Nyssa sylvatica*, *Carpinus caroliniana*, and *Acer rubrum*. Of these, *Fraxinus* and *Nyssa* were by far the most productive populations, responsible for nearly 80% of the total canopy production.

The understory was also quite prolific. Analysis of monthly harvests of understory vegetation revealed a production level of approximately 4830 kg/ha/yr. *Peltandra virginica* and *Aneilema keisak* were the most prominent of the herbaceous species, accounting for 50% of the understory production. The understory data were characterized in several different manners in order to depict the patterns of development observed in the community. Monthly importance values present the relative status of the major species at specific times during the growing season. Species-specific importance values were introduced to describe the development and senescence pattern unique to each population. The aspects of each of these importance values were combined to derive the Community importance values, which, unlike the other two, can be compared between both months and species.

MACROPHYTIC COMMUNITY DYNAMICS IN A TIDAL FRESHWATER SWAMP

INTRODUCTION

Wetlands in General

Several decades ago, wetlands were perceived by many to be offensive wastelands, suitable only for draining, filling, and developing (Brande 1980). This view is no longer prevalent due to the increasing wealth of information which confirms their importance.

In general, wetlands appear to contribute an impressive array of benefits to neighboring ecosystems. Hunters and naturalists have long appreciated their value in providing habitat for many species of furbearers, waterfowl, and other wildlife (Shaw and Fredine 1956; Palmisano 1973; Odum 1978; Odum et al. 1979). Not only do these animals find shelter in wetlands, but also a rich variety of food sources (Lynch et al. 1947; Smith and Odum 1981; Silberhorn 1982). Many fish species have also been observed to school in relatively high densities in the tidal creeks which dissect wetlands. In the shallow creeks, smaller fish escape predation and find an abundance of food (Shea and Theberge 1978; Pollard et al. 1982; Boesch and Turner 1983; Talbot and Able 1983). Analyses of gut contents have demonstrated that many fish, and the aquatic organisms on which they feed, ingest substantial proportions of wetland detritus (Odum 1970; Odum and Heald 1975). In addition to these values, wetland plants and substrate may be effective in removing certain toxic substances from the water, stabilizing them in an organic matrix (Simpson et al. 1983). Also, tidal wetland ecosystems, due to their high productivity, remove nutrients from the rivers and streams during warmer months of the year, and may thereby supress the potential for algal blooms.

Community structure and production studies are foundational in the quantitative research of specific wetland types. Through this research we can perceive much about the relationships between the composition and functions of various communities. Some plants and associations, for example, may be recognized as excellent food items whereas others are discovered to be more important in stabilizing sediments. The specific values of different wetland communities are becoming increasingly apparent as this data is collected and analyzed.

Intensive studies of saltwater marshes have been conducted during the past 20 - 30 years, providing evidence that these habitats are among the most productive in the world. More recently, quantitative research emphasis has been directed to the study of brackish and freshwater wetland communities. Although the quantity of data is limited, there are already strong indications that the high productivity of salt marshes may be surpassed by certain brackish and freshwater wetlands (Wass and Wright 1969; Odum et al. 1984). Typical values for salt marsh production along the Mid-Atlantic and Southeast coasts range from several hundred g/m^2 annually to nearly 4000 g/m^2, averaging between one and two thousand $g/m^2/yr$ (Keefe 1972; Turner 1976; Lugo and Brinson 1979). Freshwater and brackish wetlands generally have net primary production values falling within the same range as salt marshes, with an average of one to two thousand $g/m^2/yr$ (Whigham et al. 1978; Odum et al. 1984).

Numerous estimates have been generated of wetland primary production and carbon and nutrient export and uptake, but variability among these values is still fairly large (Whigham et al. 1978). However, as the data base continues to be expanded through further research, and as methods of sampling continue to be refined, the levels of confidence in these estimates will increase. It is therefore imperative that research of these ecosystems continue in order to accurately assess the functions and processes which are occurring.

Tidal Freshwater Swamps

Relatively little research has been conducted in tidal freshwater swamps to ascertain their ecological importance. It is generally conceded that swamps are highly valuable habitat for a rich variety of wildlife species. Swamps harbor a number of plant species that are excellent food resources for many animals. Tidal swamps may also be significant exporters of usable detritus in the fall and winter, while still providing an abundance of cover for wildlife.

Several of Virginia's larger river systems have expanses of tidal swamps in their watersheds. Along extensive stretches of these rivers and their tributaries, tidal freshwater swamps are the dominant wetland type. Consequently, these wetlands may be of substantial value to aquatic organisms as habitat and/or exporters of organic matter.

The purpose of this project was to examine above-ground macrophyte production in a tidal freshwater swamp system. Emphasis was directed toward estimating that portion of primary production which is made available to aquatic detritovores and other heterotrophs. The point-centered quarter method was utilized for examining the overstory, and a modification of the sequential harvest technique was employed for understory analysis. Belowground productivity was not investigated due to the difficulty and uncertainty of obtaining reliable data. Also, the sub-surface production has very little potential to be utilized by aquatic consumers.

LITERATURE REVIEW

Swamps in General

Studies of swamp productivity (as well as that of other wetlands) are essential for confirming present estimates of vegetative yield and for evaluating the fate of this production. In these habitats, a large amount of organic matter is synthesized each year which is available for consumption by terrestrial organisms. This organic production is also accessable for utilization by aquatic organisms, especially during periods of high water (Wharton et al. 1982). Thus, the organic matter produced by riverine swamps (and especially tidal swamps) has the potential to serve a more diverse array of organisms than does that produced by upland forests.

To appreciate the fate of organic production of forested wetland systems, one must consider the differences between depression swamps and riverine swamps. Depression swamps are forested wetlands in which surface outflow of water is insignificant relative to groundwater transport and evaporation. Riverine swamps are located adjacent to streams and have flowing surface waters at least occasionally during the year. Comparison of the available research indicates that both of these systems can have high levels of productivity (see, e.g., Brown 1981). Yet, it appears that those with flowing surface waters are generally more productive (Conner and Day 1976; Brison et al. 1981).

The reasons for this probably include better aerated soils and, hence, oxygen supply to roots, and greater availablilty of dissolved nutrients than in the more stagnant wetlands (de la Cruz 1978; Brinson et al. 1980). In riverine swamplands, while nutrients and organic matter are being imported from upstream and incoming tides, there is a simultaneous eflux of organic matter into the aquatic ecosystem. Water currents erode the substrate and transport particulates and leachates from the soil and litterfall to places downstream. In the water, the swamp production becomes incorporated into aquatic food webs. During periods of high water, the export of swamp organic matter is intensified (Mulholland and Kuenzler 1979). There is a corresponding increase in the potential of detritus to be consumed by aquatic organisms. Fish are able to swim further into the wetland and forage among the submersed litter (Wharton et al. 1981; Wharton et al. 1982). As they feed, they stir up debris and the smaller suspended particles are more easily washed from the swamp.

Inland depression wetlands, on the other hand, function more as sinks for nutrients and organic matter. Their soils are very rich from the many years in which rain and groundwater flow have imported materials from the surrounding uplands (Reiners 1972). Depending on the degree of soil saturation, these low areas may be more productive than neighboring habitats (Reiners 1972; Whittaker et al. 1974). Generally, the only exports of depression swamp production are via consumption by herbivorous animals and respiration by forest floor microbes.

Analytic Methods - Community Structure

The vegetation of swamp ecosystems is usually analyzed in the same manner as that of other forests. The plants are grouped on the basis of height, stem diameter, and other physiognomic characteristics. Common classes are: trees (often subdivided into dominants and subordinates), shrubs and woody vines, and herbaceous plants. Evaluating the abundances and spatial organizations of the various plant species is a preliminary task. There are numerous ways in which this is accomplished, through the use of quadrats or plotless techniques (e.g., Kershaw 1964; Newbould 1967; Mueller-Dombois and Ellenberg 1974). Generally, the classes of vegetation are evaluated independently utilizing techniques specifically suited to the type of vegetation being considered.

Plotless field procedures are often employed to assess canopy structure. The point-centered quarter method is considered superior for most woodlands. This method allows the recording of several measurements quickly at each sampling station, thereby attenuating the time required for field work. Also, the estimates provided by this method are very accurate (Cottam and Curtis 1956). The point-centered quarter method has been used in several swamp studies (e.g., Conner and Day 1976; Schlesinger 1978; Doumlele et al. 1985) to generate relative and absolute measures of density, dominance, and frequency (Cottam and Curtis 1956), and the subsequently derived Importance Value (Curtis and McIntosh 1951).

Understory composition and structure are generally evaluated by using a number of plots. Since herbaceous vegetation is more ephemeral in nature than woody plants, periodic sampling is usually necessary to assess seasonal changes in this portion of the community.

Analytic Methods - Community Production

Determining the primary productivity of swamp forests is not readily accomplished. Girth increments of trees are easily measured, but accurately assessing the production of canopy and belowground biomass is a formidable undertaking. Estimates may be obtained by first selecting a number of trees of assorted sizes for regression analyses. The trees are harvested and separated into various components (leaves and twigs, large branches, bole, roots). The mass of each component is measured, and equations are derived which predict, for each species, a component's biomass as a function of a tree's DBH (diameter at breast height), basal area (area of the trunk's cross-section at breast height), total height, or some other conveniently measured parameter. Tree ring data can provide the necessary information for estimating, with regression equations, the biomass of each component at the end of past growing seasons. Net annual production can be assumed to be the average biomass increment over the past several years (often 5-10 years; Newbould 1967). Or, some measurement (or combination of measurements) can be taken at yearly intervals and this data used to estimate biomass increases.

Sometimes, the canopy production estimates derived by regressions are evaluated in conjunction with the weight of leaves, bark, and other vegetative matter collected in litter traps. Litter traps are especially useful in deciduous forests, where the leaves collected in autumn are the product of only one season's growth and most of the leaves fall from the trees during a short period (as opposed to evergreen forests). Several corrections should be noted, though, when utilizing litterfall data. For example, herbivory of leaves will reduce the biomass which would otherwise be collected. In general, herbivory has minimal effect on forest primary production (Franklin 1970). However, defoliation of an area can sometimes be substantial, claiming a relatively high percentage of the total leaf production (Carlisle et al. 1966; Conner and Day 1976). Tilton and Bernard's (1975) procedure for accounting for this loss was simple but effective. They randomly chose and weighed 100 leaves which had signs of herbivory and 100 entire leaves. The ratio of these two weights is the average amount of leaf material consumed among affected leaves, and the total mass of such leaves was adjusted by this ratio. Another consideration in utilizing litterfall data is that organic matter is translocated from the leaves into the stems before leaf abscission (Carlisle et al. 1966; Reiners 1972). Also, leaching and decay of organic production in twigs and branches occur before they fall (Whittaker and Woodwell 1971). These processes suggest that reliance of data solely from litterfall collection will result in underestimates of actual canopy production.

Reliable data on belowground production in trees and shrubs is difficult to obtain and is uncommon in the literature on forest production. A few authors have carefully examined belowground biomass and comparisons have been made with shoot biomass (Whittaker 1962; Bray 1963; Whittaker and Woodwell 1971; Whittaker et al. 1974). In certain studies, belowground production was assumed to have the same relation to shoot production as the ratio of belowground biomass to aerial biomass (Whittaker and Marks 1975). However, it is more likely the case that belowground net production in older trees is somewhat less than the estimate generated from this relation since the ratio of root to shoot biomass usually decreases with a tree's age (Whittaker and Woodwell 1971).

Aboveground herbaceous production may be evaluated with any of a variety of methods including measurements of peak standing biomass of each species, sequential harvests of standing live and dead stems, and permanent plot techniques. The sequential harvest technique is preferred in relatively dynamic communities since it provides information on the changes in each species' biomass throughout the growing season. The net annual production obtained for each species, however, is usually the same as the peak standing biomass value since the vegetation decomposes so rapidly.

As with woody vegetation, belowground production in herbaceous plants is also difficult to assess. Whittaker (1966) suggested that the root to shoot ratios for herbaceous plants were more variable, and hence less reliable indicators than for trees. The separation of old and current production is often tedious and subject to error (Milner and Hughes 1968). Nonetheless, estimates have been generated for a variety of terrestrial herbs (Bray 1963) and marsh plants (Keefe 1972; Whigham et al. 1978; Brinson et al. 1981).

Specific Studies

Doumlele et al. (1985) utilized the point-centered quarter method for analyzing the overstory structure of a Pamunkey River (Virginia) swamp, and quadrats for examining the understory. In this particular wetland, ash (Fraxinus pennsylvanica) was by far the most prominent tree. Other important trees were black gum (Nyssa sylvatica), American hornbeam (Carpinus carolinana), and red maple (Acer rubrum). The remaining tree species encountered in the study area were relatively insignificant. The total density and dominance values for the trees in this swamp (2746.5 stems/ha and 91.35 m^2 of tree basal area/ha) are both high when compared with other swamp systems and upland forests (see Discussion section). Understory samples were harvested in August and September to evaluate community structure and its changes. This sampling revealed increases in the importance of several species (Aneilema keisak, Polygonum arifolium, and Impatiens capensis), and declines in the importance of others (Carex stricta, Saururus cernuus, and Leersia oryzoides). Few other studies have examined seasonal variations in swamp understories. This is an important consideration in swamp research, particularly if the understory exhibits significant primary productivity.

Several studies have been conducted in order to determine the primary productivity of freshwater swamplands. Most of these have focused on southern cypress swamps. Although of limited comparitive value relative to this study, the cypress research does provide information on factors influencing swamp productivity.

Brown (1981) examined the community structure and primary production of a number of cypress (Taxodium spp.) swamps in Florida. She observed, among other things, that primary production generally increased as the flow of water through the swamp increased. Production estimates for swamps which were not known to be receiving unnatural nutrient loads ranged from 2680 kg/ha/yr in a scrub cypress wetland having still water to 16,070 kg/ha/yr in a floodplain forest. A nutrient-enriched site had an even higher rate of production (17,940 kg/ha/yr).

Mitsch and Ewel's (1979) study was similar to Brown's (1981) research in comparing productivity between various cypress swamps. Their study, however, did not provide nearly as detailed a description of the differences between the swamps.

Schlesinger (1978) studied vegetative dynamics in Okefenokee Swamp (Georgia). This depression swamp consisted almost exclusively of cypress trees (98% of total forest biomass) and had a relatively low net primary production (6900 kg/ha/yr). The low productivity was attributed to the lack of hydrologic activity in depression swamps.

Conner and Day's (1976) research emphasized the composition and productivity of a cypress-tupelo swamp and a mixed hardwood swamp in Louisiana. Both of the study areas were described as having flowing surface waters, and both were discovered to have high levels of primary production. The authors estimated that net primary production was 15,160 kg/ha/yr for the cypress-tupelo forest and 17,330 kg/ha/yr for the mixed hardwood site.

Other swamp systems for which tree and understory production have been evaluated include a New York alder shrub wetland (Tilton and

Bernard 1975), a bottomland hardwood forest in Louisiana (Conner and Day 1976), and a Minnesota white cedar swamp (Reiners 1972).

The information which has been generated thus far indicates that forested wetlands (especially floodplain swamps) are very productive. When compared with the production estimates of upland forests the differences in productivity are apparent (Whittaker 1966; Whittaker and Woodwell 1968, 1969; Reiners 1972; Whittaker et al. 1974). So far, the research suggests that riverine swamps are the most productive and that depression swamps may be equivalent in productivity to upland forests.

STUDY SITE

The field work for this research was conducted in the southern portion of Cohoke Swamp, one of many extensive wetlands in the Pamunkey River watershed (Figure 1). The swamp is located 17 river miles (27 km) upstream from West Point, Virginia, where the Pamunkey River enters the York River. The Pamunkey River is tidal for approximately 60 miles (97 km) of its course, with extensive wetlands covering the broad floodplains along most of its tidal portion. At 15 river miles (24 km) from the mouth of the river, the wetlands transform rather abruptly from freshwater marsh to swamp. Further upstream, marshes are only occasional features along the margins of swamps and uplands. The tide range gradually increases from West Point to the study area and beyond due to the river basin morphology. Cohoke Swamp has a mean tide range of approximately 3 ft (0.9 m), and much of the ground is flooded during high tides.

The peninsular expanses of tidal swamp in this watershed are relatively inaccessible and have probably never been logged (Wass and Wright 1969). Consequently, the forest structure is largely, if not solely, the result of natural processes and disturbances.

The study area is typical of extensive wetland habitats in being dissected by numerous shallow muddy creeks. These drainage channels receive incoming waters during flood tides from larger tidal creeks which join the river. Between these muddy distributaries are flat

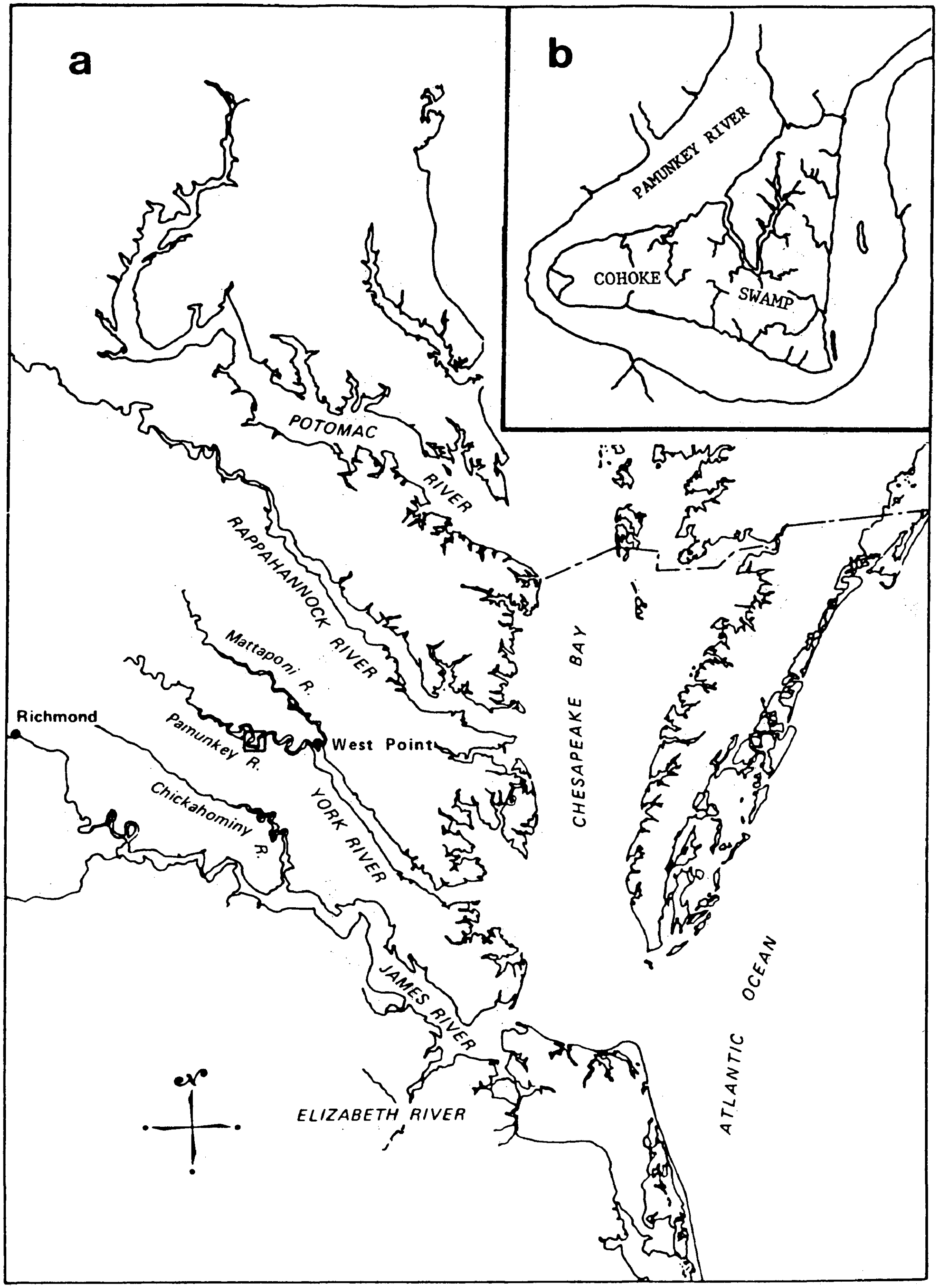

Figure 1. (a) The major tidal rivers of Virginia. Box encloses the study area on Pamunkey River.

(b) Enlargement of the study area.

islands of ground which are regularly inundated for short intervals of time. The only woody vegetation observed along the peripheries of the islands was an occasional sapling or brier. Saplings which begin growing in the guts either die within a few years or accumulate sediment around their shallow roots. This was apparent since larger trees were not observed growing in the mucky substrate. The herbaceous vegetation of the swamp varies remarkably depending on whether its growth is upon the elevated ground or within the drainage channels. Peltandra, Cicuta, Sagittaria, and other hydrophiles thrive upon the muckier substrate, whereas Carex, Leersia, Bidens, and many other species are much more common on the elevated ground. The situation of the plants is probably due to a combination of substrate preference and competition.

METHODS

Overstory

The point-centered quarter method (Cottam and Curtis 1956; Ashby 1972) was utilized for characterizing the overstory. Twenty-five permanent stations were established in the swamp in April 1984 to serve as reference points for sampling. These stations were arranged in five parallel rows with five stations per row. The spacing between the stations in a row and between rows was 65 - 130 ft (20 - 40 m). Each row of stations began near the river's edge and extended nearly 500 ft (150 m) into the swamp. From the reference points, the closest tree larger than 1 inch (2.5 cm) in diameter at breast height (4.5 ft, 1.4 m) was selected from each of the four quadrants. Nails were driven into each tree to mark the breast height level. This would ensure measuring the stem's circumference at the same level on the following year. The species, point-to-tree distances, and breast-height circumferences of the four trees were recorded at each station. This information was used to calculate estimates for population densities, dominances, and frequencies:

$$\mathrm{DENy} = \frac{(10{,}000)\,(\mathrm{Nt})\,(\mathrm{Ny})}{(\mathrm{Dt})^2} \qquad (1)$$

where: DENy = absolute density of species y (in #/ha), Nt = total number of trees sampled,

Ny = number of individuals of species y, and

Dt = sum of all point to tree distances (in m);

$$DOMy = (BAy)(DENy) \tag{2}$$

where: DOMy = absolute dominance of species y (in m^2/ha), and

BAy = mean basal area of individuals of species y (in m^2);

$$FREy = Sy/St \tag{3}$$

where: FREy = absolute frequency of species y,

Sy = number of stations at which species y occurred, and

St = total number of stations.

In addition, the relative values of each of these measures were determined for each species:

$$RDENy = DENy/DENt \tag{4}$$

where: RDENy = relative density of species y, and

DENt = sum of density values for all tree species;

$$RDOMy = DOMy/DOMt \tag{5}$$

where: RDOMy = relative dominance of species y, and

DOMt = sum of dominance values for all tree species;

$$RFREy = FREy/FREt \tag{6}$$

where: RFREy = relative frequency of species y, and

FREt = sum of frequency values for all tree species.

The three relative values are averaged to obtain a measure of each species' status in the community, referred to as its "importance value"

(Curtis and McIntosh 1951; Mueller-Dombois and Ellenberg 1974). This particular importance value (IV) derivation applies only to the overstory species, and will be referred to in this study as the "overstory importance value" or "IVo".

Biomass of each of the 100 sample trees was estimated by using species-specific regression equations of the form:

$$\log Y = A + B(\log X), \tag{7}$$

where A and B are species-specific coefficients, X is the tree's diameter at breast height (DBH), and Y is the biomass of a particular component of the tree (see Appendix I). The DBHs of the trees were calculated from the circumference measurements taken in 1984 to obtain the initial biomass estimates. In the spring of 1985, the circumference of each of the sampled trees was again measured. The new DBH values were used in the regression equations to produce new estimates of biomass for each tree. Wood production was taken to be the increase in biomass of the trees from spring 1984 to spring 1985. Litterfall data, collected from 30 litter traps positioned randomly throughout the study area, supplemented the wood production estimate to give the aboveground net primary production for the trees.

At the end of the project, increment cores were collected from a number of trees in order to examine patterns of stem growth over the past several years. The growth estimated by measuring changes in circumferences over the year was compared with that estimated from widths of radial growth bands to ascertain whether 1984-85 production had been typical of the recent past.

Understory

The swamp understory, considered to be all vegetation other than the trees, was predominantly herbaceous in composition. Several factors were considered in determining the quadrat size and the number of samples to be taken. During the previous year, I examined the understory of Cohoke Swamp and had noted its similarity to Sweet Hall Marsh of Doumlele's (1976, 1981) study. From this and other marsh research, I estimated an appropriate quadrat size to be utilized in the understory portion of my study. Time constraints were a significant factor in limiting the number of samples which could be collected and examined per excursion. A $0.25m^2$ hoop was selected, and 20 samples were collected each month from June through October. Samples were collected monthly, on two days of two consecutive weeks. This allowed analysis of each set of vegetation samples before the plants decomposed.

For each sample, the number of individuals and the biomass (oven dry weight) of each species were recorded. The species densities were combined with other data to characterize the community structure and its transformation through the growing season. Midway through the sampling program, this information was also discovered to be relevant in evaluating primary production. I had anticipated using the standard sequential harvest technique in evaluating understory production. Analysis of the understory data as early as the second month of sampling, and particularly by the third month, clearly indicated that a modified sequential harvest procedure would provide a more accurate assessment of understory production. The modification involved considering changes in both the number of individuals per species (i.e., species densities) and biomass. This analysis accounted for the loss of individuals which generally occurs throughout the growing season. Evaluating this loss through measurements of the dead vegetation would have been impractical since the succulent wetland herbs decompose very quickly.

The parameters of interest in the understory samples were similar to those analyzed in the overstory sampling. The measurements and their derivations are as follows:

$$DEN_{y,a} = \frac{NI_{y,a}}{(Q)(S_a)} \qquad (8)$$

where: $DEN_{y,a}$ = density of species y in month a,

$NI_{y,a}$ = total no. of individuals of y collected in month a,

Q = area of sampling quadrat (in m^2), and

S_a = total number of samples taken in month a;

$$DOM_{y,a} = \frac{B_{y,a}}{(Q)(S_a)} \qquad (9)$$

where: $DOM_{y,a}$ = dominance of species y in month a, and

$B_{y,a}$ = total biomass (in g) of species y collected in month a;

$$FRE_{y,a} = \frac{NS_{y,a}}{S_a} \qquad (10)$$

where: $FRE_{y,a}$ = frequency of species y in month a, and

$NS_{y,a}$ = number of samples containing species y in month a.

The composition of the understory and changes in the community structure during the growing season were depicted in several ways.

Three different importance values were calculated for the most abundant understory species. The "monthly importance value" (IVm) is similar to the traditional "importance value" (IV) often calculated to describe understory vegetation (e.g., Doumlele 1976; Doumlele et al. 1985):

$$IVm = \left(\frac{By,a}{Bt,a} + \frac{FREy,a}{FREt,a} \right) \times 50 \qquad (11)$$

where: Bt,a = total biomass of all understory species harvested in month a, and

FREt,a = sum of frequency values for all species sampled in month a.

The sum of the IVm of all species sampled in any month will always equal 100. Importance values can be compared within a month but not between months. This calculation differs from the conventional equation in substituting biomass for species cover as a measure of dominance.

A second measure of importance, the "species-specific importance value" (IVss), describes changes within a population from month to month. A single species' biomass and average density values are the only two parameters considered in the IVss calculation:

$$IVss = \left(\frac{By,a}{By,t} + \frac{DENy,a}{DENy,t} \right) \times 50 \qquad (12)$$

where: By,t = sum of each month's biomass values for species y, and

DENy,t = sum of each month's density values for species y.

In the case of the IVss, the sum of each month's values for a single species equals 100 and values of different species cannot be compared. The importance value of a species at a particular time is relative to its importance during the rest of the year.

Combining the attributes of both of these importance values, a third measure was derived. The "community importance value" (IVc), unlike either of the other IV's, provides a means for comparing the importance of a species at any time to the importance of any other species at any time. The measure is based on the assumption that the maximum possible biomass and the maximum possible frequency for any species of the community are equally important.

$$IVc = \left(\frac{By,a}{Bmax} + \frac{FREy,a}{FREmax} \right) \times 50 \qquad (13)$$

where: Bmax = the greatest biomass value of any species sampled, and

FREmax = number of samples taken each month.

Primary production of the understory was assessed in two different ways. For the more prominent species, primary production was calculated by adding the biomass of individuals which had succumbed earlier in the growing season to the peak standing crop for each species. The additional biomass was estimated as the average plant weight in the month before those individuals were lost to the population times the number of plants lost. For the less prominent understory species, net production was considered to be equivalent to the peak standing crop for each species.

RESULTS

Overstory

Seven tree and shrub species were sampled in Cohoke Swamp. Table 1 presents the absolute densities, dominances, and frequencies for each of the sampled overstory species. Relative measures for these parameters are given in Table 2, with the overstory importance value calculated for each species. Although Fraxinus pennsylvanica trees were more abundant than the other species, the Nyssa sylvatica population was by far the most dominant in terms of basal area. Similarly, Carpinus caroliniana individuals were twice as common as Acer rubrum, but the entire population had only one-third the total basal area of Acer. These four species accounted for 96% of the trees sampled. Fraxinus ranked slightly greater than Nyssa in importance (IVo), which was followed by Carpinus, then Acer. Liriodendron tulipifera, Magnolia virginiana, Viburnum dentatum, and other unsampled species were relatively insignificant components of the overstory.

The aboveground annual primary production data for the tree and shrub species are summarized in Table 3. Total overstory production was determined to be 7442 kg/ha/yr, and was attributed to the growth of tree stems and branches (calculated with regression equations; Appendix I) plus the dry weight of leaves, twigs, and bark collected in the litter traps. Nyssa trees generally had much larger stems than

TABLE 1. Absolute measures of overstory species sampled in Cohoke Swamp, Spring 1984.

	Average Density (stems/ha)	Average Dominance (m^2/ha)	Average Basal Area (cm^2/stem)	Frequency (%)
Fraxinus pennsylvanica	1119	16.79	150	92
Nyssa sylvatica	365	25.93	711	52
Carpinus caroliniana	584	1.81	31	60
Acer rubrum	268	5.60	209	40
Liriodendron tulipifera	49	2.22	456	8
Magnolia virginiana	24	0.16	64	4
Viburnum dentatum	24	0.08	33	4
All species	2433	52.59	--	--

TABLE 2. Relative measures of overstory species sampled in Cohoke Swamp, Spring 1984.

	Relative Density (%)	Relative Dominance (%)	Relative Frequency (%)	Importance Value (%)
Fraxinus pennsylvanica	46	32	35	38
Nyssa sylvatica	15	49	20	28
Carpinus caroliniana	24	3.4	23	17
Acer rubrum	11	11	15	12
Liriodendron tulipifera	2	4.2	3.1	3.1
Magnolia virginiana	1	0.3	1.5	1.0
Viburnum dentatum	1	0.1	1.5	0.6
All species	(100)	(100)	(100)	(100)

TABLE 3. Overstory net primary production.

STEMS AND BRANCHES		
Nyssa sylvatica	2135 kg/ha/yr	5.85 kg/tree/yr
Fraxinus pennsylvanica	1751	1.56
Acer rubrum	514	1.92
Carpinus caroliniana	273	0.47
Liriodendron tulipifera	202	4.12
Magnolia virginiana	43	1.79
Viburnum dentatum	*	*
Total	4918 kg/ha/yr	—
LITTERFALL		
leaves + twigs + bark	2524 kg/ha/yr	
TOTAL OVERSTORY PRODUCTION	7442 kg/ha/yr	

* no production detected for this species

Fraxinus trees. Not only do larger trees grow taller in the canopy, but they also are able to produce broader crowns which intercept more sunlight. This advantage allowed individual Nyssa trees to greatly surpass Fraxinus trees in primary production (5.85 kg/tree/yr vs 1.56 kg/tree/yr). In addition, the Nyssa population appeared to be a greater contributor to community production than the larger Fraxinus population (2135 kg/ha/yr vs 1751 kg/ha/yr). These two species had a combined net production of 3886 kg of woody biomass/ha/yr, which was 79% of the total woody production. Liriodendron was also a highly productive tree; however its low abundance limited its contribution to community production. Despite the high density and frequency of Carpinus, it was also a minor contributor to total production due to suppressed individual production rates. Acer and Magnolia trees were similar to Fraxinus in their production potentials, yet less regular in occurrence. The Acer population ranked third in overstory production. Magnolia, having a much lower population density, ranked sixth. Although it is assumed that the Viburnum grow like other trees, no production was detected in the sample population.

Litterfall was found to be a substantial contributor to the detrital pool in the swamp. Leaves, twigs, and bark which were collected in the litter traps were shed at a rate of 2524 kg/ha/yr. Small branches which fell into the litter traps accounted for another 27 kg/ha/yr. In addition to these sources of detritus, large branches and trees occasionally fell during the study, but accurate assessment of this loss of biomass was beyond the scope of this project.

Understory

Understory analysis presented an interesting problem due to the structure and dynamics of the community. Early in the study, I recognized that, within each month, substantial variability existed between samples, and among individuals of each species. The populations sampled did not appear to be representative of statistically "normal" populations, in which most of the individuals are relatively uniform in size. In general, this occurs only when the population consists of a single cohort. Instead, the raw data revealed that small and large individuals were often as numerous as, or more numerous than, the medium-sized plants. This indicated that the populations were continuously recruiting new sprouts and seedlings and/or that the growth of existing individuals was not uniform.

Since the samples had to be analyzed within a limited amount of time (i.e., before decomposition), harvesting efforts were restricted to twenty $0.25m^2$ plots per month. A summary of the data obtained for the ten most prominent understory species is presented in Table 4.

For most species, the patterns of growth depicted by the data in Table 4 did not correspond to the dynamics typical of natural populations. This was probably the result of collecting an insufficient number of samples. In order to make the data more useful for analysis, I averaged certain measurements between consecutive months. Data for the frequency of occurrence, species density, and average plant weight were averaged as necessary within populations to conform to the assumptions and principles of population dynamics outlined below:

TABLE 4. Original Data - Cohoke Swamp Understory, 1984.

	Average Density ($\#/m^2$)	Average Biomass (g/m^2)	Frequency (%)	Average Plant Weight (g)
Peltandra virginica				
June	25.40	91.21	95	3.59
July	11.60	94.66	90	8.16
Aug.	6.00	32.18	80	5.36
Sep.	5.80	23.49	85	4.05
Oct.	4.20	4.14	65	0.99
Aneilema keisak				
June	306.20	21.25	80	0.07
July	203.20	25.22	80	0.12
Aug.	171.00	29.10	65	0.17
Sep.	353.40	108.75	95	0.31
Oct.	119.80	55.81	70	0.47
Polygonum arifolium				
June	22.60	4.54	75	0.20
July	14.40	9.34	85	0.65
Aug.	19.60	37.83	75	1.93
Sep.	15.80	28.84	80	1.83
Oct.	2.80	12.98	25	4.64
Carex stricta				
June	264.60	21.88	30	0.08
July	317.40	26.47	35	0.08
Aug.	268.00	20.10	25	0.07
Sep.	247.00	19.59	35	0.08
Oct.	423.00	28.64	55	0.07
Bidens laevis				
June	1.00	0.23	10	0.23
July	7.40	2.62	40	0.35
Aug.	17.20	16.74	60	0.97
Sep.	5.40	6.09	60	1.13
Oct.	5.20	9.75	45	1.87

TABLE 4 (cont.)

	Average Density (#/m^2)	Average Biomass (g/m^2)	Frequency (%)	Average Plant Weight (g)
Saururus cernuus				
June	7.20	14.29	45	1.99
July	6.00	10.98	45	1.83
Aug.	5.40	13.02	45	2.41
Sep.	4.20	7.24	35	1.72
Oct.	2.00	4.54	30	2.27
Osmunda regalis				
June	6.80	8.38	20	1.23
July	3.40	1.01	20	0.30
Aug.	0	0	0	0
Sep.	2.40	13.59	10	5.66
Oct.	1.80	3.73	10	2.07
Leersia oryzoides				
June	44.80	5.56	85	0.12
July	61.20	11.55	50	0.19
Aug.	17.00	2.47	30	0.15
Sep.	35.80	8.60	55	0.24
Oct.	5.40	1.51	40	0.28
Cicuta maculata				
June	7.40	2.36	30	0.32
July	2.80	1.05	20	0.38
Aug.	3.80	6.93	30	1.82
Sep.	1.40	1.00	20	0.71
Oct.	0.40	0.02	5	0.05
Bidens coronata				
June	0	0	0	0
July	1.80	0.57	15	0.32
Aug.	2.80	2.93	25	1.05
Sep.	1.40	3.69	25	2.64
Oct.	0.80	3.84	15	4.81

1. The frequency of occurrence of a particular species will increase initially, and then decrease as the population senesces. I assumed that the frequency of occurrence would not increase following a true decrease.
2. A species' density will increase initially, and then decrease as the population senesces. I assumed that the average number of individuals per sample would not increase following a reduction. The sampling data supported this premise in that new individuals emerged continuously throughout the growing season and not as distinct cohorts, thereby precluding the potential for multiple peaks in population densities.
3. The average biomass per plant increases and then decreases through the growing season. I assumed that this value would not increase following a decrease. This may be a fairly weak assumption since recruitment can reduce the average biomass per plant value. However, this would occur only if growth among existing individuals had diminished and/or a large percentage of the harvest consisted of very young plants.

The adjusted data are presented in Table 5. Since these values appear to better represent the understory, they were used in calculating the different understory IV's. Production estimates were obtained from both the original and adjusted data.

Numerous species were encountered in the swamp understory, the structure being quite similar to that observed in tidal freshwater

TABLE 5. Adjusted Data - Cohoke Swamp Understory, 1984.

	Average Density ($\#/m^2$)	Average Biomass (g/m^2)	Frequency (%)	Average Plant Weight (g)
Peltandra virginica				
June	25.40	91.21	95	3.59
July	11.60	94.66	90	8.16
Aug.	6.20	33.25	82	5.36
Sep.	5.64	22.84	82	4.05
Oct.	4.20	4.14	65	0.99
Aneilema keisak				
June	306.20	21.25	80	0.07
July	242.53	29.10	80	0.12
Aug.	242.53	41.23	80	0.17
Sep.	242.53	75.19	80	0.31
Oct.	119.80	55.81	70	0.47
Polygonum arifolium				
June	22.60	4.54	75	0.20
July	18.06	11.71	85	0.65
Aug.	16.47	31.02	78	1.88
Sep.	15.31	28.84	78	1.88
Oct.	2.80	12.98	25	4.64
Carex stricta				
June	264.60	21.88	30	0.08
July	272.05	22.69	30	0.08
Aug.	321.60	24.78	30	0.08
Sep.	260.55	20.08	35	0.08
Oct.	409.44	27.72	55	0.07
Bidens laevis				
June	1.00	0.23	10	0.23
July	7.40	2.62	40	0.35
Aug.	17.20	17.38	60	1.01
Sep.	6.06	6.12	60	1.01
Oct.	4.54	8.50	45	1.87

TABLE 5 (cont.)

	Average Density (#/m^2)	Average Biomass (g/m^2)	Frequency (%)	Average Plant Weight (g)
Saururus cernuus				
June	7.20	13.78	45	1.91
July	6.00	11.49	45	1.91
Aug.	5.40	13.02	45	2.41
Sep.	4.20	8.38	35	2.00
Oct.	2.00	3.99	30	2.00
Osmunda regalis				
June	6.80	6.26	20	0.92
July	1.93	1.78	10	0.92
Aug.	1.93	6.36	10	3.29
Sep.	1.93	10.95	10	5.66
Oct.	1.80	3.73	10	2.07
Leersia oryzoides				
June	44.80	5.56	85	0.12
July	61.20	10.97	50	0.18
Aug.	26.40	4.73	42	0.18
Sep.	26.40	6.34	42	0.24
Oct.	5.40	1.51	40	0.28
Cicuta maculata				
June	7.40	2.36	30	0.32
July	3.50	1.31	25	0.38
Aug.	3.17	5.77	25	1.82
Sep.	1.44	1.02	20	0.71
Oct.	0.36	0.02	5	0.05
Bidens coronata				
June	0	0	0	0
July	1.80	0.57	15	0.32
Aug.	2.80	2.93	25	1.05
Sep.	1.40	3.69	25	2.64
Oct.	0.80	3.84	15	4.81

marshes (e.g., Doumlele 1976, 1981; Odum et al. 1984). This herbaceous community changed remarkably through the growing season as species would continually displace each other in importance. During the year, however, the dominant positions in the community were shared by relatively few species.

Tables 5-8 characterize the more abundant species in the understory during the last five months of the growing season. It was presumed that the entire understory community was growing through June, i.e., that no species began to decline until after that time. Table 5 presents the changes in various parameters for each species during each month. Interestingly, the biomass values of certain species were observed to increase in biomass from one month to the next when the number of individuals in the population dropped considerably. This was due to the growth of some individuals, at a time when others in the population were dying (compare average weight per plant vs. density in Table 5). Early in the year, Peltandra virginica far outranked all other species in ground cover (i.e., biomass). By July, Peltandra growth had begun to taper off as most of the other understory plants continued to increase in importance. Aneilema keisak and Polygonum arifolium became especially dominant as the Peltandra population declined. During this time, other species peaked in importance and then subsided, such as Cicuta maculata and Leersia oryzoides. A spectacular display was provided by the Bidens species in late summer as many individuals grew large in size, and produced a multitude of showy yellow flowers. Soon afterwards, the entire understory community began to undergo senescence.

Various measures of species importance are presented in Tables 6, 7, and 8. The conventional measure of importance among herbaceous species usually sums or averages the "relative frequency" and the "relative dominance" of each species (these values being "relative" to those of other species at a particular moment). A set of these importance values (referred to as "Monthly Importance Values" or IVm in this study; Table 6) measures the relative degree of interaction between each species and the rest of the community during each month of the study. Table 6 clearly depicts the importance of Peltandra, Aneilema, and Polygonum during the growing season. The data for the "other spp." were considered collectively, and are presented as if they described a single population.

An alternative method for analyzing the data is to consider how a particular species changes from month to month. Table 7 summarizes these changes for the most important species with Species-specific importance values (IVss). These differ from the IVm of Table 6 in that one species' values cannot be compared with those of another species. If a species increases or decreases in cover or frequency, it will show a corresponding change in its IVss irrespective of changes occurring in the other species of the community. The patterns observed in the IVm are particularly interesting when they are compared with trends in the IVss. For example, notice how the importance of Aneilema relative to the other species increases between August and October in Table 6. The population itself, however, peaks in September and declines substantially through October, as illustrated in Table 7. The Community importance values are an attempt to correct for this lack of information.

TABLE 6. Monthly Importance Values (IVm)

Cohoke Swamp Understory, 1984.

	June	July	August	September	October
P.v.*	32.6	29.5	15.0	13.0	9.0
A.k.	12.7	14.0	16.6	25.2	28.5
P.a.	7.8	10.6	14.1	14.1	7.6
C.s.	8.5	7.9	8.3	8.0	16.5
B.l.	0.9	4.4	9.4	7.0	8.3
S.c.	7.6	6.8	7.1	5.2	4.9
O.r.	3.4	1.3	2.4	3.5	2.5
L.o.	9.0	7.2	4.9	5.4	5.2
C.m.	3.3	2.6	3.6	2.1	0.6
B.c.	0	1.5	2.9	3.2	3.1
Other spp.	14.0	15.6	15.6	13.1	13.9
Total	(100)	(100)	(100)	(100)	(100)

*P.v.=Peltandra virginica, A.k.=Aneilema keisak, P.a.=Polygonum arifolium, C.s.=Carex stricta, B.l.=Bidens laevis, S.c.=Saururus cernuus, O.r.=Osmunda regalis, L.o.=Leersia oryzoides, C.m.=Cicuta maculata, B.c.=Bidens coronata.

TABLE 7. Species-specific Importance Values (IVss) for the 10 most prominent understory species Cohoke Swamp, 1984.

	June	July	August	September	October	Total
P.v.*	42.5	30.2	12.6	10.0	4.8	(100)
A.k.	18.0	17.0	19.8	27.4	17.7	(100)
P.a.	17.6	18.6	28.4	26.4	9.1	(100)
C.s.	18.0	18.6	21.1	17.1	25.2	(100)
B.l.	1.7	14.0	48.7	17.2	18.5	(100)
S.c.	28.1	23.4	23.7	16.7	8.0	(100)
O.r.	34.4	9.8	17.6	25.5	12.7	(100)
L.o.	23.2	37.5	16.2	18.9	4.2	(100)
C.m.	34.6	17.3	37.5	9.4	1.2	(100)
B.c.	0	15.8	33.9	27.0	23.3	(100)

*P.v.=Peltandra virginica, A.k.=Aneilema keisak, P.a.=Polygonum arifolium, C.s.=Carex stricta, B.l.=Bidens laevis, S.c.=Saururus cernuus, O.r.=Osmunda regalis, L.o.=Leersia oryzoides, C.m.=Cicuta maculata, B.c.=Bidens coronata

Table 8 presents the Community importance values (IVc) for the major species, combining the attributes of both the monthly and species-specific importance values. Each value in this table is related to the importance of all other species throughout the growing season. Consequently, any IVc can be compared with any other IVc to assess the importance of any species at any time, relative to the rest of the community. Differences in the frequency of occurrence of species has greater significance than differences in biomass for most species due to the overwhelming dominance of Peltandra early in the summer. Yet, it can be seen that the pattern in the IVc for each species correspond to the IVss, and the IVc for each month follow the same pattern as observed in the IVm.

The determination of herbaceous production in this study was based on evaluating changes in samples of live plants. Analysis of the Peltandra data can be used to illustrate how production was calculated for the major species. The Peltandra population during the sampling period is characterized in Table 5 as:

	Biomass (g/m^2)	Density ($inds./m^2$)	Frequency (%)	Average Plant Weight (g)
June	91.21	25.40	95	3.59
July	94.66	11.60	90	8.16
Aug.	33.25	6.20	82	5.36
Sep.	22.84	5.64	82	4.05
Oct.	4.14	4.20	65	0.99

Notice that between June and July, the average biomass increased slightly whereas the plant density diminished considerably. This indicates that the remaining plants must have increased in biomass as depicted by the change in average plant weight. The average dry mass

TABLE 8. Community Importance Values (IVc) for the 10 most prominent understory species Cohoke Swamp, 1984.

	June	July	August	September	October
P.v.*	95.7	95.0	58.6	53.1	34.7
A.k.	51.2	55.4	61.8	79.7	64.5
P.a.	39.9	48.7	55.4	54.2	19.4
C.s.	26.6	27.0	28.1	28.1	42.1
B.l.	5.1	21.4	39.2	33.2	27.0
S.c.	29.8	28.6	29.4	21.9	17.1
O.r.	13.3	5.9	8.4	10.8	7.0
L.o.	45.4	30.8	23.5	24.3	20.8
C.m.	16.2	13.2	15.5	10.5	2.5
B.c.	0	7.8	14.0	14.4	9.5

*P.v.=*Peltandra virginica*, A.k.=*Aneilema keisak*, P.a.=*Polygonum arifolium*, C.s.=*Carex stricta*, B.l.=*Bidens laevis*, S.c.=*Saururus cernuus*, O.r.=*Osmunda regalis*, L.o.=*Leersia oryzoides*, C.m.=*Cicuta maculata*, B.c.=*Bidens coronata* per plant in June was 3.59 g. In July, the average plant dry mass had increased to 8.16 g. Most of this growth would not have been detected using conventional analytic techniques, and total Peltandra production would have been reported as 94.66 g/m^2. Since we do not know the size of the plants in June which survived until July, we can assume that they had an average dry mass of 3.59 g/plant. Those plants grew an additional (8.16 - 3.59) = 4.57 g/plant between June and July, assuming that no new plants were recruited into the population. This additional production of (4.57 g/ind) x (11.60 ind/m^2) = 53.01 g/m^2, combined with the previous month's production of 91.21 g/m^2, gives an estimate of 144.22 g/m^2 primary production by July. Since the average plant weight begins to decline after this time, there is no way to assess additional growth in individual plants.

This method of determining primary production is utilized on ten species. The other species of the understory community were sampled infrequently, and this method of analysis would be of questionable value. Therefore, peak standing crops of these species are used to estimate net primary production. The understory production estimates are presented in Table 9 using the original data, and in Table 10 using the adjusted data. The original data give a net primary production estimate for the understory community of 5423 kg/ha/yr (542.3 g/m^2/yr). The estimate obtained by using the adjusted data is 4830 kg/ha/yr (483.0 g/m^2/yr), and is probably a more accurate approximation of true primary production. Peltandra and Aneilema were the most productive of the understory species, responsible for 50% of the total understory production.

TABLE 9. Understory Net Primary Production

Cohoke Swamp, 1984

(calculated from the original data).

Peltandra virginica	1442 kg/ha/yr
Aneilema keisak	1388
Polygonum arifolium	474
Carex stricta	380
Bidens laevis	214
Saururus cernuus	185
Osmunda regalis	136*
Leersia oryzoides	179
Cicuta maculata	84
Bidens coronata	69
Other species	872
TOTAL UNDERSTORY PRODUCTION	5423 kg/ha/yr

*peak standing crop

TABLE 10. Understory Net Primary Production

Cohoke Swamp, 1984

(calculated from the adjusted data).

Peltandra virginica	1442 kg/ha/yr
Aneilema keisak	986
Polygonum arifolium	406
Carex stricta	324
Bidens laevis	213
Saururus cernuus	165
Osmunda regalis	154
Leersia oryzoides	128
Cicuta maculata	71
Bidens coronata	69
Other species	872
TOTAL UNDERSTORY PRODUCTION	4830 kg/ha/yr

DISCUSSION

The vegetative community structure of this study site was, as expected, quite similar to that of another swamp immediately upstream (Doumlele et al. 1985). In both of these Pamunkey River swamps, Fraxinus pennsylvanica was by far the most commonly encountered tree species, followed by Nyssa sylvatica, Carpinus caroliniana, and Acer rubrum. These four species comprised over 95% of the individuals in the overstory of both study areas. Minor tree and shrub species observed in the swamps included: Liriodendron tulipifera, Magnolia virginiana, Viburnum dentatum, Myrica cerifera, Alnus serrulata, Vaccinium corymbosum, Kalmia latifolia, and Juniperus virginiana.

Cohoke Swamp is a relatively productive ecosystem. Total aboveground primary production in the study area was 12,272 kg/ha during 1984. The overstory contributed 60% of the net production, and the understory contributed 40%. The swamp appears to be slightly more productive than many other wetlands in the Mid-Atlantic region (Doumlele 1976, 1981; Whigham et al. 1978). In relation to other forest types of the eastern United States, Cohoke Swamp is also among the most productive (Wharton et al. 1982; Table 11). Some upland forest communities may be as productive as Cohoke Swamp (e.g., Whittaker 1966; Whittaker et al. 1974; Johnson and Risser 1974), yet riverine swamps generally appear to be the most productive forests.

TABLE 11. Production estimates of various forest types.

	Aboveground Net Primary Production (kg/ha/yr)			
	Overstory	Understory	Total	Forest type
UPLAND FORESTS				
Reiners 1972 (Minnesota)	8700	210	8910	oak
Whittaker et al. 1974 (New Hampshire)	11190	80	11270	hardwood (low elev.)
	10320	80	10410	(mid elevation)
	7690	200	7900	(high elevation)
Whittaker 1966 (Tennessee)	11100	560	11870	a number of hardwood sites (values represent the averages)
Whittaker and Woodwell 1968, 1969 (New York)	7960	630	8590	young oak/pine
Johnson and Risser 1974 (Oklahoma)	12310	300	12610	oak
Day and Monk 1974 (North Carolina)	>5620	—	>5620	mixed hardwood (values represent leaf biomass only)
Monk et al. 1970 (Georgia)	5410	—	>6000	oak/hickory

TABLE 11 (cont.)

	Aboveground Net Primary Production (kg/ha/yr)			
	Overstory	Understory	Total	Forest type
RIVERINE SWAMPS				
Brown 1981 (Florida)	16070	—	>16070	cypress/hardwood
Conner and Day 1976 (Louisiana)	11200	200	11400	cypress/tupelo
	13740	2000	15740	mixed hardwood
Tilton and Bernard 1975 (New York)	7300	2410	9710	alder shrub
Mitsch and Ewel 1979 (Florida)	9500	—	>9500	cypress/hardwood
Present study (Virginia)	7442	4830	12272	mixed hardwood
DEPRESSION SWAMPS				
Brown 1981 (Florida)	2680	—	>2680	scrub cypress
	8590	—	>8590	young cypress dome
	7820	—	>7820	young cypress dome
	9560	—	>9560	mature cypress dome
Schlesinger 1978 (Georgia)	5950	1170	7120	cypress
Reiners 1972 (Minnesota)	10140	180	10320	cedar
	6510	550	7070	mixed hardwood fen

This particular swamp is very likely being sustained in steady state. It has remained virtually undisturbed by timber harvesting practices and other human encroachment for nearly 200 years or more (Wass and Wright 1969). The present study lends support to the steady state hypothesis. During the course of the project, two trees died of the 100 that were sampled. The estimated biomass of these two trees was 136 kg, which is equivalent to a loss of 6664 kg/ha/yr. Stem and branch production in the overstory amounted to 4918 kg/ha/yr during 1984. The proximity of these values is remarkable, particularly in light of the immense standing biomass of the swamp.

This study introduced two new measures for assessing changes in the understory through the growing season. The IVss, although of limited value for describing the community, are useful for indicating patterns of development in individual species. The IVc provide a broader perspective of community structure and dynamics, and appear to be an improvement over the conventional IVm.

The method of estimating understory production that is presented in this thesis indicates that freshwater marsh communities may be even more productive than recent studies have revealed. This can be exemplified using the data of Doumlele's (1976) marsh study, some of which are contained in Table 12. The average dry weight/plant values were not specifically presented in his thesis, but were calculated from his data. Doumlele estimated Peltandra production, for example, to be 396.72 $g/m^2/yr$. This estimate does not account for the loss of individuals between May and June or between June and July, and the growth of surviving plants during those months. Also, recruitment of new individuals apparently occurred between July and August (note the

TABLE 12. Data from Doumlele's (1976) marsh study.

	Average Biomass (g/m^2)	Average Density ($\#/m^2$)	Average Plant Weight (g)
Peltandra virginica			
May	279.37	8.15	34.28
June	330.45	4.88	67.72
July	396.72	4.80	82.65
Aug.	379.31	5.45	69.60
Sep.	91.53	3.50	26.15
Leersia oryzoides			
May	1.83	12.00	0.15
June	13.71	24.00	0.57
July	28.93	25.00	1.16
Aug.	55.76	25.12	2.22
Sep.	57.95	25.00	2.32
Polygonum punctatum			
May	0.04	5.00	0.01
June	0.73	5.00	0.15
July	17.96	5.12	3.51
Aug.	31.78	6.58	4.83
Sep.	45.29	5.48	8.26
Pontederia cordata			
May	2.29	0.90	2.54
June	18.13	1.60	11.33
July	30.84	1.70	18.14
Aug.	26.94	1.52	17.72
Sep.	29.10	1.68	17.32

TABLE 12 (cont.)

	Average Biomass (g/m^2)	Average Density ($\#/m^2$)	Average Plant Weight (g)
<u>Polygonum arifolium</u>			
May	0.04	0.20	0.20
June	1.39	0.55	2.53
July	2.32	0.85	2.73
Aug.	8.43	1.15	7.33
Sep.	13.55	0.60	22.58
<u>Impatiens capensis</u>			
May	0.01	0.55	0.02
June	0.29	1.18	0.25
July	2.89	1.95	1.48
Aug.	6.62	2.80	2.36
Sep.	6.51	1.15	5.66
<u>Eleocharis quadrangulata</u>			
May	0.05	0.05	1.00
June	0.25	0.12	2.08
July	3.09	0.22	14.05
Aug.	2.73	0.82	3.33
Sep.	3.17	2.35	1.35

increase in stem density), yet the contribution of this increase in Peltandra production is not evident from the data. When these factors are considered, Peltandra production can be calculated as:

$$279.37 + 4.88(67.72 - 34.28) + 4.80(82.65 - 67.72) = 514.23\ g/m^2$$

+ an indeterminable amount from late season recruitment.

Likewise, revised production estimates for the other species are:

Leersia oryzoides	$55.76 + 25.00(2.32 - 2.22) = 58.22\ g/m^2$
Polygonum punctatum	$31.78 + 5.48(8.26 - 4.83) = 50.60\ g/m^2$
Pontederia cordata	$30.84 + (29.10 - 26.94) = 33.00\ g/m^2$
Polygonum arifolium	$8.43 + 0.60(22.58 - 7.33) = 17.58\ g/m^2$
Impatiens capensis	$6.62 + 1.15(5.66 - 2.36) = 10.41\ g/m^2$
Eleocharis quadrangulata	$3.09 + (3.17 - 2.73) = 3.53\ g/m^2$

(The estimates for P. cordata and E. quadrangulata reflect the minimum production increases from recruited plants which can be detected from the data.)

Doumlele presents net primary production for the entire marsh community as 755.16 $g/m^2/yr$. However, total community production is greater than 888.61 $g/m^2/yr$ when the data are analyzed by the method utilized here.

For future studies of this nature, understory sampling should be intensified to the point that all species of interest will be adequately sampled throughout the growing season. This would necessitate reevaluating the appropriate quadrat size and number of samples for each sampling excursion, since community structure varies considerably from month to month. In addition, permanent plots with identification and regular examination of individual plants would be of great benefit in understanding mortality and recruitment patterns. This information could then be applied to the harvested samples to give the most accurate assessment of net primary production.

APPENDIX I

Regression equations utilized for estimating primary production of the various tree species are presented below. The regressions and estimates were chosen over others (e.g., Bunce 1968; Whittaker et al. 1974) due to the closer similarities in climate and habitat. _Magnolia virginiana_ were assumed similar in form and growth to _Acer_ _rubrum_ based on data from Forbes (1961).

Nyssa _sylvatica_ - taken from Brown (1978) regression for _N_. _biflora_

$$\log_{10}(A) = -0.983 + (2.386)\log_{10}(X)$$

A = total aboveground woody biomass, in kg
X = dbh of tree, in cm

Fraxinus _pennsylvanica_ - taken from Reiners (1972) regressions for _F_. _nigra_

$$\log_{10}(B) = 2.8649 + (2.3390)\log_{10}(Y)$$

$$\log_{10}(C) = 2.2131 + (2.1085)\log_{10}(Y)$$

$$\log_{10}(D) = 1.7899 + (3.1751)\log_{10}(Y)$$

B = bole wood biomass, in g
C = bole bark biomass, in g
D = biomass of branches, in g
Y = dbh of tree, in inches

Acer rubrum - average of Reiners (1972) regressions for A. rubrum and estimates obtained by plotting and extrapolating Sollins and Anderson (1971) A. rubrum data

$$\log_{10}(B) = 2.8824 + (2.2344)\log_{10}(Y)$$

$$\log_{10}(C) = 2.2475 + (1.6287)\log_{10}(Y)$$

$$\log_{10}(D) = 2.5221 + (2.3994)\log_{10}(Y)$$

Carpinus caroliniana - taken from Reiners (1972) regressions for C. caroliniana

$$\log_{10}(B) = 3.0870 + (2.0463)\log_{10}(Y)$$

$$\log_{10}(C) = 2.2127 + (1.8428)\log_{10}(Y)$$

$$\log_{10}(D) = 2.6856 + (1.6558)\log_{10}(Y)$$

Liriodendron tulipifera - extrapolated from plotted L. tulipifera data of Sollins and Anderson (1971)

Magnolia virginiana - taken from Reiners (1972) regressions for Acer rubrum (see A. rubrum regressions above)

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