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Primary Production and Plant Community Structure in a Tidal Freshwater Marsh

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PRIMARY PRODUCTION AND PLANT COMMUNITY STRUCTURE IN A TIDAL FRESHWATER MARSH

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Damon George Doumlele

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APPROVAL SHEET

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ABSTRACT

Annual net primary production and indices of community structure for Sweet Hall Marsh, a tidal freshwater marsh in Virginia, were determined. The total marsh community sampled produced approximately 755.16 g/m^2/yr, with *Peltandra virginica* accounting for over half the amount. Other major producers were *Leersia oryzoides*, *Polygonum punctatum*, *Pontederia cordata* and *Aneilema keisak*.

Species diversity was highest in August. Both diversity and the species distribution pattern were strongly influenced by elevation and the effects of the presence of shrubs and trees.

The community was found to be largely dominated by *Peltandra* from spring through midsummer, but consequent die-back of this species allowed other species, namely *Leersia*, to increase in importance toward the end of the growing season.

INTRODUCTION

Investigations of primary productivity and community structure in tidal marshes have increased in number in recent years, mainly as a result of the discovery of their importance in estuarine production (Odum, 1961). The abundance of extensive salt and brackish marshes on the Atlantic and Gulf coasts of the U.S. made them primary study areas, particularly in regard to productivity, nutrient cycling and species distribution.

Studies of freshwater marshes in general are extensive, but most have been done on inland, non-tidal marshes. Research in tidal freshwater marshes along the Atlantic coast is almost nonexistent, due to their scarcity in comparison with salt and brackish marshes, their commonly small size and their soft substrates which hamper field activities.

Most of the few studies of tidal freshwater marshes deal with marsh classification. Studies in productivity and community structure are few; hence this investigation was undertaken. The objectives were to: 1) delineate plant communities within the marsh, 2) determine net primary productivity of the most common marsh species, 3) determine species diversity with respect to time of growing season and location within the marsh, and 4) determine interspecific relationships.

REVIEW OF LITERATURE

Productivity of marshes

Salt and brackish marshes

Odum (1961) reported *Spartina alterniflora* production in a Georgia salt marsh to be approximately 2242 g/m^2, and this high source of nutrients (the salt marsh) has since become the object of numerous productivity studies (Keefe, 1972; Hatcher and Mann, 1975). Most of the work has dealt with primary productivity of higher plants, although some authors have included macrophytic algae and phytoplankton (Udell et al, 1969) and faunal relationships (Day et al, 1973).

Spartina alterniflora, because of its relatively high abundance, has been the most intensively studied marsh plant, but considerable attention has been given to other species. In irregularly-flooded salt marshes of North Carolina, annual net productivity of *Juncus roemerianus* has been determined by Waits (1967) and Foster (1968). Standing crop values have also been reported for *Spartina patens* (Waits, 1967; Wass and Wright, 1969) and *Distichlis spicata* (Wass and Wright, 1969).

Primary productivity studies in brackish marshes have been conducted mainly for comparisons with results of salt marsh investigations. In Virginia, Mendelssohn (1973) compared three marshes--two brackish and one salt--in terms of productivity and soil and tissue nutrient concentrations, and Wass and Wright (1969) reported standing crop values for various salt, brackish, and freshwater marsh species. Odum and Fanning (1973) compared productivity of *Spartina cynosuroides* in a Georgia brackish marsh with that of *Spartina alterniflora* in a salt marsh and found that the latter equaled or exceeded the former. The authors hypothesized that even though *S. cynosuroides* spends less energy in osmoregulation, neither does it have the benefit of as much water-flow energy.

Freshwater Marshes

Productivity studies on freshwater marsh plants have focused primarily on *Phragmites australis* (=*P. communis*) and *Typha latifolia*. Considerable work has been done in Britain, where standing crop and productivity values were obtained for *Phragmites* and *Typha* by Buttery and Lambert (1965), Pearsall and Gorham (1956) and Gorham and Pearsall (1956). Westlake (1963) compared fertile reed swamps with other terrestrial communities worldwide and concluded that they are apparently the most productive temperate communities, producing 30-45 metric tons per hectare per year.

In the United States, Van Dyke (1972) reported standing crops at different times of the year for *Phragmites* and other plants in an Iowa marsh, and McNaughton (1966) investigated changes in *Typha* biomass along a transect from North Dakota to Texas. Much research has been done in the South on various marsh and swamp species. Boyd and Hess (1970) recorded *Typha* standing crop and nutrient levels over a large area of the Southeast, and Wass and Wright (1969) listed standing biomass for *Zizania aquatica*, *Leersia oryzoides*, *Phragmites australis* and *Nuphar luteum*, as well as for *Typha*. Other less common plants such as *Justicia americana* and *Alternanthera philoxeroides*

(Boyd, 1969) and *Eichornia crassipes* (Penfound and Earle, 1948) have also been studied.

Although extensive work has been done on single species or monotypic communities, few studies have been carried out in vegetationally diverse freshwater marshes. Jervis (1969), in determining community production in a diverse New Jersey marsh, found that the average (9.50 $g/m^2/day$) and maximum (20.94 $g/m^2/day$) productivities were among the highest reported for natural vegetation. Good and Good (1974), also in New Jersey, obtained aerial and subaerial standing crop values for community types in a tidal freshwater marsh and found a general agreement with values taken from nearby marshes.

Species Distribution and Community Structure of Marshes

Marshes in General

Among the earliest studies of marshes are those which relate to the delineation of plant communities or species zones (Harshberger, 1909; Johnson and York, 1915). Penfound and Hathaway (1938) described 11 community types among 7 Louisiana marsh transects ranging in salinity from salt to fresh and listed presence and relative abundance of each species in each community tpye. Wells (1928), in a comprehensive study of terrestrial plant communities of the coastal plain of North Carolina, described salt and freshwater communities as well as successional relations. In New Jersey, salt, brackish and freshwater communities of Island Beach State Park were described and mapped by Martin (1959) In Virginia, Wass and Wright (1969) gave floristic descriptions of a variety of aquatic communities, and Kerwin (1966) studied changes in community structure along a salt-to-freshwater gradient.

Salt and Brackish Marshes

Research related to species distribution in salt marshes has centered on species zonation and the controlling factors. In delineating zones of algae and seed plants in Cold Spring Harbor, New York, Johnson and York (1915) concluded that factors which influence distribution include subtratum, currents, salintiy and water temperature, but primarily tide levels which, in turn, control evaporation, aeration and light supply. The influence of tides and marsh elevation on species zonation has since been well studied in many localities. Yapp et al. (1917) looked at zonation and plant associations in a British estuary in relation to altitude, and similar studies have been conducted in the U.S. (Miller and Egler, 1950; Adams, 1963; Kerwin and Pedigo, 1971).

Community structure studies in brackish marshes are scarce in comparison with other marshes. In Virginia, Mendelssohn (1973) examined community composition and species dominance in two brackish marshes and a salt marsh, while Flowers (1973) studied zonation and succession in two brackish marshes in Maryland and concluded that marsh elevation exerts the greatest influence.

Freshwater Marshes

As one progresses from salt to freshwater marshes, plant diversity increases dramatically; lateral zonation is correspondingly reduced (Gabriel and de la Cruz, 1974); and variation in species composition among marshes is thus increased (Martin, 1959). Causes of this variation are apparently numerous and complex, as Martin states that water table depth, ground water pH, ground water salinity and substrate composition revealed no gradient along which to arrange species variation in different marshes in New Jersey.

Community structure studies in freshwater marshes have not been as concerned with zonation as in salt and brackish marshes, since species zones are not normally as distinct. Van Dyke (1972) calculated species dominance and density values for an Iowa marsh, and Jervis (1963) named and described 10 communities in Troy Meadows, N. J. and listed physiographic, edaphic, climatic and biotic influences on community composition.

MATERIALS AND METHODS

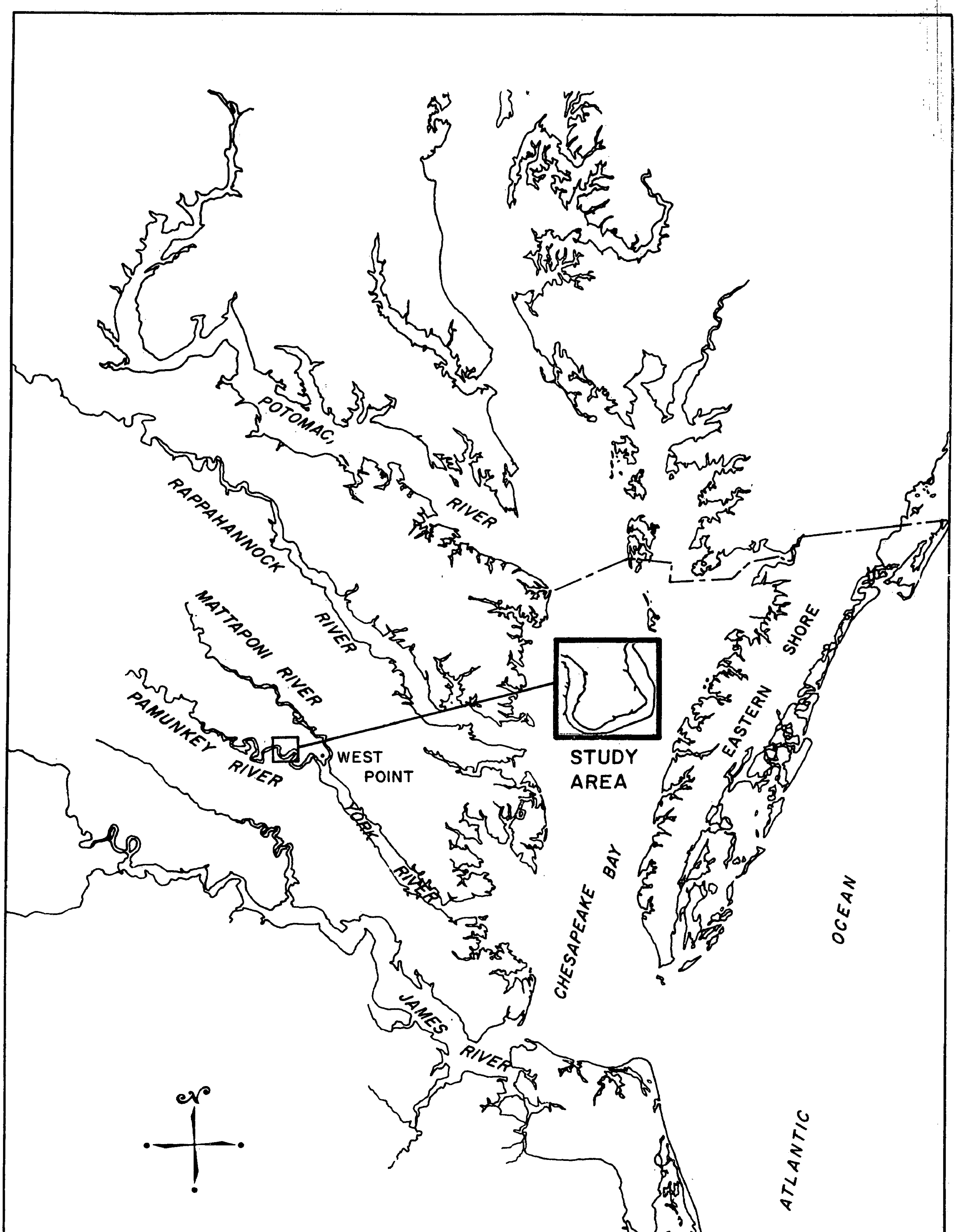
Selection of the Study Area

Sweet Hall Marsh, the area chosen for this study, is located approximately 19 km from the mouth of the Pamunkey River, a tributary of the York River, Virginia (Fig. 1). It is the fourth of the eight major fresh-mesohaline marshes and swamps of the river, which include some of the most extensive tidally-flushed wetlands in the U.S. Geologically, the area is part of the fluvial depositional system of the coastal plain of Virginia (Onuschak, 1973) and is characterized by such features as marshes, flood plains and meadering streams.

The marsh consists of over 444 ha of undisturbed wetlands, including 29 ha of wooded swamp and 30 ha of water in streams at least 15 m wide. There is also a 7.4 km border with the river, the salinity of which varies from 0 to 5 o/oo, depending on the flow (Marcellus, unpublished data).

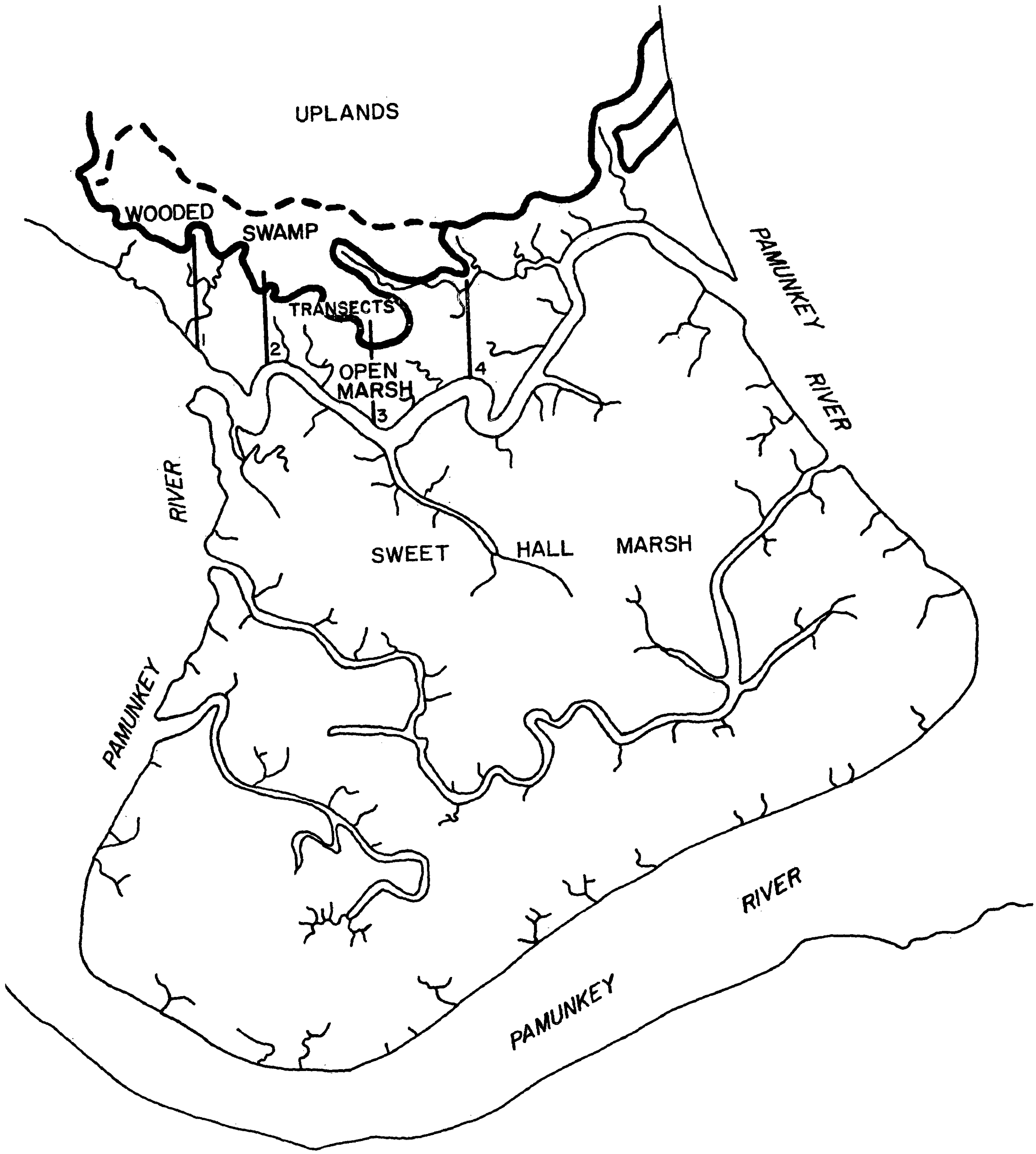
The sampling area (Fig. 2) is located in the northwest sector and consists of four parallel belt transects which extend from a transverse creek to the wooded swamp. Originally, the transects were intended to extend into the upland woods bordering the swamp, but field conditions made this unfeasible.

Figure 1. Map of eastern Virginia showing location of Sweet Hall Marsh.



POTOMAC
RIVER
RAPPAHANNOCK
RIVER
MATTAPONI RIVER
PAMUNKEY RIVER
WEST
POINT
YORK
RIVER
STUDY
AREA
EASTERN
SHORE
CHESAPEAKE BAY
JAMES
RIVER
ATLANTIC
OCEAN
N

Figure 2. Map of study area showing marsh, swamp and transect locations.


UPLANDS
WOODED
SWAMP
TRANSECTS
1
2
3
4
OPEN
MARSH
PAMUNKEY
RIVER
RIVER
SWEET HALL MARSH
PAMUNKEY
RIVER
PAMUNKEY

Sampling Procedures

After a preliminary reconnaissance in February, 1974, transects and sampling quadrat markers were established with the aid of U.S.G.S. topographic maps and aerial photographs. Sampling began in late April, when the vegetation was sufficiently high, and continued monthly through October, when most of the plants had died back. During each sampling, a one-meter-square frame was placed on the ground over each of the 40 quadrat markers, and data were taken from the plants located within the frame. Data recorded included species present, number of individuals of each species or species density, average species height and species coverage. Where certain species existed as tussocks or clumps, such as *Peltandra virginica* and *Carex stricta*, the clumps were each counted as one individual. Species coverage was defined as the percentage of the quadrat covered by a species if the shadow of the plants were vertically projected on the ground.

During the season over 80 species were identified, both from sampling plots and from nearby areas and are listed in Table A1 of the Appendix.

Near each quadrat was chosen a 0.1 m^2 plot of similar species composition in which all of the above-ground vegetation was clipped and brought back to the laboratory for determination of species biomass. Samples were separated by species, washed, placed in paper bags and allowed to dry at 120°C in an oven. This unusually high temperature was deemed necessary in order to dry certain species such as *Peltandra* and *Pontederia*, which have a high water content, before they became covered with fungi. The dried samples were weighed by species to the nearest 0.01 g.

The above procedures were followed for each monthly sampling through September. A sampling was attempted on October 31, but too little living vegetation was left to ensure reliable data. Samplings during the late fall and winter months were not made because of the many duck hunters in the marsh.

Determination of Standing Crop and Net Primary Production

Standing crop of each species was calculated as the dry weight per square meter for a given sampling date. Although 37 plant species occurred among the 200 clip samples taken (40 per month), only standing crop values for those species found in over 10% of the August clip plots were tabulated separately, as the other species were too scarce for dependable results.

Annual net primary production for each species was equal to the maximum monthly standing crop value, and productivity for the total community was the sum of these values (Odum, 1960; Jervis, 1969). Daily production rates were obtained by dividing the difference between two consecutive standing crop values by the number of days within the interval. Changes in dead standing crop could not be determined, since most of the species sampled were very fleshy and decayed rapidly after death; also, vigorous tidal flushing tends to remove most of the litter from the marsh.

Determination of Species Diversity

Species frequency was defined as the percentage of the 40 quadrats in which a species occurred. This index, along with species density and species coverage, was used to calculate the following indices (Curtis and McIntosh, 1950; Phillips, 1959):

$$\text{Relative frequency} = \frac{\text{Species frequency}}{\text{Sum of frequency values for all species}} \times 100$$

$$\text{Relative density} = \frac{\text{Number of individuals of the species}}{\text{Number of individuals of all species}} \times 100$$

$$\text{Relative dominance} = \frac{\text{Species coverage}}{\text{Sum of coverage values for all species}} \times 100$$

The species importance value (Curtis and McIntosh, 1951) was defined as the sum of these three indices. The importance values were then substituted into the Shannon-Weaver (1949) formula

$$\bar{H} = -\Sigma P_i \log P_i$$

where $\bar{H}$ represents the index of diversity, and P_i is equal to the importance probability or the species importance value divided by the total of importance values.

The diversity index was calculated for each monthly sampling and also for each quadrat in each sampling; thus changes in diversity could be observed both temporally and spatially.

Index of Sociability

The tendency of a species to have a clumped or contagious distribution is expressed by the index of sociability (Whitford, 1949; Daubenmire, 1968), which is obtained by dividing the species frequency, expressed as a decimal, into the species density. A high index indicates a high degree of aggregation, and a low index indicates a more random or regular distribution. The index of sociability was calculated for all 37 quadrat species for each sampling date, and averages for the season were taken.

Index of Similarity and Clustering Methods

The index of similarity or Sorenson's index (Kontkanen, 1957) was used as a measure of the association between two species and is calculated as follows:

$$QS = \frac{2c}{a + b} \times 100$$

where

QS = Sorenson's index
a = Number of quadrats in which species A occurred
b = Number of quadrats in which species B occurred
c = Number of quadrats in which both species occurred

This index was calculated for all possible comiinations of the 10 most common species during the August sampling. Clustering was then performed using the weighted pair-group method (Sokal and Sneath, 1963), and a dendrogram was constructed.

RESULTS AND DISCUSSION

General Observations

In Sweet Hall Marsh there exists, in addition to open marsh, an extensive area composed of both herbaceous and woody vegetation, referred to as swamp in this paper. Within the swamp, two, and possibly three communities were recognized. The mature swamp borders the fastlands and is a dense-canopied community in summer, consisting of large trees such as *Nyssa, Acer* and *Fraxinus*; an understory of *Viburnum, Smilax, Myrica* and *Cornus*; and an herbaceous flora similar to that of the open marsh. The substrate of this community is typically a very soft muck and at high tide is usually covered with several centimeters of water. A second swamp community borders the open marsh in certain areas and is less densely populated by trees and shrubs than the mature swamp. Mostly small individuals of *Acer, Rhus* and *Viburnum* comprise the woody flora of this second swamp type, with the herbaceous vegetation consisting of *Osmunda regalis, Impatiens capensis, Polygonum arifolium, Typha angustifolia* and other open marsh species. The substrate of this community is also very soft but is considerably covered by solid tussocks of *Osmunda* and interwoven with roots of trees and shrubs. A possible third type of swamp community is the ecotone between the swamp and the open marsh. However, the flora of this region is largely a mixture of the swamp and marsh floras and thus may not be distinctive enough to classify the area as a separate community.

The effects of trees and shrubs on herbaceous marsh vegetation are generally unknown, but several obvious influences were observed during the course of this study. In 1974, new shoots of *Peltandra* appeared in Sweet Hall Marsh as early as February 13 and averaged 8 cm in height by March 28, with the tallest individuals growing in the swamp and on creek banks. The pattern of tall *Peltandra* in the swamp was prevalent throughout the growing season and extended to other species as well. It was observed that nearly all herbs in the swamp sprouted earlier, flowered earlier and appeared greener and more robust than those growing in the open marsh. The reasons for this are not clear, but it is possibly related to shading or increased fertility of the soil from decaying leaves and wood.

Factors affecting vigorous growth of *Peltandra* on creek banks may be related to those which promote the similar growth of tall *Spartina alterniflora* in salt marshes (Romig, 1973), the main factor being high amounts of dissolved oxygen in the soil water. Romig hypothesized that creek bank aeration and drainage is due not only to nearness to the tidal creek, but also to burrowing crabs such as *Uca*, which are very abundant in Sweet Hall Marsh.

The trees were generally not as tall as those of the nearby uplands, and this difference can be detected from aerial photographs. The deciduous woody plants also lost their leaves earlier in the fall than did their upland counterparts, and thus the two regions could be easily distinguished from a distance at that time of the year.

Productivity Analysis

Results of the standing crop and productivity determinations are shown in Table 1 and Figs. 3, 4, 5 and 6; clip frequencies are listed in Table A2 of the Appendix. Productivity and standing crop for *Peltandra* were so high in relation to other plants that it was necessary to graph *Peltandra* in separate figures with compressed vertical axes (Figs. 3 and 5) so that the curves of the less productive species could be analyzed. The production rate was assumed to be zero at the initial sampling, although some production, especially in *Peltandra*, undoubtedly took place before that date.

It can be seen from Fig. 3 that even though the curve for the standing crop of the total community is a resultant of the 37 species sampled, the shape of the curve is largely influenced by *Peltandra*, which accounted for 53% (396.72 $g/m^2/yr$) of the total community production. Apparently, the environmental conditions found in Sweet Hall Marsh are very nearly the optimum conditions for *Peltandra*, as few of the clip samples did not contain at least one individual.

Peltandra, *Pontederia cordata* and *Leersia oryzoides* are the only common plants which produced at high rates during May and the early part of June, with most of the others reaching their highest peaks in August (Figs. 5 and 6). A few species such as *Leersia*, *Aneilema keisak* and *Polygonum arifolium* experienced a secondary rise in their production rates during late July and early August after a previous productive period in May. Possible causes of these twin peaks are changes in competition among species during the season, the production of flowers and fruits later in the season, and the ability of certain species to produce new foliage after the first leaves have

TABLE 1

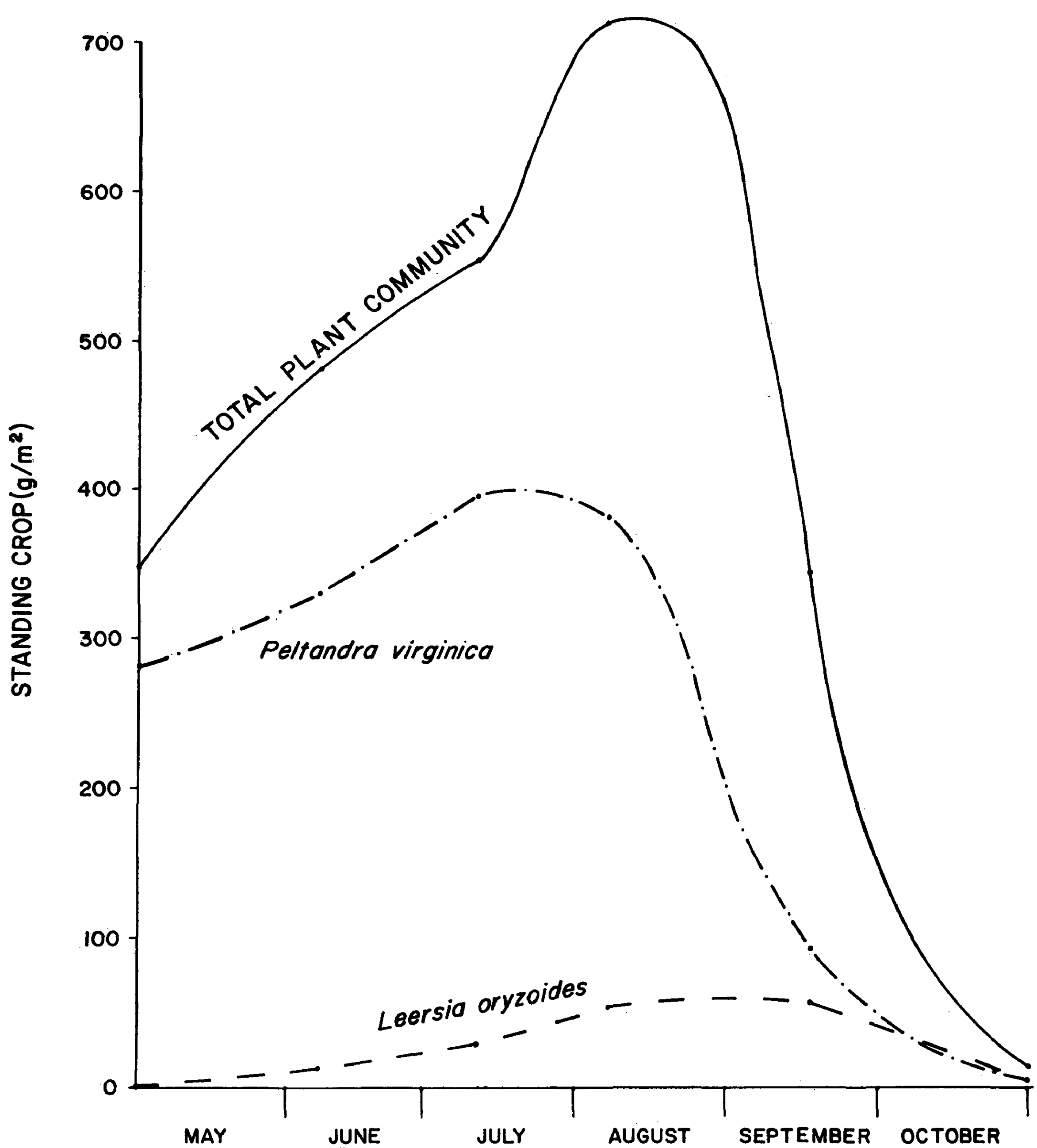
STANDING CROPS (G/M^2) AND PRODUCTION RATES ($G/M^2/DAY$) FOR THE PERIOD MAY-OCTOBER, 1974

	May 3	June 8		July 10		Aug 8		Sept 17		
Species	Initial Standing Crop	Standing Crop	Rate	Standing Crop	Rate	Standing Crop	Rate	Standing Crop	Rate	Annual Net Production
Peltandra virginica	279.37	330.45	1.42	396.72	0.98	379.31	-0.18	91.53	-2.10	396.72
Leersia oryzoides	1.83	13.71	0.33	28.93	0.23	55.76	0.28	57.95	0.02	57.95
Polygonum punctatum	0.04	0.73	0.02	17.96	0.25	31.78	0.14	45.29	0.10	45.29
Pontederia cordata	2.29	18.13	0.44	30.84	0.19	26.94	-0.04	29.10	0.02	30.84
Aneilema keisak		2.95	0.08	8.02	0.08	22.23	0.15	16.33	-0.04	22.23
Polygonum arifolium	0.04	1.39	0.04	2.32	0.01	8.43	0.06	13.55	0.04	13.55
Impatiens capensis	0.01	0.29	0.01	2.89	0.04	6.62	0.04	6.51		6.62
Eleocharis quadrangulata	0.05	0.25	0.01	3.09	0.04	2.73	-0.01	3.17		3.17

TABLE 1 (Continued)

Species	May 3 Initial Standing Crop	June 8 Standing Crop	June 8 Rate	July 10 Standing Crop	July 10 Rate	Aug 8 Standing Crop	Aug 8 Rate	Sept 17 Standing Crop	Sept 17 Rate	Annual Net Production
Scirpus americanus	0.31	0.82	0.02	2.03	0.02	1.44	0.01	2.27	0.01	2.27
Polygonum sagittatum		0.38	0.01	0.42		2.11	0.02	1.95		2.11
Others	61.12	108.94	1.33	61.89	-0.69	174.43	1.16	76.87	-0.71	174.43
Total	345.06	478.01	3.69	555.09	1.13	711.78	1.62	344.50	-2.68	755.16
Days from Initial Sampling		36		68		97		137		

Figure 3. Comparison of changes in standing crop biomass among *Leersia oryzoides*, *Peltandra virginica* and the total plant community.



700
600
500
400
300
200
100
0
STANDING CROP (g/m²)
TOTAL PLANT COMMUNITY
Peltandra virginica
Leersia oryzoides
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER

Figure 4. Comparison of changes in standing crop biomass among the seven most productive species, excluding *Peltandra virginica*.

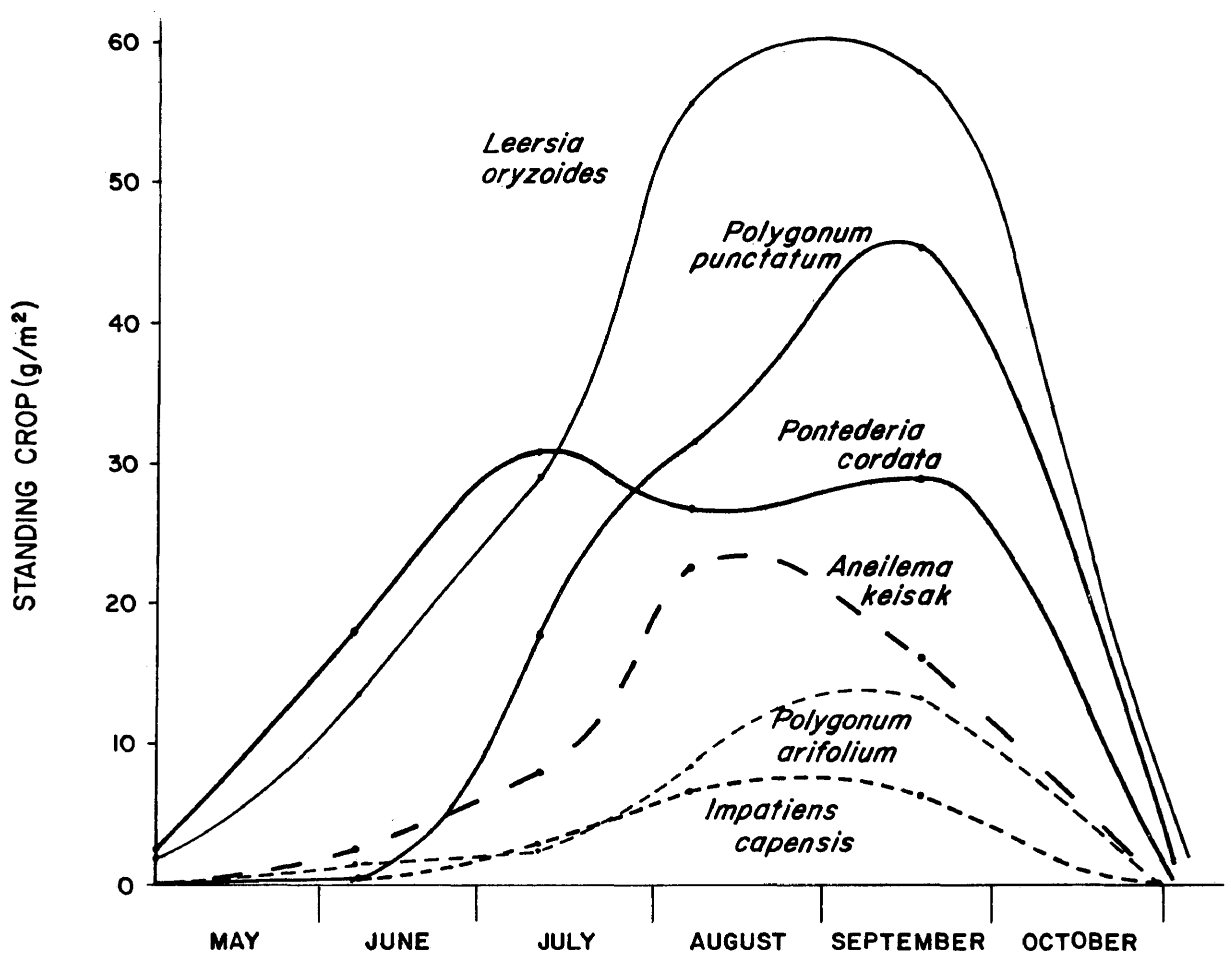
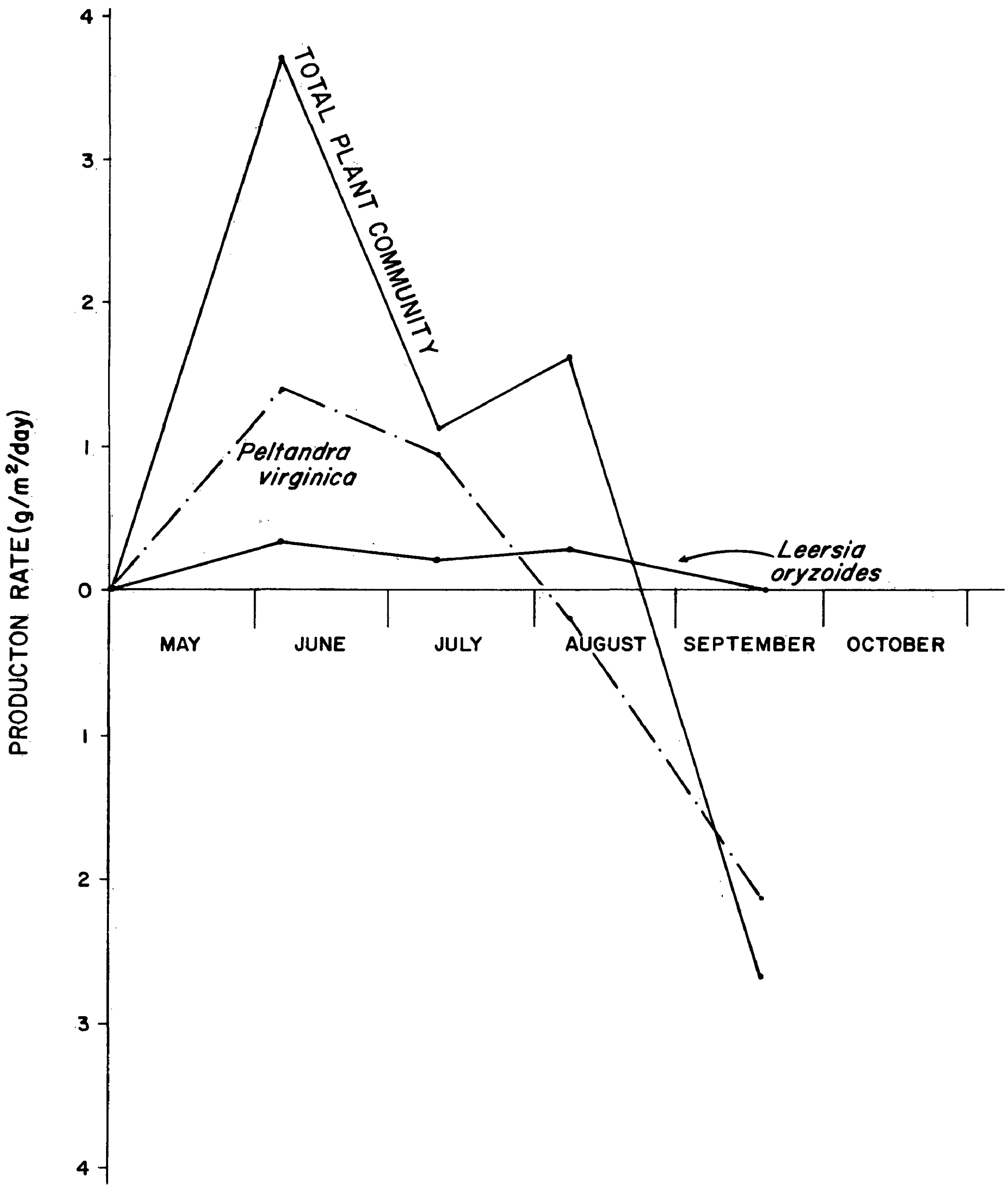
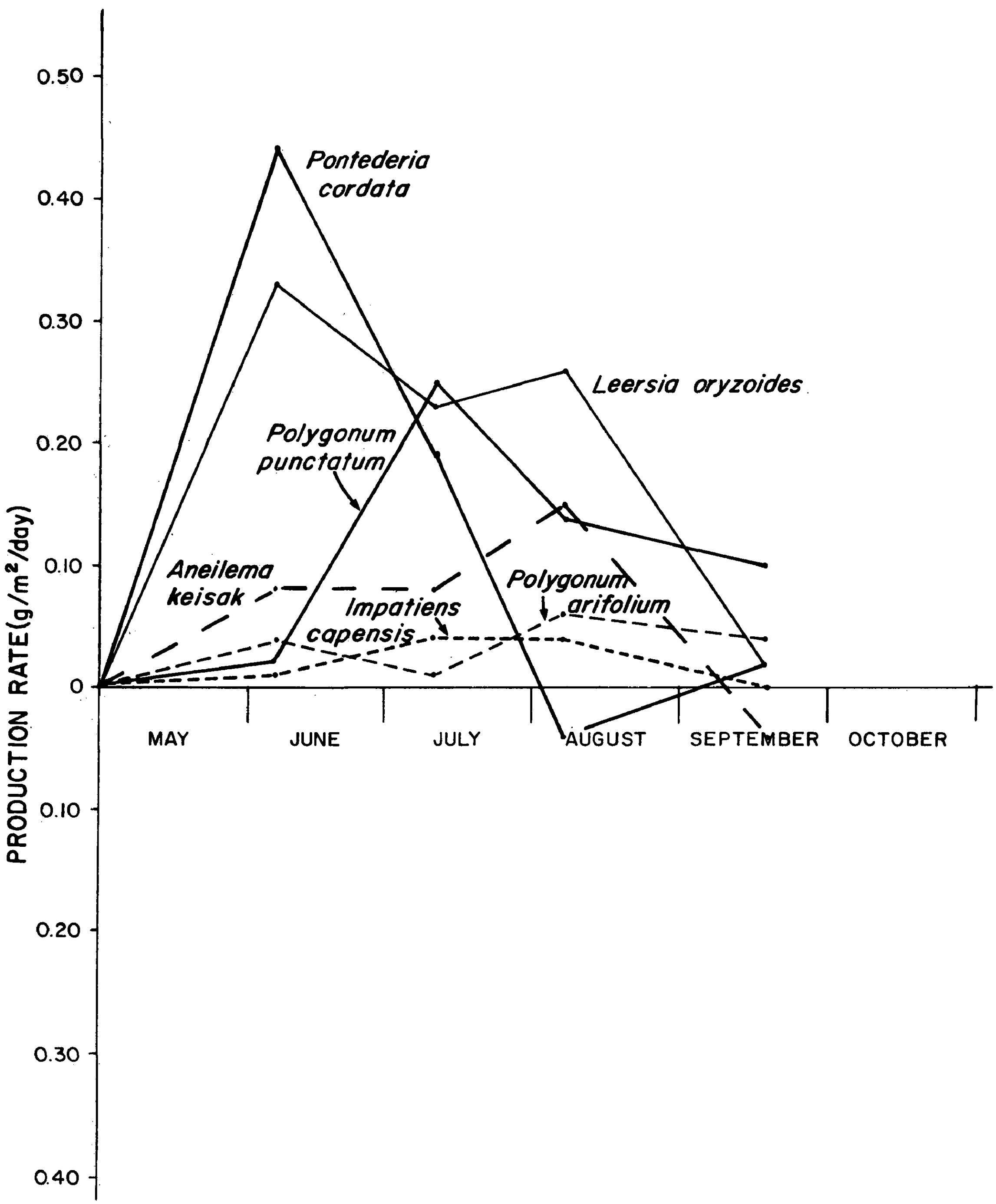

STANDING CROP (g/m²)
60
50
40
30
20
10
0
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
Leersia oryzoides
Polygonum punctatum
Pontederia cordata
Aneilema keisak
Polygonum arifolium
Impatiens capensis

Figure 5. Comparison of changes in daily production rate among *Leersia oryzoides*, *Peltandra virginica* and the total plant community.



PRODUCTON RATE (g/m²/day)
4
3
2
1
0
1
2
3
4
TOTAL PLANT COMMUNITY
Peltandra virginica
Leersia oryzoides
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER

Figure 6. Comparison of changes in daily production rate among the seven most productive species, excluding *Peltandra virginica*.


0.50
0.40
0.30
0.20
0.10
0
0.10
0.20
0.30
0.40
PRODUCTION RATE (g/m² /day)
MAY
JUNE
JULY
AUGUST
SEPTEMBER
OCTOBER
Pontederia cordata
Leersia oryzoides
Polygonum punctatum
Aneilema keisak
Impatiens capensis
Polygonum arifolium

died (Wass and Wright, 1969). A fourth cause hypothesized by Penfound (1956) may be differential changes in rates of photosynthesis and respiration. During the hot summer, photosynthesis decreases, respiration increases and productivity therefore decreases. In late summer and fall, the trend is reversed, hence a secondary production peak. Similar phenomena have been observed by Waits (1967), Boyd (1970) and Mendelssohn (1973), in which freshwater marsh production has been observed to peak in spring and early summer. Earlier productivity maxima for *Peltandra*, *Pontederia* and *Leersia* could also possibly be due to initial translocation of material stored underground during the winter to the new aerial shoots, a phenomenon known to occur in *Typha* (Jervis, 1969). The productivity peaks of these early producers and those of the other plants cause the productivity curve to be consequently two-peaked (Fig. 5).

Maximum standing crops, for the most part, occurred in late August and early September, exceptions being *Peltandra* and *Pontederia*, which peaked in July; *Aneilema*, which peaked in mid-August; and *Polygonum punctatum*, which reached a maximum in late September. *Peltandra*, as mentioned previously, was one of the first species to produce new growth in the spring; this is evidenced by the fact that as early as May 1 the plant had already produced a standing crop of 279.37 g/m^2 or over 80% of the total community standing crop at that time. Before reaching its maximum in July, *Pontederia* had a consistently higher standing crop than *Leersia*, which kept producing until September. *Pontederia* later reached a secondary peak in September, probably because of decreasing competition with *Peltandra*, which grows in a similar habitat. The community as a whole produced a maximum standing crop of 755. 16 g/m^2 during the latter half of August, and production then fell sharply, until by later October and early November the remaining living crop was negligible.

Primary production in freshwater marshes has been investigated by numerous authors (see REVIEW OF LITERATURE), but comparatively few productivity values of the species listed in Table 1 have been reported. The main reason is probably the fact that in freshwater marshes it is often difficult to obtain monospecific samples, especially of the rarer species, in sufficient quantity to arrive at reliable standing crop estimates. Despite the obvious dominance of *Peltandra* in this study, it accounted for only half of the total community production (Table 1). The surrounding plant community greatly influences the productivity of the species, since 396.72 $g/m^2/yr$ annual production for *Peltandra* would be less than the productivity of the species obtained from a pure *Peltandra* stand. As an example, Jervis (1969) reported *Typha* annual production values ranging from 44 g/m^2 in the sedge-shrub community to 1566 g/m^2 in the less competitive cattail community.

It is for this reason that productivity values of individual species in heterogeneous freshwater marshes are often only useful when compared with values derived from other marshes of similar community structure. Therefore, it appears more logical to consider total community production of freshwater mixed communities when analyzing the productivity of marshes of this type. This contrasts with salt marshes, where species usually grow in pure stands, the productivities of which can be compared with those of pure stands of the same species elsewhere.

Annual net production of the community studied in Sweet Hall Marsh was 755.16 g/m^2, which falls into the productivity range of 672 to 1121 g/m^2 for freshwater mixed communities in Virginia (Silberhorn et al, 1974). In comparison, Jervis (1969) reported 1491.69 $g/m^2/yr$ for his sedge swale community in New Jersey. Sweet Hall Marsh is located farther south and has a longer growing season but is significantly less productive. The difference in production rates, however, is due to differences in community composition rather than climatic factors. All four of the communities which Jervis examined are dominated by such prodigious producers as *Zizania aquatica*, *Typha* spp. and *Carex stricta*, which are notably less common in Sweet Hall Marsh. When these three dominants are excluded from Jervis's data, the highest productivities are 255.15 $g/m^2/yr$ (*Echinochloa*), 239.60 $g/m^2/yr$ (*Sparganium*) and 230.99 $g/m^2/yr$ (*Peltandra*), all of which are less than the 396.72 $g/m^2/yr$ produced by *Peltandra* in Sweet Hall Marsh. Another reason for the difference in productivity of the two marshes is the fact that in Jervis's marsh there is a greater degree of evenness as far as productivity of individual species is concerned, with many species producing over 20 $g/m^2/yr$. This is not the case in Sweet Hall Marsh, where only five species produced over 20 $g/m^2/yr$, and these being dominated by *Peltandra*.

The only other figures available for the major producers of Sweet Hall Marsh are those of Wass and Wright (1969) for *Leersia oryzoides*. Their clippings, however, originated from a pure stand and gave a standing crop biomass of 1545 g/m^2, whereas even though *Leersia* was found to be the second highest producer in this study, the peak standing crop was only 57.95 g/m^2. This lower value, however, is a result of competition with other species.

In comparison with salt marshes, freshwater marshes appear generally more productive (Mendelssohn, 1973). Studies by Mendelssohn (1973) and Keefe and Boynton (1973) of Virginia salt marshes list peak living standing crops of 363 g/m^2 (Wachapreague) and 558 g/m^2 (Chincoteague Bay) respectively, compared with 775.16 g/m^2 for this study. However, under favorable conditions standing crops as high as 1725 g/m^2 for tall *Spartina alterniflora* and 1545 g/m^2 for *Leersia oryzoides* have been reported (Wass and Wright, 1969).

Community Structure

Dominance and Density

A dominant species in a community is one which largely controls the energy flow and strongly affects the environment of all other species in the community (Odum, 1971). By this definition, *Peltandra virginica* is considered the dominant species of Sweet Hall Marsh, since it contributes most to community production (see previous section). Although productivity can be used as an approximate indicator of dominance, clipping injures the plants to the extent that the same plot cannot be used for repeated samplings. Species coverage, however, can be used repeatedly and provides a good index of dominance for marsh vegetation.

Coverage, density and frequency values for the 10 most common species are listed in Table 2. *Peltandra* had relatively high coverage values until September, when it was overtaken by *Leersia*. A major cause of these high values is the fact that the broad leaves of *Peltandra* easily shade more area than the narrow leaves and stems of *Leersia*; this is borne out by the high density values of *Leersia* in

TABLE 2

SPECIES FREQUENCY, DENSITY AND DOMINANCE FOR THE 10 MOST COMMONLY SAMPLED SPECIES

	Species Frequency (per cent)					Species Density (individuals per square meter)					Species Coverage (fraction of quadrat covered)				
Species	May	Jun	Jul	Aug	Sep	May	Jun	Jul	Aug	Sep	May	Jun	Jul	Aug	Sep
Peltandra virginica	100	100	98	100	90	8.15	4.88	4.80	5.45	3.50	0.210	0.469	0.367	0.161	0.036
Polygonum punctatum	40	64	62	75	72	5.00	5.00	5.12	6.58	5.48	0.010	0.020	0.026	0.037	0.021
Leersia oryzoides	12	68	78	78	70	12.00	24.00	25.00	25.12	25.00	0.002	0.036	0.058	0.123	0.055
Pontederia cordata	22	42	45	42	45	0.90	1.60	1.70	1.52	1.68	0.006	0.022	0.014	0.030	0.007
Polygonum arifolium	18	42	38	45	30	0.20	0.55	0.85	1.15	0.60	0.002	0.003	0.006	0.009	0.003
Impatiens capensis	20	32	38	32	28	0.55	1.18	1.95	2.80	1.15	0.011	0.019	0.030	0.037	0.006
Carex stricta	20	18	18	12	12	0.28	0.30	0.38	0.28	0.20	0.024	0.038	0.209	0.036	0.015
Eleocharis quadrangulata	3	5	12	22	28	0.05	0.12	0.22	0.82	2.35	---	---	---	---	---
Aneilema keisak	--	5	20	15	20	-	1.25	2.78	2.00	1.50	---	0.005	0.158	0.047	0.023
Hibiscus moscheutos	3	8	12	20	15	0.02	0.12	0.25	0.35	0.32	---	0.004	0.004	0.009	0.004

comparison to those of *Peltandra*. *Peltandra* reached its maximum coverage in June, after which competition with other species forced it to decline, although it remained the dominant species until September.

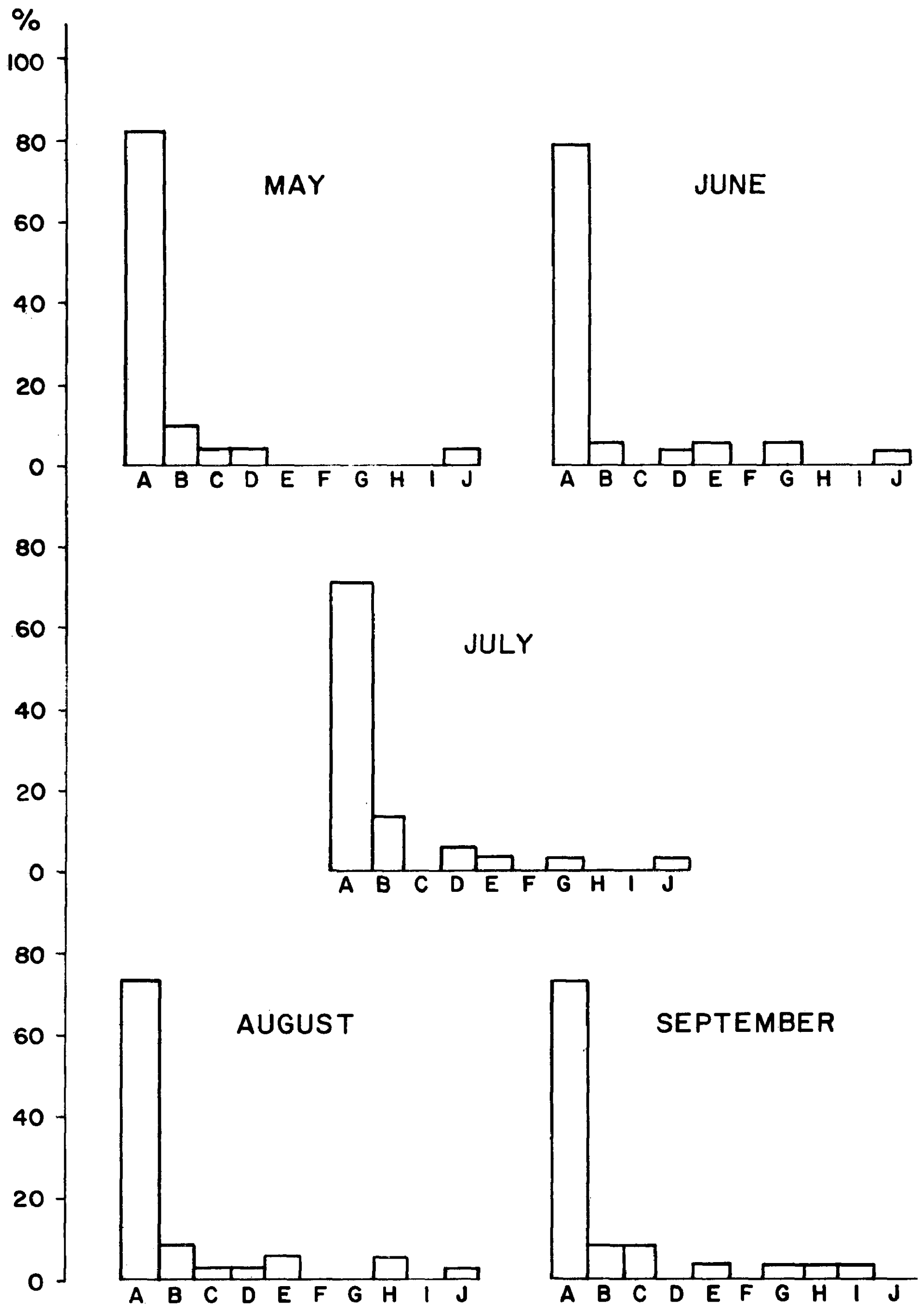
Density values, as noted from Table 2, either remained fairly constant or gradually increased through the season, as a result of germination of seeds during the later months. However, only one species, *Eleocharis quadrangulata*, attained a maximum density in September, probably because of reduced shading by broad-leaved plants. The general decrease in *Peltandra* density was largely a result of sampling procedures rather than ecological factors. The numerous scattered individuals early in the season were probably aggregated into clumps, but these clumps were not readily discernible because of the small sizes of individual plants. As the plants grew, the clumps became apparent and were therefore each counted as one individual, thereby reducing the density values.

Frequency

Frequency is a rough indicator of distribution and can often give information on the general structure of a community. Thus, one can look at the high *Peltandra* frequencies in Table 2 and conclude that the distribution of *Peltandra* is fairly uniform, as a non-evenly dispersed distribution would result in many individuals being found in a few plots and hence a lower frequency.

The diagrams in Fig. 7 are a result of grouping the frequencies into 10 classes. Roughly three-fourths of the species sampled fell into class A (frequencies between 0 and 10%). This implies that most

Figure 7. Comparison of frequency-class percentages for each sampling.


%
100
80
60
40
20
0
MAY
A B C D E F G H I J
JUNE
A B C D E F G H I J
80
60
40
20
0
JULY
A B C D E F G H I J
80
60
40
20
0
AUGUST
A B C D E F G H I J
SEPTEMBER
A B C D E F G H I J

species in the marsh are present in small numbers and/or are far from evenly distributed. The diagrams do not have the characteristic J-shape of the Raunkiaer normal (Cain and Castro, 1959), since *Peltandra* is the sole occupant of class J (except in September, when it falls back into class I) and so overwhelms the other species that the curve cannot turn up at the end. As the season progressed and species became more widespread, their frequencies increased, and consequently the sizes of the classes toward the right end increased.

Sociability

The average indices of sociability for each species for the season are listed in descending order in Table 3. As clumping or aggregation of individuals is often dependent upon the mode of reproduction, this aspect was noted for each species. Plants which spread primarily by vegetative methods, e. g. stolons or rhizomes, tend to produce offspring which are clustered about their parents, as opposed to plants which disseminate efficiently, although other environmental and phytosociological factors affect the distribution patterns of plants. Generally the effectiveness of seed dispersal can be adequately reflected by the sociability index, with high values usually indicating predominance of vegetative reproduction.

Monthly sociability index values for the common species are listed in Table 4 and graphed in Fig. 8. *Leersia, Aneilema, Polygonum punctatum* and *Peltandra,* which began the season with high values, showed more homogeneous distributions by September, when clumps had enlarged and integraded. However, some plants such as *Impatiens, Eleocharis* and *Hibiscus* actually increased in contagion through the

TABLE 3

AVERAGE INDEX OF SOCIABILITY FOR ALL SPECIES SAMPLED

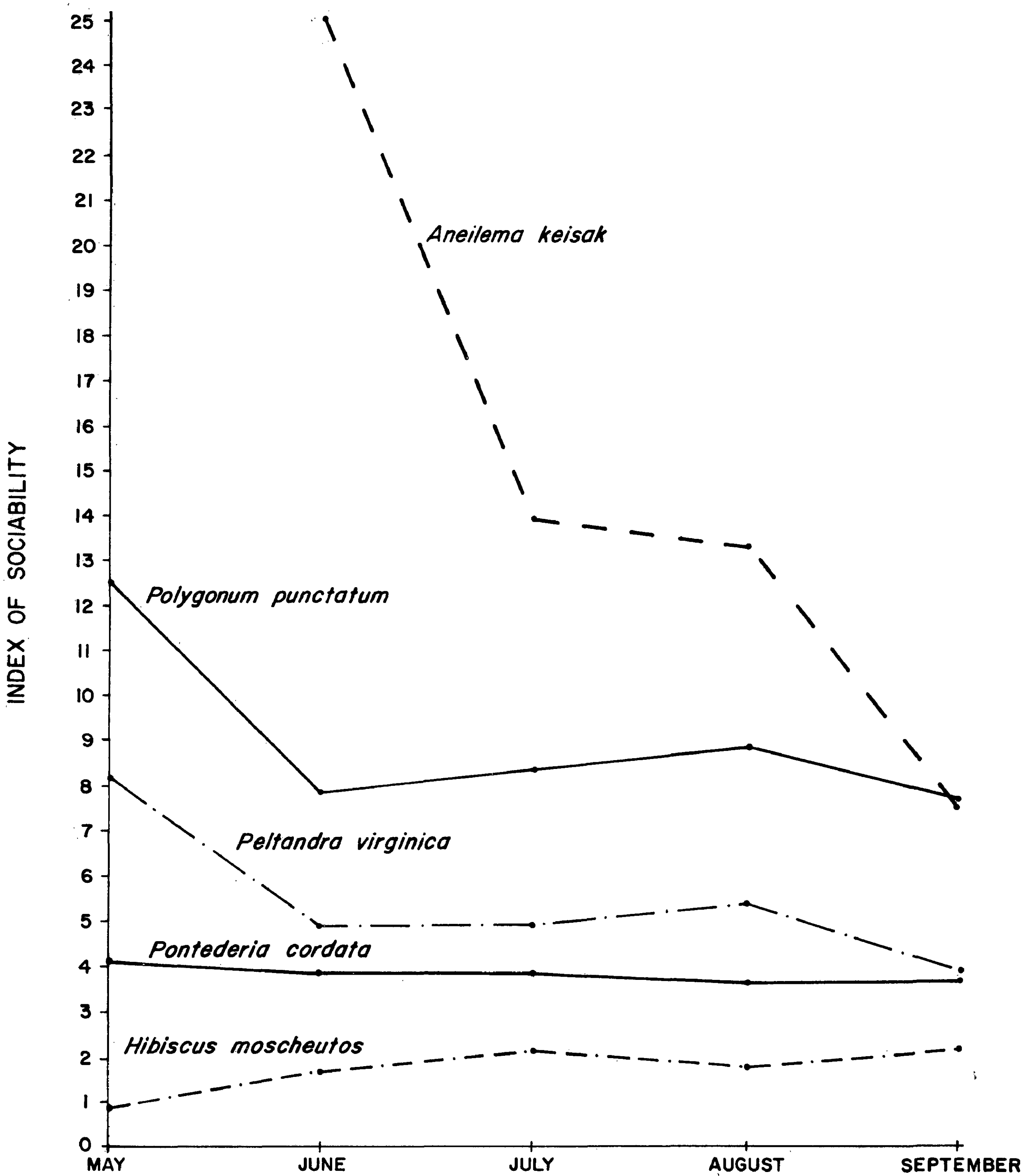
Species Sampled	Index	Reproduction Usually Vegetative	Reproduction Usually Non-vegetative
Leersia oryzoides	47.05	X	
Juncus effusus	16.67	X	
Aneilema keisak	14.93	X	
Polygonum punctatum	8.99		X
Peltandra virginica	5.45	X	
Impatiens capensis	4.88		X
Thelypteris palustris	4.76	X	
Pontederia cordata	3.81	X	
Osmunda regalis	3.70	X	
Eleocharis quadrangulata	3.64	X	
Rumex verticillatus	3.55		X
Hypericum sp.	3.50		X
Phragmites australis	3.16	X	
Spartina cynosuroides	2.71	X	
Scirpus americanus	2.25	X	
Echinochloa walteri	2.00		X
Polygonum arifolium	1.84		X
Carex stricta	1.82	X	
Typha angustifolia	1.74	X	
Hibiscus moscheutos	1.68		X
Amaranthus cannabinus	1.67		X
Zizania aquatica	1.61		X
Rhus radicans	1.57		X
Carex hyalinolepis	1.39	X	
Decodon verticillatus	1.39	X	
Polygonum sagittatum	1.32		X
Scirpus validus	1.12	X	
Acer rubrum	1.10		X
Bidens coronata	0.99		X
Rosa palustris	0.83	X	
Sagittaria latifolia	0.83	X	
Boehmeria cylindrica	0.83		X
Parthenocissus quinquefolia	0.83		X
Thalictrum sp.	0.83		X
Vitis sp.	0.83		X
Teucrium canadense	0.83		X
Galium sp.	0.83		X

TABLE 4

INDEX OF SOCIABILITY FOR THE 10 MOST COMMONLY SAMPLED SPECIES

Species	May	Jun	Jul	Aug	Sep	Av.
Peltandra virginica	8.15	4.88	4.90	5.45	3.89	5.45
Polygonum punctatum	12.50	7.81	8.27	8.77	7.60	8.99
Leersia oryzoides	100.00	35.29	32.05	32.21	35.71	47.05
Pontederia cordata	4.09	3.81	3.78	3.63	3.72	3.81
Polygonum arifolium	1.11	1.31	2.24	2.56	2.00	1.84
Impatiens capensis	2.75	3.67	5.13	8.75	4.11	4.88
Carex stricta	1.38	1.67	2.08	2.29	1.67	1.82
Eleocharis quadrangulata	1.67	2.50	1.88	3.75	8.39	3.64
Aneilema keisak	--	25.00	13.88	13.33	7.50	14.93
Hibiscus moscheutos	0.83	1.56	2.08	1.75	2.17	1.68

Figure 8. Comparison of changes in the index of sociability for five common marsh species.


INDEX OF SOCIABILITY
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
Aneilema keisak
Polygonum punctatum
Peltandra virginica
Pontederia cordata
Hibiscus moscheutos
MAY
JUNE
JULY
AUGUST
SEPTEMBER

season, possibly because of: 1) increasing competition for light and nutrients in an area of a particular species' distribution, causing the species to be aggregated in areas of less competition, and 2) die-back of *Peltandra* in the middle of the season, providing additional niches.

Diversity

The type of species importance value used in the diversity index calculations (Table 6) is that of Phillips (1959) and is expressed as the sum of the species relative frequency, relative density and relative dominance values listed in Table 5. Table 5 differs from Table 2 only in that each value in Table 5 is a per cent equal to the corresponding value in Table 2 divided by the total of all values for that month. Thus, the total of relative frequency, density or dominance values for any month of all species sampled is equal to 100, and the maximum species importance value is 300.

In obtaining importance values for species in individual quadrats during one monthly sampling, the relative frequency component was not applicable, since frequency involves more than one quadrat. Therefore, the importance values for species in individual quadrats are smaller, the maximum being 200. Because the species importance value for 40 quadrats is calculated differently from the importance value for one quadrat, the diversity indices obtained cannot be compared between the two situations. For example, the diversity indices listed in Table 7 cannot be compared with those in Fig. 9 because relative frequency was taken into account in the former but not the latter.

As the importance of *Peltandra* decreased steadily from May onward (Table 6), it was accompanied by a rise in the importance of

TABLE 5

RELATIVE FREQUENCY, DENSITY AND DOMINANCE FOR THE 10 MOST COMMONLY SAMPLED SPECIES

Species	Relative Frequency					Relative Density					Relative Dominance				
	May	Jun	Jul	Aug	Sep	May	Jun	Jul	Aug	Sep	May	Jun	Jul	Aug	Sep
Peltandra virginica	29.7	21.4	19.1	17.9	18.0	28.45	11.95	10.69	11.12	7.81	75.29	71.84	40.04	30.48	18.21
Polygonum punctatum	11.7	13.7	12.1	13.4	14.4	17.45	12.25	11.41	13.41	12.21	3.58	3.06	2.84	6.96	10.77
Leersia oryzoides	3.6	14.5	15.2	14.0	14.0	41.88	58.82	55.68	51.25	55.77	0.64	5.59	6.33	23.26	28.36
Pontederia cordata	6.5	9.0	8.8	7.5	9.0	3.14	3.92	3.79	3.11	3.75	2.08	3.42	1.47	5.58	3.59
Polygonum arifolium	5.3	9.0	7.4	8.1	6.0	0.70	1.35	1.89	2.35	1.34	0.72	0.46	0.63	1.70	1.44
Impatiens capensis	5.9	6.8	7.4	5.7	5.6	1.92	2.88	4.34	5.71	2.57	4.05	2.88	3.27	7.00	3.33
Carex stricta	5.9	3.8	3.5	2.1	2.4	0.96	0.74	0.84	0.56	0.45	8.60	5.79	22.76	6.86	7.85
Eleocharis quadrangulata	0.9	1.1	2.3	3.9	5.6	0.17	0.31	0.50	1.68	5.24	---	---	---	---	---
Aneilema keisak	---	1.1	3.9	2.7	4.0	---	3.06	6.18	4.08	3.35	---	0.77	17.29	8.89	11.79
Hibiscus moscheutos	0.9	1.7	2.3	3.6	3.0	0.09	0.31	0.56	0.71	0.73	---	0.55	0.38	1.70	1.79

TABLE 6

SPECIES IMPORTANCE VALUES AND IMPORTANCE PROBABILITIES FOR THE 10 MOST COMMONLY SAMPLED SPECIES

Species	Importance Value						Importance Probability					
	May	Jun	Jul	Aug	Sep	Av.	May	Jun	Jul	Aug	Sep	Av.
Peltandra virginica	133.44	105.19	69.83	59.50	44.02	82.40	0.450	0.354	0.235	0.200	0.149	0.276
Polygonum punctatum	32.73	29.01	26.35	33.77	37.38	31.85	0.110	0.098	0.089	0.113	0.127	0.107
Leersia oryzoides	46.12	78.91	77.21	88.51	98.13	77.78	0.156	0.266	0.260	0.297	0.332	0.261
Pontederia cordata	11.72	16.34	14.06	16.19	16.35	14.93	0.040	0.055	0.047	0.054	0.055	0.050
Polygonum arifolium	6.72	10.81	9.92	12.15	8.78	9.68	0.023	0.036	0.033	0.041	0.030	0.032
Impatiens capensis	11.87	12.56	15.01	18.41	11.50	13.87	0.040	0.042	0.050	0.062	0.039	0.047
Carex stricta	15.46	10.33	27.10	9.52	10.70	14.62	0.052	0.035	0.091	0.032	0.036	0.049
Eleocharis quadrangulata	1.07	1.41	2.80	5.58	10.84	4.34	0.004	0.005	0.009	0.019	0.037	0.015
Aneilema keisak	---	4.93	27.37	15.67	19.14	13.42	----	0.017	0.092	0.053	0.065	0.045
Hibiscus moscheutos	0.99	2.56	3.24	6.01	5.52	3.66	0.003	0.009	0.011	0.020	0.019	0.012

Leersia, which overtook *Peltandra* as early as July. High importance values for *Peltandra* were attributed to high relative dominance, owing to the broad leaves. On the other hand, the high importance values for *Leersia* were more a result of high relative density, although relative dominance increased significantly toward the end of the season and even overtook *Peltandra* in September. The only other species with high importance values was *Polygonum punctatum*, which fluctuated little during the season.

Diversity can be broken down into two components: species richness and species evenness or equitability (Lloyd and Ghelardi, 1964). Species richness is the relationship between the number of species and the total number of individuals, and species evenness is the apportionment of individuals among the species present. Values for these component indices are listed in Table 7, along with values for the diversity index. The diversity formula of Menhinick (1964) and the evenness index of Pielou (1966) were used as indicators of richness and evenness, respectively.

Species diversity in Sweet Hall Marsh reached its maximum in August. Although diversity is largely dependent on richness, the effect of evenness is also substantial, since diversity increased from May through July while richness decreased during the same period. Furthermore, the richness value for May is equal to that of August, when diversity was highest, but the low evenness value for May caused the diversity of that month to be the lowest. Thus, it appears that the species diversity of the marsh is influenced more by relative numbers of individuals per species than by fluctuations in numbers of species present.

TABLE 7

SPECIES RICHNESS, EVENNESS AND DIVERSITY

BASED ON THE 40 QUADRATS SAMPLED

	May	June	July	Aug	Sep
Species Richness ($S/\sqrt{N}$)	0.768	0.619	0.614	0.768	0.661
Species Evenness ($\bar{H}/\log S$)	0.615	0.631	0.693	0.676	0.697
Species Diversity ($\bar{H}$)	0.870	0.882	0.980	1.035	1.008

S = Number of species sampled

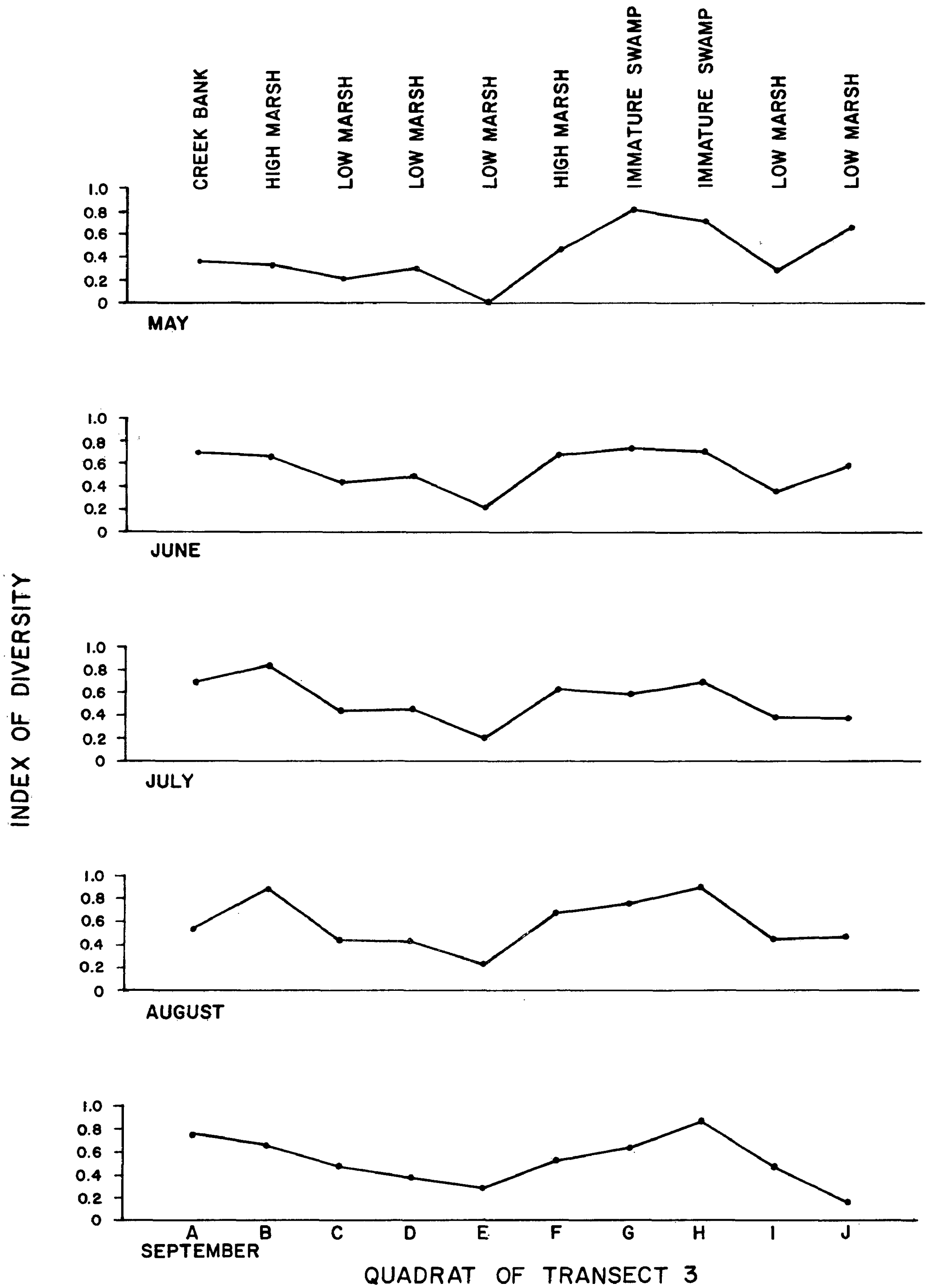
N = Number of individuals sampled

$\bar{H}$ = Index of diversity

The major environmental factors which affect diversity in the marsh appear to be soil elevation (or length of submergence) and the presence of shrubs and trees. This is illustrated in Fig. 9, in which one of the four transects was chosen to show spatial variations in diversity. The environmental conditions of each quadrat in the transect are described qualitatively at the top of the figure, with those plots receiving tidal inundation twice daily designated as low marsh and those receiving inundation less than twice daily designated as high marsh. Noticeable are the low diversities of the plots located on the creek bank and in low marsh areas and the relatively high diversities of plots in the high marsh and immature swamp. Low diversity in areas of low elevation is understandable, since only a few emergent species sampled, namely *Peltandra* and *Pontederia*, can withstand the longer and more frequent periods of submergence. The high diversity found in the immature swamp is probably a result of the additional niches provided by shade, although shading becomes limiting in the mature swamp (not represented in Fig. 9), as fewer species of herbs are found there, and the spacing between individuals is greater.

Odum (1960) states that diversity is a "structural" feature of a community, while productivity is a "functional" one. His study of primary production in old-field succession refuted beliefs that there exists a simple correlation between productivity and diversity, although a rough relationship does exist (Odum, 1971, p. 150). In studies of marsh vegetation this conclusion is further supported, as vegetationally diverse freshwater marshes are often less productive than monospecific salt marshes.

Figure 9. Index of diversity for quadrats of Transect 3 for each monthly sampling (see Fig. 2 for location of transect).


CREEK BANK
HIGH MARSH
LOW MARSH
LOW MARSH
LOW MARSH
HIGH MARSH
IMMATURE SWAMP
IMMATURE SWAMP
LOW MARSH
LOW MARSH
INDEX OF DIVERSITY
1.0
0.8
0.6
0.4
0.2
0
MAY
JUNE
JULY
AUGUST
SEPTEMBER
A
B
C
D
E
F
G
H
I
J
QUADRAT OF TRANSECT 3

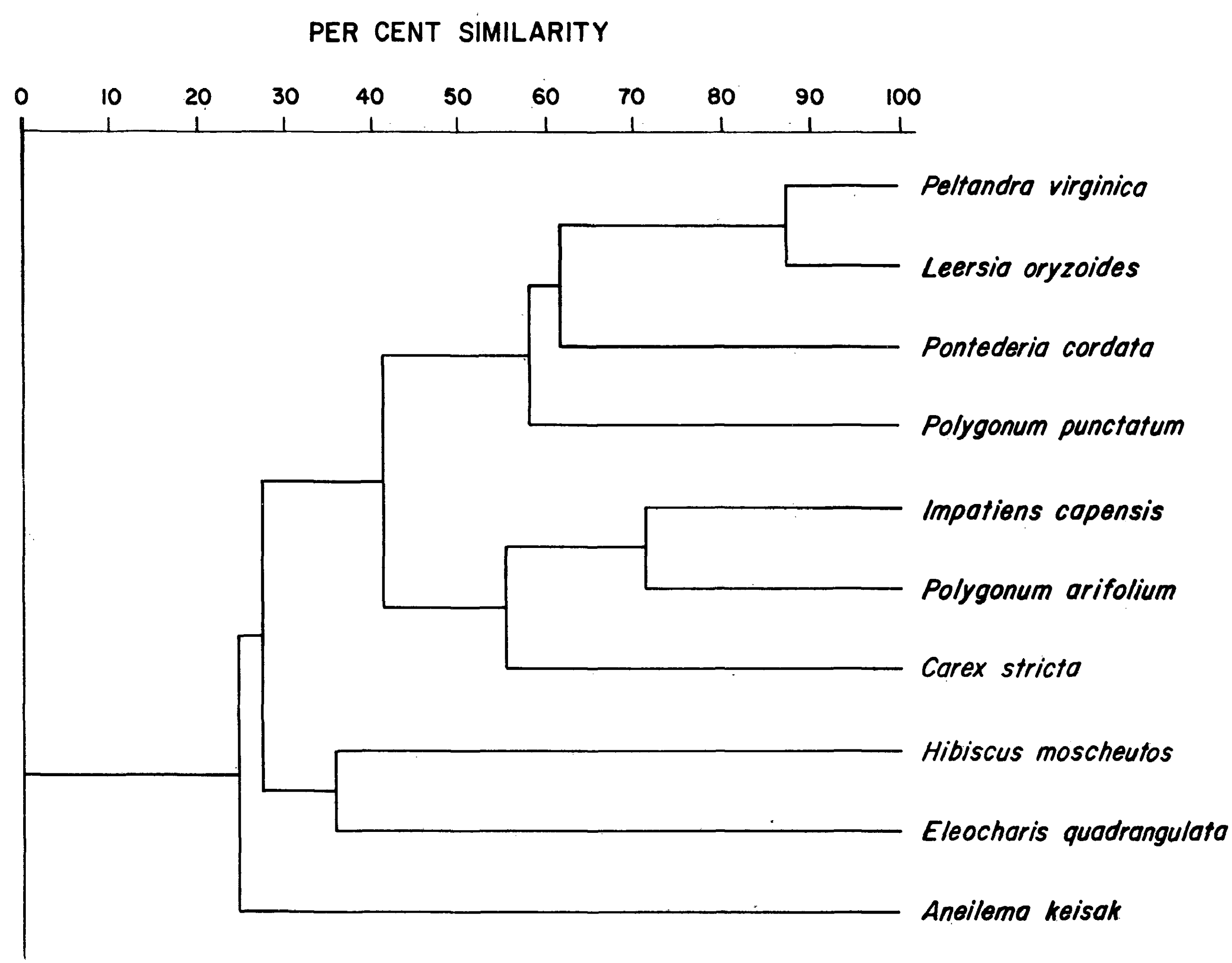
For the one growing season during which the present study was conducted, diversity and productivity trends were similar. Both increased to a peak in August, but production dropped sharply afterward, while diversity decreased only slightly. The difference in rate of decrease relates back to the "structural-functional" concept just mentioned; i.e., the community "structure" (diversity) changed little, while the community "function" (productivity) fell significantly. This imples that even though several species ceased production after August, they still remained as contributors to the structure and diversity of the community.

Margalef (1968) related construction of feedback systems to diversity and indicated that increased diversity means longer food chains, more cases of parasitism, symbiosis, etc., the final result being increased stability of the ecosystem or community. Applying this principle to marsh vegetation, higher diversity of plants means an increased variety of food sources for consumers and more varied niches for them, in addition to the general characteristics listed above. Thus, a diverse freshwater marsh such as Sweet Hall Marsh should be more stable ecologically than a salt marsh of low diversity and should be better able to adjust to changes in the environment.

Plant Associations

A dendrogram of the 10 most common species sampled in August (Fig. 10) shows two species associations, the members of which possess similarity indices of over 50%. Mendelssohn (1973) delineated similar associations for marshes of different salinities and explained the groupings on the basis of different tolerances of species to salinity.

Figure 10. Dendrogram of the 10 most common species in August based on similarity indices.


PER CENT SIMILARITY
0
10
20
30
40
50
60
70
80
90
100
Peltandra virginica
Leersia oryzoides
Pontederia cordata
Polygonum punctatum
Impatiens capensis
Polygonum arifolium
Carex stricta
Hibiscus moscheutos
Eleocharis quadrangulata
Aneilema keisak

As salinity is not a factor in the plant distribution of Sweet Hall Marsh, other factors must be responsible for the groupings in Fig. 10.

The first association consists of *Peltandra*, *Leersia*, *Pontederia* and *Polygonum punctatum*. All of these species are notably tolerant of submergence, especially *Peltandra* and *Pontederia*, although the association between *Peltandra* and *Leersia* is stronger. Apparently, the fact that *Peltandra* is often common in the high marsh, as is *Leersia*, accounts for this strong association.

The other association consists of *Impatiens*, *Polygonum arifolium* and *Carex stricta*, all of which are commonly high marsh species. The stronger association between *Impatiens* and *Polygonum* is probably due to the fact that early in the season both were common in the swamp areas, where *Carex* does not grow.

Competition and Changes in Community Composition

As noted from the data obtained, the community structure of the area studied varied considerably through the course of the growing season. Both the productivity and community structure data support the conclusion that the character of the marsh is largely determined by *Peltandra*, espeically from spring through midsummer. Even though *Peltandra* is well-adapted to growing in the lower elevations of the marsh and is often the only species found there, it apparently thrives equally well in all areas of both the open marsh and wooded swamp, although it is limited somewhat in the higher elevations by competition with other species.

As the season progressed, reduction in coverage and standing crop of *Peltandra* allowed other species, namely *Leersia*, to increase in importance, although the decrease in *Peltandra* was probably accelerated by the increasing competition. Buttery and Lambert (1965) encountered a similar situation in which *Glyceria maxima*, competing with *Phragmites communis*, formed dense swards in spring, which prohibited penetration by new shoots of *Phragmites*. However, where *Glyceria* showed reduced growth, *Phragmites* shoots could penetrate and thus intercept available light. Jervis (1969) recognized the control of the dominant *Typha* canopy over *Peltandra* production, pointing out that production of *Peltandra* peaked during spring, after which shading by *Typha* caused it to decline. However, in communities where the canopies closed more slowly, the peak production occurred during early summer.

Since the marsh was observed for only one growing season, accurate speculations concerning ecological succession cannot be made. On the surface it would appear that *Peltandra* is out-competing the other species, but whether it is "winning out" or whether the community has reached a state of equilibrium or climax is not known. Harper (1961) concluded that two species of plants can coexist if they are sensitive to a common controlling factor such as light or water at different times. Thus, the fact that *Peltandra* matures earlier in the season (i.e., is sensitive to light, etc.) than most of the other speices ensures that the subdominant species can coexist successfully, if their existence depended entirely upon the behavior of *Peltandra*. Among the subdominants themselves, the same principle applies; that is, the proliferation or elimination of a species depends upon the time at which other species are utilizing one or more essential resources.

Noticeable changes in community composition due to changing environmental conditions are gradually taking place, however. Local residents and hunters have noticed a steady replacement of *Spartina cynosuroides*, a valuable source of food and shelter for wildlife, by the less valuable *Phragmites australis*. This replacement is thought to be a result of the rise in sea level relative to the land (Marmer, 1948; Oaks, 1965) which until the last thirty years or so had been balanced by marsh buildup from accumulation of estuarine and terrestrial sediments by the watershed (Meade, 1972; Redfield, 1972; Moore, 1974). The rate of rise in sea level now seems to be greater than the sedimentation rate, with the result that erosion-deterring *Spartina* is being replaced by species which can tolerate the increased submergence (Wass and Wright, 1969).

Based on available data, large-scale changes in community composition due to man have not taken place in the marsh, but are very possible in the near future. At present, a nuclear power plant is being constructed on the North Anna River, which, together with the South Anna River, forms the Pamunkey. The power plant will use river water for cooling steam condensers, and a cooling water reservoir is being constructed in conjunction with the power plant to store river water during periods of low flow. Such alterations in river flow will undoubtedly affect the salt intrusion of the downstream reaches and thus affect the salinity regimes of the marshes in that area. In light of these possible changes and the others previously mentioned, further research in the downstream freshwater and brackish marshes is necessary in order to assess the progress and extent of changes in plant community composition.

SUMMARY

1. Community types in the marsh and swamp were recognized on the basis of plant composition. All herbs were found to mature earlier and grow larger in the swamp communities.

2. Annual net primary production for the major producers and for the marsh community as a whole was determined. The marsh was found to produce approximately 755.16 $g/m^2/yr$, which is typical for marshes of this type in Virginia. Maximum standing crop occurred in late August, while the peak daily production rate occurred in early June.

3. *Peltandra virginica* was found to be the major producer, producing approximately 396.72 $g/m^2/yr$, followed by *Leersia oryzoides*, *Polygonum punctatum*, *Pontederia cordata* and *Aneilema keisak*.

4. *Peltandra* was the dominant of the marsh in terms of coverage until September, when it was overtaken by *Leersia*. *Leersia* maintained the highest density values throughout the season.

5. Roughly three-fourths of the species sampled had frequencies of less than 10%, implying that most species are present in small numbers and/or are far from being evenly distributed. As the season progressed, they became more wide-spread, and their frequencies generally increased.

6. Species which spread primarily by vegetative methods were found to have a high index of sociability due to clustering of offspring

around their parents. Sociability increased or decreased as the season progressed, depending on the species.

7. Species diversity reached its maximum in August. Diversity in the marsh appears to be influenced more by relative numbers of individuals per species than by fluctuations in numbers of species present. Diversity was highest in the high marsh and swampy areas. Diversity and productivity trends were roughly similar.

8. Distribution of plant species was found to be strongly influenced by soil elevation and the effects of the presence of shrubs and trees.

9. The community structure of the marsh in spring is different from that of early fall, with *Peltandra* dominating the former and *Leersia* becoming prominent in the latter.

APPENDIX

TABLE A1

PLANT CHECKLIST FOR SWEET HALL MARSH STUDY AREA[1]

Plants Observed Within Sampling Quadrats

Scientific Name	Common Name
Acer rubrum L.	Red Maple
Amaranthus cannabinus (L.) J. D. Sauer	Water Hemp
Amphicarpa bracteata (L.) Fern.	Hog Peanut
Aneilema keisak Hassk.	Asiatic Dayflower
Bidens coronata (L.) Britt.	Begger Ticks
Bidens frondosa L.	Begger Ticks
Boehmeria cylindrica (L.) Sw.	False Nettle
Carex hyalinolepis Steud.	Clear-Scale Sedge
Carex stricta Lam.	Bunch Sedge
Cassia fasciculata Michx.	Partridge Pea
Clematis crispa L.	Blue Jasmine
Decodon verticillatus (L.) Ell.	Water Willow
Echinochloa walteri (Pursh) Nash	Walter's Millet
Eleocharis quadrangulata (Michx.) R. & S.	Spikerush
Galium sp.	Bedstraw
Hibiscus moscheutos L.	Rose Mallow
Hypericum sp.	St. John's-wort
Impatiens capensis Meerb.	Jewelweed
Juncus effusus L.	Soft Rush
Leersia oryzoides (L.) Sw.	Rice Cutgrass
Osmunda regalis L.	Royal Fern
Parthenocissus quinquefolia (L.) Planch	Virginia Creeper
Peltandra virginica (L.) Kunth.	Arrow Arum
Phragmites australis (Cav.) Trin. ex Steud.	Reedgrass
Polygonum arifolium L.	Halberd-leaved Tearthumb
Polygonum punctatum Ell.	Water Smartweed
Polygonum sagittatum L.	Arrow-leaved Tearthumb
Pontederia cordata L.	Pickerel Weed
Rhus radicans L.	Poison Ivy
Rosa palustris Marsh.	Swamp Rose
Rumex verticillatus L.	Water Dock
Sagittaria latifolia Willd.	Arrowhead
Scirpus americanus Pers.	Three-square
Scirpus validus Vahl.	Great Bulrush
Spartina alterniflora Loisel.	Saltmarsh Cordgrass
Spartina cynosuroides (L.) Roth	Giant Cordgrass
Strophostyles umbellata (Muhl.) Britt var. paludigena Fern.	Wild Bean

TABLE A1 (continued)

Scientific Name	Common Name
Teucrium canadense L.	Wood Sage
Thalictrum sp.	Meadow Rue
Thelypteris palustris Schott	Marsh Fern
Typha angustifolia L.	Narrow-leaved Cattail
Vitis sp.	Grape
Zizania aquatica L.	Wild Rice

Other Plants Observed Outside Sampling Quadrats

Alnus sp.	Alder
Asclepias incarnata L.	Swamp Milkweed
Aster sp.	Aster
Bidens comosa (Gray) Wieg.	Begger Ticks
Cornus florida L.	Flowering Dogwood
Cuscuta sp.	Dodder
Cyperus strigosus L.	Galingale
Erianthus giganteus (Walt.) Muhl.	Plume Grass
Eryngium aquaticum L.	Eryngo
Eupatorium perfoliatum L.	Boneset
Fraxinus americana L.	White Ash
Fraxinus caroliniana Mill.	Water Ash
Hydrocotyle sp.	Water Pennywort
Ilex laevigata (Pursh) Gray	Smooth Winterberry
Iva frutescens L.	Marsh-elder
Juncus canadensis J. Gay	Rush
Juniperus virginiana L.	Red Cedar
Kosteletzkya virginica (L.) Presl.	Seashore Mallow
Leucothoë sp.	Fetter Bush
Lilium superbum L.	Turk's-cap-lily
Lobelia cardinalis L.	Cardinal Flower
Lonicera japonica Thunb.	Japanese Honeysuckle
Myrica cerifera L.	Wax Myrtle
Nuphar luteum (L.) Sibthorp & Smith	Yellow Pond Lily
Nyssa sylvatica L.	Black Gum
Onoclea sensibilis L.	Sensitive Fern
Osmunda cinnamomea L.	Cinnamon Fern
Oxypolis sp.	Hog-fennel
Phoradendron serotinum (Raf.) M. C. Johnston	Mistletoe
Polygonum persicaria L.	Lady's Thumb
Rhynchospora macrostachya Torr.	Beak Rush
Saururus cernuus L.	Lizard's Tail
Scirpus cyperinus (L.) Kunth.	Woolgrass
Scirpus fluviatilis (Torr.) Gray	River Bulrush
Smilax rotundifolia L.	Common Greenbrier
Smilax sp.	Greenbrier

TABLE A1 (continued)

Scientific Name	Common Name
Taxodium distichum (L.) Richard	Bald Cypress
Vaccinium corymbosum L.	Highbush Blueberry
Vernonia altissima Nutt.	Ironweed
Viburnum dentatum L.	Southern Arrow-wood
Viburnum recognitum Fern.	Arrow-wood
Viola sp.	Violet

[1]Nomenclature following that of Fernald (1950) and Radford et al (1968).

TABLE A2

CLIP FREQUENCIES

(PERCENTAGE OF PLOTS IN WHICH SPECIES OCCURRED)

Species	May	June	July	Aug	Sep
Peltandra virginica	95	95	98	93	85
Leersia oryzoides	40	78	83	78	73
Polygonum punctatum	8	15	68	50	60
Pontederia cordata	20	25	30	33	30
Aneilema keisak		10	18	18	30
Polygonum arifolium	8	13	18	23	28
Impatiens capensis	3	8	23	18	18
Eleocharis quadrangulata	3	5	8	18	18
Scirpus americanus	10	8	10	10	5
Carex stricta	10	10	10	8	8
Polygonum sagittatum		5	8	10	13
Hibiscus moscheutos		10	8	3	8
Osmunda regalis	8	5	5	3	5
Carex hyalinolepis	8	8		8	
Phragmites australis	5	8		5	5
Spartina cynosuroides	5	3	5	5	3
Scirpus validus	3	5	8	3	3
Typha angustifolia	3	3	5	3	5
Bidens coronata	3		3	3	5
Thelypteris palustris		3	3	5	3
Rumex verticillatus	3		5		3
Rhus radicans		3	3	3	
Teucrium canadense	3	3			
Decodon verticillatus		5			
Vitis sp.			3		
Cassia fasciculata			3		
Amphicarpa bracteata			3		
Bidens frondosa			3		
Clematis crispa			3		
Strophostyles umbellata				5	
Hypericum sp.				3	
Zizania aquatica				3	8
Juncus effusus				3	5
Spartina alterniflora					3
Sagittaria latifolia					3
Galium sp.					3
Echinochloa walteri					18

TABLE A3

AVERAGE SPECIES HEIGHT (CM)

PER SAMPLING QUADRAT OF OCCURRENCE

Species	May	June	July	Aug	Sep
Acer rubrum	175.00	213.33	225.00	210.00	200.00
Typha angustifolia	100.00	200.00	200.00	173.33	190.00
Spartina cynosuroides	75.00	200.00	200.00	187.00	185.00
Zizania aquatica			130.00	105.00	200.00
Phragmites australis	90.00	172.50	166.67	176.67	163.33
Scirpus validus		75.00	160.00	50.00	110.00
Scirpus americanus	70.00	140.00	100.00	155.00	100.00
Carex hyalinolepis	10.00	112.00	153.33	140.00	125.00
Hibiscus moscheutos	100.00	116.67	144.00	135.00	121.00
Carex stricta	68.00	101.43	130.00	121.43	100.00
Eleocharis quadrangulata	30.00	125.00	114.00	98.89	89.09
Boehmeria cylindrica				120.00	
Rumex verticillatus	76.67	115.00	105.00	100.00	80.00
Pontederia cordata	33.33	101.88	114.44	110.00	88.42
Bidens coronata	20.00	50.00	80.00	90.00	110.00
Decondon verticillatus	20.00	110.00	110.00		
Parthenocissus quinquefolia				110.00	
Polygonum sagittatum		25.00	84.00	102.50	67.50
Vitis sp.	100.00		100.00	100.00	
Rosa palustris	100.00			100.00	
Juncus effusus				100.00	100.00
Osmunda regalis	100.00	72.50	74.00	90.00	80.00
Peltandra virginica	54.73	92.88	99.00	91.00	57.14
Leersia oryzoides	10.00	60.74	91.29	80.97	65.93
Rhus radicans	80.00	85.00	90.00	80.00	80.00
Impatiens capensis	30.00	43.57	86.25	86.67	78.85
Hypericum sp.	8.00	20.00		80.00	
Galium sp.				80.00	
Polygonum arifolium	30.00	48.75	71.25	73.89	75.00
Thelypteris palustris	20.00		73.33	73.33	60.00
Polygonum punctatum	5.00	26.74	43.20	72.00	67.59
Amaranthus cannabinus				70.00	
Teucrium canadense	30.00	60.00			
Echinochloa walteri					55.00
Thalictrum sp.				40.00	
Sagittaria latifolia					40.00
Aneilema keisak		15.00	27.50	30.00	37.50

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