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Annual Variation in Biomass and Production of a Tidal Freshwater Wetland and Comparison with other Wetland Systems

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ABSTRACT

Tidal freshwater wetlands are characterized as being highly productive and having the productivity shared by a large number of perennial and annual species. In this paper, we report results from an 11 year study of net annual aboveground production for a high marsh community in a New Jersey tidal freshwater wetland. Between year patterns of production are examined for the dominant species and for the overall community. Results from the New Jersey study are compared to similar data from other types of wetlands. Tidal freshwater wetlands appear to be unique because they have a fairly low coefficient of variation (c. 20%) and a high diversity of dominant species. Reasons for this pattern are considered.

INTRODUCTION

Most wetlands are highly productive yet there is almost nothing known about the range of variation in production that occurs from one year to the next (Good et al., 1978, Brinson et al., 1981, Mitsch and Gosselink, 1986). High levels of annual variation could have important implications as most of the net annual biomass production in wetlands enters either the detritus or grazing food chains and benefits secondary consumers. Whigham et al., (1989b), for example, found that net aboveground production of *Typha angustifolia* varied by as much as 75% in a brackish wetland. Working in the same wetland during the same time period, Jordan and Correll (1991) found significant yearly differences in the magnitude of nutrient import and/or export. How typical were those findings and what are their implications for wetland structure and function? Our objective is to consider the general question of how variable annual production is within and between different types of wetlands. We first consider annual variation in aboveground production for a tidal freshwater wetland in New Jersey and then compare those data with published data for other types of wetlands.

STUDY SITE

The Hamilton Marshes are part of the complex of tidal freshwater wetlands that are common along the eastern coast of the U.S. (Odum et al., 1984). They are the northernmost tidal freshwater wetlands in the Delaware River system and have been the site of studies on vegetation (Leck et al., 1988; West and Whigham, 1976; Whigham and Simpson, 1977, 1982; Whigham et al., 1978), water quality (Simpson et al., 1981, 1983a, 1983b), seed bank dynamics (Leck and Graveline, 1979; Leck and Simpson, 1987a and 1987b; Leck et al., 1989; Parker and Leck, 1985), decomposition (Whigham et al., 1989a), and wastewater management (Whigham and Simpson, 1976 and 1978; Simpson et al., 1983a).

In this paper, we describe results for six years of an eleven year period at one of the sites that was initially sampled in 1973 (Whigham and Simpson, 1975). The site is a high marsh habitat (Simpson et al., 1983a) that is normally flooded for two to three hours during each tidal cycle. The high marsh, typically the most diverse vegetation zone in tidal freshwater wetlands (Odum et al., 1984; Simpson et al., 1983a), has a heterogeneous mixture of annual and perennial species. The most abundant species are: Perennials - *Acorus calamus* (Sweet flag), *Peltandra virginica* (Arrow arum), *Typha latifolia* (Common cattail), *Sagittaria latifolia* (Arrowhead); Annuals - *Polygonum arifolium* (Halberd tearthumb), *Polygonum sagittatum* (Tearthumb), *Zizania aquatica* var. *aquatica* (Wild rice), *Bidens laevis* (Bur marigold), and *Impatiens capensis* (Touch-me-not).

Vegetation was sampled throughout the growing seasons of 1973-1977 and 1985. All sampling took place within an area of approximately 100 x 100 m and all aboveground biomass in seven randomly located quadrats was harvested on each sampling date. The samples were washed to remove sediment, sorted by species, and dried to constant weight. Standing crop biomass for each sampling date was summed for annuals, perennials, and all species combined. Because the species reach peak biomass at different times, net annual aboveground biomass production was estimated as the sum of the peak biomass for each species (see Whigham et al., 1978 for a detailed description of the method).

For the literature comparison, we used data from studies of three or more years in duration. Peak aboveground biomass or estimates of annual production were averaged and the coefficient of variation (C.V.) calculated to compare the amount of variation in populations having different means (Sokal and Rohlf, 1969).

RESULTS AND DISCUSSION

Seasonal biomass patterns were similar for all years. Perennial biomass (Fig. 1) was highest early in the growing season and decreased with time. The pattern for all years was similar except for 1973 when perennial biomass was lower because *Typha* was not present in any of the sampled quadrats. In contrast, biomass of annuals (Fig. 1) increased throughout the growing season and the yearly patterns were very similar. The annual:perennial biomass ratio (Fig. 2) showed the seasonal shift in dominance from perennials to annuals and demonstrated that (except in 1973 when there was not any *Typha* in the harvested samples) the ratio changes little from year-to-year.

Net annual aboveground production ranged from approximately 1500 to 2000 g/m^2 for all years except 1975 (Fig. 3) when the production estimate was higher due to the presence of *Typha latifolia* for the first time (Fig. 4) and higher biomass for *Acorus calamus* (Fig. 4) and *Bidens laevis* (Fig 5). Annual aboveground production of perennials varied widely between years for all species except *Peltandra virginica* which was also the most productive perennial species (Fig. 4). Net annual production of the dominant annuals (Fig. 5) was also quite variable for all species due to highly variable spatial patterns of distribution. The data also give some indication of successional processes. *Bidens laevis* was completely absent from the site in 1985

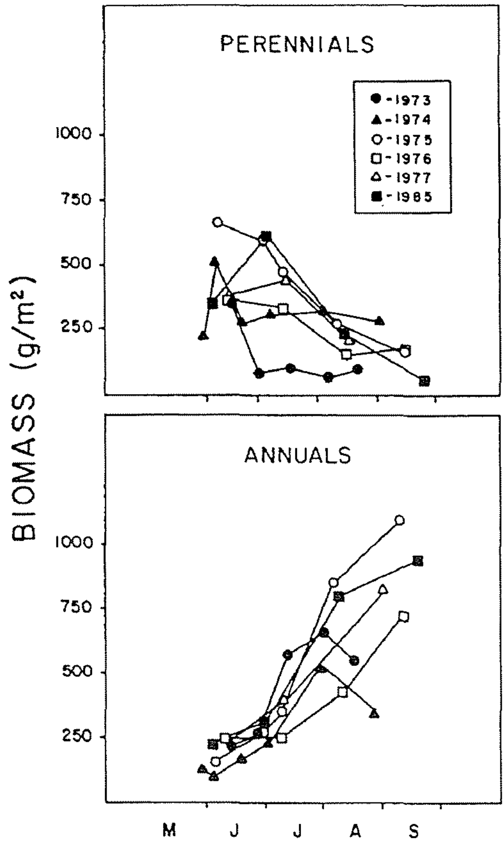


FIGURE 1. Seasonal biomass patterns for perennials and annuals in the Hamilton Marshes.

(Fig. 5) but the loss of *Bidens* was compensated for by a large increase in the biomass production of *Impatiens capensis* (Fig. 5).

There was clearly a high level of interspecific variation in annual biomass production (Figs. 4 and 5) but inter-annual differences in biomass and production were fairly small at the community level (Fig. 3) even though the presence and abundance of some species changed from 1973 to 1985. For the six years, the C.V. of net annual aboveground production was 22.8% which is fairly low considering the large number of dominant species that occur in tidal freshwater wetlands.

Table 1 is a summary of annual biomass and production data for a range of wetland types. The highest C.V.'s appear to be associated with brackish intertidal wetlands that experience large fluctuations in salinity. The C.V. for a regularly flooded *Typha angustifolia* dominated wetland in Maryland was 75% and the variation was associated with high inter-annual variation in salinity during the early part of the growing season (Whigham et al., 1989b). The C.V.'s were also high for three vegetation types in an irregularly flooded high marsh wetland (Drake et al., 1989) that is within 0.5 km of the *Typha* dominated low marsh studied by Whigham et al. (1989b). The C.V. of the high marsh ranged from 15.3 for areas dominated by *Scirpus olneyi* to 55.6 in areas dominated by *Spartina patens*. Areas dominated by *Distichlis spicata* had a C.V. of 44.3 and the mean for all three vegetation types,

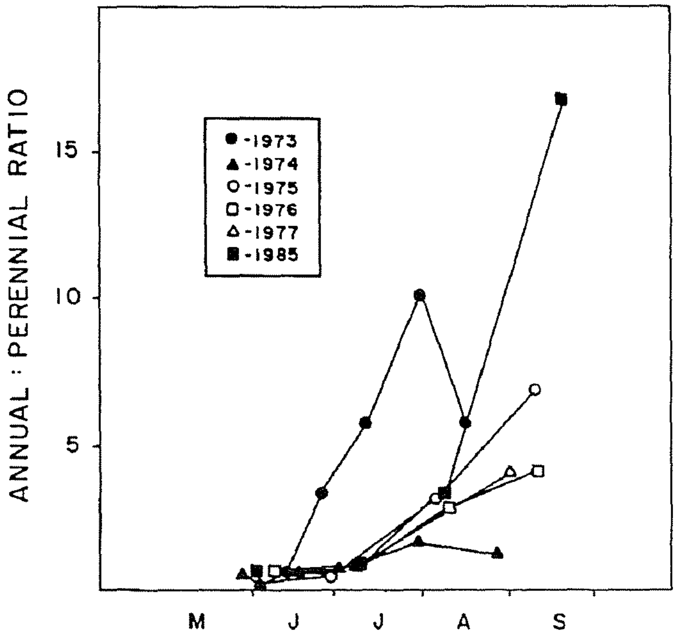


FIGURE 2. Ratios of annual:perennial biomass.

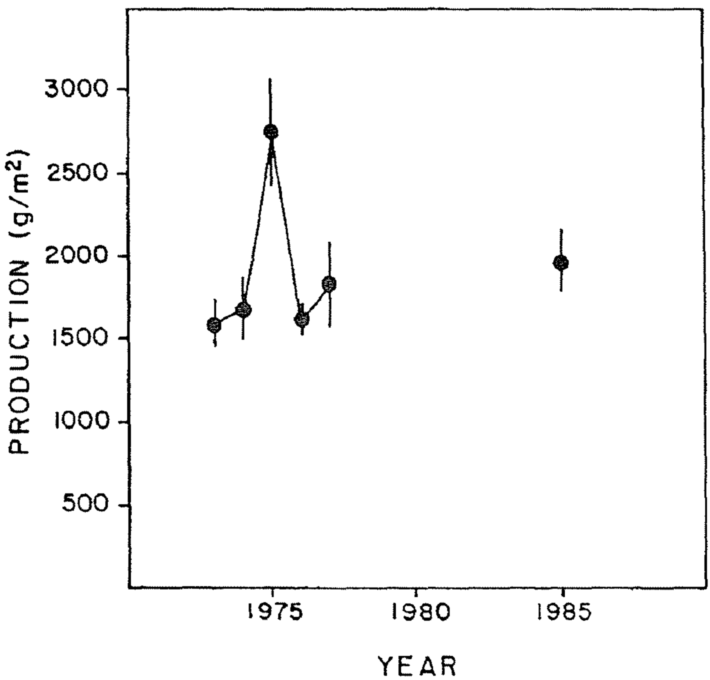


FIGURE 3. Annual net aboveground biomass production for the High Marsh habitat in the Hamilton Marshes. Values are means ± 1 standard error.

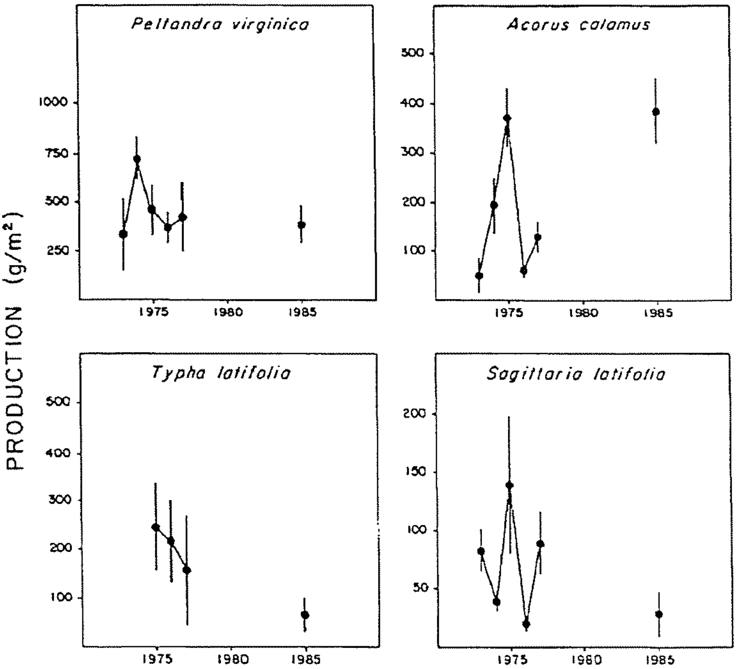
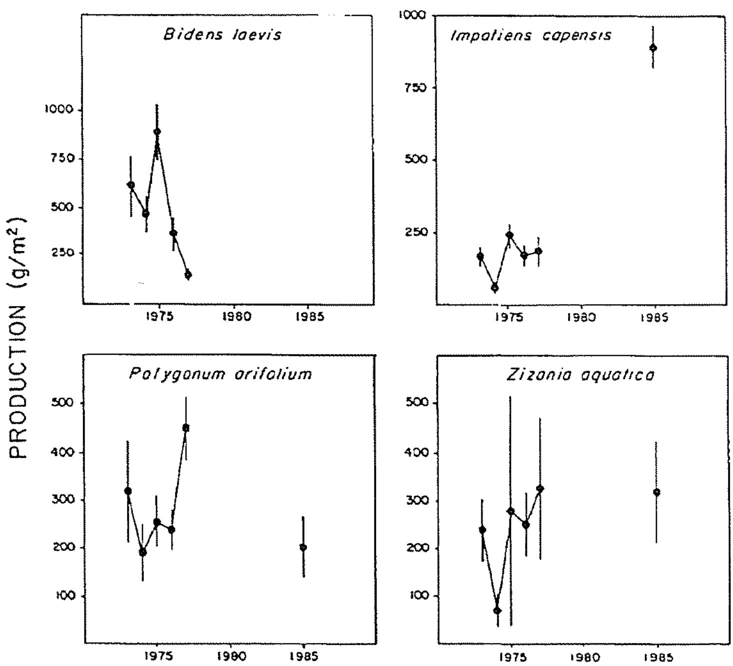


FIGURE 4. Annual net aboveground biomass production for the four dominant perennial species in the High Marsh habitat in the Hamilton Marshes. Values are means ± 1 standard error.



all located within a few meters of each other, was 43.4. The high C.V.'s for the vegetation studied by Drake et al. (1989) was most likely due to seasonal differences in precipitation which influenced interstitial salinity. *Scirpus* areas are topographically lower and are flooded more regularly and have less variation in soil salinity than topographically higher areas dominated by *Spartina*.

The range in C.V. for annual biomass production appears to be somewhat less in coastal saltmarsh wetlands (Table 1). Zedler et al., (1980) conducted a three year study of a California hypersaline wetland dominated by *Spartina foliosa*. They sampled along a flooding gradient and found that the C.V. was least in the low marsh (9.2) and highest in the high marsh (21.4). The higher C.V. in the high marsh was most likely caused by large changes in soil salinity in the high marsh habitat that floods infrequently. The reverse pattern was found by Dame and Kenny (1986) for a *Spartina alterniflora* dominated wetland in the North Inlet estuary in South Carolina (Table 1). Dame and Kenny found that the C.V. was least in the high marsh (2.2) and greatest in the low marsh (20.9). They believed that higher variability in the low marsh was due to changes in freshwater input to the estuary. Over a thirteen year period, Teal (1986) found a C.V. of 9.1 in a *Spartina alterniflora* dominated wetland in Massachusetts. One wetland that had a high C.V. (Range = 31-62; Mean = 46.5) was a managed (mowed) and infrequently flooded saltmarsh in The Netherlands (de Leeuw et al., 1990). The high annual variation in that system was caused by year-to-year variation in soil conditions (soil salinity and soil moisture content).

Five data sets (Table 1) indicate that the C.V. can be expected to range between 15 and 40% for non-tidal freshwater wetlands. In a Swedish *Carex rostrata* dominated wetland with regulated water levels, the C.V. was 16.1 for a three year period (Hultgren, 1989). Over a five year period, Solander (1983) found that the C.V. in a Swedish wetland dominated by *Carex rostrata* and *Equisetum fluviatile* was 21.2 in areas that were fertilized and 34.9 in unfertilized areas. Koerselman et al. (1990) found only small differences in the C.V. for groundwater discharge (30.7) and groundwater recharge (31.5) fens in The Netherlands. Both fens were mowed yearly during the growing season and they were surrounded by heavily fertilized pastures. Kadlec and Bevis (1990) conducted a five year study of a Michigan bog that received sewage wastewater. The bog had been undergoing dramatic vegetation changes from an oligotrophic *Picea-Carex-Chamaedaphne* dominated bog to one dominated by *Typha latifolia*. The C.V for areas dominated by *Typha* ranged from 6.9 at c. 900 m from the point of wastewater discharge to 40.9 at c. 2500 m. This suggests that conversion to a more eutrophic condition near the point of discharge provided a steady supply of water and nutrients that resulted in a decrease in the variation in annual production. In the only wetland with clear seasonality in hydrologic conditions, Rogers and Breen (1990) measured a C.V. of 31.6 over a four year period in a floodplain wetland in South Africa.

Table 1 indicates that most wetlands have a low dominance diversity and that there is a wide range of C.V.'s. Saltmarshes that experience few changes in salinity have the lowest C.V.'s and brackish tidal wetlands which experience wide fluctuations in salinity conditions have the highest C.V.'s. Tidal freshwater wetlands are in the middle of the range for freshwater wetlands but they are unique because they have a high species diversity and fairly low C.V.. The two Dutch systems with levels

TABLE 1. Comparison of coefficients of variation for different wetlands. Species refers to the number of dominant species cited by the authors.

Source	Wetland Type	Habitat	Species	Study Years	C.V.
Zedler et al., 1980	Saltmarsh	Low Marsh	1	3	9.2
		Intermediate	2	3	11.7
		High Marsh	2	3	21.4
Dame and Kenny, 1986	Saltmarsh	Low Marsh	1	4	20.9
		Intermediate	1	4	5.7
		High Marsh	1	4	2.2
de Leeuw et al., 1990	Saltmarsh	High Marsh	8	13	46.5
Teal, 1986	Saltmarsh	High Marsh	1	13	9.1
Drake et al., 1989	Brackish	High Marsh	1	4	15.3
		High Marsh	1	4	55.6
		High Marsh	1	4	44.3
Whigham et al., 1989	Brackish	Low Marsh	1	6	75.0
This study	Tidal Fresh	High Marsh	8	6	22.8
Hultgren, 1989	Freshwater	Lacustrine	1	3	16.1
Solander, 1983	Freshwater	Lacustrine	2	5	21.2
		Lacustrine	2	5	34.9
Koerselman et al., 1990	Freshwater	Fen	7	3	30.7
		Fen	7	3	31.5
Kadlec and Bevis, 1990	Freshwater	Bog	1	4	6.9
		Bog	1	4	40.9
Rogers and Breen, 1990	Freshwater	Floodplain	1	4	31.6

of diversity similar to the Hamilton Marshes and somewhat higher C.V.'s, were both managed (mowed) and received high levels of nutrient inputs.

We believe that there are three reasons why tidal freshwater wetlands have a high species diversity and low C.V.. First, the energy signature (ie., tidal flooding) is predictable and high marsh habitats are flooded for 2-3 hours during each tidal cycle. Regular tidal inundation and flushing transports sediments and nutrients to the wetland while flushing oxidizes the surface layer of the substrate and removes salts, and potential harmful chemicals that could have a negative affect on production. Second, nutrient levels are high in most tidal freshwater wetlands because they are located in the upper reaches of estuaries where nutrient levels are high due to agricultural runoff and/or wastewater effluent (Simpson et al., 1983a). High nutrient levels assure that annual primary production will be high each year. Third, the high diversity and dominance of annual species is unique among estuarine wetlands (Odum et al., 1984). This feature of tidal freshwater wetlands allows for species compensation so that annual production levels remain high and fairly constant even though there may be shifts in the distribution and abundance of species from one year to the next. Finally, data from the Hamilton Marshes and the data summarized in Table 1 suggest that the high species diversity of tidal freshwater wetlands enables them to be buffered against changing environmental conditions. This situation contrasts sharply with brackish tidal wetlands which experience wide ranges in production (Whigham et al., 1989) and pronounced changes in species diversity. The universality of these findings, however, and their implications for ecosystem structure and function await additional long-term studies.

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