BIOMASS AND PRIMARY PRODUCTION IN FRESHWATER TIDAL WETLANDS OF THE MIDDLE ATLANTIC COAST

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Abstract Although there are many measurements of peak standing crop and several estimates of aboveground annual net production, there are few accurate estimates of total net primary production for Middle Atlantic coastal freshwater tidal wetlands. Estimates of biomass and production vary widely both within and between vegetation types. The variability appears to be due to sampling techniques and/or the heterogeneous nature of freshwater tidal wetland

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vegetation. Undoubtedly, all estimates of primary production are low because they do not include data on growing season mortality of plants and plant parts, herbivore consumption, and belowground production. Most estimates of primary production are also low because freshwater tidal wetland communities usually undergo a series of physiognomic changes during the growing season and the measurements of primary production do not account for those seasonal patterns. Comparatively, freshwater macrophyte production in tidal wetlands appears to be at least equal to that of brackish water wetlands at the same geographic latitude.

Key words *Biomass, freshwater, Middle Atlantic coast, productivity, tidal, wetland.*

INTRODUCTION

Three major types of tidal wetlands form a continuum within the Middle Atlantic coastal region. At one extreme of the continuum are saline wetlands that are characterized by the presence of extensive stands of salt-marsh cordgrass (*Spartina alterniflora*). At the other extreme, freshwater wetlands occur near the inland limit of the tide in areas that are never exposed to water of elevated salinity. Species diversity is greatest at the freshwater end of the continuum with wild rice (*Zizania aquatica*) and spatterdock (*Nuphar advena*) being characteristic species. Brackish wetlands occupy the areas where fresh and salt water mix and are characteristically dominated by several species. Salt-meadow cordgrass (*Spartina patens*) and Olney three-square (*Scirpus olneyi*) frequently form the bulk of plant cover. Such species as cattail (*Typha* sp.) and marsh mallow (*Hibiscus* sp.) may be prominent either in brackish or freshwater wetlands but distinctions between them are often made based on the presence of big cordgrass (*Spartina cynosuroides*) which may be conspicuous along tidal channels of brackish wetlands.

The primary production of tidal wetlands has been purported to be very high (Odum, 1971; Westlake, 1963) and Kirby and Gosselink (1976) have recently demonstrated that saline and brackish wetland primary production may be even higher than previously suspected. With the exception of a summary by Keefe (1972) and a brief review in Whigham and Simpson (1976*a*), there has been no systematic attempt to compile and analyze data on primary production of freshwater tidal wetlands. This paper summarizes data on biomass and primary production of freshwater tidal wetlands and makes comparisons with production estimates for saline and brackish wetlands within the Middle Atlantic coastal zone.

Kirby and Gosselink (1976) have recently shown that standing crop measurements may be significant underestimates of actual annual production of Gulf Coast saline wetlands. We herein present data showing that most published estimates of production in freshwater tidal wetlands are underestimates of the actual annual net production and that the differences may be very large. Most investigations underestimate actual net production for several reasons. For example, the single harvest method of estimating annual net production has been frequently used in the past, but is not suitable for most freshwater tidal wetlands. Most sites are dominated by several species during one growing season and the single harvest not only misses senesced vegetation but it does not include production of species that may dominate later. Our recent estimates of belowground production and leaf mortality show that these components can also account for significant amounts of the total annual net production. Therefore we provide estimates of total annual net production (for 1 vegetation type), that were derived from peak biomass and multiple harvest techniques plus measurements of leaf mortality and belowground production.

ESTIMATES OF BIOMASS AND PRODUCTION

Published and unpublished data on biomass and primary production were available for freshwater tidal wetlands in Maryland, Virginia, New Jersey and Pennsylvania (Table 1). For comparison, we have also incorporated data on brackish wetlands into Table 1.

The standing crop and/or production estimates were obtained primarily from Delaware River, Delaware Bay or Chesapeake Bay freshwater tidal wetlands, mostly since 1970. All data were obtained by using 2 techniques. The single harvest method entails measuring peak biomass during the period when standing crops are thought to be maximum. There is an inherent variability and potential error in the method because there are no corrections for: (1) plant tissues that developed and died prior to the sampling time, (2) herbivory, and (3) tissues that will develop after the harvest. The multiple harvest technique, involving data collected at intervals of several days to several weeks throughout the growing season, yields better estimates of total annual net production; however, most investigations utilizing this technique have been in brackish and saline wetlands (Gosselink et al., 1977; Kirby and Gosselink, 1976; Smalley, 1959; Stroud and Cooper, 1968; Williams and Murdoch, 1969). Gosselink et al. (1977) measured production of a Gulf Coast freshwater tidal wetland species using multiple harvest techniques which also included estimates of mortality and leaf turnover.

Estimates of average peak aboveground biomass in freshwater tidal wetlands range from 432 g/m^2 in *Sagittaria latifolia* vegetation to 2,311 g/m^2 in *Spartina cynosuroides* vegetation (Table 1). Peak biomass is almost always greatest in wetlands dominated by grasses such as *S. cynosuroides* and *Phragmites* (1,850 g/m^2), or else vegetation dominated by semi-shrubs such as *Hibiscus* (1,714 g/m^2) and *Lythrum* (1,616 g/m^2). Average peak aboveground biomass is slightly less in wetlands dominated by *Typha* (1,215 g/m^2), *Zizania* (1,218 g/m^2), *Ambrosia* (1,205 g/m^2), *Bidens* (1,017 g/m^2), *Acnida* (940 g/m^2), and *Acorus* (857 g/m^2). Average peak standing crop is least in stands dominated by typical emergent macrophytes such as *Pontederia*/*Peltandra* (682 g/m^2), *Nuphar* (627 g/m^2), *Scirpus* (606 g/m^2), and *Sagittaria*

Table 1. Peak Standing Crop and Net Annual Production Estimates for Freshwater (Part 1) and Brackish (Part 2) Tidal Wetlands Within the Middle Atlantic Coastal Region[a]

Vegetation type[b]	Peak standing crop[c]			Annual production[c]	Source
	Aboveground	Belowground	Dead		
		Part 1—Freshwater tidal wetlands			
Polygonum/ Leersia	2,142 [2]	...	...	...	J. McCormick (*personal observations*)
	1,547	...	...	...	Wass and Wright (1969)
	769	507	...	...	Good and Good (1975)
	523	...	...	...	McCormick (1970)
	1,425				
Nuphar advena	513 [2]	...	...	...	J. McCormick (*personal observations*)
	245	...	...	...	Wass and Wright (1969)
	743 [2]	...	...	863 [2]	J. McCormick (*personal observations*)
	516	...	...	...	McCormick and Ashbaugh (1972)
	605	1,146	...	...	Good and Good (1975)
	529 [6]	...	...	...	Whigham and Simpson (1975)
	...	4,799	...	780	Whigham and Simpson (1975)
	1,175 [2]	...	...	...	McCormick (1970)
	627				
Pontederia/ Peltandra	648 [2]	...	...	...	J. McCormick (*personal observations*)
	988	...	132	...	Flemer et al. (*In press*)
	1,286	2,463	...	...	Good et al. (1975)
	594 [2]	...	...	...	McCormick and Ashbaugh (1972)
	486 [2]	...	...	...	Whigham and Simpson (1975)
	553	...	...	...	Good and Good (1975)
	657 [3]	...	...	650	Whigham and Simpson (1975)
	677	...	...	1,126	J. McCormick (*personal observations*)
	686			**888**	
Acorus calamus	1,174 [2]	...	...	...	J. McCormick (*personal observations*)
	605	...	...	...	McCormick and Ashbaugh (1972)
	819 [4]	...	...	...	Whigham and Simpson (1975)
	623	...	...	1,071	J. McCormick (*personal observations*)
	857				

Table 1. Continued

Vegetation type[b]	Peak standing crop[c] Above-ground	Below-ground	Dead	Annual production[c]	Source
Typha sp.	2,338	...	167	...	Heinle et al. (1974)
	1,190 [2]	...	330 [2]	...	Flemer et al. (*In press*)
	966	...	...	1,868	Johnson (1970)
	...	...	...	956[d]	Stevenson et al. (1976)
	987	...	...	...	McCormick and Ashbaugh (1972)
	850	1,800	...	...	Good and Good (1975)
	894	1,371	...	...	Good et al. (1975)
	1,297 [3]	...	...	1,320	Whigham and Simpson (1975)
	1,199	...	...	1,534	J. McCormick (*personal observations*)
	1,310 [3]	...	...	...	McCormick (1970)
	804	5,053	...	...	Walker and Good (1976)
	1,215			**1,420**	
Hibiscus palustris	1,714 [2]	...	...	...	J. McCormick (*personal observations*)
	...	...	...	489[d]	Stevenson et al. (1976)
	1,714				
Zizania aquatica	2,091 [2]	...	...	...	J. McCormick (*personal observations*)
	1,178 [4]	...	135 [3]	...	Flemer et al. (*In press*)
	560	...	...	...	Wass and Wright (1969)
	1,390	...	...	...	McCormick and Ashbaugh (1972)
	1,600	721	...	...	Good and Good (1975)
	866 [4]	...	...	1,589 [5]	Whigham and Simpson (1975)
	1,346	...	...	1,520	J. McCormick (*personal observations*)
	1,117 [2]	...	...	...	McCormick (1970)
	1,218			**1,578**	
Spartina cynosuroides	3,543[e] [2]	...	...	...	J. McCormick (*personal observations*)
	951	...	241	...	Flemer et al. (*In press*)
	1,207	...	...	1,572	Johnson (1970)
	2,311				
Phragmites communis	3,999 [2]	...	...	...	J. McCormick (*personal observations*)
	1,367 [3]	...	347 [3]	...	Flemer et al. (*In press*)
	1,451	...	...	1,678	Johnson (1970)
	1,727	...	...	...	McCormick and Ashbaugh (1972)
	1,493	...	...	2,066	J. McCormick (*personal observations*)

Table 1. Continued

Vegetation type[b]	Peak standing crop[c] Above-ground	Below-ground	Dead	Annual production[c]	Source
	654	. . .	. . .	. . .	McCormick (1970)
	1,074	7,180	. . .	. . .	Walker and Good (1976)
	1,850			**1,872**	
Acnida cannabina	1,112	. . .	. . .	1,547	J. McCormick (*personal observations*)
	768	560	. . .	. . .	Good et al. (1975)
	940				
Bidens sp.	1,026 [3]	. . .	. . .	910	Whigham and Simpson (1975)
	1,109	. . .	. . .	1,771	J. McCormick (*personal observations*)
	900	. . .	. . .	. . .	McCormick (1970)
	1,017			**1,340**	
Phalaris arundinacea	566	. . .	. . .	. . .	Whigham and Simpson (1975)
Lythrum salicaria	2,104	. . .	. . .	2,100	Whigham and Simpson (1975)
	1,373 [2]	. . .	. . .	. . .	McCormick (1970)
	1,616				
Ambrosia trifida	1,160	. . .	. . .	1,160	Whigham and Simpson (1975)
	1,227 [2]	. . .	. . .	. . .	McCormick (1970)
	1,205				
Sagittaria latifolia	649	. . .	. . .	1,071	J. McCormick (*personal observations*)
	214	. . .	. . .	. . .	Good et al. (1975)
	432				
Part 2—Brackish tidal wetlands					
Spartina patens/ Distichlis spicata	1,123 [3]	. . .	. . .	. . .	J. McCormick (*personal observations*)
	449 [3]	. . .	. . .	. . .	Heinle (1972)
	680	. . .	1,209	. . .	Flemer et al. (*In press*)
	1,525 [2]	. . .	. . .	. . .	Jack McCormick and Associates, Inc. (1973)
	480	. . .	. . .	572	Mendelssohn and Marcellus (1976)
	445	. . .	. . .	. . .	Drake (1976)
	1,145 [2]	. . .	. . .	. . .	de la Cruz (1973)
	897				
Iva/Baccharis/ Spartina patens	1,075 [2]	. . .	. . .	. . .	J. McCormick (*personal observations*)
	534	. . .	. . .	. . .	Drake (1976)
	895				

Table 1. Continued

Vegetation type[b]	Peak standing crop[c] Above-ground	Below-ground	Dead	Annual production[c]	Source
Juncus roemerianus	1,602 [2]	...	...	...	J. McCormick (*personal observations*)
	1,082 [3]	...	...	...	Heinle (1972)
	1,290				
Typha sp.	1,453 [2]	...	...	...	J. McCormick (*personal observations*)
	1,668 [3]	...	698 [3]	...	Flemer et al. (*In press*)
	1,435	...	...	...	Jack McCormick and Associates, Inc. (1973)
	919	...	...	...	Wass and Wright (1969)
	626	...	...	...	Drake (1976)
	1,361				
Hibiscus palustris	**1,354** [2]	...	...	...	J. McCormick (*personal observations*)
Panicum virgatum	4,029 [2]	...	...	...	J. McCormick (*personal observations*)
	652	...	...	...	Anderson et al. (1968)
	326	...	...	...	Drake (1976)
	2,259				
Scirpus sp.	802 [2]	...	...	...	J. McCormick (*personal observations*)
	366 [2]	...	...	...	Anderson et al. (1968)
	833 [3]	...	295 [3]	...	Flemer et al. (*In press*)
	561	...	...	...	Wass and Wright (1969)
	472	...	...	...	Drake (1976)
	193	...	...	...	Good (1965)
	606				
Spartina cynosuroides	968 [2]	...	...	...	Anderson et al. (1968)
	1,900 [2]	...	685 [2]	...	Flemer et al. (*In press*)
	1,401 [3]	...	...	...	Wass and Wright (1969)
	560	...	...	...	Mendelssohn and Marcellus (1976)
	672	...	...	563	Drake (1976)
	826 [4]	...	349 [4]	1,175 [4]	Odum and Fanning (1973)
	1,113			**1,053**	
Spartina alterniflora	1,003 [2]	...	...	...	J. McCormick (*personal observations*)
	1,020 [2]	...	...	...	Jack McCormick and Associates, Inc. (1973)
	2,410	...	...	...	Wass and Wright (1969)
	725 [4]	6,353 [4]	...	3,500	R. E. Good and R. Walker (*personal observations*)
	587	...	...	...	Drake (1976)

Table 1. Continued

Vegetation type[b]	Peak standing crop[c] Above-ground	Below-ground	Dead	Annual production[c]	Source
	1,184	. . .	. . .	. . .	G. T. Potera and E. E. MacNamara (*personal observations*)
	563 [2]	. . .	. . .	. . .	Jack McCormick and Associates, Inc. (1974)
	943				

[a] The number of estimates used to calculate the entries is shown in brackets. All estimates were used to calculate the averages shown in boldface.

[b] The classification system used in construction of this table was provided by Jack McCormick and is available from him.

[c] All data are expressed as grams per square metre dry weight.

[d] Stevenson et al. (1976) data were converted to grams per square metre using 18.83 kJ/g as a conversion factor.

[e] These are adjusted estimates; the weights of all harvested materials in the 2 samples were 5,415 and 5,875 g/m².

(432 g/m²). This sequence must be viewed with caution because of the large amount of variability within and between vegetation types (Table 1). Some variation is undoubtedly due to sampling techniques, but much variation may be an expression of the highly variable spatial and species composition of freshwater tidal wetland vegetation. Assuming that biomass and production are related, data in Table 1 fall toward the low range of expected values of net production in freshwater wetlands (Lieth and Whittaker, 1976) but correspond to primary production and standing crop measurements made by Jervis (1969) in a New Jersey nontidal freshwater wetland.

Estimates of annual net production are higher than biomass estimates for the same vegetation types but there have been few estimates of annual production and the available data suggest that there is much variation within and between vegetation types (Table 1). The lowest reported estimates are for *Pontederia/Peltandra*-dominated vegetation (650 g/m²) and the highest reported values are for *Zizania* stands in New Jersey (2,321 g/m²). The latter estimate included root production. The range of average peak aboveground standing crop estimates in freshwater tidal wetlands (566–2,311 g/m²) is as high as that measured in brackish wetlands (216–2,270 g/m²) and, in most cases, biomass was greatest in those portions of brackish wetlands where freshwater tidal wetland species occur (Table 1). Comparison of data presented in Table 1 with data on biomass and production of saline wetlands (Keefe, 1972; Turner, 1976) reveals that aboveground biomass in freshwater tidal wetlands is greater than that measured in saline wetlands at the same geographic latitudes. *Juncus roemerianus* and *Spartina alterniflora* (tall form) wetlands had the highest average peak standing crops (1,160 and 958 g/m^2, respectively) while *Spartina patens/Distichlis spicata* and *Spartina alterniflora* (short form) wetlands had the lowest average peak standing crops (341–216 g/m^2, respectively). Estimated annual net primary production ranged from 1,036 g/m^2 in tall form *Spartina alterniflora* wetlands to 365 g/m^2 in short form *S. alterniflora* wetlands. The range of values reported is very wide and there are still not enough reliable data to document clearly the differences between net annual production of the 3 types of tidal wetlands.

It would also be interesting to know the comparative relationship between macrophyte production in tidal and nontidal freshwater wetlands because Turner (1976) has recently suggested that tidal subsidy may not be an important factor in determining production of saline wetlands. Based on macrophyte production data in other chapters of this volume and in Keefe (1972) and Whigham and Simpson (1976*a*), it is impossible to make reliable comparisons between analogous communities in tidal and nontidal freshwater wetlands because the production estimates for both types of wetlands are quite variable. It is also difficult to make any definite conclusions when comparisons are made of production estimates of individual species. For example, it appears that Delaware River tidal populations of *Zizania aquatica* var. *aquatica* are more productive than Minnesota nontidal populations but the pattern does not always hold because there are no differences between tidal and nontidal populations in New Jersey (Whigham and Simpson, 1977). Similarly, *Typha* sp. production has been measured many times but there are no apparent patterns when comparisons are made between tidal and nontidal populations (Whigham and Simpson, 1976*a*). Only further research will provide an answer to the question of whether or not factors associated with tidal activity cause the net community production of freshwater tidal wetlands to be greater than their nontidal counterparts.

FACTORS RESPONSIBLE FOR UNDERESTIMATION OF PRODUCTIVITY

Jervis (1969) and Auclair et al. (1976) have documented the existence of pronounced seasonal changes in dominance in nontidal freshwater wetlands. Data from Whigham and Simpson (1975, 1976*a*, 1976*b*) in the Hamilton Marshes clearly demonstrate that there are seasonal patterns of accumulation of biomass in freshwater tidal wetlands. Seasonal patterns are also reported in McCormick (1970), McCormick and Ashbaugh (1972) and Good and Good (1975). Data from Whigham and Simpson are used to demonstrate 4 patterns of biomass accumulation (Fig. 1). Distinct seasonal variations in the distribution of aboveground biomass within most vegetation types are also illustrated (Fig. 2). In general, physiognomic changes are associated with early season dominance by perennials, senescence of the perennials

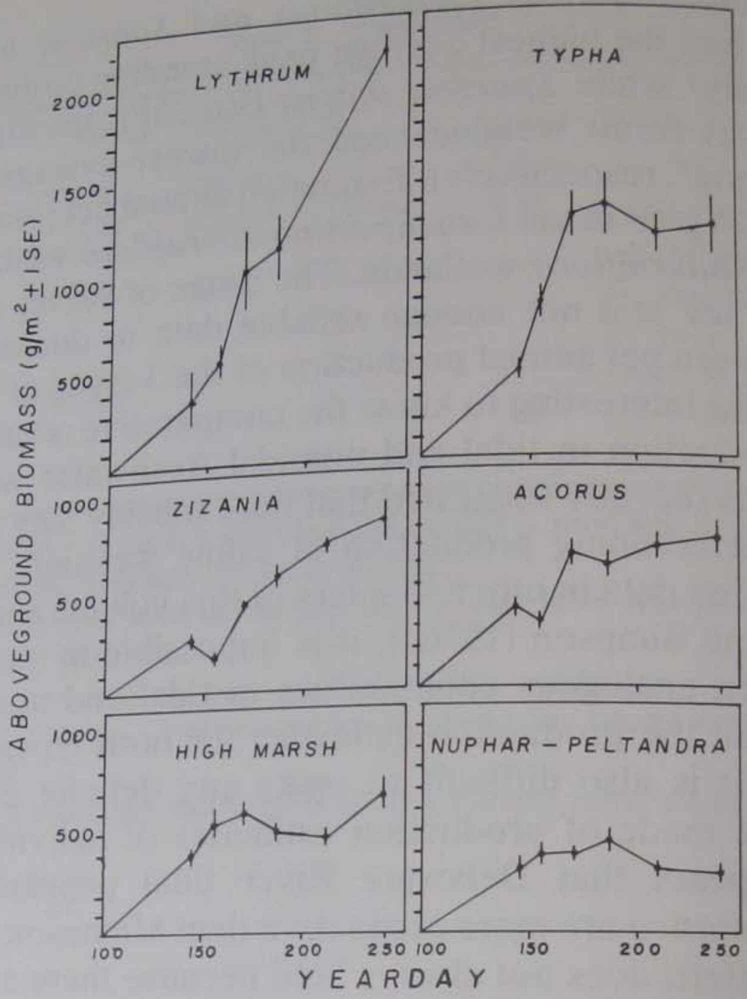

Fig. 1. Patterns of aboveground biomass accumulation in the 6 most common vegetation types in the Hamilton Marshes. Data were collected during the 1974 and 1975 growing season using 0.25 m^2 quadrats. Methods are detailed in the Whigham and Simpson (1975, 1976*a*).

and their replacement by a succession of annuals and a few perennials that reach peak biomass later in the season.

In vegetation dominated by the annual, *Zizania*, and a semi-shrub perennial, *Lythrum*, aboveground biomass increased linearly throughout the growing season and reached average peak biomass of 800 g/m^2 and 2,100 g/m^2, respectively (Fig. 1). A second pattern of biomass accumulation occurred in vegetation along stream banks and in pond-like areas. Those habitats were dominated by *Nuphar* and *Peltandra*, both perennials, early in the growing season and then by annuals (*Acnida* and *Polygonum punctatum*) and perennials (*Pontederia* and *Sagittaria*) following senescence of *Nuphar* and *Peltandra* leaves. Peak aboveground biomass (450 g/m^2) occurred prior to the senescence of *Nuphar* and *Peltandra* leaves (Fig. 1). A third pattern was observed in vegetation dominated by *Typha* and *Acorus* (Fig. 1). Aboveground biomass peaked by June and remained rather constant for the remainder of the growing season. This type of growth of *Typha* has been well documented by Boyd (1970*a*, 1970*b*, and 1971), and Dykyjová et al. (1972) reported a similar pattern for individual clones of *Acorus* grown in greenhouse cultures. In both species, initial high growth rates are due to the

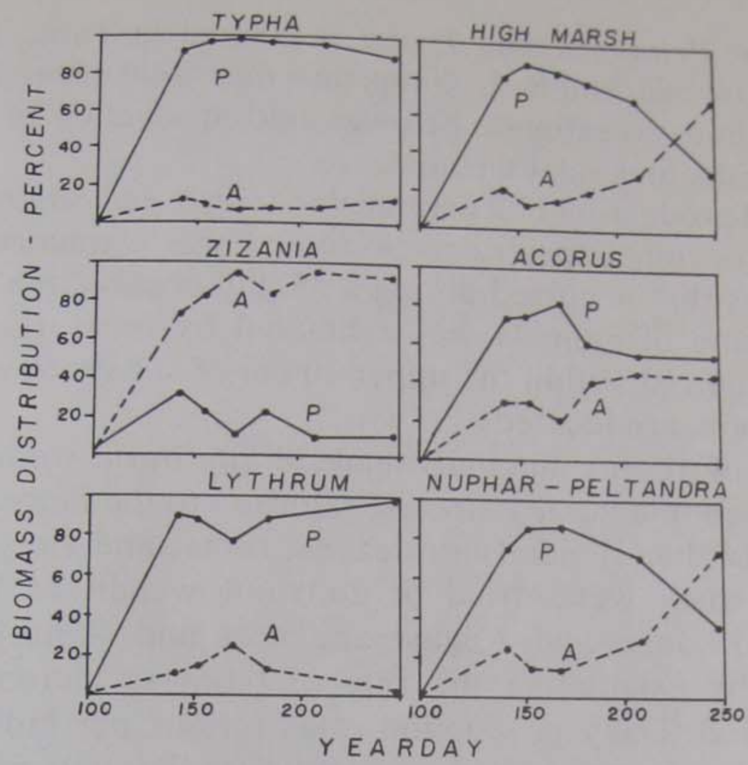

Fig. 2. Data from Fig. 1 were subdivided into perennials (P) and annuals (A) to show the changes in dominance patterns within the 6 vegetation types sampled.

mobilization of energy stored belowground from the previous growing season. Cattail vegetation was dominated by *Typha* throughout the growing season (Fig. 2) but sweet flag dominated vegetation went through a series of physiognomic changes because most *Acorus calamus* had senesced by midsummer. *Acorus* sites were then commonly dominated by a perennial (*Sagittaria*) and several annuals (*Zizania*, *Polygonum arifolium*, and *Bidens*). Peak biomass was ≈700 g/m² in *Acorus*-dominated sites and 1,200 g/m² in *Typha*-dominated vegetation (Fig. 1). A common pattern on high marsh sites (Whigham and Simpson, 1976*a*) was characterized by early growing season dominance of *Peltandra* followed by succession of other species (Fig. 2). Similar to *Acorus*- and *Typha*-dominated vegetation, biomass increased rapidly after the onset of the growing season (Fig. 1) and most of the biomass was due to the dominance of *Peltandra*. By midsummer, almost all *Peltandra* leaves had senesced and the stands usually were dominated by 2 annuals (*Zizania and Impatiens*). Following senescence of *Zizania* and *Impatiens*, *Bidens* and *Polygonum arifolium* dominated the sites when peak standing crop (680 g/m²) occurred.

There have been few measurements of belowground biomass and production in saline wetlands (Turner, 1976) and freshwater tidal wetlands (Table 1). The paucity of data reflects the inherent difficulty in sampling wetland substrates and also the difficulty in measuring root production of perennial species. Belowground production measurements must, however, be made to estimate reliably net community production. It is quite likely that belowground production is very high in some species as suggested by the belowground data for *Peltandra* and *Typha* presented in Table 1. This section details D. F. Whigham and R. L. Simpson's (*personal observations*) attempt to develop methods to estimate belowground production of perennials and annuals in a freshwater tidal wetland.

Belowground production of 2 perennials (*Acorus* and *Sagittaria*, examples of clonal and nonclonal species respectively) was estimated by measuring biomass changes that occurred during a 55 day observation period. Belowground production of annuals was estimated by measuring root biomass changes that occurred within the upper 10 cm of substrate where ≈90–95% of the annual roots are located.

Entire clones of *Acorus* and individuals of *Sagittaria* were hand extracted and gently washed in a nearby stream, returned to the laboratory, washed a second time, and then divided into leaves, roots, and stems/rhizome components before they were dried to constant weight at 105°C. Samples were collected in June and August and root and stem/rhizome production estimated by calculating the rate of biomass increment during the observation period. Daily production rates (grams per individual per day) were multiplied by the average plant density (individuals per square metre) and growing season (days) to estimate yearly production (grams per square metre per day). As stated, root production (primarily roots of annuals) within the upper 10 cm of marsh substrate was estimated by measuring the increase in root material in cores. Ten cores were collected in June and August in each of 8 study areas using a 5 cm diameter corer. The cores were washed in a series of nested soil sieves to remove inorganic material and the remaining materials were washed into white enamel trays. Roots were then handpicked from the trays and dried to determine the biomass in each core. Dry weights (grams per core) were converted to grams per square metre and daily production rates calculated (Table 2).

Acorus belowground biomass increased at a rate of 1.49 $g \cdot m^{-2} \cdot day^{-1}$ with the increase occurring in both root and rhizome components. *Sagittaria* subterranean biomass increased at a rate of 0.02 $g \cdot m^{-2} \cdot day^{-1}$ while root biomass in the upper 10 cm of marsh substrate increased at a rate of 0.4 $g \cdot m^{-2} \cdot day^{-1}$. Estimated yearly production of belowground biomass was 223.5 g/m^2 for *Acorus*, 4.0 g/m^2 for *Sagittaria* and 160 g/m^2 for all roots in the upper 10 cm of substrate. This method of estimating annual root production is probably valid for most species that form a dense root mat near the surface.

Large amounts of biomass are omitted from production and biomass measurements because of senescence of leaves and other plant parts. There are, however, few data on the magnitude of those losses within freshwater tidal wetlands. Authors Whigham and Simpson measured leaf mortality for 4 dominant species during the 1976 growing season in the Hamilton Marshes. Aluminum tags were attached to petioles of *Bidens*, *Acorus*, *Peltandra* and *Sagittaria* leaves and their disappearance rate observed over a 55-

Table 2. Seasonal Changes in Shoot, Root, and Stem Biomass for 2 Species, and for all Roots in the Upper 10 cm of Substrate[a]

		Biomass (g/m^2)			Samples, plants, or growing	Growing season	Production rate (g·	Yearly belowground production
Plant	Date	Leaves	Roots	Rhizome/stem	points (n)	(days)	$m^{-2}\cdot day^{-1}$)	(g/m^2)
Acorus calamus	24 Jun	158.4	38.5	109.5	38	150	1.49	223.5
	4 Aug	94.6	53.9	155.1	36			
Sagittaria latifolia	24 Jun	2.2	0.6	. . .	12	200	0.02	4.0
	4 Aug	4.7	1.2	0.2	12			
All roots in upper 10 cm	24 Jun	. . .	5.1	. . .	24	200	0.80	160.0
	4 Aug	. . .	22.9	. . .	11			

[a] Plants were harvested in 1976 from the Hamilton Marshes near Trenton, New Jersey. Methodology is provided in the text.

Table 3. Leaf Mortality Data for 4 Wetland Species[a]

Parameter	*Peltandra*	*Sagittaria*	*Bidens*	*Acorus*
Leaves per plant ($\bar{x} \pm$ SE)	5.3 ± 3.4 (N = 109)	3.7 ± 1.3 (N = 95)	250 (N = 133)	6 per growing point
Percent/day leaf mortality rate ($\bar{x} \pm$ SE)	1.2 ± 0.52	1.2 ± 0.2	1.11 ± 0.11	1.41 ± 0.36
Approximate growing season (days)	100	200	200	150
Wt ($\bar{x} \pm$ SE) of recently senesced leaves (g)	4.38 ± 1.82	2.12 ± 1.58	.08	1.55 ± 0.54
Density (plants/m²)	2.3	0.5	3.1	5.5
Estimated biomass loss for growing season (g/m²)	60	9.4	277	102

[a] Data were collected in 1976 from the Hamilton Marshes near Trenton, New Jersey. Methodology is provided in the text.

day period. Mortality ranged from 61.3 ± 6.4% of the tagged *Bidens* leaves to 77.7 ± 19.9% for *Acorus* (Table 3). The turnover of leaf biomass for each species was estimated by multiplying the average daily mortality rates by the average number of leaves per plant, mean weight of recently senesced leaves, and average plant density. The estimated leaf mortality losses were 60 g/m² for *Peltandra*, 9.0 g/m² for *Sagittaria*, 277 g/m² for *Bidens*, and 102 g/m² for *Acorus*. Gosselink et al. (1977) also observed that leaf turnover is high for freshwater macrophytes in Gulf Coast wetlands.

In freshwater tidal wetlands, obtaining estimates of actual net production is difficult because of phenological changes in the wetland communities, heterogeneity in community composition and the difficulty in obtaining estimates of leaf mortality, plant mortality and belowground production. An important question, therefore, is how closely do measurements of peak standing crop approximate actual net production?

Table 4 shows peak aboveground standing crop and an estimate of annual aboveground production for a high marsh site in the wetlands being studied by Whigham and Simpson (1975, 1976*a*, 1976*b*). The site that was dominated by *Peltandra* and *Acorus* during the early part of the growing season and then sequentially by *Zizania*, *Bidens*, and *Polygonum arifolium*. Twenty-four 0.25-m² quadrats were harvested during each of 4 sample periods. Aboveground biomass was determined by harvesting all vegetation at the substrate surface, washing the samples, sorting them by species and determining dry weights for each species. Root production and leaf mortality were estimated using methods previously described in this paper. Peak aboveground standing crop (844 ± 76 g/m²) occurred late in the growing season (Table 4). Annual net aboveground production was estimated to be 1,286.5 g/m². The latter was estimated by summing peak aboveground biomass values for all

Table 4. Peak Aboveground Biomass Measurements and an Estimate of Net Annual Aboveground Production for a High Marsh Site in the Hamilton Marshes near Trenton, New Jersey, During 1976

Taxa	Peak biomass (g/m²)	Date
Acorus calamus	73.6	11 Jun
Peltandra virginica	385.4	11 Jun
Scirpus validus	21.9	11 Jun
Leersia oryzoides	2.3	11 Jun
Impatiens capensis	119.3	19 Jul
Cicuta maculata	0.7	19 Jul
Cuscuta sp.	1.4	19 Jul
Zizania aquatica	84.7	11 Aug
Boehmeria cylindrica	2.6	11 Aug
Sagittaria latifolia	12.3	11 Aug
Bidens laevis	282.2	11 Aug
Polygonum arifolium	199.9	11 Aug
Typha latifolia	87.2	11 Aug
Acnida cannabina	7.2	11 Aug
Polygonum punctatum	5.8	11 Aug
	Total = 1,286.5[a]	

[a] Annual net aboveground production: estimate determined by summing peak aboveground biomass for all species.

species independent of when the samples were collected. Accounting for estimates of leaf mortality (600 g/m²) and belowground production (160 g/m² for annuals and 140 g/m² for 2 perennials), total estimated annual net production was 2,346.5 g/m². Leaf mortality and belowground production estimates are the same as those described previously. The latter is still an underestimate of total production because it does not include data on belowground production for several perennial species (especially *Peltandra*) and there is no estimate for herbivore consumption.

Clearly, the measurement of peak aboveground standing crop was not a good estimator of annual production. In addition to yielding significantly low estimates of production, peak aboveground standing crop may also have given incorrect relative estimates of species productivity due to differences in belowground production, leaf mortality and consumption (which may be expected to vary substantially between the wide range of growth habits and life histories of annual and perennial marsh species). Peak aboveground standing crop must be viewed as only a rough estimate of a single parameter, aboveground production.

CONCLUSIONS

Based on our literature review, it appears that freshwater tidal wetlands may be more productive than saline wetlands at the same latitude and that typical freshwater tidal wetland species are usually the most productive species when they occur in brackish wetlands. Due to the extensive variability in available data, it is impossible to make any valid comparisons between production of tidal and nontidal freshwater wetlands. Production estimates for freshwater tidal wetlands are low because they do not account for belowground production, leaf mortality during the growing season, herbivory and plant turnover during the growing season. Our studies in a New Jersey tidal wetland demonstrate that those factors may account for at least 50% of the total net community production. If this value is accurate we estimate that production of freshwater tidal wetlands within the Middle Atlantic coastal region ranges from $\approx$1,000 g/m^2 to 3,500 g/m^2 and that some wetlands can produce >4,000 g/m^2. Because of the pronounced physiognomic changes that occur in community composition, we suggest that investigators use multiple harvest techniques when measuring primary production within freshwater tidal wetlands. The need for more adequate data on the dynamics of belowground biomass, leaf mortality and herbivory is obvious, and future production studies should include estimates of those parameters.

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