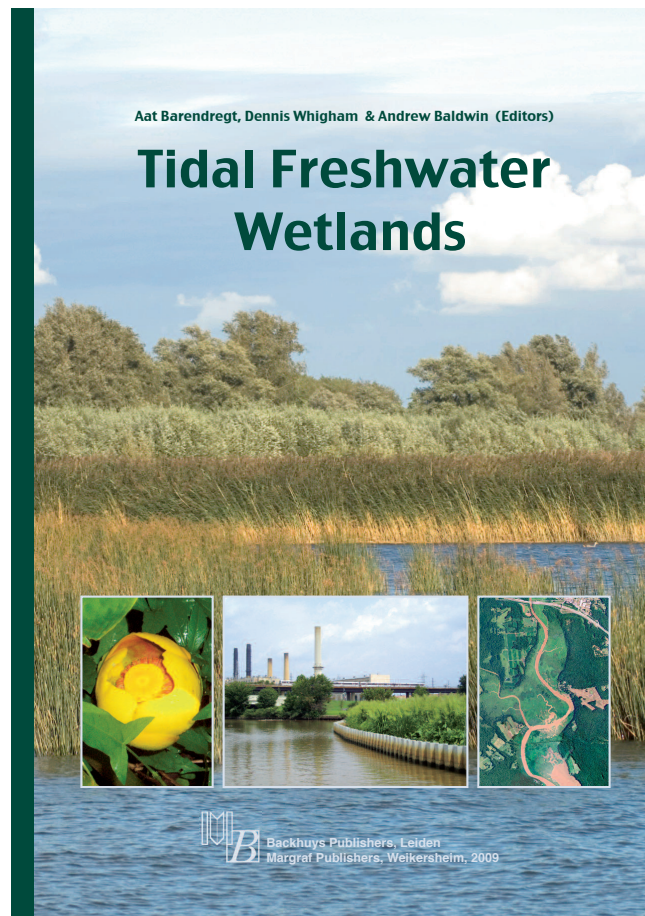


## Chapter 10

# PRIMARY PRODUCTION IN TIDAL FRESHWATER WETLANDS


*Dennis F. Whigham*

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## Chapter 10

# PRIMARY PRODUCTION IN TIDAL FRESHWATER WETLANDS

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**Abstract:** Primary production of tidal freshwater wetlands is extremely high for most habitats. High levels of primary production are the result of several factors, including their location in nutrient-rich portions of estuaries and the presence of a tide (e.g., tidal subsidy) in a fresh water habitat. Primary production is high throughout the growing season because of the almost unique combination of annual and perennial species that dominate tidal freshwater wetlands. Perennials typically dominate the vegetation in the early part of the growing season and annuals dominate in the middle and later parts of the growing season. Estimates of production of individual species are over 2,000 g/m<sup>2</sup>/yr. Belowground production is also high but there have been few studies of belowground dynamics of TFW plant species.

Nomenclature: Plant names follow the USDA PLANTS checklist ([plants.usda.gov](http://plants.usda.gov))

**Keywords:** productivity, primary production, nutrient limitations, peak biomass, tidal pulsing, annuals, perennials, belowground

## INTRODUCTION

Tidal freshwater wetlands (TFW) that exist today are considered to be young depositional landforms (see: Chapter 4) that occur at the interface between non-tidal rivers and brackish estuaries (Odum et al. 1984, Simpson et al. 1983a, Mitsch & Gosselink 2000, Barendregt et al. 2006). Because of their landscape position they have a unique combination of characteristics that support high levels of primary productivity (Whigham et al. 1978, Simpson et al. 1983a, Odum et al. 1984). First, they occur in the tidal fresh zone of rivers and are influenced by twice-daily tides, a natural subsidy that supports high levels of primary production in estuarine ecosystems (Odum et al. 1995). Two other factors related to high levels of primary production are the location of tidal freshwater habitats within the river continuum and lack of salt stress. Macrophytes in TFW have been shown to be sensitive to salt stress (Ferren et al. 1981, Tiner & Burke 1995) and except for the portion of the tidal fresh zone that is adjacent to and mixes with brackish water, salinity is always less than 0.5 parts per thousand and salinity stress does not limit plant growth. Second, the tidal freshwater zone in river systems is typically eutrophic (Barendregt et al. 2006) and thus plant growth should not be nutrient-limited. This unique combination of factors (i.e., lunar tides in a nutrient-rich freshwater environment) is not found in any other type of ecosystem,

except for a few fresh water environments (e.g., large water bodies such as the Great Lakes) that have small-scale wind-driven movements of water (seiches) that are similar to tides but do not occur at the same regularity.

In addition to high levels of primary production, other characteristic ecosystem responses are associated with fresh water tidal habitats. TFW typically have high biodiversity and support rare and endangered species (Barendregt et al. 2006). Many macrophytes that dominate TFW have high rates of decomposition (e.g., Odum et al. 1984, Morris 1986) and substantial nutrient loads are incorporated into substrates, especially in high marsh habitats, because of nutrient uptake by decomposing litter (Khan & Brush 1995), microbial processing (Fogel & Tuross 1999) and high rates of sediment deposition and subsequent burial of organic matter (Morse et al. 2004, Chapter 4). These and other subjects are the focus of other chapters in the book.

In this chapter I review the primary production literature for TFW. It is important to understand the levels of primary production in TFW in terms of the linkages between primary producers, secondary consumers, and nutrient dynamics of TFW (Odum et al. 1984). Several aspects of primary production are considered. First I compare and contrast recent estimates of primary production with literature reviews that were conducted in the 1970s, 1980s, and early 1990s. I then focus on patterns of primary production within different

habitats and among species with different life history strategies. I also compare levels of primary production for species that occur in tidal as well as non-tidal freshwater wetlands. Following a section on the relationship between primary production and nutrient limitation, the review ends with a discussion of the linkages between the products of primary production and other organisms and processes in TFW.

## ESTIMATES OF PRIMARY PRODUCTION

There have been few published journal articles or book chapters that contain estimates of primary production in TFW since early studies in the 1970s and 1980s (Table 1) and the publications of Whigham et al. (1978), Simpson et al. (1983a), Odum et al. (1984), Odum (1988), Whigham & Simpson (1992), and Mitsch & Gosselink (2000) contain many of the same estimates for TFW for North America. Very few estimates of primary production are available for TFW in Europe (Soetaert et al. 2004 and Barendregt in Table 1). The general patterns that emerged from the earlier research and syntheses have been further confirmed by a few more recent studies (Table 1).

There is a high degree of variation in estimates of primary production among different vegetation types (Table 1) in TFW (Whigham et al. 1978, Odum et al. 1984, 1995, Mitsch & Gosselink 2000), but they are almost always more productive than non-tidal freshwater wetlands with the same species (see below), and there is a large degree of overlap in estimates of primary production in TFW compared to other types of tidal wetlands. At the system level, Odum (1988) and Mitsch and Gosselink (2000) estimated that the total annual primary production of TFW ranged between 1,000 and 3,500 g/m<sup>2</sup>/yr but measurements of individual species suggest that net above- and belowground production may attain levels between 6,000 – 8,500 g/m<sup>2</sup>/yr (e.g., Sickels & Simpson 1985, Simpson et al. 1985).

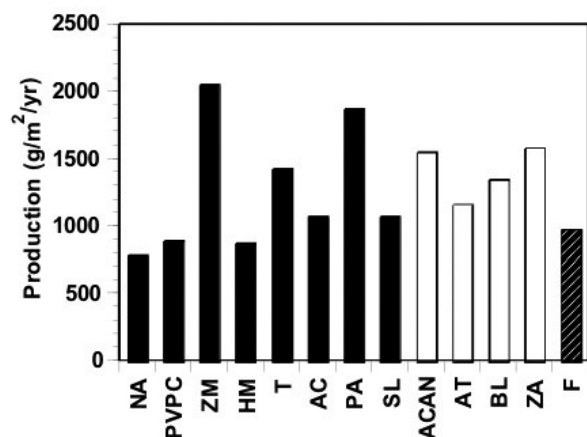
### Comparisons between vegetation types and species

Estimates of primary production vary from one vegetation type to another and differences between reported values depend on the method used to estimate production, whether or not the estimates include measurements of belowground production or biomass losses due to mortality of individuals and tissue loss during the growing season. There have been a few studies in which investigators have attempted to account for more than one of these components of annual production. Neubauer et al. (2000) offered one of the most complete analyses of primary production in a TFW, and several studies of communities and species in a TFW in New Jersey attempted to account for belowground biomass as well

as changes in biomass and tissue losses during the growing season (Whigham & Simpson 1977, 1992, Whigham et al. 1978, Sickels & Simpson 1985, Simpson et al. 1985). Odum et al. (1983) also accounted for belowground biomass in their estimate of production of a *Zizaniopsis miliacea*-dominated TFW site in Georgia.

Belowground biomass of perennial species in TFW can be very large (e.g., Whigham & Simpson 1978) but it is difficult to convert measurements of belowground biomass into estimates of production because much of the biomass is composed of tissues that persist for more than one growing season. Based on the few data available, however, the amount of the net annual production that is allocated to belowground biomass appears to be between about 50 and 25%. Booth (1989) estimated that the amount of annual production of *Peltandra virginica*, a perennial species, allocated to belowground and aboveground biomass was about equal. Neubauer et al. (2000) made similar estimates working in a *Peltandra*-dominated TFW. The proportion of net annual production allocated to roots is less than 50% for annual species, in part, because annuals do not produce any long-term storage structures such as rhizomes and bulbs. *Ambrosia trifida* (Sickels & Simpson 1985) and *Zizania aquatica* var. *aquatica* (Whigham & Simpson 1977) root biomass was 45.9 and ~ 22% of the shoot biomass, respectively.

Fig. 1 shows estimates of annual production, for aboveground biomass only, for different vegetation types in TFW. The figure was compiled from Table 7 in Odum et al. (1984). All of the vegetation types shown in black bars were dominated by perennial species and the four vegetation types in the white bars were dominated by annual species. Aver-



**Figure 1.** Estimates of productivity for herb-dominated TFW from Table 7 in Odum et al. (1984) and for forested TFW (F) from Fowler & Hershner (1989) and Megonigal (1996). Data were compiled for vegetation types dominated by perennial species (black bars), annuals (white bars) and forested TFW (stippled). Community types are: NA=*Nuphar lutea* (= *advena*), PVPC = *Peltandra virginica*-*Pontederia cordata*, ZM = *Zizaniopsis miliacea*, HM = *Hibiscus moscheutos*, T = *Typha* spp., AC = *Acorus calamus*, PA = *Phragmites australis*, SL = *Sagittaria latifolia*, ACAN = *Amaranthus cannabinus*, AT = *Ambrosia trifida*, BL = *Bidens laevis*, ZA = *Zizania aquatica*, F = forested TFW.

**Table 1.** Estimates of primary production for tidal freshwater wetlands. All values are g/m<sup>2</sup>/yr of organic matter on a dry weight basis for macrophytes and mg C/m<sup>2</sup>/hr for bacterial productivity. Many of the estimates were taken from Table 1 in Odum et al. (1984) and readers should consult that publication for the original citations.

Habitat or species	Above ground	Total	Measurement technique	Location of study	Source
High to low marsh		1,430 – 1,072 <sup>1</sup>	Gas exchange and multiple harvests	Virginia - Pamunkey River (USA)	Neubauer et al. (2000)
High to low marsh	775.7		Multiple harvests	Virginia - Pamunkey River (USA)	Doumlele (1981)
High to low marsh	2,179 – 1,176		Multiple harvests	Scheldt River (Belgium)	Soetaert et al. (2004)
High marsh	457.1 - 435.7 <sup>2</sup>		Harvest at peak biomass	Virginia - Mattaponi River (USA)	Morse et al. (2004)
High to low marsh	834 - 84 <sup>4</sup>		Multiple harvests	Quebec - St. Lawrence River (Canada)	Gilbert (1990)
High to low marsh	816 (range appr. 1,650 - 350 <sup>7</sup> )		Multiple harvests	Washington - Nooksack River (USA)	Disraeli & Fonda (1979)
High marsh ( <i>Schoenoplectus americanus</i> fresh water – to <i>Distichlis spicata</i> and <i>Jaumea carnosa</i> – slightly brackish)	1,600 – 500 <sup>3</sup>		Peak biomass	California - Sacramento and San Joaquin Rivers (USA)	Lisa Schile & Tom Parker (pers. comm.)
Low marsh ( <i>Zizania aquatica</i> , <i>Pontederia cordata</i> , <i>Peltandra virginica</i> = dominants)	1,100 - 982		Multiple harvests with focus on peak biomass	Maryland - Patuxent River (USA)	Flemer et al. (1978)
Low marsh ( <i>Schoenoplectus acutus</i> = dominant)	2,000 - 600		Peak biomass	California - Sacramento and San Joaquin Rivers (USA)	Lisa Schile & Tom Parker (pers. comm.)
<i>Calamagrostis canadensis</i>	127		Multiple harvests <sup>6</sup>	Massachusetts - North River Marsh (USA)	Bowden et al. (1991)
Forested tidal freshwater wetland	1,227.2		Allometric measurements of trees, litterfall measurements, multiple harvest of understory herbaceous vegetation	Virginia - Pamunkey River (USA)	Fowler & Hershner (1989)
Forested tidal freshwater wetland	979 - 708		Allometric measurements of trees, litterfall measurements and harvest of understory herbs	North Carolina - White Oak River (USA)	Megonigal (1996)
<i>Salix</i> -dominated stand <sup>10</sup>	2,757.4		One harvest	Oude Maas (The Netherlands)	Aat Barendregt (pers. comm.)
<i>Carex lacustris</i>	236		Multiple harvests <sup>6</sup>	Massachusetts - North River Marsh (USA)	Bowden et al. (1991)
<i>Carex lyngbyei</i>	1,742		Harvest at peak biomass	Washington - Skagit River (USA)	Ewing (1986)
<i>Carex lyngbyei</i> <sup>8</sup>	1,390 – 1,086		Harvest at peak biomass	Washington - Nisqually River (USA)	Burg et al. (1980)
<i>Impatiens capensis</i>	8,492		Multiple harvests	New Jersey - Delaware River (USA)	Simpson et al. (1985)
<i>Leersia oryzoides</i>	58 - 58 <sup>9</sup>		Multiple harvests	Virginia - Pamunkey River (USA)	Perry & Hershner (1999)
<i>Peltandra virginica</i>	769 – 1,552 <sup>2</sup>		Two harvests	Virginia - Chickahominy River (USA)	Chambers & Fourqurean (1991)
<i>Peltandra virginica</i>	423		Multiple harvests	Virginia - Pamunkey River (USA)	Doumlele (1981)
<i>Peltandra virginica</i>	214 - 370 <sup>9</sup>		Multiple harvests	Virginia - Pamunkey River (USA)	Perry & Hershner (1999)
<i>Phragmites australis</i>	2,147.7		One harvest	Oude Maas (The Netherlands)	Aat Barendregt (pers. comm.)
<i>Polygonum punctatum</i>	45		Multiple harvests	Virginia - Pamunkey River (USA)	Perry & Hershner (1999)
<i>Pontederia cordata</i>	31		Multiple harvests	Virginia - Pamunkey River (USA)	Perry & Hershner (1999)
<i>Sagittaria latifolia</i>		685 <sup>2</sup>	Multiple harvests	Quebec - St. Lawrence River (Canada)	Gilbert (1990)
<i>Sagittaria rigida</i>		89 <sup>2</sup>	Multiple harvests	Quebec - St. Lawrence River (Canada)	Gilbert (1990)
<i>Scirpus americanus</i>		436 <sup>2</sup>	Multiple harvests	Quebec - St. Lawrence River (Canada)	Gilbert (1990)
<i>Typha latifolia</i>	575		Multiple harvests <sup>6</sup>	Massachusetts - North River Marsh (USA)	Bowden et al. (1991)

continued

Table 1 (continued)

Habitat or species	Above ground	Total	Measurement technique	Location of study	Source
<i>Zizania aquatica</i>		196 <sup>2</sup>	Multiple harvests	Quebec - St. Lawrence River (Canada)	Gilbert (1990)
<i>Zizania aquatica</i>	55		Multiple harvests	Virginia – Pamunkey River (USA)	Perry & Hershner (1999)
<i>Zizania aquatica</i> var. <i>aquatica</i>	560 – 2,091 <sup>5</sup>		Multiple methods	New Jersey, Pennsylvania, Maryland, Virginia (USA)	Whigham & Simpson (1997)
<i>Zizania aquatica</i> var. <i>aquatica</i>		1,453 <sup>2</sup>	Multiple harvests	New Jersey – Delaware River (USA)	Whigham & Simpson (1977)
<i>Zizaniopsis miliacea</i>		1,531 <sup>2</sup>	Two harvests	Georgia – Augustine Creek (USA)	Odum et al. (1983)

<sup>1</sup>Estimates in Neubauer et al. (2000) were given in g C/m<sup>2</sup>/yr and were doubled (based on the assumption that half of the organic matter is carbon) to estimate g/m<sup>2</sup>/yr.

<sup>2</sup>Means.

<sup>3</sup>Range.

<sup>4</sup>Highest and lowest means for 7 vegetation types.

<sup>5</sup>Range of estimates from studies in New Jersey, Pennsylvania, Maryland, and Virginia as cited in Table 1 in Whigham and Simpson (1977).

<sup>6</sup>Total aboveground biomass based on the sum of live and dead aboveground biomass for the month when the total of the two measurements was the greatest.

<sup>7</sup>Mean biomass for four sites representing different elevations. Salinity ranged from a mean of 0.5 to 1.21 (July-October) along the elevation gradient. *Carex lyngbyei* was the dominant species at the sites with the highest biomass.

<sup>8</sup>Range of values for sites dominated by *Carex lyngbyei* and *Festuca rubra*. From the original publication it was not possible to determine if these two vegetation types were truly tidal freshwater but it is likely that there was, at times, brackish water intrusion into these two vegetation types.

<sup>9</sup>Biomass sampled in 1974 (value on left) and 1987 (value on right) in the same wetland. In 1974, the site was entirely fresh water but by 1987, brackish water had started to intrude into the site.

<sup>10</sup>Other species present at the time of the autumn sampling were: *Ranunculus repens*, *Cardamine pratense*, *Urtica dioica*, *Anthriscus sylvestris*, *Symphytum officinale*, *Heracleum sphondyleum*, *Valeriana officinalis*, *Agrostis stolonifera*, *Calystegia sepium*, *Rumex* sp., *Sonchus* sp. and moss species (e.g., *Eurhyngium praelongum*). Biomass estimate includes 204.4 g of herbaceous vegetation, 497.0 g of *Salix* leaves, and 2,056 g of the *Salix* branches/m<sup>2</sup>.

age production for the annual-dominated communities was greater than 1,000 g/m<sup>2</sup>/yr while only three vegetation types dominated by perennials averaged more than 1,000 g/m<sup>2</sup>/yr. The three perennial communities with the highest estimates of production are all dominated by clonal species (species of *Typha*, *Phragmites australis*, *Zizaniopsis miliacea*) that form dense stands and have shoots that are typically taller than 1.5 meters (McCormick & Somes 1982). The perennial communities with lower estimates of annual production are, with one exception, dominated by shorter broad-leaved perennials (*Nuphar lutea*, *Pontederia cordata*, *Peltandra virginica*, *Acorus calamus*, *Sagittaria latifolia*). The only exception to this pattern is a community type dominated by *Hibiscus moscheutos*, a species that also has tall shoots but does not spread clonally and does not have a high shoot density compared to *Typha*, *Phragmites*, and *Zizaniopsis*.

### Latitudinal comparisons

Primary production has been measured at relatively few TFW sites but general latitudinal comparisons are possible for the Atlantic and Pacific coasts of North America (Table 1). On the Atlantic coast, production of some species and habitats is lower in the north (e.g., sites in the St. Lawrence River - Canada, North River - Massachusetts) where the

growing season is shorter and where the potential impacts of ice formation and scouring would be greatest. The highest levels of production measured in the St. Lawrence River (~650 – 850 g/m<sup>2</sup>/yr) overlap, however, with production estimates for some vegetation types in the mid-Atlantic region (e.g., New Jersey, Maryland, Virginia). There are too few data from TFW in southern sites to determine if the longer growing season manifests itself in higher levels of production compared to mid-Atlantic sites (Table 1; *Zizania aquatica* in New Jersey and *Zizaniopsis miliacea* in Georgia) but data from floating TFW, a variant of TFW that occur on the Gulf coast of the USA (Sasser & Gosselink 1984, Sasser et al. 1995b, Chapter 15), indicate that production levels are comparable.

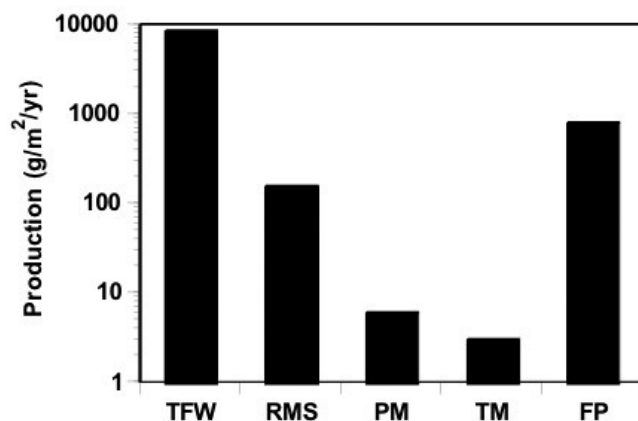
Based on only a few studies, there is no clear latitudinal pattern in primary production from Washington and Oregon in the north to California in the south and production estimates vary from about 1,700 to 500 g/m<sup>2</sup>/yr (Table 1). Production of *Carex lyngbyei*-dominated sites in tidal fresh water and slightly brackish sites on the Pacific northwest coast (e.g., Ewing 1986) appear to have the same general level of production as *Schoenoplectus americanus*-dominated sites in California (Table 1) and there does not appear to be a latitudinal trend (Hutchinson 1986). A general feature of west coast TFW is that most seem to be periodically influenced by the intrusion of brackish water during droughts or extreme

storm events. In San Francisco Bay, many wetlands occur behind dikes and breaches in the dikes allow brackish water to enter sites that are normally fresh water (T. Parker pers. comm.).

### Comparisons of species that grow in tidal and non-tidal freshwater wetlands

Few investigators have measured primary production at the same time in tidal and non-tidal freshwater wetlands but the few data that are available suggest that the tidal subsidy (Odum et al. 1995) results in increased production. Odum et al. (1983) found that the production of *Zizaniopsis miliacea*-dominated vegetation was higher in tidal portions of the Savannah River (1,531 g/m<sup>2</sup>/yr) compared to areas that had been tidal but were converted to non-tidal wetlands for purposes of rice growing (1,172 g/m<sup>2</sup>/yr). The differences in production in tidal and non-tidal habitats is likely due to elements of the tidal subsidy, which include the delivery of nutrients in flood tides, the removal of metabolic by-products in the ebb tide, and tidal pumping of the sediments which would enable oxygen to more effectively enter the substrate.

A species that occurs over a wide range of habitats, including TFW, is the annual *Impatiens capensis*. In TFW it is widespread and a common species that is among a group of annuals that often dominates the biomass from mid-summer until the end of the growing season (Whigham & Simpson 1992). Simpson et al. (1985) measured a wide range of variables for terrestrial and wetland populations of *Impatiens capensis* in New Jersey, USA and found that the highest level of production clearly occurred in TFW (Fig. 2).



**Figure 2.** Production estimates (means) of the annual species *Impatiens capensis* in a tidal freshwater wetland (TFW) and in four non-tidal wetlands (RMS = red maple swamp, PM = *Phragmites*-dominated wetland, TM = *Typha*-dominated wetland, FP = forested riverine floodplain). Source: Simpson et al. (1985).

### Inter-annual variations in primary production

The only effort to compare inter-annual variation in production in TFW was published in an article by Whigham & Simpson (1992) in which they summarized data from a multi-year study of a TFW in New Jersey. Whigham and Simpson then compared their data with production estimates from other multi-year studies in which the authors studying saline, brackish, and non-tidal freshwater wetlands had measured production for three or more years. The metric that Whigham and Simpson used to compare inter-annual variation in production was the coefficient of variation (CV). They found that the highest level of variation occurred in brackish wetlands that experienced salt stress (range = 75.0 - 43.4 %). The CV was less in saline tidal wetlands (range = 46.5 - 2.2 %) and varied between 40 - 15 % for non-tidal freshwater wetlands. The CV for the TFW studied by Whigham and Simpson was 22.8, which was in the lower end of the range for non-tidal fresh water wetlands.

Whigham and Simpson (1992) provided two explanations for the relatively low CV of TFW. First, with regular tidal inundation of nutrient-rich fresh water, vegetation in TFW is not moisture- or nutrient-limited (see below) nor salt-stressed, resulting in little year to year variation in production. Perhaps the most important feature, however, is that TFW have a high macrophyte diversity with a large number of annual and perennial species. They suggested that this feature “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”. High diversity enables the system to be buffered against changing environmental conditions, features that do not occur in most brackish and saline wetlands, which experience seasonal changes in salinity, or in non-tidal fresh water wetlands, which can experience seasonal and annual variation in water availability.

### Nutrient limitation and primary production

Primary production in saline and brackish tidal wetlands in the temperate zone has been shown to be typically nitrogen-limited (e.g., Callaway et al. 2003, Tyler et al. 2003a) but TFW, similar to other types of fresh water ecosystems, are typically phosphorus-limited. Templer et al. (1998) suggested, however, that macrophytes in TFW are most likely N-limited.

I located data from only four experimental studies of nutrient limitation in TFW. They all demonstrate that primary production is not nutrient-limited, most likely because in modern times, TFW occur in portions of river systems that receive large inputs of anthropologically derived nutrients and sediments.

Morse et al. (2004) fertilized plots in TFW along the Mattaponi River (Virginia) with N and P and found no significant increase in aboveground production. Similar results were found for fertilized *Peltandra virginica* (Chambers & Fourqurean 1991) along the Chickahominy River (Virginia). Sibylle et al. (1999) found no growth response and only minimal responses in plant tissue N for *Typha* in a Hudson River TFW. Morris (as reported in Bowden et al. 1991) found similar results for the North River Marsh in Massachusetts. Sybille et al. (1999) also found that the application of urea did not result in any significant responses of the microbial community, further demonstrating that TFW are almost always nutrient-rich.

## DISCUSSION

As suggested throughout this review, differences in estimates of primary production of TFW vary for a number of reasons. Perhaps the most common factor that has varied from one study to another is the method used to measure production. Investigators have used a variety of techniques,

including measurements of gas exchange (e.g., Neubauer et al. 2000), but most estimates have been based on harvesting vegetation at peak aboveground biomass (e.g., McCormick & Somes 1982). This technique, while valid and commonly used in all types of wetlands (Mitsch & Gosselink 2000), has been shown to lack accuracy for TFW where there is strong seasonal dynamics among annual and perennial species (Whigham & Simpson 1992, Simpson et al. 1983a, Whigham & Simpson 1992). In many of the vegetation types found in TFW, biomass in the first half of the growing season is dominated by perennial species while annuals (Fig. 3) dominate many habitats later in the growing season (Whigham & Simpson 1976a, Whigham & Simpson 1992, Chapter 5).

In habitats where there is a pronounced seasonal shift in dominance between annuals and perennials, estimates of primary production are more accurate when biomass is harvested throughout the growing season to encompass peak standing crops of as many species as possible. This technique was used by Whigham and Simpson (1992) to obtain estimates of annual primary production that ranged between approximately 1,500 and 3,000 g/m<sup>2</sup> over an 11 year period for a high marsh



**Figure 3.** Wetland ecology students in a TFW on the Patuxent River (Maryland, USA) late in the growing season (October). Two annual species, *Polygonum arifolium* and *Bidens laevis*, comprise the majority of herbaceous vegetation visible in the foreground. The predominance of annual plants over perennials late in the season is typical of many east coast TFW. Photo by A. Baldwin.

habitat in the Hamilton Marshes (Delaware River, USA). As described above, however, these estimates are certainly lower than actual production because they do not account for the allocation of net annual production to belowground biomass, a large component of total plant biomass for most perennial species (Whigham & Simpson 1978, Booth 1989, Neubauer et al. 2000). Neither do most estimates of primary production account for plant mortality during the growing season (i.e., self-thinning among annual species (Weiner & Whigham 1988) or the shedding of plant parts during the growing season (e.g., Sickels & Simpson 1985).

While it is difficult to accurately measure primary production in TFW, additional studies would not likely change existing estimates of the range primary production nor would they alter the conclusion that most vegetation types in tidal TFW are highly productive. There is a clear need, however, for additional studies of primary production, such as those of Neubauer et al. (2000), that allow us to gain a better understanding of how different components of primary production support food webs and ecosystem processes. There is also a need for additional measurements of primary production that are designed to more fully assess linkages between components of primary production and adjacent aquatic and terrestrial ecosystems. The issues that I now address are related to the fate of the biomass produced and what roles it plays in the overall functioning of TFW, including interactions with adjacent tidally influenced riverine ecosystems.

The products of primary production (e.g., leaves, seeds, tubers, rhizomes) are utilized directly or indirectly by animals (e.g., Barbour & Kiviat 1986, Anderson & Schmidt 1989, Connors et al. 2000, Barendregt et al. 2006), thus the biomass produced by plants in TFW support *in situ* and adjacent aquatic and terrestrial foodwebs (Odum et al. 1984). In addition to supporting local ecosystems, plant biomass produced in TFW also supports more distant ecosystems by providing important resting and feeding sites for migratory birds (Odum et al. 1984, Meanley 1996) and for providing rearing and breeding habitat for migratory fish (Odum et al. 1984, Barendregt et al. 2006).

With the exception of long-lived belowground biomass that turns over slowly, most of the net annual production of herb-dominated TFW enters the estuarine detritus food web. Neubauer et al. (2000), for example, estimated that almost 54% of the net annual production of a TFW in Virginia entered aquatic ecosystems through the processes of decomposition and leaching. The primary mechanism by which the products of primary production enter the detritus food web is decomposition.

Many macrophytes that dominate TFW have aboveground tissues that decompose rapidly (e.g., Odum & Heywood 1978, Whigham et al. 1989) but tissues of some plants (e.g., of *Typha* spp.) decompose more slowly (Odum et al. 1984, Findlay et al. 1990). The seasonal pattern of litter production and litter decomposition clearly influences patterns of nutrient exchange within TFW, between TFW and adjacent tidal streams (e.g., Simpson et al. 1983a, Bowden et al.

1991, Findlay et al. 2003), as well as the dynamics of microbial communities (e.g., Sinsabaugh & Findlay 1995). TFW species that produce tissues that decompose rapidly mostly influence the movement of nutrients within TFW and adjacent tidal creeks and rivers (Findlay et al. 1990, Sinsabaugh & Findlay 1995, Neubauer & Anderson 2003). Species that produce litter that decomposes more slowly, on the other hand, undoubtedly contribute to the *in situ* burial of litter and ultimate incorporation of organic and nutrients matter into the substrate of TFW (Findlay et al. 1990, Bowden et al. 1991, Morse et al. 2004).

The pattern that has emerged from the few studies of nutrient and carbon exchange that have been conducted in TFW suggest that they are mostly transformed nutrients and that the net exchanges between TFW and tidal rivers are typically small in magnitude (Simpson et al. 1978, 1983b, Findlay et al. 1998b, Bowden et al. 1991). In fact, sediment delivery from upstream non-tidal systems seems to be the primary mechanism for nutrient input to TFW (Serodes & Troude 1984, Odum 1988, Orson et al. 1990, Morse et al. 2004, Chapter 4).

Tidal freshwater wetlands are ecosystems where sediment deposition is important (references in previous para-



**Figure 4.** *Phragmites australis*, shown in this photograph from a restored TFW on the Anacostia River in Washington, DC, is a  $C_3$  species that is expected to thrive in response to increased carbon dioxide. Because a large amount of net annual production is stored in belowground roots and rhizomes, the surface elevation of wetlands dominated by this species may be able to keep pace with rising sea levels. Photo by A. Baldwin.

graph) and the relationship between primary production and sediment deposition may play an important role in determining the fate of TFW in response to sea-level rise, primarily through their ability to track changes in sea-level, an ongoing process that is accelerating (e.g., Morris et al. 2002). Within estuarine systems that are large enough to include saline, brackish and TFW, sea-level rise will likely have the greatest impact on TFW. Plant biodiversity and productivity will decrease in response to increased flooding (Simpson et al. 1983a, Baldwin et al. 2001) and salt stress (Ferren et al. 1981, Perry & Hershner 1999), and eventually existing TFW will be replaced by brackish tidal wetlands and as sea-level rises, TFW will have to migrate upstream in habitats that are now non-tidal rivers. This type of ecosystem-migration will be possible as long as the river valleys are not too narrow (i.e., there is a floodplain upon which TFW can establish) and development (i.e., landfills, docks and wharves associated with urbanization) does not preclude it (see: Chapter 13). As estuarine wetlands migrate in response to sea-level rise, primary production will play an important role in determining how abundant TFW will be in the future. As most

macrophytes in TFW have the  $C_3$  photosynthetic pathway, it is likely that primary production will increase in response to increased levels of atmospheric carbon dioxide that are associated with climate change (Curtis et al. 1989) and related sea-level rise. Higher levels of productivity of  $C_3$  plants will potentially result in increased storage of carbon belowground which, in combination with riverine inputs of sediment, will enable substrates of TFW to accrete vertically and keep pace with sea-level rise (Fig. 4). This prediction is, however, untested and a useful focus of future research on TFW would be the effects of increased carbon dioxide on primary production and substrate characteristics (e.g., changes in surface elevations).

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The references in this volume derive from the international literature (e.g., periodicals) and moreover, due to the review of many less-described aspects, also from local periodicals, books and reports from North America and Europe. To assist the reader we incorporated the town and country of publication, except for the well-known cities New York, Washington, London, Amsterdam, Berlin and Paris. Some countries frequently mentioned are indicated by an abbreviation: USA (United States of America; in the reference the town including the state), UK (United Kingdom), DK (Denmark), GER (Germany), NL (The Netherlands), BEL (Belgium), and FR (France). The sequence of the references is alphabetically for the one- and two author publications; the publications with three and more authors (et al.) are arranged by year of publication, eventually followed by the indication a or b. SI = Special Issue.

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