

The Ecology of Freshwater Tidal Wetlands

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Freshwater tidal wetlands act as buffers between upstream ecosystems and the estuary. They display high macrophyte diversity, distinct zonation patterns, and dynamic seed banks. Primary production and decomposition proceed at high rates. They serve as habitat for fish and wildlife and may act as sinks for nutrients and heavy metals. (Accepted for publication 27 October 1982)

Freshwater tidal wetlands are found in the upper estuaries of most Atlantic Coast river systems where there is sufficient freshwater flow to maintain salinities of less than one percent, but insufficient flow to dampen upstream tidal movement. Odum et al. (1979) conservatively estimate that there are 500,000–1,000,000 ha of freshwater tidal wetlands along the Atlantic and Gulf Coasts, of which 100,000–140,000 ha are in New Jersey. Almost all of the major East Coast cities from Trenton, NJ, to Richmond, VA, are near freshwater tidal wetlands. Consequently, these wetlands are greatly affected by human activities. Our discussion of the structure, function, and value of freshwater tidal wetlands is based on studies of three Delaware River wetlands: the Hamilton Marsh near Trenton, NJ, Woodbury Creek Marsh south of Camden, NJ, and Tinicum Marsh near Philadelphia, PA.

In freshwater tidal wetlands the major system components—producers, consumers, detritus, sediment, and nutrients—are coupled by biological and physical processes that transfer materials and energy (Figure 1). Materials, such as organic matter, nutrients, heavy metals, and sediment, enter freshwater tidal wetlands from sources including the atmosphere, tides, point-source effluents, non-point-source runoff, ground-

water, and consumer immigration. Outputs are via the atmosphere, tides, and consumer emigration. Along the urbanized upper Delaware River estuary, tidal waters provide the most important inputs, although point-source effluent and non-point-source runoff may locally contribute significant quantities of nutrients and heavy metals (Walton and Patrick 1973).

Wetland function is ultimately controlled by climate, but hydrologic parameters such as duration and frequency of inundation, and the velocity and source of the water determine the physical and chemical properties of wetland substrates (Gosselink and Turner 1978). In turn, substrate characteristics dictate specific ecosystem responses, including primary production, species diversity, decomposition, and uptake and release of nutrients.

Most freshwater tidal wetlands may be conveniently divided into four major habitats on the basis of hydrological regimes (Whigham and Simpson 1976): streams and tidally exposed stream banks that may or may not be vegetated, high marsh areas that are inundated twice daily for 0–4 hours by up to 30 cm of water, pond-like areas that are inundated for approximately 9 hours during each tide cycle with up to 100 cm of water, and pond areas that are continuously inundated, but show regular flow reversal coupled with changes in tidal direction. The first two zones are found in virtually all freshwater tidal wetlands, but the latter two zones most often occur in areas that have been diked or otherwise manipulated by man.

Soils of freshwater tidal wetlands are primarily silts and clays of very fine

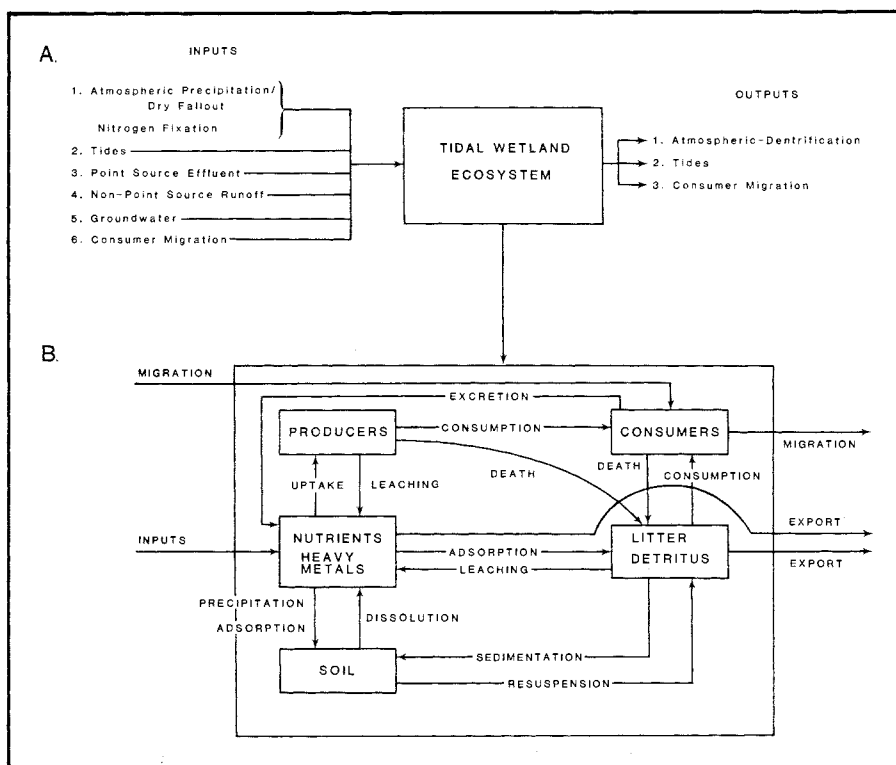


Figure 1. Diagrammatic representation of a tidal wetland ecosystem. **A.** Major inputs and outputs of materials to tidal wetlands. **B.** Major compartments in which nutrients and heavy metals are stored and pathways through which nutrients and heavy metals move. (From Simpson et al. 1981a)

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texture (Odum 1978) and often display a gradient of organic content from 10–15% at the top of actively flooded levees to 30–45% in high marsh areas with minimal tidal activity (Whigham and Simpson 1975). Rates of sediment deposition in high-marsh habitats appear to be low, but considerable erosion and deposition occurs in stream channels and lower, gently sloping stream banks.

PRIMARY PRODUCERS

Freshwater tidal wetlands are dominated by a combination of 12 or more annual and perennial emergent macrophytes that are more characteristic of North American, nontidal, freshwater wetlands than of brackish wetlands (which are usually dominated by one or two perennial grasses). Most species are widespread, but distinct associations do occur (Figure 2). Perennials such as *Nuphar advena* (water lily) and *Pontederia cordata* (pickerelweed) are dominant in stream channels, ponds, and pond-like areas, which may be inundated continuously from 9 to 12 hours during each tidal cycle. A zone of annuals dominated by *Polygonum punctatum* (water smartweed) and *Acnida cannabina* (water hemp) occurs on the stream banks; transition areas between stream banks and the high marsh are often dominated by *Ambrosia trifida* (giant ragweed). On the high marsh, *Bidens laevis* (bur marigold), *Impatiens capensis* (jewelweed), and *Polygonum arifolium* (tearthumb) are important annuals that share dominance with perennials such as *Peltandra virginica* (arrow arum), *Acorus calamus* (sweet flag), *Sagittaria latifolia* (arrowhead), *Typha* sp. (cattail), sedges, and grasses. *Zizania aquatica* var. *aquatica* (wild rice) is important in all habitats and occurs in pure or mixed stands. It is the only annual that may dominate in channels and pond-like habitats.

Although patterns of dominance occur, most species are found in almost all habitats (Whigham and Simpson 1975) because most produce seeds that are widely dispersed. Parker and Leck (1979, personal observation) studied the distribution of seeds and seedlings along a gradient from the stream channel to the high marsh (Figure 2). Fifty percent of the seeds of all the species in the seed bank and 77% of the seedlings occurred throughout the gradient. However, density and survival varied from zone to zone. Reciprocal transplant studies demonstrated that distribution of adult annual species is most likely restricted (Fig-

ure 2) by competitive interactions and the inability to survive prolonged inundation (Parker and Leck 1979). Seedlings of streambank dominants (*Acnida cannabina* and *Polygonum punctatum*) cannot successfully compete with more robust, high-marsh species. Other annual species are restricted to the high marsh as adults (*Impatiens capensis*, *Polygonum arifolium*, and *Bidens laevis*) because their seedlings cannot tolerate prolonged periods of inundation. *Zizania aquatica* occurs throughout the gradient (Whigham and Simpson 1977) because its seedlings can withstand inundation. Germination requirements also may influence the distribution of annuals. For example, *Zizania aquatica* germinates under a wide range of hydrologic conditions (Whigham and Simpson 1977), whereas *Impatiens capensis* requires aerobic conditions for afterripening and germination (Leck 1979).

Less is known about factors that limit distribution of perennial macrophytes. *Typha latifolia* produces many seeds but few seedlings (Leck and Graveline 1979, Leck and Simpson personal observation). The causes are unknown, but shading may prevent germination. *Acorus calamus* rarely produces seeds (Britton and Brown 1970); it persists and colonizes by asexual reproduction. Seeds and seedlings of *Peltandra virginica*

are widely distributed, but the occurrence of adult plants is restricted because seedlings are unable to tolerate long periods of inundation (Whigham et al. 1979). In contrast, seeds of *Pontederia cordata*, although widespread, germinate optimally at high temperatures, and plants become established in the streambank habitat where substrate surface temperatures are suitable (Whigham and Simpson 1982). *Peltandra* and *Typha* (Bonasera et al. 1979, McNaughton 1968) affect distributions by releasing chemicals that inhibit other species.

In the Hamilton Marsh, the seed bank mirrors the surface vegetation (Leck and Graveline 1979). Annuals comprise the bulk of the seed bank, but only about half the species that grow. The role of perennial and woody species in vegetation changes is not known. We do not yet know how to predict the course of vegetation change, even of annuals. For example, the high density of the annual *Ambrosia trifida* in 1982 could not have been predicted by available seed bank data (Leck and Graveline 1979, Parker and Leck personal observation). The perennials survive poorly, which raises questions about how they become established. For example, *Acorus calamus*, a common high marsh perennial, has not been documented in the seed bank, and apparently, only rarely produces fruit.

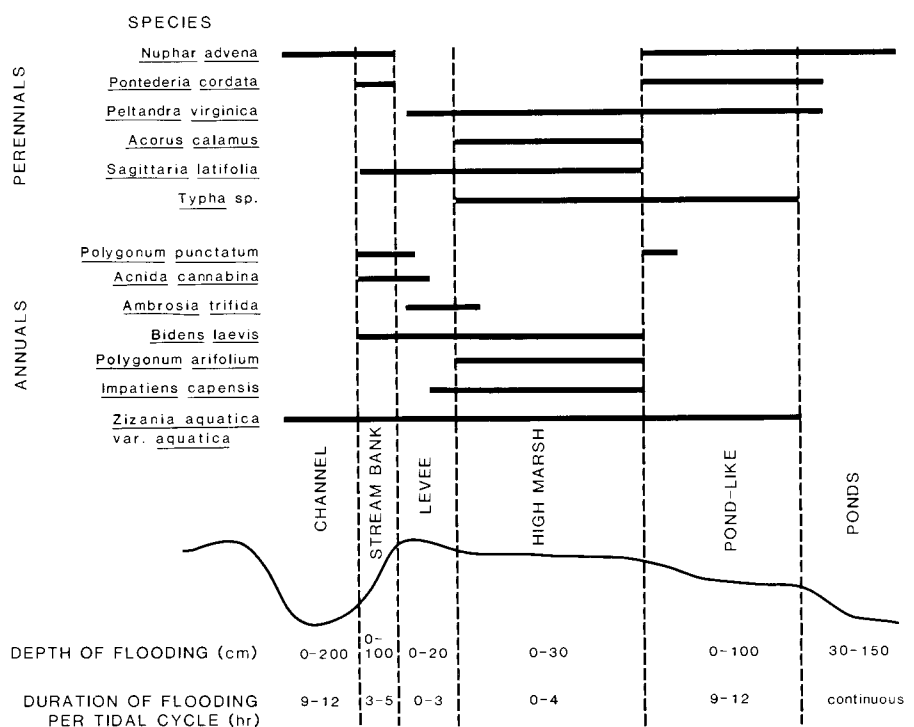


Figure 2. Diagrammatic representation of major habitats in freshwater tidal wetlands. Also depicted are distribution patterns for dominant species and information on duration and depth of flooding. All habitats are subject to tidal flow. (Data from Good and Good 1975, McCormick and Ashbaugh 1972, Parker and Leck 1979, Whigham and Simpson 1975)

Species diversity is great. Species partition both the physical environment and the temporal environment. Partitioning the temporal environment effects a seasonal change in aspect dominance in the high-marsh habitat (Whigham et al. 1978). Two perennials, *Peltandra virginica* and *Acorus calamus* reach peak biomass in early to mid-July and then give way to *Zizania aquatica* and *Impatiens capensis*, which reach peak biomass in early August. They, in turn, yield to *Polygonum arifolium* and *Bidens laevis* in mid-September. Because of these seasonal dominance patterns, production in freshwater tidal wetlands is high compared to most nontidal wetlands.

Reported peak, aboveground, standing-crop values range from 566–2312 $\text{g} \cdot \text{m}^{-2}$ (Whigham et al. 1978). Communities dominated by *Nuphar advena*, *Peltandra virginica*, and other species with little structural tissue typically have standing crop values less than 1000 $\text{g} \cdot \text{m}^{-2}$, whereas *Typha* sp. and *Lythrum salicaria*, with abundant structural material, may exceed 2000 $\text{g} \cdot \text{m}^{-2}$. Typical mixed high-marsh communities usually have intermediate standing crop values.

Belowground, standing-crop estimates range from 500 $\text{g} \cdot \text{m}^{-2}$ to over 7100 $\text{g} \cdot \text{m}^{-2}$ (Whigham et al. 1978), but it is not known whether similar patterns of biomass accrual occur belowground as aboveground for the dominants. Relationships between root standing crop and peak aboveground standing crop for freshwater tidal macrophytes show three basic patterns of belowground biomass allocation (Whigham and Simpson 1978a): perennial with a root–shoot ratio much greater than one (e.g., *Peltandra* root system may exceed 3 m depth, Walker 1981), other perennial rhizomatous species (e.g., *Acorus* and *Sparganium*) with a root–shoot ratio of approximately one, and annuals with root–shoot ratios well below one.

Net primary production in freshwater tidal wetlands of the middle Atlantic coast seems to range from 1000 $\text{g} \cdot \text{m}^{-2}$ to 3500 $\text{g} \cdot \text{m}^{-2}$ and in some wetlands may exceed 4000 $\text{g} \cdot \text{m}^{-2}$ (Odum 1978, Whigham et al. 1978). Algal production in freshwater tidal wetlands appears to contribute less than one percent of the net annual production (Whigham and Simpson 1976), far less than the 30% reported by Gallagher and Daiber (1974) for salt-marsh algae.

Actual net primary production for freshwater tidal wetlands is probably higher than these values suggest because there have been few measurements of

belowground production or leaf turnover (Whigham et al. 1978). Leaf turnover rates in freshwater tidal wetlands are known to be high (Whigham et al. 1978).

CONSUMERS

Most of the vegetation produced in freshwater tidal wetlands enters food chains via detritus pathways (Simpson et al. 1979) although the seeds of some species, such as *Zizania aquatica*, are an important component of the diet of birds (Hawkins and Leck 1977). Dominant invertebrates are largely detrital feeders and include oligochaete worms, amphipods, snails, and insect larva. Other invertebrates, such as copepods and cladocerans, which occur in high densities in tidal marsh creeks (Simpson and Roman personal observation), are important foods for many species of fish.

Fish communities are dominated by three ecologically distinct groups: freshwater, oligohaline, and anadromous species (Odum et al. 1979). Hastings and Good (1977) collected 17 species of fish in Woodbury Creek Marsh. The majority (13) were primarily freshwater, one, the mummichog (*Fundulus heteroclitus*), was typical of marine or brackish habitats, and three, the blueback herring (*Alosa aestivalis*), alewife (*Alosa pseudoharengus*), and American eel (*Anguilla rostrata*), were anadromous. Woodbury Creek and similar areas along the Delaware River appear to be important spawning and nursery areas for both *Alosa aestivalis* and *Alosa pseudoharengus*. Odum et al. (1979) list 18 important food and game fish as commonly using freshwater tidal wetlands of the east coast at some period in their life cycles.

Limited data are available on the birds of freshwater tidal wetlands (Hawkins and Leck 1977, McCormick 1970). In the Hamilton Marsh, 65 species were recorded as summer residents (Hawkins and Leck 1977). Forty-eight species were believed to be nesting in the wetland, with the red-winged blackbird and the long-billed marsh wren being the most common summer breeding residents. Omnivores composed the largest feeding class and accounted for 85% of the total avian biomass. Estimated energy flow through the bird populations ranged from 150 to 496 $\text{Kcal} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$.

Freshwater tidal wetlands support an array of amphibians, reptiles, and mammals (McCormick 1970, Odum et al. 1979), but their roles are poorly understood. The muskrat has caused widespread disturbance of Hudson River wet-

lands by grazing (Kivat 1978). Its extensive network of tunnels and burrows may also influence subsurface drainage patterns.

MATERIAL FLUXES

There is a virtual absence of litter in most freshwater tidal habitats at the beginning of the growing season. Decomposition in freshwater tidal wetlands is rapid, with up to 80% weight loss from high marsh litter in 30 days (Simpson et al. 1978). Although environmental factors such as depth and frequency of flooding may influence decomposition rates, inherent species differences are more important to the decomposition process (Odum and Heywood 1978). *Peltandra virginica*, which has much less structural material than either *Zizania aquatica* or *Bidens laevis*, decomposes much more rapidly (Whigham and Simpson personal observation).

The combination of high rates of production and decomposition determine the limits for cycling processes in freshwater tidal wetlands. However, actual nutrient and particulate fluxes result from the complex interaction of physical, chemical, and biotic processes as in other tidal systems (Nixon 1980).

Simpson et al. (1978) found higher concentrations of ammonia and nitrate nitrogen occurred in flood-tide waters than ebb-tide waters during the summer in the Hamilton Marsh. This condition persisted through the early winter in pond-like habitats, but not in creeks that drain the high marsh. Late spring–early summer input–output studies from small, contained units of wetland showed a net import of ammonia, nitrate, and organic nitrogen from tidal waters (Whigham and Simpson 1978b). Likewise, Tinicum Marsh took up dissolved inorganic nitrogen during the summer growing season (Grant and Patrick 1970). Tidal flux budgets for Woodbury Creek Marsh found nitrogen imported to the wetland early in the growing season (Simpson et al. 1983). Late in the growing season, nitrogen was exported. But following macrophyte dieback, both nitrate and organic nitrogen were again imported to the wetland.

Phosphorus flux appears to be more variable. The pond-like areas of the Hamilton Marsh were net sinks for inorganic phosphate (Simpson et al. 1978). However, tidal cycle flux studies from the small, high-marsh plots showed a net export of both reactive and total phosphorus from the surface during late

spring and early summer (Whigham and Simpson 1978b). In contrast, reactive phosphorus was never lost from Woodbury Creek Marsh and was sometimes imported; total phosphorus was imported in July, September, and November, but otherwise exported (Simpson et al. 1983).

Early in the growing season there is a rapid uptake of nitrogen and phosphorus by the vegetation (Table 1). Since there appears to be little seasonal variation in soil nitrogen and phosphorus concentrations (Simpson et al. 1983, Whigham et al. 1980), it is likely that much of this nitrogen and phosphorus comes from tidal sources. This accounts for the net input of inorganic nitrogen and phosphorus to the wetland during the spring and early summer. Late in the growing season, when the demand for nitrogen by the vegetation is reduced, inorganic nitrogen is exported from the wetland.

After dieback of the vegetation, 80% or more of the nitrogen and phosphorus of standing dead litter may be lost within one to two months (Simpson et al. 1978). However, litter in contact with the wetland surface appears to lose nutrients more slowly (Whigham and Simpson personal observation). Nitrogen concentrations in the litter increase to as much as twice initial values, and phosphorus concentrations first decline, then return to approximately initial concentrations.

Data on heavy metal flux in freshwater tidal wetlands are limited to Woodbury Creek Marsh (Simpson et al. 1983). In general fluxes appear to be quite variable with large differences in the total amount of metal entering and leaving the wetland from tidal cycle to tidal cycle. Cadmium was always exported from the wetland, whereas nickel was imported in all months except June. Copper was imported during the growing season, but zinc

and lead were imported late in the growing season and following macrophyte dieback.

The vegetation plays an important role in the retention of heavy metals during the growing season (Table 1) with the uptake of some metals continuing through the growing season. Indeed, Simpson et al. (1983) have found up to a 3- to 5-fold increase in tissue concentrations of cadmium, copper, lead, nickel, and zinc in September over July following the resurgence of *Nuphar advena* in the Hamilton Marsh late in the growing season. The allocation of heavy metals between plant parts appears to follow the pattern: roots > reproductive structures > leaves > stems (Simpson et al. 1981b).

Standing stocks of heavy metal increased dramatically following dieback of the macrophytes (Table 1) to levels up to five times higher than those found in the September vegetation (Simpson et al. 1981a). Concurrent increases in soil heavy metals were not found, suggesting that the litter, not the soil, plays a dominant role in metal retention following macrophyte dieback. High heavy-metal concentrations may be maintained in the litter for several months (Simpson and Good personal observation). Because decomposition rates in freshwater tidal wetlands are high, the litter appears to serve only as a short-term sink for heavy metals. The question of whether the metals found in the litter are ultimately incorporated in the soil or exported from the wetland is currently being addressed. It appears that the substrate does retain lead coming from non-point-source runoff (Simpson et al. 1983).

MANAGEMENT IMPLICATIONS

Many freshwater tidal wetlands, especially those adjacent to the Delaware,

James, and Potomac Rivers, lie in highly urbanized and industrialized areas. They are subject to a variety of perturbations ranging from nutrient enrichment, coming from sewage treatment facilities and agriculture, to non-point-source runoff of nutrients and heavy metals from roads and parking lots, and accidental chemical and oil spills (Walton and Patrick 1973). Destruction or disturbance of intertidal areas along the Delaware River from dredge spoil, landfill, highway construction, and other activities of man has resulted in the extirpation and range reductions of several plant species (Ferren and Schuyler 1980).

Freshwater tidal wetlands serve as important buffers between man and the estuary. Grant and Patrick (1970) suggested that they act as water purifiers, removing excess nutrients from tidal waters. This idea was extended by Whigham and Simpson (1976) who suggested that freshwater tidal wetlands could be used as natural systems for the tertiary treatment of sewage. Subsequent studies in the Hamilton Marsh (Whigham and Simpson 1978b) showed that freshwater tidal wetlands were of value for the removal of nutrients, especially nitrogen, from domestic wastewaters on a seasonal basis. More recently Simpson et al. (1983) have shown that freshwater tidal wetlands may also play an important role in the removal of heavy metals, especially lead, from non-point-source, urban runoff.

Although evidence suggests that freshwater tidal wetlands act seasonally as nutrient sinks, flux studies of one year or longer are lacking, and the question of whether freshwater tidal wetlands are sinks or sources of material to the estuary cannot now be resolved. Furthermore, the understanding of food chain relationships in freshwater tidal wetlands and the adjacent estuary is rudimentary. At best we can only guess at energy and material transfers between members of the wetland and estuarine communities. Finally, there are few data on the short- and long-term effects of pollutants such as oils, pesticides, and heavy metals on species composition and community structure, although these wetlands serve as nursery grounds for commercially important fish and other wildlife. Despite these gaps in our knowledge of freshwater tidal wetlands, it is clear that, though they share many of the same ecosystem functions of salt marshes (Niering and Warren 1980), they possess a number of unique features that must be considered in their management.

Table 1. Nutrient ($\text{g} \cdot \text{m}^{-2}$) and heavy metal ($\text{mg} \cdot \text{m}^{-2}$) standing stocks in the vegetation (June–September) and litter (November) in Woodbury Creek Marsh for 1979 (from Simpson et al. 1981a). All values $\bar{x} \pm 1$ s.e., $n = 9$.

	June	July	September	November
N	5.99 ± .48	14.37 ± 1.96 [†]	10.81 ± 2.95	9.05 ± 1.50
P	.45 ± .04	.93 ± .15	.63 ± .17	.87 ± .16
Cd	.57 ± .09	.89 ± .17	.66 ± .18	1.93 ± .37 [†]
Cu	3.14 ± .42	7.23 ± .92	6.77 ± 1.71	38.81 ± 9.84 [§]
Pb	4.57 ± .53	12.39 ± 2.88	18.51 ± 5.13 [†]	116.36 ± 21.14 [§]
Ni	1.62 ± .14	4.10 ± .48	7.94 ± .99 [*]	27.52 ± 6.06 [§]
Zn	63.45 ± 18.88	58.31 ± 10.48	59.86 ± 16.15	271.62 ± 56.07 [§]
Biomass ($\text{g} \cdot \text{m}^{-2}$)	198.6 ± 22.1	693.7 ± 87.8	487.7 ± 104.9	711.3 ± 94.8

*Significantly higher ($P = .05$) than June and July

†Significantly higher ($P = .05$) than June

‡Significantly higher ($P = .05$) than September vegetation

§Significantly higher ($P = .01$) than September vegetation

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