

# Evaluating the influence of macrophytes on algal and bacterial production in multiple habitats of a freshwater wetland

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## Abstract

Algal <sup>14</sup>C uptake and bacterial <sup>3</sup>H leucine incorporation were measured over 20 months to assess the influence of macrophytes on the spatial distribution and magnitude of microbial production and the relative importance of algae versus macrophytes to whole-system energy flow in a southeastern U.S. wetland. Algal and bacterial production were determined for water column and plant-, sediment-, and wood-surface microhabitats in four zones defined by aquatic vascular plant composition: no macrophyte, floating leaved (*Nymphaea odorata*), heterophyllous (*Proserpinaca palustris*), or emergent macrophyte (*Juncus effusus*) zones. We combined production data with detailed habitat measurements to estimate production at meter-squared and whole-wetland scales and compared microbial C fixation to concurrently determined rates of macrophyte production. Production on plant surfaces was significantly lower than on wood and benthic sediments in all zones. At a meter-squared scale, 79% of algal production and 74% of bacterial production occurred on sediments, with epiphytes contributing <6% to both algal and bacterial rates. With the exception of phytoplankton in the *Nymphaea* zone and bacteria on *Juncus* zone sediments, production in the water column or on plant or sediment surfaces did not significantly differ among macrophyte zones. Thus, plant type did not affect the spatial distribution of microbial activity except in the *Juncus* marsh, where the limited area and volume of water per square meter reduced production at larger spatial scales. However, the magnitude of bacterial production was influenced by macrophytes, as bacterial carbon demand greatly exceeded the amount supplied by algal production. At the whole-ecosystem scale, macrophytes overwhelmed algal production, which accounted for only 4–10% of total wetland C fixation.

Although significant progress has been made in understanding rates and determinants of algal and bacterial production and the contribution of these assemblages to energy flow in pelagic systems over the past two decades, microbial dynamics in other settings have received far less attention (Vadeboncoeur et al. 2002). This lack of information is particularly acute for wetlands (Goldsborough and Robinson 1996; Kirschner and Velimirov 1999), where studies of energy flow have focused on aquatic macrophytes rather than algae and where, conversely, bacterial populations are often viewed in terms of biogeochemical processes rather than productivity (but see Findlay et al. 1998). Consequently,

substantial gaps exist in our understanding of how rates of algal and bacterial production vary among different habitats, over time, or in comparison to vascular plants in wetland ecosystems.

Aquatic vascular plants are conspicuous, defining features of freshwater wetlands, and the presence and type of macrophytes have profound effects on these systems. With respect to microbial production, Goldsborough and Robinson (1996) and Wetzel and Søndergaard (1998) argued that establishment of macrophyte beds should shift the location of greatest algal and bacterial growth from the water column and benthic sediments to plant surfaces because of the multiple advantages associated with an epiphytic lifestyle. These benefits include direct access to nutrients and labile organic compounds from the plant, avoidance of particle settling and anoxia in the sediments, high insolation, and availability of extensive surface area (Wetzel 2001).

Spatial patterns of microbial production in wetlands may be further modified by the type or growth form of macrophytes present. Architectural differences among species determine the amount of surface area available for microbial colonization and create pronounced spatial variation in light, temperature, water current, and nutrient conditions within and between macrophyte beds (e.g., Wilcock et al. 1999). Moreover, if microbes rely on plant-derived organic matter, then patterns of production are likely to reflect differences

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## Acknowledgments

We are indebted to S. M. Evces for her tireless contributions to all aspects of this study. R. G. Wetzel generously provided supplies, equipment, and a wide range of other support and advice throughout this project, and G. M. Ward provided meteorological and hydrologic data. Thanks to L. S. W. Lindblom for access to her data. Pond surface area and volume estimates and wetland maps were made by Joe Partlow at the Department of Biological Sciences GIS Laboratory. This article has been greatly improved by the comments of S. R. Carpenter, P. J. Mulholland, and two anonymous reviewers. This research was supported by NSF-EPSCoR grant OSR-91-08761.

in timing, magnitude, and quality of organic matter released from different plant taxa. Differences in macrophyte species have been shown to affect the biomass (Cattaneo et al. 1998; Engelhardt and Ritchie 2001) and species composition (Pip and Robinson 1984) of attached algal communities; thus, it is reasonable to assume that plant type should also influence the location and quantity of microbial production occurring within wetlands. Therefore, our primary objective was to test the hypothesis that macrophytes dictate the spatial distribution and magnitude of wetland microbial production.

Algae can account for approximately half of aboveground primary production in newly constructed and experimental wetlands (Cronk and Mitsch 1994; Robinson et al. 1997) as well as salt marshes (e.g., Pinckney and Zingmark 1993), suggesting that they may also make a substantial contribution to primary production in natural freshwater wetlands. The diverse physical structure of these ecosystems—in large part a result of the presence of macrophytes—means that surface area available for microbial growth may be far greater than total water surface area. Unfortunately, there are little empirical data available to assess the significance of algae to net ecosystem production (NEP) (Robinson et al. 1997; Wetzel 2001). Thus, our second objective was to ask the following question: How important are algae versus macrophytes to NEP in a southeastern U.S. wetland?

We measured algal and bacterial production in the water column and on plant, benthic sediment, and wood surfaces in habitats defined by different macrophyte growth forms (i.e., emergent, floating-leaved, and heterophyllous plants or no plants), and assessed the relative contribution of algal, bacterial, and vascular plants to wetland production and carbon cycling. This comprehensive approach was imperative for a robust resolution of the hypothesis of macrophyte influence on microbial production and for establishing an unequivocal understanding of the major contributors to whole-ecosystem energy flow.

### Study site

The Talladega Wetland is located in the north-central region of the Mobile River basin within the Alabama coastal plain region (Fig. 1). The study area consisted of a small, shallow (mean depth ~0.4–0.6 m) pond embedded within a larger wetland complex and contained five distinct macrophyte-defined zones: a marsh area dominated by the emergent reed *Juncus effusus*, a shallow water zone with dense stands of *Proserpinaca palustris*, a slightly deeper area populated by fragrant water lilies (*Nymphaea odorata*), an open-water area in which macrophytes were absent, and a region of mixed macrophytes along the western edge of the pond that was not sampled because of restricted access and frequent dewatering during summer. Floating logs and stumps were present throughout all but the marsh area. Benthic sediments were loosely consolidated and highly organic in all zones. Sampling sites were established along a network of catwalks within the four main wetland zones: the *Nymphaea* (NY), *Proserpinaca* (PR), *Juncus* (JU), and open-water (OW) zones.

Pond stage was continually high during winter (Novem-

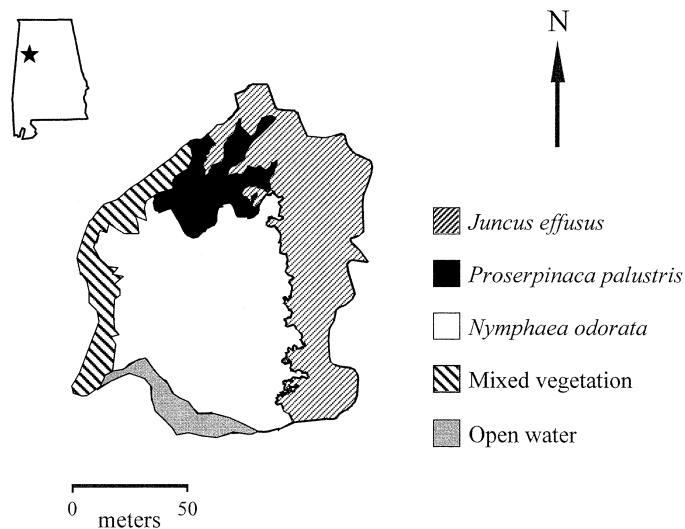


Fig. 1. Map of the major vegetative communities of the Talladega Wetland (32°E55'N, 87°E26'W), Alabama, U.S.A.

ber–March) and variable but was often low during summer (May–September), with pond surface area varying from 5,300 to 9,300 m<sup>2</sup> (Ward 1995). Surface waters of the Talladega Wetland had low alkalinity (0.05–1 meq L<sup>-1</sup>) and were weakly acidic and relatively nutrient-poor (Stanley and Ward 1997). Dissolved organic carbon (DOC) concentrations were typically <4 mg L<sup>-1</sup> during winter and varied between 4 and 14 mg L<sup>-1</sup> during summer months (Mann and Wetzel 1995). Water temperature never fell below 3°C nor exceeded 28°C during the study period.

### Methods

We combined radioisotope incorporation methods with detailed habitat measurements to determine algal and bacterial production at three spatial scales (Table 1) in the Talladega Wetland from March 1993 to October 1994. Production was measured monthly throughout the study. To test our hypothesis (macrophytes dictate the spatial distribution and magnitude of microbial production), we evaluated patterns of algal and bacterial production in three different ways (Table 2). First, macrophyte influence on microbial production may be attributable to a 'hotspot' effect (sensu Thiel-Nielsen and Søndergaard 1999)—i.e., high rates per unit area of microhabitat surface. Thus, we compared microhabitat-specific (carbon uptake per cm<sup>2</sup> of surface) production occurring on wood, plant, and benthic sediment surfaces within the NY zone over the entire 20-month period. This test was supplemented by a comparison between production on sediments versus plant surfaces within the PR and JU zones during the second year of the study (Table 2). Plankton was not included in the microhabitat-scale evaluation because such a comparison would require volumetric rates of plankton production to be converted to areal rates; thus, habitat extent (i.e., water column depth) would affect the results. Second, spatial variation in microbial production as a result of plants may result from differences in the amount of plant surface area. Therefore, we assessed the 'surface-area' effect by

Table 1. Definition, description, and units for algal and bacterial production measurements at each of the three spatial scales considered in this study.

Scale	Description and calculation	Units
Microhabitat-specific	Production within a fixed volume of water (plankton) or on a fixed area of sediment, wood, or plant surface	$\mu\text{g C L}^{-1} \text{d}^{-1}$ (plankton) $\mu\text{g C cm}^{-2} \text{d}^{-1}$ (surfaces)
Area-specific	Microhabitat-specific production weighted by microhabitat extent within $1 \text{ m}^2$ of each zone = [microhabitat-specific production $\times (\text{m}^2 \text{ microhabitat} \times \text{m}^{-2} \text{ zone})$ ]	$\text{mg C m}^{-2} \text{d}^{-1}$
Whole-pond	Whole-pond production; sum of production of all zones = $\left\{ \sum \left[ \sum (\text{area-specific production/zone}) \times \text{zone area} \right] \right\}$	$\text{g C d}^{-1}$

comparing microhabitat-specific rates weighted by microhabitat extent (i.e., area-specific rates) among the NY, PR, and JU zones (Table 2). Finally, macrophytes may have a 'general habitat' effect. For example, light reaching benthic sediments may differ substantially between areas with floating leafed plants versus submersed plants. Thus, we compared microhabitat-scale planktonic production among the four zones over the entire 20-month period and epiphytic and sediment production among the three plant-dominated zones during Year 2 (Table 2). Differences among rates for all comparisons were evaluated using a nonparametric Friedman two-way (repeated-measure) analysis of variance along

with Kendall's coefficient of concordance (W) or a Wilcoxon paired sample test for tests involving only two surfaces.

Whole-pond algal and bacterial production values were estimated by combining area-specific rates for all microhabitats with monthly measures of zone sizes (Table 1) during Year 2. Daily production measurements were multiplied by number of days in the appropriate month to generate monthly values, and monthly values were summed to determine an annual rate for each plant zone (Wetzel and Likens 2000). Since Year 2 measures of surface productivity were made over 8 months (March–October 1994), rates from NY zone microhabitats were applied to other zones for the November 1993–February 1994 period to calculate annual whole-pond production. For benthic algae in the OW zone, NY rates were adjusted based on the assumption that production in the deeper OW zone decreased in proportion to light extinction. Irradiance was measured at 10-cm intervals in the OW zone each month in 1993 using a Li-Cor LI-185B light meter attached to an underwater quantum sensor, and the extinction coefficient was calculated from these vertical profiles. Primary production on OW sediments was calculated as:

algal production of OW sediments

$$= \text{algal production of NY sediments}(e^{-\eta Z}) \quad (1)$$

where  $\eta$  = the month-specific light extinction coefficient and  $Z$  = difference in average water depth between the NY and OW zones for each month. This calculation assumes that the photosynthesis–irradiance relationship for benthic algal communities in both zones is similar. Annual microbial production was then compared to production of *Juncus*, *Proserpinaca*, and *Nymphaea* determined concurrently with this study by Wetzel and Howe (1999), Lindblom (1997), and Carter (1995).

Table 2. Tests to evaluate possible effects of macrophytes on spatial differences in algal and bacterial production in the Talladega Wetland. See Table 1 for definition of spatial scales.

Null hypothesis tested	Spatial scale	Months of data
1. Hot-spot effect:		
1A: sediments = wood = plant surfaces within the NY zone	Microhabitat	20
1B: sediments = plant surfaces with the PR zone	Microhabitat	8
1C: sediments = plant surfaces within the JU zone	Microhabitat	8
2. Surface-area effect:		
2A: sediments = wood = plankton = plant surfaces within the NY zones	Area-specific	20
2B: sediments = plankton = plant surfaces within the PR zone*	Area-specific	8
2C: sediments = plankton = plant surfaces within the JU zone	Area-specific	8
3. General habitat effect:		
3A: OW plankton = NY plankton = PR plankton = JU plankton†	Microhabitat	20
3B: NY sediments = PR sediments = JU sediments	Microhabitat	8
3C: NY plant surfaces = PR plant surfaces = JU plant surfaces	Microhabitat	8

NY, *Nymphaea* zone; PR, *Proserpinaca* zone; JU, *Juncus* zone; OW, open-water zone.

\* Wood surface production was not measured in the PR zone.

† Algal production of plankton in the PR zone was not measured during year 1 and thus was excluded from the analysis.

**Bacterial production**—Bacterial carbon production was determined by  $^3\text{H}$ -leucine incorporation into protein (Kirchman et al. 1985). Assays were conducted under in situ light and temperature conditions in the laboratory for plankton and in the field for surfaces during Year 1; all Year 2 incubations were conducted in the field. For each microhabitat, productivity was assessed using three live samples and three formalin-killed controls. Wood and *Nymphaea* leaf samples were collected using a 0.97-cm<sup>2</sup> cork borer (one core/leaf or log), and measured sections (2–4 cm) were taken from the middle third of *Nymphaea* petioles and submerged *Juncus* culms. *Proserpinaca* leaves were gently removed from plants using forceps. Sediments from the top 1 cm were collected with an open-ended syringe (open end area = 1.61 cm<sup>2</sup>) and a flat piece of plastic to hold in the sample. Samples were placed in glass tubes filled with sterile-filtered (0.2  $\mu\text{m}$ ) surface water and equilibrated for approximately 20 min before adding a mixture of labeled (specific activity =  $5.29\text{--}6.55 \times 10^3$  Gbq mmol<sup>-1</sup>; Amersham) and unlabeled leucine (10 nmol L<sup>-1</sup>  $^3\text{H}$ -leucine + 100 nmol L<sup>-1</sup> unlabeled leucine for plankton [Jørgensen 1992] and 10 nmol L<sup>-1</sup>  $^3\text{H}$ -leucine + 400 nmol L<sup>-1</sup> unlabeled leucine for surfaces [Thomaz and Wetzel 1995]). Following incubation, samples were killed with 0.4 ml formalin, and bacteria were removed from surfaces by sonication. Lindblom (1997) found that this method removed ~85% of all cells on plant surfaces. Sonicated material was collected on a 0.2  $\mu\text{m}$  polycarbonate membrane for protein extraction in hot trichloroacetic acid (TCA) (Kirchman et al. 1985) and radioassayed on a Beckman LS 3801 liquid scintillation counter. Rates of leucine incorporation were converted to bacterial carbon production using conversion factors and equations from Simon and Azam (1989) and Wetzel and Likens (2000). Extrapolation of hourly rates to daily production values was based on the assumption that productivity did not vary over 24 h.

**Algal production**—Primary production was measured by  $^{14}\text{C}$  uptake (Wetzel and Likens 2000). Plankton samples were collected from and suspended in the middle of the water column in each zone. Surface samples were collected in the same fashion used for bacterial measurements, except that we used entire *Nymphaea* leaves rather than small discs and 5–7-cm lengths of *Nymphaea* petioles and *Juncus* culms. All samples were incubated in situ at depths and positions appropriate for each surface. Therefore, our sample design incorporated realistic variation in light intensity experienced by microbial communities attached to different surfaces and in different macrophyte zones. Sediment samples were placed gently on the benthic surface for incubations. Tubes containing *Nymphaea* petioles were sealed with a dark screw cap and suspended at an 80° angle from the sediment surface to mimic natural positioning and leaf shading. *Nymphaea* leaf productivity was measured in 250-ml wide-bottomed, clear plastic jars, which were inverted to permit the *Nymphaea* leaves to float on the water surface inside the container. Tubes containing *Juncus* culms were placed horizontally alongside the stems where samples had been collected. Three replicate light bottles and one dark bottle were collected for each microhabitat type, and each sample was injected with 185 KBq NaH<sup>14</sup>CO<sub>3</sub>, mixed gently, then incu-

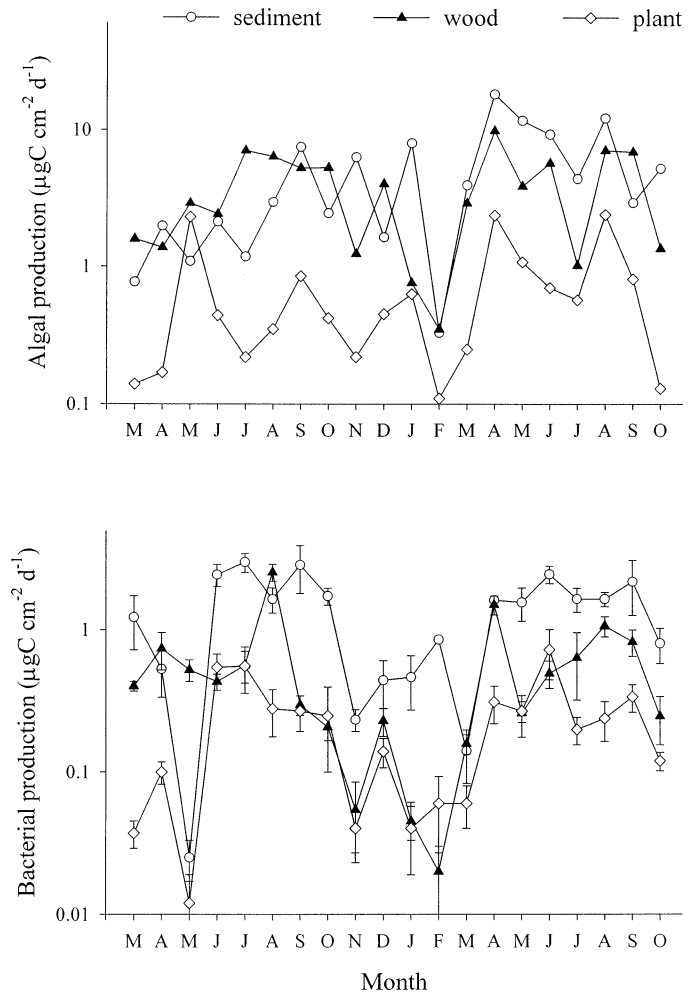


Fig. 2. Microhabitat-scale algal and bacterial production on sediment, wood, and plant surfaces in the NY zone of the Talladega Wetland from March 1993 to October 1994. Values are means ( $\pm 1$  standard error [SE] for bacterial production). Note log scale of the y-axis.

bated for 2–3 h from mid-morning to midday. After incubation, bottles were placed in darkened containers and returned to the laboratory for processing.

Plankton samples were filtered (0.45  $\mu\text{m}$  HA membranes), processed, and radioassayed following Wetzel and Likens (2000). For surface samples, pond water was slowly decanted out of incubation bottles, and any surface material that had detached was collected on a filter. Attached algae were removed by sonication or scraping, and the loosened material was collected on a filter. Filters were radioassayed following methods described in Palumbo et al. (1987), and activity in disintegrations per minute (dpm) was converted to  $\mu\text{g C L}^{-1}$  (plankton) or  $\mu\text{g C cm}^{-2}$  (surfaces) based on net uptake and ratios of C added : dissolved inorganic carbon (DIC) of water calculated from water temperature, pH (Orion model 710A pH/ISE meter), and alkalinity (gran titration). Daily primary production rates were determined by multiplying the value of primary productivity over the incubation period by the ratio of total daily light flux : incubation period

Table 3. Results of Friedman's tests ( $\chi^2$ ) and Kendall's coefficient of concordance (W) for comparisons involving multiple microhabitats within and between different microhabitats and zones. For W, values range between 0 and 1, and W = 1 indicates complete concordance. See Table 2 for statements of tests. See text for statistical results for Wilcoxon paired sample tests of hypotheses 1B and 1C.

Test	Variable	Rank sum	$\chi^2$	W	P
1A, algae	Sediments	50.0	27.1	0.68	<0.001
	Wood	49.0			
	Plant	21.0			
1A, bacteria	Sediments	57.0	25.9	0.65	<0.001
	Wood	38.0			
	Plant	25.0			
2A, algae	Sediments	80.0	44.3	0.74	<0.001
	Wood	53.0			
	Plant	37.0			
	Plankton	30.0			
2A, bacteria	Sediments	79.0	48.7	0.81	<0.001
	Plankton	58.5			
	Plant	33.0			
	Wood	29.5			
2B, algae	Sediment	23.0	9.75	0.61	0.008
	Plant	14.0			
	Plankton	11.0			
2B, bacteria	Sediment	22.0	7.8	0.48	0.02
	Plankton	15.0			
	Plant	11.0			
2C, algae	Sediment	23.0	14.2	0.89	0.001
	Plankton	17.0			
	Plant	8.0			
2C, bacteria	Sediment	22.0	13.0	0.81	0.02
	Plankton	18.0			
	Plant	8.0			
3A, algae	JU*	51.0	22.3	0.56	<0.001
	OW	46.0			
	NY	23.0			
3A, bacteria	Plankton, OW, NY, PR, JU zones		5.9	0.10	NS
3B, algae	Sediments, NY, PR, JU zones		4.7	0.30	NS
3B, bacteria	NY	20.0	7.0	0.44	0.03
	PR	18.0			
	JU	10.0			
3C, algae	Plant surfaces, NY, PR, JU zones		5.2	0.33	NS
3C, bacteria	Plant surfaces, NY, PR, JU zones		0.06	0.004	NS

\* JU, *Juncus* zone; OW, open-water zone; NY, *Nymphaea* zone; PR, *Proserpinaca* zone; NS, not significant.

light flux (i.e., the diurnal expansion factor), as calculated from measures of insolation over the lighted period of each sampling day (described in Wetzel and Likens 2000). This approach assumes a linear relationship between photosynthesis and light. We consider this assumption to be valid because >90% of our flux measurements varied between 20 and 250  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for pond depths of 10–60 cm, which is below the  $I_k$  (photosaturation) values reviewed by Hill (1996) for a variety of lentic and lotic environments. Furthermore, extinction coefficients calculated from monthly light profiles (1.46–6.79) mostly fall within a range indicative of a light environment that is subsaturating for algal photosynthesis (Hill 1996). Light flux was continuously monitored with a Li-Cor LI-185B quantum flux sensor at a central meteorological station at the NY/JU border throughout the study. Water temperature was recorded at 5-min in-

tervals with model 107B temperature probes and Campbell CR-10 dataloggers at the NY (in the water column and at the sediment surface) and OW (mid-water column) zones.

*Habitat quantification*—Surface areas were quantified for all samples not collected with a fixed-size sampler after biofilm removal. Lengths and diameters of all *Nymphaea* petioles and *Juncus* culms were measured with Vernier calipers, and surface area was calculated using the formula for the surface area of a cylinder. Outlines of *Nymphaea* leaves were traced onto a plastic sheet and digitized. Lengths and diameters of all *Proserpinaca* leaflets were measured on dissecting or inverted microscopes, and we assumed a cylindrical leaflet shape for calculating surface areas. Leaflet surface areas were then summed to determine total sample surface area.

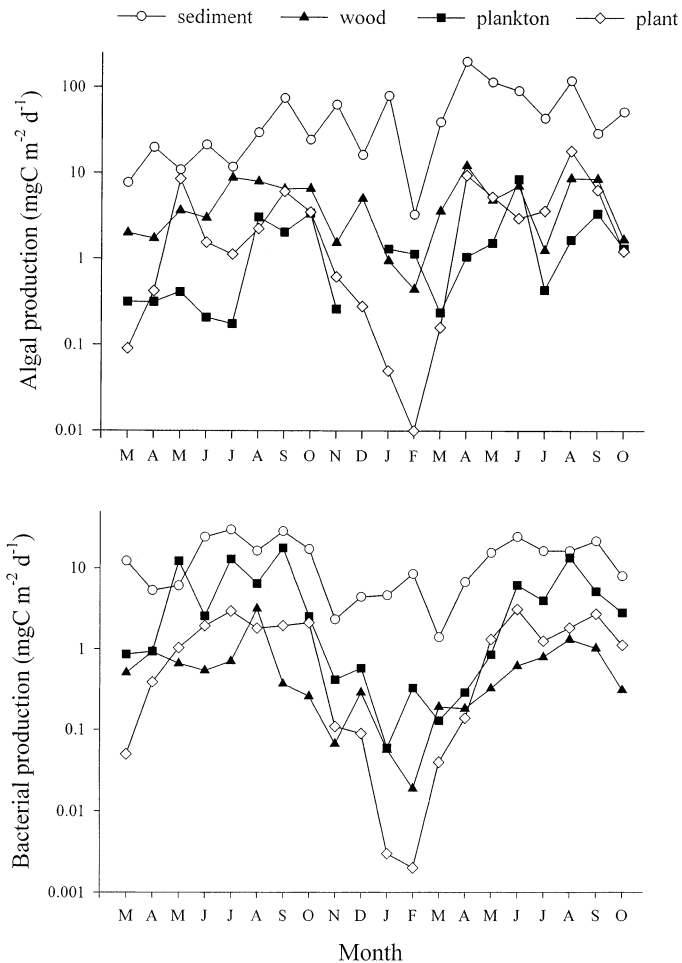


Fig. 3. Area-specific algal and bacterial production in the NY zone from March 1993 to October 1994. Note log scale of the y-axis.

Total wood surface area throughout the wetland, *Nymphaea* density, and *Nymphaea* leaf surface area in the NY zone were measured in 1993 by Pickard and Benke (1996). *Nymphaea* petiole surface area was calculated from monthly measurements of petiole lengths and diameters ( $N = 20-50$ ). Final rates of *Nymphaea* epiphytic production presented herein are surface-area-weighted averages of petiole and leaf rates, as there were no significant differences between leaf and petiole-associated production for either algae or bacteria. *Nymphaea* densities were not measured in 1994, so monthly values from 1993 were used for Year 2 calculations.

The number of submersed *Proserpinaca* leaves per plant and number of plants per square meter were measured weekly over the entire study period (Lindblom 1997). Weekly values were averaged for each month and combined with leaf surface area measurements to calculate square meter of leaf surface area per square meter of the PR zone.

*Juncus* culm surface area was determined by collecting culms from five pools in the JU zone (two samples per pool). A polyvinyl chloride ring (diameter = 15.24 cm) was tossed into the pool, and culms lying within the ring were collected for length and diameter determination. Surface area per culm

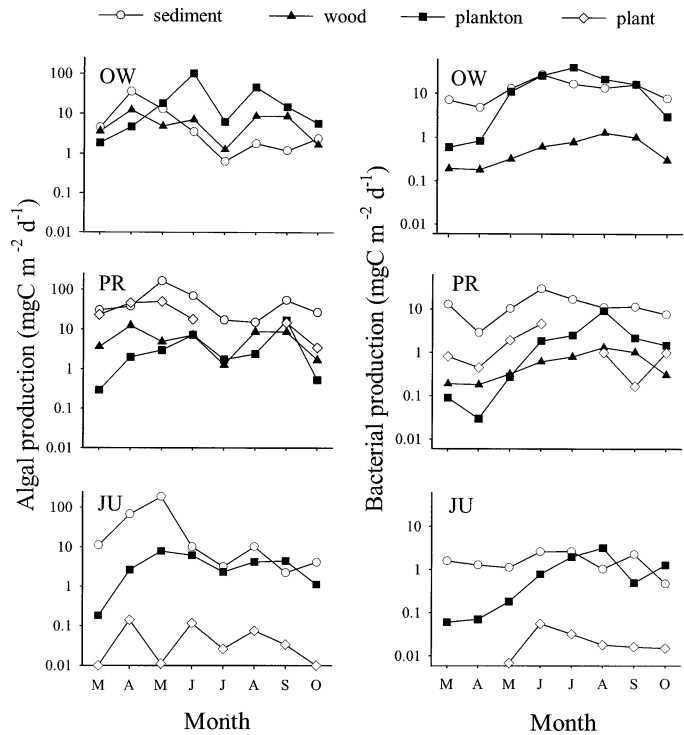


Fig. 4. Area-specific algal and bacterial production in the open water (OW), *Proserpinaca* (PR), and *Juncus* (JU) zones during Year 2. Note log scale of the y-axis.

was calculated using the formula for a cylinder, and surface areas of all culms were summed to estimate plant surface area per square meter of JU pool.

For NY and PR zones, we assumed a 1:1 ratio of surface water to sediment area (i.e., 1 m<sup>2</sup> of sediment surface area for each 1 m<sup>2</sup> of NY or PR zone). However, a correction factor of 0.65, representing water surface per square meter, was used to compensate for the uneven pool/hummock topography of the JU zone (Wetzel and Howe 1999). Surface areas and volumes of all zones were calculated for each sampling date by combining stage data with a digital terrain model based on 1,000 fixed elevation measurements using ARC/INFO® software (Environmental Systems Research Institute). Pond stage height was measured over 5-min intervals at the OW site with a PS9104 pressure transducer (Instrumentation Northwest).

## Results

*Evaluation of hot-spot effects*—Algal production at the microhabitat scale was characterized by pronounced month-to-month variability with little or no seasonality (Fig. 2). Production differed significantly among surfaces, as plant surface rates were consistently lower than for wood and sediments in the NY zone (Fig. 2; Table 3). Bacterial activity also differed among surfaces, with sediment production outstripping rates on both wood and plant surfaces on most dates (Fig. 2; Table 3). Epiphytic production was also significantly lower than sediments for both algae ( $Z = -2.10$ ,  $P < 0.05$ ) and bacteria ( $Z = -2.52$ ,  $P < 0.05$ ) within the

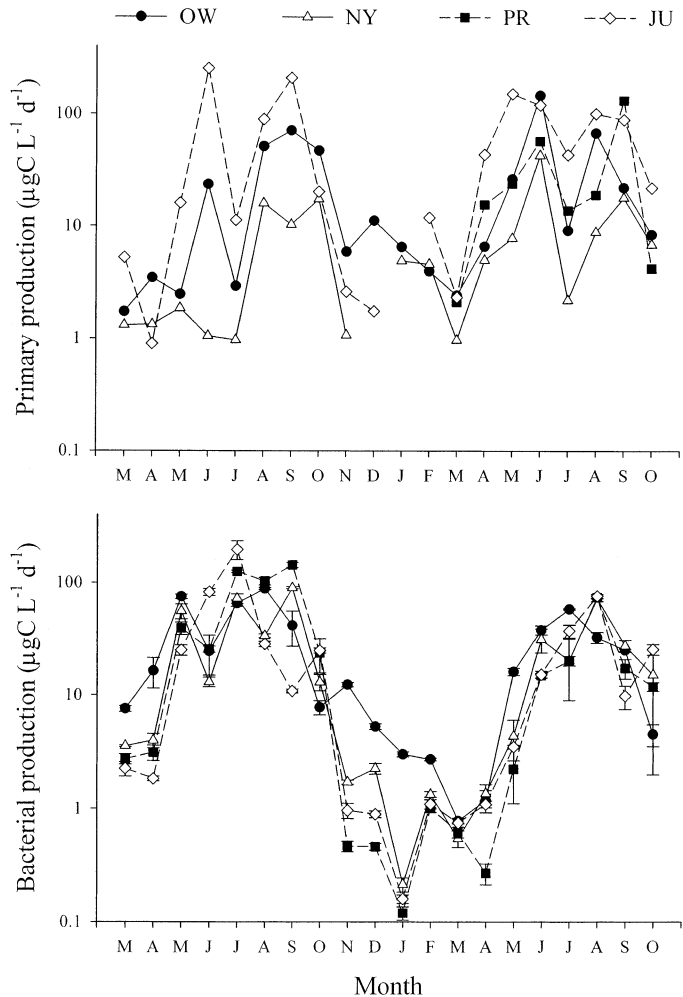


Fig. 5. Phytoplankton and bacterioplankton production in the four macrophyte zones of the Talladega Wetland from March 1993 to October 1994. Values are means ( $\pm 1$  standard error [SE] for bacterial production). OW = open-water zone, NY = *Nymphaea* zone, PR = *Proserpinaca* zone, and JU = *Juncus* zone. Note log scale of the y-axis.

PR zone and for algae in the JU zone ( $Z = -2.52$ ,  $P < 0.05$ ). Differences in bacterial production between plant surfaces and sediments in the JU zone were marginally significant, however ( $Z = -1.82$ ,  $P = 0.07$ ).

**Evaluation of area-specific effects**—Production weighted by microhabitat extent (area-specific rates) for the NY zone reflected patterns apparent at the microhabitat scale. Sediment carbon uptake was significantly higher than on other surfaces or in the water column (Fig. 3; Table 3). Although microhabitat-specific rates of algal production were similar on wood and sediments, the limited extent of wood surfaces minimized rates per square meter for this community. Conversely, extensive leaf surface area was insufficient to override low intrinsic rates of microbial production on plant surfaces at this larger scale. Sediments accounted for an average of 79% of total algal production summed over a square meter, followed by wood (11%), epiphytes (6%), and plankton (4%). For bacteria, carbon uptake associated with benthic

sediments was typically one to two orders of magnitude greater than area-weighted rates for all other microhabitats (Fig. 3; Table 3) and represented an average of 74% of total bacterial production per square meter in the NY zone. Plankton, epiphytes, and wood surfaces represented 17, 5, and 4% of areal production, respectively, over the 20-month period.

Microhabitat-weighted rates of production in the other macrophyte zones repeated the same pattern of sediment domination for both algae and bacteria (Fig. 4). The OW zone represented an apparent exception based on assumptions we made regarding diminished benthic primary production due to light attenuation and because of increased water depth ( $>1.0$  m), which increased the contribution of planktonic production. Total epiphytic algal production in the PR zone equaled or was slightly less than that on sediments during March through May; however, rates were not measurable in mid-summer, when plants became emergent and submersed leaves were rare. Total production per square meter was similar among the three pond zones (OW, NY, and PR zones) but was consistently lower in the JU zone. Lower areal production in this latter zone was attributable in large part to the limited amount of total submersed habitat and shallow depths characteristic of this semiaquatic marsh.

**Evaluation of general habitat effects**—Algal and bacterial planktonic production was significantly correlated with water temperature ( $R = 0.72$ – $0.90$  and  $P < 0.001$  for all zones) and demonstrated distinct seasonal variability throughout the study (Fig. 5). Greatest phytoplankton production per liter occurred in the JU and OW zones, and production was lowest in the NY zone, but bacterioplankton rates showed no significant zone-to-zone differences (Table 3).

Rates of algal and bacterial production on epiphytes did not differ among the NY, JU, or PR zones, nor were there differences in algal production on sediments among these three zones (Fig. 6; Table 3). The only significant difference in microhabitat-specific production among plant zones occurred for bacteria on sediments as a result of low production rates in the JU zone (Fig. 6; Table 3).

**Whole-wetland production**—The final scale of analysis considered microbial activity of the entire pond weighted by the extent of each microhabitat and plant zone. High area-specific rates and large extent made sediments the dominant contributor to whole-pond production during 1994 (Fig. 7), accounting for 85% and 70% of all algal and bacterial production, respectively. Plankton accounted for 22% of bacterial carbon production but less than 5% of algal production. Epiphytes added less than 6% to both algal and bacterial totals.

Microbial activity was dwarfed by annual macrophyte production in the Talladega Wetland (Table 4), as algae accounted for only 4% of wetland NEP. If the marshy, hydrologically variable JU zone was excluded from our calculations, algal contribution to pond primary production increased to 10.5% annually. This difference is due both to the tremendously high production of *Juncus effusus* (Wetzel and Howe 1999) and to the low rates of algal production in the JU zone. Algae in the PR zone made the highest relative

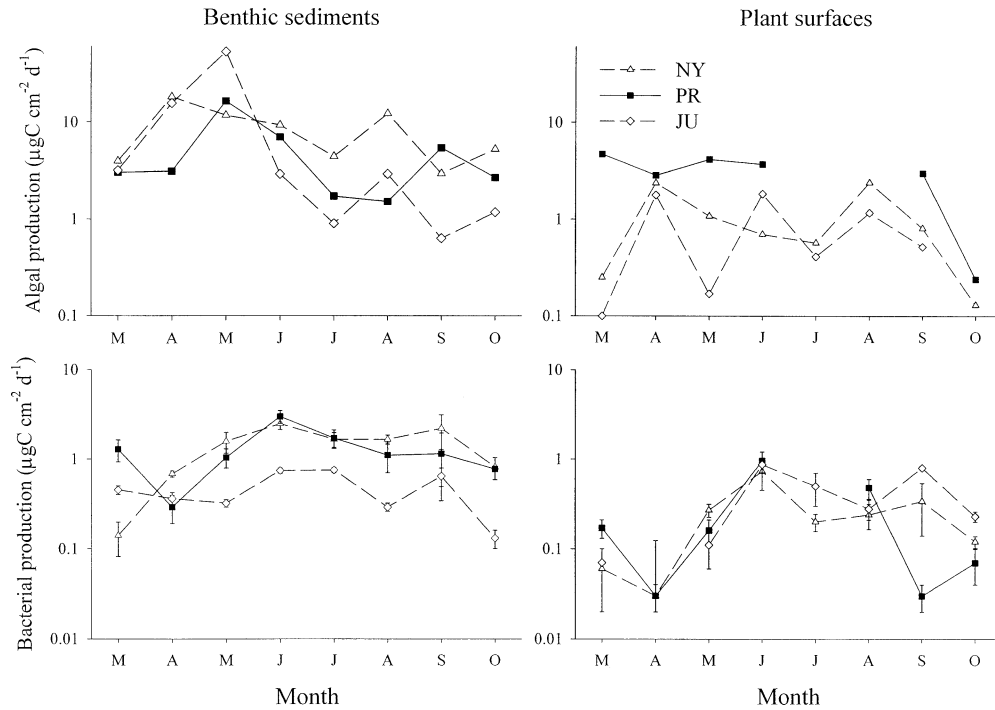


Fig. 6. Comparison of microhabitat-specific rates of production on benthic sediments and on plant surfaces among the NY, PR, and JU zones in the Talladega Wetland during Year 2. Values are means ( $\pm 1$  standard error [SE] for bacterial production).

contribution within its respective zone, representing ca. 15% of NEP.

## Discussion

*Macrophyte influence on algal and bacterial production*—At the microhabitat scale, production was consistently high on benthic sediments and low on plant surfaces, regardless of season or vegetative zone. For bacteria, these results are consistent with one-time and seasonal measures of production of sediment bacteria and epiphytes in a seagrass bed (Moriarty et al. 1985) and a lowland German river (Fischer and Pusch 2001), respectively. However, algal production on benthic sediments has been reported to be both higher (Robinson et al. 1997, this study) and lower (Hart and Lovvorn 2000) than on plant surfaces in other systems, indicating a lack of consensus regarding the spatial distribution of hot-spot activity for algae in wetlands. Nonetheless, our first test of macrophyte influence on microbial activity—that plant surfaces are hotspots of microbial production—must be rejected for both algae and bacteria in the Talladega Wetland. Indeed, if plants had any effect on production at this scale, it was a negative one. These patterns of epiphytic production indicate either a cost associated with growth on plant surfaces or strong advantages associated with benthic sediments. Allelopathy has been suggested as a possible cause of low bacterial and algal production on plant surfaces (e.g., Moriarty et al. 1985), but the importance of this mechanism remains to be investigated. Alternatively, the benthic environment is typically nutrient- and organic matter-rich, and in shallow wetland systems, in which sediments are well lit,

these advantages are likely to fuel high algal and bacterial production.

The second test of macrophyte influence considered habitat provision by plants. The epiphytic contribution to total algal and bacterial production per square meter was trivial in the Talladega Wetland because of low microhabitat rates coupled with only moderate surface-area provision by macrophytes. Epiphytic production in excess of planktonic or benthic communities has been associated with systems in which plant surface area exceeds  $10 \text{ m}^2$  per  $\text{m}^2$  of water surface (e.g., Theil-Nielsen and Søndergaard 1999). In contrast, plant surface areas averaged  $1 \text{ m}^2 \times \text{m}^2$  and never exceeded  $4 \text{ m}^2 \times \text{m}^2$  in our study. It would appear that macrophytes must provide substantial amounts of surface area for epiphytes to become an important contributor to microbial production.

The final evaluation of macrophyte influence addressed differences in production for a specific microhabitat among the different plant zones. The only between-zone differences were low rates of phytoplankton production in the NY zone and low benthic bacterial production on JU zone sediments. The cause of low phytoplankton rates in the NY zone was not readily apparent, and in general, planktonic activity appeared to be strongly influenced by seasonal variables such as temperature. Low bacterial production in the JU zone was likely a result of the limnological extremes of the small pools in this part of the wetland. Pools interspersed among *Juncus* hummocks were often hypoxic or anoxic during summer months (Stanley and Ward 1997), which would have inhibited leucine uptake and thus underestimated bacterial production.

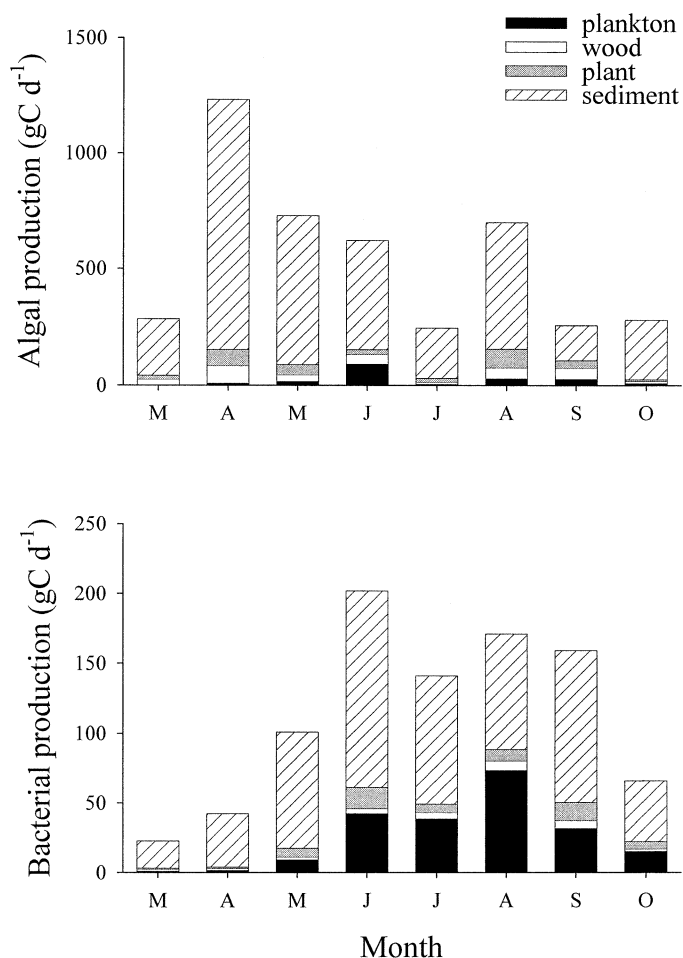


Fig. 7. Whole-wetland algal and bacterial production during Year 2, indicating the contribution of different microhabitats to total carbon uptake.

Although production of specific microhabitats was relatively uniform from zone to zone, total production per square meter revealed an important habitat difference. Specifically, production per square meter in the JU zone was lower than in the main pond zones because of the limited area and volume of water per square meter. The hummock growth form of *Juncus* means that approximately one third of the marsh environment is above the water surface (Wetzel and Howe 1999) and thus does not contribute to area-specific or zone-scale algal and bacterial production. However, other than this effect, we found little evidence that general habitat conditions associated with different macrophytes influenced rates of microbial production.

The lack of consistent differences in production among macrophyte zones does not equate to a complete absence of vascular plant influence on microbial activity. Bacterial growth efficiencies in the Talladega Wetland vary from 17% to 28% for bacteria supplied with DOC either leached from *Juncus* culms (Mann and Wetzel 1996) or from surface water (Mann and Wetzel 1995). These efficiencies translate to an average summer bacterial carbon demand of 576–948  $\mu\text{g C L}^{-1} \text{d}^{-1}$  (112–184  $\text{mg C m}^{-2} \text{d}^{-1}$ ) for the NY zone. If 20% of algal production is available to bacteria (Cole et al. 1988;

Findlay et al. 1992), then algae can only supply an average of 8–14% of daily bacterial C demand during summer months. An additional 505–877  $\mu\text{g C L}^{-1} \text{d}^{-1}$  would be required to support observed rates of bacterial production. These values are similar to estimates by Findlay et al. (1992), who calculated a bacterial C demand of 140–318  $\mu\text{g C L}^{-1} \text{d}^{-1}$  beyond algal C supply for a riverine wetland. If only 10% of *Nymphaea* production is also available to bacteria in the NY zone, then approximately 46–76% of bacterial demand would be met, and summertime bacterial C uptake could be met if an average of 14–24% of plant production were available. We suspect that bacterial C demand in excess of algal production and reliance on macrophyte carbon sources are widespread among wetlands (e.g., see also Findlay et al. 1992; Kirschner and Velimirov 1999). So although the type of macrophyte and the surface area provided by macrophytes had little influence on microbial production, plants played a key role in supplying, and perhaps limiting, bacterial C uptake.

*Contribution of microbial production to NEP*—Very few studies have measured both algal and macrophyte production among the range of habitats present in most aquatic ecosystems at the same time, so the relative importance of these two groups to whole-system carbon fixation, and controls on the balance between algal and macrophyte production, are not well established (Wetzel 2001). Estimates for wetlands are particularly scarce, and those that exist have important limitations in terms of the scope and/or resolution of productivity measurements. With these cautions in mind, algae accounted for 38% of NEP in a dystrophic Carolina Bay wetland (Schalles and Shure 1989) and for 17–57% in a newly constructed wetland (Cronk and Mitsch 1994). Similarly, Robinson et al. (1997) reported that rates of algal production in experimental wetland cells were equal in magnitude to plant production in the adjacent unmanipulated marsh. In contrast, we estimated that algae accounted for only 4% of NEP. Even if we limited our consideration to the non-marsh pond area, algal production still only made a minor contribution (10%), despite the fact that macrophyte production in this part of the wetland was not remarkably high.

In conclusion, we found little evidence that growth on, or availability of, plant surfaces appreciably enhances microbial production in the Talladega Wetland. With the exception of the marsh zone, where the hummock topography reduced total production by reducing habitat extent, differences in plant type did not create variation in algal or bacterial production among macrophyte zones. That is, plants did not appear to affect the spatial distribution of microbial activity at any spatial scale. Macrophyte presence had little detectable influence on the magnitude of algal production, but it did bolster bacterial production. However, plant growth and bacterial production were spatially uncoupled; macrophyte-derived organic matter fueled bacterial production in the sediments, and to a lesser degree in the water column throughout the wetland, but did not enhance epiphytic production. Thus, macrophytes had a diffuse rather than spatially explicit effect on bacterial growth. Finally, although plants did not influence the location in which the greatest algal and bacterial production occurred, they reduced the significance of

Table 4. Estimated annual macrophyte, algal, and bacterial production in the Talladega Wetland. Area-specific rates at the scale of the whole wetland are zone-weighted averages. Pond-only values include those associated with open-water (OW), *Nymphaea* (NY), and *Proserpinaca* (PR) zones (i.e., *Juncus* [JU] zone rates are excluded).

		Area-specific (g C m <sup>-2</sup> y <sup>-1</sup> )	Whole-pond (kg C y <sup>-1</sup> )
Within-zone production			
NY zone	<i>Nymphaea odorata</i>	262*	
	Algae	30	
OW zone	Algae	12	
JU zone	<i>Juncus effusus</i>	2,086†	
	Algae	15	
PR zone	<i>Proserpinaca palustris</i>	142‡	
	Algae	25	
Whole-wetland primary production			
Macrophytes—all zones		523	3,668
Macrophyte—pond only		232	1,373
Algae—all zones		30	168
Algae—pond only		31	166
Whole-wetland bacterial production			
Whole wetland		6	33
Pond only		6	32

\* Carter (1995).

† Wetzel and Howe (1999).

‡ Lindblom (1997).

this production by exceeding microbial growth by an order of magnitude in the Talladega Wetland. The extremely small contribution of algae to NEP stands in strong contrast to prior studies (Schalles and Shure 1989; Cronk and Mitsch 1994) and conceptual models (Goldsborough and Robinson 1996) of wetland production. These disparate results indicate that our general understanding of determinants of rates and relative contributions of algal production to net ecosystem production in wetlands is in need of further refinement and development.

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Received: 2 April 2002

Accepted: 15 January 2003

Amended: 19 January 2003