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# Contributions of Three Subsystems of a Freshwater Marsh to Total Bacterial Secondary Productivity

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**Abstract.** Rates of bacterial production were measured in the water column, on the surface of plant detritus, and in the surface sediments of a freshwater marsh in the Okefenokee Swamp, Georgia, USA. Bacterioplankton production rates were not correlated with several measures of quantity and quality of dissolved organic matter, including an index of the relative importance of vascular plant derivatives. Bacterioplankton productivity was high (mean: 63 $\mu$g C liter$^{-1}$ day$^{-1}$) compared with rates reported for other aquatic ecosystems. Somewhat paradoxically, bacterial productivity on plant detritus (mean: 13 $\mu$g C g$^{-1}$ day$^{-1}$) and sediments (mean: 15 $\mu$g C g$^{-1}$ day$^{-1}$) was low relative to other locations. On an areal basis, total bacterial productivity in this marsh ecosystem averaged 22 mg C m$^{-2}$ day$^{-1}$, based on sample dates in May 1990 and February 1991. Marsh sediments supported the bulk of the production, accounting for 46% (May) and 88% (February) of the total. The remainder was contributed approximately equally by bacteria in the water column and on accumulated stores of plant detritus.

## Introduction

The contribution of heterotrophic bacterial production to carbon and energy flow in aquatic ecosystems has been widely recognized in recent years. Reported rates of bacterioplankton production range, on an areal basis, from 18 to 576 mg C m$^{-2}$ day$^{-1}$ and average 30% percent of the net primary production [6]. Measured rates of bacterial production in surface sediments range from 3 to 925 mg C m$^{-2}$ day$^{-1}$ [13]. Little is known, however, about the relative importance of these two subsystems (water column vs sediment) within particular environments in supporting total growth of bacteria; what evidence is available suggests roles that vary significantly from one ecosystem to another [6, 7].

While most attempts to quantify bacterial production in aquatic environments have focused on water column or sediment habitats, accumulated detrital material constitutes a third subsystem, which has the potential to be an important source of

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bacterial biomass. Where shallow water permits the growth of rooted plants, significant amounts of particulate detritus derived from senescing plant tissue can accumulate. Thus, for example, in wetlands and lentic zones of lake ecosystems, detritus-attached bacteria may contribute a significant, and perhaps even dominant, fraction of the total bacterial secondary production. Yet only a few measurements of bacterial growth rates on aquatic plant detritus (ranging widely from 10 to 4,500 μg C g plant material$^{-1}$ day$^{-1}$) have been reported [8, 14, 16, 22]. The system level importance of this process has generally not been considered.

In the Mizell Prairie marsh in the Okefenokee Swamp (Georgia, USA; 30° 45′ N, 82° 15′ W), all three aquatic subsystems (planktonic, sediment, and detrital surface) are well represented and support active microbial populations. A sedge (*Carex walteriana*) and a *Sphagnum* moss annually produce about 900 g above ground plant material per square meter, much of which accumulates on the marsh surface in a 1:4 ratio of live to dead biomass [10]. Undegraded plant material and other types of particulate organic matter (POM) are gradually incorporated into the accumulating sediments, resulting in a deep layer of highly organic peat. The standing water in the marsh has extremely high concentrations of dissolved organic carbon (DOC), averaging 40 mg C liter$^{-1}$. Sources of DOC include exudates, leachates, and degradation intermediates from marsh plants (*C. walteriana, Sphagnum* sp., and algae), and much of the DOC (about 80%) is humic in nature [18]. Rates of bacterial production in the marsh water column have been measured previously by Murray and Hodson [20] and found to average 64 μg C liter$^{-1}$ day$^{-1}$. Rates of bacterial production at the expense of particulate plant detritus and in surface sediments have not previously been measured.

We report here a 10-month study of bacterial secondary productivity in the water column, sediment, and detrital subsystems of Mizell Prairie marsh. During the study, large fluctuations in water levels occurred, spanning levels typical of drought conditions as well as those representative of normal water conditions in the marsh. Marsh DOC was characterized with regard to quantity and composition (concentrations of dissolved humic substances and vascular plant derivatives) in order to identify possible correlations with measured rates of bacterial protein production in the water column. The relative contributions of the three subsystems to the total bacterial secondary productivity were estimated based on bacterial production rates for each subsystem and the abundance of each type of substrate within the marsh.

## Methods

### *Sampling Regime*

Litterbags containing *C. walteriana* lignocellulose were placed in the Mizell Prairie marsh on April 4, 1990. The 10 × 10 cm litterbags were constructed of polyethylene screening with 110 μm mesh size. Each bag contained 4 g of ground *Carex* lignocellulose (225–450 μm particle size), prepared by sequential chemical extraction of *Carex* culms with ethanol, ethanol:benzene (1:2 v:v), and water to remove all but the structural polysaccharide (cellulose and hemicellulose) and lignin components of the plant tissue [2]. Litterbags were placed inside plastic test tube baskets (95% open area; 4 bags per basket) and suspended in a deep-water area (>1 m in depth at the start of the study) at the edge the marsh.

Field samplings were conducted in 1990 on May 4, June 6, July 17, September 11, and November 15 and in 1991 on February 19. Water levels in the marsh dropped during the course of the study because of a severe drought, but recovered by early 1991. At each sample date, two 4-liter samples of water were collected from the marsh in acid-washed Nalgene carboys. During low water periods, samples were collected from a deep-water area at the edge of the marsh. Two samples of *Carex* detritus (pieces of dead culms no longer attached to a living plant) and two litterbags containing *Carex* lignocellulose were randomly collected from the marsh surface and placed in sterile plastic bags. The culm pieces represented natural *Carex* detritus of unknown age, whereas the lignocellulose represented a major chemical component of *Carex* to be collected at known intervals after initiation of decomposition. The flocculent surface of the marsh peat was also sampled in duplicate, by drawing sediment into 35 $cm^3$ cut-off plastic syringes. Water samples could not be collected at the November 15 sampling due to extremely low water levels. The drought conditions also resulted in intermittent exposure of the litterbags to air between July and December 1990.

Samples were returned to an on-site laboratory within 30 min of collection. From each water sample, 10 ml were removed and placed in a plastic scintillation vial containing 0.6 ml formalin for later determination of bacterial numbers, and 20 ml were removed for determination of bacterial production. Two liters of the remaining water were filtered sequentially through Gelman AE and Whatman GF/F glass fiber filters using a large-diameter (293 mm) Plexiglas filtration unit; water was acidified to pH 2 using 6 N HCl and stored refrigerated until later DOC characterizations.

## *Bacterial Protein Production Measurements*

For determination of water column bacterial productivity by $^3$H-leucine incorporation [15], a 20 ml subsample from each of the water samples was divided into four glass scintillation vials (5 ml each). One vial of each set of four was established as a killed control by the addition of 250 μl 5 N NaOH and 500 μl 100% trichloroacetic acid (TCA). $^3$H-Leucine was added to both live and killed control vials to a final concentration of 10 nM, and incubation allowed to proceed for 1 hour. Live vials then received 250 μl 5 N NaOH (to lyse bacterial cells) (26), and contents were mixed and incubated at 25°C for 15 min. A 500 μl aliquot of 100% TCA was added, and vial contents were mixed and incubated for 30 min in a 95°C water bath. All vials were then cooled in ice water for 10 minutes and the contents filtered through 0.22 μm pore-size Millipore filters (type GS), rinsing three times with 1-ml washes of 5% TCA and once with 1 ml cold 80% ethanol. Filters, containing precipitated bacterial protein, were placed in scintillation vials with 1 ml ethyl acetate. After the filters dissolved, 10 ml scintillation fluid was added and radioactivity quantified using a Beckman LS900 scintillation counter and external standard quench correction.

Leucine incorporation into bacterial protein was corrected for killed controls and converted to rates of carbon production based on an empirical conversion factor determined for Mizell Prairie bacterioplankton. A tenfold diluted culture of marsh water was incubated with gentle stirring at 25°C for 24 hours. At the initiation of the incubation and at five subsequent time points, 30 ml subsamples were withdrawn for simultaneous determination of rates of $^3$H-leucine incorporation (three live incubations, one killed control) and bacterial biomass (see below). A leucine-to-carbon conversion factor was calculated by the integrative method of Riemann et al. [23].

For determination of bacterial productivity on *Carex* detritus, a 4–5 cm long piece of leaf detritus was measured to determine length and width, cut into 4 smaller pieces, and placed in a scintillation vial containing 5 ml of filter-sterilized distilled water. Four vials (three live and one killed control) were set up from each detritus sample. For determination of productivity on *Carex* lignocellulose, lignocellulose particles were removed from the litterbags and packed into a cut-off 3 $cm^3$ syringe. A subsample of 0.25 $cm^3$ was extruded into a scintillation vial containing 5 ml filter-sterilized distilled water. Four vials (three live and one killed control) were set up from each litterbag. Use of distilled water in these incubations eliminated the possibility of bacterial growth occurring at the expense of dissolved organic matter; no effect on rates was found during the 1-hour incubation if the distilled water was amended with inorganic nutrients (5–25 μM $NO_3$, 1–5 μM $PO_4$). For determination of productivity on surface sediment, 5-ml of the sediment/water mixture were removed from the 35 $cm^3$ syringe into a glass scintillation vial; four vials (three live and one killed control) were set up from each sediment sample.

It was necessary to modify the standard $^3$H-leucine incorporation protocol for measurement of bacterial productivity on plant detritus and in surface sediment. Following precipitation of proteins, the filter was placed in a vial with 3 ml of 3% sodium dodecyl sulfate (SDS) and incubated at 80°C. This additional step was included to separate protein (soluble in 3% SDS) from the insoluble plant material or sediment matrix that might interfere with counting through quench and/or adsorption of unincorporated label. After 30 min, vials were cooled in ice water for 10 minutes and contents were filtered through a second Millipore filter. The filtrate was collected in graduated test tubes, total volume was recorded, and a 1-ml subsample was quantified for radioactivity. Final leucine concentration used for plant detritus and sediment incubations was 35 nM rather than 10 nM, as preliminary experiments showed that uptake kinetics were not saturated below 30 nM for bacteria attached to plant detritus.

Additional samples of detritus, lignocellulose, and sediment (three replicates of each) were collected, washed, and dried at 55°C for calculation of volume-to-weight or area-to-weight conversions. Samples were combusted at 500°C for determination of ash content, and all production values were calculated on an ash-free dry weight basis. Ash content ranged from 3–15% for *Carex* detritus, 1–9% for *Carex* lignocellulose, and 12–18% for sediment.

## *Microscopy*

Bacterial numbers in duplicate water samples were determined by filtering bacteria onto pre-blackened Nuclepore filters, staining cells with 0.01% acridine orange, and counting cells via epifluorescence microscopy [12]. Ten microscope fields were counted per slide. Bacterial volumes (for the leucine conversion factor) were determined by image analysis of acridine orange-stained cells using fluorescent latex beads of 1.7 μm diameter for calibration. Average cell volume was calculated based on at least 200 cells for each time point. Individual cell lengths and widths were estimated from area and perimeter measurements [9] and converted to volumes by two formulae, one assuming prolate spheroid cell shape and one assuming capped cylinder shape [16]. We averaged values obtained with these two formulae as a best approximation of the shape of the natural bacterial. Volumes were converted to bacterial carbon assuming $2.2 \times 10^{-13}$ g C $\mu m^{-3}$ [5].

## *DOC Characterization*

Aquatic humic substances are hydrophobic organic acids operationally defined as those compounds that adhere to an Amberlite XAD-8 resin at pH 2 [1]. To quantify humic substances, duplicate acidified water samples were pumped at a rate of 50 ml $min^{-1}$ through a 2.2 × 40 cm column of XAD-8 resin. Subsamples of water were collected in combusted 3-dram vials before and after passage through the column for determinations of total DOC and carbon budgets. Humic substances were eluted from the column in 200 ml of 0.1 N NaOH and deionized by passage through a BioRad AGMP-50 resin. The humic eluant was rotoevaporated and then freeze-dried. Recovered humics were weighed and their carbon content determined on a Perkin-Elmer 240C CHN analyzer.

Samples for DOC analysis were stored frozen until analysis by direct high-temperature combustion (Shimadzu TC500). Samples were sparged with nitrogen for 4 min prior to injection. At least three replicate injections were made for each sample. Carbon budgets showed that 88 ± 3% of the DOC (measured before passage through the XAD-8 resin) was accounted for by the sum of the DOC in column effluent and the recovered humic substances.

Chemically recognizable dissolved lignin-derived material was quantified by oxidation of 30 mg of freeze-dried humic substances with alkaline cupric oxide for 3 hours at 170°C to produce a suite of eight simple lignin phenols (vanillic acid, vanillin, acetovanillon, syringic acid, syringaldehyde, acetosyringone, ferulic acid, and ρ-coumaric acid). Phenols were extracted from the oxidation mixture with ether and converted to trimethylsilyl derivatives. Quantification of lignin phenols was carried out on an HP 5890 gas chromatograph using Supelco SE-30 and J & W DB-1701 columns, with normalization between the two columns based on vanillic acid concentrations [11].

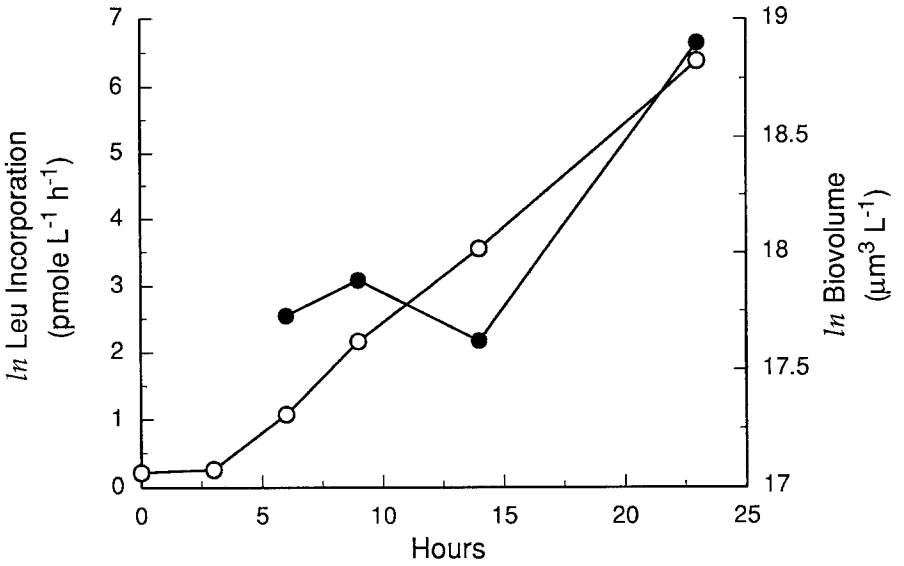


**Fig. 1.** Rates of leucine incorporation (○) and bacterial biovolume (●) in tenfold diluted cultures of Mizell Prairie bacterioplankton.

## Results and Discussion

Based on simultaneous measurements of rates of leucine incorporation and changes in bacterial biovolume in Okefenokee Swamp water (Fig. 1), we calculated a leucine conversion factor of 8.6 ng C pmole$^{-1}$ leucine incorporated. This factor is similar to other carbon-based leucine conversion factors reported for a variety of aquatic ecosystems, including 3.1 ng C pmole$^{-1}$ [24], 3.0 ng C pmole$^{-1}$ [4], and 7.2 ng C pmole$^{-1}$ [19].

Bacterial productivity in the marsh water column, calculated from rates of leucine incorporation and the above conversion factor, varied 25-fold during the course of the study (Fig. 2), from a low in February 1991 of 4 µg C liter$^{-1}$ day$^{-1}$ to a high in May 1990 of 111 µg C liter$^{-1}$ day$^{-1}$ (mean: 63 µg C liter$^{-1}$ day$^{-1}$). Bacterial production rates reported by Murray and Hodson [20] for the Mizell Prairie water column from August 1983 through August 1984 (recalculated using the same volume-to-carbon conversion factor as used in this study) range from 6 to 330 µg C liter$^{-1}$ day$^{-1}$ (mean: 117 µg C liter$^{-1}$ day$^{-1}$). Agreement between the two studies is relatively good, despite the different methods used (Murray and Hodson [20] used $^{3}$H-thymidine incorporation), and suggests similar ranges in rates of bacterioplankton secondary production (within a factor of two) during the different years sampled. Our measured rates of production were not correlated with the number of bacterioplankton present in the water column ($r = 0.50$, $P > 0.05$; Table 1), nor with water temperature at the time of sampling ($r = 0.72$, $P > 0.05$; Table 1).

We calculated growth rates and doubling times for planktonic bacteria from the concentration of bacterial cells in the water and the leucine incorporation rates (converted to change in cell number based on an average measured cell size of 0.08

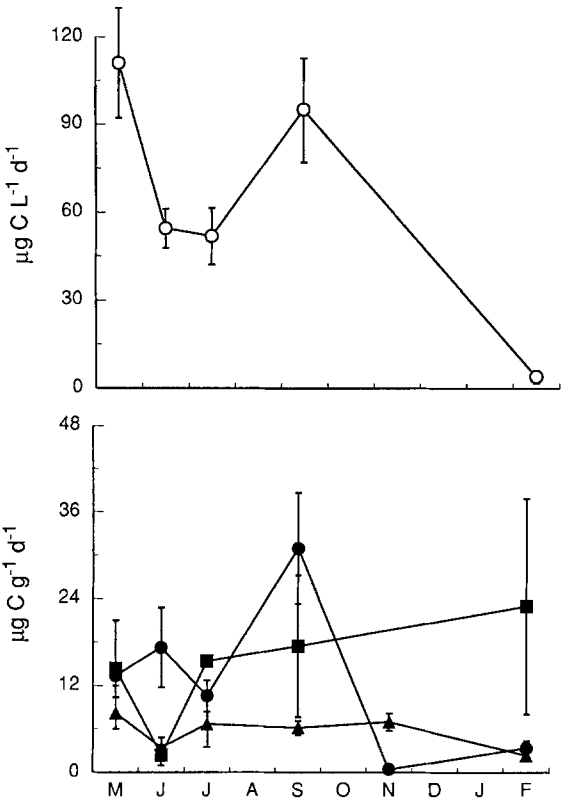


**Fig. 2.** Rates of bacterial secondary production in the water column (○), on *C. walteriana* detritus (●), on *C. walteriana* lignocellulose (▲), and in the surface sediments (■) of the Mizell Prairie marsh in the Okefenokee Swamp. Vertical bars represent the standard error of the mean of two samples (with three replicate determinations per sample).

**Table 1.** Biological and chemical characteristics of Mizell Prairie water (n = 2, ±1 SE)

| Sampling date | Water temperature (°C) | Bacterial production (µg C liter$^{-1}$ day$^{-1}$) | Cell numbers ($10^6$ ml$^{-1}$) | DOC (mg C liter$^{-1}$) | Humic substances (mg C liter$^{-1}$) | Lignin phenols (µg C liter$^{-1}$) |
|---|---|---|---|---|---|---|
| May 1990 | 26 | 111 ± 19 | 4.7 ± 0.2 | 41.3 ± 0.3 | 28.9 ± 1.8 (70.0 ± 3.8)[a] | 118 ± 13 (0.29 ± 0.03)[a] |
| June 1990 | 27 | 54 ± 7 | 4.1 ± 0.2 | 38.9 ± 0.7 | 28.2 ± 2.2 (72.7 ± 7.1) | 83 ± 18 (0.21 ± 0.05) |
| July 1990 | 28 | 52 ± 9 | 6.2 ± 0.1 | 43.6 ± 0.3 | 31.5 ± 1.5 (72.2 ± 4.0) | 75 ± 0 (0.17 ± 0.01) |
| Sept 1990 | 28 | 95 ± 18 | 18.9 ± 1.4 | 27.5 ± 3.6 | 19.1 ± 0.3 (73.9 ± 10.8) | 50 ± 0 (0.18 ± 0.02) |
| Feb 1991 | 15 | 4 ± 2 | 2.8 ± 0.3 | 60.2 ± 1.1 | 28.0 ± 0.5 (46.6 ± 1.4) | 152 ± 9 (0.25 ± 0.02) |

[a] Percent of DOC in parentheses

$\mu m^3$ and assuming $2.2 \times 10^{-13}$ g C $\mu m^{-3}$ [5]). Average specific growth rates of bacteria in the Mizell Prairie water column ranged from 0.003 to 0.055 $hour^{-1}$ during the course of the study. The average doubling time for bacterial biomass was 3 days (range: 0.5 to 9.6 days). Specific growth rates as high as 0.16 $hour^{-1}$ were measured in Mizell Prairie water during the leucine conversion factor experiment, based on changes in bacterioplankton biovolume (Fig. 1); this rate is threefold greater than the highest in situ growth rate we measured.

Various chemical parameters of the water were measured in order to characterize the dissolved organic matter available to marsh bacterioplankton. Total DOC concentrations in the marsh averaged 42 mg C $liter^{-1}$, with relatively high (twofold) variation among the five dates on which water was sampled (Table 1). Humic substances were found to make up a significant fraction (from 47 to 74%) of the total DOC (Table 1). In the Okefenokee Swamp, humics are thought to have a strong vascular plant component [25], and previously have been found to support bacterioplankton growth, although they are less biologically available than nonhumic compounds by a factor of four [18]. Concentrations of characteristic dissolved lignin phenols were measured in order to provide a relative index of vascular plant influence; *Carex* and other vascular plants produce a lignin phenol signal in the DOM, while nonvascular plants present in the marsh, such as planktonic and epiphytic algae and *Sphagnum* moss, do not. Concentrations of dissolved lignin phenols varied threefold during the study, although the percent contribution to the total DOC pool varied less than twofold (Table 1).

We looked for possible correlations between these three measures of DOC quantity or composition and measured rates of bacterioplankton production. There was no statistically significant relationship between total DOC concentration and rates of bacterial production ($r = 0.79$, $P > 0.05$), or between humic carbon concentrations and rates of production, considering either absolute concentrations of humics ($r = 0.35$, $P > 0.05$) or concentrations expressed as a percent of total DOC ($r = 0.76$, $P > 0.05$). Likewise, lignin phenol concentrations were not correlated with rates of bacterial production ($r = 0.51$, $P > 0.05$), despite the probability that the relative importance of refractory, high C:N ratio vascular plant sources, as indicated by lignin phenol concentrations, would negatively affect DOC quality. Rates of bacterial growth in the water column of the marsh are apparently controlled by factors other than, or more complex than, concentrations of bulk DOC or the humic and vascular plant-derived components of DOC. Inhibitory compounds leaching from plant material (e.g., plant tannins), particularly during times of extreme water fluctuation in the Okefenokee Swamp, may have an important influence on bacterial activity [21].

On *Carex* detritus, rates of bacterial production ranged from a low of 0.5 $\mu$g C $g^{-1}$ $day^{-1}$ in November 1990 to a high of 31 $\mu$g C $g^{-1}$ $day^{-1}$ in September 1990 (mean: 13 $\mu$g C $g^{-1}$ $day^{-1}$) (Fig. 2). Rates of production on *Carex* lignocellulose particles, which had been chemically extracted prior to incubation to remove the nonstructural fraction of the plant material, were generally lower than those measured on natural plant detritus, ranging from 2 to 8 $\mu$g C $g^{-1}$ $day^{-1}$ (mean: 6 $\mu$g C $g^{-1}$ $day^{-1}$) (Fig. 2). Bacterial production at the expense of lignocellulose generally decreased during the course of the study, with rates at the last sample point averaging only 30% of initial rates, although a regression of production vs time was not statistically significant ($r^2 = 0.19$, $P > 0.05$). Previously, specific rates of

mineralization of radiolabeled *C. walteriana* lignocellulose were shown to decrease during decomposition [3].

Surface sediment bacterial productivity was comparable to productivity on plant detritus and generally greater than that measured on lignocellulose. Rates of production on surface sediment ranged from 0.4 to 3.5 mg C $m^{-2}$ $day^{-1}$ (to a 1 cm depth) or 2.4 to 23 μg C $g^{-1}$ $day^{-1}$ (mean: 15 μg C $g^{-1}$ $day^{-1}$) (Fig. 1).

Certain features of the Okefenokee Swamp ecosystem, such as the low pH and the accumulation of peat, suggest an unusual, possibly adverse, environment for microbial growth relative to other marsh ecosystems. However, our measured rates of bacterial production in the water column, like those reported by Murray and Hodson [20], instead indicate a highly active bacterioplankton population. The average production rate (63 μg C $liter^{-1}$ $day^{-1}$) was more than twice the average value reported by Cole et al. [6] based on a survey of over 50 aquatic systems (26 μg C $liter^{-1}$ $day^{-1}$). By contrast, however, bacteria attached to plant detritus exhibited relatively depressed productivity. Bacterial production rates on *Carex* detritus and lignocellulose were not only lower than those measured previously on fresh plant detritus (up to 4,500 μg C $g^{-1}$ $day^{-1}$ [8]; 1,130 μg C $g^{-1}$ $day^{-1}$ [14]), but also were low relative to rates measured on standing dead grass (*Spartina alterniflora*) leaves (675 μg C g organic $mass^{-1}$ $day^{-1}$ [22]) and on lignocellulose from emergent macrophytes degrading in a freshwater reservoir (10 to 810 μg C $g^{-1}$ $day^{-1}$ [16]). Previously, degradation of plant detritus in Mizell Prairie, as measured by mineralization of $^{14}C$-labeled plant material, was also found to proceed slowly relative to other aquatic ecosystems [3]. A comparison of bacterial growth rates indicates that observed differences in productivity are paralleled by differences in specific growth rates. Growth rates of bacterioplankton measured in this study averaged 0.024 ± 0.009 $hour^{-1}$, while growth rates of detritus-attached bacteria (measured in December 1989 and August 1990; S. Y. Newell, M. A. Moran, R. J. Wicks, R. E. Hodson; in preparation) averaged 0.006 ± 0.0004 $day^{-1}$. Thus, our measured rates of bacterial production are consistent with earlier studies of the Okefenokee Swamp showing an active population of bacterioplankton yet a relatively inactive population of surface-attached bacteria. For sediment bacterial production, the area-based values (per $m^2$) are in the low end of the range found in a variety of other aquatic ecosystems (3–925 mg C $m^2$ $day^{-1}$ [13]), although weight-based values (per g) are comparable with other sites (due to the low density of Okefenokee sediments; 1 ml sediment = 0.09 g).

We calculated areal rates of bacterial production in order to assess the contribution of each subsystem (water column, plant detritus, and surface sediment) to total bacterial productivity in the marsh. The quantity or volume of each substrate type per square meter of marsh (Table 2) was multiplied by the measured rate of bacterial production per unit of substrate (Fig. 2). For purposes of this calculation, we used only the pre- and post-drought samples (May 1990 and February 1991), at which time water levels were within normal range and standing water was present on the marsh. Because bacterial productivity on *Carex* culms is extremely low until stems have senesced and fallen into the water column (M. A. Moran and R. E. Hodson, unpublished data), only fallen, dead plant material was considered to be available substrate.

Calculations show that total bacterial productivity was similar on the two dates, yet the relative contributions of the three subsystems varied considerably (Table 2).

**Table 2.** Contributions of three Mizell Prairie subsystems to total bacterial production

| Date | Substrate abundance | | | Bacterial productivity (mg C $m^{-2}$ $day^{-1}$) | | | |
|---|---|---|---|---|---|---|---|
| | Water[a] (liter $m^{-2}$) | Detritus[b] (g $m^{-2}$) | Sediment[c] (g $m^{-2}$) | Water | Detritus | Sediment | Total |
| May 1990 | 70 | 483 | 750 | 7.8 | 5.0 | 10.8 | 23.6 |
| February 1991 | 250 | 430 | 750 | 1.0 | 1.4 | 17.3 | 19.7 |

[a] Water depth on the marsh was 7 cm (May 1990) and 25 cm (February 1991)

[b] Stocks of accumulated *C. walteriana* detritus were calculated as the mean of measurements of dead, fallen material made in May 1982 and 1985 and February 1983 and 1986 ([10]; H. S. Greening, unpublished data)

[c] Measured production rates were assumed to apply to the top 5 cm of sediment

The water column was an important source of new bacterial biomass in May 1990 (33% of total productivity), but was relatively unimportant in February 1991 (5%); this was the case despite the deeper water during the February sample (25 cm) relative to the May sample (7 cm). Likewise, there was a high overall contribution from the bacteria attached to detrital material in May (21%) compared to February (7%).

Calculated areal rates of production on vascular plant detritus, however, should be considered underestimates of the contribution of vascular plant-derived organic matter to overall bacterial production in the marsh. We have observed that approximately 25% (by weight) of surface sediment is composed of recognizable fragments of *C. walteriana* leaves and much of the amorphous material is likely to be plant-derived, as well. Furthermore, during the degradation of *Carex* lignocellulose by attached bacteria, up to 40% of the plant material is solubilized and released into the water column prior to utilization by bacteria [17]. Thus vascular plant-derived organic matter is the basis for some portion of the bacterial production measured in both the sediment and water column subsystems. However, in spite of this likely underestimate of total vascular plant-derived production, bacteria attached to accumulated plant detritus made a contribution to overall bacterial secondary productivity approximately equal to that of the bacterioplankton. The most important subsystem on both sample dates was the surface sediment, which contributed 46% (May) and 88% (February) of the total bacterial production in this marsh ecosystem.

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