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METABOLIC ACTIVITY OF THE EPIPHYTIC COMMUNITY ASSOCIATED WITH *SPARTINA ALTERNIFLORA*

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ABSTRACT Primary production and respiration rates were determined for two epiphytic communities associated with *Spartina alterniflora* Loisel., in the southwestern Barataria Bay area of Louisiana. The communities studied were: (1) a shoreline community and (2) a community 1.5 meters inland from the shoreline site. Annual mean net production and respiration rates for the shoreline community were 25.8 and $-19.6 \text{ mg C} \cdot (\text{m}^2 \text{ substrate area})^{-1} \cdot \text{h}^{-1}$ respectively; whereas the inland community showed corresponding rates of -3.3 and $-12.5 \text{ mg C} \cdot (\text{m}^2 \text{ substrate area})^{-1} \cdot \text{h}^{-1}$, respectively. Thus, the shoreline community was a net contributor to system production; the inland community was an energy sink. The inland community was elevated 15 to 20 cm above the shoreline community, lacked the conspicuous filamentous algal growth common at the shoreline location, and had a significantly smaller diatom population. The role of epiphytes is speculated to be one of quality rather than quantity production.

INTRODUCTION

Production by epiphytic algae has been found to vary in different environments. Using the ¹⁴C method, Allen (1971) found epiphytic production on submerged substrates to be $600 \text{ g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ and $71 \text{ g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ on emergent substrates. In the spring of the year, Jones (1980) using radioisotope technique observed a rate of $24.8 \text{ mg C} \cdot (\text{m}^2 \text{ substrate area})^{-1} \cdot \text{h}^{-1}$ for epiphytes associated with *Spartina alterniflora* in a Georgia salt marsh. Jones (1968) found the epiphytes on *Thalassia testudinum* König. produced $315 \text{ g C} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, or about 35% of the host-epiphyte complex production. Studies by Sand-Jensen (1977) showed a significant reduction of host productivity as a result of epiphytosis. Penhale (1977) suggested that epiphyte shading could reduce host photosynthesis.

While the community structure of the microalgal population attached to (Stowe 1980, 1982) and beneath (Blum 1968, Sullivan 1978) the *S. alterniflora* canopy have been studied, only the report of Jones (1980) has investigated the productivity of the *S. alterniflora* epiphytic community. Others (Pomeroy 1959, Gallagher and Daiber 1973) have investigated sediment production beneath the grass canopy. This report describes the productivity and respiration of the epiphytic community associated with *S. alterniflora* in a salt marsh of the Barataria estuary, Louisiana.

DESCRIPTION OF THE STUDY AREA

The Barataria estuary is an interdistributary, deltaic basin of the Mississippi River system (Russell 1936, Gagliano and van Beek 1970). It is a large ($6,300 \text{ km}^2$), shallow series of bays and lakes flanked by marshes. The water is saline at the coast, grading through brackish to fresh at the upper reaches of the estuary (Day et al. 1973). Tidal cycles are diurnal rather than semidiurnal with a

0.3 m average amplitude (Baumann 1980).

Airplane Lake (N 29°13.25', W 90°06.18') was selected because a number of other ecological parameters were being studied at this site (Day et al. 1973). This marsh lies at a +5 cm relative to local mean water level. A natural levee rises from the shoreline, cresting about 1.5 to 3 m inland with an elevation of 15-20 cm. Maximum average water level of +20 cm occurs in September and a minimum level of -12 cm occurs in January. Baumann's inundation studies (1980) reported 260 marsh floodings per year with a mean duration of 17 hours per flood. The physical environment of the sampling area has been described further by Day et al. (1973) and Stowe (1980, 1982).

MATERIALS AND METHODS

Twelve times between June 1970 and May 1971, *S. alterniflora* culms were collected from the Airplane Lake site. Twenty-four culms were collected immediately along the exposed edge of the marsh and an equal number from the crest of the natural levee 1.5 m inland from the shoreline site. The inland site was elevated about 15 cm above the shoreline site. The culms were severed at the sediment surface, placed in individual plastic bags and returned to the field laboratory under refrigeration.

Macroscopic algal biomass was determined from culm scraping, dried at 80°C for 24 hours, and weighed on an analytical balance. Microscopic algal density (almost all diatoms) was determined by the methods described by Stowe (1982).

Production of the epiphytic community was measured by a modification of the light-dark bottle method (Howard and Menzies 1969). Two bottom 10-cm lengths of the collected culms were placed in each of 24 BOD bottles. Water used for incubation was collected from Airplane Lake in a 20-liter carboy and allowed to settle for at least 2 weeks. The BOD bottles were filled by syphoning from

the middle of the carboy, allowing each bottle to overflow, replacing the volume in the BOD bottles approximately three times. Two uninoculated control bottles were also filled in the manner previously described.

The bottom 10 cm of the culms were used because structural studies indicated that 70% of the diatoms and practically all of the macroscopic algae were confined to this region (Day et al. 1973 and Stowe 1982). Gosselink et al. (1977) observed no net CO₂ uptake by the bases of epiphyte-free, greenhouse-grown *S. alterniflora* and very low respiration rates. Therefore it was assumed that all O₂ changes were the result of epiphytes.

Six shoreline and six inland bottles were incubated in a dark ice chest at ambient temperatures. Six other bottles with shoreline culms were incubated in direct sunlight while submerged in ambient temperature tap water in a large wash tub. Six bottles with inland culms were incubated in the shade of *Distichlis spicata*. Both light regimes approximated the natural conditions of the field. Incubation of these culms began by mid-morning within 1.5 hours of collection and was carried out for 2 hours.

Dissolved oxygen (DO) was determined from control bottles at the beginning of incubation and on the control and test bottles at the end of the 2-hour incubation period. Initially, DO determination was done by a modified Winkler titration method (Strickland and Parsons 1968). Later, DO was determined polarographically with the O₂ sensor membrane fitting approximately one-third of the way down into the bottle. The water, during DO measurement, was stirred moderately with a magnetic stirrer. After determination of DO, the total water volume was measured to the nearest ml.

Net production and respiration were calculated as the difference between initial and final DO in the light and dark bottles, respectively, with control correction. Dissolved oxygen concentration was converted to mg carbon fixed or released by a modification of the method described by Strickland and Parsons (1968).

The average surface area of the culms was calculated by measuring the diameter of the lower portion of the culm and assuming it to be a cylinder 10 cm long. Fifteen culms collected from each site monthly were used in this determination.

RESULTS AND DISCUSSION

Four genera of macroscopic algae dominated the epiphytic community at the shoreline site. The macroscopic algae showed distinct seasonal variations in abundance (Figure 1) (Day et al. 1973). *Polysiphonia* sp. and *Bostrychia* sp. dominated from spring to fall. *Ectocarpus* sp. and *Enteromorpha* sp. dominated during the winter. These algae rarely occurred more than 50 cm inland. They were usually limited to a horizontal band 10 cm wide parallel to the shoreline. *Ectocarpus* sp. and *Enteromorpha* sp. grew on mud flats and other substrates as well as on *S. alterniflora*.

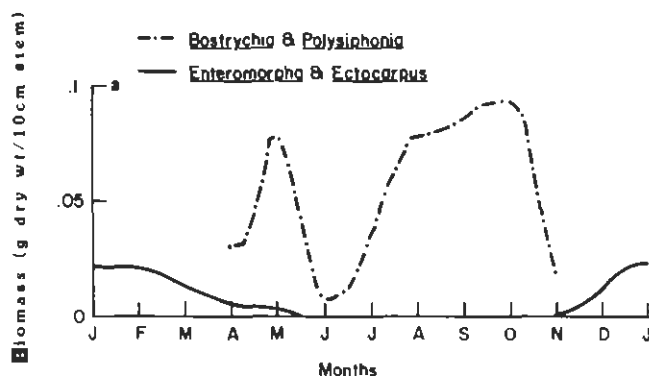


Figure 1. Seasonal biomass of the four dominant macroscopic algae.

The dominant microscopic epiphytes were diatoms. Diatoms occurred at densities of about 1.8×10^5 per cm² of culm surface area and decreased in density with distance from the shoreline and height on the culm (Stowe 1982). They also varied seasonally with peak density on the bottom 10 cm of the host culm occurring in December–January (Stowe 1982). Further discussion of the epiphytic diatoms can be found in Stowe (1982).

Shoreline community mean metabolic rates were 25.9 (± 12.4) and -19.6 (± 11.3) mg C \cdot (m² substrate area)⁻¹ \cdot h⁻¹ for net production and respiration, respectively (mean \pm standard deviation). Inland community rates were -3.3 (± 9.5) and -12.5 (± 8.3) mg C \cdot (m² substrate area)⁻¹ \cdot h⁻¹ respectively. Table 1 presents the F values calculated for separate one-way analyses of variance for shoreline and inland net production and respiration. Highly significant F values indicate that net production was significantly influenced by location and time of year. Respiration rate was not influenced by location; however, significant F values indicated that respiration varied seasonally. Culm counts of standing material indicated a density of 220 m⁻² and 360 m⁻² for the shoreline and inland communities, respectively. The average culm surface area for a bottom 10-cm section was 27.9 and 27 cm², respectively, for the shoreline and inland sites. Culm surface area per square meter of marsh surface was 6124 and 9207 cm² for the lower 10-cm section of shoreline and inland culms.

TABLE 1

F values for separate one-way ANOVA calculations for the following interactions.

Net Production	
shoreline vs inland	44.72**
shoreline vs sampling date	18.33**
inland vs sampling date	27.30**
Respiration	
shoreline vs inland	2.41
shoreline vs sampling date	32.47**
inland vs sampling date	30.44**

**Significant at the .99 probability level.

Seasonal trends of net production with standard deviations are presented in Figure 2. Shoreline net production

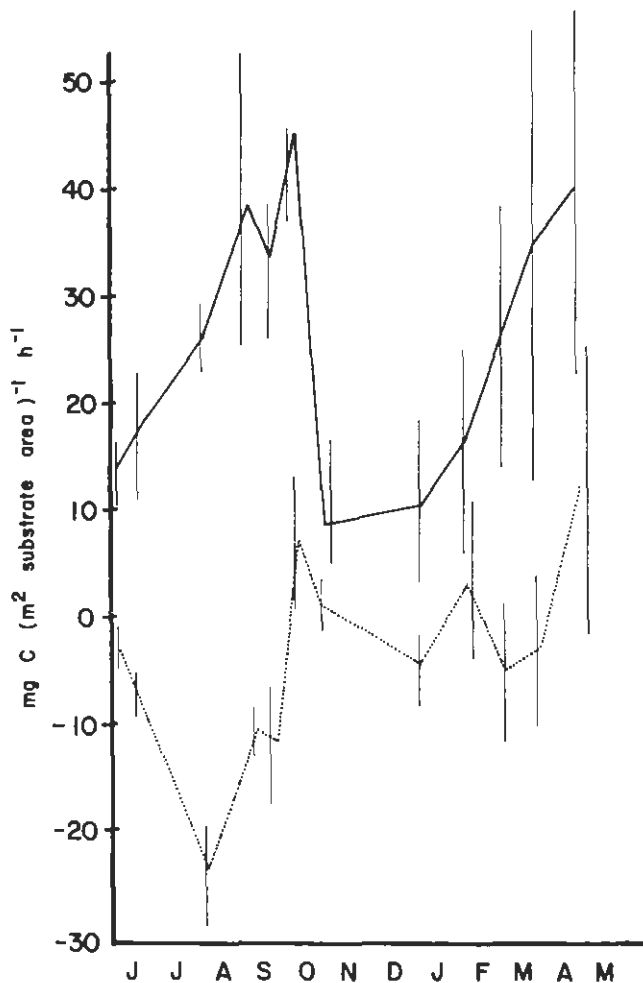


Figure 2. Seasonal variation in net production for the shoreline (—) and inland (.....) communities.

shows a bimodal distribution with midspring and October–November peaks. This bimodality follows closely the seasonal biomass distribution of *Bostrychia* and *Polysiphonia* (Figure 1). Following the November decline, the production rate remains constant during the winter, then begins a spring rise. *Bostrychia* and *Polysiphonia* were seldom found in the inland community. Inland net production was positive during the late fall and early spring, but was negative the remainder of the year. The two communities had similar production rates during the winter when filamentous epiphytes were scarce. Even though epiphytic diatoms peak during the winter (Stowe 1982), they do not contribute significantly to net production. This observation is supported by the reports of several other authors (Penhale 1977, Pomeroy 1960, Sand-Jensen 1977, and Gosselink et al. 1977).

In contrast, the inland community was dominated by unicellular algae, predominately diatoms. Net production

was low and negative in the late summer when *S. alterniflora* stands were most dense reducing light penetration to the marsh floor. Conversely, net production became a positive contributor during the winter when the *S. alterniflora* canopy was more open. Shading and dessication were possible controlling factors of inland productivity. Since light could reach the shoreline community from the water side, low light was not considered to be a limiting factor here. The inland community with its elevation of 15–20 cm above the shoreline community was less frequently flooded, therefore more likely to have dessication stress. The work of Dawes et al. (1978) and unpublished work of one of the present authors (WCS) indicates that macroscopic estuarine algae recover rapidly from dessication; we are not certain that the same can be said for the unicellular forms.

Very high seasonal respiratory rates were calculated for the epiphytic community (Figure 3). At times these respira-

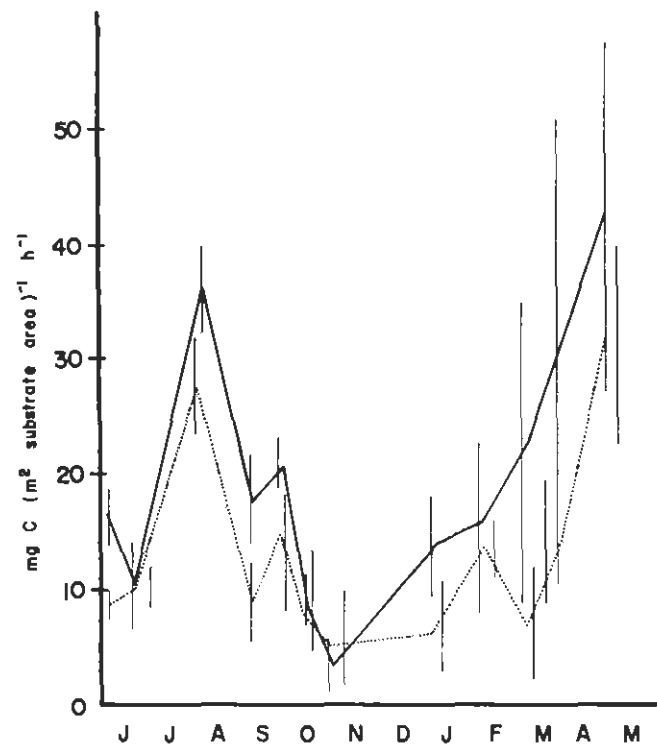


Figure 3. Seasonal variation in respiration for the shoreline (—) and inland (.....) communities.

tion rates equaled or exceeded calculated net production values. Since there was no significant difference between the two communities and because the curves of Figure 3 are very similar, one might assume that the communities are similar. However, this is not the case (see description of the area and Stowe 1980, 1982). The shoreline macroscopic algae were often inhabited by invertebrates (such as small crustaceans and nematodes) which contributed to respiration. These herbivores reached maximal levels during peak net production. Contributors to greater respiration rates were the larger bacterial (Hood and Colmer 1971), fungal,

and meiofaunal (Meyers et al. 1970) communities which have been observed inland. These communities, although different, are sufficiently dense to give similar rates. The communities had similar respiration rates per substrate area. The rate per marsh surface area was significantly higher inland because of the greater culm density.

Metabolic averages did not present a complete picture of this community. High variability was a significant characteristic of these communities (note standard deviations in Figures 2 and 3). Variation in colonization among culms was shown by large standard deviations in the calculated metabolic rates. The calculated standard deviations in this study were often greater than half the corresponding mean values. These large deviations should be expected when considering the patchy distribution of macroscopic algae.

Grazing impact, while not assessed, could be significant. During the spring and fall, amphipod populations were concentrated in the epiphytic macroalgal masses (personal observation) and were present in much larger numbers than at any other time. R. E. Condrey (personal communication) had observed several other types of crustaceans grazing in the epiphytic algal masses. These herbivore maxima occurred during peak net production. While we are convinced that the November production and biomass decline was related to seasonal lowering of the water level (Stowe 1982), the decline of *Bostrychia* and *Polysiphonia* in May

was not so easily attributed to water level fluctuation. Perhaps the observations of Cattaneo (1983) in Canada are applicable and grazers were responsible for the May decline.

Jones (1980), working on Sapelo Island, Georgia, in early April, calculated an epiphytic production of $24.8 \text{ mg C} \cdot (\text{m}^2 \text{ substrate area})^{-1} \cdot \text{h}^{-1}$ with a range of 15.3 to 45.5. Since Sapelo Island is a little farther north than Barataria Bay, their early April could be comparable to our late March. Our late March net production average was $25.4 \text{ mg C} \cdot (\text{m}^2 \text{ substrate area})^{-1} \cdot \text{h}^{-1}$ ($s = 13$). Considering the differences in techniques used and the areas studied, these results are remarkably similar. On this basis, it is tempting to speculate that these results have broader application than just to the Louisiana coast.

Initially the authors thought of the salt marsh *S. alterniflora* as a massive substratum for production of epiphytes. This was not true in Airplane Lake. In this study, net epiphytic productive contribution was limited to a narrow active band paralleling the shoreline. Inland from this band the epiphytic community was an energy sink. Thus epiphytic contribution to total marsh production was low (Day et al. 1973). Mason and Bryant (1975) found a freshwater epiphytic community to be a richer source of total nitrogen and phosphorous than the nearby sediments. Perhaps the role of the epiphytic community is one of quality production rather than quantity.

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