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Decomposition and CO_2 Evolution from Standing Litter of the Emergent Macrophyte *Erianthus giganteus*

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Abstract

Decomposition of standing litter of the emergent macrophyte *Erianthus giganteus* (plumegrass) was quantified in a small freshwater wetland in Alabama, USA. Living green shoots of *E. giganteus* were tagged and periodically retrieved for determination of leaf and culm mass loss, litter-associated fungal biomass (ergosterol), and nitrogen and phosphorus concentrations. Laboratory studies were also conducted to examine the effects of plant litter moisture content and temperature on rates of CO_2 evolution from plant litter. Culm and leaf material lost 25 and 32% AFDM, respectively, during plant senescence and early litter decay. Fungal biomass, as determined by ergosterol concentrations, increased significantly in both leaf and culm litter during decomposition, with maximum biomass accounting for 3.7 and 6.7% of the total detrital weight in culm and leaf litter, respectively. Spatial differences in fungal biomass were observed along the culm axis, with upper regions of the culm accumulating significantly greater amounts of fungal mass than basal regions ($p < 0.01$, ANOVA). Rates of CO_2 evolution from both leaf and culm litter increased rapidly after wetting (0 to 76 μg CO_2–C g^{-1} AFDM h^{-1} within 5 min). In addition, rates of CO_2 evolution from water saturated culms increased exponentially as the temperature was increased from 10 to 30°C. These results provide evidence that considerable microbial colonization and mineralization of standing emergent macrophyte litter can occur before collapse of senescent shoot material to the water and sediment surface.

Introduction

Emergent macrophytes often constitute a major fraction of the organic matter produced in freshwater wetlands and littoral zones of lakes [27, 28]. A substantial portion of macrophyte production eventually enters the detrital pool where microbial assemblages (bacteria and fungi) are important agents involved in litter breakdown and mineralization [17, 27]. Consequently, the fate of vascular plant detritus represents an important component in understanding energy flow and nutrient cycling within these ecosystems.

In most emergent macrophytes, abscission and collapse of leaf and shoot material to the sediment surface does not occur immediately after senescence and death. As a result, large

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amounts of standing dead plant matter often occur in wetland and littoral habitats dominated by the growth of emergent macrophytes [5, 7, 16, 28], and decomposition of this plant litter commences while it is in the aerial standing dead phase [2, 12]. Growing evidence has established that this litter is colonized and degraded by fungal assemblages that are adapted to the harsh environmental conditions experienced in the standing dead phase [13, 14], suggesting that these microorganisms can contribute to plant litter decay before its entry into the aquatic environment.

Despite this evidence, few studies have examined the microbial decay dynamics of standing litter in freshwater habitats [2, 12, 13, 20]. Most studies of emergent macrophyte decomposition have focused on plant litter decay at the sediment surface, since perhaps many investigators have assumed that microbial colonization and decay of plant litter is minor prior to its entry into the aquatic environment [18]. In these studies, plant litter was harvested, enclosed in bags of variable mesh sizes, and placed at the sediment surface [e.g., 6] or buried beneath the peat surface [e.g., 26]. Such methodological approaches circumvent the standing dead phase and may lead to experimental conditions that do not accurately reflect the natural decay sequence [1, 9, 18].

The present study examined the decomposition and microbial dynamics associated with naturally standing litter of a freshwater emergent macrophyte, *Erianthus giganteus* (giant plumegrass). The specific objectives were to determine the mass loss, nutrient content, and associated fungal biomass in leaves and culms of *E. giganteus* during shoot senescence and early litter decay. Additional studies were conducted to examine the effect of moisture and temperature on the respiratory activity of microbial assemblages associated with standing dead leaf and culm litter.

Methods

Field Procedures

This study was conducted in a small freshwater wetland located in Hale County, Alabama, USA (32° 54′30″ N, 87° 26′30″). *Erianthus giganteus* is a tall reed-like perennial common to wetland habitats in the southeastern United States [10]. Plant shoots arise from underground rhizomes and form circular clumps. Shoot culms (i.e., jointed stems of grasses) are cylindrical in shape and at the study site reach a mean height of 2.3 m. Leaf blades are long and flat, becoming narrow at both the blade base and tip. In mid-October 1997, live, fully green standing shoots of *E. giganteus* were tagged using small red flags and cable ties. At this time, 25 living shoots were collected, returned to the laboratory, and separated into leaf and culm material. Leaf sheaths were left attached to culms and the panicles removed. Morphometric measurements, including total length and diameter (base, middle, and upper culm sections), were recorded for each culm collected (Table 1). Length and mid-leaf width measurements were recorded for each leaf collected (Table 1). Culm and leaf material was then dried at 60°C to a constant weight and ground to pass through a number 40 mesh screen (ca. 400 μm mesh size) using a Wiley mill. Subsamples of ground plant material were combusted overnight at 550°C to determine ash free dry mass (AFDM). Stepwise multiple linear regressions were performed to generate models to predict initial AFDM of tagged culm and leaf material that was collected later during shoot senescence and decay. The following regression models provided the best prediction of initial culm and leaf AFDM:

$$\text{Culm initial AFDM} = 0.180 \cdot L + 22.5 \cdot D - 35.4,\ r^2 = 0.93$$

$$\text{Leaf initial AFDM} = 0.0136 \cdot L + 0.262 \cdot W - 0.58,\ r^2 = 0.92$$

where AFDM is given in grams and the symbols in equations are as follows: L = length, D = middle culm diameter, and W = mid-leaf width in centimeters. Climatic conditions at the wetland site were monitored continuously throughout the study period (Fig. 1) using a Campbell-CM6 meteorological station and CR-10 data logger (Campbell Scientific, Inc.). Statistical analyses were performed using SYSTAT [29] and values were considered significant at the $p < 0.05$ level. Symbols and error bars illustrated in Figs. 2–5 are the mean ± SE. Symbols in which error bars are not visible denote SEs which are smaller than the plotted symbol.

Table 1. Morphometric measurements recorded for living *E. giganteus* shoots collected in October 1997[a]

Type	Mean ± SD	Range
Leaves		
Length	49.5 ± 14.7	21.0–96.5
Mid-width	1.96 ± 0.43	1.1–3.0
Culms		
Length	230 ± 46	142–333
Diameter		
Upper	0.60 ± 0.10	0.4–0.7
Middle	0.78 ± 0.16	0.5–1.1
Base	0.94 ± 0.16	0.6–1.2

[a] $N = 25$ for culms, $N = 102$ for leaves. Values are given in cm.

Mass Loss and Nutrient Contents

Tagged shoots (9–15) were periodically collected at random over 190 d during shoot senescence and early litter decay. In the present study, visible senescence of shoot material began shortly after tagging of shoots, with leaves and culms becoming fully brown within

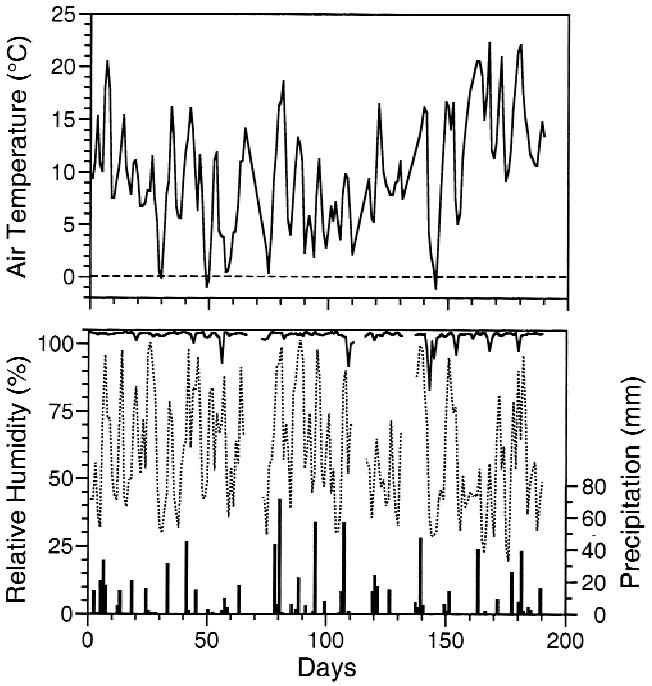

Fig. 1. Mean daily air temperature, maximum and minimum relative humidity, and total precipitation during the study period between October 19, 1997, and April 25, 1998. Dark vertical bars denote total precipitation; dotted and solid line denote minimum and maximum relative humidity, respectively.

2 and 4 weeks, respectively. At each sampling date, 3–10 shoots were used to estimate mass loss of culm and leaf material. The remaining shoots were used to estimate litter associated fungal biomass or litter-associated microbial respiratory activities (see below). Collected shoots were separated into leaves and culms and morphometric measurements recorded. Litter was then dried, weighed, ground, and subsamples washed as above. The percentage AFDM remaining of leaf and culm material was then estimated following calculation of the initial AFDM using the above regression equations.

Additional subsamples of ground leaf and culm litter were analyzed for N and P contents. Carbon and N contents were determined using a CHNS analyzer (Carlo Erba, Inc.). Phosphorus contents were determined using a Lachet Flow Injection Analyzer (ascorbic acid spectrophotometric method) following high-temperature sulfuric acid digestion (Lachet Inc.).

Fungal Biomass

During each sampling date, three shoots were used to estimate litter associated fungal biomass. Fungal biomass was monitored by the collection and extraction of ergosterol from decaying plant litter [8]. Three leaf discs (0.79 cm^2/disc) or one 2-cm culm piece were cut from each replicate shoot, placed into a vial containing 5 ml of methanol, and stored at −20°C until extracted. Separate culm samples were taken at the base, middle, and upper regions of the culm. Additional leaf and culm pieces were also cut, dried at 60°C, and combusted overnight at 550°C to determine AFDM of plant material in ergosterol samples. Ergosterol in leaf and culm litter was extracted by refluxing in alcoholic base (4% KOH in 95% methanol) for 30 min in a water bath at 80°C [25]. The resultant extract was partitioned into *n*-pentane and evaporated to dryness under a stream of N_2 gas at 30°C. Ergosterol was redissolved in 2 ml of methanol using an ultrasonic bath (10 min, Branson Inc.), filtered (Acrodisc, 0.45 μm), and stored in 4-ml screw-cap vials at −20°C until analyzed. Separation and analysis of ergosterol was performed using a Shimadzu high performance liquid chromatography (HPLC) system (LC-10A5 pump and SPD-10A UV-VIS detector) and a Whatman Partisphere C-18 reverse phase column (12.5 cm long, 20 μl sample loop, mobile phase HPLC grade methanol at 1 ml/min). Ergosterol was detected at 282 nm (R_t = ca. 6.5 min) and quantified based on comparison with ergosterol standards.

Microbial Respiratory Activities

Three replicate dry standing dead shoots of *E. giganteus* were collected in the field in January 1998 and April 1998, returned to the laboratory, and separated into leaf and culm material. Culm and leaf litter were cut into 5–6 pieces (10 cm in length; middle section of culms and leaves) and the rate of CO_2 evolution immediately monitored from one 10-cm piece using a Li-Cor Li-6250 Infrared Gas Analyzer [13]. All leaf and culm pieces were then placed into sterile Petri dishes (150 × 20 mm) containing filter paper (Whatman), wetted with sterile distilled water (ca. 30 ml) and drained of excess water. Rates of CO_2 evolution were repeatedly monitored from the same leaf and culm pieces 5 min after initial wetting and then periodically over 24 h. After 24 h, samples were allowed to air dry under laboratory conditions (22°C, ca. 50% rel. humidity). Rates of CO_2 evolution were also monitored during this drying period. Additional leaf and culm pieces placed in Petri dishes were removed at each CO_2 rate measurement for simultaneous determination of plant litter water potentials and fungal biomass. Water potentials were monitored using a Wescor (HR-33T) Dew-Point Microvoltmeter [13]. Briefly, three leaf discs or one 2-cm culm section was placed in each of two replicate (C-30) sample chambers. Chambers were placed in a Styrofoam box and allowed to equilibrate for 3 h. Measurements were made using the dew-point hygrometric mode and recorded when readings were stable and reproducible.

Additional experiments were conducted to examine the effect of temperature on rates of CO_2 evolution from water-saturated culm litter. Culm pieces were collected from three replicate shoots, cut into 10-cm pieces, placed into sterile Petri dishes, and wetted as above. Additional culm pieces were autoclaved and wetted to serve as negative controls. Samples were placed in an incubator at ca. 10°C, allowed to equilibrate for 1.5 h, and rates of CO_2 evolution monitored. The incubator temperature was then increased in increments of ca. 10°C up to 40°C. The same culm samples were

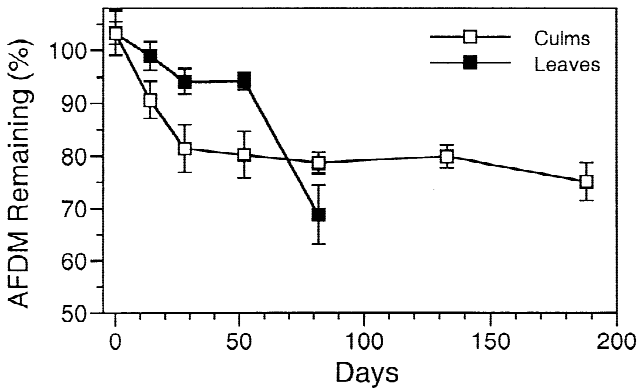

Fig. 2. Percent ash free dry mass (AFDM) remaining of standing *E. giganteus* leaf and culm material during plant senescence and early litter decay. Symbols indicate the mean ± SE ($N \geq 3$).

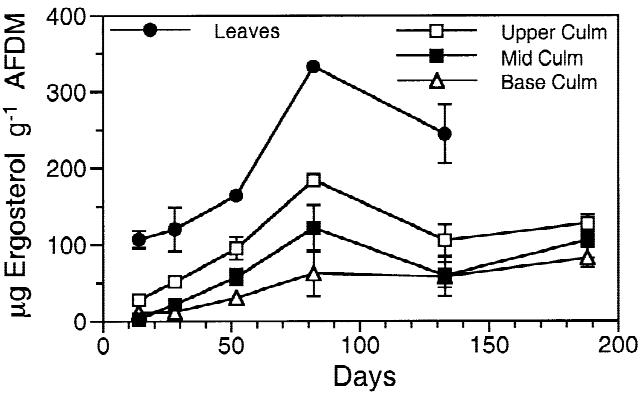

Fig. 3. Changes in ergosterol concentrations of standing dead *E. giganteus* leaf and culm litter. Symbols indicate the mean ± SE ($N = 3$).

allowed to equilibrate at each temperature 1.5 h before measurements of CO_2 evolution rates were repeated.

Results and Discussion

Mass Loss

Culm and leaf material lost 25 and 32% AFDM, respectively, during plant senescence and early standing litter decomposition (Fig. 2). These mass loss estimates are consistent with results from previous studies examining the decomposition of standing litter in freshwater emergent macrophytes [2, 3, 4, 11, 12, 20], although only a few of these previous studies have considered the decay of naturally intact standing litter [2, 4, 20], and no data are currently available for *E. giganteus*. Bärlocher and Biddiscombe [2] reported 55% mass loss from standing attached leaves of *Typha latifolia* in 210 days, with the overall mass loss pattern a combination of microbial decomposition, leaching, and fragmentation. In a similar study, Newell et al. [20] observed between 37 and 46% mass loss in tagged standing leaves of *Carex walteriana* during senescence and early litter decay. Results obtained in the present study provide additional evidence that appreciable mass loss of emergent macrophyte tissue can occur in the aerial standing phase prior to the entry of plant litter into the aquatic environment. However, note that part of the observed mass loss in *E. giganteus* may have resulted from translocation of shoot photosynthate rather than microbial decomposition, as indicated by the finding that in some emergent macrophytes (e.g., *Phragmites australis*) the starch content of rhizomes may increase during shoot senescence [23, see also 22]. In addition, mass loss of *E. giganteus* leaves appeared to have been partially caused by fragmentation, particularly after 52 d when most of the leaves remaining in the upper canopy were extremely brittle, with the laminae splitting down the main axis (pers. obs.); correspondingly, leaf mass loss accelerated greatly between days 52 and 82 (Fig. 2). Eighty-two days after tagging, most of the standing dead leaves had become detached from the plant shoot and were accumulating around the base of standing culms. At this point, mass loss continues under environmental conditions that differ from standing decay, but this aspect was not investigated in the present study.

Fungal Biomass

Fungal biomass as measured by ergosterol concentrations increased significantly ($p < 0.05$, ANOVA) during the first 82 d of leaf and culm decay, then decreased and/or leveled off during the remaining study period (Fig. 3). Significantly higher ergosterol concentrations were found in leaf than in culm litter ($p < 0.01$, ANOVA). Furthermore, ergosterol concentrations varied significantly along the culm axis ($p < 0.01$, ANOVA), with the highest concentrations observed in the upper sections of culms (Fig. 3). Using a conversion factor of 5 µg ergosterol mg^{-1} living fungal biomass [8], maximum fungal biomass values in leaf and culm litter were 67 ± 2 and 37 ± 2 mg g^{-1} AFDM, respectively. Similar patterns of ergosterol accumulation in standing litter have been reported in standing dead litter of *Carex walteriana* [20] and *Typha latifolia* [2]. Bärlocher and Biddiscombe [2] observed a gradual increase in ergosterol in standing dead *Typha* leaves during leaf senescence and early decay, with maximum ergosterol concentrations occurring in the tips of attached leaves 8 weeks after tagging (ca. 200 µg ergosterol

g^{-1} AFDM). Furthermore, Bärlocher and Biddiscombe [2] also found spatial differences in ergosterol concentrations within *Typha* leaves, with the leaf tips accumulating nearly twice the ergosterol content of middle leaf sections. Spatial differences in ergosterol concentrations have also been observed within standing dead culms of *Phragmites australis* collected from a lake littoral site in Switzerland and a freshwater tidal marsh in New York, USA [Kuehn, Gessner, and Findlay, unpublished data].

In the present study, increases in ergosterol concentrations from 14 to 82 d were fit to an exponential growth equation and indicated the following growth rates of fungi within decaying litter: 1.2 ± 0.2% d^{-1} (leaves), 2.5 ± 0.2% d^{-1} (upper section of culms), 4.0 ± 0.7% d^{-1} (middle), and 2.3 ± 0.9% d^{-1} (base). These growth rates can be considered conservative, since losses in fungal biomass (i.e., hyphal fragmentation, sporulation, etc.) may have occurred during this period. Nevertheless, these rates are within the range (1–5% d^{-1}) reported for fungal communities associated with decomposing standing litter of the freshwater sedge *Carex walteriana* [20] and the salt marsh grass *Spartina alterniflora* [19] using radioisotopic incorporation techniques, but are lower than those observed for fungal communities associated with deciduous leaf litter in streams (up to 28% d^{-1}) [24].

Nutrient Dynamics

Substantial decreases in N and P concentrations of leaf and culm material were observed during plant senescence and early decay (Fig. 4) (ANOVA, $p < 0.01$), resulting in corresponding increases in the C:N, C:P, and N:P ratios within litter (Table 2). A large initial decrease in N and P was observed during plant senescence (14 d after tagging for leaves, and 28 d for culms). Nitrogen concentrations decreased by 57% in leaves and 42% in culms. Phosphorus concentrations decreased by 87% in leaves and 99% in culms (Fig. 4). Much of the N and P was presumably translocated to the parent rhizome [15], although other processes such as leaching may have also contributed to these decreases. After the initial decrease, no significant fluctuations in N and P were observed ($p > 0.05$, ANOVA, Tukey), indicating that the observed accumulation of fungal biomass (Fig. 3) was not accompanied by a notable microbial nutrient immobilization from external sources (e.g., atmospheric deposition). Higher concentrations of both N and P were observed in leaf litter as compared to culms (Fig. 4 and Table 2), possibly in accordance with the significantly greater amount of fungal biomass observed in leaf material during this study.

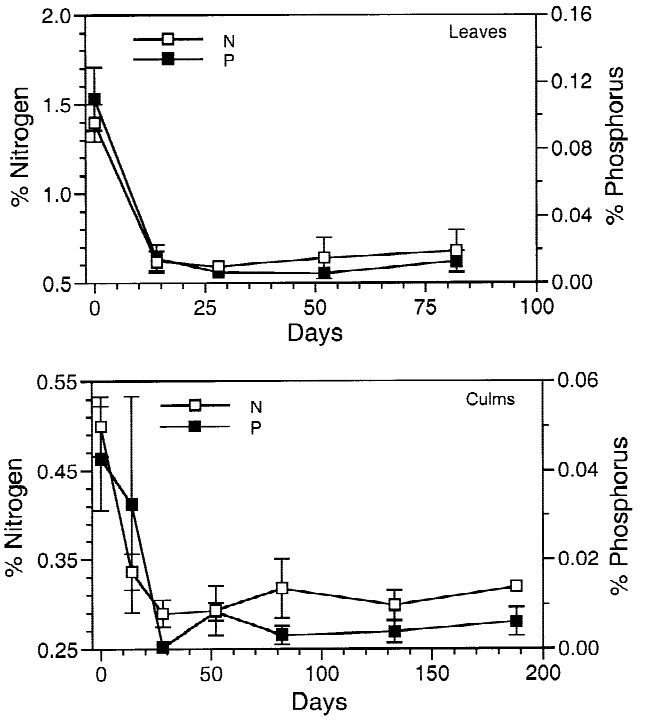

Fig. 4. Changes in N and P concentrations of standing dead *E. giganteus* leaf and culm material during shoot senescence and early litter decay. Symbols indicate the mean ± SE ($N = 3$).

Response of Microbial Assemblages to Environmental Parameters

Microbial assemblages associated with decaying leaf and culm litter collected in January 1998 responded rapidly to increased water availability (Fig. 5). Rapid increases in rates of CO_2 evolution from both leaf and culm litter were observed within 5 min after exposure to water saturating conditions ($p < 0.001$, ANOVA), as has been previously noted for microbial assemblages associated with standing litter of the salt marsh grass *Spartina alterniflora* [21] and the freshwater rush *Juncus effusus* [13, 14]. Five times higher rates of CO_2 evolution were observed in leaf compared to culm litter (Fig. 5), whereas a similar marked difference in mass loss was not observed during field studies (Fig. 2). Rates of CO_2 evolution from litter remained high for up to 24 hr after initial wetting with no significant fluctuations ($p > 0.05$, ANOVA, Tukey), indicating that the high initial microbial activities observed are not restricted to an initial burst of respiration, but can be maintained for prolonged periods as long as environmental conditions are favorable for inhabitant microbiota. When plant litter was exposed to drying conditions, rates of CO_2 evolution declined rapidly, con-

Table 2. Changes in N and P concentrations within *E. giganteus* plant matter during senescence and early litter decay[a]

Litter Type	Day	% N	% P	C:N	C:P	N:P
Leaves	0	1.39 ± 0.10	0.11 ± 0.02	38 ± 3	1,122 ± 212	30 ± 6
	28	0.59 ± 0.03	0.01 ± 0.002	89 ± 5	13,542 ± 6,240	146 ± 66
	82	0.67 ± 0.11	0.01 ± 0.01	81 ± 13	14,231 ± 5,365	162 ± 43
Culms	0	0.50 ± 0.03	0.04 ± 0.01	110 ± 7	3,230 ± 755	29 ± 6
	52	0.29 ± 0.03	0.01 ± 0.002	193 ± 46	16,708 ± 4,358	87 ± 22
	188	0.32 ± 0.004	0.006 ± 0.003	173 ± 2	13,678 ± 2,338	78 ± 12

Atomic C:N, C:P, and N:P rations are also given.
[a] Leaves and culms collected at day 0 were living. Values are the mean ± SE ($N = 3$). Differences among initial, intermediate, and final concentrations were highly significant ($p < 0.01$, ANOVA).

comitant with decreasing litter water potentials. Rates of CO_2 evolution from culms decreased only slowly after exposure to drying conditions, which is in accordance with the prolonged maintenance of elevated moisture levels in culm litter. Rates of CO_2 evolution were positively correlated with leaf ($r = 0.92$) and culm ($r = 0.68$) litter water potentials ($p < 0.05$). No significant changes in ergosterol concentrations of leaf (ANOVA, $p = 0.72$) or culm ($p = 0.92$) litter were noted during incubations (data not shown). Culm litter collected in April 98 showed qualitatively identical responses to leaf and culm litter collected in January. However, with only slightly greater fungal biomass concentrations, maximum rates of CO_2 evolution from culms were significantly higher than in January and approached rates observed for leaves (Table 3). Taken together, these results lend further support to the hypothesis that water availability is a primary controlling factor of microbial activities associated with standing dead macrophyte litter [13].

In addition to moisture, microbial assemblages associated with standing *E. giganteus* litter responded to changes in temperature (Fig. 6). Rates of CO_2 evolution from water saturated culms increased markedly as the temperature was increased from 10 to 30°C. Note that rates of CO_2 evolution from control (autoclaved) culm samples were negligible compared to experimental samples (live), confirming that CO_2 evolution from plant litter was the result of the respi-

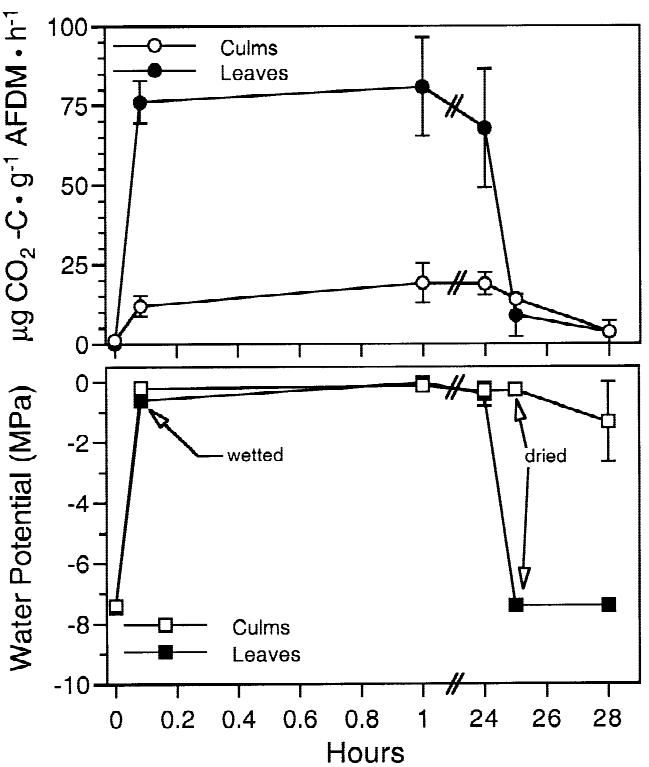

Fig. 5. Changes in plant litter water potentials and rates of CO_2 evolution from standing dead leaf and culm litter of *E. giganteus* after litter was wetted and dried in the laboratory. Symbols indicate the mean ± SE ($N = 3$).

Table 3. Fungal biomass (ergosterol), water potential, incubation temperature, and CO_2 evolution rate during periods of highest activities of microbial assemblages associated with leaves and culms of *E. giganteus* in short-term laboratory experiments[a]

Date	Litter type	Ergosterol (μg g^{-1} AFDM)	Water Potential (MPa)	Temperature (°C)	CO_2 Evolution Rate (μg C g^{-1} AFDM h^{-1}
January 97	Leaves	236 ± 35	−0.04 ± 0.05	24.5 ± 0.3	80.9 ± 15.5
	Culms	90 ± 5	−0.13 ± 0.0	22.6 ± 0.1	19.1 ± 6.0
April 98	Culms	121 ± 13	0 ± 0	23.3 ± 0.1	71.2 ± 10.0

[a] Values are the mean ± SE ($N = 3$).

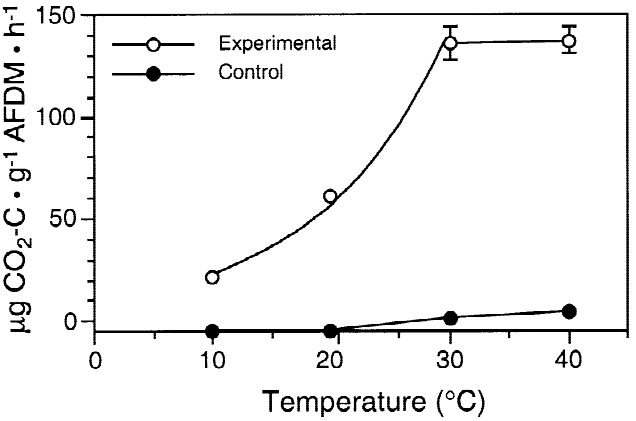

Fig. 6. Effect of temperature on rates of CO_2 evolution from water-saturated standing dead culm litter of *E. giganteus* under laboratory conditions. Symbols indicate the mean ± SE ($N = 3$).

ratory activity of inhabitant microbial assemblages rather than physical processes. The relationship between rates of CO_2 evolution and temperature is well described by the exponential equation $C = 8.40e^{0.094T}$ ($r^2 = 0.99$, $p < 0.01$), where C is the rate of CO_2 evolution, and T is temperature in °C. The temperature coefficient of 0.094 corresponds to a Q_{10} of 2.56 for data spanning this temperature range. Similar metabolic responses to temperature increases have been reported by Kuehn and Suberkropp [13] for microbial assemblages associated with standing litter of *J. effusus* (Q_{10} = 1.95). In addition, CO_2 evolution at temperatures exceeding 30°C continued at high rates, but leveled off to those values observed at 30°C (Fig. 6) [also see 13]. These results indicate that, under adequate moisture conditions, inhabitant microbial assemblages in standing litter of emergent macrophytes can remain metabolically active even when the ambient temperatures become high.

Conclusion

The findings obtained in this study strongly support conclusions from previous investigations that emergent macrophyte plant litter is colonized by microorganisms and that decay begins while litter is in a standing condition. Furthermore, these findings provide additional evidence that microbial assemblages associated with standing litter are metabolically adapted to the fluctuating moisture conditions experienced in the standing dead environment, as indicated by the rapid shift from the metabolically inactive to active state, and vice versa, when water becomes available to or is removed from litter-associated microbial assemblages. Thus, it would appear that a complete understanding of the decay dynamics of freshwater emergent macrophytes must include decay processes that occur in the standing dead phase.

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