

Diel fluctuations in rates of CO₂ evolution from standing dead leaf litter of the emergent macrophyte *Juncus effusus*

Kevin A. Kuehn*, Keller Suberkropp

Department of Biological Sciences, Aquatic Biology Program, Box 870206, University of Alabama, Tuscaloosa, Alabama 35487-0206, USA

ABSTRACT: Standing dead plant litter of emergent macrophytes often forms a considerable portion of the detrital mass in wetland habitats. We examined the effects of varying environmental conditions on the diel respiratory activity (rate of CO₂ evolution) of microbial assemblages associated with standing dead litter of the emergent macrophyte *Juncus effusus* L. from a small freshwater wetland in central Alabama, USA. Availability of water was a major factor affecting rates of respiration in standing litter. Under field conditions, rates of CO₂ evolution from plant litter fluctuated greatly, with the highest rates occurring at night and in the early morning hours, coinciding with increasing relative humidity (>90%) and plant litter water potentials (>-1.0 MPa). Rates ranged from 2 to 285 µg CO₂-C g⁻¹ organic mass h⁻¹ over 24 h. Daily CO₂ flux from microbial decomposers inhabiting standing litter ranged between 1.37 and 3.35 g C m⁻² d⁻¹. After controlled laboratory additions of water, rates of CO₂ evolution from standing litter increased significantly, with sustained maximal rates occurring within 5 min after being wetted (>100 µg CO₂-C g⁻¹ organic mass h⁻¹). Results of these investigations establish that *J. effusus* litter is colonized by active microbial decomposers while in the standing dead phase. Furthermore, these microbial assemblages make significant contributions to ecosystem metabolism and may represent an important CO₂ output not previously recognized or incorporated in estimates of CO₂ flux from wetland habitats.

KEY WORDS: Freshwater wetlands · CO₂ emissions · *Juncus effusus* · Standing litter · Fungi

INTRODUCTION

Wetlands are among the most productive ecosystems known, with annual above ground plant production frequently exceeding 1000 g dry mass m⁻² yr⁻¹ (Mitsch & Gosselink 1993). The growth of emergent macrophytes often constitutes a significant portion of this annual plant production (Wetzel 1990, Gessner et al. 1996), with much of the fixed carbon residing in the structural material of cell walls (i.e. lignocellulose). Very little (e.g. <5%) of the plant matter produced within these habitats is directly consumed by herbivores (Teal 1962, Mann 1988). Consequently, most plant litter eventually enters the detrital food web

where microbial populations (bacteria and fungi) are involved in its decomposition and mineralization. Thus, wetland ecosystems are often viewed as detritus-based, with decaying vascular plant litter representing an important energy input (Mann 1988).

In many emergent macrophytes, leaf abscission does not occur following senescence, resulting in the accumulation of standing dead leaves that begin to decay while still attached to the parent plant (Newell 1993, 1996, Bärlocher & Biddiscombe 1996, Samiaji & Bärlocher 1996). Large amounts of standing dead plant material can accumulate in wetlands, and at certain times of the year may exceed the above ground mass of living plant matter (Jordan & Whigham 1988, Christian et al. 1990, Lee 1990). Diverse fungal assemblages have been identified from standing dead litter of both freshwater and salt marsh emergent macrophytes (e.g.

*E-mail: kkuehn3@biology.as.ua.edu

Apinis et al. 1975, Kohlmeyer et al. 1995, 1996, Samiaji & Bärlocher 1996). However, despite evidence of extensive fungal colonization, few investigators have examined the role of microbial assemblages in standing litter decay (Newell 1993, 1996, Bärlocher & Biddiscombe 1996, Newell et al. 1996, Samiaji & Bärlocher 1996). Most studies of marine and freshwater vascular plant decomposition have focused on plant detritus that has been harvested and placed at the sediment surface (e.g. Thormann & Bayley 1997), leading to an alteration in the natural decay sequence (Newell 1993).

In *Spartina* salt marshes, microbial assemblages associated with standing litter appear to be well adapted to fluctuations in moisture levels, as their rates of respiration vary greatly depending on moisture availability (Gallagher et al. 1984, Newell et al. 1985, 1996, Buth & Voeselek 1988). Furthermore, Newell et al. (1985) demonstrated that microbial assemblages could mineralize a considerable fraction of the plant carbon while in the standing dead phase. The frequent occurrence of fungal decomposers in standing litter suggests that these microorganisms contribute significantly to plant litter decay before its entry into the aquatic environment, and have important impacts on carbon mineralization and nutrient recycling in wetland and littoral habitats.

Wetland ecosystems have generally been considered net carbon sinks due to the large annual plant production associated with these habitats and anaerobic sediment conditions that contribute to the slow decomposition and accumulation of deposited organic matter. However, several investigators have speculated that increases in global temperatures and anthropogenic disturbance of natural wetlands may lead to increased litter decomposition, thus shifting wetlands from net carbon sinks to net sources of atmospheric CO₂ and CH₄ (Gorham 1991, Moore 1994, Bridgman et al. 1995). As a result, wetland ecosystems have been implicated as potential sources of greenhouse gases (CO₂ and CH₄), thereby providing a positive feedback on global warming (Bridgman et al. 1995), and highlighting the need for further studies examining the ecology and biogeochemistry of wetland ecosystems (Gorham 1994).

In the present study, we examined the effect of temperature and moisture availability on the rates of microbial respiratory activity (CO₂ evolution) associated with standing litter of the freshwater emergent macrophyte *Juncus effusus* L. under both laboratory and field conditions. Specifically, we measured the short-term diel responses of microbial assemblages to the daily changes in environmental conditions that are experienced in the standing dead phase. Since fungi are common inhabitants of standing dead litter, we also examined the dynamics of fungal propagules

within the atmosphere above decomposing *J. effusus* litter. Lastly, we estimated the potential contribution of microbial assemblages inhabiting standing litter to overall wetland metabolism.

METHODS

Study site. These investigations were conducted in a small (13.6 ha) freshwater wetland located in the Talladega National Forest, Hale County, Alabama, USA (32° 54' 30" N, 87° 26' 30" W). The wetland is in the Coastal Plain physiographic province of the Mobile River drainage basin and occupies the southern portion of a stream valley impounded by beaver. The surrounding catchment is 384 ha and is composed of mixed coniferous-deciduous forests. Two predominant vegetative zones occur at the wetland site: an open water zone dominated by the white water lily *Nymphaea odorata* Ait. covering 8.8 ha, and a marginal region dominated by the rush *Juncus effusus* L. covering 4.5 ha.

Field studies. Diel fluctuations in rates of microbial respiration (CO₂ evolution) associated with standing dead plant litter were monitored under a variety of environmental conditions from August 1993 to September 1994. Two sampling dates included periods of rainfall so that effects of precipitation could be assessed. During these studies, standing dead leaves of *Juncus effusus* were randomly collected from the outer periphery of replicate plant tussocks at intervals ranging from 1 to 14 h. Leaf litter samples (upper 3/4 portion of leaf) were cut into 10 cm leaf pieces and rates of CO₂ evolution measured as described below. Plant material was also cut into 2 cm leaf pieces to determine plant litter water potentials (see below). Environmental conditions and airborne fungal spore concentrations were also monitored (see below). Plant litter samples were also collected at the completion of diel studies for determination of fungal biomass within decaying plant matter.

Laboratory studies. The effects of temperature and moisture on rates of CO₂ evolution from standing litter were studied under controlled environmental conditions in the laboratory. Dry standing litter was collected from 3 plant tussocks at the wetland, placed on ice, and returned to the laboratory. Subsamples of dry litter were immediately cut and rates of CO₂ evolution measured. Samples were also collected to determine plant litter water potentials and fungal biomass. After recording initial rates of CO₂ evolution and water potentials, the remaining plant litter was wetted with deionized water and enclosed in a ventilated plexiglass chamber (0.7 × 0.5 × 1.4 m). A mist-generating vaporizer (Kaz Inc.) placed within the chamber kept

plant litter water saturated. Subsamples of litter were removed 5 min after initial wetting and then periodically over 24 h for measurement of microbial respiration rates, water potentials and fungal biomass. Temperature was held constant at $20.3 \pm 1.7^\circ\text{C}$.

The effect of temperature on rates of CO_2 evolution from plant litter was monitored on 2 dates (September and December 1993). Dry standing litter was collected and returned to the laboratory (as above). Leaf litter was cut into 10 cm leaf pieces and 10 leaf pieces placed into sterile culture plates (150×20 mm) containing filter paper (Whatman, qualitative #2). Leaf samples were wetted with deionized water (ca 10 ml) and drained of excess water. Samples were then placed in a 10°C incubator, allowed to equilibrate for 2 h, and rates of CO_2 evolution were monitored. The incubator temperature was increased in increments of ca 10°C up to 30°C and then in increments of ca 5°C up to 45°C , allowing the same leaf litter samples to equilibrate at each temperature setting for 2 h before measurements of CO_2 evolution rates were repeated. Leaf piece samples and filter paper were kept water saturated throughout these studies by repeated addition of deionized water (as above).

Respiration rates. In both laboratory and field studies, rates of CO_2 evolution from standing *Juncus effusus* plant litter were measured by enclosing leaf litter samples in a LiCor Li-600-11, 0.25 l sample chamber connected to a LiCor Li-6250 Infrared gas analyzer (LiCor Inc.). The instrument allows changes in CO_2 concentration to be monitored *in situ* over short time periods. In addition, the instrument provided temperature data during sample incubations. Collected leaf litter samples were cut into 10 cm pieces and 10 leaf pieces were enclosed in the LiCor sample chamber. After a period of instrument stabilization (1 to 2 min, see LiCor Inc. 1987), the linear rate of CO_2 evolution was monitored for 10 min. After respiration rates were determined, plant material was stored on ice, returned to the laboratory, dried at 60°C to a constant weight, and organic content determined after combustion overnight (>12 h) at 550°C .

Laboratory experiments were conducted to examine the potential involvement of epiphytic algae and abiotic factors on rates of CO_2 evolution from plant litter. Plant litter was collected from 3 plant tussocks, placed on ice and returned to the laboratory. Leaf pieces were cut and wetted as described above. Rates of carbon dioxide evolution from plant litter were then monitored for untreated and autoclaved litter samples. Rates of CO_2 evolution from sterilized plant litter samples were negligible compared to untreated samples (Table 1). Similar results were obtained for plant litter samples incubated at 10 and 30°C (data not shown). These experiments established that CO_2 evolution from standing plant

Table 1 *Juncus effusus*. Rates of carbon dioxide evolution from water saturated standing dead plant litter exposed to different treatments in the laboratory. Light treatment conducted under intensities of ca $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. OM: organic matter

Sample treatment	$\mu\text{g CO}_2\text{-C g}^{-1} \text{ OM h}^{-1}$ at 20°C (mean \pm SE)
Untreated	99.1 ± 21.8
Autoclaved	0.9 ± 0.9
Autoclaved ^a	-2.8 ± 2.4
Light	110.1 ± 35.1
Dark	125.1 ± 30.2

^aAfter wetting with sterile deionized water enriched with NaHCO_3 (10 mg l^{-1})

litter was the result of the metabolic activities of inhabitant microbiota. Rates of CO_2 evolution from untreated samples were also monitored under both full sunlight (ca $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) and dark incubation conditions. No significant differences in rates of CO_2 evolution were observed for plant samples incubated under full sunlight or dark conditions ($p = 0.76$, Student's *t*-test) (Table 1), indicating the absence of any appreciable carbon fixation by epiphytic algal assemblages.

Plant litter water potentials. Water potentials of plant litter were recorded using a dew-point microvoltmeter (model HR-33T, Wescor Inc.). Five leaf pieces (2 cm) were placed in each of 3 replicate sample chambers (C-30, Wescor Inc.). Chambers were placed in a Styrofoam cooler and allowed to equilibrate for 3 h. Measurements were made using the dew-point hygrometric mode and recorded when readings were stable and reproducible. A salt solution (0.55 M NaCl) of known water potential (-2.5 MPa) was used for chamber/instrument calibration. Sensitivities of (C-30) chambers used in this investigation were confined to a narrow range of measurable water potentials, as determined by the manufacturer (Wescor Inc. 1986, see Newell et al. 1991). Maximum sensitivity (i.e. lowest measurable water potential) of chambers averaged $-7.6 \pm 0.3 \text{ MPa}$. Water potentials lower than these values were assumed to be equal to the corresponding chamber sensitivity.

Environmental conditions. A Campbell-CM6 meteorological station and CR-10 data logger (Campbell Scientific Inc.) monitored temperature ($^\circ\text{C}$), precipitation (mm), relative humidity (%), wind speed (m s^{-1}) and light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$). Temperature data of plant litter enclosed within the LiCor sample chamber was also obtained directly from the LiCor Li-6250 gas analyzer.

Airborne spore concentration. Airborne fungal spores were sampled within the *Juncus effusus* dominated portion of the wetland using a Kramer-Collins volumetric spore trap (Kramer et al. 1976). The sampler

was positioned ca 10 cm above the *J. effusus* canopy. Airborne particulates (pollen, fungal spores etc.) were collected on an adhesive coated tape applied to the outer surface of a removable sampling wheel (15 cm diameter). The adhesive tape was coated with a thin layer of hexa-silicone (n-hexane + silicone grease) (Smith 1990) containing 0.05% v/v thimerosal to facilitate particle retention and prevent spore germination and growth. Ten minute air samples were collected every 2 h. Upon completion of diel studies, the sampling wheel was removed and returned to the laboratory. The tape was then removed, sectioned and mounted on glass slides. Airborne particulates (pollen and fungal spores) retained on the tape were stained with 1% Calberla's solution (Smith 1990) and microscopically counted and identified if possible.

Fungal biomass. Fungal biomass was determined by the extraction and quantification of ergosterol from plant litter samples (Gessner & Newell 1997). Sixty leaf pieces (2 cm) were collected from each replicate *Juncus effusus* tussock at the completion of respiratory experiments. Three replicates, each containing 10 leaf pieces, were placed into 5 ml of methanol and stored at -20°C until extracted. An additional 3 replicates (10 leaf pieces each) were dried at 60°C to a constant weight and combusted overnight at 550°C to determine organic mass of leaf material. Ergosterol was extracted by refluxing samples in alcoholic KOH (25 ml methanol + 5 ml 4% KOH in 95% methanol) for 30 min (Suberkropp & Weyers 1996). The resultant extract was partitioned into n-pentane and evaporated to dryness under a stream of nitrogen gas at 30°C . Dried samples were redissolved by water bath sonication (Branson Inc.) in 2 ml of methanol and filtered (0.45 μm Acrodisc PTFE filters). Samples were stored tightly sealed at -20°C until analyzed. Ergosterol was separated with a Whatman partisphere C-18 reverse phase column (0.46 \times 12.5 cm with 20 μl sample loop) (Whatman Inc.) connected to a Shimadzu LC-10A5 liquid chromatography system (HPLC) (Shimadzu Scientific Inc.). The mobile phase was methanol (HPLC grade) at a constant flow rate of 1 ml min^{-1} . Ergosterol was detected at 282 nm with a Shimadzu SPD-10A UV-VIS detector (retention time of 6.5 min). Ergosterol contents were identified and quantified based on comparison with known ergosterol standards (Fluka Chemical Co.).

RESULTS

Field studies

Microbial respiration associated with standing litter exhibited significant diel periodicity in August 1993 ($p < 0.01$, Kruskal-Wallis) (Fig. 1A). Rates of CO_2 evo-

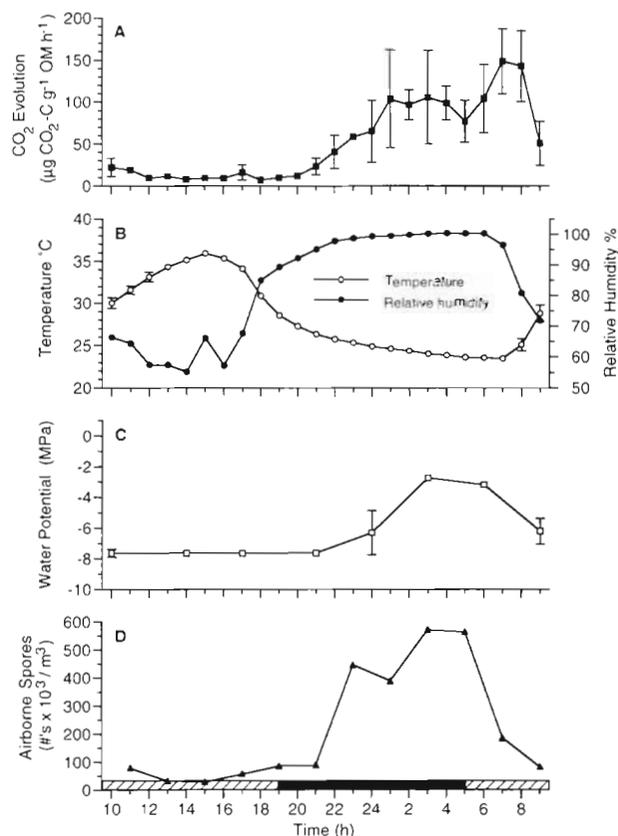


Fig. 1. Diel changes in (A) rates of CO_2 evolution from standing litter of *Juncus effusus* and (B) air temperatures and relative humidity above decaying litter on August 19–20, 1993. Diel changes in (C) water potentials of plant litter and (D) airborne spore concentrations are also illustrated. Means \pm SD for CO_2 and temperature ($n = 2$); means \pm SE for water potential values ($n = 3$). Symbols for airborne spore concentrations and relative humidity are single point measurements ($n = 1$). Dark horizontal bar on x-axis in (D) indicates nighttime; hatched horizontal bar indicates daytime

lution ranged between 5 and $176 \mu\text{g CO}_2\text{-C g}^{-1}$ organic mass h^{-1} (Table 2) and were significantly correlated with environmental conditions (Table 3). At night, decreasing temperatures and increasing relative humidity ($>90\%$) (Fig. 1B) contributed to dew formation on standing litter, leading to increased plant litter water potentials (i.e. greater water availability) (Fig. 1C). The highest rates of CO_2 evolution (Fig. 1A) occurred during these wetting periods. During the day, increasing temperatures (Fig. 1B) and exposure to sunlight contributed to the desiccation of plant litter and had a negative effect ($r = -0.85$, $p < 0.001$, Spearman) on rates of CO_2 evolution (Table 3). Concentrations of airborne fungal spores above decomposing *Juncus effusus* litter also showed a diel periodicity (Fig. 1D), with peak concentrations coinciding with maximal rates of CO_2 evolution ($r = 0.75$, $p < 0.001$, Spearman).

Table 2. Summary of data obtained during diel field studies. OM: organic matter

Date	$\mu\text{g CO}_2\text{-C g}^{-1}\text{ OM h}^{-1}$		$\text{g CO}_2\text{-C m}^{-2}\text{ d}^{-1}$		Temperature ($^{\circ}\text{C}$)		Water potential (MPa)		Precipitation (mm)		Relative humidity (%)		Airborne spores ($\times 10^3\text{ m}^{-3}$)		$\mu\text{g ergosterol g}^{-1}\text{ OM}$	
	Mean	Range	Mean \pm SE	Mean \pm SE	Mean	Range	Mean	Range	Total	Range	Range	Mean	Range	Mean	Range	Mean \pm SE
August 1993	51.9	5.1–175.6	2.35 \pm 0.44	28.4	23.2–36.1	≤ -7.63 –(-2.75)	0.00	55.2–100.0	217.5	28.6–571.4	357.7 \pm 3.1					
September 1993	91.7	14.4–196.4	2.64 \pm 1.28	23.3	21.1–26.7	≤ -7.87 –(-0.22)	0.00	81.8–100.0	148.3	32.1–410.7	339.8 \pm 64.6					
December 1993	39.9	3.1–95.6	1.87 \pm 0.74	9.3	6.1–12.3	-6.28–(-0.04)	2.54	79.9–100.0	19.9	4.9–39.8	296.4 \pm 48.4					
March 1994	33.2	0.0–111.4	1.37 \pm 0.95	14.2	3.2–26.8	≤ -7.87 –(-0.58)	0.00	39.5–100.0	15.0	0.0–32.1	302.1 \pm 55.6					
June 1994	152.9	1.8–284.7	3.35 \pm 0.13	24.9	20.4–31.5	≤ -7.87 –(0.00)	10.67	63.3–100.0	58.8	19.4–151.8	398.7 \pm 71.1					
September 1994	84.4	6.7–193.3	2.43 \pm 0.74	24.8	19.5–33.1	≤ -7.87 –(-0.13)	0.00	62.2–100.0	133.6	14.3–346.4	352.2 \pm 114.7					

In December 1993, microbial assemblages in standing litter remained active throughout the daytime with no significant fluctuations in rates of CO_2 release ($p = 0.11$, Kruskal-Wallis) (Fig. 2A). Cooler temperatures (Fig. 2B) and precipitation (Fig. 2C) in the afternoon hours prevented litter from drying. Rates of CO_2 evolution were lower than those recorded during warmer sampling periods, ranging between 3 and 96 $\mu\text{g CO}_2\text{-C g}^{-1}$ organic mass h^{-1} (Table 2). Water potentials of plant litter remained high until drying conditions contributed to the desiccation of litter on the last day of that study (Fig. 2C). Water potentials decreased from -1.4 to -6.3 MPa, with a corresponding decrease in microbial respiration rates (Fig. 2A). Even under relatively constant moisture and temperature conditions, airborne fungal spore concentrations still showed a diel

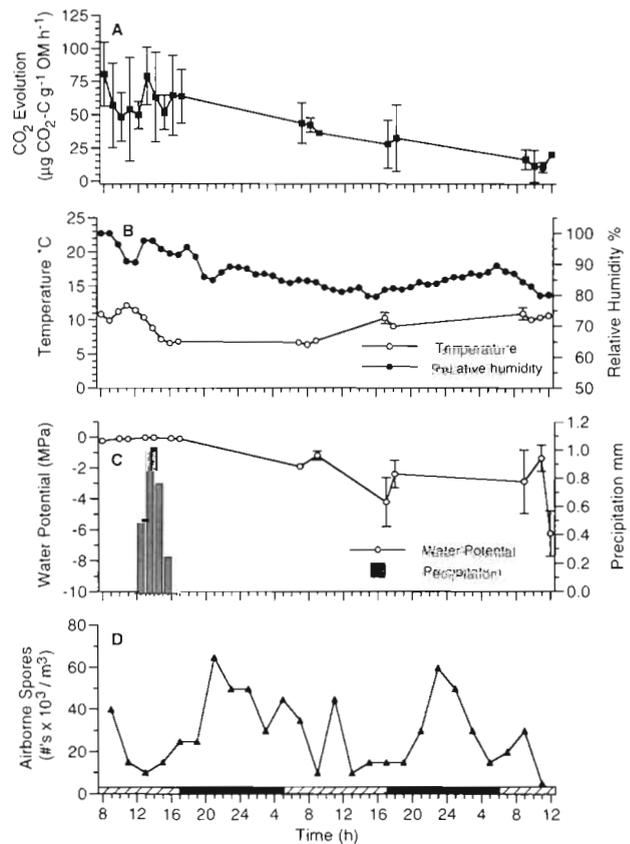


Fig. 2. Diel changes in (A) rates of CO_2 evolution from standing litter of *Juncus effusus* and (B) air temperatures and relative humidity above decaying litter on December 14–16, 1993. Diel changes in (C) precipitation and water potentials of plant litter and (D) airborne spore concentrations are also illustrated. Means \pm SD for CO_2 and temperature ($n = 2$); means \pm SE for water potential values ($n = 3$). Values for precipitation (mm) indicate the amount accumulated over a 1 h period. Symbols for airborne spore concentrations and relative humidity are single point measurements ($n = 1$). Dark horizontal bar on x-axis in (D) indicates nighttime; hatched horizontal bar indicates daytime

Table 3. Spearman rank-order correlation coefficients showing the relationship between rates of CO₂ evolution versus plant litter water potentials and environmental variables collected over the study period

Carbon dioxide in	vs Temperature	Relative humidity	Water potential	Light intensity	Wind speed
August 1993	-0.85***	0.72***	0.85***	-0.45**	-0.49***
September 1993	-0.17	-0.27	0.69**	-0.36**	-0.09
December 1993	-0.11	0.72***	0.76**	-0.30	-0.22
March 1994	-0.21	0.12	0.48**	-0.13	-0.17
June 1994	-0.40**	0.45**	0.75***	-0.44**	-0.39**
September 1994	-0.77***	0.37*	0.86***	-0.30	-0.14

***p < 0.001, **p < 0.01, *p < 0.05

pattern, with peak concentrations occurring at night (Fig. 2D). However, maximum concentrations were half those reported during warmer periods (Table 2).

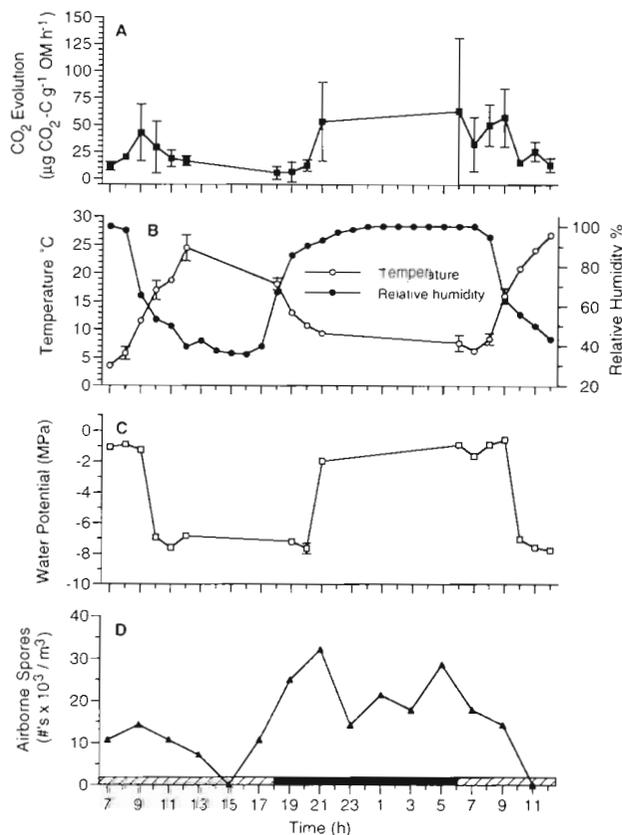


Fig. 3. Diel changes in (A) rates of CO₂ evolution from standing litter of *Juncus effusus* and (B) air temperatures and relative humidity above decaying litter on March 4–5, 1994. Diel changes in (C) water potentials of plant litter and (D) airborne spore concentrations are also illustrated. Means \pm SD for CO₂ and temperature (n = 2); means \pm SE for water potential values (n = 3). Symbols for airborne spore concentrations and relative humidity are single point measurements (n = 1). Dark horizontal bar on x-axis in (D) indicates nighttime; hatched horizontal bar indicates daytime

Rates of CO₂ evolution associated with standing litter in March 1994 were low and highly variable (Fig. 3A), with no significant differences in rates of CO₂ evolution observed (p = 0.13, Kruskal-Wallis). Both cold temperatures and low water potentials may have affected rates of respiration from standing litter during this study period. Low rates of CO₂ evolution were noted in the morning hours at the start of diel experiments when temperatures were low (3°C) (Fig. 3B), despite the presence of high litter water potentials (-1.0 MPa) (Fig. 3C). As the tempera-

tures increased during the day, litter water potentials decreased due to the drying of exposed plant matter. Water potentials remained low until dew formation on standing litter at night, leading to increased rates of microbial respiration. However, even under optimal moisture conditions, lower nighttime temperatures appeared to affect the respiratory rates of resident microbial assemblages. Rates of CO₂ evolution ranged between 0 and 111 $\mu\text{g CO}_2\text{-C g}^{-1}$ organic mass h^{-1} (Table 2). Airborne fungal spore concentrations continued to show a diel periodicity (Fig. 3D).

The remaining diel field studies (Table 2) consistently pointed to the availability of water (i.e. rainfall, dew formation) as an important factor affecting microbial respiratory activities in standing litter. In the absence of precipitation, a distinct diel response in rates of CO₂ evolution was observed, with increasing rates occurring only at night when high relative humidities resulted in dew condensation on standing litter. Maximum rates of CO₂ evolution were noted during the early predawn hours, when plant litter had been exposed to dew-forming conditions for several hours. Significant positive correlations were observed between rates of CO₂ evolution and plant litter water potentials during each field sampling date (Table 3). Furthermore, using combined data from all field dates, plant litter water potentials were a significant predictor of rates of CO₂ evolution (Fig. 4). Rates of CO₂ evolution ranged from below 15 (0 in March 1994) during periods of desiccation to as high as 285 $\mu\text{g CO}_2\text{-C g}^{-1}$ organic mass h^{-1} (June 1994) during periods of water saturation (Table 2). During the daytime, increasing temperatures led to the desiccation of standing litter and a decrease in rates of microbial respiration. However, temperatures exhibited significant negative correlations with respiratory activities only during sampling dates when maximum temperatures exceeded 30°C (Table 3). Average hourly rates of CO₂ evolution were significantly different among sampling dates (p < 0.05,

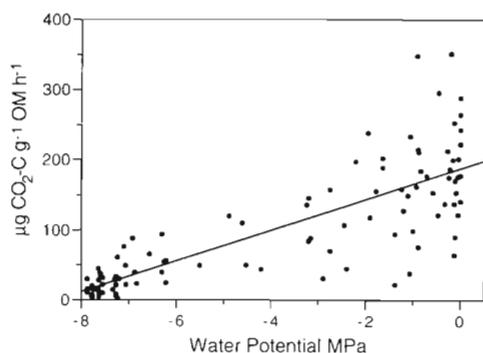


Fig. 4. Effect of litter water potentials on rates of CO_2 evolution from standing dead *Juncus effusus* litter using combined data from all field sampling dates. Rates of CO_2 evolution adjusted to a temperature of 25°C using a Q_{10} of 1.95. Linear regression model: rate of CO_2 evolution = $21.4(\text{water potential}) + 186$, $r^2 = 0.63$, $p < 0.0001$

Kruskal-Wallis), ranging between 33 and $153 \mu\text{g CO}_2\text{-C g}^{-1}$ organic mass h^{-1} , with lower rates occurring during periods of lower average temperatures (Table 2). Based on estimates of above ground standing detrital mass of *Juncus effusus* (annual mean 1310 g m^{-2} , range 571 to 2302 g m^{-2} ; R. G. Wetzel pers. comm.), the microbial respiration rates reported here represent a net carbon flux of between 1.37 and $3.35 \text{ g m}^{-2} \text{ d}^{-1}$ from microbiota inhabiting standing litter (Table 2).

Airborne fungal spore concentrations above decomposing *Juncus effusus* litter continued to show a diel pattern during the remaining field investigations, with the highest atmospheric concentrations occurring at night. In the absence of precipitation, airborne fungal spore concentrations were negatively correlated with light intensities and positively correlated with relative humidity (Table 4). However, spore concentrations were significantly correlated with rates of CO_2 release on only 1 sampling date (August). Spore concentrations were higher during

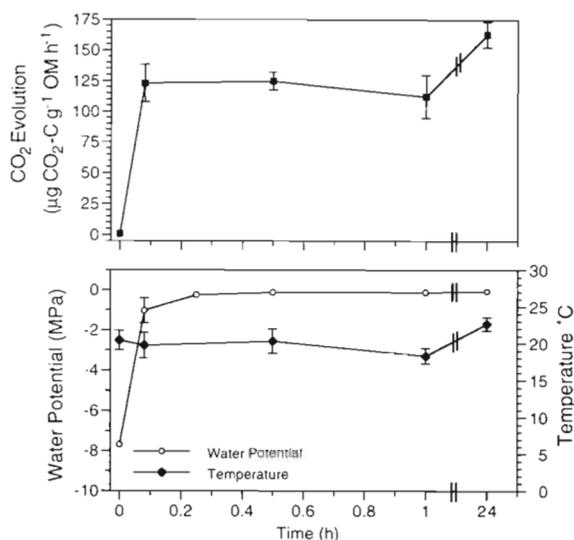


Fig. 5. Changes in rates of CO_2 evolution from standing dead *Juncus effusus* litter and corresponding plant litter water potentials after litter was wetted in the laboratory. Changes in temperature are also illustrated. Means \pm SE ($n = 3$)

the warmer periods of the year. Spores identified in collected air samples were small ($<10 \mu\text{m}$) hyaline spherical and rod shape spores, which were similar to spores of the dominant coelomycete and basidiomycete taxa identified from standing dead litter (i.e. *Phoma* sp., *Panellus copelandii* (Pat.) Burdsall & Miller, *Marasmiellus* sp.) (Kuehn & Suberkropp unpubl. data).

Ergosterol concentrations of decomposing *Juncus effusus* litter ranged between 296 and $399 \mu\text{g ergosterol g}^{-1}$ organic mass and were not significantly different among sampling periods ($p = 0.68$, ANOVA) (Table 2). Based on the conversion factor of $5 \mu\text{g ergosterol mg}^{-1}$ fungal mass (Gessner & Newell 1997) this represents 48 to $64 \text{ mg living fungal biomass g}^{-1}$ detrital organic mass.

Table 4. Spearman rank-order correlation coefficients showing the relationship between airborne spore concentrations versus environmental variables collected over the entire study period

Airborne spores in	vs Temperature	Relative humidity	Light intensity	Wind speed
August 1993	-0.92***	0.96***	-0.84***	-0.74***
September 1993	-0.08	0.88***	-0.87***	-0.75**
December 1993	-0.51**	0.14	-0.54**	-0.13
March 1994	-0.56**	0.69**	-0.83***	-0.63*
June 1994	-0.48	0.29	-0.15	-0.33
September 1994	-0.89***	0.81***	-0.79***	-0.56

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Laboratory studies

In the laboratory, microbial assemblages responded rapidly to being wetted (Fig. 5), under constant temperature conditions. Significant increases ($p < 0.001$, ANOVA) in rates of CO_2 evolution from leaf litter were observed within 5 min after exposure to water saturating conditions (from 2 to $123 \mu\text{g CO}_2\text{-C g}^{-1}$ organic mass h^{-1}). Rates of CO_2 evolution remained high for up to 24 h after initial wetting with

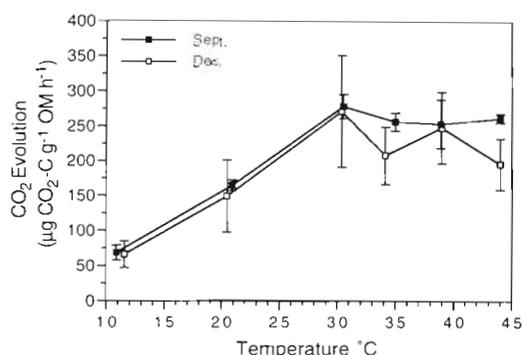


Fig. 6. Effect of temperature on rates of CO₂ evolution from water saturated leaves of standing dead *Juncus effusus* in the laboratory. Means \pm SE (n = 3)

no significant change in rates of CO₂ released ($p > 0.05$, ANOVA, Tukey). Rates of CO₂ evolution were positively correlated with changes in plant litter water potentials ($r = 0.92$, $p < 0.001$, Pearson). No significant changes in ergosterol contents were noted after wetting of plant litter ($p > 0.05$, ANOVA).

When wetted, microbial assemblages associated with standing dead litter also responded to changes in temperature (Fig. 6). As the temperature was increased from 10 to 30°C, the rate of CO₂ evolution from water saturated plant litter increased markedly. From 10 to 30°C, the relationship between CO₂ evolution and temperature could be described by the exponential model: (September 1993, $C = 40.0e^{0.064T}$, $r^2 = 0.98$, $p < 0.001$); (December 1993, $C = 32.6e^{0.070T}$, $r^2 = 0.85$, $p < 0.001$; where C is the rate of CO₂ evolution and T is temperature in °C). The calculated Q₁₀ for data spanning this range in both experiments averaged 1.95. Rates of CO₂ evolution at temperatures exceeding 30°C remained high, but leveled off between 200 and 278 µg CO₂-C g⁻¹ organic mass h⁻¹ (Fig. 6).

DISCUSSION

Results obtained in this study indicate that microbial colonization of *Juncus effusus* litter occurred while in the standing dead phase. Fungal biomass associated with standing *J. effusus* litter in the present study varied between 5 and 6% of the total detrital dry weight, and is similar to values reported previously for standing dead litter in marine and freshwater habitats (Newell & Fallon 1989, Newell et al. 1989, 1995, 1996, Newell 1993). Furthermore, measurement of rates of CO₂ evolution indicated that significant mineralization of plant litter can occur while it is in the exposed standing position, before it comes in contact with microbial assemblages associated with the water or surface sediments. Thus, standing *J. effusus* litter has a well-

established microbiota, which appears to be metabolically adapted to the cyclic environmental conditions that are experienced while in the standing dead phase.

In the present study, both field and laboratory investigations indicated that the water potential of plant litter was a major factor affecting microbial respiration. These results agree with previous studies of standing salt marsh litter, which found that plant litter moisture contents significantly affect the rates of both CO₂ evolution and litter mass loss (e.g. Gallagher et al. 1984, Newell et al. 1985, Halupa & Howes 1995). Halupa & Howes (1995) established that tidally mediated moisture contents were a dominant factor controlling standing litter decay of *Spartina alterniflora* Loisel. and *Spartina patens* (Ait.) Muhl. Standing dead litter exposed to greater frequency and magnitude of tidal inundation experienced greater rates of decay versus plant litter found higher in the tidal zone. In addition, under laboratory conditions, respiratory activity of microbial decomposers in standing litter increased significantly as moisture content increased (Halupa & Howes 1995). In an earlier study, Newell et al. (1985) found that respiratory activity of microbial assemblages associated with standing dead salt marsh litter can fluctuate rapidly after exposure to wetting (dew-formation) or drying conditions. During periods of desiccation (water content <30%, ~ -6.0 MPa, see Newell et al. 1991), microbiota associated with plant litter of both *S. alterniflora* and *Juncus roemerianus* Scheele released CO₂ at very low rates (1 to 10 µg CO₂-C g⁻¹ dry wt h⁻¹). However, upon exposure to water (water content >50%, ~ -2.5 MPa), rates of CO₂ evolution from plant litter increased dramatically (>100 µg CO₂-C g⁻¹ dry wt h⁻¹), maintaining high rates until exposure to drying conditions (Newell et al. 1985).

In a more recent study, Newell et al. (1996) found that frequent periodic misting of standing *Spartina alterniflora* litter had a negative effect on fungal productivity and densities of ascospores of *Phaeosphaeria spartinicola* Leuchtman, the predominant fungal decomposer of standing dead leaf blades of *S. alterniflora*. These findings provide evidence that fungal decomposers of *S. alterniflora* litter are adapted to the standing dead environment, and are apparently dependent upon the cyclic episodes of desiccation/wetness for optimal growth and reproduction (Newell et al. 1996). In the present study, large increases in fungal spore concentrations above decomposing plant litter occurred at night, during periods of high water availability. These results suggest that fungal decomposers of *Juncus effusus* and other substrates may require dark conditions and/or increased nighttime moisture conditions for release of spores. Moisture requirements for spore release have been documented in several fungal species (Ingold 1971).

Maximum rates of CO₂ evolution observed for litter of *Juncus effusus* are within the range reported for standing litter in salt marsh habitats (Gallagher & Pfeiffer 1977, Gallagher et al. 1984, Newell et al. 1985, 1989, 1996, Buth & Voeselek 1988, Newell & Fallon 1989, Halupa & Howes 1995). However, the values reported in many of these studies represent only the maximum rates of CO₂ evolution possible, as plant litter samples were submersed or saturated with water prior to incubation and measurement. The present study and those of Gallagher et al. (1984) and Newell et al. (1985) represent the only investigations that have determined rates of CO₂ evolution from standing litter under natural field moisture conditions. Furthermore, to our knowledge, Newell et al. (1985) is the only published study that examined changes in rates of microbial respiration in standing litter over short time scales. The results of the present study show that the activities of the microbiota associated with standing litter in freshwater environments respond to wetting as rapidly as standing litter in salt marsh systems.

It is not surprising that the dynamics of standing litter decay have been largely neglected, since measurements of CO₂ evolution from standing litter during the day would reveal very low rates of respiration from inhabitant microbiota. Such observations could lead to the assumption that colonization and subsequent microbial decay of plant litter commences only as plant litter falls to the sediment-water interface. However, in this case, the researcher has imposed a '...perceptual bias, a filter through which the system is viewed.' (Levin 1992). It is only when these rates are examined at a finer temporal scale that we begin to distinguish and appreciate the potential contribution and adaptive qualities of microbial assemblages inhabiting standing litter. The rationale behind this argument is illustrated in the present study (Fig. 1A), where peak metabolic activities of microbial decomposers occurred primarily at night when field investigations are not likely to be conducted.

The effect of temperature on microbial respiratory activities in standing dead litter further illustrates how completely different conclusions can be drawn at different observational scales. When examined on a fine temporal scale (hours), increasing temperature had a negative effect on microbial activities, as high temperatures contributed to the desiccation of plant litter and caused increased water stress of inhabitant microbiota. However, when analyzed over an annual cycle, increasing temperature had a significant positive relationship with maximum rates of CO₂ evolution ($r = 0.69$, $p < 0.01$, Pearson), since higher nighttime temperatures during the summer together with optimal moisture conditions resulted in higher rates of microbial respiration. Therefore, the relationship between

respiration and temperature (and possibly other environmental factors) may vary depending on the specific scale of observation.

Carbon dioxide emission rates have been reported from a variety of wetland habitats (Table 5). However, in wetland habitats dominated by emergent macrophytes, very few studies have attempted to incorporate the contribution of above-ground microbial decomposers (standing dead litter) in CO₂ flux measurements. Emphasis has often been placed on the dynamics of plant litter decay in the sediments, by determining rates of carbon mineralization from sediment cores (e.g. Howes et al. 1985, Nyman & DeLaune 1991, Updegraff et al. 1995), or from small *in situ* chambers in which above-ground plant material had been removed (e.g. Smith et al. 1983, Luken & Billings 1985, Kim & Verma 1992, Martikainen et al. 1995, Silvola et al. 1996). Additional studies have monitored CO₂ emissions from wetlands using chambers that may have included standing plant litter (Whiting 1994, Paludan & Blicher-Mathiesen 1996). However, these studies were conducted under conditions in which the respiratory activity of microbial inhabitants in standing litter is likely to be minimal (i.e. daytime desiccating conditions). Whiting (1994) used a large climate controlled incubation chamber (see Whiting et al. 1992) to monitor net CO₂ flux from a *Carex*-dominated wetland. During these studies, the chamber temperature was decreased and the chamber was shaded during the day in an attempt to simulate natural nighttime conditions. However, the chamber was equilibrated for only 20 to 30 min prior to gas flux measurements. Such short-term incubations may not allow time for sufficient dew formation on standing litter, and may result in nearly minimal activities from inhabitant microbiota. Thus, CO₂ flux rates reported in these investigations may be an underestimate, since the contribution of above-ground microbial assemblages was nearly or fully excluded from total gas flux measurements.

In another recent study, Magenheimer et al. (1996) also used large incubation chambers to measure CH₄ and CO₂ emissions from salt marsh habitats in New Brunswick, Canada, where standing dead plant matter is known to occur (Samiaji & Bärlocher 1996). However, the timing of chamber incubation and sampling (daytime vs nighttime) was not clearly indicated. Thus, it is not clear whether respiratory activities of microbial assemblages inhabiting standing litter were incorporated in the reported gas flux estimates. Diel studies which use large chambers that include above-ground vegetation may incorporate respiratory activities of microbial decomposers inhabiting standing litter (e.g. Grulke et al. 1990, Whiting et al. 1992, Vourlitis et al. 1993, Yavitt 1994). If standing litter is exposed to natural wetting conditions (i.e. precipitation, dew) prior to

Table 5. Rates of CO₂ release reported from various wetland habitats and estimates from standing dead plant litter. Conditions of flux incubations: PS, peat surface; SS, sediment surface; SDL, standing dead litter. NR: not recorded. (–) Above-ground vegetation clipped and removed prior to flux measurements. (+) Flux measurements including above-ground vegetation and litter. (*) Flux measurements taken from the sediment surface adjacent to *Juncus effusus* plant tussocks; flux measurements do not include above-ground vegetation or litter

g CO ₂ -C m ⁻² d ⁻¹		Temperature (°C)	Location	Conditions	Habitat	Source
Average	Range	Range				
9.80	2.70 – 16.70	7 – 20	Minnesota, USA	PS, –	Bog	Kim & Verma (1992)
1.92	0.05 – 7.20	–4 – 22	West Virginia, USA	PS, +	Freshwater bog	Yavitt et al. (1993) ^a
			Ontario, Canada		Freshwater	Whiting (1994)
9.25	0.84 – 22.46	11 – 33		PS, +	Bog	
5.67	1.73 – 10.37	18 – 23		PS, +	Interior fen	
7.16	1.73 – 12.96	14 – 30		PS, +	Coastal fen	
0.78	0.03 – 2.99	NR	Maryland /	PS, +	Bog	Yavitt (1994)
1.76	0.00 – 6.22	NR	West Virginia, USA	PS, +	Swamp	
1.13	0.03 – 4.09	NR		PS, +	Marsh	
0.52	0.43 – 10.80	0 – 18	Finland	PS, –	Fen	Martikainen et al. (1995)
0.46	0.74 – 7.68	0 – 19		PS, –	Bog	
2.50	0.30 – 3.70	NR	New Brunswick	PS, –	Salt marsh	Magenheimer et al. (1996)
			Denmark	PS, +	Forested wetland	Paludan & Blicher-Mathiesen (1996)
0.63	0.30 – 1.26	0.7 – 13			Site 1 (LN)	
0.27	0.11 – 0.42	2 – 14			Site 2 (LF)	
			Finland	PS, –	Fen (virgin)	Silvola et al. (1996)
0.79	1.80 – 10.80	5 – 20			Sedge site (L–21)	
1.24	0.12 – 2.44	7 – 20	Alabama, USA	SS, *	Forested swamp	Roden & Wetzel (1996)
			Alabama, USA	SDL	Forested swamp	This study
2.33	1.37 – 3.35	3 – 36			<i>Juncus effusus</i> L.	
			Georgia, USA	SDL	Salt marsh	Newell et al. (1996) ^b
					<i>Spartina alterniflora</i> Loisel.	
0.62	0.00 – 1.66	10 – 30			Short form	
1.67	0.00 – 4.46	10 – 30			Tall form	

^aMedian CO₂ release in g CO₂-C m⁻² d⁻¹
^bCO₂ flux based on average respiration rate of 75 µg CO₂-C g⁻¹ dry wt h⁻¹ from standing litter (see Newell et al. 1985), and detrital mass of 930 and 345 g m⁻² for standing dead litter of tall and short form *S. alterniflora*, respectively (see Gallagher et al. 1980)

chamber incubations, then such diel studies would provide a more accurate assessment of CO₂ emissions from wetlands dominated by emergent macrophytes.

Rates of CO₂ evolution from microbial assemblages inhabiting standing litter of *Juncus effusus* were within the range of CO₂ flux rates reported from other wetland habitats, and are equal to or exceed those CO₂ flux rates reported for sediments from this same wetland system (see Roden & Wetzel 1996) (Table 5). These findings suggest that microbial assemblages inhabiting standing litter can make a significant contribution to total ecosystem metabolism. Furthermore, our findings support Newell et al. (1985) who reported the potential for high CO₂ flux from standing litter in salt marsh systems. The increasing evidence that standing dead litter of emergent macrophytes supports an active microbiota (Newell 1993, 1996) and serves as major conduits for plant gas exchange (e.g. Brix 1990, Brix et al. 1996, Whiting & Chanton 1996) suggests that standing litter may play a greater role in CO₂ emissions from wetlands than previously considered. Further-

more, high rates of CO₂ evolution from standing litter in wetland habitats may have potential ramifications for CO₂ flux measurements in terrestrial systems, particularly grasslands, which are known to have a substantial standing dead component (Seastedt 1988).

Acknowledgements. The authors thank Dr R. G. Wetzel for the use of LiCor instrumentation and Dr G. M. Ward for access to meteorological-station field data. We also express gratitude to Drs P. F. Churchill, R. V. Gessner, M. O. Gessner, S. Y. Newell, and R. G. Wetzel, Mr Colin Jackson and 3 anonymous reviewers for their comments on an earlier version of this manuscript. This research was supported by a grant OSR 9108761 from the National Science Foundation, and by a Sigma Xi Grant-in-Aid of Research to K.A.K.

LITERATURE CITED

- Apinis AE, Chesters CGC, Taligoola HK (1975) Microfungi colonizing nodes and internodes of aerial standing dead culms of *Phragmites communis* Trin. Nova Hedwigia 26: 495–507

- Bärlocher F, Biddiscombe NR (1996) Geratology and decomposition of *Typha latifolia* and *Lythrum salicaria* in a freshwater marsh. *Arch Hydrobiol* 136:309–325
- Bridgman SD, Johnston CA, Pastor J, Updegraff K (1995) Potential feedbacks of northern wetlands on climate change. *BioSci* 45:262–274
- Brix H (1990) Gas exchange through the soil-atmosphere interphase and through dead-culms of *Phragmites australis* in a constructed reed bed receiving domestic sewage. *Water Res* 24:259–266
- Brix H, Sorrell BK, Schierup HH (1996) Gas fluxes achieved by *in situ* convective flow in *Phragmites australis*. *Aquat Bot* 54:151–163
- Buth GJC, Voeselek LACJ (1988) Respiration of standing and fallen plant litter in a Dutch salt marsh. In: Verhoeven JTA, Heil GW, Werger MJA (eds) *Vegetation structure in relation to carbon and nutrient economy*. SPG Academic Publishing, The Hague, p 51–60
- Christian RR, Bryant WL, Brinson MM (1990) *Juncus roemerianus* production and decomposition along gradients of salinity and hydroperiod. *Mar Ecol Prog Ser* 68:137–145
- Gallagher JL, Kibby HV, Skirvin KW (1984) Community respiration of decomposing plants in Oregon estuarine marshes. *Estuar Coast Shelf Sci* 18:421–431
- Gallagher JL, Pfeiffer WJ (1977) Aquatic metabolism of the communities associated with attached dead shoots of salt marsh plants. *Limnol Oceanogr* 22:562–565
- Gallagher JL, Reimold RJ, Linthurst RA, Pfeiffer WJ (1980) Aerial production, mortality, and mineral accumulation-export dynamics in *Spartina alterniflora* and *Juncus roemerianus* plant stands in a Georgia salt marsh. *Ecology* 61:303–313
- Gessner MO, Newell SY (1997) Bulk quantitative methods for the examination of eukaryotic organoosmotrophs in plant litter. In: Hurst CJ, Knudsen GR, Melueruey MJ, Stetzenbach LD, Walter MV (eds) *Manual of environmental microbiology*. American Society for Microbiology, Washington, DC, p 295–308
- Gessner MO, Schieferstein B, Müller U, Barkmann S, Lenfers UA (1996) A partial budget of primary organic carbon flows in the littoral zone of a hardwater lake. *Aquat Bot* 55:93–105
- Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecol Appl* 1:182–195
- Gorham E (1994) The future of research in Canadian peatlands: a brief survey with particular reference to global change. *Wetlands* 14:206–215
- Grulke NE, Riechers GH, Oechel WC, Hjelm U, Jaeger C (1990) Carbon balance in tussock tundra under ambient and elevated atmospheric CO₂. *Oecologia* 83:485–494
- Halupa PJ, Howes BL (1995) Effects of tidally mediated litter moisture content on decomposition of *Spartina alterniflora* and *S. patens*. *Mar Biol* 123:379–391
- Howes BL, Dacey JH, Teal JM (1985) Annual carbon mineralization and belowground production of *Spartina alterniflora* in a New England salt marsh. *Ecology* 66:595–605
- Ingold CT (1971) *Fungal spores: their liberation and dispersal*. Clarendon Press, Oxford
- Jordan TE, Whigham DF (1988) The importance of standing dead shoots of the narrow leaved cattail *Typha angustifolia* L. *Aquat Bot* 29:319–328
- Kim J, Verma SB (1992) Soil surface CO₂ flux in a Minnesota peatland. *Biogeochemistry* 18:37–51
- Kohlmeyer J, Volkmann-Kohlmeyer B, Eriksson OE (1995) Fungi on *Juncus roemerianus*. 4. New marine ascomycetes. *Mycologia* 87:532–542
- Kohlmeyer J, Volkmann-Kohlmeyer B, Eriksson OE (1996) Fungi on *Juncus roemerianus*. 8. New bitunicate ascomycetes. *Can J Bot* 74:1830–1840
- Kramer CL, Eversmeyer MG, Collins TI (1976) A new 7-day spore sampler. *Phytopathology* 66:60–61
- Lee SY (1990) Net aerial primary productivity, litter production and decomposition of the reed *Phragmites communis* in a nature reserve in Hong Kong: management implications. *Mar Ecol Prog Ser* 66:161–173
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967
- LiCor Inc. (1987) *The LI-6200 primer: an introduction to operating the LI-6200 portable photosynthesis system*. LiCor Inc, Lincoln, NE
- Luken JO, Billings WD (1985) The influence of microtopographic heterogeneity on carbon dioxide efflux from a subarctic bog. *Holarct Ecol* 8:306–312
- Magenheimer JF, Moore TR, Chmura GL, Daoust RJ (1996) Methane and carbon dioxide flux from a microtidal salt marsh, Bay of Fundy, New Brunswick. *Estuaries* 19:139–145
- Mann KH (1988) Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. *Limnol Oceanogr* 33:910–930
- Martikainen PJ, Nykänen H, Alm J, Silvola J (1995) Changes in fluxes of carbon dioxide, methane and nitrous oxide due to forest drainage of mire sites of different trophic. *Plant Soil* 168–169:571–577
- Mitsch WJ, Gosselink JG (1993) *Wetlands*, 2nd edn. Van Nostrand Reinhold, New York
- Moore TR (1994) Trace gas emissions from Canadian peatlands and the effect of climatic change. *Wetlands* 14:223–228
- Newell SY (1993) Decomposition of shoots of a saltmarsh grass: methodology and dynamics of microbial assemblages. *Adv Microb Ecol* 13:301–326
- Newell SY (1996) Established and potential impacts of eukaryotic mycelial decomposers in marine/terrestrial ecotones. *J Exp Mar Biol Ecol* 200:187–206
- Newell SY, Arsuffi TL, Kemp PF, Scott LA (1991) Water potential of standing-dead shoots of an intertidal grass. *Oecologia* 85:321–326
- Newell SY, Arsuffi TL, Palm LA (1996) Misting and nitrogen fertilization of shoots of a saltmarsh grass: effects upon fungal decay of leaf blades. *Oecologia* 108:495–502
- Newell SY, Fallon RD (1989) Litterbags, leaf tags and decay of nonabscised intertidal leaves. *Can J Bot* 67:2324–2327
- Newell SY, Fallon RD, Cal Rodriguez RM, Groene LC (1985) Influence of rain, tidal wetting and relative humidity on release of carbon dioxide by standing-dead salt-marsh plants. *Oecologia* 68:73–79
- Newell SY, Fallon RD, Miller JD (1989) Decomposition and microbial dynamics for standing, naturally positioned leaves of the salt marsh grass *Spartina alterniflora*. *Mar Biol* 101:471–481
- Newell SY, Moran MA, Wicks R, Hodson RE (1995) Productivities of microbial decomposers during early stages of decomposition of leaves of a freshwater sedge. *Freshwat Biol* 34:135–148
- Nyman JA, DeLaune RD (1991) CO₂ emission and soil Eh responses to different hydrological conditions in fresh, brackish and saline marsh soils. *Limnol Oceanogr* 36:1406–1414
- Paludan C, Blicher-Mathiesen G (1996) Losses of inorganic carbon and nitrous oxide from a temperate freshwater wetland in relation to nitrate loading. *Biogeochemistry* 35:305–326

- Roden EE, Wetzel RG (1996) Organic carbon oxidation and suppression of methane production by microbial Fe(III) oxide reduction in vegetated and unvegetated freshwater wetland sediments. *Limnol Oceanogr* 41:1733–1748
- Samiaji J, Bärlocher F (1996) Geratology and decomposition of *Spartina alterniflora* Loisel in a New Brunswick salt-marsh. *J Exp Mar Biol Ecol* 201:233–252
- Seastedt TR (1988) Mass, nitrogen and phosphorus dynamics in foliage and root detritus of tallgrass prairie. *Ecology* 69:59–65
- Silvola J, Alm J, Ahlholm U, Nykänen H, Martikainen PJ (1996) CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions. *J Ecol* 84:219–228
- Smith CJ, Delaune RD, Patrick WH Jr (1983) Carbon dioxide emission and carbon accumulation in coastal wetlands. *Estuar Coast Shelf Sci* 17:21–29
- Smith EG (1990) Sampling and identifying allergenic pollens and molds. Blewstone Press, San Antonio, TX
- Suberkropp K, Weyers H (1996) Application of fungal and bacterial production methodologies to decomposing leaves in streams. *Appl Environ Microbiol* 62:1610–1615
- Teal JM (1962) Energy flow in a salt marsh ecosystem of Georgia. *Ecology* 43:614–624
- Thormann MN, Bayley SE (1997) Decomposition along a moderate-rich fen-marsh peatland gradient in boreal Alberta, Canada. *Wetlands* 17:123–137
- Updegraff K, Pastor J, Bridgham SD, Johnston CA (1995) Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. *Ecol Appl* 5:151–163
- Vourlitis GL, Oechel WC, Hastings SJ, Jenkins MA (1993) A system for measuring *in situ* CO₂ and CH₄ flux in unmanaged ecosystems: an arctic example. *Funct Ecol* 7:369–379
- Wescor Inc (1986) Instruction/service manual HR-33T dew point microvoltmeter. Wescor Inc, Logan, UT
- Wetzel RG (1990) Land-water interfaces: metabolic and limnological regulators. *Verh Internat Verein Theor Angew Limnol* 24:6–24
- Whiting GJ (1994) CO₂ exchange in the Hudson Bay lowlands: community characteristics and multispectral reflectance properties. *J Geophys Res* 99(D):1519–1528
- Whiting GJ, Bartlett DS, Fan S, Bakwin PS, Wofsy SC (1992) Biosphere/atmosphere CO₂ exchange in tundra ecosystems: community characteristics and relationships with multispectral surface reflectance. *J Geophys Res* 97(D):16671–16680
- Whiting GJ, Chanton JP (1996) Control of the diurnal pattern of methane emission from emergent aquatic macrophytes by gas transport mechanisms. *Aquat Bot* 54:237–253
- Yavitt JB (1994) Carbon dynamics in appalachian peatlands of West Virginia and Western Maryland. *Water Air Soil Pollut* 77:271–290
- Yavitt JB, Wieder RK, Lang GE (1993) CO₂ and CH₄ dynamics of a *Sphagnum*-dominated peatland in West Virginia. *Global Biogeochem Cycles* 7:259–274

Editorial responsibility: John Dolan,
Villefranche-sur-Mer, France

Submitted: July 3, 1997; Accepted: October 13, 1997
Proofs received from author(s): January 23, 1998