DIEL MINERALIZATION PATTERNS OF STANDING-DEAD PLANT LITTER: IMPLICATIONS FOR CO$_2$ FLUX FROM WETLANDS

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Abstract. We examined the effects of environmental conditions on the microbially mediated CO$_2$ evolution from standing-dead litter (leaf blades, leaf sheaths, and culms) of the common reed, *Phragmites australis* (Cav.) Trin. ex Steud., in two temperate littoral freshwater marshes. Water availability was the major factor affecting CO$_2$ evolution rates. In the laboratory, microbial assemblages responded rapidly to controlled additions of water, with large increases in CO$_2$ evolution occurring within five minutes after wetting of litter (e.g., leaf blades: 10–295 μg CO$_2$-C·(g ash-free dry mass [AFDM])$^{-1}$·h^{-1}). Under field conditions, CO$_2$ evolution in the absence of precipitation exhibited a pronounced diel periodicity, with the highest rates occurring during periods of increased water availability resulting from a temperature-induced rise in relative humidity (>95%) and corresponding litter water potential (>−2.0 MPa) during nighttime. For example, in October, rates of CO$_2$ evolution over a 24-h cycle ranged from 5 to 223 μg CO$_2$-C·(g AFDM)$^{-1}$·h^{-1} for leaf blades and from 10 to 155 μg CO$_2$-C·(g AFDM)$^{-1}$·h^{-1} for leaf sheaths. Maximum rates of CO$_2$ evolution from sheaths were consistently lower than those for leaf blades (by ~25%), but were typically an order of magnitude higher than those observed from culm litter (e.g., 1.0–18 μg CO$_2$-C·(g AFDM)$^{-1}$·h^{-1} over a diel cycle in August) exposed to identical environmental conditions. Much of the differences in maximum CO$_2$ evolution rates from different litter types were related ($r^2 = 0.72$) to differences in litter associated fungal biomass (leaf blades 34–74 mg dry mass/g AFDM, leaf sheaths 16–67 mg dry mass/g AFDM, and culms 2–7 mg dry mass/g AFDM), which was estimated from litter ergosterol concentrations. Based on measured stocks of standing-dead plant litter, estimated daily CO$_2$ flux from standing-dead shoots ranged between 51 and 570 mg C/m^2 of wetland surface area. These values translate into a roughly estimated annual carbon mineralization equivalent to a mean of 8% (leaf blades), 29% (leaf sheaths), and 3% (culms) of net aboveground plant production. These data provide compelling evidence that microbial decomposition of plant litter in the aerial standing-dead phase can contribute appreciably to overall carbon flux from marshes to the atmosphere, even in cool temperate climates, where most wetlands occur.

Key words: carbon cycling; CO$_2$ flux; decomposition; diel patterns; fungi; macrophytes; organic matter; Phragmites; *respiration; standing-dead litter; temperate wetlands.*

INTRODUCTION

Wetlands occupy only 4–6% of the earth's land surface, yet many are considered to be globally important carbon stores due to their often large annual plant production (particularly marshes and swamps) and anaerobic sediments that favor the slow decomposition and accumulation of plant derived organic matter (e.g., Matthews and Fung 1987, Mitsch and Gosselink 2000). Increases in temperature and anthropogenic changes in flooding regimes of wetlands predicted by global change scenarios may lead to enhanced litter decomposition, thereby shifting wetlands from net carbon sinks to sources of atmospheric CO$_2$ and/or CH$_4$ (e.g.,

Gorham 1991, Bridgham et al. 1995, Chapin et al. 2000, Moore 2002). Consequently, in view of the potential positive feedback of wetland carbon dynamics on climate change, global-scale predictions of future atmospheric emissions of CO$_2$ and CH$_4$ require a sound understanding of the underlying pathways and mechanisms controlling carbon cycling and gas fluxes from wetland ecosystems (Gorham 1994, Bridgham et al. 1995, Chapin et al. 2000).

In many wetlands, including freshwater marshes and littoral zones of lakes, emergent vascular plants, such as *Typha*, *Phragmites*, *Carex*, and *Juncus*, frequently constitute a major fraction of organic matter produced (e.g., Gessner et al. 1996, Kvêt and Westlake 1998, Wetzel and Howe 1999, Windham 2001). Most of this plant biomass is not consumed during the growing season (e.g., Dvorák and Imhof 1998, Wetzel and Howe 1999), but eventually enters the detrital pool, where it is transformed and mineralized by microbial assem-

blages and detritus-feeding consumers. As a result, many characteristics related to wetland carbon cycling and energy flow are regulated by the metabolic activities of microbial assemblages associated with decaying plant material.

Past analyses of emergent wetland plant decay have generally ignored an important phenologic characteristic during the plants' life cycle. In many emergent macrophytes, as well as other grass-like plants, the collapse of aboveground plant matter and incorporation of plant litter into the sediments does not typically occur immediately after shoot senescence and death. Much of the dead plant matter remains in an aerial standing-dead position for extended periods (Newell 1993), resulting in conspicuously large amounts of standing-dead plant matter in wetland habitats for much of the year (e.g., Findlay et al. 1990, Windham 2001, Asaeda et al. 2002).

It has been known for well over 100 years that fungi pervasively colonize and reproduce on and within standing-dead litter of wetland plants. For example, Saccardo (1898) reported 168 fungal taxa associated with shoots of the common reed, *Phragmites australis* (Cav.) Trin. ex Steud., and to date, over 600 species of fungi have been recorded from this single cosmopolitan plant species (Apinis et al. 1972, 1975, Poon and Hyde 1998). Despite the wealth of qualitative evidence and detailed studies on plant litter decay and carbon cycling at wetland sediment and soil surfaces (e.g., Brinson et al. 1981, Updegraff et al. 1995, Emery and Perry 1996, Aerts and de Caluwe 1997, Thormann and Bayley 1997, Bridgham et al. 1998, Aerts et al. 1999, Windham 2001, Larmola et al. 2003), quantitative data on microbially mediated carbon dynamics associated with standing-dead litter (Newell et al. 1995, Gessner 2001, Newell 2001, Findlay et al. 2002, Welsch and Yavitt 2003) and their potential contribution to total wetland ecosystem metabolism are scarce (Newell et al. 1985, Kuehn and Suberkropp 1998, Newell 2001). This discrepancy suggests that our current knowledge of wetland plant decay and carbon and nutrient dynamics is incomplete and potentially biased.

Results from subtropical climates suggest that microbiota, particularly fungi, associated with standing-dead wetland plants are well adapted to the fluctuating temperature and moisture conditions that prevail in that type of habitat (Kuehn et al. 1998). In the absence of precipitation, microbial decomposers become active at night when water becomes available as a result of dew formation on plant litter surfaces (Newell et al. 1985, Kuehn and Suberkropp 1998). In contrast, during the day, microbial activity virtually ceases as a result of desiccation stress. This regular diel pattern suggests that microbial decomposers may mineralize a portion of the total plant carbon prior to the collapse of leaves and shoots to the sediments, a pathway of carbon flow that has potentially gone unnoticed in past chamber-based estimates of wetland CO$_2$ flux. Consequently,

metabolic activities of standing-litter microbial communities may represent a source of CO$_2$ emission from wetlands that is missing in extant budgets of carbon flux at the ecosystem scale.

The central question addressed in the present investigation is whether microbially mediated carbon release from standing-dead litter in temperate wetlands follows similar diel patterns as observed in subtropical climates (e.g., Newell et al. 1985, Kuehn and Suberkropp 1998). Are diel changes in temperature and relative air humidity sufficient to bring about substantial CO$_2$ evolution during the night in cooler climates, where most wetlands occur on a global scale (Mitsch and Gosselink 2000)? In addition, we sought (a) to determine the extent to which CO$_2$ evolution differs among plant tissues of differing structural and chemical characteristics (i.e., leaf blades, leaf sheaths, and culms), (b) to test whether such differences are related to litter-associated living fungal biomass (ergosterol), and (c) to provide an estimate of the contribution of CO$_2$ flux from standing-dead litter to total wetland metabolism and atmospheric gas emission. Littoral marshes of the common reed, *P. australis*, were chosen as the model system for this study, since this plant is distributed worldwide, typically forms extensive monospecific stands and is a dominant wetland plant throughout much of Eurasia. Furthermore, *P. australis* is aggressively invading both freshwater and salt marshes in North America, where it replaces native wetland vegetation such as cattail and cordgrass (Findlay et al. 2002, Saltonstall 2002).

METHODS

Field sites

Field studies were conducted in permanently aquatic reed stands in the littoral zones of two lakes (Table 1). One of the stands was located in western Switzerland on the southeastern shore of Lake Neuchâtel, an oligotrophic hardwater lake. This reed stand is specifically located in the Grande Cariçaie, a wetland of national importance near the village of Forel. The second site was situated within a littoral reed stand on the eastern shore of Lake Hallwil, a eutrophic hardwater lake in central Switzerland, northwest of the city of Lucerne. *Phragmites australis* is the dominant emergent macrophyte in both lakes, forming dense, monospecific stands. More detailed information on the lakes and the two study sites is provided in Komínková et al. (2000) and Buesing (2002).

Temperature and relative humidity were continuously monitored during field studies using Onset Hobo H8 Pro series data loggers (accuracy of ±3.0% relative humidity; Onset Computer, Pocasset, Massachusetts, USA) placed at middle height in the canopy within the reed stands. Precipitation data was provided by the Swiss Meteorological Institute from official stations located near each study site.[2]

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[2] ⟨http://www.meteoswiss.ch/en/index.shtml⟩

TABLE 1. Selected characteristics of Lakes Neuchâtel and Hallwil, and of the littoral reed stands where litter samples were collected.

Characteristics	Lake Neuchâtel	Lake Hallwil
Location coordinates	46°54′ N, 6°54′ E	47°17′ N, 8°14′ E
Lake surface area (km²)	215	10
Width of reed stand (m)	50	800
Water depth within reed stand (m)	0.3–1.0	0.3–0.7
Shoot density (shoots/m²)	42 ± 12	47 ± 12
Shoot height (m)	3.11 ± 0.35	3.05 ± 0.40
Culm diameter (mm)	10.0 ± 1.2	8.4 ± 0.9
Maximum aboveground biomass (g AFDM·m⁻²·yr⁻¹)	2326 ± 627	1177 ± 335

Notes: Values are the means ± 1 SD or ranges. ''AFDM'' indicates ash-free dry mass.

Shoot biomass

Aboveground standing-dead shoot mass of *P. australis* was determined monthly at both field sites in order to provide estimates of carbon mineralization from standing-dead litter on an aerial basis. At Lake Hallwil, shoot densities (shoots/m²) were randomly determined in one subplot (0.25 m²) within each of six permanently established transects (~15 m) running perpendicular to the lakeshore through the reed stand (Buesing 2002). These transects were located adjacent to the sites where diel studies were conducted. At Lake Neuchâtel, shoot densities were estimated based on the persistence through time of 200 shoots randomly tagged at the end of the growing season along a ~50 m transect running parallel to the lakeshore through the center of the reed stand. Shoot densities at the time of tagging were determined in six randomly selected plots along the reed transect. At each sampling date, six (Hallwil) or twelve (Neuchâtel) individual standing-dead shoots were collected at random, returned to the laboratory and separated into dead, brown leaf blades, leaf sheaths, and culms (hereafter referred to as leaves, sheaths, and culms). Green plant material was discarded. All shoot fractions were dried at 105°C, weighed, and subsamples ashed overnight at 500°C to determine ash-free dry mass (AFDM). Plant matter carbon content was assumed to be 50% of AFDM. Estimates of aboveground standing-dead mass (g/m²) in each month were calculated as the mean shoot mass of the different plant fractions multiplied by the shoot density.

In situ diel patterns of CO_2 evolution from standing-dead litter

Fluctuations in rates of microbial CO_2 evolution from standing-dead litter over diel cycles were periodically examined in situ under a variety of environmental conditions. Measurements were made on a total of seven dates between October 1998 and May 2000 at Lakes Neuchâtel and Hallwil. Standing-dead litter (leaves, sheaths, culms) of *P. australis* was randomly collected at middle height within the reed stand. Samples were collected over 22–26-h periods at intervals ranging from 1 to 3 h. Collected samples were cut into two ~10-cm pieces, and rates of CO_2 evolution were immediately monitored.

Rates of CO_2 evolution were measured by enclosing litter samples into a custom-built U-shaped plexiglass chamber (total volume 135 cm³) connected to a LiCor LI-6400 Infrared Gas Analyzer (LiCor, Lincoln, Nebraska, USA). The instrument operates on a unidirectional flow-through method in which two analyzers measure CO_2 concentrations simultaneously in a sample and reference flowpath (LiCor 1998). Rates of CO_2 evolution (μmol/s) were monitored over short periods (~3 min) based on flow rates and differences in CO_2 concentrations between sample and reference analyzers. Readings were taken after the instrument had stabilized for 2–5 min to avoid any fluctuations in the CO_2 concentration of air entering the instrument during measurements. CO_2 was purged from incoming air and subsequently re-injected from a CO_2 injector (LiCor 6400-01) to a constant air concentration of 400 ppm. This ensured that the incoming air was at a constant concentration of CO_2. Thus, even small differences in CO_2 concentrations between sample and reference analyzers could be accurately quantified. Airflow from the sample analyzer was periodically diverted to the reference analyzer during measurements in order to calibrate both analyzers to the same gas source. This electronic matching of the gas analyzers ensured removal of any potential offsets that might have influenced the accuracy of measurements. Following measurements, litter samples were placed on ice, returned to the laboratory and stored at −20°C. Frozen samples were later freeze-dried for 24 h (Liovac GT2, Leybold, Cologne, Germany), weighed, and subsamples combusted to determine AFDM (as described in *Methods*: *Shoot biomass*, above).

Plant-litter water potential

Water potential of the collected plant litter was monitored using a dew-point microvoltmeter (model HR-33T, Wescor, Logan, Utah, USA) as described by Newell et al. (1991) and Kuehn and Suberkropp (1998). Subsamples of collected litter (two 2-cm pieces) used in CO_2 measurements were simultaneously enclosed in C-30 sample chambers. The chambers were placed in

a styrofoam box and allowed to equilibrate for 3 h. Water potentials were determined using the dew-point hygrometric mode and recorded when readings of the instrument were stable. Sensitivities of sample chambers used were confined to a narrow range of measurable water potentials (Wescor 1986, see also Newell et al. 1991 and Kuehn and Suberkropp 1998). The mean maximum sensitivity (i.e., lowest measurable water potential) of the chambers used in this study was -7.6 ± 0.3 MPa. Water potentials lower than these values were assumed to be equal to the corresponding maximum chamber sensitivity. A salt solution (0.55 mol NaCl) of known water potential (-2.5 MPa at 25°C) was routinely used to verify calibration of individual chambers.

Fungal biomass

Fungal biomass associated with plant litter samples was estimated by extracting and quantifying ergosterol, a fungal membrane sterol (Gessner and Newell 2002). Subsamples of plant litter used for monitoring CO$_2$ evolution were freeze-dried, weighed, and ergosterol was extracted in 10 mL of alcoholic KOH (143 μmol/L in HPLC grade methanol; ergosterol extraction efficiencies >95%) for 30 min at 80°C in tightly capped, pressure-resistant glass extraction tubes (26 × 100 mm) with constant stirring. The crude extract was cleaned by solid-phase extraction (SPE; Gessner and Schmitt 1996) and ergosterol was quantified by high-pressure liquid chromatography (HPLC). A LiChrospher 100 RP-18 column (0.46 × 25 cm, Merck, Darmstadt, Germany) maintained at 32°C and connected to a Jasco AS-950 autosampler (Jasco, Easton, Maryland, USA) and PU-980 liquid chromatograph was used for separation and analysis. The mobile phase was HPLC-grade methanol at a flow rate of 1.5 mL/min. Ergosterol was detected with a Jasco UV-970 UV/VIS detector (Jasco, Easton, Maryland, USA) by measuring absorbance at 282 nm (retention time = ~8 min), and it was identified and quantified based on comparison with ergosterol standards (99% purity, Fluka Chemical, Buchs, Switzerland). Ergosterol concentrations within plant litter samples were converted to fungal biomass assuming an ergosterol content of 5 μg/mg fungal dry mass (Gessner and Chauvet 1993, Gessner and Newell 2002).

Laboratory experiments

A series of laboratory experiments were conducted to examine the effects of moisture and temperature on rates of microbial CO$_2$ evolution from standing-dead plant litter under controlled conditions. Three fully brown, standing-dead shoots of *P. australis* were randomly collected from the reed stand at Lake Neuchâtel in November and December 1998 and returned to the laboratory. Leaves and sheaths were removed at middle height from shoots, cut into three or four pieces each 10-cm long, and the rate of CO$_2$ evolution was immediately monitored (as described in the *Methods*:

In situ diel patterns of CO$_2$ evolution from standing-dead litter). Leaf and sheath pieces were then placed into sterile Petri dishes (150 × 20 mm) containing sterile filter paper, wetted with sterile distilled water (~30 mL) and drained of excess water. Rates of CO$_2$ evolution were monitored five minutes after initial wetting and then 0.5, 1, and 24 hours, thereafter. After 24 hours, litter samples were removed from the Petri dishes and allowed to air dry under ambient laboratory conditions (25 ± 0.7°C). Rates of CO$_2$ evolution were monitored every 30 minutes for two hours during this drying period. After respiration rates were determined, samples were frozen (-20°C), freeze-dried, weighed, and subsamples were combusted to determine AFDM. Subsamples of litter were used following each CO$_2$ rate measurement for determination of plant litter water potentials and fungal biomass.

On two separate dates in November and December 1998, the effects of temperature were determined on rates of CO$_2$ evolution from water-saturated plant litter. Three replicate standing-dead shoots were collected from the reed stand at Lake Neuchâtel, returned to the laboratory and 10-cm pieces (leaves and sheaths) were cut from the mid-section of the shoots. Samples (3–4 pieces) were placed into sterile Petri dishes (150 × 20 mm) containing a sterile filter paper, wetted with sterile deionized water (~30 mL) and drained of excess water (as in previous paragraph). Additional leaf and sheath pieces (December only) were autoclaved before wetting to serve as controls. Samples were placed in an incubator at 5°C and allowed to equilibrate for 2 h before rates of CO$_2$ evolution were monitored. The incubator temperature was then increased in increments of ~10°C up to 45°C, allowing the same litter samples to equilibrate at each temperature setting for 2 h before CO$_2$ evolution was measured again. Litter samples were kept water-saturated throughout these studies by repeated addition of sterile deionized water. After respiration rates were determined, samples were frozen, freeze-dried, weighed, and subsamples combusted to determine sample AFDM (as described in the previous paragraph). Litter subsamples taken at the beginning and end of the experiment were used to determine litter-associated fungal biomass.

Data analyses

All statistical analyses were performed using SYSTAT (Wilkinson et al. 1992), with differences considered significant at the $P < 0.05$ level. Repeated-measures analysis of variance (ANOVA) was used to detect trends over time in laboratory studies. Field data were analyzed using a Student's t test when only two means were compared, and ANOVA in all other cases. ANCOVA was used to test for differences in slopes of regression lines. Correlation analyses of data collected in both laboratory and field studies were conducted
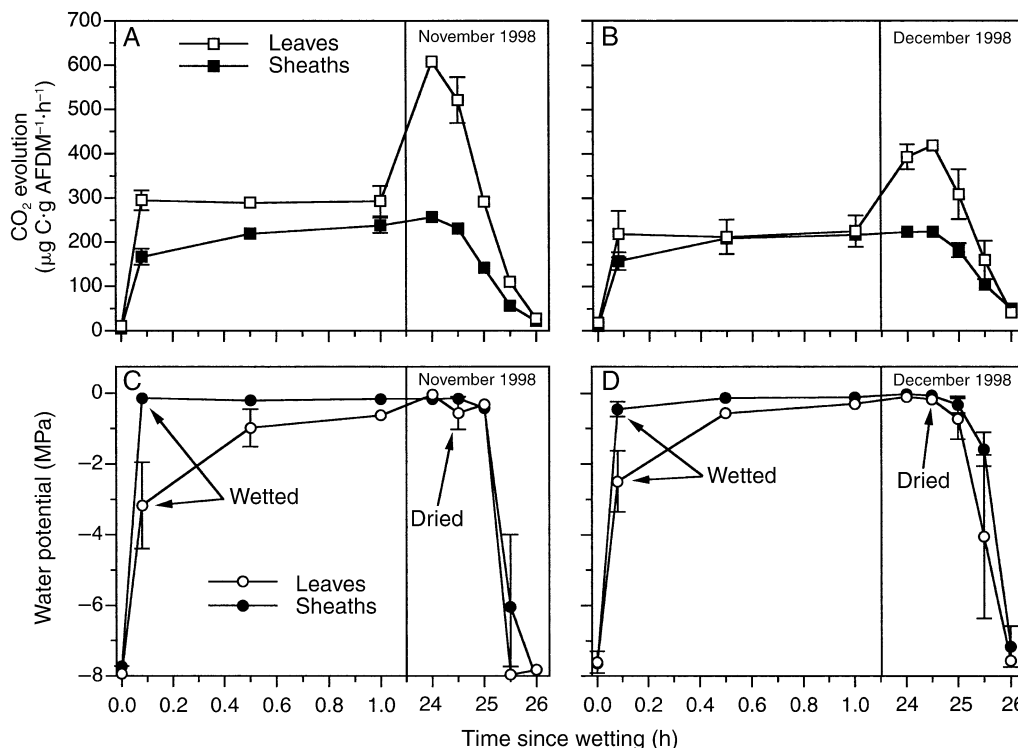
FIG. 1.   Changes in rates of CO_2 evolution from standing-dead *Phragmites australis* (A) leaf and (B) sheath litter, and (C, D) corresponding plant-litter water potentials after litter was wetted and air-dried in the laboratory. Note the varied scale in the x-axes. Open symbols show leaf data; solid symbols show sheath data. Means ± 1 SE are shown (*n* = 3). "AFDM" indicates ash-free dry mass.

using the Pearson product-moment correlation coefficient.

RESULTS

Controlled laboratory experiments

Under constant temperature conditions, microbial assemblages associated with standing-dead leaves and sheaths showed near-instantaneous responses to controlled experimental wetting in the laboratory. Significant increases in plant litter water potentials and up to a 30-fold increase in rates of CO_2 evolution ($P < 0.05$) were observed within 5 min after wetting of litter (Fig. 1A–D). Thereafter sheaths sustained constantly high rates of CO_2 evolution for up to 24 h after wetting ($P \geq 0.30$, repeated-measures ANOVA), whereas rates of CO_2 evolution from leaves increased further (two-fold) between 1 and 24 h after the initial wetting. Once exposed to drying conditions, rates of CO_2 evolution from both leaves and sheaths declined within 2 h ($P < 0.001$) (Fig. 1A–D). The dynamics and magnitudes in plant litter water potentials and CO_2 evolution rates were both remarkably similar in November and December 1998. Overall, litter water potential consistently showed a highly significant positive correlation with rates of CO_2 evolution ($r = 0.83$ to 0.95 for leaves and sheaths, respectively; $P < 0.001$).

No significant changes in fungal biomass (ergosterol) of leaves or sheaths were observed during either experiment. Grand means ± 1 SE (*n* = 12) of fungal biomass in leaves were 34 ± 2 mg dry mass/g ash-free dry mass (AFDM) in November and 38 ± 2 mg dry mass/g AFDM in December. The corresponding fungal biomass in sheaths was 29 ± 3 and 27 ± 2 mg dry mass/g AFDM in November and December, respectively.

Rates of CO_2 evolution from wetted litter increased as temperature was increased from 5 to 35°C or 25°C (November) ($P < 0.001$, $r^2 = 0.93$ for leaves and 0.89 for sheaths; Fig. 2A–B). Leaves showed a slightly stronger response than sheaths. Above 35°C, rates of CO_2 evolution declined slightly. No appreciable CO_2 evolution was observed from sterilized (autoclaved controls) leaf ($P = 0.44$) or sheath litter ($P = 0.78$; Fig. 2A–B). A Q_{10} relationship for rates of CO_2 evolution was derived from an Arrhenius plot (Winkler et al. 1996) over the temperature range from 5 to 35°C. The Q_{10} in both experiments averaged 1.94 and 1.62 for leaves and sheaths, respectively. Mean pooled fungal biomass (±1 SE; *n* = 6) of samples collected at the beginning and end of the temperature incubations were 35 ± 3 (November) and 74 ± 7 (December) mg dry mass/g AFDM for leaves, and 17 ± 4 and 45 ± 6 mg
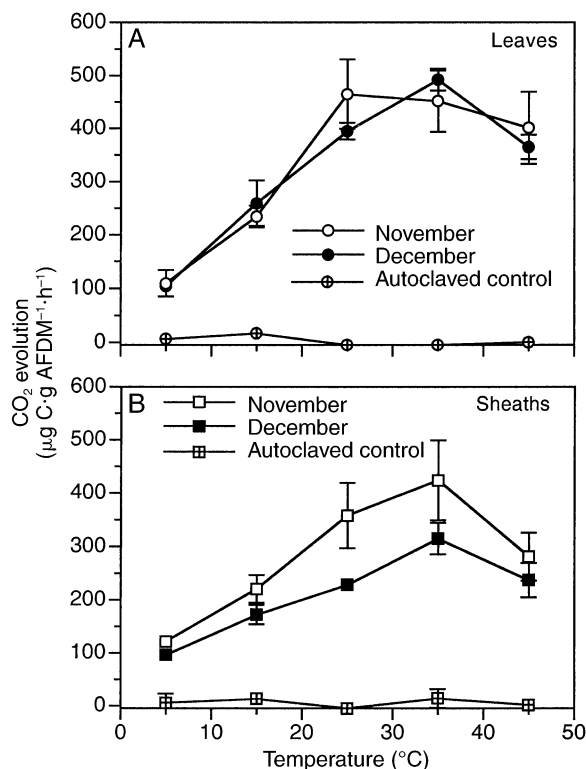
FIG. 2. Effect of temperature on rates of CO$_2$ evolution from water-saturated leaves and sheaths of standing-dead *P. australis* litter in the laboratory. Rates of CO$_2$ evolution from water-saturated autoclaved control leaves and sheaths are also illustrated. Means ± 1 SE are shown (*n* = 3). "AFDM" indicates ash-free dry mass.

dry mass/g AFDM for sheaths. No significant changes in fungal biomass were observed.

CO$_2$ evolution under in situ conditions

Results of field measurements consistently point to temperature-driven changes in relative humidity and litter water potential as the primary mechanism underlying diel changes in CO$_2$ evolution from standing-dead *P. australis* shoots. The temporal changes depicted in Figs. 3–5 typified the diel pattern observed under constant weather conditions in all seasons and with all types of plant litter. Rates of CO$_2$ evolution were high in the morning (Figs. 3A, 4A, and 5A), concurrent with high plant-litter water potentials (Figs. 3C, 4C, and 5C) resulting from either dew formation or, in one case (Fig. 4C), slight rainfall that occurred during the preceding night. Subsequent increases in temperature during daytime resulted in decreases in relative humidity and drying of plant litter (Figs. 3B, 4B, and 5B). Litter water potential (Figs. 3C, 4C, and 5C) and rates of CO$_2$ evolution (Figs. 3A, 4A, and 5A) decreased rapidly during these drying periods. Both the water potential of and, therefore, CO$_2$ evolution from plant litter remained consistently low throughout the day, even when the relative humidity was moderately

high (>80%), as observed in May 1999 (Fig. 5B). At night, relative humidity (Figs. 3B, 4B, and 5B), and hence litter water potential (Figs. 3C, 4C, and 5C), increased as air temperature decreased (Figs. 3B, 4B, and 5B), thus, inducing dew formation on standing-dead litter as relative humidity eventually reached 100%. Rates of CO$_2$ evolution rose sharply concomitant with this temperature-induced increase in microbial water availability (Figs. 3A, 4A, and 5A). Overall, rates of CO$_2$ evolution from plant litter showed strong positive correlations with relative humidity and, especially, plant litter water potential (Table 2), whereas significant negative correlations between CO$_2$ evolution rate and temperature were observed.

Distinct differences in rates of CO$_2$ evolution were observed among *P. australis* litter fractions. Maximum rates from culm litter were consistently an order of magnitude lower than rates observed from leaves and sheaths. For example, in May 2000, sheaths released
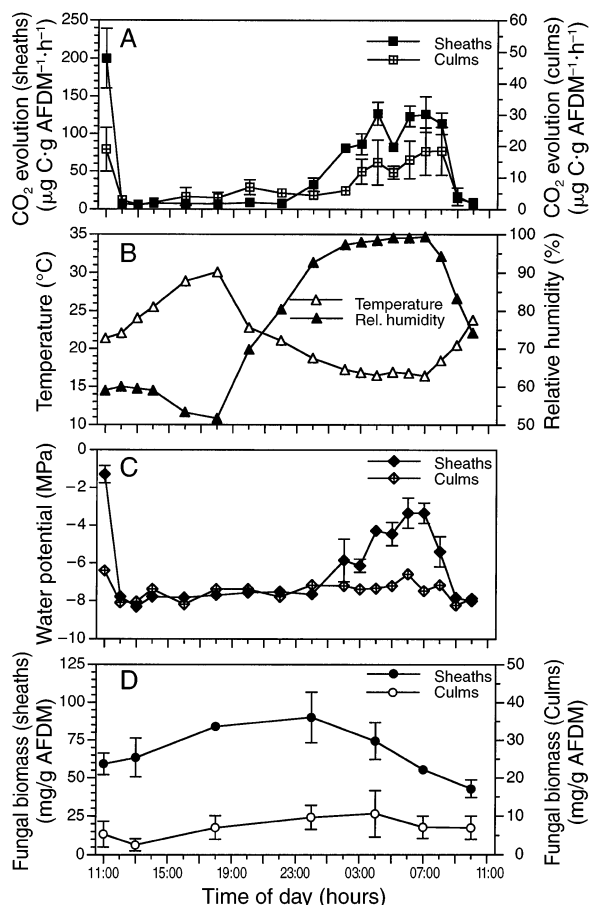

FIG. 3. Diel changes in (A) rates of CO$_2$ evolution from standing-dead sheath and culm litter of *P. australis* and (B) air temperatures and relative humidity at middle height within the reed stand at Lake Neuchâtel on 3–4 August 1999. Diel changes in (C) plant-litter water potentials and (D) litter-associated fungal biomass are also illustrated. Means ± 1 SE are shown (*n* = 3). "AFDM" indicates ash-free dry mass.
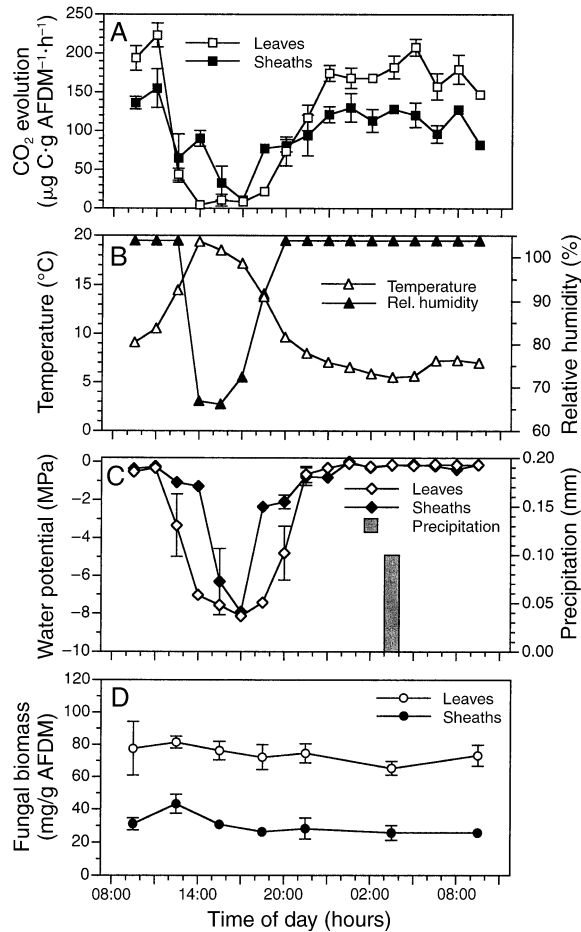
FIG. 4. Diel changes in (A) rates of CO_2 evolution from standing-dead leaf and sheath litter of *P. australis* and (B) air temperatures and relative humidity at middle height within the reed stand at Lake Hallwil on 26–27 October 1999. Diel changes in (C) plant-litter water potentials and (D) litter-associated fungal biomass are also illustrated. Means ± 1 SE are shown (*n* = 3). "AFDM" indicates ash-free dry mass.

up to 144 ± 25 μg C·g AFDM^{-1}·h^{-1}, whereas only 29 ± 5 μg C·g AFDM^{-1}·h^{-1} were recorded from corresponding culm litter (Fig. 5A). Furthermore, 24–42% higher maximum rates were recorded from leaves compared to sheaths experiencing identical environmental conditions (e.g., Fig. 4A, Table 3). Sheaths, however, responded more rapidly to drying and wetting events than leaves (Fig. 4A), whereas culm litter required longer periods to become notably wet (Fig. 5A). As an extreme, dead culms collected in August 1999 experienced only very slight increases in water potential and rates of CO_2 evolution, whereas sheath tissue responded markedly to the same changes in environmental conditions (Fig. 3A and 3C).

No significant fluctuations in litter associated fungal biomass were observed in any type of litter during diel cycles (Figs. 3D, 4D, and 5D). However, differences in fungal biomass concentrations were observed be-

tween litter types at any given date. For example, in October 1999, fungal biomass in sheaths was only about half of that in corresponding leaves (Fig. 4D, Table 3), and in May 2000, it was about five times higher in sheaths compared to culm litter (Fig. 5D, Table 3).

Abrupt weather changes greatly affected diel patterns of CO_2 evolution from *P. australis*, as observed in November 1999 (*data not shown*). Low rates of CO_2 evolution from plant litter during the daytime increased during the evening as a result of increasing relative humidity (>90%), leading to significant increases in plant litter water potentials (*P* < 0.001). Rates of CO_2 evolution from standing-dead litter also increased during this time, despite low air temperatures of <4°C. At about midnight, however, a warm weather front moved through the area, resulting in a marked increase in nighttime air temperatures and a concomitant decrease

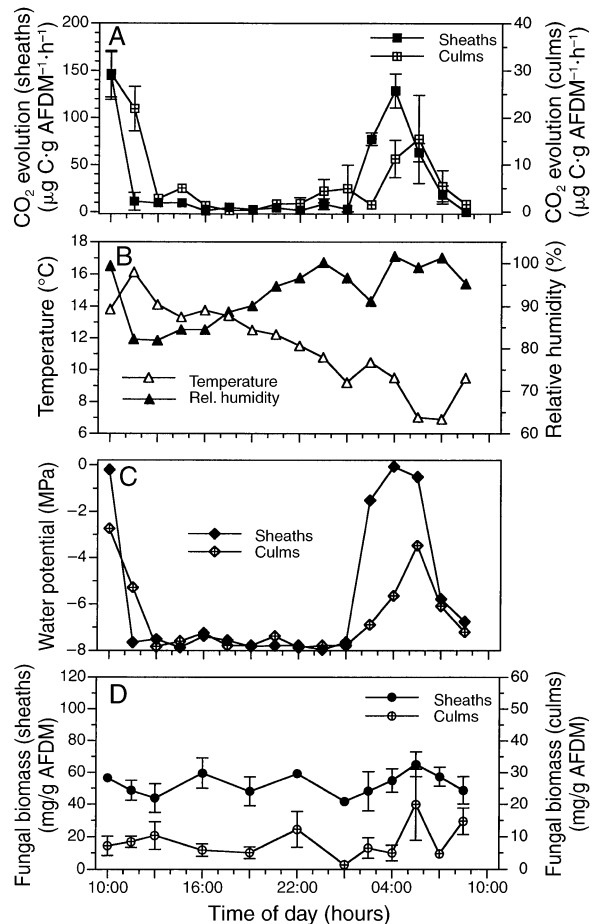FIG. 5. Diel changes in (A) rates of CO_2 evolution from standing-dead sheath and culm litter of *P. australis* and (B) air temperatures and relative humidity at middle height within the reed stand at Lake Hallwil on 18–19 May 1999. Diel changes in (C) plant-litter water potentials and (D) litter-associated fungal biomass are also illustrated. Means ± 1 SE are shown (*n* = 3). "AFDM" indicates ash-free dry mass.

TABLE 2. Pearson correlation coefficients (r) showing the relationship between litter-asso-
ciated microbial respiratory activities (rates of CO_2 evolution from leaves, sheaths, or culms)
and temperature, relative humidity, and plant-litter water potentials during diel field studies.

Site and date	Plant organ	Temperature	Relative humidity	Water potential
Lake Neuchâtel				
October 1998	leaves	0.12	−0.03	0.77***
	sheaths	0.22	−0.11	0.70***
November 1998	leaves	−0.30	0.42*	0.55**
	sheaths	−0.15	0.15	0.18
May 1999	sheaths	−0.68***	0.65***	0.71***
	culms	−0.47***	0.44**	0.32**
August 1999	sheaths	−0.60***	0.47***	0.92***
	culms	−0.46***	0.40**	0.66***
Lake Hallwil				
October 1999	leaves	−0.85***	0.75***	0.90***
	sheaths	−0.595***	0.58***	0.75***
March 2000	sheaths	0.25	−0.16	−0.18
	culms	0.08	0.03	−0.08
May 2000	sheaths	−0.14	0.43**	0.90***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

in relative humidity. As a consequence, plant-litter wa-
ter potentials and rates of CO_2 evolution decreased, as
observed in both laboratory experiments during drying
periods and in field measurements during the daytime
under stable weather conditions.

Temporal patterns in temperature, relative humidity,
litter water potential, and CO_2 evolution during the
remaining three field studies differed in detail from
those shown in Figs. 3–5. However, all field data con-
sistently pointed to a day–night temperature-induced
availability of water as the critical factor controlling
CO_2 evolution. As a consequence, strong positive re-
lationships were observed between rates of CO_2 evo-
lution and plant-litter water potentials for nearly all of
the diel field studies (Table 2). A notable exception was
March 2000, when rates of CO_2 evolution were very
low throughout the diel cycle (Table 3). This lack of
activity is consistent, however, with the constantly low
plant-litter water potentials on that day, despite high
recorded relative humidities during the nighttime.

When data from all diel studies are combined, rates
of CO_2 evolution from litter fractions show a positive
linear relationship with plant-litter water potential (Fig.
6A–C), with significant differences between plant or-
gans ($P < 0.001$, ANCOVA). Closer inspection of the
data suggests that rates of CO_2 evolution from leaves
tended to increase more strongly as water potential ex-
ceeded −1 MPa (Fig. 6A). In contrast, water potentials
of the culm material never reached −1 MPa, with most
values clustering at or below −6 MPa (Fig. 6C), ex-
plaining the invariably low CO_2 evolution rate mea-
sured from this type of litter. Maximum rates of CO_2
evolution were significantly related to litter-associated
fungal biomass (Fig. 7, $P < 0.001$, $r^2 = 0.72$), with
the greatest variability associated with sheaths.

Standing-dead litter stocks

Amounts of standing-dead litter varied substantially
over the year with an overall range in total standing-
dead shoot biomass of 103–965 g AFDM/m² (Fig. 8A).
Leaves were only present during fall for about three
months. Sheaths were present year-round, although the
highest standing stock was also observed during fall.
Using these estimates of total standing-dead organic
matter for leaves sheaths and culms of *P. australis*,
microbial CO_2 evolution rates obtained in the present
study represent a net daily carbon flux of between 51
and 570 mg C/m² of wetland surface area (Fig. 8B). In
spite of the lower maximum standing stock of leaves
and sheaths (October 1998) compared to culms (May
1999), daily CO_2 flux from leaves and sheaths exceeded
the flux from culms about four-fold.

Discussion

Results obtained in this investigation are in accor-
dance with observations in subtropical wetlands of Al-
abama and Georgia that large day-and-night fluctua-
tions in air temperature drive nighttime evolution of
CO_2 from standing-dead plant litter (Newell et al. 1985,
Kuehn and Suberkropp 1998). The mechanism under-
lying this cyclic pattern is straightforward. Relative
humidity increases as air temperatures decrease during
the night; this translates into increased litter water po-
tential, which tends towards equilibrium with ambient
air humidity and gives rise to CO_2 evolution resulting
from the increased respiratory activities of standing
litter-associated microbial decomposers. Conversely,
increasing temperatures and concomitant declines in
relative humidity and water potential curb CO_2 evo-
lution during the day.

How general is this diel pattern in microbial respi-
ratory activity and what are the implications for carbon
cycling at larger scales? The evolution of CO_2 observed
during our field studies attests that carbon mineraliz-
ation of standing-dead litter is by no means limited
to subtropical wetlands. The typical pattern of night-

TABLE 3. Summary of data obtained during diel field studies.

Site and date	Plant organ	CO$_2$ evolution (μg C·g AFDM^{-1}·h^{-1})		Standing-litter biomass (g AFDM/m^2) Mean ± 1 SE	CO$_2$ flux (mg C·m^{-2}·d^{-1}) Mean ± 1 SE
		Mean	Range		
Lake Neuchâtel					
October 1998	leaves	59.6	5.6–142.1	171 ± 19	244 ± 27
	sheaths	46.0	8.0–92.2	295 ± 32	326 ± 36
November 1998	leaves	61.7	6.7–133.0	55 ± 6	82 ± 9
	sheaths	37.9	17.9–93.2	281 ± 31	256 ± 28
May 1999	sheaths	21.2	0.0–80.4	189 ± 20	96 ± 11
	culms	3.3	0.1–11.9	776 ± 86	61 ± 7
August 1999	sheaths	58.1	2.4–275.7	21 ± 2	29 ± 3
	culms	8.4	0.2–32.9	110 ± 12	22 ± 2
Lake Hallwil					
October 1999	leaves	123.1	2.3–243.4	45 ± 11	132 ± 33
	sheaths	97.7	2.2–185.4	58 ± 12	136 ± 27
March 2000	sheaths	19.3	2.9–34.7	79 ± 19	37 ± 9
	culms	5.3	1.8–13.3	270 ± 74	34 ± 9
May 2000	sheaths	30.6	0.0–177.6	55 ± 15	41 ± 11
	culms	6.8	0.0–36.9	245 ± 57	40 ± 9

Note: Key to abbreviations: AFDM, ash-free dry mass; dm, dry mass.

time activity that is disrupted during the day also prevails in cooler temperate climates. Although the highest gas fluxes are sustained under continual wet conditions at high summer temperatures, significant CO$_2$ evolution occurs even during the cold season, when temperatures may approach freezing. The implication of this finding is that microbially-mediated nighttime evolution of CO$_2$ from standing-dead plant litter is widespread even at northern latitudes, where most wetlands occur (Mitsch and Gosselink 2000).

A key feature of the microbial assemblages associated with standing-dead litter in wetlands is their capacity to rapidly shift their metabolism ($\leq$5 min) from an inactive to fully active state when sufficient water becomes available (Fig. 1). Such rapid responses have been shown for microbial assemblages on standing-dead litter in subtropical wetlands (Newell et al. 1985, Kuehn and Suberkropp 1998) and, as shown by our laboratory experiments, in temperate wetlands. The lack of response from autoclaved litter provides unambiguous evidence that the large shifts in CO$_2$ evolution rates are driven by microbial metabolic processes, rather than by physical phenomena (see also Kuehn and Suberkropp 1998). The ability of microbial decomposers to switch their metabolism instantly is a crucial adaptation for growth and survival in the standing-dead litter environment, allowing the microbes to take advantage of even short-term periods of moisture availability. This ability may be especially advantageous in climates characterized by highly variable weather conditions throughout the year, as is typical in much of Europe and other regions influenced by oceanic climate. The ecosystem consequence of this adaptation is that the onset of nighttime dew formation, or rainfall, will induce microbial CO$_2$ evolution from standing-dead litter almost instantaneously.

The fact that water availability is a key factor regulating microbial activity in standing-dead plant litter may seem obvious in view of its established importance for soil microbial activity (e.g., Raich and Schlesinger 1992, Rustad et al. 2000, Smith et al. 2003). However, the idea that water can limit microbial activity in wetlands has generally been viewed indirectly in terms of fluctuating water tables that affect the balance between aerobic and anaerobic sediment processes, rather than in terms of directly controlling microbial metabolic processes (e.g., Silvola et al. 1996a, Updegraff et al. 2001). This restricted notion probably reflects the widespread perception that carbon mineralization in wetlands occurs exclusively at or within the sediments, but not within the standing-dead plant canopy.

The observed differences between *P. australis* litter fractions in both the timing and magnitude of CO$_2$ evolution during periods of wetting (Figs. 3A, 4A, and 5A) are likely related to differences in water absorption patterns resulting from distinct physical and chemical characteristics of plant litter tissues. In particular, sheaths of *P. australis* possess a large proportion of aerenchymatous tissue with intercellular gas spaces (e.g., Armstrong et al. 1996), whereas culm litter is composed primarily of refractory sclerenchymatous tissue with a thick water-repellent cuticle (Rodewald-Rudescu 1975). In addition, most of the culm surface area in *P. australis* is surrounded by sheaths, so that any free water must absorb into and saturate sheath tissues before coming in contact with culm tissue. Thus, plant tissue quality appears to control rates of CO$_2$ evolution not only through variations in the chemical makeup of litter, which determines intrinsic litter decomposability (e.g., Gessner and Chauvet 1994), but also as a result of differences in water absorption capacities that ultimately delineate the scope of microbial colonization and activity.

The observed differences in water absorption patterns and structural characteristics of plant litter frac-

TABLE 3. Extended.

Fungal biomass (mg dm/g AFDM) Mean ± 1 SD	Relative humidity (%) Range	Temperature (°C)		Total precipitation (mm)	Water potential (MPa)	
		Mean	Range		Minimum	Maximum
34 ± 10	73–94	10.3	8.5–12.6	0.00	≤−7.33	0.00
16 ± 10					≤−6.67	0.00
38 ± 11	80–100	6.2	1.3–9.7	0.00	≤−7.60	−0.83
22 ± 7					−6.67	−0.67
51 ± 9	61–99	13.8	8.4–21.5	0.00	≤−8.40	−2.80
2 ± 2					≤−8.40	−5.60
67 ± 21	51–99	21.0	16.4–30.1	0.00	≤−8.67	−0.37
7 ± 6					≤−8.40	−4.40
74 ± 13	66–100	10.1	5.5–19.4	0.10	≤−8.27	0.00
30 ± 8					≤−8.40	0.00
44 ± 19	42–100	9.5	4.8–18.5	0.00	≤−8.53	−6.93
6 ± 5					≤−8.40	−6.93
53 ± 13	82–100	11.5	6.9–16.1	0.00	≤−8.27	0.00
6 ± 8					≤−8.40	−1.60

tions are also consistent with the patterns of microbial colonization seen among litter types. Fungal biomass concentrations in sheaths were 7–25-fold higher than in corresponding culms, and ~two-fold lower than in corresponding leaves. As a result, differences in maximum CO$_2$ evolution rates among litter fractions were partly accounted for by differences in litter-associated fungal biomass (Fig. 7, $r^2 = 0.72$, $P < 0.001$). These differences among litter fractions suggest that the direct effects of litter quality and water absorption capacities on CO$_2$ evolution are exacerbated by the degree of microbial colonization, which is likely to be ultimately controlled by plant litter quality.

Maximum rates of CO$_2$ evolution from standing-dead litter measured under in situ conditions in the present study (Table 3) are comparable to those reported for standing emergent plant litter in other wetland habitats (Table 4). Moreover, maximum respiration rates observed from standing *P. australis* litter are equal to or often exceed those rates reported from *P. australis* litter under submerged conditions at the same (Komínková et al. 2000, Buesing 2002) and other wetland sites (e.g., Hargrave 1972, Andersen 1978). For example, Komínková et al. (2000) reported respiration rates from submerged *P. australis* leaves in Lake Neuchâtel that varied between 29 ± 9 and 127 ± 20 μg CO$_2$-C·(g AFDM)$^{-1}$·h^{-1}, with fluctuations following changes in lake water temperature. Rates measured in Lake Hallwil range from 31 ± 2 and 319 ± 32 μg CO$_2$-C·(g AFDM)$^{-1}$·h^{-1} (Buesing 2002). These comparisons with submerged decaying litter reveal that carbon mineralization by microbial decomposers associated with standing-dead litter can be a sizeable component of carbon flux from wetlands to the atmosphere.

CO$_2$ evolution from standing-dead plant shoots may represent trace gas emissions that have not been fully recognized or included in flux estimates from wetlands, although that research area has attracted great interest since biological carbon fluxes have been incorporated into global climate change models. As a result, the effects of environmental factors on the production and emission of CO$_2$ and CH$_4$ from wetlands have received wide attention (e.g., Whiting 1994, Updegraff et al. 1995, 2001, Silvola et al. 1996*a,* Yavitt 1997, Bridgham et al. 1998, Bubier et al. 1998, Frolking et al. 1998, Alm et al. 1999, Scanlon and Moore 2000, Dalva et al. 2001, Wickland et al. 2001, Clair et al. 2002, Moore et al. 2002, Christensen et al. 2003, Larmola et al. 2003), whereas attempts at assessing the contribution of standing-dead litter to total CO$_2$ flux even approximately (Newell et al. 1985, Kuehn et al. 1998) have been notably scarce. Most estimates were generally restricted to chamber-based measurements of wetland soils/sediments (i.e., cores or monoliths) with aboveground plant biomass and standing litter either removed before flux measurements (e.g., Updegraff et al. 1995, Bridgham et al. 1998, Scanlon and Moore 2000), or measurements were made under conditions when CO$_2$ evolution from standing-dead litter is likely minimal, namely during the daytime (e.g., Whiting 1994, Yavitt 1997, Bridgham et al. 1998, Updegraff et al. 2001, Dalva et al. 2001, Wickland et al. 2001, Clair et al. 2002, Moore et al. 2002, Christensen et al. 2003, Larmola et al. 2003). As a consequence, models predicting ecosystem carbon flux in wetlands may not have incorporated the standing-dead plant litter compartment (e.g., Frolking et al. 2001, Chimner et al. 2002). CO$_2$ flux estimates with micrometeorological methods (eddy covariance) include microbial CO$_2$ flux from the standing-dead litter compartment (e.g., Baldocchi et al. 2001). However, they do not provide a detailed understanding or quantification of individual processes occurring within the plant canopy or sediments and are often not suitable for measuring fluxes near distinct
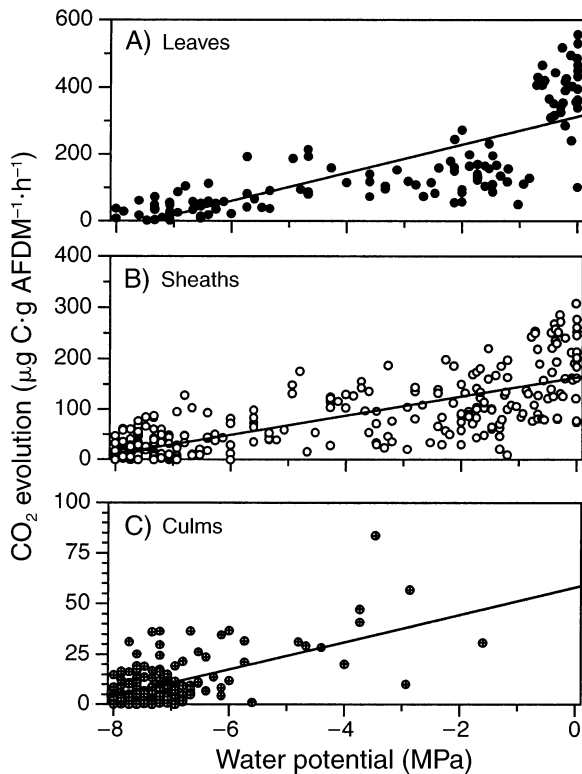
FIG. 6. Relationship between litter water potentials (ψ) and rates of CO_2 evolution (R) from standing-dead *P. australis* (A) leaf, (B) sheath, and (C) culm litter using combined data from all field sampling dates. Linear regression models: $R = 42(\psi) + 314$, $r^2 = 0.62$ for leaves; $R = 19(\psi) + 164$, $r^2 = 0.64$ for sheaths; $R = 6.7(\psi) + 58$, $r^2 = 0.38$ for culms; $P < 0.0001$ in all instances. "AFDM" indicates ash-free dry mass.
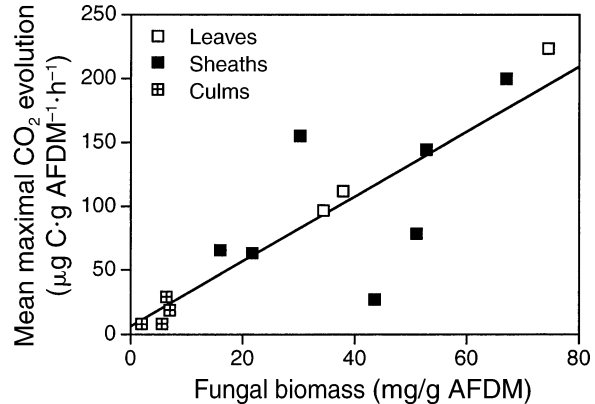

FIG. 7. The effect of litter-associated living fungal biomass (ergosterol) on the mean maximum rate of CO_2 evolution observed from standing-dead *P. australis* leaf, sheath, and culm litter using combined data from all field sampling dates ($r^2 = 0.72$, $P < 0.001$). "AFDM" indicates ash-free dry mass.

plant litter in a subtropical freshwater marsh dominated by *Juncus effusus* L. (from 1.37 ± 0.95 to 3.35 ± 0.13 g $C \cdot m^{-2} \cdot d^{-1}$; Kuehn and Suberkropp 1998), were equal to or exceeded sediment CO_2 flux rates from the same wetland system (from 0.12 ± 0.02 to 2.43 ± 0.24 g $C \cdot m^{-2} \cdot d^{-1}$; Roden and Wetzel 1996). Thus, including CO_2 flux from standing-dead litter at the rates determined in the present study, or higher, would appreciably augment the estimates of total wetland CO_2 flux reported in other studies. Consequently, greater attention to the standing-dead litter seems warranted to better assess the potential role of this litter compartment in both the global and local carbon cycles, and to incorporate such fluxes into current ecosystem models.

landscape transitions such as relatively narrow lake littoral wetlands (Baldocchi et al. 2001).

When integrated on an areal and temporal basis, diel fluctuations in CO_2 evolution in the present study translate to a flux of 51–570 mg $C \cdot m^{-2} \cdot d^{-1}$, which are within the range of total flux estimates reported from wetland soil/sediments in temperate climates. Paludan and Blicher-Mathiesen (1996), for example, found CO_2 flux rates of ~106–1260 mg $C \cdot m^{-2} \cdot d^{-1}$ from peaty sediments of a Danish freshwater wetland extensively colonized by emergent vegetation (e.g., *Carex*, *Scirpus*, and *Typha* spp.). Scanlon and Moore (2000) reported static chamber CO_2 flux rates ranging between ~130 and 2800 mg $C \cdot m^{-2} \cdot d^{-1}$ from fen and beaver pond littoral sediments that were also colonized by emergent vascular plants (see Fig. 1 in Scanlon and Moore 2000). Total CO_2 flux reported in these studies included only the CO_2 evolved from the respiratory activities of microbial assemblages on or within the peat layer and from the respiratory activities of living plant roots, which can be a sizable component (~35–45%) of sediment CO_2 flux (Silvola et al. 1996b). Similarly to the present study, CO_2 flux estimates from standing-dead
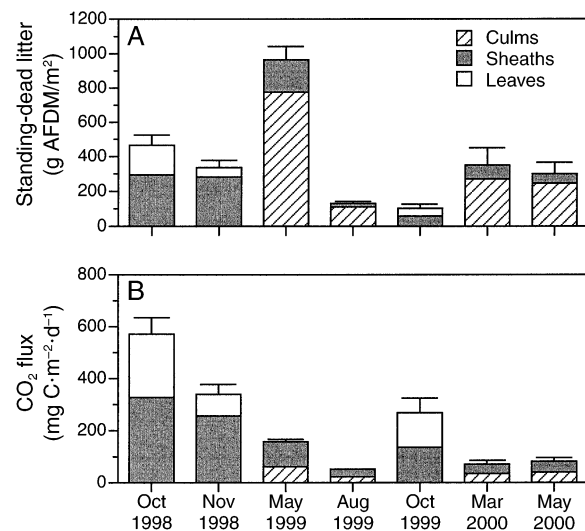

FIG. 8. Standing-dead *P. australis* (A) litter mass and (B) daily CO_2 flux from leaf, sheath, and culm litter during diel field studies. Error bars show $+ 1$ SE. "AFDM" indicates ash-free dry mass.

TABLE 4. Published maximum rates of CO$_2$ evolution reported from standing-dead plant litter from saltmarsh and freshwater wetland ecosystems.

Wetland climate and location, plant litter composition	Litter type	CO$_2$ evolution (μg C·g^{-1}dm·h^{-1})	Tempera-ture (°C)	Reference
Saltmarsh				
Temperate				
Oregon, USA				Gallagher et al. (1984)
Carex lyngbyei Hornem.	shoots	125	NR	
Deschampsia caespitosa (L.) P. Beauv	shoots	60	NR	
Distichlis spicata (L.) Greene	shoots	78	NR	
Juncus balticus Willd.	shoots	100	NR	
Potentilla pacifica Howell	shoots	225	NR	
Salicornia virginica L.	shoots	123	NR	
Scirpus americanus Pers.	shoots	160	NR	
Triglochin maritima (L.)	shoots	550	NR	
The Netherlands				Buth and Voesenek (1988)
Triglochin maritima (L.)	leaves	509	15	
Limonium vulgare Mill.	leaves	227	14	
Spartina anglica Hubbard	leaves	335	6	
Subtropical				
Georgia, USA				
Spartina alterniflora Loisel.	shoots	118	NR	Gallagher and Pfeiffer (1977)
Juncus roemerianus Scheele	leaves	45	NR	
Juncus roemerianus	leaves	115	12	Newell et al. (1985)
Spartina alterniflora	culms	136	30	
Spartina alterniflora	leaves	188	30	
Spartina alterniflora	leaves	202†	25	Newell and Fallon (1989)
Spartina alterniflora	leaves	110†	22	Newell et al. (1989)
Spartina alterniflora	leaves	208	25	Newell et al. (1996)
Freshwater				
Temperate				
The Netherlands				
Carex acutiformis Erhl.	leaves	90	20	Aerts et al. (1995)
Carex lasiocarpa Ehrh.	leaves	55	20	
Carex acutiformis Erhl.	leaves	95	20	Aerts and de Caluwe (1997)
Carex diandra	leaves	109	20	
Carex lasiocarpa Ehrh.	leaves	82	20	
Carex rostrata	leaves	123	20	
New York, USA				Welsch and Yavitt (2003)
Lythrum salicaria L.	stems	97	NR	
Typha latifolia L.	shoot	99	NR	
Michigan, USA				K. A. Kuehn, *unpublished data*
Typha angustifolia L.	leaves	63†	16	
Switzerland				this study
Phragmites australis (Cav.) Trin.	leaves	243†	10	
Phragmites australis ex Steud	sheaths	276†	21	
Phragmites australis	culms	37†	14	
Subtropical				
Alabama, USA				Kuehn and Suberkropp (1998)
Juncus effusus L.	leaves	285†	23	
Florida, USA				DeBusk and Reddy (1998)
Typha domingensis Pers.	leaves	66	25	
Cladium jamaicense Crantz	leaves	54	25	
Alabama, USA				Kuehn et al. (1999)
Erianthus giganteus (Walt.) Muhl	leaves	81†	25	
Erianthus giganteus	culms‡	71†	23	

Note: Key to abbreviations: NR, not reported; dm, dry mass.
† Reported as μg C·(g AFDM)$^{-1}$·h^{-1}.
‡ Culm plus attached leaf sheath.

As indicated by the present results, litter quality (which may be related to both plant species and plant organ) is an important factor for large-scale flux estimates because large differences exist among litter types in terms of the response of attached microbes to moisture availability. A rough budget suggests, for example, that a considerable portion of *Phragmites* leaves and particularly sheaths are likely to be mineralized under standing-dead conditions on an annual basis (Table 5). Only a small portion of this carbon flux is due to rainfall, the bulk being accounted for by nighttime moistening by dew formation. Culm material, in contrast,

TABLE 5. Estimate of the annual net aboveground production of *Phragmites australis* that is mineralized by microbial assemblages while in the standing-dead litter phase.

Lake and plant organ	Production (g C·m^{-2}·yr^{-1})	Mineral-ization (g C·m^{-2}·yr^{-1})	Percentage mineralized	
			Total (%)	Due to rainfall (%)
Neuchâtel				
Leaves	272	23	8.5	1.0
Sheaths	191	57	29.8	5.7
Culms	631	13	2.0	0.4
Hallwil				
Leaves	193	15	7.8	1.2
Sheaths	88	25	28.0	3.9
Culms	308	11	3.6	0.6

Notes: CO_2 flux estimates were calculated by taking the mean daily respiration rate from respective plant organs, adjusting for mean daily temperature (assumed Q_{10} for leaves of 1.9, for sheaths of 1.6, and for culms of 2.0) and multiplying by the estimated daily standing-dead biomass. Rain events were included only if precipitation occurred throughout the entire day. In these instances, the temperature-adjusted mean daily maximum respiration rate from the respective plant organs was used.

appears to undergo decomposition mainly at the sediment surface once shoots have collapsed. Because culms of *P. australis* are particularly water repellent and difficult to decay (Hietz 1992, Gessner 2000), they may represent an extreme among emergent wetland plants. Less recalcitrant emergent plants, such as cattails (*Typha* spp.), which dominate most of North America's freshwater wetlands, may have a much greater portion of their biomass mineralized under standing-dead conditions, possibly approaching our estimate of near 30% of the net aboveground production of *Phragmites* leaf sheaths. The current large-scale invasions of cattail marshes by *P. australis* in North America (e.g., Findlay et al. 2002) may therefore have consequences for carbon fluxes well beyond the individual site.

In permanent wetlands, water supply is always large enough to ensure high relative humidity when daytime temperatures drop. In view of the potential global significance of CO_2 flux from standing-dead litter, it would be important to assess whether similar diel patterns as described here for marshes are observed in other types of ecosystems. Grasslands, for example, are known to possess a large standing-dead litter component (Risser et al. 1981, Seastedt 1988, Biondini and Manske 1996) that is inhabited by microbial decomposers similar to those occurring on emergent wetland plants (e.g., Ellis and Ellis 1997, Farr et al. 1989). Quantifying the role of heterotrophic microbial decomposers within standing-dead litter canopy of these systems would appear to be a priority in future ecosystem research.

LITERATURE CITED

Aerts, R., and H. de Caluwe. 1997. Nutritional and plant-mediated controls on leaf litter decomposition of *Carex* species. Ecology **78**:244–260.

Aerts, R., R. van Logtestijn, M. van Staalduinen, and S. Toet. 1995. Nitrogen supply effects on productivity and potential leaf litter decay of *Carex* species from peatlands differing in nutrient limitation. Oecologia **104**:447–453.

Aerts, R., J. T. A. Verhoeven, and D. F. Whigham. 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology **80**:2170–2181.

Alm, J., L. Schulman, J. Walden, H. Nykänen, P. J. Martikainen, and J. Silvola. 1999. Carbon balance of a boreal bog during a year with an exceptionally dry summer. Ecology **80**:161–174.

Andersen, F. O. 1978. Effects of nutrient level on decomposition of *Phragmites communis* Trin. Archiv für Hydrobiologia **84**:42–54.

Apinis, A. E., C. G. C. Chesters, and H. K. Taligoola. 1972. Colonisation of *Phragmites communis* leaves by fungi. Nova Hedwigia **23**:113–124.

Apinis, A. E., C. G. C. Chesters, and H. K. Taligoola. 1975. Microfungi colonizing nodes and internodes of aerial standing dead culms of *Phragmites communis* Trin. Nova Hedwigia **26**:495–507.

Armstrong, J., W. Armstrong, P. M. Beckett, J. E. Halder, S. Lythe, R. Holt, and A. Sinclair. 1996. Pathways of aeration and the mechanisms and beneficial effects of humidity- and venturi-induced convections in *Phragmites australis* (Cav.) Trin. ex Steud. Aquatic Botany **54**:177–197.

Asaeda, T., L. H. Nam, P. Hietz, N. Tanaka, and S. Karunaratne. 2002. Seasonal fluctuations in live and dead biomass of *Phragmites australis* as described by a growth and decomposition model: implications of duration of aerobic conditions for litter mineralization and sedimentation. Aquatic Botany **73**:223–239.

Baldocchi, D., E. Falge, L. Gu, R. Olson, D. Hollinger, S. Running, P. Anthoni, C. Bernhofer, K. Davis, R. Evans, J. Fuentes, A. Goldstein, et al. 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bulletin of the American Meteorological Society **82**: 2415–2434.

Biondini, M. E., and L. Manske. 1996. Grazing frequency and ecosystem processes in a Northern mixed prairie, USA. Ecological Applications **6**:239–256.

Bridgham, S. D., C. A. Johnston, J. Pastor, and K. Updegraff. 1995. Potential feedbacks of northern wetlands on climate change. BioScience **45**:262–274.

Bridgham, S. D., K. Updegraff, and J. Pastor. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. Ecology **79**:1545–1561.

Brinson, M. M., A. E. Lugo, and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Annual Review of Ecology and Systematics **12**:123–161.

Bubier, J. L., P. M. Crill, T. R. Moore, K. Savage, and R. K. Varner. 1998. Seasonal patterns and controls on net eco-

system CO$_2$ exchange in a boreal peatland complex. Global Biogeochemical Cycles **12**:703–714.

Buesing, N. 2002. Microbial productivity and organic matter flow in a littoral reed stand. Dissertation. Swiss Federal Institute of Technology, Zurich, Switzerland.

Buth, G. J. C, and L. A. C. J. Voesenek. 1988. Respiration of standing and fallen plant litter in a Dutch salt marsh. Pages 51–60 *in* J. T. A. Verhoeven, G. W. Heil, and M. J. A. Werger, editors. Vegetation structure in relation to carbon and nutrient economy. SPB (Simon Peter Bakker) Academic Publishing, The Hague, The Netherlands.

Chapin, F. S., A. D. McGuire, J. Randerson, R. Pielke, D. Baldocchi, S. E. Hobbie, N. Roulet, W. Eugster, E. Kasischke, E. B. Rastetter, S. A. Zimov, and S. W. Running. 2000. Arctic and boreal ecosystems of western North America as components of the climate change Global Change. Biology **6**(S1):211–223.

Chimner, R. A., D. J. Cooper, and W. J. Parton. 2002. Modeling carbon accumulation in Rocky Mountain fens. Wetlands **22**:100–110.

Christensen, T. R., N. Panikov, M. Mastepanov, A. Joabsson, A. Stewart, M. Öquist, M. Sommerkorn, S. Reynaud, and B. Svensson. 2003. Biotic controls on CO$_2$ and CH$_4$ exchange in wetlands—a closed environment study. Biogeochemistry **64**:337–354.

Clair, T. A., P. Arp, T. R. Moore, M. Dalva, and F. R. Meng. 2002. Gaseous carbon dioxide and methane, as well as dissolved organic carbon losses from a small temperate wetland under a changing climate. Environmental Pollution **116**:S143–S148.

Dalva, M., T. R. Moore, P. Arp, and T. A. Clair. 2001. Methane and soil and plant community respiration from wetlands, Kejimkujik National Park, Nova Scotia: measurements, predictions, and climate change. Journal of Geophysical Research **106**(D):2955–2962.

DeBusk, W. F., and K. R. Reddy. 1998. Turnover of detrital organic carbon in a nutrient-impacted Everglades marsh. Soil Science Society of America Journal **62**:1460–1468.

Dvorák, J., and G. Imhof. 1998. The role of animals and animal communities in wetlands. Pages 211–318 *in* D. F. Westlake, J. Kvêt, and A. Szczepanski, editors. The production ecology of wetlands. Cambridge University Press, Cambridge, UK.

Ellis, M. B., and J. P. Ellis. 1997. Microfungi on land plants: an identification handbook, new enlarged edition. Richmond, London, UK.

Emery, S. L., and J. A. Perry. 1996. Decomposition rates and phosphorus concentrations of purple loosestrife (*Lythrum salicaria*) and cattail (*Typha* spp.) in fourteen Minnesota wetlands. Hydrobiologia **323**:129–138.

Farr, D. F., G. F. Bills, G. P. Chamuris, and A. Y. Rossman. 1989. Fungi on plants and plant products in the United States. American Phytopathological Society Press, St. Paul, Minnesota, USA.

Findlay, S. E. G., S. Dye, and K. A. Kuehn. 2002. Microbial growth and nitrogen retention in litter of *Phragmites australis* compared to *Typha angustifolia*. Wetlands **22**:616–625.

Findlay, S., K. Howe, and H. K. Austin. 1990. Comparison of detritus dynamics in two tidal freshwater wetlands. Ecology **71**:288–295.

Frolking, S. E., J. L. Bubier, T. R. Moore, T. Ball, L. M. Bellisario, A. Bhardwaj, P. Carroll, P. M. Crill, P. M. Lafleur, J. H. McCaughey, N. T. Roulet, A. E. Suyker, et al. 1998. Relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. Global Biogeochemical Cycle **12**:115–126.

Frolking, S., N. T. Roulet, T. R. Moore, P. J. H. Richard, M. Lavoie, and S. D. Muller. 2001. Modeling Northern peatland decomposition and peat accumulation. Ecosystems **4**:479–498.

Gallagher, J. L., H. V. Kibby, and K. W. Skirvin. 1984. Community respiration of decomposing plants in Oregon estuarine marshes. Estuarine, Coastal and Shelf Science **18**:421–431.

Gallagher, J. L., and W. J. Pfeiffer. 1977. Aquatic metabolism of the communities associated with attached dead shoots of salt marsh plants. Limnology and Oceanography **22**:562–565.

Gessner, M. O. 2000. Breakdown and nutrient dynamics of submerged *Phragmites* shoots in the littoral zone of a temperate hardwater lake. Aquatic Botany **66**:9–20.

Gessner, M. O. 2001. Mass loss, fungal colonisation and nutrient dynamics of *Phragmites australis* leaves during senescence and early decay in a standing position. Aquatic Botany **69**:325–339.

Gessner, M. O., and E. Chauvet. 1993. Ergosterol-to-biomass conversion factors for aquatic hyphomycetes. Applied and Environmental Microbiology **59**:502–507.

Gessner, M. O., and E. Chauvet. 1994. Importance of stream microfungi in controlling breakdown rates of leaf litter. Ecology **75**:1807–1817.

Gessner, M. O., and S. Y. Newell. 2002. Biomass, growth rate, and production of filamentous fungi in plant litter. Pages 390–408 *in* C. J. Hurst, R. L. Crawford, G. R. Knudsen, M. J. McInerney, and L. D. Stetzenbach, editors. Manual of environmental microbiology. Second edition. ASM, Washington, D.C., USA.

Gessner, M. O., B. Schieferstein, U. Müeller, S. Barkman, and U. A. Lenfers. 1996. A partial budget of primary organic carbon flows in the littoral zone of a hard water lake. Aquatic Botany **55**:93–105.

Gessner, M. O., and A. L. Schmitt. 1996. Use of solid-phase extraction to determine ergosterol concentrations in plant tissue colonized by fungi. Applied and Evironmental Microbiology **62**:415–419.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecological Applications **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.

Hargrave, B. T. 1972. Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. Limnology and Oceanography **17**:583–596.

Hietz, P. 1992. Decomposition and nutrient dynamics of reed (*Phragmites australis* (Cav.) Trin. ex Steud.) litter in Lake Neusiedl, Austria. Aquatic Botany **43**:211–230.

Komínková, D., K. A. Kuehn, N. Büsing, D. Steiner, and M. O. Gessner. 2000. Microbial biomass, growth, and respiration associated with submerged litter of *Phragmites australis* decomposing in a littoral reed stand of a large lake. Aquatic Microbial Ecology **22**:271–282.

Kuehn, K. A., P. F. Churchill, and K. Suberkropp. 1998. Osmoregulatory strategies of fungal populations inhabiting standing dead litter of the emergent macrophyte *Juncus effusus*. Applied and Environmental Microbiology **64**:607–612.

Kuehn, K. A., M. O. Gessner, R. G. Wetzel, and K. Suberkropp. 1999. Standing litter decomposition of the emergent macrophyte *Erianthus giganteus*. Microbial Ecology **38**:50–57.

Kuehn, K. A., and K. Suberkropp. 1998. Diel fluctuations in microbial activity associate with standing-dead litter of the freshwater emergent macrophyte *Juncus effusus*. Aquatic Microbial Ecology **14**:171–182.

Kvêt, J., and D. F. Westlake. 1998. Primary production in wetlands. Pages 78–268 *in* D. F. Westlake, J. Kvêt, and A.

Szczepanski, editors. The production ecology of wetlands. Cambridge University Press, Cambridge, UK.

Larmola, T., J. Alm, S. Juutinen, P. J. Martikainen, and J. Silvola. 2003. Ecosystem CO_2 exchange and plant biomass in the littoral zone of a boreal eutrophic lake. Freshwater Biology 48:1295–1310.

LiCor. 1998. The LI-6400 Primer: an introduction to operating the LI-6400 portable photosynthesis system. LiCor, Lincoln, Nebraska, USA.

Matthews, E., and I. Fung. 1987. Methane emissions from natural wetlands: global distribution, area, and environmental characteristics of sources. Global Biogeochemical Cycles 1:61–86.

Mitsch, W. J., and J. G. Gosselink. 2000. Wetlands. Third edition. John Wiley and Sons, New York, New York, USA.

Moore, P. D. 2002. The future of cool temperate bogs. Environmental Conservation 29:3–20.

Moore, T. R., J. L. Bubier, S. E. Frolking, P. M. Lafleur, and N. T Roulet. 2002. Plant biomass and production and CO_2 exchange in an ombrotrophic bog. Journal of Ecology 90:25–36.

Newell, S. Y. 1993. Decomposition of shoots of a saltmarsh grass: methodology and dynamics of microbial assemblages. Advances in Microbial Ecology 13:301–326.

Newell, S. Y. 2001. Multiyear patterns of fungal biomass dynamics and productivity within naturally decaying smooth cordgrass shoots. Limnology and Oceanography 46:573–583.

Newell, S. Y., T. L. Arsuffi, P. F. Kemp, and L. A. Scott. 1991. Water potential of standing-dead shoots of an intertidal grass. Oecologia 85:321–326.

Newell, S. Y., T. L. Arsuffi, and L. A. Palm. 1996. Misting and nitrogen fertilization of shoots of a saltmarsh grass: effects upon fungal decay of leaf blades. Oecologia: 108:495–502.

Newell, S. Y., and R. D. Fallon. 1989. Litterbags, leaf tags and decay of nonabscised intertidal leaves. Canadian Journal of Botany 67:2324–2327.

Newell, S. Y., R. D. Fallon, R. M. Cal Rodriguez, and L. C. Groene. 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, S. Y., R. D. Fallon, and J. D. Miller. 1989. Decomposition and microbial dynamics for standing, naturally positioned leaves of the salt marsh grass *Spartina alterniflora*. Marine Biology 101:471–481.

Newell, S. Y., M. A. Moran, R. Wicks, and R. E. Hodson. 1995. Productivities of microbial decomposers during early stages of decomposition of leaves of a freshwater sedge. Freshwater Biology 34:135–148.

Paludan, C., and G. Blicher-Mathiesen. 1996. Losses of inorganic carbon and nitrous oxide from a temperate freshwater wetland in relation to nitrate loading. Biogeochemistry 35:305–326.

Poon, M. O. K., and K. D. Hyde. 1998. Biodiversity of intertidal estuarine fungi on *Phragmites* at Mai Po Marshes, Hong Kong. Botanica Marina 41:141–155.

Raich, J. W., and W. H. Schlesinger. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B:81–99.

Risser, P. G., E. C. Birney, H. D. Blocker, S. W. May, W. J. Parton, and J. A. Wiens. 1981. The true prairie ecosystem. United States/International Biological Program Synthesis Series 16. Hutchinson Ross Publishing, Stroudsburg, Pennsylvania, USA.

Roden, E. E., and R. G. Wetzel. 1996. Organic carbon oxidation and suppression of methane production by microbial Fe(III) oxide reduction in vegetated and unvegetated freshwater wetland sediments. Limnology and Oceanography 41:1733–1748.

Rodewald-Rudescu, L. 1975. Das Schilfrohr. Die Binnengewässer. Volume 27. Schweizerbart, Stuttgart, Germany.

Rustad, L. E., T. G. Huntington, and R. D. Boone. 2000. Controls on soil respiration: implications for climate change. Biogeochemistry 48:1–6.

Saccardo, P. A. 1898. Sylloge Fungorum Omnium Hucusque cognitorum 13. Index Universalis. Verlag Gebrüder Bornträger, Leipzig, Germany.

Saltonstall, K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proceedings of the National Academy of Sciences (USA) 99:2445–2449.

Scanlon, D., and T. Moore. 2000. Carbon dioxide production from peatland soil profiles: the influence of temperature, oxic/anoxic conditions and substrate. Soil Science 165:153–160.

Seastedt, T. R. 1988. Mass, nitrogen and phosphorus dynamics in foliage and root detritus of tallgrass prairie. Ecology 69:59–65.

Silvola, J., J. Alm, U. Ahlholm, H. Nykänen, and P. J. Martikainen. 1996a. CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions. Journal of Ecology 84:219–228.

Silvola, J., J. Alm, U. Ahlholm, H. Nykänen, and P. J. Martikainen. 1996b. The contribution of plant roots to CO_2 fluxes from organic soils. Biology and Fertility of Soils 23:126–131.

Smith, K. A., T. Ball, F. Conen, K. E. Dobbie, J. Massheder, and A. Rey. 2003. Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. European Journal of Soil Science 54:779–791.

Thormann, M. N., and S. E. Bayley. 1997. Decomposition along a moderate-rich fen–marsh peatland gradient in boreal Alberta, Canada. Wetlands 17:123–137.

Updegraff, K., S. D. Bridgham, J. Pastor, P. Weishampel, and C. Harth. 2001. Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. Ecological Applications 11:311–326.

Updegraff, K., J. Pastor, S. D. Bridgham, and C. A. Johnston. 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecological Applications 5:151–163.

Welsch, M., and J. B. Yavitt. 2003. Early stages of decay of *Lythrum salicaria* L. and *Typha latifolia* L. in a standing-dead position. Aquatic Botany 75:45–57.

Wescor. 1986. Instruction/service manual HR-33T dew point microvoltmeter. Wescor, Logan, Utah, USA.

Wetzel, R. G., and M. J. Howe. 1999. High production in a herbaceous perennial plant achieved by continuous growth and synchronized population dynamics. Aquatic Botany 64:111–129.

Whiting, G. J. 1994. CO_2 exchange in the Hudson Bay lowlands: community characteristics and multispectral reflectance properties. Journal of Geophysical Research 99(D):1519–1528.

Wickland, K. P., R. G. Striegl, M. A. Mast, and D. W. Clow. 2001. Carbon gas exchange at a southern Rocky Mountain wetland, 1996–1998. Global Biogeochemical Cycles 15:321–335.

Wilkinson, L., M. A. Hill, J. P. Welna, and G. K. Birkenbeuel. 1992. SYSTAT 5 for the Macintosh. Version 5.2. Systat, Evanston, Illinois, USA.

Windham, L. 2001. Comparison of biomass production and decomposition between *Phragmites australis* (common reed) and *Spartina patens* (salt hay grass) in brackish tidal marshes of New Jersey, USA. Wetlands 21:179–188.

Winkler, J. P., R. S. Cherry, and W. H. Schlesinger. 1996. The Q_{10} relationship of microbial respiration in a temperate forest soil. Soil Biology and Biochemistry 28:1067–1072.

Yavitt, J. B. 1997. Methane and carbon dioxide dynamics in *Typha latifolia* (L.) wetlands in central New York State. Wetlands 17:394–406.