7 Decomposition in Boreal Peatlands

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7.1 Introduction

Peatlands are characterized by substantial amounts of organic matter, with stocks commonly 50–150 kg C m^{-2} and accumulation rates between 10 and 30 g C m^{-2} $year^{-1}$ (Gorham 1991; Turunen et al. 2001). These accumulations represent an imbalance between input of C from plant production and its export from the peatland as CO_2, CH_4, or dissolved organic carbon, which are the products of the decomposition of plant tissues and organic matter in the soil. Rates of net primary production in peatlands are generally small (Campbell et al. 2000; Moore et al. 2002; Chap. 8), as are rates of net ecosystem exchange of CO_2 and soil respiration (Frolking et al. 1998; Chap. 9). Thus, the accumulation of organic matter in peatlands is generally ascribed to slow rates of decomposition associated with cool temperatures, anoxic conditions, functionally limited decomposer communities, and litter and organic matter substrates that are naturally slow to decompose. Many studies have measured the rates of litter and organic matter decomposition in peatlands and the controls on these rates. In this chapter, we review their major findings and present some new results. Although the change from plant tissues to peat is part of a continuum, the techniques used to determine rates of litter and peat decomposition are different and thus we treat them separately.

7.2 Litter Decomposition

A common method of determining rates of litter or plant tissue decomposition in soils is to enclose the material in mesh bags, place the bags in the soil profile at the position in which the litter would normally decompose, and then retrieve subsets of the initially placed bags over a number of years and establish the residual mass in the bag and associated changes in

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chemistry, such as C, N, and P contents. This litter-bag method has been criticized because monospecific litters are usually employed, the bags may either exclude soil organisms if the mesh is small or allow litter particles to fall through if the mesh is large and separation of original litter from incorporated soil humus becomes difficult in the late stages of decomposition. Furthermore, there are concerns that the bags may create their own environment in terms of chemistry, water content, and temperature distinct from the environment of the bulk soil. Nevertheless, the method is relatively inexpensive and easily allows comparisons to be made of decomposition rates of distinct litter types at different locations or at different depths in the soil profile. Decomposition rates are fast in warm, well-drained soils with rich litters, but rates are slow in peatlands, so most peatland litter-bag studies lasting for 2 or 3 years show that only a small proportion of the mass has been decomposed, thus tracing only a small proportion of the continuum from litter to peat.

Results may be reported as the proportion of original litter mass remaining after a defined period and/or by assuming a mathematical relationship between the mass and time. A simple exponential decay pattern is assumed in most cases, providing a regression with a constant term (a, the mass at time zero) and a decay constant, frequently given the symbol k, usually on a per year basis (mass remaining equals ae^{kt}). Litter-bag experiments have rarely been run for long enough to evaluate whether a simple exponential decay model adequately explains the longer-term decomposition rate. The exception is a study by Latter et al. (1998), in which four litters (*Rubus* leaves, *Eriophorum* leaves, and *Calluna* stems and shoots) were placed in mesh bags, hair nets, or left unenclosed and retrieved for up to 23 years. Mass loss after 5 years ranged from 70 % (*Rubus* leaves) to 24–55 % for the other tissues. The use of a double exponential decay regression for the 23-year data resulted in an improvement in the proportion of variance explained by 1.5 % (*Calluna* stems), 10.0 % (*Calluna* shoots), to 29.2 % (*Eriophorum*), and an asymptotic model provided the best fit. Nevertheless, a single exponential model commonly fits data from short-term studies of mass loss and facilitates comparison between litter types and environments.

Typical short-term (6 years) decomposition rates of litter in northern peatlands (bog, fen, and swamp) are illustrated in Fig. 7.1. In general, the simple exponential decay model works well, with k values ranging from –0.01 to –0.45 year^{-1} and high coefficients of determination (r^2>0.8) when litter decays rapidly. Coefficients of determination, however, can be small (r^2<0.2) when decomposition rates are slow, such as in wood blocks or *Sphagnum fuscum*. The intercept value (a) of the regression of mass remaining against time relates to the early mass loss, such as water-soluble material and other labile material within the tissues (Trofymow et al. 2002). Simple exponential decay constants (k) for peatlands collated by lit-

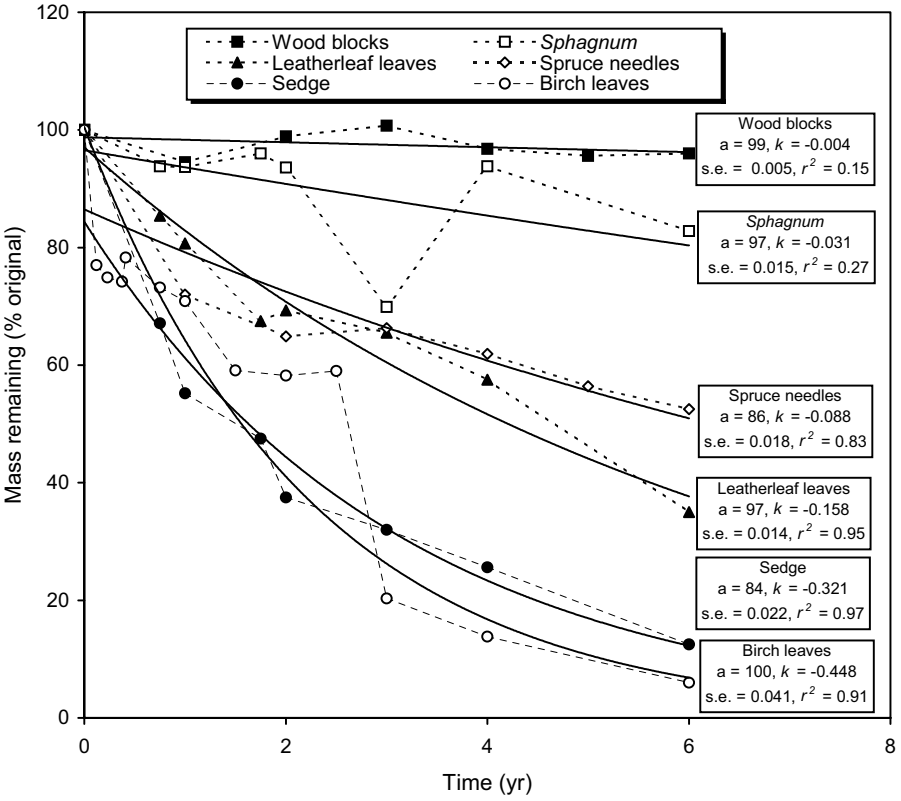

Fig. 7.1. Decomposition rates of litters in representative Canadian peatlands. Western hemlock (*Tsuga heterophylla*) wood blocks and spruce needles (*Picea mariana*) decomposed at a bog near Nelson House, Manitoba (Moore et al. 2006); *Sphagnum* (*S. fuscum*) and sedge (*Carex rostrata*) decomposed at a poor fen near Schefferville, Quebec; leatherleaf leaves (*Chamaedaphne calyculata*) decomposed in a bog near Sept-Îles, Quebec; and yellow birch leaves (*Betula alleghaniensis*) decomposed at a swamp, Mont St. Hilaire, Quebec (Moore, unpublished data). Each value represents the mean of three to four replicate bags collected at each date. The *curved lines* represent the exponential decay regression for each litter type: mass remaining (% original) = ae^{kt}, with t in years. The values for a and k (year^{-1}) are indicated for each tissue, along with the standard error (*s.e.*) of k and the coefficient of determination (r^2)

ter type based on studies at several Canadian peatlands in which mass loss has been measured for 6 years are presented in Table 7.1. In general, the k values follow the sequence of decomposition from slowest to fastest of woody material<hummock *Sphagnum*<hollow/lawn *Sphagnum*<tree needles<tree leaves<shrub leaves<sedge. Within the trees and shrubs, evergreen material decomposes at a slower rate than deciduous material. These results are similar to those collated by Aerts et al. (1999), based on k

Table 7.1. Exponential decay constants (k) for different litter types in northern peatlands, based on studies lasting 6 years (Moore et al. 2005; Moore unpublished data)

Litter type	k value Range	Mean	Locations
Wood blocks[a]	–0.00 to –0.01	–0.01	Boreal bogs, central Canada
Tree foliage			
Needles	–0.08 to –0.23	–0.15	Bogs and swamp
Needles[a]	–0.04 to –0.12	–0.09	Bogs and pothole peatland
Leaves	–0.07 to –0.38	–0.22	Bogs and swamp
Leaves[a]	–0.09 to –0.12	–0.11	Bogs and pothole peatland
Shrub stems	–0.23 to –0.27	–0.21	Temperate bog
Shrub leaves			
Evergreen	–0.12 to –0.19	–0.15	Bogs and swamp
Deciduous	–0.19 to –0.23	–0.21	Bogs and swamp
Sedges	–0.16 to –0.44	–0.28	Subarctic fens and boreal bogs
Sphagnum moss			
Hummock species (e.g., *S. fuscum*, *S. rubellum*, *S. capillifolium*)	–0.01 to –0.03	–0.02	Subarctic, boreal, and cool temperate bogs and fens
Hollows/lawn species (e.g., *S. angustifolium*, *S. lindbergii*)	–0.07 to –0.15	–0.08	
Lichen	–	–0.08	Boreal bog

Most results were obtained with litter bags with openings of 1 mm × 2 mm.
[a] Part of the Canadian Intersite Decomposition Experiment in which litter bags with 0.25-mm × 0.50-mm openings were used at sites in central Canada

values calculated for the first year of study. Although there is a general correlation between first-year k values and those found after 6 years, differences in decomposition rate develop as the tissues decompose.

7.2.1 Controls on Litter Decomposition

The main controls on litter decomposition in peatlands can be identified as macroclimate and microclimate, position within the peat profile, and litter and peat chemistry. The influence of macroclimate on decomposition rates in forest litters has been well established, showing that decomposition slows as temperatures decrease and becomes faster with increasing precipitation (Meentemeyer 1978; Moore et al. 1999; Trofymow et al. 2002). There have been few litter transplant experiments in peatlands, so this pattern has not been clearly established in peatlands. In a study of leaf

litter decomposition rates in Canadian forests, an increase in mean annual temperature from 0 to 10 °C resulted in an average increase in decomposition rates, shown by 6-year k values changing from –0.13 to –0.23 year^{-1}, and a decrease from 50 to 22 % of the original mass (Trofymow et al. 2002). At three peatland sites in central Canada, Moore et al. (2005) showed that the overall rate of decomposition of 12 litter types decreased as the mean annual temperature declined, although this pattern was confounded by microclimatic and other effects.

It is often assumed that rates of litter decomposition are slower in upland, well-drained forests than in adjacent peatlands. This pattern is variable. There was a slower decomposition (as shown by less negative k values) over 6 years of three tree leaf types in a temperate swamp than in an adjacent deciduous forest (Fig. 7.2). In central Canada, however, the pattern was variable among 12 litters decomposing over 6 years between three pairs of upland and peatland sites (Fig. 7.3). Strong differences between upland and peatland decomposition rates may only develop in

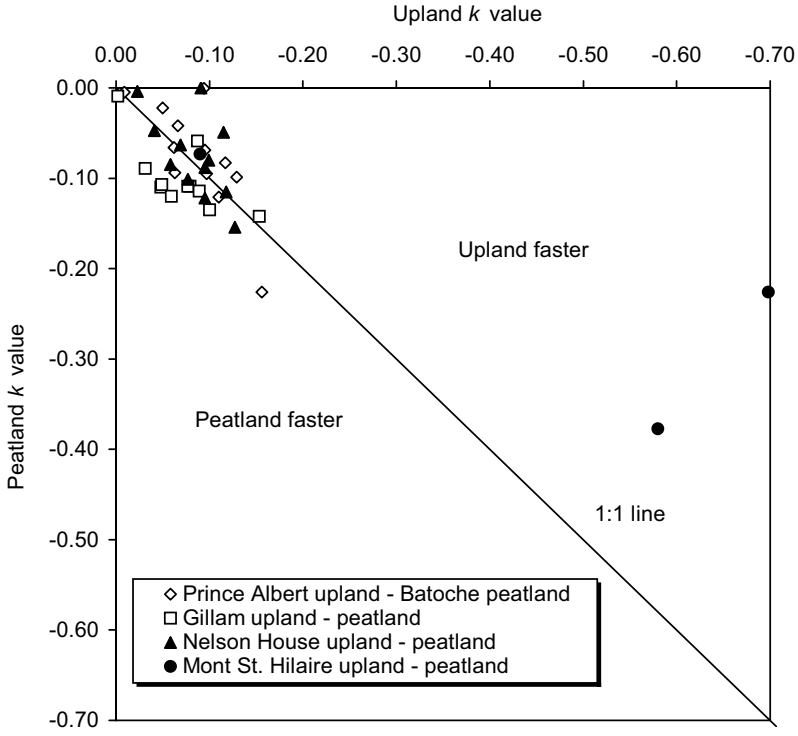

Fig. 7.2. Comparison of exponential decay k values for plant tissues decomposing at three peatland and nearby upland forest sites, Canada. Data for the swamp–deciduous forest were obtained at Mont St. Hilaire, southern Quebec (Moore, unpublished data) and for the CIDET sites in central Canada from Moore et al. (2005)

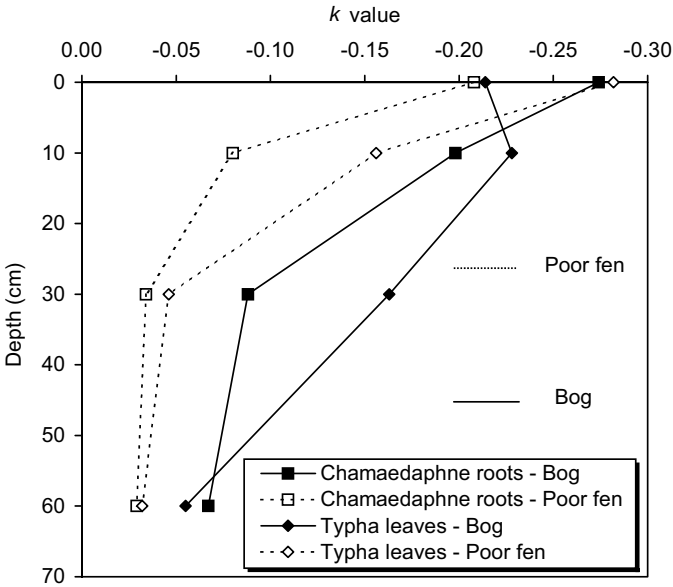

Fig. 7.3. Exponential decay *k* values for *Chamaedaphne calyculata* roots (2–5-mm diameter) and *Typha latifolia* leaves placed in litter bags from the peat surface to 60 cm at a cool temperate bog and poor fen, Mer Bleue, eastern Ontario, calculated over 6 years (Moore, unpublished data). The *horizontal lines* represent the average summer water table position at the two sites. Standard errors of the estimate of the *k* values are not shown, but average 0.02

the later stages of decomposition. The effect of flooding on litter decomposition rates has been examined in several studies with variable results, depending on duration, litter type, and influence of water chemistry (Day 1983, Wylie 1987, Lockaby et al. 1996, Baker et al. 2001). Short periods of flooding may stimulate decomposition, while prolonged flooding may slow rates. Thus, the effect of drainage class on litter decomposition in peatlands may become important after several years for slowly decomposing litter or when the litter is inundated for long periods.

Position within the peat profile can have a profound influence on the rates of litter decomposition, as the lower sections of the peat profile are both cooler and exposed to more frequent anoxic conditions than the surface layers (Clymo 1965). At an ombrotrophic bog and poor fen in eastern Canada, the exponential decay *k* value showed a pronounced change from –0.2 to –0.3 year^{-1} for *Typha latifolia* leaves and *Chamaedaphne calyculata* roots (2–5-mm diameter) placed on the peat surface to –0.05 to –0.10 year^{-1} at depths of 10, 30, and 60 cm (Fig. 7.3). The greatest change was observed in the poor fen, where the water table was closer to the peat

surface, keeping the 30- and 60-cm depths waterlogged for nearly all the year, whereas the water table dropped beneath 30 cm for most of the summer at the bog site. In a Swedish bog, Johnson and Damman (1991) also observed a decrease in decomposition rate (mass loss over 22 months) of *Sphagnum* samples placed in oxic or anoxic zones in a hummock. Although much of plant production in peatlands occurs belowground, studies of decomposition of root and rhizomes lag behind those of aboveground components. Thormann et al. (2000) observed rapid decomposition of sedge rhizomes and willow roots placed 3–10 cm beneath the surface of boreal peatlands, and collated data on belowground 1-year mass losses ranging from 15 to 60 % in temperate and boreal peatlands. At a temperate bog, sedge and shrub roots lost between 16 and 52 % and 18 and 66 %, respectively, of their original mass over 5 years, the larger losses occurring at a depth of 10 cm and the smaller losses at 30 or 60 cm in the peat profile (Moore, unpublished data).

Litter chemistry plays an important role in controlling rates of decomposition in peatlands. From studies of upland forests, the lignin and N concentration of litter has been found to exert an important influence on decomposition rate (Meentemeyer, 1978; Trofymow et al. 2002). At three peatland sites in central Canada, the decomposition rate (expressed as the *k* value over 6 years) of ten upland foliar litters was significantly correlated with the lignin-to-N ratio of the initial litter (Fig. 7.4). This relationship, however, breaks down when nonvascular litters, such as lichen and *Sphagnum* mosses, are included, because of their specific organic composition.

The cause of the very slow decomposition rates of *Sphagnum* (Table 7.1) has been linked to specific organic compounds within the plant tissue, as well as to low concentrations of nutrients such as N and P. Verhoeven and Liefveld (1997) reviewed organochemical compounds produced by *Sphagnum*, noting the production of phenolics and uronic acids as well as "sphagnol" and "sphagnum acid," which negatively affect vascular plant growth and aid in the preservation of bodies (Painter 1991). These compounds also slow down the rate of decomposition of plant tissues, through acidification and the inhibition of microbial decay of litter. The latter is supported by the inhibition of Gram-positive bacteria by *Sphagnum* extracts (Banerjee and Sen 1979) and the slowed rates of decomposition of sedge and moss tissues in laboratory experiments when homogenized *Sphagnum* capitula were added (Verhoeven and Toth 1995). There are variations in the rate at which *Sphagnum* mosses decompose: hummock mosses decompose at slower rates than those found in hollows, even though the decay environment is less favorable in the hollows (Johnson and Damman 1993). Johnson and Damman (1993) suggested that rates of *Sphagnum* decay could be negatively correlated to the concentration of polyuronic acid and positively to the nonstructural carbohydrate content,

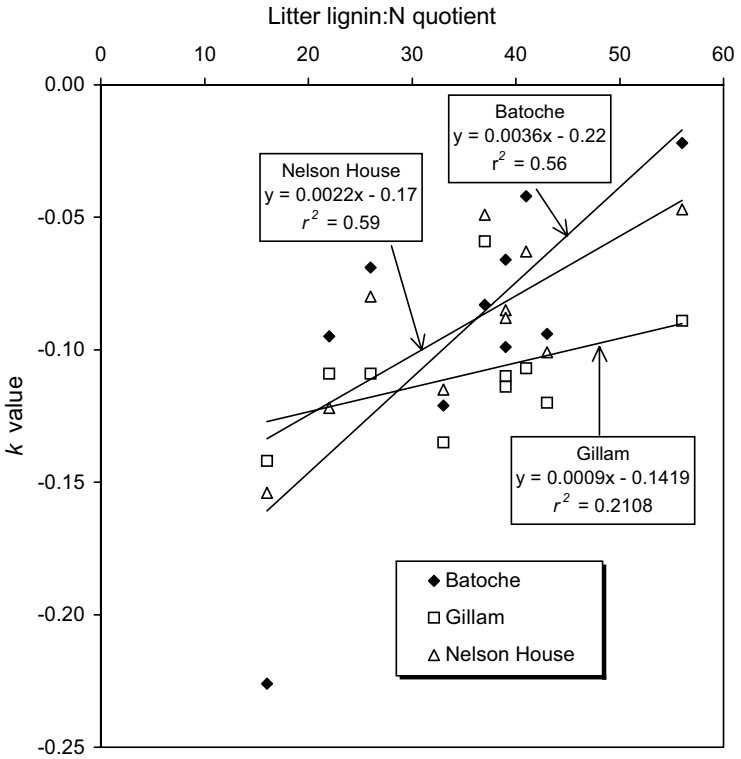

Fig. 7.4. Relationship between lignin-to-N quotient and exponential decay *k* value for ten leaf litters over 6 years placed on the peat surface at three peatland sites in central Canada. The litters comprised aspen, beech, and birch leaves; western red cedar, Douglas fir, jack pine, black spruce, and tamarack needles; and grass and bracken fern. The regression between the quotient and *k* value is shown. (Moore et al. 2005)

and Limpens and Berendse (2003) also suggested that N concentration is important, although P concentration may also play a role.

7.2.2 Peat Decomposition

Plant litter becomes peat through partial decomposition. Peat mineralization is constrained by many of the same factors as litter mineralization; however, because rates are slower and particle sizes can be too small for containment within mesh bags, in vitro incubations and measurement of gaseous mineral products have more commonly been used to investigate controls. Although many of the specific microbial mechanisms involved in both partial decomposition of plant litter resulting in peat formation and

subsequent peat mineralization are still not fully understood, a great deal of work has been done investigating broad controls on peat mineralization.

Lignin and other polymeric phenolic molecules, including sphagnum acid, originally derived from woody tissues and *Sphagnum*, are degraded to monomeric phenolics only under aerobic conditions by various microbial oxidase enzymes (Freeman et al. 2001); however, decomposition proceeds slowly even under aerobic conditions owing to pH constraints of these enzymes (Williams et al. 2000). As a result, mineralization is rapider under aerobic than anaerobic conditions (Moore and Dalva 1993; Yavitt et al. 1997; Glatzel et al. 2004), a key factor in peat accumulation. Although the anoxic separation of polymeric phenolic molecules either cannot occur or has not yet been characterized, anaerobic metabolic pathways leading to and including methanogenesis still contribute to production of organic decomposition products and partial mineralization of peat. In the 1920s, Waksman and Stevens (1929) described *Sphagnum*-derived peat soils as a mixture of partially decomposed plant residue and secondary microbial products. Owing to analytical constraints, since the 1920s our understanding of molecular structures of microbially formed peat has not improved greatly, especially for high molecular weight polymeric molecules.

The partial decomposition of phenolic molecules through anaerobic fermentations produces, in part, several short-chain fatty acids that provide a C substrate for other microbial activities and ultimately a suitable redox potential and a C substrate for methanogenesis (Bräuer et al. 2004; Chap. 9). In the presence of more energetically profitable electron acceptors, particularly oxidized inorganic N, Fe, or S, methanogens, especially when they utilize the aceticlastic pathway, cannot compete well for fatty acids. Rates of microbial denitrification are usually low and do not contribute largely to C turnover, as incoming inorganic oxidized N in unpolluted to moderately polluted sites is largely retained by vegetation (Li and Vitt 1997; Williams et al. 1999; Chap. 10). Microbial Fe reduction has not been demonstrated to contribute substantially to C turnover, and total Fe concentrations are low particularly in northern bogs (Robert et al. 1999; Basiliko and Yavitt 2001). Despite relatively low inputs of S to most northern peatlands, microbial S reduction can contribute to the anaerobic mineralization of C (Vile et al. 2003a, b; Chap. 12). Sulfate reduction potentials measured in the laboratory are often high, despite low inputs of oxidized S (Blodau and Moore 2003). This probably indicates internal recycling between oxidized and reduced S species (Wieder and Lang 1988; Wieder et al. 1990) either by the temporary presence of O_2, perhaps as delivered by vascular roots as demonstrated in other ecosystems (Wind and Conrad 1997), or there may be a yet-unidentified organic electron acceptor that could reoxidize reduced S (Blodau et al. 2002).

Many studies have quantified production of CO_2 and CH_4 as a proxy for peat decomposition (Chap. 9). Measuring gaseous release of mineral C is both rapid and a relevant measure of microbial activity to C and greenhouse gas budgets of peatlands, but it is important to note that these are only terminal decomposition products. Although controls on mineralization rates of peat to CO_2 and CH_4 often are assumed to correlate with controls on bulk decomposition, it must be recognized that mineralization of peat is a final step of a much more detailed, and poorly understood, set of processes.

Microbial CO_2 production cannot be measured directly in situ because living *Sphagnum* and vascular roots throughout peat also produce CO_2. In vitro incubation of peat in the absence of plant respiration has commonly been used to investigate controls on relative rates of decomposition between sites, throughout depths or under different laboratory conditions (Moore and Dalva 1997; Yavitt et al. 1997; Scanlon and Moore 2000; Basiliko and Yavitt 2001; Blodau et al. 2004; Glatzel et al. 2004). Advantages to using in vitro incubation techniques include utilizing peat of any age as opposed to fresh plant litter with mesh bags, rapidity, and the ability to capture the effects of nutrient and chemical changes in recently formed plant litter and peat arising; for example, from increased nutrient deposition. On the other hand, incubation techniques inevitably involve severe sample disturbance, introduce artificial environmental conditions, and estimate decomposition rates over very short periods of time. At best, these techniques may indicate relative rates of peat decomposition, and because they are carried out under controlled and often idealized conditions they are often described as potential CO_2 production measurements.

We suggest that potential CO_2 production rates likely occur as a function of in situ substrate, nutrient, and microbial biomass potential to mineralize peat. For example, aerobic CO_2 production potentials determined in 416 samples from a wide range of sites in eastern Canadian peatlands revealed positive correlations with extractable organic N and P and microbial biomass C and N (Figs. 7.5, 7.6). Within more constrained sets of samples, for example indicated with closed circles in Figs. 7.5 and 7.6, correlations with single potentially controlling factors were stronger, similar to patterns reported by Turetsky (2004) across peatlands in the boreal discontinuous permafrost region of central Canada. The size of the microbial biomass, which presumably results from substrate and nutrient availability and suitable environmental conditions and relates to decomposition and mineralization rates, may be similar to that of forest soils. On average, our 416 peat samples from eastern Canadian sites had biomass values similar to those reported for organic layers of southern Canadian conifer forests, and both organic portions of forest soils and peats had much smaller biomass than mineral agricultural soils when normalized for soil organic C (Table 7.2). Our samples were biased toward less humified peat

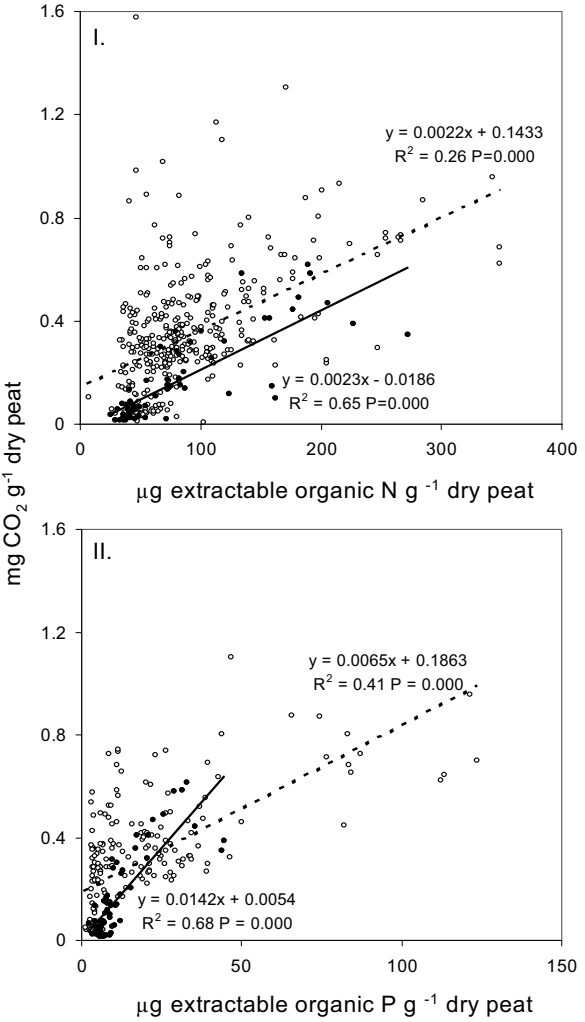

Fig. 7.5. Relationships between K_2SO_4-extractable organic N (*I*) and P (*II*) and aerobic CO_2 production potential in peat from nine eastern Canadian peatlands in pristine condition or undergoing commercial harvesting or nutrient fertilization taken at different times of year and throughout depth (Basiliko and Moore, unpublished data). *Data points* and regressions in *closed circles* represent peat collected on one sampling date at sites from one region near Shippagan, New Brunswick

from the upper 0.5 m of the peat deposit, whereas highly humified peat had much less biomass than forest soils, and it may be this highly recalcitrant fraction that supports small biomass and is responsible for the larger C storage functions in peatlands relative to forests (Table 7.2). Owing to both different measurement techniques and differential C extraction efficiencies among soils, comparisons of microbial biomass must be interpreted with caution.

Potential CO_2 production has been used in many previous studies to determine controls on peat decomposition. Rates generally depend on peat temperature, availability of oxygen, vascular plant activity, environmental fluctuations, and chemical characteristics (Moore and Dalva 1993;

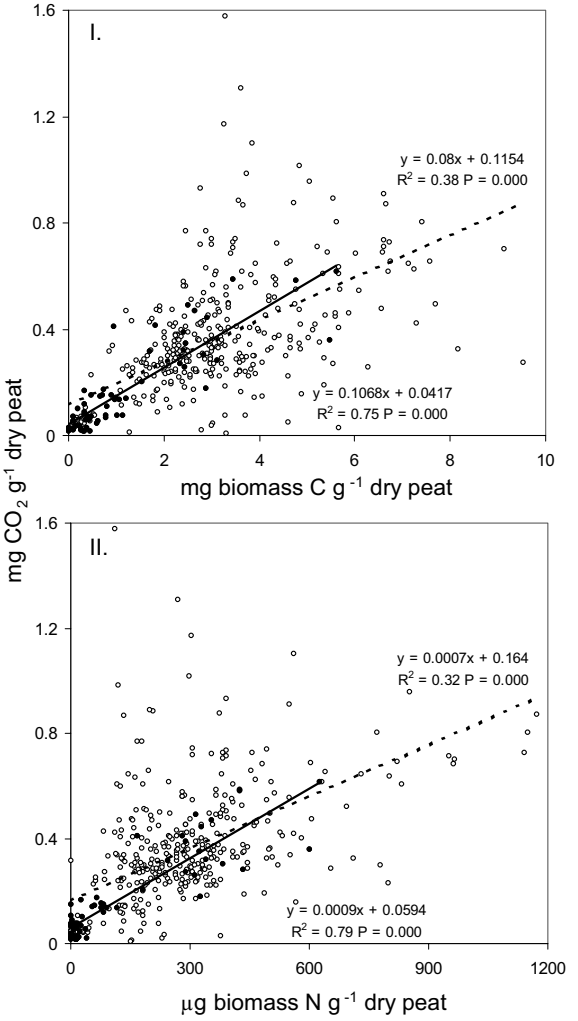

Fig. 7.6. Relationships between microbial biomass C (*I*) and N (*II*), determined with $CHCl_3$ fumigation–extraction and CO_2 production potential in peat from nine eastern Canadian peatlands in pristine condition or undergoing commercial harvesting or nutrient fertilization taken at different times of year and throughout depth (Basiliko and Moore, unpublished data). *Data points* and regressions in *closed circles* represent peat collected on one sampling date at sites from one region near Shippagan, New Brunswick

Thomas et al. 1996; Yavitt et al. 1997). Potential CO_2 production responds to a 10 °C change in temperature, within the 2–23 °C range, by a factor of approximately 2.2–2.4 (Moore and Dalva 1993; Yavitt et al. 1997), although smaller, and site- and depth-specific, responses to changing temperatures have also been reported (Scanlon and Moore 2000). Potential CO_2 production in aerobic incubations is greater than in anaerobic incubations, but the pattern is very variable, varying by a factor of 1.2 (Yavitt et al. 1997) to 200 (Hogg 1993), although factors of 2–6 are more common (Moore and Dalva 1997; Glatzel et al. 2004) The activity of vascular plants (Thomas et al. 1996) and *Sphagnum* mosses (Fenner et al. 2004) in releasing photosynthates to the peat profile also apparently provides a labile C source that

Table 7.2. Microbial biomass C in Canadian mineral agricultural soils under various crops (Arshad et al. 2004), organic soils in mixed conifer stands (Leckie et al. 2004), and nine eastern peatlands (Basiliko and Moore, unpublished data) expressed per gram of dry soil and per gram of soil organic C (*SOC*). Humified peat samples were from commercially harvested sites, where harvesting exposed deep, old peat to the surface. Organic C content of forest humus and peat was assumed to be 50 %

Soil type	Microbial biomass mg microbial C g^{-1} soil	mg microbial C g^{-1} SOC
Mineral soils with crops		
Smooth brome	1.08	25.0
Red fescue	1.16	25.9
Continuous wheat	0.93	23.7
Wheat–canola rotation	0.86	21.4
Wheat–pea rotation	0.86	23.1
Wheat–fallow rotation	0.87	23.5
Forest soils		
Cedar–hemlock, forest floor	4.27	8.5
Cedar–hemlock, upper humus	2.88	5.8
Cedar–hemlock, lower humus	1.84	3.7
Hemlock–amibilis fir, forest floor	3.75	7.5
Hemlock–amibilis fir, upper humus	2.77	5.5
Hemlock–amibilis fir, forest floor	1.49	3.0
Peatlands		
All peat samples (n=416)	2.80	5.6
Humified peat (n=60)	0.31	0.6

contributes to microbial CO_2 production (however, Thomas et al. 1996 and Fenner et al. 2004 used isotope tracer techniques and not CO_2 production potential assays). Labile trigger molecules may enhance decomposition of bulk peat (Basiliko et al., unpublished data). Water table fluctuations leading to drying and wetting of peat, or freeze–thaw cycles, may also increase decomposition rates (Wynn-Williams 1982; Freeman et al. 1997).

Peat chemical characteristics play a large role in decomposition and mineralization rates (Updegraff et al. 1996; Yavitt et al. 1997; Turetsky 2004); however, Yavitt et al. (1997) has suggested that among *Sphagnum*-dominated sites, very subtle chemical differences may be responsible for variability in mineralization rates. Chemical fractionation or proximate analyses as well as total and extractable nutrient concentrations have been used to characterize the chemical nature of peat (Waksman and Stevens 1928; Yavitt et al. 1997; Turetsky 2004). Although these methods do not illustrate exact molecular composition, they group molecules and compounds into classes that may relate to bioavailability. Fractionation meth-

ods traditionally rely, at least in part, on high-temperature oxidation in strong acids and extractions. N and P concentrations or quality have the potential to influence decomposition rates (Turetsky 2004; Fig. 7.5); however, traditional measures, such as lignin-to-N or acid insoluble material-to-N quotients that can predict organic matter mineralization rates across other terrestrial ecosystems, are apparently only successful across some (Turetsky 2004), but not all, *Sphagnum*-derived peats (Yavitt et al. 1997).

Methanogenesis, an important terminal anaerobic decomposition step, is carried out in peatlands by a group of strictly anaerobic euryarchaeota that utilize nine 1-C or 2-C organic acids or H_2 (Zinder 1993), and it is unclear if and when aceticlastic or hydrogenitrophic methanogenesis is the more common methanogenic pathway in peatlands (Hornibrook et al. 1997; Duddleston et al. 2002; Chap. 9). Similar to microbial CO_2 production, many studies utilize laboratory incubations to examine controls on CH_4 production. Methanogens rely on substrates produced by fermentative bacteria, and peat organic matter quality has been related to rates of CH_4 production (Updegraff et al. 1996; Yavitt et al. 1997). Substrates otherwise available for methanogenesis may be more readily utilized by sulfate reducers in the presence of oxidized S, through inferior thermodynamic competition (Nedwell and Watson 1995). Alternatively, buildup of moderate to large concentrations of acetate inhibits CH_4 production (Bräuer et al. 2004). Methanogens are strict anaerobes, and following flooding and initiation of anoxia, CH_4 production is usually characterized by a lag period until rapid rates are achieved (Basiliko and Yavitt 2001). Methane production is also dependent on temperature and pH (Dunfield et al. 1993; Moore and Dalva 1993), and response to temperature is greater than for potential CO_2 production with Q_{10} factors of about 4 (Segers 1998). Micronutrients that are not limiting for many other organisms may limit methanogenesis (Basiliko and Yavitt 2001). Simultaneous anaerobic CH_4 and CO_2 production potential measurements have shown that more CO_2 than CH_4 (molar basis) is produced, although CH_4 and CO_2 production potentials often correlate, indicating that similar controlling factors may exist (Moore and Dalva 1997; Glatzel et al. 2004). In peat from North American peatlands, anaerobic CH_4 production potential over 30 days ranged from 3 to 21 % of CO_2 produced (Basiliko and Yavitt 2001).

Some estimate of relative decomposition rates, compared with rates for fresh litter, can be made. Scanlon and Moore (2000) incubated undisturbed cores from the upper part of peat profiles in a temperate bog under varying temperature and oxic/anoxic conditions. From these results, and thermal and water table regimes at the site, they estimated that k values ranged from –0.05 year^{-1} at a depth of 10–20 cm to –0.002 to –0.02 year^{-1} at a depth of 40–50 cm. Using transplants of peat, Belyea (1996) estimated rates of –0.01 to –0.08 year^{-1} from beneath the water table to close to the surface in a Scottish peatland. Wieder (2001) used ^{210}Pb-dating of the sur-

face layers of three bogs in Alberta to estimate k values ranging from 0 to –0.12 year^{-1}, with average values over the top 30 cm of –0.02 to -0.03 year^{-1}. Analyzing profiles of bogs, Clymo et al. (1998) estimated that decay rates in the catotelm of bog profiles ranged from -1×10^{-4} to -1×10^{-8} year^{-1}, showing an increase with mean annual temperature. Thus, there is consistency in boreal peatland decomposition k values ranging from –0.03 to –0.30 year^{-1} in fresh plant tissues (from mosses to nutrient-rich leaves) to –0.02 to –0.0001 year^{-1} in the upper and lower parts of the profile.

Many boreal and cool temperate peatlands have been harvested for their peat, especially for horticultural peat moss. Global production of peat amounted to 28×10^6 t in 2000 (Jasinski 2001). Most of the harvested peat decomposes in an aerobic environment, mixed with mineral soil or other substrates or fertilizer and exposed to a wider range of soil fauna than in a bog. There are few studies of the rates of peat decomposition when added to well-drained soils, but the results of Aendekerk (1997) and Murayama et al. (1990) suggest that decomposition rates are much accelerated, with first-year mass losses of between 5 and 25 % when placed in mineral aerobic soils. Cleary et al. (2005) have shown that for the peat extraction industry in Canada, this poorly understood rate of decomposition of the harvested peat dominates the C cycle, and deserves further attention.

7.3 Conclusions

The slow rates of decomposition of plant tissues and peat are critical to the accumulation of large amounts of organic matter in boreal peatlands. This slowness is a combination of the poor nutrient content and high refractory content of most peatland plants and the underlying peat, the generally cool and frequently anoxic conditions in which the plant tissues and peat decompose, and small microbial populations, when normalized to soil organic C content. Although several studies have identified and quantified the influence of these controls of decomposition rates for individual peatlands, we still lack a coherence, compared with forest or grassland systems, in the application of this knowledge to the broad range of peatlands that occur with boreal environments under both natural and disturbed (such as drained, harvested, or flooded) conditions or under climate-change scenarios.

References

Aendekerk TGL (1997) Decomposition of peat substances in relation to physical properties and growth of chamaecyparis. Acta horticulturae 450:191–198

Aerts R, Verhoeven JTA, Whigham DF (1999) Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology 80:2170–2181

Arshad MA, Franzluebbers AJ, Azooz RH (2004) Surface-soil structural properties under grass and cereal production on a Mollic Cyroboralf in Canada. Soil Tillage Res 77:15–23

Baker TT, Lockaby BG, Conner WH, Meier CE, Stanturf JA, Burke MK (2001) Leaf litter decomposition and nutrient dynamics in four southern forested floodplain communities. Soil Sci Soc Am J 65:1334–1347

Banerjee RD, Sen SP (1979) Antibiotic activity of bryophytes. Bryologist 82:141–153

Basiliko N, Yavitt JB (2001) Influence of Ni, Co, Fe, and Na additions on methane production in *Sphagnum*-dominated northern American peatlands. Biogeochemistry 52:133–153

Belyea LR (1996) Separating the effects of litter quality and macroenvironment on decomposition rates in a patterned peatland. Oikos 77:529–539

Blodau C, Moore TR (2003) Micro-scale CO_2 and CH_4 dynamics in a peat soil during a water fluctuation and sulfate pulse. Soil Biol Biochem 35:535–547

Blodau C, Roehm CL, Moore TR (2002) Iron, sulfur, and dissolved carbon dynamics in a northern peatland. Achiv Hydrobiol 154:561–583

Blodau C, Basiliko N, Moore TR (2004) Carbon turnover in peatland mesocosms exposed to different water table levels. Biogeochemistry 67:331–351

Bräuer SL, Yavitt JB, Zinder SH (2004) Methanogenesis in McLean Bog, an acidic peat bog in upstate New York: stimulation by H_2/CO_2in presence of rifampicin, or by low concentrations of acetate. Geomicrobiol J 21:433–443

Campbell C, Vitt DH, Halsey LA, Campbell ID, Thormann MN, Bayley SE (2000) Net primary production and standing biomass in northern continental wetlands. Canadian Forestry Service information report NOR-X-369. Canadian Forestry Service, Edmonton

Cleary J, Roulet NT, Moore TR (2005). Greenhouse gas emissions from Canadian peat extraction, 1990-2000: a life-cycle analysis. Ambio 34:456–461

Clymo RS (1965) Experiments on breakdown of *Sphagnum* in two bogs. J Ecol 53:737–757

Clymo RS, Turunen J, Tolonen K (1998) Carbon accumulation in peatland. Oikos 81:368–388

Day FP (1983) Effects of flooding on leaf litter decomposition in microcosms. Oecologia 56:180–184

Dunfield P, Knowles R, Dumont RT, Moore TR (1993) Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. Soil Biol Biochem 25:321–326

Duddleston KN, Kinney MA, Kiene RP, Hines ME (2002) Anaerobic microbial biogeochemistry in a northern bog: acetate as a dominant metabolic end product. Global Biogeochem Cycles 16. DOI 10.1029/2001GB001402

Fenner N, Ostle N, Freeman C, Sleep D, Reynolds B (2004) Peatland carbon efflux partitioning reveals that *Sphagnum* photosynthate contributes to the DOC pool. Plant Soil 259:345–354

Freeman C, Liska G, Ostle NJ, Lock MA, Hughes S, Reynolds B, Hudson J (1997) Enzymes and biogeochemical cycling in wetlands during a simulated drought. Biogeochemistry 39:177–187

Freeman C, Ostle N, Kang H (2001) An enzymatic 'latch' on global carbon store. Nature 409:149

Frolking S, Bubier JL, Moore TR, Ball T, Bellisario LM, Bhardwaj A, Carroll P, Crill PM, Lafleur PM, McCaughey JH, Roulet NT, Suyker AE, Verma SB, Waddington JM, Whiting GJ (1998) The relationship between ecosystem productivity and photosynthetically active radiation for northern peatlands. Global Biogeochem Cycles 12:115–126

Glatzel SN, Basiliko N, Moore TR (2004) Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, eastern Québec, Canada. Wetlands 24:261–267

Gorham E (1991) Northern Peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1:182–195

Hogg HE (1993) Decay potential of hummock and hollow *Sphagnum* peats at different depths in a Swedish raised mire. Oikos 66:269–278

Hornibrook ERC, Longstaff FJ, Frye WS (1997) Spatial distribution of microbial methane production pathways in temperate zone wetland soils: stable carbon and hydrogen isotope evidence. Geochim Cosmochim Acta 61:745–753

Jasinski SM (2001) Peat. Mineral Commodity Summaries, January, 2001. US Department of the Interior: US Geological Survey, Washington, DC

Johnson LC, Damman AWH (1991) Species controlled *Sphagnum* decay on a south Swedish raised bog. Oikos 61:234–242

Johnson LC, Damman AWH (1993) Decay and its regulation in *Sphagnum* peatlands. Adv Bryol 5:249–296

Latter PM, Howson G, Howard DM, Scott WA (1998) Long-term study of litter decomposition on a Pennine peat bog: which regression? Oecologia 113:94–103

Leckie SE, Prescott CE, Grayston SJ, Neufeld JD, Mohn WW (2004) Characterization of humus microbial communities in adjacent forest types that differ in nitrogen availability. Microbial Ecol 48:29–40

Li Y, Vitt DH (1997) Patterns of retention and utilization of aerially deposited nitrogen in boreal peatlands. Écoscience 4:106–116

Limpens J, Berendse F (2003) How litter quality affects mass loss and N loss from decomposing *Sphagnum*. Oikos 103:537–547

Lockaby BG, Wheat RS, Clawson RG (1996) Influence of hydroperiod on litter conversion to soil organic matter in a floodplain forest. Soil Sci Soc Am J 60:1989–-1993

Meentemeyer V (1978) Macroclimate and lignin control of litter decomposition rates. Ecology 59:465–472

Moore TR, Dalva M (1993) The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatlands soil. J Soil Sci 44:651–664

Moore TR, Dalva M (1997) Methane and carbon dioxide exchange potentials of peat in aerobic and anaerobic laboratory incubations. Soil Biol Biochem 29:1157–1164

Moore TR, Bubier JL, Frolking SE, Lafleur PM, Roulet NT (2002) Plant biomass and production and CO_2 exchange in an ombrotrophic bog. J Ecol 90:25–36

Moore TR, Trofymow JA, Taylor B, Prescott C, Camiré C, Duschene L, Fyles J, Kozak L, Kranabetter M, Morrison I, Siltanen M, Smith S, Titus B, Visser S, Wein R, Zoltai S (1999) Litter decomposition rates in Canadian forests. Global Change Biol 5:75–82

Moore TR, Trofymow JA, Siltanen M, Prescott C, CIDET Working Group (2005) Patterns of decomposition and carbon, nitrogen and phosphorus dynamics of litter in upland forest and peatland sites, central Canada. Can J For Res 35:133–142

Moore TR, Trofymow JA, Prescott CE, Fyles J, Titus BD, CIDET Working Group (2006) Patterns of carbon, nitrogen and phosphorus dynamics in decomposing foliar litter in Canadian forests. Ecosystems (in press)

Murayama S, Asakawa Y, Ohno Y (1990) Chemical properties of subsurface peats and their decomposition kinetics under field conditions. Soil Sci Plant Nutr 36:129–140

Nedwell D, Watson A (1995) CH_4 production, oxidation and emissions in a UK ombrotrophic peat bog: influence of SO_4^{2-} from acid rain. Soil Biol Biochem 27:893–903

Painter TJ (1991) Lindow Man, Tollund Man and other peat-bog bodies: the preservative and antimicrobial action of Sphanan, a reactive glycurnoglycan with tanning and sequestering properties. Carbohydr Polym 15:123–142

Robert EC, Rochefort L, Garneau M (1999) Natural revegetation of two block-cut mined peatlands in eastern Canada. Can J Bot 77:447–459

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

Segers R (1998) Methane production and methane consumption: a review of processes underlying wetland methane fluxes. Biogeochemistry 41:23–51

Thomas KL, Benstead J, Davies KL, Lloyd D (1996) Role of wetland plants in the diurnal control of CH_4 and CO_2 fluxes in peat. Soil Biol Biochem 28:17–23

Thormann MN, Bayley SE, Currah RS (2000) Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta. Can J Bot 79:9–22

Trofymow JA, Moore TR, Titus B, Prescott C, Morrison I, Siltanen M, Smith S, Fyles J, Wein R, Camiré C, Duschene L, Kozak L, Kranabetter M, Visser S (2002) Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can J For Res 32:789–804

Turetskey MR (2004) Decomposition and organic matter quality in continental peatland: the ghost of permafrost past. Ecosystems 7:740–750

Turunen J, Pitkänen A, Tahvanainen T, Tolonen K (2001) Carbon accumulation in West Siberian mires, Russia. Global Biogeochem Cycles 15:285–296

Updegraff K, Pastor J, Bridgham SD, Johnston CA (1996) Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecol Appl 5:151–163

Verhoeven JTA, Liefveld WM (1997) The ecological significance of organochemical compounds in *Sphagnum*. Acta Bot Neerl 46:117–130

Verhoeven JTA, Toth E (1995) Decomposition of *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibition by living tissue homogenates. Soil Biol Biochem 27:271–275

Vile MA, Bridgham SD, Wieder RK, Novak M (2003a) Atmospheric sulfur deposition alters pathways of gaseous carbon production in peatlands. Global Biogeochem Cycles 17:1058. DOI 10.1029/2002GB001966

Vile MA, Bridgham SD, Wieder RK (2003b) Response of anaerobic carbon mineralization rates to sulfate amendments in a boreal peatland. Ecol Appl 13:720–734

Waksman SA, Stevens KR (1928) Contribution to the chemical composition of peat I. Chemical nature of organic complexes in peat and methods of analysis. Soil Sci 26:113–137

Waksman SA, Stevens KR (1929) Contribution to the chemical contribution of peat. II. The role of microorganisms in peat formation. Soil Sci 28:315–340

Wieder RK (2001) Past, present and future carbon balance – an empirical model based on ^{210}Pb-dated cores. Ecol Appl 11:321–336

Wieder RK, Lang GE (1988) Cycling of inorganic and organic sulfur in peat from Big Run Bog, West Virginia. Biogeochemistry 5:221–242
Wieder RK, Yavitt JB, Lang GE (1990) Methane production and sulfate reduction in 2 Appalachian peatlands. Biogeochemistry 10:81–104
Williams B, Silcock D, Young M (1999) Seasonal dynamics of N in two *Sphagnum* moss species and the underlying peat treated with $^{15}NH_4{}^{15}NO_3$. Biogeochemistry 45:285–302
Williams CJ, Shingara EA, Yavitt JB (2000) Phenol oxidase activity in peatlands in New York state: response to summer drought and peat type. Wetlands 20:416–421
Wind T, Conrad R (1997) Localization of sulfate reduction in planted and unplanted rice field soil. Biogeochemistry 37:253–278
Wylie GD (1987) Decomposition and nutrient dynamics of litter of *Quercus palustris* and *Nelumbo lutea* in a wetland complex of Southeast Missouri, U.S.A. Arch Hydrobiol 111:95–106
Wynn-Williams DD (1982) Simulation of seasonal changes in microbial activity of maritime Antarctic peat. Soil Biol Biochem 14:1–12
Yavitt JB, Williams CJ, Wieder RK (1997) Production of methane and carbon dioxide in peatland ecosystems across North America: effects of temperature, aeration, and organic chemistry of peat. Geomicrobiol J 14:299–316
Zinder SH (1993) Physiological ecology of methanogens. In: Ferry JG (ed) Methanogenesis: ecology, physiology, biochemistry, and genetics. Chapman and Hall, New York, pp 128–206