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Controls over carbon storage and turnover in high-latitude soils

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Abstract

Despite the importance of Arctic and boreal regions in the present carbon cycle, estimates of annual high-latitude carbon fluxes vary in sign and magnitude. Without accurate estimates of current carbon fluxes from Arctic and boreal ecosystems, predicting the response of these systems to global change is daunting. A number of factors control carbon turnover in high-latitude soils, but because they are unique to northern systems, they are mostly ignored by biogeochemical models used to predict the response of these systems to global change. Here, we review those factors. First, many northern systems are dominated by mosses, whose extremely slow decomposition is not predicted by commonly used indices of litter quality. Second, cold temperature, permafrost, waterlogging, and substrate quality interact to stabilize soil organic matter, but the relative importance of these factors, and how they respond to climate change, is unknown. Third, recent evidence suggests that biological activity occurring over winter can contribute significantly to annual soil carbon fluxes. However, the controls over this winter activity remain poorly understood. Finally, processes at the landscape scale, such as fire, permafrost dynamics, and drainage, control regional carbon fluxes, complicating the extrapolation of site-level measurements to regional scales.

Keywords: Arctic, boreal, carbon, decomposition, global change, soil

Introduction

Understanding the factors that control fluxes of carbon from arctic and boreal soils is essential for predicting how carbon fluxes in these regions will respond to global change. Arctic and boreal regions have long been recognized as potentially important players in the global carbon cycle because of the large stocks of carbon stored in northern soils. Estimates of arctic and boreal soil carbon pools vary considerably; they range from 90 to 290 Pg (10^{15} g) of carbon in upland boreal forest soils, 120–460 Pg of carbon in peatland soils, and 60–190 Pg of carbon in arctic tundra soils (Schlesinger 1977; Post *et al.* 1982; Post *et al.* 1985; Oechel 1989; Gorham 1991; Chapin & Matthews 1992). In total, this represents 20–60% of the global soil carbon pool, and 1–2 orders of magnitude more carbon than is emitted annually to the atmosphere from fossil fuel burning and deforestation. Yet the magnitude and even the sign of feedbacks from northern regions to climate change induced by rising concentrations of CO_2 in the atmosphere are disputed (Lashof 1989; Post 1990; Shaver *et al.* 1992; Oechel *et al.* 1993; Goulden *et al.* 1998).

Despite the importance of arctic and boreal ecosystems in the global carbon cycle, our understanding of controls over carbon storage in these systems is lacking. For example, observations of atmospheric $\delta^{13}CO_2$ suggest a large terrestrial sink ($> 3\,Pg\,C\,y^{-1}$ in 1992 and 1993) in temperate and boreal regions of the northern hemisphere (Ciais *et al.* 1995). In contrast, estimates of temperate, boreal, and arctic carbon uptake based on forest inventories, forward modelling simulations, and regional extrapolations yield a range of source and sink estimates with a much smaller absolute magnitude (Dixon *et al.* 1994; Schimel *et al.* 1995; Houghton 1996; McGuire *et al.*

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2000; Oechel *et al.* 2000). Identifying why these estimates of terrestrial carbon storage differ is critical for predicting future concentrations of atmospheric CO_2 over the next several centuries.

The discrepancy among carbon flux estimates arises in part from our lack of understanding about the controls over carbon residence times in mid- and high-latitude ecosystems. Within forest stands, rates of carbon turnover are regulated by species composition, allocation, litter decomposition, and fine root turnover (Vogt *et al.* 1986). At the regional scale, residence times of carbon are also determined by mortality events such as fires, harvesting, and insect outbreaks (Kurz & Apps 1994; Harden *et al.* 1997). The $\delta^{13}CO_2$, forest inventory, and forward modelling approaches to calculating terrestrial carbon fluxes depend on accurate descriptions of these processes.

In the $\delta^{13}CO_2$ approach, rates of terrestrial carbon turnover determine the isotopic disequilibrium of the gross exchange between the land and the atmosphere. Disequilibria are created in all terrestrial ecosystems by decreasing atmospheric $\delta^{13}CO_2$ driven by fossil fuel emissions (that are relatively depleted in $\delta^{13}C$). Because of this, carbon released through respiration can be significantly enriched in $\delta^{13}C$ compared to that currently fixed from the atmosphere if the residence time of carbon in plants and soils is long enough (Tans *et al.* 1993; Fung *et al.* 1997). Terrestrial CO_2 uptake also causes atmospheric CO_2 to become enriched in $\delta^{13}C$ because of discrimination against $\delta^{13}C$ during photosynthesis (Lloyd & Farquhar 1994). Because disequilibria and terrestrial sinks both cause the atmosphere to become relatively enriched in $\delta^{13}C$, they can both potentially explain the recent atmospheric $\delta^{13}CO_2$ trend (Francey *et al.* 1995). In other words, if analyses of atmospheric $\delta^{13}CO_2$ (e.g. Ciais *et al.* 1995) had assumed slower turnover of terrestrial carbon, they would have obtained a smaller estimate of a boreal carbon sink.

In the forest inventory approach, carbon turnover dynamics determine the length of the recovery (and uptake) period following a disturbance. During the 19th and early 20th centuries, large tracts of forest were cleared across Europe and the east coast of North America (Houghton 1994; Kohlmaier *et al.* 1995). With low rates of slash and soil decomposition and carbon stocks that were decimated at the time of disturbance, many of these previously cleared forests may currently function as carbon sinks (Kauppi *et al.* 1992). There is evidence, however, for increasing rates of disturbance and thus a mean annual release of carbon in other temperate and boreal regions, including the west coast of North America (Kasischke *et al.* 1999).

In forward modelling analyses, the magnitude of the carbon sink is directly proportional to the rate of change in NPP and the residence time of carbon with ecosystems (Thompson *et al.* 1996). In recent decades, increasing levels of atmospheric CO_2 (Keeling *et al.* 1989) and nitrogen deposition (Holland *et al.* 1997) may have stimulated rates of net primary production (NPP) in high-latitude ecosystems (Melillo *et al.* 1996). A critical component of forward modelling simulations is the response of decomposition to temperature, and in particular, the response during winter months when low but persistent rates of respiration under the snow pack can influence seasonal and annual carbon balances (McGuire *et al.* 2000b).

Accurate estimates of carbon residence times in soils are necessary for accurate descriptions of the present carbon balance of high-latitude ecosystems. In this paper we review the major controls over carbon turnover through soils in arctic and boreal ecosystems, highlighting those controls that are unique to high latitudes and pointing out how current biogeochemical models might be misrepresenting these processes for northern systems.

Controls over litter decomposition

As in other regions, the major controls over decomposition of fresh litter in arctic and boreal regions include temperature, moisture, and substrate quality. Numerous studies have demonstrated the importance of cold temperature in limiting rates of decomposition in arctic and boreal systems. In laboratory incubations, litter decomposition rates increase from subzero temperatures (−5 °C) up to 25 °C (Flanagan & Veum 1974; Rosswall 1974; Heal *et al.* 1981; Clein & Schimel 1995). Optimal moistures average near 400% of dry weight, but decrease at higher temperatures (Flanagan & Veum 1974). Across broad arctic-boreal regions, both mean annual temperature and actual evapotranspiration are good predictors of decomposition rates (Johansson *et al.* 1995).

Substrate quality, particularly carbon chemistry, is also a strong limitation to decomposition rate in arctic and boreal ecosystems. Decomposition is generally slower for litter with high lignin concentrations and low concentrations of soluble carbohydrates (Van Cleve 1974; Heal *et al.* 1981; Hobbie 1996). Large differences occur among plant growth forms and among plant organs within species. Woody stems, mosses, lichens, and evergreen leaf litter decompose slowly, while deciduous and forb leaf litter decompose rapidly (Heal & French 1974; Moore 1984; Hobbie 1996; Shaver *et al.* 1997).

Several studies have suggested that the influence of substrate quality over decomposition can be large relative to the effects of temperature in arctic and boreal systems, perhaps reflecting the diversity of growth forms found in these regions. Differences in decomposition rate among Alaskan tundra species were sometimes larger than the effects of a 6 °C warming (Hobbie 1996). Similarly, faster decomposition rates in birch than in spruce forests in Alaskan taiga were caused primarily by the better substrate quality of birch litter rather than by the warmer soils in birch forests (Flanagan & Van Cleve 1983).

To evaluate the broad-scale controls over decomposition rate in arctic and boreal regions, we searched for general patterns among a number of published decomposition studies (Appendix). To allow comparison, we restricted our analysis to those studies that measured decomposition rates of senesced tissues using the litter bag technique. Studies of decomposition of organs other than leaves were rare, so we analysed only leaf litter decomposition (for the vascular species). From most studies we were able to extract the following information: latitude and longitude, mean annual temperature (MAT), mean annual precipitation (MAP), the dominant vegetation of the study, and the species studied. When climate data were not included or readily obtained from citations, we estimated MAT from nearby studies. Topographic position (i.e. upland or lowland) was determined from descriptions of the vegetation type. Bogs, forested bogs, mires, fens, laggs, and wet meadow tundra were considered lowlands. Forests, and heath, tussock, and shrub tundras were considered uplands. Insufficient information was available to include analyses of litter chemistry.

Our results are consistent with laboratory and field studies and suggest that temperature, topography (i.e. the degree of inundation), and vegetation composition are the primary controls over litter decomposition at the regional scale. Decomposition rate was positively affected by MAT but MAT explained less than 15% of the variation in decomposition rate (Fig. 1, $F_{1,111} = 13.07$, $P < 0.001$; $R^2 = 0.11$;% mass loss = 23.01 + 1.02 × MAT). In contrast, decomposition rate was not significantly related to MAP ($F_{1,89} = 1.12$, $P = 0.29$, $R^2 = 0.01$). So, despite relatively low precipitation rates, cold temperatures are the primary climatic factor limiting decomposition at high latitudes.

Whether decomposition occurred in upland or lowland ecosystems also significantly affected rates of litter mass loss. Litter in upland ecosystems decomposed more rapidly than litter in ecosystems characterized by poor drainage (Fig. 1a). In an analysis of covariance (ANCOVA) with topographic position as a categorical variable and MAT as a covariate, both variables were significant ($F_{1,107} = 13.26$, $P < 0.001$ and $F_{1,107} = 19.96$, $P < 0.001$, respectively; $R^2 = 0.21$; slopes were homogeneous). Slow decomposition in poorly drained areas likely results from low oxygen availability in saturated soils with little water flow.

Substrate quality was just as important as temperature in explaining variation in decomposition rates in arctic and boreal regions. To determine the importance of vegetation composition relative to abiotic factors, we grouped species into the dominant growth forms found in high-latitude ecosystems [mosses, evergreens, deciduous species, and herbs (graminoids and forbs); insufficient data existed to include lichens], because species within these growth forms have previously been shown to decompose similarly (Hobbie 1996). Together, growth form and MAT explained greater than 50% of the variation in decomposition rate (Fig. 1b). In an ANCOVA including growth form as a categorical variable and MAT as a covariate, both variables were significant ($F_{3,102} = 31.09$, $P < 0.001$ and $F_{1,102} = 52.38$, $P < 0.001$, respectively; $R^2 = 0.54$; slopes were homogeneous). Overall, litter of deciduous and herbaceous species decomposed more quickly than other litter types (Tukey's HSD, $P < 0.001$) but had similar rates of decomposition to each other (Tukey's HSD, $P = 0.49$). Evergreen litter decomposed significantly more slowly than that of deciduous and herbaceous species (Tukey's HSD, $P < 0.001$), and moss litter decomposed even more slowly than that of evergreens (Tukey's HSD, $P = 0.02$).

Decomposition rates of the vascular growth forms probably reflect differences in both carbon and nutrient chemistry, because evergreen species tend to have both higher lignin and lower nutrient concentrations than do deciduous species (Coley *et al.* 1985). Despite the strong association of moss with poorly drained ecosystems (80% of the cases of moss decomposition studied here were in lowland ecosystems), their slow decomposition appears to be a function of their poor substrate quality. When we narrowed our analysis to lowland ecosystems and compared moss decomposition with that of deciduous and herbaceous litter, we still found that mosses decompose significantly more slowly (Fig. 1c). In an ANCOVA that compared just herbaceous and deciduous litter with that of moss litter decomposing within lowland ecosystems and included MAT as a covariate, both growth form and MAT were significant ($F_{1,27} = 34.60$, $P < 0.001$ and $F_{1,27} = 16.00$, $P < 0.001$, respectively; $R^2 = 0.58$; slopes were homogeneous). The reason why mosses decompose so slowly is elusive but widely observed (Clymo & Hayward 1982; Hobbie 1996). Slow decomposition of *Sphagnum* spp. may result from their low nutrient concentrations (Coulson & Butterfield 1978) or from recalcitrant carbon compounds (Karunen & Ekman 1982; Chapin *et al.* 1986; Johnson & Damman 1991). In addition, *Sphagnum* spp. are known to produce compounds with antimicrobial properties (Painter 1991; Verhoeven & Toth 1995).

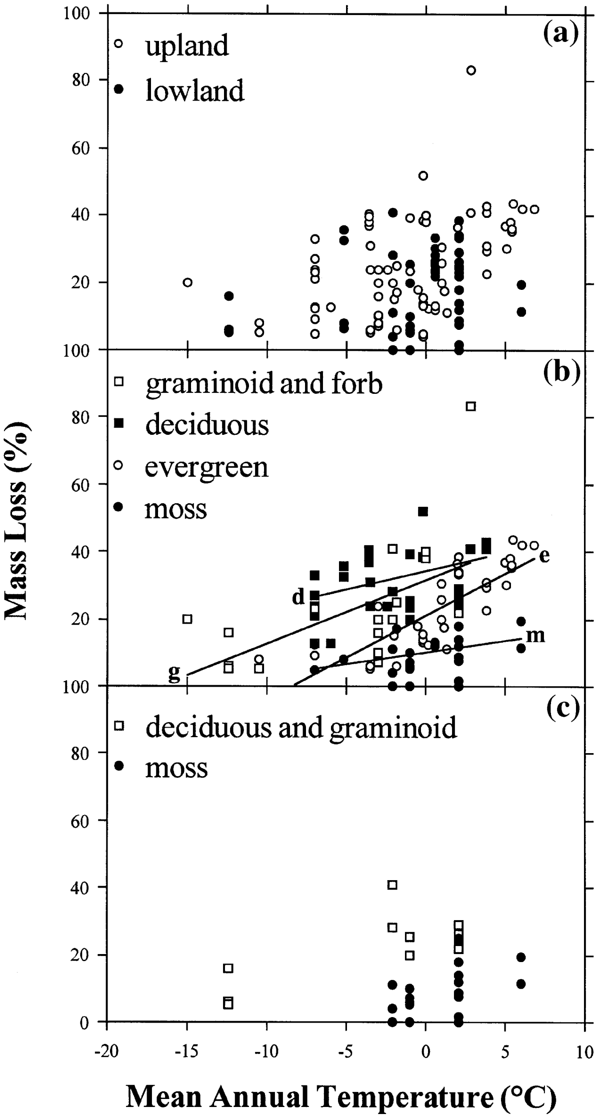

Fig. 1 (a) Litter mass loss after one year vs. MAT in upland and lowland ecosystems. (b) Litter mass loss after one year vs. MAT for different dominant growth forms. Lines represent regression lines obtained for individual growth forms (g, graminoid and forb; e, evergreen; d, deciduous; m, moss). (c) Litter mass loss after one year vs. MAT in lowland ecosystems only.

Differences in decomposition rates among growth forms were large relative to the effect of temperature. Litter of deciduous species decomposed twice as quickly as moss litter. Temperature would have to increase by approximately 5 °C to cause a comparable doubling of decomposition rate. Thus, understanding variation in carbon storage across landscapes or predicting the response of carbon storage to global changes requires accounting for variation in the abundances of the dominant growth forms or predicting how growth form abundance will change, respectively. Although for the vascular plants these growth-form differences in decomposition might be summarized accurately by some index of litter quality (e.g. lignin concentration), slow moss decomposition is not predicted by its carbon chemistry (Hobbie 1996). Current biogeochemical models that use litter quality indices appropriate for vascular plants to predict decomposition rates may overestimate rates of moss-derived peat decomposition in response to climate warming (e.g. Schimel *et al.* 1994), perhaps contributing to the discrepancy among estimates in high-latitude carbon sinks discussed earlier.

Recent reviews suggest that the dominant growth forms in arctic ecosystems make logical functional groups in which to lump species with respect to their influence on biogeochemical processes (Chapin *et al.* 1995, 1997). Our analysis provides evidence that across arctic and boreal regions, growth forms are distinct in their effect on decomposition and may provide a useful way of simplifying species for inclusion in ecosystem models. Boreal and arctic ecosystems differ from other regions because growth forms with such contrasting effects on biogeochemical processes, such as mosses and deciduous species, can dominate adjacent landscapes. Also, different growth forms can dominate the same landscape during different stages of succession (e.g. postfire or postflooding). Notably, we did not consider decomposition of woody litter in our analysis. Depending on allocation, the slow decomposition of woody litter may reduce the overall decomposition rates of litter from deciduous and evergreen shrubs and trees (Hobbie 1996).

Accumulation, storage and decomposition of soil organic matter

Most of the carbon stored in northern soils has decomposition rates that are slower than those found in fresh litter ($k < 0.1$ y^{-1}) as revealed by radiocarbon data (e.g. Clymo 1984; Trumbore & Harden 1997; Clymo *et al.* 1998) and chronosequence studies (Harden *et al.* 1992). Slow decomposition rates of soil organic matter result from several factors. First, recalcitrant compounds may dominate soils because of selective preservation of components that decompose slowly, like mosses, as decomposers break down more labile material. Secondly, recalcitrant compounds may form because of microbial processing (humification) or by fire (charcoal). Thirdly, persistent cold soil temperatures associated with permafrost, as well as anaerobic conditions, slow *in situ* decomposition rates. For example, the largest carbon inventories exist in poorly drained soils and wetlands (Ping *et al.* 1997), where high moss abundance, low oxygen, and cold temperatures combine to retard decay. In boreal uplands, large stores of decomposed and charred material are found below the litter layer and above the mineral soil (Harden *et al*. 1997) and decomposition rates in this humic layer are 10-fold slower than those of the overlying litter (Trumbore & Harden 1997). In areas dominated by permafrost, cryoturbation (mixing of soils by freeze-thaw processes) may be an additional important process by which organic matter from surface horizons is stabilized in permanently frozen horizons, making it inaccessible to microbes. Where carbon stocks in permafrost have been measured, they are large and can double estimates of soil carbon based on carbon measured in the active layer that thaws during the growing season (Michaelson *et al*. 1996). The long-term storage of this nonlitter carbon contrasts with lower-latitude systems where interaction with mineral surfaces (approximated by soil texture) is a dominant control of the storage and dynamics of carbon on millennial time scales. Indeed some biogeochemical models assume that soil organic matter decomposition is a function of soil texture (e.g. CENTURY, Parton *et al*. 1987). However, soil organic matter decomposition may be unrelated to soil texture in ecosystems where much of the decomposition occurs in an organic horizon with little mineral content.

In wetland ecosystems, stores of carbon in deep, humified layers are so large that even at very slow rates of decomposition, the flux of CO_2 derived from these layers contributes significantly to annual soil respiration (Tolonen & Turunen 1996; Clymo *et al*. 1998). This may also be true in moderately to poorly drained upland soils in boreal regions (Trumbore & Harden 1997). In a black spruce/moss stand in central Manitoba, an overall increase in soil respiration in the late summer/early fall was linked to the timing of thawing and warming of deep humified organic matter (Goulden *et al*. 1998). Radiocarbon measurements in soil CO_2 confirmed that much of the CO_2 respired in fall and winter months was derived from decomposition of organic matter that was between 50 and several hundred years old (Winston *et al*. 1997). Hence the lag time between carbon fixation and decomposition for a significant portion of the annual net carbon flux may be quite long, which may increase estimates of isotope disequilibrium in boreal regions. Year-to-year differences in soil respiration may be caused by climate variability as it impacts the timing and degree of deep soil thaw in upland soils (Goulden *et al*. 1998).

Incubation of these organic materials shows that decomposition rates may increase dramatically if the soils are dried or warmed (Billings *et al*. 1982; Moore & Knowles 1989; Goulden *et al*. 1998). If high-latitude regions dry or thaw as a result of future climate change, net decomposition of the vast stores of deep carbon could result in a large positive feedback to rising atmospheric CO_2. Alternatively, if nutrients associated with mineralized carbon stimulate plant production, high-latitudes could prove sinks for carbon (Shaver *et al*. 1992). Indeed, models used to predict future carbon balance with climate warming that consider thawing of carbon stored in permafrost are extremely sensitive to assumptions about the amount of carbon stored in permafrost and its carbon to nutrient ratio (Waelbroeck *et al*. 1997). Yet, little is known about the characteristics of frozen carbon pools for large regions. A better understanding of the importance of limitation by substrate quality vs. limitation by abiotic conditions (permafrost or waterlogging) is required to predict the storage of carbon in soil organic matter for high-latitude regions and its response to changes in temperature and precipitation.

Winter decomposition

A unique aspect of arctic and boreal systems is their long, cold winter. Microbial decomposition processes during this period have long been assumed to be insignificant in the annual cycling of carbon and nutrients (e.g. Steudler *et al*. 1989). Yet, recent data indicate that litter decomposition and soil respiration occur over winter in both arctic and boreal ecosystems (Sommerfeld *et al*. 1993; Zimov *et al*. 1993; Clein & Schimel 1995; Wagener 1995; Brooks *et al*. 1996; Hobbie & Chapin 1996; Zimov *et al*. 1996; Oechel *et al*. 1997; Winston *et al*. 1997; Fahnestock *et al*. 1998; Fahnestock *et al*. 1999; Grogan & Chapin 1999). In fact, winter fluxes of CO_2 are substantial in annual carbon budgets (Table 1) and likely influence both the magnitude and direction of annual carbon fluxes.

Winter activity accounts for roughly 20% of annual soil respiration, although estimates range between 3 and 50% across different arctic and alpine tundra and boreal forest communities (Table 1). Many of the methods used to estimate winter fluxes are problematic. For example, atmospheric CO_2 may be concentrated in freezing snow and transported to the base of the snowpack (Williams 1949), resulting in overestimates of net efflux based on CO_2 concentration profiles in snow. Nevertheless, all of the methods used to date indicate net fluxes of CO_2 during the winter, although the magnitude of these fluxes is uncertain. Winter CO_2 fluxes vary both spatially and temporally. They are highest and most variable during the autumn–winter and winter–spring transitional periods as soils are subjected to repeated freeze–thaw events, but can continue through winter (Jones *et al*. 1997; Oechel *et al*. 1997; Fahnestock *et al*. 1998; Fahnestock *et al*. 1999; Grogan & Chapin 1999).

Our understanding of the processes involved in winter CO_2 efflux remains poor. We know little about the microbial processes controlling winter decomposition and CO_2 fluxes: do they operate similarly, but more slowly, to those in the summer, or do they behave quite differently? For example, CO_2 during the summer comes

Table 1 Comparison of the magnitude of wintertime fluxes of CO_2 from studies in Alaska and Russia

Vegetation Type	Magnitude of wintertime fluxes	Method	Reference
Tussock tundra	61% of net annual CO_2 exchange	Flux chambers	Oechel *et al*. 1997
Wet sedge	81% of net annual CO_2 exchange	''	''
Forest tundra	41% of net annual CO_2 exchange	Snow CO_2 profiles	Zimov *et al*. 1996
Mixed types	18% of total annual soil respiration	''	Zimov *et al*. 1993; Fahnestock *et al*. 1998
Shrub	7% of total annual soil respiration	Snow CO_2 profiles	Fahnestock *et al*. 1998
Tussock	21% of total annual soil respiration	''	''
Wet meadow	17% of total annual soil respiration	''	''
Various types	>50% of total annual soil respiration	Soda lime traps	Grogan & Chapin 1999
Tussocks	34% of total annual soil respiration	Extrapolation of lab data	Clein & Schimel 1995
Intertussock	12% of total annual soil respiration	''	''
Wet meadow	21% of total annual soil respiration	''	''
Black spruce/ jack pine forests	3–17% of total annual soil respiration	Flux chambers	Winston *et al*. 1997; Savage *et al*. 1997

primarily from root respiration and decay of plant detritus in the surface organic horizon (J.P. Schimel, unpubl. data, Grogan & Chapin 1999), but during the winter it appears that microbial respiration may be driven by soluble material remaining in water films or deeper in the profile or into the mineral soils (Clein & Schimel 1995). If this is the case, then models of carbon dynamics developed for summer activity would be fundamentally flawed in modelling winter activity.

Litter mass and N loss appear to occur primarily during winter in arctic systems (Hobbie & Chapin 1996), though it was unclear from that work whether the winter mass and N loss were biological or associated with spring leaching. Wagener (1995), however, showed that litter decomposition occurred in the taiga before snowmelt, suggesting that overwinter decomposition may also result from microbial activity. Several laboratory studies have shown that significant microbial activity can occur in soils at temperatures in the range of −5 to −7 °C (Flanagan & Bunnell 1980; Coxson & Parkinson 1987; Clein & Schimel 1995). Soil temperatures in this range are common in the tundra during early and late winter, and throughout the winter in areas where snow insulates the soil.

The controls on this activity in frozen soils, however, are complex. Temperature responses vary in different tundra and taiga soils, with Q_{10} responses ranging from 1 to 9.8 over the range from −5 °C to −2 °C (Clein & Schimel 1995). The temperature below which activity ceases also varies among soils. Brooks *et al*. (1996) reported activity down to −5 °C for two alpine sites, while Mosier *et al*. (1991) found that respiration only continued in a short-grass steppe down to about −2 °C. In a treeline site no CO_2 production occurred when the soil was below 0 °C (Brooks *et al*. 1996). This critical temperature can even vary between nearby sites: the alpine and treeline sites described by Brooks *et al*. (1996) were within 100 m of each other.

Decomposition during the winter appears to be controlled by both physical and biological factors. Physical factors include the thermal regime of the soil and the quantity of unfrozen water it contains. How large a thawed layer exists in the soil and how long into the winter it exists is critical in controlling winter decomposition activity (Zimov *et al*. 1993). Perhaps equally important is the amount of unfrozen water that remains in 'frozen' soil, as substantial microbial activity can occur in films of liquid water that remain on soil particles even after the bulk of the water has frozen. For example, Clein & Schimel (1995) showed significantly less respiration in a white spruce taiga soil when that soil was incubated frozen at 10% vs. 50% of water holding capacity. The amount of unfrozen water that remains in soil or litter at a particular temperature depends on soil composition (particle size distribution) and chemistry. There are several existing models for predicting the amount of unfrozen water in soil (Lovell 1957; Nakano & Brown 1971), but it is not yet clear which is most appropriate for modelling microbial activity in frozen soils, particularly organic soils. This area needs further study. It is also likely that the physical and biological factors interrelate with each other, as microbes may produce enough heat to affect the soil thermal regime (Zimov *et al*. 1996).

Because different soils appear to have variable responses to increased temperature, these soils must differ in other factors that control microbial activity during the winter. For example, the nature of the available substrates is probably an important control on winter activity and none of the few studies at subzero temperatures evaluated microbial substrate use. During the summer, respiration in arctic and boreal regions is almost certainly dominated by activity in the surface organic horizon, because the bulk of the decomposable litter and organic matter is found there. However, during winter, it is quite possible that much of the decomposition activity occurs deeper in the profile in warmer (and possibly unfrozen) horizons. In areas where there are not deep peat accumulations, activity in the mineral soil may become important. Dissolved organic carbon (DOC) fractions may also be more important than nondissolved ones in supplying carbon to microbes even within the organic horizons (Clein & Schimel 1995). In tussock tundra the ^{13}C of respired CO_2 varied by up to 5‰ between summer and winter (Welker pers. comm.), indicating changes in substrate use. Dramatic seasonal changes in the radiocarbon in soil CO_2 in boreal forest soils demonstrate a significant shift in substrate age, with older carbon respired in the fall and winter (Winston *et al*. 1997). Thus, it seems likely that there are major shifts in the zone of microbial activity and of substrates between summer and winter. Models of annual activity must account for these shifts to accurately model winter activity.

Basic thermodynamics also supports the idea that substrate use may change as temperature drops. The fundamental control on the temperature response of biochemical reactions is the activation energy of the reaction, as described by the Arrhenius equation. The higher the activation energy, the higher the temperature sensitivity, and the comparatively slower the rates that would occur at low temperature. Metabolizing complex, aromatic structures should have a higher activation energy and temperature sensitivity than metabolizing simpler, carbohydrate-based structures. Equally important, temperature can affect the activation energy of enzymatic reactions by causing changes in enzyme conformation. Linkins *et al*. (1984) noted a dramatic increase in the activation energy of endocellulase in a tundra soil below 5 °C, which would greatly reduce cellulose use at low temperature.

Landscape controls over soil carbon storage

A number of factors in arctic and boreal regions interact to control soil carbon storage at the landscape scale. Fires are uncommon in tundra (Wein 1976), but in boreal regions, the timing and spatial distribution of fires (as well as the distribution of wetland areas that do not burn) control whether landscapes are sources or sinks for carbon. Fire is an especially important control over carbon storage in soils of upland boreal forests. These forest stands are carbon sources to the atmosphere during and in the years immediately following fire, and carbon sinks as trees and mosses regrow (e.g. Kasischke *et al*. 1995; Harden *et al*. 1997; Rapalee *et al*. 1998). Approximately equal amounts of carbon are lost to burning in fires and during decomposition in the years immediately following fires, when less shade and reduced insulating ground cover combine to increase soil temperatures (Kasischke *et al*. 1995). Between burning events, decomposition rates of mosses are slow enough that large stores of carbon (several kg C m^{-2}) accumulate in moss and detrital layers. For ecosystems where fire is the principal mode of disturbance, the loss of carbon during burning must be considered along with decomposition rates as a control on the amount of accumulated litter material.

Topographic position is an important factor controlling carbon storage in both arctic and boreal landscapes because it influences the drainage and formation of wetland areas. In tundra, soil carbon stocks are greatest in low-lying poorly drained wet meadow tundra and in tussock tundra that forms on stable, gentle slopes with relatively shallow thaw (Giblin *et al*. 1991; Michaelson *et al*. 1996). Wetlands can be significant sinks of carbon, accumulating on average about $30\,g\,C\,m^{-2}\,y^{-1}$ (Gorham 1991). Small landscape elements, such as beaver ponds (Roulet *et al*. 1997), or local areas of permafrost collapse, may act as large local sources of carbon to the atmosphere that offset carbon gains in the remainder of the landscape. Drainage of northern wetlands results in a short-term release of carbon, as water tables drop and decomposable substrates are exposed to oxygen (Billings *et al*. 1982; Moore & Dalva 1993; Schurpali *et al*. 1996; Waddington & Roulet 1996).

Conclusions

Despite the importance of arctic and boreal systems in the present carbon cycle, controls over carbon storage in northern soils are not well-understood. Biogeochemical models used to predict the response of ecosystems to changing climate may be inadequate for use at high latitudes, where a number of unique factors strongly influence soil carbon turnover:

1 Differences in litter decomposition between growth forms are large relative to the effects of abiotic factors such as temperature. Of particular importance is the slow decomposition rate of moss litter, which is not predicted by commonly used indices of litter quality.

2 Cold temperature, anaerobiosis, and permafrost interact with substrate quality to determine the degree of organic matter stabilization. The relative importance of these factors, and how they will respond to climate change, is unknown.

3 Recent evidence suggests that biological activity occurring in frozen soils can contribute significantly to annual soil carbon fluxes. Yet the controls over this activity remain poorly understood.

4 Landscape-level processes, such as fire and inundation, can be just as important as processes within landscape units in controlling regional carbon fluxes.

By explicitly considering these unique aspects of soil carbon turnover in high-latitude systems, we may be able to refine our understanding of present carbon fluxes and better predict the influence of these systems on the future climate.

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Appendix

Sources of decomposition data used analyses of controls over litter decomposition in arctic and boreal ecosystems. Dashes indicate no information available.

Location	MAP (mm)	MAT (°C)	Site	Topographic position	Growth form	Litter source	Mass loss (% after 1 y)	Reference	Notes
–	540	−5.2	Sivaya Maska, USSR	–	deciduous	*Betula nana*	32.4	Heal & French (1974)	
–	″	″	″	–	″	*Rubus chamaemorus*	35.6	″	
–	″	″	″	–	moss	*Pleurozium shreberi*	8	″	
48°30′N, 95°W	700	2.8	Little Sioux Wildfire, MN, USA	upland	deciduous	*Populus tremuloides*	41.075	Grigal & McColl (1977)	climate data from Climatology Working Group[1]
″	″	″	″	″	″	*Aster macrophyllum*	83.5	″	″
49°40′N, 93°43′W	623	2.1	Exp. Lakes Area, Ont., Canada	lowland	moss	*Sphagnum fuscum*	12	Rochefort *et al.* (1990)	
″	″	″	″	″	″	*Sphagnum magellanicum*	18	″	
″	″	″	″	″	″	*Sphagnum angustifolium*	25	″	
49°53′N, 95°54′W	–	2.1	Elma, Manit., Canada	lowland	deciduous	*Salix bebbiana*	29	Reader & Stewart (1972)	
″	–	″	″	″	″	*Salix serissima*	26.1	″	
″	–	″	″	″	evergreen	*Ledum groenlandicum*	33.2	″	
″	–	″	″	″	″	*Picea mariana*	24.3	″	
″	–	″	″	″	″	*Ledum groenlandicum*	17.8	″	
″	–	″	″	″	″	*Vaccinium vitis-idaea*	34.3	″	
″	–	″	″	″	″	*Picea mariana*	33.7	″	
″	–	″	″	″	″	*Ledum groenlandicum*	13.8	″	
″	–	″	″	″	″	*Vaccinium vitis-idaea*	38.7	″	
″	–	″	″	″	herbaceous	*Calamagrostic canadensis*	23.1	″	
″	–	″	″	″	″	*Carex rostrata*	22	″	
″	–	″	″	″	moss	*Aulacomnium palustre*	7.6	″	
″	–	″	″	″	″	*Pleurozium schreberi*	24.7	″	
″	–	″	″	″	″	*Sphagnum fuscum*	1.7	″	
″	–	″	″	″	″	″	0.1	″	
″	–	″	″	″	″	*Polytrichum juniperinum*	13.9	″	
″	–	″	″	″	″	*Aulacomnium palustre*	8.9	″	
53°38′N, 106°13′W	456	−0.2	Pr. Albert Natl. Park, Sask.,Canada	upland	deciduous	*Populus tremuloides*	38.5	Huang & Schoenau (1997)	
″	″	″	″	″	″	*Corylus cornuta*	52	″	
53°57′N, 105°30′W	–	0.6	Candle Lake, Sask., Canada	″	moss	*Hylocomium splendens*	12.1	Nakatsubo *et al.* (1997)	
″	–	″	″	″	″	″	13.2	″	
54°15′N,116°W	–	0.2	Whitecourt, Alberta, Canada	″	evergreen	*Pinus banksiana* × *P. contorta*	12.2	Prescott & Parkinson (1985)	MAT from Nakatsubo *et al.* (1997)

Location	MAP (mm)	MAT (°C)	Site	Topographic position	Growth form	Litter source	Mass loss (% after 1 y)	Reference	Notes
54°43′N, 66°42′W	785	−0.2	Schefferville, Quebec, Canada	″	″	*Picea mariana*	13.9	Moore (1984)	MAT from Finer *et al.* (1997)
″	″	″	″	″	″	″	13.1	″	″
″	″	″	″	″	″	″	15.6	″	″
56°36′N, 13°15′E	1070	6.8	Mastocka, Sweden	″	″	*Pinus sylvestris*	42.2	Berg *et al.* (1993)	
57°10′N, 19°50′E	702.5	6	Akhelt Mire, Sweden	lowland	moss	*Sphagnum cuspidatum*	19.4	Johnson & Damman (1991)	
″	″	″	″	″	″	*Sphagnum fuscum*	11.4	″	
58°04′N, 14°08′E	595	5.1	Sanskjon, Sweden	upland	evergreen	*Pinus sylvestris*	30	Berg *et al.* (1993)	
58°06′ N, 13°17′E	600	5.4	Tveten, Sweden	″	″	″	36.3	″	
58°28′N, 13°39′E	550	5.4	Remningstorp, Sweden	″	″	″	35.2	″	
58°33′N, 15°51′E	525	6.1	Grensholm, Sweden	″	″	″	42	″	
59°07′N, 15°44′E	550	5.5	Dimbo, Sweden	″	″	″	43.7	″	
59°31′N, 17°16′E	470	5.3	Kungs-Husby, Sweden	″	″	″	38.1	″	
59°49′N, 16°33′E	500	5	Tomta, Sweden	″	″	″	36.9	″	
60°17′N, 7°40′E	700	−3	Hardangervidda, Norway	″	″	*Vaccinium* sp.	24	Heal & French (1974)	location, MAP, MAT, elev. from French (1974), Rosswall (1974)
″	″	″	″	″	herbaceous	barley straw	10	″	″
″	″	″	″	″	″	*Juncus trifidus*	7	″	″
″	″	″	″	″	″	*Carex bigelowii*	20	″	″
″	″	−1.8	″	″	evergreen	*Dryas octopetala*	6	″	″
″	″	″	″	″	herbaceous	barley straw	25	″	″
″	″	″	″	″	moss	mixed mosses	17	″	″
60°18′N, 7°41′ E	752	−2.1	″	lowland	deciduous	*Salix* sp. shoots	28	″	″
″	″	″	″	″	herbaceous	*Carex nigra*	41	″	″
″	″	″	″	upland	″	barley straw	20	″	″
″	″	″	″	lowland	moss	mixed mosses	4	″	″
″	″	″	″	″	″	*Drepanocladus uncinatus*	0	″	″
″	″	″	″	″	″	mixed mosses	11	″	″
60°25′N, 7°21′ E	1013	0	″	upland	herbaceous	barley straw	38	″	″
″	″	″	″	″	″	barley straw small mesh	40	″	″
60°49′N, 16°30′E	609	3.8	Ivantjarnsheden, Sweden	″	deciduous	*Betula pubescens*	40.9	Berg & Ekbohm (1991)	
″	″	″	″	″	evergreen	*Pinus sylvestris*	29.4	″	
″	″	″	″	″	″	*Pinus contorta*	22.5	″	
″	″	″	″	″	deciduous	*Betula pubescens*	43	″	
″	″	″	″	″	evergreen	*Pinus sylvestris*	31.1	″	
63°13′N, 14°28′ E	455	2	Vastbyn, Sweden	″	″	″	36.4	Berg *et al.* (1993)	

Location	MAP (mm)	MAT (°C)	Site	Topographic position	Growth form	Litter source	Mass loss (% after 1 y)	Reference	Notes
64°21′N, 20°53′E	595	1.2	Norrliden, Sweden	″	″	″	17.4	″	
64°53′N, 147°45′W	286	−3.5	Bonanza Creek, AK, USA	″	deciduous	*Betula papyrifera*	24	Flanagan & Van Cleve (1983)	
″	″	″	″	″	″	″	31	″	
64°53′N, 147°45′W	305	−3.6	Fairbanks, AK, USA	″	″	″	40.6	Van Cleve (1971)	
″	″	″	″	″	″	*Alnus crispa*	37.1	″	
″	″	″	″	″	″	*Populus tremuloides*	38.3	″	
″	″	″	″	″	″	*Alnus crispa*	39.7	″	
64°53′N, 147°45′W	286	−3.5	Bonanza Creek, AK, USA	″	evergreen	*Picea mariana*	5	Flanagan & Van Cleve (1983)	
″	″	″	″	″	″	″	6	″	
65°28′N, 145°23′W	–	−10.5	Eagle Summit, AK, USA	″	″	*Dryas integrifolia*	8	Heal & French (1974)	location, MAP, MAT, elev. from French (1974), Rosswall (1974)
″	″	″	″	″	herbaceous	*Eriophorum vaginatum*	5	″	″
65°47′N, 20°37′E	700	1	Manjarv 3 : 1, Sweden	″	evergreen	*Pinus sylvestris*	19.8	Berg *et al.* (1993)	
″	″	″	″	″	″	″	25.9	″	
″	″	″	″	″	″	″	30.7	″	
66°08′N, 20°53′E	650	−1.3	Harads, Sweden	″	″	″	11.1	″	
66°32′N, 20°11′E	500	−0.5	Skallarimsheden, Sweden	″	″	″	17.9	″	
68°21′N, 18°49′E	300	−1	Abisko, Sweden	″	deciduous	*Vaccinium uliginosum*	39.2	Robinson *et al.* (1995)	
″	″	″	″	″	″	*Betula pubescens*	23.6	″	
″	″	″	″	lowland	″	*Rubus chamaemorus*	20	Heal & French 1974	location, MAP, MAT, elev. from French (1974), Rosswall (1974)
″	″	″	″	″	″	*Betula nana*	25.5	″	″
″	″	″	″	″	moss	*Sphagnum fuscum*	0	″	″
″	″	″	″	″	″	*Sphagnum balticum*	6	″	″
″	″	″	″	″	″	*Sphagnum riparium*	10	″	″
″	″	″	″	″	″	*Sphagnum lindergii*	7	″	″
″	″	″	″	″	″	*Sphagnum recurvum*	5	″	″
68°38′N, 149°34′W	300	−7	Toolik Lake, AK, USA	upland	deciduous	*Betula nana*	23.2	Shaver *et al.* (1997)	
″	″	″	″	″	″	*Polygonum bistorta*	23.2	″	
″	″	″	″	″	″	*Salix pulchra*	27.1	″	
″	″	″	″	″	″	*Rubus chamaemorus*	21.1	″	
″	″	″	″	″	″	*Betula papyrifera*	24	Hobbie & Chapin (1996)	

Location	MAP (mm)	MAT (°C)	Site	Topographic position	Growth form	Litter source	Mass loss (% after 1 y)	Reference	Notes
″	″	″	″	″	″	″	32.8	″	
″	″	″	″	″	evergreen	*Ledum palustre*	9.0	Shaver *et al.* (1997)	
″	″	″	″	″	herbaceous	*Eriophorum vaginatum*	12.9	″	
″	″	″	″	″	moss	*Aulacomnium turgidum*	4.7	″	
″	″	″	″	″	″	*Sphagnum spp.*	12.4	″	
69°45′N, 27°01′E	420	−2.4	Kevo, Finland	″	deciduous	*Betula tortuosa*	24	Heal & French (1974)	location, MAP, MAT, elev. from French (1974), Rosswall (1974)
″	″	″	″	″	evergreen	*Pinus sylvestris*	15	″	″
71°20′N, 156°39′W	108	−12.4	Barrow, AK, USA	lowland	herbaceous	*Dupontia fischeri*	16	″	″
″	″	″	″	″	″	*Eriophorum angustifolium*	6	″	″
″	″	″	″	″	″	*Carex aquatilis*	5	″	″
75°N, 95°W	196	−15	Devon Island, Canada	upland	″	*Carex stans*	20	″	″
78°56′N, 11°50′E	371	−6	Svalbard, Norway	″	deciduous	*Salix polaris*	12.7	Robinson *et al.* (1995)	climate data from Wookey *et al.* (1995)

[1] http://www.soils.agri.umn.edu/research/climatology/