Patterns of Biogeochemistry in Alaskan Boreal Forests

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Introduction

As the northernmost forest on Earth, boreal forests endure a combination of environmental challenges common only in subalpine forests elsewhere: extremely cold winters, short growing seasons, cold soils, and limited nutrient availability. Consequently, decomposition has lagged plant production, making circumpolar boreal forest soils one of the largest terrestrial reservoirs of carbon (C). Soil organic matter also constitutes a major source of nutrients, particularly nitrogen (N), that promote plant productivity when released during decomposition. If current trends in high-latitude warming continue (Chapter 4), how will accelerated soil C losses from decomposition compare to the C gains from enhanced plant productivity? This remains an open question of great interest to climate modelers seeking to incorporate biological feedbacks into future generations of general circulation models. This chapter builds on earlier chapters on plants (Chapters 11 and 12), herbivores (Chapter 13), and soil microbes (Chapter 14) to describe the patterns and processes of C and N dynamics in Alaska’s boreal forest, paying particular attention to responses of these processes to the interacting influences of disturbance and climatic variations that occur across the landscape and through time. Other nutrients have received less attention in Alaskan research, and that data gap is reflected in this chapter.

Landscape Context and Permafrost

Interior Alaska’s boreal forest is a patchwork of successional forest types. The major physiographic zones into which we categorize them reflect the contrasting influences
of two major disturbance types: fire in upland and lowland areas results in multiple secondary successional pathways, while a more ordered array of forest types results from a combination of primary succession and variation in flooding frequency during succession on active floodplains (Chapter 7). Within each general physiographic zone (uplands and lowlands, floodplains), differences in the postdisturbance environment further influence vegetation establishment, plant species composition, and, ultimately, element cycling.

The state factor approach has proven useful in understanding landscape variation in biogeochemistry (Chapter 1; Van Cleve et al. 1991). As with other aspects of ecosystem function, element cycling reflects control exerted by major state factors: climate, parent material, potential vegetation, topography, and time since the most recent disturbance event. At one end of the spectrum, black spruce ecosystems occupy the coldest soils, exhibit the slowest growth, and have the least demand for nutrients to support growth. Organic materials produced by black spruce and bryophytes tend to display the greatest resistance to decomposition and therefore the slowest resupply of elements for plant uptake (Van Cleve and Harrison 1985, Van Cleve et al. 1986). Production of slowly decomposing organic matter initiates a positive feedback loop that results in low element supply and increased forest floor thickness, reducing soil temperatures that allow relatively labile organic compounds to persist. More productive forest types (birch, aspen, poplar, and some white spruce) generally display the opposite characteristics, producing less decay-resistant organic matter that recycles elements faster, and do not accumulate thick, insulating forest floors. Early-successional communities, dominated by deciduous vegetation, also tend to display more rapid element cycling.

Small differences in microclimate have more profound influences on biogeochemistry in Alaska’s boreal forest than in other biomes because these small temperature differences govern the distribution of permafrost across the landscape. Permafrost, in turn, restricts internal soil drainage and root penetration in the soil profile, which further restricts decomposition and focuses C accretion near the soil surface (Chapter 12). Local climate and vegetation, particularly mosses, interact strongly to govern permafrost characteristics (Chapter 4). The accumulation of an insulating organic surface horizon slows heating in the summer, restricting the depth of the active layer (that portion of the soil profile that thaws seasonally). In extreme cases, the active layer becomes thinner than the O horizon, and the underlying mineral soil no longer participates meaningfully in element cycling.

Correspondence between landscape position, permafrost presence or depth of the active layer, and biogeochemical processes is complex, however. In areas with wide seasonal temperature fluctuation (e.g., valley bottoms that experience the coldest temperatures during winter atmospheric inversions), annual average temperatures may be below freezing and thus be underlain by permafrost. Yet their surface soils may be warmer during the growing season than soils that have higher annual mean temperatures but narrower seasonal temperature amplitudes, such as higher elevation areas that are above winter inversions yet are cooler during summer months). This can result in the counterintuitive situation in which soils in permafrost areas are warmer than those higher in elevation with no permafrost (Vogel 2004) and thus experience more rapid rates of decomposition during the summer months.
Major Element Cycles

Productivity in Alaska’s boreal forest is constrained more directly by availability of moisture and nutrients than by low temperatures (Chapter 11). Nutrient supply rates in turn are governed by litter decomposition and C mineralization rates, so the dynamics of decomposing residues and soil C are of primary concern in any treatment of biogeochemistry.

Carbon

The patterns of C storage, release, and internal dynamics in boreal forest soils have captured the attention of earth scientists owing to the enormous C reservoir that these soils contain and the potential for its release as CO₂ into the atmosphere. Because C balance is the relatively small difference between two much larger and highly variable rates—photosynthesis versus multiple pathways of loss—its assessment entails a challenging integration of complex processes and controls occurring over multiple temporal and spatial scales.

Soil C Stocks

Most authors agree that the boreal forest contains large stocks of soil C, which is most usefully expressed per unit area (e.g., Mg ha⁻¹ = megagrams per hectare). However, such measurements must be interpreted carefully because two questions are not always clearly answered: “Are peatlands included?” and “To what depth are measurements made?” Summaries differ in whether they include the surface O horizon, consisting of layers of recent litter (the Oi horizon; Chapter 3) and increasingly decomposed organic matter (Oe and Oa horizons), in their assessments of C stocks. In nearly all biomes (including the boreal forest), most soil C is in the mineral soil. The O horizon accounts for less than 5% of the total soil C stock in most biomes, but in temperate and boreal forests the percentage is two or three times as large, respectively (Schlesinger 1997).

One recent review of global soil C reservoirs (Jobbágy and Jackson 2000) considered only the surface 1 meter of mineral soil horizons in estimating a pool size of 93 Mg C ha⁻¹ in boreal forest soils. This figure is lower (per unit area) than all other surveyed biomes except deserts and sclerophyllous shrublands. Additional C also exists below the surface meter of soil that is the basis of the estimates described earlier, so Jobbágy and Jackson (2000) also expanded the depth to the surface 3 m of soil. This raised the total boreal forest mineral soil C inventory to 125 Mg C ha⁻¹ but also increased total C stocks in the soils of all other biomes even more in absolute terms, so boreal forests stand ahead of only deserts in total C stored in mineral soil.

Most other estimates include the surface O horizon and are much larger. One early estimate (Schlesinger 1977, repeated in Schlesinger 1997) put average boreal forest soil C content at 149 Mg C ha⁻¹, of which 20 Mg C ha⁻¹ (13.4%) is in the O horizon. This is in relatively good agreement with the estimate from Jobbágy and Jackson (2000). Others have arrived at larger figures. Anderson (1991) (also
cited in Van Cleve and Powers 1995) estimated C stored in boreal forest soils at about 170 Mg C ha$^{-1}$, and Apps et al. (1993) estimated a still larger C inventory of 185 Mg C ha$^{-1}$, larger than that for nearly any other biome.

These issues dramatically highlight the unique distribution of C in boreal forest soils. The O horizon is larger in boreal forests than in any other biome in terms of global total and per unit area and as a fraction of total soil C, so the difference between C in the mineral soil and C in the organic horizons is least in boreal forest soils (Schlesinger 1997). This top-heavy distribution reflects differences both in vectors and in rates of vertical movement of C within the soil profile and in the vulnerability of soil C to changes in moisture and temperature at the soil surface. As such, the quantities of surface soil C may vary over time more rapidly than total soil C in other biomes, belying the notion that overall boreal forest soil C inventories may not change rapidly in response to a changing climate.

The foregoing discussion does not include the vast northern peatlands embedded within the boreal forest. On average, these wetlands store more than 1600 Mg C ha$^{-1}$ as peat on a land area a fifth the size of the boreal forest biome. This corresponds to a global total nearly twice that of the rest of the boreal forest (419 vs. 231 Pg C; Apps et al. 1993).

In summary, because of their large aerial extent (1.2 billion ha), boreal forest soils represent a total reservoir (179–231 Pg C) that is larger than that in any biome except the tropical forest, which has more than twice the spatial extent (Schlesinger 1997). These figures triple when we include embedded wetlands (Apps et al. 1993). Because of their historic success in sequestering C and their potential responsiveness to changes in climate and disturbance regime, the boreal forest and its associated wetlands have become foci of interest and concern for future changes in C storage and methane release (see later discussion and Chapter 19).

Soil C Dynamics

The rate at which soils accumulate C depends on the relative rates of litter input, soil respiration, and combustion. As in most forests, boreal soils lose C with disturbance but accumulate C between disturbances (Harden et al. 1997, Goulden et al. 1998). Many boreal ecosystems are characterized by frequent disturbances (Chapter 17) and modest aboveground tree productivity (Chapters 11, 12). Why, then, does soil C accumulate so dramatically in many boreal soils? Part of the answer lies in changes in the source of litter—roots and mosses account for a large proportion of litter input in many boreal ecosystems (Chapter 12). However, controls over decomposition, as described in this section, also play a critical role.

Surface litter and the underlying SOM differ substantially in their controls over decomposition. Plant chemistry appears to dominate patterns of foliar litter decomposition rates, whereas environment and organic matter chemistry both contribute to landscape variation in SOM decomposition.

The most dramatic differences in litter decomposition rate observed among Alaskan boreal forests are between black spruce and other forest types. Birch foliar litter decomposes four to five times faster than black spruce foliar litter in the field (Flanagan and Van Cleve 1983). Reciprocal transplants of these litter types dem-
onstrate that the inherent properties of the litter are much more important than environment in explaining this large difference in litter decay rate. Differences in carbon chemistry account for much of the observed variation in foliar litter decomposition rate. Poplar litter, for example, decomposes more slowly than willow or alder litter on the Tanana floodplain in part because of higher concentrations of complex tannins and lignin (Chapter 14; Yarie and Van Cleve 1996). Other patterns of decomposition are less easily explained. White spruce needle litter, for example, decomposes relatively rapidly (Chapter 12), despite its high lignin and tannin concentrations (Yarie and Van Cleve 1996). Litter N concentration also correlates with litter decomposition rate (Flanagan and Van Cleve 1983), as in many biomes, but tests often show that this correlation does not reflect a causal relationship (Prescott 1995, Hobbie 1996). In the boreal forest, for example, enhanced N and P availabilities inhibited wood decomposition relative to both untreated litter and litter to which glucose had been added (Fig. 15.1; Flanagan and Van Cleve 1983). Thus, litter decomposition appears to be constrained more by C chemistry (resistance of C compounds to decay) than by nutrient composition (Chapter 14).

Most litter decomposition studies have focused on the leaf litter or wood produced by vascular plants. The largest proportion of litter input in black spruce forests comes from fine roots and moss (Chapter 12; Ruess et al. 2003), which complicates our understanding of overall litter decomposition dynamics. The role of root litter carbon chemistry in controlling decomposition rates has not been examined, but roots appear and disappear rapidly from serial minirhizotron images, suggesting rapid production and decomposition (Chapter 12; Ruess et al. 1996). The proportion of the root-derived C that is mineralized to CO$_2$ or transformed into humic substances is unknown. It is apparent, however, that root litter contributes substantially to belowground C dynamics. In the absence of root inputs, Vogel (2004) found that the forest floor mass of three black spruce stands decreased rapidly, suggesting

![Graphs showing mass loss relative to control for Birch forest and Spruce forest](image)

**Figure 15.1.** Effects of carbon and nutrient additions on decomposition rates of wood substrates placed in different organic horizons (L1 = upper litter layer [undecomposed or Oi]; L2 = lower litter layer [undecomposed or Oi]; F = fermentation layer [partially decomposed or Oe]; H = humus layer [fully decomposed or Oa]. Rates are expressed relative to untreated control plots, set at zero. Data recalculated from Flanagan and Van Cleve (1983).
that a large fraction of the forest floor consists of root litter that turns over rapidly, with much of the decomposition products being lost from the forest floor as either CO₂ or soluble C. Mosses, on the other hand, decompose slowly (Turetsky 2003), perhaps contributing more to long-term SOM accumulation in black spruce forests.

In contrast to litter, the decomposition and turnover of the soil organic mat appear to be controlled by both environment and chemistry. Reciprocal transplants (Flanagan and Van Cleve 1983) and laboratory incubations of soil organic matter (Vance and Chapin 2001) both show that black spruce SOM decomposes more slowly than SOM from other forest types, suggesting an important role of SOM chemistry, just as described for foliar litter. Unlike foliar litter, however, SOM turnover is also strongly influenced by the subsurface environment. Soils on south aspects often warm to temperatures typical of temperate soils during the summer, enabling instantaneous rates of litter decomposition that rival those of their southern counterparts—but over a much shorter time period. Once coniferous forests develop thick moss layers and underlying O horizons, their cold, wet environment strongly limits decomposition. Laboratory incubations of this organic layer under favorable conditions of temperature and moisture demonstrate that most of this organic matter is highly labile and decomposes rapidly (Neff and Hooper 2002; Vogel 2004), just as in arctic tundra (Weintraub and Schimel 2003). Field warming experiments also lead to rapid decomposition of black spruce SOM (Van Cleve et al. 1990). Temperature may also alter the nature of the residual humus and increase the relative quantities of CO₂ evolved per unit of organic matter processed (Thornley and Cannell 2001). Decomposition of SOM accumulated under cold conditions responds sensitively to changes in temperature. For example, soils sampled from cold environments exhibited higher Q₁₀’s (R₉/₅₄/R₁) where R is microbial respiration at two temperatures differing by 10°C than did soils sampled from warmer environments (Kirschbaum 1995). Together, these observations suggest that there may be large positive feedbacks between climate warming and C release from the cold soils of boreal forests (Kirschbaum 2000).

Ecosystem carbon turnover is often indexed as the mean residence time (MRT) of the forest floor, which strictly speaking requires measurement of C loss from the forest floor. This is often approximated as litterfall rates by assuming steady state, that is, that the forest floor is neither aggrading nor degrading. This assumption is questionable in most biomes, especially the boreal forest, where the forest floor clearly aggrades during succession. By measuring mass loss of forest floor samples in litterbags placed back into the forest floor, Flanagan and Van Cleve (1983) avoided this assumption. They found that the MRT of spruce litter in forest floor increased with increasing forest floor thickness, while MRT for broad-leaved litter did not differ across a range of deciduous forest floor thicknesses (Fig. 15.2; Flanagan and Van Cleve 1983). These patterns and rates are very similar to the litter MRTs measured across a range of mature black spruce stands in interior Alaska, which ranged from 76–102 years (Vogel 2004).

A recent paper presented a simple model of soil C accumulation with potentially important implications for the geographic distribution of changes in C balance with climate. Because C fixation occurs aboveground and C mineralization is largely a belowground process, Swanson et al. (2000) reasoned that the difference between
above- and belowground growing degree-days (GDD, Chapter 4; thus AGDD-BGDD) would constitute an “above-ground thermal advantage.” Larger advantages would correspond to higher rates of peat accumulation. AGDD and BGDD converge at low latitudes (both are high) and at extreme high latitudes (both are near zero; Fig. 15.3). At intermediate latitudes, AGDD-BGDD reaches a maximum at approximately the 0°C mean annual soil temperature (MAST) isotherm, which corresponds to the major zone of peat accumulation across North America (Swanson et al. 2000). This model also implies that climate warming might differ in its effect on soil C storage across the boreal forest; in the southern boreal forest, there should be a net C loss resulting from a shrinking aboveground thermal advantage; whereas in the northern boreal forest there should be a net C gain resulting from an increasing aboveground thermal advantage. Incorporation of simple models such as this could improve biome-scale assessments of C balance.

Disturbance Impacts

Although boreal forests historically are disturbance-driven ecosystems, Alaska’s boreal forests are unusual in the circumpolar north because non-anthropogenic disturbance patterns, especially wildfire, still dominate the landscape. Depending on severity, wildfire transfers varying amounts of organic C from the ground surface, where most fires are carried in coniferous forests, to the atmosphere (Chapter 17). Severe fires, especially those in late summer, burn deep into the O horizon because of chronic drying, releasing more C than would be likely in the
Figure 15.3. Annual cycle of soil and air temperature, soil and air growing degree-days (GDD), and aboveground thermal advantage (air GDD–soil GDD) in high-arctic, boreal, and subtropical ecosystems. Adapted from Swanson et al. (2000).
same stand earlier in the growing season (Kasischke and Johnstone in press). Less severe fires may do little more than scorch the surface of the forest floor, leaving most C in place.

In early July 1999, a major experimental examination of wildfire behavior and the role of wildfire on boreal forest dynamics began. Dubbed “Frostfire” to embrace the contrasts in extremes inherent in the boreal forest, the “prescribed wildfire” achieved moderate severity in about 35% of the 11 km² watershed C4 within the Caribou Poker Creeks Research Watershed, primarily in closed-canopy black spruce vegetation. Previous studies had suggested that the warm, moist conditions typical of postfire periods drive a sharp increase in heterotrophic respiration (Richter et al. 2000). However, measurements of surface CO₂ exchange have not provided evidence of such a spike, either at Frostfire (Valentine 2002, unpublished) or elsewhere in interior Alaska (O’Neill 2000). Depending on how slowly productivity recovers, the integrated C losses for postfire years can equal or exceed direct fire losses (Zhuang et al. 2002).

Repeated fires further complicate trends in soil C accumulation owing to the pyrogenic transformation of biomass into charred materials (“black carbon”). Harden et al. (1997, 2000) hypothesized that fires cause not only the single largest loss of C from surface soils but also the single largest input of C into mineral soil (Fig. 15.4), resulting from the movement of small pieces of charred materials deeper

![Figure 15.4. Conceptual model of temporal changes in shallow and deep-soil C storage associated with succession and wildfire. During succession, C accumulates in shallow soils and is lost from deep soils, whereas wildfire causes a loss of shallow-soil C to the atmosphere (combustion) and to deep soils (leaching). Redrawn with permission from Blackwell Publishing, Ltd. (Harden et al. 2000).](image)
into the soil profile. Their hypothesis also predicts that, between fires, litter inputs to surface soils exceed respiratory losses, whereas C losses exceed inputs in mineral soils. Black carbon accumulation is potentially a major contributor to the long-term C balance of boreal forests.

The overall pattern after wildfire is C loss from soils until litter inputs exceed microbial respiration, after which rapid regrowth causes rapid net C accretion. Later in stand development, rates of NPP and C accretion slow (Fig. 15.5; Van Cleve et al. 1993), and variability in net C accretion increases among older, otherwise similar stands, even among otherwise similar sites.

Methane

Boreal forests in Alaska and elsewhere contain an abundance of peatlands resulting from poor drainage, often the combined result of permafrost and the insulating and drainage-impeding nature of mosses. Under these conditions, C metabolism proceeds more slowly via anaerobic pathways that generate a variety of reduced trace gases, such as methyl sulfides and, ultimately, methane (CH₄). Although CH₄ emissions are constrained by both slow anaerobic metabolism and partial oxidation in surface sediments and are far lower than CO₂ emissions would be from an aerated environment, CH₄ is 20 times more powerful than CO₂ (per mole) as a “greenhouse gas” (Chapter 19). Northern wetlands may be a major potential source

Figure 15.5. Organic C accretion in organic matter and carbonate disappearance during floodplain succession. Redrawn with permission from the Canadian Journal of Forest Research (Van Cleve et al. 1993).
of CH$_4$ to the atmosphere, and a great deal of effort has been expended quantifying CH$_4$ emissions in northern wetlands (Hamilton et al. 1994, Suyker et al. 1996). Measured CH$_4$ emissions rates vary substantially depending on water table, substrate quality, temperature, and pH.

Methane fluxes from wetlands in Alaska’s boreal forests have not received as much attention as those in Canada, and the importance of methane biogeochemistry remains a gap in our knowledge. Methane fluxes from Alaskan wetlands appear to be comparatively low, however (Bartlett et al. 1992, Martens et al. 1992). This may be the result of temperature or other constraints on the acetate metabolic pathway that is thought to dominate methane production in freshwater wetlands (Hines et al. 2001).

As in most uplands elsewhere, bacteria in well-drained or otherwise aerobic boreal forest soils consume atmospheric CH$_4$ (Whalen et al. 1990, Gullledge and Schimel 2000). Rates of CH$_4$ consumption are very low (generally <0.5 mg C m$^{-2}$ d$^{-1}$) and are inhibited by ammonium in soils (Gullledge et al. 1997). These patterns are similar to those observed in other ecosystems (Steudler et al. 1989, Mosier et al. 1996).

**Nitrogen**

As with carbon, boreal forests have very large stocks of soil organic N (Van Cleve and Alexander 1981). Nonetheless, N supply rates directly limit plant productivity throughout Alaska’s interior forests (Chapter 11). Recent estimates suggest that the annual inputs of inorganic N (dry and wet deposition, N fixation and mineralization) cannot account for observed plant N uptake (Ruess et al. 1996). In black spruce forests, these conventional measures of N flux represent less than 50% of the annual N requirement of the vegetation (Table 15.1). Part of the reason for this discrepancy between N supply and N demand is that boreal trees absorb part of their N in an organic form (Näsholm et al. 1998, Kielland 2001, McFarland et al. 2002). This recent discovery of the central role of organic N in boreal N cycling has led to major changes in our paradigm of how N cycles through ecosystems (Chapin 1995, Atkin 1996).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Alder$^1$</th>
<th>Balsam Poplar$^1$</th>
<th>Birch$^1$</th>
<th>White Spruce$^1$</th>
<th>Black Spruce$^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Supply$^3$</td>
<td>4.34</td>
<td>2.40</td>
<td>2.45</td>
<td>1.47</td>
<td>0.38</td>
</tr>
<tr>
<td>Requirement$^3$</td>
<td>7.46</td>
<td>2.23</td>
<td>5.25</td>
<td>1.35</td>
<td>0.92</td>
</tr>
<tr>
<td>S/R($^4$100)$^4$</td>
<td>58</td>
<td>107</td>
<td>47</td>
<td>109</td>
<td>41</td>
</tr>
</tbody>
</table>

Source: Data calculated from Ruess et al. (1996) and Van Cleve et al. (1983).

$^1$Floodplain stands.

$^2$Upland stands.

$^3$Units are in g m$^{-2}$ yr$^{-1}$.

$^4$Proportion of annual requirement supplied by inorganic N (%).
N inputs

On floodplains, N cycling is dominated by inputs from thinleaf alder (A. tenuifolia), especially in early- to mid-succession. These inputs establish an N legacy that carries through later stages of forest development. Because of the low precipitation and lack of industrial development in interior Alaska, N deposition is relatively minor (Chapter 16), except in the earliest successional stands of willow, which have very low rates of N fixation and N mineralization. Initially, N fixation accounts for nearly 80% of the N that is absorbed by vegetation. In later successional stages, N fixation typically accounts for 10–20% of the N budget (Ruess et al. 1996). Ultimately, in late succession, the amounts of N accumulated in mineral soil in the floodplain and in upland/lowlands may be similar. However, N accumulates more rapidly in floodplain than in upland forests because of the higher rates of N fixation by the floodplain alder (Anderson et al. 2004). This difference in N inputs is reflected in the generally higher foliar N concentrations of deciduous trees on the floodplain than in the uplands (Yarie and Van Cleve 1983), although this difference is not apparent in white spruce.

In upland secondary successional forests, a substantial legacy of N remains after fire because variable burn intensities can consume little of or nearly the entire forest floor. It would be interesting to know the age of organic materials (C) in these postburn ecosystems. Accumulation of decay-resistant organic materials (e.g., lignin, charcoal, and humus) over several fire cycles may also influence supplies of N from mineralization through chemical stabilization, physical protection, and cooling.

Soil Organic N Turnover

Average concentration of total N in the forest floor varies approximately 15-fold through primary floodplain succession in interior Alaska, being lowest in the willow stage and highest in the poplar stage (Walker 1989). This contrasts to a mere twofold variation of total N in the mineral soil. Extractable concentrations of ammonium are typically orders of magnitude greater than nitrate, except in the N-fixing alder stands, where nitrate concentrations approximate those of ammonium. Concentrations of dissolved organic N (DON) in mineral soil are typically two to three times greater than concentrations of ammonium (Walker 1989).

Except in early succession, organic N inputs from plants are the largest N inputs to the soil. The controls over the breakdown of this insoluble organic N to soluble forms is not well understood but may be the rate-limiting step in going from dead organic matter to N forms that are available to plants and microbes. Insoluble organic N is acted upon by a range of proteases, which, in conjunction with the direct release of free amino acids from cell lysis, results in amino acid concentrations in the soil solution on the order of 20–250 µM (Kielland 1995, Raab et al. 1999). The breakdown of proteins to dissolved organic N (DON) is positively correlated with total soil N (Raab et al. 1999) and negatively correlated with soil depth and organic matter quality (Chapin et al. 1988, Jones 1999). Plants are an additional direct source of DON. They can contain up to 30% protein by weight and free amino acids at
concentrations between 5–10 mM (Jones and Darrah 1994, Kielland 1994). Rupture of root cells by freeze-thaw cycles, herbivory, or senescence can release substantial DON to the soil.

In boreal surface soils, free amino acid concentrations are about 4–8 μg N g⁻¹ dry weight (Kielland 2001, Jones and Kielland 2002), similar to values in arctic tundra soils (Kielland 1995). This DON pool is several-fold (50-fold in black spruce) larger than the ammonium pool (Fig. 15.6; Jones et al. 2002). Because N typically originates as insoluble or soluble organic N and subsequently is transformed to soluble inorganic N forms, the probable gross supply rate must be in this order: soluble organic N > ammonium > nitrate.

Both laboratory and in situ field estimates of amino acid turnover (i.e., complete replacement of the pool) suggest that this pool is highly dynamic, even under the prevailing cold conditions of late-successional boreal ecosystems. In the field, free amino acid turnover times in soils are generally 1–12 hours, depending on soil physicochemical characteristics (Jones et al. 1994), and the N flux through the amino acid pool is large—over an order of magnitude greater than the rate of gross mineralization in black spruce soils (Jones et al. 2002). The turnover of the amino acid pool is approximately three times more rapid in the organic horizon than in the mineral soil (Fig. 15.7 top). This is in part explained by the much more rapid microbial uptake rate of amino acids in the forest floor (Fig. 15.7 bottom). However, in the willow stage of succession, the in situ turnover rates of simple amino acids, such as glycine, alanine, and aspartate, appear to be as rapid as those in the organic horizon in white spruce stands. The large pools and the rapid turnover of free amino acids imply that their production and consumption rates must be very high, both during times of high biological activity and on an annual basis. The rapid consumption

![Figure 15.6. Relative proportions of ammonium, amino acids, and other uncharacterized dissolved organic nitrogen (DON) in soil extracts of black spruce forests of the Tanana floodplain. Nitrate was undetectable. Data from Jones et al. (2002).]
of amino acids suggests that the transformation of protein to amino acids (rather than the mineralization of amino acids to NH₄⁺) is the major bottleneck in the N cycle in boreal soils. Although organic N turnover has not been thoroughly studied in most ecosystems, we suspect that patterns observed in boreal soils are widely applicable. In both marine and terrestrial ecosystems, the potential and actual turnover of free amino acids are very rapid. For example, the alanine pool in marine sediments turns over in about two to four hours (Jørgensen and Søndergaard 1984, Henrichs and Doyle 1986).

Both proteolysis and N mineralization are positively correlated with total soil N (Marion and Miller 1982, Raab et al. 1999) and negatively correlated with soil depth and organic matter quality (owing to N immobilization potentials; Chapin et al. 1988, Jones 1999). Further, amino acid decomposition appears to exhibit qualitatively different temperature responses than does N mineralization. Whereas amino acid turnover is very sensitive to increases in temperature below 10°C (Jones 1999), N mineralization and nitrification in taiga soils do not respond significantly to temperature until it exceeds 15–20°C (Klingensmith and Van Cleve 1993). Moreover, soil proteolytic activity, unlike N mineralization, is tightly controlled by pH (Leake and Read 1989). In addition, pH strongly affects amino acid uptake in boreal plants (Falkengren-Grerup et al. 2000).
Soil N Mineralization

Short growing season and environmental conditions adverse to decomposition result in a low annual flux of inorganic N in boreal forests. Growing-season (May–September) rates of net N mineralization vary eight-fold across successional stands in interior Alaska (Fig. 15.8). The seasonal dynamics of N mineralization are highly variable, and microbial N immobilization may predominate anytime during the growing season (Gordon and Van Cleve 1983, Boone 1992, Klingensmith and Van Cleve 1993). Van Cleve et al. (1993) found the highest rates of N mineralization early in the season, whereas other studies have found different patterns (Gordon and Van Cleve 1983, Klingensmith and Van Cleve 1993). Moreover, the peak in N mineralization does not always occur synchronously in mineral soil and in the forest floor. Net mineralization rates during the short summer season are much more rapid than over winter (Gordon and Van Cleve 1983). However, cumulative net N production over the winter accounts for nearly 40% of the annual total flux because of the long winter season.

N mineralization in interior forests is strongly affected by substrate quality (Flanagan and Van Cleve 1983), attesting to the importance of vegetation control over ecosystem processes in the north (Chapin et al. 1997). By contrast, temperature appears to have very little effect on N mineralization under ambient soil temperatures between 5–20 °C (Klingensmith and Van Cleve 1993; Viereck et al. 1993). Likewise, soil moisture has negligible effects on N mineralization, except in the white spruce stage of succession, where drought stress significantly reduces tree growth (Chapter 11; Barber et al. 2000).

Though midwinter air and soil temperatures are typically low in boreal forests, the duration of autumn freeze-up can be prolonged, even in these high-latitude ecosystems. High soil moisture, and thus increased soil heat capacity, coupled with

![Net N mineralization](chart)

**Figure 15.8.** Successional changes in summer, winter, and annual net N mineralization in the Tanana River floodplain.
an increasingly insulating snow cover, often leaves the top 10 cm of the soil, where most of the biological activity is concentrated, unfrozen for many weeks after freeze-up has occurred. Indeed, much of the N flux through the soil system occurs after ecologists have returned to their classrooms in the fall. Net N mineralization rates during the growing season from green-up (late May) through freeze-up (late September) accounts for about 60% of the annual inorganic N flux, with the remaining 40% released during the nearly eight months of the apparent dormant season. Similarly, in the Arctic about half of the annual N mineralization occurs during winter (Hobbie and Chapin 1996). Boreal N release during winter occurs primarily from October through January, with negligible N mineralization during early spring in stands of willow, alder, balsam poplar, and white spruce. Conversely, black spruce stands exhibit substantial mineralization after snowmelt during early spring. The high rates of N mineralization in late autumn through early winter coincide with high turnover of fine-root biomass in these stands, suggesting that labile substrate production, rather than temperature, is a major factor in controlling N mineralization in these ecosystems. The results are consistent with the low temperature sensitivity of boreal N mineralization described earlier. These findings suggest that the biogeochemically active season in these ecosystems is much longer than previously recognized. The shoulder seasons of spring and fall may turn out to be as important as the summer growing season for many biogeochemical processes in boreal forests.

Organic Solutes from Plants May Affect N Availability

Some recent studies have suggested that secondary metabolites leached from understory species may have deleterious effects on forest growth. Swedish researchers (Zackrisson and Nilsson 1992, Nilsson et al. 1993, Zackrisson et al. 1996, 1997, Wardle et al. 1998) noted that intensively managed Scots pine (Pinus sylvestris) forests in Sweden had declined in productivity and sought an explanation. They found that a ubiquitous understory shrub, crowberry (Empetrum hermaphroditum), leached a compound—Batatasin III—that had deleterious effects on germination and early growth of pine, and they suggested that one mechanism to explain this may be depression of N availability. They also noted that charcoal—no longer produced by wildfire in Swedish forests—adsorbed Batatasin III, mitigating its negative effects.

In Alaskan interior forests, Castells et al. (2003) did not find such activity resulting from crowberry but did find evidence that foliar and litter leachates from another common understory shrub in hardwood forests, Labrador tea (Ledum palustre), stimulated N immobilization and thereby reduced net N mineralization. The effects of plant secondary metabolites on microbial processes are often complex (Chapter 14).

Plant N Uptake

As described earlier, interior Alaskan forests appear to be dominated by one of two modes of N dynamics. On the one hand, there is strong, direct evidence that addition of inorganic N stimulates the productivity of taiga ecosystems (Chapter 11), a
conclusion that is also suggested by significant relationships that link productivity, decomposition, and N mineralization (Van Cleve et al. 1983, 1993). On the other hand, in the N budget of stands such as black spruce, birch, and alder, the combined inorganic N fluxes (mineralization, deposition, and fixation) account for only about 50% of the annual N requirement. This discrepancy suggests that "unconventional" mechanisms of N acquisition, such as direct uptake of amino acids, may play a role in these forests.

Boreal plants exhibit a substantial capacity to absorb organic N, just as do plants from alpine (Raab et al. 1999) and arctic ecosystems (Kielwand 2001). In plots labeled with U-13C,15N glycine, 45–90% of the label is taken up as an intact amino acid (Nåsholm et al. 1998). Conservative estimates of glycine uptake in interior Alaskan forests show similar results (McFarland et al. 2002). Moreover, estimates of ammonium and glycine uptake in situ show that the forest vegetation takes up these N forms in roughly equal proportions (Fig. 15.9). Thus, despite very rapid microbial turnover of amino acids in the soil, which might compete with uptake by vegetation (Jones 1999), amino acids appear to play a significant role in the N economy of boreal forests.

There are several physiological mechanisms that enable plants to obtain organic N, including direct uptake by roots and association with mycorrhizal fungi that have a high capacity to break down proteins and absorb the resulting amino acids. The direct acquisition of organic N is not an exclusive trait of species in natural ecosystems. Important agricultural species can also take up organic N (Nåsholm et al. 2000, Yamagata et al. 2001), suggesting that plant species under radically different edaphic conditions mine the soil for N in both mineral and organic form. It is still unclear how important organic N is to the overall N economy of other ecosystems.

![Figure 15.9. Relative plant uptake rates of 15N-labeled NH4+ and glycine from boreal forest soils. Data are means + SE. Redrawn with permission from Ecosystems (McFarland et al. 2002).](image)
Rates of absorption of most nutrients vary predictably among boreal tree species as a function of their intrinsic growth rate, nutrient availability in the soil they occupy, and the ion in question (Chapin et al. 1986). Nutrient uptake rate is typically most temperature-sensitive in species such as aspen that occupy warm soils, compared to species such as black spruce, which occur in very cold soils. Moreover, species from high-fertility soils tend to have higher nutrient absorption rates than species from low-fertility soils because of their greater nutrient demands for growth. The availability/production of mineral N in taiga soils is dominated by ammonium, except in the older stage of primary succession where nitrate predominates (Van Cleve et al. 1993). Nevertheless, ammonium appears to be the preferred mineral N source for the majority of boreal species, as estimated from laboratory absorption experiments (Chapin et al. 1986).

Isotopic Signatures of Taiga Forest Species

The isotopic signature of N (δ¹⁵N) in tissues of northern species also provides evidence of niche differentiation regarding the acquisition of different N forms (Schulze et al. 1994, Michelsen et al. 1996, Nadelhoffer et al. 1996, Kielland et al. 1998). For example, arctic species of different functional types differ substantially in leaf δ¹⁵N values, suggesting differences in the source and possibly the composition of absorbed soil N. Graminoids, which rely primarily on inorganic N and exploit deeper soil horizons, are enriched in the heavy isotope (¹⁵N), implying that they are relying on N that has cycled within the ecosystem for a relatively long time. Conversely, mosses and deciduous and evergreen shrubs, which rely more heavily on organic N, are depleted in ¹⁵N (Kielland 1997). The patterns of isotope values among boreal species are similar to those in arctic tundra, with δ¹⁵N values ranging from +4‰ in aquatic plants to -10‰ in black spruce (Fig. 15.10; Schulze et al. 1994, Kielland et al. 1998). This variation is consistent with the hypothesis that plants in both ecosystems have evolved diverse strategies for acquiring soil N.

Species in high-fertility soils, such as alder, differ greatly in δ¹⁵N from species such as willow and black spruce, which grow in low-fertility soils (Fig. 15.11). This divergence underscores the differences in N dynamics among ecosystems and suggests variation of N sources across successional gradients. In particular, the very depleted isotope signature of black spruce (Picea mariana) is the opposite of what is expected of species growing in century-old peat, where a long history of soil N processing should have enriched soils in ¹⁵N via chronic losses of ¹⁴N.

Phosphorus

Although most of Alaska’s boreal forest soils escaped glaciation (Chapter 2), they have experienced little chemical weathering and hence tend to be relatively “young” (Chapter 3). Along the Tanana River floodplain, for example, total phosphorus (P) content of soils (mass basis) exceeds that of N for nearly the first 200 years of stand development, despite large inputs of alder-fixed N early in succession (Van Cleve et al. 1993). In upland soils, total P contents are similarly high, in some stands rivaling those of N on a mass basis (Van Cleve et al. 1983). Since plants typically
require about 14 times more N than P, these observations suggest that P should seldom limit production in these forests (Chapter 11). Three factors may, however, limit P availability in some boreal forest soils.

First, soil pH varies from slightly alkaline (pH 7.5) to strongly acidic (pH 4), largely driven by differences in disturbance regimes and changes through succession (Van Cleve et al. 1993). The higher pH values occur in poorly weathered parent material typical of recently deposited alluvium rich in calcite (Marion et al. 1993), in which calcium phosphates and hydroxyapatite are only sparingly soluble and restrict P availability. Surface soils become mildly acidic later in succession and in upland/lowland areas of all ages in the absence of calcite deposition. Moreover, periodic fire releases P from organic matter and acts as a mildly alkalinizing influence, replenishing soluble P supplies. Greater P availability for plant growth in upland ecosystems is reflected in the substantially higher current foliage P concentrations in both deciduous and white spruce tissue in upland forests compared with floodplain forests. P availability reaches its maximum at pH 6.5, below which precipitation with iron begins to restrict solubility. Surface soil pH values are lowest in the organic horizons under white and black spruce cover types (with associated bryophytes). Available P does not always diminish at low pH in these soils, however. On the Tanana River floodplain, for example, peak concentrations of extractable P occurred at pH 5—well below the theoretical P solubility maximum at pH 6.5 (Van Cleve et al. 1993). In summary, there are several potential mechanisms that might alter the relative availability of N and P in boreal soils, but future research will be required to assess their relative importance.
Second, in excessively well-drained, coarse-textured soils, chemical weathering may be too slow to keep pace with plant demands. In Alaska’s boreal forests, these conditions may occur in sandy and gravelly deposits in river floodplains early in succession, in stabilized sand dunes, or anywhere else that parent materials are exposed at the surface.

Third, soils in which restricted drainage or low temperatures limit decomposition accumulate a thick, acidic organic horizon on the soil surface. Over time, this process may become self-reinforcing (paludification) as the accumulating peat not only restricts drainage but also insulates the subsoil from surface heating and enables permafrost to rise, often up into the organic horizon. This severely curtails the rates of mineral weathering and the access of roots to mineral P. Although total P in these organic-rich soils may be relatively high, the poor drainage and low temperatures of the organic horizon restrict mineralization of P from the organic matter, while low soil pH limits its solubility, especially in the presence of soluble iron or aluminum. Although it is not clear which of these processes (restricted mineralization or low solubility) is the dominant mechanism, this pattern frequently occurs in nutrient-poor black spruce stands (Van Cleve et al. 1983).

**Conclusions**

Biogeochemistry in Alaska’s boreal forest is variable both across the landscape and over time. This variability reflects the exceptionally broad dynamic range of conditions imposed by the major state factors on biogeochemical processes, exemplified in the extreme by the interaction of frequent wildfires with underlying permafrost.
to govern rates of decomposition and nutrient return to vegetation. We have learned a great deal from chronosequence studies by substituting space for time; future repeated measurements within single stands will permit us to verify these patterns.

The major changes that govern boreal forests’ productivity and C balance occur rapidly over relatively short time scales. Interannual climatic variability can change the sign of ecosystem C balance by changing both disturbance regimes (fire and insect, Chapters 17 and 9, respectively) and plant root litter inputs (Chapter 12) and decomposition. Rapid root production and turnover rates (Chapter 12) contribute substantially not only to C accretion but also to interannual variation in total surface organic C stocks (Vogel 2004). Because a relatively large fraction of soil C is at or near the soil surface, boreal forest C dynamics track interannual fluctuations in climate and disturbance more closely than in other biomes. This sensitivity, coupled with the large size of the boreal forest soil C reservoir and the predicted magnitude of climate change at high latitudes, reinforces the widely held view that the boreal forest will strongly influence future atmospheric CO₂ levels (Chapter 19).

It is nonetheless clear that long-term assessments of the decomposition rates of major litter types, including roots, coarse woody debris, and bryophytes, are needed to complete our understanding of C balance and nutrient cycling.

As with most other terrestrial biomes, the dynamics of N availability generally limit vegetative growth. In the cold soils of Alaska’s boreal forest, however, alternative pathways of N availability that do not require mineralization are important, even dominant—especially in late-successional spruce forests. The quantity of N taken up by vegetation as amino acids, as well as the factors that control the uptake rate, are poorly known. Similarly, it remains to be identified when during succession organic N becomes an important N uptake pathway. These basic questions underscore the fundamental shift in our understanding of the N cycle brought about by the discovery of the dominance of organic N in boreal forest nutrition.

References


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