Carbon Dynamics in the Boreal Forest

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Executives Summary

As one of the largest and most intact biomes, the boreal forest occupies a prominent place in the global carbon budget. While it contains about 13% of global terrestrial biomass, its organic-rich soils hold 43% of the world's soil carbon. A growing body of research has attempted to measure how climate influences the processes governing carbon uptake and release, and to predict further changes due to climate change. A review of this body of research produces the key findings outlined below.

Current research on boreal forest carbon pools and the processes that affect them suggest that this biome acts as a weak sink for atmospheric carbon. However, evidence of rapid climate change at northern latitudes has raised concern that the boreal forest could readily shift to a net carbon source if the ecophysiological processes facilitating carbon uptake are sufficiently disrupted. Changes in soil temperatures, respiration rates, and disturbance dynamics (type, extent, and frequency) brought about by climate change or other factors could switch the biome to a net source of carbon. Based on current knowledge, it appears that a warming climate will likely create the conditions for increased carbon release from boreal forests.

The boreal is a large and complex ecosystem and uniform response due to warming is unlikely. Empirical evidence suggests non-linear response, and this will affect forest carbon storage on varied temporal and spatial scales. Furthermore, determining the balance of carbon uptake and release is highly complex, and methods of carbon flux measurement will need to improve for more accurate conclusions of climate change impacts to be made. The following points represent generalizations across all boreal ecosystems.

What We Know About Carbon Storage and Flux in Boreal Forests

- Research indicates that boreal forests across North America and Eurasia have acted as weak sinks for atmospheric carbon in the last century. Storage of carbon in living and dead vegetation and the organic soil pool have generally exceeded carbon release through respiration and combustion. The "sink" status of the boreal forest is largely dependent on factors that keep heterotrophic respiration (release of CO_2 by microbial decomposition of organic matter) lower than carbon uptake through plant growth and accumulation in the soil. Heterotrophic respiration varies with the amount of decaying organic matter, soil moisture, soil temperature, vegetation type, and species/types of decomposers, which in turn

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are influenced by disturbance (particularly fire and insect outbreaks, but also harvesting and ice and wind storms), temperature, precipitation, and duration of thaw.
- The soil carbon pool plays a disproportionately large role in sequestration in boreal forests, frequently constituting the largest pool in the system. In general, carbon accumulation rates in the soil are highest in low-lying, poorly drained sites such as peat bogs or black spruce swamps. More productive, well-drained sites on uplands may produce greater tree growth but store less carbon in the soil pool. Likewise, north-facing aspects that maintain permafrost and cooler temperatures support reduced productivity and higher carbon accumulation rates compared to other topographic positions.
- Studies in Canada have shown that lichens and bryophytes in lowland saturated sites contain upwards of 20% of the above ground carbon. These communities have important effects on how carbon is stored in boreal soils. Thick moss layers limit heat gain from the atmosphere, creating cold and wet conditions that promote the development of permafrost, with limited decomposition, thus are important for carbon storage. These positive feedbacks can be altered by novel disturbance regimes, including severe fire, which alter successional trajectories and increase carbon loss through decomposition and respiration.

What We Do Not Know About Carbon Storage and Flux in Boreal Forests

- Certain regions of the boreal are well studied, including those areas in Canada and Fennoscandia. However, many other regions are underrepresented in global carbon budget projections, and as a result, there is a tremendous amount of uncertainty in estimates of boreal carbon pools.
- There is little quantifiable information about several important carbon pools, including fine root biomass and mycorrhizae, bryophyte and understory layers and coarse woody debris and litter.
- Research is lacking on poorly drained sites, including those found in the larch forests of Siberia, which may be the most vulnerable to soil carbon loss with changes in disturbance regimes and climate.
- Considering the importance of fire in boreal carbon dynamics, there is much that is still not well understood, including extent, frequency, and intensity across the biome; and the interactions among fire intensity, nitrogen, and carbon.

What We Think Are the Major Influences on Carbon Storage and Flux in Boreal Forests

Disturbance

- Increased fire frequency could greatly increase carbon release, especially if it increases the decomposition of "old" carbon from the soil pool by increasing soil temperatures and degrading permafrost. More frequent fires could greatly reduce storage in woody biomass, and cause a concurrent increase in decomposition. Of even greater importance is the enhanced rate of heterotrophic respiration observed after fire. Increased soil temperatures from surface blackening and loss of the insulating bryophyte and litter layers that keep soil respiration low, increased nutrient availability from ash, and carbon inputs from fire-killed trees all contribute to enhanced decomposition rates post-burn. In addition, fire regimes determine the forest age class distribution across the landscape, and influence what vegetation communities develop (with their differing carbon dynamics). On the other hand, an often-overlooked impact of fire is the conversion of woody biomass to charcoal, a very persistent form of carbon that can remain in the soil for centuries. Thus fire may contribute to carbon storage in the soil through charcoal inputs to long-term carbon pool.
- While fire is recognized as the dominant natural disturbance type over much of the boreal forest, secondary disturbances such as insect outbreaks (and "background" insect damage during non-outbreak years) are also critically important. In some circumstances, such as the Canadian boreal and north temperate forests, insects and pathogens annually cause forest volume losses through mortality and growth reductions that are three times the volume lost to fire. Unlike fire, insect damage does not produce a direct emission, but rather exerts its influence through altered rates of decomposition and growth. In

some forest types, insect outbreaks exert the primary influence on age class distribution.

- Drought events have been increasingly implicated as a critical driver of stand dynamics and forest mortality, particularly in the boreal zone. Increased temperatures and extended periods of below-average precipitation have triggered forest dieback and mortality across large areas, with drier regions of the boreal appearing particularly vulnerable. Drought affected regions may also be more vulnerable to insect outbreaks thereby enhancing mortality rates. Resulting massive waves of mortality that have been documented represent a dramatic and sharp increase of carbon in dead standing biomass, with significant consequences for long-term carbon flux.

Age Class Distribution

- The balance of carbon uptake versus respiration loss changes with the stage of stand development in boreal forests, and research indicates that two distinct scenarios may be possible. In the first more frequently observed scenario, a brief period of enhanced post-disturbance (fire or logging) release is followed by a return to sink conditions and, eventually, equilibrium, The “sink” status of boreal forests is thus dependent on a disturbance regime that creates a forest age-class distribution that is skewed towards vigorous, maturing stands. However, other research indicates that decomposition of post-fire detritus may not occur early in stand development, but rather during stand maturation. Such a delayed decomposition response could counteract the high carbon uptake rates observed in maturing stands, making them a weaker sink than traditionally thought.

Climate and Topography

- Extremely high rates of carbon storage are possible in many boreal soils due to insulating bryophyte layers, low temperatures, poor drainage, high moisture content and permafrost formation. Cold and wet conditions slow decomposition rates and allow organic matter to accumulate faster than it is respired away.

How We Think the Carbon Status of Boreal Forests Changes with Changing Climate

- The question of whether moisture availability will decline with climatic warming will probably determine whether warming enhances the boreal carbon sink or turns it into a source. The balance of growth and respiration is significantly influenced by climatic conditions such as temperature, precipitation, and duration of the growing season. Increasing temperatures without concurrent increases in precipitation can cause drought stress, increased respiration, and the loss of carbon from boreal forests. However, if precipitation increases along with temperature, growing conditions could significantly improve and greater carbon uptake could occur. Increasing temperatures in early spring could also increase carbon uptake by lengthening the growing season.
- Sustained increased temperatures could possibly cause the breakdown of permafrost layers in boreal soils. If this occurs, the large stores of carbon bound in these frozen soils could be released.
- It appears that climatic warming is shortening the fire return interval in many boreal forests, speeding up the life cycles of damaging insects, and amplifying drought-driven dieback events. This could result in a large release of carbon, quickly turning the boreal forests from a sink to a source of carbon.
- Peatlands are possibly at greater risk from climate warming than forested areas and there is very little research on these un-forested wetlands, which may hold the majority of the carbon found in the boreal system.
- Over 97% of the total carbon stored in the vast tundra systems to the north of the boreal forest is found in the soil. This has huge implications for the global carbon budget, with the potential for a shifting boreal-tundra border with climate change. It is unclear whether the massive carbon pool in tundra soils would remain intact if converted to a forested biome.

1 Introduction

This chapter reviews the research literature on boreal and sub boreal forests of Eurasia and North America. It first describes the region, the forest

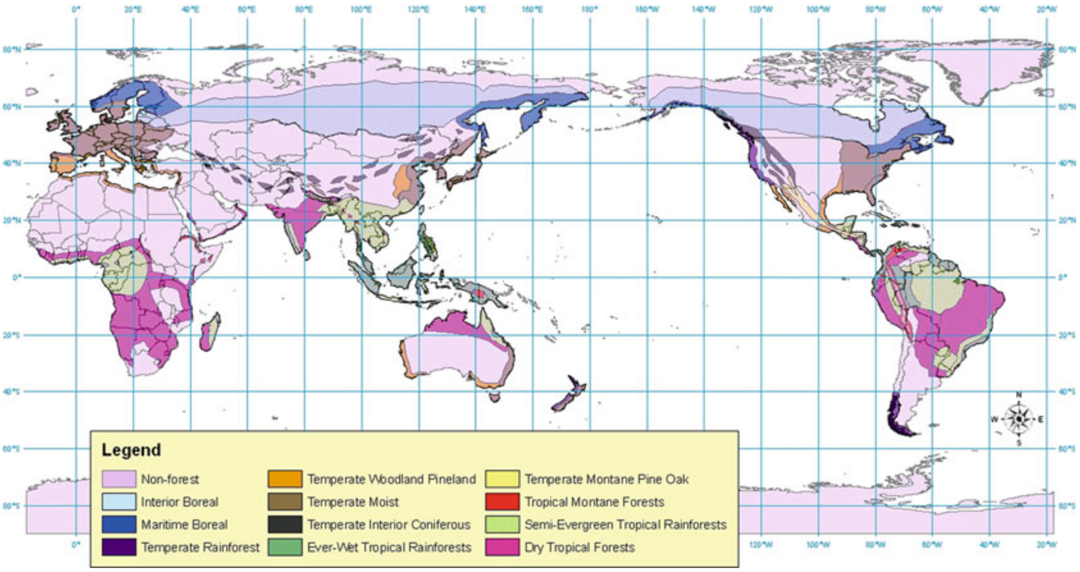

Fig. 6.1 Original extent of boreal, temperate, and tropical forest types of the world prior to land clearing

types, and their climatic variations. It then describes the stocks of carbon within the different components of the forest – above-ground biomass, below-ground biomass, lichens and bryophytes, the litter layer, and the soil. The next part of the chapter is focused on changes among carbon stocks – in particular understanding the biotic interactions of uptake (photosynthesis) and loss (respiration, decomposition); and then how abiotic influences of disturbance (fire, insect outbreaks, drought, forest management) can affect carbon stocks. The chapter highlights areas of carbon forest science that we understand well versus those areas that represent critical gaps in our knowledge and demand further investigation.

1.1 The Boreal Forest System

The boreal forest occupies a vast swath of the northern hemisphere, including much of Canada, Alaska, Fennoscandia, Russia, Mongolia, and northeast China (Fig. 6.1). Its northern limit is close to 68°N in North America and nearly 71°N in Eurasia, north of which tundra vegetation dominates. The southern limit is more variable, blending into temperate mixed forests or grassland and steppe systems, depending on moisture availability (Larsen 1980). Certain temperate forests that border the boreal (such as the Laurentian forest types of eastern North America or the Ussuri Taiga of the Russian Far East) or that occur at high elevations (such as spruce-fir communities in the Rocky Mountains or the Alps) have similar dynamics of carbon storage and release, and much of the research cited in this paper may apply to these regions.

Across their global range, boreal forests share certain key features. Only six tree genera are found as canopy dominants: spruce (*Picea*), fir (*Abies*), pine (*Pinus*), larch (*Larix*), birch (*Betula*), and aspen (*Populus*). Mature stands tend to exhibit very simple structure, dominated by a single stratum of conifers with a well-developed bryophyte layer at ground level (Gower et al. 2001). Understory communities are generally of low diversity (Larsen 1980), but shrub and herb diversity can vary substantially between stands related to overstory composition and soil type (e.g. MacDonald and Fenniak 2007; Légaré et al. 2001). In sub-boreal forests along the southern edge of the zone, aspens and birches may become more dominant, with a concomitant increase in understory diversity (e.g. MacDonald and Fenniak 2007). Boreal landscapes in North America and Eurasia feature vast plains (often the beds of ancient glacial lakes) interspersed with numerous bogs and fens. These plains are bounded by mountain ranges such as the Northern Rockies and the Altai (Fig. 6.1). Soils types vary across the boreal. Higher fertility luvisolic (alfisols) soils are characteristic of some interior regions of the southern boreal, but organic soils (histosols), permafrost soils (gelisols), and heavily leached and nutrient-poor podzols predominate over large areas (Larsen 1980). In lowland areas with sufficient moisture and temperature conditions, large peat deposits form above the mineral soil, sometimes covering many millions of hectares (Gorham 1991).

Differences in climate, moisture availability, and disturbance regimes create distinct zones within the greater boreal continuum. In North America, interior boreal forests characterized by a continental climate occupy the majority of the area. Dominant species assemblages include white spruce (*Picea glauca*), jack pine (*Pinus banksiana*) and spruce-aspen (*Populus tremuloides*) mixedwoods on upland sites, and black spruce (*P. mariana*) with components of Larch (*Larix* sp.) on cold, poorly drained sites. These interior boreal forest types are primarily characterized by a disturbance regime of catastrophic fires. In contrast, maritime influence from the Pacific in the west, and the Atlantic Ocean in the east create moister, more productive conditions in the Cordillarean and Maritime boreal zones, respectively (Apps et al. 1993; Baldocchi et al. 2000) (Fig. 6.1). These forests include a larger component of fir (*Abies* spp.) and cyclical outbreaks of forest insects play a greater role in structuring forest dynamics. In addition, most regions of the North American boreal are heavily influenced by industrial forest use.

In Eurasia, boreal forests west of the Ural Mountains tend to be dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), and are significantly influenced by catastrophic fire and industrial forest management practices. The Baltic and White Seas produce a moderating climatic effect for Fennoscandian and northwest Russian forests (Baldocchi et al. 2000), which may explain the higher productivity observed in these areas compared to continental Siberian forests (Schulze et al. 1999) (Fig. 6.1). East of the Urals, a combination of extreme moisture stress and extensive permafrost shifts the competitive advantage to larch species (*Larix* spp.), which are adapted to these difficult growing conditions (Gower and Richards 1990). Large areas of Scots pine are also found in Siberia. A regime of frequent, non-catastrophic ground fires is characteristic of these forests (Harden et al. 1997). Fennoscandian forests have a long history of local forest utilization and commercial forestry (e.g. Berg et al. 2008), while industrial forest use in the Siberian boreal has expanded rapidly in recent years (Archard et al. 2006).

2 Pools of Carbon in the Boreal System

Carbon storage in the boreal forest occurs in distinct but interrelated pools, each of which demonstrates unique response to environmental change. As such, it is very important to address these pools separately before attempting an integrated understanding of boreal carbon dynamics. The major pools are aboveground biomass (ranging from 11% to 59%); soil (ranging from 20% to 85%); and bryophytes/mosses (ranging from 5% to 26%) (Table 6.1). Litter and belowground biomass are much smaller, although the litter pool can be as high as 50% in young Jack pine stands. Belowground biomass is hard to measure and consequently there are limited data for this pool.

2.1 Aboveground Biomass

This pool consists of the live or dead standing biomass of trees, shrubs and herbs. In contrast with tropical and temperate forests, this aboveground pool is usually not the largest in the boreal system but is strongly influenced by site productivity. For example, in relatively productive

Table 6.1 Distribution of carbon among different pools in boreal forests

	Site characteristics			Carbon pools			
Source	Location	Forest type	Age	Aboveground biomass	Bryophytes/ mosses	Litter	Soil
Malhi et al. (1999)	Interior Canada	Black Spruce	115	49.2 Mg/ha (11%)		6.2 Mg/ha (1%)	390.4 Mg/ha (85%)
Goulden et al. (1998)	Interior Canada	Black Spruce Sphagnum site	120	40 ± 20 tons/ha (14%)	45 ± 13 tons/ha (16%)		200 ± 50 tons/ha (70%)
Goulden et al. (1998)	Interior Canada	Black Spruce Pleurozium site	120	40 ± 20 tons/ha (23%)	45 ± 13 tons/ha (26%)		90 ± 51 tons/ha (70%)
Gower et al. (1997)	Interior Canada	Black spruce	115–155	49.2–57.2 Mg/ha (11–12%)			390.4–418.4 Mg/ha (87–88%)
		Aspen	53–67	57.0–93.3 Mg/ha (32–59%)		15.9–19.4 Mg/ha (9–12%)	36.0–97.2 Mg/ha (23–55%)
		Jack pine	25	7.8–12.3 Mg/ha (10–24%)		18.1–40.3 Mg/ha (36–53%)	20.2–28.4 Mg/ha (37–40%)
		Jack pine	65	29.0–34.6 Mg/ha (42–51%)	3.5–5.1 Mg/ha (5–7%)	11.5–14.6 Mg/ha (17–21%)	14.2–25.8 Mg/ha (20–38%)

upland aspen and jack pine sites in central Canada, aboveground vegetation and soil contained roughly equal amounts of carbon. In contrast, in lowland swamps of stunted black spruce (*Picea mariana*), only about 12–13% of the carbon was found aboveground (Gower et al. 1997). Black spruce stands in Manitoba had 40 ± 13 tons carbon ha^{-1} (living and dead biomass), which comprised around 15–23% of total stand carbon depending on whether the sites were saturated swamps or well-drained uplands (Goulden et al. 1998). In southern Siberia, biomass carbon exceeded soil carbon in Scots pine stands, while it was near equal in birch stands, and was exceeded by soil carbon in larch stands (Vedrova et al. 2002). In an interior Canadian black spruce forest, Malhi et al. (1999) reported that aboveground biomass makes up on average around 11% of total stand carbon (see Table 6.1).

Overstory (tree) vegetation appears to dominate the aboveground pool of which approximately 5% may be dead trees (Yarie and Billings 2002). The woody understory comprises a minor component of total forest carbon (Nalder and Wein 1999; Li et al. 2003), and was measured in one study as less than 2% (Wang et al. 2001).

Aboveground productivity in boreal forests is limited by a number of environmental factors, including seasonal distribution of precipitation, timing of soil thaw, soil type, nutrient availability, site aspect, topography, and length of the growing season (Jarvis and Linder 2000; Gower et al. 2001). Many of these factors affect productivity primarily by controlling rates of respiration and decomposition, which will be explained further in the section on “Means of Uptake and Release.” One example, nitrogen availability, is often identified as a growth limitation in boreal forests (Bonan and Van Cleve 1992). This limitation is related to very slow decomposition rates, which ties up nitrogen in undecomposed litter (Wirth et al. 2002). Thus, decomposition and its drivers (soil warming, water table depth, forest fire) determine the extent to which nitrogen limits aboveground productivity. In a related way, pollution driven N-deposition in Northern Europe may be increasing aboveground carbon pools in Scandinavia (Mäkipää et al. 1999).

Aboveground carbon storage also appears to differ across forest types. It is greater in mixed woods than pure stands of either deciduous or coniferous trees, perhaps due to the greater foliage mass in stratified mixed stands (Martin et al. 2005). Additionally, aboveground and total net primary production (NPP) are generally higher in deciduous than coniferous stands (Gower et al. 1997, 2001).

Research from the Russian taiga indicates that disturbance and extreme climatic events (i.e. drought) may prevent boreal forests from attaining the maximum density and productivity possible under site conditions (Schulze et al. 1999; Vygodskaya et al. 2002). For instance, southern Siberian forests were kept below the theoretical self-thinning line by frequent ground fires that reduced stand density beyond the levels associated with competition mortality (Schulze et al. 1999). The importance of such events must be considered along with site factors in quantifying the aboveground carbon pool.

2.2 Belowground Biomass

The belowground biomass carbon pool consists of coarse and fine tree roots and their associated mycorrhizae. It is considered one of the most difficult pools to quantify, as labor-intensive destructive sampling is often required to achieve exact figures, and even then measuring fine root mass may not be possible (Table 6.2). Gower et al. (2001) found that the most common bias in estimations of NPP in boreal forests was the exclusion of fine roots and mycorrhizae from the calculation. The few studies that have measured these features show high variability and thus cannot be extrapolated accurately to quantify the belowground carbon pool for the biome.

While precise quantification of belowground biomass is difficult, researchers have been able to identify the approximate proportion of total stand carbon that this pool accounts for (Table 6.1). Data from limited studies show that belowground biomass is highly variable, influenced by such stand and site factors as species composition, stand age, and available moisture. A greater

Table 6.2 Sources of uncertainty in Boreal carbon modeling

	References
Inadequately quantified carbon pools	
Fine root biomass/mycorrhizae	Gower et al. (1997, 2001)
Magnitude of labile soil carbon pool	Rustad and Fernandez (1998); Jarvis and Linder (2000); Bronson et al. (2008)
Bryophyte/understory layers	Gower et al. (2001)
CWD and litter in Russia	Krankina et al. (2002)
Changing allocation patterns within trees	Lapenis et al. (2005)
Poorly understood environmental variables	
Quantifying burned area in Russia	Dixon and Krankina (1993); Conard and Ivanova (1997); Soja et al. (2007)
Recognizing refugia in burned areas	Amiro et al. (2001); Kang et al. (2006)
Fire intensity vs. simply fire occurrence	Wooster and Zhang (2004)
Influence of burn severity on carbon and nitrogen consumption	Balshi et al. (2007)
Accounting for ground vs. crown fires	Wirth et al. (2002)
Changes in insect life cycles	Malmstrom and Raffa (2000)
Possibility of poor post-disturbance stocking	Auclair and Carter (1993); Shvidenko et al. (1997)
Accounting for potential vegetation dieback	Kasischke et al. (1995)
Rates of permafrost degradation	Prokushkin et al. (2005)
Lag time on migration of temperate species into boreal zone	Smith and Shugart (1993)
Quantifying area, depth and bulk density of boreal peatlands	Gorham (1991)
Balance of CO_2 and CH_4 emissions from peatlands	Gorham (1991)
Lack of research on poorly-drained forests	Bond-Lamberty et al. (2004)
Rates of precipitation change	Pastor and Post (1988); Flannigan et al. (1998)
Accuracy of estimation of crown and soil temperatures	Arain et al. (2002)
Varying temperatures of different carbon pools	Lindroth et al. (1998)
Assumption of increased productivity with increased temperature	Briffa et al. (1998); Barber et al. (2000); Wilmking et al. (2004)
Timing of increased temperatures	Lindroth et al. (1998)
Using monthly temperature anomalies as opposed to daily temperature data	Flannigan et al. (1998)
Thresholds in NEP response to climate change	Grant et al. (2006)
Albedo effect of boreal forest cover	Bonan et al. (1992, 1995); Betts (2000); Bala (et al. 2007)
Lack of data on Eurasian larch forests	Gower et al. (2001)

The table summarizes portions of the boreal carbon budget (pools, processes and environmental variables) that are currently poorly understood or quantified, and indicates potential areas for future research on boreal carbon dynamics

percentage of total NPP is allocated to roots in coniferous than in hardwood stands (Bond-Lamberty et al. 2004). One comparative study found that 41–46% of total NPP was allocated to roots in conifer stands but only 10–19% in aspen stands (Gower et al. 1997). However, research in Alaska has shown that hardwood forests can exceed coniferous forests in the production of *fine* roots, which can make up 11–29% of stand biomass (Ruess et al. 1996). Stand age appears to affect the belowground biomass pool by regulating root production. Bond-Lamberty et al. (2004) found that coarse and fine root production peaked at around 70 years in a Canadian black spruce chronosequence, but was 50–70% lower in 151-year-old stands.

Soil moisture limitations may cause trees to allocate more biomass to belowground structures.

Schulze et al. (1999) found that a greater proportion of stand biomass was allocated to roots in Siberian boreal forests than in European Russia or temperate European forests, perhaps due to the extreme moisture deficits that occur in some areas of Siberia. Indeed, increasing aridity across northern Siberia may be causing a shift in allocation from photosynthetic tissues to roots, while increasing moisture in European Russia and southern Siberia is having the opposite effect (Lapenis et al. 2005). Other environmental factors besides moisture could also be at play here: Prokushkin et al. (2005) attributed the high relative allocation of carbon to roots in Siberian forests to low soil temperatures and nutrient availability. It appears that under stressful conditions with low levels of water and nutrients, trees develop larger root systems to access these resources.

2.3 Lichens and Bryophytes

This pool is largely composed of lichens and mosses, which frequently form a dense mat at the ground level in boreal forests. This pool is relatively unique in importance to boreal forests compared to temperate and tropical zones where it is a relatively insignificant component of the carbon budget.

Bryophyte tissues decompose more slowly than woody or non-woody tissue (Turetsky 2003; Turetsky et al. 2010), and thus tend to accumulate between fire events. Soil drainage seems to influence the magnitude of this pool (Turetsky et al. 2005), which is largest in boreal peatlands, where bryophytes are the major vegetation type. In mature lowland black spruce forests, mosses may sequester as much or more carbon than trees, and ten times the amount sequestered by understory vegetation (Harden et al. 1997) (Table 6.1). Czimczik et al. (2006) found that bryophytes made up 20% of total aboveground NPP in black spruce stands. The dominant bryophytes in such saturated sites are *Sphagnum* mosses. In upland spruce sites with better drainage, the moss dominance switches to *Pleurozium* feathermosses, which accumulate significantly less carbon that *Sphagnum* types (Goulden et al. 1998). Moving even further "upland," only 3.2% of stand carbon is stored in mosses in xeric jack pine stands, and in aspen stands the bryophyte pool is even smaller (Nalder and Wein 1999).

Unfortunately, no research on the importance of bryophytes in Eurasian boreal forests was found for this review. Given the circumpolar range of *Sphagnum* and *Pleurozium* species, and the widespread presence of saturated lowland boreal forests in Eurasia, it seems likely that bryophytes also play a large role in that region. Little is also known about the dry lichen communities (often composed of *Cladonia* species) that blanket the floor of xeric conifer woodlands in North America and Eurasia. Despite recognition of their unique importance, lichens and bryophytes remain one of the least studied carbon pools in the boreal forest (Table 6.2).

In addition to their direct role as a carbon pool, bryophyte communities have important effects on how carbon is stored in boreal soils. Thick moss layers (including live mosses and moss-derived organic material) limit heat gain from the atmosphere (Startsev et al. 2007). In black spruce stands, for example, this creates cold and wet conditions near the soil surface that promote the development of permafrost (O'Neill et al. 2002). The limitations on decomposition imposed by such conditions are very important for carbon storage in the soil profile. In white spruce and aspen stands with less-developed bryophyte communities, more rapid transfer of heat, moisture, and oxygen through the soil profile is possible, resulting in warmer and drier subsoil conditions and less stored carbon (O'Neill et al. 2002).

The flammability of different bryophyte communities influences their rates of carbon storage and release. *Pleurozium* mosses dry out completely; consequently, a fire can release the carbon stored therein and expose the soil surface to greater heat and drying. In contrast, *Sphagnum* mosses remain saturated through most of their profile, even during dry seasons. Fires only remove the upper layers, leaving moist lower layers intact to insulate the soil (Harden et al. 1997). In addition, a dense layer of sphagnum moss contributes to higher soil acidity, which facilitates formation of an impermeable soil layer (Bonan and Shugart 1989). This acts as a positive feedback to soil moisture conditions by reducing the movement of moisture through the upper soil horizons, and increases moisture levels near the soil surface. When vigorous, sphagnum moss can even regulate successional trajectories by limiting colonization to species capable of layering, such as spruce (Johnstone et al. 2010). The reduced flammability and decomposition brought about by *Sphagnum* communities contribute to the general trend of greater ground-level and belowground carbon storage in saturated lowland sites than in well-drained uplands. However, this also hints at the potential re-organizing that would take place if fire events in the sphagnum-dominated portions of the boreal were to become more severe (Chapin et al. 2010; Johnstone et al. 2010).

2.4 Litter Layer and Coarse Woody Debris

This pool is made up of dead organic matter that has not decomposed and entered the soil profile. The coarse woody debris component represents an increasingly important element of forests at higher latitudes, and thus may be most at risk of becoming a carbon source under increased warming. Malhi et al. (1999) found that the litter layer composes on average only about 1% of total stand carbon in boreal forests (Table 6.1). The size of this pool is primarily driven by rates of decomposition and disturbance. Disturbances such as fire or insect infestation contribute pulses of dead material to the pool, but fire can also reduce it through direct burning or by raising ground temperatures and stimulating increased decomposition. Also litter and coarse woody debris additions vary by stand type and age (Brassard and Chen 2008). Young post-disturbance stands often have very large litter pools (composed of the dead remains of the previous cohort), which diminish through stand development before increasing again as overstory mortality increases during stand maturation (Goulden et al. 2010). Increased overstory mortality as stands age can thus gradually replenish the supply of litter. As a consequence, coarse woody debris becomes an increasingly significant pool in older-growth stands (Siitonen et al. 2000). In contrast, studies have shown that the forest floor may actually lose carbon as the stand matures, as was identified in Canadian jack pine stands (Nalder and Wein 1999). This sequence of depletion and re-accumulation demonstrates that there is no simple relationship between litter, coarse woody debris, carbon and stand age.

Rates of litter accumulation vary across boreal zones. In Russian boreal forests, these differences may be associated with species composition. Stocks of coarse woody material are greater in Siberia, where rot-resistant larch species predominate, than in pine- and spruce-dominated European Russia (Krankina et al. 2002). Nalder and Wein (1999) found that the density of forest floor carbon was 68% higher in jack pine stands in eastern Canada than in western Canada. The reasons for such differences across the same vegetation community are not entirely clear. Differing site productivity, decomposition rates or fire levels could be involved.

The litter layer also interacts with bryophyte communities to affect soil properties. Like mosses, thick litter layers can insulate the soil, affecting depth of thaw, available moisture and belowground respiration (Bonan et al. 1990). The insulating and moisture-retaining capacity of the forest floor (including both litter and bryophytes) is highest in black spruce forests among all Canadian boreal forest types (Van Cleve et al. 1990). In such stands, the combined litter-bryophyte "ground" layer may store three to four times the carbon held in aboveground biomass (Kasischke et al. 1995).

2.5 Soil Carbon

The soil pool (found below the litter layer, consisting of decomposed organic matter and mineral soil) is the most important in the boreal carbon budget. The amount of carbon held in the soil profile often dwarfs the amount of carbon in forest vegetation (Malhi et al. 1999; Goulden et al. 1998; Kasischke et al. 1995; Wirth et al. 2002), and is a unique feature of the boreal forest (Table 6.1).

Many of the same factors responsible for carbon accumulation in bryophyte and litter layers help explain the prominence of soil carbon: cold, saturated soils have low rates of decomposition allowing carbon-rich organic matter to accumulate in the soil profile faster than respiration losses. Thus, the soil pool is greatest in the coldest, most saturated sites. Unforested wetlands may hold the majority of the carbon found in the boreal system, significantly out of proportion to their position in the landscape (Kasischke et al. 1995; Rapalee et al. 1998). For example, lowland (*Sphagnum* site) black spruce soils contain 200 ± 50 tons carbon ha^{-1}, while upland (*Pleurozium* site) soils contain only 90 ± 20 tons ha^{-1} (Goulden et al. 1998). Soil carbon storage in well-drained (and more productive) aspen and jack pine stands is 2.8–2.9 times less than in saturated black spruce soils, which contain 87–88% of stand carbon (Gower et al. 1997). In contrast, total biomass carbon in the xeric Scots pine stands of Siberia may exceed that of the soil carbon pool (Vedrova et al. 2002; Wirth et al. 2002).

The disproportionately large amount of belowground carbon is even more pronounced in the tundra systems to the north. Over 97% of the total carbon stored in these systems is found in the soil (Billings 1987). If current projections hold, a northward shift in the boreal-tundra ecotone is occurring (Soja et al. 2007), with potentially huge implications for the global carbon budget. It is unclear whether the massive soil pool in tundra sites would remain intact if converted to a forested biome (Kasischke et al. 1995).

The specific location of carbon within the soil profile also varies across time and space. In saturated black spruce sites, soil carbon is often found in the organic horizons or directly below (Goulden et al. 1998; O'Neill et al. 2002), while the majority of soil carbon in upland aspen (92%) and white spruce (82%) stands is found in the mineral soil (O'Neill et al. 2002). Mineral soil carbon typically declines with depth, but the trend varies among soils reflecting prevailing ecosystem processes. For example, in upland larch (*Larix gmelinii*) forests in northeast China, soil carbon concentration decreases relatively rapidly with soil depth across a range of mesic to xeric sites. This may be attributable to pulses of charcoal added to upper layers by recent fires (Wang et al. 2001).

Fires appear to be very important for transferring carbon from vegetation to the soil profile through conversion to charcoal, which is decay-resistant and can reside in the soil 3,000–12,000 years (Deluca and Aplet 2008). While some is transferred into lower soil horizons by cryoturbation (mixing of soil layers by the freeze-thaw process) (Hobbie et al. 2000), the large majority remains above 30 cm in depth, with approximately 70% remaining in the upper 10 cm of the soil profile (Deluca and Aplet 2008). One study estimated that 30% of the biomass killed in a fire enters the soil as charcoal or unburned material, at least half of which may enter the long-term soil pool; the rest is lost to decomposition or re-burning over the next century (Harden et al. 1997). Globally, charcoal additions probably represent about 1% of stored carbon in boreal forest types (Ohlson et al. 2009), but in some forest types may be significantly higher. For example, in the Rocky Mountains, charcoal are estimated to comprise as much as 60% of soil carbon (Deluca and Aplet 2008), while in southern Siberia this figure is 20–24% (Schulze et al. 1999).

3 Biotic Drivers of Uptake and Release

Biosphere-atmosphere carbon flux consists primarily of three processes: photosynthesis, autotrophic respiration (respiration by plants), and heterotrophic respiration (by microbial organisms during decomposition of organic matter). Along with biomass burning, these processes determine the balance between uptake and release of carbon from forests.

3.1 Photosynthesis and Autotrophic Respiration

Plant photosynthesis and respiration processes are coupled, their balance determining net carbon fixation by plants. These two processes are essentially paired because photosynthesis cannot proceed without energetic (respirational) expenditures on the maintenance and production of organs (roots, stems, and leaves) involved in carbon fixation. Carbon uptake by photosynthesis must therefore be paired with carbon loss through autotrophic respiration, which consumes 54–77% of annual net photosynthesis in boreal forests (Ryan et al. 1997). While autotrophic and heterotrophic respiration are often considered together (due to the difficulty of distinguishing them during measurement), only the former is closely paired with photosynthesis. Heterotrophic respiration rates are not necessarily proportional to tree growth (Li et al. 2003; Barr et al. 2007).

The pairing of photosynthesis and autotrophic respiration does not imply that they necessarily respond the same way to environmental stimuli. In one study in a mature Canadian aspen forest, interannual variability of photosynthesis was controlled primarily by growing season length and secondarily by drought, whereas interannual variability in respiration was primarily controlled by drought and secondarily by temperature (Barr et al. 2007). Jarvis and Linder (2000) support the idea that canopy duration (i.e. length of growing season as controlled by spring temperature) is more important in determining total photosynthesis levels than average temperature or soil moisture levels. Indeed, twentieth century increases in spring temperatures attributed to rising atmospheric CO_2 levels may have increased productivity in boreal aspen stands by allowing for earlier leaf out (Chen et al. 1999).

Rising temperatures (especially if encountered in early spring) may stimulate increased photosynthesis, but they also cause a rise in autotrophic respiration. Respiration rates rise faster under rising temperatures than photosynthesis rates, potentially causing carbon release to the atmosphere (Lindroth et al. 1998). Many models of boreal carbon flux assume that respiration responds directly to rising temperature, while photosynthesis is limited by other factors such as light levels, growing season length, and water and nutrient availability. However, in a study of these processes in Canadian peatlands, increasing annual temperature was unexpectedly correlated with increased net carbon uptake, suggesting that photosynthesis may be more responsive than previously thought, and that respiration will not necessarily offset increased carbon uptake in a warming climate (Dunn et al. 2007).

That said, the unexpected results from Dunn et al. (2007) may have been related to the abundant soil moisture available in peatlands. In drier upland forests, soil moisture availability imposes limitations on forest productivity (Chen et al. 1999; Gower et al. 2001; Bond-Lamberty et al. 2007). Rising temperatures unaccompanied by increasing precipitation could cause moisture stress, reducing photosynthesis. But importantly, drought also lowers respiration levels, potentially balancing out the reduced carbon uptake (Barr et al. 2007). The duration and severity of drought is important for several reasons. Mild drought suppresses respiration while photosynthesis remains largely unchanged, whereas severe drought suppresses both, with a dramatic drop in photosynthesis levels as it intensifies (Barr et al. 2007). In addition, drought events will promote species with strong stomatal conductance, such as Scots pine over species less tolerant to arid conditions, including larch (Dulamsuren et al. 2009). In the Mongolian boreal, Dulamsuren et al. (2009) note the competitive advantage of Scots pine under dry conditions, and conclude that a dark conifer for light conifer transition may occur if drought events become more frequent. This will create numerous feedbacks to the carbon budget of these systems (Bonan 2008).

3.2 Heterotrophic Respiration and Decomposition

Heterotrophic respiration, caused by decomposition of organic matter in the soil and litter layers, is the largest source of carbon emissions in the boreal system. Conceptually, decomposition and organic matter accumulation act as opposite influences on the soil and litter carbon pools; if decomposition exceeds organic inputs, there is a net loss of carbon from the system (Harden et al. 1997). Heterotrophic respiration is a large enough component of carbon flux that it might offset not only organic matter accumulation, but also carbon gains from photosynthesis. Indeed, because photosynthesis and autotrophic respiration often rise and fall together, the real determinant of whether a stand is a carbon sink or source may be its rate of heterotrophic respiration.

Certain environmental factors determine this rate. Vegetation type influences respiration rates through the differing qualities of litter produced. For instance, softwood litter decomposes slower than hardwood litter due to its high lignin content (Hobbie et al. 2000), and larch coarse woody material contains chemicals that slow the rate of decay relative to other softwoods (Krankina et al. 2002). Soil moisture exerts an even stronger influence on soil respiration rates (Harden et al. 2000) and needs to be considered along with temperature when simulating ecosystem responses (Krishnan et al. 2008). The high heat capacity of water and thick mats of bryophytes slow the warming of saturated soils. These factors limit baseline respiration rates, and also mitigate large spikes in respiration that follow fires (Harden et al. 1997). This explains the overall trend of higher soil carbon storage in lowland boreal forests than in upland forests. However, the constant saturation that limits release of CO_2 in boreal peatlands also promotes the release of methane (CH_4), an important greenhouse gas. Drying of peatlands would have the opposite result, namely, decreased CH_4, but increased CO_2 emissions (Gorham 1991). This dynamic could become an important element of carbon flux under changing climatic conditions.

Soil temperature may be even more limiting to decomposition rates than soil moisture (O'Neill et al. 2002). Increasing soil temperatures are widely expected to stimulate increased decomposition and respiration rates, but studies suggest that decomposition rates may actually diminish as a consequence of shifts in microbial community structure with soil warming (Allison and Treseder 2008). So responses to increased temperature may not be so easily predicted. Temperature is also important in determining rates of winter respiration, a frequently overlooked process that may make up 20% of yearly respiration (Hobbie et al. 2000). Young deciduous stands that are carbon sinks during the growing season may become sources after senescence due to winter respiration (Pypker and Fredeen 2002; Trofymow et al. 2002). Such respiration appears to take place in deeper soil layers where temperatures remain high enough in the winter to support decomposition (Goulden et al. 1998). The organic matter in these layers is generally composed of much older, less mobile carbon than that which is decomposed in the summertime (Winston et al. 1997; Dioumaeva et al. 2002). The temperature and duration of thaw in these soil layers control the decomposition rate of "old" soil carbon. Whether sustained soil warming associated with climate change would cause significant increases in carbon flux from this long-term pool is unclear (Table 6.2).

Many studies have attempted to quantify how the balance of decomposition and vegetative growth shifts across a post-disturbance chronosequence (Fig. 6.2). Increased respiration after a fire can be a significant source of carbon release. In fact, research has shown that post-fire decomposition may equal (Amiro et al. 2001) or exceed (Auclair and Carter 1993) direct emissions from burning. Fire has a short-term impact on heterotrophic respiration rates by raising soil temperatures, stimulating increased decomposition of soil organic matter (Harden et al. 1997). There is a longer-term respiration response as well, when the trees killed by the fire begin to decompose a few years later. This process can potentially make young post-fire stands a source of carbon despite the vigorous regrowth of trees and mosses (Rapalee et al. 1998; Vedrova et al. 2002; Wirth et al. 2002). At the same time, increased heterotrophic respiration in young post-disturbance stands may be somewhat balanced by a decrease in autotrophic respiration, caused by tree mortality (Wang et al. 2001). Similarly, in a chronosequence of post-harvest stands in central Canada, Li et al. (2003) found that stands younger than 20 years were carbon sources (releasing 193–239 g carbon/m^2 per year), but by 40 years of age had become weak sinks as growth outpaced decomposition. However, a post-fire chronosequence from the same region showed that

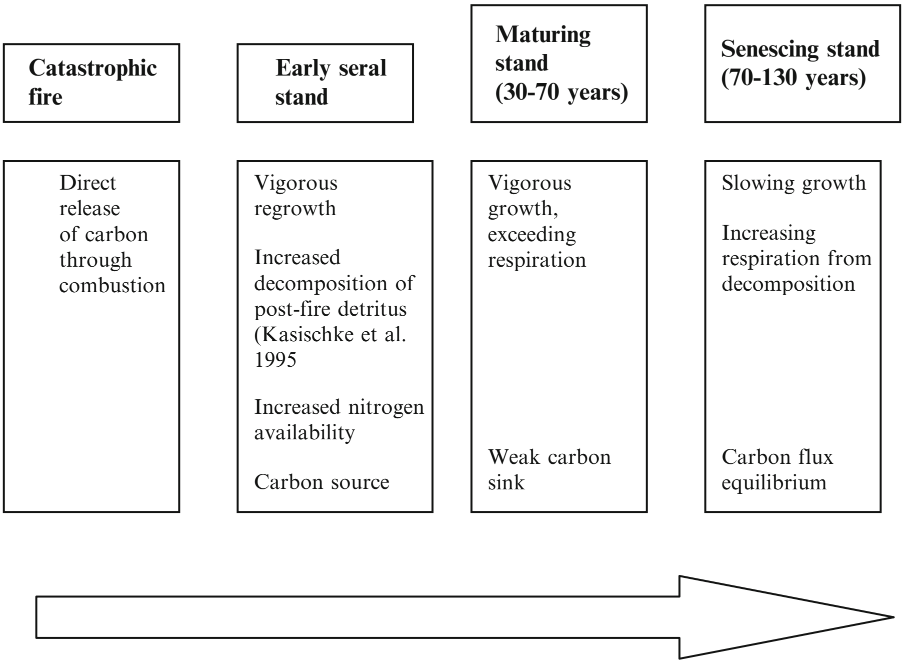

Fig. 6.2 Model of carbon dynamics through stand development in a Canadian black spruce forest (Derived from Litvak et al. (2003) unless otherwise noted in the figure)

significant decomposition of fire-killed litter did not occur in the first few decades and that young stands showed the lowest levels of respiration (Litvak et al. 2003). Czimczik et al. (2006) also did not observe a rise in decomposition in young post-fire stands in Canada. In fact, heterotrophic respiration did not become significant until black spruce dominated the canopy (around 70 years post-fire). Generally, studies suggest an overall pattern of decline in carbon production efficiency as stands age, with older stands tending to show increased carbon losses, in large part due to increased tree mortality (Goulden et al. 2010). These examples demonstrate that disturbance effects on decomposition rates may lag and occur later in stand development, and depend on the type of disturbance. These patterns and lag effects have not been well explored in relation to dieback and tree mortality driven by drought and insects. However, data from the massive mountain pine beetle outbreak in western Canada indicates that forests can rapidly become large net carbon sources in the years following insect attack (Kurz et al. 2008a).

4 Disturbance: Abiotic Drivers of Uptake and Release

Disturbances such as fire, insect and pathogen outbreaks, and logging have important impacts on the boreal carbon budget. Disturbances influence the size of carbon pools by directly destroying (fire) or removing biomass (logging) from the system, and by altering the rates of photosynthesis and respiration as discussed earlier. In fact, disturbance may be the overriding factor in whether or not the boreal forest is a source or sink of carbon. For instance, Kurz et al. (2008c) have estimated that large-scale insect outbreaks have turned Canada's managed forests from a carbon sink to a carbon source. Using Monte Carlo simulations, they predict that this trend will continue due the effects of natural disturbances.

4.1 Fire

The direct emission of carbon to the atmosphere through combustion is a significant component of boreal carbon flux. In upland sites in boreal Canada, Harden et al.'s (2000) model of long-term carbon balance estimated that 10–30% of the annual carbon production has been released as fire emissions, while 40–80% has been released during decomposition and 8–30% fixed as soil carbon. This estimate fits with other observations that increased post-fire decomposition has a greater impact than direct fire emissions (Auclair and Carter 1993; Conard and Ivanova 1997). Quantifying direct emissions is a complicated task, beginning with the process of identifying the area burned in a given year across the vast boreal landscape. Underestimation of burnt area in Russia can significantly bias models, potentially missing a vital source of emissions to the atmosphere (Dixon and Krankina 1993). In contrast, satellite estimation of forest fire extent in Canada overestimated cumulative burned area by approximately 22% because unburned inclusions were not recognized (Kang et al. 2006). These examples demonstrate the difficulty of accurately calculating this component of carbon flux (Table 6.2).

As discussed earlier, fire affects soil properties through changes in temperature and moisture conditions, removal of insulating litter and bryophyte layers, and contribution of decay-resistant charcoal to the soil pool. Fire may also increase nitrogen input from the organic layer to the soil, increasing nitrogen mineralization and vegetation productivity (Kasischke et al. 1995; Johnson and Curtis 2001; Kang et al. 2006). One study in the Canadian boreal demonstrated that deciduous stands are able to respond more rapidly to the increased supply of nitrogen than conifers, due to their faster rate of leaf canopy turnover. Thus, deciduous forests exhibited increased productivity with increasing fire frequency, while the opposite was true of both dry and wet coniferous types (Kang et al. 2006).

Across much of the boreal region, fire exerts a dominant influence on forest age class distribution. Fire-prone landscapes are characterized by a mosaic of age classes, each with differing rates of growth and respiration. Boreal carbon budgets must account for the different patterns of carbon uptake and release that accompany different age class distributions. In Canadian black spruce forests, most of the net biomass accumulation appears to take place from 20 to 70 years after a fire. Stands younger than 20 years lack sufficient leaf area for rapid carbon accumulation and stands older than 70 years are at or near zero carbon balance with the atmosphere (Fig. 6.2). Only a small proportion (9%) of the black spruce stands in central Canada are in the most productive age class (around 36 years old) (Litvak et al. 2003). In boreal Quebec, biomass increased from 27 to 75 years following a fire, and decreased thereafter due to stand degradation. In the Alberta Boreal Plains ecoregion, it took between 15 and 30 years for post-fire stands to attain the same photosynthetic rates as mature areas while biomass continued to increase to at least 60 years of age (Amiro et al. 2000). Kasischke et al. (1995) reported, however, that biomass levels in upland black spruce forests in Alaska and northwest Canada continue to increase for 140–200 years after a fire, before increased overstory mortality sets in.

Such growth rate comparisons across stand age must be paired with rates of post-fire decomposition. In Siberian Scots pine forests, young post-fire stands are sources of carbon, and may take 70 years to reach pre-fire carbon levels (Wirth et al. 2002). Canadian studies also point to high initial rates of decomposition (Li et al. 2003; Litvak et al. 2003), although this trend may not always hold. Using eddy covariance measurements of growing season net ecosystem CO_2 exchange, Litvak et al. (2003) estimated that recently disturbed black spruce stands in Canada are sources of carbon, middle-aged (20–70 years old) stands are sinks, and older (70–130 years old) stands in near balance with the atmosphere. In Siberia, the trajectory is somewhat different: an initial decrease in carbon pools during first 30–40 years after a fire, fairly rapid carbon accumulation over the next 50 years, and lower but steady rates of accumulation in the centuries thereafter (Wirth et al. 2002).

The frequency and intensity of fire determines how forest age classes are distributed in many boreal landscapes (Table 6.3). In boreal forests of North America, Fennoscandia and European Russia, fires have historically been high-intensity and stand-replacing (Harden et al. 2000), and have

Table 6.3 Fire regimes in the boreal forest

Forest type/location	Disturbance type	Return interval (years)	Reference
Pinus sylvestris, NW Russia	Ground fire	20–40	Gromtsev (2002)
Pinus sylvestris, Siberia	Ground fire	25–50	Conard and Ivanova (1997)
Larix sibirica, Siberia	Ground fire	90–130	Conard and Ivanova (1997)
Picea abies, NW Russia	Stand-replacing fire	130–200	Gromtsev (2002)
Dark taiga[a],central Siberia	Stand-replacing fire	400–500	Schulze et al. (2005)
Continental taiga[b], interior Canada	Stand-replacing fire	40–110	Amiro et al. (2000)
Spruce/fir/birch[c], eastern Canada	Stand-replacing fire	136 ± 29	Lesieur et al. (2002)
Boreal/tundra interface[d], NW Canada	Stand-replacing fire	110	Johnson and Rowe (1975)

[a] *Picea obovata*, *Abies sibirica*, *Pinus sibirica*
[b] *Picea glauca*, *P. mariana*, *Pinus banksiana*, *P. contorta*, *Populus tremuloides*
[c] *Picea glauca*, *P. mariana*, *Abies balsamea*, *Betula papyrifera*
[d] *Picea glauca*, *Pinus banksiana*, muskeg vegetation

a return interval of 40–110 years (Amiro et al. 2000). In Siberia, ground fires that are not stand-replacing are the norm, accounting for about 80% of the area burned. Such fires may burn through Scots pine stands on a short 25–50 year return interval, and larch stands on a 90–130 year interval, leaving many live trees. However, intervals seem to be considerably longer for spruce/fir stands, with fires in this type more likely to be catastrophic (Conard and Ivanova 1997). The total number of fires and the area burned are higher in Siberia than in North America, but the lower intensity of these fires means that more carbon is not necessarily released (Wooster and Zhang 2004). Models that fail to consider that detail can overestimate carbon emissions from Russian forest fires.

Stand-replacing fires have different impacts on carbon dynamics than low-intensity ground fires. The post-fire chronosequences described above tend to occur in catastrophic fire systems, in which the aftermath of fire is nearly always mass mortality and decomposition, and a return to early-successional condition. Ground fires have a more complex result. They can produce uneven-aged communities (Harden et al. 2000), and cause multiple small pulses of mortality and decomposition within the same stand. Rather than causing sudden, complete changes in stand development, ground fires alter competition and productivity levels within the existing cohort. Low-intensity fires in Siberian Scots pine stands result in a 10–20 year growth depression of the surviving trees due to fire damage, followed by 10–15 years of accelerated growth under reduced competition and higher nutrient supply (Schulze et al. 1999). In this forest type, young growth does not appear to necessarily replace the trees lost to ground fires. Instead, low-density stands persist and may never attain the maximum possible stocking (Schulze et al. 1999; Wirth et al. 2002). This "lost" productivity has a significant impact on carbon uptake in Siberian forests; Shvidenko et al. (1997) calculated a 45–50% reduction in forest productivity due to ground fires across large areas of Siberia.

Suppression of forest fires also affects the carbon budget. For example, temperate oak (*Quercus*) forests under fire suppression management had 90% more total ecosystem carbon than those with a frequent fire regime (Tilman et al. 2000). If fire suppression is practiced across a significant portion of the landscape, pools of biomass and litter carbon may exceed estimates for forests under a natural fire regime (Price et al. 1997). However, there is an inherent danger in fire suppression because larger fuel loads may, if ignited, produce much more intense fires than might have occurred in a natural fire regime.

4.2 Insect Outbreaks

While fire is recognized as the dominant natural disturbance type over much of the boreal forest, insect outbreaks (and "background" insect damage during non-outbreak years) are also critically important. Across the Canadian boreal and north temperate forests, insects and pathogens annually cause forest volume losses through mortality and growth reductions that are three times the volume lost to fire. Malstrom and Raffa (2000) found that insects are especially dominant in the moist eastern regions of Canada. Indeed, in the balsam fir (*Abies balsamea*) dominated forests of the Maritime Provinces, cyclical outbreaks of the defoliating insect spruce budworm (*Choristoneura fumiferana*) supplant fire as the primary influence on age class distribution (Baskerville 1975). Unlike fire, insect damage does not produce a direct emission, but rather exerts its influence through altered rates of decomposition and growth (Kurz et al. 2008c).

Kurz et al. (2008c) modeled the impact of spruce budworm and western mountain pine beetle (*Dendroctonus ponderosae*) outbreaks on carbon flux in the Canadian forest. They concluded that these events could switch the region from a carbon sink to a source due to the massive increases in decomposition of dead trees that follow outbreaks. Background levels of insect herbivory are also important. In Fennoscandian and Russian birch (*Betula pubescens*) forests, defoliating insects had a significant effect on leaf area index and net primary production. If certain levels of herbivory are reached, coniferous species may take over the growing space relinquished by damaged birches, speeding stand development and causing related changes in carbon dynamics (Wolf et al. 2008). The combination of drought and defoliating insects can result in significantly reduced production in Canadian aspen forests. If climate change results in an increase in drought and insect outbreaks, closed aspen forests may transition to sparse parklands (Hogg et al. 2002).

4.3 Drought

There is increasing global concern about the potential consequences of altered climate conditions on the extent, duration and severity of drought events and their impacts on forest mortality (Allen et al. 2010). Drought events have been increasingly implicated as a critical driver of stand dynamics and forest mortality, particularly in the boreal zone. Widespread dieback in aspen in western North America (reviewed by Frey et al. 2004) has been attributed to extended periods of unusually severe drought in the region. A function of increased temperatures and periods of below-average precipitation, such events appear to have triggered forest dieback and mortality across large areas, with drier regions of the boreal appearing particularly vulnerable (Hogg et al. 2008). Drought affected regions may also be more vulnerable to insect outbreaks thereby enhancing mortality rates (Frey et al. 2004). Resulting massive waves of mortality that have been documented represent a dramatic and sharp increase of carbon in dead standing biomass (Hogg et al. 2008), with significant consequences for long-term carbon flux.

4.4 Forest Management

Besides its impacts on growth and decomposition rates, the commercial harvest of trees has a direct impact on carbon stocks through the removal of biomass from the forest. The eventual decomposition or combustion of this pool must be considered (refer to Chapter 12 for an analysis of wood products). The greatest difference between timber harvesting and other disturbance types is in the altered contribution it makes to the litter pool compared to fire or insect outbreak. Logging adds litter in pulses that are concentrated around harvest events, and the litter tends to lack stemwood, which is removed from the site for forest products. Intensive site preparation techniques, such as slash burning, can limit this pool even further. Krankina et al. (2002) found that intensively managed European Russian forests had much larger stocks of coarse woody material than unmanaged Siberian forests of similar productivity. In addition, logged stands may maintain higher carbon pools in live biomass compared to post-wildfire stands, where trees are retained in silvicultural activities and their additional beneficial effect on promoting faster regeneration of stand post-disturbance are considered (Seedre and Chen 2010).

Field studies by Martin et al. (2005) suggest that the stand-level impacts of logging on soil carbon dynamics are limited. Harvesting has no consistent effect on carbon levels in soil detritus. Johnson and Curtis (2001) came to a similar conclusion, although they found that whole-tree harvests (as opposed to stem-only harvests that leave tree crowns in the forest) could cause slight decreases in soil carbon. In contrast, Thiffault et al. (2008) observed lower stable C fractions and nutrient retention in soils post-harvest compared to post-wildfire soils of similar age (Thiffault et al. 2008). Furthermore, long-term modeling of managed boreal forests has shown a consistent decline in soil carbon across a 300-year time period compared to forests under a natural disturbance regime (Seely et al. 2002). Long term research plots in managed forests will be necessary to determine if such predictions are accurate.

Timber harvesting is concentrated in certain regions of the boreal forest. Fennoscandia and Maritime Canada are under near-complete management, while vast swathes of interior Canada and Siberia have experienced virtually no logging (although this could change in coming decades). Thus the impacts of forest management on the boreal carbon budget are uneven and difficult to compare with natural disturbances. In south Siberia, the decomposition of logging slash comprised an insignificant proportion of carbon flux to the atmosphere compared to fire emissions and post-fire decomposition (Vedrova et al. 2002). It should also be noted that, unlike natural disturbance, harvesting tends to be concentrated on the most productive portions of the landscape. This could give it an impact out of proportion to area affected (Li et al. 2003).

4.5 Nitrogen-Deposition

Deposition of nitrogen compounds related to pollution has affected several regions, most importantly eastern Europe and Scandinavia. Studies suggest that increased nitrogen-deposition has enhanced productivity in this region (Magnani et al. 2007). While carbon uptake is understood to be highly coupled to nitrogen status, recent findings suggest that increased canopy nitrogen conditions correlate positively with surface albedo, which may represent a further feedback on carbon uptake (Ollinger et al. 2008).

5 Climate Change Impacts on Boreal Carbon Dynamics

The most pressing question is how climate change will affect the carbon balance in the boreal forest. A warming climate could change the productivity/respiration balance, change disturbance regimes, shift forest types, and possibly cause dramatic changes in the extent of the biome itself.

5.1 Increased Productivity Versus Increased Respiration

Much of the uncertainty regarding carbon flux under a changing climate revolves around whether rates of respiration (both autotrophic and heterotrophic) will increase faster than rates of photosynthesis. There is also a question of whether such increased rates will be sustained, or will only constitute a short-term reaction.

Increased CO_2 availability can benefit plant growth, as it is a major constraint on photosynthetic efficiency. Studies have suggested that atmospheric enrichment, or “fertilization” of CO_2 that has been occurring over the past century can enhance growth and may offset increased losses expected from wildfire frequency (Balshi et al. 2007, 2009). Others (e.g. Kurz et al. 2008b) using modeling approaches have suggested that increased productivity is unlikely to offset increased carbon losses due to disturbance.

If climate change results in warmer temperatures in early spring, forest productivity could respond positively thanks to the extension of the growing season (Chen et al. 1999). This could have the greatest effect in deciduous forests due to the stronger response to early-season warmth (Barr et al. 2007). On the other hand, if rising spring temperatures are erratic, they could cause growth reductions by stimulating early de-hardening of tree buds which are then susceptible to frost damage (Hanninen et al. 2005). If rising temperatures come later in the growing season, when moisture stress is a potential problem, then either growth increases could be outstripped by respiration increases (Lindroth et al. 1998), or photosynthesis could actually decrease (Kang et al. 2006). For example, twentieth century decreases in white spruce growth in Alaska have been linked to increased drought stress caused by rising temperatures (Barber et al. 2000). The most common response of trees at the northern Alaskan treeline to increasing temperature is growth reduction, especially on productive sites where competition for moisture is high (Wilmking et al. 2004). Exclusion of such drought impacts from boreal models could potentially skew projections of the carbon budget (Briffa et al. 1998).

Satellite monitoring of boreal forests reveals that productivity declines may be occurring in some regions, perhaps attributed to moisture stress. Goetz et al. (2007) found that more than 25% of boreal forests in Canada that were not recently disturbed showed a decline in productivity with rising global temperatures. Large areas of Siberia showed increased productivity, but this is likely the result of rigorous post-fire regrowth in the wake of many extreme fire seasons.

Thus, whether or not precipitation rises along with temperature has very important consequences for carbon flux (Pastor and Post 1988). If temperature and precipitation increase in tandem, Fennoscandian forests may demonstrate increased productivity (Kellomaki et al. 1997). Predictions of future precipitation changes show strong variation across the boreal system, and even within select ecozones. For instance, while precipitation is expected to increase across most of northern Europe, it is forecasted to decrease in southern Fennoscandia (Flannigan et al. 1998). Similarly, while increased drought stress is modeled for interior Canadian forests, precipitation could rise in maritime eastern Canada (Amiro et al. 2001).

Changing temperature and precipitation regimes will affect decomposition rates in the future. Increasing soil temperatures could increase mineralization and breakdown of organic matter, potentially making more nutrients available for tree growth (Van Cleve et al. 1990). However, the supply of labile nitrogen in the soil may be depleted fairly quickly. In addition, any nitrogen-induced increases may be outweighed by concomitant increases in soil respiration (Bonan and Van Cleve 1992). Soil respiration may be particularly important if a greater proportion of the increased growth goes into roots than aboveground structures (Niinisto et al. 2004). Also, work by Karhu et al. (2010) highlights how responses vary among soil fractions in soil, from labile fractions cycled annually to more recalcitrant material cycled over centuries. Soil organic fractions and sensitivity to warming as estimated by Q_{10} (doubling rates) increases in all soil organic fractions, but most substantially in intermediate fractions. Moreover, the 30–45% increase in carbon loss estimated for soil fractions at current rates of warming would require a 100–120% increase in growth to offset.

However, it is heterotrophic respiration that holds the greatest potential for turning boreal forests from sinks to sources in a warming climate. Bonan and Van Cleve (1992), using models that simulated production and decomposition under warming conditions in Canadian forests, found that respiration increases would balance out photosynthesis gains in black spruce and paper birch (*Betula papyrifera*) forests, and would exceed them in white spruce forests. In a simulation of climatic warming in Finland, gross primary production increased by 12%, but respiration by 22% (Mäkipää et al. 1999). However, climatic simulation in Alaska predicted that increases in heterotrophic respiration would only exceed productivity increases in paper birch stands, while the opposite would be true in white spruce and balsam poplar (*Populus balsamifera*) stands (Yarie and Billings 2002).

Experimental soil warming (+5°C) in north-temperate forests in Maine increased respiration by 25–50% (Rustad and Fernandez 1998). Much of the increase could come from decomposition of deep soil carbon, which currently comprises a small proportion of the whole (Winston et al. 1997; Goulden et al. 1998). In Siberian forests with extreme buildup of organic matter, warming conditions could cause long-term, sustained increases in heterotrophic respiration from humified materials (Dioumaeva et al. 2002). Increased heterotrophic respiration may be limited by certain factors, however. Since the amount of labile organic matter is limited in many boreal soils, respiration rates may tail off after this pool is "burned off" by increased decomposition, (Rustad and Fernandez 1998). In addition, microbial communities in the soil may acclimate to higher temperatures, regulating decomposition rates (Jarvis and Linder 2000; Bronson et al. 2008).

The potential for increases in deep soil decomposition is greatly increased if significant soil thawing and permafrost degradation occurs. This will largely be determined by how a changing climate affects the litter and bryophyte layers that insulate the soil profile. Increasing fire in a warming climate could reduce the thickness of these insulating layers (Harden et al. 2000), and warmer air temperatures would increase the period of time in which there is a positive heat flow from the atmosphere to the ground layer (Kasischke et al. 1995). Both of these factors could cause degradation of permafrost. Camill (2005) found that increasing air temperatures in the latter half of the twentieth century (without an accompanying increase in precipitation) resulted in widespread degradation across the discontinuous permafrost zone of Manitoba. However, drying of the litter layer could reduce decomposition rates (Niinisto et al. 2004), and reduce the layer's thermal conductivity, thereby decreasing the depth of soil thawing (Bonan et al. 1990). If precipitation increased along with temperature, this drying would be prevented and permafrost thaw could increase (Gorham 1991).

The impact of changing temperatures and precipitation is especially hard to understand in boreal peatland systems. On one hand, permafrost degradation and increased heterotrophic respiration are significant possibilities (Hobbie et al. 2000). On the other hand, peat accumulates twice as fast on "collapse scars" as on bogs with intact permafrost (Camill et al. 2001). Thus, the increased productivity of these areas could offset some of the carbon losses. There is also a tradeoff in peatlands between aerobic decomposition (which releases CO_2) and anaerobic decomposition (which releases CH_4). If water tables drop, aerobic decomposition is likely to increase, since waterlogged peat is oxygen-poor, but affected areas could also experience reductions in CH_4 emissions as anaerobic decomposition declines. Under this scenario, it is unclear whether peatlands will become a source or sink. Dried-out peatlands will have accelerated oxidation of organic matter, but reduced emissions of CH_4, whereas waterlogged, collapsed thermokarst basins will accumulate more peat resulting in increased CH_4 emissions (Gorham 1991).

5.2 Changing Disturbance Regimes

Cycles of forest fire and insect outbreak are controlled by weather and the condition of the fuel or host. Both of these factors could be altered by climate change. One possibility is a more rapid buildup of pandemic insect populations as increasing temperatures could cause drought stress in their host tree species as well as shorten insect life cycles. A massive spruce beetle outbreak in Alaska has been attributed to abnormally warm and dry summers since the 1960s (Berg et al. 2006), and similar climatic triggers may be causing the widespread devastation by mountain pine beetle across western North America (Malmstrom and Raffa 2000; Powell and Logan 2005). Indeed, the prospect of future pine beetle and spruce budworm outbreaks caused one model to predict that Canadian boreal forests will be a net source of greenhouse gases in the coming decades (Kurz et al. 2008c).

Climate change may also allow pests that are less cold tolerant to extend their distribution into the boreal zone (Wolf et al. 2008). However, it may also be possible that a warming climate could suppress insect populations under certain conditions. One model predicts that rising temperature without an accompanying rise in precipitation will decrease the area affected by spruce budworm in temperate forests of Oregon (Williams and Liebhold 1995).

There is evidence that fire return intervals have been shortening across the boreal forest during the twentieth century, and this trend could continue (Stocks et al. 1998). Annual area of North American boreal forests burned increased approximately by a factor of three between the 1960s and the 1990s (Kang et al. 2006). One study predicted that Canadian fire return intervals could decline from an average of 150 years to 100–125 years, with significant associated emissions (Kasischke et al. 1995). And just as future rates of photosynthesis and respiration will depend on how precipitation changes in relation to rising temperatures, so too will future fire return intervals (Flannigan et al. 1998; Amiro et al. 2001). It is possible that the most significant impact of rising CO_2 levels in the atmosphere thus far has been an increase in fire frequency, thus altering the boreal forest age-class distribution (Bond-Lamberty et al. 2007).

The potential for altered fire regimes in response to climate change is another topic that will hold implications for the boreal carbon budget. In certain boreal forest-types, climate change is expected to facilitate shorter fire return intervals, which will promote early successional deciduous species (Soja et al. 2007). Because deciduous species accumulate less carbon than spruce stands, a deciduous for coniferous shift in species composition will affect the boreal carbon cycle in many spruce-dominant regions (Kasischke et al. 2010). Additionally, if fire severity changes, more organic matter will be consumed during burn events, subsequently reducing the negative feedbacks associated with Sphagnum moss accumulation and seed germination (Johnstone et al. 2010). Deep thawing would arise in conditions where insulating mosses were removed, and site drainage would likely facilitate drying of the organic layer and subsequently increase fire severity. Newly exposed mineral soils would promote seed germination by different forest species, most likely including light-seeded pioneers (Johnstone et al. 2010).

5.3 Changes in Biome and Forest Type

Some research predicts significant compositional changes within the boreal zone with a changing climate, as well as a shift of its southern border northward with expansion of temperate forests and steppe and invasion of its northern border into the tundra. Some predictions are dramatic: Emanuel et al. (1985) modeled that boreal forests will decrease by 37% if there is a doubling of atmospheric CO_2 concentration. Rising temperatures and degrading permafrost are allowing Siberian pine (*Pinus sibirica*) to invade the understory of larch stands across southern Siberia and Mongolia, and coniferous forests are displacing montane tundra in the mountain ranges of these regions (Soja et al. 2007). In boreal Canada, climate change may make deciduous forest types more competitive (Kasischke et al. 1995), perhaps due to increased fire that favors the hardwood pioneers birch and aspen. A shift to hardwood dominance could change future fire regimes, nutrient dynamics, and even the boreal climate, since the albedo of deciduous forests is higher than coniferous types (Amiro et al. 2006; Goetz et al. 2007). However, caution should be used in predicting major compositional changes through modeling. Models are convenient for parametizing and testing assumptions about complex questions, but the results are only as good as the available data, the assumptions used, and the ability to calibrate and verify the model. Data on feedback between climate and boreal forests are very limited and highly variable, leading to highly variable model results. For example, one model in Alaska predicted that moisture-induced stress would cause the disappearance of existing forest types and their replacement by aspen woodlands (Bonan et al. 1990), but later refinement of the model to include more parameters of biophysical complexity indicated that moisture deficits would likely not reach levels that could cause such widespread mortality (Bonan and Van Cleve 1992).

Compositional changes within the boreal zone could significantly alter carbon dynamics, but conversion of boreal forests to temperate forests, or tundra to boreal forests, could have a greater impact. Such transitions will not be rapid. Rather, the existing community will likely degrade at a faster rate than new vegetation types can invade. During the lag, large CO_2 emissions are possible (Apps et al. 1993). Smith and Shugart (1993) predicted a net carbon loss of 36.6 Pg over a

50–100 year period as other forest types invade the boreal region. The movement of boreal forests into the tundra could greatly increase fuel loads, bringing fire into a system in which it is rare (Kasischke et al. 1995). The impact on soil carbon pools in the tundra is unknown, but concerning. In addition, northward migration of the tree line will change albedo levels in high northern latitudes.

5.4 Albedo Effect

Albedo is not directly related to carbon storage and release; rather, it controls the absorption of heat by the biome. At high northern latitudes, forest cover increases heat absorption because dark conifer crowns have lower albedo (less reflectivity) than light conifers or low, snow-covered tundra vegetation. A growing body of research suggests that light conifer competitiveness is on the wane, and replacement by dark conifers is likely (Kharuk et al. 2009; Lloyd et al. 2011; Shuman et al. 2011). The result of this competitive shift would be a boreal forest that actually exerts a warming influence on regional and global climate, subsequently outweighing their current role as carbon sinks (Betts 2000). The presently high albedo of tundra creates a feedback with the Arctic Ocean, maintaining high levels of sea ice; forest invasion of the tundra zone could alter this interaction, changing dynamics across the entire polar region (Bonan et al. 1995). One modeling exercise that replaced global boreal forests with grass and shrub vegetation predicted a cooling of the earth's climate because of the greater reflectance of these vegetation types (Bala et al. 2007). This research suggests that albedo effects may have a dominant influence on climate at high latitudes. It should be considered, however, that these conclusions are heavily reliant on modeling, and are a relatively recent addition to boreal zone research. At the very least, however, the albedo effect should be considered as a potential balance to any effect that boreal forests may have on slowing climate change through carbon sequestration.

6 Conclusion and Summary Recommendations

Much of the research regarding the impacts of climate change on the boreal carbon budget is based on modeling, and can only predict potential changes.

- Some observations of existing impacts are available, and seem to point toward the potential for greater carbon loss from boreal forests.
- Steadily increasing temperatures across boreal and arctic North America in the past fifty years have been associated with drought-induced growth reductions, permafrost degradation, increased fire frequency, increased soil respiration, and potentially larger outbreaks of insect pests.
- Under increased temperatures, increased respiration associated with rising temperatures seems to outstrip any increases in carbon uptake through growth.
- The possibility of greatly altered carbon dynamics due to permafrost degradation also exists.

However, there is also research suggesting that some of the impacts of climate change may not be as extreme as predicted.

- It is unclear whether increased soil temperatures will cause a sustained increase in carbon release. The pool of labile carbon in the soil may not be large, resulting in only a brief increase in decomposition. While the degradation of permafrost may increase the release of CO_2, it could also result in reduced emissions of CH_4, a potent greenhouse gas.
- Some models also predict an increase in precipitation across much of the boreal zone, which in concert with rising temperatures could cause increased productivity.

Recommendations for further research are necessary particularly on the following topics.

- Understand whether the massive carbon pool in tundra soils would remain intact if converted to a forested biome.
- Concentrate on regions under-represented in global carbon budget projections (e.g. Siberia).

These regions have large uncertainties in estimates of boreal carbon pools.

- Further quantify information about several important carbon pools, including fine root biomass and mycorrhizae, bryophyte and understory layers and coarse woody debris and litter.
- Better understand poorly drained sites, including those found in the larch forests of Siberia, which may be the most vulnerable to soil carbon loss with changes in disturbance regimes and climate.
- Further consider the impacts of fire in boreal carbon dynamics, including extent, frequency, and intensity across the biome; and the interactions among fire intensity, nitrogen, and carbon.

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