

Boreal forest soil carbon: distribution, function and modelling

THOMAS H. DELUCA^{1*} AND CELINE BOISVENUE^{2,3}

¹ SENRGy, 2nd Floor ECW, Bangor University, Bangor, Gwynedd LL57 2UW, UK

² Forest Research Branch, Ministère de resource naturelles et de la faune, 2700 Einstein, Québec, Canada G1P 3W8

³ Present address: 506 West Burnside Road, Victoria, British Columbia, Canada V8Z 1M5

*Corresponding author. E-mail: t.h.deluca@bangor.ac.uk

Summary

Increasing accumulation of CO₂ in the atmosphere has led to calls for terrestrial mechanisms for CO₂ abatement and given that soils represent the largest terrestrial body of C on Earth, there is a great deal of interest in soils as a sink for atmospheric C. This emphasis on sequestration in boreal forest soils is understandable given the sheer mass of this C reservoir (~1700 Pg of C) but diverts our attention from the importance of soil C in soil physical, chemical and biotic functions, and importantly, it ignores the possibility that soils may also represent a source of C. In this review, we address these issues through a discussion of the size and character of boreal forest soil C pool, its role in ecosystem function, the potential impacts of climate change on soil C, efforts to model these processes and the role of soil C in boreal resilience to the impacts of climate change. Soil C is fundamental to ecosystem function in terms of improving soil physical properties, increasing soil biotic activity and enhancing insulation all of which improve site productivity. Managing upland soils for C sequestration will achieve little in terms of offsetting fossil fuel emissions but would likely improve soil quality. Most of the C stored in the boreal biome is found in permafrost and wetland soils and events related to climatic change could shift these soils from C sink to C source. Melting of permafrost soils with predicted warming trends within the circumpolar region could result in the release of 30–60 Pg C by the year 2040. Such predictions, however, are limited by uncertainty in both climatic changes and soil response to these changes. Prediction of shifts in soil C dynamics with climate change relies on our ability to link C transformations to N dynamics and climatic variables. Improvement in ecosystem models will advance our ability to assess the resilience of the boreal biome under future climatic conditions.

Introduction

Concern over C loading of the atmosphere from anthropogenic activities has greatly increased interest in soil as a receptacle for long-term storage of carbon (C) in an attempt to offset C emissions associated with global consumption of fossil fuels. This increased interest in ecosystem C is reflected in the number of articles published on forest C and soil C. The Institute for Scientific Information lists only seven papers indexed on 'forest carbon' in 1979–1980 compared with 4572 papers in 2009–2010 with many of these works focused on C storage or C flux as related to greenhouse gas (GHG) emissions. This C storage focus may be misplaced and has likely led many to ignore the far more important role of soil C as a mediator of soil productivity and sustainability. As a preface to this review, it must be emphasized that soils are far more than an 'ecosystem

service' of C storage. Soils represent a fundamental life support system for terrestrial and aquatic organisms, and in this, capacity will play a vital role in ecosystem resilience to the conditions created by anthropogenically driven climate change. Forest ecosystems will be subjected to a great deal of stress in a changing climate. Changes in the occurrence of temperature extremes, occurrence and extent of wildfires and insect infestation are a few examples of the impacts on forest ecosystems that are being attributed to climatic change (Soja *et al.*, 2006; Raffa *et al.*, 2008; Turetsky *et al.*, 2011).

Building an understanding of the ecosystem C storage potential associated with forest soils is an interesting and important exercise; however, we would argue that this emphasis should be coupled with an effort to further understand the role of soil C in ecological processes that will affect and be affected by climate change. Therefore,

the purpose of this review is to: (1) provide an overview of soil C storage in boreal ecosystems; (2) discuss the distribution of C in boreal forest soils; (3) describe the process of C accumulation in these systems; (4) Discuss the status of current soil C models commonly used in boreal ecosystems in terms of capacity to predict soil C storage, dynamics and loss rates with a changing climate; (5) Discuss the influence of climate change on soil C storage and (6) Describe the role of soil C in the sustainability and resilience of boreal forest ecosystems.

Carbon storage in the boreal biome

Recent studies estimate that one third of total global fossil fuel emissions are taken up by forests (Pan *et al.*, 2011). Forest soils and specifically those of the boreal region are a reservoir for long-term storage of boreal C and a significant contributor to global C storage (Jones *et al.*, 2009) and therefore have the potential to greatly influence the global GHG balance as either a sink or a source. In fact, boreal forest ecosystems account for ~50 per cent, or more, of world forest ecosystem C stocks compared with 14 per cent for temperate and 37 per cent for tropical systems (Malhi *et al.*, 1999). Boreal forest soils also hold more total ecosystem C than is found in the overstory (Havas and Kubin, 1983; Gower *et al.*, 1997; Schultze *et al.*, 1999; Martin *et al.*, 2005). Indeed, soil C in boreal ecosystems has been reported to account for about five times the total C in the standing biomass or ~85 per cent of the total biome C (Malhi *et al.*, 1999). Boreal forests account for ~33 per cent of the total land area of the circumpolar region (Jones *et al.*, 2009), but most of the C stored in high-latitude ecosystems is found within peat bog and permafrost soils (Tarnocai *et al.*, 2009). Of all permafrost soils, about 40–55 per cent are found in boreal forests with the remaining portion found in the Arctic (Allison and Treseder, 2011).

The large mass of C stored at depth in these systems resulted in a focus on boreal forests as C sink (Jobba and Jackson, 2000). Circumpolar forest biomass accounts for approximately 60–80 Pg of total C, whereas upland soils of this biome hold between 90 and 500 Pg C and boreal peatlands hold an additional 260–600 Pg C (Apps *et al.*, 1993; Jobba and Jackson, 2000; Kasischke and Stocks, 2000; Tarnocai *et al.*, 2009; Allison and Treseder, 2011). There is, however, a great deal of variation between studies in terms of depth of soil sampling, differences in soil type and components of forest considered in an ecosystem wide assessment and methods of scaling up individual observations such as root mass.

Historical estimates place high latitude, permafrost soils inclusive of boreal forest and tundra ecosystems at less than 700 Pg of C (Schlesinger, 1997; Kasischke and Stocks, 2000). More recent estimates by Tarnocai *et al.* (2009) suggest that more careful consideration of the surface metre of soil results in greater C estimates (by a factor of nearly two), and the inclusion of subsurface (2–3 m) soils of permafrost zones into global C inventories raise

total C estimates by an additional 20–40 per cent. There is far less C storage per unit area in the non-permafrost portion of the boreal, but the size of the region makes up for the amount contained per unit area in wetland and permafrost soils and together the circumpolar region holds a C mass equivalent to ~1700 Pg total C (Tarnocai *et al.*, 2009; Hugelius *et al.*, 2010). This value is nearly 18 times greater than that stored in the plant biomass of the boreal, emphasizing the important role of boreal and Arctic soils as a long-term reservoir of C. The majority of permafrost soils are located in North America and Siberia (see Figure 1 and discussion below), their distribution can be observed in detail elsewhere (http://www.interboreal.org/global_warming/, <http://nsidc.org/fgdc/maps/>).

Boreal forest soils: carbon distribution and accumulation

Boreal forest soils collectively represent an immature, somewhat sensitive, mosaic of sandy acidic mineral soils and organic rich peat soils of moderate productivity. Being relatively young, they retain a great deal of the mineral content of the parent material; however, low temperatures, surface area (low clay contents) and soil pH result in low-nutrient availability. The importance of soil C in ecosystem function and specifically in the internal physical, chemical and biological processes of soil cannot be overstated (Jurgensen *et al.*, 1997). Soil organic C (SOC) increases soil water holding capacity, cation exchange capacity, soil microbial activity and improves soil aggregation. The benefits of maintained or improved soil organic matter storage in soils and the role that soil organic matter plays in soil resilience to land use change or climate change should not be shrouded by the potential for C storage in forest soils.

Table 1 provides a summary of ecosystem C distribution in some northern temperate and boreal coniferous forest ecosystems providing examples of different forest and land types. Total ecosystem C storage in boreal forests varies by age, structure and stand history, all of which have a great influence on total C storage as reflected by changes in forest biomass, coarse woody debris, forest floor, and to a lesser extent, mineral soil. Mineral soil C (to 1.0 m depth) remains relatively stable and accounts for the majority of total ecosystem C across forest maturity and disturbance regimes. This notion is supported by the data of Stinson *et al.* (2011) which suggest that mineral soils account for nearly 40 per cent of total ecosystem C, while aboveground C accounts for closer to 23 per cent of total ecosystem C.

In this review, soils of the boreal region are described using the soil taxonomic classifications as described in the World Reference Base for soils (International Union of Soil Scientists, 2006). Figure 1 provides a soil map for the circumpolar region and emphasizes the presence of Podzols, Cambisols and Fluvisols, Gleysols, Histosols and Cryosols as the dominant soils of the boreal biome (Fisher and Binkley, 2000; Jones *et al.*, 2009). Podzols and Cambisols make up the majority of upland forest soils throughout the circumpolar region (Figure 1). There are ~4.8 million ha of Podzols in boreal forests

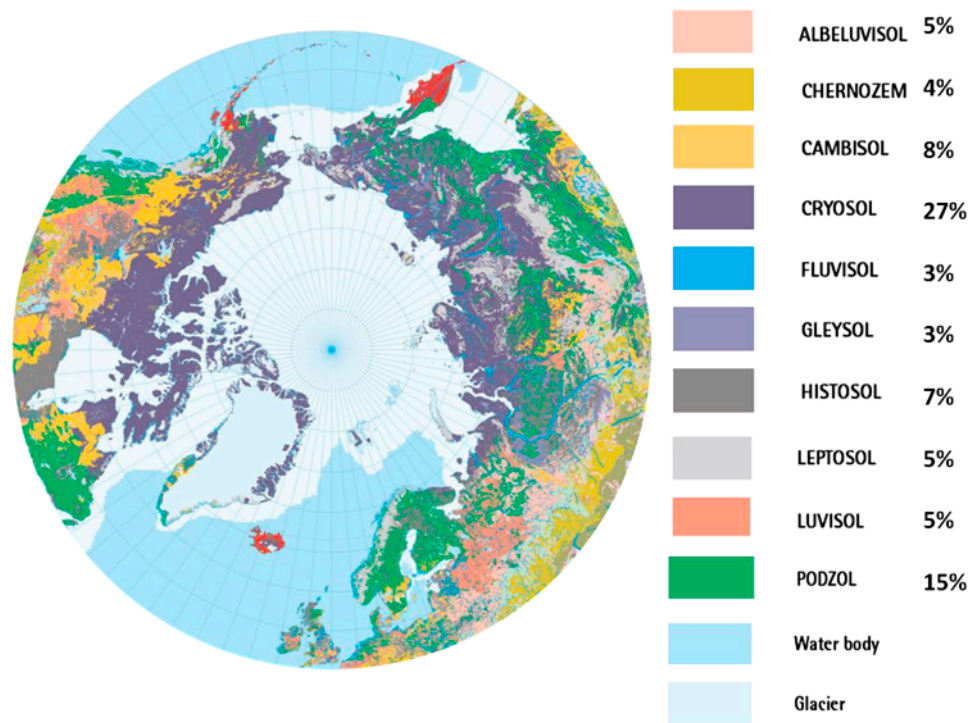


Figure 1. Map of major soil taxonomic groups (FAO World Reference Base) of the circumpolar region. Percentages on legend represent portion of land surface of circumpolar region accounted for by individual soil types that dominate the boreal region. The Map and legend are adapted from Jones *et al.* (2009).

(International Union of Soil Scientists, 2006) which is over 30 per cent of boreal biome and 15 per cent of the circumpolar region. Podzols generally possess a relatively thin, 1–20 cm, surface organic horizon that is characterized by the presence of a litter layer (L or Oi) and fragmentation layer (F or Oe) and often a humus layer (H or Oa) overlying humus poor surface mineral horizons (Fisher and Binkley, 2000; Buol *et al.*, 2003) but often having increasing C accumulation at depth in Bh or Bhs horizons particularly in nutrient poor or periodically saturated soils where organic C decomposition is reduced (Buurman and Jongmans, 2005). Accumulation of C with depth is, however, highly variable and controlled in part by soil texture, climatic influences and environmental influences such as fire frequencies and N deposition. Boreal Podzols have been found to contain less C at depth than nemoral or southern boreal forest soils across Scandinavia possibly as a result of warmer temperatures and differences in N deposition (discussed below) and biomass inputs (Callesen *et al.*, 2003). Cambisols and Fluvisols are less well-developed soils and found predominantly along river corridors, on steep slopes or on particularly resistant or nutrient poor parent materials. These soils lack any significant soil development with depth but can support thick O horizons and organic rich surface horizons.

Carbon distribution in common boreal forest soils is given in Figure 2. In this figure, the limited C accumulation in Cambisols and Podzols (generally well-drained) is clearly demonstrated as is the high level of C accumulation at depth in permafrost soils and histic permafrost soils (poorly

drained). Cambisols and Podzols house 5–40 Mg C ha⁻¹ in the O horizon and about 10–90 Mg C ha⁻¹ in surface mineral soils (0–15 cm). An additional 10–150 Mg C ha⁻¹ at depth (15–45 cm) in upland forest soils, but generally there is little C below 1 m of upland soils in these environments (Rapalee *et al.*, 1998; Berg *et al.*, 2001; Verje *et al.*, 2003; Ping *et al.*, 2010). Subsurface humus accumulation was historically considered to be strictly illuvial (leached into place); however, humus accumulation in the B horizon is highly variable and is the combined effect of translocation, root deposition and vertical mixing (Buurman and Jongmans, 2005). In a survey of over 2100 soil profiles in Sweden, Olsson *et al.* (2009) reported C concentration in the O horizon of 389 g C kg⁻¹; however, the low bulk density and shallow depth (~8 cm) results in a total C density of only 28 Mg C ha⁻¹. Mineral soils in Podzols have a C concentration of ~9 g kg⁻¹ and a C density of 53 Mg C ha⁻¹ resulting in an average profile C density of ~82 Mg C ha⁻¹ (Olsson *et al.*, 2009). Given that there are ~480 million ha of Podzols in boreal forests, these soils store a total of ~39 Pg C in the surface 50 cm of soil.

Histosols, Gleysols and Histic Cambisols of the boreal forest occupy seasonally or permanently saturated soils characterized by the presence of thick carpets of sphagnum or other mosses and the noted accumulation of deep organic horizons often referred to as peatlands. There are over 3 million km² of Histosols in the boreal biome (International Union of Soil Scientists, 2006) accounting for most of the World's wetland soils. An organic horizon by definition contains greater

Table 1: Example of values for total ecosystem C with varied forest stand age and its distribution in different components of boreal and northern temperate forest ecosystems

Stand type	Age (years)	Soil	O horizon	CWD	Overstory	Understory	Coarse roots	Ecosystem C	Source
<i>Picea abies</i>	250	121	2	-	48	1.9	10	183	Havas and Kubin (1983)
<i>Pinus sylvestris</i>	28	11	0	11	8	-	-	33	Schultze <i>et al.</i> (1999)
	36	14	3	28	36	-	-	81	
	383	22	7	10	71	-	-	111	
Mixedwood*	11	52†	44	16	13	0.9	2	127	Martin <i>et al.</i> (2005)
	30	46	33	3	27	0.8	4	115	
	65	53	25	9	50	0.8	9	147	
<i>Picea mariana</i>	155	390	-	6	48	1.1	-	446	Gower <i>et al.</i> (1997)
	115	418	-	3	57	0.9	-	479	
<i>Pinus banksia</i>	65	28	12	2	23	5.7	-	68	
<i>Populus tremuloides</i>	67	97	16	6	56	0.6	-	176	
<i>Pinus sylvestris</i>	75	133	34	-	70	-	12	249	Yuste <i>et al.</i> (2005)
<i>Larix occidentalis</i>	200	76	24	20	144	0.2	41	305	Bisbing <i>et al.</i> (2010)
	40	61	50	11	24	0.4	6	98	
Range	11–383	11–418	0–44	1–28	8–144	0.6–5.7	2–41	68–479	
Mean	109	109	17	10	48	1	12	187	
SE	29	36	4	2	9	0	4	38	

CWD = Coarse woody debris.

* Mixedwood stand is dominated by *Betula papyrifera*, *Larix laricina*, *Picea mariana*, *Picea glauca*, *Pinus banksiana*, *Populus balsamifera* and *Populus tremuloides*.† Soil depths: 30 cm (Martin *et al.*, 2005); 70 cm (Gower *et al.*, 1997); 1 m (Havas and Kubin, 1983; Schultze *et al.*, 1999; Bisbing *et al.*, 2010).

than 200 g ka⁻¹ of organic matter or 120 g organic C kg⁻¹ but often are in excess of 500 g C kg⁻¹ (Gorham, 1991) yielding values of 100–150 kg C m⁻² when measured to depths of greater than a metre depth (Rapalee *et al.*, 1998). Although Histosols account for only ~5 per cent of the boreal biome they house about 270–450 Pg C (Gorham, 1991; Turunen *et al.*, 2002) which is a majority of total C stored within soils across the boreal (Rapalee *et al.*, 1998).

There are ~16.6 million km² of Cryosols or permafrost soils in the circumpolar region accounting for 22 per cent of the boreal and Arctic landscape (Schuur *et al.*, 2008). Most of the permafrost soils found in the boreal biome reside in western Siberia (Kasischke and Stocks, 2000). Cryosols are also often enriched in organic C to depths of more than a metre (Bockheim and Hinkel, 2007; Tarnocai *et al.*, 2009) and are thought to hold 1024 Pg of C to a depth of 3 m (Tarnocai *et al.*, 2009). Permafrost soils accumulate organic C as a result of anoxia from wet conditions and from cold temperatures which retard decomposition rates (Buol *et al.*, 2003; Hugelius *et al.*, 2010; McGuire *et al.*, 2010). Carbon distribution in permafrost soils varies with depth depending on the type of surface mineral soil or surface organic horizons, with as much as 30 per cent of the total soil profile C existing at depths of 2–3 m (Tarnocai *et al.*, 2009). Tarnocai *et al.* (2009) reported the greatest C accumulation per unit area in all major soil groups within the circumpolar north as being found in Cryosols formed in alluvial sediments.

Forest succession and C accumulation

Soil development initiates with the exposure of geologic strata following redeposition (alluvial, eolian, colluvial), glacial retreat (till) or draining of lake basins and the establishment of pioneer plant communities often composed of bryophytes, lichen and a limited number of small vascular plants which eventually give way to N fixing herbs and shrubs such as *Alnus* spp, *Hippophae* spp. and *Dryas* spp (Chapin *et al.*, 1994). Once N capital is accumulated, then non-N-fixing shrubs and birch or aspen trees begin to dominate the overstory shading out the light demanding N fixing trees and shrubs. Pine and spruce species often succeed birch and aspen and spruce ultimately reaching a retrogressive stage in the absence of disturbance (Peltzer *et al.*, 2010). Carbon content of the mineral soil and O horizon tend to increase linearly in early primary succession (Kasischke *et al.*, 2000; Kimmins, 2003) and plateaus in late succession (Figure 3) potentially declining in a retrogressive (late successional decline in productivity and diversity) stand (Wardle *et al.*, 2008). Responses to disturbances may lead to a decrease in net annual productivity and SOC and N pools and an increase in respiration (e.g. Chertov *et al.*, 2009). The intensity and frequency of disturbance, be it fire, insects, windthrow or prolonged drought, which are themselves closely related to climate variables, leave no doubt as per their influence on forest C dynamics (Kurz *et al.*, 2008; Running, 2008; Chertov *et al.*, 2009). Across much of the boreal, fire functions as a fundamental disturbance process that consumes the

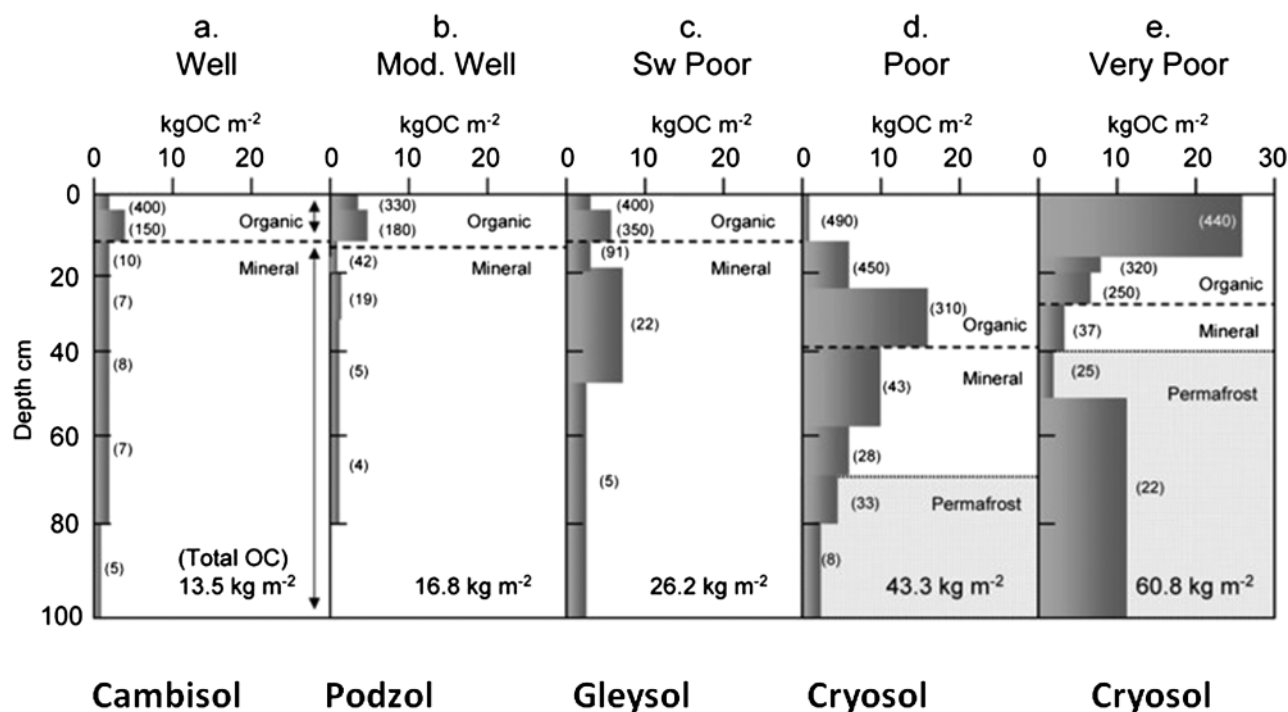


Figure 2. Soil organic C distribution with depth in common boreal forest soil types representing upland well-drained soils to poorly drained permafrost soils. Bars represent C content for horizons up to a depth of 1 m (from Ping *et al.*, 2010, reprinted with permission from Soil Science Society of America).

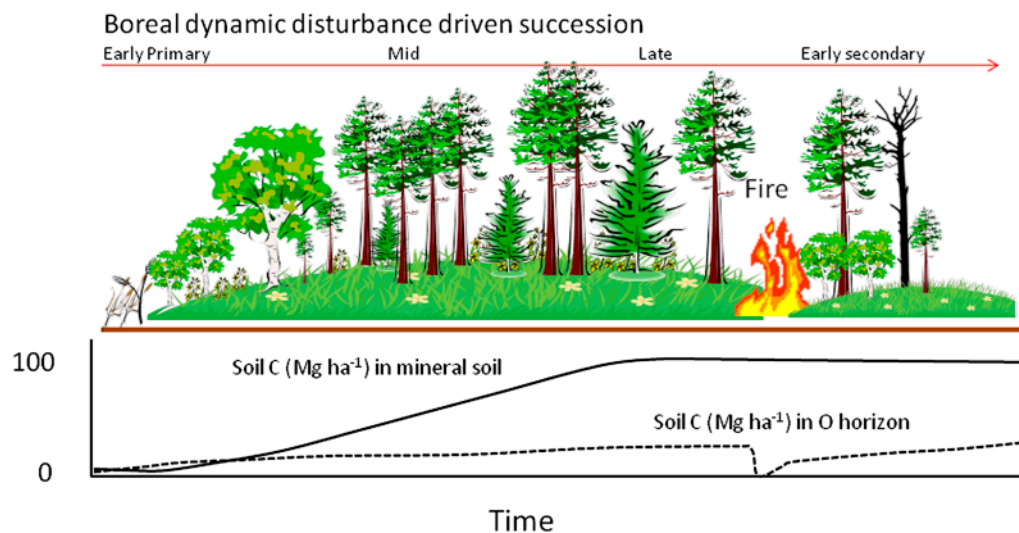


Figure 3. A hypothetical schematic diagram of the change in C density in the O horizon and mineral soil with time since inception or disturbance in succession in boreal forest ecosystems.

understory and moss bottom layer along with a portion of the humus pool and with a significant portion of the total C stored in the O horizon (Kasischke and Stocks, 2000) and partially resets the successional clock (Engelmark, 1999) with mineral soil C remaining greatly unchanged (Seedre *et al.*, 2011).

Mature boreal forest ecosystems of North America are dominated by black spruce (*Picea Marianna* Mill BSP), white spruce (*Picea glauca*), Jack pine (*Pinus banksiana* Lamb.) and lodgepole pine (*Pinus contorta*). Western Eurasian boreal forests are dominated by Scots pine and Norway spruce (*Picea abies*). After fire events, pioneer

species establish including bryophytes (e.g. *Polytricum*), grasses (*Deschampsia flexuosa*), herbs (e.g. *Ebolobium*) and trees (*Betula*, *Populus*, *Picea*). In North America, black spruce, lodgepole pine in the west and Jack pine in the east are normally killed by crown fires leaving the forest to regenerate via germination of the serotinous cones associated with these species or open to 'invaders' such as white spruce and aspen (Bourgeau-Chavez *et al.*, 2000). In northern Eurasia, Scots pine forests are more likely to survive fire events but also experience establishment of various birch species as an early successional invader. In North America and in Eurasia, feather mosses re-establish during the 20–50 years following fire and bring with them the capacity to accumulate N through their cyanobacterial associates (DeLuca *et al.*, 2002). In instances where permafrost forms under the insulating layer of feather moss, sphagnum may succeed the feather mosses, further reducing soil temperatures and increasing rates of accumulation of organic matter (Kimmins, 2003).

Nitrogen fixation in feather moss communities after fires is an important ingredient in maintaining forest in fire-maintained ecosystems (DeLuca *et al.*, 2002) and is therefore essential for the re-accumulation of C. Recurrent fire on an excessively short interval has the potential to result in a net loss of N from the ecosystem and may inhibit ecosystem recovery after fire (DeLuca and Sala, 2006). Timing of fire also influences the amount of C consumed in surface fire events as fires during early summer will generally consume far less C than fires in late summer due to the dry conditions allowing for greater organic matter combustion (Kasischke *et al.*, 2000). Fire frequency in boreal ecosystems is greatly dictated by climatic conditions. Fire return intervals in boreal ecosystems have been found to range from 70 to 150 years in interior portions of Europe (Zackrisson, 1976, 1977), Russia, Alaska (Johnstone *et al.*, 2010) and Canada (Kasischke and Stocks, 2000) with fire suppression extending this range to 400 years in parts of Canada (Bergeron *et al.*, 2009).

About 10–15 million ha of boreal forest burn annually in boreal forests of Canada, Russia, Alaska and Europe (Flannigan *et al.*, 2008). This is a relatively small area considering that ~650 million ha of Savannah and ~250 million ha of tropical forests burn each year (Levine and Cofer, 2000). Only ~20 per cent of the vegetative biomass and less than 50 per cent of the humus layer are consumed (Lynch *et al.*, 2004) in wildfire events. These 10–15 million ha of boreal forest exposed to wildfire on an annual basis release ~270 Tg of C each year (Levine and Cofer, 2000). Climate change will likely increase fire severity and occurrence across the boreal biome (Flannigan *et al.*, 2008) and with these changes, there will be an increase in total annual C emissions (Turetsky *et al.*, 2011).

Approximately 10 per cent of the woody biomass consumed by fire is converted to charcoal, a uniquely stable form of C with mean residence times measured in thousands of years (Figure 4) as opposed to months for twigs and small stems (DeLuca and Aplet, 2008). This stable form of C is often not accounted for when evaluating the influence of fire on total C storage in soil ecosystems.

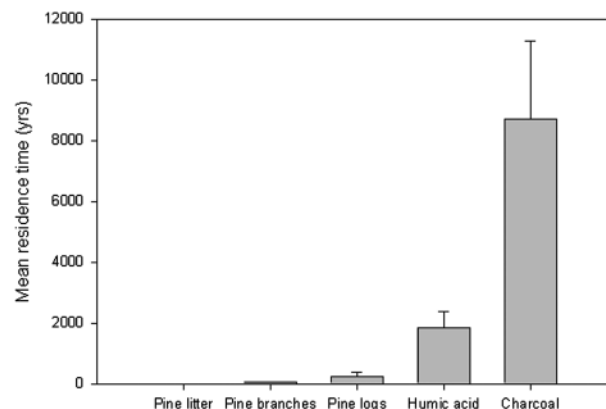


Figure 4. Mean residence time for litter, twigs, stems, logs, humic acid and charcoal (adapted from DeLuca and Aplet, 2008).

Interestingly, charcoal commonly accounts for approximately 500–1000 kg C ha⁻¹ in the O horizon of boreal forest soils with estimated mean ages of 600–2000 years old (Zackrisson *et al.*, 1996; Ohlson *et al.*, 2009). The quantity of charcoal accumulated in mineral soil depends upon numerous factors including the severity and frequency of fire dictated by whether there is an opportunity for charcoal to be mixed from the surface O horizon into the mineral soil prior to the next fire (Gavin *et al.*, 2003). Much of the charcoal left in the forest floor during a fire may actually be consumed in subsequent fire events limiting its total accumulation in fire maintained ecosystems. Charcoal that is buried by pedoturbation (from mixing organisms, tree tip, frost dynamics) is far more likely to be preserved in soils for millennia (Gavin *et al.*, 2003). Landscape position appears to greatly influence charcoal accumulation in the O horizon and surface soils, likely owing to microclimatic influences on the occurrence of fire on the landscape (Kane *et al.*, 2010). While more frequent fire on south slopes has been shown to increase charcoal occurrence in surface soil (Kane *et al.*, 2010), studies on permafrost soils in Siberia indicate that charcoal accumulation is greater in cooler organic rich north facing slopes than dry south facing slopes, perhaps again as a result of charcoal consumption in recurrent fire events (Guggenberger *et al.*, 2008). To date, modelling efforts have not effectively accounted for charcoal generation in long-term C accounting in boreal forest systems; however, charcoal can account for 1–50 per cent of total C in mineral soil C of boreal forest surface soils (DeLuca and Aplet, 2008; Guggenberger *et al.*, 2008).

Timber harvest results in the removal of forest biomass for the production of woody products, paper products or biomass energy. This removal results in an immediate short-term loss of C from the forest environment, but most of the forest biomass is recaptured once the forest reaches maturity (Jandl *et al.*, 2007). Harvesting of timber resources from these environments on a rotation that outpaces nutrient regeneration rates will ultimately lead to long-term

declines in productivity (Thiffault *et al.*, 2011). The forest floor is consistently reduced with forest harvest (Nave *et al.*, 2010) but recovers relatively rapidly. Timber harvest often has little direct influence on mineral soil C stocks (Martin and Bolstad, 2005; Jandl *et al.*, 2007; Nave *et al.*, 2010; Seed *et al.*, 2011). Some of the C put into durable woody products has the potential to be stored in that state for tens to hundreds of years (Nunery and Keeton, 2009), but it must be kept in mind that approximately 25–50 per cent of the forest C can be rapidly emitted during slash pile burning and burning of mill residues and more slowly lost during decomposition of forest residues in soil or as woody products post-consumer in the landfill (Ingerson, 2008).

While boreal wetland soils accumulate C at a rate of about 20–30 g C m⁻² year⁻¹ (Gorham, 1991; Rapalee *et al.*, 1998), draining of wetland soils to facilitate timber production also directly and indirectly influences total C storage in these high C systems. Between the 1960s and 1980s, over 15 million ha of wetlands were drained for forest management purposes across boreal regions with 70 per cent of this practice taking place in Finland, Russia and Sweden (Minkinen *et al.*, 2008). Although draining of peatlands can increase short-term C emissions, drainage can also increase vascular plant productivity, root growth and soil C storage resulting in a net increase in C storage per unit area (Minkinen *et al.*, 2002). Furthermore, draining of boreal forest peatlands may reduce phenol oxidase activity (an enzyme system responsible for the oxidation of complex, polyphenolic organic materials) resulting in slowed rates of decomposition of peat which was aerated following drainage (Toberman *et al.*, 2010). These increases in net C storage, however, do not take into account the potential increase in boreal forest fire events and consumption of organic materials in drained peatlands (Turetsky *et al.*, 2011). Drained peatlands would likely function more like the upland sites in study described Turetsky *et al.* (2011), resulting in deeper burning of organic materials than undrained peatlands.

Carbon cycling and boreal forest soils

The C cycle in the boreal biome primarily differs from temperate forests in that the C turnover rates are limited by cool temperatures and a relatively short frost-free season. Carbon fixation, accumulation, turnover and release are all slowed by the cool temperatures at these northern latitudes. Litter decomposition reactions generally follow first order kinetics (Tate, 1995) and generally adhere to the Arrhenius equation (temperature effect on reaction rate), wherein reaction rates approximately double with every 10°C change in temperature (Craine *et al.*, 2010) except at temperatures less than 5°C upon which decomposition departs from Arrhenius relationships. Soils of the boreal region generally fall into Cryic (mean annual temperature (MAT) < 8°C, but no permafrost) or Pergelic (MAT < 0°C) temperature regimes. The MAT for soils across the boreal range from -10 to +3°C, in contrast, MAT for soils of temperate coniferous forests range from 5 to 10°C and trop-

ical forest systems from 15 to 25°C (Schlesinger, 1997). In addition to cool temperatures, boreal litter forest litter tends to be composed of phenol rich substrates that are relatively resistant to decomposition (Nilsson *et al.*, 2008). These factors reduce rates of litter decomposition and increase rates of soil organic matter accumulation. Most of the C accumulates as surface organic matter as a result of the acidic litter types and poorly drained forest conditions. Importantly, organic matter decay is influenced by temperature and oxygen contents including moisture, soil physical properties, substrate quality (recalcitrance of litter) and nutrient availability (Stevenson and Cole, 1999).

Temperature controls and forest C cycling

Temperature is a dominant driver of organic matter decomposition rates in soil environments. Temperature regulates C accumulation through direct controls on microbial activity and indirect controls on moisture and substrate quality. In the temperature range expected in boreal forest soils, microbial decomposition increases exponentially with increasing temperature, thus the cool annual and seasonal temperatures experienced in the boreal results in slow rates of organic matter decomposition. Carbon accumulation in boreal ecosystems is inversely related to temperature and is generally described by the following simple equation:

$$L_t = L_0 e^{-kt} \quad (1)$$

Where L_t = litter remaining at time t , L_0 = initial litter input, t = temperature and k = the decay constant for litter assuming one rate of decay. Mean residence time refers to the time required for litter to completely decompose under steady state conditions and can be described by $1/k$. More complex models incorporate a second constant for the microbial uptake of litter carbon and turnover of microbial tissue (Tate, 1995). Both single and double compartment equations demonstrate the direct role of temperature in dictating decomposition rates but also greatly oversimplify the myriad of factors controlling C decomposition rates and CO₂ emissions.

Indirect effects of temperature on decomposition rates include soil drying as influenced by heat input and conversely moisture accumulation with reduced evaporation rates under cool temperatures. Waterlogged conditions (described below) greatly retard decomposition rates as a result of restricted oxygen conditions. Freezing and thawing of soils and litter layers result in the rupture of cell walls and the physical disintegration of leaf litter (Skogland *et al.*, 1988; DeLuca *et al.*, 1992). This commonly results in a stimulation of microbial activity and a net release of soluble organic C and N, which is available for net mineralization or leaching (DeLuca *et al.*, 1992; Grogan *et al.*, 2003). Increased moisture conditions created during snow melt and thawing of subsoils during thaw result in an increase in nitrous oxide emissions associated with the respiratory burst after thaw (Skogland *et al.*, 1988; Teepe *et al.*, 2000).

Decreasing temperatures result in a decrease in vegetative C production and total net primary productivity (NPP)

with increasing northerly latitudes (Chapin *et al.*, 2002) which reduces litter fall, root exudation and root turnover. All these factors yield less C input per unit time in boreal soils. In spite of minimal biomass production in Arctic tundra, cold temperatures and seasonally oxygen-limited conditions slow decomposition rates and result in C accumulation levels in these soils that rivals the soil C contents of boreal or temperate forest ecosystems (Tarnocai *et al.*, 2009; Hugelius *et al.*, 2010).

Carbon accumulation in the soil environment is greatest under water-saturated conditions but is not nearly so sensitive to dry soil conditions as compared with C inputs associated with NPP. Drying and rewetting cycles enhance substrate decomposition similar to freeze thaw effects (Fierer and Schimel, 2002). Drying of soils results in cell mortality and subsequent release of C available for decomposition once soils are rewetted (Miller *et al.*, 2005). Repeated drying and rewetting of soils may reduce each subsequent pulse of respiration with rewetting (Fierer and Schimel, 2002). In boreal ecosystems, drying cycles are common during summer months and likely play a significant role in dictating net C efflux from soil.

Creation of saturated soil conditions through excess rainfall, melting of snowpack or physical impediments to drainage results in slowed decomposition rates. Initially, saturated conditions slow oxygen diffusion to soil microbes, pushing the microbial community to conduct oxidative decomposition using alternative electron acceptors and reducing the efficiency of decomposition (Tate, 1995). Ultimately saturated conditions result in anoxic conditions under which fermentation pathways are emphasized and decomposition rates slow and result in accumulation of acids and alcohols that further slow decomposition rates. This partially explains the great degree of C accumulation in low lying peatlands and bogs in boreal ecosystems; however, of equal or greater importance is the presence of sphagnum mosses that dominate areas with shallow water tables throughout the Boreal (Halsey *et al.*, 2000). Sphagnum species 'paludify' soils through the production of a recalcitrant acidic biomass that reduces the presence of other litter types (Simard *et al.*, 2009). Draining of peatlands and wetlands potentially releases large quantities of peat C (Gorham, 1991), but as discussed above, may also lead to a net increase in C storage due to collapse of peat strata, increased forest productivity and reduced long-term decomposition rates (Minkinen *et al.*, 2008).

Influence of substrate quality on soil C accumulation

Substrate quality refers to the ease with which organic materials are degraded in the soil ecosystem. Boreal forest litter is generally of relatively poor quality and the associated soils are inherently C rich and exhibit low nutrient availability, especially N. Substrate quality is dictated by two primary factors: (1) The recalcitrance of organic compounds that make up the material (e.g. lignin or phenol contents); (2) The nutrient content, and in particular, the N and P content of the matter (Prescott *et al.*, 2000; Berg and McCaughey, 2008). Litter in boreal forests originates predominantly from stems, branches, twigs and needles of

coniferous trees and the stems and waxy leaves of ericaceous plants. The forest floor is then carpeted by feather mosses which are known to have high C : N (C to N ratio) for an herbaceous plant and generate particularly recalcitrant litter. The C : N of labile materials (such as manures or herbaceous plants) is a good indicator of decomposition potential (Stevenson and Cole, 1999). However, in the phenolic rich, recalcitrant litter of the boreal forest, C : N alone is often a poor predictor of decomposition rate (Prescott *et al.*, 2000). And while initially lignin : N has been identified as a more suitable predictor of N mineralization rates from litter (Scott and Binkley, 1997), incubation experiments have suggested that lignin : N may be a poor predictor of litter decomposition, especially where more labile substrates are involved (Taylor *et al.*, 1989). During litter decomposition, phenolic compounds are liberated which then complex with proteins to form secondary compounds of limited bioavailability (Hattenschwiler and Vitousek, 2000; Gundale *et al.*, 2010). This process confounds attempts to predict litter decomposition. Combining of climatic variables with litter N content and indices of litter recalcitrance may be the most effective means of predicting litter decomposition rates; however, further work is necessary to better capture litter quality estimates.

Similarly, rates for organic matter within the mineral soil are at least partially dictated by substrate quality (Stevenson and Cole, 1999; Hartley and Ineson, 2008). The decomposition of non-humic materials such as sugars, amino acids, peptides and proteins is extremely rapid compared with more recalcitrant materials (chitin, waxes and lignin). Humic materials (humic acid, fulvic acid and humin) and char represent uniquely stable materials with half-lives of hundreds of years. The labile fraction drives short-term microbial activity where the stable forms of organic matter represent long-term C storage. It should be emphasized that mineral soil organic matter C : N is a poor predictor of decomposition rates due to the high humic matter content of soil organic matter and the relatively high N content of humic materials. Therefore, soil organic matter quality must be described by the complementary presence of both humic and non-humic materials.

Enzyme kinetics indicate that the temperature sensitivity of decomposition increases with increasing recalcitrance of litter (Craine *et al.*, 2010). This is also described as the C quality-temperature hypothesis. Ecological adherence to this hypothesis was recently supported in several studies (Craine *et al.*, 2010; Karhu *et al.*, 2010; Wetterstedt *et al.*, 2010). The findings of Craine *et al.* (2010) clearly support the notion that recalcitrant litter (lignin and hemicelluloses) and soil organic matter (humic materials) will be most sensitive to increasing temperatures with climatic change. However, some studies are less clear on this issue and may actually counter claims of higher temperature sensitivity for more recalcitrant substrates (Fissore *et al.*, 2009). In other studies, soil substrates in boreal forests were found to be highly temperature sensitive (Karhu *et al.*, 2010). These researchers reported that soils of boreal regions could lose 30–45 per cent more C with warming

conditions in the near future assuming no increase in vegetative C input. This is of great importance because existing attempts to predict C loss with warming conditions often assume a single temperature sensitivity for all organic matter fractions which could greatly underestimate C emission rates from a region of extremely high C density (see subsequent section on modelling).

Effects of climate change on soil C storage

Observed changes

The fourth assessment report (AR4) of the Intergovernmental Panel on Climate Change (IPCC) unequivocally shows that the environment in which forest have developed in the recent past, conditions that drive forest dynamics, have changed and will most probably change more drastically in the future (IPCC, 2007). The United States' National Ocean and Atmosphere Administration measurement records at Mauna Loa show a sustained increase in CO₂ concentrations (HI – <http://co2now.org/> – Keeling and Whorf, 2002), a major contributor to the greenhouse effect, and temperatures are following suite (Hansen *et al.*, 2010). As previously mentioned, atmospheric N deposition also contributes to changes in forest soil C dynamics (Ashmore, 2005; Höglberg, 2007) and anthropogenic contributions of N to the atmosphere are increasing along with CO₂ concentrations and temperature. These changes have direct and indirect impacts on boreal forest C content. Forests have already responded to these environmental changes with many study areas showing an increase in productivity (Boisvenue and Running, 2006).

There is much speculation regarding the consequences of these changes on forest soil C, including the potential for large C release into the atmosphere from boreal systems and the effects of such a release on the global C budget (e.g. Bellamy *et al.*, 2005). Different forest systems will have different responses to these changing conditions with some forests projected to become C sources to the atmosphere even without considering disturbances (Boisvenue and Running, 2010). Observed responses to the major global change drivers are somewhat conflicting. In general, well-documented single-factor forest productivity responses have included higher photosynthetic rate (the main CO₂ response), increasing length of growing season (the main temperature response) and higher leaf-area index (the main N deposition and partly CO₂ response) (Hyvonen *et al.*, 2007). All these factors would directly impact soil C dynamics: higher photosynthesis affects total litter inputs, litter quality and fine-root production. Increases in growing season length will increase time for C turnover with higher soil temperatures and consequently, all physiochemical processes and higher leaf-area index will again influence litter quality and quantity. Other findings show a pattern of insensitivity to climate for global net ecosystem productivity (NEP = NPP – heterotrophic respiration) (Luyssaert *et al.*, 2007) attributing changes in forest NEP to non-climatic conditions, such as successional stage,

management, site history and site disturbance and not to CO₂ and/or changes in temperatures and/or N deposition. Millard *et al.* (2007) found forest growth to not be C-limited, and as such, forests would not respond to CO₂ increases, contradicting the general increase in productivity described above. The divergence in findings may in some cases be credited to differences in scale of study or variables measured, but mostly, divergences seem to point to some missing understanding in forest soil C processes. More multifactor experiments and simulations (in which process and observations are linked) are needed to quantify these responses to climate change.

Feedback loops

The partial loss to the atmosphere of the enormous C pool contained in boreal forest soils as a result of poor land management, melting of permafrost and large-scale fire events could create a highly damaging feedback loop in which increasing warming would fuel increasing loss of boreal C to the atmosphere (Fan *et al.*, 2008). It has been estimated that by 2100 (doubling of atmospheric CO₂), the globe could experience a net loss of as much as 9 million km² of permafrost soils as a result of thawing and drying of permafrost resulting in an increase in CO₂ evolution (Schuur *et al.*, 2008) and a temporary increase in CH₄ emissions (Lawrence and Slater, 2005; Allison and Treseder, 2011; Koven *et al.*, 2011). This equates to a net release of more than 100 Pg C from the melting of permafrost (Schuur *et al.*, 2008). Relatively conservative estimates of 20 per cent increase in CH₄ emissions have been proposed for permafrost soils exposed to a 2–3°C increase in air temperatures at northern latitudes (Anisimov, 2007). In a recent survey of permafrost researchers, Schuur and Abbott (2011) suggest that the combined impact of CO₂ and CH₄ release upon thawing of permafrost soils of the circumpolar region could be between 30 and 63 Pg C (CO₂ eq) by the year 2040. These are potentially extremely important figures for boreal ecosystems, permafrost or discontinuous permafrost soils make up 40–55 per cent of the boreal biome (Allison and Treseder, 2011) and beg the question of the long-term impacts of such feedbacks on global climatic change (Schuur and Abbott, 2011).

Currently, there is little or no collective agreement on the amount and time of the likely C release from these soils with the melting of permafrost. Conversely, the sheer scale of boreal biome C causes many to consider the capacity of this system to absorb the burden of fossil fuel emissions by trading forest ecosystem C for future fuel consumption (i.e. carbon credits). In the short-term, forests may be identified as C sources or sinks and up to now for boreal forests, recent disturbance history determines if a forest is a sink or source (Bond-Lamberty *et al.*, 2007). A young forest, growing some years post fire or harvest or land clearing yields a net sink (Fahey *et al.*, 2010; Stinson *et al.*, 2011). In contrast, a forest exposed to a recent insect infestation or fire event would be a C source (Kurz *et al.*, 2008). Regardless, boreal forest ecosystems are often identified as potential C sinks or systems that can take on additional C, based on estimates of C accumulation in biomass and soils

(Myneni *et al.*, 2001; Ågren *et al.*, 2007). Negative feedbacks have been described wherein increased CO₂ loading of the atmosphere and N deposition would increase NPP and long-term C storage (Magnani *et al.*, 2007). However, the extent and duration of the productivity increase with CO₂ fertilization from anthropogenic C emissions or N deposition is unclear and the associated C storage in forests or forest soils more so (de Vries *et al.*, 2006; Bonan, 2008; Janssens *et al.*, 2010; Silva *et al.*, 2010). To date, disturbance and time since disturbance seem to determine if a boreal forest is a C sink or source, and mature forests C fluxes hover around zero from year to year. However, in the case of melting permafrost soils, the shift from sink to source has clear implications for a positive feedback loop that enhances C loss with increasing greenhouse gas emissions from the permafrost soils (Koven *et al.*, 2011).

Based on the previously stated control that temperature exerts on decomposition rates and on soil C in general, another possible positive feedback process is that the projected temperature increase would be reinforced by additional CO₂ emissions from soils owing to rising temperature which would increase decomposition and consequently respiration, releasing CO₂ (rising CO₂ is a precursor to rising temperatures). Many studies have explored this possibility but no consensus has yet arisen (Jenkinson *et al.*, 1991; Cao and Woodward, 1998; Cox *et al.*, 2000; Davidson *et al.*, 2000; Giardina and Ryan, 2000; Fang *et al.*, 2005; Knorr *et al.*, 2005; Powlson, 2005). The potential extra C emissions from forest soils in response to increases in temperatures could come from either plants or microbial respiration (Bond-Lamberty and Thomson, 2010).

Respiration is difficult to estimate which most probably contributes to much uncertainty around projections of the effects of climate change on forests. Theoretical models on the effects of temperature on respiration often conflict with observations (e.g. Chen *et al.*, 2010). Our understanding of soil respiration (represented in our models) has to date maintained a tight relationship between temperature and respiration (e.g. Q10). However, synthesis data now seem to show that respiration is not as sensitive to temperatures as previously thought (Mahecha *et al.*, 2010). Perhaps, autotrophic and heterotrophic respiration in forest soils differ in their responses to temperature and precipitation change as indicated by Wei *et al.* (2010) and Lavigne *et al.* (2003). Microbial activity (heterotrophic respiration) has been shown to eventually reach a threshold with increasing temperatures and to grow more slowly beyond this threshold (Allison *et al.*, 2010) and hence temperature increases alone would not stimulate soil C decomposition (Giardina and Ryan, 2000), as was initially predicted. There appears to be a missing cog in the decomposition cycle, perhaps it is the pinion of precipitation-, vegetation- or possibly specific-microbial community factors (Balser and Wixon, 2009; Angel *et al.*, 2010; Muhr *et al.*, 2010) that are presently being considered that would help explain the discrepancy in research findings on the effects of climate change on forest ecosystem respiration.

In addition to this missing multiple factor interaction, productivity changes, including increased litter production are predicted to occur with the changing climatic condi-

tions (Liu *et al.*, 2004) which may trigger the mineralization of organic C in deep soil layers (Fontaine *et al.*, 2007). Mineralization of soil organic matter plays a key role in supplying essential nutrients for plant growth (Zhang *et al.*, 2009) and may itself function as a feedback to the already changing level of productivity. But as with many (and previous) interesting findings, other results temper these findings. For example, Feng *et al.* (2008) showed that warming could alter soil organic matter at the molecular level, accelerating lignin degradation and increasing leaf cuticle-derived C sequestration. Combinations of *in situ* temperature, precipitation level, specific vegetation and its productivity and microbial community seem to give each site a specific context and site-specific responses to changing conditions (Crow *et al.*, 2009). Furthermore, studies in boreal black spruce forests suggest that warming does not seem to affect gross primary productivity (GPP) or above-ground respiration, both of which are directly related to soil C emissions (Bronson and Gower, 2010). Generally, if increases in plant-derived C inputs to soils exceed increases in decomposition, the feedback would be negative (forest soils store more C) and the reverse would result in a positive feedback (more C to the atmosphere), for example increased levels of disturbances would create a positive feedback.

In 2008, global emissions of fossil fuel C were ~8.8 Pg C year⁻¹ (Myhre *et al.*, 2009). The expansion of temperate and boreal forest ecosystems back into glaciated landscapes resulted in the net accumulation of 500–1350 Pg of C on the Earth's surface (Malhi *et al.*, 1999), leading many to consider these ecosystems as net sinks for the burning of fossil fuel C. Current knowledge shows these ecosystems may be functioning in a long-term dynamic quasi-equilibrium where, in the absence of disturbance, production nearly matches respiration resulting in an insignificant potential sink for human releases of fossil fuel C (Schlesinger, 1997). Forests are dynamic systems and any increases in storage are reversible, and land management that leads to increases in C storage may lead to increased losses of other greenhouse gasses. Changes in climate may already have changed the equilibrium of boreal systems, and projections of climatic conditions point towards increased emissions. Therefore, it is unlikely that any large quantity of current C emissions could be sequestered into boreal ecosystems as a net additional sink for fossil fuel C.

As Davidson and Janssens (2006) point out, unravelling feedback effects is particularly difficult because the diverse soil organic compounds exhibit a wide range of kinetic properties, which determine the intrinsic temperature sensitivity of their decomposition. Moreover, controls over observed temperature responses, as opposed to the intrinsic temperature response of decomposition, may themselves be sensitive to climate. Until a consensus emerges on the temperature sensitivity of soil carbon decomposition, continued research efforts must be sustained.

Nitrogen

Nitrogen is the primary limiting nutrient in boreal forest ecosystems (Tamm, 1991), a condition that remains true

today in spite of increases in atmospheric N deposition associated with anthropogenic pollution (LeBauer and Treseder, 2008). Nitrogen fertilizer amendment studies in semi-natural boreal forest ecosystems generally result in an increase in plant productivity and thus increased litter inputs and in some instances increased belowground C inputs (Tamm, 1991). There is no real consensus on whether increased N deposition associated with anthropogenic pollution will sustain increased productivity associated with long-term increases in N deposition (Magnani *et al.*, 2007; de Vries *et al.*, 2008; Janssens and Luyssaert, 2009).

Increasing N deposition in the presence of CO₂ enrichment has been reported to lead to increased forest productivity in boreal and temperate forest ecosystems (de Vries *et al.*, 2006, 2009; Magnani *et al.*, 2007; Janssens and Luyssaert, 2009; Quinn *et al.*, 2009), which is likely a consequence of increased photosynthetic C inputs to soils accompanied by no net change or a decrease in heterotrophic respiration (Fog, 1988; Janssens *et al.*, 2010). The cause of a decrease in respiration rates with N enrichment may be somewhat counter intuitive, as a decrease in lignin : N should yield an increase in litter decomposition similar to a decrease in C : N (Scott and Binkley, 1997). However, the decline in decomposition is likely related to shifts in the decomposer community or potentially due to an increase in the production of N-polyphenol complexes (Janssens *et al.*, 2010). The influence of N-enrichment on shifts in soil C storage appear to be less pronounced in more northern forest ecosystems (de Vries *et al.*, 2006) although all species with mycorrhizal fungi association in the north-east and north central US seem to benefit from increase N inputs of the 80s and 90s (Quinn *et al.*, 2009). It is important to note that long-term trials involving high rates of N enrichment demonstrate an eventual decline in forest response to N (Högberg *et al.*, 2006). Also important to consider is the fact that N deposition rates across the boreal biome remain relatively low compared with temperate forest ecosystems of North America and Europe (Bobbink *et al.*, 2010; Gundale *et al.*, 2011). Hence, either boreal specific experiments and/or monitoring over time are needed to determine the effects of increased N deposition on the boreal system.

Part of the controversy surrounding the impacts of increased CO₂ concentrations and increasing temperatures might be partially explained by N₂ fixation in boreal ecosystems. As previously noted, feather mosses and sphagnum peat mosses cover the forest floor of most boreal ecosystems. Both moss types harbour N₂ fixing cyanobacteria creating a niche for N₂ fixation in an otherwise hostile (temporally dry or excessively wet) environment (DeLuca *et al.*, 2002). Although N₂ fixation in individual moss shoots is relatively low, collectively, the mosses provide the vast majority of fixed N in secondary successional boreal forests (Zackrisson *et al.*, 2004). In N enrichment conditions, early succession forests (our best C absorbers) have shown a rapid cycling of N resulting in increased through-fall N deposition, which in turn decreased the N fixation by cyanobacterial associates in feather moss carpets that reside on the forest floor (DeLuca *et al.*, 2008). This down-

regulation thereby buffers inputs from anthropogenic sources (Gundale *et al.*, 2011).

Forest soil C models

The main motivators for the elaboration of forest soil carbon (C) models are: (1) the scientific need for understanding C-related processes in forest soils and linkages across scales (soil ↔ ecosystem ↔ physical environment) and (2) quantifying ecosystem C stores. These are not mutually exclusive. In case 1, models permit us to account for the multiple processes across scales of time and space, furthering our understanding of the system. The complexity of the processes involved in soil C accumulation make it difficult to develop accurate models, however, our need to predict process outcomes requires that we create models based on our current understanding of processes. Models certainly oversimplify the dynamism of forest ecosystems and they are unable to perfectly emulate natural phenomena as a result of our limited understanding of forest soil processes compounded by the complexity and variability of the system.

The development of models in case 2 is now being fuelled by established international requirements for national C budgets that include changes in soil and litter C (United Nations Framework Convention of Climate Change (UNFCCC)–LULUCF, Kyoto Protocol (UNFCCC, 1997, 1998)). The UK (Bellamy *et al.*, 2005), Sweden (Stahl *et al.*, 2004) and Belgium (Lettenens *et al.*, 2005) are some of the few countries that have large-scale forest soil C inventory databases that can satisfy these C budgeting requirements and the UK in particular includes forest land across the UK countryside (Chamberlain *et al.*, 2010). Most models use a mix of mathematical representation of process and empirical approaches. Large uncertainties in empirical data make it difficult to parameterize exceedingly sophisticated models. The level of sophistication in models varies tremendously and mostly according to their intended applications and application scale. In this section, we give an overview of the types of forest soil C models that can be found in the scientific literature in two arbitrary categories: process and empirical.

Process models

Models based on our understanding of biogeochemical and ecological exchanges in forest soils or on interactions among forest vegetation, soils, the underlying geology and geomorphology and the atmosphere are referred to as process models. Some forest soil process models represent an ensemble of processes and interactions; others represent specific processes such as decomposition and respiration, while others represent whole ecosystems including soils. Table 2 provides a partial list of existing soil process models that are used to predict soil C dynamics.

Most forest soil-specific process models either require vegetation turnover estimates as inputs from above and below-ground live biomass components or produce their own turnover estimate. For example, Wutzler and Mund (2007) uses

Table 2: List of models containing varying degrees of process-based representation of soil carbon dynamics

Model name	Main reference	Soil specific?	Modelling goal	Decomposition drivers	Other processes	Soil depth
YASSO	Liski <i>et al.</i> (2005)	Yes	Soil C dynamics in forestry appl.	Litter, climate	None	100 cm
CENTURY	Parton <i>et al.</i> (1993)	Yes	Organic matter dynamics	Litter, climate, soil texture, C : N	N and other nutrient dynamics	0–20 cm
ROMUL	Chertov <i>et al.</i> (2001)	Yes	Soil organic matter	Soil biota, litter, climate data,	N cycling	100 cm
RothC	Coleman and Jenkinson (1996)	Yes	Soil C turnover	Litter, climate, soil biota	None	100 cm
Biome-BGC	Thornton (1998)	No	Atmosphere and ecosystem exchanges	Water, temperature	Mass and energy exchange, light interception, drainage and run-off, snow dynamics, evaporation and evapotranspiration, photosynthesis, N uptake, C allocation, plant mortality	User defined
SMART2	Kros <i>et al.</i> (2002)	Yes	Soil acidification	Soil biota	Nutrient cycling	User defined
PATCIS	Saiz <i>et al.</i> (2007)	Yes	CO ₂ production and transport	Water, temperature, soil biota	None	User defined
Ecosys	Grant <i>et al.</i> (2006)	No	Representation of all processes in ecosystems	Water, temperature, soil biota	Photosynthesis, mass and energy exchange, water and energy transfer, plant growth, solute and gas transfer, microbial activity, management activities	User defined
FORECAST	Kimmins <i>et al.</i> (1999)	No	Forest management effects	Set quantitative curves by litter type	Plant growth, nutrient cycling, light competition, plant mortality	User defined
N/A	Kutsch <i>et al.</i> (2010)	Yes	Respiration	Litter, climate, photosynthesis, mycorrhiza	None	60 cm
SOILN	Eckersten <i>et al.</i> (1998)	Yes	N cycling	Other model estimates	Physio-chemical processes	N/A
Q-model	Ågren and Bosatta (1987)	Yes	C and N dynamics in soils	Litter, climate, soil biota	Physio-chemical processes	N/A
Soil OC	Fan <i>et al.</i> (2008)	Yes	Post fire soil C dynamics	Differential equations of isotope decay	None	User defined
SMART2	Wamelink <i>et al.</i> (2009)	Yes	Soil chemistry with atmospheric deposition	Climate, available nutrients	Nutrient cycling	User defined
Forest-DNDC	Li <i>et al.</i> (2000)	No	Environmental impacts on ecosystem	Climate, litter, soil texture and acidity	photosynthesis–evapotranspiration, N cycling	User defined
3-PG	Landsberg and Waring (1997)	No	Forest management effects	Constant NPP to GPP ratio	Light interception, photosynthesis, C allocation, tree mortality	User defined
CBM-CFS3	Kurz <i>et al.</i> (2009)	No	Forest C accounting	Annual temperature and precipitation	Growth, C allocation, disturbances	N/A

N/A = not applicable.

yield tables as a source of foliage turnover. Litter is often qualified in soil models by its ease of decomposition (e.g. lignin or cellulose content, lignin to nitrogen (N) and C to N ratios). Smith (2001, 2002) reviews the representation of decomposition processes in different soil organic matter (SOM) models. Decomposition rates, based on litter input and quality, are either a function of temperature (e.g. Q10 as in Biome-BGC (Thornton, 1998)) or of the type of micro flora or fauna on site (Kros *et al.*, 2002) or both (e.g. PATCIS model, Saiz *et al.*, 2007). Some models detail physio-chemical processes (humification, aggregation, sorption-desorption, hydrophobicity) and/or detail enzymatic processes (e.g. 'Ecosys', Grant *et al.*, 2006), while some follow individual elements such as C, N, P, S and/or K (e.g. FORECAST, Kimmins *et al.*, 1999). Virtually all forest soil C models provide some means of estimating soil respiration, and some models are specific to respiration (e.g. Kutsch *et al.*, 2010). A few models provide a very coarse scale description of biological control: ROMUL regulates the translocation of SOM between soil layers with soil biota (Chertov *et al.*, 2001) and decomposition in SOILN (Eckersten *et al.*, 1998) and Q-model (Ågren and Bosatta, 1987; Ågren *et al.*, 2007) is controlled by microbial biomass.

Two models emerge as the most widely used and published forest soil models, YASSO (Tuomi *et al.*, 2009) and CENTURY (Parton *et al.*, 1993). ROMUL (Chertov *et al.*, 2009) and RothC (Jones *et al.*, 2005) also have a high-frequency occurrence in the literature but not as wide of an application as YASSO and CENTURY for forest soils. All four of these models are commonly linked to vegetation or ecosystem models and all four models have been used to provide large-scale C balance estimation.

YASSO is a SOM decomposition model developed in Finland specifically for forestry applications (Liski *et al.*, 2005). YASSO models SOC to a depth of 100 cm (organic and mineral layers). The model requires estimates of litter quantity and chemistry as inputs. Decomposition rates depend on litter chemistry, litter diameter, temperature and precipitation. YASSO has been used all over Scandinavia (e.g. de Wit *et al.*, 2006), Switzerland (e.g. Thürig and Kaufmann, 2010) and in parts of North America (e.g. Johnson *et al.*, 2010). Figure 5 provides a conceptual representation of the YASSO model (Liski *et al.*, 2005).

CENTURY was initially developed for grassland system (Parton *et al.*, 1987) and has since been modified to apply to forest systems (e.g. tropical, subtropical (Cerri *et al.*, 2004; Lopes *et al.*, 2008; Shrestha *et al.*, 2009), western north American pines (Smithwick *et al.*, 2009) and boreal forests (Nalder and Wein, 2006)). CENTURY simulates active, passive and slow SOM pools between 0 and 20 cm depth and has five live biomass pools, and while decomposition rates are modified by temperature and moisture, each SOM pool decomposition rate relies on different variables; the slow and passive pools similarly use lignin to N and C to N ratios to determine decomposition, while the active pool rate relies on soil texture. When calibrated for the same sites, YASSO and CENTURY gave comparable projections of SOC under repeated and various harvesting scenarios for hardwoods sites in the Green Mountains

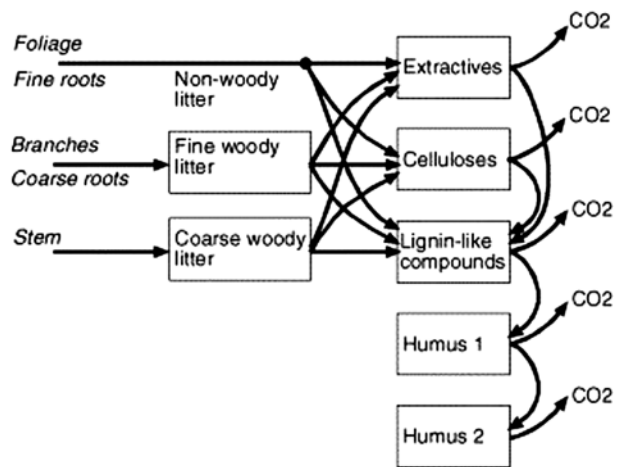


Figure 5. A conceptual flow chart of the Yasso Model. Boxes represent individual carbon compartments and the arrows represent carbon fluxes (reprinted from Liski *et al.*, 2005, with permission from Elsevier).

of Vermont (Johnson *et al.*, 2010). Differences are mostly traceable to each model's representation of soil C dynamics (e.g. CENTURY maintains C to N ratios in soil compartments). SOC estimates from both models are sensitive to litter input and both models have been extensively tested.

Many other soil-specific process models exist, ROMUL and RothC are popular models, but the list goes on: PATCIS is a one-dimensional process-based model (Fang and Moncrieff, 1999) that simulates production and transport of CO₂ in soil (e.g. Hui and Luo, 2004; Saiz *et al.*, 2007); SOC dynamics (Fan *et al.*, 2008) is a model used for post-fire soil C modelling based on work by Carrasco *et al.* (2006) who looked at both short- and long-term C accumulation in boreal forest soils using multi-isotopes (¹²C, ¹⁴C); SMART2 a soil chemistry model developed by Kros *et al.* (2002) and used by Wamelink *et al.* (2009) for soil acidification which together simulate soil chemistry as affected by atmospheric deposition. All models perform best when used in the context for which they were developed.

Whole ecosystem process models represent soil processes with varying complexity. Forest-DNDC (Li *et al.*, 2000), BIOME-BGC (Thornton, 1998), Mixfor-3D (Olchev *et al.*, 2009) and CoupModel (Svensson *et al.*, 2008) are among those of somewhat higher complexity and model climate (with atmospheric interactions), vegetation and soils. Although soil compartments within these process models are quite simple relative to the complexity of the system they attempt to emulate, they do represent C and N cycling, decomposition and weather interactions in forest soils. With less atmospheric detail but still representing C and N cycling are: FORCCHN (Yan and Zhao, 2007), SIMA (Alam *et al.*, 2008), SAFED (Yarie, 2000), CANDY (Franko *et al.*, 1995), LINKAGE (Post and Pastor, 1996) and a model by Larocque *et al.* (2006). The model FORECAST (Kimmins *et al.*, 1999) follows a longer list of nutrients and is of similar complexity level as the later models. All the above models incorporate some representation of

respiration. The models FORESEE (Lasch *et al.*, 2005) and 3-PG have no N cycling component, and 3-PG only represents respiration by an NPP/GPP ratio (Landsberg and Waring, 1997), although some modifications have been published that incorporate N cycling (3-PGN, Xenakis *et al.*, 2008) and respiration (Nole *et al.*, 2009).

Among the most complex published ecosystem model is Ecosys (Grant *et al.*, 2006). In Ecosys, the key biological processes controlling N₂O generation – mineralization, immobilization, nitrification, denitrification, root and mycorrhizal uptake (with microbe functional types) are coupled with key physical processes – convection, diffusion, volatilization, dissolution controlling the transport of gaseous reactants and products of these biological processes. Ecosys models the population behaviour of destructor groups (microorganisms, fungi and soil micro- and mesofauna) and their interactions with mycorrhiza. Such models are valuable for fundamental science but are cumbersome to apply due to the high number of difficult to estimate parameters (Komarov, 2008).

Carbon budget models such as CBM-CFS3 (Kurz *et al.*, 2009) which is a C accounting model used by Canada for international reporting purposes, represent another category of models. Its soil C compartments are stabilized through modelling iterations (similarly to Biome-BGC), it models decomposition (using Q10 and mean annual temperatures and precipitation) but has no N cycling representation other than the release of N₂O from forest fire. CBM-CFS3 is partially a process model but driven by growth curves, which facilitates the link with forest management data and makes it extremely useful for carbon accounting in managed forests. In its present form, is only partially sensitive to changing environmental conditions.

Global C models that attempt to model vegetation dynamics, atmosphere–biosphere interaction or global C budgets increasingly incorporate soil representation. For example, IBIS (Liu *et al.*, 2005), a global-scale model, incorporates a simple N-cycling representation. Most global models have one pool for SOM (e.g. AVIM model for China, Ji, 1995; PnET for US Aber *et al.*, 1995), but some represent soils much like whole ecosystems models with many pools for SOM and give SOC estimates (e.g. GTEC, King *et al.*, 1997; LPJ and DyN, Haxeltine and Prentice, 1996; Xu and Prentice, 2008). The mere incorporation of simple representation of soil C dynamics in the global C models was a giant leap forward. As the spatial resolution increases, models can incorporate more processes and increase the complexity of the process representation. The state-of-the-art modelling approach, when looking at process-based models, is mostly scale and goal dependent. For forestry applications, YASSO and CENTURY seem to perform the best, and they are increasingly used in data assimilation contexts.

Empirical models

Models are rarely completely process based nor are they fully empirical. There are models at the empirical end of this continuum that use statistical methods to expand

field measurements over a large land base. For example, the USA Forcarb model (Smith and Heath, 2002) estimates SOC with statistical models from the STATSGO database (http://dbwww.essc.psu.edu/dbtop/doc/statsgo/statsgo_info.html). Tate *et al.* (2005) similarly estimated soil C for New Zealand; Grimm *et al.* (2008) used an imputation method to estimate SOC and C stocks of Barro Colorado Island (Panama canal), Martin *et al.* (2009) provided SOC estimates empirically from quadratic equations for the Canadian Great Lakes region, and Bellamy *et al.* (2005) provided soil C estimates for Wales and England from a sampling plan. There are few systematic large-scale belowground C measurements, inhibiting good statistical estimates. Regression methods have also been used to estimate respiration from landscape data (e.g. Tang *et al.*, 2005; Verbeeck *et al.*, 2006) and Chen *et al.* (2010) used regression to provide global respiration estimates from a meta-analysis of respiration estimates. Other examples of empirical soil respiration models at different scales include Li *et al.* (2010), Abnee *et al.* (2004), the C-Fix Remote Sensing Model (Verstraeten *et al.*, 2006) and Yuste *et al.* (2005).

From a practical perspective empirical models are generally simpler than process models and easier to use, and they may, in certain cases, give similar results (e.g. Hui and Luo, 2004). If for an intended application, processes are poorly understood and no temporal or spatial projections are needed than empirical models, which are usually simpler, may be the best choice. They do not, however, generally advance our understanding of the forest system the way process models do and they are not appropriate for use under changing environmental conditions. For temporal projections or for spatial projections outside the data range, process representation provides valuable constraints to the modelling system, while fitting the model (or parameters) to actual data grounds the projections in reality. Empirical representations of soil C may be improved by a link to process representation, as suggested by Vargas *et al.* (2010). This is evident by the increasing practice of linking various data sources with empirical methods to provide soil C estimates (e.g. Lecoate *et al.*, 2006) and to link process models with field and experimental datasets. Kuchment *et al.* (2006) and Zobitz *et al.* (2008) use data assimilation techniques to estimate parameters for their model from flux-tower data. In Willams *et al.* (2005), the authors demonstrated why data assimilation techniques – which combine stock and flux observations with a process model – improve estimates of and provide insights into ecosystem C exchanges.

Fortunately, linkages at other scales can also expand our potential for better modelling and may provide cross-scale C estimates. CENTURY, which already compared relatively well with eddy-flux measurements (Kirschbaum *et al.*, 2007), has been linked to satellite data and forest inventory systems (Potter *et al.*, 2008), providing a potential for wide application. Liski *et al.* (2006) provided countrywide C estimates with a combination of YASSO and aggregated forest inventory data, and Peltoniemi *et al.* (2006) combined forest inventory, models of biomass and turnover and YASSO for large-scale C estimates. Post *et al.*

(2001) proposed a combination of process-based models and multiple data sources including flux-tower measurements, forest inventory data and soil measurements, for better countrywide C estimates. Even at the global modelling scale model data linkages seem to be more and more common (e.g. LPJ constrained by satellite data, [Smith et al., 2008](#)) and soil-specific process models such as CENTURY are increasingly used to represent the soil portion of the modelling system (e.g. in [Piao et al., 2009](#)).

Given the present availability of models, model choice must take into consideration the intended application, the level of understanding of soil processes at that scale, the specific model representation of that understanding and input data availability. In comparison to agricultural systems, little calibration data are available for soil C content in forests systems. A model that requires easily available input data will at least function to its full potential. Previously, difficult to obtain input data (e.g. rooting depth, recalcitrant carbon fraction) is becoming more and more available as forest soil databases expand and new measurement methods are used. For example, soil bulk density estimates, which are needed to convert organic C content to mass of organic C per unit area, have shown potential to be estimated via remote sensing ([Moreira et al., 2009](#)), and [Sankey et al. \(2008\)](#) measured soil texture via remote sensing. For international obligations and policy development, the choice if model should be a function of its ability to interact with disturbances and land use change and represent their impacts.

Model findings

Models have helped to identify the main drivers of change in soil C in the recent past. According to simulations using the model InTEC (soil modelling portion based on CENTURY), climate was the biggest driver of the increase in total soil C content during 1901–2000 simulations for Canada, followed by CO₂ fertilization and N deposition ([Page-Dumroese and Jurgensen, 2006](#)). In the later part of the century (1981–2000), the same study shows that CO₂ fertilization was the biggest driver of the increase in soil C, while climate change caused soil C to decrease. For Europe, the model RothC attributes soil C changes of the recent past to N deposition and predicts that CO₂ concentrations will become the main driver of change in soil C ([Milne and Oijen, 2005](#)). Forest-DNDC simulations for southwestern China indicated the importance of temperature and precipitation for soil C ([Lu and Cheng, 2009](#)), and the effect of this interaction on soil respiration rates was also apparent in other systems using other models (e.g. PATCIS Sitka spruce—[Saiz et al., 2007](#)). However, in the NE USA forests, the variability in precipitation and light was more influential on soil C than temperatures ([Medvigy et al., 2010](#)), and [Smith et al. \(2006\)](#) maintains that while climate change will be a key driver in soil C dynamics, changes in age class structure and land use will have a much greater effect on forests soil C.

Modelling studies seem to show that controls are system specific. For example, unlike more temperate ecosystems, one of the key mechanisms involved in C preservation in

boreal soils is the cooling of subsurface soil layers as soil depth increases rather than increasing recalcitrance in subsurface soils ([Carrasco et al., 2006](#)). The initial spike in respiration followed by stabilization with increase in soil temperature (discussed previously) is also apparent in some modelling simulations ([Eliasson et al., 2005](#)) even without a representation of changes in soil microbes populations which act as a major point of C transfer between plants and soil ([Drigo et al., 2010](#)).

Models have also been useful for figuring out the relative effects of change: they may not point to the same absolute value but they generally agree on trend directions and relative change. A number of modelling studies show ecophysiological responses to be minor (but not negligible) compared with the potential impact of changes in disturbance patterns ([Kurz et al., 2008](#); [Negrón-Juárez et al., 2008](#); [Raffa et al., 2008](#); [Grant et al., 2009](#)).

Carbon flux over the next century will reflect complex relationships between climate and its influence on the physiological and physio-chemical responses, age structure and disturbance-recovery patterns of the landscape ([Smithwick et al., 2009](#)). Models that can manipulate multiple conditions are needed ([Wullschlegel and Strahl, 2010](#)). Many modelling exercises show that under IPCC future climate scenarios, specific forests become more productive and increase their soil C content (e.g. Europe's boreal and temperate forests with RothC ([Milne and Oijen, 2005](#)), forests of north eastern China with CENTURY (TRIPLEX) ([Peng et al., 2009](#)), black spruce forests of central Canada with EFIMOD ([Chertov et al., 2009](#)), Finnish forests with SIMA ([Alam et al., 2008](#))), while others show decline in soil C (e.g. European Mediterranean forests with RothC ([Milne and Oijen, 2005](#)), forests of the northern USA Rockies with Biome-BGC ([Boisvenue and Running, 2010](#))). Both the predicted warmer temperatures and the increased CO₂ concentrations are generally associated with decreases in forest soil C (e.g. [Weslien et al., 2009](#)). Modelled responses to disturbances are essential for quantifying potential impacts and consequently, adaptation scenarios. Patterns in the boreal are still unclear; recent studies show an increase in mortality ([Peng et al., 2011](#)) across the boreal but their findings are based a very few plots.

Until our understanding of the system improves and our capacity to accurately quantify processes and include some data links expand, model users must understand the consequences of the structure of the model they are using and how this affects model simulations results. The simplification of reality chosen for each model can have dramatic implication for modelling the effects of environmental changes on soil C ([Wutzler and Reichstein, 2007](#)). Factors such as the depth of soil temperature measurements ([Wei et al., 2010](#)) and modelling of rooting depth, turnover and C and N cycling at depth ([Iversen, 2010](#)) can dramatically alter model simulation results.

Boreal soil carbon and ecosystem resilience

Beyond C storage, wetlands, peat ecosystems and boreal forests serve a multitude of important ecosystem functions

including purification of water, creation of habitat and generation of a historically valuable resource. In a healthy forest stand, soils are often completely overlooked, however, when the standing timber in a forest is killed by drought, fire or insects; the role of soil in forest ecosystem resilience becomes that much more evident. Soil provides a buffer against aboveground impacts (e.g. insulation against heat transfer during fire, water storage during drying conditions, absorption of inhibitory compounds) and is the very foundation of the forest seed bank thereby providing the starting point for post-disturbance secondary succession. Soil organic matter enhances water holding capacity, ion exchange capacity, provides microbial refugia and soil tilth and is a reservoir of fertility all of which function to aid in the establishment and growth of a regenerating forest (Jurgensen *et al.*, 1997). To soil scientists, ecosystem ecologists, farmers and devoted land stewards, soils play a pivotal role in general ecosystem function. However, the vast majority of papers published on soil organic matter today are focused on the role of organic matter in ecosystem service of C storage. While a focus on C storage is generally benign, a lack of recognition of the broader value of soil C logically alleviates any pressure to manage for organic matter if the value of soil C in the greater ecosystem balance is deemed unimportant or unpredictable as a source or a sink.

Soil C serves to improve soil condition thereby increasing the resilience and long-term sustainability of forest ecosystems. Chapin *et al.* (2010) recently characterized the vulnerability of boreal Alaskan ecosystems to the impacts of climate change. They defined vulnerability as the degree to which a system is likely to change due to an applied stress. In contrast, resilience can be defined as the capacity of the system to maintain its function, structure and feedbacks in the face of warming associated with climate change. In the case where the resilience of an ecosystem is exceeded, transformation may occur that pushes the system into a new state that exhibits unique properties and characteristics (Chapin *et al.*, 2010). The resilience of boreal ecosystems to the impacts of anthropogenic climate change is directly and indirectly linked to soil organic matter pools and the role they play in forest ecosystem processes. Soil organic C simultaneously represents a fundamental feature of a resilient ecosystem and a display of vulnerability of forest ecosystems to climatic feedbacks in the form of C release potential. The very capacity for boreal forest systems to store C makes them a target for C offsetting and a threat of massive C emissions.

As previously indicated, a warming climate across the boreal will have the potential to greatly alter the nature of boreal forest soils through increased decomposition rates or increases in the occurrence and severity of disturbances. Perturbation, in the form of timber harvest, fire, insect kill all have the potential to temporarily shift the forest floor to a net C source and clearly the thawing of permafrost associated with climate warming may result in the evolution of an enormous mass of stored C. Conversely, pollution in the form of N deposition may increase the rate of soil C accumulation even with no net increase in biomass production associated with increasing N input. The loss of forest

floor and humus layer in upland Podzolic soils threatens the potential for these soils to facilitate regeneration. We are obliged to protect these C reserves to avoid positive feedback effects, protect soil resource sustainability and help maximize the resilience of boreal ecosystems to the impacts of climate change.

Process models that have been developed to simulate ecosystem C dynamics with specific relevance to soils are being used to predict the response of soil organic C pool to perturbation or climatic warming. They are essential for the continued stewardship of these ecosystems and to monitor the effects of the C exchanges in this system on the global C budget. They can also be used to evaluate the resilience of natural and managed ecosystems to the impacts of global climatic change. Such predictions are valuable from a planning or management perspective, but more importantly, they serve to identify knowledge gaps that can be partially addressed through empiric research.

Even though models are simplifications of reality, they can serve as a platform to incorporate the increasingly available data on climate change responses. Boreal forest soils are diverse and their responses to changing environment will also be diverse. Consequently, to be able to anticipate effects of changing conditions, our analyses need to be flexible. The use of remote sensing may not only help in providing previously difficult to obtain data but also provides a means to scaling-up modelling results, another important challenge of the forest soil C modelling research field.

Conclusion

The boreal biome accounts for ~17 per cent of the worlds terrestrial land mass, but accounts for more than 30 per cent of total terrestrial organic C with the majority of this C residing in the soil environment. It is unlikely that the boreal biome will function as a long-term sink for anthropogenic increases in C emissions; however, climate change may ultimately lead to large increases in C emissions from soils at northern latitudes. Melting of permafrost soils and warming of surface soils will lead to increased C emissions that will likely outstrip increases in biomass production. Permafrost soils of the circumpolar region alone could emit 30–63 Pg of C (CO₂ equivalent) by the year 2040, the equivalent of 4–8 years of fossil fuel emissions at today's rates. This potentially daunting feedback emphasizes the importance of boreal soils in dictating the future rates of greenhouse gas emissions in becoming more of a source than as a sink for C. The same concerns go for the increasing occurrence of boreal forest fires and shift from C sink to source. Thus, we believe that the emphasis placed on C storage in soils and forests as a means of offsetting the C emitted by fossil fuel consumption is misplaced and may ultimately prove damaging if assumptions are made regarding ecosystem C sinks that prove to be C sources.

As emphasized in this review, soil C represents so much more than a potential CO₂ source or sink, it improves physical and chemical soil properties and it represents the very currency of life and the basis of all energy transfer between

soil organisms. Forests must be managed to minimize disturbance of soils in a manner that may enhance losses of soil organic matter. This will enhance ecosystem productivity, increase resilience to climate change and reduce C feedbacks that further enhance C loss. Process models allow us to predict soil organic C losses but we presently lack a clear understanding of all the processes involved in forest soil C dynamics. Currently, this incomplete understanding of forest soil C dynamics and linkages to other cycles and responses to different disturbances all contribute to what we consider an over simplification of forest soil representation in models as a 'C reservoir.'

Effective modelling of these processes dictates our ability to predict future C dynamics and feedbacks. Data-model combination studies and data-assimilation techniques (combining process and empirical data) seem to provide an opportunity for combining both the information content of field and experimental data and the acquired understanding of processes. This may be the mechanism by which we might dispel the old paradigm that process models are generally not suitable for operational applications. Data-assimilation techniques that combine process models and empirical data also provide a means to quantify uncertainty in both the model and the data and make possible a realistic evaluation of the resilience of the boreal system. Accurate prediction of shifts in soil C dynamics with shifts in N limitation or C recalcitrance (including the presence of charcoal in the mineral soil) will ultimately require a clear and empirically founded simulation of the link between C transformations and N limitations and transformations in boreal ecosystems. This improved capacity to predict soil C dynamics will allow us to assess the role of soils and soil C in the resilience of boreal forest ecosystems to the impacts of anthropogenic climate change.

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Conflict of interest statement

None declared.

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