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The role of fire in the boreal carbon budget

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Abstract

To reconcile observations of decomposition rates, carbon inventories, and net primary production (NPP), we estimated long-term averages for C exchange in boreal forests near Thompson, Manitoba. Soil drainage as defined by water table, moss cover, and permafrost dynamics, is the dominant control on direct fire emissions. In upland forests, an average of about 10–30% of annual NPP was likely consumed by fire over the past 6500 years since these landforms and ecosystems were established. This long-term, average fire emission is much larger than has been accounted for in global C cycle models and may forecast an increase in fire activity for this region. While over decadal to century times these boreal forests may be acting as slight net sinks for C from the atmosphere to land, periods of drought and severe fire activity may result in net sources of C from these systems.

Keywords: boreal, carbon, decomposition, fire, forest, soil

Introduction

Boreal systems contain one of the largest carbon reserves in the world (Post *et al*. 1982; Gorham 1991; Chapin *et al*. 1993) and include vast regions of wetlands, forests, and permafrost. Boreal wetlands are renowned for both their areal extent and carbon density (Gorham 1991; Chapin & Mathews 1993). Both forested and wetland systems are underlain by permafrost, which is susceptible to cycles of degradation (thermokarst) and aggradation (Thie 1974), the cycles of which have in some cases been related to the occurrence of fires (Zoltai 1993). In better-drained uplands, boreal forests are known for the size and intensity of wildfires, which play a defining role in the establishment of the forested ecosystems (Payette 1992). The occurrence of discontinuous permafrost, large fires, and thermokarst wetlands are clues to an interaction among climate, fire disturbance, hydrology, and ecosystem structure.

Fire disturbance in the boreal region may become increasingly important to the global carbon budget, because climate is changing in a region where carbon reserves are large and where fire disturbance dominates the distribution of plant and soil carbon. Fire disturbance

in North America's boreal forests was higher in the 1980s than in any previous decade on record (Murphy *et al*. 1999). Concurrently, annual surface temperatures have increased by about 5 °C over the past 30 years in Alaskan boreal and arctic regions (Lachenbruch & Marshall 1986), in the Canadian boreal (Beltrami & Mareschal 1994) and in North America in general (Oechel & Vourlitis 1994). Moreover, the prospect of summer drought, indicated by recent trends in Alaska (Wotton & Flannigan 1993), threatens an increase in fire occurrence. Although it is unclear whether the changes documented in climate records have forced or are forcing changes in fire activity, changes in fire disturbance in these C-rich systems are likely to result in profound changes in C exchange.

In North America and western Russia, most fires occur as crown fires (Stocks & Kauffman 1997) which have high intensity and severity. In addition, these fires are large in areal extent, which may be related to the large fuel loads that accumulate in the moss-rich forest floor (Stocks 1991). Crown fires are generally stand-replacing fires, and the most dominant coniferous species propagate their seeds by high-temperature fire conditions (serotinous cones). As a result, forests in these regions tend to be of a single age and have a limited number of tree species. Eurasian forests, by contrast, typically have milder ground fires and are of mixed age and mixed

species. In all boreal regions, deciduous species such as birch (*Betula*), poplar (*Populus*), willow (*Salix*) and alder (*Alnus*) occur, usually after fire disturbance, in single stands or in mixtures with coniferous species. In North America, most pine species are found in well-drained, commonly sandy soils (Nalder & Wein, 1999). In the more poorly drained landscapes throughout the boreal forests, black spruce dominates over pine and in mixtures with birch and aspen. In some regions, aspen may be more likely than spruce to replace severe fires (Dyrness *et al*. 1986**),** while black spruce is likely to replace itself after milder fires.

Boreal forest fires have only recently been considered to be of potential importance to the global carbon cycle. Biomass burning in the tropics, largely stemming from savanna and forest conversions, are thought to greatly outweigh (by 10-fold) the emissions generated by boreal forests (Crutzen & Andreae 1990). However, wildfires in boreal forests appear to show tremendous interannual variation in both area burned and severity of burning; fire emissions may be greater than previously assumed or may be on the increase since the turn of the century. For example, in the 1980s in Canada, 10 times more land area burned than in any previous decade on record (Murphy *et al*. 1999). Estimates of fuel consumption and fire severity also vary greatly (Kasischke *et al*. 1995b). Implications for dramatic shifts in fire disturbance, whether interannual or interdecadal, involve not only direct C emissions but also shifts in stand-age and species composition for the region. Disturbance and regrowth patterns were found to have a large effect on seasonal amplitude of net carbon exchange in high latitudes, an effect that was larger than interannual or growing-season temperatures, and that has contributed an increase of about 15% to high-latitude amplitudes since the 1960s (Zimov *et al*. 1999). As a result of the large variations and uncertainties in fire emissions and their importance to C exchange at high latitudes, we attempt to introduce a different approach to understanding the controls and constraints on C losses to fire. Our method uses modern estimates for production, decomposition, and storage of carbon, a model of fire dynamics developed over millenial time-scales, and an assessment of the long-term carbon balance for a variety of boreal landscapes in North America.

Methods for a mass balance model

Because soils represent the net accumulation of carbon over long time-periods, soils also contain information about the balance between plant production, decomposition, and fire emissions. Boreal soils store large amounts of carbon (Chapin & Matthews 1993), which is evidence for net C exchange onto land since the time of glacial ice

retreat (Harden *et al*. 1992). Carbon studies typically describe soils as net sink terms for modern C budgets (Apps *et al*. 1993). However, there is compelling evidence that at least some of these systems are no longer large sinks for C onto land (Goulden *et al*. 1998) and that they have changed over time in their potential for net C storage (Harden *et al*. 1992). Soil drainage strongly affects the amount of carbon stored in soils (Harden *et al*. 1997; Trumbore & Harden 1997), and several workers (e.g. Gorham 1991) have attributed decreased decomposition in wetland peats as the reason for their large carbon storage. However, fire may also be an important factor in the association of soil carbon and soil drainage class. It is critically important today to understand: (i) whether or not these systems have been taking up carbon for recent centuries; (ii) whether these systems have undergone a recent change in net C exchange in response to recent warming of the region; and (iii) how C exchange will respond to future changes in regional climate and fire disturbance. Based on the size and frequency of fires and on the presence of permafrost in these regions, mechanisms that control carbon exchange are likely to involve fire disturbance and regrowth as well as carbon burial into deeper, colder soil environments where carbon is protected from decomposition. To this end, a model was developed that includes fire disturbance, burial of C in cold soil layers, soil drainage, and plant regrowth simulated over millenial timescales using a decadal time-step. Our main purpose was to understand the relative importance of production, decomposition, and fire in controlling C storage in well-drained to very poorly drained systems.

As a first principal, it is clear that C that is added to soil as plant residue must either decompose, accumulate, or burn.

For the entire system:

$$
\begin{aligned}
dC/dt &= NPP - C_h - F \\
&= NPP - k_s{}^*C_s - k_s{}^*C_c - k_d{}^*C_d - f^*(C_s + C_{tr}) \quad (1)
\end{aligned}
$$

where NPP is net primary production; C_h is C lost to heterotrophic respiration (decomposition), and F is carbon lost to fire. C_h is the sum of respiration from shallow detritus (s), fire-killed plant matter 'char' (c), and deep (d) soil layers expressed as C storage times fractional decomposition coefficient k for shallow (s) and deep (d). C_{tr} is C stored in trees. Loss of C to dissolved organic C and to herbivory are not included at this time. As part of the Boreal Ecosystem Atmosphere Study, we can estimate terms NPP, k, C but have no direct estimates of fire emissions. As a result, we treated f as an unknown and solved (1) to estimate C lost to fire in each soil drainage class (Table 1). This approach to estimating f is unprecedented in the literature, where

determination of f has been based on measurements of area burned, fire frequency, and fuel consumption estimated from control vs. burn comparisons. The present approach also differs from other estimates of f because soil carbon represents a long-term balance (decadal, century, and millennial) of the carbon budget, whereas other methods rely on the more recent (annual to decadal) past.

Emphasizing the fire cycle and the mechanism of burial by regrowing moss, the present model partitions soil into a shallow (C_s) layer that accumulates between fires and a deep (C_d) layer that is buried by regrowing C_s (Fig. 1). C_s consists of roots, plant litter, and moss that decomposes at a first order rate constant k_s and typically has C/N ratios of 40–60, bulk densities $0.05\,\mathrm{g\,cm^{-3}}$ or less, and carbon contents of about 50%. Deep carbon C_d consists of roots, dead wood and 'char' and humus that decomposes at a first-order rate constant k_d with C/N ratios of 10–20, bulk densities around $0.1\,\mathrm{g\,cm^{-3}}$, and carbon contents of about 20% (Fig. 2). The coefficient k_d is generally about $10\times$ slower than k_s (Table 1) as a result of C_d being older (radiocarbon dated) and more decomposed and of burial into colder conditions (Goulden *et al.* 1998). Upon burning, a proportion (f) of C_s and C_{st} (tree stems) burns at a prescribed, average fire return time. After fire, the remains that include dead wood (Fig. 1) decompose at a rate of k_s in the shallow compartment for one burn cycle before input into the deep soil (Input deep in Table 1) where it decomposes at a rate k_d. By subjecting the fire-killed wood and 'char' to decomposition at a rate k_s for an entire burn cycle, decomposition is maximized before the material enters the deep layer. Other scenarios, including a 50-y period before burial into deep or an immediate transfer into deep, result in much higher inputs to deep layers and infer even higher C losses to fire in order to balance the deep C storage.

As part of the Boreal Ecosystem Atmosphere Study in northern Manitoba, we used soil carbon and moss inventories (Harden *et al.* 1997), soil gas-exchange chambers (Trumbore & Harden 1997), and measurements of radiocarbon in soil and deep sediment (Trumbore & Harden 1997 for uplands; Trumbore *et al.* 1999 for wetlands) to determine the rate at which soil components decompose or accumulate as fuel between fires. Dead moss (Harden *et al.* 1997) and phytomass inventories (Gower *et al.* 1997) and growth increments of live trees (Gower *et al.* 1997) were used to determine Net Primary Production of moss and trees. Carbon inventories of fire-killed trees (Harden *et al.* 1997) were used to determine a minimum of how much fuel is left after burning (tree stems don't burn) and tree-ring analysis of fire recurrence (Stocks 1989, 1980, 1991) were used to determine the average return time for intensive, stand-killing fires. Model input terms such as decomposition coefficients

(Table 1) have large uncertainties; in model runs, NPP and k_s were allowed to vary within the range of observations as long as the value of C_s was satisfied within its range of observation. To solve for C_d after 6500 years, the term f (fraction of shallow C burned) was allowed to vary as a model unknown.

The model was run separately for each drainage/ecosystem type and can be visualized as though each ecosystem were re-established repeatedly at the same site. The char component was allowed to decompose at the rate of the shallow layer (k_s) for a period of 1 burn cycle following each fire; then the char was decomposed at the rate of the deep layer (k_d). This likely overestimated decomposition of the charred material because burial by moss is sufficiently widespread and deep by about 50 years after fire (Harden *et al.* 1997). Also, NPP was modelled to recover within 10 years of the fire event, although areal spread of moss likely takes longer (Harden *et al.* 1997); this oversimplification likely overestimates NPP by about 10–25%. We did not attempt to simulate the effects of succession, variations in weather that might affect NPP or decomposition, variations in fire severity, nor accelerated decomposition following fire; however, some of these effects counteract each other and should be examined separately for net effects on the C budget. Model output, including totals for C gains (by NPP), losses (to C_h and f), and net exchange (NEP) were summed over the entire model period (Tables 1, 2) and represent long-term averages for these systems.

As a sensitivity test and as a method to find a 'best estimate' for model results, several model scenarios were run for the 6500 years since deglaciation. The variations in decomposition rate k_s and NPP of moss and litter were constrained by C_s and therefore did not significantly affect C stored in the deep soil. However, model results were highly sensitive to the rate at which charred remains decomposed (k_{char}, eqn 1) before entering the deep soil (Fig. 3). Typically, the upper estimate of fire emissions is constrained by lower limits to decomposition rates: not more than about 14% of NPP for sphagnum and 40% for spruce and pine could be lost as fire emissions. However, the lower limit for fire emissions is more problematic because the mechanisms of decomposition and burial of charred material is so poorly known: if charred material decomposes at upper ranges of shallow decomposition rates then very little C loss ($<1\%$ of NPP) is required to balance the soil C budget. Our best estimates for fire losses are derived from model runs in which means were used for input terms of (most critically) k_s and k_d. We also used an optimization procedure in Microsoft Excel® to minimize the differences between model results and data for C_s, C_d, k_s, k_d in determining the best estimates for fire

Table 1. Model inputs and constraints for determining longterm C losses to fire and decomposition. Terms defined in text (Eq. 1).

	Model inputs and constraints						Model unknowns			Model output	
	NPP[1] (kgC m^{-2} y^{-1})	1/k shallow[2] (y)	1/k deep[2] (y)	Cs mature[3] (kgC m^{-2})	Cd today[3] (kgC m^{-2})	C mature trees[1] (kgC m^{-2})	Cc (dead)[5] (kgC m^{-2}) at t = event	Input deep[3] (kgC m^{-2} y^{-1})	%Fuel burned	Fire emission[6] kg C m^{-2} event^{-1}	%NPP to fire
Pine/lichen: burn interval 60 y											
Model	0.15	13	100	1.1	1.18	4	3	0.009	41%	2	25% (range 1–26%)
Observed data	0.1–0.15	6–14	100	1.1	1.8	2–4	> 2–3	0.01		1.1–2.5	
Spruce/Feathermoss: fire interval 80 y											
Model	0.15	55	550	3.3	9	3.6	3.87	0.04	44%	3	33% (range 18–44%)
Observed data	0.096–0.17	55–250	200–500	2–4	9–11	2.9–5.7	> 1.2–4.7	0.002–0.005		1.4–7	
Spruce/Sphagnum: fire interval 200 y											
Model	0.12	56	1100	4.3	18	2.9	5.03	0.012	30%	2	12% (range 1–26%)
Observed data	0.12–0.16	55–250	1000–2000	2–4	18–22	2.5	> 1–3	0.007–0.033		–	
Wetland bryophytes, sedges: fire interval 200 y											
Model	0.3	37	0.0003	5.26	70	0	5.3	0.0495	0.05	<1	2% (range 0–6%)
Observed data[4]	0.26–0.42	17–37	2000–3300	4.6–5.2	78–120	0.038–0.064		–			

Data sources:

[1] from Gower *et al.* (1997) based on 1994 data of mature forests; Harden *et al.* (1997) based on average over fire cycle.
[2] from Trumbore & Harden (1997); *k* for char is = *k*$_s$ for one burn cycle except for pine, where *k* for char = 0.02 required to allow inputs to deep layer.
[3] from Harden *et al.* (1997) and Trumbore & Harden (1997); at mature Black Spruce site with both moss types; at mature Jack Pine site; at mature fen site.
[4] from Trumbore *et al.* (1999).
[5] stem data for mature live stands (stems do not burn) and standing dead inventories of burned stands; minimum estimates because remnants of burned moss not inventoried.
[6] data from Stocks & Kauffman (1997) for pine; Kasischke *et al.* (2000a) for spruce).

(a) Initial stand of spruce and moss

(b) Fire event

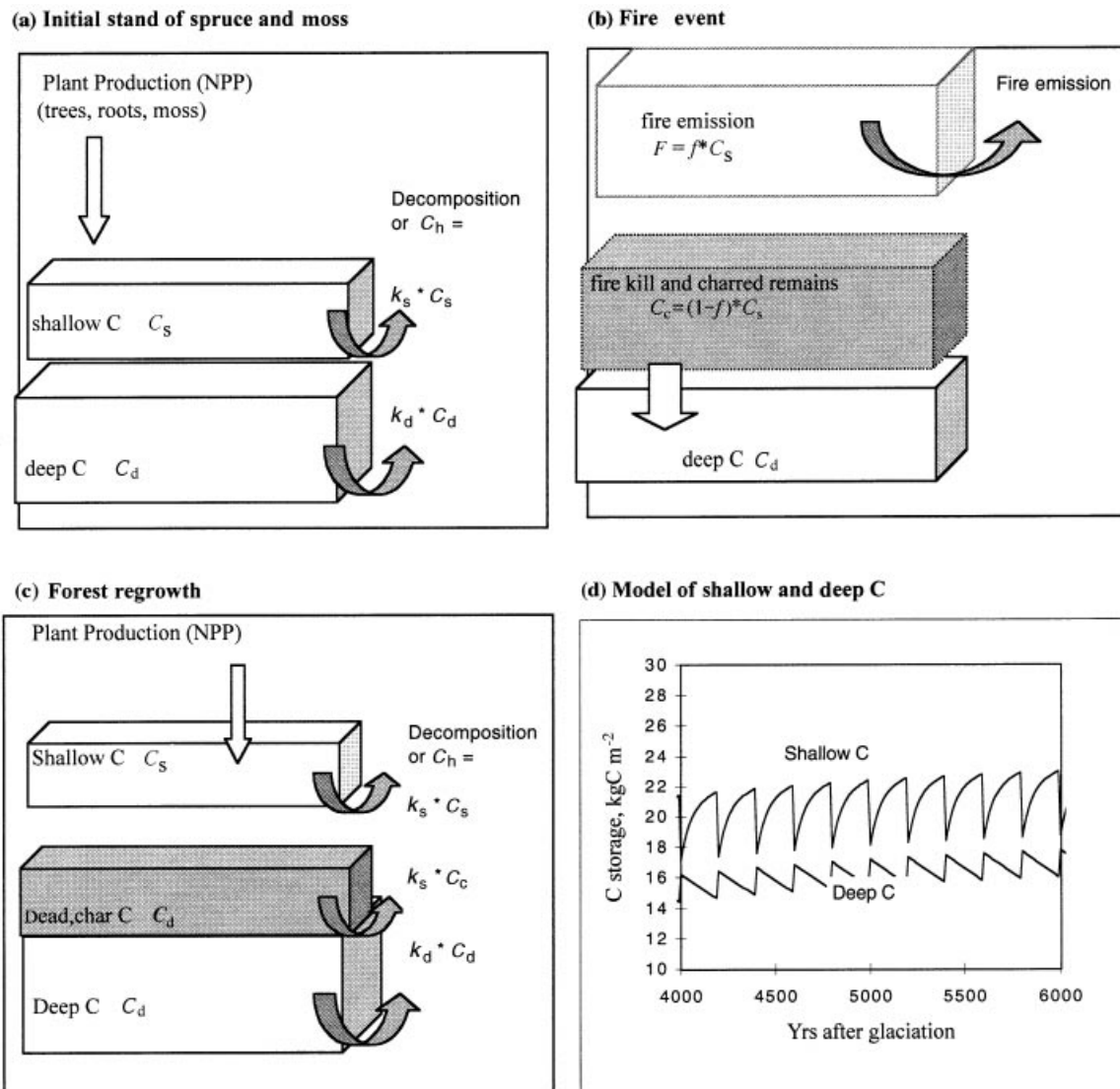## (c) Forest regrowth

(d) Model of shallow and deep C

Fig. 1 A model of soil carbon storage showing C loss to fire events, C burial by mosses during regrowth, and protection from decomposition in deep layers. In a pre-fire condition, the C transfers of the forest represent inputs from NPP and losses to decomposition. When fire occurs, carbon that is not lost to direct fire emissions is transferred from the shallow soil and tree layer to an intermediate layer C_c that decomposes at the surface until burial by moss allows the material to decompose at slower rates of the deep layer. Data in Table 1 are used to define terms including t, time t in years; NPP, net primary production in $kg\,m^{-2}\,y^{-1}$; k_s, k_d, decomposition coefficients in units of $kgC\,m^{-2}\,y^{-1}$; $t-1$, year previous to time t; C_s carbon storage (in units of $kgC\,m^{-2}$) in shallow soil and trees, including moss, roots, plant litter, trees; C_d, carbon storage ($kgC\,m^{-2}$) in deep soil layers; C_c, C storage ($kgC\,m^{-2}$) in fire-killed trees and remains of burning; C_{tr}, carbon storage ($kgC\,m^{-2}$) in tree stem; F, fractional percentage loss to fire; C_h, heterotrophic respiration in $kgC\,m^{-2}$ in one year. Equations for calculations between fire events are $C_s + C_{tr}$ at time $t = C_{tr}(t-1) + ANPP_{stem} + C_s(t-1) + NPPs - k_s*C_s(t-1)$ for shallow carbon and tree layer; C_d at $t = C_d(t-1) - k_d C_d(t-1)$ for deep carbon layer; $C_h = k_s*C_s(t-1) + k_d*C_d(t-1) + k_s*C_c(t-1)$ for heterotrophic respiration in one model year; C_c at time $t = C_c(t-1) - k_s*C_c(t-1)$ for fire-killed remains. For years in which fire occurs, equations are C_s at time of fire = 0; C_d at t of fire = $C_d(t-1) + C_c(t-1)$ for carbon storage of deep carbon; F (fire) = $f * (C_s)$ for C consumed by fire and released as CO_2 and other C trace gases; $C_h = k_d*C_d(t-1) + k_s*C_c(t-1)$ for decomposition or heterotropic respiration; $C_c = (1-f)*(C_s + C_{tr})$ for carbon storage of fire-killed remains.

emissions (Table 1, output). The modelled best estimates for direct fire emissions per event are comparable to data on experimental burns in pine and spruce forests (Stocks 1980, 1989).

Results

There is a zig-zag pattern of carbon storage in both the shallow and deep soil layers (Figs 1, 3) that is caused by
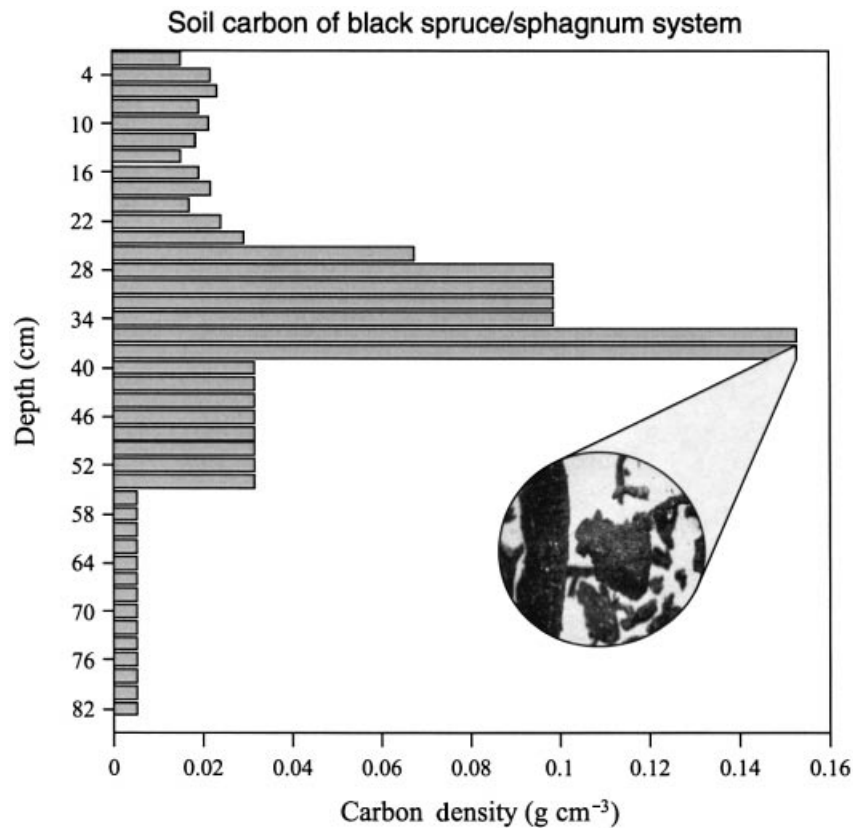
Fig. 2 Evidence for fire: Residues of decomposed and burned plant debris are concentrated in deep organic layers. Initial forms of 'black carbon' may exist in these layers, but more labile, easily decomposed material also exists, suggesting that these deep layers are protected from decomposition by burial and cold temperatures. C density = %C/100 × bulk density.

the shallow layer burning and the deep layer receiving the fire-killed, partially decomposed remains. Well-drained sandy sites, which are generally warmer at the soil surface, have rapid rates of decomposition that limit the storage of fuel and thereby limit the inputs to the deep soil layers (Table 1 – note the small deep inputs; Fig. 4). Poorly drained upland sites, which have higher C storage in moss layers (owing to greater moss NPP but lower tree NPP; see Gower *et al*. 1997; Harden *et al*. 1997), have plenty of fuel for combustion (Table 1, see C_s at maturity) but deep C storage varies two-fold according to the severity of burning (Fig. 4).

The importance of fire emissions as a mechanism of C loss is best seen in a comparison of all four drainage systems (Fig. 4), where estimates of NPP and decomposition are relatively similar, but carbon storage varies by 10× as a result of fire emissions. Better drained ecosystems generally have greater C losses to fire than wetter ecosystems (Fig. 5) but the maximum fire emissions are derived from intermediate soils with black spruce stands. These patterns are reflected in model results; for example, because decomposition is so fast in the pine sites, they store small amounts of shallow C (C_s), and therefore the burn emissions are lower than for spruce sites (Table 1). Pine sites, although productive, put more of their NPP into tree stems (which do not

burn) than into fine fuels such as moss and litter. As a result, both high decomposition rates and the allocation of C into coarse stems accounts for a slightly lower fire emission in pine than spruce. On the other end of the spectrum, wetland sites also do not burn as much as spruce stands, but it is the deep, wet conditions that offer protection from fire. As a result, the ratios of fire emissions to total emissions ($F/(C_h + F)$) along the drainage gradient are 0.27, 0.43, 0.26, and 0.08 for driest to wettest sites (Fig. 4). In uplands of our study area, 10–30% of the annual CO_2 that is fixed as NPP has been released in the form of fire emissions, while about 40–80% of NPP has been released to decomposition and 8–30% fixed as soil carbon (Table 1).

Following a fire, exposure of charred and dead material at the surface leads to a high decomposition efflux during the warm season. A change in the surface energy balance is evident from a thickening of the active layer (Viereck 1983; O'Neill *et al*. 1997). In the laboratory, charred material appeared to be a mixture of more stable carbon, that resisted digestion by strong acid and base (method of Gillespie *et al*. 1992; data not shown), and more labile carbon, that at room temperature decomposed at rates similar to shallow, preburn material (Goulden *et al*. 1998; see footnote 23). On fire-scars of various ages, O'Neill and colleagues found net losses of

Table 2. Boreal ecosystem classes and long-term carbon mass balance terms (does not include forest-tundra).

Drainage class	Vegetation[1]	Area % of boreal forest	Area[2] (m²)	Range of NPP[1] (kg C m⁻² y⁻¹)	Boreal NPP[3] (range in gC y⁻¹)	Annual fire emission[4] (range in gC y⁻¹)	Annual decomposition[4] (range in gC y⁻¹)	NEP (NPP-F-Ch)[6] (range in gC y⁻¹)
Well-drained	Jack Pine/lichen	26%	3.80E+12	0.18 to 0.26	6.8E+14 to 9.9E+14	1.7E+14 to 2.5E+14	5.1E+14 to 7.4E+14	0.0E+01 to 0.0E+01
Mixed drainage	Deciduous 5	40%	5.90E+12	0.22 to 0.43	1.3E+15 to 2.5E+15	4.3E+14 to 8.4E+14	8.6E+14 to 1.7E+15	1.3E+13 to 2.5E+13
Poorly drained	B. Spruce/Sphagnum	13%	1.90E+12	0.18 to 0.43	3.4E+14 to 8.2E+14	4.1E+13 to 9.8E+13	2.9E+14 to 6.9E+14	1.0E+13 to 2.5E+13
Moderately drained	B. Spruce/Feathermoss	13%	1.90E+12	0.18 to 0.43	3.4E+14 to 8.2E+14	1.1E+14 to 2.7E+14	1.9E+14 to 4.7E+14	3.4E+13 to 8.2E+13
Very poorly drained	Wetland mosses, sedge	8%	1.10E+12	0.15 to 0.38	1.7E+14 to 4.2E+14	3.3E+12 to 8.4E+12	1.6E+14 to 3.8E+14	0.0E+01 to 3.4E+13
		1.00E+00	1.46E+13		2.5E+15 to 4.8E+15	6.4E+14 to 1.2E+15	1.8E+15 to 3.5E+15	2.3E+13 to 8.4E+13

Data sources:

[1]Trees and moss from synthesis by Gower *et al.* (1997) for pine, broadleaf, and spruce forests around the world. See also Randerson *et al.* (1997) with 0.3 to 0.5 range. See Trumbore *et al.* (1999) for wetlands. The NPP in Manitoba sites used in model are low end of the range.

[2]Most global inventories of boreal phytomass lump pine and spruce into evergreen needleleaf (Chapin & Matthews 1993). For Canada, the ratio of well-drained Spodosols to poorly drained peats and Inceptisols (from Harden *et al.* 1992) is 60% Spodosols, 40% other; whereas forests are 36% pine to 64% spruce (For. Canada, written commun.). We used 50% for global pine/spruce breakdown for all boreal forests.

Within Spruce forests, we also used 50% mixture for poorly drained black spruce (BS)/sphagnum and moderately drained BS/feathermoss.

[3]Multiplying NPP range by area; compares with 2.9 PgC y⁻¹ (Whittenburg *et al.* 1997, 1998) and 5.2 PgC y⁻¹ (Randerson *et al.* 1997).

[4]Best-estimate value from Table 1 of %NPP burned and %NPP decomposed is multiplied by NPP range. Compare totals with 0.3 PgC y⁻¹ of Kasischke *et al.* (2000b).

[5]Very few data for broadleaf exist; we used NPP, C, and litter turnover of aspen from Gower *et al.* (1997) and soil data of H.Velduis, Agriculture Canada (written comm.).

[6]Although a net C sink has been postulated for boreal systems (Gorham 1991; Harden *et al.* 1992) measurement and model based estimates range enormously from sources to sinks (Goulden *et al.* 1998).
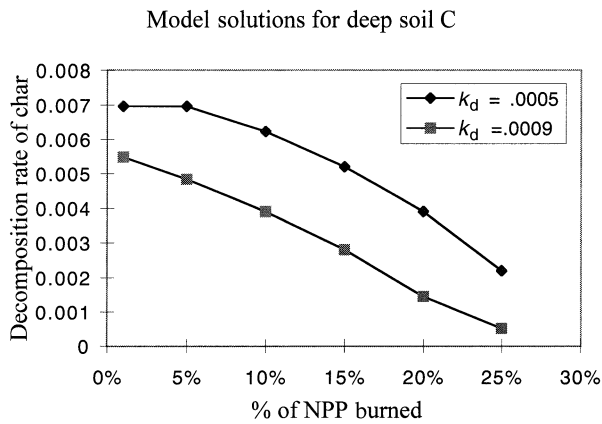
Model solutions for deep soil C

Fig. 3 The sensitivity of burn emissions to decomposition rate of charred remains (k_{char}) required to balance the C budget for deep soil. Using a decomposition rate for deep soil of $k_d = 0.0005$ (turnover time of 2000 years; shown as lower line with circles) to 0.0009 (1111 years; upper line with boxes) for black spruce/feathermoss site, model results require a combination of faster turnover time for charred material or higher burn emission to balance the C stored in deep soil. Shown as horizontal lines, decomposition rates for char may lie somewhere between ranges measured for k_d and k_s (Table 1).

Fig. 4 A model of deep soil carbon storage (C_d) for wetland fen systems that burn very lightly, poorly drained spruce systems that burn severely, and well drained pine systems that decompose and burn severely. The zig-zag pattern represents input of dead and burned material from shallow to deep layers and subsequent decline by decomposition between fires. For a site maturing after a burn, local Net Ecosystem Production (NEP) is represented by C accumulation in deep soil layers. Extrapolating NEP from local site measurements to a regional scale or long-term average must include fire emission losses that account for the major differences in carbon storage in fen, spruce and pine systems.

carbon as a result of increased heterotrophic respiration (O'Neill et al. 1997) and absence of vegetative cover. As the site recovers with new vegetation, dead and charred material is protected by burial into deeper, colder layers (Goulden et al. 1998), and decomposition is offset by net primary production. Based on the work of Rapalee et al. (1998), fire scars are net C sources for about 30 years after burning, after which time the systems become net sinks for C. The loss of the insulating organic layers probably also has an effect on winter fluxes in which soils would be colder to greater depths and may remain frozen for a longer period. However, the thickening of the active layer after fire suggests an overall warming. Although our model does not explicitly include a post-fire warming or winter cooling, nor a slow transition during regrowth, a sensitivity test suggested that a two-fold increase in decomposition sustained for 20 years resulted in an underestimate of decomposition comparable to about 3%NPP. This estimate, however, may change as different model scenarios include changes in fire return interval and shifts in the C_h and F terms.

For a regional and global perspective on carbon exchange, carbon storage and decomposition may be extrapolated best by soil drainage class in association with ecosystem structure. For each drainage and ecosystem class, we assigned relationships of C_h, F, and NPP to areas of the globe based on the distribution of soil drainage and ecosystem class. Because the discontinuous permafrost that underlies our study may disproportionately affect ratios of $F/(C_h + F)$ relative to regions
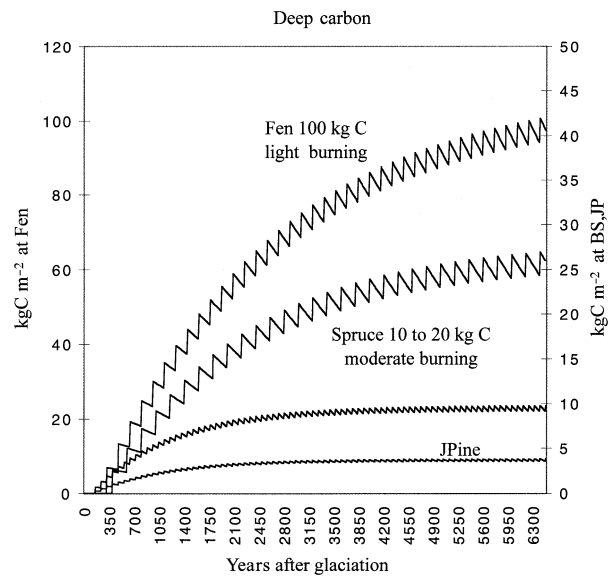
lacking permafrost, the $F/(C_h + F)$ relationship may not hold true for the boreal forest in the absence of permafrost. Based on our areal extrapolations in the presence of permafrost, however (Table 2), global boreal fire emissions could have been about 0.5–1 Pg C y^{-1} over the past century or millennia. This overlaps at least the low end of some recent boreal fire studies (Kasischke et al. 1995a; Conard & Ivanova 1998) but is at least three times larger than extrapolations from some direct emission estimates (Cahoon et al. 1994) and 3–10 times larger than estimates used in general circulation models (Houghton 1991; Randerson et al. 1997; Wittenburg et al. 1998; see discussion below). While our estimates are highly uncertain, they do emphasize the importance of fire emissions in closing the C budget over century-to-millenial timescales, and they emphasize the links between NPP, decomposition and fire.

Discussion

If the distribution of stand age were to change through fire suppression or through changes in climate, then the relationships of NPP, k, C, and F would change and
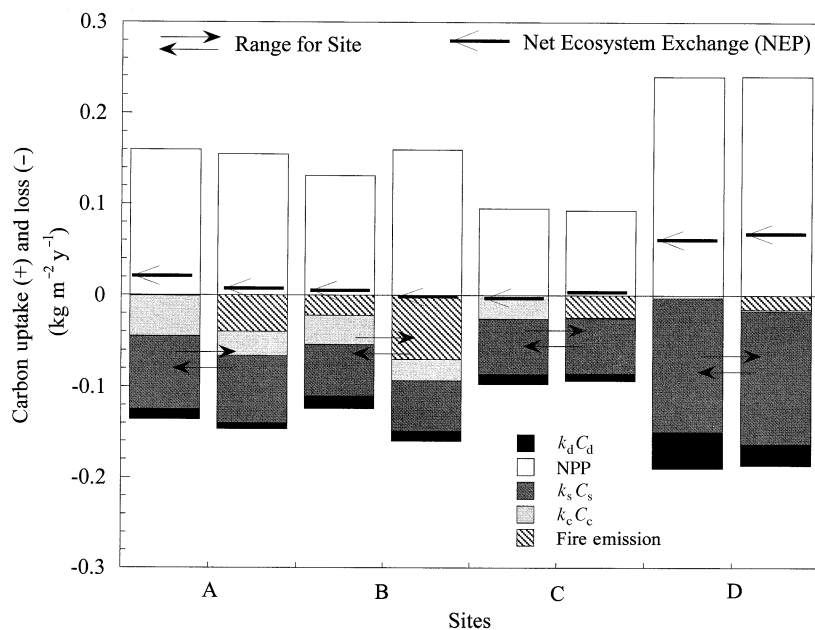
Fig. 5 Carbon losses to fire and decomposition were calculated from model results described in text. Long-term sums for NPP, C_h for shallow (k_sC_s), C_h for deep (k_dC_d) and C_h for dead (k_sC_c), and fire emission F were divided by years of simulation for annual uptake and loss rates of C exchange. Each drainage class was modelled separately for runs where fire emissions were minimized (all C_h values generally maximized within data constraints of Table 1) and maximized (C_h minimized) to show range of possible fire emissions. Best estimates for F and C_h are not shown here but are summarized in Tables 1 and 2.

result in a shift in $F/(C_h + F)$ and in NEP. Looking back through the past century, some investigators have noted variations in fire occurrence that coincided with variations in fire-season climate, but regional results vary. Compared to ad1850, burn areas and fire occurrence were notably low in tree-ring records in Quebec from 1870 to 1988 (Payette *et al.* 1989; Bergeron & Archambault 1993) and in charcoal deposition of Minnesota in the 19th Century (Clark 1988). By contrast, fires in the rest of Canada after the 1980s have been more extensive than in previous decades (Murphy *et al.* 1999). These variations in climate and in fire disturbance likely resulted in shifts of $F/(C_h + F)$ and therefore in shifts of how fast and in what forms C was lost from the systems. More discreet stand-age information is needed before we can understand how such shifts may relate to NEP or how shifts in climate will affect $F/(C_h + F)$ and NEP.

The reasons for the discrepancy between our estimates of the long-term average carbon emissions and direct estimates of C emissions are unclear but potentially important. First, estimates derived from observations before the 1980s (Murphy *et al.* 1999) may be biased toward a lower fire activity of the last century, as suggested by Bergeron & Archambault (1993). In this case, our long-term estimates suggest that we are entering a period of fire activity that is atypical of the past century but more typical for the boreal forest. Secondly, the technology for estimating emissions has advanced to increase the area burned by two-fold over the past 5 years (Cahoon *et al.* 1994; Conard & Ivanova 1998). Fire severity estimates have increased steadily also, as studies include a wider variety of stands (such as

black spruce with more moss and ground fuels) and a more careful accounting of ground fuels in general (Stocks 1989; Kasischke *et al.* 2000a). Whether fire activity is actually on the rise or is being more carefully accounted, CO_2 emissions from boreal fires are likely to be much greater than have been assumed (e.g. compare Seiler & Crutzen 1980 with Cahoon *et al.* 1994 and French *et al.* 2000). In addition, fire emissions may increase in the future, particularly if summer droughts are sustained in these regions leading to more episodic fire events.

Interactions between fire disturbance and the active layer above permafrost have demonstrated the importance of insulating moss and soil layers in maintaining a frozen soil near the ground surface (Viereck 1983). In these regions species composition is highly dependent on soil drainage (Rapalee *et al.* 1998), and NEP and decomposition are sensitive to soil drainage class (Trumbore & Harden 1997); thus it would follow that changes in fire return intervals could potentially invoke changes in forest structure and carbon exchange. As fire is episodic and sudden in the boreal forest, relative to gradual changes in temperature and decomposition, the mechanism by which carbon may respond to regional climate change is inherently different from other ecosystems where fire is managed or of smaller scale. Furthermore, changes in permafrost regions can be irreversible when shallow and deep freeze layers become separated (formation of talik and massive soil drainage). Depending on the balance between colder, deeper winter freezes and warmer, deeper summer thaws in areas where organic mats were burned, a change to more frequent fires may prevent insulating layers from

recovering and therefore might favour the degradation of permafrost (Landhausser & Wein 1993; Kasischke *et al.* 2000b).

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