Modeling physical and biogeochemical controls over carbon accumulation in a boreal forest soil

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Abstract

Boreal soils are important to the global C cycle due to large C stocks, repeated disturbance from fire, and the potential for permafrost thaw to expose previously stable, buried C. To evaluate the primary mechanisms responsible for both short and long-term C accumulation in boreal soils, we developed a multi-isotope ($^{12}$C,$^{14}$C) soil C model with dynamic soil layers that develop through time as soil organic matter burns and re-accumulates. We then evaluated the mechanisms that control organic matter turnover in boreal regions including carbon input rates, substrate recalcitrance, soil moisture and temperature, and the presence of historical permafrost to assess the importance of these factors in boreal C accumulation. Results indicate that total C accumulation is controlled by the rate of carbon input, decomposition rates and the presence of historical permafrost. However, unlike more temperate ecosystems, one of the key mechanisms involved in C preservation in boreal soils examined here is the cooling of subsurface soil layers as soil depth increases rather than increasing recalcitrance in subsurface soils. The propagation of the $^{14}$C bomb spike into soils also illustrates the importance of historical permafrost and 20th century warming in contemporary boreal soil respiration fluxes. Both $^{14}$C and total C simulation data also strongly suggest that boreal SOM need not be recalcitrant to accumulate; the strong role of soil temperature controls on boreal C accumulation at our modeling test site in Manitoba, Canada indicates that carbon in the deep organic soil horizons is probably relatively labile and thus subject to perturbations that result from changing climatic conditions in the future.

Keywords: black spruce, boreal, carbon, decomposition, model, soil
Introduction

Poorly-drained boreal soils are rich in organic matter and play a critical role in the global carbon (C) cycle due to the large accumulation of soil C via the long-term preservation of old, deep C. The mechanisms responsible for accumulation of C in boreal soils include the physical and chemical properties of soils and the biophysical regulation of decomposition. Within boreal soils several factors are important to the control of decomposition rates; most notably, temperature, substrate recalcitrance, and moisture (Hobbie et al., 2000). In addition to these factors, fire also contributes to boreal soil C dynamics through combustion of organic matter and production of highly recalcitrant black carbon compounds (Harden, 2000; Czimczik, 2003). Understanding the influence of these factors on C stabilization in boreal soils is essential to improving predictions of how boreal soil C might respond to a warming climate.

Soil temperature influences the rate of microbial activity in soils and therefore, regulates the rate of soil organic carbon (SOC) decomposition. Indeed, decomposition in arctic and boreal soils is sensitive to temperature based on both field observations (Goulden et al., 1998) and laboratory incubations (Dioumaeva et al., 2002; Mikan et al., 2002; Neff and Hooper, 2002). This response to soil temperature influences the seasonal dynamics of soil respiration in boreal soils. Warm surface organic soils appear to be the dominant source of CO$_2$-C released in the summer, though the insulated humic organic layer and thawed mineral soil contributes as much as 20% of the annual CO$_2$-C loss during the fall through early spring (Winston et al., 1997). The stability of the deeper soil C is of particular interest as climate change may increase soil temperatures at depth, thereby increasing the flux of old C from the deep soil.

The influence of substrate quality and recalcitrance on the rate of decomposition in boreal soils has been explored primarily through examination of decomposition rates for leaf litter substrate from different growth forms (Flanagan and van Cleve, 1983; Hobbie, 1996) and soil beneath various arctic and boreal plants (Neff and Hooper, 2002). It is evident from these studies that the rate of decomposition varies considerably due to growth form, but the recalcitrance of buried humic material relative to the less humified soil organic matter (SOM) in the surface horizon is not known. While it is clear from radiocarbon dating that the deeper, humic layers are indeed older, it is unclear why. Substrate age does not necessarily correspond
with recalcitrance if other factors such as cold temperatures or high moisture content are
protecting the carbon from decomposition.

Fire is the other critical process that we need to understand in order to predict boreal soil
responses to climate changes. Fire influences the C cycle through direct combustion loss of
biomass and surface soil organic C (Kasischke et al., 1995; Kasischke and Johnstone, 2005),
creation of recalcitrant black carbon (Czimczik et al., 2003), and through the legacy of fire that
persists for decades following fire through changes in NPP and soil temperature (O'Neill et al.,
2003; Bond-Lamberty et al., 2004). One of the additional effects of fire on soils is the influence
on soil temperature regime that occurs following combustion of the surface layer. This loss of
live and dead moss layers exposes previously buried soil to warmer temperatures near the
surface, and thus, may increase decomposition (Harden et al., submitted). As with substrate
recalcitrance and soil physical factors, fire is part of the mosaic of interacting controls that
influence contemporary boreal decomposition processes and will control future carbon dynamics
in these ecosystems.

The quantitative influence of multiple interacting controls on soil organic matter
decomposition is difficult to establish in field studies but is well suited to examination in a
simulation model environment. In this paper, we describe a new layered soil decomposition
model that can be used to assess the mechanisms of C accumulation in poorly-drained boreal
soils. We use this model and data from a well characterized, poorly drained ecosystem in
Manitoba, Canada to carry out an assessment of what factors influence decomposition and C
accumulation in this setting. We chose poorly-drained boreal soils as they represent soils
intermediate in decomposition and C accumulation compared to well-drained upland soils and
organic rich, very poorly drained ecosystems (Rapalee, 1998). The model simulates both $^{12}$C
and $^{14}$C isotopes in order to evaluate the formation and aging of soil C as it accumulates in the
soil profile. The results of this study indicate that, in contrast to many temperate ecosystems,
SOC accumulation depends strongly on the interaction between carbon inputs and losses
(controlled by carbon inputs and decomposition rate) and the thermal characteristics of the soil
profile. The study also suggests that boreal soils need not be highly recalcitrant to accumulate
large stores of carbon. Rather, historically cold conditions and cool temperatures deep in the soil
profile, between wildland fire events, appear to play a large role in historic carbon accumulation.
rates. The potential lability of subsurface boreal soils suggests that carbon release from these ecosystems could be highly sensitive to future warming trends.

Methods

Model Structure

The model was developed in a Matlab modeling environment and uses a series of coupled ordinary differential equations (Table 1) which are solved by a Runge-Kutta 4th-order algorithm. The distribution of $^{12}$C and $^{14}$C through pools and layers are solved simultaneously for each isotope. The equations governing $^{12}$C and $^{14}$C are identical (Table 1) with the exception of radiocarbon decay which is modeled as a loss of $^{14}$C from each discrete carbon pool at each timestep based on the following equation:

$$\text{Decay } ^{14}C = \frac{1}{8267 \text{yr}}$$

Each carbon isotope is simulated as separate C pools and then calculations of $\Delta ^{14}C$ are made for each time step after the simulation ends. Input of $^{12}$C or $^{14}$C to organic matter pools is based on productivity as discussed below, however in the case of $^{14}$C, we simulate the time course of incorporation of the atmospheric $^{14}$C spike into plants and soils from 1950 to the present. All simulations were run with a monthly time step for 6500 years in order to capture the ecosystem and soil development following the retreat of the Laurentide ice sheet in boreal Canada (Harden et al., 1992). Many of the parameterizations given below may be appropriate in a range of boreal settings. However, for our model sensitivity testing, we parameterize the model for a well studied, poorly drained black spruce stand in Manitoba, Canada (see below).

Site Description

We use soils in poorly-drained boreal forests in northern Manitoba as the target for our initial model testing. The soil used to evaluate our simulations is from the Northern Study Area Old Black Spruce (NOBS) site of the Boreal Ecosystem and Atmosphere Study (BOREAS) (Sellers et al., 1995). While about half of the area under the flux tower is underlain by moderately drained soils with tall black spruce/feathermoss cover, the other half of the area is mapped as more poorly drained (imperfect, poor, and very poorly drained) soils, much of which is overlain by Sphagnum moss and sparse cover of black spruce (Veldhuis, 2000). This poorly
drained, *Sphagnum* covered soil, is the target of our study because it includes a thick mat of organic soil layers that are amenable to radiocarbon dating (Trumbore and Harden, 1997) and because many poorly drained soils were underlain by permafrost in the region over the past 20 years (Veldhuis et al, 2002). Sample OBSP9 (Trumbore et al., 1998) was collected in 1994 and analyzed for bulk density, C, and radiocarbon; this profile contains 2 cm of living sphagnum moss, dead moss from 4 to 30 cm, moss and dead roots from 30 to 41 cm, and humified organic matter from 43 to 69 cm depth. The stand age at NOBS was approximately 120 years old at the time of field data collection (Trumbore and Harden, 1997). Aboveground NPP for the NOBS site is estimated to be 0.120 kg C m\(^{-2}\) yr\(^{-1}\) but ranges from 0.098 kg C m\(^{-2}\) yr\(^{-1}\) in a young jack pine stand to 0.349 kg C m\(^{-2}\) yr\(^{-1}\) in an aspen stand (Gower et al., 1997).

*Dynamic model layer development*

The model simulates multiple organic soil layers and soil depth, the latter of which changes through time as organic matter is consumed and re-accumulates between disturbance events (fire). We do not simulate the dynamics of carbon in mineral soil horizons in this model. Layers in the simulation model develop through time following fire and are tracked in the model as vertically discrete SOC layers with each new layer containing the regrowing surface moss, roots and the surface SOC. In the final 120 years of a simulation, soil layers are generated every five years in order to create sufficient detail to evaluate the propagation of the radiocarbon bomb-spike into soils. The number of model layers at the end of the run is thus equivalent to the total number of fire events that occur during the simulation plus 24 additional layers created during the final 120 years of the simulation. This layering structure is not intended to mimic the creation of diagnostic soil horizons but rather to allow the depth of soils to change through time as organic matter accumulates. The thickness of each layer is determined from a parameterized relationship between soil organic matter content and bulk carbon density for multiple depths within a soil profile (Figure 1). This structure is markedly different from existing soil organic matter models but is able to represent the transition from low bulk C density in dead moss and fibric horizons to higher bulk C density in mesic and humic horizons. This depth/carbon relationship is essential to modeling of boreal soils because of strong thermal gradients from surface to deep soils. Stated more directly, by converting carbon content to soil depth we are
able to simultaneously model the thermal properties and SOM pool distributions in a boreal soil profile.

**Model parameters and simulations**

We assembled a suite of model scenarios to evaluate the performance of the model with a range of parameters that included fixed (Table 2) and intentionally varied parameters (Table 3) designed to examine the quantitative importance of several factors on boreal soil C storage. The central focus of our model analysis included factorial combinations of two levels for the soil thermal regime, fire return interval, fire severity, decomposition quotient (Q10), and soil moisture regulation of decomposition. We also used three levels for net primary production and SOC pool structure/turnover dynamics. Combined, these variables allow comparison of the relative importance of soil thermal history, fire disturbance, the temperature and moisture sensitivity of decomposition, variability in NPP and the nature of SOC pool structure and turnover.

The model simulations were parameterized with several static parameters used in all simulations. These parameters controlled the allocation of NPP into the various biomass pools, the residence time for C in each of the biomass pools and standing-dead pool, root depth distribution, and the burn severity for standing live black spruce stems (Table 2).

The parameters that were varied were done so in a factorial design so that every level of each parameter was combined with each level of the other parameters (Table 3). This was done to identify the combinations of parameters that performed well with respect to the observed NOBS data and those combinations that resulted in poor model-data fit. The model was unconstrained allowing the simulations to accumulate as little or as much C as the model parameters dictated. A total of 288 individual model runs were performed.

**Net primary productivity**

For our model simulations, we varied total NPP values from 0.135, 0.180, and 0.225 kg C m$^{-2}$ yr$^{-1}$ following simulations for this site by Harden et al. 2000. The above and belowground NPP pools included aboveground black spruce stem and branch C ($C_{s+b}$) and belowground root C ($C_r$), as well as aboveground Sphagnum moss and black spruce needle C ($C_{m+n}$). The root NPP and the root biomass distribution both followed a negative exponential model with depth (Jackson et al., 1996). The root biomass C ($C_{r,z}$) was a single pool within each layer based on layer depth $z$ and thickness. Net primary productivity allocation was as shown in Table 2. To
reflect the low NPP during post-fire forest regrowth, we scaled all NPP values up to their
prescribed values over the first 50 years post-fire (O'Neill et al., 2003).

We parameterized C residence times for the live biomass pools to reflect the mean age of
C within each pool (Table 2). We used decay constants of 0.015 yr\(^{-1}\) for \(C_{s+b}\), 0.167 yr\(^{-1}\) for \(C_{m+n}\)
(Schuur et al., 2003), and 0.125 yr\(^{-1}\) for \(C_t\) (Steele et al., 1997). After burning, stem C enters the
standing-dead pool \((C_{s-d})\) before entering the soil. The residence time for \(C_{s-d}\) is 0.094 yr\(^{-1}\)
(Manies, 2005), resulting in a large input of coarse woody debris to the soil shortly after fire.

**SOC pool structure**

We developed three different model SOC pool structures to evaluate the influence of
carbon pool structure, turnover time and humification on the pattern and amount of C
accumulation. These three structures include two representations of organic matter
decomposition that assume that SOM is a homogenous slow or homogeneous fast turnover pool
of carbon and an additional representation that uses a multiple pool structure (Figure 2). In these
two structures, carbon is simulated as a single pool with uniform inherent turnover time through
the profile. The actual turnover time of these simulations is determined by the temperature and
moisture controls described below. These pool structures are described by the simple
designations single-pool labile (S\(_l\)) and single-pool recalcitrant (S\(_r\)). The third structure is
analogous to more contemporary ecosystem model structures that have fast, slow and recalcitrant
material (Parton, 1987, 1987). This multiple-pool structure represents increasing recalcitrance
with decomposition as organic matter becomes progressively humified and is designated as the
multiple-pool humic (M\(_h\)) C pool structure. The effect of this structure is that organic matter
becomes increasingly recalcitrant as it is cycles through decomposition and so therefore results
in increasing recalcitrance in older, deeper, more-decomposed organic matter. We do not
include an explicit black carbon (BC) pool in this model because the fraction of soil contained in
black carbon tends to be very small (<1\%) (Czimczik et al., 2003) and because there is currently
not enough information to parameterize the turnover of this pool with much confidence. We did
however evaluate the potential impact of highly recalcitrant black carbon produced at low rates
during fires in an earlier version of this model and found that neither total carbon nor \(^{14}\)C profiles
were sensitive to the inclusion of BC in the model (data not shown). This is a research area
where further modeling is certainly warranted as more information becomes available.
We parameterized our three organic matter structures based on field and laboratory studies as described below. The recalcitrant single SOC pool structure had a $k = 0.018$ yr$^{-1}$ at 5°C. This was based on the determination of field based turnover time for the surface soil at the Northern Old Black Spruce (NOBS) site in Manitoba (Trumbore and Harden, 1997). This field-based turnover time implicitly includes both environmental and substrate level controls on decomposition in the surface soil layer, including any level of recalcitrance whether chemical or physical. This parameter set is hereon referred to as single-recalcitrant (Sr). To evaluate a faster single pool model, we increased the field-based decay constant by 50% to $k = 0.027$ yr$^{-1}$ at 5°C to account for the field temperature and moisture regulation (single-labile, Sl). The multiple pool SOC structure was based on the results of a laboratory incubation using respired $\Delta^{14}$C-CO$_2$ and the $\Delta^{14}$C of C pools in the NOBS soil (Dioumaeva et al., 2002). Normalized $k$ values at 5°C for these pools were: fine $k = 0.107$ yr$^{-1}$, coarse $k = 0.037$ yr$^{-1}$ and humic $k = 0.023$ yr$^{-1}$.

Carbon from the moss and needle litter, along with the fine root fraction of $C_r$ enters either the single C pool or the fine fraction C pool ($C_f$) upon senescence. Woody biomass, including standing-dead C and the coarse fraction of root C, flows to either the single C pool or to a coarse fraction pool ($C_c$). As these pools decompose, carbon flows to a separate humic C pool ($C_h$) in the multiple-pool set or is recycled into the single C pool in the recalcitrant and labile single pool sets. Carbon loss (CO$_2$-C) resulting from microbial growth efficiencies during turnover is prescribed at 50% following Parton et al. (1987).

**Soil thermal regime and $Q_{10}$**

Soil temperature profiles in the model are based on data collected during 1994-1996 at depths of 5-100 cm in the Old Black Spruce site at the BOREAS Northern Study Area (Sutton, 1998). We reduced the dataset to a record of average monthly soil temperatures by depth for this period (Figure 3a). In order to determine a soil temperature profile for each month, the modeled soil layer midpoint was calculated and the corresponding soil temperature was interpolated from the record. As soils develop during a simulation, increases in soil depth translate into alteration of soil thermal properties following these depth/temperature relationships. The relationship between soil depth and temperature is purely correlative in this model but is consistent with temperature profiles in other boreal soils (Harden, unpublished data).

Soil carbon decay constants (i.e., $k$'s) were normalized to 5°C to reflect the inherent lability of the various C substrates at 5°C as described above, and then were adjusted up or down.
by $f[T(t,z)]$, a function of temperature in month $t$ and for layer midpoint depth $z$. For this
function, we used a $Q_{10}$ response which was normalized to a value of 1.0 at 5°C. When soil
temperature is below 0°C, we set $f[T(t,z)]$ to 10% of the $Q_{10}$ value. This was done to capture the
reduced rate of decomposition in very cold soils and to reflect the large decline in free soil water
as soils freeze, reducing the interaction of microbes and enzymes with the soil C. However, due
to the lag in deep soil freeze relative to the surface soil (Figure 3a), deep soil respiration
continues well into the fall and early winter, as has been observed in the field (Winston et al.,
1997). The layer temperature was then applied to the decay constant as $f[T(t,z)]$ based on the $Q_{10}$
relationship.

We evaluated the sensitivity of C accumulation to variation in $Q_{10}$ by carrying out
simulations with a $Q_{10}$ of either 2 or 3. Boreal soil incubation studies have shown soil
decomposition $Q_{10}$ values generally range from 2 to 3 (Clein, 1995; Dioumaeva, 2002; Neff,
2002). We used both values to assess the influence of $Q_{10}$ on the resulting accumulation and the
pattern of C accumulation throughout the soil profile in our model.

Permafrost is probably currently absent on the NOBS site, but in some years may be
sporadically present in some of the larger Sphagnum hummocks. Permafrost was more
widespread in the early 1990s, and it may have underlain the whole area in the past as is evident
from small collapses (H. Veldhuis, personal communication). Studies on other shallow peatlands
have revealed that permafrost can be widespread, but that its distribution is controlled by depth
of peat, shading, fire history, and slope (Mills et al., 1987; Veldhuis et al., 2002). To examine
the potential influence of changing modern temperature regimes we used a modern temperature
simulation (assumes modern temperatures are the same as the past 6500 yr) and a historically
colder scenario based on borehole thermometry. The historically colder scenario assumes a 2°C
warming over the past 500 years to bring model input temperatures up to modern values by the
end of the simulations, which is consistent with warming trends for northern latitude ecosystems
inferred from borehole thermometry (Beltrami et al., 1995).

### Moisture regulation

The influence of soil moisture content on decomposition was handled in a similar manner
to soil temperature. We calculated the soil profile water filled pore-space (WFPS) for each
month based on monthly average volumetric moisture content from NOBS during 1994-1996.
NOBS data were recorded at depths of 7.5, 22.5, 45, 75, and 105 cm (Figure 3b). We used the
WFPS record and the decomposition/moisture response curve from a prior modeling study (Frolking, 1996) that slowed decomposition under 20% WFPS and above 50% WFPS. To provide an assessment of model sensitivity to moisture, we included two moisture response curves in our simulations; one that allows optimal decomposition between 30-50% WFPS (strong regulation) and one that allowed optimal conditions from 30-70% WFPS (weak regulation). Both curves were otherwise similar to the Frolking et al. (1996) parameterization.

Fire return interval and fire severity

The influence of fire in the model includes the effects of combustion and soil thermal changes. Fire is modeled to burn a small fraction of $C_{s+b}$ (Table 2) and a fraction of all other exposed C pools, which includes the surface SOC pool(s), and $C_r$ in the surface organic layer (Kasischke et al., 1995; Harden et al., 2000). All fires are stand killing, resulting in the transfer of all $C_r$ into the single SOC pool for the single pool model simulations or into both $C_f$ (85% of $C_r$) and $C_c$ (15% of $C_r$) in the multiple pool simulations. All unburned surface moss and needles immediately become $C_f$, while in the aboveground pools, the black spruce stems and branches ($C_{s+b}$) become standing-dead stems and branches ($C_{s-d}$) and have a lag before entering the soil and contributing to the detrital soil C. This model version does not attempt to include changes in the soil thermal regime due to changes in soil albedo or soil water content following fire, although these effects may be large and important (Chapin, 2000).

We tested the model sensitivity to fire return interval by using a 200 year interval as supported by research from continental Canada (B. J. Stocks, personal communication) as well as a fire return interval of 150 years based on measures of fire intervals observed in Alaska for moderately drained systems (Kasischke, 1995). In addition, we used two different levels of burn severity for consumption of surface moss, black spruce needles, and surface organic soil. One set was based on a burn severity of 30% of available fuels (Harden, 2000) and the other was based on a lower burn severity of 20% (Table 3).

Evaluation of model scenarios

Since boreal forests can vary widely based on soil drainage and stand age, we selected the NOBS site as our reference site in order to test the model structure and parameterizations. To evaluate the model simulations, we employed two different measures of goodness of fit that represent different aspects of model function. We compared modeled total C to site C to
examine which parameters have the largest effect on C estimates. We also compared modeled and site soil $^{14}$C profiles to examine the distribution of C through the soil. For total C, we calculated the relative deviation (RD) in total soil C from the NOBS soil profile for each simulation. For the goodness of fit in the radiocarbon profile, we interpolated the NOBS radiocarbon depth record and compared simulated radiocarbon values throughout the profile to the interpolated radiocarbon values for NOBS at the same layer depth. We used an unweighted root-mean square deviation (RMSD) for this measure. In order to combine the two different measures of fit, we ranked the values of the two measures separately and then calculated the average of the rank for each simulation with equal weighting for both total C RD and the $^{14}$C RMSD. The lower the average rank, the better the overall fit to the NOBS data.

**Statistical Tests**

The series of parameters described above were run in a full factorial design resulting in 288 hundred individual simulations. To evaluate the quantitative importance of each factor on soil C accumulation (total C) or distribution ($^{14}$C RMSD), we carried out main effects analysis of variance (ANOVA). All statistical tests were carried out in Statistica (Statsoft Inc., Version 7, Tulsa, OK, USA). We also carried out a rank based analysis by evaluating the 10 simulations that had the lowest, equally weighted combination, of $^{14}$C RMSD and total C RD.

**Results**

The batch simulations resulted in a span of C accumulation from 10.4 kg C m$^{-2}$ to 207 kg C m$^{-2}$. The distribution of C, and $^{14}$C in particular, throughout the soil profile, shows that the model simulations were capable of capturing the observed $^{14}$C depth pattern quite well (Figure 4). The simulation data were plotted accordingly, and show that the simulations varied considerably in the depth of the primary bomb-spike from a low of 18 cm to a high of 34 cm, reflecting either too little (18 cm) or too much (34 cm) C accumulation since the late 1950s. The model simulations were able to dynamically grow soil layers and resulted in the change in total organic soil layer depth with time and especially immediately following fire.

The structure of the SOC pool (and associated lability or recalcitrance) and carbon input rate (NPP) were the two most important factors in determining total C and the $^{14}$C RMSD in simulations (Figure 5, ANOVA results in Table 4). The accuracy ($^{14}$C RMSD) of model-data comparisons of the $^{14}$C soil profile was primarily determined by the rate of carbon input (and rate
of increase in soil depth) whereas a greater number of variables had a statistically significant
effect on total carbon content estimates including soil permafrost history, $Q_{10}$, and fire severity
(ANOVA F values in Table 4).

The overall behavior of individual model runs for both total C RD and $^{14}$C RMSD is
illustrated in Figure 5. The average simulation rank of the total C deviation and the $^{14}$C RMSD
values suggests that the historically colder scenarios were consistently important in accurate
simulation of the NOBS data. Among the top ten simulations, the optimal $Q_{10}$ was 3 and the top
6 simulations all had fire severity of 20% with the remaining 4 simulations at 30% fire severity.

Of the two parameter sets that were most influential (based on the ANOVAs), the top ten
simulations either had 225 g C m$^{-2}$ yr$^{-1}$ NPP coupled with the multiple-pool humic SOC structure
or 180 g C m$^{-2}$ yr$^{-1}$ NPP coupled with the single-labile SOC pool structure (Table 5). The single-
recalcitrant SOC pool structure consistently yielded a poor fit to the data based on the goodness
of fit criteria used. Examination of the top ten simulations shows that while the simulated $^{14}$C
data tracked very well from 20-48 cm, the surface 0-20 cm and the deeper 48-70 cm were two
areas where there was more significant model/data mismatch (Figure 4). The best adjustment to
the mismatch was provided by model runs with historic permafrost.

Discussion

The ability of boreal soils to store soil C over millennia has resulted in a large
accumulation of terrestrial C (Gorham 1991; Harden et al., 1992; Rapalee et al., 1998) and this
modeling analysis suggests that the rate of NPP and the lability/recalcitrance of soil organic
matter are the most critical factors in determining the rate of accumulation and distribution of
soil carbon in a boreal forest. Boreal ecosystems have relatively large stocks of organic matter
compared to other ecosystems and a number of investigators have suggested that boreal and
arctic surface vegetation (particularly mosses) produce recalcitrant organic matter (Hobbie,
2000) that may be responsible, in part, for rapid rates of C accumulation. Measurements of soil
radiocarbon profiles (Trumbore and Harden, 1997) also show slow apparent turnover times that
decline substantially with soil depth and which are much older than values at comparable depths
in temperate ecosystems (Trumbore, 2000). However, various suggestions of high boreal
organic matter recalcitrance and slow apparent turnover times contrast, to some degree, with
other work that indicates that boreal soils have relatively rapid potential turnover rates compared
to temperate zone soils (Neff and Hooper, 2002, Dioumaeva et al., 2002). The resolution of the
debate over what factors control boreal decomposition is critical in light of rapid temperature
changes leading to thawing permafrost, changes in fire frequency and severity, and the
possibility of large soil carbon losses in coming decades (Gorham 1991; Shaver et al., 1992;
Kasischke et al., 1995; Chapin et al., 2000; McGuire et al., 2002).

The model analysis presented here for a black spruce/Sphagnum moss system illustrates
that carbon input rates and disturbance are important factors controlling boreal SOM cycling. In
this sense, boreal ecosystems are similar to temperate and tropical ecosystems (Randerson, 1996
#6). However, SOM dynamics in boreal ecosystems are substantially different from temperate
or tropical ecosystems in some critical ways. This modeling exercise suggests that, unlike many
tropical or temperate ecosystems, boreal SOM does not need to be exceptionally recalcitrant to
accumulate (Krull, 2003 #4). Consistently, the best model fits to both total C and 14C SOC
distributions were scenarios with the fastest inherent/potential turnover time which are based on
laboratory incubations (Neff, 2002, 2002, Dioumaeva et al., 2002), but which are then modified
based on temperature and moisture conditions. For both our single pool labile (S_l) and
recalcitrant (S_r) cases, we started with field-based turnover times and in the case of the S_r
scenarios, further reduced turnover with our temperature and moisture scalars. In the S_l scenario
a faster inherent turnover is introduced and then adjusted downward by temperature and
moisture. One interesting result of these scenarios is that the labile decomposition scenario (S_l)
combined with the highest NPP inputs and temperature regulation of decomposition can be used
to explain both the C stock and isotope profile (Figure 5). By contrast, the slow decomposition
(S_r) scenario, especially when combined with the two highest NPP input values lead to
substantial overestimation of soil carbon stocks. Overall, simulation of isotopic profiles in soils
is more sensitive to parameter variation than simulation of total carbon. Whereas many of the
simulations accurately predict total soil carbon, they do a very poor job predicting the
propagation of the bomb spike through the soil profile (seen as high 14C RMSD in figure 5).
These results indicate that accurate simulation of total carbon (a typical metric for model
performance) may not be evidence for appropriate representation of underlying model
mechanisms.

This analysis suggests that one mechanism for carbon preservation in boreal soils is the
interaction between organic surface layers and the thermal characteristics of boreal soil profiles.
As boreal soils develop, slowly decomposing moss litter provides an increasingly thick organic
mat which in turn causes deeper soils to become progressively colder (Yoshikawa, 2002 #2246).
In this model analysis, both $Q_{10}$ and the history of soil thermal properties (i.e., historical
permafrost and 20th century warming) played a role in carbon accumulation in the model
simulations. Neither of these scenarios, however, fully addresses the basic role of temperature in
boreal C preservation. The temperature gradient between surface and deep soils in the Manitoba
site in summer months can exceed 10°C (Figure 2). Even within the top 50 cm of soil, there are
gradients of 5-8°C during July and August. Given a $Q_{10}$ of 2-3, these gradients can result in a
50-300% difference in mid summer decomposition between surface and deep soils of similar
recalcitrance. Following the factorial analyses described in the results, we carried out an
additional simulation in which we set the temperature of the entire soil profile equal to that of
surface soils. This constant temperature simulation is inherently unrealistic but it offers insight
into the role of the thermal characteristics of the soil profile on decomposition. When the
thermal gradients of the soil profile are removed, total simulated SOM content at the end of a
model run was 30-40% of the top ten runs shown in Table 5. This feedback between soil depth
(as influenced by C input rate and SOM decomposition structure), temperature, and carbon
preservation is critical to understanding and modeling boreal soil C accumulation. In a general
sense, boreal SOM accumulates because there is an interaction between moderate litter
recalcitrance and the cooling that occurs in soils as organic matter accumulates in a boreal
ecosystem. The resulting organic matter profile can have exceptionally old radiocarbon values
if C persists between fire events, but this modeling analysis highlights how the interaction of
temperature and recalcitrance yields soil organic matter with exceptionally slow apparent (but
much faster inherent) turnover times.

For all the reasons discussed above, boreal soils appear to have very different
mechanisms influencing decomposition than all but the most extreme (e.g. alpine) temperate or
tropical soils, particularly in the interactions between organic layer depth and soil profile
temperatures. However boreal soils are also very diverse, particularly with regard to soil
moisture content. In a drier setting, fire may play a larger role in recalcitrance and turnover than
presented here, particularly when fires can burn to mineral soils and have large impacts on
nutrient content, plant substrates, and SOM composition (Harden et al., 2004; Neff et al., 2005).
For drier boreal systems, changes in fire return intervals with climate change (Gillett, 2004 #2),
could be a major future control on soil C flux. There are also much wetter soils than those
modeled here and for those soils, more work is needed to understand (and parameterize for
modeling) moisture limitations to decomposition. Finally, permafrost cover through much of the
boreal region is discontinuous (Brown 1969). The site used in this analysis in Manitoba,
Canada does not currently have permafrost but the soil $^{14}$C profile suggests that the loss of
permafrost may have been relatively recent. The discontinuity around 50 cm in the $\Delta^{14}$C
accumulation curve at the NOBS site (Figure 4) suggests that permafrost used to be present but
has disappeared over the past century. Loss of permafrost, coupled with a relatively high,
inherent decomposability of boreal soils, suggest that more attention should be paid to the
mechanisms that control both surface and deep boreal carbon storage in both models and field
experiments.

**Implications**

In this paper, we used a range of techniques to estimate parameters for modeling, but the
accuracy of this exercise is to some degree limited by the data available from field and laboratory
studies. This is particularly true for estimates of soil organic matter turnover times and above
and belowground NPP. These factors play a major role in boreal C accumulation rates in the site
we examined and in general remain difficult to estimate. While better boreal parameter
estimates might improve our modeling ability, much more work is needed to better represent the
unique characteristics of boreal ecosystems in regional and global ecosystem models. This
analysis clearly illustrates that boreal soil carbon models need to be vertically resolved,
mechanically sophisticated, and capable of simulating millennial scale changes in soil carbon
dynamics in order to capture key aspects of contemporary boreal C cycling, let alone predict
future changes in boreal C cycling. The carbon pool structure for northern soils is probably best
captured by discreet representation of soil depth as it relates to physical processes (Trumbore,
1997). Several factors are critically important to include in future boreal modeling exercises.
First, most large scale ecosystem models simulate only a single layer of SOC dynamics and this
analysis illustrates the potential risk of ignoring the role of deeper soils (and historical
permafrost) in current day modeling analyses. Second, most ecosystem models have their
origins in the temperate zone, and include parameterizations that represent the role of
aggregation and sorption on soil carbon storage. Such mechanisms do not apply to the deep
organic horizons of boreal systems, which illustrates that inclusion (implicit or explicit) of
recalcitrance due to physical stabilization mechanisms in boreal models may risk significant
underestimates of the potential for decomposition in a changing climate. Finally, this study illustrates that boreal decomposition dynamics are tightly coupled to the physical/thermal properties of soils; the same coupling is needed in models if we hope to simulate the fundamental controls on boreal carbon cycling.

Acknowledgements

We thank H. Veldhuis, Q. Zhuang, A. D. McGuire, and two anonymous reviewers for their helpful comments on an earlier manuscript and to Merritt Turetsky for earlier discussions. This work was supported by grants from the NSF (DEB 0077881) and (OPP 0115744).

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Substrate limitations for heterotrophs: Implications for models that estimate the seasonal


FIGURE CAPTIONS:

Figure 1. Depth profile of carbon density used in the model to determine soil layer depth. Layer thickness was based on a relationship between cumulative C calculated from this C density curve and the basal depth of each layer. Data used to develop this C density curve is based on poorly drained soils in the BOREAS Northern Study Area.

Figure 2. Diagram of the layered boreal C cycle model. Carbon enters the system in the live pools shown here in gray. Detrital soil carbon pools are shown in thick black boxes. In single pool simulations (a), a humic C pool is not used and so byproducts from decomposition are recycled into the single C pool. However, in the multi-pool simulations (b) a humic C pool is incorporated and receives C from both fine and coarse C pools. Following fire the surface layer (z1) is created, burying the deep layers beneath it during regrowth.

Figure 3. Monthly temperature and water filled pore-space profiles based on data collected from the BOREAS Northern Study Area Old Black Spruce site. Data shown is average of record from 1994-1996 with (a) temperature recorded at 5, 10, 20, 50, and 100 cm depth and (b) water filled pore-space content recorded at 7.5, 22.5, 45, 75, 105 cm depth. Note that the extreme soil temperatures are found in the top 10-20 cm of the soil with temperature fluctuations dampened in the deeper soil. Water filled pore space increases in the surface soil in May and June and water moves into deeper soil for the remaining summer months and into fall. The white line across both panels indicates the transition from organic to mineral soil in the figure.

Figure 4. Modeled radiocarbon profile distributions for all 288 simulations overlaid on the plot of NOBS data. NOBS data is represented by error bars showing the value of $\Delta^{14}C$ and the layer thickness represented by the value. The primary bomb-spike in the surface soil is based on sphagnum only, while the smaller bomb-spike and old radiocarbon of the deeper soil reflects the bulk soil radiocarbon for that depth. The 10 simulations with the best overall fit to the NOBS data are shown in black.
Figure 5. A scatterplot showing the distribution of simulations based on the two measures of fit to the observed NOBS data. Data are categorized based on net primary productivity parameters (135, 180, 225 g C m$^{-2}$ yr$^{-1}$) and the soil C pool structure (single pool – recalcitrant, single pool – labile, and a multi-pool humic approach). The relative deviation of cumulative C indicates whether accumulation of C in the simulation met the target amount and values close to zero on both axes are closest to field data.
Table 1. Model equations. The variable $t$ is time in years since fire. The function $f[T(z), M(z)]$ represents the temperature ($T(z)$) and moisture ($M(z)$) scalars used to regulate depth-dependent turnover rates. Soil pools are layer dependent and are indicated as such by the subscript $z$ representing soil layer depth. Refer to methods for further details.

Table 2. Fixed model parameters used in all model simulations.

Table 3. Model parameterizations.

Table 4. Main effects ANOVAs for all simulations based on total C RSD and $^{14}$C RMSD.

Table 5. The 10 best simulations based on average rank of total C RSD and $^{14}$C RMSD and the corresponding parameters used for each simulation.
<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Equation</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$C_{m+n}$</td>
<td>Live moss and needle C</td>
<td>$\frac{dC_{m+n}}{dt} = NPP(alloc_{m+n})(1 - e^{-0.1t}) - k_{m+n} C_{m+n}$</td>
<td>kg C m$^{-2}$</td>
</tr>
<tr>
<td>$C_r$</td>
<td>Live root C</td>
<td>$\frac{dC_r}{dt} = NPP(alloc_{r,z})(1 - e^{-0.1t}) - k_{r} C_{r,z}$</td>
<td>kg C m$^{-2}$</td>
</tr>
<tr>
<td>$C_{s+b}$</td>
<td>Live stem and branch C</td>
<td>$\frac{dC_{s+b}}{dt} = NPP(alloc_{s+b})(1 - e^{-0.1t}) - k_{s+b} C_{s+b}$</td>
<td>kg C m$^{-2}$</td>
</tr>
<tr>
<td>$C_{s-d}$</td>
<td>Standing dead C</td>
<td>$\frac{dC_{s-d}}{dt} = k_{s+b} C_{s+b} - k_{s-d} C_{s-d}$</td>
<td>kg C m$^{-2}$</td>
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<tr>
<td>$C_c$</td>
<td>Coarse soil C</td>
<td>$\frac{dC_c}{dt} = k_{s-d} C_{s-d} + (1 - frac_e) k_{r} C_{r,z} - f[T(z)M(z)] k_{c} C_{c,z}$</td>
<td>kg C m$^{-2}$</td>
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<tr>
<td>$C_f$</td>
<td>Fine soil C</td>
<td>$\frac{dC_f}{dt} = k_{m+n} C_{m+n} + frac_f k_{r} C_{r,z} - f[T(z)M(z)] k_{f} C_{f,z}$</td>
<td>kg C m$^{-2}$</td>
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<tr>
<td>$C_h$</td>
<td>Humic soil C</td>
<td>$\frac{dC_h}{dt} = f[T(z)M(z)](1 - m_{eff})(k_{f} C_{f,z} + k_{c} C_{c,z} - k_{h} C_{h,z})$</td>
<td>kg C m$^{-2}$</td>
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<tr>
<td>$C_{CO2}$</td>
<td>Respired C</td>
<td>$\frac{dC_{CO2}}{dt} = f[T(z)M(z)][m_{eff}(k_{f} C_{f,z} + k_{c} C_{c,z} + C_{h,z})]$</td>
<td>kg C m$^{-2}$</td>
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*This pool acts as the single soil C pool in the single-labile and single-slow model versions.*
TABLE 2.

<table>
<thead>
<tr>
<th>Variable</th>
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<th>Value</th>
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<td>alloc_{m+n}</td>
<td>Moss + needle NPP allocation</td>
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<td>alloc_{r}</td>
<td>Root NPP allocation</td>
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<td>alloc_{s+b}</td>
<td>Stem and branch NPP allocation</td>
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<td>frac_{fr}</td>
<td>Fine root fraction of root C</td>
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<td>m_{eff}</td>
<td>Microbial efficiency</td>
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<td>k_{s+b}</td>
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<td>yr^{-1}</td>
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<td>k_{s-d}</td>
<td>Standing dead stem and branch decay constant</td>
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<td>Live moss and needle decay constant</td>
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<td>k_{r}</td>
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<td>1.25 x 10^{-1}</td>
<td>yr^{-1}</td>
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<td>--</td>
<td>Root zone distribution (exponential decline)</td>
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<td>Φ_{s+b}</td>
<td>Stem and branch fire severity (combustion loss)</td>
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<td>%</td>
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TABLE 3.

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<td>Net primary production ($NPP$)</td>
<td>0.135, 0.180, 0.225 (kg C m$^{-2}$ yr$^{-1}$)</td>
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<td>SOC pool structure decay constants</td>
<td>Single pool–recalcitrant ($S_r$) ($k$: 0.018 yr$^{-1}$), single pool–labile ($S_l$)($k$: 0.027 yr$^{-1}$), multi-pool–humic ($M_h$) ($k_c$: 0.037 yr$^{-1}$, $k_c$: 0.107 yr$^{-1}$, $k_h$: 0.023 yr$^{-1}$)</td>
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<td>Soil fire severity</td>
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<td>Fire return interval</td>
<td>150, 200 (yr)</td>
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<td>Moisture regulation</td>
<td>Weak, strong</td>
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<tr>
<td>C pool structure (Sl, Sr, Mh)</td>
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<td>Fire Return Interval</td>
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<td>Soil Moisture Regulation</td>
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