Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage

K.L. Manies, J.W. Harden, B.P. Bond-Lamberty, and K.P. O'Neill

Abstract: This study investigated the role of fire-killed woody debris as a source of soil carbon in black spruce (*Picea mariana* (Mill.) BSP) stands in Manitoba, Canada. We measured the amount of standing dead and downed woody debris along an upland chronosequence, including wood partially and completely covered by moss growth. Such woody debris is rarely included in measurement protocols and composed up to 26% of the total amount of woody debris in older stands, suggesting that it is important to measure all types of woody debris in ecosystems where burial by organic matter is possible. Based on these data and existing net primary production (NPP) values, we used a mass-balance model to assess the potential impact of fire-killed wood on long-term carbon storage at this site. The amount of carbon stored in deeper soil organic layers, which persists over millennia, was used to represent this long-term carbon. We estimate that between 10% and 60% of the deep-soil carbon is derived from wood biomass. Sensitivity analyses suggest that this estimate is most affected by the fire return interval, decay rate of wood, amount of NPP, and decay rate of the char (postfire) carbon pool. Landscape variations in these terms could account for large differences in deep-soil carbon. The model was less sensitive to fire consumption rates and to rates at which standing dead becomes woody debris. All model runs, however, suggest that woody debris plays an important role in long-term carbon storage for this area.

Résumé : Cette étude porte sur le rôle des débris ligneux laissés par le feu en tant que source de carbone dans le sol sous des peuplements d'épinette noire (*Picea mariana* (Mill.) BSP) du Manitoba, au Canada. Les auteurs ont mesuré la quantité de chicots et de débris ligneux au sol le long d'une chronoséquence sur des hautes terres, incluant le bois partiellement et complètement couvert de mousse. Ce genre de débris ligneux qui est rarement inclus dans les protocoles expérimentaux compte pour 26 % de la quantité totale de débris ligneux dans les vieux peuplements, indiquant qu'il est important de mesurer tous les types de débris ligneux dans les écosystèmes où ces débris peuvent être recouverts par de la matière organique. Sur la base de ces données et des valeurs existantes de productivité primaire nette, ils ont utilisé un modèle de bilan massique pour évaluer l'impact potentiel du bois tué par le feu sur le stockage de carbone à long terme dans ce site. La quantité de carbone emmagasiné dans les horizons organiques plus profonds du sol a été utilisée pour représenter ce carbone qui persiste pendant des milliers d'années. Ils ont estimé que 10 % à 60 % du carbone enfoui profondément dans le sol provient de la biomasse ligneuse. Des analyses de sensibilité indiquent que cette estimation est surtout affectée par l'intervalle entre les feux, le taux de décomposition du bois, la productivité primaire nette et le taux de décomposition du pool de carbone sous forme de résidus carbonisés (après feu). Sur cette base, les variations du paysage pourraient expliquer les grandes différences dans la quantité de carbone enfoui dans le sol. Le modèle est moins sensible au taux auquel la forêt est consumée par le feu et au taux auquel les chicots deviennent des débris ligneux. Cependant, tous les essais avec le modèle indiquent que les débris ligneux jouent un rôle important dans le stockage à long terme du carbone dans cette région.

[Traduit par la Rédaction]

Introduction

Although woody debris has long been recognized as an important component of forested ecosystems for factors such as animal habitat (Pedlar et al. 2002), sediment transport (Harmon et al. 1986), and nutrient cycling (Sollins 1982; Hart 1999; Holub et al. 2001), the role of woody debris in carbon (C) cycling is a relatively new focus (Krankina and Harmon 1995; Tarasov 2000; Yatskov et al. 2003). Many of these studies have concentrated on the potential of woody debris to be a source of atmospheric carbon dioxide (CO_2; Krankina and Harmon 1995; Knohl et al. 2002; Wang et al. 2002; Bond-Lamberty et al. 2003). However, given its low surface area and high lignin content (Harmon et al. 1986), woody debris is also important to long-term C storage, particularly in ecosystems such as the boreal forest.

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Boreal forests, which usually occur between latitudes 45°N and 70°N, contain over 30% of the world's terrestrial C (combined plant and soil; Post et al. 1982; Kasischke 2000). The large amount of C stored within this biome results from a unique combination of long periods of light during the growing season (which promote relatively high rates of plant growth) and cold soil temperatures that limit annual rates of decomposition. The balance of these inputs and losses has tended to result in a small long-term net C sink (Ciais et al. 1995; Harden et al. 1997; Kasischke 2000). However, boreal forests are projected to undergo significant changes due to global climate change (Cubasch et al. 2001). Therefore, there is great interest in furthering our understanding of the boreal C cycle and what changes may occur within this system in the future (cf. Sellers et al. 1997; Kasischke and Stocks 2000; Hom 2003).

Two main pathways of C loss from boreal forests are decomposition and fire. On average, over 5.6×10^6 ha of boreal forest burn annually (Stocks 1991), and the amount of C lost through fire emissions alone can be quite large (Amiro et al. 2001). Over millennial timescales, Harden et al. (2000) estimated that 10% to 40% of C gained through net primary productivity (NPP) could be lost to the atmosphere as a result of combustion. Their study used soil C storage as an index for long-term net ecosystem production (NEP), which is the balance between the inputs (NPP) and losses (decomposition, combustion, and lateral exports) of C to an ecosystem (Randerson et al. 2002). Harden et al. (2000) recognized the large impact of coarse wood on their model results and that the effects of this pool had not been fully investigated. To address this problem, we measured the amount of woody debris along a boreal chronosequence, used these data to estimate the decay rate of this material, and added wood as a separate component to their model. This new model was used to test the impact of wood-based C inputs on the long-term C storage of a feather moss – black spruce (*Picea mariana* (Mill.) BSP) ecosystem in Manitoba, Canada.

Methods

Field data

Woody debris inventories were performed near Thompson, Manitoba (55°53′N, 98°20′W), an area associated with the Boreal Ecosystem Atmosphere Study (BOREAS), and a subsequent investigation was performed of black spruce stands that regenerated from fires in 1998, 1995, 1989, 1981, 1964, 1930, and 1850 (Bond-Lamberty et al. 2004; Wang et al. 2003). The 1850 site, known as the northern study area – old black spruce site (NSA–OBS) was extensively studied during the BOREAS project (Sellers et al. 1997).

Downed woody debris was measured using the line intersect method (Brown 1974; Harmon and Sexton 1996). Eighteen to 20 transects that were 20 m long were located at each site. To reduce directional effects (e.g., dominant wind direction and slope effects), transects were placed along two main axes that were set at right angles to each other. Fine woody debris (<7 cm diameter) was tallied into one of five size classes (diameters of 0.0–0.49, 0.50–0.99, 1.0–2.99, 3.0–4.99, and 5.0–6.99 cm) and its location was classified as either above or below ground (<50% or 50%–99% buried by forest floor organic matter, respectively). Species, diameter (cm) at transect intersection, and decay class were also recorded for coarse woody debris (≥7 cm diameter). Decay class categories were (1) bark and wood intact, knife unable to penetrate samples; (2) wood beginning to get mealy, still hard for knife to penetrate sample; (3) wood mealy throughout, knife can penetrate sample somewhat; (4) wood can be broken into pieces, knife easily penetrates sample; and (5) sample no longer holds shape and splits into small pieces. At sites where moss regrowth was extensive enough to bury fire-killed remains, 10-m sections of three randomly selected transects were excavated to the mineral soil. Any woody debris entirely covered by organic matter (buried wood) was recorded using the same protocol as defined above. It was also noted whether the wood showed evidence of fire (e.g., charring). Data were converted to mass of wood per unit ground area using formulas and fuel load multipliers (based on species and size class) for central Manitoba (Nalder et al. 1999). Mass values were converted to C and a concentration of 48% was assumed (Schlesinger 1997).

Model structure

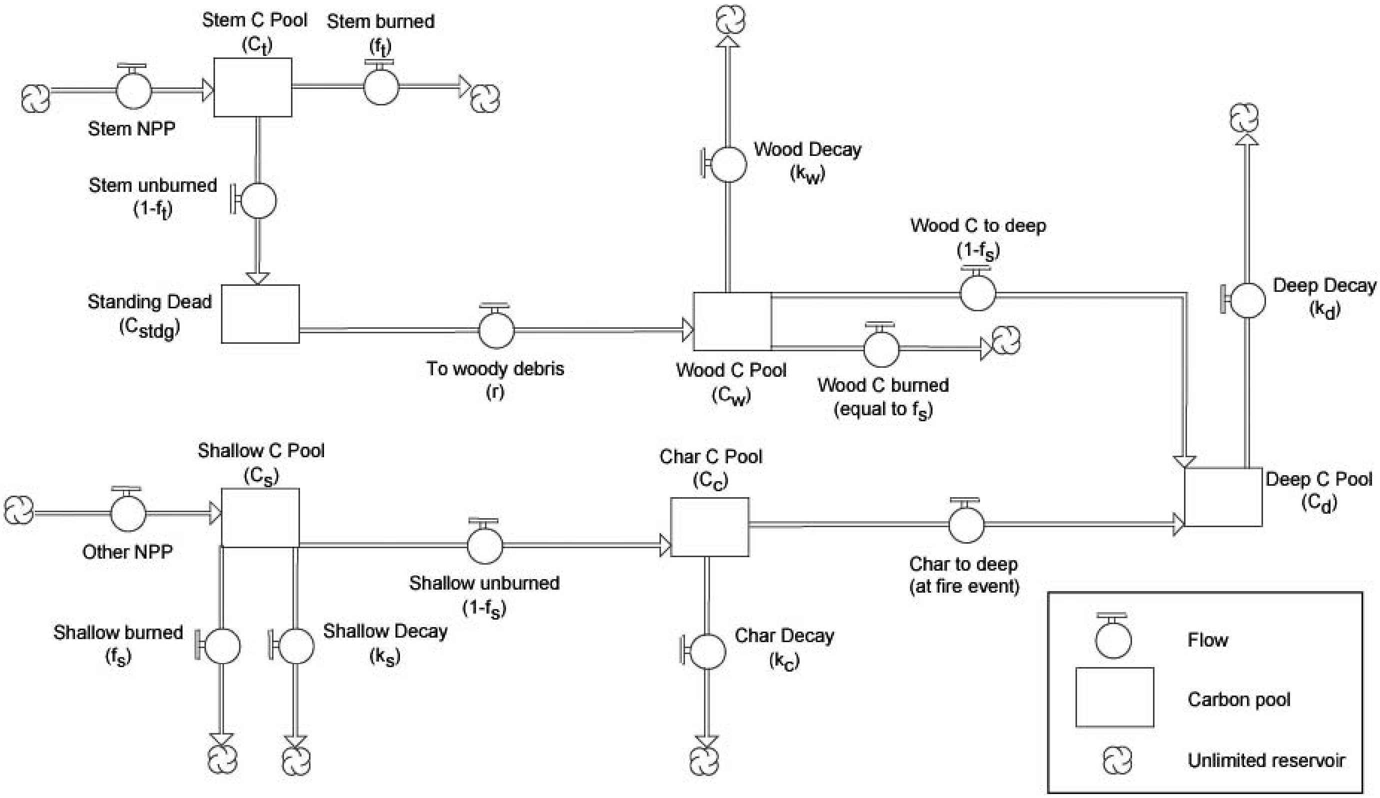
The model structure of Harden et al. (2000) is based on a mass-balance approach in which changes in ecosystem C over time are calculated as the difference between system inputs and outputs. This model accounts for inputs from NPP and losses from fire and decomposition by implementing fire cycles during which vegetation growth, decay, and loss from burning occurred in different soil C pools. Losses to herbivory and exports of dissolved organic C were not addressed. We modified this model by explicitly allocating aboveground NPP between tree stems and other aboveground components (tree branches and foliage, understory, and moss) and by allowing this stemwood to burn and decay at different rates than the other ecosystem components (Fig. 1). The model structure, which was created with Stella version 6.0.1 software (High Performance Systems, Inc., Lebanon, New Hampshire) using Euler's method of integration, takes the following form:

$$[1] \quad dC/dt = \mathrm{NPP}_{\mathrm{stem}} + \mathrm{NPP}_{\mathrm{other}} - C_{\mathrm{s}}(k_{\mathrm{s}} + f_{\mathrm{s}}) - C_{\mathrm{t}} f_{\mathrm{t}} - C_{\mathrm{w}}(k_{\mathrm{w}} + f_{\mathrm{s}}) - C_{\mathrm{c}}k_{\mathrm{c}} - C_{\mathrm{d}}k_{\mathrm{d}}$$

where C is carbon, t is time, $\mathrm{NPP}_{\mathrm{stem}}$ is the net primary productivity of tree stems, $\mathrm{NPP}_{\mathrm{other}}$ is the net primary productivity of other aboveground components, C_{s} is the pool of shallow, or more labile, carbon (see text below), k_{s} is the decay rate of shallow carbon, f_{s} is the fraction of biomass lost to fire from the shallow C pool, C_{t} is the pool of carbon in stemwood, f_{t} is the fraction of biomass lost to fire from tree stems, C_{w} is the pool of carbon in downed woody debris, k_{w} is the decay rate of downed woody debris, C_{c} is the pool of charred carbon (created from previous fire events), k_{c} is the decay rate of the char pool, C_{d} is the pool of deep, or more recalcitrant, carbon (see text below), and k_{d} is the decay rate of the deep carbon pool.

The shallow pool of carbon (C_{s}) consists of all aboveground components other than tree stems (e.g., moss, tree, and understory litter). In the 1850 (NSA–OBS) burn site this pool is analogous to the recently created (within decades) organic matter usually found within the top 10 cm of the forest floor (data not shown). Carbon within this pool is considered

Fig. 1. The basic model structure. Long-term carbon storage is modeled as the net balance of carbon inputs from net primary production (NPP) and losses due to decomposition and fire combustion. Incorporation into tree stems provides one pathway for carbon to reach deep-soil C. Other ecosystem components (tree foliage, tree branches, understory, and moss) provide another pathway.



fairly labile and decomposes at a relatively fast rate (k_s; Table 1). After a fire, unburned material within C_s ($1 - f_s$) is transferred to the char pool (C_c). This pool decays at its own first-order decomposition rate, k_c. Very little is currently known about the value k_c, despite its importance to C storage (Harden et al. 2000). Therefore, k_c was set equal to k_s for these analyses. Ultimately, C within the char pool (C_c) is buried by moss growth and becomes part of the deep-soil C pool (C_d). The deep-soil C pool is composed of partially decomposed organic material, which persists for centuries or millennia. In the 1850 (NSA–OBS) burn site, these horizons are usually found just above the mineral soil, 10–25 cm below the moss surface (data not shown). As a result of burial, C within C_d exists in cooler and moister conditions than C_s and is also composed of more recalcitrant material. Therefore, C within C_d decays at a much slower rate, k_d (Trumbore and Harden 1997). Transfers from C_s to C_c and from C_c to C_d were set to occur only at each fire event.

The current version of the model differs from that of Harden et al. (2000) in its treatment of tree stems. In the new model, C is explicitly allocated to tree stems (C_t), which combust at a severity independent of other ecosystem components (f_t). After a fire, unburned tree stems are transferred to a pool of standing dead (C_{stdg}), defined as trees that stand at an angle ≥45° from the forest floor (Harmon and Sexton 1996). The model assumes that the decay of standing dead is negligible (Sander and Wein 2000; Storaunet and Rolstad 2002). Standing dead is transferred over time (at rate r) to the pool of downed woody debris (C_w). C_w is allowed to decay at its own rate, k_w. At the next burn cycle, remaining downed woody debris is combusted at the rate of other ecosystem components (f_s) and the remainder is transferred to C_d. Annual mortality and a lag between the creation of standing dead and the time when the trees begin to fall over are not included in the model. Tests indicated that these factors had little impact on our results and did so in ways that increased the contribution of woody debris on long-term C storage. Therefore, these factors were excluded to maintain as simple a model structure possible. Model runs lasted over 6400 years with an annual time step.

Model parameters

To assess the effects of changes in the model structure, an initial model run was made using the same input parameters as used by Harden et al. (2000). Next, the model was run using default parameters, which were our best estimate for each parameter. These values reflect the current state of knowledge and should provide a more accurate portrayal of the role of wood inputs on long-term storage. To address natural variability and measurement error in each parameter, model runs were also performed using minimum and maximum estimates for each parameter, with each parameter run individually. These runs allowed us to explore the sensitivity of deep-soil C to the range of possible values for each wood-based input parameter. An additional run was performed in which parameters were adjusted to minimize the impact of wood on the deep-soil C pool (e.g., minimum stem NPP, maximum k_w, etc.). Some model runs resulted in unrealistic values of

Table 1. Model inputs and initial constraints for an upland feather moss – black spruce boreal ecosystem.

	Stem NPP (kg C ·m^{-2}·year^{-1})^{a,b}	Other NPP (kg C·m^{-2}·year^{-1})^{b}	Shallow C pool turnover time, $1/k_s$ (year)^{c}	Wood C pool turnover time, $1/k_w$ (year)^{d}	Deep C pool turnover time, $1/k_d$ (year)^{c}	Standing dead turnover time ($1/r$) (year)	Fire return interval (year)^{e}	Bole consumption, f_t (%)	Other consumption, f_s (%)^{f}
Harden et al. 2000	0.070	0.080	55	55	550	n/a	80	44	44
Default	0.064	0.069	55	52	550	9.0	80	5	44
Minimum	0.053	0.063	—	30	—	5.4	—	0	22
Maximum	0.072	0.116	—	103	—	27.5	—	26	53
Literature	0.064–0.070	0.055–0.082	55–250	30–103	250–1667	—	70–500	—	22–53

Note: The decay rate of wood (k_w) was calculated using data presented in this paper. Other values are based on previously published data by the authors or literature sources. See the text for more information regarding the source of data and the determination of minimum and maximum values for sensitivity analyses. (Dashes indicate that sensitivity analyses were not performed for that variable.)

[a] Values used by Harden et al. (2000) for stem NPP included both stem and branch NPP.

[b] Default stem NPP based on data presented by Bond-Lamberty (2004). Literature values based on Bond-Lamberty (2004) and stem plus branch NPP values in a publication by Gower et al. (1997) assuming 89% of stem plus branch NPP is stem-based.

[c] Default values, used by Harden et al. (2000), are based on values from Trumbore and Harden (1997). Literature values also from Trumbore and Harden (1997).

[d] Default value based on field data presented in this paper. Literature values based on values given by Bond-Lamberty et al. (2004) and Storaunet and Rolstad (2002).

[e] Default value based on value used by Harden et al. (2000). Literature values from Johnson (1992), Kasischke et al. (1995), and Harden et al. (2000).

[f] Default and literature values based on value used by Harden et al. (2000).

C_d (i.e., outside of literature values; see Table 2). When this occurred, parameter values were increased or decreased until C_d was within these limits, and this is noted in the results.

NPP_{stem} and NPP_{other}

NPP values for each individual ecosystem component were based on field measurements for the 1850 (NSA–OBS) burn site. Default NPP values for tree stem, branches, and foliage as well as understory were based on the data of Bond-Lamberty et al. (2004). The default moss NPP value was based on adjusted NPP estimates of Trumbore and Harden (1997). Because their value represents all inputs to surface organic matter (moss plus foliar), it was corrected by subtracting foliage detritus using the values of Gower et al. (1997). Nonstem NPP was estimated as the sum of moss, understory, tree branch, and tree foliage values. Sensitivity runs were based on 95% confidence intervals calculated for each individual ecosystem component. The upper and lower limits for each component were used to calculate minimum and maximum NPP values for four runs: (*i*) minimum stem NPP with minimum nonstem NPP, (*ii*) minimum stem NPP with maximum nonstem NPP, (*iii*) maximum stem NPP with minimum nonstem NPP, and (*iv*) maximum stem NPP with maximum nonstem NPP. These combinations allowed us to examine the effects of variable total ecosystem NPP as well as differences in the proportion of NPP allocated to stem versus nonstem components.

Tree stem fire consumption (f_t)

Because living tree trunks do not burn readily, fire ecologists often assume that bole consumption by wildfire is minimal and do not measure this value (Albini and Reinhardt 1995; Stocks and Kauffman 1997). However, the average amount of bole consumption within northern black spruce forests has been estimated to be 5% (Roger Ottmar, personal communication). Field observations of recently burned black spruce sites indicate that often only the bark is consumed during fire, which supports this estimate. Therefore, this value was used as our default estimate. However, C isotope measurements by Schuur et al. (2003) indicated that bole consumption rates could be much higher (16% ± 10% standard deviation). Therefore, the upper limit of bole consumption used in sensitivity analyses was 26% (mean plus 1 standard deviation). The minimum value for bole consumption was set at 0%.

Rates of tree fall (r)

Flow rates between the standing dead and downed woody debris pools were estimated by modeling changes in standing dead within the 1998, 1995, 1981, and 1964 sites (Bond-Lamberty et al. 2003). Fall rate was determined by fitting a single exponential model to these data using SPSS SigmaStat software version 3.0.1 (SPSS Inc., Chicago, Illinois) (a = 1.65 (0.18 SE); b = 0.1108 (0.0192 SE); adjusted r^2 = 0.93), resulting in a turnover time of 9.0 years. Minimum and maximum values used for sensitivity analyses were based on curve fitting for the data plus or minus one standard deviation and resulted in fall rates of 5.4 and 27.5 years. Data for sites that burned before 1964 were not used, because the amount of deadwood in these sites appeared to be influenced

Table 2. Output from the new model, including three main carbon (C) pools: tree stems (C_t); the shallow pool (C_s), which represents a fairly labile pool of C; and the deep pool (C_d), which represents slower decaying long-term soil C.

Source of input values	Tree stem C pool, C_t (kg·m^{-2})[a]	Shallow C pool, C_s (kg·m^{-2})[b]	Deep C pool, C_d (kg·m^{-2})[c]	Deep C pool (C_d) from wood (%)	NPP lost to fire (%)[d]	Fire emissions (kg·m^{-2}·event^{-1})[e]
Harden et al. 2000	5.6	3.4	6.5	49	36	4.3
Default	5.1	4.3	9.5	55	20	2.7
Sensitivity analyses with C_d constrained	4.2–5.8	2.7–4.9	7.0–10.0	39–74	18–27	1.8–3.6
Most conservative wood estimates with k_c constrained by C_d	4.2	4.9	10.0	10	25	3.4
Literature	1.8–6.7	2–4	7–10	no data	18–44	1.4–7.7

Note: Results from four sets of input variables are listed. (1) those used by Harden et al. (2000); (2) our default values; (3) minimum–maximum estimates (modified when the C in the deep pool (C_d) exceeded literature values, see text); and (4) minimum–maximum estimates chosen to minimize the impact of stem-based C on the deep-soil C pool (C_d) while constraining C_d through adjustments to the decay of the char pool (k_c; see text). Output is compared with values found in the literature.

[a] Gower et al. (1997); Van Cleve et al. (1983); and data presented by Bond-Lamberty et al. (2004).

[b] Harden et al. (1997).

[c] Harden et al. (1997); Trumbore and Harden (1997); and Rapalee et al. (1998).

[d] Harden et al. (2000).

[e] Kasischke et al. (2000); Stocks and Kauffman (1997).

by the mortality of trees that were established postburn (see Results).

Decay rates (k_s, k_d, and k_w)

Decay rates of both the shallow (k_s) and deep (k_d) C pools were based on soil gas-exchange chambers and radiocarbon measurements from BOREAS (Trumbore and Harden 1997). The turnover time of the shallow pool ($1/k_s$; 55 years), which is composed of fresh as well as decades-old plant material, is slower than decay rates often associated with fresh material only (Flanagan and Van Cleve 1983). Turnover of the deep pool ($1/k_d$; 550 years) is even slower because of increased recalcitrance and colder–moister conditions. Sensitivity analyses were not performed for variations in these rates.

Decomposition of downed woody debris (k_w) was based on deadwood inventories of the chronosequence (see Field data methods above). The amount of material for each transect within a site was calculated as the sum of above- and belowground woody debris for that transect combined with the average amount of buried woody debris and average amount of standing dead (Wang et al. 2002; Bond-Lamberty et al. 2003) for that site. Wood decay was estimated as the change in the amount of dead woody material when regressed against stand age using a single negative exponential model (a = 53 451 (7 061 SE); b = 0.0194 (0.0036 SE); adjusted r^2 = 0.46; SPSS SigmaStat software). Only three time periods were used in this analysis: 1981, 1964, and 1930. Data from the 1998 and 1995 sites were not used because no change was observed in the amount of dead woody material, only in the form of the material (see Results). Data from the 1850 site were not included because the amount of dead woody material increased at this site, likely because of the influence of postfire mortality (see Results). This mortality may also influence values for those sites included in the decay rate calculation. Because postfire mortality does not occur until at least 30 years postfire (Carleton and Wannamaker 1987), the location most likely affected is the 1930 site. We assumed this influence was small relative to the natural variability of the data. Sensitivity values for wood decay were literature-based: the upper limit was based on decay estimates by Bond-Lamberty et al. (2002) for a black spruce ecosystem (0.0334), and the lower limit (0.0097) was based on decay rates for Norway spruce (*Picea abies* (L.) Karst.; Storaunet and Rolstad 2002).

Fire return interval and overall consumption rate (f_s)

Fire was modeled to occur every 80 years. This value, also used by Harden et al. (2000), is based on tree-ring analysis of fire recurrence within black spruce dominated boreal forests (B.J. Stocks, written communication). This value is similar to the fire return interval calculated for this region using the Canadian Large Fire Database version 2.0 (fire return interval = 94 years for ecoregions 88 and 89; Amiro et al. 2001). However, published estimates of fire return intervals for boreal forests range from 70 to 500 years (Johnson 1992; Payette 1992; Kasischke et al. 1995). This range was used for initial minimum–maximum values for sensitivity analyses.

The amount of nontree stem C consumed during a fire (f_s) was based on the results of Harden et al. (2000). Optimization runs done in their study suggested that long-term consumption rates averaged approximately 44%. This value was, therefore, used as our default value. This value is similar to consumption estimates (49%) calculated using average fuel consumption (Amiro et al. 2001) and total aboveground biomass (Kurz and Apps 1999) values for the Boreal West ecozone. Our sensitivity analyses used the range of other possible values found by the Harden et al. (2000) model (22%–53%).

Results

Dead woody material

The amount of buried woody debris varied depending on whether evidence of burning was present (Fig. 2). The amount slowly increases over time, when all buried wood is considered. However, the amount of wood decreases over time,

Fig. 2. The amount of buried wood found at the three sites where it was measured differs depending on whether all buried wood or only wood with evidence of charring is included. Error bars represent one standard deviation.

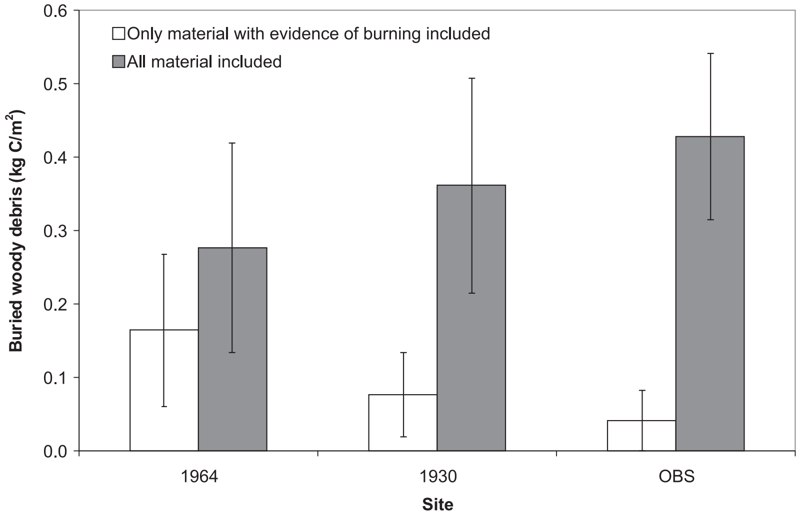
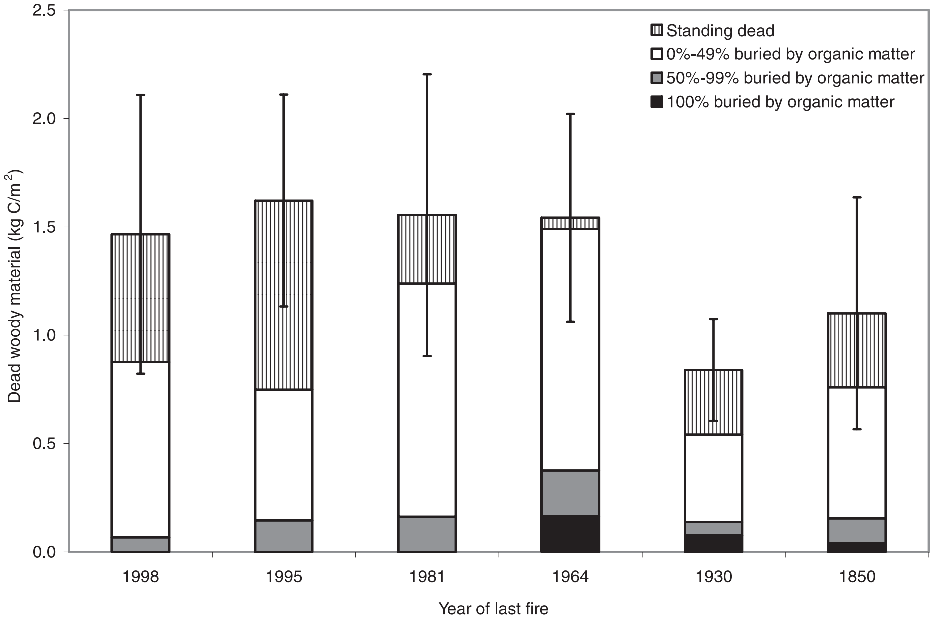


Fig. 3. Average amount of standing dead and woody debris along a chronosequence. Downed woody debris is classified in one of three categories: (1) aboveground (0%–49% buried by organic matter), (2) belowground (50%–99% buried by organic matter), and (3) buried (100% buried by organic matter). Large error bars, one standard deviation of summed dead woody material, are the result of large spatial variability within each site.



when only wood with evidence of burning is measured. *T*-tests performed among individual sites showed that there was a significant difference between values calculated with and without noncharred debris for all but the 1964 site (*p*-value = 0.335, 0.035, and 0.005 for 1964, 1930, and 1850 sites, respectively). These data imply that sometime between 40 and 70 years postfire, buried wood becomes dominated by wood resulting from postfire mortality. Subsequent analyses were, therefore, made using values that only included woody debris with burn evidence. This decision may result in overestimation of the decay rate of woody debris.

Changes in the amount of dead woody material (downed woody debris plus standing dead) within our chronosequence only occur after many decades (Fig. 3; Table 3). While total amounts of dead woody material are not significantly different during the first half of the chronosequence, the form of this material does change. Initially, almost half of wood-based C is found as standing dead. The remaining material is composed of aboveground (0%–49% buried) woody debris, which is found in quantities similar to prefire amounts, if one assumes year 1850 values represent preburn conditions. Over time, the standing dead fall to become aboveground woody debris. The amount of aboveground woody debris appears to peak between 20 and 40 years postfire in this chronosequence. Changes in belowground (50%–99% buried) and buried woody debris are much smaller and occur on longer timescales; increases in belowground woody debris and the existence of buried wood are not seen until approximately

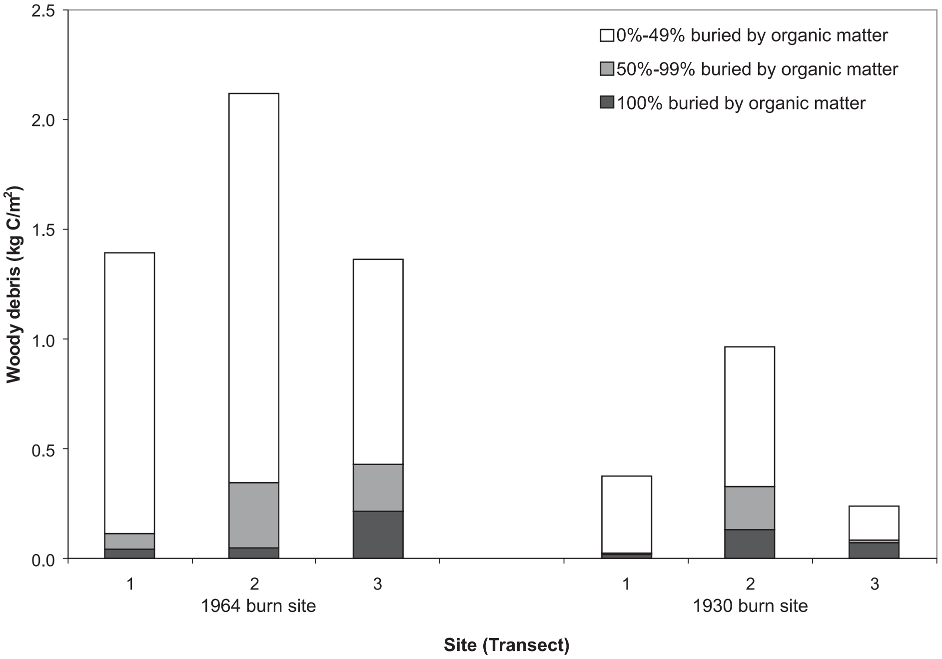
Table 3. Mean and standard deviations (in parentheses) for the woody debris inventory (kg C·m^{-2}).

Site	Standing dead	Above ground	Below ground	Buried[a]
1998	0.589 (0.208)	0.810 (0.656)	0.067 (0.063)	—
1995	0.872 (0.305)	0.603 (0.414)	0.146 (0.143)	—
1981	0.316 (0.382)	1.076 (0.659)	0.163 (0.218)	—
1964	0.052 (0.032)	1.115 (0.444)	0.211 (0.122)	0.165 (0.109)
1939	0.298 (0.107)	0.403 (0.196)	0.062 (0.063)	0.077 (0.056)
1850	0.341 (0.619)	0.604 (0.463)	0.114 (0.132)	0.041 (0.049)

Note: Trees standing at an angle ≥45° in relation to the forest floor were classified as standing dead. Woody material at angles less than this value were grouped into one of three categories: (1) above ground (0%–49% buried by organic matter), (2) below ground (50%–99% buried by organic matter), and (3) buried (100% buried by organic matter).

[a] Sites with a dash did not have buried wood measured because of insufficient moss regrowth; this value was assumed to be zero.

Fig. 4. The variability in amount of woody debris (aboveground, belowground, and buried) as demonstrated by two sites within the chronosequence (three transects per site).



40 years postfire. The largest change in woody debris is found 72 years postfire, when a significant decrease occurs. At this time, we also see an increase in the standing dead pool.

Independent of stand age, we found a large amount of spatial variability in the amount of woody debris (Fig. 4), which resulted in large standard deviations when the data were examined on a site basis (Fig. 3). The greatest amount of variability was found in the 1981 stand, followed by the oldest and youngest stands (1850, 1998, and 1995). The 1930 stand had about half the amount of variation as the other stands.

Modeling

Effects of changes in model structure

When using the same parameter values as Harden et al. (2000), we found that the new model resulted in a decrease in long-term carbon (C_d), from 9 to 6.5 kg·m^{-2} (Table 2). These differences are caused by two changes to the model structure. (1) Dead tree stems are initially classified as standing dead in our model. Wood in this stage does not decay, which creates a lag time between tree death and wood decomposition. (2) Wood-based C is allowed to burn a second time, in the form of woody debris. While the creation of a standing dead pool increases the amount of wood-based C available, most of this C is released into the atmosphere by allowing this pool to burn a second time, thereby decreasing the amount of C sent to the deep-soil C pool.

Model runs using default parameters

Model runs using the default parameter values resulted in 9.5 kg·m^{-2} of long-term C storage (C_d), which is within the 7–10 kg C·m^{-2} that has previously been found in these forests (Table 2; Harden et al. 1997; Trumbore and Harden 1997; Rapalee et al. 1998). This run indicates that approximately 20% of C inputs from NPP were lost to fire, over the 6400-year run period (Table 2), a decrease from the 33%

Table 4. Results of sensitivity analyses examining the impact of several parameters on the amount of long-term carbon storage (C_d), how much of this carbon is wood derived, and the percentage of inputs to the system (NPP) lost to fire through combustion.

Parameter	Parameter values[a]	Change in deep pool (C_d) (%)	Wood-based C in deep pool (C_d) (%)	NPP lost to fire (%)
Fire return interval	78–92 years	4–27	55–57	18–20
Turnover time of downed woody debris ($1/k_w$)	35–54 years	4–26	39–57	18–20
NPP amount and allocation (kg C·m^{-2}·year^{-1})	Stem: 0.053–0.057 Nonstem: 0.063–0.108	3–27	47–69	19–21
Turnover time of char pool ($1/k_c$)	35–60 years	5–26	52–74	20
Fire severity of nonstem components (f_s)	41%–53%	5–16	55	19–24
Fire severity of tree stems (f_t)	0%–26%	3–12	49–56	18–27
Turnover time from standing dead to downed woody debris ($1/r$)	5.4–13.0 years	4–5	53–57	20–21

[a] Parameter values listed may differ from values presented in Table 1 and the text where the parameter value resulted in values outside of the range of literature-based values for the deep C pool (C_d). Such values were adjusted by constraining the amount of C_d to the literature-based range (see text for more information). The range of acceptable values is presented here.

found by Harden et al. (2000). Results also indicate that 55% of the deep-soil C is potentially wood based (Table 4).

Sensitivity analyses

Long-term carbon storage (C_d) was most sensitive to changes in the fire return interval, decay rate of wood, the amount and allocation of NPP, and the decay rate of char. However, many of these scenarios resulted in unrealistic values of deep-soil C storage (C_d) compared with the literature, suggesting that our maximum estimates of stem NPP, nonstem NPP, and k_w may be too high. Minimum estimates for fire severity, fall rate, and k_w also resulted in unrealistic C_d values. Simulations with modified values for these variables (by constraining the amount of C_d to literature values, see Table 2) suggest that 18%–27% of NPP is lost to fire and that 39%–74% of the C found in the deep soil is wood based (Table 4). A conservative run, which minimized the impact of wood on C_d and constrained C_d through modifications of k_c (turnover = 96 years), resulted in the contribution of 10% of the long-term C from wood (Table 2).

Discussion

Field

While most of the dead woody material is composed of standing dead and aboveground (<50% buried) woody debris, in the 1964 and 1930 stands, more than 12% and 16% of the postfire woody debris, respectively, was buried. These values are likely a minimum estimate, because only wood that showed evidence of being burned was measured. Partially buried or belowground woody debris composed 8% to 20% of the downed woody debris within all stands. Excluding inventories of belowground and buried woody debris could, therefore, lead to underestimates of the amount of woody debris as well as overestimates of inventory-based decay rates. For example, the decay rates found in the present study would have increased by over 30% when estimated using aboveground woody debris alone. Differences in amounts of downed woody debris tend to occur in mid-aged and mature stands, when sufficient moss regrowth occurs.

The high spatial variability of downed woody debris at each site has implications for future inventories within this forest type. Independent of survey technique, a sufficient number of plots or transects must be measured to capture this variability and minimize the resulting errors. A power analysis on our data suggests that no fewer than 15 transects should be measured when using the line intersect method in these forests, and many more transects may be required to find differences between sites with the highest amount of variability. We found the most spatial variability 20 years after a fire, likely the result of the stochastic manner in which trees fall over and create pockets with greater amounts of downed woody debris, while other areas had none.

Model

Our results indicate that from 10% to more than 60% of the deep-soil C (C_d) originates from woody material (Table 2). This range likely represents the real world variability of both the model parameters and the role of wood-based carbon across spatial landscapes. For example, our inventory data showed that the amount of woody debris is quite heterogeneous on small spatial scales (Fig. 4). Areas with large amounts of woody debris could result in a greater quantity of wood-based soil C being stored at these locations. Additionally, variations in woody debris occur with changes in soil drainage (Bond-Lamberty et al. 2003). Soil drainage also affects fire return intervals, NPP allocation, and rates of decay. For example, the role of bryophytes becomes more important and the proportion of wood-based aboveground NPP decreases on wetter sites (Bond-Lamberty et al. 2004; Grant 2004). As a result, the fraction of deep-soil C derived from woody debris likely diminishes as soil moisture increases.

Contributions of woody debris to C storage may also change over time, especially with projected climate change. A warmer, drier climate would likely result in poorly drained ecosystems becoming better drained, changing the dominant contributor to NPP from moss to trees. This change could not only increase the amount of C available for long-term storage, but also increase the amount of that C that is wood derived. However, these inputs could be offset by increases in both decomposition rates (Robinson 2002; O'Neill et al. 2003) and combustion losses (Stocks et al. 1996).

Model assumptions and limitations

Interpretation of our results requires several caveats, because this model was created to test the impact of wood on long-term C storage as simply as possible. This model does not explicitly account for roots, which significantly affect inputs, storage, and turnover of the organic layers. A test model run was, therefore, performed to examine the potential impact of belowground processes on our results. The highest root NPP values for fine (<2 mm), medium (2–5 mm), and coarse (>5 mm) roots from Bond-Lamberty et al. (2004) were used to maximize the impact of roots on our results. Decay rates for each pool size were also chosen to maximize the impact of roots on deep-soil C (e.g., the slowest rates found were used). Values from Ruess et al. (1996) were used for fine and medium roots, while coarse roots decayed at the same rate as wood. We found minimal change (49% to 55%) in the amount of wood-based deep-soil C in this test run. This small change is due to the high turnover rate for small and medium roots, which represent most of the root NPP at these sites (Bond-Lamberty et al. 2004).

Our basic model also employs constant NPP and decomposition rates throughout the stand age, yet both of these parameters vary over time (O'Neill et al. 2003; Zhuang et al. 2003; Bond-Lamberty et al. 2004). A test run was made to investigate the impact of variable NPP on our results using equations based on the data of Bond-Lamberty et al. (2004). This run resulted in a reasonable value of C within tree stems, but a very high amount of C within the shallow pool. This value resulted because changes in decomposition rates over time were not modeled along with the changes in NPP. We feel that additional data are needed to realistically model the links between changing NPP and decomposition rates and that adding these effects to our model at this time would be too conjectural. We also note that even with the overestimation of C in the shallow pool, wood continued to play an important role in creating long-term C (48% of the deep C pool was wood-based).

Finally, our modeling efforts are based on data from one site per age-class and one region within the boreal forest. Our results are also limited to organic soil layers, which account for most of the soil C in clayey soils of the boreal region (Rapalee et al. 2000). Bond-Lamberty et al. (2004) compared our main chronosequence sites with a set of secondary sites within the same region and found similar patterns in coarse woody debris, and thus it seems likely that our results also apply to other feather moss – black spruce forests on clay soils within this region. However, this must be confirmed with additional testing. It is important to note that other storage and stabilization processes may play a more prominent role within other soil types (Wynn et al., in press), even within this region. For example, boreal sandy soils, which have faster decomposition rates (Trumbore and Harden 1997), may have a lower proportion of wood-based deep-soil C. Additionally, Nalder et al. (1999) found that region influenced variables that are important for estimating woody debris. Our results, therefore, cannot be extrapolated to black spruce dominated forests within other regions.

Conclusions

Our results suggest that 10% to 60% of deep-soil C within upland, feather moss – black spruce boreal forests on clay soil in central Manitoba may be derived from woody material. Model estimates were most sensitive to fire return interval, decay rate of wood, system inputs (NPP), and the decay rates of the char C pool. To understand C cycling within the boreal forest of this region, we, therefore, must also understand the amount and transfer rates of wood-based C within this ecosystem. Our results suggest that the potential impact of wood must be taken into account when studying the source and fate of soil C in boreal forests. Additionally, all forms of woody debris, including partially and (or) completely buried wood from sites where burial is possible, must be used to fully characterize a site's woody debris and its contribution to carbon cycling.

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