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Decomposition and Fragmentation of Coarse Woody Debris: Re-visiting a Boreal Black Spruce Chronosequence

Ben Bond-Lamberty* and Stith T. Gower

Department of Forest and Wildlife Ecology, University of Wisconsin, 1630 Linden Drive, Madison, Wisconsin 53706, USA

Abstract

We re-visited a seven-stand boreal chronosequence west of Thompson, Manitoba, Canada, in which coarse woody debris (CWD) and its instantaneous decomposition were measured in 2000. New CWD measurements were performed in 2007, and tree inventories updated to provide mortality and snag failure data. These data were used to model CWD changes, compare methods of estimating decomposition, and infer possible fragmentation rates. Measured CWD was between 9.7 (in both the 77- and 43-year-old stands) and 80.4 (in the 18-year-old stand) Mg ha^{-1} in 2007. Spatial variability was high; at most stands CWD levels had not changed significantly from 2000 to 2007. Tree mortality was a significant flux only in older stands, whereas snag fall rate varied by an order of magnitude, from 2.9% y^{-1} (0.2 Mg ha^{-1} y^{-1}) in the 9-year-old stand to 9.8% y^{-1} (2.3 Mg ha^{-1} y^{-1}) in the 12-year-old stand. A one-pool model based on these inputs underestimated actual 2000–2007 CWD decomposition in the younger stands, suggesting that fragmentation could be an important part of the carbon flux exiting the CWD pool. We compared three independent measures of annual decomposition (k): direct measurements of CWD respiration, rates based on the 7-year re-sampling effort described here, and rates inferred from the chronosequence design itself. Mean k values arrived at via these techniques were 0.06 ± 0.03, 0.05 ± 0.04, and 0.05 ± 0.05 y^{-1}, respectively. The four-pool model suggested that the transition rate between decay classes was 0.14–0.19 y^{-1}; the model was most sensitive to initial CWD values. Although the computed k values implied a problem with chronosequence site selection for at least one site, the overall CWD trend was consistent with a larger number of sites surveyed in the region.

Key words: coarse woody debris; boreal forest; decomposition; fragmentation; snag failure; black spruce; chronosequence.

Introduction

In forest ecosystems, coarse woody debris (CWD) influences nutrient cycling, humus formation, carbon storage, fire frequency, and water cycling, and serves as a habitat for both heterotrophic and autotrophic organisms (Harmon and others 1986; Rayner and Boddy 1988; Nalder and Wein 1999; Brais and others 2006). Accurately modeling CWD inputs and decomposition is necessary to track long-term dynamics of snags and woody debris and their effects on habitat, forest management, and carbon cycling (Harmon and others 1990; Janisch and others 2005; Vanderwel and others 2006). Woody debris has not been always included in re-

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*Corresponding author; e-mail: bpbond@wisc.edu

gional and global carbon budgets (Houghton and Woodwell 1989; Post and others 1990), but it influences short- and long-term biogeochemical cycling and carbon balance (Harmon and others 1990; Harden and others 2000; Manies and others 2005; Gough and others 2007).

Inventories of CWD are straightforward to perform, but measuring the decomposition rates of CWD is difficult due to the slow nature of the decomposition process and physical fragmentation (Franklin and others 1987); there are few long-term studies in the boreal forest (Krankina and Harmon 1995). One way around this difficulty is to substitute space for time by employing a chronosequence, although this design choice has its own limitations (Powers and Van Cleve 1991; Harmon and others 2000). A number of studies have used age sequences to examine boreal CWD distribution and infer decomposition rates (Krankina and Harmon 1995; Lee and others 1997; Sturtevant and others 1997; Næsset 1999; Siitonen and others 2000; Boulanger and Sirois 2006; Moroni 2006). Direct measurements of heterotrophic respiration in CWD have been performed, and annual fluxes estimated (Marra and Edmonds 1996; Progar and others 2000; Chambers and others 2001; Bond-Lamberty and others 2002a; Wang and others 2002; Gough and others 2007), but to our knowledge no independent check on these measurements has subsequently been made. In addition, although fragmentation is presumed to be an important process contributing to CWD decomposition, continuously exposing more substrate surface area to heterotrophic activity and removing material from the CWD pool, few studies have attempted to quantify it (Mattson and others 1987).

Bond-Lamberty and others (2002a) measured CWD and its instantaneous CO_2 fluxes for a seven-stand boreal chronosequence, and calculated annual decomposition rates and carbon fluxes from these data. In the current study we re-visited the chronosequence, 7 years later, and evaluated the projections made by Bond-Lamberty and others (2002a). Such a CWD re-sampling was first performed by Harmon and others (2000), who estimated decomposition rates based on biomass, density, and volume changes in individual logs; they termed this the ''decomposition vector'' method. Paired with a chronosequence, a decomposition vector permits a detailed examination of decomposition processes and woody debris dynamics over the course of stand succession.

The main goals of this study were to (i) re-measure CWD in a boreal chronosequence; (ii) evaluate how well CWD changes can be modeled based on previously measured respiration rates and known inputs from tree mortality; and (iii) use the chronosequence design to infer changes in CWD over the length of the fire cycle in central Canada. Three independent measures of decomposition were compared: direct measurements of CWD respiration; rates based on the 7-year re-sampling effort described here; and rates inferred from the chronosequence progression itself.

Materials and Methods

Site Descriptions

The study was conducted in a well-drained black spruce (*Picea mariana* Mill. BSP)-dominated chronosequence west of Thompson, Manitoba, Canada, near the BOREAS northern study area (55°53′ N, 98°20′ W). The chronosequence consisted of seven different-aged black spruce forests, all of which originated from stand-killing wildfire in mature forests. The oldest stand in the chronosequence (157 years) is the BOREAS NSA tower site (Dunn and others 2007). The stands have been extensively studied and differed in their species mix (Bond-Lamberty and others 2002b) and structure (Table 1). The stands were dominated by three tree

Table 1. Chronosequence Stand Characteristics as Measured 1999–2000, by Stand Age

Site characteristic	Years since fire (as of 2000)						
	2	5	11	19	36	70	150
Leaf area index ($m^2\ m^{-2}$)	0.0 (–)	0.1 (0.2)	0.0 (–)	0.9 (0.2)	1.8 (0.7)	6.8 (0.7)	5.3 (0.9)
Basal area ($m^2\ ha^{-1}$)	0.0 (–)	0.5 (1.1)	0.0 (–)	4.1 (1.0)	11.6 (3.9)	36.7 (4.0)	42.2 (8.6)
Snags (Mg ha^{-1})	10.6 (8.0)	23.5 (4.8)	0.0 (–)	9.9 (11.8)	2.7 (3.7)	4.5 (3.2)	3.4 (1.9)
DWD (Mg ha^{-1})	12.9 (13.0)	2.5 (1.6)	160.2 (43.9)	47.2 (20.9)	9.9 (6.8)	1.5 (1.2)	5.5 (5.6)

Standard deviations, in parentheses, are based on the plot as experimental unit (N = 4).
Tree basal area (Bond-Lamberty and others 2002b), snag biomass, and downed woody debris (DWD) data (Bond-Lamberty and others 2002a) were reported previously, although the snag values above are corrected from the latter publication.

species: trembling aspen (*Populus tremuloides* Michx), black spruce, and jack pine (*Pinus banksiana* Lamb.). Early successional deciduous tree species are replaced by black spruce in the older stands; the black spruce canopy closure, at 50–60 years, is associated with drastic thinning of the understory and growth of thick feather mosses (usually *Ptilium*, *Pleurozium* or *Hylocomium* spp.). All stands are within a 40 km^2 area except the two most recently burned stands, located in Leaf Rapids, Manitoba, 100 km northwest of the older stands. Mean annual temperature was 0.8°C; annual precipitation was 438.5 mm.

Field Measurements

Surveys of CWD, defined as woody debris 5 cm or larger in diameter, standing or down, were performed in both 2000 and 2007. In 2000, snag inventories were performed, and downed woody debris (DWD) was cut and measured in the field in four 10 m × 1 m transects at each site; dry mass was determined from subsamples dried in the lab. Before drying, instantaneous respiration rates were measured and used to compute annual respired CO_2 flux from the CWD, based on annual temperature and moisture data. These measurements were described in detail by Bond-Lamberty and others (2002a).

In July 2007, DWD was re-measured using line intercepts (Harmon and Sexton 1996). Four non-crossing survey lines (50 m) were surveyed in each stand, randomly oriented and at least 50 m from the edge of the stand. Diameter and decay class (Lambert and others 1980; Bond-Lamberty and others 2002a) of CWD that crossed the line were recorded. Burial state was assessed as 0, 25, or 75% (Manies and others 2005). CWD volume, computed from the line intercept data, was converted to biomass using decay-class-specific densities measured at these sites (Bond-Lamberty and others 2002a).

We also re-inventoried trees in the study plots that were first measured in 1999 (Bond-Lamberty and others 2002b) and subsequently in 2002 (Bond-Lamberty and others 2004). Permanent tags had been affixed to all trees and snags in 1999 were checked in 2007, with absences (tree or snag fall) and transitions (live tree to dead snag) noted. Updated diameter at breast height (1.37 m) was recorded for all trees.

Data Analysis and Modeling

The change in the coarse woody debris pool (D) over time (t) is a function of its inputs (D_i) and outputs (D_o):

$$\frac{dD}{dt} = D_i - D_o = D_m - (D_r + D_f + D_l). \qquad (1)$$

Bond-Lamberty and others (2002a) and Wang and others (2002) measured D and its respiration flux D_r; the D_m (input from live tree mortality) term can be estimated from biomass data published for these stands (Bond-Lamberty and others 2002b; Wang and others 2003; Bond-Lamberty and others 2004) and mortality data from the current surveys. This left fragmentation (D_f) and leaching (D_l) losses unknown; we assume, in this relatively low-precipitation system, that $D_l \approx 0$ and do not consider it further here (compare Mattson and others 1987). Thus

$$\frac{dD}{dt} = D_i - kD = D_i - (k_r D + k_f D) \qquad (2)$$

where k_r and k_f are the annual rate constants of respiration and fragmentation, respectively; the former term was estimated by Bond-Lamberty and others (2002a) whereas the latter was unknown.

Expected CWD levels in 2007 were first calculated using a one-pool model in each stand (equation 2). The data used included CWD levels in 2000, measured CWD respiration rates (Bond-Lamberty and others 2002a; Wang and others 2002), and the tree inputs to CWD based on the 2007 survey described above. At each annual time step, input from tree mortality was added to the CWD pool, and outputs computed based on the stand-specific k_r computed by Bond-Lamberty and others (2002a). The difference between measured and modeled 2007 levels of CWD was then assessed.

A four-pool model was used to elucidate decay class transitions. The model operated similarly to the one-pool model except that DWD decay classes I–III, as well as snags, were tracked as separate pools. We assumed that all trees that died entered the CWD pool as snags, which then fell and became decay class I on the ground, that is, that very little decomposition occurred while they remained standing; this has been observed with black spruce snags (Boulanger and Sirois 2006). Based on the data of Bond-Lamberty and others (2002a), we assumed that decay classes I, II, and III had CO_2 respiration rates 75, 125, and 100%, respectively, of the site-specific k_r means reported in that study. Snags were initially assumed to have a decomposition rate constant of 0.01 y^{-1}. Transition rates between these pools (τ_0, snags to decay I; τ_1, decay I–II; τ_2, decay II–III; τ_3, fragmentation of decay III) were then sequentially fit to minimize errors between predicted and observed data.

We examined the sensitivity of both the one- and four-pool models by varying each parameter (input to the CWD pool; transitions between snags and decay classes; annual respiration rates for each decay class) by both a set amount (10%) as well as one standard deviation, if the parameter was measured in the field. The significance of CWD changes between 2000 and 2007 was tested with a Welch two sample *t*-test in R 2.6.0 (R Development Core Team 2006). Unless otherwise noted, all calculations and statistical analyses used the plot or transect as the experimental unit and a significance level of $\alpha = 0.05$.

Results

Measured CWD in the stands was between 9.7 (in both the 77- and 43-year-old stands) and 80.4 (in the 18-year-old stand) Mg ha^{-1} in 2007 (Table 2). Although the 77- and 43-year-old stands had the same amount of total CWD, in the former stand 34% of CWD was downed woody debris (DWD), whereas at the latter DWD comprised 91% of CWD; at other stands this percentage was between 53 and 100% (Table 2). Spatial variability was high, and the coefficient of variability—standard deviation divided by the mean in each stand—averaged 0.46 (compared to 0.70 in the 2000 survey). As a result, CWD values did not significantly differ from 2000 to 2007 at most stands; the two exceptions were the 12- and 18-year-old stands ($T_{3.4} = -7.22$; $P = 0.004$ and $T_{3.7} = 3.43$; $P = 0.029$, respectively; other *P*-values between 0.10 and 0.82).

Tree mortality ranged from 0.0 to 13.7% stems y^{-1} (Table 2); on a biomass basis this was 0.0–0.9 Mg ha^{-1}y^{-1}; mortality occurred disproportionately among smaller trees. The highest mortality occurred in the oldest stands (and the 12-year-old stand, where a very few live trees had survived the fire in 1999 but died by 2007). The failure rate for snags varied by almost an order of magnitude, from 2.9% y^{-1} in the 9-year-old stand to 9.8% y^{-1} in the 12-year-old stand, with flux rates of 0.0 to 2.3 Mg ha^{-1} y^{-1} (note that snag failure rates were only calculated for stands with standing dead trees in 1999, whereas the flux was calculated for all stands).

Size and decay class distribution of CWD did not change at most of the stands between 2000 and 2007 (data not shown). In the 12-year-old stand (1995 burn), the low CWD levels in 2000 (Table 1) and the high rate of snag failure during the following 7 years (Table 2) resulted in decay class I jumping from 56 to 96% of CWD, and the largest size class from 0 to 20%. At the 18-year-old stand, there were no snags and thus no CWD inputs; this meant that the size class distribution was unchanged from 2000 to 2007, but decay class I went from 91 to 14% of CWD, and decay class III from 0 to 27% (Figure 1). Older stands had approximately 0% of their DWD buried, but percentages at the younger stands were higher (4–22%; Table 2).

The one-pool model based on the directly measured rates of Bond-Lamberty and others (2002a) generally underpredicted CWD decomposition at the younger stands (Figure 2), particularly when the CWD pool was large and its inputs were low. The overall error rate, across all stands, was 12%, and varied from 0.1 to 21%. This discrepancy may be due to measurement variability (compare error bars in Figure 2), but it is also possible that the mean difference between measured and modeled across all sites (a rate of ~0.02 y^{-1}) is due to CWD fragmentation. This in turn would imply that the rate of fragmentation (k_f) was about two-thirds that

Table 2. Tree Mortality Rate and Flux, Snag Failure Rate and Flux, Mass-Weighted Burial State and Mass of Downed Woody Debris (DWD), and Total Coarse Woody Debris (CWD) in 2007, by Stand Age

Site characteristic	Years since fire (as of 2007)						
	9	12	18	26	43	77	157
Tree mortality (% y^{-1})	–	13.7 (0.0)	–	0.0 (–)	0.0 (–)	1.4 (1.0)	2.0 (1.4)
Tree mortality (Mg ha^{-1} y^{-1})	0.0 (–)	0.1 (0.2)	0.0 (–)	0.0 (–)	0.0 (–)	0.8 (0.6)	0.9 (0.6)
Snag failure (% y^{-1})	2.9 (3.6)	9.8 (2.7)	–	6.8 (2.2)	9.1 (7.9)	9.0 (4.1)	3.4 (6.8)
Snag failure (Mg ha^{-1} y^{-1})	0.2 (0.3)	2.3 (1.0)	0.0 (–)	0.6 (0.9)	0.1 (0.1)	0.3 (0.3)	0.2 (0.3)
Burial of DWD (%)	9% (6%)	4% (4%)	22% (8%)	5% (3%)	0% (0%)	0% (0%)	1% (3%)
DWD (Mg ha^{-1})	7.7 (6.8)	25.7 (6.2)	80.4 (15.5)	23.3 (7.7)	8.9 (4.1)	3.3 (1.6)	8.0 (3.8)
Total CWD (Mg ha^{-1})	16.6 (11.8)	31.2 (7.0)	80.4 (15.5)	28.2 (8.7)	9.7 (3.4)	9.7 (2.0)	14.2 (6.2)

Tree mortality and snag failure data are based on difference between 1999 and 2007 surveys.
Standard deviations, in parentheses, are based on either the plot or survey line as experimental unit (N = 4).

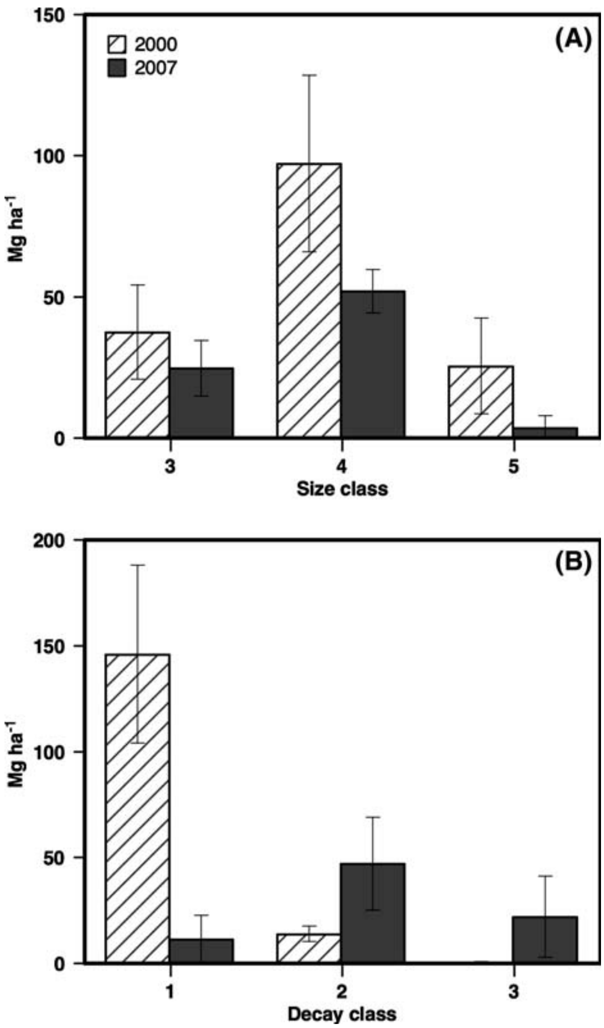

Figure 1. Shifts in (**A**) size and (**B**) decay classes of coarse woody debris between 2000 and 2007 measurements, at the 1989 burn site. Size classes were 5–10 cm (*class 3*), 10–20 cm (*class 4*), and 20+ cm (*class 5*). Errors bars are based on plot or survey line as experimental unit (N = 4).

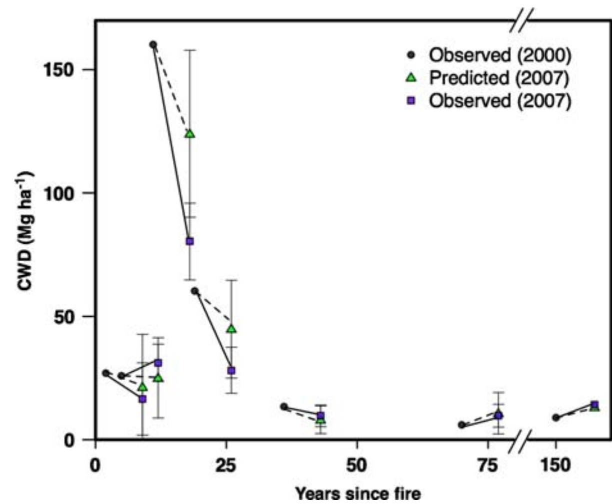

Figure 2. Coarse woody debris (CWD) measurements in 2000 and 2007, with one-pool model predictions assuming no fragmentation. Solid and dashed lines connect observed 2000 data with observed and predicted 2007 data. Errors bars are based on the survey line as experimental unit (N = 4).

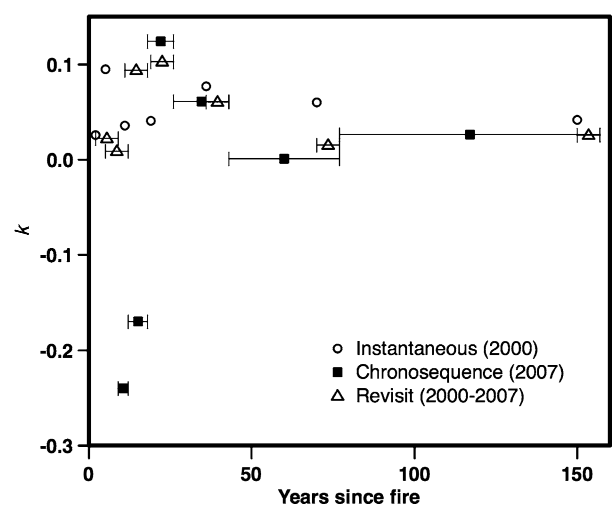

Figure 3. Measured and inferred values for decomposition rate k, based on instantaneous respiration rates (Bond-Lamberty and others 2002a), chronosequence revisit described here, and the chronosequence design itself. Error bars show time span over which each particular value was computed.

of decomposition (k_r). We discuss this possibility further below.

Figure 3 compares CWD decomposition rates (k) computed by three methods: the direct respiration measurements of Bond-Lamberty and others (2002a); the difference between the 2000 and 2007 measurements described here, and values based on the chronosequence design itself (that is, computing what rate of decomposition was necessary to account for CWD differences between different stand ages). The mean overall k rate constants based on these different techniques were, respectively, 0.06 ± 0.03, 0.05 ± 0.04, and 0.05 ± 0.05 y^{-1}. This last value is based on the 2007 survey data (mean k based on the 2000 data was 0.07 ± 0.04 y^{-1}) and excludes two negative values (Figure 3) caused by improper site selection: the 12-year-old stand had more CWD than the sum of CWD and snag biomass at the 9-year-old stand (that is, it was not possible for the 9-year-old stand to ''turn into'' the 12-year-old stand in 3 years); a similar problem occurred between the 12- and 18-year-old stands. Across the chronosequence, the

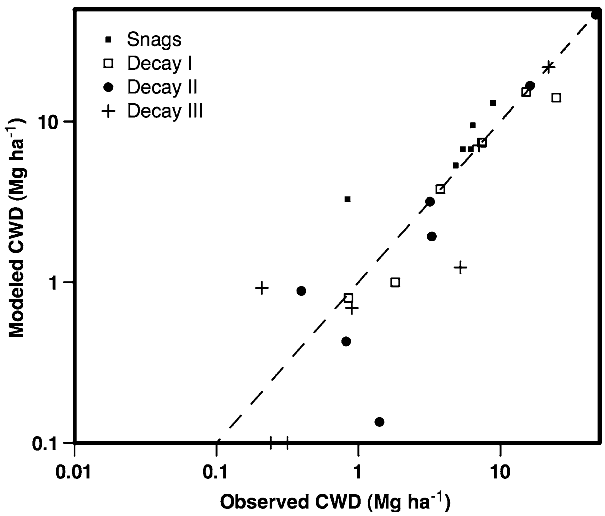

Figure 4. Observed versus modeled levels of coarse woody debris (CWD), by decay class (I-III), using the four-pool model. Dashed 1:1 line is also shown.

decomposition rate measured by all methods was low immediately after fire, peaked in the 18- and 26-year-old stands, and declined in the oldest stands (Figure 3).

The four-pool model, fit with varying decay class transitions, provided no better a fit than the simple one-pool model (Figure 4). Mean values for τ_0–τ_3 were 0.05 ± 0.07, 0.14 ± 0.18, 0.13 ± 0.18, and 0.19 ± 0.24 y^{-1}, respectively, across all stands. Mean error rates (modeled minus observed divided by observed) were 72, 15, 44, and 86% for snags and decay classes I–III, respectively, and 15% for total CWD. The high errors for snags and decay class III were driven by the older stands, where these pools were very low (<1 Mg ha^{-1}); thus in absolute terms, the error was small.

Measured CWD in 2000 (that is, the initial starting state) was the most influential parameter in both the one- and four-pool models (Table 3), with a 10% parameter change producing a 9% change in predicted 2007 CWD for both. All other parameters produced only 0–2% change. When the field-measured parameters were varied by their observed error, 2000 CWD remained the most influential parameter although both CWD input rate and measured respiration rate produced approximately 10% changes (Table 3).

Discussion

CWD Decomposition Through Time

Many studies have found a ''U-shaped'' temporal pattern in CWD levels, as initial high levels of disturbance debris decline and give way first to gradual input from the regenerating stand, and ultimately to higher inputs as the mature stand senesces into an uneven age structure (Lambert and others 1980; Spies and others 1988; Lee and others 1997; Sturtevant and others 1997); this model can vary because of the presence or absence of pre-disturbance debris or species replacement (Hély and others 2000). Although the 2000–2007 increases in CWD at the 77- and 157-year-old stands in this study were not significant, their direction of change is consistent with the above model; a similar argument applies to the 26-year-old stand's CWD decrease.

Black spruce woody debris decomposes at different rates while passing through different decomposition stages (Bond-Lamberty and others 2002a; Wang and others 2002). Harmon and others (2000) found that a single rate constant could be used within a certain range of input variability. Boulanger and Sirois (2006) reported CWD of 6–29 Mg ha^{-1} in a black spruce chronosequence, with inferred decomposition rates of $k \approx 0.02$ y^{-1}, although their definition of CWD differed from the one used here. This compares to a mean k of 0.05–0.06 y^{-1} reported here. This single mean k was not sufficient, however, to properly model CWD changes across time at all stands (Figure 3); these data support a more complex model, one taking into account both time and decomposition status.

Table 3. Sensitivity Analysis of the One- and Four-Pool Models described in the Text, by Parameter Tested

Parameter	ΔCWD 2007 for parameter: ±10%	±1 SD
One-pool model		
CWD levels in 2000	9%	58%
CWD input (tree mortality)	1%	8%
k_r (DWD respiration rate)	2%	12%
Four-pool model		
CWD levels in 2000	9%	57%
CWD input (tree mortality)	1%	8%
τ_0 (snag to decay I transition)	0%	–
τ_1 (decay I to II transition)	1%	–
τ_2 (decay II to III transition)	1%	–
τ_3 (fragmentation)	1%	–
K_0 (snag respiration rate)	2%	–
k_r (DWD respiration rate)	2%	11%

Parameters were varied by ±10%, to test their relative sensitivity compared to each other, and by their observed error rates in the field (S.D., standard deviation, N = 4) where applicable.
Mean percentage change in total 2007 CWD predicted by the models is shown for each parameter.

Finally, although CWD decomposition varies markedly with tree species (Alban and Pastor 1993; Harmon and others 2000; Brais and others 2006; Mäkinen and others 2006), this is a lesser concern in the black spruce-dominated stands studied here.

CWD Variability and Measurement Techniques

The chronosequence design is useful for studying long-term ecosystem structure and function, but problematic because distinguishing the effects of time and changes in treatment can be difficult. The chronosequence discussed here has not been formally replicated, but was shown to be consistent with an additional 28 stands in northern Manitoba (Bond-Lamberty and others 2004); in addition, Goulden and others (2006) used Landsat TM and ETM+ data to conclude that this chronosequence comprised a valid space-for-time substitution. The data presented here, however, show that at least for CWD, two of the younger stands were not valid space-for-time substitutions, as their CWD pools were too large relative to the next-younger stand in the chronosequence (Figure 3). The 12-year-old stand's discrepancy in this regard might be due to measurement error (compare Table 2 and Figure 2), but the 18-year-old stand clearly had 'too much' CWD, relative to the rest of the chronosequence. As noted above, the two youngest stands were located approximately 100 km northwest of the main study area; the slightly harsher climate in this region is a possible explanation for why these two stands do not, from a CWD perspective, fit with the chronosequence comprising the other five stands.

The spatial variability of CWD is typically large (Harmon and others 1986). The variability observed here was less than that reported in the same stands by Bond-Lamberty and others (2002a). At certain stands (for example, the 12-year-old stand), CWD may in fact have become less variable in the time period between these studies, but we also used a different measurement technique (50 m line intercepts in 2007 versus 10 m^2 cut plots in 2000), and this was likely an important factor. The ease of line intercepts, allowing for the measurement of much larger spatial areas, means that this technique is to be preferred, assuming that accurate wood density estimates are available to convert CWD volume to biomass.

Extrapolating long-term decomposition from short-term measurements of the CO_2 flux from CWD (Progar and others 2000; Chambers and others 2001; Bond-Lamberty and others 2007; Gough and others 2007) may seem questionable, subject as it is to measurement error (of both CWD levels and CO_2 fluxes), future interannual climate variability, and temporal changes in local conditions due to succession or disturbance. One of the values of the current study is that, by re-measuring chronosequence stand structure, it allows for us to use two completely independent techniques to assess the decomposition rates estimated by Bond-Lamberty and others (2002a): decomposition *k* values could be computed based on changes in CWD levels and tree mortality at individual stands (both of which can be measured easily and accurately), and based on changes between the chronosequence stands themselves (which, as noted above, is subject to a valid space-for-time substitution). Across the entire chronosequence, results from these techniques closely matched those from direct respiration measurements (mean *k* of 0.05–0.06 y^{-1}); on an individual-site basis, our results show a marked change in *k* across the chronosequence, consistent with the pattern found by Bond-Lamberty and others (2002a). The use of multiple techniques thus increases our confidence in direct respiration measurements of CWD, while significantly constraining values of *k* across time and space.

Snags and CWD Fragmentation

The dynamics of snag failure can strongly affect the vegetation re-growth, successional dynamics, and carbon balance of the developing stand (Harmon and others 1986). The snag fall rates of 3–10% y^{-1} found here were lower than aspen snag fall rates of 9–21% reported by Lee (1998) but comparable to other reported black spruce forest dynamics (Moroni 2006). Similar to the results of Lee (1998), we found that large snag failure rates were associated with older stands and smaller trees; these were also the only stands in which tree mortality comprised a significant carbon source to the CWD pool. Vanderwel and others (2006) reported 5-year snag fall probabilities of 0.00–0.33 for *Pinus* spp. in Ontario. We note however that an annual loss rate is not the ideal way to report these data; Weibull survivor models are more appropriate tools for this type of analysis (Garber and others 2005).

Once CWD is lying on the ground, decomposition proceeds more quickly because of increased moisture availability (Boddy 1983; Marra and Edmonds 1996; Wang and others 2002). This could potentially swing a stand from being a carbon sink to a source, for example, as observed by Bond-Lamberty and others (2004), resulting in a double compensation point in the lifetime of a developing post-fire stand: first, when autotrophic NPP exceeds soil heterotrophic respiration while most snags remain standing; and second, after the failure of the majority of the snag population, when the respiration pulse from this downed woody debris is overcome. This will depend greatly on the variability of snag failure.

We hypothesize above that the difference between the one-pool model (based only on CWD respiration) and observed data might provide an estimate of CWD fragmentation. This is difficult to assess, as few estimates have been made of woody debris fragmentation rates, and no direct measurement was made here. Mattson and others (1987) found that fragmentation and leaching accounted for about one-third of total debris mass loss in a southern Appalachian, USA, forest. Fragmentation accounted for 10% of CWD mass loss in a North American *Acer* spp. wetland forest (Chueng and Brown 1995), although the time period studied was short (1.5 years). Our study suggested that mass loss from fragmentation was about two-thirds that from respiration, although our estimate of fragmentation was indirect (via subtraction) and thus inferential and subject to large errors. Whether the carbon in CWD exits this pool via respiration (to the atmosphere) or fragmentation (to the soil) has large consequences for the biogeochemical cycling during stand development (Brais and others 2005; Gough and others 2007). Carefully tracking litterfall and soil organic matter in a future study would help constrain fragmentation estimates, as would careful monitoring of the changes in individual logs over time (Yatskov and others 2003).

There are few studies of transition rates between CWD decay classes; Vanderwel and others (2006) used plot re-measurements and time-dependent transition models to calculate such rates for *Pinus* spp., but the large spread in their results (calculated over 5 years), and the species and ecosystem differences between their study and the current one, make comparisons difficult. The arbitrary nature of decay classes, such as those used here, complicates the constraining of transition rates; decomposition fluxes and rate-constants may be more useful in this regard. The results of the sensitivity analysis (Table 3), however, suggest that it is far more important to measure CWD levels precisely and accurately; transition rates in the model had only a small effect on final modeled CWD.

Conclusion: Implications at the Ecosystem Level

The stands studies here are broadly representative of the central Canadian boreal forest (Figure 5),

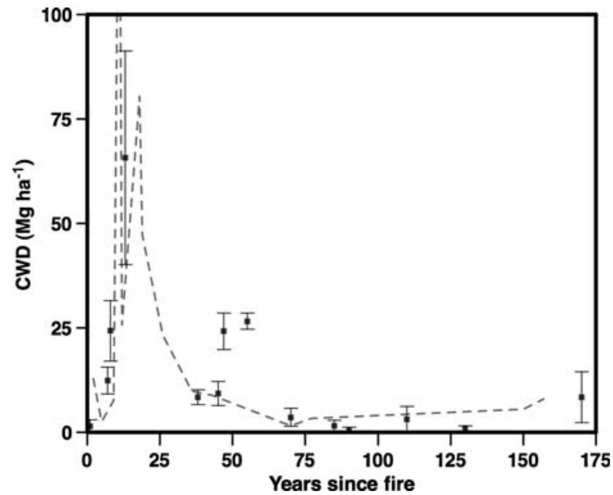

Figure 5. Comparison of chronosequence sites (line) with the extensive replicate survey sites (points) surveyed by Bond-Lamberty and others (2004) through north-central Manitoba, Canada. Errors bars are based on the plot or survey line as experimental unit (N = 4).

although the data presented here show clear evidence of at least one problem with chronosequence site selection. In North American boreal forests, stand-killing wildfires leave entire forests of snags, and the timing of their transition to the downed CWD pool and then to burial in the organic layer can potentially affect the carbon balance of the entire re-growing stand (Bond-Lamberty and others 2004). Because such wildfires exert a large effect over landscape and even biome carbon balance (Kasischke and others 1995; Harden and others 2000; Bond-Lamberty and others 2007), the timing of this ''compensation point,'' when the post-disturbance stand transitions from being a carbon source to a carbon sink, is important to quantify (Janisch and Harmon 2002; Litvak and others 2003). Over longer time periods, the rate of snag failure and woody debris incorporation into the organic soil layers will affect both ecosystem dynamics and landscape-level carbon storage (Harmon and others 1990; Tinker and Knight 2000; Manies and others 2005).

Accurately quantifying CWD dynamics—input rates, biomass, and decomposition and fragmentation—is thus important to model and manage the trajectories of post-disturbance forests. These dynamics are highly variable in both time and space, and capturing as much of this variability as possible is important in future projections, as the sensitivity analysis here shows. In at least some forests, the use of biased decomposition estimates can produce errors in calculated carbon fluxes comparable to net primary production (Janisch and others 2005). More multi-method studies are needed, in particular, we suggest, studies that re-visit the same areas across time. Such repeated measurements—both temporally and methodologically—will allow researchers to constrain decomposition estimates and increase the accuracy and precision of CWD pool and flux modeling.

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