Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement

C. Hély, Y. Bergeron, and M.D. Flannigan

Abstract: Quantities and structural characteristics of coarse woody debris (CWD) (logs and snags) were examined in relation to stand age and composition in the Canadian mixedwood boreal forest. Forty-eight stands originating after fire (from 32 to 236 years) were sampled on mesic clay deposits. The point-centered quadrant method was used to record canopy composition and structure (living trees and snags). The line-intersect method was used to sample logs of all diameters. Total log load, mean snag density, and volume per stand were similar to other boreal stands. Linear and nonlinear regressions showed that time since fire and canopy composition were significant descriptors for log load changes, whereas time since fire was the only significant factor for snag changes. Coarse woody debris accumulation models through time since fire were different from the U-shaped model because the first initial decrease from residual pre-disturbance debris was missing, the involved species had rapid decay rates with no long-term accumulation, and the succession occurred from species replacement through time.

Résumé : Les caractéristiques quantitatives et qualitatives des débris ligneux au sol et debout (CWD) ont été analysées en relation avec l'âge et la composition des peuplements de la forêt boréale mixte canadienne. Quarante-huit peuplements âgés de 32 à 236 ans, régénérés après feu, ont été échantillonnés sur les argiles mésiques. La méthode du point quadrant centré a été utilisée pour analyser la composition de la canopée et sa structure (arbres morts et vivants). La méthode de la ligne d'intersection a servi à échantillonner tous les débris ligneux couchés. La charge totale au sol, la densité moyenne des chicots et leur volume par peuplement étaient similaires aux charges rencontrées dans différents écosystèmes boréaux. Des régressions linéaires et non linéaires ont montré que le temps depuis le dernier feu et la composition de la canopée expliquaient significativement les changements temporels enregistrés par les débris au sol, alors que seul le temps depuis le dernier feu intervenait significativement dans les changements concernant les chicots. Les modèles d'accumulation des CWD dans le temps étaient différents du modèle "en U" en raison de l'absence d'une diminution de charge initiale, de taux de décomposition rapides des espèces (responsables d'une accumulation à court terme), et de la succession par le remplacement des espèces dans le temps.

Introduction

Coarse woody debris (CWD), as standing dead trees (snags) and fallen boles and branches (logs), contribute to the structure, microhabitat diversity, and nutrient cycling of forests (Harmon et al. 1986; Lambert et al. 1980; Stauffer and Best 1980). The functional importance of CWD depends not only on their quantities but also on their size distribution, degree of decay, species, position (snags vs. logs), and spatial arrangement (Harmon et al. 1986). Insight into the dynamics of CWD will guide managers in understanding the impacts of current management regimes on the CWD cycle and their consequences on biodiversity, stand health, and ecosystem productivity (Harmon et al. 1987; Keddy and Drummond 1996; Lee et al. 1997; Sturtevant et al. 1997).

The availability of CWD in early stages of forest development is almost entirely dependent on individual stand history (Spies et al. 1988), i.e., predisturbance- and disturbance-generated debris, and residual standing trees. Coarse woody debris within the accumulation stage is generated by the regenerating stand, and CWD is related to the standing forest structure, stem growth and mortality (Harmon et al. 1986), disturbance return interval, and decay rates. However, previous attempts relating standing tree structure (living basal area) to CWD have often yielded poor results (Sturtevant et al. 1997; Muller and Liu 1991). Several studies of CWD within forest chronosequences have described a general U-shaped temporal pattern observed in northern hardwoods (Bormann and Likens 1994), wave-regenerated balsam fir (*Abies balsamea* (L.) Mill.) (Lambert et al. 1980), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests (Agee and Huff 1987; Spies et al. 1988). This temporal pattern seems to characterize the dynamics of undisturbed forests (Lambert et al. 1980), naturally disturbed forests (Lee et al. 1997; Sturtevant et al. 1997; Tyrrell and Crow 1994), and managed forests that have been clearcut (Bormann and Likens 1994; Sturtevant et al. 1997). In general, debris levels are high following the initial stand disturbance. Residual

Received April 26, 1999. Accepted December 10, 1999.

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debris then declines over time, while there is a gradual additional input from the regenerating stand. As stands mature, tree mortality increases, and contributes to the CWD reservoir. Debris levels usually peak during a transitional stage as the even-aged stand senesces into a more uneven-aged structure. Finally, levels decline resulting in the reverse J-shaped diameter distribution of uneven-aged forests (Harmon et al. 1986; Spies et al. 1988).

In the Canadian mixedwood boreal forest, the forest vegetation is characterized by a gradual change in canopy species dominance following major disturbances such as fires (Bergeron and Dubuc 1989; Payette 1992; Roussopoulos 1978). All tree species regenerate within a few years following the fire, but the different growth rates create a successive dominance in the canopy from shade-intolerant deciduous species to shade-tolerant coniferous species. Paré and Bergeron (1995) have shown that the species replacement and the occurrence of spruce budworm outbreaks affect the aboveground biomass. As trees are the CWD producers, it would be interesting to see if CWD accumulation through time follows the same pattern as compared with the aboveground biomass. Our objectives in this study were twofold. First, we wanted to document the CWD quantities, species composition, and distributions to determine the appropriate CWD accumulation models for the Canadian mixedwood boreal forest. Secondly, we wanted to test the effect of stand composition and time since fire as potential factors that could simultaneously influence changes in CWD components. Our hypothesis is that, in the southeastern Canadian boreal forest, temporal patterns will differ from the traditional U-shaped model because there is a species replacement with time, and the involved species produce different CWD loads that have rapid but different decay rates.

Materials and methods

Study area description

The study area is located around Lake Duparquet (Bergeron et al. 1995), located in the Clay Belt of northwestern Quebec (48°30′N, 79°20′W), a large physiographic region characterized by lacustrine clay deposits left by the proglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). The area surrounding Lake Duparquet has forests that have never been commercially harvested. Lake Duparquet is situated at the southern limit of the boreal forest in the Missinaibi-Cabonga section, which is characterized by an association of balsam fir, black spruce (*Picea mariana* (Mill). BSP), paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), and trembling aspen (*Populus tremuloides* Michx.) (Rowe 1972). The mean annual temperature is 0.6°C; mean annual precipitation is 822.7 mm; and mean annual frost-free period is 64 days. However, freezing temperatures may occur throughout the year (Environment Canada 1993).

Data collection

Sampling design

Forty-eight stands initiated after lethal fires dating from 32 to 236 years ago were selected on gently sloping mesic clay deposits. Time of stand initiation has been determined in previous dendrochronological studies (Bergeron 1991; Dansereau and Bergeron 1993). Each stand was sampled with a 30-m-sided equilateral triangle (McRae et al. 1979). The triangular layout was used to minimize bias in situations where logs are not randomly oriented and to cover the variation in CWD distribution (Van Wagner 1980). This delineated sampling area was used to evaluate CWD composition and loads and to analyze the living canopy composition (Appendix 1).

Canopy composition

We sampled canopy characteristics (tree species, diameter at breast height (DBH), total height of trees, and status in the canopy as dominant or subdominant tree) using the point-centered quadrant method (Mueller-Dombois and Ellenberg 1974; McRae et al. 1979). Six points were set up along triangle edges and 48 trees were recorded per stand: 24 dominant trees and 24 sub-dominant trees. The 48 distances between trees and the quadrant centers were measured to calculate densities and basal areas per stand and per species (McRae et al. 1979).

Coarse woody debris

In the analyses, logs represent boles and branches, while snags represent standing dead trees. The line-intersect method (Van Wagner 1968, 1980) was used along each triangle side to sample logs. All surficial woody pieces crossing the line were recorded in six diameter size classes. Pieces less than 7 cm in diameter were recorded within the five classes recommended by McRae et al. (1979) using different intersect-line lengths for each diameter class: class I, 0–0.49 cm on a 15 m long line; class II, 0.5–0.99 cm on a 30-m line; class III, 1–2.99 cm on a 45-m line; class IV, 3–4.99 cm on a 60-m line; class V, 5–6.99 cm on a 75-m line. For these classes, total number of woody pieces and species proportions were measured (Appendices 2 and 3).

We recorded the species and diameter size (to the nearest 0.1 cm) of each item greater than 7 cm in diameter. These large logs constitute the sixth class. We did not use decay classes because only logs on the litter (upper duff logs) were measured, and few showed different decay states. Moreover, the moss cover was very infrequent in all stands, as reported previously by De Grandpré et al. (1993). The equation to calculate corrected fuel loading per species and diameter size class (Van Wagner 1980) is

$$[1] \qquad W = \frac{(Gk)}{L} \sum d^2 ac$$

where W is weight per unit ground area (t/ha); G is specific gravity (g/cm^3); k is a constant with a value of 1.234 (see Van Wagner 1980, p 3.); L is length of sample line (m); d is piece diameter at intersection (cm); a is correction factor for nonhorizontal angle of fuel pieces, and it has a value of 1.13 (see Brown 1974); and c is slope correction factor (see McRae et al. 1979, Table 4) computed from the tilt angle of each triangle side. Moreover

$$[2] \qquad \sum d^2 = n(dq^2)$$

where n is number of intercepts per species and diameter size class, and dq^2 is squared quadratic-mean diameter (cm^2). As no previous study focusing on CWD has been done in Quebec, we used specific multiplication factors Z from Ontario (McRae et al. 1979, Tables 2 and 3) for balsam fir, white birch, white spruce, and trembling aspen, with the Z factor corresponding to

$$[3] \qquad Z = \frac{Gk(dq)^2 a}{L}$$

For white cedar, we used original quadratic-mean diameters and particle specific gravities in Minnesota from Roussopoulos (1978). As quadratic-mean diameters and specific gravities were provided for the American diameter size classes, we used simple linear interpolations to calculate the corresponding quadratic diameters and gravities in our CWD diameter size classes. We then calculated Z multiplication factors for white cedar (see footnote of Appendix 3)

Table 1. Canonical correspondence analysis results for species log loads and snag basal areas in relation to basal areas of living canopy trees.

	Axis 1	Axis 2	Axis 3	Axis 4	Total variance in the CWD[a] data
Eigenvalues	0.303	0.164	0.052	0.036	1.38
Variance in the CWD data					
Percent explained per axis	22	11.9	3.8	2.6	
Cumulative percent explained	22	33.9	37.7	40.3	42.90
Pearson correlation between CWD and basal area of the living trees	0.846	0.828	0.527	0.512	
Monte Carlo test on correlation (p)	0.01	0.01			
CWD scores					
Log load of balsam fir	–0.275	–0.362			
Log load of white birch	–0.283	0.71			
Log load of white spruce	–0.386	–0.305			
Log load of trembling aspen	0.857	0.092			
Log load of white cedar	–0.918	–0.13			
BA of balsam fir snags	–0.294	–0.197			
BA of white birch snags	–0.792	1.37			
BA of white spruce snags	–0.103	–1.181			
BA of trembling aspen snags	0.888	–0.211			
Correlation of time since fire with axes	–0.672	–0.596			

[a] CWD, coarse woody debris.

to compute the cedar log loads per diameter size class. Both Ontario and Minnesota are the nearest geographically and ecologically relevant data sources for our study area.

Snags were sampled within six 1 m radius circles centered on the point-centered quadrants. Snag species, height, and diameter at the top were recorded (DBH if taller than 1.3 m). Densities, basal areas, and volumes of snags were calculated, but decay class was not recorded as all snags were into an intermediate decay class that no longer had bark.

Analyses

Canonical correspondence analysis

Canonical correspondence analysis (CCA) (Ter Braak 1987–1992) was used to analyze the distribution of the 48 stands according to species log loads and species snag basal areas. Basal area of living trees (dominant and subdominant trees) are the active descriptive variables, while time since fire was included in the analysis as a passive variable (Jongman et al. 1987) to evaluate the degree of association between this variable and the two first canonical axes. Further, Monte Carlo permutation tests (Ter Braak 1987–1992) were performed on the two first canonical axes to investigate the statistical significance of the impact variables on axes.

Covariance analysis

The pathway types found in the CCA have been analyzed through a covariance analysis (SAS Institute Inc. 1985). This analysis was conducted on total log loads with time since fire as the continuous variable and the pathway type (birch or aspen) as classification variable. Because a positive effect for both variables was found, the covariance analysis was extended to all CWD components. The 236-year-old coniferous stands were not included as they were the same for both pathways.

Effect of time since the last fire

Nonlinear regressions (SAS Institute Inc. 1985) were computed to study the potential effect of time since fire on log loads (total per stand, per diameter size classes, and per species) and on snag volumes (total per stand and per species).

Effects of time since the last fire and stand composition

We used multiple linear regression with the forward stepwise procedure (SAS Institute Inc. 1985) to test the significant effect of time since fire and basal areas of living tree species on log and snag components. For each species we distinguished two canopy layers (BA and ba for basal area of dominant and dominated trees, respectively). This partitioning of the living basal areas is used to represent the canopy composition and its variability. If time is the only significant descriptor, it will then correspond to the real change in CWD accumulation with time. Conversely, if living basal areas are also descriptors of CWD accumulation changes, then changes are the result of canopy composition changes through the successional process.

Results

CWD characteristics for the 48 stands sampled

Appendix 1 presents the characteristics of stands sampled for CWD components, while Appendices 2 and 3 report on logs in terms of counts, diameters, and species composition. Density of living trees per stand varied from 437 stems/ha in a 236-year-old white cedar stand to 3422 stems/ha in a pure 80-year-old aspen stand. The aspen stand also had the largest living tree basal area (125.6 m^2/ha); the old white cedar stand had the lowest living tree basal area (15.1 m^2/ha). Total log load per stand varied from 17.8 to 111.5 t/ha (mean 51.1 t/ha). Snag density varied from 0 to 7000 stems/ha, corresponding with 0–108 m^2/ha in basal area and from 0 to 700 m^3/ha in snag volume.

Analysis for multivariate potential factors

Results of the CCA, reported in Table 1 and Fig. 1, show that 42.9% of the initial variance in the CWD data set can be explained by the basal area of living trees in the canopy (33.8% on the two first axes; see Table 1). Monte Carlo tests show that the two first canonical axes are good linear combinations of these descriptive variables. The upper graph

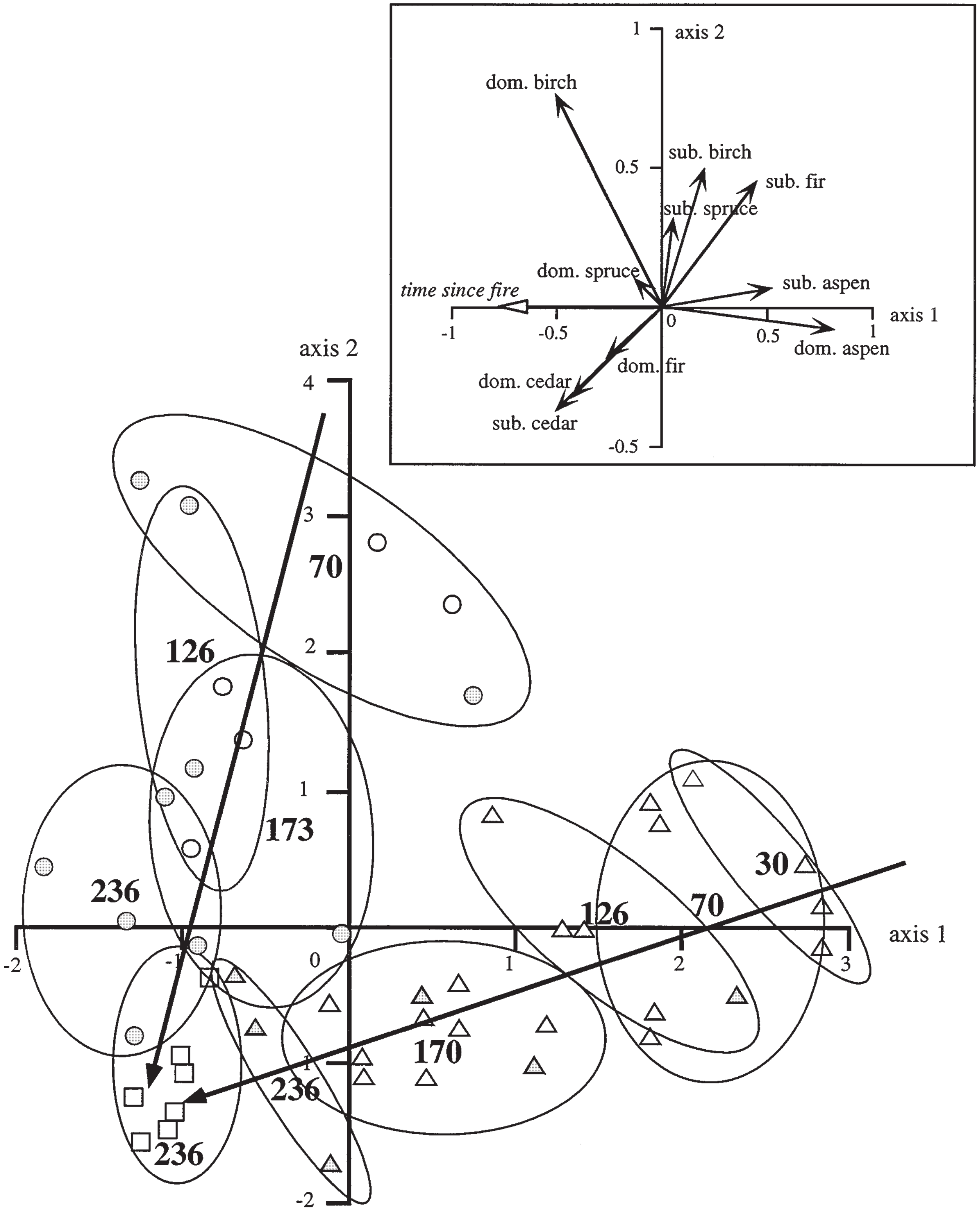
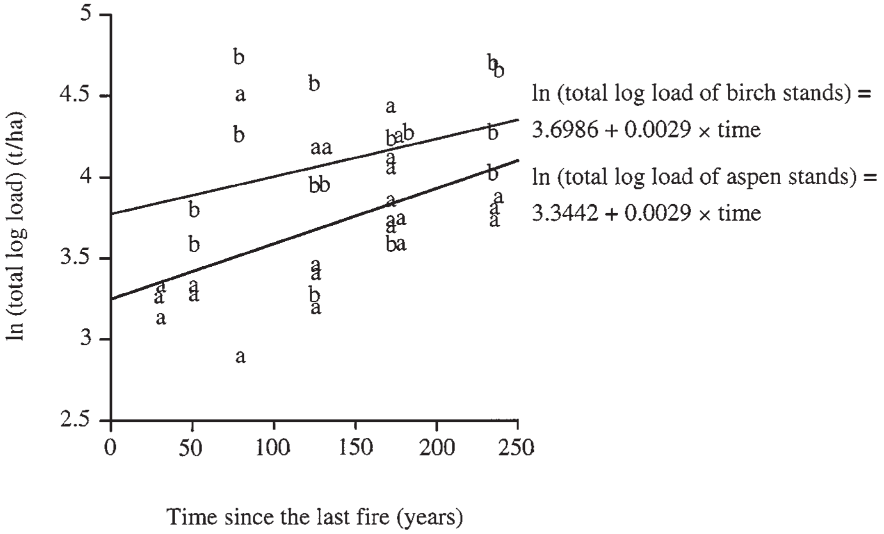


Fig. 1. Canonical correspondence analysis on coarse woody debris characteristics (species log loads and snag basal areas) in relation to basal areas of living canopy species. Arrows on the upper graph represent vectors for living basal areas of species (dom., dominant trees; sub., sub-dominant trees). On the main graph the numbers in the ellipses are the mean stand age. The symbols of stand scores are as follows: (△) aspen stands; (○) birch stands; (□) conifer stands. Shaded symbols represent mixed stands (based on coniferous basal area between 25 and 74% of total stand). Arrow directions on the main graph symbolize the successional pathway trends.

Fig. 2. Results of the covariance analysis conducted on the natural logarithms of total log loads with time since the last fire as continuous variable and successional pathway (a, trembling aspen; b, white birch) as classification variable.



shows the descriptive basal areas with time since fire as passive variable (Fig. 1). On the main graph, birch and aspen stands are segregated according to the first axis, and they present two successional pathways (the two arrow directions). These two patterns converge at the end of the succession (after 200 years since fire) towards coniferous stands. The upper graph shows that all trembling aspen, tall white birch, and white cedar are the best represented variables defining the two axes. These living basal areas are well correlated with both the basal area of snags and the log loads of their respective species (see scores in Table 1). Finally, time since fire is well correlated with canonical axes (Table 1) and it is related positively with the dominating coniferous basal areas and negatively with the trembling aspen basal areas and the subdominant conifer basal areas.

The covariance analysis on total log load (Fig. 2) shows that birch and aspen stands have the same slope parameter but significantly different intercepts. Log loads in birch stands tend to be heavier than in aspen stands. This analysis supports the existence of two successional pathways shown by the CCA. However, covariance analyses carried out on each CWD component showed that time since fire was the most significant factor (not shown). For these reasons, we have chosen to only consider time since fire as a significant factor, and we have analyzed the 48 stands together.

Effects of time since the last fire

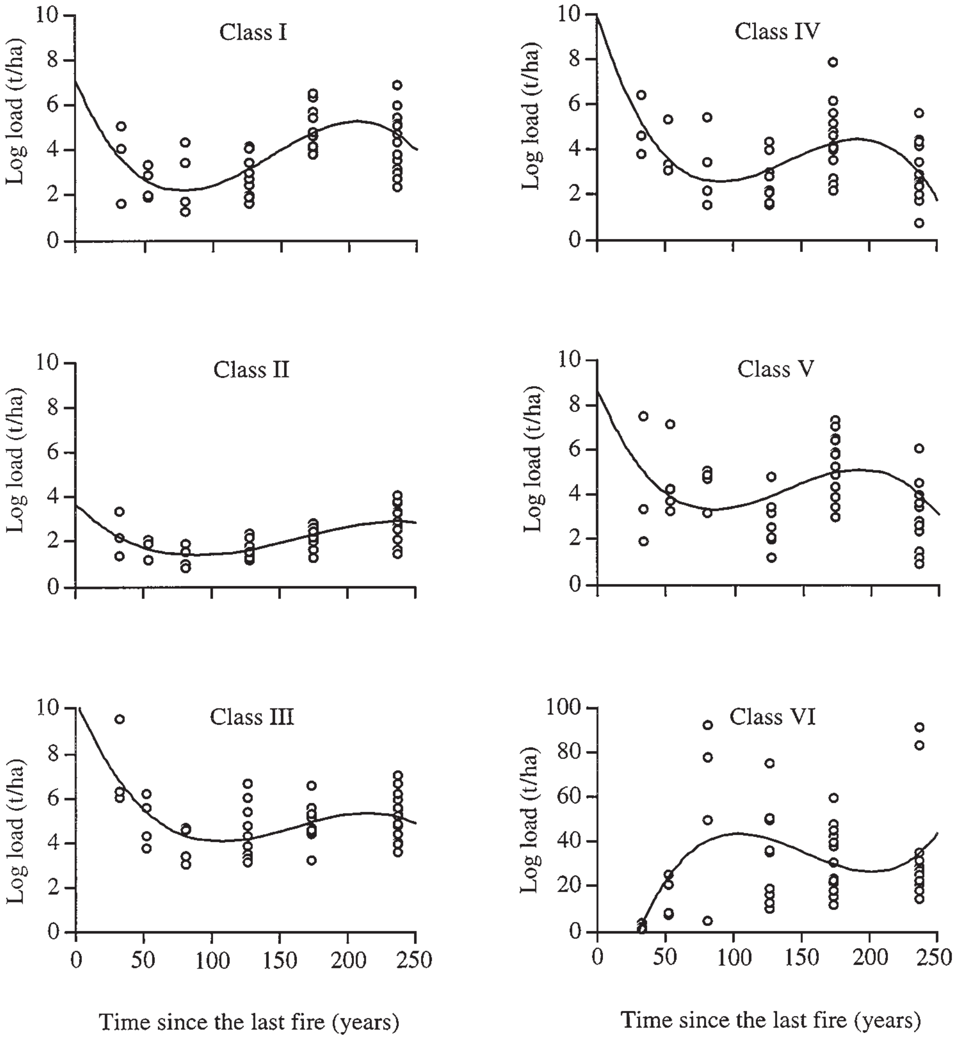
The first five diameter size classes of logs present the same general trend in relation to time since fire (Fig. 3), with a U-shaped curve prolonged by a plateau or a decrease in the very late successional stages. All these fine debris levels tend to be variable but quite high 30 years following the fire. Log loads decrease with stand age to a low at 80–120 years. An accumulation period follows then for a 100-year period and then plateaus or decreases again at late stages. However, the cumulative five class loads represent on average 43 ± 18% (mean ± SD) of total log load. The class VI load presents a significantly different pattern through time since fire (Fig. 3): coarse debris levels are the lowest 30 years after fire, but they increase up to 100 years. In stands older than 120 years, log loads tend to slightly decrease before increasing again in the late stages. These two different patterns among log class loads associated to the proportions of fine and coarse debris loads imply that total log loads (Fig. 4) fit a different pattern from the above ones, with a general load increasing with time. Among the species, only balsam fir and trembling aspen log loads had significant trends through time (Fig. 4). Aspen log loads decreased with time, whereas fir log loads increased through time. White birch log loads remained high over the entire period, while white spruce log loads were consistently the lowest. White cedar log loads increased significantly in stands older than 200 years.

Among snags, the only significant relationships between volumes and time since fire were for the total snag and balsam fir snag volumes (Fig. 5). In both cases, volumes increased with time. Volumes of trembling aspen snags present a U-shaped pattern from 30 to 170 years and then disappear after 200 years. Some birch snags are present in young and very old stands and show no particular trend. White spruce and white cedar did not have a sufficient number of stands with snags.

Effects of time since the last fire and stand composition

Results for logs and snags (Tables 2 and 3, respectively) show different behaviours of CWD in relation to time since fire and canopy basal areas. Log loads of classes V and VI, white spruce, and white cedar are not reported in Table 2 as they did not show significant linear relationships with time or basal areas. However, basal areas and time since fire are significant descriptors in four of the eight significant models (Table 2). Basal areas are the only significant descriptors in three models, whereas time since fire is the only significant descriptor for the class I log load. This implies that changes in the log accumulation (total and species log loads) are influenced both by the effect of time since fire and by the change in canopy species dominance, reflecting successional process. Moreover, the species composition effect is as

Fig. 3. Changes in log loads by diameter size class with time since the last fire. n = 48; critical $R^2_{(47,\ 0.05)}$ = 0.081. Equations for log load through time are as follows: class I = $-0.000\,003\,t^3 + 0.0026t^2 - 0.1442t + 7.1656$ (R^2 = 0.387; p = 0.0001); class II = $-0.000\,001\,t^3 + 0.0005t^2 - 0.0598t + 3.7074$ (R^2 = 0.484; p = 0.0001); class III = $-0.000\,002\,t^3 + 0.0010t^2 - 0.1444t + 10.5044$ (R^2 = 0.271; p = 0.0028); class IV = $-0.000\,004\,t^3 + 0.0016t^2 - 0.1969t + 10.1109$ (R^2 = 0.245; p = 0.0058); class V = $-0.000\,004\,t^3 + 0.0016t^2 - 0.1893t + 9.8683$ (R^2 = 0.219; p = 0.0119); class VI = $-0.000\,003\,7\,t^3 - 0.0170t^2 + 2.330t$ (R^2 = 0.175; p = 0.0360).



important as time (see Table 2 for outcome order entries from the forward stepwise selection).

Conversely, time is always the first variable selected for snags (Table 3), with four cases where it is the only significant variable. Even in models where basal areas are part of significant descriptors, only one species basal area is included. This implies that changes in snag components (species composition, density, basal area, and volume) are almost only influenced by time since fire.

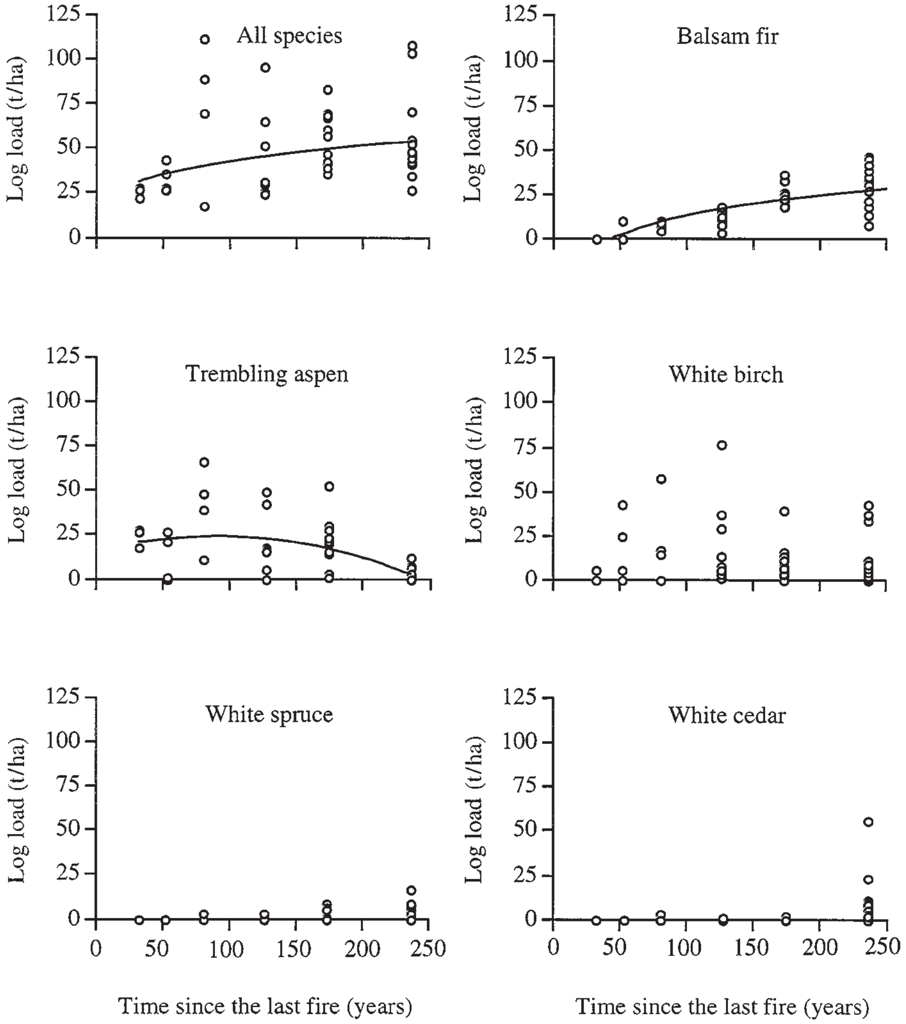
Discussion

Comparisons of CWD characteristics with other boreal ecosystems

The presented snag components (mean volume 140.5 m^3/ha; mean density 1570 stems/ha) are at the upper limit of ranges found to date in boreal forests (Lee et al. 1997; Linder et al. 1997; Schimmel and Granström 1997; Sturtevant et al. 1997). If we only focus on snags larger than 10 cm in DBH, the mean snag volume per stand increases from 140 to 143 m^3/ha, corresponding with a slight decrease of mean snag basal area from 22 to 19 m^2/ha and a mean density dropping from 1570 to 830 snags/ha. These values fit better to those of other studies. Moreover, snag density and basal area may reflect some processes such as self-thinning and natural disturbance effects. Indeed, the maximum density of 6900 snags/ha (all diameters included) was recorded in the youngest aspen stands, where trees are undergoing self-thinning (snag basal area is only 17 m^2/ha). However, only one of these stands recorded a snag larger than 10 cm in DBH. In mixed and conifer stands, snag densities higher than 3000 stems/ha represent mostly balsam firs killed during the last and most severe spruce budworm outbreak (Bergeron et al. 1995; Morin et al. 1993). Insects may have also fed on sub-dominant trees (from 5 to 10 cm in DBH) during the maximum defoliation period.

Comparisons between log characteristics found in our study area (mean log load 51 t/ha) and other boreal ecosystems

Fig. 4. Changes in the total and species log loads with time since the last fire. $n = 48$; critical $R^2_{(47,\ 0.05)} = 0.081$. Residual homoscedasticity was not accepted for white birch, white spruce, and white cedar log loads. Equations for log load through time are as follows: all species, $y = 11.96t^{0.276}$ ($R^2 = 0.139$; $p = 0.0091$); balsam fir: $y = 0.2725t - 2.565t^{0.5} + 6.0221$ ($R^2 = 0.636$; $p = 0.0001$); trembling aspen: $y = 0.0003t^2 - 0.2080t + 33.3853$ ($R^2 = 0.241$; $p = 0.0004$).



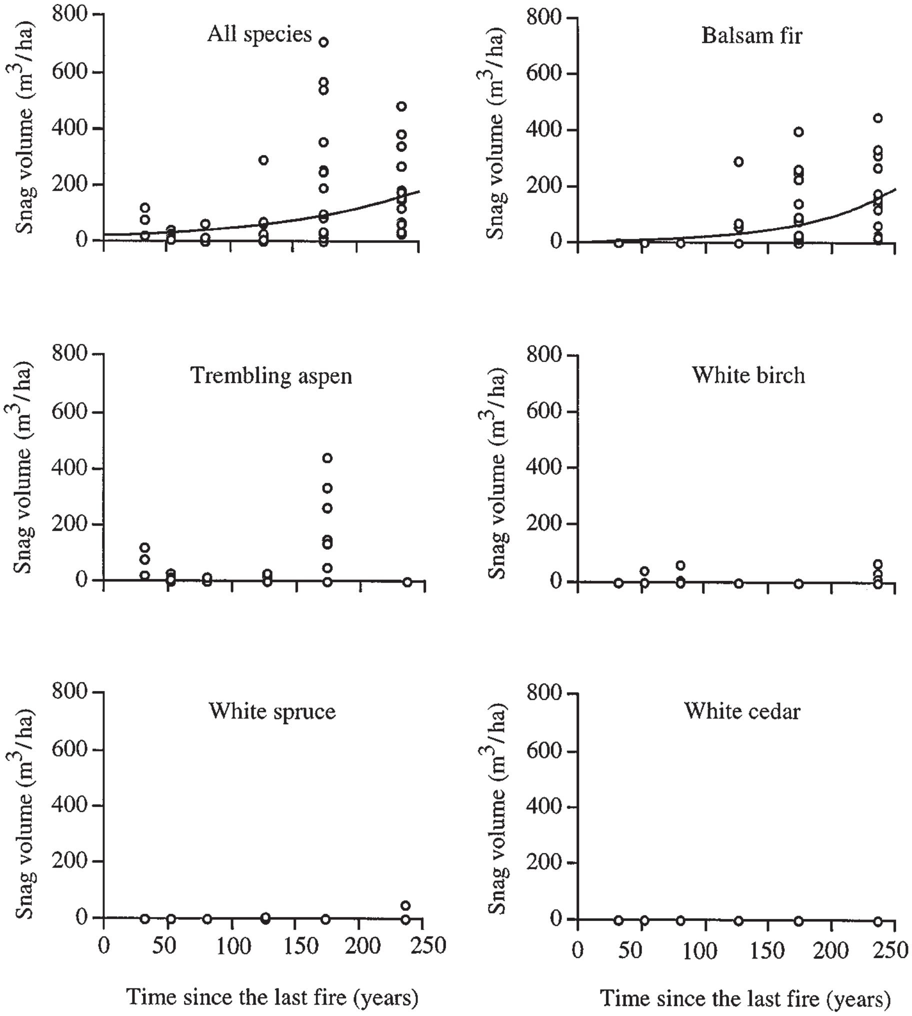
showed (Hély 2000) differences with deciduous stands in Alberta (109–124 m^3/ha; Lee et al. 1997) and mixedwood boreal stands in New Brunswick (7–20 t/ha; Freedman et al. 1996). It is likely that the drier climate in Alberta creates a less favourable environment for decomposer fungi. This would slow down bole decay rate and result in a greater log accumulation. Conversely, in New Brunswick, the moister climate has inverse effects, and it favours log decay. Moreover, Freedman et al. (1996), by sampling only logs greater than 5 cm in diameter, have not taken into account small diameter log loads that comprise up to 43% of the total load in our study area.

Stand composition and time since the last fire as descriptors of the change in the CWD accumulation

The analyses have shown that time since fire and stand canopy composition are two significant descriptive factors in CWD changes. However, while logs are influenced by both factors, snags are mainly influenced by time since fire.

The high correlation between species log loads and living basal areas show that logs reflect the stand dynamics through the successional process: the dominant deciduous species die and deciduous stands are replaced by mixed and conifer stands in later successional stages (Bergeron and Dubuc 1989). Other studies have recorded poor correlation between the stand basal area and log composition (Muller and Liu 1991; Sturtevant et al. 1997), but species composition of CWD reflected the species composition of the standing forest (Muller and Liu 1991). In our study, log loads respond almost immediately to the canopy species replacement by a rapid change in their species composition. This rapid change can be explained by the rapid replacement of the dominant canopy species that is also the largest log producer at that time. Paré and Bergeron (1995) have shown that total aboveground biomass closely corresponds to the trembling aspen biomass, and when this species is replaced by conifer species, the total aboveground biomass decreases in the same way. Moreover, the involved species are known to have rapid decay rates (Alban and Pastor 1993; Lambert et al. 1980). The log load at a given time corresponds

Fig. 5. Changes in snag characteristics with time since the last fire. n = 48 when not mentioned; critical $R^2_{(47,\ 0.05)} = 0.081$. Residual homoscedasticity was not accepted for trembling aspen, white birch, white spruce, and white cedar snag volumes. Equations for snag volume through time are as follows: all species: $y = 20.184 \times 10^{0.004t}$, ($R^2 = 0.253$; $p = 0.0006$; $n = 43$); balsam fir, $y = 0.004t^2 - 0.419t + 9.778$ ($R^2 = 0.461$; $p = 0.0001$).



closely to the present load (input and decay likely in equilibrium) and also to the actual canopy composition. It seems that there is no long-term accumulation process.

Conversely, the snags component changes are, when they exist, mainly influenced by time since fire, and to a lesser extent by the canopy composition changes. Snags, because they are standing, are drier and less exposed to decomposers, would have a slower decay rate than logs. Thus, snags can then remain standing for a long time, even though their species no longer dominates the living stand canopy. This explains why snag composition does not fit the actual living tree canopy composition, but that it is instead related to stand age and to its history. Snags reflect the transition from deciduous towards conifer dominance occurring during succession (Bergeron and Dubuc 1989): the percentage of conifer snags (mainly represented by balsam fir) increases with time, whereas trembling aspen, which is the most prolific deciduous snag producer, has a snag density that varies with time. After fire, shade-intolerant species such as trembling aspen dominate the stand canopy and the snag compartment from self-thinning. From 50 to 120 years after fire, snag volume is low but still dominated by deciduous species. After 150 years, overmature aspen die and constitute high snag inputs. Conifer species, mostly balsam fir, finally replace deciduous species in the canopy, and produce at that time, the largest snag volumes particularly from outbreaks. These intrinsic and extrinsic events created, within a short time period, large amounts of snags, standing for a long time after the disturbance event. Moreover, we also have to consider the relationship between the timing of the sampling period and spruce budworm outbreak events. If CWD were sampled 25–30 years ago, the last spruce budworm outbreak would not have occurred yet, and the balsam fir CWD (logs and snags) would have been less important. Additionally, if we were to sample CWD 20 years from now with no spruce budworm outbreaks ocurring, the balsam fir snags would have fallen and so would be less important.

CWD accumulation models in the southern boreal forest

Coarse woody debris accumulation models in the mixedwood boreal forest (Figs. 3–5) are different from other CWD

Table 2. Significant multiple regressions for the log load components.

Variable	Total	Class I	Class II	Class III	Class IV	ln(fir)	$(\text{Birch})^{0.5}$	$(\text{Aspen})^{0.5}$
p	0.0004	0.0003	0.0001	0.0010	0.0280	0.0001	0.0001	0.0001
Multiple *R*	0.5430	0.5030	0.6850	0.5140	0.3170	0.8820	0.7078	0.8370
R^2	0.2640	0.2360	0.4690	0.2320	0.1010	0.7770	0.5010	0.7010
Intercept	0.0000	2.2370	1.6110	5.2040	3.3691	0.0000	1.3071	3.6940
Time	0.1303 (2)	0.0110 (1)	0.0061 (1)			0.0151 (1)		–0.0099 (2)
BA fir								
BA birch							0.2103 (1)	–0.1267 (4)
BA spruce			–0.0827 (2)					
BA aspen				–0.0197 (2)				0.0413 (1)
BA cedar								
ba fir	5.3814 (1)		–0.0869 (3)			0.1674 (2)		0.3716 (3)
ba birch							0.4195 (2)	
ba spruce								
ba aspen				0.1875 (1)	0.1608 (1)			
ba cedar								

Note: Only the significant parameters are given. Values in parentheses give the order in which the variables entered the model. *p*, overall model probability; BA, basal area of dominant trees; ba, basal area of subdominant trees.

Table 3. Significant multiple regressions for the snag components.

Variable	$(\text{Stand vol.})^{0.5}$	$(\text{Stand BA})^{0.5}$	Conifer snags (%)	ln(fir dens.)	ln(fir BA)	$(\text{Fir vol.})^{0.5}$	ln(aspen dens.)
p	0.0015	0.0068	0.0001	0.0001	0.0001	0.0001	0.0001
Multiple *R*	0.4447	0.3858	0.6162	0.6756	0.7080	0.7114	0.6940
R^2	0.1977	0.1489	0.3797	0.4564	0.5018	0.5061	0.4816
Intercept	0.0000	1.8548	0.0000	0.0000	0.0000	–4.297	7.8627
Time	0.0445 (1)	0.0136 (1)	0.3005 (1)	0.0333 (1)	0.0156 (1)	0.7990 (1)	–0.0259 (1)
BA fir							
BA birch			–2.3327 (2)				–0.2468 (2)
BA spruce							
BA aspen							
BA cedar							
ba fir							
ba birch							
ba spruce							
ba aspen							
ba cedar						–0.5436 (2)	

Note: Only the significant parameters are given. Values in parentheses give the order in which the variables entered the model. *p*, overall model probability; BA, basal area of dominant trees; ba, basal area of subdominant trees; vol., volume (m^3/ha); dens., density (stems/ha).

accumulation models (Agee and Huff 1987; Bormann and Likens 1994; Harmon et al. 1986; Spies et al. 1988; Sturtevant et al. 1997). As we have seen above, the key factors explaining these differences (for total or species loads) are the species replacement occurring during succession (Bergeron and Dubuc 1989), differences in species productivity (Paré and Bergeron 1995), rapid decay rates (Lambert et al. 1980; Harmon et al. 1986), and disturbances such as cyclic spruce budworm outbreaks killing mature balsam firs and favouring white birch and (or) balsam fir regeneration (Kneeshaw and Bergeron 1998). The CWD models in our study do not show the high initial post-fire CWD load resulting from the fire event, as in the traditional U-shaped model (Agee and Huff 1987; Bormann and Likens 1994; Spies et al. 1988; Sturtevant et al. 1997). The initial load at 30 years is composed of small-diameter pieces (that would not have withstood the fire event) and not from pre-fire or fire residual debris. The absence of large pre-fire CWD can be explained by the faster decay rate of burned pieces a few years after fire (Harmon et al. 1986) and by the absence of large-diameter trees in pre-fire stands. Indeed, even in old stands, conifers that dominate stands are much smaller trees and snag producers than deciduous species (Paré and Bergeron 1995). The log pattern of trembling aspen through time found and discussed in our study shows the same trend as the aboveground biomass found by Paré and Bergeron (1995) in the same study area and also as the trembling aspen snags in western Canada found by Lee et al. (1997). This pattern is characterized by a first load increase until stand maturity, followed by a period of load decrease during the late successional stages. It resembles the aboveground living biomass of forest stands presented by Peet (1981), who assigned this accumulation pattern to boreal stands such as feathermoss – black spruce stands with very thick organic layer. In our case, the period of load decrease is not a decrease in the successive cohort productivity because of less favorable abiotic conditions but to the species replacement with a resulting decrease in the abundance of trembling aspen (Bergeron and Dubuc 1989; Paré and Bergeron 1995). Aspen and birch have no difference in decay rates, but white birch log accumulation is significantly higher than trembling aspen (same trend in Fig. 2). Moreover, the birch trend through time is more variable (nonsignificant trend in Fig. 4) than for aspen logs. This variability difference may come from the distinct life-history patterns of these species: white birch is a long-lived species with one postfire cohort that can stand more than 200 years (Frelich and Lorimer 1991; Dansereau and Bergeron 1993) and create logs and snags along the entire succession, whereas the mean life-span of trembling aspen is 80 years in eastern North America (Hosie 1979); aspen regenerates through successive cohorts over a comparable period. Thus, aspen produces high episodic amounts of CWD (Fig. 5 for snags). The birch pattern variability could also be explained by periodic openings of stand canopy from balsam fir death during spruce budworm outbreaks. Large gaps are favourable to white birch regeneration (Kneeshaw and Bergeron 1998). For white cedar, this study would have required a longer time window to record a significant trend, as this shade-tolerant species only begins to regenerate in the late stages (Bergeron and Dubuc 1989). A recently discovered mesic forest dominated by white cedar and regenerated at least 400 years ago after a fire had a total log load of 29 t/ha. Balsam fir, white cedar, and white birch were responsible for 18, 8, and 3 t/ha, respectively. This suggests that mixed stands can be maintained for a long time (high variability of old stand composition also shown by the CCA) and that high balsam fir log load was probably created by the last spruce budworm outbreak. However, because of the longevity of white cedar, it produces only small log loads even in 236-year-old stands. White spruce seems the least active species in the successional replacement process, with a low abundance of living trees and few logs and snags. This could explain why there was no significant trend over time for this species. Finally, balsam fir accumulates CWD during the entire succession. The trend seems to be dependent on both disturbance and decay rate. Because the outbreak periods seem to be as long as the decay rate, the log pattern should stay stable over the long term, until another fire occurs.

Acknowledgments

This research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Quebec Ministry of Education (Fonds pour la formation de chercheurs et l'aide à la recherche), and the Network of Centres of Excellence in Sustainable Forest Management. We thank Samuel Alleaume, Catherine Boudreault, and Marie-Hélène Longpré for assistance in the field; Thuy Nguyen, Daniel Gagnon, and two anonymous reviewers for valuable comments on an earlier version of this manuscript; and Patricia Wood and Brenda Laishley for linguistic amelioration. We thank the members of the Groupe de recherche en écologie forestière and Northern Forestry Centre staff in Edmonton for their help.

References

Agee, J.K., and Huff, M.H. 1987. Fuel succession in a western hemlock/Douglas-fir forest. Can. J. For. Res. **17**: 697–704.

Alban, D.H., and Pastor, J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. **23**: 1744–1749.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology, **72**: 1980–1992.

Bergeron, Y., and Dubuc, M. 1989. Succession in the southern part of the Canadian boreal forest. Vegetation, **79**: 51–63.

Bergeron, Y., Leduc, A., Morin, H., and Joyal, C. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. Can. J. For. Res. **25**: 1375–1384.

Bormann, F.H., and Likens, G.E. 1994. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA For. Serv. Gen. Tech. Rep. No. INT-16.

Dansereau, P., and Bergeron, Y. 1993. Fire history in the southern boreal forest of northern Québec. Can. J. For. Res. **23**: 25–32.

De Grandpré, L., Gagnon, D., and Bergeron, Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. J. Veg. Sci. **4**: 803–810.

Environment Canada 1993. Canadian climate normals 1961–90. Canadian Climate Program, Atmospheric Environment Service, Environment Canada, Downsview, Ont.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Flemming, S., Forbes, G., Gerrow, J.S., Johnson, G., and Woodley, S. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. **4**: 238–265.

Frelich, L.E., and Lorimer, C.G. 1991. Natural disturbance regimes in hemlock–hardwood forests of the Upper Great Lakes region. Ecol. Monogr. **61**: 145–164.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. No. 15. pp. 133–302.

Harmon, M.E., Cromack, H., Jr., and Smith, B. 1987. Coarse woody debris in mixed-conifer forest, Sequoia National Park, California. Can. J. For. Res. **17**: 1265–1272.

Hély, C. 2000. Influence de la végétation et du climat dans le comportement des incendies en forêt boréale mixte canadienne. Ph.D. thesis, Université du Québec à Montréal, Montréal.

Hosie, R.C. 1979. Native trees of Canada. 8th ed. Fitzhenry and Whiteside Ltd., Toronto, Ont.

Jongman, R.H.G., Ter Braak, C.J.F., and Can Tongeren, O.F.R. 1987. Data analysis in community and landscape ecology. Pudoc, Wageningen, the Netherlands.

Keddy, P.A., and Drummond, C.G. 1996. Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems. Ecol. Appl. **6**: 748–762.

Kneeshaw, D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology, **79**: 783–794.

Lambert, R.L., Lang, G.E., and Reiners, W.A. 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology, **61**: 1460–1473.

Lee, P.C., Crites, S., Nietfeld, M., Van Nguyen, H., and Stelfox, J.B. 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecol. Appl. **7**: 691–701.

Linder, P., Elfving, B., and Zackrisson, O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. For. Ecol. Manage. **98**: 17–33.

McRae, D.J., Alexander, M.E., and Stocks, B.J. 1979. Measurement and description of fuels and fire behaviour on prescribed burns: a handbook. Can. For. Serv. Great Lakes For. Cent. Inf. Rep. No. O-X-287.

Morin, H., Laprise, D., and Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Can. J. For. Res. **23**: 1497–1506.

Mueller-Dombois, D., and Ellenberg, H. 1974. Aims and methods of vegetation ecology. Wiley, New York.

Muller, R.N., and Liu, Y. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland plateau, southeastern Kentucky. Can. J. For. Res. **21**: 1567–1572.

Paré, D., and Bergeron, Y. 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. J. Ecol. **83**: 1001–1007.

Payette, S. 1992. Fire as controlling process in the Northern American boreal forest. *In* A systems analysis of the global boreal forest. *Edited by* H.H. Shugart, R. Leemans, and G.B. Bonan. Cambridge University Press, New York. pp. 144–169.

Peet, R.K. 1981. Changes in biomass and production during secondary forest succession. *In* Forest succession: concepts and application. *Edited by* D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, New York. pp. 325–338.

Roussopoulos, P.J. 1978. An appraisal of upland forest fuels and potential fire behavior for a portion of the boundary waters canoe area. Ph.D. thesis, Department of Forestry, Michigan State University, East Lansing.

Rowe, J.S. 1972. Forest regions of Canada. Environment Canada, Ottawa, Ont. Publ. No. 1300.

SAS Institute Inc. 1985. SAS user's guide: statistics, version 6 edition. SAS Institute Inc., Cary, N.C.

Schimmel, J., and Granström, A. 1997. Fuel succession and fire behavior in the Swedish boreal forest. Can. J. For. Res. **27**: 1207–1216.

Spies, T.A., Franklin, J.F., and Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology, **69**: 1689–1702.

Stauffer, D.F., and Best, L.B. 1980. Habitat selection by birds of riparian communities: evaluating effect of habitat alteration. J. Wildl. Manage. **44**: 1–15.

Sturtevant, B.R., Bissonette, J.A., Long, J.M., and Roberts, D.W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol. Appl. **7**: 702–712.

Ter Braak, C.J.F. 1987–1992. CANOCO—a FORTRAN program for canonical community ordination. Microcomputer Power, Ithaca, N.Y.

Tyrrell, L.E., and Crow, T.R. 1994. Dynamics of dead wood in old-growth hemlock–hardwood forests of northern Wisconsin and northern Michigan. Can. J. For. Res. **24**: 1672–1683.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. For. Sci. **14**: 20–26.

Van Wagner, C.E. 1980. Practical aspects of the line intersect method. Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep. No. PI-X-12.

Vincent, J.S., and Hardy, L. 1977. L'évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québecois. Geogr. Phys. Quat. **31**: 357–372.

Appendix 1

Table A1. Characteristics of sampled stands.

Stand No.	Time since last fire (years)	Total living density (stems/ha)	Total living basal area (m^2/ha)	Deciduous living basal area (%)	Total log load (t/ha)	Total basal area of snags (m^2/ha)	Total volume of snags (m^3/ha)	Total snag density (stems/ha)
p0301	32	2382	51.27	100	27.70	17.41	81.57	6897
p0302	32	1978	42.80	100	22.60	3.58	25.26	2122
p0303	32	1234	35.33	100	26.20	7.15	125.13	531
b0551	52	1072	39.41	70	35.40	13.80	42.45	1592
b0552	52	1478	18.98	96	43.61	15.59	28.84	1061
p0551	52	1055	22.43	93	27.59	8.46	17.26	1592
p0552	52	1901	37.53	96	26.96	2.67	5.60	531
b0801	80	2309	64.94	77	111.51	2.87	8.41	1592
b0802	80	1139	45.06	72	70.02	6.69	62.59	1061
p0801	80	3422	125.57	93	89.22	0.00	0.00	0
p0802	80	2823	60.49	92	17.80	9.81	18.40	1061
b1201	126	1702	31.81	81	51.10	55.85	294.63	4244
b1202	126	1581	25.91	74	26.02	0.00	0.00	0
b1203	126	2168	21.20	81	51.90	9.60	63.87	1061
b1204	126	1057	25.80	52	95.58	0.00	0.00	0
p1201	126	1205	47.73	92	29.76	14.84	15.59	1061
p1202	126	1265	35.81	71	24.05	32.51	32.51	1061
p1203	126	753	44.08	81	64.86	16.92	74.01	2122
p1204	126	632	54.67	78	31.37	0.00	0.00	0
p1205	126	712	70.96	91	65.35	2.28	10.27	531
b1701	173	1065	15.50	36	69.76	8.76	83.22	531
b1702	173	878	22.83	78	67.86	0.00	0.00	0
b1703	173	1650	29.57	29	35.64	15.52	97.78	531
p1701	173	1160	31.40	68	56.75	5.90	19.18	1061
p1702	173	1646	26.69	78	68.14	41.50	254.53	1592
p1703	173	861	32.36	77	36.10	25.20	251.14	1592
p1704	173	825	64.38	85	60.99	7.64	32.09	1592
p1705	173	1800	39.50	84	82.56	107.89	708.50	3183
p1706	173	1111	47.09	96	41.20	7.89	34.72	1592
p1707	173	748	31.66	95	46.60	74.93	569.44	3183
p1708	173	627	32.14	68	42.42	35.06	358.35	2653
p1709	173	1430	57.41	82	56.96	70.82	540.57	1592
p1710	173	1045	50.90	93	39.63	23.95	196.38	1592
b2101	236	444	30.44	59	70.49	84.39	485.84	3714
b2102	236	673	37.74	65	54.90	11.90	29.75	531
b2103	236	775	22.98	49	103.42	19.75	147.10	1061
b2104	236	1084	24.06	59	108.31	25.43	149.18	1592
p2101	236	906	52.66	54	44.49	10.17	70.15	1061
p2102	236	570	37.15	56	41.13	22.68	123.98	1592
p2103	236	1002	68.88	70	46.40	6.86	37.76	1592
s2101	236	999	23.30	21	46.89	47.87	380.60	3714
s2102	236	961	26.30	18	34.85	14.31	64.39	1592
t2101	236	820	36.33	34	47.23	33.49	159.09	2122
t2102	236	578	68.12	22	41.98	20.99	185.40	1592
t2103	236	1086	15.10	0	44.68	26.43	179.36	2122
t2104	236	1288	33.03	7	47.97	33.78	340.29	2122
t2105	236	437	43.58	11	26.77	10.97	67.47	1061
t2106	236	1136	37.33	10	52.24	21.55	272.63	1061

Appendix 2

Table A2. Characteristics of sampled logs: number of woody counts per class for the first five diameter size classes, and sum of square diameters per species for the sixth diameter size class.

Stand	No. of wood pieces					Sum of square diameters per species in class VI				
No.	Class I	Class II	Class III	Class IV	Class V	Fir	Birch	Spruce	Aspen	Cedar
p0301	285	157	132	50	32	0	0	0	890	0
p0302	705	228	127	26	13	0	0	0	537	0
p0303	850	372	208	36	8	0	0	0	289	0
b0551	385	114	85	19	11	1312	1762	0	0	0
b0552	580	195	102	15	11	0	3014	0	204	0
p0551	345	129	78	37	28	59	146	0	1284	0
p0552	565	210	121	24	18	0	50	0	1638	0
b0801	940	145	94	21	18	535	5628	0	8909	0
b0802	705	183	87	30	16	1351	263	0	7488	848
p0801	220	111	65	16	13	1716	1624	0	11202	0
p0802	315	96	79	12	21	0	282	0	587	0
b1201	545	154	133	13	14	1008	3599	0	0	0
b1202	605	142	97	10	18	1329	483	0	0	0
b1203	890	220	88	13	9	2236	2350	149	1029	0
b1204	960	205	133	25	11	2089	7879	0	0	231
p1201	315	134	86	24	14	1288	145	0	1875	0
p1202	390	133	74	20	5	240	132	139	2045	0
p1203	695	193	135	17	9	1009	420	0	8309	0
p1204	345	137	85	12	14	1263	860	0	999	0
p1205	595	172	73	30	9	1924	659	533	6446	0
b1701	1080	198	101	17	27	3314	456	1389	3863	0
b1702	1035	217	97	49	22	2590	3220	149	576	0
b1703	1470	230	120	33	15	1802	420	0	0	0
p1701	1060	245	124	19	13	5221	1024	0	400	250
p1702	800	238	140	32	29	5111	243	0	3605	0
p1703	865	138	80	17	15	2337	0	0	1741	317
p1704	770	237	111	33	26	2550	636	1001	3255	0
p1705	710	176	127	38	28	3675	594	0	7441	0
p1706	860	304	161	44	23	1683	0	0	1228	388
p1707	990	264	85	36	31	1903	0	0	2814	0
p1708	800	235	116	28	22	2113	365	916	793	0
p1709	1420	277	114	47	25	1623	1011	77	2874	0
p1710	1020	259	111	32	19	2097	803	0	345	0
b2101	730	258	107	35	67	1565	2819	773	0	168
b2102	1760	266	151	28	12	4563	86	0	0	1368
b2103	740	206	163	20	20	6480	3622	0	0	5716
b2104	690	161	89	17	14	689	3214	1156	0	1399
p2101	1470	319	155	27	16	3206	135	0	625	106
p2102	940	143	89	12	6	2877	189	1146	1024	0
p2103	1400	313	137	15	11	3680	703	0	586	135
s2101	1165	330	142	34	28	4638	0	0	0	0
s2102	1270	224	104	20	13	2639	0	0	0	1174
t2101	1125	247	126	13	7	2559	0	2614	0	811
t2102	900	202	129	17	14	2876	1138	0	0	541
t2103	1475	337	153	6	14	4193	59	502	0	279
t2104	2020	329	164	31	12	4495	0	0	0	178
t2105	1065	192	106	15	4	1140	650	0	625	291
t2106	1345	221	152	28	17	4622	1076	0	0	67

Appendix 3

Table A3. Species percentages of sampled logs for the different diameter classes.

Stand	Percentage in class I					Percentage in class II					Percentage in classes III–V				
No.	Fir	Birch	Spruce	Aspen	Cedar	Fir	Birch	Spruce	Aspen	Cedar	Fir	Birch	Spruce	Aspen	Cedar
p0301	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0
p0302	0	0.2	0	0.8	0	0	0.2	0	0.8	0	0	0.2	0	0.8	0
p0303	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0
b0551	0.1	0.9	0	0	0	0.4	0.6	0	0	0	0.4	0.6	0	0	0
b0552	0	1	0	0	0	0	0.9	0	0.1	0	0	1	0	0	0
p0551	0	0.2	0	0.8	0	0	0.2	0	0.8	0	0	0.2	0	0.8	0
p0552	0	0	0	1	0	0	0.1	0	0.9	0	0	0	0	1	0
b0801	0.3	0.7	0	0	0	0.2	0.8	0	0	0	0.2	0.5	0	0.3	0
b0802	0.2	0.7	0	0.1	0	0.2	0.7	0	0.1	0	0.2	0.7	0	0.1	0
p0801	0.1	0.1	0	0.8	0	0.1	0.1	0	0.8	0	0.1	0.1	0	0.8	0
p0802	0.2	0	0	0.8	0	0.2	0	0	0.8	0	0.2	0	0	0.8	0
b1201	0.6	0.4	0	0	0	0.6	0.4	0	0	0	0.6	0.4	0	0	0
b1202	0.5	0.5	0	0	0	0.5	0.5	0	0	0	0.4	0.6	0	0	0
b1203	0.3	0.7	0	0	0	0.3	0.7	0	0	0	0.4	0.6	0	0	0
b1204	0.6	0.3	0	0	0.1	0.5	0.4	0	0	0.1	0.4	0.6	0	0	0
p1201	0.3	0	0	0.7	0	0.3	0	0	0.7	0	0.4	0	0	0.6	0
p1202	0.3	0.2	0	0.5	0	0.3	0.2	0	0.5	0	0.3	0.2	0	0.5	0
p1203	0.5	0	0	0.5	0	0.5	0	0	0.5	0	0.5	0	0	0.5	0
p1204	0.2	0.3	0	0.5	0	0.2	0	0	0.8	0	0.2	0	0	0.8	0
p1205	0.1	0.1	0	0.6	0.2	0.3	0	0	0.7	0	0.2	0.1	0	0.6	0.1
b1701	0.6	0.4	0	0	0	0.5	0.5	0	0	0	0.5	0.5	0	0	0
b1702	0.5	0.5	0	0	0	0.6	0.4	0	0	0	0.6	0.4	0	0	0
b1703	0.7	0.2	0	0.1	0	0.7	0.3	0	0	0	0.6	0.4	0	0	0
p1701	0.3	0	0	0.7	0	0.4	0	0	0.6	0	0.4	0	0	0.6	0
p1702	0.5	0	0	0.5	0	0.6	0	0	0.4	0	0.5	0	0	0.5	0
p1703	0.8	0	0	0.2	0	0.5	0	0	0.5	0	0.5	0	0	0.5	0
p1704	0.3	0	0	0.7	0	0.6	0	0	0.4	0	0.5	0	0	0.5	0
p1705	0.3	0	0	0.7	0	0.4	0	0	0.6	0	0.3	0	0	0.7	0
p1706	0.3	0	0	0.7	0	0.4	0	0	0.6	0	0.4	0	0	0.6	0
p1707	0.5	0	0	0.4	0.1	0.8	0	0	0.2	0	0.8	0	0	0.2	0
p1708	0.4	0	0	0.6	0	0.3	0	0.1	0.6	0	0.6	0	0	0.4	0
p1709	0.6	0.2	0	0.2	0	0.7	0	0	0.3	0	0.6	0.1	0	0.3	0
p1710	0.3	0	0	0.7	0	0.5	0	0	0.5	0	0.4	0	0	0.6	0
b2101	0.1	0.9	0	0	0	0.4	0.6	0	0	0	0.6	0.4	0	0	0
b2102	0.5	0.2	0.2	0	0.1	0.4	0.3	0	0	0.3	0.4	0.3	0	0	0.3
b2103	0.6	0.4	0	0	0	0.5	0.5	0	0	0	0.9	0.1	0	0	0
b2104	0.2	0.7	0	0	0.1	0.6	0.4	0	0	0	0.4	0.6	0	0	0
p2101	0.7	0	0	0.3	0	0.6	0	0	0.3	0.1	0.5	0	0	0.4	0.1
p2102	0.2	0.6	0.1	0.1	0	0.1	0.7	0.1	0.1	0	0.5	0.2	0.1	0.2	0
p2103	0.6	0.1	0	0.1	0.2	0.7	0.1	0	0.1	0.1	0.6	0.1	0	0.2	0.1
s2101	0.7	0.1	0	0.2	0	0.9	0	0	0.1	0	1	0	0	0	0
s2102	0.7	0.1	0	0	0.2	0.5	0.2	0	0	0.3	0.9	0	0	0	0.1
t2101	0.2	0.3	0	0	0.5	0.3	0.3	0.1	0	0.3	0.4	0.1	0	0	0.5
t2102	0.3	0	0	0.1	0.6	0.5	0	0	0.1	0.4	0.5	0.1	0	0.1	0.3
t2103	0.7	0.2	0	0	0.1	0.8	0.1	0	0	0.1	0.8	0	0	0	0.2
t2104	0.6	0.1	0	0	0.3	0.7	0.1	0	0	0.2	0.6	0.2	0	0	0.2
t2105	0.1	0	0	0	0.9	0.8	0.1	0	0	0.1	0.9	0.1	0	0	0
t2106	0.8	0.1	0	0	0.1	0.8	0	0	0	0.2	0.9	0	0	0	0.1

Note: The calculated multiplication factors for white cedar are as follows: class I = 0.0002; class II = 0.0020; class III = 0.0047; class IV = 0.0141; class V = 0.0113; class VI = 0.0004.