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Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity

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Abstract

The long-term relationships between coarse woody debris (CWD) dynamics, soil characteristics and site productivity have, so far, received little attention. The objectives of the study were to describe CWD dynamics along a post-fire chronosequence (43–86 years after fire) in jack pine (*Pinus banksiana* Lamb.) stands, assess the importance of buried CWD in terms of soil available water holding capacity (AWHC), and investigate relationships between CWD, AWHC, nutrient retention and site productivity.

Twelve jack pine stands on sandy, mesic sites of glaciolacustrine origin were surveyed. Buried wood volume within the forest floor varied between 1 and 57 m^3 ha^{-1} (4–92% of total site CWD volume) and showed no relationship with time. Downed log mass accumulation followed a ''U shaped'' successional pattern with time since fire. Buried wood AWHC was negligible compared with that of the 0–20 cm mineral soil layer. The most productive sites were characterised by higher forest floor dry weight, effective CEC and water holding capacity in the mineral soil. Path analyses of relationships between organic matter content, CWD and forest floor CEC showed that CEC was conditioned by forest floor organic matter and buried wood content.

Keywords: Jack pine; Soil organic matter; Coarse woody debris; Site index; Forest fire

1. Introduction

Coarse woody debris (CWD) made up of snags and downed logs, is part of forest ecosystem structures, or legacies, remaining from disturbances such as fires, windthrow, or insect outbreaks that consume small amounts of wood (Franklin, 1992). As such, CWD affects a disturbed ecosystem's ability to maintain key processes (Perry and Amaranthus, 1997). For example, CWD provides habitat, seedbed and food for numerous organisms (Harmon et al., 1986); stores substantial amounts of carbon (Fleming and Freedman, 1998) and nutrients (Arthur and Fahey, 1990; Means et al., 1992); provides substrate for nitrogen fixation (Hendrickson, 1991; Griffiths et al., 1993; Crawford et al., 1997); and contributes to on-site nitrogen retention through immobilization following severe disturbance (Vitousek and Matson, 1985). Downed logs can also store large quantities of water (Means et al., 1992).

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The amount of CWD in an ecosystem reflects the cumulative balance between inputs through tree mortality and outputs through respiration and export (Harmon et al., 1986). In natural stands originating from fire, causes and rates of tree mortality change with successionnal status from fire-induced mortality to self-thinning, and finally, senescence (Lee et al., 1997). Dynamics of snags and downed wood in post-disturbance stands often follow a "U shaped" successional pattern with higher biomass in young and older stands (Harmon et al., 1986; Sturvenant et al., 1997; Clark et al., 1998). Eventually these residues become part of the forest floor as buried wood (McFee and Stone, 1966), and finally, part of soil organic matter (SOM) stable fraction (N'dayegamiye and Angers, 1993). Hyvönen and Ägren (2001) estimated stem wood and coarse-root litter may account for 70% of forest soils' C pool.

A continuous input of organic matter is of particular relevance for coarse-textured soils where stabilisation of organic C by clay is minimal (Oades, 1988) and where most of the soil cation exchange capacity (CEC) depends primarily on its organic fraction (Baldock and Nelson, 1999). Soil organic matter also contributes to soil water retention directly through its own ability to absorb water and indirectly through its effects on soil structure. The effect of SOM on soil available water holding capacity (AWHC) increases as soil sand content increases (Baldock and Nelson, 1999). Available water holding capacity (Pawluk and Arneman, 1961; Béland and Bergeron, 1996) or site characteristics controlling soil moisture (Schmidt and Carmean, 1988) have been shown to explain a high percentage of the productivity of jack pine stands growing on coarse-textured sites. The slow organic matter decomposition rates of species such as jack pine (95% breakdown time of 71 years) (Alban and Pastor, 1993) adapted to coarse-textured sites may contribute to their ability to sustain productive forest ecosystems.

CWD water characteristics have received little attention, but Harmon and Sexton (1995) have shown that CWD ability to store water increases with decay during the first years of decomposition. We hypothesised that as decomposition proceeds and wood density decreases, the capacity of CWD to store water should increase. Buried wood contained in the forest floor of coarse-textured soils should make a significant contribution to overall soil AWHC, and as a source of organic matter, it should also contribute to CEC.

This study (1) assesses the dynamics of CWD – snags, downed logs and buried wood – in jack pine stands in relation to time since fire; (2) measures AWHC of downed logs and buried wood in relation to decomposition status; (3) compares CWD's AWHC to that of the mineral soil; and (4) tests causal relationships between time since fire, amounts of CWD, soil characteristics and site productivity.

2. Material and methods

2.1. Study area

The study area is located in northwestern Quebec, Canada (48°20′–49°20′N; 78°40′–79°15′ W). Climate is continental with mean annual temperature of 0.7 °C and total precipitation of 890 mm, falling mainly as rain (Environment Canada, 2002). The region is part of the Precambrian Shield and the topography is generally gentle. Most of the bedrock is covered with Quaternary surface deposits. Because of their dimensions, eskers are an important feature of the landscape, while a clay plain formed by sedimentation at the bottom of glacial Lake Barlow-Ojibway lies between the eskers (Allard, 1974). The transition zone between the eskers and the clay plain is covered with reworked glaciofluvial material overlaying the bottom of the lake. Soils from the study have evolved from these coarse-textured glaciolacustrine deposits and are classified as humo-ferric podzols (perudic cryorthods) (Soil Classification Working Group, 1998).

2.2. Stands selection

Potential stands where first localised using Quebec Natural Resources Ministry's forest inventory database which provides information such as stand composition, surface deposit, moisture regime and slope. All selected stands were pure jack pine, growing on coarse-textured glaciolacustrine deposits with a fresh soil moisture regime and a slope ranging from 4 to 8%. An initial visit was conducted to confirm this information. The soil moisture regime was validated using Brais and Camiré (1992) field keys. Only natural stands (originating from fire) were selected. Time since fire was assessed by locating trees with fire scars. When present, cross-sections of three trees bearing fire scars were collected from the base of the tree. When scars were not found, time since fire was assessed by dating stand age, again using cross-sections. All stands presenting signs of recent or past forest management interventions were rejected. In Quebec, successful fire exclusion started in 1972; accessible natural jack pine stands younger than 30 years were not found in the course of the study.

2.3. Field methods

In each selected stand, CWD volume and mass were estimated on a surface basis by decay (Daniels et al., 1997) and diameter classes using the line intercept method (Van Wagner, 1982). A triangular layout (30 m sides) was used to minimise bias. Within the triangles (three per stand), all snags were measured (dbh in cm and height by 0.5 m classes) and the dominant living jack pine tree was cut down for stem analysis. Downed log samples from each category of decay class were taken to the lab to be measured for density and water retention. Five 0.5 m^2 quadrats were sampled systematically within each triangle for a total of 15 for each stand. In each quadrat, all forest floor material down to the mineral soil was excavated by hand. Material was classified as distinct wood residue (buried wood, decomposition classes 4 and 5) or forest floor originating from fine litter or mosses. Both components were weighed in the field and subsampled for dry weight estimation. Buried wood was also sampled for density and water retention. Forest floor originating form fine litter and mineral soil (0–20 cm) were sampled within the quadrats for organic matter concentration, pH, effective CEC and permanent wilting point. An undisturbed 100 cm^3 soil sample was taken at a 10–15 cm depth to measure bulk density and field capacity in the lab. An additional bulk sample (25 cm depth) was taken for particle-size analysis.

2.4. Laboratory methods

Fifty-one downed and buried wood samples were analysed for density and water retention. Density was estimated from two sections of each sample. The first section was weighed (fresh) and coated in hot paraffin before its volume was measured by water displacement. The second section was weighted (fresh) and oven dried for moisture content estimation. The density was estimated from the first section after its fresh weight was corrected for moisture content. Masses of downed wood were estimated for three large decomposition classes (1–2, 3, 4–5) from volume (on a hectare basis) and density measurements.

Water retention properties of downed logs and buried wood samples were determined using soil sample procedures (Klute, 1986; Cassel and Nielsen, 1986). Undisturbed CWD samples were immersed in water for 48 h before they were brought to equilibrium with a tension value of −1500 kPa (permanent wilting point, PWP) using a pressure membrane apparatus (soil moisture equipment). Samples were weighed and immersed again in water for 48 h and brought to equilibrium with a tension value of −10 kPa (field capacity, FC) using a sandbox apparatus (Eijkelkamp Agrisearch Equipment). The CWD samples were finally dried (65 °C) for 48 h and weighed a last time. Available water holding capacity (AWHC) corresponds to the water retained (on a percent weight basis) between field capacity and permanent wilting point. Mineral soil samples (15 per site) were subjected to the same procedure for macroporosity (%, volume basis) and field capacity (%, ww) but bulk samples (six per site) were sieved before they were submerged and subjected to permanent wilting point measurements. Soils were dried for 48 h at 105 °C. The AWHC values were applied to downed logs, buried wood and mineral soil (0–20 cm) masses in order to obtain site values (m^3 of water ha^{-1}).

Forest floor and mineral soil samples were sieved (2 mm) and pooled within each triangular plot. Soil chemical analyses were conducted on three pooled samples per soil layer per site. Samples' organic matter concentration was determined by loss on ignition (McKeague, 1976). Soil pH was determined in 0.01 M $CaCl_2$ (Hendershot et al., 1993). Samples were analysed for exchangeable cations (Ca, Mg, K, Na) (inductively coupled plasma atomic emission (ICP, Perkin-Elmer Plasma 40) and acidity (titration, Metler DL-40) after extraction with $NH_4Cl–BaCl_2$ (Amacher et al., 1990). Effective cation exchange capacity (CEC_E) was estimated by adding base cations and exchangeable acidity ($acidity_e$). Soil texture determination was estimated by the Bouyoucos hydrometer method (McKeague, 1976). Soils were also sieved in order to estimate individual sand factions.

Cross-sections collected for dating stands and for stem analyses were sanded to expose rings clearly. Time since fire was dated with a precision of 1 year. Stem analysis was conducted according to Zarnovican (1985) to estimate site index at age 25.Snag volume (V_{snag}) was estimated using a truncated cone formula (Rondeux, 1993):

$$V_{snag} = \frac{\pi H_s}{12}[D^2 + d^2 + Dd]$$

where H_s is the snag height, D the stem diameter at ground level and d the stem diameter at the top of the snag. In order to estimate D and d from dbh, tree height before breakdown (H_t, m) was calculated form field dbh measurements (mm) according to the following Chapman–Richards equation:

$$H_t = \frac{(130 + B_0[1 - e^{-B_1\,\mathrm{dbh}}]^{B_2})}{100}$$

Two different sets of coefficients, developed specifically for jack pine (B_0 = 3332, 1900, B_1 = 0.001578, 0.007660 and B_2 = 0.688810, 1.059698), were used as the study area straddled two ecological regions (Grenier and Harvey, 2001). Thereafter, diameter at the base of the snag (D) and diameter at the top of the snag (d) were derived from simple geometric proportions:

$$D = \frac{H_t \times \mathrm{dbh}}{H_t - 1.3}$$

and

$$d = \frac{D[H_t - H_s]}{H_t}$$

2.5. Data analysis

Changes in CWD in relation to time were described by a linear polynomial model. In order to summarise site characteristics, a principal component analysis was conducted on-site variables excluding site index. Path analyses (Sokal and Rohlf, 1981; Legendre and Legendre, 1998) were used to assess causal relationships among time since fire, CWD (snags, downed logs and buried wood) properties, soil characteristics and site productivity. Causal ordering among variables was determined from ecological theory and was depicted by arrows (Legendre and Legendre, 1998). Multiple linear regressions were conducted using a stepwise procedure. Levels of significance for addition or deletion of variables were set to 0.10. In order to assess the relative importance of explanatory variables, all variables were first standardized (hence correlation coefficients and simple regression coefficients were equal). Data analyses were conducted using REG, MEANS, PRINCOMP, STANDARD and CORR procedures of the SAS statistical package (SAS Institute Inc., 1988).

3. Results

3.1. Stand characteristics

Twelve stands were sampled (Table 1). Time since the last fire ranged from 43 to 81 years. Particle size analyses confirmed the uniformity of soil parent material, with total sand content ranging from 83 to 93%. Nonetheless, fine sand content was more variable ranging from 9 to 65% (Table 1). Variation in forest floor (Table 1) and 0–10 cm mineral soil (Table 2) characteristics as measured by the coefficient of variation (CV) ranged from 10% of forest floor OM to 30% for mineral soil AWHC. The mean mineral soil AWHC was 12% (S.D. = 4) of soil dry weight. For the 0–10 cm layer, AWHC ranged from 158 to 393 $m^3\,ha^{-1}$ or, in terms of water storage, from 1.58 to 3.93 cm. Field capacity was significantly correlated with mineral soil OM content (r = 0.65, p = 0.021, n = 12) and with time since fire (r = −0.71, p = 0.001, n = 12). Some undisturbed soil samples showed signs of water repellency that increased with time since fire and reduced field capacity. No significant correlation was found between permanent wilting point and sand fractions or organic matter content. Despite similar soil texture, slope and moisture regime, site index at age 25 was variable, ranging from 3.3 to 9.3 m (CV = 29%) and was within the range of site indexes reported by Pothier and Savard (1998) and Béland and Bergeron (1996) for natural jack pine stands.

3.2. Coarse woody debris dynamics

Coarse woody debris volumes were highly variable (Fig. 1a–e) with a CV of 52% for snags, 97% for

Table 1
Selected site and soil properties of natural boreal jack pine stands growing on glacio-lacustrine surface deposits

Site	Time since fire (years)	Site index (25 year, m)	Total sand content (%)	Fine sand content (<0.25 mm) (%)	Forest floor OM (%)	Forest floor pH	Forest floor effective CEC (cmol(+) kg^{-1})	Downed logs (kg ha^{-1})	Buried wood (kg ha^{-1})
1	43	6.5	93	47	89	3.2	24.6	7216	4373
2	49	9.3	91	44	91	3.3	25.9	1737	11948
3	55	9.2	91	65	84	3.2	24.3	574	9609
4	57	8.4	93	41	94	3.3	23.5	2880	1252
5	64	6.4	83	23	91	3.2	22.0	1976	1332
6	66	5.8	92	45	93	3.3	24.7	1352	233
7	66	7.3	92	9	91	3.1	24.6	3633	380
8	66	7.2	87	20	85	3.3	21.3	1942	671
9	79	5.6	92	23	91	3.3	21.1	3272	288
10	79	3.7	91	37	64	3.4	17.0	2357	6872
11	81	7.1	90	36	86	3.1	25.0	13179	14980
12	86	3.3	88	11	72	3.4	18.4	11649	2367
Mean	66	6.6	90	33	86	3.3	22.7	4314	4525
S.D.	13	1.9	3	16	9	0.1	2.8	4142	5132

downed logs volume of decomposition classes 1–3, 142% for downed logs volume of decomposition classes 4–5, and 113% for buried wood. Some sites had very little CWD (total volume = 16.1 m^3 ha^{-1}). Some sites' CWD was made up mostly of snags while some were mostly made up of buried wood. The highest total CWD volume observed was 113.1 m^3 ha^{-1}. Buried wood volume varied between 1 and 57 m^3 ha^{-1} or 233–14 980 kg ha^{-1} (Table 1) and represented between 5 and 92% of total site CWD volume and between 0.1 and 24% of the total forest floor dry weight. No significant relationship was found between time since fire and total CWD volume (Fig. 1a, $r^2 = 0.345$, $p = 0.147$), snag volume (Fig. 1b) or buried wood (Fig. 1e) but as the proportion of dead wood volume present as snags decreased, the proportion of the total volume present as buried dead wood increased ($r = -0.81$, $p = 0.001$, $n = 12$). Downed volume for both fresh (classes 1–3) and well decomposed (classes 4–5) logs followed a significant

Table 2
Mineral soil properties of natural boreal jack pine stands growing on coarse-textured glacio-lacustrine deposits

Site	Depth	0–10 cm			0–20 cm			
	Time since fire (years)	OM (%)	pH	Effective CEC (cmol(+) kg^{-1})	Macroporosity −10 kPa (%, v/v)	FC −10 kPa (%, w/w)	PWP −1 500 kPa (%, w/w)	AWHC (m^3 ha^{-1})
1	43	2.2	3.9	1.56	31	16.8	2.3	306
2	49	3.3	4.0	1.47	25	21.3	2.4	393
3	55	2.9	4.0	1.45	34	16.7	4.1	271
4	57	1.7	3.9	1.39	30	14.8	3.4	236
5	64	2.0	3.7	2.05	28	16.0	3.3	278
6	66	3.1	3.9	1.61	21	18.0	3.3	313
7	66	3.3	3.9	1.89	23	19.3	2.7	358
8	66	2.4	4.0	1.87	33	12.7	3.5	209
9	79	2.0	4.2	0.93	25	11.1	4.3	158
10	79	2.4	4.0	1.40	28	11.4	3.3	183
11	81	2.4	3.5	1.79	32	14.3	3.3	244
12	86	2.5	4.0	1.24	29	11.3	3.2	191
Mean	66	2.5	3.9	1.55	28	15.3	3.3	262
S.D.	13	0.5	0.2	0.31	4	3.3	0.6	72

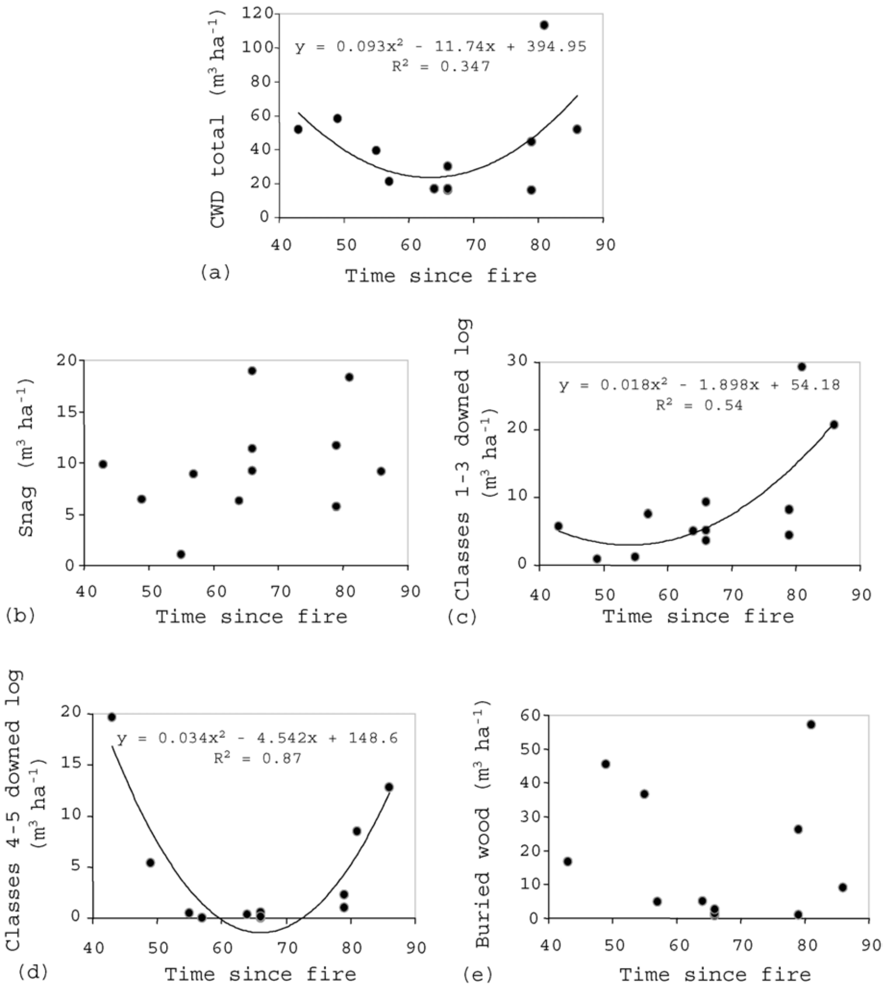

Fig. 1. Volume of (a) CWD (snags, downed logs and buried wood), (b) snags, (c) fresh downed logs, (d) well decomposed downed logs and (e) buried wood, in natural boreal jack pine stands in relation to time since the last fire.

($p < 0.05$) "U shaped" successional pattern (Fig. 1c and d), with higher biomass in young and older stands. The increase in fresh log volume in old stands preceded that of the well decomposed logs. The smallest volumes for well decomposed, downed logs and buried wood were observed between 55 and 80 years after fire (Fig. 1d and e).

3.3. Soil and CWD water retention characteristic

As density of dead wood decreased with decomposition, its water holding capacity increased but its AWHC remained stable (Fig. 2a and b). Available water holding capacity (volume basis) of well decomposed wood (classes 4 and 5 combined) was 9%. At the site level and on a hectare basis, downed log and buried wood AWHC were negligible (mean = 1.4 (S.D. = 1.4) and 1.7 $m^3\ ha^{-1}$ (S.D. = 2.0), respectively) compared with that of the 0–20 cm mineral soil layer (262 $m^3\ ha^{-1}$) (Table 2).

3.4. Site productivity

Fourteen variables were included in the principle component analysis (time since fire; snag volume; AWHC of downed log and buried wood; forest floor dry weight, OM content, effective CEC and pH; mineral soil OM content, effective CEC, pH, AWHC,

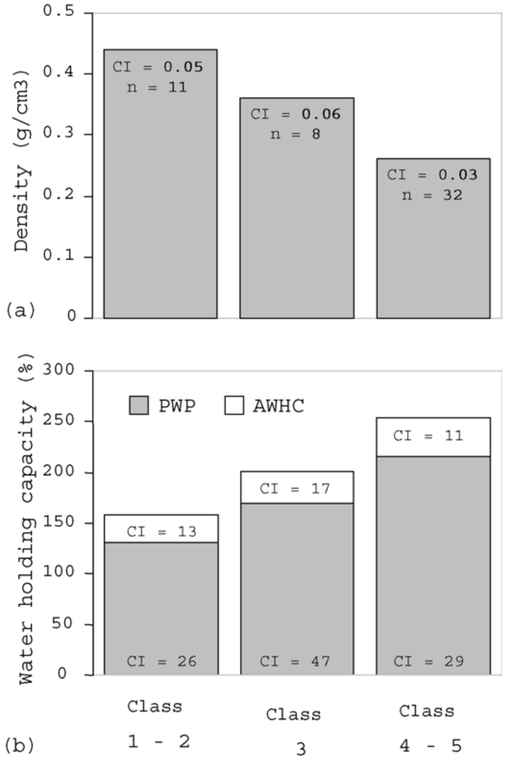

Fig. 2. Jack pine (a) wood density and (b) permanent wilting point (PWP) and available water holding capacity (AWHC) in relation to decomposition classes. CI: 95% confidence interval for population mean.

fine and very fine sand content). The first component explained 35% of the total variance and was correlated with soil characteristics (Fig. 3). The second component explained 21% of variance and was correlated with snag volume ($r = 0.83$, $p < 0.001$, $n = 12$), AWHC of fresh downed logs ($r = 0.67$, $p = 0.016$, $n = 12$), fine sand content ($r = -0.61$, $p = 0.033$, $n = 12$) and mineral soil pH ($r = -0.83$, $p = 0.011$, $n = 12$). Only the first component was correlated with site index ($r = 0.74$, $p = 0.006$, $n = 12$).

Effective CEC had a strong ($r^2 = 0.64$) positive and direct effect (path coefficient = 0.83) on-site productivity while AWHC of downed log had a lesser ($r^2 = 0.15$) direct but negative effect (path coefficient = −0.40). Mineral soil macroporosity also had a significant ($r^2 = 0.10$) and positive effect on-site index (path coefficient = 0.41) (Fig. 4). Eighty-nine percent of site index was explained by the simple model. The model also showed that buried wood ($r^2 = 0.22$) and forest floor OM concentration ($r^2 = 0.64$) had a direct and positive effect on forest floor effective CEC, hence both factors had an indirect effect on-site productivity through their relation with CEC (path coefficient of 0.40 (0.48×0.83) between buried wood and site index and of 0.75 (0.90×0.83) between organic matter concentration and site index).

4. Discussion

4.1. Coarse woody debris dynamics

Most of the literature on CWD originates from western North America (see Harmon et al., 1986). Despite some recent studies (Sturvenant et al., 1997; Fleming and Freedman, 1998; Pedlar et al., 2002; Hély et al., 2000), data on CWD dynamics in relation to

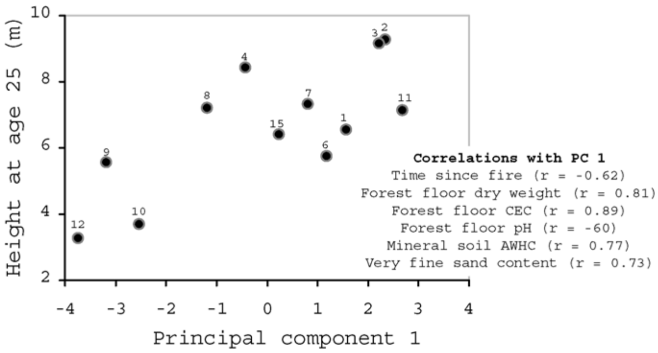

Fig. 3. Relationship between site index at age 25 and site characteristics as summarised by the first principal component of PCA. The first component explained 35% of total site variance. Site numbers correspond to numbers given in Table 1.

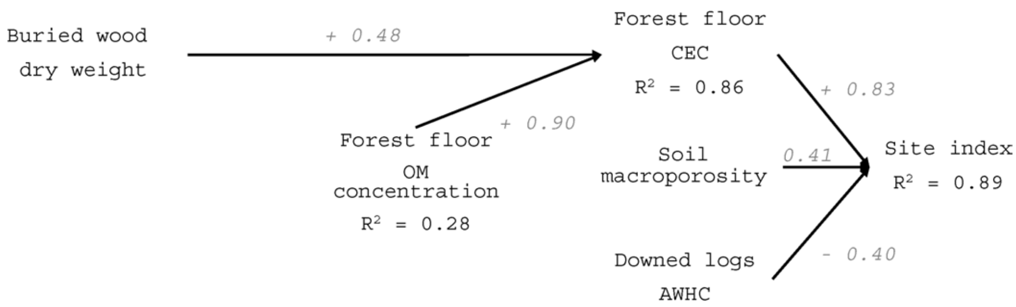

Fig. 4. Path analysis of causal relations between CWD, forest floor and mineral soil characteristics, and site productivity. Path coefficients (in italic and grey) are a measure of the strength of the relation between dependant variable and independent variables.

disturbances and succession for eastern boreal forests are scarce. Our values for total above ground CWD volume fall within the range of those reported for eastern boreal forests (Sturvenant et al., 1997; Pedlar et al., 2002). However differences in species composition, disturbances history and stand age make comparisons of absolute CWD amounts virtually meaningless. Nonetheless, ‘‘U-shaped’’ distributions of downed logs volume along chronosequences following stand replacing disturbances have been reported by Clark et al. (1998) and Duval and Grigal (1999) for sub-boreal spruce forests and by Sturvenant et al. (1997) for eastern boreal forests.

The reasons behind the absence of a clear pattern for snag volume or density (results not shown) in relation to time since fire are not clear. As an early successional species, jack pine has evolved regeneration strategies that enable natural stands to attain high stand densities in the first years following fire (Chrosciewicz, 1983). Stand establishment is then followed by waves of natural thinning starting around 25 years of age (Kenkel et al., 1997). The youngest stand measured in this study was 43 years old and already passed through the first wave of self-thinning.

Forty to 50 years following fire, the volume of fresh downed logs was low while the volume of well decomposed logs was still high. Assuming that most of the well decomposed material observed in 40–70-year-old stands dates from the last fire event and, to a lesser degree, from early self-thinning, the period with the smallest amounts of well decomposed downed logs or buried wood (55–70 years after fire) is consistent with the decomposition rate of jack pine logs. Alban and Pastor (1993) estimated the 95% breakdown time of jack pine to be 71 years. The highly significant and inverse relationship between snags and buried wood abundance suggests that part of the trees fell on the ground immediately or soon after the last fire and were buried progressively under the regenerating forest floor. They appeared to have decomposed at a similar rate as that of the logs on top of the forest floor. How much of this buried wood, if any, predated the last fire remains an open question.

Little reference is made to buried wood in the literature, but McFee and Stone (1966) gave a thorough description of buried wood found within the mor horizon of yellow birch–red spruce stands of New York State. Absolute weights of buried wood in these stands were higher than what we found in the present study, but amounted to similar proportions of the total forest floor (17.5–26% of total humus layer). Volume of buried wood found by Harvey et al. (1981) in Douglas fir–western larch stands were much higher (373–230 m^3 ha^{-1}) but reflected higher inputs.

Stand break-up is characterised by the breakage and fall of individual or groups of trees. An increase in fresh downed wood volume was observed between 60 and 70 years after fire. This would be consistent with estimates of rotation age for jack pine stands ranging between 55 and 112 years, depending on stand productivity and density (Pothier and Savard, 1998). The observed increase in well-decomposed downed logs lagged behind that of fresh logs.

4.2. *Soil and CWD water retention characteristics*

Differences in site AWHC are related to differences in SOM that can be, in part, explained by site specific disturbance histories (Bouma and Droogers, 1999), assuming that the soils have developed from similar parent material, are on similar topographical conditions and are under a similar moisture regime. We hypothesised that besides SOM, CWD and especially buried wood would also contribute to site AWHC. While the capacity of dead wood to retain water increased with decomposition, the proportion of this water available to plants remained stable. Contrary to our hypothesis, downed logs and buried wood stored small quantities of water between field capacity and permanent wilting point values while large quantities were retained at a lower potential than the permanent wilting point. The storage capacity of dead wood (water contained below field capacity) compared with that of the mineral soil (0–20 cm depth) remained very small. We recognise that field capacity and permanent wilting point are arbitrary criteria that do not take into account the dynamics of the soil–plant–atmosphere continuum (Hillel, 1998) and water availability to other soil organisms. Also, the reasons why roots preferentially grow within the dead wood material contained within the forest floor (personal observation) at these study sites remain to be elucidated.

Our AWHC values for the mineral soil were very similar to those reported by Pawluk and Arneman (1961) for jack pine stands in Minnesota. The permanent wilting point appeared to be independent from soil organic matter content or any other measured parameter. On the other hand, the soil water repellency and concomitant decrease in field capacity that were observed in older stands were somewhat unexpected and may be linked to the presence of soil fungi (Pritchett and Fisher, 1987).

4.3. Site productivity

The observed relationship between forest floor characteristics, soil AWHC and site productivity, as expressed by site index, where expected, given the information provided by other studies (Pawluk and Arneman, 1961; Schmidt and Carmean, 1988). What we aimed to do was to assess the direct and indirect contribution of CWD to site organic matter and productivity. Our results showed that CWD may have both positive and negative effects on productivity and that these effects were mediated by vegetation dynamics and site disturbance. While a positive and direct correlation could have been expected between site productivity and amounts of CWD, this was not the case.

The negative relationship between downed logs AWHC and site productivity could be related to water interception. Harmon and Sexton (1995) have estimated that downed logs may intercept a small but significant proportion (2–5%) of canopy throughfall to the forest floor. For fresh coarse-textured soils, the reduction in water reaching the root zone appeared to have a significant effect on-site productivity. On the other hand, high buried wood content in the forest floor increased forest floor CEC and, indirectly, site productivity. The mechanisms involved between buried wood and forest floor CEC have yet to be investigated but may be linked to the high lignin content of these residues which offers protection against microbial attack. Once part of the soil organic matter stable fraction (N'dayegamiye and Angers, 1993) CWD would contribute to soil nutrient and water retention (Baldock and Nelson, 1999).

5. Conclusion

The functions of snags and downed wood have been considered from the standpoint of their habitat characteristics (e.g. Cline et al., 1980; Lee et al., 1997) or of their carbon or nutrient content (e.g. Busse, 1994; Laiho and Prescott, 1999) but buried wood, as a morphological structure of boreal forest soils, has been largely ignored (McFee and Stone, 1966). These limited results imply that current estimates of CWD that limit sampling to material lying on the forest floor underestimate the downed wood component in boreal forests. The high variability of CWD estimates may be linked to specific site disturbance histories and more specifically to variations in fire intensity. Although jack pine stands are generally characterised by an even-aged structure resulting from high intensity stand replacing fires, four of the study stands originated from fires of moderate intensity.

Causal relationships are always difficult to tackle in observational studies. We recognise the proposed model linking CWD and site productivity is a working hypothesis. The function of CWD and more specifically of buried wood in the maintenance of site productivity needs further investigations. Moreover, forest management activities have the potential to alter the balance between inputs and losses of soil organic matter and the importance of CWD in this balance needs to be assessed.

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