

**Structure of Forest Stands Disturbed by  
Wildfire and Logging  
in the Rocky Mountain Foothills**

Daniel R. Farr<sup>1</sup>, Christopher P. Spytz<sup>2</sup>, and E. George Mercer<sup>3</sup>

<sup>1</sup> Foothills Model Forest, Box 6330, Hinton, Alberta, Canada, T7V 1X6

<sup>2</sup> Weldwood of Canada Limited, Hinton Division, 760 Switzer Drive, Hinton, Alberta, Canada, T7V 1V7

<sup>3</sup> Jasper National Park, Box 10, Jasper, Alberta, Canada, T0E 1E0

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## Contents

Disclaimer.....	2
Abstract.....	4
Introduction.....	5
Methods .....	6
Results .....	11
Discussion.....	23
Management implications.....	26
Acknowledgements.....	28
Literature cited.....	29

## Tables

<b>Table 1.</b> Summary of study site characteristics and species composition of live trees greater than 2 m tall .....	12
<b>Table 2.</b> Number of standing dead trees in burned and logged sites in the Rocky Mountain Foothills of Alberta.....	16
<b>Table 3.</b> Density and volume of down deadwood in burned and logged sites in the Rocky Mountain Foothills of Alberta .....	17
<b>Table 4.</b> Factor loadings of 3 principal components from a PCA of down deadwood attributes of 195 plots in burned and logged sites in the Rocky Mountains and Foothills of Alberta .....	21

## Figures

<b>Figure 1.</b> Map showing locations of the four burns sampled in this study.....	7
<b>Figure 2.</b> Sample plot locations for each study site .....	8
<b>Figure 3.</b> Density and basal area of live trees greater than 2 m tall by diameter class in burned and logged sites in the Rocky Mountain Foothills.....	13
<b>Figure 4.</b> Distribution of standing dead trees across a range of decay and diameter classes in burned and logged sites in the Rocky Mountain Foothills.....	14
<b>Figure 5.</b> Volume of down deadwood greater than 7 cm diameter in recently burned or logged sites in the Rocky Mountain Foothills .....	15
<b>Figure 6.</b> Volume of down deadwood in recently burned and logged sites in the Rocky Mountain Foothills .....	18
<b>Figure 7.</b> Distribution of down deadwood across a range of diameter, height, decay, texture, and epiphyte cover classes, in burned and logged sites in the Rocky Mountain Foothills.....	19
<b>Figure 8.</b> A. Site means for the first three principal components from a PCA of nine attributes related to down deadwood (Table 4). B. Plot values for the first two principal components from the same PCA.....	22

## Abstract

Efforts to conserve the biological diversity of boreal forest stands disturbed by logging are constrained by a lack of information on the structural variability of such stands relative to stands disturbed by natural processes such as wildfire. In this study, we examined the abundance, size, condition, and origin of deadwood and live trees in recently burned (34-40 yr) and logged (23-27 yr) coniferous stands in the Rocky Mountains and Foothills of western Alberta, Canada. The structure of fire-origin stands was more variable than that of harvest-origin stands, as measured by live and standing dead trees > 2 m tall and down deadwood > 7 cm diameter. In stands of both origin types, > 90% of standing dead trees were derived from the cohort of live trees germinating after disturbance. Standing dead trees of post-disturbance origin were five times more abundant in burned stands ( $25.9 \pm 4.9$  trees per plot, mean  $\pm$  SD) than logged stands ( $4.9 \pm 4.6$  trees per plot). Few large fire-killed standing dead trees were present in the burned stands ( $3.1 \pm 1.3$  trees per plot), with most having fallen and contributed to a large pool of down deadwood. Down deadwood derived from the previous stand was a dominant feature of burned stands, reaching volumes of over  $150 \text{ m}^3 / \text{ha}$ , approximately four times the volume of pre-harvest origin down deadwood in logged stands. Stands of both disturbance types contained similar amounts of down deadwood from trees derived from trees germinating after fire or logging. Forest managers attempting to increase the range of deadwood in future logged stands should retain variable amounts of standing live and dead trees during harvesting that can provide a source of down deadwood several decades later. Within protected areas, where prescribed fire may be the preferred management tool, this study suggests a range of deadwood supply in burned stands which managers may wish to strive for in support of objectives to maintain natural processes.

## Introduction

Wood is a defining attribute of forest ecosystems (Hunter 1990), and in many forests, woody tissue comprises over 90% of the total biomass (Packham and Harding 1982). Until recently, the importance of dead wood to the biological diversity of forest stands has largely been overlooked. Deadwood contributes to biodiversity and ecological function by modifying microclimate and providing habitat for vertebrates (Maser and Trappe 1984; Hayes and Cross 1987; Bunnell et al. 1997; Lindenmayer and Franklin 1997), invertebrates (Niemela 1997), plants (Andersson and Hytteborn 1991; McAlister 1995), fungi (Boddy and Watkinson 1994) and lichens (see review by Harmon et al. 1986). Decomposing deadwood within upper soil horizons, which may persist for several decades or more (McFee and Stone 1966; Harvey et al. 1981), provides a suitable medium for non-symbiotic nitrogen-fixing bacteria (Jurgensen et al. 1992), and ectomycorrhizal associations with root tips that facilitate the transport of nutrients and water in trees and other woody vegetation (Larson et al. 1978, Harvey et al. 1987, Vare 1989).

The abundance and condition of deadwood in forests is highly dynamic. The amount present in a stand reflects the combined processes of accumulation through tree growth and mortality, and losses through decomposition (Franklin et al. 1987). Pulses of tree mortality caused by sudden disturbances such as wildfire can create a large pool of deadwood, consisting of both standing dead trees and down deadwood that may persist for many decades (Harmon et al. 1986). Post-fire establishment of trees may result in very high tree densities followed by mortality that contributes additional deadwood to the stand (Lotan et al. 1985, Lee et al. 1997). Because periodic disturbance by wildfire is characteristic of many boreal forest ecosystems (Rowe and Scotter 1973; Arno 1980; Mooney et al. 1981), standing and down fire-killed trees are significant elements of boreal forest stand infrastructure (Jeske and Bevins 1979; Brown and See 1981; Fahey 1983).

Two human activities, wildfire suppression and tree harvesting, have the potential to alter ecological functions associated with deadwood over much of the boreal forest in Canada. Fire suppression may reduce the frequency of pulses of high tree mortality, while tree harvesting removes much of the wood biomass that would otherwise remain after fire (Lee et al. 1995, 1997, Spies et al. 1998). Repeated logging over successive rotations would maintain a relatively low supply of deadwood in logged stands. In this way, harvesting may be similar to repeated burning, at short intervals. Practices such as clear-cutting, thinning, and other silvicultural interventions that reduce the supply of deadwood in forest stands have been suggested as a primary cause of decline in certain birds, arthropods, bryophytes

and fungi associated with deadwood in boreal regions (Haapanen 1965; Samuelsson et al. 1994; Siitonen and Martikainen 1994; Atlegrim and Sjöberg 1995; Niemelä 1997; Rydin et al. 1997).

One strategy to conserve deadwood and its associated biota in boreal forest stands is to increase the amount of residual woody material remaining after logging to more closely resemble the range occurring in fire-origin stands (Hansen et al. 1991). This material would supplement that which occurs in buffers, sub-merchantable stands and inaccessible stands. While increasing the amount of deadwood in logged stands would likely reduce the risk of many undesirable ecological effects (Jurgensen et al. 1992; Rydin et al. 1997), it is constrained by issues relating to safety, legislation, silviculture, cost, infrastructure investments and wood supply commitments. In addition, a lack of baseline information on the ranges of abundance and condition of deadwood in fire-origin stands make it difficult to judge the merits of alternative deadwood retention strategies relative to the natural range of variability (Swanson et al. 1993).

The Rocky Mountains and Foothills in Alberta offer opportunities for retrospective comparisons of deadwood in fire-origin and logging-origin stands that could inform management strategies intended to maintain future deadwood supply that better approximate a natural range of variability. Wildfire is common in this region (DeLisle and Hall 1987; Government of Alberta 1998), and logging has occurred in the Foothills on an industrial scale since the mid-1950's (Crossley 1978). In this study, we estimated and compared ranges of variability in the structure of stands disturbed by wildfire and by clear-cut harvesting, with structure defined as the abundance, size and condition of deadwood and live trees.

## **Methods**

All study sites were located in western Alberta, between 52° to 54° N, and 115° to 119° W (Fig. 1), and ranged from 1300 to 1600 m asl. The region is topographically diverse, including the East Slope Rockies, Upper Foothills, and Lower Foothills forest sections (Rowe 1972). Four sites burned 34 to 40 years prior to sampling, and three were logged 23 to 27 years prior to sampling. Forest cover in undisturbed residual patches within each site and in the surrounding area was primarily coniferous stands or coniferous-dominated mixedwood stands ranging in age from 20 to >150 years. Logging activities to support local sawmills prior to 1956 probably affected forest cover in most sites, but detailed records were not available.



Topographic and edaphic differences between burned and logged sites were reduced by selecting logged stands adjacent to the three Foothills burns (Fig. 2). All logged stands were clear-cut between 1970 and 1974 by North Western Pulp and Power (see Crossley 1978 for a summary of the forest management system used in this area at the time). The primary logging method was tree-length harvesting, with de-limbing and topping done in the cutblock by power saw. Wheeled skidders moved wood to roadside for de-limbing and loading. Most blocks were scarified 1 -10 years after harvesting, and some were planted with nursery stock. In parts of each burned site, evidence of salvage logging and firewood collection was observed (particularly in the Gregg River Burn), but the extent and timing of such activities are not known. In some cutblocks, evidence of pre-commercial thinning occurring between 1976 and 1986 was observed.

Sample plots were randomly selected for each of the seven study sites using a map grid overlay. Plots remote from motorized ground access (over 2 hours travel from a road) were replaced. The resulting distribution of sample plots was therefore not completely random, but achieved a broad spatial distribution across each study area (Fig. 2). A total of 195 plots were sampled, 30 plots per site except for the Chaba River Burn (14 plots), and the Gregg River Burn (31 plots).

Field sampling procedures were based on methods for estimating volume of down deadwood described by McRae et al. (1979). Data were recorded along a triangular transect measuring 30 m on a side (total length 90 m), and within the 390 m<sup>2</sup> triangular plot enclosed by the transect. All pieces of down deadwood crossing the transect that measured at least 7 cm in diameter at the point of intersection were tallied, with the following information recorded: piece diameter at the point of intersection; decay class of entire piece; wood texture class at the point of intersection; distance from the ground to the underside of the piece at the point of intersection; and proportion of the piece directly under the transect line that was covered by bark and attached plants, fungi, or lichens. Volume of down deadwood greater than 7 cm diameter was estimated using the equation given by Van Wagner (1968) and Brown (1974), converted to cubic metres per hectare:

$$v = 10\,000 (\pi^2 \Sigma (d_i^2)) / (8l),$$

where  $v$  = volume of down deadwood, in m<sup>3</sup> / ha,  $d$  = diameter of each piece of deadwood crossing the transect in metres,  $l$  = length of transect in metres.

All free-standing dead trees over 2 m tall within the plots were tallied. Diameter at breast height (dbh) and decay class (see Results) were also recorded for each.





Standing dead trees and down deadwood were divided into two categories of origin: pre-disturbance and post-disturbance. If the dbh of a standing dead tree or the diameter of a piece of down deadwood at the transect line was greater than the dbh of the largest live tree in a plot, it was considered pre-disturbance origin (see Lee et al. 1995). All other deadwood was considered post-disturbance origin. Pre-disturbance deadwood smaller than post-disturbance live trees would be incorrectly classified as post-disturbance in origin. Therefore our estimates of the structural components of the previous stand are likely conservative. The amount of pre-disturbance material provided an estimate of the structural legacy of the previous stand, while the amount of post-disturbance origin material provided an estimate of deadwood recruitment through mortality of trees germinating after disturbance.

All live trees over 2 m tall were tallied within the 390 m<sup>2</sup> plot, except when a preliminary assessment indicated that density was very high, in which case only trees within the three 5x5x5 m corner plots (combined sample area 32 m<sup>2</sup>) were tallied. For each tree, species and dbh were recorded.

The abundance, size and condition of down deadwood, standing dead trees and live trees in burned and logged sites were compared using Student's t-test (Zar 1984). Since assumptions of the t-test (normality and homogeneity of variance) were not met in all cases, we also performed the non-parametric equivalent (Mann-Whitney U test) and reported any discrepancies with respect to significance. All statistical comparisons included only the six sites in the Foothills in order to minimize the effects of topographic and edaphic variability. For each t-test, the minimum power to correctly reject the null hypothesis of no difference between means was estimated using a Type I error probability of 0.05. We estimated the power to detect two magnitudes of differences between means, set at  $\pm 50\%$  of the overall mean and  $\pm 10\%$  of the overall mean. For example, if the sample mean abundance of down deadwood in burned and logged sites equaled 130 and 140 pieces respectively, we estimated power to detect a difference between means of 135 pieces ( $\pm 50\%$  of the overall mean) and 27 pieces ( $\pm 10\%$  of the overall mean). Power was estimated using the formula given by Nemeč (1991:14) and accompanying SAS functions (SAS 1989).

To more fully understand the pattern of differences in down deadwood among the seven study sites, we also used principal components analysis (PCA) to construct a set of new, uncorrelated factors which accounted for a known proportion of the variability within the correlation matrix of nine deadwood attributes (Johnson and Wichern 1988). To improve the interpretability of the resulting factors, varimax rotation was used to minimize the number of attributes that were strongly correlated with a single factor (Norušis 1992). We interpreted factors by inspecting their correlations, or loadings, with the original nine attributes, and differences among sites were illustrated using mean values of each factor. Although many

attributes were positively skewed (skewness values ranging -0.12 to 2.06), no transformations were performed, permitting assessments of the influence of actual attribute values on the resulting factors. Interpretations of the PCA results should therefore be made with caution.

## Results

Inspection of annual growth rings of selected trees in each plot confirmed that mortality in almost all plots was complete, and was followed by the establishment of a new cohort. In fire-origin sites, the average size of the largest live tree in a plot ranged from 11.1 cm (range 5 - 30 cm) dbh at Smith Creek, to 20.4 cm (range 12 - 33 cm) dbh at Chaba River. In harvest-origin sites, the average size of the largest live tree in a plot ranged from 12.9 cm (range 7 - 19 cm) dbh at Smith Creek to 14.1 cm (range 4 - 37 cm) dbh at Gregg River.

The mean density of live trees > 2 m tall in the four burned sites was highly variable, ranging from 1 791 to 18 656 trees / ha (median 1 001 - 14 780 trees / ha, Table 1). All four burns were dominated (70-91% of basal area) by lodgepole pine (*Pinus contorta* Dougl. ex Loud var *latifolia* Engelm., with smaller proportions of black spruce (*Picea mariana* (Mill.) BSP), white spruce (*P. glauca* (Moench) Voss), Engelmann spruce (*P. Engelmannii*), white x Engelmann spruce hybrids (*P. glauca* x *Engelmannii*) fir spp. (*Abies lasiocarpa* (Hook.) Nutt, *A. balsamifera* (L.) Mill.) and deciduous tree species including *Populus tremuloides* Michx., *P. balsamifera* L. and *Betula papyrifera* Marsh. (Table 1).

The mean density of live trees > 2 m tall in the three logged sites ranged from 3 719 to 5 979 trees / ha (median 2 707 to 4 734 trees / ha, Table 1), and was not significantly different from burned sites ( $t = 2.60$ ,  $df = 4$ ,  $p = 0.060$ ). The power of this test was low (46% probability of detecting a difference of  $\pm 50\%$  of the overall mean). However, the variability in tree density (estimated by SD) was significantly less in logged sites ( $t = 3.31$ ,  $df = 4$ ,  $p = 0.030$ , Table 1). Two logged sites were dominated by lodgepole pine (75% and 97% of basal area) but the third (Lynx Creek) contained 40% pine, with 35% deciduous trees and 18% subalpine fir (Table 1).

In the three Foothills burned sites, most live trees were relatively small. Trees less than 5 cm dbh comprised almost 75% of the tree cohort (average 9 249 trees / ha), compared to 52% (average 2 360 trees / ha) in the three logged sites (Fig. 3). These small trees represented relatively minor contributions to total stand basal area in both burned sites (23%) and logged sites (12%, Fig. 3).

**Table 1.** Summary of study site characteristics and species composition of live trees greater than 2 m tall.

	Chaba River		Gregg River		Lynx Creek		Smith Creek	
	Burned	Burned	Logged	Burned	Logged	Burned	Logged	
<b>Number of sample plots</b>	14	31	30	30	30	30	30	
<b>Years since disturbance</b>	34	40	23-27	36	23-27	40	23-27	
<b>Tree density (number per ha)</b>								
Mean	1 791	10 372	5 979	9 157	3 842	18 656	3 719	
Median	1 001	8 006	4 734	8 160	3 015	14 780	2 707	
SD	1 819	9 055	4 282	8 172	3 021	14 505	3 255	
Interquartile Range	2 066	10 469	7 448	9 526	4 804	23 248	2 245	
<b>Tree species composition</b>								
Mean basal area (m <sup>2</sup> / ha)	12.5	28.0	16.3	22.3	12.7	19.7	9.0	
Lodgepole pine (%)	82.9	91.3	75.2	70.2	40.2	89.8	96.5	
Black spruce (%)	7.7	3.9	4.3	1.0	0.5	8.7	0.8	
White/ Engelmann spruce (%)	9.0	3.0	4.3	6.5	6.3	1.4	0.2	
Subalpine/ Balsam fir (%)	0.4	0.9	7.6	0.9	18.1	0.0	2.4	
Poplar / Birch (%)	0.0	0.9	8.7	21.4	35.0	0.0	0.1	

Most (> 90%) of the standing dead trees observed in the study sites were recruited from the cohort of live trees that germinated after disturbance and subsequently died. Most of these post-disturbance origin dead trees were relatively small and in relatively early stages of decay (Figure 4). Abundance was particularly high in the three Foothills burned sites, with an average density of 664 post-disturbance origin dead trees / ha (Table 2). Abundance in the three logged sites was significantly lower, at 126 post-disturbance origin dead trees / ha (Table 2). Standard deviation among sites was three times greater in burned stands than logged stands (Table 2).

Very few standing dead trees in any site were classified as pre-disturbance origin (Table 2). However, as with post-disturbance origin standing dead trees, abundance was significantly higher and more variable in burned sites than in logged sites (Table 2); mean densities of 79 trees / ha and 3 trees / ha were observed in burned and logged sites, respectively.

The total volume of down deadwood > 7 cm dbh observed in each study site was highly variable (Fig. 5), with standard deviations considerably higher in burned sites ( $134.5 \pm 17.0 \text{ m}^3 / \text{ha}$ ), than in logged sites ( $51.4 \pm 19.2 \text{ m}^3 / \text{ha}$ ;  $t=5.59$ ,  $df=4$ ,  $p=0.005$ ). Mean volumes in the Foothills burned sites were significantly greater ( $200.0 \pm 10.9 \text{ m}^3 / \text{ha}$ ) than in logged sites ( $69.0 \pm 17.1 \text{ m}^3 / \text{ha}$ ;  $t=11.18$ ,  $df=4$ ,  $p<0.001$ ).







**Table 2.** Number of standing dead trees in burned (n=3) and in logged (n=3) sites<sup>1</sup> in the Rocky Mountain Foothills of Alberta. Mean and SD are for all plots sampled in each site; see Table 1 for number of sample plots per site. Power = minimum probability of rejecting the null hypothesis of no difference between means if p=0.05 and the difference between the two means was equal to the specified percentage (50% and 10%) above and below the average of the two means. (See text for further explanation.)

Number of standing dead trees	Burned		Logged		t	P	Power	
	mean ± SD	mean ± SD	t	P			±50%	±10%
<b>Post-disturbance origin</b>								
Mean	25.9 ± 4.9	4.9 ± 4.6	5.39	0.006	56	7		
SD	30.5 ± 6.6	9.4 ± 7.3	3.71	0.021	47	7		
<b>Pre-disturbance origin</b>								
Mean	3.1 ± 1.3	0.1 ± 0.2	3.93	0.017	21	6		
SD	4.7 ± 2.5	0.3 ± 0.5	3.03	0.039	15	5		

<sup>1</sup> Excluding Chaba River Burn

Most of the down deadwood in burned sites was carried over from the pre-disturbance stand (Table 3, Fig. 6). In the three Foothills burned sites, pre-disturbance origin down deadwood contributed an average of 81% of the total down deadwood volume, and 66% of the total density (Table 3). In logged sites, 62% of volume and 35% of density was of pre-disturbance origin (Table 3), but average volume and density were much lower and less variable than in burned sites (Table 3). The average volume and density of post-disturbance origin down deadwood did not differ significantly between burned and logged stands, although variability was greater in burned stands (Table 3).

The size, height, and condition of down deadwood in all Foothills sites were highly variable, but the following trends were evident (Fig. 7). Size distributions were similar, but in burned sites, 54% of the pieces were elevated above the ground (average height of all pieces = 10 cm), compared to only 18% in logged sites (average height of all pieces = 2 cm, Fig. 7). Relatively few down deadwood pieces were in an early stage of decay, although burned sites contained a mean of 9.3 pieces per plot of pre-disturbance material having a decay class of 1 or 2, compared to virtually no (mean = 0.3) such pieces in logged sites (Fig. 7). Patterns of surface colonization by plants, fungi and lichens appeared to be similar, averaging 43% cover in burned sites, and 53% cover in logged sites. Very little bark was present on any of the pieces of down deadwood observed, with 98% of all pieces completely bark-free under the transect line in both burned and logged sites.



**Table 3.** Density and volume of down deadwood in burned (n=3) and in logged (n=3) sites<sup>1</sup> in the Rocky Mountain Foothills of Alberta. Mean and SD are for all plots sampled in each site; see Table 1 for number of sample plots per site. Power = minimum probability of rejecting the null hypothesis of no difference between means if p=0.05 and the difference between the two means was equal to the specified percentage (50% and 10%) above and below the average of the two means. (See text for further explanation.)

	<b>Burned</b> mean $\pm$ SD	<b>Logged</b> mean $\pm$ SD	t	P	Power	
					$\pm 50\%$	$\pm 10\%$
<b>Number of pieces</b>						
<b>Post-disturbance origin</b>						
Mean	22.2 $\pm$ 5.3	18.7 $\pm$ 10.1	0.53	0.622	39	6
SD	22.0 $\pm$ 5.2	13.6 $\pm$ 6.8	1.72	0.161	50	7
<b>Pre-disturbance origin</b>						
Mean	43.7 $\pm$ 11.0	9.9 $\pm$ 2.3	5.19	0.007	60	7
SD	36.2 $\pm$ 9.1	10.2 $\pm$ 5.0	4.35	0.012	55	7
<b>Total volume (m<sup>3</sup> / ha)</b>						
<b>Post-disturbance origin</b>						
Mean	38.1 $\pm$ 9.8	25.9 $\pm$ 11.2	1.41	0.230	52	7
SD	49.7 $\pm$ 11.6	23.1 $\pm$ 4.8	3.67	0.021	75	9
<b>Pre-disturbance origin</b>						
Mean	161.9 $\pm$ 5.5	43.1 $\pm$ 8.6	20.18	0.001	100	47
SD	130.6 $\pm$ 22.3	43.9 $\pm$ 20.4	4.97	0.008	75	9

<sup>1</sup> Excluding Chaba River Burn

The three factors generated from principal components analysis together accounted for 80% of the variability in the original nine variables related to down deadwood (Table 4). The first factor (PC 1) was interpreted as the degree to which pieces were decayed, the second (PC 2) was related to piece size, height above ground, and the amount of down deadwood of pre-disturbance origin. The third factor (PC 3) was related to the amount of post-disturbance origin down deadwood. The positions of the seven study sites in relation to these three factors suggested separation of burned sites from logged sites along the second axis (Fig. 8), but considerable variability along PC 1 and PC 3.







**Table 4.** Factor loadings of 3 principal components from a PCA of down deadwood attributes of 195 plots in burned and logged sites in the Rocky Mountains and Foothills of Alberta. Factor loadings of less than | 0.10 | are not shown.

	<b>PC 1</b>	<b>PC 2</b>	<b>PC 3</b>
Eigenvalue	3.57	1.98	1.60
Variance explained	40%	22%	18%
<b>Attribute</b>	<b>Factor loading</b>		
Wood texture class of deadwood pieces	0.88		-0.12
Decay class of deadwood pieces	0.86	-0.29	
Plant cover on deadwood pieces	0.84		0.14
Volume of pre-disturbance origin down deadwood pieces	-0.27	0.90	
Diameter of deadwood pieces	0.33	0.78	0.18
Number of pre-disturbance origin down deadwood pieces	-0.43	0.64	-0.36
Height of deadwood pieces	-0.46	0.62	0.15
Volume of post-disturbance origin down deadwood pieces		0.11	0.96
Number of post-disturbance origin down deadwood pieces	-0.21		0.92



## Discussion

The woody infrastructure of fire-origin stands sampled in this study was more variable than harvest-origin stands. This variability was propagated largely by the presence of fire-killed trees, some of which remained standing and relatively intact up to 40 years after fire. Once fallen, these trees from the previous stand contributed to a large, but variable, pool of down deadwood that subsequently decayed. Post-fire conditions for germination and establishment probably facilitated a high density of small live trees, with subsequent mortality contributing additional deadwood to the stand. Unlike fire, logging removed much of the source for recruitment of down deadwood in harvest-origin stands. In addition, the lower density of live trees in such stands may be less likely to create conditions in which mortality during succession contributes additional deadwood, although mortality in some stands was accelerated by thinning operations.

This interpretation of stand dynamics in fire-origin stands is consistent with the results of previous observations from chronosequences in northern Alberta (Lee et al. 1995, 1997), Glacier National Park (Jeske and Bevins 1979), Olympic National Park (Agee and Huff 1987) and the Cascade Range in Washington and Oregon (Spies et al. 1988). In each of these studies, fire-killed trees contributed to initially high amounts of deadwood, which gradually decreased with time through decomposition, then becoming higher in older stands through tree mortality. Deviations from this U-shaped pattern were observed in stands in the Oregon Coast Range that were probably immature at the time of burning (Spies et al. 1988).

The magnitude of the pulse of tree mortality in the four sampled burns is unknown without data from immediately after the wildfire, but it is reasonable to assume that the density of pre-disturbance origin standing dead trees at the time of sampling was much lower than immediately after the fire. This assumption was supported by examination of photographs taken shortly after each fire, in which high densities of standing dead trees were observed in each burn. Lyon (1977) estimated that fire-killed lodgepole pine snags in a Montana burn fell at a rate of 8.9% per year during the first 15 years, which extrapolates to 2.6% remaining after 40 years. Other studies indicate that standing dead trees frequently decay very slowly (e.g., Johnson and Greene 1991), with some fire-killed lodgepole pine trees still standing after 110 years (Fahey 1983). Small standing dead trees probably fall at higher rates than large ones (Lyon 1977; Cline et al. 1980; Raphael and Morrison 1987; but see Johnson and Greene 1991, Harrington 1996).

During the initial few decades following wildfire, the falling of standing dead trees in boreal forest stands is accompanied by an increase in the volume of down deadwood (Harmon et al. 1986; Agee and Huff 1987, Spies et al. 1988), unless the decomposition rate of down deadwood is high. For example, Lee et al. (1995) found no differences in the volume of pre-fire origin down deadwood between young (25 years) and mature (55 years) aspen dominated stands despite a significant decline in the density of standing dead trees, suggesting that rates of removal through decomposition were similar to rates of input from falling dead trees. The decomposition rate of wood in coniferous forests is frequently very slow (McFee and Stone 1966; Harvey et al. 1981). Fahey (1983) found that pre-disturbance origin down deadwood was abundant in lodgepole pine stands that burned between 80 and 110 years prior to sampling. Elevation above the ground surface caused by fallen boles lying on top of one another (Fig. 7) probably contributes to increased longevity, as such material decays more slowly than material in contact with the ground (Fahey 1983; Barber and Van Lear 1984; Erickson et al. 1985; Edmonds et al. 1986; Wei et al. 1997). Elevated coniferous logs in northern Sweden had few lichen or bryophyte species compared to logs in contact with the ground (Söderström 1988). Coverage by lichen, fungi and bryophytes is probably associated with accelerated decomposition rates (McCullough 1948; Mattson et al. 1987).

The abundance of deadwood of post-disturbance origin in the four burned sites (Tables 2, 3) corresponds to natural thinning, which probably explains the presence of relatively intact post-disturbance down deadwood (Fig. 7). Tree mortality is frequently very high in young fire-origin lodgepole pine stands (Fahey 1983; Lotan et al. 1985). The high density of live trees in the burns sampled in this study (Table 1) indicates that high mortality rates and input of deadwood are likely to continue, although mortality rates may decrease as stands age (e.g., Douglas-fir, Cline et al. 1980).

While the above discussion suggests successional trends within fire-origin stands sampled in this study, the wide variability in woody stand structure observed (Tables 2, 3, Figs. 5, 6) is also typical of recently burned temperate forests (Fahenstock 1976; Alexander 1979; Brown and See 1981). The primary source of this variability is probably pre-disturbance vegetation structure and composition, although fire severity and other factors may also contribute (see below). In samples from a wide range of stands, Lotan et al. (1985) found that stand age at the time of burn was considerably more important than time since fire in predicting quantities of down deadwood. Burning of relatively young stands would result in less carry-over of woody material to the next stand (Spies et al. 1988), with frequent repeated disturbances probably reducing the overall supply of deadwood (Mattson et al. 1987). Smaller tree boles may also decay more quickly than larger boles due to their proportionally higher surface area to provide access for decay-causing organisms (Abbott and Crossley 1982; Edmonds et al. 1986; Wei et al. 1997),



although Barber and Van Lear (1984) and Erickson et al. (1985) suggested that small pieces of wood may decay more slowly because of their lower moisture content relative to larger pieces.

Some additional variability among sites may have been associated with regional climatic differences which in turn may influence decomposition rates. Decomposition of down deadwood may have been slower in the higher elevation Chaba River Burn due to a shorter growing season (Fahey 1983). Variable aspect exposure probably also affects decomposition rates, as suggested by Erickson et al. (1985) and Mattson et al. (1987).

Tree species composition probably also influences deadwood abundance through variable decay rates of different species (Harmon et al. 1986). For example, lodgepole pine logs (Fahey 1983) probably decay more slowly than trembling aspen (Miller 1983; Gosz 1980), possibly due to their higher lignin content (Harmon et al. 1986). Decomposition rates in general tend to be faster in deciduous forests compared to coniferous forests (Arthur and Fahey 1990). Without data on fire severity in the burns sampled in this study, it is difficult to assess the potential contribution of this factor to variability in stand structures observed. Few sample plots contained survivors of the pre-disturbance stand, suggesting almost complete tree mortality over much of each burn. Such a pattern is typical in many coniferous forests (Rowe and Scotter 1973; Johnson 1992), as is the relatively small amount of wood biomass combusted and exported during most forest fires (Arno 1980; Lotan et al. 1985; Wei et al. 1997).

Interpretation of differences between burned and logged stands would be assisted by information on pre-disturbance forest structure and composition. The logged stands sampled in this study contained a merchantable wood volume of at least  $72 \text{ m}^3 / \text{ha}$  to be eligible for harvesting (Crossley 1978), although most probably contained greater than  $200 \text{ m}^3 / \text{ha}$ . Their pre-disturbance structure and composition was probably more uniform than burned stands given that fires disturb a wide range of stand types (Rowe and Scotter 1973). This, in addition to the removal of trees during logging, probably contributed to the lower variability in the volume of pre-disturbance origin deadwood observed in logged stands compared to burned stands (Table 3).

In logged sites, existing deadwood and logging debris in the form of small trees, large branches and tops would have contributed some down deadwood to the subsequent stand after logging, as would the thinned material from spacing operations. The decay rate of this down deadwood may be higher in logged sites relative to burned sites because much of the deadwood is in contact with the ground (Fig. 7), facilitating a higher moisture content favorable to decay-causing organisms (Fahey 1983; Mattson et al.

1987, Wei et al. 1997). Fragmentation of down deadwood during harvest operations and site preparation may also accelerate decomposition rates (Sollins 1982; Spies et al. 1988).

### **Management implications**

Overall, the results of this study suggest that the temporal dynamics of stand structure differ considerably between the burned and logged stands sampled (Figs. 6, 8). Since the amount of deadwood originating in the previous stand can only decline during succession through decomposition (Harmon et al. 1986), and since standing dead trees of pre-disturbance origin were scarce in the logged stands sampled (Table 2), the lower volume (Fig. 6A), lower position relative to the ground (Fig. 7) and possibly more advanced decay (Fig. 7) of down deadwood suggest that pre-disturbance deadwood will be depleted in logged stands earlier during succession than in burned stands. Because the density of live and recently dead trees was lower in logged stands than burned stands (Tables 1, 2), mortality during succession is not likely to reverse this trend.

Changes in biodiversity associated with deadwood may occur at a regional scale if efforts to limit disturbance by suppressing wildfires are successful. Prescribed burning of non-merchantable stands adjacent to logged stands would increase the regional supply of deadwood, although these would represent a limited range of stand types relative to those burned by wildfire.

One proposed solution is to expand the range of structural conditions created through harvesting to more closely approximate the range of variability produced by natural disturbance (Hansen et al. 1991, Swanson et al. 1993). Although this model is appealing, our data suggest that the substantial differences in deadwood structures propagated by current logging practices compared to fire offer a considerable challenge to successful implementation in conifer-dominated forests. For example, while the distribution and frequency of stand-replacing wildfires have been suggested as an appropriate spatial model for harvesting (Hunter 1993), the within-stand structural legacy of clear-cutting appears to be dissimilar to that of wildfire (Lee et al. 1997, Wei et al. 1997, this study). In Canada, over 85% of harvesting is done by clear-cutting (Canadian Council of Forest Ministers 1996), a method that receives considerable support for its economic and silvicultural benefits (Keenan and Kimmins 1993).

Application of the "natural disturbance model" (Swanson et al. 1993) to harvesting methods within stands would require managers to expand the range of variability in the amount of deadwood in logged stands to more closely resemble amounts present after natural disturbance such as wildfire.

Because economic and silvicultural considerations will tend to limit the total amount of wood left in cutblocks, decisions on how to provide present and future deadwood need to be made carefully. Of particular concern is the provision of an adequate range of deadwood supply in stands several decades after disturbance, e.g., during the latter half of a planned rotation interval of approximately 80 years.

Though emulation of wildfire-origin stands immediately after harvest is unlikely, retention of standing live and dead trees in some stands at the time of harvest supplies deadwood in future logged stands (Lee et al. 1995; Alberta Forest Products Association 1996). Retention of standing stems in clumps rather than single trees would increase the probability that fallen boles would decay slowly. Fallen boles would have a greater probability of being propped above the ground on boles that fell previously, as occurs in fire-origin stands (Fig. 7). If the recruitment of down deadwood through mortality of live trees was insufficient, it could be accelerated by killing some live trees (e.g., Bull and Partridge 1986; Siitonen and Martikainen 1994) later during succession.

Additional strategies for providing deadwood include the protection of down deadwood present prior to harvest, and the retention of down deadwood created by harvest operations (Lee et al. 1995; Greater Fundy Ecosystem Research Group 1997). Down deadwood in advanced stages of decay may be easily fragmented by machinery used for harvesting and site preparation (Edmonds et al. 1986; Wei et al. 1997). Minimizing the impacts of this machinery in at least some stands would potentially slow decomposition and increase future deadwood supply. The piling of down deadwood in the form of large branches, small boles, and other unutilized material would also delay decomposition, although piling would also contribute to lower deadwood abundance over the rest of the stand. The burning of residue piles, believed to reduce the risk of fire and colonization by tree pathogens in the regenerating stand, further reduces the supply of deadwood (Graham et al. 1994), and perhaps maintaining only large diameter material in debris piles would alleviate these concerns. Graham et al. (1994) recommended amounts of down deadwood to be retained after forest harvesting in a variety of Rocky Mountain cover types, based on optimal levels of ectomycorrhizal activity. Setting different targets for deadwood supply among harvest units (e.g., low, medium, high) would assist in propagating a desired future range of variability.

Finally, if these or other approaches intended to approximate the effects of natural disturbance regimes were implemented, it would also be prudent to monitor structural dynamics and biological response under a range of retention strategies, and identify thresholds for attributes such as down deadwood volume for selected species or processes (e.g., Volney et al. 1999). In this way, ecological benefits could be more accurately quantified against the potential economic costs of attempting to emulate

natural disturbance in harvested stands. Within protected areas, where prescribed fire may be the preferred management tool, this study suggests a range of deadwood supply in burned stands which managers may wish to strive for in support of objectives to maintain natural processes.

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