Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 233 (2006) 176–191
Forest Ecology and Management
www.elsevier.com/locate/foreco

Abundance and attributes of wildlife trees and coarse woody debris at three silvicultural systems study areas in the Interior Cedar-Hemlock Zone, British Columbia

Susan K. Stevenson *, Michael J. Jull, Bruce J. Rogers

University of Northern British Columbia, Ecosystem Science and Management, 3333 University Way, Prince George, BC, V2N4Z9 Canada

Received 21 February 2006; received in revised form 19 June 2006; accepted 19 June 2006

Abstract

Unmanaged cedar (*Thuja plicata*)-hemlock (*Tsuga heterophylla*) forests of the northern Interior Wetbelt of British Columbia support standing and dead trees with a variety of structural features that provide habitat for wildlife. We describe the pre-harvest abundance and characteristics of wildlife trees (standing trees with special characteristics that provide habitat for wildlife) and coarse woody debris (CWD) at three silvicultural systems trials in cedar-dominated stands, and the short-term effects of forest harvesting on the abundance and attributes of CWD. The treatments were clearcut, group retention (70% volume removal), group selection (30% volume removal), and unlogged control. We measured standing trees in 75 0.125-ha plots and CWD along 225 24-m transects, using a functional classification system to characterize habitat attributes of trees and logs. CWD assessments were repeated on the same transects after the harvest. The relationship between tree size and occurrence of habitat features was strong for both standing trees and logs. Each of the four major tree species in the study area was associated with specific habitat features that occurred more often in that species than in any other. Large concealed spaces at the bases of trees, providing den sites and escape cover, were associated with hybrid white spruce (*Picea engelmannii* × *glauca*). We suggest that these trees had originated on nurse logs that subsequently rotted away; if that supposition is correct, there may be shortages of these structures in future stands that originate from plantations. Forest harvesting had little effect on the volume of CWD, but did affect the decay class distribution, reduce the proportion of pieces having structural habitat attributes, and reduce piece lengths; these effects were generally proportional to the level of harvest removal. Partial-cut silvicultural systems have the potential to mitigate anticipated deficits in large wildlife trees and logs in managed stands, if components of the stand are managed on longer rotations than those planned for timber production alone.

Keywords: Wildlife trees; Coarse woody debris; Wildlife habitat; Silvicultural systems; Interior Cedar-Hemlock Zone; Inland rainforest

1. Introduction

Whereas the coastal rainforests of the Pacific Northwest are widely known for their large trees, complex structures, and longevity (Kirk, 1996; Schoonmaker et al., 1997), the wet forests on the windward side of the northern Rocky Mountains, which share these characteristics, have received less public or scientific attention. The Interior Wetbelt of British Columbia is characterized by mountainous terrain; high precipitation; long, snowy winters; and old, predominantly uneven-aged forests. It is dominated by western redcedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) at low elevations and Engelmann spruce (*Picea engelmannii* Parry ex Englm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) at higher elevations. Stand-destroying fires occur infrequently; recent studies in one watershed have reported median estimated time since fire of 467 years (Sanborn et al., 2006), although fire frequency appears to vary with topography. On many sites, intervals between stand-destroying events are long enough that small disturbances in which one or a few trees are killed become important agents of natural forest regeneration (BC Ministry of Forests and Ministry of Environment, 1995). As well, dead or damaged trees provide a rich variety of habitats for 61 vertebrate species of north-central British Columbia that are obligate or frequent users of wildlife trees (standing trees with special characteristics that provide habitat for wildlife), and 51 vertebrate species that are obligate or frequent users of coarse woody debris (CWD) (Keisker, 2000).

* Corresponding author at: Silvifauna Research, 101 Burden St., Prince George, BC, V2M2G8 Canada. Tel.: +1 250 564 5695; fax: +1 250 562 8419.
E-mail address: sksteven@pgweb.com (S.K. Stevenson).

0378-1127/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2006.06.023

In a wide variety of forest types in western North America, the way in which a tree is damaged or killed has been shown to affect its value as wildlife habitat. Trees that have been attacked by insects provide foraging habitat for bark-foraging woodpeckers, nuthatches (*Sitta* spp.), brown creepers (*Certhia americana* Bonaparte) and foliage-gleaning chickadees (*Poecile* spp.); these birds also play a significant role in maintaining pests at endemic levels (Perry, 1988; Machmer and Steeger, 1995). Recently burned trees attract a variety of insectivorous birds, especially black-backed woodpeckers (*Picoides arcticus* Swainson) (Hutto, 1995; Hoyt and Hannon, 2002; Morrissette et al., 2002). Heartwood decay is characteristic of trees selected for nest sites by primary cavity excavating birds (Mannan et al., 1980; Winternitz and Cahn, 1983; Harestad and Keisker, 1989). Some trees that are infected by heartwood fungi develop large cavities that provide habitat for a variety of wildlife, including den sites for black bears (*Ursus americanus* Pallas) (Bull et al., 2000), night roosts for pileated woodpeckers (*Dryocopus pileatus* Linn.) (Bull et al., 1992), nesting and roosting sites for Vaux's swift (*Chaetura vauxi* Towns.) (Summers and Gebauer, 1995), and roosting sites for bats (Parsons et al., 2002; Psyllakis and Brigham, 2006). Broken tops resulting from wind damage not only provide an entrance point for heartwood fungi, they may also form nest sites for a variety of large birds, including osprey (*Pandion haliaetus* Linn.), red-tailed hawk (*Buteo jamaicensis* Gmel.), northern goshawk (*Accipiter gentilis* Linn.), great horned owl (*Bubo virginianus* Gmel.), and barred owl (*Strix varia* Barton) (Campbell et al., 1990). Witches' brooms resulting from rusts (*Chrysomyxa* spp.) or dwarf mistletoe (*Arceuthobium* spp.) are used as den sites by northern flying squirrels (*Glaucomys sabrinus* Shaw) (Mowrey and Zasada, 1984; Cotton and Parker, 2000), resting sites by fishers (*Martes pennanti* Erxleben) (Weir, 1995), and nest sites by great gray owl (*Strix nebulosa* Forster) and great horned owl (Campbell et al., 1990).

Structural attributes resulting from the action of disturbance agents seem to have less influence on the habitat value of fallen trees than of standing trees. Some relationships have been identified. Hollow logs result from the action of heartwood fungi in living trees, and cannot be created by post-mortality decay processes (Bull et al., 1997). They are important as cover or denning sites for a variety of large mammals, including snowshoe hares (*Lepus americanus* Erxleben), bushy-tailed woodrats (*Neotoma cinerea* Ord), weasels (*Mustela* spp.), skunks, and black bears (Maser et al., 1979; Bull et al., 2000). Some animals, such as red squirrels (*Tamiasciurus hudsonicus* Erxleben), cache winter food supplies in hollow logs (Maser et al., 1979). The elevated root wad of uprooted trees is an important habitat feature that is used by flycatchers for perching, by grouse for dusting, by dark-eyed juncos (*Junco hyemalis* Linn.) for nesting, and by winter wrens (*Troglodytes troglodytes* Linn.) for both foraging and nesting (Campbell et al., 1997). Aside from these structural attributes, the use of fallen trees by wildlife is largely determined by size, decay stage, orientation, and quantity (Caza, 1993).

While it is valuable to understand the mechanisms by which specific wildlife habitat features develop in standing trees and, to a lesser extent, in logs, forest management decisions are rarely made at that level. Instead, managers need to know how the occurrence of these features is related to easily-measured attributes, such as tree species, diameter, and stage of decay. This kind of information helps managers plan how wildlife habitat will be maintained within stands and across the landscape, and to predict the outcomes of various possible management scenarios.

Many of the structural features of standing and fallen trees that provide habitat for wildlife require large trees and considerable time to develop. They will be absent or substantially reduced in a landscape in which clearcutting on a short rotation is the dominant silvicultural regime. Recently, an increasing body of scientific research on the unique characteristics of old forests, and increasing public attention to the maintenance of biodiversity, wildlife habitat, visual quality, and other non-timber values, has led to a reappraisal of management objectives that focussed largely on regeneration and growth of commercially important tree species (Coates and Burton, 1997; Franklin et al., 1997; McCarthy, 2001; McClellan, 2004). Emerging silvicultural systems aim to create structurally complex managed stands that produce timber products without compromising ecosystem functioning. In 1996, we began to establish a set of silvicultural systems trials in the northern Interior Wetbelt of British Columbia in which to examine the effects of various harvest patterns on stand structure and development (including regeneration, growth, damage, and mortality), and on the loss and creation of structural biodiversity attributes associated with standing trees and CWD.

At the landscape level, harvest patterns have been shown to influence the distribution of a variety of disturbance agents, including defoliating insects, bark beetles, fire, and windthrow (Perry, 1988). However, at the stand level, there is little information on the long-term effects of silvicultural systems on the incidence of disturbance agents or the structural biodiversity attributes that result from them. Their occurrence will depend on the agents and attributes that were present in the stand before harvest, and the subsequent influence of the harvesting. The harvest disturbance itself may affect the frequency, severity, and nature of other disturbances in the residual stand. One of the long-term objectives of our study is to evaluate the effects of harvest patterns on the occurrence of biotic and abiotic disturbance in the residual stand, as well as the wildlife habitat features associated with damaged trees.

In the short-term, our baseline data allow us to examine the occurrence of wildlife habitat features in standing trees and logs, and the tree attributes with which they are associated. The purposes of this study are (1) to describe the pre-harvest abundance and characteristics of wildlife trees and CWD at three silvicultural systems trials in cedar-dominated stands in the Interior Wetbelt of British Columbia and (2) to describe the short-term effects of partial cutting on the abundance and attributes of CWD.

2. Methods

2.1. Study areas

The three study areas were located in the wet and very wet subzones of the Interior Cedar-Hemlock Zone (Meidinger and Pojar, 1991) in east-central British Columbia, an area also

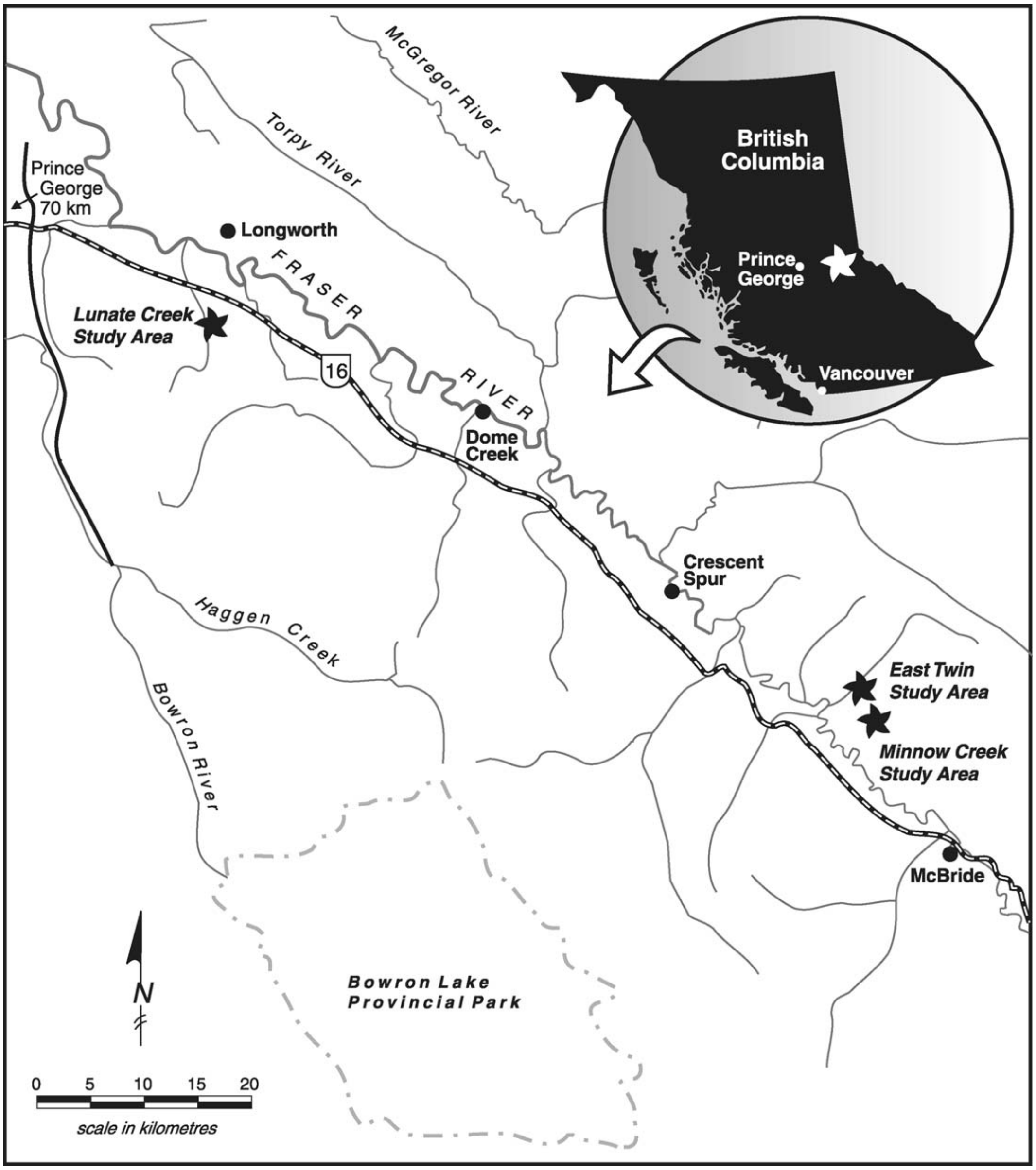

Fig. 1. Location of the study areas.

known as the inland rainforest (Arsenault and Goward, 2000). The main criteria used to select the study areas were: relatively homogeneous cedar-dominated stands large enough to include several comparable treatment units; availability of the area for harvest; willingness of the forest licensee to accept the extra time and costs required for planning and implementation; and accessibility. The three sites were located between the communities of Prince George and McBride, British Columbia (Fig. 1); their physical characteristics are summarized in Table 1.

Stands at both Minnow Creek and East Twin Creek appeared to be late seral, and similar in age; the oldest trees were estimated to be about 300–350 years old. Internal decay precluded exact aging of most of the large trees, but calibrated

Table 1
Physical characteristics of the study areas

Study area	Subzone and variant	Latitude/longitude	Elevation range (m)	Aspect	Mean slope (%)	Area (ha)
East Twin Creek	ICHwk3[a]	53°28′46″N/120°21′07″W	900–1050	NW	40	26.0
Minnow Creek	ICHwk3[a]	53°27′56″N/120°21′02″W	1050–1200	SW	30	39.2
Lunate Creek	ICHvk2[b]	53°49′53″N/121°28′44″W	950–1200	N	35	72.4

[a] Goat river wet cool ICH (Meidinger et al., 1988).
[b] Slim very wet cool ICH (DeLong, 2003).

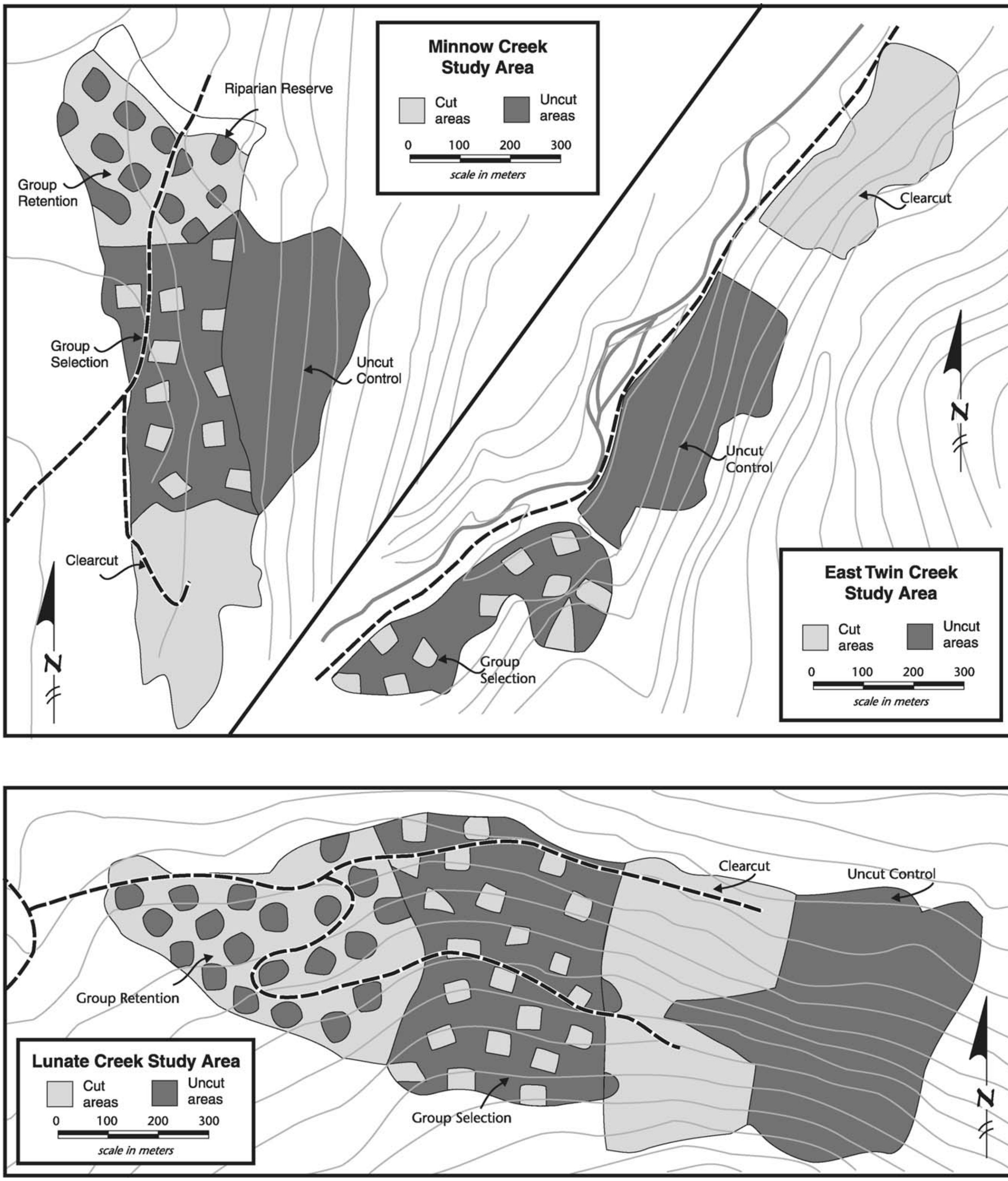

Fig. 2. Layout of the treatment units.

radiocarbon dating of surficial charcoal layers in the forest floor indicated that these sites burned approximately 400–450 years ago (Sanborn et al., 2006). Stand structure and relative tree size at the Lunate Creek site suggested that the stand was substantially older, but no charcoal was found in the forest floor for radiocarbon dating. Trees at all three sites had a high level of damage and decay. Sporophores of the heartrot fungus *Echinodontium tinctorium* (Ellis & Everh.) Ellis & Everh. were present on most western hemlock trees, and most of the larger western redcedar trees were internally decayed or hollow at stump height.

2.2. Treatments

Four treatments were applied at each study area except East Twin Creek, which was only large enough to

Table 2
Summary of sample plots and CWD transects

Study area	Treatment unit	Treatment unit area (ha)	Number of 0.125-ha large tree plots	Number of 24-m CWD transects
East Twin Creek	UN	9.9	7	21
	GS	8.7	6	18
	CC	7.8	6	18
Minnow Creek	UN	9.9	6	18
	GS	11.2	8	24
	GR	10.7	6	18
	CC	7.4	5	15
Lunate Creek	UN	20.3	7	21
	GS	20.8	8	24
	GR	16.7	8	24
	CC	14.6	8	24

accommodate three of the four treatments (Fig. 2). The treatments were: 0% post-harvest retention or ‘‘clearcut’’ (CC), 30% post-harvest retention or ‘‘group retention’’ (GR), 70% post-harvest retention or ‘‘group selection’’ (GS), and 100% retention or ‘‘unlogged control’’ (UN). Group retention patches were 1–2 tree heights in diameter, or approximately 0.1–0.4 ha, and group selection openings were similar in size. Wherever possible, we randomly allocated harvesting treatments among available treatment units. In one case, visual quality objectives precluded a particular treatment location, and in all cases, the unlogged control areas were placed where they would be least affected by access roads or adjacent logging.

All harvesting was done in winter on a settled snowpack. The East Twin Creek site was harvested in March 2000, and the other two sites were logged concurrently in January–March 2001. Ground-based methods (hand- or machine-felling with skidder yarding to a central location) were used in all treatment units except the clearcut at East Twin, where steep slopes required use of a high-lead cable system in about 75% of the treatment unit.

2.3. Pre-harvest sampling

Before harvest, temporary 0.125-ha sample plots to sample standing trees were systematically established in each treatment unit in each study area to a minimum intensity of 5% of the treatment unit area (Table 2). For each tree $\geq$17.5 cm dbh and $\geq$1.5 m high, we recorded species, dbh, height, percent live crown, and pathological indicators (BC Ministry of Forests, 1998). We rated the decay stage of each tree according to the British Columbia decay classification system for conifers (BC Ministry of Forests and Ministry of Environment, 1995), a nine-class system similar to that of Thomas et al. (1979) in which class 1 represents living, healthy trees and class 9 represents decayed stumps. Evidence of wildlife use, if any, was recorded. Evidence of damage agents was recorded, using Allen et al. (1996) as a field reference.

We also recorded any wildlife tree types (Keisker, 2000) associated with each tree. A type is a configuration of habitat features required by one or more wildlife species for specific functions. For example, type 1 trees (WT1), those with hard outer wood surrounding decay-softened inner wood, are needed by strong primary cavity excavators as substrates for the excavation of nest holes. Types are not mutually exclusive; a tree may be associated with zero, one, or more types. The 10 wildlife tree types are described in Table 3.

Associated with each tree plot were a set of three independently located 24-m line transects for CWD measurements (Table 2). Each piece of CWD > 7.5 cm in diameter at the point of intersection of the sampling line was marked with paint at the point of intersection and measured according to Resource Inventory Committee (1998) procedures. We recorded species, diameter at the point of intersection, tilt angle, length, diameter at stump height (if possible), origin (stem break, stock break, root break, tree throw, or unknown) and decay class according to the five-class system of Maser et al. (1979), in which class 1 represents solid, recently fallen trees and class 5 represents logs in an advanced state of decay. For odd-shaped pieces, we recorded the dimensions of a rectangle with an equivalent cross-sectional area to the cross-section of the piece (Resource Inventory Committee, 1998). Evidence of use by wildlife, if any, was noted. We also recorded any CWD types (Keisker, 2000) associated with each piece. The six CWD types are described in Table 4.

CWD types 1, 2, and 3 may apply to the lower bole (below 1.3 m) of standing trees as well as logs. We included CWD1 and CWD3 in our assessments of standing trees, but not CWD2, because it applied to almost every tree. CWD1 was recorded only if the concealed space had an entrance large enough to accommodate two fists. Thus, references to ‘‘wildlife tree types’’ in standing trees include CWD1 and CWD3 as well as WT types 1–10.

2.4. Post-harvest sampling

The summer after logging, the CWD transects were re-established in the same locations as the pre-harvest samples. We searched for each piece of CWD that had been present before harvest and recorded it as present or absent. Any changes in the condition or attributes of pieces were also recorded. New pieces were measured and described.

Table 3
Types of wildlife trees required by wildlife of north-central British Columbia (Keisker, 2000)

Main function		Type	Main users
Reproduction/resting			
Substrates for cavity excavation	WT-1	Hard outer wood surrounding decay-softened inner wood	Woodpeckers (stronger excavators)
	WT-2	Outer and inner wood softened by decay	Woodpeckers (weaker excavators), chickadees, nuthatches
Existing cavities	WT-3	Small, excavated or natural cavities	Chickadees, nuthatches, swallows, bats
	WT-4	Large, excavated or natural cavities	Ducks, owls, bluebirds, swallows, bats, squirrels, mustelids
	WT-5	Very large natural cavities or hollow trees	Swifts, owls, bats, mustelids
	WT-6	Cracks, loose bark, or deeply furrowed bark	Creepers, bats
Large open-nest supports and other non-cavity sites	WT-7	Witches' brooms	Diurnal raptors, owls, squirrels, mustelids
	WT-8	Large branches, multiple leaders, or large-diameter broken tops	Herons, diurnal raptors, owls
Foraging			
Feeding substrates	WT-9	Arthropods in wood or under bark	Woodpeckers
Hunting perches	WT-10	Open-structured trees in or adjacent to open areas	Diurnal raptors, owls

2.5. Data analysis

Analysis of the attributes associated with wildlife tree and coarse woody debris types was restricted to pre-harvest data. We used binary logistic regression (SPSS Inc., 2000) to identify the explanatory categorical variables that were most closely associated with the presence of each type. Wildlife tree types 1 and 2, both of which apply to trees with decay-softened inner wood, were grouped for analysis because WT2 numbers were relatively low. The explanatory variables included in the logistic regression models for wildlife tree types were study area (Minnow, Lunate, or East Twin), tree species (hybrid spruce, subalpine fir, western hemlock, or western redcedar), decay class (1–2, 3, 4, 5, or 6–8) and DBH class (1 = 17.5 to <32.5 cm; 2 = 32.5 to <47.5 cm; 3 = 47.5 to <62.5 cm; 4 = 62.5 to <100 cm; 5 = >100 cm). The explanatory variables included in the logistic regressions for CWD types were study area, tree species (hybrid spruce, subalpine fir, western hemlock, western redcedar, branch, or unknown), decay class (1, 2, 3, 4, 5), origin (stem break, stock break, root break, tree throw, or unknown), and length class (≤10 m, 11–20 m, 21–30 m, or >30 m). The explanatory variables were dummy coded with Minnow, hybrid spruce, decay class 1–2 (living trees), and DBH class 1 (17.5–32.5) as reference values for standing trees, and Minnow, unknown tree species, decay class 1, unknown origin, and length ≤10 m as reference values for CWD. We used a backward stepwise model in which variables with an alpha value >0.15 were removed. We did not include

Table 4
Types of coarse woody debris required by wildlife of north-central British Columbia (Keisker, 2000)

Main function		Type	Main users
Reproduction/resting/escape			
Concealed spaces	CWD-1	Large concealed spaces	Grouse, hare, woodrat, porcupine, fox, cats, some mustelids, bears
	CWD-2	Small concealed spaces (or soft substrate allowing excavation of such spaces) at or below ground-level beneath hard material	Salamander, toad, treefrog, snakes, wrens, shrews, voles, deer mouse, golden-mantled ground squirrel, chipmunk, jumping mice, weasels
	CWD-3	Small concealed spaces above ground-level	Treefrog, yellow-bellied flycatcher, wrens, townsend's solitaire, some wood warblers, some sparrows
Travel			
Concealed runways	CWD-4	Long concealed spaces (or soft substrate allowing construction of runways)	Salamander, some snakes, wrens, shrews, voles, deer mouse, weasels
Exposed, raised travel lanes	CWD-5	Large or elevated, long material clear of dense vegetation	Tree squirrels, chipmunk
Foraging			
Feeding substrates	CWD-6	Invertebrates in wood, under bark or moss-cover, or in litter/humus accumulated around CWD	Salamander, treefrog, woodpeckers, wrens, some sparrows, shrews, deer mouse, skunk, bears

interactions in any of the models, because interaction terms were often correlated with other variables (a violation of the non-collinearity assumption), and because the addition of interactions would have resulted in a very large number of variables. Fit of the model was evaluated using the *p*-value of the likelihood ratio statistic and McFadden's rho-squared (SPSS Inc., 2000).

We had measurements of diameter at stump height (DSH) for only a subset of the CWD pieces; therefore we did not include DSH in the logistic regression, but instead used *t*-tests with Bonferroni adjusted probabilities on that subset of the data to compare the size of pieces with and without each type.

Comparison of pre- and post-treatment conditions was limited to CWD. The likelihood ratio chi-square statistic (Sokal and Rohlf, 1995; SPSS Inc., 2000) was used to compare pre- and post-treatment values of binary categorical variables, and distributions of multinomial categorical variables. Piece length distributions of CWD were non-normal and heterogeneous, in some cases approaching a bimodal distribution, and were not normalized by transformation. Therefore, the Mann–Whitney test was used to compare piece lengths of CWD before and after harvest.

CWD volume was calculated according to Van Wagner (1982), except that volume of odd-shaped pieces was calculated according to Marshall et al. (2000). The CWD volume distributions were skewed right and had unequal variances; therefore, a cube root transformation was applied to the data to meet the assumptions of statistical tests. The effects of study area and treatment on CWD volume were examined using analysis of variance with repeated measures. A paired samples *t*-test was used to compare pre- and post-harvest CWD volumes within individual treatment units.

3. Results

3.1. Pre-harvest conditions

At all three sites, the mature forest cover was dominated by western redcedar, with smaller components of hybrid white spruce (*P. engelmannii* × *glauca*), subalpine fir, and western hemlock. Western redcedar made up over 90% of the basal area at the Lunate and East Twin blocks, and 75% of the basal area at the Minnow block. The rest of the stand at Minnow was composed of hybrid spruce and subalpine fir; very little (<2%) western hemlock was present. Live basal area ranged from 93.7 m^2/ha at Minnow Creek to 133.6 m^2/ha at Lunate Creek; basal area of dead standing trees ranged from 9.8 m^2/ha at East Twin to 17.0 m^2/ha at Lunate Creek.

In the pre-harvest stands, as a whole, 86–91% of the standing trees ≥17.5 cm dbh and 1.5 m in height were living. Fig. 3A shows how the dead trees were distributed among decay classes 3–8. Numbers of standing dead trees ranged from 28 stems/ha at Lunate Creek to 65 stems/ha at Minnow Creek.

Most trees were not associated with any wildlife tree types. Numbers of trees with types ranged from 22.4% (110 stems/ha) at East Twin to 30.3 % (93 stems/ha) at Lunate Creek. Most trees with types exhibited only one, but 3–7% of trees exhibited two types, and a few exceptional trees were associated with three or more (Fig. 3A). The percentage of trees with one or more wildlife tree types increased steadily with diameter, from 14.1% in the 17.5–32.5 cm diameter class to 63.7% in trees >100 cm in diameter.

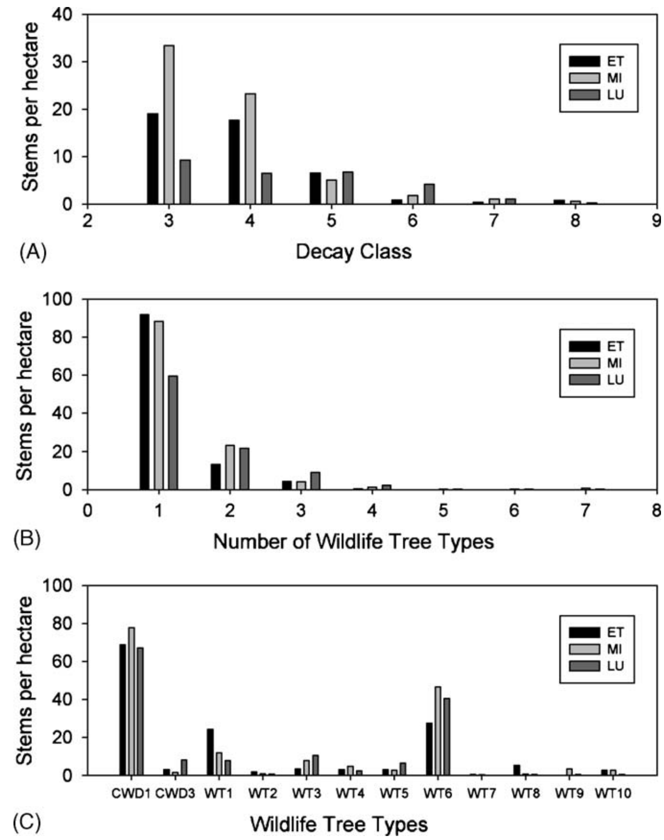

Fig. 3. Pre-harvest frequencies (stems/ha) of decay classes 3–8 of standing trees (A), trees having one or more wildlife tree types (B), and occurrence of specific wildlife tree types (C) at East Twin (ET), Minnow (MI), and Lunate (LU) study areas.

Individual wildlife tree types differed greatly in their frequency of occurrence (Fig. 3C), and the occurrence of types differed among tree species (Table 5). The most common types were CWD1 (trees with large concealed spaces at the base),

Table 5
Percent occurrence of wildlife tree types in four tree species

WLT type	Species			
	Subalpine fir (*n* = 474)	Western redcedar (*n* = 2670)	Western hemlock (*n* = 364)	Hybrid spruce (*n* = 311)
CWD1	13.50	18.09	6.04	24.76
CWD2	0.84	1.39	0.27	0.00
WT1	4.22	0.90	14.01	7.72
WT2	0.42	0.19	0.27	0.32
WT3	1.90	2.06	0.55	1.29
WT4	1.27	0.67	0.27	1.29
WT5	0.63	1.31	0.27	0.64
WT6	21.94	8.69	2.47	3.22
WT7	0.21	0.00	0.00	0.32
WT8	0.21	0.24	1.65	0.96
WT9	1.05	0.04	0.00	1.93
WT10	1.27	0.19	0.27	1.29

Table 6
Parameters that distinguished trees with wildlife tree types from those without types using logistic regression

WLT type	Model rho-squared	Parameter	Parameter estimate	S.E.	*t*-ratio	*p*	Odds ratio
CWD1	0.132	Western redcedar	−0.764	0.163	−4.675	<0.001	0.466
		Western hemlock	−0.920	0.283	−3.253	0.001	0.398
		Decay class 4	0.825	0.231	3.568	<0.001	2.282
		Decay class 6–8	1.029	0.386	2.667	0.008	2.798
		DBH class 2	0.616	0.181	3.411	0.001	1.852
		DBH class 3	1.201	0.178	6.741	<0.001	3.322
		DBH class 4	1.917	0.163	11.765	<0.001	6.800
		DBH class 5	2.900	0.191	15.187	<0.001	18.177
CWD3[a]	0.298	Decay class 3	2.472	0.558	4.429	<0.001	11.851
		Decay class 4	3.013	0.530	5.684	<0.001	20.352
		Decay class 5	2.979	0.545	5.470	<0.001	19.661
		Decay class 6–8	3.402	0.546	6.227	<0.001	30.026
		DBH class 5	2.886	0.677	4.261	<0.001	17.928
WT1–2	0.295	Subalpine fir	−1.143	0.364	−3.141	0.002	0.319
		Western redcedar	−2.160	0.361	−5.987	<0.001	0.115
		Western hemlock	1.112	0.376	2.960	0.003	3.041
		Decay class 3	1.977	0.339	5.826	<0.001	7.223
		Decay class 4	2.653	0.327	8.125	<0.001	14.197
		Decay class 5	3.411	0.389	8.763	<0.001	30.293
		Decay class 6–8	3.722	0.499	7.457	<0.001	41.349
WT3	0.227	Decay class 3	1.565	0.529	2.959	0.003	4.782
		Decay class 4	2.813	0.419	6.709	<0.001	16.656
		Decay class 5	2.001	0.541	3.696	<0.001	7.398
		Decay class 6–8	2.919	0.494	5.914	<0.001	18.525
		DBH class 4	1.814	0.597	3.040	0.002	6.133
		DBH class 5	3.374	0.607	5.561	<0.001	29.210
WT4	0.225	Decay class 3	2.688	0.627	4.286	<0.001	14.698
		Decay class 4	3.550	0.514	6.909	<0.001	34.814
		Decay class 5	2.869	0.690	4.156	<0.001	17.611
		Decay class 6–8	2.718	0.815	3.332	0.001	15.144
		DBH class 4	3.031	1.061	2.857	0.004	20.714
		DBH class 5	3.488	1.110	3.142	0.002	32.721
WT5	0.148	Decay class 4	2.360	0.546	4.318	<0.001	10.581
		DBH class 5	3.879	1.034	3.752	<0.001	48.398
WT6	0.312	East Twin	−0.624	0.199	−3.137	0.002	0.536
		Subalpine fir	2.568	0.419	6.129	<0.001	13.038
		Western redcedar	1.373	0.406	3.384	0.001	3.945
		Decay class 3	2.166	0.240	9.032	<0.001	8.721
		Decay class 4	3.806	0.250	15.244	<0.001	44.971
		Decay class 5	1.830	0.366	5.000	<0.001	6.237
		Decay class 6–8	1.367	0.445	3.069	0.002	3.922
		DBH class 2	0.698	0.250	2.789	0.005	2.010
		DBH class 3	0.978	0.279	3.500	<0.001	2.658
		DBH class 4	2.127	0.261	8.155	<0.001	8.389
		DBH class 5	3.814	0.278	13.742	<0.001	45.321
WT8	0.248	East Twin	2.242	0.844	2.656	0.008	9.408
		DBH class 4	2.716	0.909	2.988	0.003	15.123
WT9	0.332	Western redcedar	−4.390	1.237	−3.550	<0.001	0.012
		Decay class 4	2.086	0.706	2.954	0.003	8.053
WT10	0.251	Decay class 3	3.566	0.700	5.079	<0.001	35.362
		Decay class 4	3.896	0.664	5.864	<0.001	49.207

[a] CWD1 was not found in hybird spruce; western hemlock was used as the reference.

WT6 (trees with cracks, loose bark, or deeply furrowed bark), and WT1 (trees with hard outer shells and internal decay). Other types occurred at frequencies of 11 stems/ha or less.

All logistic regression models for wildlife tree types had *p*-values <0.001), indicating that the coefficients (other than that of the constant) differed from zero, and most models had rho-squared values between 0.2 and 0.4 (Table 6), indicating an acceptable fit (SPSS Inc., 2000). WT7 was not modeled because it was rare at our study sites. Table 6 also shows the attributes that were most closely associated with the occurrence

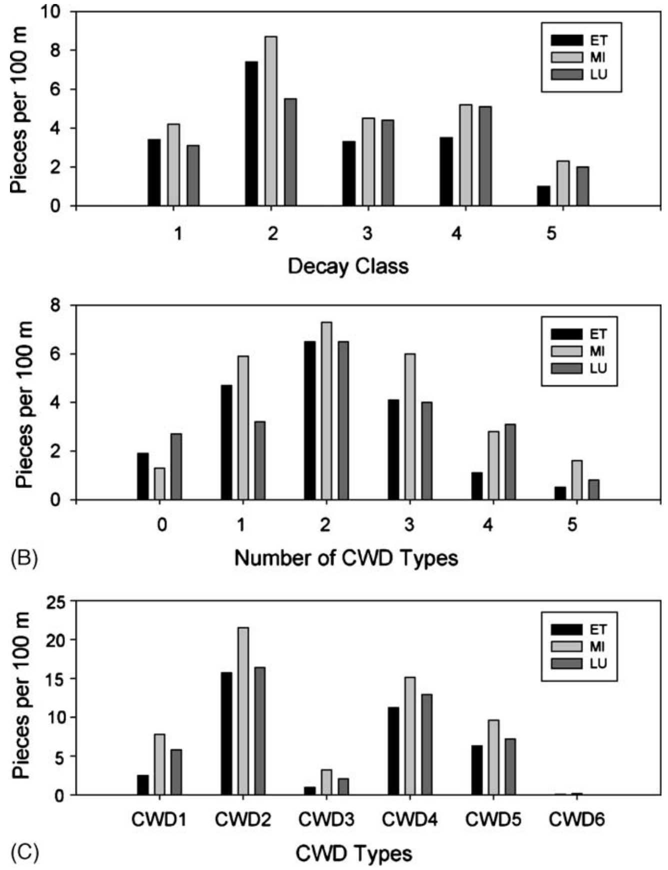

Fig. 4. Pre-harvest frequencies (pieces/100 m) of decay classes of coarse woody debris (A), number of coarse woody debris types (B), and CWD types (C) at East Twin (ET), Minnow (MI), and Lunate (LU) study areas.

of the various wildlife tree types; only those attributes with $p < 0.01$ and odds ratios with lower confidence bounds >1 or upper confidence bounds <1 are included. The odds ratio indicates the factor by which the odds change, in relation to a reference value of the explanatory variable, when the attribute is present. Thus, a western redcedar tree was only about half as likely as a hybrid spruce (the reference value for tree species) to be classified as CWD1 (odds ratio 0.466), but almost four times as likely to be classified as WT6 (odds ratio 3.945).

Mean pre-harvest volume of CWD ranged from 220 m^3/ha at East Twin to 387 m^3/ha at Lunate Creek. Of the 1148 pieces that were sampled pre-harvest, 42% were sufficiently decayed that they could not be identified to species. The greatest number of CWD pieces occurred in decay class 2 at all three sites, but the distribution of decay classes was more uniform at Lunate Creek than in the other study areas (Fig. 4A). CWD types occurred with a much greater frequency than wildlife tree types; most (86–95%) CWD pieces had one, two or three CWD types (Fig. 4B). CWD types 2 (small concealed spaces at or below ground-level) and 4 (long concealed spaces that can be used as runways) occurred most commonly, and CWD6 (pieces with invertebrates used for foraging by vertebrates) were extremely rare (Fig. 4C).

Logistic regression models for CWD types also had p-values <0.001, and had rho-squared values in the same range as the models for wildlife tree types (Table 7). Diameter at stump height of pieces with CWD types was significantly greater than that of pieces without types for CWD types 1–5; sample sizes of CWD6 were too small for statistical tests (Table 8).

3.2. Effects of harvesting on CWD

There were significant differences in the pre- and post-harvest distributions of decay classes of CWD in the clearcut (likelihood ratio chi-square = 109.240; d.f. = 4; $p < 0.001$), group retention (likelihood ratio chi-square = 35.829); d.f. = 4; $p < 0.001$), and group selection (likelihood ratio chi-square = 25.350; d.f. = 4; $p < 0.001$) treatment units. As expected, the decay class distribution did not change in the unlogged control area (likelihood ratio chi-square = 0.061; d.f. = 4; $p = 0.100$). The changes in decay class distributions in harvested units occurred largely in decay class 1, which increased by factors of 6.6 in the clearcut, 3.1 in the group retention area, and 2.2 in the group selection area.

The proportion of CWD pieces having CWD types 1, 2, 3, 4, or 5 was reduced by logging (Table 9). The occurrence of CWD types 2 and 4 was significantly reduced in all three harvested treatment units. The occurrence of CWD types 1, 3, and 5 was also reduced, but the response was less consistent among replicates. Occurrences of CWD6 were too few for statistical tests.

Volume of CWD differed significantly among study areas and with time (pre- and post-harvest); interactions of time with

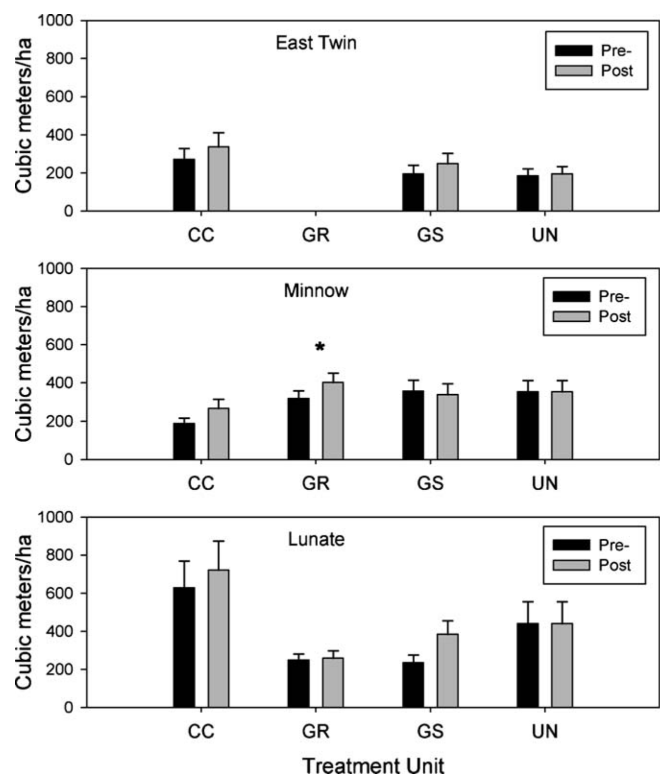

Fig. 5. Pre- and post-harvest volumes of CWD in clearcut (CC), group retention (GR), group selection (GS), and unlogged (UN) treatment units at three ICH study areas. Asterisks indicate statistically significant differences (paired sample t-tests performed on cube root transformed data).

Table 7
Parameters that distinguished logs with CWD types from those without types using logistic regression

CWD type	Model rho-squared	Parameter	Parameter estimate	S.E.	*t*-ratio	*p*	Odds ratio
CWD1	0.213	East Twin	−1.071	0.252	−4.248	<0.001	0.343
		Western redcedar	0.797	0.236	3.369	0.001	2.218
		Hybrid spruce	1.212	0.387	3.132	0.002	3.361
		Decay class 2	0.673	0.241	2.795	0.005	1.961
		Decay class 3	1.285	0.279	4.603	<0.001	3.616
		Decay class 4	0.888	0.326	2.722	0.006	2.431
		Tree throw	1.353	0.284	4.770	<0.001	3.868
		Length 11–20 m	1.139	0.202	5.636	<0.001	3.142
		Length 21–30 m	1.767	0.244	7.231	<0.001	5.851
		Length >30 m	2.820	0.447	6.306	<0.001	16.780
CWD2	0.194	Decay class 2	1.595	0.246	6.478	<0.001	4.930
		Decay class 3	3.260	0.485	6.723	<0.001	26.037
		Decay class 4	2.424	0.407	5.961	<0.001	11.294
		Branch	−0.935	0.322	−2.902	0.004	0.393
		Length 11–20 m	0.667	0.254	2.630	0.009	1.948
		Length 21–30 m	1.021	0.332	3.072	0.002	2.777
CWD3	0.238	Tree throw	2.159	0.491	4.400	<0.001	8.663
		Length 21–30 m	1.652	0.334	4.798	<0.001	5.216
		Length >30 m	2.164	0.469	4.617	<0.001	8.705
CWD4	0.239	Decay class 2	1.773	0.235	7.536	<0.001	5.890
		Decay class 3	2.736	0.306	8.938	<0.001	15.420
		Decay class 4	1.505	0.303	4.971	<0.001	4.504
		Tree throw	0.824	0.314	2.627	0.009	2.280
		Length 11–20 m	1.241	0.188	6.582	<0.001	3.457
		Length 21–30 m	2.046	0.285	7.183	<0.001	7.738
		Length >30 m	3.312	0.776	4.268	<0.001	27.436
CWD5	0.416	Lunate Creek	0.624	0.227	2.744	0.006	1.866
		Subalpine fir	1.709	0.311	5.491	<0.001	5.526
		Western redcedar	1.409	0.252	5.588	<0.001	4.092
		Western hemlock	1.348	0.412	3.274	0.001	3.850
		Hybrid spruce	1.550	0.428	3.618	<0.001	4.710
		Decay class 4	−1.268	0.348	−3.646	<0.001	0.281
		Stem break	1.339	0.291	4.606	<0.001	3.817
		Stock break	1.170	0.403	2.906	0.004	3.222
		Root break	1.565	0.379	4.126	<0.001	4.784
		Tree throw	1.093	0.331	3.306	0.001	2.985
		Length 11–20 m	1.395	0.207	6.744	<0.001	4.035
		Length 21–30 m	2.214	0.264	8.392	<0.001	9.152
		Length >30 m	2.649	0.545	4.861	<0.001	14.142

study area and with treatment were not significant (Table 10). Although CWD volume tended to increase in the harvested units, the difference was statistically significant ($p = 0.011$) in only one case (Fig. 5).

Table 8
Univariate comparisons (*t*-test) of diameter at stump height of logs with and without CWD types

CWD type	Type present		Type absent		*p*
	Mean ± S.E.	*n*	Mean ± S.E.	*n*	
1	65.9 ± 2.3	132	39.6 ± 1.8	142	<0.001
2	54.4 ± 1.7	247	32.5 ± 2.8	27	<0.001
3	71.7 ± 3.6	66	46.1 ± 1.6	208	<0.001
4	56.2 ± 1.9	217	36.9 ± 2.5	57	<0.001
5	55.9 ± 1.9	171	46.1 ± 3.0	103	0.006
6	51.3	3	52.2 ± 1.6	274	–

Between the pre-harvest and the post-harvest observations, piece length of CWD declined by an average of 36.7% in the clearcuts, 32.9% in the group retention units, and 18.1% in the group selection units. Piece length declined by only 1.2% in the unlogged units during the same period. Differences between pre-harvest and post-harvest piece lengths were statistically significant ($p < 0.05$, using the Mann–Whitney test statistic) in all three clearcut units, both group retention units, one of the three group selection units, and none of the unlogged units.

4. Discussion

4.1. Attributes of trees and logs with habitat value

The type classification system (Keisker, 2000) for standing trees and CWD was a useful tool with which to rapidly distinguish trees and logs with high potential to provide habitat

Table 9
Percentage of CWD pieces having CWD types, pre-harvest and post-harvest

TU	Study area	CWD types											
		CWD1		CWD2		CWD3		CWD4		CWD5		CWD6	
		Pre-harvest	Post-harvest	Pre-harvest	Post-harvest	Pre-harvest	Post-harvest	Pre-harvest	Post-harvest	Pre-harvest	Post-harvest	Pre-harvest	Post-harvest
UN	ET	10.6	10.2	79.8	77.8	2.0	1.9	58.7	57.4	28.8	29.6	0.0	0.0
UN	MI	23.2	23.0	93.7	92.9	8.0	8.0	66.1	64.6	40.2	38.9	0.01	0.01
UN	LU	44.4	44.4	77.7	77.7	16.5	16.5	52.2	52.2	42.4	43.4	0.0	0.0
p		0.908		0.733		0.954		0.875		0.991		–	
GS	ET	15.5	11.5	90.1	81.2	5.6	4.2	56.3	52.1	40.8	34.4	0.0	0.0
GS	MI	25.0	17.9	87.8	75.0	12.8	10.3	68.3	55.8	42.1	33.3	0.01	0.01
GS	LU	19.8	21.8	71.7	59.2	8.1	13.6	58.6	43.5	32.3	32.0	0.0	0.0
p		0.280		<0.001		0.948		0.001		0.101		–	
GR	MI	44.2	23.7	78.8	62.8	17.7	5.8	57.5	43.6	35.4	27.6	0.01	0.02
GR	LU	27.0	19.7	86.5	67.6	7.1	6.3	66.7	50.0	31.0	26.1	0.0	0.0
p		0.001		<0.001		0.013		<0.001		0.118		–	
CC	ET	15.0	7.2	82.5	58.8	10.0	4.6	65.0	42.5	32.5	26.8	0.0	0.01
CC	MI	35.3	9.4	85.3	36.7	13.2	1.6	44.1	17.2	35.3	18.7	0.0	0.0
CC	LU	24.5	15.2	84.8	55.7	10.8	7.4	63.9	39.5	35.4	28.1	0.0	0.0
p		0.002		<0.001		0.110		<0.001		0.037		–	

p-values indicate probability of the likelihood ratio chi-square for the treatment unit as a whole.

for wildlife from those with low potential. Although the classification system of Keisker (2000) was developed for the forests of central British Columbia, we expect that both the classification system and our results are applicable in other forest types. The broad pattern of occurrence of wildlife tree and CWD types in this study was similar to that observed at a silvicultural systems site in a higher-elevation stand composed of subalpine fir and Engelmann spruce (Stevenson and Keisker, 2002). In both cases, wildlife tree types were relatively uncommon—22–30% of standing trees in the cedar-dominated study areas and 36% in the fir-spruce study area were classified as having one or more wildlife tree types (including CWD1 and CWD3). CWD types were common—about 90% of logs were classified as having one or more CWD types in both studies.

The relationship between tree size and the occurrence of habitat features was strong for both standing trees and logs. In standing trees, the probability of occurrence of large concealed spaces at tree bases (CWD1) and cracks or loose bark (WT6) increased consistently with diameter class. Other features, such as small concealed spaces below 1.3 m (CWD3), hollow trees and trees with cavities (WT3–5), and trees suitable for large open nests (WT8) were strongly associated with one or both of the two largest diameter classes. Only trees with internal decay (WT1–2), trees with arthropods (WT9), and trees suitable as hunting perches (WT10), showed no relationship with diameter class. The absence of a relationship between diameter class and trees with internal decay was unexpected, because of the relationship between tree age and the presence of decay columns due to heartrot fungi, especially in conifers (Bunnell et al., 2002). At our study sites, there were substantial numbers of suppressed western hemlock trees in the smallest diameter class (17.5–32.5 cm) that bore sporophores of the heartrot fungus *E. tinctorium*, and were therefore classified as WT1. These hemlocks, which may have been relatively old despite their small size, skewed the distribution of WT1–2 trees away from the larger diameter classes. None of the small hemlocks had actually been used for nest hole excavation.

Larger tree size was also associated with the presence of CWD types in logs, as shown by the comparisons of mean diameter at stump height of logs with and without types, and by the prominence of piece length as a significant factor in the logistic regression models.

Our study areas were not ideally suited for examining relationships between types and tree species, because of the preponderance of one species. About 70% of the stems ≥17.5 cm were western redcedar, and the remainder subalpine fir (12.4%), western hemlock (9.5%), or hybrid spruce (8.1%). The association between WT1–2 and western hemlock was evident,

Table 10
Analysis of variance with repeated measures of CWD volume performed on cube root transformed data

Source	Sum of squares	d.f.	Mean square	*F*	*p*
Between subjects					
Study area	82.384	2	41.192	4.748	0.010
Treatment	34.539	3	11.513	1.327	0.266
Error	1873.942	216	8.676		
Within subjects					
Time	6.758	1	6.758	6.135	0.014
Time × study area	0.368	2	0.184	0.167	0.846
Time × treatment	1.812	3	0.604	0.548	0.650
Error	237.927	216	1.102		

but only three western hemlocks actually had cavities (WT3 or 4). Two of these were large (DBH class ≥3), dead trees, and the other was a living 45-cm tree with a natural cavity. Primary cavity excavators may be averse to drilling through live sapwood of western hemlock, as is the case for many other conifers (Keisker, 2000). If that is true, then the presence of *E. tinctorium* in living western hemlocks should be treated as an indicator of potential future habitat, rather than as current habitat.

In contrast, western redcedar was rarely classified as WT1–2. Sporophores of heartrot fungi, which are indicators of WT1–2, were rare in cedar. Where cracks or scars extended into the heartwood of the cedar, the tree was often found to be hollow, and classified as WT5 rather than WT1–2. Most (85%) of the trees classified as WT5 were cedars, and we expected to see a strong association between western redcedar and hollowness, but that was not reflected in the logistic regression. Trees were only classified as WT5 if they had a hole or crack that would allow wildlife to enter them; many cedars were undoubtedly hollow, but lacked visible openings. As well, many of the cedars that were hollow near the base probably had decay-softened inner wood higher on the bole, but were not classified as WT1–2 because they lacked external indicators. Most (74%) of the trees associated with WT3 or 4 were cedars, and these included a number of trees in which the only external indicator of decay was an excavated nest hole. Thus, our assessments of WT1–2 may have underestimated wildlife habitat potential in cedar, because there were few external indicators of decay.

WT6 was associated strongly with subalpine fir, and to a lesser extent with western redcedar. Loose bark suitable as roosting cover for bats occurred most commonly in dead subalpine fir, which tends to develop ideal bark conditions in decay class 4. Cracks in the bole or the bark wide enough for bats occurred most often in cedar. Loose slabs of bark suitable for brown creeper nests also occurred in cedar, and one probable brown creeper nest was found in a sample tree. Trees with arthropods in the stem or under the bark (WT9) were associated with hybrid spruce, but occurred infrequently, indicating a low level of bark beetle activity in the study areas at present.

Large concealed spaces at the base of the tree were most strongly associated with hybrid spruce. CWD1 differs from other wildlife tree types in that it is not closely associated with any disturbance agent, except in cedar, where large concealed spaces were often associated with internal decay. In other species, these spaces were often found under large roots, apparently independent of any damage or decay. We speculate that trees with root-sheltered cavities often originate on nurse logs, which subsequently rot away, leaving openings beneath some of the roots.

The association between CWD1 and spruce may have occurred because that species is more likely than the others to have originated on nurse logs in this and similar ecosystems. Literature reviews have reported that decaying wood is a preferred seedbed, and sometimes the dominant seedbed, for spruce in northern ecosystems, especially under a mature forest canopy where little mineral soil is available as a substrate (Coates et al., 1994; McCarthy, 2001). Conifer regeneration on nurse logs is a well-known process, but the long-term development of these seedling cohorts has not often been studied. In general, survival of seedlings originating on rotten wood seems to be lower than survival on other seedbeds (Harmon and Franklin, 1989; Brang et al., 2003). In some cases, poor survival may be associated with failure of root systems to reach the soil. Heineman (1991) observed that white spruce seedlings experimentally planted on rotten wood that had roots extending into the F or H layer appeared to be healthier than seedlings with roots that remained within the rotten wood.

Various authors (Harmon and Franklin, 1989; Harris, 1989; Narukawa and Yamamots, 2005) have suggested that ‘‘stilt-rooted’’ trees have resulted from the collapse of decaying logs on which regeneration has become established. Regenerating trees that originated on decaying wood and that extended their root systems into the surrounding forest floor were described by Wagg (1967), Heineman (1991), and Narukawa and Yamamots (2005), but in these studies the supporting logs were still present. The processes by which logs decay and subside into the forest floor have been described (Maser and Trappe, 1984; Harmon et al., 1986), but we have not found any documentation of the concurrent development of the root morphology of the saplings that grew on these logs. We hypothesize that the association we observed between CWD1 and spruce occurred because spruce is more likely than the other tree species to have originated on nurse logs in our study area. Evidence for this supposition is largely anecdotal at present; further studies would be necessary to support or refute this hypothesis.

Occurrence of CWD types in logs was not generally associated with tree species. The apparent association of raised travel lanes (CWD5) with all four tree species was an artifact that occurred because the reference species used in the logistic regression was ‘‘unknown’’. Logs that could not be identified to species were mainly in the older decay classes, which were unlikely to be elevated enough to be classified as travel lanes.

In both standing trees and downed logs, some habitat attributes were associated with the stage of decay. Odds of wildlife tree types occurring were generally higher in decay classes ≥3, indicating that the types were more likely to occur in dead than living trees, but odds did not necessary increase with decay class in dead trees. Cracks and loose bark (WT6) and trees with arthropods (WT9) were associated with decay class 4. Hunting perches (WT10) were associated with decay classes 3 and 4, probably because trees in these classes had branches as perch sites, but lacked the visual obstruction of foliage.

Habitat functions of logs varied with the elevation of the log. Our results were similar to those of DeLong et al. (2005), who used the same functional classification system in their study of decaying log habitats in wet subzones of the sub-boreal spruce zone (Meidinger and Pojar, 1991). In our study, small concealed spaces at ground level (CWD2) and long concealed spaces for runways (CWD4) tended to peak in decay class 3, the class in which logs are no longer elevated, but are still solid enough to provide overhead cover. DeLong et al. (2005) observed the same pattern of occurrence of ground-level runways, although in their study area concealed ground-level spaces continued to increase in decay class 4–5. We found that logs providing raised travel lanes (CWD5) were negatively associated with decay class 4, and absent in decay class 5; DeLong et al. (2005) reported a similar decline in elevated runways with increasing stage of decay.

Coarse woody debris pieces that originated from the uprooting of trees (tree throw) were associated with some CWD types. Both large (CWD1) and small (CWD3) concealed spaces were often found within or beneath root wads of uprooted trees. Logs providing raised travel lanes were associated with any recognizable origin (stem break, stock break, root, break, or tree throw, as opposed to ‘‘unknown’’ or ‘‘branch’’), for the same reason that these logs were associated with any recognizable tree species—elevated logs were likely to be sufficiently intact that their origin could be identified.

4.2. Effects of harvesting on CWD

Pre-harvest CWD volumes observed in this study fall within the range of values reported in old-growth stands in wet ICH subzones (158–557 m^3/ha) by Feller (2003). The more uniform distribution of decay classes at Lunate, which we believe to be the oldest stand, probably reflects a longer period of stand development and CWD input.

Other studies of the effects of forest harvesting on volume of CWD in central British Columbia have found inconsistent or insignificant trends between pre- and post-harvest conditions (Lloyd, 2002; Densmore et al., 2004), and that was true in this study. However, harvesting may generate important differences in CWD size, structure, decay stage, and spatial distribution; these changes in CWD attributes may affect wildlife, even if volume is unchanged. In our study, the greatest change in decay class distribution after harvest was the input of decay class 1 logs, probably because many living trees with high levels of internal decay were considered unmerchantable and left on the block, as there is currently no economically-viable market for whole logs for pulp in this region. The change we observed in decay class distribution differs from that in many other study areas, in which harvested sites are often dominated by pieces in intermediate decay classes (Densmore et al., 2004). Across all treatments at our study sites, the input of decay class 1 pieces, with little loss of more decayed pieces, will likely prolong wildlife habitat values, compared to cutblocks in which there are few additions of decay class 1 pieces.

The reduction in piece length we observed, even in the clearcut units, was less extreme than that in other cutblocks in the wet ICH, where investigators found that 70% of the post-harvest CWD volume was in pieces <6 m long (Densmore et al., 2004). Informal observations at our study sites suggested that the decline in piece length resulted mainly from input of short pieces of logging debris, and to a lesser extent, from damage to pre-existing pieces by logging equipment. Similarly, the reduced occurrence of CWD pieces with types in our study resulted mainly from input of pieces that lacked wildlife habitat attributes. The scheduling of logging on a winter snowpack probably helped to protect and maintain pre-existing CWD pieces – especially those at ground level – and the habitat attributes that are associated with them.

The effects of harvesting that we observed on distribution of decay classes, occurrence of CWD types, and piece length, were generally proportional to the level of harvest removal. However, the most significant effects of forest harvesting on amount and function of CWD occur over time, as new input is produced by the residual and regenerating stands. Densmore et al. (2004) have projected that 90 years after clearcut harvesting, CWD volumes at their sub-boreal spruce sites and Interior Douglas-fir sites would have declined to 15% and 1.5%, respectively, of the volumes found in mature unmanaged stands. We expect that likewise, CWD volumes and habitat attributes will decline most dramatically in the clearcut treatments at our study sites, in the long-term. However, because the residual stand in the partial-cut treatments will continue to provide stand-level input of diverse pieces over the rotation, we expect that significant differences in CWD trends will emerge between the clearcut and partial-cut treatments.

4.3. Management implications

Many authors have stressed the positive association between tree size and specific ecological values, both in standing trees and CWD (Samuelsson et al., 1994; Bull et al., 1997; Stevens, 1997; Lofroth, 1998; Bunnell et al., 2002). The anticipated shortage of large wildlife trees and logs in managed stands of the future has emerged as a major management concern. Our study likewise supports the contention that large tree size is associated with a wide range of attributes that enhance the value of standing trees and logs as habitat for wildlife.

Considering only tree size, it is likely that the occurrence of trees with wildlife habitat features will be greatly reduced in even-aged managed stands in the wet ICH at anticipated rotation ages of 80–100 years. In this study, most types were strongly associated with trees in the two largest diameter classes (>62.5 cm). We suspect that many of the trees ≥62.5 cm dbh observed in this study were more than 300 years old. Such large trees will be rare under planned even-aged management regimes in north-central British Columbia (e.g. BC Ministry of Forests, 2001), and probably in many other forest types throughout western North America.

To maintain and promote wildlife habitat attributes, the biotic and abiotic disturbance agents that create wildlife trees must be included and accepted in managed stands of the future. There is a growing recognition among forest health professionals that damaged trees serve important ecosystem functions and therefore have a place in managed forests (BC Ministry of Forests, 1997; Henigman et al., 1999). However, we note that these values are not always reflected in operational management practices in our region. To meet ecosystem management goals, silviculturists and forest health managers must balance the negative impacts of forest disturbance agents with their capacity to create structures needed by wildlife.

In this study, each of the four major tree species was associated with specific habitat features that occurred more often in that species than in any other. Our results provide empirical support for the general principle that maintaining the full range of native tree species at the stand level and across the landscape is an important component of biodiversity management. Past silvicultural practices in the northern Interior Wetbelt have resulted in the conversion of old cedar-hemlock stands to young spruce-dominated stands with few or no residual trees, but today silviculturists are increasingly managing for cedar and hemlock as well as spruce regeneration (BC Ministry of Forests, 2002), and for retention of residual trees individually and in groups. This shift toward a more balanced species mix will result in stands with a greater potential to provide future wildlife habitat than stands dominated by a single species.

The association between large concealed spaces at tree bases and spruce warrants further investigation, and may have implications for stand-level management practices. If nurse log origins are in fact an important factor predisposing trees to develop root-sheltered cavities, there may be shortages of these structures in future stands that originate from plantations, even if the planted trees are allowed to grow past rotation age. It may be possible to address the anticipated deficiency of this habitat feature by increasing the use of management practices that protect existing nurse logs and promote the retention of advanced regeneration on at least part of the managed forest area. The silvicultural practices that have predominated in British Columbia (and in other parts of western North America) since the late 1960s have not encouraged the retention of advanced regeneration. However, some recommendations for the management of forest ecosystems driven by gap dynamics include shifts toward smaller openings and increased structural retention within openings; these recommendations, if put into practice, may make the use of advanced regeneration and other forms of natural regeneration more attractive (McCarthy, 2001; Brang et al., 2003).

Canopy replacement through the release of advanced regeneration is a normal process in unmanaged Wetbelt forests, and thus the retention of some advanced regeneration within harvest openings is a strategy consistent with the concept of mimicking natural forest processes during management (Parish and Antos, 2005). We still need to learn more about the prospects for survival, growth, and root development of trees originating on nurse logs, especially in relation to canopy openings and patches retained during harvesting. Information on these topics will help inform strategies for promoting the development of trees with root-sheltered cavities. Likewise, research is needed on the manner in which root-sheltered cavities develop, and on how the processes that produce them can be maintained in managed stands.

This study has reinforced the importance of managing for large and diverse pieces of CWD. The occurrence of most habitat features increased with piece length, but piece length decreased in harvested areas. As well, different decay classes are associated with different functions in CWD, as they are in standing trees. In the short-term, measures that protect existing CWD will help to maintain piece size and diversity. Such measures include winter logging on settled snowpacks and use of designated skid trails. As well, we recommend that uprooted trees with large root wads be recognized as valuable habitat features to be protected where possible. In the long-term, maintaining an adequate supply of CWD that includes well-distributed large pieces and pieces at various stages of decay will be a challenge to forest managers. The potential of partial-cut silvicultural systems to address this challenge should be considered in long-term forest planning.

The creation of wildlife habitat features in standing trees and downed logs requires enough time for trees to grow large, to be acted upon by agents of damage, decay, or mortality, and subsequently to develop the critical structures. While some habitat features may develop in even-aged second-growth stands within a conventional 80- to 100-year rotation, others will not. Alternative silvicultural strategies, including partial-cut silvicultural systems, have the potential of ameliorating anticipated deficits in large wildlife trees and logs by carrying forward older trees with habitat attributes, or the potential to develop them, into managed stands of the future. However, if these alternative strategies are to be effective in recruiting desired wildlife habitat attributes, some groups or cohorts of trees will have to be managed under much longer rotations than those planned for purposes of timber production. It will be a challenge for forest managers to develop and maintain appropriate silvicultural prescriptions and durable administrative mechanisms to track and protect such retained forest structures over many decades.

Acknowledgements

This project was funded by Forest Renewal British Columbia and Forest Innovation Investment. We acknowledge the cooperation of forest licensees, contractors, and Ministry of Forests staff whose special efforts contributed to the success of the silvicultural systems trials. Dan Eriksen, Bill Floyd, Dev Khurana, Becky L'Hirondelle, Sarah Parsons, Chad Renzie, Mike Stricker, and Dave Stuart assisted with field data collection. We thank Dieter Ayers for statistical advice and William Owens for his statistical review. The manuscript was much improved by the comments of two anonymous reviewers.

References

Allen, E., Morrison, D., Wallis, G., 1996. Common Tree Diseases of British Columbia. Natural Resources Canada, Canadian Forest Service.

Arsenault, A., Goward, T., 2000. Ecological characteristics of inland rain forests. In: Darling, L. (Ed.), Proceedings of the Biology and Management of Species and Habitats at Risk, vol. I, BC Ministry of Environment, Lands and Parks, Victoria, BC and University College of the Cariboo, Kamloops, BC, pp. 437–439.

Brang, P., Moran, J., Puttonen, P., 2003. Regeneration of *Picea engelmannii* and *Abies lasiocarpa* in high-elevation forests of south-central British Columbia depends on nurse logs. Forest. Chron. 79, 273–279.

BC Ministry of Forests, 1997. Tree wounding and decay guidebook. In: Forest Practices Code of British Columbia, BC Ministry of Forests, Victoria, BC.

BC Ministry of Forests, 1998. Guidelines for Establishment and Maintenance of Growth and Yield Permanent Sample Plots. BC Ministry of Forests, Victoria, BC.

BC Ministry of Forests, 2001. Prince George Timber Supply Area Analysis Report. BC Ministry of Forests, Victoria, BC.

BC Ministry of Forests, 2002. Prince George Timber Supply Area: Rationale for Allowable Annual Cut Determination. BC Ministry of Forests, Victoria, BC.

BC Ministry of Forests and Ministry of Environment, 1995. Biodiversity guidebook. In: Forest Practices Code of British Columbia, BC Ministry of Forests and Ministry of Environment, Victoria, BC.

Bull, E.L., Akenson, J.J., Henjum, M.G., 2000. Characteristics of black bear dens in trees and logs in northeastern Oregon. Northwest. Nat. 81, 148–153.

Bull, E.L., Holthausen, R.S., Henjum, M.G., 1992. Roost trees used by Pileated Woodpeckers in northeastern Oregon. J. Wildlife Manage. 56, 786–793.

Bull, E.L., Parks, C.G., Torgerson, T.R., 1997. Trees and logs important to wildlife in the Interior Columbia River basin. US Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-GTR-391, Portland, OR.

Bunnell, F.L., Wind, E., Boyland, M., Houde, I., 2002. Diameters and heights of trees with cavities: their implications to management. In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E. (Eds.), Proceedings of the Ecology and Management of Dead Wood in Western Forests. US Dep. Agric. For. Serv. Gen. Tech. Rep. PSW-GTR-181, pp. 717–737.

Campbell, R.W., Dawe, N.K., McTaggart-Cowan, I., Cooper, J.M., Kaiser, G.W., McNall, M.C.E., 1990. The Birds of British Columbia, vol. II. Non-passerines: Diurnal Birds of Prey through Woodpeckers. Royal BC Museum, Victoria, BC.

Campbell, R.W., Dawe, N.K., McTaggart-Cowan, I., Cooper, J.M., Kaiser, G.W., McNall, M.C.E., Smith, G.E.J., 1997. The Birds of British Columbia, vol. III. Passerines: Flycatchers through Vireos. UBC Press, Vancouver, BC.

Caza, C.L., 1993. Woody debris in the forests of British Columbia: a review of the literature and current research. BC Ministry of Forests Land Manage. Rep. 78, Victoria, BC.

Coates, K.D., Burton, P.J., 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. For. Ecol. Manage. 99, 337–354.

Coates, K.D., Haeussler, S., Lindeburgh, S., Pojar, R., Stock, A.J., 1994. Ecology and silviculture of interior spruce in British Columbia. For. Can. and BC Ministry of Forests FRDA Rep. 220.

Cotton, L., Parker, K.L., 2000. Winter habitat and nest trees used by northern flying squirrels in sub-boreal forests. J. Mammal. 81, 1071–1086.

DeLong, C., 2003. A field guide to site identification and interpretation for the southeast portion of the Prince George Forest Region. BC Ministry of Forests Land Manage. Hdbk. 51.

DeLong, S.C., Daniels, L.D., Heemskerk, B., Storaunet, K.O., 2005. Temporal development of decaying log habitats in wet spruce-fir stands in east-central British Columbia. Can. J. For. Res. 35, 2841–2850.

Densmore, N., Parminter, J., Stevens, V., 2004. Coarse woody debris: inventory, decay modeling, and management implications in three biogeoclimatic zones. BC J. Ecosystems Manage. 5, 14–29., www.forrex.org/jem/2004/vol5/no2/art3.pdf.

Feller, M.C., 2003. Coarse woody debris in the old-growth forests of British Columbia. Environ. Rev. 11, S135–S157.

Franklin, J.F., Berg, D.R., Thornburgh, D.A., Tappeiner, J.C., 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century: the Science of Ecosystem Management. Island Press, Washington, DC, pp. 111–139.

Harestad, A.S., Keisker, D.G., 1989. Nest tree use by primary cavity-nesting birds in south central British Columbia. Can. J. Zool. 67, 1067–1073.

Harmon, M.E., Franklin, J.F., 1989. Tree seedlings on logs in *Picea–Tsuga* forests of Oregon and Washington. Ecology 70, 48–59.

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, K.J., Cromack, K.J., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.

Harris, A.S., 1989. Wind in the forests of southeast Alaska and guides for reducing damage. US Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-GTR-244.

Heineman, J.L., 1991. Growth of interior spruce seedlings on forest floor materials. M.Sc. Thesis. University of British Columbia, Vancouver, BC.

Henigman, J., Ebata, T., Allen, E., Holt, J., Pollard, A., 1999. Field guide to forest damage in British Columbia. BC Ministry of Forests and Canadian Forest Services Joint Publication 17, Victoria, BC.

Hoyt, J.S., Hannon, S.J., 2002. Habitat associations of black-backed and three-toed woodpeckers in the boreal forest of Alberta. Can. J. For. Res. 32, 1881–1888.

Hutto, R.L., 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain (USA) conifer forests. Conserv. Biol. 9, 1041–1058.

Keisker, D.G., 2000. Types of wildlife trees and coarse woody debris required by wildlife of north-central British Columbia. BC Ministry of Forests Working Paper 50, Victoria, BC.

Kirk, R. (Ed.), 1996. The Enduring Forests. The Mountaineers, Seattle.

Lloyd, R., 2002. A comparison of coarse woody debris in harvested and unharvested sites. Morice and Lakes Innovative Forest Practices Agreement. Summary No. 12, pp. 1–8. URL: www.moricelakes-ifpa.com/publications/ecosystem_function.htm#debris_sites.

Lofroth, E.C., 1998. The dead wood cycle. In: Voller, J., Harrison, S. (Eds.), Conservation Biology Principles for Forested Landscapes. UBC Press, Vancouver, BC, pp. 185–214.

Machmer, M.M., Steeger, C., 1995. The ecological roles of wildlife tree users in forest ecosystems. BC Ministry of Forests Land Manage. Hdbk. 35, Victoria, BC

Mannan, W.R., Meslow, C.E., Wight, H.M., 1980. Use of snags by birds in Douglas-fir forests, western Oregon. J. Wildlife Manage. 44, 787–797.

Marshall, P.L., Davis, G., Lemay, V.M., 2000. Using line intersect sampling for coarse woody debris. Forest Research Technical Report TR-003. BC Ministry of Forests, Vancouver Forest Region, Nanaimo, BC.

Maser, C., Trappe, J.M., 1984. The seen and unseen world of the fallen tree. US Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-164.

Maser, C., Anderson, R.G., Cromack Jr., K., Williams, J.T., Martin, R.E., 1979. Dead and down woody material. In: Thomas, J.W. (Ed.), Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. US Dep. Agric. For. Serv. Agric. Hdbk. 553, Washington, DC, pp. 78–95.

McCarthy, J., 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environ. Rev. 9, 1–59.

McClellan, M.H., 2004. Development of silvicultural systems for maintaining old-growth conditions in the temperate rainforest of southeast Alaska. For. Snow Landscape Res. 78, 173–190.

Meidinger, D., Pojar, J., 1991. Ecosystems of British Columbia. BC Ministry of Forests Spec. Rep. Series 6, Victoria, BC.

Meidinger, D., McLeod, A., MacKinnon, A., DeLong, C., Hope, G., 1988. A field guide for identification and interpretation of ecosystems of the Rocky Mountain Trench, Prince George Forest Region. BC Ministry of Forests Land Manage. Hdbk. 15.

Morrissette, J.L., Cobb, T.P., Brigham, R.M., James, P.C., 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Can. J. For. Res. 32, 2169–2183.

Mowrey, R.A., Zasada, J.C., 1984. Den tree use and movements of northern flying squirrels in interior Alaska and implications for forest management. In: Meehan, W.R., Merrell, Jr., T.R., Hanley, T.A. (Eds.), Proceedings of the Symposium on Fish and Wildlife Relationships in Old-Growth Forests, Am. Inst. Fish Res. Biol., Morehead City, NC, pp. 351–356.

Narukawa, Y., Yamamots, S., 2005. Development of conifer seedlings roots on soil and fallen logs in boreal and subalpine coniferous forests of Japan. For. Ecol. Manage. 175, 131–139.

Parish, R., Antos, J., 2005. Advanced regeneration and seedling establishment in small cutblocks in high-elevation spruce-fir forests at Sicamous Creek, southern British Columbia. Can. J. For. Res. 35, 1877–1888.

Parsons, S., Lewis, K.J., Psyllakis, J.M., 2002. Relationships between roosting habitat of bats and decay of aspen in the sub-boreal forests of British Columbia. For. Ecol. Manage. 177, 559–570.

Perry, D., 1988. Landscape pattern and forest pests. Northwest Environ. J. 4, 213–228.

Psyllakis, J.M., Brigham, M.R., 2006. Characteristics of diurnal roosts used by female *Myotis* bats in sub-boreal forests. For. Ecol. Manage. 223, 93–102.

Resource Inventory Committee, 1998. BC Vegetation Resources Inventory: Sampling Procedures. BC Ministry of Forests and BC Ministry of Environment, Lands and Parks. Victoria, BC.

Samuelsson, J., Gustafsson, L., Ingelög, T., 1994. Dying and dead trees: a review of their importance for biodiversity. Swedish Environmental Protection Agency Rep. No. 4306. Swedish Threatened Species Unit, Uppsala, Sweden.

Sanborn, P., Geertsam, M., Jull, A.J.T., Hawkes, B., 2006. Soil and sedimentary charcoal evidence for Holocene forest fires in an inland

temperate rainforest, east-central British Columbia, Canada. Holocene 16, 415–427.
Schoonmaker, P.K., von Hagen, B., Wolf, E.C., 1997. The Rain Forests of Home. Island Press, Washington, DC.
Sokal, R.R., Rohlf, F.J., 1995. Biometry, 3rd ed. Freeman and Co., New York.
SPSS Inc., 2000. SYSTAT 10 Statistics I. SPSS Inc., Chicago, IL.
Stevens, T., 1997. The ecological role of coarse woody debris: an overview of the importance of CWD in BC forests. BC Ministry of Forests, Res. Br., Work. Pap. 30, Victoria, BC.
Stevenson, S.K., Keisker, D.G., 2002. Evaluating the effects of partial cutting on wildlife trees and coarse woody debris. In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E. (Eds.), Proceedings of the Ecology and Management of Dead Wood in Western Forests. US Dep. Agric. For. Serv. Gen. Tech. Rep. PSW-GTR-181, pp. 753–763.
Summers, K., Gebauer, M. 1995. Status of the Vaux's Swift in British Columbia. BC Ministry of Environment, Lands and Parks Wildlife Working Report WR-67, Victoria, BC.
Thomas, J.W., Anderson, R.G., Maser, C., Bull, E.L., 1979. Snags. In: Thomas, J.W. (Ed.), Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington. US Dep. Agric. For. Serv. Agric. Hdbk. 553, Washington, DC, pp. 60–77.
Van Wagner, C.E., 1982. Practical aspects of the line intersect method. Can. For. Serv. Info. Rep. PI-X-12. Petawawa National Forestry Institute, Chalk River, Ont.
Wagg, J.W.B., 1967. Origin and development of white spruce root-forms, Can. Dep. For. and Rural Dev., Forestry Branch Pub. 1192.
Weir, R.D., 1995. Diet, spatial organization, and habitat relationships of fishers in south-central British Columbia. M.Sc. Thesis. Simon Fraser University, Burnaby, BC.
Winternitz, B.L., Cahn, H., 1983. Nest holes in live and dead aspen. In: Davis, J.W., Goodwin, G.A., Ockenfels, R.A. (Eds.), Proceedings of the Symposium on Snag Management. June 7–9, 1983, Flagstaff, Arizona. US Dep. Agric. For. Serv. Gen. Tech. Rep. RM-99, Fort Collins, CO, pp. 102–106.