Influence of variable retention harvests on forest ecosystems. I. Diversity of stand structure

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Summary

1. Variable retention harvests or 'green-tree retention systems' are important to the management of coniferous forests in the temperate zone. Green-tree retention leaves large live trees after harvest (i.e. residual trees) to increase structural diversity of the regenerating stand and provide mature forest habitat that develops sooner than in typical even-aged management by clear-cutting. The seed-tree system is one method of harvesting that leaves a few wind-firm seed trees standing singly, or in groups, to provide seed to regenerate an area naturally. Green-tree retention may increase biological diversity and help to enhance functional links among forest structures or ecological processes.

2. This study was designed to test the hypothesis that the abundance (e.g. basal area and density of residual trees and amount of vegetation) and diversity (e.g. species diversity and structural diversity of the herb, shrub and tree layers) of various aspects of stand structure will decline with lower levels of tree retention. In particular, abundance and diversity should be greater in sites with green-tree retention than in clear-cut sites.

3. Stand structure attributes were measured from 1996 (immediately after harvesting) to 1999 in replicated clear-cut, single seed-tree, group seed-tree, patch-cut and uncut forest sites in mixed forests of Douglas fir *Pseudotsuga menziesii*–lodgepole pine *Pinus contorta* in southern British Columbia, Canada.

4. In terms of abundance, clear-cut, single seed-tree and group seed-tree sites had similar mean basal areas of residual trees, ranging from 0·1 to 2·5 m² ha⁻¹, with significantly higher levels on patch-cut (23·4 m² ha⁻¹) and uncut forest (39·0 m² ha⁻¹) sites. Mean densities of residual trees also followed this pattern, ranging from 0·7 to 16·3 stems ha⁻¹ on the clear-cut to group seed-tree sites, to 769·4 and 2050·0 stems ha⁻¹ on the patch-cut and uncut forest sites, respectively. However, mean volume (m³ ha⁻¹) of fallen wood (i.e. dead wood or woody debris) was similar among sites, ranging from 116·7 in the single seed-tree to 210·2 in the patch-cut sites. Contrary to our hypothesis, the mean index of total crown volume of herbs, shrubs, mosses and lichens was similar among sites.

5. Mean species richness of herbs, shrubs and total plants was similar among sites. Mean richness of trees in seed-tree sites was similar to that in uncut forest in three of four post-harvest years. The mean species diversity of herbs was similar among sites, but that of shrubs and trees was generally lowest in the patch-cut sites and similar among the other sites.

6. The mean structural richness and diversity of herbs was lowest in the uncut forest and similar at the other sites 3 and 4 years post-harvest. The mean structural richness of trees and total plants in the patch-cut and uncut forest sites had more vegetation layers than the other sites.

7. Our hypothesis was partly supported in terms of basal area and density of residual trees and structural richness of total vegetation layers across a gradient of tree retention from uncut forest to clear-cut sites. However, this pattern was not supported for abundance or diversity of understorey vegetation. Thus, the structural attributes of residual

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trees and layers of vegetation, but not the abundance, species richness or species diversity of understorey vegetation, lend support to the aims of variable retention harvesting, at least up to 4 years post-harvest.

Introduction

Variable retention harvests or 'green-tree retention systems' are becoming a standard component of harvest prescriptions for temperate zone coniferous forests (Ciancio & Nocentini 1994; Watanabe & Sasaki 1994; Larsen 1995; Franklin *et al*. 1997). Green-tree retention leaves large live trees after harvest (i.e. residual trees) to increase structural diversity of the regenerating stand and provide mature forest habitat that develops sooner than in typical even-aged management by clear-cutting. The seed-tree harvesting system leaves a few wind-firm seed trees standing singly, or in groups, to provide seed to regenerate an area naturally (Smith 1986). The patch-cut system harvests timber from small (< 1-ha) units dispersed over a given area of forest. Conventional silvicultural systems evolved to manage forests sustainably but unfortunately in practice have not come anywhere near this goal, particularly in North America. Forest harvesting has been dominated by clear-cutting, but variable retention harvests have become more common over the past decade.

Clear-cutting appears to mimic the natural disturbance regime of catastrophic (i.e. stand-replacing) wildfires (Franklin & DeBell 1973). However, it has become apparent that this harvest practice does not produce the same pattern of complexity thought to underlie the recovery of forest ecosystems following large-scale disturbance (Franklin, Frenzen & Swanson 1995; Perry & Amaranthus 1997).

Historically, wildfires in the Pacific north-west of North America, for example, were highly variable, ranging from low-frequency stand-replacing fires in coastal areas to high-frequency variable-intensity fires in interior regions (Agee 1993). Individual trees or groups of trees often survived catastrophic fires, along with large amounts of woody debris (logs and snags, i.e. standing dead trees). The structure and composition of these surviving features may differ markedly from those left by conventional clear-cutting (Spies, Franklin & Thomas 1988; Hansen *et al*. 1991; Spies & Franklin 1991; Halpern & Spies 1995; Tappeiner *et al*. 1997).

Forest harvesting systems are now designed to mimic more closely the processes and outcomes of natural disturbance and succession by retaining structural characteristics of the former forest, such as large live trees or 'green-trees', snags and logs (Franklin 1989; Franklin *et al*. 1997). These techniques are designed to maintain ecosystem structure and function, provide regenerating stands with structural features that would otherwise be absent, and enhance connectivity across the landscape. The conceptual basis for green-tree retention lies in the strong functional links among forest structures, ecological processes and biological diversity found in natural forest ecosystems (Franklin *et al*. 1981; Harmon *et al*. 1986; Spies & Franklin 1991).

Large-scale harvest studies in mature, late-successional, forests are lacking (Aubry *et al*. 1999). However, some retrospective studies investigating potential long-term consequences of green-tree retention in two-tiered (two-aged) stands have been conducted. The effects of green-tree retention on biodiversity include impacts on growth and tree species composition of future forests (Rose & Muir 1997; Zenner, Acker & Emmingham 1998), canopy lichen communities (Peck & McCune 1997; Sillett & Goslin 1999), understorey vegetation (North *et al*. 1996) and stand structural complexity (Zenner 2000). In additional studies of green-tree retention, the positive relationship between canopy tree retention and diversity of birds has been reported by Hansen & Hounihan (1996) and Chambers & McComb (1997). Sullivan, Sullivan & Lindgren (2000) reported that a seed-tree silvicultural system, at 17–19 years after harvest, had a positive influence on diversity of stand structure attributes and small mammal communities.

No studies have been published that examine the effects of a gradient of green-tree retention (i.e. variable numbers or basal areas of residual trees) on stand structure attributes and small mammal communities during the early years immediately after harvest. As a component of a forest ecosystems study with large-scale (operational) treatments across a range of variable retention harvests, we report on responses of stand structure attributes to experimentally manipulated levels of basal area and density of residual trees over 4 years following harvesting. Investigation of the responses of small mammal communities to these treatments is reported in Sullivan & Sullivan (2001).

This study was designed to test the hypothesis that the abundance (e.g. basal area and density of residual trees and amount of vegetation) and diversity (e.g. species diversity and structural diversity of herb, shrub and tree layers) of various aspects of stand structure will decline with lower levels of tree retention. In particular, abundance and diversity should be greater in sites with green-tree retention than in clear-cut sites.

Materials and methods

STUDY AREA

The study was located in mixed Douglas fir *Pseudot-suga menziesii*–lodgepole pine *Pinus contorta* mature and old-growth forests in the Bald Range, 25 km west of Summerland in south-central British Columbia, Canada (49°40′ N; 119°53′ W). This area is within the upper Interior Douglas Fir (IDF$_{dk}$) and Montane Spruce (MS$_{dm}$) biogeoclimatic zones (Meidinger & Pojar 1991). Topography ranges from hilly to rolling hills at 1300–1520 m elevation. The upper IDF and the MS have a cool continental climate, with cold winters and moderately short, warm, summers. The average temperature is below 0 °C for 2–5 months and above 10 °C for 2–5 months, with mean annual precipitation ranging from 30 to 90 cm. Open to closed mature forests of Douglas fir cover much of the IDF zone, with even-aged post-fire lodgepole pine stands at higher elevations. The MS landscape has extensive, young and maturing seral stages of lodgepole pine, which have regenerated after wildfire. Hybrid interior spruce *Picea glauca* × *P. engelmannii* and subalpine fir *Abies lasiocarpa* are the dominant shade-tolerant climax trees. Douglas fir is an important seral species in zonal ecosystems and is a climax species on warm south-facing slopes in the driest ecosystems. Trembling aspen *Populus tremuloides* is a common seral species and black cottonwood *Populus trichocarpa* occurs on some moist sites (Meidinger & Pojar 1991).

Candidate sites were chosen to represent five treatments of variable retention harvests: clear-cut, single seed-tree, group seed-tree, patch-cut and uncut forest (Figs 1–3). Prior to harvesting, all stands were composed of a mixture of lodgepole pine with variable amounts of Douglas fir, spruce and subalpine fir. Average ages of lodgepole pine ranged from 82 to 120 years, and for Douglas fir ranged from 120 to 228 years. Average tree heights ranged from 10·5 to 19·5 m for lodgepole pine and from 16·7 to 27·5 m for Douglas fir. In all cases, Douglas fir was left as residual trees on harvested sites, with most lodgepole pine and spruce removed as crop trees. The area of the sites ranged from 4·6 to 12·8 ha for clear-cuts, 3·6 to 6·8 ha for single seed-trees, 3·6 to 10·9 ha for group seed-trees, 0·5 to 0·7-ha openings for patch-cut, and 10 to 100+ ha for mature and old-growth stands, which represented uncut forest.

The clear-cut and seed-tree sites were harvested in February–March and July 1996. These sites were mechanically raked in August 1996 to distribute and pile coarse woody debris in preparation for planting of lodgepole pine, Douglas fir and interior spruce seedlings in the spring of 1997. This scarification treatment provided sufficient planting spots and mineral soil exposure for planting of tree seedlings. The patch-cut sites were chosen from the 31 openings (mean area of patch-cuts was 0·7 ha with a total of 21·5 ha) over a 65-ha cutting area, which was harvested in June–July 1996. Because approximately one-third of the area was partially cut, three replicate sites were chosen that had 30–40% logged area (with retention of some understorey conifers and Douglas fir trees) and 60–70% uncut forest. These patch-cut sites had no site preparation and were planted with seedlings in autumn 1997. Three sites of uncut forest were selected for comparison with harvested sites.

EXPERIMENTAL DESIGN

The study had a completely randomized design with three replicate sites of each treatment. The 15 sites (5 treatments × 3 replicates) were selected on the basis of operational scale, reasonable proximity to one another, and availability of variable retention harvest sites that were the size of typical forestry operations. All sites were far enough apart (0·12–0·84 km) to be statistically independent, except for two adjacent sites (a single seed-tree and a group seed-tree) on the same harvested unit. This latter arrangement may have constituted sacrificial pseudoreplication (Hurlbert 1984) but was necessary to complete the range of treatments and replicates in a balanced design.

STAND STRUCTURE

Stand structure attributes were measured in three 20 × 20-m plots randomly located within each of the patch-cut and uncut forest sites. For each of the patch-cut sites, one plot was located in the patch-cut opening and two plots were located in the adjacent uncut forest to sample accurately the one-third cut and two-thirds uncut pattern of this harvesting treatment. Each plot was divided into four 10 × 10-m subplots for ease of sampling. Species and diameter at breast height (d.b.h.; 1·3 m above soil surface) were recorded for each tree within a subplot. Representative heights and ages were measured for two to three trees in each plot. A complete count and measurement of d.b.h. of all residual trees was done on each of the clear-cut, single seed-tree and group seed-tree sites.

Fallen wood was recorded along two transect lines of 20 m each on the perimeter of the 20 × 20-m plot. As each piece of fallen wood was encountered the following attributes were recorded: (a) species; (b) diameter where line crossed wood (cm); (c) hardness (five decay classes: 1, intact; 2, intact to partially soft; 3, hard large pieces; 4, small soft blocky pieces; 5, soft and powdery or hollow; Hunter 1990). Volume of fallen wood (m^3 ha^{-1}) was calculated by the method of Van Wagner (1968).

UNDERSTOREY VEGETATION

Understorey vegetation was sampled on three 25-m transects, each consisting of five 5 × 5-m plots, in each of the 15 sites. Each plot contained three sizes of nested subplots: a 5 × 5-m subplot for sampling trees, a 3 × 3-m subplot for sampling shrubs, and a 1 × 1-m subplot for sampling herbaceous species, mosses and lichens. A
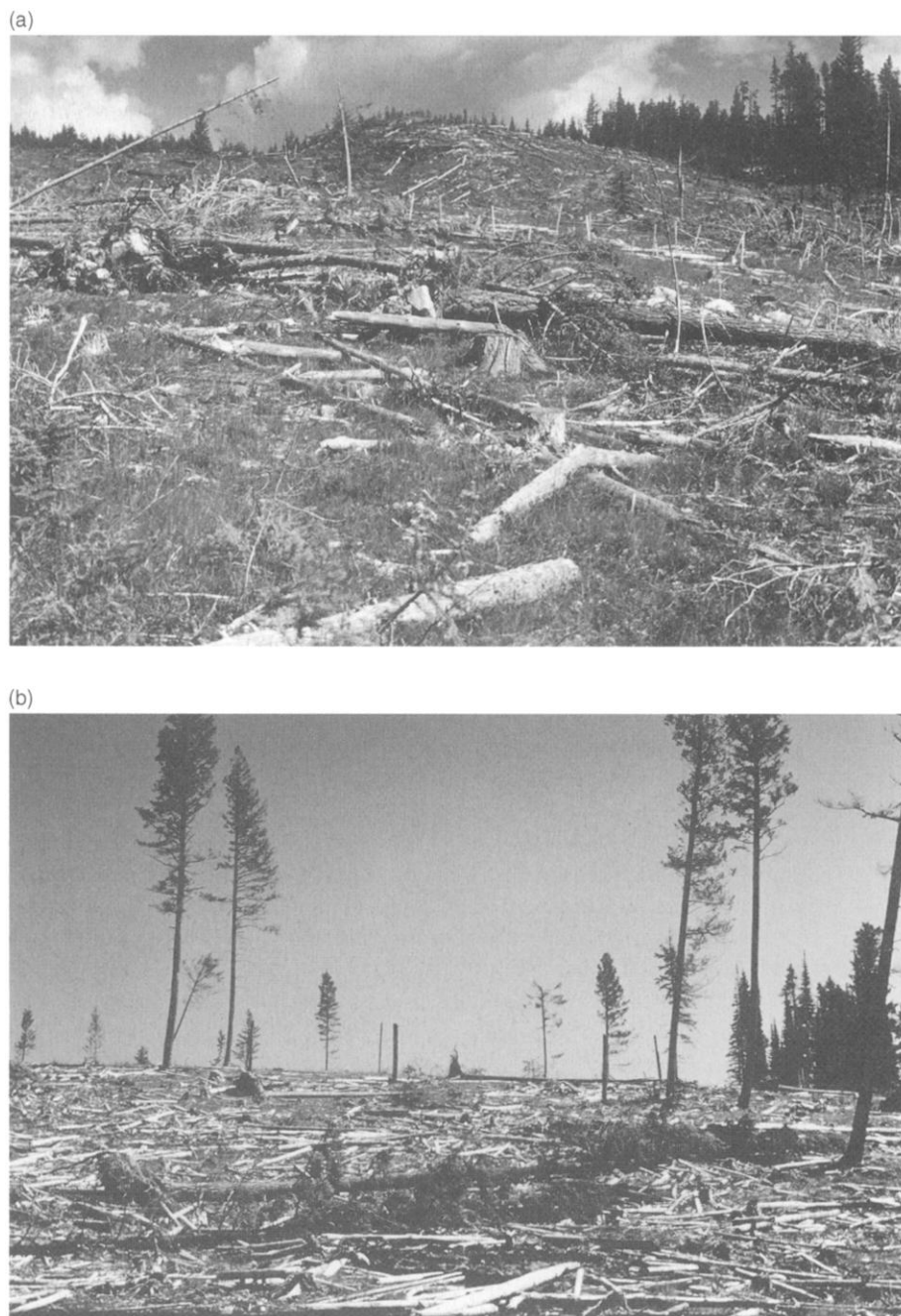
Fig. 1. Photographs of (a) a clear-cut site and (b) a single seed-tree site.

shrub was any woody species that was not a tree, in any height class. These layers were subdivided into height classes: $0-0.25$, $0.25-0.50$, $0.50-1.0$, $1.0-2.0$, $2.0-3.0$ and $3.0-5.0$ m. A visual estimate of percentage ground cover was made for each species/height class combination within the appropriate nested subplot. Total percentage cover for each subplot was also estimated. These measurements were used to calculate crown volume index (m^3 0.01 ha^{-1}) for each species (Stickney 1980). The product of percentage cover and representative height gave the volume of a cylindroid that represented the space occupied by the plant in the community. Crown volume index values were averaged by species for each plot size, and converted to 0.01-ha

base to produce the values given for species and layers. Sampling was conducted in July–August 1996, 1997, 1998 and 1999. Grasses, mosses and lichens were not identified to species. Plant species were identified in accordance with Hitchcock & Cronquist (1973) and Parish, Coupe & Lloyd (1996). Authorities for scientific names of vascular plants follow Hitchcock & Cronquist (1973). Species richness, species diversity and structural diversity were calculated for these data.

DIVERSITY MEASURES

Diversity of stand structure attributes was measured by species richness, species diversity and structural
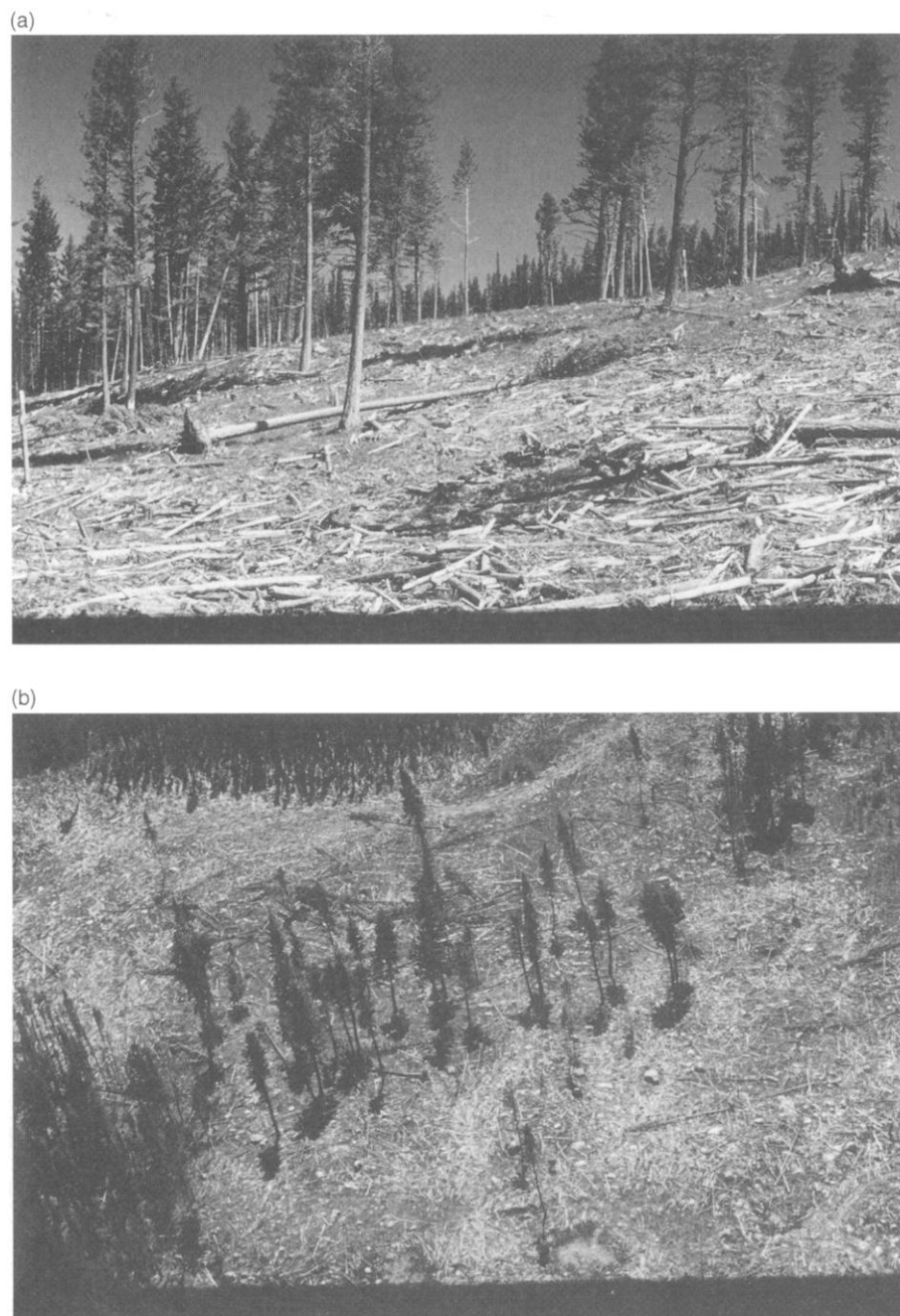
**Fig. 2.** Photographs of (a) a group seed-tree site and (b) an aerial view of a group seed-tree site.

diversity. Species richness was the total number of species sampled for the plant (herbs, shrubs and trees) community in each site (Krebs 1989). Species diversity was based on the Shannon–Wiener index (Pielou 1966), which is well represented in the ecological literature (Magurran 1988; Burton *et al.* 1992). Species diversity was calculated using the crown volume index for each plant species averaged across the three transects in a given site. Species diversity was calculated separately for herbs, shrubs and coniferous trees.

Structural diversity, or foliage height diversity (MacArthur & MacArthur 1961), was based on the same indices as for species richness and diversity, with the height classes of each of the herb, shrub and tree layers acting as 'species'. Thus, structural richness was the total number of height classes occupied by the various vegetative layers. Structural diversity used the Shannon–Wiener index with plant species represented by height classes and the amount (crown volume index) of vegetation in each class.

STATISTICAL ANALYSES

A one-way analysis of variance (ANOVA) (Zar 1984) was used to determine the effect of harvest treatments on mean basal area (BA), density and diameter classes of coniferous trees and mean volume, diameter and decay classes of fallen wood. A repeated-measures (RM) ANOVA (SPSS Institute Inc. 1997) was conducted to
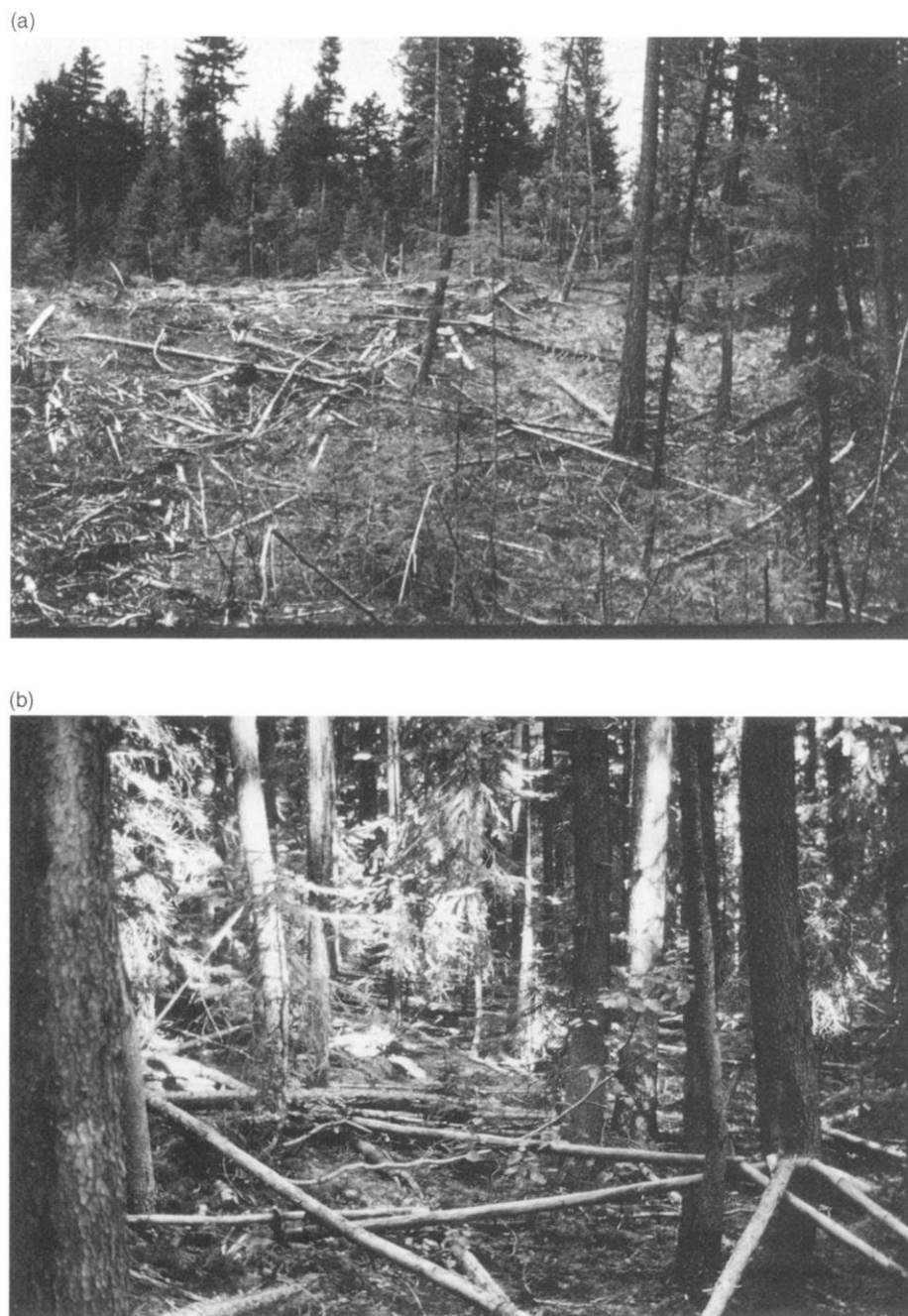
Fig. 3. Photographs of (a) a patch-cut site and (b) an uncut forest site.

determine the effects of treatment and time (1–4 years post-harvest) on mean crown volume index of mosses, lichens, herbs, shrubs and trees. Mean species richness and diversity and mean structural diversity of the herb, shrub and tree layers was also compared using this RM ANOVA model. Before performing any analyses, data not conforming to properties of normality and equal variance were subjected to various transformations to best approximate the assumptions required by any ANOVA (Zar 1984). Mauchly's *W*-test statistic was used to test for sphericity (independence of data among repeated measures) (Littel 1989; Kuehl 1994). For data found to be correlated among years, the Huynh–Feldt correction (Huynh & Feldt 1976) was used to adjust the

degrees of freedom of the within-subjects *F*-ratio. Duncan's multiple range test (DMRT) was used to compare mean values based on ANOVA results (Saville 1990). In all analyses, the level of significance was at least $P = 0.05$.

Results

STAND STRUCTURE

The variable retention harvests had a significant ($F_{4,10} = 41.08$; $P < 0.01$) effect on BA of residual coniferous trees (Table 1). The clear-cut, single seed-tree and group seed-tree sites had similar mean BA (m^2 ha^{-1}) ranging from 0.1 to 2.5, with significantly (DMRT;

Table 1. Summary of mean ($n = 3$ replicate sites) ± SE basal area, density, percentage cover and diameter (d.b.h.) of coniferous trees (primarily Douglas fir) and volume, diameter classes and decay classes of fallen wood and results of analyses. Mean values followed by different letters are significantly different according to DMRT

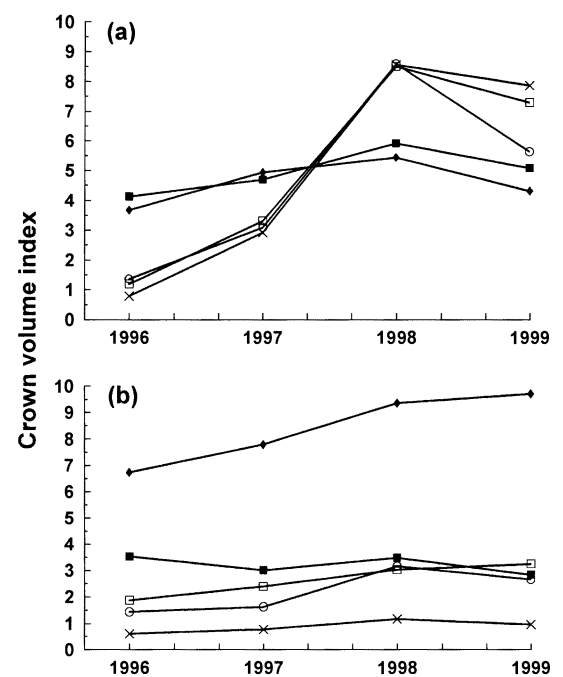| Parameter	Clear-cut	Single seed-tree	Group seed-tree	Patch-cut	Uncut forest	$F_{4,10}$	P
Basal area (m^2 ha^{-1})	$0.1^a \pm 0.1$	$0.7^a \pm 0.1$	$2.5^a \pm 1.0$	$23.4^b \pm 1.9$	$39.0^c \pm 5.7$	41.08	< 0.01
Density (stems ha^{-1})	$0.7^a \pm 0.7$	$9.0^a \pm 3.4$	$16.3^a \pm 4.2$	$769.4^b \pm 179.8$	$2050.0^b \pm 429.8$	18.33	< 0.01
Cover (%)	$0.7^a \pm 0.7$	$4.1^b \pm 1.4$	$8.4^b \pm 3.7$	$34.1^c \pm 3.1$	$32.9^c \pm 5.2$	28.44	< 0.01
d.b.h. (cm)							
< 30	–	$21.3^a \pm 1.8$	$19.4^a \pm 0.7$	$11.5^b \pm 1.8$	$12.0^b \pm 0.6$	10.15^1	< 0.01
30–60	–	39.7 ± 1.8	43.3 ± 1.5	38.0 ± 1.3	35.9 ± 1.5	2.95^1	0.09
> 60	–	72.8 ± 0.4	69.2 ± 1.5	67.9 ± 3.6	–	1.33^2	0.39
Volume of fallen wood (m^3 ha^{-1})	136.1 ± 29.0	116.7 ± 27.0	179.7 ± 25.6	210.2 ± 9.7	140.9 ± 40.9	1.78	0.21
No. of wood pieces Diameter classes (cm)							
< 5	$122.2^a \pm 22.6$	$130.6^{ab} \pm 7.4$	$126.0^{ab} \pm 14.9$	$183.1^b \pm 19.4$	$38.2^c \pm 20.7$	8.50	< 0.01
5–25	$30.4^a \pm 4.9$	$23.6^a \pm 2.8$	$27.3^a \pm 0.8$	$44.8^b \pm 3.6$	$11.8^c \pm 4.5$	10.83	< 0.01
> 25	0.9 ± 0.1	0.9 ± 0.5	1.5 ± 0.2	0.8 ± 0.5	1.2 ± 0.4	0.56	0.70
Decay classes							
1	0.2 ± 0.2	1.1 ± 0.3	2.1 ± 1.1	2.2 ± 0.2	0.2 ± 0.2	3.14	0.06
2	0.4 ± 0.3	3.1 ± 2.3	0.9 ± 0.3	3.3 ± 0.2	4.2 ± 0.8	2.27	0.13
3	$143.7^a \pm 20.5$	$143.8^a \pm 7.9$	$141.7^a \pm 17.5$	$217.2^b \pm 23.0$	$40.8^c \pm 21.6$	11.09	< 0.01
4	7.6 ± 3.4	5.1 ± 2.2	6.3 ± 2.4	4.4 ± 2.1	3.2 ± 1.6	0.48	0.75
5	1.7 ± 0.8	1.9 ± 1.1	3.8 ± 2.0	1.5 ± 0.4	3.0 ± 1.7	0.57	0.69

$^1 F_{4,8}$ $^2 F_{4,4}$

$P = 0.05$) higher levels on patch-cut (23·4) and uncut forest (39·0) sites. This pattern was also recorded for the effect of these harvests on density of trees ($F_{4,10} = 18.33$; $P < 0.01$). Numbers ranged from 0·7 to 16·3 stems ha^{-1} on the clear-cut to group seed-tree sites and up to 769·4 and 2050·0 stems ha^{-1} in the patch-cut and uncut forest sites, respectively (Table 1). Mean cover of coniferous trees was significantly ($F_{4,10} = 28.44$; $P < 0.01$) different among sites with higher (DMRT; $P = 0.05$) cover on the patch-cut and uncut forest sites than on the two seed-tree sites, followed by the clear-cut site. Mean diameters of trees in the 30–60 cm and > 60 cm classes were similar across the sites, but were significantly ($F_{4,8} = 10.15$; $P < 0.01$) different among sites in the < 30 cm class (Table 1).

Mean volume (m^3 ha^{-1}) of fallen wood was similar among sites, ranging from 116·7 in the single seed-tree to 210·2 in the patch-cut sites (Table 1). The clear-cut, seed-tree and patch-cut sites had a greater number ($F_{4,10} = 8.50$; $P < 0.01$) of wood pieces in the < 5 cm class than the uncut forest. The patch-cut sites had more (DMRT; $P = 0.05$) medium (5–25 cm) diameter pieces than any of the other sites (Table 1). Similarly, the clear-cut and seed-tree sites had more (DMRT; $P = 0.05$) medium diameter pieces of fallen wood than the uncut forest. This same pattern was evident for the most common decay class 3 (Table 1), possibly owing to an accumulation of woody debris from the various harvesting operations.

UNDERSTOREY VEGETATION

Mean total crown volume index of herbs was similar ($F_{4,10} = 0.02$; $P = 1.00$) across sites, but increased

Fig. 4. Mean ($n = 3$ replicate sites) crown volume index (m^3 0.01 ha^{-1}) for (a) herbs and (b) shrubs for the five treatments 1996–99. Clear-cut (open squares); single seed-tree (open circles); group seed-tree (crosses); patch-cut (diamonds); uncut forest (filled squares).

significantly ($F_{3,30} = 7.69$; $P < 0.01$) through time, particularly on the clear-cut and seed-tree sites (Fig. 4). Prominent herb species on these sites included wild strawberry *Fragaria virginiana*, fireweed *Epilobium angustifolium*, grasses, white-flowered hawkweed

Hieracium albiflorum, heart-leaved arnica *Arnica cordifolia*, Arctic lupine *Lupinus arcticus*, racemose pussytoes *Antennaria racemosa* and one-sided wintergreen *Pyrola secunda*.

Mean total crown volume indexes of mosses ($F_{4,10} = 2\cdot89$; $P = 0\cdot08$) and lichens ($F_{4,10} = 1\cdot44$; $P = 0\cdot29$) were similar among sites. Volume of mosses was highly variable within the three replicate sites of uncut forest. Although not statistically significant, mean value of mosses in the uncut forest was 2·4–5·9 times higher than the average of the other four treatments.

Mean total crown volume index of shrubs was similar ($F_{4,10} = 1\cdot93$; $P = 0\cdot18$) among sites (Fig. 4), but did change over time ($F_{4,30} = 2\cdot89$; $P = 0\cdot05$) from 1996 to 1999. Prominent shrubs included kinnikinnick *Arctostaphylos uva-ursi*, twinflower *Linnaea borealis*, Utah honeysuckle *Lonicera utahensis*, falsebox *Pachistima myrsinites*, birch-leaved spirea *Spiraea betulifolia* and grouseberry *Vaccinium scoparium*.

Mean total crown volume index of trees was significantly ($F_{4,10} = 24\cdot07$; $P < 0\cdot01$) different among sites, with the patch-cut and uncut forest sites higher (DMRT; $P = 0\cdot05$) in crown volume than the other sites. Prominent tree species on these sites were Douglas fir, lodgepole pine, subalpine fir and interior spruce.

SPECIES AND STRUCTURAL DIVERSITY

A total of 45 species of herbs, 26 species of shrubs and six species of trees was sampled in this study. Mean species richness of herbs ($F_{4,10} = 0\cdot25$; $P = 0\cdot90$) and shrubs ($F_{4,10} = 1\cdot08$; $P = 0\cdot42$) was similar among sites. However, mean richness of trees was significantly ($F_{4,10} = 6\cdot91$; $P < 0\cdot01$) different among sites. Mean number of tree species was highest in the uncut forest sites, followed by both seed-tree sites and the clear-cut sites, and lowest in the patch-cut sites (DMRT; $P = 0\cdot05$). Total species richness of plants was similar among sites, but increased ($F_{3,30} = 5\cdot64$; $P < 0\cdot01$) with time.

Mean species diversity of herbs was similar among sites, but shrubs were significantly ($F_{4,10} = 7\cdot70$; $P < 0\cdot01$) different (Fig. 5). Shrub species diversity was generally highest in the seed-tree and clear-cut sites, followed by the uncut forest, and patch-cut sites (DMRT; $P = 0\cdot05$). There were no differences over time for either herb or shrub species diversity. Mean species diversity of trees was significantly ($F_{4,10} = 7\cdot38$; $P < 0\cdot01$) different among sites (Fig. 5). Diversity of trees was similar in the uncut forest, clear-cut and seed-tree sites, which were all higher than the patch-cut sites (DMRT; $P = 0\cdot05$). Tree diversity increased significantly ($F_{3,30} = 16\cdot90$; $P < 0\cdot01$) with time, particularly from 1996 to 1997–99, because of the planting in 1997 of Douglas fir, lodgepole pine and spruce seedlings on the clear-cut and seed-tree sites.

Mean structural richness of height classes (or layers) of vegetation) of herbs was significantly ($F_{4,10} = 3\cdot60$; $P = 0\cdot05$) different among sites, with a lower richness
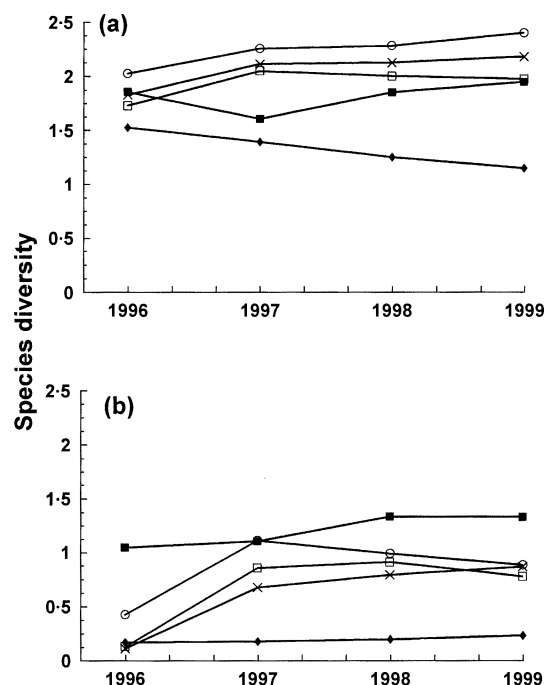
Fig. 5. Mean ($n = 3$ replicate sites) species diversity for (a) shrubs and (b) trees for the five treatments 1996–99. Symbols as for Fig. 4.
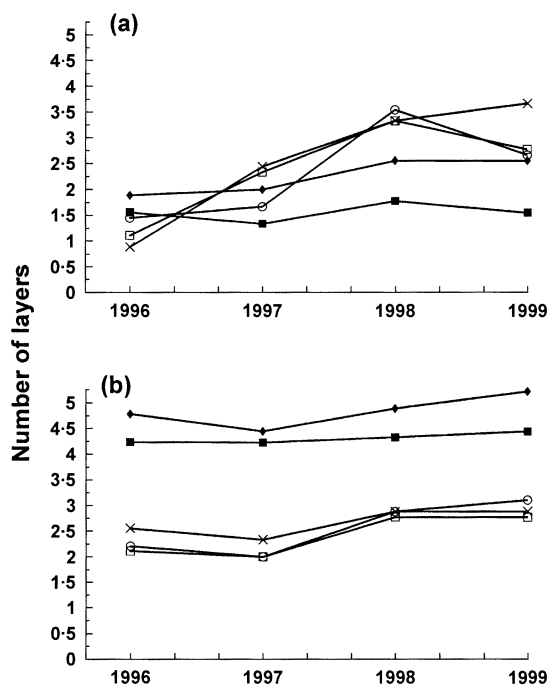

Fig. 6. Mean ($n = 3$ replicate sites) structural richness for (a) herbs and (b) trees for the five treatments 1996–99. Symbols as for Fig. 4.

(DMRT; $P = 0\cdot05$) of herb layers in the uncut forest than at the other sites in 1998 and 1999 (Fig. 6). Structural richness of shrubs was similar ($F_{4,10} = 1\cdot74$; $P = 0\cdot22$) among sites (Table 2). Mean structural diversity of the herb ($F_{4,10} = 6\cdot87$; $P < 0\cdot01$) and shrub layers ($F_{4,10} = 2\cdot31$; $P = 0\cdot13$) also followed this pattern (Table 2 and Fig. 7). Herb structural richness and

Table 2. Mean (n = 3 replicate sites) structural richness and diversity for shrubs and total plants for the five treatments during the study 1996–99. Mean values followed by different letters are significantly different according to DMRT

Parameter and layer		Clear-cut	Single seed-tree	Group seed-tree	Patch-cut	Uncut forest
Structural richness						
Shrubs	1996	2·33	1·89	1·33	2·33	2·22
	1997	2·33	1·67	1·55	2·33	1·67
	1998	2·22	2·22	1·67	2·67	2·33
	1999	2·66	2·33	1·55	2·00	1·78
Total	1996	2·78[b]	2·78[b]	2·77[b]	5·44[a]	4·78[a]
	1997	3·22[c]	2·55[c]	3·55[bc]	5·55[a]	4·67[ab]
	1998	3·67[b]	4·00[b]	4·00[b]	5·22[a]	5·22[a]
	1999	3·44[c]	3·67[bc]	4·00[c]	5·55[a]	5·00[b]
Structural diversity						
Shrubs	1996	0·71	0·57	0·18	0·65	0·67
	1997	0·69	0·40	0·29	0·48	0·31
	1998	0·68	0·73	0·36	0·59	0·66
	1999	0·88	0·80	0·43	0·38	0·48
Total	1996	0·87	0·71	0·43	0·77	0·49
	1997	0·98	0·65	0·72	0·91	0·53
	1998	1·36	1·55	1·18	0·89	0·64
	1999	1·22	1·27	1·26	0·80	0·50

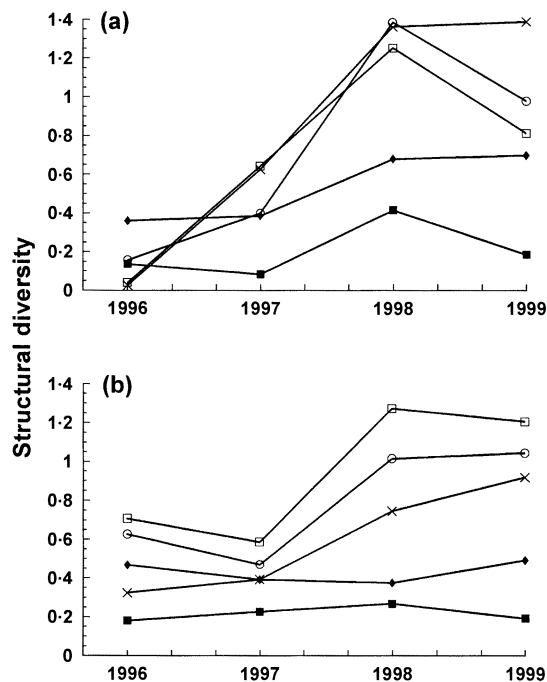**Fig. 7.** Mean (n = 3 replicate sites) structural diversity for (a) herbs and (b) trees for the five treatments 1996–99. Symbols as for Fig. 4.

diversity increased ($P < 0·01$) dramatically with time (Figs 6 and 7).

Mean structural richness was significantly different among sites for trees ($F_{4,10} = 7·58$; $P < 0·01$) and for total plants ($F_{4,10} = 7·49$; $P < 0·01$), with the richness in vegetation layers of patch-cut and uncut forest sites higher than in the other three sites (Fig. 6 and Table 2). Conversely, mean structural diversity of the tree layer ($F_{4,10} = 3·40$; $P = 0·05$) was significantly different among sites, with the patch-cut and uncut forest having a lower structural diversity of trees than the other sites

(Fig. 7). Total structural diversity was similar ($F_{4,10} = 3·26$; $P = 0·06$) among sites, and both of these diversity components increased ($P < 0·01$) with time (Fig. 7 and Table 2).

Discussion

VARIABLE RETENTION HARVESTS

Variable retention harvest is a flexible silvicultural system that maintains some structural features of mature forest after harvesting. Our study covered the period from the time of harvest through to the first 4 post-harvest years of early successional change. Structural elements, outlined by Franklin *et al.* (1997) to define variable retention harvests, included large-diameter live Douglas fir trees, some with large limbs and clusters of limbs, some snags (5–10 ha⁻¹), fallen wood in various stages of decay, and understorey vegetation (Figs 1–3). The fifth criterion of Franklin *et al.* (1997), namely undisturbed layers of forest floor, were present in the patch-cut and uncut forest sites, but not in the other sites, which had been mechanically prepared for the planting of tree seedlings.

The single and group seed-tree sites originated from the harvest of lodgepole pine with retention of all Douglas fir on a given operating unit. This seed-tree silvicultural system (Smith 1986) is common across the southern interior of British Columbia in mixed forests of Douglas fir–lodgepole pine and western larch *Larix occidentalis*–lodgepole pine. Thus, single seed-tree sites differed from group seed-tree sites based on the number and distribution of Douglas fir in the original late-successional stands. These large live fir trees are important hosts and energy sources for many soil organisms, including fungal species that form mycorrhizae (Perry 1994). The canopies of these trees help to

ameliorate the microclimate for understorey species and also benefit many bird species (Hansen *et al.* 1995; Hansen & Hounihan 1996). They are also future sources of large-diameter snags and logs. The importance of snags and fallen wood to a wide variety of cavity-using and roosting wildlife species is well known for temperate forests (Harmon *et al.* 1986; Maser *et al.* 1988).

STAND STRUCTURE ATTRIBUTES

This is the first study to report on initial changes in stand structure after harvesting forest sites using variable retention methods. In terms of our hypothesis, that abundance and diversity of herb, shrub and tree layers would decline with decreasing levels of tree retention, abundance of herbs was similar among treatment sites and increased significantly with time, particularly on the clear-cut and seed-tree sites. The abundance of shrubs was similar across the treatments. Thus, the hypothesis was not supported in terms of abundance. Similarly, species richness, species diversity and structural diversity of herbs and shrubs did not support the hypothesis. This latter result was contrary to those of Halpern & Spies (1995) and Meehan, Merrell & Hanley (1984), who reported that understorey vascular plants may require long periods of time to develop diverse assemblages after clear-cutting. However, at least six species of herbs and four species of shrubs occurred in the uncut forest only. Thus, it was possible that these species were present in the harvested sites prior to cutting and were lost from these sites, at least temporarily.

Conversely, eight species of herbs and three species of shrubs occurred in at least one of the clear-cut and seed-tree sites only. Of these, *Melampyrum lineare* and an unknown species of *Vaccinium* were observed in 1996, immediately after harvest, but not in subsequent years. Similarly, of those species in the uncut forest only, *Galium triflorum*, *Streptopus amplexifolius*, *Veratrum viride*, *Betula glandulosa* and *Rubus parviflorus* were found in 1996 and not thereafter. Clearly, these sites need to be monitored for several years post-harvest to determine if any of these species of herbs and shrubs reappear, and to chart the potential invasion of new species.

Six species of herbs and one species of shrub occurred in the uncut forest and in one or more of the seed-tree or patch-cut sites, but not in the clear-cut sites. Three of these herbs, *Osmorhiza chilensis*, *Plantanthera orbiculata* and *Pyrola asarifolia*, are forest interior species that apparently found the understorey conditions tolerable in the sites with residual trees, at least up to 4 years post-harvest. Contrary to the prediction of Halpern *et al.* (1999) that abundance of forest interior species will increase with percentage of green trees retained, our results indicated that herbs such as *Clintonia uniflora*, *Cornus canadensis* and *Viola canadensis* occurred mainly in the clear-cut and seed-

tree stands. However, *Goodyera oblongifolia* and *Lilium columbianum* did increase in abundance with the percentage of green trees retained. Shrubs such as *Chimaphila umbellatum*, *Pachistima myrsinites*, *Vaccinium scoparium* and *Linnaea borealis* are considered forest interior species but they occurred across all treatment sites at variable levels of abundance.

The species richness and diversity of trees was highest in the uncut forest. Structural richness of the tree layer and for all layers was also highest in the patch-cut and uncut forest sites. Mean structural diversity of the tree layer and total layers did not fit this pattern because tree cover dominated the diversity measurement, thereby lowering evenness among the relative abundances of the various layers.

Forest development and tree growth on sites with variable levels of green-tree retention appear to be negatively affected in terms of BA growth of residual Douglas fir (North *et al.* 1996). Retrospective studies of two-tiered stands also indicate that above densities of approximately 15 trees ha⁻¹, residual stems can affect the composition of younger cohorts and reduce their BA growth (Rose & Muir 1997). These latter effects may also occur in harvest-age coniferous trees that occur in stands with residual tree densities of 5 trees ha⁻¹ (Zenner, Acker & Emmingham 1998) or BA of 5–10 m² ha⁻¹ (Acker, Zenner & Emmingham 1998). Our seed-tree stands were clearly within these ranges of residual tree effects. A retrospective study of young (17–19 years post-harvest) lodgepole pine stands with and without Douglas fir seed-trees indicated significantly greater numbers of fir seedlings in the regeneration cohort of stands with seed-trees than those without residual trees. Conversely, this regeneration cohort was probably limited by the residual Douglas fir as there were lower numbers of lodgepole pine seedlings and saplings in the subcanopy and main canopy of the seed-tree than young pine stands (Sullivan, Sullivan & Lindgren 2000). It is likely that our sites may develop similar stand characteristics by 20 years post-harvest.

Although our clear-cut, single seed-tree and group seed-tree sites had statistically similar levels of mean BA (range of 0·1–2·5 m² ha⁻¹) of residual trees, this range was widened to 0·1–13·2 m² ha⁻¹ if the BA for the group seed-tree sites was calculated over the aggregate of trees rather than the overall site. Similarly, the range of density of residual trees increased to 0·7–72·2 trees ha⁻¹. The single seed-tree sites represented a dispersed, and the group seed-tree sites an aggregated, pattern of retention (Franklin *et al.* 1997). Thus, our retention levels did provide a reasonable range of post-harvest conditions to evaluate changes in stand structure attributes. Our particular harvesting treatments also provided similar levels of fallen wood.

Our aggregate units were not intended to provide habitat for interior forest species that require large areas, because of the edge influences associated with small residual forest patches. However, some microclimatic benefits may be achieved even with relatively

small aggregates (< 1 ha in size) (Chen, Franklin & Spies 1992, 1993). The mean area of the three aggregate groups of trees on these sites was 0·70 ha, which was in the range of 0·05–1·0 ha, typical of aggregates in the Pacific north-west of North America (Franklin *et al.* 1997).

EXPERIMENTAL DESIGN

Our study began in the late summer of 1996 after completion of harvest and site preparation treatments. Although we did not have pretreatment measurements to separate the potential effects of retained trees from initial species composition and other site-level variation, we did have three true replicates of treatment sites (Hurlbert 1984). These sites were the size of typical forestry operations in southern British Columbia, and the Pacific north-west of North America, for interior mixed forests of lodgepole pine and Douglas fir. However, two sites on the same experimental unit may not be independent of the treatment being tested, and hence would constitute sacrificial pseudoreplication (Hurlbert 1984). Duplicate sites in one experimental unit, however deemed independent, may reduce among-replicate variability and increase the probability of detecting effects that are not real. We acknowledge this concern, but the situation was part of the logistical constraints associated with our field study.

The experimental design tested operational-scale treatments of varying levels and patterns of green-tree retention on forest ecosystem components (Walters & Holling 1990; Franklin *et al.* 1997; Aubry *et al.* 1999). Inferences from this study reflect responses in stand structure attributes in the first 4 post-harvest years only. Clearly, an understanding of relatively long-term (> 5 years) responses of these and other variables will require repeated measures over a longer time-frame.

CONCLUSIONS

This study began with the hypothesis that variable retention harvests in temperate zone coniferous forests can integrate ecological and economic objectives by (i) structurally enriching the subsequent forest stand, (ii) maintaining some species and ecological processes from the original forest, particularly in aggregated or group seed-tree patterns, and (iii) maintaining some connectivity in the managed forest landscape. If true, there should be a gradient in abundance and diversity of stand structure and plant communities from clear-cut to uncut forest through the intermediate stages of variable green-tree retention. In particular, abundance and diversity should be higher in sites with tree retention than in clear-cut sites. Our study showed that this was only partly true.

In terms of abundance, there was a gradient in BA and density of residual trees across treatment sites. However, the crown volume index of herbs, shrubs, mosses and lichens was similar among sites. Mean species richness of herbs, shrubs and total plants was

similar among sites. Tree species richness in seed-tree sites was similar to that in uncut forest in three of four post-harvest years. Mean species diversity of herbs was similar among sites, but that of shrubs and trees was generally lowest in patch-cut sites and similar among the other sites. Mean structural richness of trees and total plants in the patch-cut and uncut forest sites had more vegetation layers than the other sites. Thus, the structural attributes of residual trees and layers of vegetation, but not the abundance, species richness or species diversity of understorey vegetation, lend support to the basis of variable retention harvesting. Our study represents an initial 'snapshot' in time, and future monitoring of these sites over many years will determine if these trends continue.

References

Acker, S.A., Zenner, E.K. & Emmingham, W.H. (1998) Structure and yield of two-aged stands on the Willamette National Forest, Oregon: implications for green tree retention. *Canadian Journal of Forest Research*, **28**, 749–758.

Agee, J.K. (1993) *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, DC.

Aubry, K.B., Amaranthus, M.P., Halpern, C.B., White, J.D., Woodard, B.L., Peterson, C.E., Lagoudakis, C.A. & Horton, A.J. (1999) Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. *Northwest Science*, **73**, 12–26.

Burton, P.J., Balisky, A.C., Coward, L.P., Cumming, S.G. & Kneeshaw, D.D. (1992) The value of managing for biodiversity. *Forestry Chronicle*, **68**, 225–237.

Chambers, C.L. & McComb, W.C. (1997) Effects of silvicultural treatments on wintering bird communities in the Oregon Coast Range. *Northwest Science*, **71**, 298–304.

Chen, J., Franklin, J.F. & Spies, T.A. (1992) Vegetation responses to edge environments in old-growth Douglas fir forests. *Ecological Applications*, **2**, 387–396.

Chen, J., Franklin, J.F. & Spies, T.A. (1993) Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology*, **63**, 219–237.

Ciancio, O. & Nocentini, S. (1994) Gurnaud's control method and silviculture on natural basis: a forest management and silvicultural question. *L'Italia Forestale e Montana*, **49**, 336–356.

Franklin, J.F. (1989) Toward a new forestry. *American Forests*, **95**, 37–44.

Franklin, J.F. & DeBell, D.S. (1973) Effects of various harvesting methods on forest regeneration. *Even-Aged Management* (eds R.K. Hermann & D.P. Lavender), pp. 29–57. Proceedings of a Symposium held 1 August 1972, Corvallis, Oregon, USA. School of Forestry, Oregon State University, Corvallis, OR.

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

Franklin, J.F., Cromack, K. Jr, Denison, W., McKee, D., Maser, C., Sedell, J., Swanson, F. & Juday, G. (1981) *Ecological Characteristics of Old-Growth Douglas Fir Forests.* General Technical Report PNW-118. USDA Forest Service, Portland, Oregon.

Franklin, J.F., Frenzen, P.M. & Swanson, F.J. (1995) Re-creation of ecosystems at Mount St Helens: contrasts in artificial and natural approaches. *Rehabilitating Damaged Ecosystems* (ed. J. Cairns Jr), pp. 287–333, 2nd edn. Lewis Publishers, Boca Raton, FL.

Halpern, C.B. & Spies, T.A. (1995) Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications*, **5**, 914–934.

Halpern, C.B., Evans, S.A., Nelson, C.R., McKenzie, D., Liguori, D.A., Hibbs, D.E. & Halaj, M.G. (1999) Response of forest vegetation to varying levels and patterns of green-tree retention: an overview of a long-term experiment. *Northwest Science*, **73**, 27–44.

Hansen, A.J. & Hounihan, P. (1996) Canopy tree retention and avian diversity in the Oregon Cascades. *Biodiversity in Managed Landscapes Theory and Practice* (eds R.C. Szaro & D.W. Johnston), pp. 402–421. Oxford University Press, New York, NY.

Hansen, A.J., McComb, W.C., Bega, R., Raphael, M.G. & Hunter, M. (1995) Bird habitat relationships in natural and managed forests in the West Cascades of Oregon. *Ecological Applications*, **5**, 555–569.

Hansen, A.J., Spies, T.A., Swanson, F.J. & Ohmann, J.L. (1991) Conserving biodiversity in managed forests. *Bioscience*, **41**, 382–392.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr & Cummins, K.W. (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, **15**, 133–302.

Hitchcock, C.L. & Cronquist, A. (1973) *Flora of the Pacific Northwest.* University of Washington Press, Seattle, WA.

Hunter, M.J. Jr (1990) *Wildlife, Forests and Forestry.* Prentice Hall, Englewood Cliffs, NJ.

Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.

Huynh, H. & Feldt, L.S. (1976) Estimation of the Box correction for degrees of freedom from sample data in the randomized block and split-plot designs. *Journal of Educational Statistics*, **1**, 69–82.

Krebs, C.J. (1989) *Ecological Methodology.* Harper & Row, New York, NY.

Kuehl, R.O. (1994) *Statistical Principles of Research Design and Analysis.* Duxbury Press, Belmont, CA.

Larsen, J.B. (1995) Ecological stability of forests and sustainable silviculture. *Forest Ecology and Management*, **73**, 85–96.

Littel, R.C. (1989) Statistical analysis of experiments with repeated measures. *Hortscience*, **24**, 36–40.

MacArthur, R.H. & MacArthur, J.W. (1961) On bird species diversity. *Ecology*, **42**, 594–598.

Magurran, A.E. (1988) *Ecological Diversity and its Measurement.* Princeton University Press, Princeton, NJ.

Maser, C., Tarrant, R.F., Trappe, J.M. & Franklin, J.F. (1988) *From the Forest to the Sea: A Story of Fallen Trees.* General Technical Report PNW-GTR-229. USDA Forest Service, Washington, DC.

Meehan, W.R., Merrell, T.R. Jr & Hanley, T.A. (1984) *Fish and Wildlife Relationships in Old-Growth Forests.* American Institute of Fishery Research Biologists, Morehead City, NC.

Meidinger, D. & Pojar, J. (1991) *Ecosystems of British Columbia.* Special Report Series No. 6. Research Branch, Ministry of Forests, Victoria, Canada.

North, M., Chen, J., Smith, G., Krakowiak, L. & Franklin, J. (1996) Initial response of understorey plant diversity and overstorey tree diameter growth to a green tree retention harvest. *Northwest Science*, **70**, 24–35.

Parish, R., Coupé, R. & Lloyd, D. (1996) *Plants of Southern Interior British Columbia.* Lone Pine Publishing, Vancouver, Canada.

Peck, J.E. & McCune, B. (1997) Remnant trees and canopy lichen communities in western Oregon: a retrospective approach. *Ecological Applications*, **7**, 1181–1187.

Perry, D.A. (1994) *Forest Ecosystems.* Johns Hopkins University Press, Baltimore, MD.

Perry, D.A. & Amaranthus, M.P. (1997) Disturbance, recovery, and stability. *Creating a Forestry for the 21st Century: The Science of Ecosystem Management* (eds K.A. Kohm & J.F. Franklin), pp. 31–56. Island Press, Washington, DC.

Pielou, E.C. (1966) The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology*, **13**, 131–144.

Rose, C.R. & Muir, P.S. (1997) Green-tree retention: consequences for timber production in forests of the western Cascades, Oregon. *Ecological Applications*, **7**, 209–217.

Saville, D.J. (1990) Multiple comparison procedures: the practical solution. *American Statistician*, **44**, 174–180.

Sillett, S.C. & Goslin, M.N. (1999) Distribution of epiphytic macrolichens in relation to remnant trees in a multiple-age Douglas fir forest. *Canadian Journal of Forest Research*, **29**, 1204–1215.

Smith, D.M. (1986) *The Practice of Silviculture.* John Wiley & Sons, New York, NY.

Spies, T.A. & Franklin, J.F. (1991) The structure of natural young, mature, and old-growth Douglas fir forests in Oregon and Washington. *Wildlife and Vegetation of Unmanaged Douglas fir Forests* (technical co-ordinators L.F. Ruggiero, K.B. Aubry, A.B. Carey & M.H. Huff), pp. 91–109. General Technical Report PNW-GTR-285. USDA Forest Service, Portland, Oregon.

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

SPSS Institute Inc. (1997) *Statistical Programs for the Social Sciences.* SPSS Institute Inc., Chicago, IL.

Stickney, P.F. (1980) *Data Base for Post-Fire Succession, First 6–9 Years, in Montana Larch–Fir Forests.* US Forest Service General Technical Report INT-62. Intermountain Research Station, Ogden, UT.

Sullivan, T.P. & Sullivan, D.S. (2001) Influence of variable retention harvests on forest ecosystems. II. Diversity and population dynamics of small mammals. *Journal of Applied Ecology*, **38**, 1234–1252.

Sullivan, T.P., Sullivan, D.S. & Lindgren, P.M.F. (2000) Small mammals and stand structure in young pine, seed-tree, and old-growth forest southwest Canada. *Ecological Applications*, **10**, 1367–1383.

Tappeiner, J.C., Lavender, D., Walstad, J., Curtis, R.O. & DeBell, D.S. (1997) Silvicultural systems and regeneration methods: current practices and new alternatives. *Creating a Forestry for the 21st Century: The Science of Ecosystem Management* (eds K.A. Kohm & J.F. Franklin), pp. 151–164. Island Press, Washington, DC.

Van Wagner, C.E. (1968) The line intersect method in forest fuel sampling. *Forest Science*, **14**, 20–26.

Walters, C.J. & Holling, C.S. (1990) Large-scale management

experiments and learning by doing. *Ecology*, **71**, 2060–2068.

Watanabe, S. & Sasaki, S. (1994) The silvicultural management system in temperate and boreal forests: a case history of the Hokkaido Tokyo University Forest. *Canadian Journal of Forest Research*, **24**, 1176–1185.

Zar, J.H. (1984) *Biostatistical Analysis*. Prentice Hall Inc., Englewood Cliffs, NJ.

Zenner, E.K. (2000) Do residual trees increase structural complexity in Pacific Northwest coniferous forests? *Ecological Applications*, **10**, 800–810.

Zenner, E.K., Acker, S.A. & Emmingham, W.H. (1998) Growth reduction in harvest-age, coniferous forests with residual trees in the western central Cascade Range of Oregon. *Forest Ecology and Management*, **102**, 75–88.