Small Mammals and Stand Structure in Young Pine, Seed-Tree, and Old-Growth Forest, Southwest Canada

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SMALL MAMMALS AND STAND STRUCTURE IN YOUNG PINE, SEED-TREE, AND OLD-GROWTH FOREST, SOUTHWEST CANADA

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Abstract. Alternative silvicultural systems to clearcutting are receiving considerable attention in Pacific Northwest forests of North America. Understanding the implications of these harvesting systems on stand structure and biodiversity through time is a fundamental aspect of forest ecosystem management. This study was designed to test the hypothesis that diversity of stand-structure attributes and forest floor small-mammal communities will increase from young pine to seed tree to old-growth forest. The study area was within mixed Douglas-fir (*Pseudotsuga menziesii*)–lodgepole pine (*Pinus contorta*) forests within the Montane Spruce biogeoclimatic zone near Summerland in south-central British Columbia, Canada. This retrospective study had three replicate stands each of 17-yr-old "young pine" (clear-cut harvested), "seed tree" composed of young pine with Douglas-fir seed trees, and uncut "old-growth" composed primarily of Douglas-fir and lodgepole pine. Stand-structure attributes (coniferous tree layers and understory vegetation) were measured in each stand. Small-mammal populations were sampled intensively from 1995 to 1997 in all stands.

The mean total percentage cover and crown-volume index of herbs and mosses were similar among treatment stands, but for shrubs–deciduous trees were highest in young pine and lowest in old growth. Mean species richness of herbs and coniferous trees was similar among treatment stands, but for shrubs–deciduous trees was highest in the young pine. Mean species diversity of herbs and shrubs–deciduous trees was similar among treatment stands, but for coniferous trees was higher in the seed-tree and old-growth stands than in the young pine stands. Mean richness of layers of herbs and shrubs–deciduous trees appeared consistently highest in the young pine, but for coniferous trees was highest in the seed-tree stands. Mean abundance of red-backed voles (*Clethrionomys gapperi*) was consistently higher in the old-growth than in young pine or seed-tree stands. Mean numbers of Northwestern chipmunks (*Tamias amoenus*), heather voles (*Phenacomys intermedius*), western jumping mice (*Zapus princeps*), montane shrews (*Sorex monticolus*), and common shrews (*S. cinereus*) were higher in the seed-tree or young pine stands than in old growth. Mean abundance of meadow voles (*Microtus pennsylvanicus*) was highest in seed-tree stands. Deer mice (*Peromyscus maniculatus*), long-tailed voles (*M. longicaudus*), and short-tailed weasels (*Mustela erminea*) had similar mean numbers among treatment stands. Mean species richness and diversity of small mammals was higher in the seed-tree and young pine stands than in old growth. Each of these stand types offers its own structural diversity to the forest landscape and should help manage for a range of biodiversity goals.

Key words: biodiversity; British Columbia, Canada; forest management; green-tree retention; old-growth forest; Pinus contorta; Pseudotsuga menziesii; *seed trees; silvicultural systems; small mammals; species richness and diversity; stand structure.*

INTRODUCTION

Throughout the Pacific Northwest of Canada and the United States, an ecosystem approach to forest management is being adopted (Franklin et al. 1989, Swanson and Franklin 1992). A common definition of "ecosystem management" involves the recognition that provision of diverse benefits from forests may be achieved by allowing natural processes to occur or by emulating natural processes through management (Slocombe 1993, Grumbine 1994, Rose and Muir 1997). Forest

management regimes that emulate natural disturbances (e.g., wildfires and windthrow events) leave standing green and dead trees, as well as variable levels and structural complexity of woody debris.

The silvicultural practice of clear-cutting has often been justified on the basis that it emulates stand-replacing fires (Franklin and DeBell 1973). However, Agee (1993) reported that prior to fire suppression (ca. 1910), fire regimes in the Pacific Northwest were highly variable, ranging from low-frequency, stand-replacing fires in coastal areas to high-frequency, variable-intensity fires in interior regions. In most fire events, some pockets of live trees were often left following a fire (Franklin and Waring 1979, Morrison and Swanson

1990). This pattern of patchy fires or moderate-intensity windthrow that leaves live trees as individuals and in clumps forms the basis for green-tree retention following timber harvest. In terms of ecosystem management, green-tree retention leaves large live trees after harvest to persist through the next rotation 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 (McComb et al. 1993, North et al. 1996). This structural diversity retains some later seral conditions such as a multi-layered canopy, provides a future supply of large snags and downed logs, and may increase microsite variability for a more diverse understory (Franklin 1989, Gillis 1990).

In mixed stands of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and lodgepole pine (*Pinus contorta* var. *latifolia*) in the southern interior of British Columbia, Canada, pine is often harvested by clear-cutting and the fir are left as residual standing trees. These "seed trees" provide a source of fir regeneration to provide a secondary species to lodgepole pine, which regenerates naturally from abundant cone slash. This is a relatively widespread practice that has been in place since the early to mid-1970s when lodgepole pine became an important commercial timber species. Thus, green-tree retention is not a new management approach to timber harvesting in this region.

The seed-tree silvicultural system is a method of even-aged management whereby a few wind-firm seed trees are left standing singly, or in groups, to furnish seed to regenerate the cleared area naturally (Smith 1986). After a new crop is established, these seed trees may be removed in a second harvest or left indefinitely. The major distinction from shelterwood cutting is that the crown cover on standing trees is not sufficient to make the cleared area different in microclimate compared to an open clearcut area (Smith 1986). Compared with the clear-cutting silvicultural system, the seed sources are retained within the harvested area rather than near the perimeter of a given unit.

A major question is: what role do these seed-tree stands play in managing the forest landscape for biodiversity objectives? Except for simulation models that provide some insights into the long-term impacts of alternative harvesting systems on forest ecosystems (McComb et al. 1993, Hansen et al. 1995*a*), field studies covering decades have yet to be completed. Retrospective studies of the effects of green-tree retention on biodiversity include impacts on growth and tree species composition of future forests where past wildfire was used as an analogue for timber harvest (Rose and Muir 1997, Zenner et al. 1998), canopy lichen communities (Peck and McCune 1997), and understory plant communities in western Oregon (Traut 1995) and western Washington (North et al. 1996). Hansen and Hounihan (1996) reported on canopy tree retention and diversity of birds in western Oregon.

Forest-floor small mammals are an integral part of temperate forest ecosystems because of their roles as prey for a wide range of predators, distributors of beneficial mycorrhizal fungi (Maser et al. 1978), and consumers of invertebrates (Buckner 1966, Elkinton et al. 1996) and plants (Sullivan et al. 1990). Comparison of small-mammal communities between old-growth forests and young (35–79 yr old) unmanaged forests in Washington and Oregon reported few ecologically interpretable patterns across age classes of forest stands (Aubry et al. 1991). Carey and Johnson (1995) found abundance and productivity of most small-mammal species were greatest in old-growth than in managed even-aged stands (44–67 yr old) in western Washington, but all species were still abundant in the managed stands. Those authors suggested that coarse woody debris and understory vegetation (stand structure) were key factors affecting small-mammal abundance, and these factors could potentially be maintained or enhanced by partial-cutting systems. Abundance and diversity of understory vegetation are determined by the interaction of canopy closure, site conditions, and stand history (Spies 1991).

No studies have reported on the responses of stand-structure attributes and small-mammal communities to harvesting using a seed-tree silvicultural system. Because of the relatively long-term history of seed-tree systems in Douglas-fir–lodgepole pine forests in the southern interior of British Columbia, we studied a "natural" experiment at a snapshot in time: naturally regenerated stands of young (17 yr since harvest) lodgepole pine with and without Douglas-fir seed trees, compared with old-growth stands of mixed Douglas-fir and lodgepole pine. The seed-tree system in this forest type may mimic the natural-disturbance regime of frequent variable-intensity fires whereby some residual old-growth Douglas-fir survive amidst fire-regenerated stands of lodgepole pine.

The present study was designed to (1) test the hypothesis that diversity of stand-structure attributes and forest-floor small-mammal communities will increase from young pine to seed-tree to old-growth forest, and (2) discuss the relationship of variable stand structure to managing the forest landscape for biodiversity objectives.

MATERIALS AND METHODS

Study areas

This study was located 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 Montane Spruce ($MS_{d,m}$; d,m = dry precipitation regime, mild temperature regime) biogeoclimatic zone (Meidinger and Pojar 1991) at an elevation range of 1400–1520 m. The MS has a cool, continental climate with cold winters and moderately short, warm summers. Mean annual temperature is 0.5–4.7°C and pre-

cipitation ranges from 380 to 900 mm. 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 and Pojar 1991).

Clear-cut harvesting of lodgepole pine with both uniform and group seed-tree reserves of Douglas-fir began in this area in 1977 in response to an outbreak of mountain pine beetle (*Dendroctonus ponderosae*). Depending on the original composition of the harvested stands and the degree of windthrow damage after harvesting, the number of residual Douglas-fir ranged from a few trees per hectare up to a maximum of ~100 trees/ha. The original silvicultural goal with seed trees was to maintain, and perhaps increase, the proportion of Douglas-fir in the regenerated forest. Lodgepole pine regenerated naturally after harvesting and was the dominant tree species in these young stands.

Stands without seed trees were called "young pine," stands with residual fir were "seed tree," and uncut stands were termed "old growth" (Fig. 1). At the start of our study in 1995, young pine stands were 17-yr-old, seed-tree stands had understory pine stands 17-yr-old (one 18-yr-old stand) with overstory Douglas-fir ranging in average age from 106 to 149 yr. Old-growth stands had a tree species composition of lodgepole pine, Douglas-fir, subalpine fir, and spruce, and ranged in average age from 70 to 133 yr. Veteran or "emergent" trees have survived previous wildfire disturbance (old-growth stands) or been left as seed trees after harvesting (seed-tree stands).

Tree heights ranged from an average of 21.6 to 28.3 m for emergents in all stands with an overstory layer of mature or old-growth trees, 4.2–5.5 m for the main canopy and 2.1–3.0 m for the subcanopy for lodgepole pine in the young pine and seed-tree stands. In the old-growth stands, average tree heights ranged from 16.7 to 21.5 m in the main canopy and from 5.5 to 7.1 m in the subcanopy. Area ranged from 16.9 to 22.9 ha in young pine, 16.5 to 24.0 ha in seed-tree, and 10 to >100 ha for the old-growth stands. The lodgepole pine components of the young pine and seed-tree stands were pre-commercially thinned to a range of 1371–1674 stems/ha in 1985 or 1987.

Experimental design

The experimental design was a randomized-block design with replicate blocks of young pine, seed-tree, and old-growth units (stands) at each of three locations (blocks) at the study area. These nine stands were selected on the basis of operational scale, proximity, and
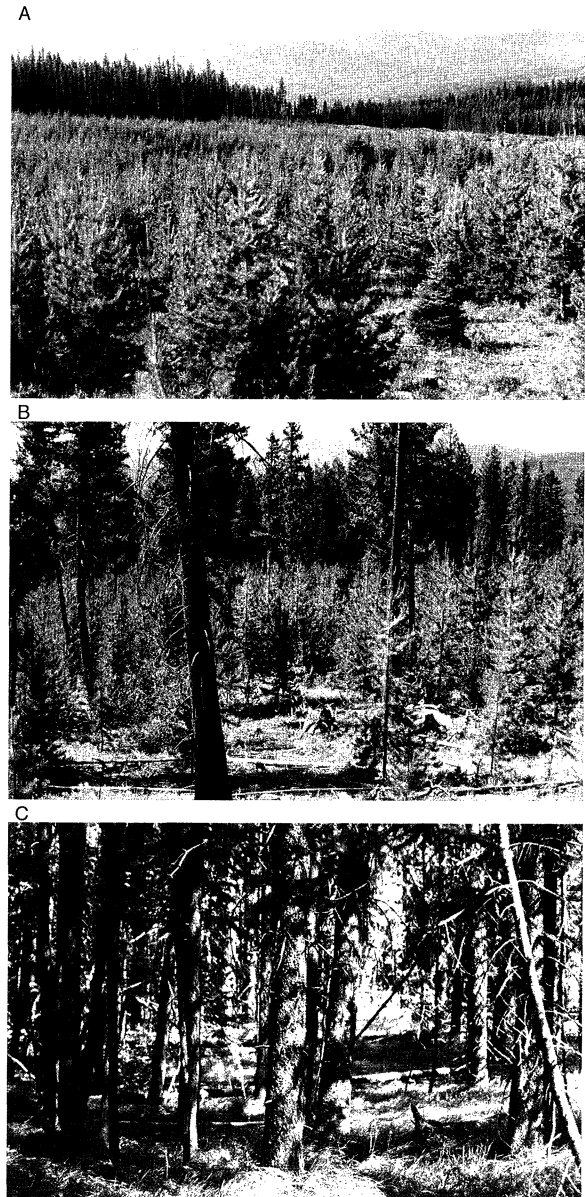
FIG. 1. Photographs of treatment stands at the Summerland study area in south-central British Columbia, Canada: (A) young pine stand, (B) seed-tree stand, and (C) old-growth stand.

reasonable grouping into respective blocks based on location and elevation. Because of the retrospective nature of our study, we did not intersperse the three treatment units randomly within each block. However, there would appear to be little, if any, bias in assignment of treatment units based on past cutting history, subsequent successional development, and availability of particular experimental units with which to test our hypothesis. Because none of these factors was under our control, it could be argued that the treatment units were essentially randomized within each block. Treat-

ment units within a block were spatially segregated to enhance statistical independence (Hurlbert 1984). Within a given block the three stands were separated by a range of 0.2–3.1 km, 0.2–0.7 km, and 0.4–1.0 km. These distances provided a sufficient degree of independence among sampling units as only 1.1% (6/538 individuals) of deer mice (*Peromyscus maniculatus*) and 0.2% (1/425 individuals) of southern red-backed voles (*Clethrionomys gapperi*) were captured on trapping grids in two stands. No individuals of the other small-mammal species were captured on more than one trapping grid.

Stand structure

Stand-structure attributes were measured in five 20 × 20 m plots randomly located within each stand. Each plot was divided into four 10 × 10 m subplots for ease of sampling. For each tree and snag within a subplot, the following parameters were recorded: (a) species; (b) diameter at breast height (dbh, in centimeters); (c) height class: R = regeneration (<1.3 m), S = subcanopy (1.3–5 m), M = main canopy (5–20 m), E = emergent (>20 m); and (d) hardness (five decay classes): 1 = intact, 2 = intact to partially soft, 3 = hard large pieces, 4 = small soft blocky pieces, and 5 = soft and powdery or hollow (Luttermerding et al. 1990). The subcanopy and main canopy tree height categories varied according to stand structure in the different treatment stands.

Down wood was recorded along two transect lines of 20 m each on the perimeter of the 20 × 20 m plot. As each piece was encountered the following attributes were recorded: (a) species, (b) diameter where line crosses wood (in centimeters), and (c) hardness (five decay classes). The volume of down wood (in cubic meters per hectare) was calculated by the method of Van Wagner (1968).

The physical characteristics of each 20 × 20 m plot were recorded with respect to aspect, slope, site position, and other ecologically relevant features.

Understory vegetation

Within each 10 × 10 m subplot, two sizes of nested subplots were established: a 3 × 3 m subplot for sampling shrubs, and a 1 × 1 m subplot for sampling herbs and mosses. These nested subplots were located 2 m in from the quadrat perimeter. Shrub and herb layers were subdivided into height classes: 0–0.25 m, 0.25–0.50 m, 0.50–1.0 m, 1.0–2.0 m, 2.0–3.0 m, and 3.0–5.0 m (Walmsley et al. 1980). A visual estimate of percentage cover of the ground was made for each species height-class combination within the appropriate nested subplot. Total percentage cover for each layer was also estimated for each subplot. These data were then used to calculate crown-volume index (in cubic meters per 0.01 hectare) for each plant species (Stickney 1980, 1985). The product of percentage cover and representative height gives the volume of a cylindroid that represents the space occupied by the plant in the community. Crown-volume-index values were then averaged by species for each plot size and converted to 0.01-ha base to produce a tabular value given for each species and layer (mosses, herbs, and shrubs–deciduous trees). Sampling was done in July–August 1995 and 1996. Grasses were not identified to species. Plant species were identified in accordance with Hitchcock and Cronquist (1973) and Parish et al. (1996). Species richness, species diversity, and structural diversity were calculated for these data.

Small-mammal communities

Forest-floor small-mammal populations were sampled at 4-wk intervals from June to October 1995, May to October 1996, and May to September 1997 for a total of five sampling periods per year. One old-growth grid had only three sampling periods for 1997, prior to harvesting of the stand in late summer-fall of that year. Trapping grids (1 ha) had 49 (7 × 7 array) trap stations at 14.3-m intervals with one Longworth live-trap at each station (Ritchie and Sullivan 1989). Traps were supplied with whole oats and carrot, and cotton as bedding. Traps were set on the afternoon of day 1, checked on the morning and afternoon of day 2 and morning of day 3, and then locked open between trapping periods.

Forest-floor small-mammal species sampled by this procedure included the deer mouse, northwestern chipmunk (*Tamias amoenus*), meadow vole (*Microtus pennsylvanicus*), long-tailed vole (*M. longicaudus*), southern red-backed vole, heather vole (*Phenacomys intermedius*), western jumping mouse (*Zapus princeps*), montane shrew (*Sorex monticolus*), common shrew (*S. cinereus),* and short-tailed weasel (*Mustela erminea*).

All small mammals (except shrews and weasels) captured were ear-tagged and immediately released at the point of capture (Krebs et al. 1969). There was a high mortality rate for shrews because of the overnight trapping technique. Shrews that died in traps were collected and identified according to Nagorsen (1996). The pygmy shrew (*S. hoyi*) and water shrew (*S. palustris*) may also have been present in our sampling areas but were not captured. The pygmy shrew ranges in density from 0.5 to 1.2 animals/ha and is relatively uncommon (Nagorsen 1996). The water shrew is strongly associated with wet habitats at densities similar to the pygmy shrew (Nagorsen 1996). The northern pocket gopher (*Thomomys talpoides*) also occurred in our study area, but rarely appeared aboveground and only one individual was captured. This latter burrowing species and the primarily arboreal red squirrel (*Tamiasciurus hudsonicus*), northern flying squirrel (*Glaucomys sabrinus*), and bushy-tailed woodrat (*Neotoma cinerea*) were not considered part of the forest-floor small-mammal community.

Abundance

To determine the effects of stand treatments on abundance of the major species, we measured trappability and population density. Jolly trappability was calculated according to the trappability estimate discussed by Krebs and Boonstra (1984).

Population estimates of the deer mouse, northwestern chipmunk, southern red-backed vole, and heather vole were derived from the Jolly-Seber stochastic model (Seber 1982). The minimum number of animals known to be alive (MNA) (Krebs 1966) was used as the population estimate for the first and last sampling weeks of the study when the Jolly-Seber estimate was not calculated. The reliability of the Jolly-Seber model declines when population sizes are very low and no marked animals are captured (Krebs et al. 1986). In those cases, the total number of individuals captured was used to compare populations of the meadow vole, long-tailed vole, western jumping mouse, montane shrew, common shrew, and short-tailed weasel.

Diversity measures

Diversity of stand-structure attributes was measured by species richness, species diversity, and structural diversity. *Species richness* was the total number of species sampled for the plant (mosses, herbs, shrubs–deciduous trees, and coniferous trees) and small-mammal communities in each stand (Krebs 1989). *Species diversity* was based on the Simpson (1949) and Shannon-Wiener (Pielou 1966) diversity indices, which are well represented in the ecological literature (Magurran 1988, Burton et al. 1992). Simpson's index is sensitive to changes in the more abundant species and is the probability of picking two organisms at random that are different species. This index has values that range from 0 to almost 1. The Shannon-Wiener index is sensitive to changes in the rare species in a community sample (Peet 1974). This index is based on the degree of difficulty in predicting correctly the species of the next individual sampled. It increases with the number of species in the community, and ranges from 0 to approximately 5.0 for biological communities (Washington 1984).

Structural diversity was based on the same indices as for species richness and diversity, with the height classes of each of the herb, shrub–deciduous tree, and coniferous tree layers acting as "species." Thus, structural richness was the total number of height classes occupied by the various vegetative layers. Structural diversity utilized the same Simpson's and Shannon-Wiener indices, with plant species represented by height classes and the amount (crown-volume index) of vegetation in each class. Basal area was used in these calculations of structural diversity for coniferous trees.

For the plant communities, species diversity was calculated using the crown-volume index for each plant species averaged across the five plots, each of which was an average of four subplots, in a given stand. Species diversity was calculated separately for mosses, herbs, shrubs–deciduous trees, and coniferous trees. Diversity for small mammals was calculated using the estimated abundance of each species for a given sampling period and averaged over the five sampling periods for each year. Log-series alpha was also calculated for the small-mammal communities as this index shows good discriminant ability in a wide range of circumstances (Southwood 1978). This index is less affected by species dominance than either the Shannon-Wiener or Simpson indices (Magurran 1988).

Statistical analysis

For the analysis of stand structure, a randomized-block ANOVA (Zar 1984) was conducted to test differences in mean stand density, diameter, and basal area within height classes for each of the four coniferous tree species. As an additional part of this stand-structure analysis, this ANOVA was also used to compare mean volume, diameter, and decay classes of down wood among treatment stands. Mean percentage cover and crown-volume index of mosses, herbs, and shrubs–deciduous trees, as well as mean species richness and diversity of these same three layers, plus the coniferous tree layer, were also compared among treatment stands by this randomized-block ANOVA. Mean structural diversity of the herb, shrub–deciduous tree, and coniferous tree layers was also compared using this ANOVA model.

This retrospective study represented a brief period of successional change (17–19 yr) for young lodgepole pine compared to the first 5–10 yr after disturbance. Therefore, the randomized-block design incorporated both spatial (three stands per treatment) and temporal (three years per treatment) replication for the small-mammal data. This analysis was conducted to test differences in mean number of each small-mammal species, mean species richness, and mean species diversity. For these analyses, a mean estimate of the given parameter for each year and treatment was derived to use the variability among years and blocks to test for differences among levels of the treatment.

Percentage data were arcsine-transformed prior to analysis. Duncan's multiple-range test was used to compare mean values. In all analyses, the level of significance was at least $P = 0.05$.

RESULTS

Stand structure

Douglas-fir emergent trees averaged 77 stems/ha in the seed-tree stands compared with 12 stems/ha in the old-growth stands (Table 1). However, the main canopy in the old-growth stands averaged 303 stems/ha of Douglas-fir, and contained some trees that would have been emergent in the seed-tree stands. The lodgepole pine main canopy in the young pine stands had a sig-

TABLE 1. Summary of stand-structure attributes (density, diameter, and basal area) for three height classes of emergent (Emerg.), main canopy (MC), subcanopy (SC), and regeneration (Regen.) coniferous tree species together with results of ANOVAs, for data collected at Summerland, British Columbia, Canada, 1995–1997.

Species	Density (stems/ha)				Diameter (cm)		
	Emerg.	MC	SC	Regen.	Emerg.	MC	SC
Douglas-fir							
Young pine	0.00	0.00	41.7	63.3	0.00	0.00	2.27
			(22.1)	(20.5)			(0.24)
Seed tree	76.7	0.00	53.3	731.7	37.69	0.00	1.84
	(10.9)		(19.7)	(212.9)	(0.24)		(0.19)
Old growth							
Live	11.7	303.3	488.3	1668.3	54.58	21.47	6.17
	(6.0)	(123.1)	(109.0)	(873.4)	(3.96)	(0.71)	(0.82)
Dead	1.7	5.0	109.0	0.00	47.50	13.63	6.52
	(1.7)	(2.9)	(64.1)			(3.64)	(0.89)
$F_{2,4}$	...	...	7.64	2.10	...	...	16.07†
P	...	...	0.05	0.25	...	...	0.03
Lodgepole pine							
Young pine	0.00	1135.0	1563.3	1495.0	0.00	7.52	2.01
		(61.2)	(96.3)	(167.9)		(0.28)	(0.10)
Seed tree	0.00	575.0	885.0	1500.0	0.00	7.08	2.28
		(112.6)	(460.7)	(1001.2)		(0.31)	(0.26)
Old growth							
Live	0.00	390.0	40.0	3.3	0.00	19.74	9.11
		(130.9)	(23.7)	(3.3)		(1.38)	(1.57)
Dead	0.00	273.3	240.0	0.00	0.00	19.57	9.46
		(79.6)	(79.5)			(0.67)	(0.69)
$F_{2,4}$	...	47.23	6.85	2.20	...	91.85	18.94
P	...	<0.01	0.05	0.24	...	<0.01	<0.01
Subalpine fir							
Young pine	0.00	0.00	15.0	111.7	0.00	0.00	2.04
			(5.0)	(49.2)			(0.35)
Seed tree	0.00	6.7	35.0	63.3	0.00	13.65	2.59
		(3.3)	(21.8)	(41.0)		(3.66)	(0.40)
Old growth							
Live	0.00	118.3	103.3	821.7	0.00	20.21	10.17
		(70.3)	(39.5)	(822.6)		(3.06)	(1.09)
Dead	0.00	6.7	56.7	0.00	0.00	17.05	9.93
		(6.7)	(54.3)				(3.58)
$F_{2,4}$	...	2.57	2.22	0.82	...	...	37.34†
P	...	0.21	0.24	0.50	...	...	<0.01
Spruce							
Young pine	0.00	0.00	85.0	405.0	0.00	0.00	2.06
			(32.6)	(101.2)			(0.33)
Seed tree	0.00	6.7	5.0	45.0	0.00	0.00	1.75
		(3.3)	(2.9)	(26.0)			(0.75)
Old growth							
Live	0.00	11.7	8.3	18.3	0.00	21.29	4.29
		(11.7)	(8.3)	(18.4)			
Dead	0.00	0.00	0.00	0.00	0.00	0.00	0.00
$F_{2,4}$	...	...	6.74	10.90	...	...	...
P	...	...	0.05	0.02	...	...	...

Note: Data entries are means with 1 SE in parentheses.

† $F_{2,3}$

nificantly ($F_{2,4} = 47.23$; $P < 0.01$) higher density (1135 stems/ha) than either of the seed-tree (575 stems/ha) or old-growth (390 stems/ha) stands (Table 1). In the subcanopy height classes, Douglas-fir occurred at a significantly ($F_{2,4} = 7.64$; $P = 0.05$) higher density (488 stems/ha) in the old-growth stand than in either of the young pine (42 stems/ha) or seed-tree (53 stems/ha) stands. Conversely, lodgepole pine dominated ($F_{2,4} = 6.85$; $P = 0.05$) the subcanopy in the young pine stand

(1563 stems/ha) followed by the seed-tree (885 stems/ha) and old-growth (40 stems/ha) stands (Table 1).

Douglas-fir dominated the regeneration layer (<1.3 m height) in the old-growth stands (1668 stems/ha) followed by the seed-tree (732 stems/ha) and young pine (63 stems/ha) stands. Lodgepole pine was at comparable numbers in the young pine and seed-tree stands, with very few pine seedlings occurring as regeneration in the old-growth stands (Table 1). Some subalpine fir

TABLE 1. Extended.

Basal area (m²/ha)		
Emerg.	MC	SC
0.00	0.00	0.02 (0.00)
8.54 (1.19)	0.00	0.01 (0.003)
4.20 (1.18)	11.57 (0.14)	1.53 (0.62)
0.89	4.94 (0.10)	0.50 (0.05)
...	...	4.45†
...	...	0.13
0.00	5.09 (0.62)	0.50 (0.07)
0.00	2.22 (0.32)	0.29 (0.08)
0.00	13.14 (5.52)	0.36 (0.23)
0.00	7.94 (2.06)	1.55 (0.38)
...	3.76	0.47
...	0.14	0.67
0.00	0.00	0.01 (0.002)
0.00	0.16 (0.08)	0.03 (0.02)
0.00	4.24 (2.17)	0.72 (0.21)
0.00	0.46	0.30 (0.23)
...	...	7.50†
...	...	0.07
0.00	0.00	0.02 (0.01)
0.00	0.00	0.003 (0.002)
0.00	1.25	0.04
0.00	0.00	0.00
...	...	...
...	...	...

and spruce were present in the main canopy of the seed-tree and old-growth stands. These two tree species were present in all stands in the subcanopy and regeneration height classes, with subalpine fir occurring most often as regeneration in old-growth stands, but with highly variable densities across replicates. Spruce occurred at significantly higher densities in the subcanopy ($F_{2,4}$ = 6.74; P = 0.05) and regeneration ($F_{2,4}$ = 10.90; P = 0.02) height classes of the young pine than in the other stands.

Because of the difference in vertical stratification of

the main canopy and subcanopy layers between the old-growth stands and seed-tree and young pine stands, it is not surprising that mean diameters of Douglas-fir, lodgepole pine, and subalpine fir were highest in the old-growth stands (Table 1). Despite these differences in diameters, basal area of each species was similar within height classes among treatment stands.

Dead standing trees (snags) were present in the old-growth stands only. In terms of density, Douglas-fir snags varied from 5 to 109 stems/ha in the main and subcanopy layers, respectively. Lodgepole pine snags were at similar numbers in the main canopy (273 stems/ha) and subcanopy (240 stems/ha). Subalpine fir had 7 dead stems/ha in the subcanopy and 57 dead stems/ha in the main canopy.

Mean volume of down wood was similar among treatment stands, ranging from 83 m³/ha in the seed-tree, to 114 m³/ha in the young pine, to 120 m³/ha in the old-growth stands (Table 2). The young pine stands had a greater number ($F_{2,4}$ = 9.20; P = 0.03) of wood pieces in the 5–25 cm diameter class than the seed-tree or old-growth stands. Conversely, the old-growth stands tended to have more large (>25 cm) diameter pieces than the other stands in these down wood samples (Table 2). The young pine and seed-tree stands had more pieces in decay classes 3 and 4 than the old-growth stands, possibly owing to an accumulation of woody debris from the harvesting operations.

Understory vegetation

Mean total percentage cover of herbs ($F_{2,4}$ = 0.07; P > 0.75) and mosses ($F_{2,4}$ = 0.17; P > 0.75) was similar among treatment stands (Table 3). Mean total crown-volume index was also similar across stands for herbs ($F_{2,4}$ = 0.95; P = 0.47) and mosses ($F_{2,4}$ = 0.20; P > 0.75). Prominent herb species in these stands included fireweed (*Epilobium angustifolium*), grasses, Arctic lupine (*Lupinus arcticus*), heart-leaved arnica (*Arnica cordifolia*), wild strawberry (*Fragaria virginiana*), and white-flowered hawkweed (*Hieracium albiflorum*).

In terms of total herbaceous species, three species occurred in the young pine only: fir clubmoss (*Lycopodium selago*), mountain sweet-cicely (*Osmorhiza chilensis*), and pink wintergreen (*Pyrola asarifolia*); and two species in the seed-tree stands only: common mitrewort (*Mitella nuda*) and common dandelion (*Taraxacum officinale*). There were 12 species that occurred in the old-growth stands only, and they were: yarrow (*Achillea millefolium*), field pussytoes (*Antennaria neglecta*), Lindley's aster (*Aster ciliolatus*), fairyslipper (*Calypso bulbosa*), common red paintbrush (*Castilleja miniata*), sweet-scented bedstraw (*Galium triflorum*), narrow-leaved hawkweed (*Hieracium umbellatum*), yellow monkey-flower (*Mimulus guttatus*), bracted lousewort (*Pedicularis bracteosa*), self-heal (*Prunella vulgaris*), roseroot (*Sedum integrifolium*), and American vetch (*Vicia americana*).

TABLE 2. Summary of characteristics of down wood (volume and number of pieces of wood in diameter classes and decay classes) together with results of ANOVAs for three types of stands at Summerland, British Columbia, Canada.

| | Stands | | | | |
Variable	Young pine	Seed tree	Old growth	$F_{2,4}$	P
Volume (m³/ha)	114.48 ± 11.85	82.74 ± 16.12	120.06 ± 17.56	1.19	0.42
No. of wood pieces					
Diameter classes (cm)					
<5	27.87 ± 3.96	36.80 ± 2.60	32.87 ± 8.58	1.60	0.34
5–25	31.73 ± 4.44	17.13 ± 0.55	12.80 ± 5.54	9.20	0.03
>25	0.40 ± 0.20	0.53 ± 0.29	1.67 ± 0.27	5.88	0.07
Decay classes					
1	0.00	1.07 ± 0.68	2.40 ± 1.10	2.69	0.21
2	26.47 ± 3.88	23.00 ± 1.40	30.80 ± 8.05	0.57	0.62
3	21.80 ± 3.61	18.93 ± 1.53	8.07 ± 4.18	6.65	0.06
4	9.13 ± 1.38	8.87 ± 1.23	3.47 ± 1.45	57.01	<0.01
5	2.60 ± 0.35	2.60 ± 0.35	2.60 ± 0.90	0.00	>0.75

Note: Data are means ± 1 SE.

Prominent moss species included common lawn moss (*Brachythecium albicans*), broom moss (*Dicranum* sp.), fire moss (*Ceratodon purpureus*), and juniper haircap moss (*Polytrichum juniperinum*). In terms of total moss species, three species (*Plagiomnium insigne, P. undulata,* and *Rhytidiadelphus triquetrus*) occurred in the old-growth stands only.

Mean total percentage cover of shrubs–deciduous trees was significantly ($F_{2,4}$ = 10.70; P = 0.02) higher in the young pine (40.8%) (Duncan's multiple range test [DMRT]; P = 0.05) than old-growth (9.4%) stands (Table 3). The seed-tree stands had 25.0% mean cover of shrubs–deciduous trees. Although not significant ($F_{2,4}$ = 4.67; P = 0.09), mean total crown-volume index of shrubs–deciduous trees also tended to follow this pattern: young pine (41.8 m³/0.01 ha), seed tree (21.6 m³/0.01 ha), and old growth (5.8 m³/0.01 ha). Prominent shrubs included Sitka alder (*Alnus sinuata*), kinnikinnick (*Arctostaphylos uva-ursi*), twinflower (*Linnaea borealis*), Utah honeysuckle (*Lonicera utahensis*), falsebox (*Pachistima myrsinites*), birch-leaved spirea (*Spiraea betulifolia*), and grouseberry (*Vaccinium scoparium*).

In terms of total shrubs–deciduous tree species, seven species occurred in the young pine only: Labrador tea (*Ledum groenlandicum*), black cottonwood (*Populus trichocarpa*), stink currant (*Ribes bracteosum*), five-leaved bramble (*Rubus pedatus*), thimbleberry (*Rubus parviflorus*), red elderberry (*Sambucus race-*

mosa), and Sitka mountain-ash (*Sorbus sitchensis*). There were six species in the seed-tree stands only: red-osier dogwood (*Cornus stolonifera*), white-flowered rhododendron (*Rhododendron albiflorum*), soopolallie (*Shepherdia canadensis*), common snowberry (*Symphoricarpos albus*), dwarf blueberry (*Vaccinium caespitosum*), and high-bush cranberry (*Viburnum edule*). There were two species in the old-growth stands only: tall Oregon-grape (*Mahonia aquifolium*) and saskatoon (*Amelanchier alnifolia*).

Diversity of stand-structure attributes

Total species richness was similar among the young pine (45 species present), seed-tree (43), and old-growth (49) stands. Mean species richness of herbs and coniferous trees was similar among treatment stands, whereas richness of shrubs–deciduous trees was significantly ($F_{2,4}$ = 9.34; P = 0.03) different among treatment stands. The young pine stands had a mean richness of 8.73 which was higher (DMRT; P = 0.05) than that in the old-growth stands (5.00) (Table 4). Mean species richness of mosses was similar ($F_{2,4}$ = 0.97; P = 0.47) among treatment stands. Mean species diversity of herbs and shrubs–deciduous trees was similar among treatment stands for both diversity indices (Table 4). This response was the same for moss species diversity regardless of indices: Simpson's ($F_{2,4}$ = 0.60; P = 0.61) and Shannon-Wiener ($F_{2,4}$ = 0.83; P = 0.50). These measures indicated that species diversity of co-

TABLE 3. Total percent cover and crown-volume index for plant species in the understory vegetation layers for three types of stands at the Summerland, (British Columbia, Canada) study area.

| | Total (%) | | | Crown-volume index (m³/0.01ha) | | |
Vegetation layer	Young pine	Seed tree	Old growth	Young pine	Seed tree	Old growth
Herbs	22.80	23.24	25.20	10.54	8.78	7.42
Mosses	11.13	8.92	9.99	2.79	2.23	2.50
Shrubs–deciduous trees	40.76	24.95	9.38	41.84	21.61	5.79

Note: Data are means.

TABLE 4. Species diversity and structural diversity of three vegetation layers (herbs, shrubs–deciduous trees and coniferous trees), together with results of ANOVAs for data collected at the Summerland, British Columbia, Canada study area.

	Species diversity			Structural diversity		
	Richness	Simpson's index	Shannon-Wiener index	Height class	Simpson's index	Shannon-Wiener index
Herbs						
Young pine	5.80	0.48	1.33	3.67	0.63	1.62
	(0.50)	(0.03)	(0.14)	(0.13)	(0.02)	(0.05)
Seed tree	5.33	0.41	1.16	2.80	0.35	0.93
	(1.60)	(0.05)	(0.02)	(0.58)	(0.14)	(0.38)
Old growth	5.33	0.45	1.30	1.93	0.22	0.52
	(0.93)	(0.06)	(0.20)	(0.35)	(0.10)	(0.23)
$F_{2,4}$	0.16	1.00	0.40	4.82	3.80	4.16
P	0.75	0.46	0.71	0.09	0.13	0.11
Shrubs–deciduous trees						
Young pine	8.73	0.54	1.67	5.20	0.64	1.80
	(0.84)	(0.10)	(0.30)	(0.31)	(0.04)	(0.12)
Seed tree	7.20	0.38	1.20	3.67	0.40	1.05
	(0.83)	(0.02)	(0.02)	(0.73)	(0.07)	(0.23)
Old growth	5.00	0.53	1.47	2.60	0.30	0.77
	(0.81)	(0.02)	(0.07)	(0.70)	(0.08)	(0.26)
$F_{2,4}$	9.34	2.00	1.74	5.80	30.00	24.97
P	0.03	0.25	0.31	0.07	<0.01	<0.01
Coniferous trees						
Young pine	3.63	0.03	0.12	3.00	0.23	0.64
	(0.09)	(0.01)	(0.03)	(0.00)	(0.04)	(0.08)
Seed tree	3.13	0.35	0.74	4.00	0.38	0.89
	(0.37)	(0.05)	(0.11)	(0.00)	(0.06)	(0.06)
Old growth	2.73	0.38	0.89	3.07	0.22	0.56
	(0.18)	(0.10)	(0.24)	(0.07)	(0.06)	(0.10)
$F_{2,4}$	2.86	7.86	6.23	234.50	2.27	3.60
P	0.19	0.04	0.06	<0.01	0.23	0.15

Note: Data are means with 1 SE in parentheses.

niferous trees was higher in the seed-tree and old-growth stands than in the young pine stands (Table 4). This latter result is not surprising considering the dominance of lodgepole pine in the young pine stands.

Mean structural diversity in terms of richness of height classes (or layers of vegetation) of herbs and shrubs–deciduous trees appeared consistently higher in the young pine than in the seed-tree and old-growth stands (Table 4). Richness of height classes was significantly ($F_{2,4} = 234.50$; $P < 0.01$) different for coniferous trees with the seed-tree stands higher (DMRT;

$P = 0.05$) than either of the young pine or old-growth stands. Structural diversity based on the Simpson's and Shannon-Wiener indices indicated no difference in herb and coniferous tree layers (Table 4). However, mean structural diversity of the shrub–deciduous tree layer was significantly different among treatment stands for both Simpson's ($F_{2,4} = 30.00$; $P < 0.01$) and Shannon-Wiener ($F_{2,4} = 24.97$; $P < 0.01$) indices. The young pine stands had significantly (DMRT; $P = 0.05$) higher structural diversity of shrubs–deciduous trees than the seed-tree stands. In addition, the seed-tree stands also

TABLE 5. Total numbers of individuals captured of each small mammal species in the three replicate stands of each treatment during the 3-year study at Summerland, British Columbia, Canada.

Species	Young pine	Seed tree	Old growth	Total
Deer mice (Peromyscus maniculatus)	204	133	201	538
Red-backed voles (Clethrionomys gapperi)	79	79	267	425
Northwestern chipmunks (Tamias amoenus)	86	110	38	234
Heather voles (Phenacomys intermedius)	15	28	0	43
Meadow voles (Microtus pennsylvanicus)	10	17	5	32
Long-tailed voles (M. longicaudus)	3	23	9	35
Western jumping mice (Zapus princeps)	8	15	0	23
Montane shrews (Sorex monticolus)	97	128	8	233
Common shrews (S. cinereus)	36	27	8	71
Short-tailed weasels (Mustela erminea)	10	7	6	23
Total	548	567	542	1657

TABLE 6. Jolly trappability estimates (mean values and 95% confidence intervals) for the major small-mammal species in the replicate stands of each treatment during the 3-yr study at Summerland, British Columbia, Canada.

Treatment	Deer mice $\bar{x}$ (%)	Deer mice 95% CI	Red-backed voles $\bar{x}$ (%)	Red-backed voles 95% CI	Northwestern chipmunks $\bar{x}$ (%)	Northwestern chipmunks 95% CI	Heather voles $\bar{x}$ (%)	Heather voles 95% CI
Young pine								
1	92.9	83.1–102.7	66.9	39.7–94.1	65.8	46.7–85.0	40.2	10.2–70.1
2	89.0	79.1–98.9	96.2	87.8–104.5	80.7	62.1–99.3	23.1	−3.4–49.6
3	89.7	77.3–102.1	53.8	22.5–85.2	52.3	33.0–71.6	46.2	14.8–77.5
Seed tree								
1	88.5	70.4–106.6	23.1	−3.4–49.6	55.7	40.7–70.7	53.8	22.5–85.2
2	82.8	69.3–96.4	72.4	45.6–99.2	63.5	42.5–84.4	30.8	1.7–59.8
3	83.2	60.7–105.8	90.9	82.1–99.8	68.3	50.6–86.0	15.4	−7.3–38.1
Old growth								
1	74.9	58.1–91.8	79.2	69.7–88.7	50.5	22.7–78.2	···	···
2	88.7	70.8–106.6	83.8	70.0–97.6	65.1	39.7–90.4	···	···
3	78.2	64.8–91.7	97.8	92.9–102.6	23.1	−3.4–49.6	···	···

had higher (DMRT; $P = 0.05$) structural diversity of this vegetative layer than the old-growth stands for the Shannon-Wiener index (Table 4).

Small-mammal abundance

The total numbers of individuals captured of all small-mammal species are listed in Table 5. Estimates of trappability (susceptibility to capture) tended to be variable among species, with overall mean values ranging from 85.3% for deer mice, 73.8% for red-backed voles, and 58.3% for northwestern chipmunks, to 34.9% for heather voles (Table 6). Therefore, for reasons outlined in Jolly and Dickson (1983), Jolly-Seber population estimates were used for this study.

Mean numbers of deer mice were similar ($F_{2,16} = 1.35$; $P = 0.30$) among treatment stands (Table 7) and changes in abundance through the summer and fall of 1995 to 1997 reflect this pattern (Fig. 2A). Mean numbers of red-backed voles were significantly ($F_{2,16} = 17.78$; $P < 0.01$) different, with consistently higher (3.1–7.3 times) abundance in the old-growth than in either of the young pine or seed-tree stands (Table 7). This difference was evident in all years (Fig. 2B).

The northwestern chipmunk also exhibited significantly ($F_{2,16} = 14.25$; $P < 0.01$) different mean numbers among treatment stands. The seed-tree (3.1 times) and young pine (2.4 times) stands had higher (DMRT; $P = 0.05$) abundance of chipmunks than the old-growth stands (Table 7; Fig. 3A). There was no difference (DMRT; $P = 0.05$) in mean number of chipmunks between the seed-tree and young pine stands. Heather voles were consistently present at low numbers (~ 1 animal/ha) in both young pine and seed-tree stands, but were absent from the old-growth stands (Fig. 3B). This difference in mean numbers of heather voles was significant ($F_{2,16} = 13.23$; $P < 0.01$) overall and also between (DMRT; $P = 0.05$) the old-growth stand and each of the young pine and seed-tree stands (Table 7). Another relatively uncommon species, the western jumping mouse, also tended ($F_{2,16} = 3.13$; $P = 0.08$) to have consistently higher mean numbers in the young pine (0.21 animals/ha) and seed-tree (0.33 animals/ha) than in the old-growth stands, where it was absent.

There was no difference ($F_{2,16} = 1.65$; $P = 0.23$) in mean numbers of long-tailed voles among treatment stands. However, mean abundance of meadow voles tended to be higher ($F_{2,16} = 3.53$; $P = 0.06$) in the seed-tree (0.61 animals/ha) than in either of the young pine (0.33 animals/ha) or old-growth (0.27 animals/ha) stands (Table 7).

TABLE 7. Abundance of small mammal species during each year in the three treatment stands for Jolly-Seber population estimates at the Summerland (British Columbia, Canada) study area.

Species	1995 Young pine	1995 Seed tree	1995 Old growth
Peromyscus maniculatus	8.91 ± 2.06	7.05 ± 2.04	10.21 ± 2.35
Clethrionomys gapperi	2.70 ± 1.46	1.53 ± 0.94	10.17 ± 3.54
Tamias amoenus	5.79 ± 0.53	8.92 ± 3.66	2.79 ± 1.65
Phenacomys intermedius	0.67 ± 0.22	0.73 ± 0.29	0
Microtus pennsylvanicus	0.47 ± 0.37	0.67 ± 0.34	0.50 ± 0.50
M. longicaudus	0.13 ± 0.13	1.70 ± 1.41	0.40 ± 0.40
Zapus princeps	0	0.20 ± 0.20	0
Sorex monticolus	2.07 ± 0.77	2.13 ± 1.01	0.20 ± 0.12
S. cinereus	1.07 ± 0.35	0.07 ± 0.07	0.13 ± 0.13
Mustela erminea	0.13 ± 0.13	0.13 ± 0.13	0.33 ± 0.07

Note: Data are means ± 1 SE.

The insectivore members of these small-mammal communities exhibited significant differences among treatment stands: montane shrew ($F_{2,16} = 14.72$; $P < 0.01$) and common shrew ($F_{2,16} = 4.84$; $P = 0.02$) (Table 7). The overall mean abundance of montane shrews was significantly (DMRT; $P = 0.05$) higher in the young pine (2.16 animals/ha) and seed-tree (2.42 animals/ha) than in the old-growth (0.18 animals/ha) stands. This difference (DMRT; $P = 0.05$) in mean numbers was also true for common shrews between the young pine (0.80 animals/ha) and old-growth (0.18 animals/ha) stands. On average, montane shrews occurred at 3.2 times greater numbers than common shrews.

Mean numbers of the short-tailed weasel, a principal predator of several of these small-mammal species, were similar ($F_{2,16} = 0.33$; $P = 0.73$) among treatment stands (Table 7).

Species diversity

Mean species richness of the small-mammal communities was significantly ($F_{2,16} = 70.54$; $P < 0.01$) different among treatment stands. Both the young pine (5.71) and seed-tree (6.24) stands had more (DMRT; $P = 0.05$) species (1.4–1.6 times) than the old-growth (3.96) stands and this pattern was consistent throughout the three years of the study (Fig. 4A). Similarly, small-mammal richness was higher (DMRT; $P = 0.05$) in the seed-tree than in the young pine stands.

Mean species diversity was significantly (DMRT; $P = 0.05$) higher in the young pine and seed-tree stands than in the old-growth stands as represented by the log-series index ($F_{2,16} = 51.86$; $P < 0.01$) (Fig. 4B). Both the Simpson's ($F_{2,16} = 10.00$; $P < 0.01$) and Shannon-Wiener ($F_{2,16} = 25.38$; $P < 0.01$) indices also followed this pattern. There was no difference in species diversity between the young pine and seed-tree stands, and these differences were consistent throughout the study.

DISCUSSION

Seed-tree silvicultural system

The seed-tree silvicultural system has been in use in the southern interior of British Columbia for nearly 30 years, particularly in mixed Douglas-fir–lodgepole pine forests but also in mixed western larch (*Larix occidentalis*)–lodgepole pine forests as well. As a means of regenerating Douglas-fir in the understory, our seed-tree stands at 17–19 yr post-harvest were successful with greater numbers (11.6 times) of fir seedlings than in the young pine stands (Table 1). Thus, the goal of adding a significant component of Douglas-fir to the naturally regenerated lodgepole pine seemed to be achieved. The lower numbers of lodgepole pine seedlings and saplings in the subcanopy and main canopy, respectively, of the seed-tree than young pine stands suggested that the residual Douglas-fir may have limited the regeneration cohort as reported by Rose and Muir (1997) for coastal forests with remnant trees. Acker et al. (1998) and Zenner et al. (1998) reported growth reductions in harvest-age coniferous forests with residual trees. Part of this effect of residual trees on regeneration and growth was likely owing to occupation of space by residuals and the concurrent competition for light, water, and nutrients. Although important to future fibre production and silvicultural flexibility, the smaller regeneration cohort in our seed-tree stands was more than compensated for by the higher species diversity provided by a substantial component of Douglas-fir mixed with lodgepole pine. Because of this species mix, the seed-tree and old-growth stands had similar levels of species diversity of coniferous trees, significantly higher than that in the young pine stands.

The remnant trees that comprise the uniform or group seed-tree systems will, in most cases, be retained to provide a biological legacy from the original stand to the regenerating stand. Remnant trees probably affect the recovering ecosystem in many different ways (Rose and Muir 1997). In addition to the seed source that enhanced diversity of coniferous trees to a level found in our old growth stands, the residual Douglas-fir may also provide shade and amelioration of temperature and surface desiccation for both tree seedlings and understory herbs and shrubs. These seed trees also provide a source of snags and large-diameter down wood in the future forest. In addition, they provide some large high-value timber if retained and included in the next harvest.

TABLE 7. Extended.

|	1996			1997	
Young pine	Seed tree	Old growth	Young pine	Seed tree	Old growth
12.76 ± 5.09	9.02 ± 2.89	11.96 ± 2.73	6.87 ± 2.73	2.67 ± 1.57	5.56 ± 1.12
1.70 ± 0.36	2.57 ± 1.51	12.41 ± 3.34	3.77 ± 0.63	6.14 ± 2.84	18.76 ± 4.52
9.16 ± 1.85	11.57 ± 2.22	3.46 ± 2.10	7.79 ± 1.66	10.99 ± 2.09	3.10 ± 1.27
1.17 ± 0.32	0.60 ± 0.06	0	1.40 ± 0.67	1.77 ± 0.52	0
0.23 ± 0.23	0.57 ± 0.32	0.17 ± 0.17	0.30 ± 0.30	0.60 ± 0.20	0.13 ± 0.13
0	0.20 ± 0.20	0.20 ± 0.20	0.13 ± 0.13	0.33 ± 0.33	0.33 ± 0.33
0.20 ± 0.12	0.33 ± 0.33	0	0.43 ± 0.34	0.47 ± 0.47	0
2.53 ± 0.27	2.93 ± 0.88	0.33 ± 0.24	1.87 ± 0.68	2.20 ± 0.92	0
1.07 ± 0.29	0.73 ± 0.47	0.40 ± 0.12	0.27 ± 0.13	0.40 ± 0.40	0
0.07 ± 0.07	0	0	0.47 ± 0.24	0.33 ± 0.13	0.07 ± 0.07
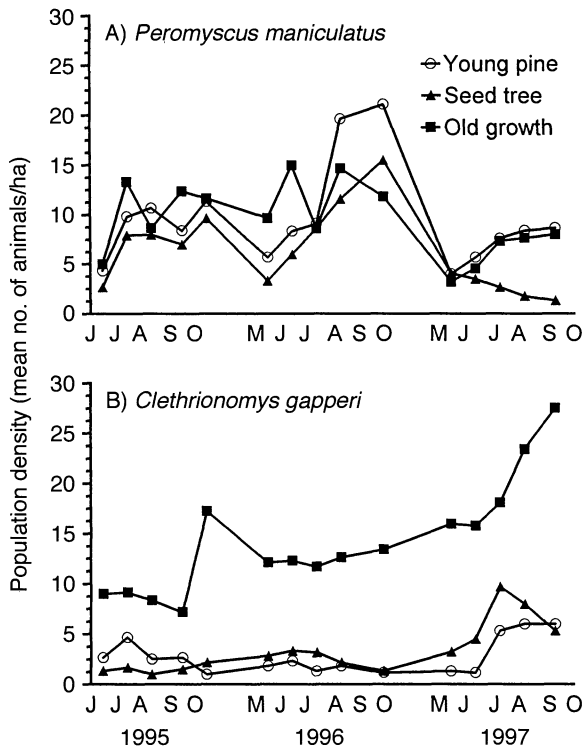
FIG. 2. Population density from Jolly-Seber estimates in the young pine, seed-tree, and old-growth stands from 1995 to 1997 for (A) *Peromyscus maniculatus* and (B) *Clethrionomys gapperi* at the Summerland study area (*n* = 3 replicates).
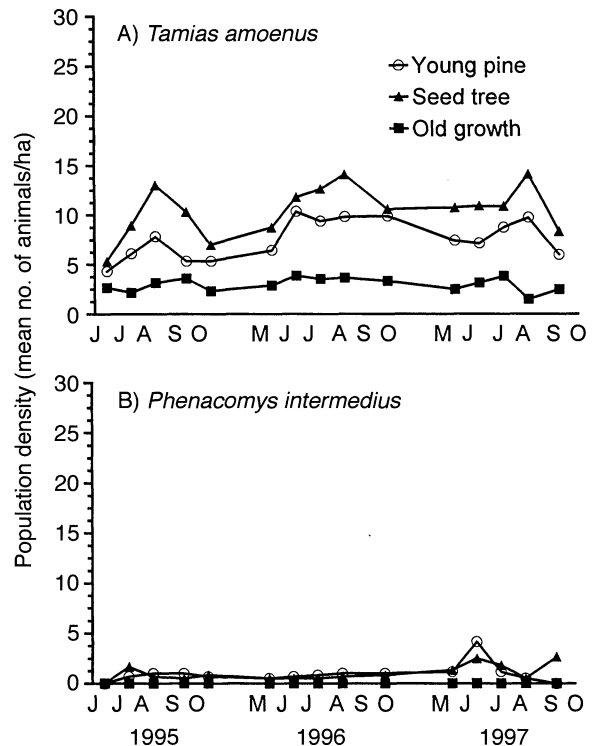

FIG. 3. Population density from Jolly-Seber estimates in the young pine, seed-tree, and old-growth stands from 1995 to 1997 for (A) *Tamias amoenus* and (B) *Phenacomys intermedius* at the Summerland study area; *n* = 3 replicates.

The goal of promoting a multistoried canopy appeared to be achieved by the significantly higher number of height classes of coniferous trees in the seed-tree than in the young pine and old-growth stands. Similarly, the high structural richness and diversity of herbs and shrubs–deciduous trees found in the young pine stands also occurred to some degree in the understory component of the seed-tree stands.

Stand structure and habitat diversity

Stand-structure attributes have been related to habitat complexity for wildlife through species diversity and structural-diversity measurements at a "snapshot" in time (17–19 yr post-harvest). Based on the results of this analysis, we cannot accept our hypothesis that stand-structure attributes (species diversity and structural diversity of herb, shrub, and tree layers) will increase from young pine to seed-tree to old-growth forest. Comparison of vertical stratification between the young pine and old-growth stands was difficult because of the considerable difference in tree heights within the main and subcanopies. In addition, there are many dimensions to stand structure, not all of which can be incorporated into one index. Our index of structural diversity might best be called "layer diversity." Thus, although structural richness appeared low in the old-growth stands, species diversity of coniferous trees and

provision of snags for cavity-using wildlife species was high (Thomas et al. 1979, Neitro et al. 1985). There tends to be a positive relationship between foliage height diversity and species richness of various taxa, particularly birds (MacArthur and MacArthur 1961, Aber 1979, Hunter 1990) and small mammals (Adler 1987, Harney and Dueser 1987). In particular, canopy tree retention after forest harvesting benefits many bird species (Hansen et al. 1995b, Hansen and Hounihan 1996, Chambers and McComb 1997, Norton and Hannon 1997). In addition, canopy structure may direct many ecological processes, including species diversity, as suggested by Hansen and Hounihan (1996). Therefore, it could be argued that the retention of seed trees in these particular forests does provide some aspects of the vertical stratification and habitats found within old-growth forests.

Total species richness of our plant communities was similar, which was different from the study reported by North et al. (1996) where richness was highest in green-tree-retention stands. However, richness and diversity measurements are strictly quantitative rather than qualitative, and hence do not reflect the actual species composition of a given community. This similarity in total species richness overlooks the 12 herb, 3 moss, and 2 shrub species that occurred in the old-growth stands only. Clearly, the combination of canopy closure and
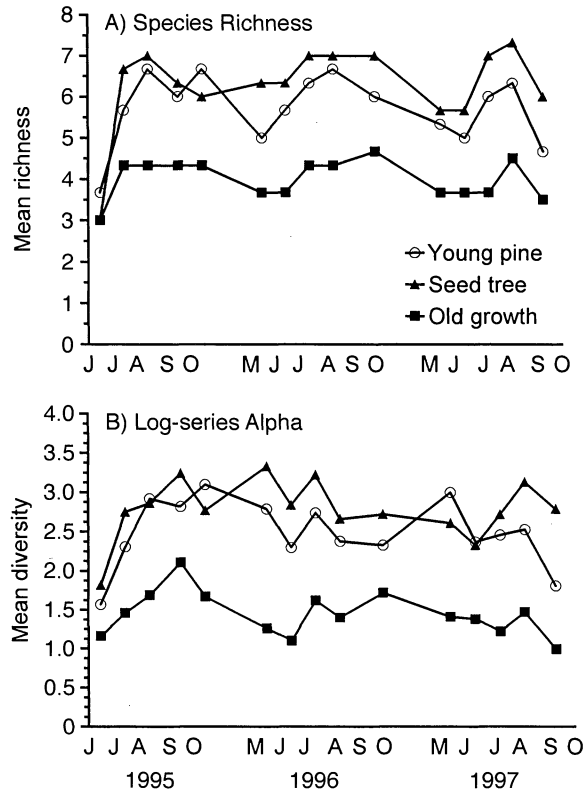
FIG. 4. Species richness and species diversity at the Summerland study area, 1995–1997. (A) Species richness and (B) log-series alpha for small-mammal communities in the young pine, seed-tree, and old-growth stands.

lack of disturbance provided microhabitats for these plant species. Harvesting disturbance either by clear-cutting or seed-tree systems did not provide conditions to maintain these particular species, at least at 17–19 yr post-harvest. The shrub–deciduous tree species unique to the young pine (seven species) and seed-tree (six species) stands were not surprising as the understory vegetation at this successional stage is dominated by this layer. The shrub species occurring only in the seed-tree stands appear to be somewhat shade tolerant and able to grow in "open" forest conditions under a partial canopy of Douglas-fir (Parish et al. 1996). Similarly, those wildlife species requiring shrub-dominated "open"-canopy forests would be accommodated in these stands. Wildlife species requiring cavities and structurally complex forests would do well in the old-growth stands. The variable plant species assemblages found in each of our stand types supports the premise of managing forests for biodiversity with a mosaic of different stand types across the landscape (Hunter 1990).

Small-mammal communities

Our hypothesis that species richness and diversity of forest-floor small-mammal communities would increase from young pine to seed-tree to old-growth for-

est is also not accepted, based on our results. In fact, we conclude that species richness and diversity of small mammals was highest in the seed-tree and young pine stands than in old-growth forest. The higher richness of forest floor small mammals in the young pine and seed-tree stands than in old-growth stands does reflect differences related to young vs. old forest. However, the small-mammal community in the seed-tree stands was composed of up to 10 species including the heather vole and western jumping mouse, which are both relatively uncommon across their ranges (Whitaker 1972, McAllister and Hoffmann 1988). Thus, this difference was not a high relative species richness composed of widespread and abundant species. No species of forest floor small mammals occurred in old-growth forest only, at least with respect to our sampling protocol. In fact, the old-growth stands were composed primarily of two common forest rodents: the deer mouse and red-backed vole (84.5% of mean abundance).

This conclusion is relevant for those forest floor small mammals sampled by Longworth live traps (Penlon Limited, Abingdon, UK). Our sampling methodology provided reasonable estimates of abundance for the eight species of surface-active rodents. However, live traps and certain types of snap traps may underestimate abundance of insectivores such as *Sorex* spp. (Pucek 1969, Wiener and Smith 1972, West 1985). In addition, small soricids are particularly difficult to sample (Wolfe and Esher 1981). *S. hoyi* may have occurred in our study area but was not captured by our live traps. *S. palustris* lives primarily near water and was unlikely to occur in our particular treatment stands.

Although live traps are not considered suitable for sampling shrews, there are no published studies comparing the efficacy of Longworth traps vs. other live traps, snap traps, and pitfall traps. In fact, Hawes (1977) used Longworth traps for a population study of *S. vagrans* and *S. obscurus* (now *S. monticolus,* Nagorsen 1996) in coastal coniferous forest of southwestern British Columbia. Thus, our sampling of shrews may have underestimated abundance, but the same protocol was used in all treatment units and did provide a relative measure of shrew numbers.

Other sampling protocols would be required to measure abundance of red squirrels, northern flying squirrels, bushy-tailed woodrats, and northern pocket gophers in our treatment stands. Similarly, track transects for short-tailed weasel (and other small carnivores) would have supplemented the minor amount of data collected for this mustelid.

Zapus may live in a variety of habitats, particularly abandoned grassy fields and riparian or wooded areas with abundant herbaceous vegetation (Whitaker 1972). Heather voles are found primarily in dry, open coniferous forests with an understory of low shrubs, as well as shrubby vegetation on the borders of forests and in moist, mossy meadows (Banfield 1974). The young pine and seed-tree stands evidently provided habitat

for these two species with average densities ≤1 animal/ha. This low density was at the lower end of a range of 0.5–4.3 animals/ha for heather voles reported in montane forest in southwestern Alberta, Canada (Innes and Millar 1982). As in our study, heather voles were not trapped in closed pine or spruce–fir forests in Alberta (Millar et al. 1985), but this species did occur in pine forests of Ontario (Naylor et al. 1985).

Compared with old-growth forest, the young pine and seed-tree stands also provided suitable habitat for the meadow vole, montane shrew, and common shrew. All of these species like dense understory ground cover typical of early successional stages after disturbance (Reich 1981, Gunther et al. 1983, Doyle 1990, Nagorsen 1996). In particular, the montane shrew was positively associated with various shrub species in the Oregon Cascade Range (Gilbert and Allwine 1991). In Hawe's (1977) population study, peak numbers of montane shrews reached 5–12 animals/ha. Abundance of this soricid ranged up to 9 shrews/ha in our seed-tree stands.

The northwestern chipmunk prefers shrub-dominated habitats interspersed with herbaceous vegetation as well as open conifer stands (Sutton 1992). Thus, it is not surprising that this sciurid occurred at higher abundance in the young pine and seed-tree stands than in old growth. These results are similar to those reported for *Tamias amoenus* by Sullivan and Klenner (2000), but contrast with Townsend's chipmunk (*T. townsendii*), which appeared more abundant in old forests than in young managed forests (Raphael 1984, Carey 1991, West 1991, Rosenberg and Anthony 1993). Conversely, Hayes et al. (1995) reported that Townsend's chipmunk was a generalist across stand age and seral stage of coastal forests in Oregon (USA).

Deer mouse numbers were predictably similar in all stand types as this species occupies many different habitats, ranging from old-growth forests to open fields (Baker 1968). Our population data on red-backed voles fit their association with later successional coniferous, deciduous, and mixed-wood forests (Merritt 1981). This species is dependent on hypogeous ectomycorrhizal fungi (Maser et al. 1978, Ure and Maser 1982) and mesic conditions associated with heavy ground cover of organic matter (Martell and Radvanyi 1977, Yahner 1986). Although amounts of down wood were similar across our stand types, moisture levels and fungal development in the young pine and seed-tree stands may not have developed to levels found in old-growth forest. Red-backed voles occurred consistently in these younger stands but numbers averaged 3.1–7.3 times higher in the old-growth stands.

Experimental design

Retrospective studies are based on the assumption that past disturbances (either natural or harvesting) provide experimental units that have undergone successional change, often over decades, but still allow reasonably rigorous comparisons to be made among treatments. Our young pine and seed-tree stands were 17 yr old at the start of the study. We have assumed that the original forest composition on these sites prior to harvesting in 1978 (one stand in 1977), and subsequent successional development, were reasonably similar among stands. It would have been ideal to follow changes in plant and small-mammal communities from pre-harvest to nearly 20 yr of post-harvest successional change. However, such studies have yet to be completed.

Another potential source of variation in this design was the 2-yr difference in timing of pre-commercial thinning (1985 and 1987) in the seed-tree stands, compared with the 1985 thinning in all young pine stands. However, the mean diameter and height of main-canopy lodgepole pine appeared to be reasonably similar in young pine (7.5 ± 0.3 cm and 5.0 ± 0.1 m, respectively [mean ± 1 SE]) and seed-tree (7.1 ± 0.3 cm and 4.8 ± 0.4 m, respectively) stands.

The three study blocks acted as site replicates in an experimental design with true replicates of experimental units (Hurlbert 1984). These units were all as large as typical forestry operations. We acknowledge the concern that we did not actually intersperse the three treatment units randomly within each block. However, because past events (harvesting system and proximity of units) tended to control assignment of treatment units within a block, this was considered a randomized design.

Inferences from this study reflect responses in stand-structure attributes that have developed in the 17–19 yr after harvest. These attributes also need to be monitored immediately after harvest and on a long-term (decades) basis thereafter (McComb et al. 1993). Responses of the forest-floor small-mammal communities to treatment stands represented spring to autumn seasons, and may not have been the same during winter months. However, the study did cover three years and there were no dramatic changes in abundance from one year to the next during the overwinter periods when data were not available. Species richness and diversity also followed this pattern. In terms of the consistency of these responses to treatments, these years were considered temporal replicates.

Conclusions

Our results indicate that (1) stand-structure attributes (species diversity and structural diversity of herbs, shrubs, and trees), at 17–19 yr post-harvest, across young pine, seed-tree, and old-growth stands suggest that each stand type offers its own structural diversity to the forest landscape; and (2) the species richness and diversity of forest floor small mammals was higher in seed-tree and young pine stands than in old-growth forest. Because of these differences in stand structure and forest-floor small-mammal communities, these three stand types, as well as a range of canopy tree

densities arising from other silvicultural systems, need to be maintained across the landscape. It would be prudent to investigate the response of other wildlife communities, e.g., birds, amphibians, large mammals, to these stand types since other species may have quite different responses to these particular forest conditions. This approach would best meet the goal of managing the forest landscape for biodiversity.

Seed-tree systems in this forest type emulate a natural disturbance whereby some residual old-growth Douglas-fir survive amidst fire-regenerated stands of lodgepole pine and fir. Stand-replacement fires have also occurred, resulting in some patches of pure pine stands. In this light, it would be most interesting to compare the young pine and seed-tree stands to structurally similar, and same-age, stands arising from wildfire disturbance. This case would have been the "true" ecological comparison. Presumably amounts of coarse woody debris would be higher in the post-harvest stands than in those occurring from wildfire.

The structural richness and diversity of coniferous trees in the multistoried canopy of seed-tree stands provide some components of old-growth or mature-forest habitat. Similarly, the structural richness and diversity of herb and shrub–deciduous tree layers found in young pine stands also occur to some degree in the understory component of the seed-tree stands. Although these residual trees provide attributes of old-growth forest structure such as a source of snags and down wood in the future forest, they also appear to impact understory stand regeneration and growth. The silvicultural implications of this impact must also be addressed on a landscape basis, in terms of future timber production.

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