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STAND STRUCTURE AND SMALL MAMMALS IN YOUNG LODGEPOLE PINE FOREST: 10-YEAR RESULTS AFTER THINNING

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Abstract. Management of forested landscapes for biological diversity is a major objective across North America. Perhaps the greatest potential to diversify future forests lies in the vast areas of young second-growth stands which may be managed silviculturally to accelerate ecosystem development. This study was designed to test the hypotheses that large-scale precommercial thinning, at ages 17–27 yr, to various stand densities would, over the 10-yr period since treatment, enhance: (1) productivity of lodgepole pine (*Pinus contorta*) crop trees, (2) stand structure attributes, and (3) species richness and diversity of forest floor small-mammal communities. Study areas were located near Penticton, Kamloops, and Prince George in south-central British Columbia, Canada, in three forest ecological zones. Each study area had three stands thinned to densities of ~500 (low), ~1000 (medium), and ~2000 (high) stems/ha, with an unthinned juvenile pine and old-growth pine stand for comparison. Understory vegetation was measured in all stands in 1990, 1993, and 1998, and coniferous tree layers were measured in 1998. Small-mammal populations were sampled intensively in 1990, 1991, and 1998.

Mean diameter increments of trees in the low-density stands were significantly higher than those in the medium- and high-density stands at all study areas. Mean height increments of trees were similar in the medium- and high-density stands and significantly higher than that in the low-density stands at Penticton and Prince George. Crown volume index (biomass) of herbs was highest in the thinned stands by 1998, but there was no difference among stands for shrubs and trees; volume of mosses was highest in the old-growth stands. Mean species richness and diversity of herbs, shrubs, and trees were similar among stands at 2, 5, and 10 yr after thinning. However, mean species diversity and structural diversity of coniferous trees were significantly higher in the low- and medium-density stands than in the high-density and unthinned stands 10 yr after thinning. Total structural diversity of all vegetation in the low-density stands was significantly greater than that of the medium-density, unthinned, and old-growth stands in 1998.

Mean total abundance of all small mammals was similar among stands in 1990–1991, but the low-density and old-growth stands had the most mammals in 1998. Mean abundance of southern red-backed voles (*Clethrionomys gapperi*) was consistently higher (2.1–3.3 times) in the old-growth stands than in unthinned stands. In seven of nine cases, mean abundance of red-backed voles was similar among old-growth and thinned stands. Mean species richness and species diversity of small mammals were highest in the low-density and medium-density stands. Heavily thinned lodgepole pine stands developed structural attributes such as large diameter trees, large crowns, and structurally diverse vegetative understories. Forest floor small-mammal communities reflected the compositional and structural diversity of these managed stands.

Key words: *biodiversity; crop trees; old-growth forest;* Pinus contorta; *precommercial thinning; silviculture; small mammals; species richness and diversity; stand density; stand structure; tree growth; wildlife habitat.*

INTRODUCTION

Managing and conserving forests for biological diversity has become a major objective for forested landscapes in North America and elsewhere (Carey 2000). This objective may be achieved by a combination of practices that provide a variety of forest successional stages (including old-growth), tree species, and stand structures in a mosaic of habitats across a landscape (Hunter 1990). Perhaps the greatest opportunity to diversify forests for the future lies in the vast areas of young second-growth stands which are amenable to silvicultural practices to accelerate ecosystem development (Carey and Curtis 1996, Hayes et al. 1997).

There are hundreds of thousands of forested hectares in early seral stages (1–30-yr-old) across the interior lands of the Pacific Northwest. Lodgepole pine (*Pinus contorta*) is the dominant coniferous tree species comprising these young forests, having regenerated after

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both forest harvesting and wildfire (Koch 1996*a*). Overall, this species is the fourth most extensive timber type in the western United States occupying six million hectares. In Canada, lodgepole pine forests occupy ~20 million ha, mostly in British Columbia (B.C.) and Alberta (Koch 1996*b*).

As discussed by Hayes et al. (1997), most young seral stands are structurally simple with a single canopy layer, limited number of tree species, relatively little understory vegetation, and variable numbers of standing or fallen dead trees. Young lodgepole pine forests are a classic example of stands with these attributes. A silvicultural practice which could help diversify these simple stands and contribute to both volume and quality increases in wood fiber is the use of precommercial thinning or stand density management (Johnstone 1985). Young lodgepole pine stands are currently thinned to within a very narrow range of stand densities in precommercial thinning programs in B.C. (typically 1600–2000 stems/ha; Johnstone 1985). Thinning is a tool that could dramatically alter stand structure and the rate and direction of ecological succession, and hence diversification of thinning prescriptions could have profound implications for wildlife habitat and biological diversity.

Low-density or open stands delay canopy closure and provide an opportunity to create early successional stages of herb and shrub layers in understory vegetation. This vertical structure provides forage and cover for several wildlife species (Lyon 1987, Nyberg 1990, Carey and Johnson 1995, Hayes et al. 1995, Hagar et al. 1996). In addition, open-grown crop trees have large diameters and canopies that tend to simulate late seral forest and old-growth conditions (McComb et al. 1993, Carey and Curtis 1996). Heavily thinned stands have reduced wood volume (O'Hara 1988) but are tailored to large-diameter timber and the production of quality products (Jozsa and Middleton 1994). Barbour et al. (1997) and Lippke and Fretwell (1997) concluded that appropriately managed Douglas-fir (*Pseudotsuga menziesii*) stands could be managed for both structural diversity and quality wood products.

Stands of higher density, both managed and unmanaged, provide important thermal, security, and nesting cover for wildlife (Lyon 1987, Hagar et al. 1996). Thickets and patches of dense lodgepole pine provide important habitat for many fur-bearing species and their prey such as lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*; Koehler 1990). These higher density stands are well suited for wood volume production for the construction lumber market (Jozsa and Middleton 1994).

The abundance and diversity of forest floor small-mammal communities may provide measures of the integrity of ecosystem function within temperate coniferous forests (Aubry et al. 1991, Carey and Johnson 1995, Carey et al. 1999, Sullivan et al. 2000). Ecosystem function (i.e., the internal dynamics of the forest) is crucial to biological diversity and forest health (Spies and Franklin 1988, 1991). There are several small mammal species whose ecological roles overlap. These roles have shared functions within the forest ecosystem and include distribution of beneficial mycorrhizal fungi (Maser et al. 1978); consumption of invertebrates (Buckner 1966); aeration of soil and distribution of nutrients; consumption of plants, seeds, lichen, and fungi; and prey for a wide variety of avian, reptilian, and mammalian predators (Craighead and Craighead 1956, Martin 1994, Carey and Johnson 1995). Thus, forest floor small mammals, as a group, may serve as indicators of change in forest structure.

The combination of a very limited range of stand density regimes and extensive distribution of young stands of lodgepole pine seems paradoxical if we are truly managing forests for biological diversity. In particular, development of old-growth structural attributes (large dominant trees, smaller shade-tolerant trees, multilayered canopies, snags, and an abundance of coarse woody debris; Franklin et al. 1981, Carey and Johnson 1995) in thinned stands needs to be assessed through time. Development of young coniferous forests in the Pacific Northwest appear to have five processes of development: crown-class differentiation (dominance and suppression of different individuals and species), canopy stratification, decadence, understory development, and development of habitat breadth (Carey 1998, Spies 1998). Habitat breadth is a function of structural and compositional diversity produced by tree species diversity, foliage-height diversity, and variety of vegetation types (Carey 1998). Unfortunately, there is a paucity of studies that actually document changes in stand structure and forest floor small mammals with stand management of lodgepole pine or other second-growth coniferous species.

This study was designed to test the hypotheses that large-scale stand thinning to various densities, over the 10-yr period after treatment, would enhance: (1) productivity and structural features (crown volume, diameter, and height growth) of lodgepole pine crop trees (dominant trees destined for harvest); (2) stand structure attributes (species diversity and structural diversity of herb, shrub, and tree layers); and (3) abundance and diversity of forest floor small-mammal communities.

METHODS

Study areas

Study areas were selected on the basis of having several thousand hectares of young lodgepole pine stands. Candidate stands within each of the three study areas had relatively uniform tree cover and comparable diameter, height, and density of lodgepole pine trees prior to stand thinning. Location, proximity (boundaries), and size (15–39 ha) of candidate stands were determined by a balance between adequate interspersion of experimental units (Hurlbert 1984) and oper-

TABLE 1. Characteristics of lodgepole pine stands at the Penticton, Kamloops, and Prince George study areas, British Columbia.

Study area and stand	Density (stems/ha)	Area (ha)	Mean age (yr)	1988†			1998		
				n	dbh (cm)‡	Height (m)‡	*n*	dbh (cm)‡	Height (m)‡
Penticton									
A	475	20	17	194	8.0 ± 0.2	5.1 ± 0.1	194	14.8 ± 0.2	8.9 ± 0.1
B	1170	20	17	190	8.5 ± 0.1	5.6 ± 0.1	190	13.9 ± 0.2	9.8 ± 0.1
C	1490	20	17	196	7.7 ± 0.1	5.3 ± 0.1	196	12.7 ± 0.2	9.7 ± 0.1
D	4755	100+	17	···	···	···	100	8.3 ± 0.3	7.0 ± 0.1
Kamloops									
A	455	22	24	195	11.5 ± 0.2	8.2 ± 0.1	195	16.5 ± 0.2	12.3 ± 0.1
B	895	15	23	199	11.7 ± 0.2	8.6 ± 0.1	199	15.2 ± 0.2	12.5 ± 0.1
C	1555	19	27	187	8.7 ± 0.1	8.4 ± 0.1	187	12.2 ± 0.2	11.0 ± 0.1
D	7665	100+	27	···	···	···	99	9.8 ± 0.3	11.7 ± 0.2
Prince George									
A	480	39	20	171	11.3 ± 0.3	8.7 ± 0.2	171	17.8 ± 0.3	12.3 ± 0.2
B	765	32	19	189	11.0 ± 0.3	8.6 ± 0.2	189	16.1 ± 0.3	13.0 ± 0.2
C	1640	30	15–20	188	8.8 ± 0.3	7.0 ± 0.2	188	13.5 ± 0.3	11.3 ± 0.2
D	4300	41	20	···	···	···	100	12.1 ± 0.3	11.6 ± 0.2

† 1989 for the Kamloops study area.
‡ Values are means ± 1 SE.

ational feasibility, in terms of road access and logistics for crews to conduct the thinning.

The Penticton Creek study area was located in south-central British Columbia, Canada, 15 km northeast of Penticton (49°34′ N, 119°27′ W). This area is within the Interior Douglas-fir (IDF_{dk}) biogeoclimatic zone (Meidinger and Pojar 1991). Topography in the area is hilly with sandy loam soil at 1340–1500 m elevation and southeast aspect, with a mean slope of 10%. The climate is characterized by warm dry summers and cool winters. The mean temperature is below 0°C for 2–5 mo, and above 10°C for 3–5 mo, with mean annual precipitation ranging from 30 to 75 cm. Open to closed mature forests of Douglas-fir cover much of this zone, with even-aged postfire lodgepole pine stands at higher elevations. This area (several thousand hectares) was burned by wildfire in 1970, salvage logged in 1971, and planted with lodgepole pine in 1972. Natural regeneration increased the density of pine to 18 500–30 000 stems/ha. Minor components of the stands include Douglas-fir, Engelmann spruce (*Picea engelmannii*), western larch (*Larix occidentalis*), willow (*Salix* spp.), Sitka alder (*Alnus sinuata*), and trembling aspen (*Populus tremuloides*).

Precommercial thinning was conducted in 1978, leaving ~1000–2000 stems/ha. Additional ingress of pine during the 10-yr post-thinning period up to 1988 resulted in the need to conduct further thinning. In 1988, dbh (1.3 m above the soil surface) ranged from 7.7 ± 0.1 (mean ± 1 SE) to 8.5 ± 0.1 cm, with a mean age of 17 yr. Stand height ranged from 5.1 ± 0.1 to 5.6 ± 0.1 m (Table 1). In 1998, the mean stand diameter ranged from 12.7 ± 0.2 to 14.8 ± 0.2 cm and mean stand height ranged from 8.9 ± 0.1 to 9.8 ± 0.1 m (Table 1). All stands were 0.2–2.3 km apart.

The Kamloops study area was located 30 km south of Kamloops, British Columbia (50°28′ N, 120°32′ W) within the Montane Spruce (MS_{dm}) biogeoclimatic zone (Meidinger and Pojar 1991). Engelmann and hybrid spruce (*P. engelmannii* × *P. glauca*) and varying amounts of subalpine fir (*Abies lasiocarpa*) are the characteristic tree species. Due to past wildfires, successional forests of lodgepole pine, Douglas-fir, and trembling aspen are common. This zone has a cool continental climate characterized by cold winters and moderately short, warm summers. The mean temperature is below 0°C for 5 mo, and above 10°C for 2–4 mo, with mean annual precipitation ranging from 38 to 90 cm. The topography is hilly at 1400–1500 m elevation, with northerly aspects. This area (~15 000 ha) was burned by wildfire in 1960 and regenerated naturally to lodgepole pine with a mean density of 20 000 stems/ha. Minor components of the stands include Engelmann spruce, subalpine fir, willow, Sitka alder, and trembling aspen.

Precommercial thinning was conducted from 1975 to 1978, leaving 1100–1600 stems/ha over ~200 ha. However, additional ingress of pine up to 1989 suggested that further thinning was warranted. In 1989, the mean stand diameter and height ranged from 8.7 ± 0.1 to 11.7 ± 0.2 cm and 8.2 ± 0.1 to 8.6 ± 0.1 m, respectively. In 1998, mean stand diameter ranged from 12.2 ± 0.2 to 16.5 ± 0.2 cm, and mean stand height ranged from 11.0 ± 0.1 to 12.5 ± 0.1 m (Table 1). Area of stands ranged from 15 to 22 ha. These stands were 0.5–5.0 km apart.

The Prince George study area was located 60 km west of Prince George, British Columbia (53°52′ N, 123°32′ W) in the Sub-boreal Spruce (SBS_{dw}) biogeoclimatic zone (Meidinger and Pojar 1991). The general topography is gently rolling, at 800 m elevation and variable aspects. In mature stands, hybrid Engelmann

TABLE 2. Characteristics of the old-growth stands at the Penticton, Kamloops, and Prince George study areas in 1998.

Study area	Relative abundance (%)	dbh (cm) Understory (dbh ≤ 15 cm)	dbh (cm) Overstory (dbh > 15 cm)	Height (m)	Density (stems/ha) Understory (dbh ≤ 15 cm)	Density (stems/ha) Overstory (dbh > 15 cm)	Snags (snags/ha)† Understory (dbh ≤ 15 cm)	Snags (snags/ha)† Overstory (dbh > 15 cm)
Penticton							850	90
L. pine	64.6	11.7 ± 0.4	18.8 ± 0.3	21.5 ± 0.5	480	620	(6.7 ± 0.3)	(21.0 ± 5.9)
Spruce	14.6	8.9 ± 0.7	25.0 ± 2.5	20.2 ± 1.0	350	140		
S. fir	20.8	6.9 ± 0.6	22.0 ± 1.3	22.4 ± 1.3	540	200		
Kamloops							30	140
L. pine	21.1	9.9	29.3 ± 1.4	23.9 ± 1.3	10	160	(11.4 ± 2.3)	(27.0 ± 2.5)
Spruce	10.5	3.9 ± 0.7	30.8 ± 6.2	20.1 ± 1.7	100	80		
S. fir	68.4	6.8 ± 0.4	21.8 ± 0.7	19.5 ± 0.7	1060	520		
Prince George							340	90
L. pine	57.5	12.2 ± 0.7	23.2 ± 0.9	23.3 ± 0.8	100	460	(6.3 ± 0.6)	(20.6 ± 1.4)
Spruce	42.5	6.7 ± 0.4	21.7 ± 0.9	23.5 ± 1.5	1060	340		
S. fir	0.0							

Note: Values for dbh and height are means ± 1 SE. L. pine = lodgepole pine; S. fir = subalpine fir.

† Snags were not identified to species; the values shown are the total number of snags for each study area. Snag dbh is shown in parentheses beneath each value (mean ± 1 SE).

× white spruce and subalpine fir are mixed with extensive stands of lodgepole pine, which regenerated after wildfires. Stands of young lodgepole pine covered ~1000 ha; this area was harvested 1966–1972 and left to natural regeneration of pine. Stand densities ranged from 2700 to 4700 stems/ha. Minor components of the stands included white spruce, black spruce (*P. mariana*), Douglas fir, willow, alder, and aspen. In 1988, mean stand diameter and height ranged from 8.8 ± 0.3 to 11.3 ± 0.3 cm and 7.0 ± 0.2 to 8.7 ± 0.2 m, respectively. Age of trees ranged from 15 to 20 yr (Table 1). In 1998, the mean stand diameter ranged from 13.5 ± 0.3 to 17.8 ± 0.3 cm and mean stand height ranged from 11.3 ± 0.2 to 13.0 ± 0.2 m (Table 1). The area of the stands ranged from 30 to 39 ha. These stands were 0.5–1.7 km apart.

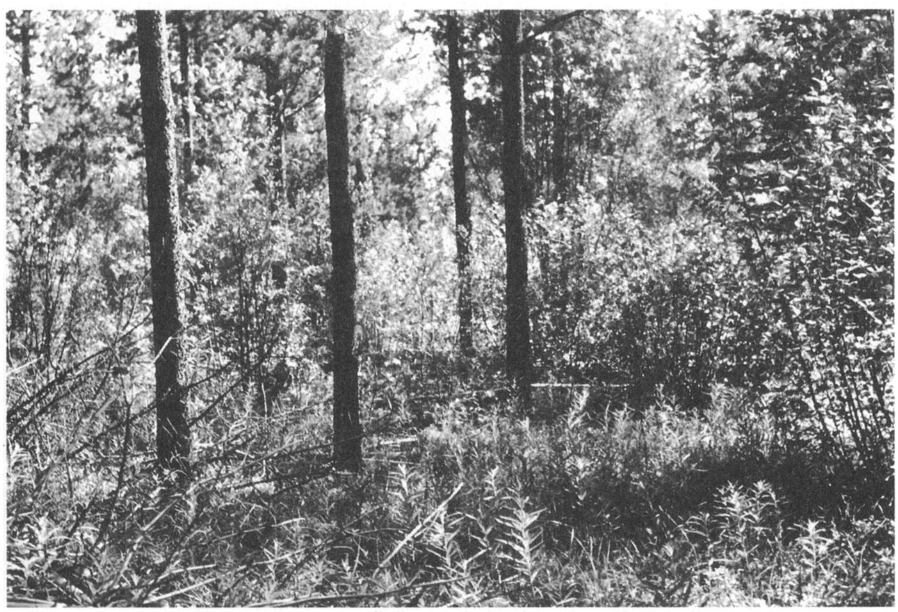
The old-growth stands at the three study areas were all in the age range of 160–250 yr. The Penticton stand was dominated by lodgepole pine with a 64.6% relative abundance, followed by spruce (14.6%) and subalpine fir (20.8%) for overstory trees (Table 2). The Kamloops stand was dominated by subalpine fir (68.4%) with lesser proportions of somewhat larger diameter pine and spruce. The Prince George old-growth stand had similar abundance of lodgepole pine (57.5%) and spruce (42.5%) trees. Heights of overstory trees ranged from 19.5 to 23.9 m and were similar in all stands (Table 2). Overall stand density in stems/ha was 2330 (Penticton), 1930 (Kamloops), and 1960 (Prince George). Overstory snag densities ranged from 90 stems/ha at Penticton and Prince George to 140 stems/ha at Kamloops (Table 2).

Experimental design

The usual prescription (>90% of stands) for precommercial thinning of lodgepole pine in B.C. is 1600–2000 stems/ha after thinning; variations from this range tend to be higher, rather than lower, based on local site conditions and silvicultural programs. Thus, we investigated a low, medium, and high density in our experimental design. In addition, unthinned juvenile and old-growth lodgepole pine stands were included at each study area in the following design: stand A is low density, target 500 stems/ha; stand B is medium density, target 1000 stems/ha; stand C is high density, target 2000 stems/ha; stand D is unthinned >2000 stems/ha; and stand E is old growth (Figs. 1, 2, 3, and 4). This range of stand densities, after thinning, was considered large enough to allow detection of changes in productivity of crop trees, stand structure attributes, and diversity of small-mammal communities through time in response to habitat alteration. It also provided an opportunity to analyze 10-yr (1988–1998) diameter and height increments of lodgepole pine growing at these three densities. This broad range of densities was considered sufficient to cause measurable changes in these growth attributes. Treatments were assigned to stands in a randomized block design. Each of the three study areas was considered a regional replicate (block).

Operational thinning was conducted after the growing season in the fall of 1988 at the Penticton and Prince George study areas, and after the growing season in the fall of 1989 at the Kamloops study area. Trees in the low-density stands were pruned to a 2.8-m lift (above ground level) at Penticton (October 1992), Kamloops (September 1992), and Prince George (November 1991). The unthinned and old-growth stands (Table 2) were added to the design at each study area in 1990, primarily to compare stand structure attributes and small-mammal communities between thinned and unthinned stands of juvenile pine and old-growth pine.

1988



1998

FIG. 1. Photographs of thinned stands with 500 stems/ha in 1988 and 1998.

Densities of pine (in stems/ha) in the unthinned stands were 5000 at Penticton, 6000 at Kamloops, and 4700 at Prince George in 1988. These densities were 4755, 7665, and 4300, respectively, in 1998.

Tree growth and stand structure

All sampling of lodgepole pine crop trees was done with 20 variable-radius plots, systematically located in each stand, to accommodate variations in stand density. For the thinned stands, the 10 crop trees closest to each plot center were permanently tagged. Measurement of the total height and dbh (both in cm) at a permanent reference point was done at the initial sampling period in October and November 1988 (Penticton and Prince George) and November 1989 (Kamloops). Diameter and height remeasurements were conducted in October 1998 to provide 10-yr growth increments at Penticton and Prince George, and 9-yr growth increments at Kamloops. Height and width (both in cm) of tree crowns were measured for all sample crop trees in ev-

1988

1998

FIG. 2. Photographs of thinned stands with 1000 stems/ha in 1988 and 1998.

ery other plot in the three thinned stands at each study area (after Schmidt and Seidel 1988).

Permanent sample plots were not installed in the unthinned stand at each study area because the greater diameter and height growth of trees in thinned than unthinned stands is well established in previous studies (Johnstone 1985, Sullivan et al. 1993). However, 10 temporary plots were located every 50–100 m in a grid pattern throughout each of the unthinned stands in 1998 to provide measurements of mean dbh and representative heights for descriptive comparisons with the thinned stands. The 10 potential crop trees closest to each plot center were sampled. Crop trees were chosen on the basis that those trees would be left as the future crop if the stand was thinned. Height and width of tree crowns of sample trees in all plots were also measured for comparison with trees in the thinned stands.

Sampling of coniferous tree species in layers in 0–1, 1–2, 2–3, and >3 m height classes was done in a

1988

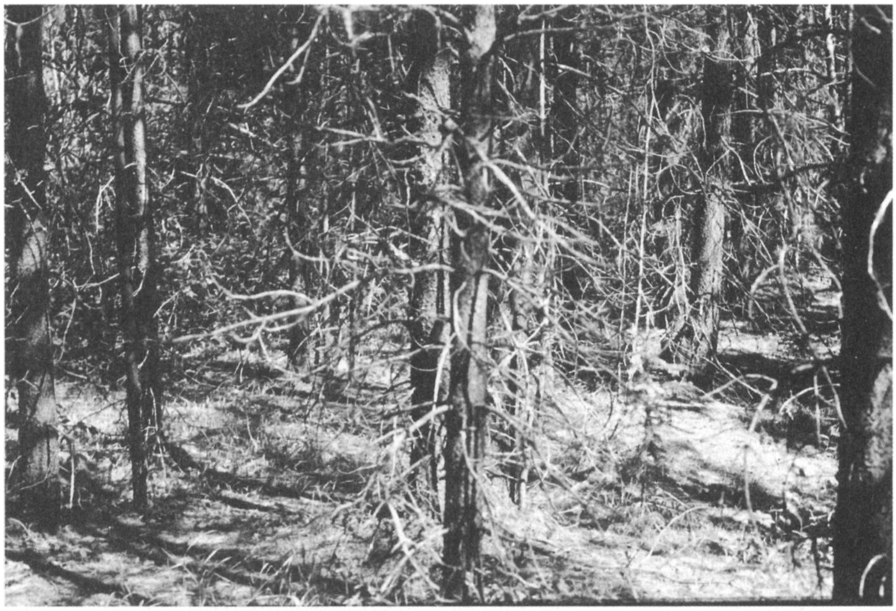
1998

FIG. 3. Photographs of thinned stands with 2000 stems/ha in 1988 and 1998.

5.64 m radius circular plot (100 m^2) located in the center of each crop tree plot. This sampling was conducted in the three thinned stands and one unthinned stand at each study area.

To provide a descriptive summary of the old-growth stands, 10 temporary plots were established in 1998 in a grid pattern throughout each stand as described above. The species and dbh of all trees in a given plot were recorded as well as whether they were alive or dead. Representative heights and crown measurements were taken for two trees in each plot. Coniferous tree layers were sampled in twenty 5.64 m radius plots established in a grid pattern.

Downed wood was recorded along two 20-m transect lines at five locations within each of the five stands at each study area. As each piece was encountered, its diameter where the transect line crossed the wood (cm) and hardness (using five decay classes) were recorded. The volume of downed wood (m^3/ha) was calculated by the method of Van Wagner (1968).



Unthinned lodgepole pine stand

Old-growth pine stand

FIG. 4. Photographs of the (top) unthinned young lodgepole pine and (bottom) old-growth lodgepole pine stands in 1998.

Understory vegetation

Three 25-m transects, consisting of five 5 × 5 m plots, were randomly located in each of the five stands at each of the study areas. Each plot contained three sizes of nested sub-plots: the 5 × 5 m plot for sampling trees, a 3 × 3 m subplot for sampling shrubs, and a 1 × 1 m subplot for sampling herbs and mosses. Tree, shrub, and herb layers were subdivided into height classes: 0–0.25, 0.25–0.5, 0.5–1.0, 1.0–2.0, 2.0–3.0, 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 a crown volume index (m^3/0.01 ha) for each plant species (Stickney 1980, 1985). The product of percentage cover and representative height gives the volume of a cylindroid which 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 a 0.01-ha base to produce the values given for species and layer (mosses, herbs, shrubs, and trees). Sampling was done in July–August 1990, 1993, and 1998. Only two transects were available for sampling in the old-growth stand at Penticton in 1993 because of salvage logging associated with spot outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) at the location of the third transect. A new transect was added for the sampling in 1998. Plant species were identified in accordance with Hitchcock and Cronquist (1973), MacKinnon et al. (1992), and Parish et al. (1996). Grasses and mosses were not identified to species.

Species richness, species diversity, and structural diversity (foliage height diversity; MacArthur and MacArthur 1961) were calculated for these data.

Small-mammal communities

Forest floor small-mammal populations were sampled at 2-wk intervals from May to September 1990 and 1991, and at 4-wk intervals from June to October 1998. Trapping grids (1 ha) had 49 (7 × 7) 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 coarse brown 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 (*Peromyscus maniculatus*), northwestern chipmunk (*Tamias amoenus*), meadow vole (*Microtus pennsylvanicus*), long-tailed vole (*M. longicaudus*), southern red-backed vole (*Clethrionomys gapperi*), heather vole (*Phenacomys intermedius*), montane shrew (*Sorex monticolus*), common shrew (*S. cinereus*), wandering shrew (*S. vagrans*), and short-tailed weasel (*Mustela erminea*).

All small mammals (except shrews and weasels) captured were ear-tagged and 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 to genus in 1990–1991 and to species in 1998 according to Nagorsen (1996).

The pygmy shrew (*Sorex hoyi*) and water shrew (*S. palustris*) may also have been present in our sampling areas but were not captured. The pygmy shrew is relatively uncommon, ranging in density from 0.5 to 1.2 animals/ha (Nagorsen 1996). The water shrew is strongly associated with wet habitats at densities similar to the pygmy shrew (Nagorsen 1996). The western jumping mouse (*Zapus princeps*), meadow jumping mouse (*Z. hudsonius*), and northern bog-lemming (*Synaptomys borealis*) all occurred in or near our study areas but are relatively uncommon (Banfield 1974) and were not captured. The northern pocket gopher (*Thomomys talpoides*) occurred in our study areas at Penticton and Kamloops, but rarely appeared above ground and was not 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 estimate discussed by Krebs and Boonstra (1984). Population estimates for the deer mouse, northwestern chipmunk, southern red-backed vole, and in some cases for the meadow vole and long-tailed 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 these cases, the total number of individuals captured was used to compare populations of the meadow vole, long-tailed vole, heather vole, montane shrew, wandering shrew, common shrew, and short-tailed weasel.

Diversity measures

Habitat diversity was measured by species richness, species diversity, and structural diversity. Species richness was the total number of species sampled for the plant (herbs, shrubs, and trees) and small-mammal communities in each stand (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).

Structural diversity 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 utilized the same Shannon-Wiener index with plant species represented by height classes and the amount (crown volume index) of vegetation in each class. Density of trees in each height class 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 three transects, each of which was a mean of five subplots, in a given stand. Species diversity was calculated separately for herbs, shrubs, and trees (1990, 1993, and 1998), and coniferous trees (1998). Diversity for small mammals was calculated using the estimated abundance of each spe-

TABLE 3. Summary of analysis of covariance determining the effect of stand density (500, 1000, and 2000 stems/ha) on diameter and height increments (cm) of lodgepole pine at each study area.

	Penticton			Kamloops			Prince George		
Parameter	500	1000	2000	500	1000	2000	500	1000	2000
Mean initial diameter	8.02	8.51	7.70	11.51	11.66	8.68	11.33	10.97	8.83
Mean diameter increment	6.81[a]	5.25[b]	5.05[b]†	4.95[d]	3.52[e]	3.53[e]‡	6.47[g]	5.14[h]	4.55[i]§
Mean height increment	378.1[a]	421.1[b]	438.0[b]‖	404.8[d]	388.6[d]	271.9[e]¶	367.7[g]	444.2[h]	427.6[h]#
Mean initial height	512.7	561.0	535.0	818.5	855.6	837.0	868.2	858.3	701.3
Mean height increment	380.0[a]	420.3[b]	436.9[b]††	410.5[d]	393.7[d]	261.1[e]‡‡	371.0[g]	447.6[h]	420.9[h]§§
Sample size	194	190	196	195	199	187	171	189	188

Notes: Within a study area, mean values followed by different letters are significantly different according to Duncan's multiple range test. Mean height increment was regressed on initial diameter in row 3, and on initial height in row 5.

† $F_{2,576} = 98.3$, $P < 0.01$.
‡ $F_{2,577} = 71.3$, $P < 0.01$.
§ $F_{2,544} = 78.1$, $P < 0.01$.
‖ $F_{2,576} = 24.0$, $P < 0.01$.
¶ $F_{2,577} = 72.3$, $P < 0.01$.
# $F_{2,544} = 25.7$, $P < 0.01$.
†† $F_{2,576} = 21.4$, $P < 0.01$.
‡‡ $F_{2,577} = 118.6$, $P < 0.01$.
§§ $F_{2,544} = 25.5$, $P < 0.01$.

cies for a given sampling period and averaged over the number of 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 the Shannon-Wiener index (Magurran 1988).

Statistical analysis

For the tree measurements, data were summarized according to initial diameter and height classes, and this format was maintained throughout the analyses. Because growth rates are dependent on initial diameter and height, an analysis of covariance (ANCOVA) was used to determine the effect of stand density on diameter and height increments at each study area.

A randomized block three-way ANOVA Model III (Zar 1984) with fixed effects of factors stand treatment (three stand densities, unthinned, and old-growth) and time (1990, 1993, and 1998) and with factor blocks as a random effect was used to test for differences in mean crown volume index of mosses, herbs, shrubs, and trees. Mean species richness and diversity and structural diversity of herb, shrub, and tree layers were also compared among treatment stands by this randomized block ANOVA.

A similar two-way analysis omitting time was used to evaluate differences in the following parameters measured in 1998: crown volume and crown ratio (crown length/total height) of crop trees; species diversity and structural diversity of coniferous tree layers; and mean volume, diameter, and decay classes of downed wood. This same analysis was used to test differences in vegetation parameters within a given sample year in some cases.

This two-way ANOVA was also used to test differences in mean abundance of each small mammal species, and mean species richness and mean species diversity for the small-mammal community. For these analyses, a mean estimate of a given parameter for each year and treatment was derived to use the variability among blocks to test for differences among levels of the treatments. Thus, there were six replicates (three spatial × two temporal) for the pooled small-mammal data in 1990–1991 and three replicates (three spatial) in 1998. Percentage data were arcsine transformed prior to analysis. Duncan's multiple range test (DMRT) was used to compare mean values. In all analyses, the level of significance was at least $P = 0.05$.

RESULTS

Tree growth and stand structure

Mean diameter increments of trees in the low-density stands were significantly higher than those in the medium- and high-density stands at all study areas (Table 3). At a stand density of 500 stems/ha, 10-yr diameter increments were 6.81 cm at Penticton and 6.47 cm at Prince George; the 9-yr diameter increment for this low-density stand at Kamloops was 4.95 cm. There was no difference in diameter increment between the medium- and high-density stands at Penticton nor at Kamloops. However, trees grew significantly faster in diameter in the medium-density stand than in the high-density stand at Prince George (Table 3). Mean height increment of trees was similar in the medium- and high-density stands and significantly higher than that in the low-density stands at Penticton and Prince George (Table 3). However, mean 10-yr height increment was similar in the low- (404.8–410.5 cm) and medium-density (388.6–393.7 cm) stands at Kamloops, but significantly higher than that (261.1–271.9 cm) in the high-density stand.

Lodgepole pine has relatively consistent crown shape. The upper portion of the tree is a long tapered cone and the lower portion is sometimes an inverted,

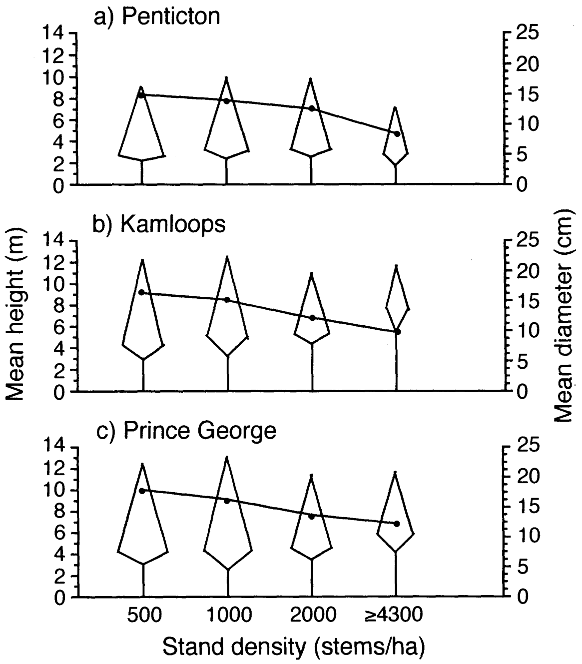


FIG. 5. Mean crown configuration of trees in 1998 for the three thinned stands and one unthinned stand at each study area. Mean height (m) is represented by the top of each tree depiction, and mean tree diameter (cm) is represented by the connected data points.

but short, tapered cone. Mean crown volume of trees was significantly ($F_{3,6}$ = 28.62, P < 0.01) different among treatment stands of young lodgepole pine (Fig. 5). Trees in both the low- (42.3 m^3) and medium-density (42.9 m^3) stands had greater crown volumes than those in the high-density (27.3 m^3) and unthinned (12.5 m^3) stands (DMRT, P = 0.05). The difference in mean crown volume between the high-density and unthinned stands was also significant (DMRT, P = 0.05).

Mean crown ratio (crown length/total height) of trees was also significantly different among treatment stands ($F_{3,6}$ = 4.68, P = 0.05). Crown ratios were similar in the low- (0.73), medium- (0.76), and high-density (0.66) stands, but both the low- and medium-density stands had higher mean crown ratios than that (0.56) in the unthinned stand (DMRT, P = 0.05).

Mean stem density of coniferous tree species and layers indicated substantial recruitment of individuals, particularly in the 0–1 and 1–2 m height classes. Ingress of conifers increased total density to 1135–3035 stems/ha in the low-density stands, 1675–2415 in the medium-density stands, and 1895–1970 in the high-density thinned stands. Total density of conifers ranged from 4600 to 7885 stems/ha for the unthinned stands and from 2690 to 19 370 for the old-growth stands. This very high density in the old-growth was composed primarily of seedling subalpine fir (16 990 stems/ha) at Kamloops.

Mean volume of downed wood was similar among treatment stands, ranging from 176 to 229 m^3/ha (Table 4). There were no differences among stands in number of wood pieces in diameter classes or decay classes, with some considerable variation within the high-density stands (Table 4).

Incidence of snags

Second-growth stands of lodgepole pine typically have few, if any, standing live or dead (snags) trees from the original stand. Although few in number, some crop trees died during the 10-yr period since thinning. The percentages (of total live and dead trees) of snags in the low-, medium-, and high-density stands at Penticton were 1.5, 0.5, and 3.0%, at Kamloops were 1.5, 0, and 1.0%, and at Prince George were 2.5, 1.5, and 1.0%, respectively. Of the dead trees which could be located in the three thinned stands, the percentage still standing was 83.3% (10 of 12) at Penticton, 55.6% (5 of 9) at Kamloops, and 22.7% (10 of 44) at Prince George. The relatively high percentage of downed trees at Prince George was due primarily to snow-press mortality in the first winter after thinning.

TABLE 4. Summary of characteristics of downed wood (volume and number of pieces of wood in diameter classes and decay classes) together with results of ANOVAs for five stands at the three study areas.

Variable	Low	Medium	High	Unthinned	Old-growth	$F_{4,8}$	P
Volume (m^3/ha)	204.6 ± 26.2	175.9 ± 45.4	194.8 ± 83.0	228.8 ± 8.3	225.4 ± 55.6	0.43	>0.75
No. of wood pieces							
Diameter classes (cm)							
<5	241.1 ± 39.6	92.4 ± 25.7	237.6 ± 114.0	101.9 ± 15.2	203.2 ± 40.1	1.35	0.35
5–25	43.8 ± 3.0	24.5 ± 4.4	41.8 ± 13.9	48.9 ± 16.5	27.3 ± 3.2	1.30	0.37
>25	1.6 ± 1.3	1.5 ± 0.5	1.3 ± 0.9	1.1 ± 0.7	3.1 ± 2.2	0.73	0.61
Decay classes							
1	0.2 ± 0.2	0.0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.41	>0.75
2	0.0	0.3 ± 0.3	0.2 ± 0.1	0.0	2.3 ± 2.1	1.05	0.45
3	197.3 ± 63.0	69.2 ± 24.8	238.3 ± 128.6	91.2 ± 9.7	185.1 ± 51.9	0.97	0.48
4	80.6 ± 24.7	42.0 ± 10.6	35.8 ± 14.6	52.1 ± 27.6	39.4 ± 14.4	1.38	0.34
5	7.7 ± 0.7	7.1 ± 1.6	6.3 ± 1.1	8.7 ± 1.8	6.6 ± 0.6	0.47	0.75

Note: Data are means ± 1 SE.

TABLE 5. Summary of analysis of variance results determining the effect of stand treatment on mean (n = 3) crown volume index, species richness and diversity, and structural diversity of herbs, shrubs, and trees at the three study areas in British Columbia.

Parameter and layer	Statistic	Crown vol. index	Species diversity: Richness	Species diversity: Diversity	Structural diversity: Richness	Structural diversity: Diversity
Herbs						
Stand	$F_{4,8}$	4.67	1.16	0.41	3.25	2.54
	P	0.03*	0.42	>0.75	0.08	0.13
Time	$F_{2,4}$	0.31	0.28	0.61	0.04	0.42
	P	0.75	>0.75	0.60	>0.75	0.70
Stand × Time Interaction	$F_{8,16}$	2.29	2.28	2.19	1.31	1.56
	P	0.08	0.08	0.09	0.32	0.22
Shrubs						
Stand	$F_{4,8}$	2.53	1.77	0.72	7.16	2.28
	P	0.14	0.24	0.61	<0.01**	0.17
Time	$F_{2,4}$	3.92	0.67	19.64	0.33	2.87
	P	0.13	0.58	<0.01**	0.74	0.19
Stand × Time Interaction	$F_{8,16}$	1.39	0.57	2.25	3.75	1.48
	P	0.28	>0.75	0.08	0.01*	0.24
Trees						
Stand	$F_{4,8}$	3.52	0.65	0.63	1.85	0.75
	P	0.07	0.65	0.66	0.22	0.59
Time	$F_{2,4}$	13.24	1.06	1.52	2.64	5.53
	P	0.02*	0.45	0.35	0.21	0.08
Stand × Time Interaction	$F_{8,16}$	1.79	1.40	0.96	2.43	1.02
	P	0.17	0.27	0.50	0.07	0.47
Total						
Stand	$F_{4,8}$		1.26	3.08	1.06	2.83
	P		0.38	0.09	0.45	0.10
Time	$F_{2,4}$		0.48	2.92	6.80	13.27
	P		0.67	0.19	0.05*	0.02*
Stand × Time Interaction	$F_{8,16}$		1.77	1.62	1.52	0.74
	P		0.17	0.21	0.22	0.66

* $P \leq 0.05$; ** $P < 0.01$.

Understory vegetation

A total of 79 species of herbs, 35 species of shrubs, and eight species of trees were sampled in this study. Mean total crown volume index of herbs was significantly different among treatment stands (Table 5). This index of herb biomass was similar ($F_{4,8}$ = 1.42, P = 0.33) among stands in 1990 but significantly different in 1993 ($F_{4,8}$ = 10.56, P < 0.01) and 1998 ($F_{4,8}$ = 6.08, P = 0.02). The medium- and high-density stands had a higher (DMRT, P = 0.05) crown volume index of herbs than that of either of the unthinned or old-growth stands in 1993, and all three thinned stands followed this pattern in 1998 (Fig. 6a). Prominent herb species in these stands included fireweed (*Epilobium angustifolium*), grasses, Arctic lupine (*Lupinus arcticus*), wild strawberry (*Fragaria virginiana*), heart-leaved arnica (*Arnica cordifolia*), white-flowered hawkweed (*Hieracium albiflorum*), showy aster (*Aster conspicuus*), bunchberry (*Cornus canadensis*), and one-sided wintergreen (*Orthilia secunda*).

Mean total crown volume index of shrubs was similar among stands (Table 5). However, shrub volume appeared to decline in the old-growth stands averaging 15.67 m^3/0.01 ha in 1990 and 8.83 in 1998. Mean crown volume index ranged from 46.33 to 57.27 m^3/0.01 ha in the four stands of young lodgepole pine in 1998 (Fig. 6b). Shrub layers in these stands were composed primarily of Sitka alder, twinflower (*Linnaea borealis*), willow, wild rose (*Rosa* sp.), black twinberry (*Lonicera involucrata*), and various species of *Vaccinium.*

Mean total crown volume index of deciduous and coniferous trees was similar among stands and increased significantly through time (Table 5, Fig. 6c). This index of tree biomass followed a predictable trend from highest volume in the unthinned stands to lowest volume in the low-density stands. Prominent trees, in addition to lodgepole pine, included aspen, interior spruce, Douglas fir, and subalpine fir.

There were the following unique assemblages (number of species) of vascular plants in the low-density (15), medium density (3), high-density (7), unthinned (0), and old-growth (12) stands. In stand comparisons, there were 11 herb and two shrub species that occurred in both the low-density and old-growth stands only. There was only one herb species that occurred in both the unthinned and old-growth stands only. A total of nine herb and eight shrub species were common to one or more of the thinned stands and old-growth stands but were not found in the unthinned stands.

Mean total crown volume index of mosses was sig-

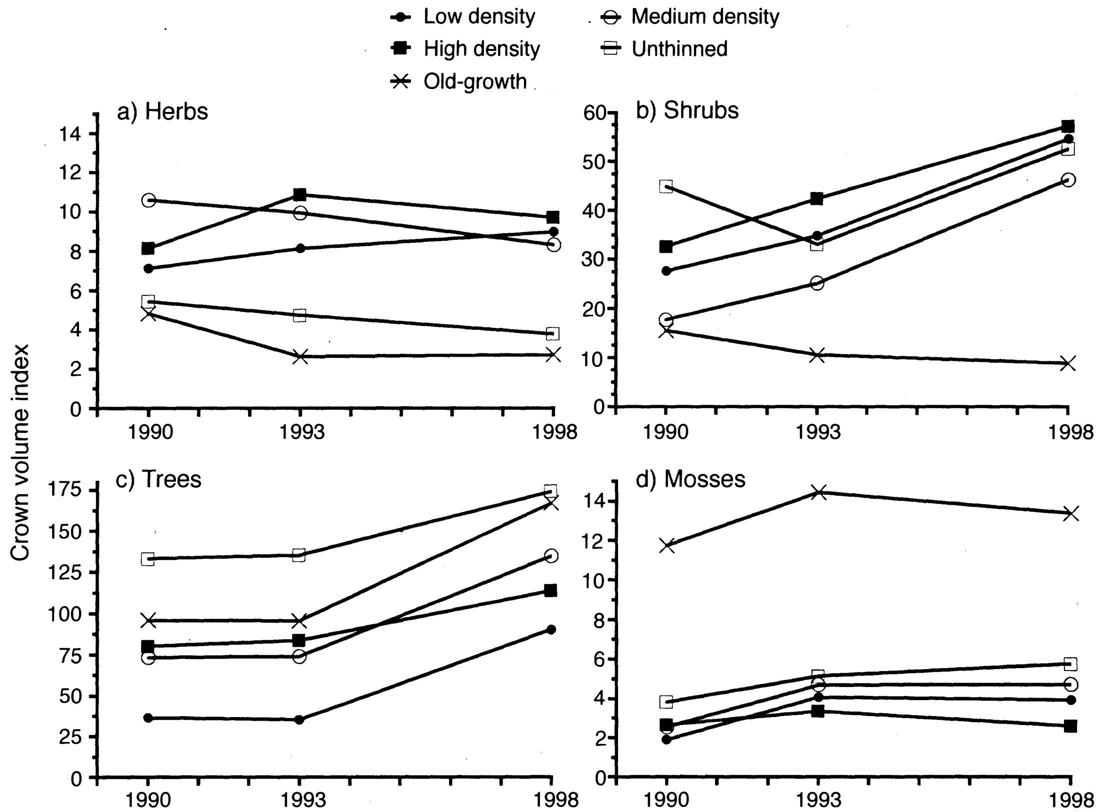


FIG. 6. Mean crown volume index (m³/0.01 ha; $n = 3$) for (a) herbs, (b) shrubs, (c) trees, and (d) mosses for the five treatment stands at 2 (1990), 5 (1993), and 10 (1998) years post-thinning.

nificantly different among treatment stands ($F_{4,8}$ = 7.12, $P < 0.01$) and over time ($F_{2,4}$ = 12.15, P = 0.02; Fig. 6d). Volume of mosses was significantly higher in the old-growth stands than in any of the other stands in all three sample years (DMRT, P = 0.05).

Species and structural diversity

Mean species richness and diversity of herbs, shrubs, and trees were similar among treatment stands (Table 5). Total species richness of all plants was similar among stands (Fig. 7a). Total species diversity also followed this pattern although the low-density stands appeared to have a consistently high diversity of plants throughout the 10 yr since thinning (Fig. 7b). Species diversity of shrubs declined over the course of the study (Table 5).

Mean species diversity of coniferous trees, based on stem counts in 1998, was significantly different among treatment stands ($F_{4,8}$ = 6.95, P = 0.01), with a more diverse component of coniferous species in the low- and medium-density stands than in the high-density and unthinned stands (DMRT, P = 0.05; Fig. 8a).

Mean structural diversity of herbs, in terms of richness of height classes (or layers of vegetation), appeared to be different among stands by 1998, but the overall comparison was not significant ($F_{4,8}$ = 3.25, P = 0.08; Fig. 9a). Comparison of stands in 1998 indicated a significant difference among stands ($F_{4,8}$ = 7.95, $P < 0.01$), with the three thinned stands having a greater richness of herb layers than the old-growth stands and the low-density stands higher than that of the unthinned stands (DMRT, P = 0.05). Species diversity also followed this pattern but there were no differences among stands (Table 5, Fig. 9b).

Mean structural diversity of shrubs was significantly different among treatment stands in terms of richness of shrub layers, but not for diversity (Table 5, Fig. 9c and D). Comparison of stands in each year approached significance in 1990 ($F_{4,8}$ = 3.73, P = 0.06), and was significantly different in 1993 ($F_{4,8}$ = 8.45, $P < 0.01$) and 1998 ($F_{4,8}$ = 7.24, $P < 0.01$). The old-growth stands had fewer shrub layers than any of the four young pine stands in both 1993 and 1998 (DMRT, P = 0.05).

There were no significant differences in richness of tree layers (both deciduous and coniferous species, based on crown volume index) or structural diversity for trees among treatment stands (Table 5). However, mean structural diversity of coniferous trees, based on stem counts in 1998 was significantly different among treatment stands ($F_{4,8}$ = 11.76, $P < 0.01$). There was greater structural diversity within coniferous tree layers in the low- and medium-density stands than in the high-density and unthinned stands (DMRT, P = 0.05; Fig.

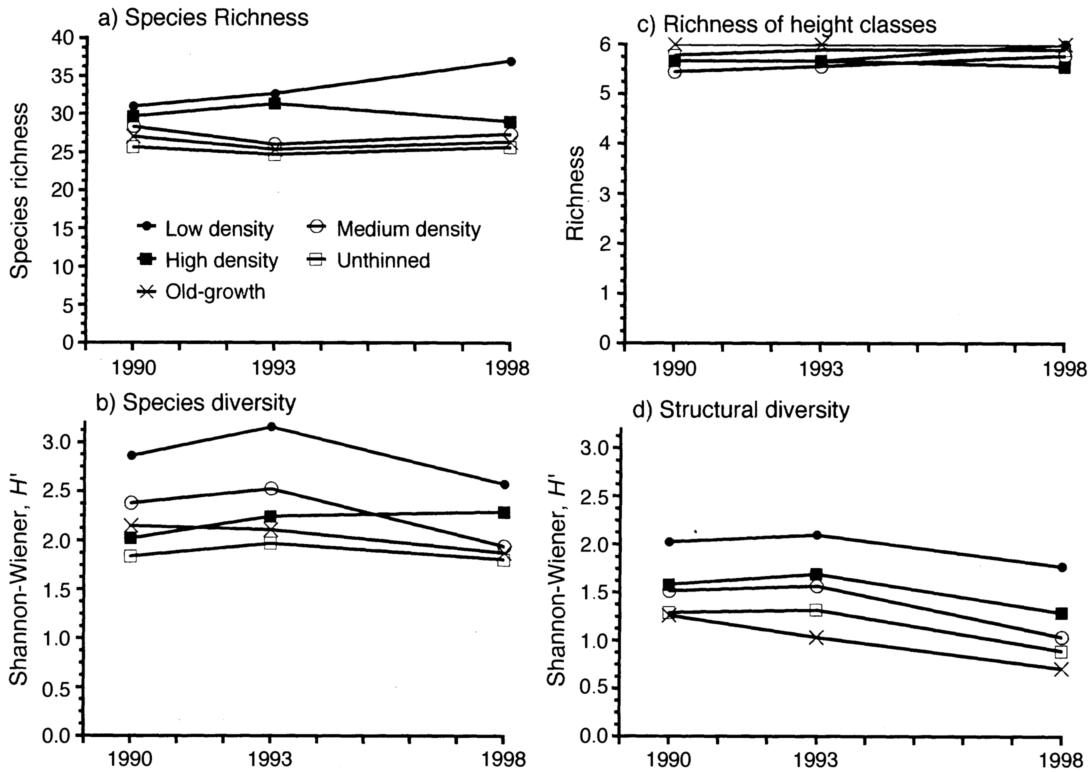


FIG. 7. Mean total species diversity and total structural diversity of vegetation (n = 3) represented by (a, c) richness, and (b, d) diversity for plants in the five treatment stands at 2 (1990), 5 (1993), and 10 (1998) years post-thinning.

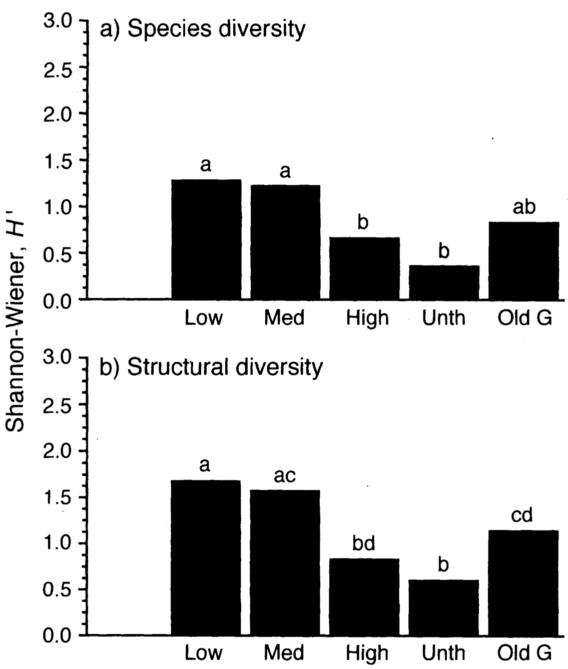


FIG. 8. Mean (a) species diversity and (b) structural diversity for coniferous trees (n = 3) in the five treatment stands in 1998, 10 yr post-thinning. Mean values represented by histograms with different letters are significantly different according to Duncan's multiple range test. Low = low density, Med = medium density, High = high density, Unth = unthinned, and Old-G = old-growth.

8b). In addition, the low-density stands were more diverse in coniferous tree layers than the old-growth stands (DMRT, P = 0.05).

Mean total structural diversity of all vegetation was similar among treatment stands for richness of layers of herbs, shrubs, and trees (Table 5, Fig. 7c). The mean total diversity index also followed this pattern but comparison of stands in 1998 indicated a significant difference among stands ($F_{4,8}$ = 5.34, P = 0.02). Total structural diversity of the low-density stand was significantly greater than that of the old-growth, unthinned, and medium-density stands in 1998 (DMRT, P = 0.05). Total structural richness and diversity declined significantly over the 10 yr of the study (Table 5).

Small-mammal abundance

Estimates of trappability (susceptibility to capture) were variable among species with mean values ranging from 65.5% to 100.0% for deer mice, from 59.0% to 91.7% for red-backed voles, from 53.6% to 97.7% for northwestern chipmunks, and from 42.9% to 90.8% for meadow voles. Therefore, for reasons outlined in Jolly and Dickson (1983), Jolly-Seber population estimates were used for this study.

Mean abundance of deer mice was significantly different among treatment stands in 1990–1991, but not in 1998 (Table 6). This common rodent occurred at higher numbers in the unthinned pine than in old-

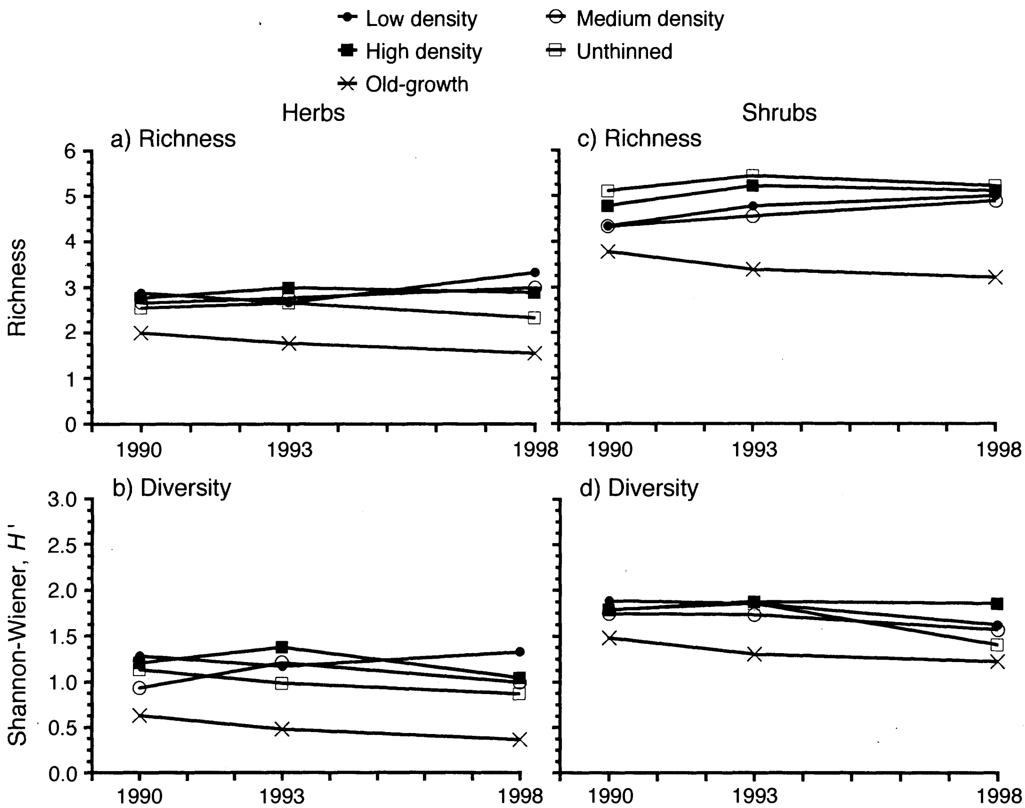


FIG. 9. Mean structural diversity of herb and shrub species (n = 3) represented by (a, c) richness of layers, and (b, d) diversity for the five treatment stands at 2 (1990), 5 (1993), and 10 (1998) years post-thinning.

growth (4.7 times) or low- and medium-density stands (1.9 times) in 1990–1991 (DMRT, P = 0.05). Mean abundance of red-backed voles was significantly different among stands in both sampling periods at 2–3 yr and 10 yr post-thinning (Table 6). There were 2.1–3.3 times as many red-backed voles in the old-growth than unthinned stands in both periods (DMRT, P = 0.05). However, their numbers were comparable in the three thinned stands and old-growth in 1990–1991, but mean abundance of this microtine was significantly lower in all young pine stands than in old-growth in 1998. However, evaluation of mean abundance and 95% confidence limits over the consecutive trapping periods each year indicated that old-growth forest had the highest density of red-backed voles in two of nine cases (Penticton in 1990 and Kamloops in 1998) compared with the three thinned stands (Fig. 10). In all cases, numbers of red-backed voles were the same or significantly higher in the three thinned than unthinned pine stands (non-overlapping 95% confidence limits).

Mean numbers of the northwestern chipmunk were similar among treatment stands in 1990–1991, with significantly more animals in the low- and medium-density stands than in the unthinned and old-growth stands in 1998 (DMRT, P = 0.05; Table 6). There were no differences in mean abundance of *Microtus* spp., heather voles, or shrews among stands (Table 6). Mean abundance of short-tailed weasels was significantly higher in the low-density stands than high-density, unthinned, or old-growth stands in 1990–1991 (DMRT, P = 0.05), with no difference in 1998.

Mean total abundance of all small mammals was similar among stands in 1990–1991, but the low-density and old-growth stands had more mammals than the high-density and unthinned stands in 1998 (DMRT, P = 0.05; Table 6).

Species diversity

Mean species richness of the small-mammal communities was significantly different among stands (Table 7), with higher richness in the low- and medium-density stands than in the unthinned and old-growth stands at 2–3 and 10 yr post-thinning (DMRT, P = 0.05). Species richness averaged over consecutive trapping periods, with 95% confidence limits, indicated a trend through time since thinning for more small mammal species in the heavily thinned pine stands than in the high-density, unthinned, and old-growth stands (Fig. 11). This difference was due primarily to the presence of meadow voles, long-tailed voles, and heather voles in these thinned stands (Table 6). In addition, the wandering shrew was present only in the low- and medium-density stands at Penticton.

Mean species diversity (Shannon-Wiener, H') was

TABLE 6. Mean values in 1990–1991 ($n = 6$) and 1998 ($n = 3$) and results of analysis of variance for population estimates per hectare.

	Stand (1990–1991)						
Species	Low	Med	High	Unth	OG	$F_{4,20}$	P
P. maniculatus	7.69[ac]	7.57[ac]	12.75[ab]	14.63[c]	3.12[b]	6.61	<0.01**
C. gapperi	6.85[ab]	7.50[ab]	6.98[ab]	3.62[b]	11.78[a]	3.49	0.03*
T. amoenus	9.12	10.10	9.51	8.31	7.58	0.35	>0.75
M. longicaudus	0.07	0.12	0	0	0	1.00	0.44
M. pennsylvanicus	0.02	0.09	0.07	0.02	0.02	0.75	0.58
P. intermedius	0	0	0	0	0		
Total rodents	23.75	25.38	29.31	26.58	22.50	1.15	0.38
S. monticolus	…	…	…	…	…		
S. cinereus	…	…	…	…	…		
S. vagrans	…	…	…	…	…		
Total shrews	0.88	0.56	0.44	0.74	0.51	0.34	>0.75
M. erminea	0.34[a]	0.16[ab]	0.09[b]	0.05[b]	0.02[b]	2.85	0.05*
Total small mammals	24.63	25.94	29.75	27.32	23.01	1.02	0.44

Notes: Within a species or group, mean values followed by different letters are significantly different according to Duncan's multiple range test. Shrews that died in traps were collected and identified to genus in 1990–1991 and to species in 1998. Unth = unthinned stand, OG = old-growth stand.
* $P \leq 0.05$; ** $P < 0.01$.

significantly different among treatment stands in both 1990–1991 and 1998 (Table 7). Log-series alpha approached significance in 1990–1991 and was significantly different among treatment stands in 1998. In general, the significant comparisons of mean species diversity indicated higher diversity of small mammals in the low- and medium-density stands than in the unthinned and old-growth stands (DMRT, $P = 0.05$). Mammal diversity in the high-density stands tended to be similar to the other thinned stands and the unthinned and old-growth stands (Table 7). This same pattern was evident in the diversity measurements averaged over consecutive trapping periods each year at each study area (Fig. 12).

Discussion

Experimental design

This study was conducted on an operational scale with treatment stands ranging in size from 15 to 39 ha. The size of these experimental units were all as large as typical forestry operations. As discussed by Walters and Holling (1990), there is a challenge in identifying experimental designs that distinguish between localized and large-scale effects, and which make the best possible use of opportunities for replication and comparison. To this end, replication in our study with such large management units precluded site replication at a given study area. Thus, the three study areas acted as regional replicates in a design with true replication of experimental units (Hurlbert 1984). This design was particularly meaningful in terms of extrapolation to lodgepole pine stands across the interior of British Columbia.

Pretreatment sampling prior to stand thinning in 1988 at Penticton and Prince George and in 1989 at Kamloops would have indicated that these study areas provided a suitable comparison of treatment stands. As outlined in Table 1 and by Sullivan et al. (1996), these stands had similar densities and growth characteristics of lodgepole pine up to the time of thinning. It is likely that pretreatment stands also had similar plant and small-mammal communities. The one-year difference in initiation of the experiment at Kamloops was due to operational logistics and was typical of step-wise adaptive management experiments (Walters et al. 1988). We have assumed that plant and mammal responses were reasonably similar between the Kamloops stands and those at Penticton and Prince George despite the one-year difference within the time frame of the study. In addition, sampling on an annual basis over the 10-yr period would have been ideal, but was not possible in this study. Measurement of vegetation change at 2, 5, and 10 yr post-thinning provided an assessment of early successional plant communities. Estimates of the volume of downed wood were quite variable in these stands and longer sample lines may have been needed.

Inferences from this study reflect responses in stand structure attributes and small-mammal abundance and diversity for the first 10 yr after precommercial thinning. Responses should be monitored through time to determine if growth rates of trees continue on the present trajectory and how vegetative succession and stand structure develop. Responses of small-mammal communities represented the early 2 to 3 yr post-thinning and then 10 yr after treatment. It is not clear if the results reported for these periods would have been recorded in the intervening years as well, particularly in light of the fluctuating populations of *Microtus* spp.

Tree growth and structure

Lodgepole pine responded positively to precommercial thinning in terms of diameter growth but the response in height growth was variable, which has been reported elsewhere for this species (Johnstone 1985,

TABLE 6. Extended.

Stand (1998)						
Low	Med	High	Unth	OG	$F_{4,8}$	*P*
8.37	3.94	9.01	7.40	7.49	0.66	0.65
7.61[a]	9.84[a]	8.07[a]	10.99[a]	23.35[b]	3.75	0.05*
6.15[a]	5.73[ab]	3.84[bc]	3.43[c]	2.22[c]	6.33	0.02*
7.61	0.80	0.20	0	0	1.04	0.46
0.20	7.78	0.33	0	0.13	1.70	0.24
0.40	0.20	0.07	0	0	3.22	0.08
30.34	28.29	21.52	21.82	33.19	3.32	0.07
2.40	2.73	1.07	0.80	0.80	2.48	0.14
0.80	0.47	1.07	1.00	0.60	0.52	0.73
0.87	0.47	0	0	0	1.00	0.47
4.07	3.67	2.14	1.80	1.40	1.39	0.34
0.20	0.47	0.07	0.27	0.40	0.93	0.49
34.41[a]	31.96[ab]	23.66[b]	23.62[b]	34.59[a]	3.90	0.05*

Johnstone and Cole 1988). This result was also reported for the five-year growth increments of pine in these same stands (Sullivan et al. 1996). As predicted by Barbour et al. (1997), diameter growth of trees in our heavily thinned stands was almost double that of trees in unthinned stands, based on 1998 mean diameters. Heavy thinning reduces the total volume of wood

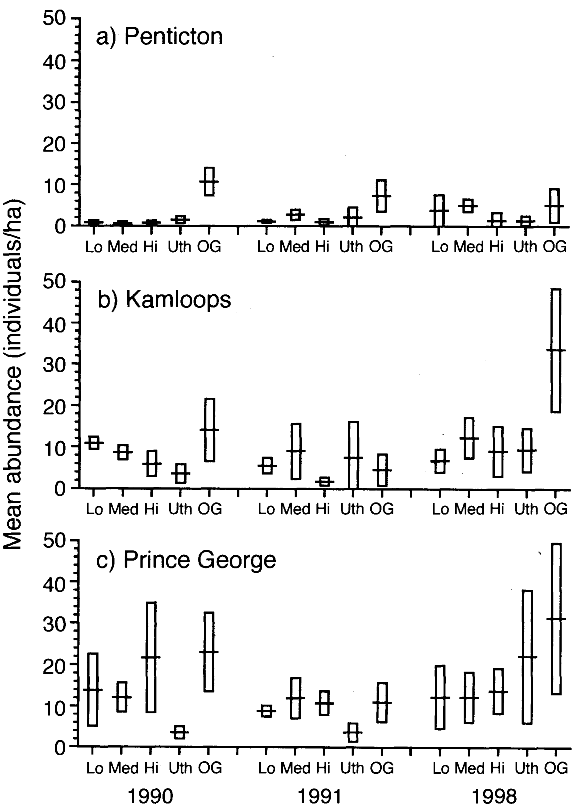


FIG. 10. Mean abundance and 95% confidence intervals for red-backed voles for the five treatment stands at each study area in 1990, 1991, and 1998. Lo = low density, Med = medium density, Hi = high density, Uth = unthinned, and OG = old-growth.

(O'Hara 1988), but does promote rapid growth of individual trees by lessening competition for light, water, and nutrients. Because of this enhanced growth, thinning could move stands out of the closed-canopy stage, at least temporarily, and accelerate the development of conditions found in late seral forests (McComb et al. 1993, Bailey 1996, Carey and Curtis 1996, Hayes et al. 1997).

The significantly larger crown volumes and crown ratios in our heavily thinned stands compared to our lightly thinned stands was similar to that recorded by Long et al. (1983) and Bailey (1996) for dominant and codominant trees in thinned 20- to 50-yr-old stands. These crowns should provide larger areas for some species of birds to nest and forage. In addition, large crowns and branch structures provide nest sites for arboreal sciurids such as the red squirrel (Rothwell 1979) and northern flying squirrel (*Glaucomys sabrinus*; Carey 1995). Large-diameter branches provide bases for bird nests and roost sites (Hamer and Nelson 1995). Forest carnivores such as the American marten (*Martes americana*) prefer to live under mature tree canopies to avoid predation from avian and mammalian predators (Thompson and Harestad 1994). Several ungulate species such as mule deer (*Odocoileus hemionus*) require winter range habitat which has stands with large canopy trees to intercept snowfall and permit movement and foraging for deer during winter (Armleder et al. 1989)

As discussed by Carey (1995), Carey and Johnson (1995), and Hayes et al. (1997), wildlife species generally respond to ecological characteristics of forest stands rather than to stand age. It may be possible to accelerate development of some structural attributes in young forest stands as documented for tree growth in this study. Thus, our hypothesis 1, that thinning would enhance productivity and structural features (crown volume, diameter but not necessarily height growth) of lodgepole pine crop trees, is apparently acceptable.

Clearly, there were few snags in the thinned stands

TABLE 7. Mean values in 1990–1991 ($n = 6$) and 1998 ($n = 3$) and results of analysis of variance for species diversity measurements for small-mammal communities.

	Stand (1990–1991)						
Parameter	Low	Med	High	Unth	OG	$F_{4,20}$	P
Species richness	3.81[a]	3.69[ab]	3.16[bc]	3.09[c]	2.88[c]	4.49	<0.01**
Shannon-Wiener, H'	1.53[a]	1.46[ab]	1.28[bc]	1.18[c]	1.22[c]	4.00	0.02*
Log-series alpha	1.41	1.39	1.06	1.08	1.20	2.66	0.07

Notes: Within a parameter, mean values followed by different letters are significantly different according to Duncan's multiple range test. Unth = unthinned stand, OG = old-growth stand.
* $P \leq 0.05$; ** $P < 0.01$.

and some program of snag creation will be required for cavity-using wildlife (McComb et al. 1993, Hayes et al. 1997). Some snags will develop naturally in these stands through time but numbers per hectare were much lower in the thinned than old-growth stands. Populations of some cavity-using birds, such as Hairy Woodpeckers (*Dendrocopos villosus*) and Red-breasted Nuthatches (*Sitta canadensis*) appear to increase after thinning, despite lower snag densities (Hagar et al. 1996). This behavior may be related to changes in availability of forage (Weikel 1997, cited in Hayes et al. 1997).

Vegetation and habitat diversity

Biomass of herbaceous plant species, as measured by crown volume index, responded positively to stand thinning at five and ten years post-treatment. This response was predictable based on vegetation development in gaps and openings in old forests which provide spatial variability in microhabitats and resources (Halpern and Spies 1995). Similar results were reported for response of understory vegetation to thinning (Crouch 1986, Hungerford 1987, Klinka et al. 1996, Stone and Wolfe 1996, Thomas et al. 1999). Several studies have related increases in forage production in thinned stands to use by ungulates during certain seasons (Blair and Enghardt 1976, Crouch 1986, Lyon 1987, Winn et al. 1988). The similarity in crown volume indices of shrubs across the four young pine stands may change with time as shrub species appeared slower than herbs in responding to the different stand densities. Although not significant, shrub volume declined by 54.4% in the old-growth stands from 1990 to 1998, but tended to increase in the young pine stands during this period. The high volume of mosses in the old-growth stands reflected the variable conditions of substrate, humidity, and age for the moss community to develop. Provision of some old-growth legacies, at the time of harvesting, would help to maintain moss communities in regenerated young stands (Franklin et al. 1989).

Habitat diversity was reflected in the structural richness of herbs and species diversity and structural diversity of coniferous trees in the heavily thinned stands. In addition, there was the tendency for high species richness and total structural diversity of the plant community in the low-density stands in 1998. This result fits the prediction of Halpern and Spies (1995) whereby plant species diversity would likely be maintained in association with old-growth attributes in managed stands, and the positive relationship between plant species richness and thinning intensity reported by Thomas et al. (1999). Overall, plant species diversity appeared to be unaffected by stand thinning and was comparable or higher than that recorded in old-growth forest, at least in these lodgepole pine ecosystems. Thus, our hypothesis 2, that thinning would enhance stand structure attributes of species diversity and structural diversity of herb, shrub, and tree layers, is partially acceptable.

Small-mammal communities

Red-backed voles are considered to be a good indicator of old-growth forest conditions (Aubry et al. 1991, Nordyke and Buskirk 1991), or at least later successional coniferous, deciduous, and mixed wood forests (Merritt 1981). Because of their dependency on hypogeous ectomycorrhizal fungi (Maser et al. 1978, Ure and Maser 1982) and associated organic matter (Yahner 1986) in old forests, abundance of red-backed voles should be predictably lower in young forests. Our thinned stands generally had the same number or more red-backed voles than the unthinned stands at 2–3 and 10 yr post-thinning, but lower abundance than in the old-growth stands. However, at Penticton in 1998, Kamloops in 1991, and Prince George in 1990–1991 there was no difference in abundance of red-backed voles between the thinned stands and old-growth stands.

The southern red-backed vole appears not to have cyclic population fluctuations (Merritt 1981, Hansson and Henttonen 1985), but abundance may vary from year to year (Vickery et al. 1989, Nordyke and Buskirk 1991). The overall higher relative abundance of red-backed voles at Kamloops and Prince George than Penticton may have been related to the higher component of spruce or subalpine fir (Table 2) in the original forests of our study areas in these two ecological zones (Montane Spruce and Sub-boreal Spruce). Nordyke and Buskirk (1991) reported old-growth spruce–fir in the central Rocky Mountains to have the highest abundance and best body condition of red-backed voles.

Thus, we conclude that in years of low or moderate numbers of red-backed voles, our thinned stands pro-

TABLE 7. Extended.

Stand (1998)						
Low	Med	High	Unth	OG	$F_{4,8}$	P
5.60[a]	5.67[a]	3.67[b]	3.47[b]	3.33[b]	5.79	0.02*
1.99[a]	2.03[a]	1.51[ab]	1.18[b]	1.00[b]	7.99	<0.01**
1.98[ab]	2.19[a]	1.24[bc]	1.22[bc]	1.05[c]	4.36	0.04*

vide habitat for this old-growth indicator species. In years of high numbers, microhabitat development for this microtine in thinned stands is as yet insufficient to support high populations. This pattern has relevance to predators of red-backed voles such as marten, weasels, and birds of prey. However, the similar mean total abundance of small mammals in the low-density and old-growth stands in 1998 suggested that other species contributed to the small-mammal community in the low-density stand. This pattern became evident in the analysis of species richness and diversity.

The higher richness and diversity of small mammal species in the heavily thinned stands was reasonably consistent over the three study areas and at 2–3 and 10 yr post-thinning. Because of the positive response in crown volume index of herbs and herb layers, it is not surprising that *Microtus* spp. and *P. intermedius* appeared in the thinned stands. These voles prefer early successional stages after forest disturbance and open coniferous forests with understory vegetation (Whitaker 1972, Banfield 1974, Reich 1981). In addition, the wandering shrew, which occurred in the low- and medium-density stands at Penticton, also inhabits grassy meadows and open patches in forests (Nagorsen 1996).

Our third hypothesis that species richness and diversity of forest floor small mammals would be enhanced by the thinning treatments is supported by the data. However, we must ask what exactly the diversity measurements are telling us about the ability of the various stands to support diverse communities of small

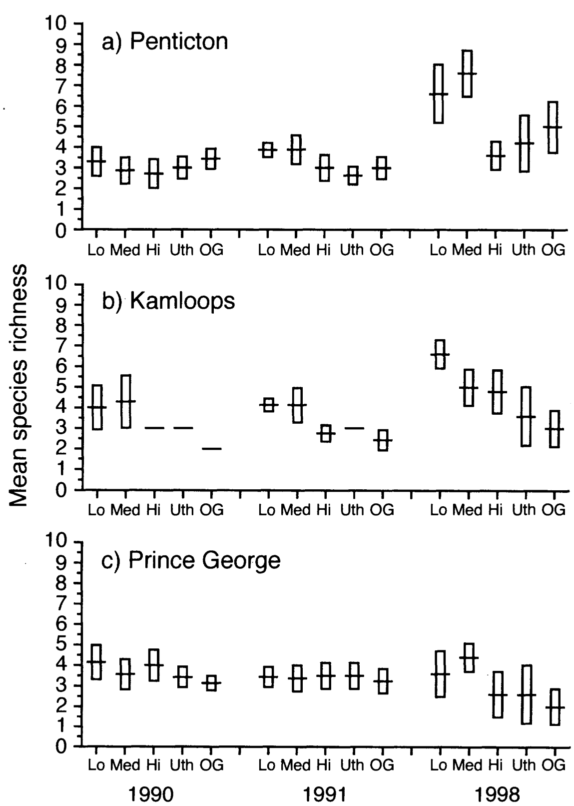


FIG. 11. Mean species richness and 95% confidence intervals for small-mammal communities for the five treatment stands at each study area in 1990, 1991, and 1998. Lo = low density, Med = medium density, Hi = high density, Uth = unthinned, and OG = old-growth.

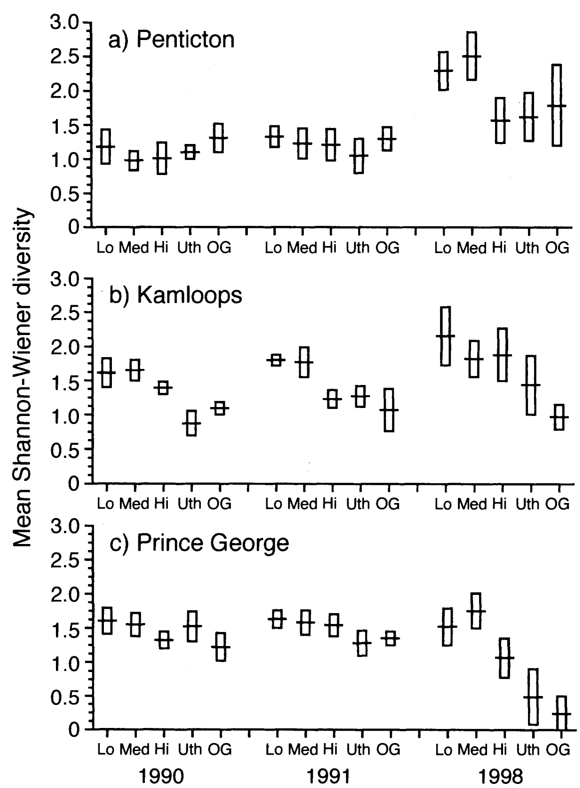


FIG. 12. Mean species diversity (Shannon-Wiener, H') and 95% confidence intervals for small-mammal communities for the five treatment stands at each study area in 1990, 1991, and 1998. Lo = low density, Med = medium density, Hi = high density, Uth = unthinned, and OG = old-growth.

mammals? Taylor et al. (1976) and Magurran (1988) discussed the discriminant ability of diversity measures and concluded that log-series alpha, Shannon-Wiener H', and species richness were the best at discriminating differences between sites. In general, indices weighted towards species richness were more useful for detecting differences between sites than indices which emphasized the dominance/evenness component of diversity (Magurran 1988). In an attempt to provide a meaningful analysis of small-mammal diversity, three measures were chosen and all generally followed the same pattern (Table 7). This higher diversity in the heavily thinned stands suggested that there was a greater number of microhabitats for small mammals because of the complex stand structure developing since the time of thinning, as predicted by Carey and Johnson (1995).

Management Implications

The structure of old-growth forests consists of large trees in the overstory, smaller trees of varying sizes and species in the lower and middle story, large standing and fallen dead trees, and patchy herb and shrub communities (Spies and Franklin 1991). Tappeiner et al. (1997) have suggested that, at least in coastal Oregon, regeneration of old-growth stands occurred over a prolonged period and trees grew at low density (<250 trees/ha). Young second-growth stands tend to have much higher densities (≥1000 stems/ha) and this is particularly true for lodgepole pine (Johnstone 1985).

Our old-growth stands averaged 953 trees/ha of ≥15 cm dbh of lodgepole pine, interior spruce, and subalpine fir which was very similar to the medium-density stands at 943 crop trees/ha. Mean density of lodgepole pine only was 413 trees/ha in this diameter class of large trees in the old-growth stands. Clearly, even old stands of lodgepole pine tend to have relatively low densities similar to the pattern discussed by Tappeiner et al. (1997). Although old-growth characteristics do, indeed, develop in lodgepole pine stands which have originated at high density, this process may take 100–250 yr in the absence of disturbance. Therefore, if our management objective is to accelerate development of old-growth attributes, rather than waiting for "long rotations" to develop these structures, then thinning should be conducted in these young stands. Our results suggest that tree diameter growth, tree crown volume, herbaceous vegetation, multilayered coniferous stand structure, total structural diversity, and species richness and diversity of small mammals may be enhanced by heavy thinning of lodgepole pine stands to ≤1000 trees/ha.

Old-growth attributes may be produced in heavily thinned stands, perhaps decades sooner than waiting for the alternative of no management intervention and long rotations of hundreds of years. However, because of eventual canopy closure, additional thinning treatments will likely be necessary to achieve and maintain old-growth features in managed stands. As discussed by McComb et al. (1993), Carey and Curtis (1996), and Hayes et al. (1997), appropriate thinning regimes may contribute to ecosystem management and emulation of natural disturbance patterns. Managing for a variety of stand treatments, structures, species, and successional stages in a mosaic of habitats across a landscape should conserve biological diversity (Hunter 1990). Stands thinned to high density and unmanaged stands would be part of this mosaic as well.

Responses of other wildlife groups such as amphibians, birds, and insects should be investigated in these stands and other variously treated young second-growth stands. Monitoring should continue for several decades after silvicultural treatments to determine if and when stands might develop old-growth compositional and structural characteristics.

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