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Influence of alternative vegetation management treatments on conifer plantation attributes: abundance, species diversity, and structural diversity

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Abstract

This study was designed to test the hypothesis that alternative vegetation management treatments (manual cutting and cut-stump applications of glyphosate herbicide) would decrease plant community abundance, species diversity, and structural diversity of young mixed conifer plantations in southern British Columbia, Canada. The experimental design consisted of nine operational-sized plantations, stratified into three blocks (1 control, 1 manual, and 1 cut-stump plantation per block), with five permanent strip-transects to sample vegetation within each plantation. Vegetation management treatments did not significantly ($p>0.10$) affect the crown volume index of herb, shrub, or coniferous tree layers. However, both manual and cut-stump treatments significantly reduced crown volume index of deciduous trees in the first post-treatment year ($p=0.05$ and $p<0.01$, respectively). Due to prolific regrowth of stump sprouts, the manual treatment effect did not last beyond the first post-treatment year. In contrast, the cut-stump treatment impeded sprouting and, relative to control and manual treatments, continued to significantly suppress deciduous growth for at least 4 years ($p<0.05$). Species richness, diversity, and turnover of the herb, shrub, and tree layers were not significantly ($p>0.10$) different between treatments and control. Similarly, the structural diversity of herb, shrub, and tree layers were also not significantly ($p>0.10$) different between treatments and control. By opening the canopy and decreasing the dominance of the deciduous tree layer, both manual and cut-stump treatments showed greater total structural diversity (herb, shrub, and tree layers combined) relative to the control. However, differences in total structural diversity between treatments and control were, for the most part, not significant ($p>0.10$). Therefore, these vegetation management treatments affected only the volume of the targeted deciduous tree layer and did not adversely affect the species richness, diversity, turnover, or structural diversity of the plant community. These results may be applicable to other temperate forest ecosystems where conifer release is practised in young plantations. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Alternative vegetation management; Herbicide; Species diversity; Structural diversity; Cut-stump treatment; Manual cutting

1. Introduction

Vegetation management is increasingly important in temperate forests of North America as a means to increase the survival and growth rates of crop trees, and to quickly achieve free-to-grow status for regenerating stands (Newton and Comeau, 1990). If annual

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harvest levels are to be maintained, accelerated development of new plantations, as well as rehabilitation of backlog sites is required. Intensive silviculture programs must deal with the problem of reducing competing herbs, shrubs, and other non-commercial species in order to increase production of merchantable trees (Walstad and Kuch, 1987; McDonald and Radosevitch, 1992). Vegetation management is, therefore, a tool which can help provide rates of tree growth necessary to sustain the forest industry.

In order to accelerate the development of a second-growth stand (i.e. reduce rotation age), vegetation management is particularly important during the first few years following planting. This is the time when a site, managed for coniferous trees, is naturally dominated by non-crop pioneer species, such as species of the genera *Betula* (birch), *Alnus* (alder), *Populus* (poplars and aspens), *Acer* (maple), *Prunus* (cherry), and *Rubus* (raspberry and thimbleberry). However, in other parts of North America, some of these hardwood species are the desired crop and conifers create a vegetation management problem. There are several methods for reducing the competition created by non-crop species, such as (1) manual (hand-held chain saws, brush saws, and girdling tools), (2) mechanical (machines that mow, rake, crush, and chip), (3) burning, (4) biological (use of grazing livestock and pathogens), and (5) the use of herbicides.

As the goal of vegetation management is to modify the plant community to favor the rapid development of crop trees, it undoubtedly has, therefore, profound effects on the abundance of some plant species inhabiting treated areas (Santillo et al., 1989). Because of growing public concern about the environment, forest managers are no longer charged with only regenerating forests (McGee and Levy, 1988; Freedman, 1991; Lautenschlager, 1993; Halpern and Spies, 1995). The conservation of biological diversity (biodiversity) is becoming an integral part of forest management. Biodiversity is recognized as an important ecological criterion of sustainability. Therefore, if forest management is to encompass both timber production and the conservation of biodiversity, vegetation management procedures must be critically examined within the context of both of these objectives.

Aerial spraying of glyphosate (Vision[®], commercial formulation containing glyphosate, 356 g/l present as isopropylamine salt) as a broadcast treatment is

the most common form of vegetation management within Canadian forests (Campbell, 1990). Although glyphosate poses minimal toxicological risks at prescribed rates, in terms of mortality and reduced reproduction in wildlife, and does not accumulate in the environment (Morrison and Meslow, 1983; Newton et al., 1984; Freedman, 1991), public opinion about the use of forest herbicides is often negative (Freedman, 1991). Research has shown that glyphosate does not have a direct effect on the survival or reproduction of small mammals (Sullivan and Sullivan, 1981; Sullivan, 1990a; Sullivan et al., 1997). In addition, several studies have shown that small mammal population responses to aerial application of this herbicide have ranged from an overall increase in population density (Anthony and Morrison, 1985), to no change in density (Sullivan and Sullivan, 1982; D'Anieri et al., 1987; Sullivan, 1990b), to others which have reported a decrease in abundance (Clough, 1987; Santillo et al., 1989). Other studies have also reported that glyphosate does not have any significant effects on the survival or health of ungulates (Sullivan and Sullivan, 1979; Cambell et al., 1981; Jones and Forbes, 1984).

A review of eight studies on the effect of herbicide treatments on northern songbird populations in regenerating clearcuts indicates that total songbird populations are seldom reduced during the growing season following treatment (Lautenschlager, 1993). Densities of species that use early successional brushy, deciduous cover are sometimes reduced, while densities of species which commonly use more open areas sometimes increase (Easton and Martin, 1998). However, more information is needed, particularly the effects of alternative treatments, on both the timber resource and non-timber values, such as habitat quality (Campbell, 1990).

Two alternative vegetation management treatments include the ground-based methods of manual cutting of competing vegetation and the application of herbicide to the cut-stump surface of manually-cut deciduous trees. Manual cutting and herbicide applications are used commonly, but the cut-stump herbicide treatment is less common. The non-broadcast and species-specific approach of these treatments suggest that they may be effective and environmentally sensitive methods of vegetation management. However, except for Bell et al. (1997), there is a dearth of studies reporting

on the responses of plant communities to these alternative treatments.

Studies designed to investigate the effects of vegetation management on biodiversity often monitor changes in plant abundance and diversity (Tomkins and Grant, 1977; Pollack et al., 1990; Freedman et al., 1993; Sullivan, 1994; Sullivan et al., 1996). However, a habitat attribute that is frequently overlooked by such studies is structural diversity or 'layer diversity'. Because of the well-documented direct relationship between the structural diversity (foliage height diversity) of a habitat and the diversity of species that live there (MacArthur and MacArthur, 1961; MacArthur, 1965; Balda, 1969; Sutton and Hudson, 1980; Adler, 1987; Harney and Dueser, 1987; Hunter, 1990), structural diversity should be carefully examined to determine the effects of vegetation management treatments on habitat quality.

This study was designed to test the hypothesis that alternative vegetation management treatments (manual cutting and cut-stump applications of glyphosate) applied in young mixed-conifer plantations would adversely affect the plant community (herbs, shrubs, and trees) by decreasing (1) abundance, (2) species diversity, and (3) structural diversity.

2. Materials and methods

2.1. Study areas

This study was conducted within two similar areas in the Shuswap Highlands of south-central British Columbia, Canada. The Eagle Bay (50°55'N, 119°11'W) and Sicamous (50°52'N, 118°59'W) sites are both located within the Thompson moist-warm subzone of the Interior Cedar-Hemlock biogeoclimatic zone (Lloyd et al., 1990). These sites are characterized by similar topography, elevation, climate, and climax vegetation. The topography of this area is hilly to steeply sloping and elevation ranges from 550 to 1237 m. Summers are generally warm and dry and winters cool and wet. Mean annual temperature ranges from 2 to 8.7°C and precipitation ranges from 500 to 1200 mm, with as much as 50% falling as snow (Ketcheson et al., 1991). Climax forests are characterized on mesic sites by western red cedar (*Thuja plicata*) and western hemlock (*Tsuga hetero-*

phylla), while interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), lodgepole pine (*Pinus contorta* var. *latifolia*), and paper birch (*Betula papyrifera*) are common seral species. Nomenclature for all plant species follows Hitchcock and Cronquist (1973).

Nine plantations, ranging from 16 to 47 ha in area, and 2–9 years in age when selected, were chosen on the basis of operational scale, proximity, and initial similarity in requiring vegetation management treatments. The six plantations found at the Eagle Bay site were located on a north to north-east facing slope. These areas were logged between 1978 and 1986 and planted predominantly to lodgepole pine between 1985 and 1990. Site inspections indicated that Douglas-fir, western larch (*Larix occidentalis*), and hybrid spruce (*Picea engelmannii* × *P. glauca*) were also present. The remaining three plantations at the Sicamous site were located on a southeast slope. These areas were logged between 1977 and 1988 and planted between 1982 and 1989, largely with Douglas-fir. Inspections of these sites indicated that lodgepole pine was also present with lesser amounts of hybrid spruce and western white pine (*Pinus monticola*).

2.2. Experimental design

This study followed a randomized-block design. Study plots were established in eight of the nine plantations in September 1991, and the ninth in April 1992. Assignment of control and vegetation management treatments was done subjectively among these nine plantations due to logistic and economic constraints. The first of these constraints was related to the close proximity of the Eagle Bay plantations to a residential community. To facilitate the approval of the herbicide application permits, the cut-stump herbicide treatments had to be applied to the two plantations furthest from these residents. The second constraint was related to a minimum acceptable outcome anticipated for the cost of the vegetation management treatments. This required that the more expensive treatment, the cut-stump herbicide treatment, be applied to the Sicamous plantation that was most dominated with deciduous trees.

The nine plantations were stratified into three blocks on the basis of (1) site, and (2) elevation. Consequently, plantations A, B, and C (Sicamous site) formed Block 1, and the remaining six plantations

from the Eagle Bay site (D to I) were stratified into Blocks 2 and 3, on the basis of elevation.

In addition to untreated controls, the vegetation management treatments used in this study were applied in the following manner. Manually treated plantations had all trembling aspen (*Populus tremuloides*), paper birch, and black cottonwood (*Populus trichocarpa*) cut with power saws, except for a few individual stems that were left in the openings of the plantation. All stems of willow (*Salix* spp.), Douglas maple (*Acer glabrum*), bitter cherry (*Prunus emarginata*), and speckled alder (*Alnus incana*) that were within 1 m of a crop tree were also cut. All other vegetation was left uncut.

Cut-stump treated plantations were treated in a similar manner as those receiving the manual treatment, with the additional application of the herbicide glyphosate, diluted 2:1 in water, to the cut stump surfaces of the felled deciduous trees. A small amount of Basacid Blue[®] dye was added to the herbicide mixture to mark the treated stumps. Most maple, cherry, and alder stems were left uncut. These prescriptions were applied between September 25 and October 22 1992.

2.3. Vegetation sampling

Vegetation was assessed annually within each plantation to determine the presence and abundance of individual species for the purpose of monitoring the plant community's composition and structure. Five permanent 5 m×25 m strip-transects, each consisting of five contiguous 5 m×5 m subplots with nested 3 m×3 m and 1 m×1 m subplots (Fig. 1), were established within each of the nine plantations (Stickney, 1980, 1985). Transects were randomly placed within each plantation as long as they were at least 50 m from the nearest stand edge, and did not cross any roads, skid-trails, or landings.

Within a strip-transect, each of the three different-sized subplots were used to sample different plant forms: the 5 m×5 m (25 m²) subplot for sampling trees, the 3 m×3 m (9 m²) subplot for sampling shrubs, and the 1 m×1 m (1 m²) subplot for sampling herbs. In addition, trees, shrubs, and herbs were each sampled within six height classes of 0–0.25, 0.25–0.50, 0.50–1.0, 1.0–2.0, 2.0–3.0, and 3.0–4.0 m (Walmsley et al., 1980). Abundance of a given species

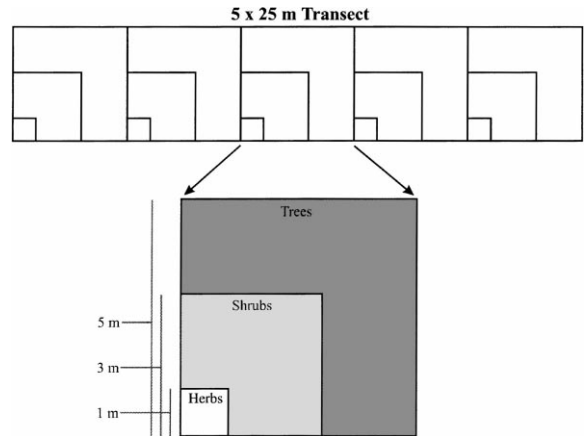


Fig. 1. Design of strip-transects used to sample vegetation.

was estimated within each of the height classes by a visual estimate of percent cover. Individual plants were only measured once within the height class containing the topmost growth of that plant.

All plants were initially classified into one of three life forms; herb, shrub, or tree. However, these classes were sometimes further subdivided or, conversely, grouped together to create additional classes of plants. For example, the tree layer was subdivided into deciduous and coniferous tree classes. Also, herbs, shrubs, and trees were sometimes grouped together to form a class including all plant forms. Hereafter, the *tree* class included both, deciduous and coniferous trees, and the *total* class included all plant forms.

A crown volume index was calculated for each species within each of the five nested subplots of a transect by multiplying the percent cover values by the top of the corresponding height class (Stickney, 1985). The product of these values gave the volume of a cylindroid and represented the space occupied by the plant in m³/0.01 ha.

2.4. Diversity calculations

Species richness (*S*) was calculated as the total number of species of a given plant form (herb, shrub, or tree) sampled within a transect (Krebs, 1989).

Species turnover (TO) was also calculated for herb, shrub, and tree layers. TO was defined as the number of species lost and gained during a set period, divided by the total number of species sampled during the

same period (Schoonmaker and McKee, 1988), and calculated as follows:

$$TO = \frac{L + G}{A + B}$$

where L is the number of species lost and G the number of species gained during a defined period from t_1 to t_2 , and A and B the total number of species sampled during times t_1 and t_2 , respectively. Because a species turnover calculation required a minimum of two sample periods, this measure is undefined for the first year of sampling (pre-treatment year).

Two diversity indexes were used: Simpson's index which is sensitive to changes in abundant species (Simpson, 1949), and the Shannon–Wiener index which is sensitive to changes in rare species (Pielou, 1966a; Peet, 1974). Simpson's index of species diversity is the probability of picking two organisms at random that are different species, and ranges from 0 to almost 1. The Shannon–Wiener index of diversity is based on information theory and the degree of difficulty in predicting correctly the next individual sampled. As such, this index increases with number of species sampled, and ranges from 0 to ≈ 5 for biological communities.

The above definition of Simpson's and Shannon–Wiener diversity indexes, although referring to species diversity, applies equally to structural diversity. While *species* is the object of a species diversity index, *height class* or *layer* is the object of a structural diversity index.

Pre-treatment vegetation sampling was initiated in July 1992. The first post-treatment sampling of vegetation was conducted in July 1993 and was conducted annually to July 1996, when the study was terminated. All plant community attributes (e.g. crown volume

index, diversity indexes) were calculated on a subplot basis, and then averaged across the five subplots of a transect. Consequently, each transect represents one datum.

2.5. Statistical analysis

A repeated measures analysis of variance (RM-ANOVA, SPSS Institute Inc., 1997) was used to test for significant differences among treatment means (Table 1). Both pre- and four post-treatment years were analyzed together, resulting in five levels (years) for the within-subjects factor (time). Both the treatment and block were assigned as between-subjects factors. Before performing any analyses, data not conforming to properties of normality and equal variance were subjected to various transformations to best approximate the assumptions required by any ANOVA (Zar, 1984). Mauchly's W test statistic was used to test for sphericity (independence of data among repeated measures) (Littel, 1989; Kuehl, 1994). For data found to be correlated among years, the Huynh–Feldt correction was used to adjust the degrees of freedom of the within-subjects F -ratio. The Bonferroni post-hoc test (adjusted for multiple contrasts) was used to locate differences among treatment means within each sample year (Rosenthal and Rosnow, 1985). Significance levels for all analyses (i.e., RM-ANOVA and Bonferroni significance tests) was set at $p=0.10$. Although conclusions made from statistical results with the standard significance level of 0.05 may be stated with more confidence than those resulting from tests with a probability of 0.10, significance tests with $p \leq 0.10$ may be biologically significant and deserve comment (Cherry, 1998). Tests regarding data properties, such

Table 1

Repeated measures analysis of variance (RM-ANOVA) model used for investigating plant volume, species diversity, and structural diversity

Source of variation	Factor type	Level	Degrees of freedom	F -test (d.f.)
Block	Random	$n=3$	$n-1=2$	
Treatment	Fixed	$k=3$	$k-1=2$	MS-treatment/MS-error I (2,4)
Error I			$(n-1)(k-1)=4$	
Time	Fixed	$t=5^a$	$t-1=4$	
Time \times treatment			$(t-1)(k-1)=8$	MS-treatment \times treatment/MS-error II (8,24)
Error II			$k(n-1)(t-1)=24$	

^a There are five levels of time ($t=5$) for all plant attributes, except species turnover. Because species turnover is not defined for the pre-treatment year, there are only four levels ($t=4$) for this attribute.

as Leven's homogeneity test and Mauchly's W sphericity test, were made with a significance level of $p=0.05$.

3. Results

3.1. Site similarity

There were no statistical differences ($p>0.10$) among the treatment and control plantations for any of the plant attributes (crown volume index, species richness, species turnover, species diversity indexes, and structural diversity indexes) during the pre-treatment year (Figs. 2–7).

3.2. Crown volume index

3.2.1. Herb layer

Prominent herb species found within the study area included fireweed (*Epilobium angustifolium*), white

hawkweed (*Hieracium albiflorum*), common dandelion (*Taraxacum officinale*), wild strawberry (*Fragaria virginiana*), and pearly everlasting (*Anaphalis margaritacea*) (Table 3). Although the mean total crown volume index of the herb layer appeared to change over time (Fig. 2), differences among control and treatment plantations were not significant ($F_{2,4}=1.26$; $p=0.38$). Both the control and treatment groups showed similar time trends during the four post-treatment years. The mean total crown volume index of the herb layer for the control, manually, and cut-stump treated plantations peaked during the second post-treatment year (1994) and then gradually decreased during the final two years of the study. Both the manually and cut-stump treated plantations appeared to show a decrease in volume of herbs in the first post-treatment year, in contrast to the increase in herb volume observed within the control during this same period, although differences were not significant (Fig. 2).

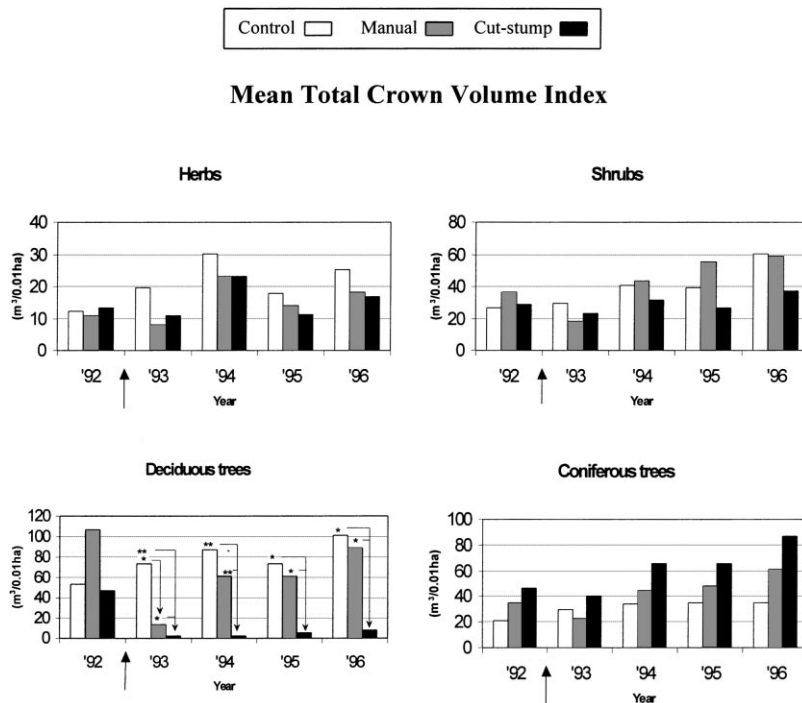


Fig. 2. Mean total crown volume index ($m^3/0.01$ ha) for herb, shrub, deciduous tree, and coniferous tree layers among control, manually, and cut-stump treated plantations. No statistical differences ($\alpha=0.10$) were observed for herb, shrub, or coniferous tree volume. However, the deciduous tree layer was significantly affected by the treatments. Arrow on horizontal axis indicates timing of treatments. * $p<0.10$, ** $p<0.05$, *** $p<0.01$; significance by Bonferroni post-hoc test.

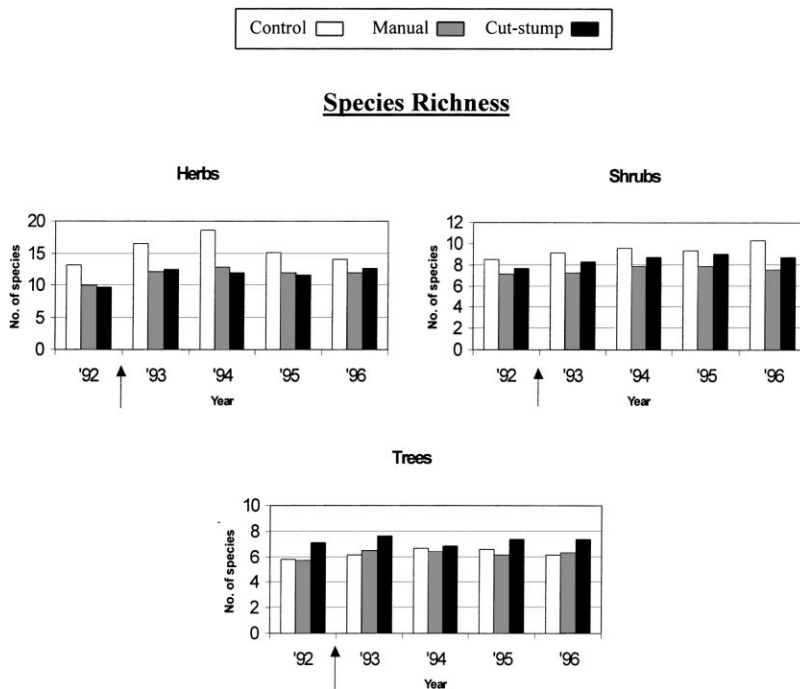


Fig. 3. Mean species richness for herb, shrub, and tree layers among control, manually, and cut-stump treated plantations. No statistical differences ($\alpha=0.10$) in species richness were observed among the control and treatment plantations for any of the plant forms (herbs, shrubs, or trees) during any of the 5 sample years. Arrow on the horizontal axis indicates timing of treatments.

3.2.2. Shrub layer

Prominent shrub species found within the study area included falsebox (*Pachistima myrsinites*), thimbleberry (*Rubus parviflorus*), red raspberry (*Rubus idaeus*), bitter cherry (*Prunus emarginata*), and willow (*Salix* spp.) (Table 3). Although the mean total crown volume index of the shrub layer appeared to change over time (Fig. 2), differences among control and treatment plantations were not significant ($F_{2,4}=0.86$; $p=0.49$). The control plantations showed a steady increase in mean total crown volume index of shrubs throughout the 5 years of the study. Both the manually and cut-stump treated plantations also increased in shrub volume during the post-treatment years.

3.2.3. Deciduous tree layer

The three deciduous tree species that were found within the study area were paper birch, black cottonwood, and trembling aspen. The mean total crown volume index of deciduous trees was similar (Bonferroni; $p=\geq 0.17$) among control and treatment

plantations during the pre-treatment year. The treatments resulted in significant ($F_{2,4}=40.63$; $p=0.002$) reductions in deciduous tree volume, 87% ($106.5-13.5$ m³/0.01 ha) and 95% ($46.8-2.2$ m³/0.01 ha) within the manually and cut-stump treated plantations, respectively, during the first post-treatment year (Table 2; Fig. 2). This decline was in direct contrast to the control plantations, which showed an increase in mean total crown volume index of 38% ($53.2-73.3$ m³/0.01 ha) during this same period (Fig. 2). Consequently, both the manually and cut-stump treated plantations had significantly less (Bonferroni; $p=0.05$ and $p<0.01$, respectively) deciduous tree volume than that of the control plantations during the first post-treatment year. In addition, during the first post-treatment year, the cut-stump treated plantations had significantly less (Bonferroni; $p=0.02$) deciduous tree volume than those treated manually (Fig. 2).

Both the control and cut-stump treated plantations gradually increased in mean total crown volume index of deciduous trees throughout the four post-treatment

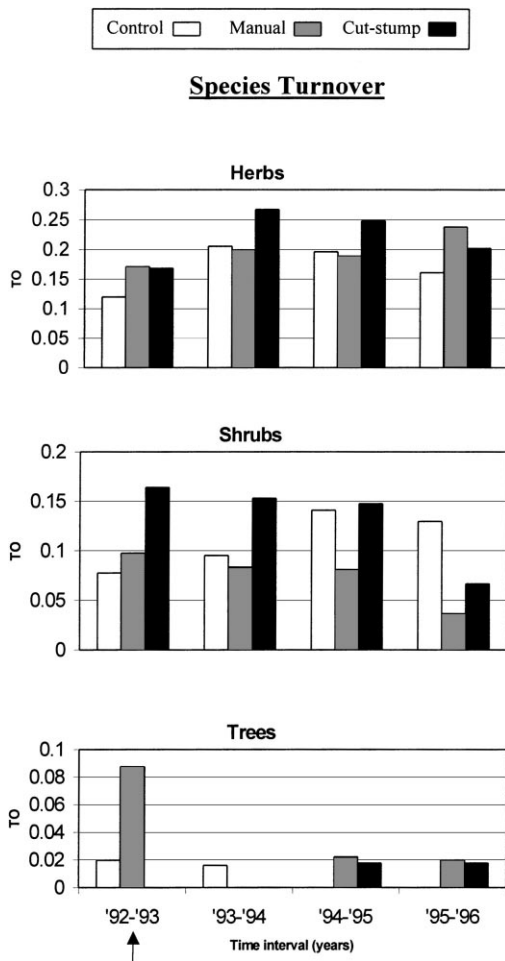


Fig. 4. Mean species turnover for herb, shrub, and tree layers within control, manually, and cut-stump treated plantations. No statistical differences ($\alpha=0.10$) in species turnover were observed among the control and treatment plantations for any of the plant forms (herbs, shrubs, or trees) during any of the 5 sample years. Arrow indicates timing of treatment.

years. The dramatic suppression of deciduous tree volume one year after treatment was maintained during the post-treatment years for the cut-stump treatment. As a result, deciduous tree volume within the cut-stump treatment was less (Bonferroni; $p<0.02$) than that of the control during all four post-treatment years. The suppression of deciduous tree volume within the manually treated plantations was short-lived. There was a rapid increase in growth by the second post-treatment year (1994), which resulted in deciduous volumes similar (Bonferroni; $p=1.00$) to

that of the control during the 1994 sample year, and thereafter (Fig. 2).

3.2.4. Coniferous tree layer

Prominent coniferous tree species included interior Douglas-fir, western red-cedar, lodgepole pine, western hemlock, hybrid spruce, and western white pine. Western larch, subalpine fir (*Abies lasiocarpa*), and western yew (*Taxus brevifolia*) were also found, but were less common.

Although the mean total crown volume index of the coniferous tree layer appeared to change over time (Fig. 2), differences among control and treatment groups were not significant ($F_{2,4}=0.99$; $p=0.45$). The control plantations showed only a slight increase in mean total crown volume index of coniferous trees throughout the 5 years. However, both the manually and cut-stump treated plantations had accelerated growth rates of coniferous tree volume relative to that of the control during the four post-treatment years. The mean annual percentage increment of coniferous tree volume (see formula below) was 5, 44, and 29% for control, manually, and cut-stump treated plantations, respectively:

Mean annual percentage increment of

$$\text{crown volume} = \frac{(B - A)/A}{C} \times 100\%$$

where A is the crown volume at time t_1 , B the crown volume at time t_2 , and C the number of years between t_1 and t_2 .

Although the differences in coniferous tree volume among treatment and control plantations were not statistically significant, increased coniferous growth rates of 5–8 times that of control plantations suggested a biologically and, most likely, economically significant treatment effect.

3.3. Species richness

During this study, a total of 75 herb, 37 shrub, and 12 tree species was sampled. There was no difference in mean species richness among the control and treatment plantations for herbs ($F_{2,4}=3.29$; $p=0.14$), shrubs ($F_{2,4}=2.75$; $p=0.18$), or trees ($F_{2,4}=1.17$; $p=0.40$), at any time during the study (Table 2; Fig. 3). Some temporal trends common to both, control and treatment groups, did occur.

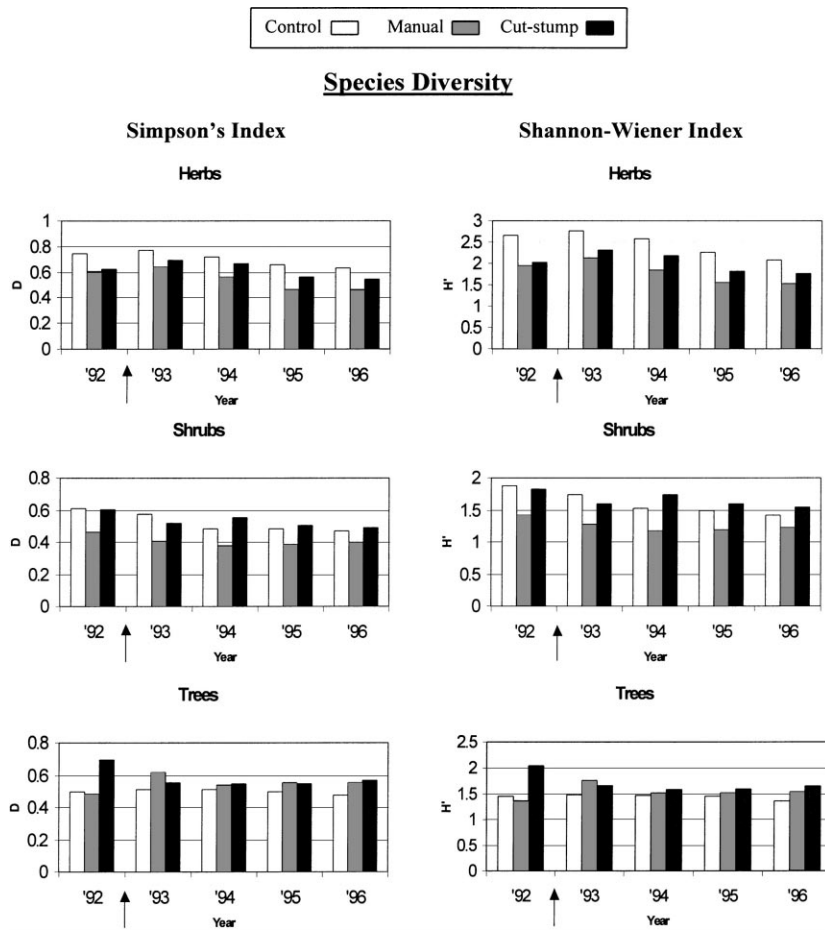


Fig. 5. Mean species diversity indexes (Simpson's and Shannon–Wiener) for herb, shrub and tree layers among control, manually, and cut-stump treated plantations. No statistical differences ($\alpha=0.10$) in species diversity were observed among the control and treatment plantations for any of the plant forms (herbs, shrubs, or trees) during any of the 5 sample years. Arrow on horizontal axis indicates timing of treatments.

3.4. Species turnover

There were no significant ($F_{2,4}=0.72$; $p=0.54$) differences in herb species turnover among control and treatment plantations during any consecutive year intervals (Table 2; Fig. 4). The lowest species turnover occurred between the pre-treatment and first post-treatment year (1992–1993), and the highest occurred in the next year (1993–1994). Control, manual, and cut-stump treatments all showed similar time trends throughout the study.

There were no significant ($F_{2,4}=1.66$; $p=0.30$) differences in shrub species turnover among control

and treatment plantations during any consecutive year intervals (Table 2; Fig. 4). Although not statistically significant, differences in shrub species turnover among treatment and control plantations did suggest some trends. Both manual and cut-stump treated plantations showed the highest species turnover during the pre-treatment and first post-treatment time interval (1992–1993) and then declined thereafter. This is in contrast to the shrub species turnover within the control plantations which was lowest during this same period, followed by an increase in consecutive years, peaking during the 1994–1995 interval.

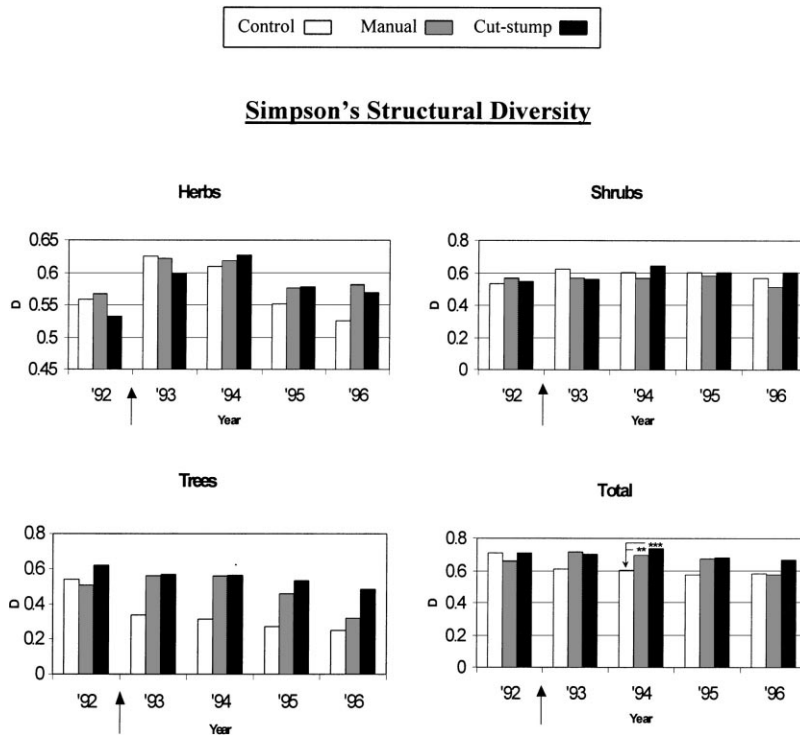


Fig. 6. Mean Simpson's structural diversity indexes for herb, shrub, tree, and combined total layers among control, manually, and cut-stump treated plantations. Bonferroni post-hoc tests indicated no statistical differences ($\alpha=0.10$) in structural diversity among any of the control and treatment plantations within the herb and shrub layers, pre- and post-treatment. However, some statistical differences among the treatment and control groups were observed within the combined total layer. Arrow on horizontal axis indicates timing of treatments. * $p<0.10$, ** $p<0.05$, *** $p<0.01$; significance by Bonferroni post-hoc test.

There were no significant ($F_{2,4}=2.14$; $p=0.23$) differences in tree species turnover among control and treatment plantations during any consecutive year intervals (Table 2; Fig. 4). The small changes in tree species turnover were caused by a single species being gained or lost within a given time interval. An exception to this was observed during the pre-treatment to first post-treatment year interval (1992–1993) when, within one of the three manually treated plantations, two tree species were gained.

By the final post-treatment year (1996), no tree species present during the pre-treatment year had been lost within any of the control or treatment plantations. However, during this same interval western yew, western white pine, and western larch were gained within the control, manually, and cut-stump treated plantations, respectively (Table 3).

3.5. Species diversity

Mean species diversity of the herb layer was similar (Simpson's [$F_{2,4}=3.34$; $p=0.14$] or Shannon–Wiener [$F_{2,4}=2.78$; $p=0.18$]) among control and treatment plantations (Table 2; Fig. 5). Both Simpson's and the Shannon–Wiener indexes showed similar time trends among the control and treatment plantations.

Mean species diversity of the shrub layer was similar (Simpson's [$F_{2,4}=1.26$; $p=0.38$] or Shannon–Wiener [$F_{2,4}=1.17$; $p=0.40$]) among control and treatment plantations (Table 2; Fig. 5). Both control and treatment plantations demonstrated the highest level of shrub species diversity during the pre-treatment year and showed a gradual decline in diversity thereafter.

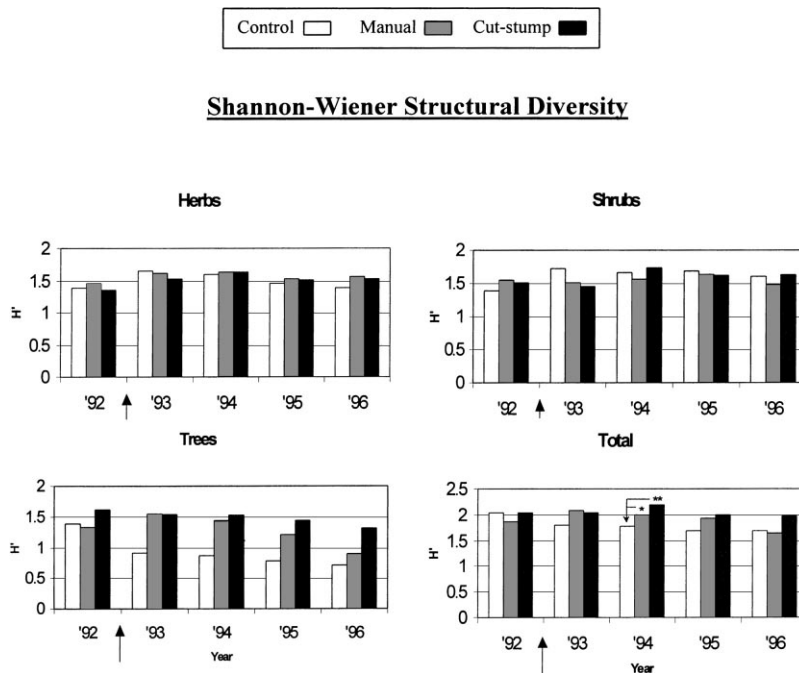


Fig. 7. Mean Shannon–Wiener structural diversity indexes for herb, shrub, tree, and combined total layers among control, manually, and cut-stump treated plantations. A Bonferroni post-hoc test suggested no statistical differences ($\alpha=0.10$) in structural diversity among any of the control and treatment units within the herb, shrub, and tree layers, pre- and post-treatment. However, some statistical differences among the treatment and control groups were observed within the combined total layer. Arrow on horizontal axis indicates timing of treatments. * $p<0.10$, ** $p<0.05$, *** $p<0.01$; significance by Bonferroni post-hoc test.

Mean species diversity of the tree layer was similar (Simpson's [$F_{2,4}=1.49$; $p=0.33$] or Shannon–Wiener [$F_{2,4}=1.22$; $p=0.39$]) among control and treatment plantations (Table 2; Fig. 5). The greatest change in both Simpson's and Shannon–Wiener tree species diversity indexes occurred between the pre-treatment and first post-treatment year and accounted for the significant ($F_{7,22}=2.66$; $p=0.04$ and $F_{7,23}=2.70$; $p=0.03$, respectively) Time \times Treatment interactions.

3.6. Structural diversity

3.6.1. Herb and shrub layers

Mean structural diversity indexes of the herb layer were similar (Simpson's [$F_{2,4}=0.09$; $p=0.92$] or Shannon–Wiener [$F_{2,4}=0.16$; $p=0.85$]) among the control and treatment plantations (Table 2; Figs. 6 and 7). The control plantations appeared to peak in herb structural diversity in the first post-treatment year (1993) and gradually declined thereafter. Similarly, the planta-

tions that received treatments also appeared to peak in structural diversity, however, this peak lagged behind that of the control by one year. Mean structural diversity indexes of the shrub layer were similar (Simpson's [$F_{2,4}=0.05$; $p=0.95$] and Shannon–Wiener [$F_{2,4}=0.09$; $p=0.92$]) among the control and treatment plantations (Table 2; Figs. 6 and 7).

3.6.2. Tree layer

Mean structural diversity indexes of the tree layer were similar (Simpson's [$F_{2,4}=3.68$; $p=0.12$] and Shannon–Wiener [$F_{2,4}=3.70$; $p=0.12$]) among the control and treatment plantations (Table 2; Figs. 6 and 7). Structural diversity of the tree layer decreased for both the control and cut-stump treated plantations from the pre-treatment year through to the final year of sampling. The manually treated plantations increased slightly in tree-layer structural diversity in the first post-treatment year, followed by a gradual decline during the final three years of sampling.

Table 2

Statistical results obtained from repeated measures analysis of variance (RM-ANOVA) conducted on several plant community attributes (five years of data — one pre-treatment year and four post-treatment years — were included in these analyses)^a

Attribute	Treatment effects		Time × Treatment interaction	
	$F_{(2,4)}$	<i>p</i>	F^b	<i>p</i>
<i>Volume index</i>				
Herbs	1.26	0.38	$F_{(6,19)}=0.73$	0.63
Shrubs	0.86	0.49	$F_{(8,24)}=1.15$	0.37
Deciduous trees	40.63	<i>0.002</i>	$F_{(6,19)}=9.94$	<i><0.001</i>
Coniferous trees	0.99	0.45	$F_{(8,24)}=0.33$	0.94
<i>Species richness</i>				
Herbs	3.29	0.14	$F_{(8,24)}=1.77$	0.13
Shrubs	2.75	0.18	$F_{(8,24)}=0.31$	0.95
Trees (deciduous and coniferous)	1.17	0.40	$F_{(8,24)}=0.85$	0.57
<i>Species turnover</i>				
Herbs	0.72	0.54	$F_{(6,18)}=0.37$	0.89
Shrubs	1.66	0.30	$F_{(6,18)}=1.24$	0.33
Trees (deciduous and coniferous)	2.14	0.23	$F_{(6,18)}=1.06$	0.42
<i>Species diversity — Simpson's</i>				
Herbs	3.34	0.14	$F_{(7,22)}=0.34$	0.93
Shrubs	1.26	0.38	$F_{(7,22)}=0.29$	0.95
Trees (deciduous and coniferous)	1.49	0.33	$F_{(7,22)}=2.66$	<i>0.04</i>
<i>Species diversity — Shannon-Wiener</i>				
Herbs	2.78	0.18	$F_{(7,22)}=0.24$	0.97
Shrubs	1.17	0.40	$F_{(7,21)}=0.36$	0.92
Trees (deciduous and coniferous)	1.22	0.39	$F_{(7,23)}=2.70$	<i>0.03</i>
<i>Structural diversity — Simpson's</i>				
Herbs	0.09	0.92	$F_{(8,24)}=0.24$	0.97
Shrubs	0.05	0.95	$F_{(8,24)}=0.62$	0.75
Trees (deciduous and coniferous)	3.68	0.12	$F_{(7,23)}=1.73$	0.15
Total (herbs, shrubs, and trees)	6.34	<i>0.06</i>	$F_{(7,23)}=2.39$	<i>0.05</i>
<i>Structural diversity — Shannon-Wiener</i>				
Herbs	0.16	0.85	$F_{(8,24)}=0.30$	0.96
Shrubs	0.09	0.92	$F_{(8,24)}=0.70$	0.69
Trees (deciduous and coniferous)	3.70	0.12	$F_{(7,23)}=1.73$	0.15
Total (herbs, shrubs, and trees)	7.09	<i>0.05</i>	$F_{(7,22)}=1.60$	0.19

^a Note: Significant *p*-values ($\alpha = 0.10$) are indicated in italic text.

^b Degrees of freedom for tests of Time × Treatment interactions are 8 and 24 (or 6 and 18 for species turnover) for an ideal situation when the data are not correlated among years. Correlation among data is a violation of ANOVA assumptions and requires an adjustment (Huynh-Feldt correction) which decreases the d.f. from those mentioned above.

3.6.3. Total (herb, shrub, and tree layers combined)

Differences in total structural diversity among control and treatment plantations were indicated by a significant ($F_{2,4}=7.09$; $p=0.05$) treatment effect for the Shannon–Wiener index (Table 2). During the second post-treatment year, total Shannon–Wiener structural diversity within both manual (Bonferroni; $p=0.08$) and cut-stump treated plantations (Bonfer-

roni; $p=0.01$) was greater than that of the control plantations (Fig. 7).

A significant Time × Treatment interaction for mean total Simpson's structural diversity ($F_{7,23}=2.39$; $p=0.05$) made it difficult to comment on the significant main treatment effect. However, a significant treatment effect ($F_{2,4}=7.37$; $p=0.04$) without interaction ($F_{6,18}=1.63$; $p=0.20$) was observed when a

Table 3

Mean total crown volume index ($\text{m}^3/0.01 \text{ ha}$) and S.E. (in parentheses) of the five most common^a herb, shrub, and tree species for the pre-treatment year (1992) and four post-treatment years within the control, manual, and cut-stump treatments

Species	Control					Manual					Cut-stump				
	1992	1993	1994	1995	1996	1992	1993	1994	1995	1996	1992	1993	1994	1995	1996
<i>Herbs</i>															
<i>Epilobium angustifolium</i>	2.55 (0.51)	4.25 (0.76)	7.28 (1.27)	4.65 (0.83)	6.23 (0.89)	4.14 (0.83)	2.51 (0.33)	8.8 (1.06)	6.16 (1.01)	7.92 (0.86)	7.29 (1.61)	3.69 (0.72)	9.58 (1.88)	6.01 (1.15)	8.08 (1.3)
<i>Hieracium albiflorum</i>	0.59 (0.13)	1.38 (0.34)	1.62 (0.3)	0.5 (0.1)	0.76 (0.16)	0.63 (0.13)	0.74 (0.15)	1.26 (0.26)	0.38 (0.07)	0.43 (0.06)	1.33 (0.46)	1.15 (0.26)	2.49 (0.51)	0.53 (0.14)	0.54 (0.14)
<i>Taraxacum officinale</i>	0.13 (0.03)	0.27 (0.08)	0.11 (0.04)	0	0	0.26 (0.06)	0.46 (0.16)	0.18 (0.04)	0	0	0.41 (0.16)	0.22 (0.07)	0.2 (0.09)	0	0
<i>Fragaria virginiana</i>	0.88 (0.36)	1.1 (0.35)	1.17 (0.41)	0.94 (0.36)	0.75 (0.25)	0.26 (0.11)	0.33 (0.21)	0.44 (0.15)	0.33 (0.18)	0.39 (0.18)	0.1 (0.06)	0.1 (0.05)	0.32 (0.15)	0.22 (0.16)	0.42 (0.27)
<i>Anaphalis margaritacea</i>	0.2 (0.1)	0.17 (0.05)	0.37 (0.16)	0.05 (0.04)	0.03 (0.01)	0.09 (0.04)	0.11 (0.04)	0.21 (0.08)	0.06 (0.02)	0.06 (0.03)	0.26 (0.11)	0.16 (0.1)	0.53 (0.22)	0.11 (0.04)	0.14 (0.06)
<i>Shrubs</i>															
<i>Paxistima myrsinites</i>	2.09 (0.53)	3.22 (0.85)	2.83 (0.97)	2.91 (0.86)	4.61 (1.46)	1.5 (0.44)	1.98 (0.64)	1.69 (0.6)	2.34 (0.81)	2.93 (1.07)	2.93 (1.05)	3.06 (1.16)	2.31 (0.8)	3.87 (1.53)	6.08 (2.54)
<i>Rubus parviflorus</i>	14.32 (3.97)	17.00 (3.42)	23.84 (6.54)	24.89 (6.59)	34.39 (7.76)	21.63 (5.52)	12.2 (2.65)	33.89 (7.44)	44.9 (11.98)	44.21 (10.61)	10.63 (2.47)	9.56 (1.82)	14.96 (3.83)	13.74 (4.05)	15.73 (3.21)
<i>Rubus idaeus</i>	1.15 (0.38)	1.32 (0.52)	0.95 (0.51)	0.86 (0.48)	1.23 (0.68)	0.43 (0.19)	0.22 (0.06)	0.33 (0.11)	0.2 (0.06)	0.22 (0.07)	2.18 (0.7)	1.05 (0.38)	0.73 (0.22)	0.33 (0.11)	0.34 (0.08)
<i>Prunus emarginata</i>	2.55 (1.07)	2.08 (0.82)	6.00 (3.87)	4.76 (2.63)	8.48 (4.93)	5.44 (2.85)	1.3 (0.82)	2.74 (1.37)	1.89 (0.98)	2.7 (1.39)	0.92 (0.39)	0.12 (0.04)	0.25 (0.08)	0.28 (0.08)	0.46 (0.14)
<i>Salixsp.</i>	1.48 (0.65)	1.15 (0.5)	1.21 (0.66)	1.09 (0.51)	2.09 (1.07)	3.3 (1.51)	0.85 (0.31)	2.22 (0.55)	3.07 (1.12)	4.77 (1.59)	3.42 (1.67)	0.86 (0.39)	1.01 (0.53)	1.26 (0.73)	3.05 (1.87)
<i>Trees</i>															
<i>Betula papyrifera</i>	30.4 (9.46)	44.76 (10.14)	56.49 (10.89)	57.19 (14.31)	75.26 (15.83)	81.53 (13.91)	6.93 (1.48)	46.61 (7.52)	43.79 (7.21)	65.98 (11.85)	32.91 (24.00)	1.48 (0.74)	0.43 (0.21)	4.04 (1.16)	6.21 (1.72)
<i>Populus trichocarpa</i>	19.83 (6.3)	24.33 (7.96)	27.39 (8.45)	13.84 (5.8)	15.42 (6.78)	13.00 (12.35)	6.47 (3.4)	18.07 (10.32)	16.79 (9.05)	22.42 (13.58)	9.13 (2.18)	0.55 (0.13)	0.9 (0.29)	0.74 (0.22)	0.67 (0.15)
<i>Pseudotsuga menziesii</i>	1.86 (0.77)	3.8 (1.69)	4.77 (1.42)	4.47 (1.3)	7.02 (2.57)	5.21 (1.3)	4.2 (1.49)	7.73 (2.12)	9.03 (2.25)	11.81 (2.79)	10.93 (5.1)	8.32 (3.43)	12.98 (5.46)	14.31 (6.08)	20.49 (6.67)
<i>Thuja plicata</i>	3.98 (1.93)	6.13 (3.14)	4.79 (2.53)	4.3 (2.07)	4.52 (2.12)	8.79 (2.75)	6.59 (2.32)	11.77 (3.47)	11.83 (3.45)	14.91 (4.26)	15.27 (8.03)	8.77 (3.39)	17.64 (6.46)	11.4 (4.24)	15.67 (4.55)
<i>Pinus contorta</i>	12.35 (5.63)	14.41 (5.84)	19.81 (7.58)	20.08 (7.41)	18.07 (5.92)	4.5 (1.56)	5.31 (2.18)	6.57 (2.73)	9.48 (3.39)	13.88 (4.82)	5.97 (2.73)	8.45 (4.46)	8.94 (3.45)	15.32 (6.14)	17.2 (6.46)

^a The most common herb and shrub species represent the species that were most frequently sampled within the control plantations during the pre-treatment year.

RM-ANOVA was performed on the post-treatment years only. This suggested that the interaction was caused by a change in total Simpson's structural diversity among control and treatment plantations from the pre- to post-treatment year and that a treatment effect did exist during the post-treatment years. Post-hoc tests indicated that, as with the Shannon–Wiener index, total Simpson's structural diversity was significantly greater than that of the control within both the manual (Bonferroni; $p=0.02$) and cut-stump treated plantations (Bonferroni; $p<0.01$), during the second post-treatment year (Fig. 6).

4. Discussion

4.1. Experimental design

The subjective allocation of the cut-stump herbicide treatment was a potential concern as this was not consistent with an ideal randomized-block design. However, although natural variation was apparent among the plantations, the similarity of control and treatment units during the pre-treatment year (Figs. 2–7) suggested that the allocation of cut-stump treatments did not significantly bias our experimental design. In addition, treatment allocation was well interspersed among the nine plantations (and among the three blocks), a condition that is considered by some to be more important than randomization. Hurlbert (1984) states that "...interspersion is the more critical concept or feature; randomization is simply a way of achieving interspersion in a way that eliminates the possibility of bias and allows accurate specification of the probability of a type I error." This is especially true when replication is low, as is often the case with large-scale ecological studies.

4.2. Crown volume index

4.2.1. Herb and shrub layers

Since the manual and cut-stump treatments targeted only specific deciduous tree species, it is not surprising that there was not a significant effect on crown volume index of herbs or shrubs. However, these treatments appeared to temporarily depress the growth of these plant forms, relative to the control.

The small and temporary decrease in abundance of understory vegetation contrasted with the significant, albeit short-term, decreases in understory biomass reported in several studies treated with broadcast applications of glyphosate (Pollack et al., 1990; MacKinnon and Freedman, 1993; Sullivan, 1994; Simard and Heineman, 1996a, b, c; Sullivan et al., 1998; Whitehead and Harper, 1998). Relative to the more commonly prescribed broadcast applications of herbicides, the species-specific approach of cut-stump herbicide application appeared to have minimal effects on the biomass of understory vegetation.

The deciduous tree slash resulting from the treatments probably resulted in the short-term decrease in herb and shrub volume observed 1 year after treatment. The physical obstruction caused by the slash may have (1) impeded the growth of both herbs and shrubs, and (2) damaged some perennial shrubs. The expected recovery of both herb and shrub volume observed by the second post-treatment year was likely due to plants taking advantage of the increased resources (light and moisture) created by the treatments.

4.2.2. Deciduous tree layer

As treatments targeted the deciduous tree layer, the dramatic decrease in mean deciduous crown volume was expected in the first post-treatment year. However, rapid regrowth of paper birch and trembling aspen via prolific stump sprouts occurred within manually treated plantations. Consequently, by the second post-treatment year, deciduous tree volume within the manually treated plantations had returned to levels similar to that of the control. Other studies have also recorded the vigorous sprouting ability of paper birch and other hardwood species following manual cutting (Hart and Comeau, 1992; Simard and Heineman, 1996a). As reported by Johansson (1985) and Marrs (1985), treatment of cut-stumps with glyphosate limited the sprouting behavior of hardwoods, resulting in continued suppression of the deciduous tree layer for the four post-treatment years of our study. Relative to the volume of deciduous trees within the control plantations, the manually treated plantations had a treatment effect that lasted only 1 year.

Our findings, and those of other studies (Christensen, 1984; Lund-Høje, 1984; Johansson, 1985; Marrs, 1985), suggest that treatments to suppress deciduous

tree species capable of growing prolific stump sprouts, such as paper birch and trembling aspen, should employ measures to impede this sprouting behavior. Our results indicate that application of glyphosate to cut-stumps of paper birch and trembling aspen is a recommended approach to reduce competition of these species with coniferous crop trees in the Interior-Cedar-Hemlock zone, and probably in other similar ecosystems as well.

4.2.3. *Coniferous tree layer*

Although our sampling methods did not measure specific attributes of coniferous tree growth (such as DBH and exact heights), the mean crown volume index did measure the growth response of the entire coniferous tree (branches and bole). Therefore, the crown volume index of the coniferous tree layer is likely directly related to coniferous bole production, which is of primary importance to the silviculturalist gauging the success of vegetation management treatments.

Although no statistical differences in coniferous tree volumes were observed among control and treatment plantations, pre- or post-treatment, trends in growth response during the post-treatment years did suggest a treatment effect. The mean annual percentage increment of coniferous tree volume (accumulation of volume) within the control units was very gradual during the four post-treatment years (5% annual increase). This result was in contrast to the 44 and 29% mean annual percentage increment of coniferous tree volume observed during this same period among the manually and cut-stump treated plantations, respectively. This pattern suggests that the coniferous tree layer did benefit from the treatments in terms of an increased rate of growth. The benefits of vegetation management on growth and survival of coniferous crop trees is well-documented (Berry, 1982; MacLean and Morgan, 1983; Yang, 1991; Wang et al., 1995).

Differences in coniferous tree growth within treated plantations may increase relative to that of the control with time. Simard and Heineman (1996a) reported that responses of Douglas-fir height to treatments were not fully expressed even 9 years after treatment. Also, a more sensitive measure to determine the treatment effects on crop tree growth may have been possible if we had included measurements of stem diameter.

Simard and Heineman (1996b) reported that stem diameter was the most sensitive measure of early response of lodgepole pine to release from competing vegetation.

The slight decrease in coniferous tree volume in the first post-treatment year in the manually and cut-stump treated plantations might be attributed to a phenomenon known as 'thinning shock' (Reukema, 1964; Brix, 1981; Harrington and Reukema, 1983). Thinning shock, of course, does not actually reduce the stem volume of an affected tree, rather it temporarily reduces the rate of tree growth due to increased exposure (e.g., sunscald) and increased physical damage (e.g. wind, snow, and ice) (Harrington and Reukema, 1983). The decrease in coniferous tree cover within the treated plantations during the first post-treatment year was consistent with the effects of thinning shock.

4.3. *Species richness and turnover*

Other studies also reported no significant differences in species richness among control plantations and those treated with manual methods or glyphosate applications (Boyd et al., 1995; Simard and Heineman, 1996a, b; Sullivan et al., 1998). The number of herb species gained was always greater than species lost during the first two or three years of the study within control and treatment plantations. The contrary was true for the final years of the study, when more herb species were lost than gained. This suggested that the 5-year sampling period may have captured a transition period for the herb layer, perhaps changing from a community of shade-intolerant to more shade-tolerant herbs in association with increased canopy closure of the tree layer. Plant species gained early in the study may have represented the last wave of shade-intolerant herbs invading the sites while light conditions still permitted germination. Conversely, plant species lost during the final years of the study may have represented the loss of shade-intolerant species as light conditions declined. Schoonmaker and McKee (1988) reported similar findings during such transitional periods in a study of secondary succession within coniferous forests of the western Cascade Mountains. They described the transition period from one plant assemblage to another as a time of unresolved competition. An analysis that groups herb

species into classes of shade-tolerance, as well as a sampling method that specifically measures canopy closure and light conditions beneath the forest canopy would be important for testing this hypothesis (Halpern and Spies, 1995).

A weak trend of increasing shrub turnover within control plantations and a decrease in shrub turnover within the treated plantations over the study suggested a possible treatment effect. We hypothesize that the treatments may have maintained a more stable shrub community by delaying the canopy closure of the tree layer. The control plantations may have experienced a more rapid change in shrub community due to the decreasing light conditions associated with the closing canopy of the tree layer.

4.4. Species diversity

When interpreting species diversity results, it is important to consider the two components that define diversity: (1) the number of species sampled, or species richness, and (2) the frequency distribution, or relative abundance, of these species. For our study, crown volume index was used to calculate the proportions of species sampled within an area. Therefore, crown volume index is useful for inferring information about the proportional component of a diversity index.

4.4.1. Herb and shrub layers

Herb species diversity began to decline in 1994, even though this was the year that experienced the greatest species richness of any of the sample years. However, when combined with the fact that the greatest herb volume of any of the sample years was also recorded during 1994, we conclude that a few herb species thrived (causing the increased herb volume) and dominated the herb layer during this time, resulting in a decline in herb species diversity. In particular, during 1993, the combined crown volumes of fireweed and grass made up 44, 62, and 63% of the total crown volume of the common herbs (Table 3) within control, manual, and cut-stump treated plantations, respectively. In the following year (1994), these same two herbs had increased in dominance and made up 57, 80, and 67% of the total crown volume of the common herbs within control, manual, and cut-stump treated plantations, respectively.

Shrub species diversity gradually declined from the pre-treatment year (1992) to the end of the study (1996) in all plantations (Fig. 5). Although shrub species richness was relatively constant throughout all 5 sample years, shrub volume generally increased during the 4 post-treatment years. This inverse relationship between species diversity and volume suggested that a few shrubs, as was concluded for the herb layer, became increasingly dominant, resulting in a decline in diversity. In particular, during the first post-treatment year, the combined crown volumes of thimbleberry, bitter cherry, and willow made up 77, 83, and 63% of the total crown volume of the common shrubs within control, manual, and cut-stump treated plantations, respectively. By the final year of sampling, these same three species had increased in dominance to combined volumes of 86, 91, and 70% of the total crown volume of common shrubs within control, manual, and cut-stump treated plantations, respectively.

4.4.2. Tree layer

The manual treatment increased tree species diversity while the cut-stump treatment resulted in a decrease in diversity from the pre-treatment to first post-treatment year. Because tree species richness was relatively constant and coniferous tree volume changed little in the first post-treatment year, the dramatic changes in deciduous tree volume were likely the cause of changes in tree species diversity within the manual and cut-stump treatments. The dramatic reduction of deciduous tree volume observed within the cut-stump treated plantations (95% decrease relative to pre-treatment year), while not eliminating any deciduous species, increased the relative dominance of the coniferous trees. Of the total crown volume index for the tree layer, coniferous trees made up 50% during the pre-treatment year. During the first post-treatment year, the proportion of coniferous trees had increased to 94% within plantations receiving the cut-stump treatment. Moreover, during this first post-treatment year, 88% of the total tree volume was made up of only four out of the 12 tree species found within the cut-stump treated plantations, all coniferous (Douglas-fir, western red-cedar, lodgepole pine, and western hemlock). Conifer dominance was, therefore, the most likely cause for the decline in tree species diversity during the first post-treatment year.

Manually treated plantations also resulted in a volume reduction (87% decrease relative to pre-treatment year) of deciduous trees. During the pre-treatment year, 76% of the total tree volume was made up of just three out of the 11 tree species found within the manually treated plantations, all deciduous (paper birch, black cottonwood, and trembling aspen). During the year following treatment, these three deciduous tree species made up only 37% of the total tree volume. The removal of a substantial proportion of this deciduous tree layer resulted in a more evenly distributed, and, therefore, more diverse tree layer during the first post-treatment year. Pielou (1966b) described this type of increase in species diversity (one caused by the thinning of a dominant tree layer) as resulting from an increase in pattern-diversity.

4.5. Structural diversity

We predicted that the treatments should not significantly alter the structural diversity of the herb layer. This was because of the annual nature of herbs which allow this plant layer to respond quickly to changing environmental conditions, growing into many of the same height classes as it had the year before. In contrast, perennial plants such as shrubs, because of their interdependence on the previous year's growth, are predicted to take longer, as a group, to respond to new environmental conditions.

As a stand of trees ages and canopy closure increases, the structural diversity of the tree layer will probably decline. Shading created by increasing canopy closure begins to thin out and simplify the understory height classes (Pielou, 1966b). By removing a substantial portion of the canopy, the manual and cut-stump treatments had effectively delayed this process of canopy closure within treated plantations. Because overstory shading, to a large extent, governs what can grow in the understory, canopy closure is a driving force that will largely determine the total (herb, shrub, and tree layers combined) structural diversity of a stand. Therefore, as the control plantations grew unimpeded towards canopy closure, there was a steady decline in structural diversity throughout all 5 years of the study. Treatments, on the other hand, temporarily opened the overstory canopy, and consequently the total structural diversity, although decreasing through the post-treatment years, was statistically

more structurally diverse than that of the control in 1994.

5. Conclusions

Our study suggested that conifer release from deciduous trees (capable of stump sprouts) was best achieved with a cut-stump application of herbicide, such as glyphosate. Methods that do not employ some means of impeding stump sprouts, such as the manual cutting method, are not likely to maintain suppression of deciduous trees for extended periods following treatment. Therefore, successful conifer release by manual methods alone is unlikely, and this result should be expected in most temperate forest ecosystems.

Although the cut-stump application of glyphosate significantly reduced deciduous tree volume for 4 post-treatment years, this treatment had little effect on species richness, species diversity, or structural diversity of the plant community. In fact, reduced dominance of the deciduous tree layer and opening of the tree canopy created by both treatments appeared to increase total structural diversity during post-treatment years, relative to that of the control.

This is the first published study to analyze a plant community's response to alternative vegetation management treatments applied to young mixed-conifer plantations. Results suggested that, while suppressing volume of the targeted deciduous tree layer, the species-specific approach of the cut-stump herbicide treatment achieved its objective of conifer release without adversely affecting species richness, species diversity, or structural diversity of the plant community. This result would likely be achieved in other temperate and boreal forest ecosystems as well.

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References

- Adler, G.H., 1987. Influence of habitat structure on demography of two rodent species in eastern Massachusetts. *Can. J. Zool.* 65, 903–912.
- Anthony, R.G., Morrison, M.L., 1985. Influence of glyphosate herbicide on small mammal populations in western Oregon. *Northwest Sci.* 59, 159–168.
- Balda, R.P., 1969. Foliage use by birds of the oak–pine juniper woodland and ponderosa pine forest in southeastern Arizona. *Condor* 71, 399–412.
- Bell, F.W., Lautenschlager, R.A., Wagner, R.G., Pitt, D.G., Hawkins, J.W., Ride, K.R., 1997. Motor manual, mechanical, and herbicide release affect early successional vegetation in northwestern Ontario. *For. Chron.* 73, 61–68.
- Berry, A.B., 1982. Response of suppressed conifer seedlings to release from aspen–pine overstory. *For. Chron.* 58, 91–92.
- Boyd, R.S., Freeman, J.D., Miller, J.H., Edwards, M.B., 1995. Forest herbicide influences on floristic diversity 7 years after broadcast pine release treatments in central Georgia, USA. *New For.* 10, 17–37.
- Brix, H., 1981. Effects of thinning and nitrogen fertilization on branch and foliage production in Douglas-fir. *Can. J. For. Res.* 11, 502–511.
- Cambell, D.L., Evans, J., Lindsey, G.D., Dusenberry, W.E., 1981. Acceptance by black-tailed deer of foliage treated with herbicides. USDA For. Serv., Pacific Northwest Forest and Range Experiment Station Portland, OR, USDI, Fish and Wildlife Service, Forest-Animal Damage Control Research Project. Olympia, WA. Res. Pap. PNW-290, 31 p.
- Campbell, R.A., 1990. Herbicide use for forest management in Canada: where we are and where we are going? *For. Chron.* 66, 355–360.
- Cherry, S., 1998. Statistical tests in publications of The Wildlife Society. *Wildl. Soc. Bull.* 26, 947–953.
- Christensen, P., 1984. Review of Danish results from chemical/mechanical control of deciduous vegetation. *Aspects Appl. Bio.* 5, 135–142.
- Clough, G.C., 1987. Relations of small mammals to forest management in northern Maine. *Can. Field-Nat.* 101, 40–48.
- D'Anieri, P., Leslie Jr., D.M., McCormack Jr., M.L., 1987. Small mammals in glyphosate-treated clearcuts in northern Maine. *Can. Field-Nat.* 101, 547–550.
- Easton, W.E., Martin, K., 1998. The effect of vegetation management on breeding bird communities in British Columbia. *Ecol. Applic.* 8, 1092–1103.
- Freedman, B., 1991. Controversy over the use of herbicides in forestry, with particular reference to glyphosate usage. *J. Environ. Sci. Health C8*, 277–286.
- Freedman, B., Morash, R., MacKinnon, D., 1993. Short-term changes in vegetation after the silvicultural spraying of glyphosate herbicide onto regenerating clearcuts in Nova Scotia, Canada. *Can. J. For. Res.* 23, 2300–2311.
- Halpern, C.B., Spies, T.A., 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecol. Applic.* 5, 913–934.
- Harney, B.A., Dueser, R.D., 1987. Vertical stratification of activity of two *Peromyscus* species: an experimental analysis. *Ecology* 68, 1084–1091.
- Harrington, C.A., Reukema, D.L., 1983. Initial shock and long-term stand development following thinning in a Douglas-fir plantation. *For. Sci.* 29, 33–46.
- Hart, D., Comeau, P.G., 1992. Manual brushing for forest vegetation management in British Columbia: a review of current knowledge and information needs. BC Min. For., Victoria, BC, Land Manage. Handbook No. 7.
- Hitchcock, C.L., Cronquist, A., 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.
- Hunter, M.L., Jr., 1990. Vertical structure. In *Wildlife, forests, and forestry: principles of managing forests for biological diversity*. Prentice Hall, Englewood Cliffs, NJ, pp. 181–199 (Chapter 11).
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr* 54, 187–211.
- Johansson, T., 1985. Herbicide injections into stumps of aspen and birch to prevent regrowth. *Weed Res.* 25, 39–45.
- Jones, R., Forbes, J.M., 1984. A note on effects of glyphosate and quinine on the palatability of hay for sheep. *Anim. Prod.* 38, 301–303.
- Ketcheson, M.V., Braumandl, T.F., Meidinger, D., Utzig, G., Demarchi, D.A., Wikeem, B.M., 1991. Interior Cedar–Hemlock zone. In: Meidinger, D., Pojar, J.(Eds.), *Ecosystems of British Columbia*. BC Ministry of Forests, Victoria, BC, pp 167–181.
- Krebs, C.J., 1989. *Ecological Methodology*. Harper and Row, New York, NY.
- Kuehl, R.O., 1994. Repeated measures designs. In: *Statistical Principles of Research Design and Analysis*. Duxbury Press, Belmont, CA. pp. 499–528 (Chapter 15).
- Lautenschlager, R.A., 1993. Response of wildlife to forest herbicide applications in northern coniferous ecosystems. *Can. J. For. Res.* 23, 2286–2299.
- Littel, R.C., 1989. Statistical analysis of experiments with repeated measures. *HortScience* 24, 36–40.
- Lloyd, D.A., Angove, K., Hope, G., Thompson, C., 1990. *A Guide for Site Identification and Interpretation of the Kamloops Forest Region*, vols. 1 and 2. BC Ministry of Forests, Victoria, BC Land Manage. Handbook 23.
- Lund-Høie, K., 1984. Growth response of Norway spruce (*Picea abies* L.) to different vegetation management programmes — preliminary results. *Aspects Appl. Bio.* 5, 127–133.
- MacArthur, R.H., 1965. Patterns of species diversity. *Biol. Rev.* 40, 510–533.
- MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. *Ecology* 42, 594–598.
- MacKinnon, D.S., Freedman, B., 1993. Effects of silviculture use of the herbicide glyphosate on breeding birds of regenerating clearcuts in Nova Scotia, Canada. *J. Appl. Ecol.* 30, 395–406.

- MacLean, D.A., Morgan, M.G., 1983. Long-term growth and yield response of young fir to mechanical and chemical release from shrub competition. *For. Chron.* 59, 177–183.
- Marrs, R.H., 1985. Birch control by the treatment of cut stumps with herbicides. *Arbor. J.* 9, 173–182.
- McDonald, P.M., Radosevitch S.R., 1992. General principles of forest vegetation management. In: Black, H.C. (Technical Editor), *Silvicultural Approaches to Animal Damage Management in Pacific Northwest Forests*. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-287, pp. 67–91.
- McGee, A.B., Levy, E., 1988. Herbicide use in forestry: communication and information gaps. *J. Environ. Manage.* 26, 111–126.
- Morrison, M.L., Meslow, E.C., 1983. Impacts of forest herbicides on wildlife: toxicity and habitat alteration. *Trans. N. Am. Wildl. Nat. Resour. Conf.* 48, 175–185.
- Newton, M., Comeau, P.G., 1990. Control of competing vegetation. In: Lavender, D.P., Parish, R., Johnson, C.M., Montgomery, G., Vyse, A., Willis, R.A., Winston, D. (Eds.), *Regenerating British Columbia's Forests*. University of British Columbia Press, Vancouver, pp. 256–265.
- Newton, M., Howard, K.M., Kelpas, B.R., Danhaus, R., Lottman, C.M., Dubelman, S., 1984. Fate of glyphosate in an Oregon forest ecosystem. *J. Agric. Food Chem.* 32, 1144–1151.
- Peet, R.K., 1974. The measurement of species diversity. *Annu. Rev. Ecol. Syst.* 5, 285–307.
- Pielou, E.C., 1966a. The measurement of species diversity in different types of biological collections. *J. Theor. Biol.* 13, 131–144.
- Pielou, E.C., 1966b. Species-diversity and pattern-diversity in the study of ecological succession. *J. Theor. Biol.* 10, 370–383.
- Pollack, J.C., LePage, P., van Thienen, F., 1990. Some effects of different forest herbicides on upland *Salix* spp. *Can. J. For. Res.* 20, 1271–1276.
- Reukema, D.L., 1964. Crown expansion and stem radial growth of Douglas-fir as influenced by release. *For. Sci.* 10, 192–199.
- Rosenthal, R., Rosnow, R.L., 1985. *Contrast Analysis: Focused Comparisons in the Analysis of Variance*. Cambridge University Press, London.
- Santillo, D.J., Leslie Jr., D.M., Brown, P.W., 1989. Response of small mammals and habitat to glyphosate application on clearcuts. *J. Wildl. Manage.* 53, 164–172.
- Schoonmaker, P., McKee, A., 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *For. Sci.* 34, 960–979.
- Simard, S.W., Heineman, J., 1996a. Nine-year response of Douglas-fir and the mixed-hardwood–shrub complex to chemical and manual release treatments on an ICHmw2 site near Salmon Arm. *Can. For. Serv. and BC Min. For., Victoria, BC, FRDA Rep. No. 257*.
- Simard, S.W., Heineman, J., 1996b. Nine-year response of lodgepole pine and the dry alder complex to chemical and manual release treatments on an ICHmk1 site near Kelowna. *Can. For. Serv. and BC Min. For., Victoria, BC, FRDA Rep. No. 259*.
- Simard, S.W., Heineman, J., 1996c. Nine-year response of Englemann spruce and the willow complex to chemical and manual treatments on an ICHmw2 site near Vernon. *Can. For. Serv. and BC Min. For., Victoria, BC, FRDA Rep. No. 258*.
- Simpson, E.H., 1949. Measurement of diversity. *Nature* 163, 688.
- SPSS Institute Inc., 1997. *Statistical Programs for the Social Sciences*. Chicago, IL.
- Stickney, P. F., 1980. Data base for post-fire succession, first 6 to 9 years, in Montana Larch-fir forests. USDA Forest Service General Technical Report, INT-62, Ogden, UT, U.S. Department of Agriculture, Forest Service, Intermountain Research Station.
- Stickney, P.F., 1985. Data base for early post-fire succession on the Sundance Burn, northern Idaho. USDA Forest Service General Technical Report, INT-189, Ogden, UT, U.S. Department of Agriculture, Forest Service, Intermountain Research Station.
- Sullivan, T.P., Sullivan, D.S., 1982. Responses of small mammal populations to a forest herbicide application in a 20-year-old conifer plantation. *J. Appl. Ecol.* 19, 95–106.
- Sullivan, T.P., 1990a. Influence of forest herbicide on deer mice and Oregon vole population dynamics. *J. Wildl. Manage.* 54, 566–576.
- Sullivan, T.P., 1990b. Demographic responses of small mammal populations to a herbicide application in coastal coniferous forest: population density and resiliency. *Can. J. Zool.* 68, 874–883.
- Sullivan, T.P., 1994. Influence of herbicide-induced habitat alteration on vegetation and snowshoe hare populations in sub-boreal spruce forest. *J. Appl. Ecol.* 31, 717–730.
- Sullivan, T.P., Sullivan, D.S., 1979. The effects of glyphosate herbicide on food preference and consumption in black-tailed deer. *Can. J. Zool.* 57, 1406–1412.
- Sullivan, T.P., Sullivan, D.S., 1981. Response of a deer mouse population to a forest herbicide application: reproduction, growth, and survival. *Can. J. Zool.* 59, 1148–1154.
- Sullivan, T.P., Lautenschlager, R.A., Wagner, R.G., 1996. Influence of glyphosate on vegetation dynamics in different successional stages of sub-boreal spruce forest. *Weed Tech.* 10, 439–446.
- Sullivan, T.P., Sullivan, D.S., Lautenschlager, R.A., Wagner, R.G., 1997. Long-term influence of glyphosate herbicide on demography and diversity of small mammal communities in coastal coniferous forest. *Northwest Sci.* 71, 6–17.
- Sullivan, T.P., Wagner, R.G., Pitt, D.G., Lautenschlager, R.A., Chen, D.G., 1998. Changes in diversity of plant and small mammal communities after herbicide application in sub-boreal spruce forest. *Can. J. For. Res.* 28, 168–177.
- Sutton, S.L., Hudson, P.J., 1980. The vertical distribution of small flying insects in lowland rainforests of Zaire. *Zool. J. Linnaean Soc.* 68, 111–123.
- Tomkins, D.J., Grant, W.F., 1977. Effects of herbicides on species diversity of two plant communities. *Ecology* 58, 398–406.
- Walmsley, M.E., Utzig, G., Vold, T., Van Barneveld, J., 1980. *Describing ecosystems in the field*. BC Ministry of Environment and Ministry of Forests, Land Management Report Number 7.
- Walstad, J.D., Kuch, P.J. (Eds.), 1987. *Forest vegetation management for conifer production*. Wiley, NY, 523 pp.
- Wang, J.R., Simard, S.W., Kimmins, J.P., 1995. Physiological responses of paper birch to thinning in British Columbia. *For. Ecol. Manage.* 73, 177–184.

- Whitehead, R.J., Harper, G.J., 1998. A comparison of four treatments for weeding Englemann spruce plantations in Interior Cedar Hemlock Zone of British Columbia: ten years after treatment. Information Report BC-X-379. Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, 21 pp.
- Yang, R.C., 1991. Growth of white spruce following release from aspen competition: 35-year results. *For. Chron.* 67, 706–711.
- Zar, J.H., 1984. Data transformations. In: *Biostatistical Analysis*. 2nd Edition. Prentice Hall, Englewood Cliffs, NJ, pp 236–243 (Chapter 14).