EFFECTS OF COMMERCIAL THINNING ON GENETIC, PLANT SPECIES AND STRUCTURAL DIVERSITY IN SECOND GROWTH DOUGLAS-FIR (*PSEUDO-TSUGA MENZIESII* (MIRB.) FRANCO) STANDS

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ABSTRACT

The impact of commercial thinning on biodiversity was studied in two Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantations, Weeks Lake (WL) and Fairservice Creek (FC) located on southern Vancouver Island, British Columbia. The age of the stands at thinning was 53 and 70 years for FC and WL, respectively. Other tree species were also present in both sites due to natural regeneration. Biodiversity was evaluated before and after commercial thinning with respect to tree species composition/abundance, tree species genetic diversity assessed by allozyme analysis and stand structural diversity represented by the diameter class (5-cm) distribution. In addition, understorey plant species diversity was monitored in WL and FC for 4 and 5 years following thinning, respectively.

Tree species composition changed in both plantations in a similar fashion as the proportion of Douglas-fir increased at the expense of all other tree species. Stand structural diversity was simplified due to the decreased number of trees in small diameter classes. These results were expected since the commercial thinning was conducted to promote the growth of Douglas-fir. Genetic diversity parameters (average number of alleles per locus, percent polymorphic loci, and expected heterozygosities) did not differ significantly before and after thinning; however, thinning resulted in a loss of 8 and 7 alleles across species for FC and WL, respectively. Most of the allelic loss occurred in the naturally regenerated species (93%). This allelic loss represents 7 and 6% of the total alleles present in FC and WL, respectively. Thus, only one allele was lost from the crop tree in the FC plantation.

Understorey vegetation species richness decreased the year following commercial thinning and then consistently increased over time in both plantations. A total of 17 and 9 new species colonized FC and WL, respectively. One species was replaced in each plantation. In FC, diversity of the understorey plant community based on the Shannon diversity index (*H*) changed in an increasing linear trend that corresponded to the increase in species richness. On the other hand, H in WL remained stable. Species evenness (H/H_{max}) did not change in WL and FC over the course of study except for seasonal fluctuations. Rare species diversity increased over time in both plantations.

Key words: Commercial thinning, species diversity, genetic diversity, structural diversity, understorey plant community diversity, *Pseudotsuga menziesii*.

INTRODUCTION

The development of successful forest management strategies requires an understanding of a wide array of topics such as: the extent and diversity of forest ecosystems, the impact of forest management practices on biological diversity, and tactics and strategies for gene conservation. Such understanding will allow forest managers and gene conservationists to work together to combine utilization with conservation in the most efficient manner. This is necessary to maintain competitiveness in world markets and to meet increasing demands on an ever shrinking forest land base without compromising sustainability of forest ecosystems.

Biological diversity or biodiversity refers to the full variety of life that occurs in an area (i.e., types and

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amounts of flora and fauna in their natural surrounding). Biodiversity encompasses ecosystem diversity (i.e., the variety of habitats), species diversity (i.e., number and abundance of species), and genetic diversity (i.e., genetic differences/breadth among individuals of the same species). The maintenance of habitat diversity ensures the availability of favourable ecological conditions for a wide variety of species; species diversity provides security in facing unpredictable environmental conditions; and genetic diversity buffers and enhances species in adapting to changing environments.

Young even-aged forest plantations often appear in disharmony with the notion of biodiversity conservation. Such plantations are usually less structurally diverse than naturally regenerated stands (HANSEN *et* *al.*, 1991). Typically they are characterised by a single canopy layer, low diversity of tree species in terms of composition and abundance, suppressed ground vegetation and lack of large woody debris. Low spatial heterogeneity is in turn linked to low wildlife diversity (HUNTER, 1990). Therefore, it is important that silvicultural treatments practised in managed forests do not further reduce plantation biodiversity but ideally enhance it. One practise that can potentially change structural diversity is commercial thinning (HAYES *et al.*, 1997).

"Commercial thinnings are simply defined as those in which all or part of the felled trees are extracted for useful products, regardless of whether their value is great enough to defray the cost of operation" (SMITH, 1962). Other reasons for conducting commercial thinning include: a) reducing the stand density, b) removal of disease infected or damaged trees, c) modifying stand species composition, and d) improving the overall stand productivity and quality. In most cases there is an opportunity to significantly alter or change tree species diversity. As a by-product of the thinning operation, the species and the structural diversity of the understorey plant community will be altered either due to the disturbance caused by the thinning operation and/or the change in the local environmental conditions (such as the level of light penetration, competition, and availability of water and nutrients). Although partial tree removal may reduce structural diversity of trees in terms of their size and composition, it can also enhance habitat heterogeneity by promoting growth of understorey vegetation and tree seedlings.

Despite the large increase in the number of managed second growth forests, there is a paucity of studies investigating the impact of forest management practices on plant species diversity (HALPERN & SPIES, 1995) and genetic diversity. The impact of management practices on tree species diversity and stand structural diversity was investigated in mixed species northern hardwood forests (NIESE & STRONG, 1992; LU & BUONGIORNO, 1993; BUONGIORNO et al., 1994). NIESE & STRONG (1992) compared five partial-cut treatments and control and found that medium to heavy selection produced the highest tree species diversity. LU & BUONGIORNO (1993) concluded that felling all trees with diameter at breast height above 41 cm every 15 years resulted in species diversity almost the same as in a natural stand. On the other hand, the highest sustainable diversity of tree size in the studied hardwood forests in Wisconsin would be attained by undisturbed stands (BUONGIORNO et al., 1994). SHULTE & BUON-GIORNO (1998) reported that loblolly pine (Pinus taeda L.) stands in the southern USA subject to management regimes producing higher maximum diameters of pines had the greatest tree size diversity while those treatments that retained a hardwood component would produce stands with greater tree species diversity.

With respect to understorey vegetation, the majority of studies investigated effects of tree removal on only one component of diversity: vegetation abundance. In general, understorey cover increases with increased canopy openings. For example, ANDERSON et al. (1969) reported the presence of linear relationship between percent open canopy and understorey cover in pine forests of northern Wisconsin. The percent of understorey vegetation was greater in thinned than unthinned stand of ponderosa pine (Pinus ponderosa Laws.) in northern California (AGEE & BISWELL, 1970). Likewise, TAPPEINER & ZASADA (1993) found that several understorey species had higher seedling emergence and survival in thinned stands in coastal Oregon. However, the increase in the ground vegetation cover in response to thinning is not always observed. For example, KRUEGER (1960) found that understorey vegetation cover in Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) stands did not change significantly six years after thinning that removed 27 % of tree volume. Similarly, the 17-year response of most vascular plants to thinning in terms of abundance was highly variable and not significant in Picea-Tsuga forests on the Oregon coast (ALABACK & HERMAN, 1988).

The impact of partial tree removal on genetic diversity have been examined in several studies using isozyme markers. HOSIUS (1993) showed that the genetic structure of a 70-year old Norway spruce (Picea abies (L.) Karst.) stand was affected by both high thinning and low thinning and that the results differed depending on the type of thinning and the enzyme systems examined. KONNERT & SPIECKER (1996) reported that selective felling operation conducted in a beech (Fagus sylvatica L.) stand affects the genetic structure of the species; however, if the felling is based in natural selection criteria, then the danger of altering genetic structures is reduced to a minimum. For the same species LAUBER et al. (1997) found that repeated thinning had no negative influence on genetic diversity in a 60-year old naturally regenerated stand and reported that heterozygosity was somewhat higher in the thinned beech stand compared to the natural stand. Thinning can influence species genetic structure not only by the removal of individuals in some diameter classes but also in situations where a certain morphological type is favoured during the thinning operation by the selective removal of a less desirable type (HER-TEL & KOHLSTOCK, 1994).

Sound management of the genetic resources in British Columbia's forests is an integral and indispens-

able element of a successful sustainable development strategy in the province. The attainment of this goal encounters at least two major and sometimes conflicting challenges. These are: (1) the maintenance of the rich biological diversity currently found in natural forest ecosystems and (2) yield enhancement of the commercially valuable wood products per unit area. The number of monoculture forests in British Columbia (B.C.) has increased prompting concerns about the reduction of biological diversity in simplified forest ecosystems.

The present study deals with factors affecting biodiversity at the stand level. Since stands are subject to various harvesting and silvicultural activities, a rigorous evaluation of the impact of these activities on plant species and their genetic diversity is required. We examined the impact of commercial thinning on biodiversity in two second growth Douglas-fir plantations on southern Vancouver Island, B.C. Evaluated components of biodiversity included tree species composition/abundance, stand structural diversity, tree species genetic diversity, and understorey vegetation composition/abundance.

MATERIALS AND METHODS

Study sites

The study was conducted in two Douglas-fir plantations, Weeks Lake (WL) and Fairservice Creek (FC) located on southern Vancouver Island, B.C. (proximal to latitude 49°, longitude 124°, elevation 19-67 m) in the Coastal Western Hemlock biogeoclimatic zone (POJAR et al., 1987). WL and FC were planted with Douglas-fir in 1925 and 1941, respectively. As a result of natural regeneration, other tree species were also present in both sites (Table 1). Salal (Gaultheria shallon Pursh) was the most abundant understorey species in WL while dull Oregon-grape (Mahonia nervosa Pursh), vanilla-leaf (Achlys triphylla (Smith) DC) and sword fern (Polystichum munitum (Kaulf.) Presl) were the main components of understorey vegetation in FC. Initial stand density in terms of number of trees per hectare was different in WL than in FC but similar when expressed as basal area per hectare (Table 1). The plantations were fertilized: WL in 1954, FC in 1969 and 1973.

In both plantations, one study site with an area of 0.25 ha was established to estimate the impact of commercial thinning on tree species diversity. To monitor changes in the understorey plant community following commercial thinning, three transect plots per study site were established. The transects were parallel, 1×30 m in size and were 15 m apart from each other

measured from the transect centre. Commercial thinning from "below" (low thinning) was completed during the early spring of 1994 and 1995 in FC and WL, respectively. Stand density expressed as number of trees per hectare was reduced by 64% in WL and 62% in FC. Stand density expressed as basal area per hectare was reduced by 37% in WL and 30% in FC.

Stand structural diversity and tree species diversity

Stem maps were generated before and after thinning. The maps show the spatial arrangement of all living trees in the study plots. The species of every individual tree was determined and the diameter at breast height (DBH) was measured. Individuals smaller than the breast height were counted. For each tree species, a diameter class distribution profile was generated with 5-cm increments. The Shannon diversity index (PIE-LOU, 1966) was calculated for tree species as explained below.

Tree species genetic diversity

For each study site, dormant vegetative buds were collected from every standing living tree. Samples were then placed in plastic bags and stored on ice to prevent protein deterioration. The branch samples were shipped to the laboratory and stored at 2°C until protein extraction. Newly developed vegetative bud primordia were removed from the bud scales and proteins were extracted using a slightly modified extraction buffer of CHELIAK & PITAL (1984). Protein electrophoresis was conducted on 11 % horizontal starch gels using four gel-electrode buffer systems. The buffer systems used were: Histidine citrate pH 7.0 (FILDES & HARRIS, 1966), Morpholine citrate pH 6.1 (CLAYTON & TRE-TIAK, 1972), Tris citrate: lithium borate pH 8.5 (RIDGE-WAY et al., 1970), and Tris citrate pH 7.0 (SICILIANO & SHAW, 1976). Depending on the species, a total of 11 (Pacific silver fir (Abies amabilis (Dougl.)) Forbes) to 22 (Douglas-fir) loci were resolved for 12 enzyme systems: phosphoglucose isomerase (Pgi-1, Pgi-2) E.C. 5.3 .1.9, phosphoglucomutase (*Pgm-1*, *Pgm-2*) E.C. 5.4.2.2, fructose diphosphatase (Fdp-2) E.C. 3.1.3.11, 6-phosphogluconic dehydrogenase (6pgd-1, 6pgd-2) E.C.1.1.1.44, shikimate dehydrogenase (Skdh-1) E.C. 1.1.1.25, aspartate amino-transferase (Aat-1, Aat-2) E.C. 2.6.1.1, malate dehydrogenase (Mdh-1, Mdh-2, MDH3) E.C. 1.1.1.37, leucine aminopeptidase (Lap-1, Lap-2) E.C. 3.4.11.1, aconitase (Aco-1, Aco-2) E.C. 4.2.1.3, isocitrate dehydrogenase (Idh) E.C. 1.1.1.42, glutamate dehydrogenase (Gdh) E.C. 1.4.1.2, and glucose-6-phosphate dehydrogenase (G6p) E.C. 1.1.1 .49. The staining methods used followed those of O'MALLEY *et al.* (1980) and CONKLE *et al.* (1982).

For each of the two study sites, gene and genotypic frequencies were compiled for each tree species. For each species/site combination, the following genetic parameters were calculated: 1) total number of alleles, 2) number of alleles per locus (N_a) , 3) proportion of polymorphic loci (PLP_{95%}), 4) expected heterozygosity (H_e) , and 5) allelic loss. Differences in mean N_a and H_e before and after thinning were assessed using t-test.

Understorey vegetation diversity

The number of understorey plant species and the frequency of individuals of every species encountered was determined in each of the three transect plots per study site. Individuals that overlapped transect boundaries were included in the study. All surveyed understorey plants were perennial. Ramets, if present, were counted as individuals. Parts of the transects were disturbed by the thinning operation and others were left intact. Transects were assessed before and immediately after thinning to determine the level of disturbance. Changes in species demography were monitored by 14 and 13 seasonal surveys in FC and WL, respectively. The surveys occurred over the period of 5 years in FC and 4 years in WL.

Impact of commercial thinning on composition and abundance of understorey vegetation was evaluated using several diversity measures: 1) species richness, 2) the Shannon diversity index, and 3) index-free diversity orderings. Species richness was defined as the total number of species found in the study plots (each transect) on each sampling date. The Shannon index has been widely used in ecological studies to describe the species diversity (e.g. SULLIVAN *et al.*, 1996; RICE *et al.*, 1997). Based on the Shannon index (*H*), species evenness of a plant community can be expressed as a ratio of the calculated value of the index to the value of the index if all individuals were evenly distributed among species, i.e. to the maximum value of the index (H_{max}).

Shannon index (H):

$$H = -\sum_{i=1}^{s} P_i \ln P_i$$

Evenness based on the Shannon index (E_H) :

$$E_H = H / H_{\text{max}} = H / \ln S$$

where S = total number of species in the sampling area, $P_i =$ proportion of individuals of the *i*th species with respect to the total number of individuals in the sampling area.

Species richness and H were subjected to the linear regression analysis with sampling date as an independent variable using AUTOREG procedure of SAS (SAS, 1993). Means of the three transects per plantation were used in the analysis. No significant first order autocorrelations were found using the Durbin-Watson statistic (DURBIN & WATSON, 1951). Due to the small sample size, higher order autocorrelation coefficients were deemed to be unreliable and were not taken into consideration even though the data fluctuated with seasons. The purpose of the regression analysis was to find a model describing trends in species diversity following commercial thinning. The cyclic component of the variations was of no interest since the seasonal variations were in large part artificial as some herbs were not visible in winter causing the species count to go down.

In addition to species richness and the diversity index, index-free diversity orderings (diversity profiles) were used (SWINDEL *et al.*, 1987). These are graphical techniques that compare diversities of two communities by plotting ranked cumulative abundance of species in each community starting with the most abundant species. If the plotted curve is above the diagonal line (representing situation when there are equal proportions of species in both communities) then community X (xaxis) is more diverse than community Y (y-axis). Diversity orderings can show not only how the community diversity was affected by disturbance (i.e., thinning) but also how the disturbance affected abundance of common and rare species.

Comparative diversity profiles were constructed for both study sites with data collected before the thinning on x-axis (winter 1994 for FC and winter 1995 for WL) and data collected after the thinning on y-axis (winters 1995–1997 for FC and winters 1996–1997 for WL). Since the vegetation survey before the thinning occurred in winter, the diversity profiles were constructed only for data collected in winter to eliminate the seasonal factor in the species count. Comparative diversity profiles for each site were based on the species mean cumulative proportional abundance of the three transect plots.

RESULTS

Stand structural diversity and tree species diversity

Commercial thinning affected several stand structure characteristics. Reduction in stand density was accompanied by the shift in tree species proportional abundance as well as change in diameter class distributions. As expected, tree species composition changed in both study plots in the same fashion as the proportion of Douglas-fir increased while the number of trees of all other species decreased as a result of thinning (Table 1). Specifically, in FC, the species composition changed from 51.4, 31.3 and 17.3 % to 75.9, 16.9 and 7.2 % for Douglas-fir, western hemlock (Tsuga heterophylla (Raf.) Sarg.), and western redcedar (Thuja plicata Donn.), respectively. In WL, the initial species composition was 72.4, 22.2, 3.0, 1.8 and 0.6 % for Douglasfir, western hemlock, western white pine (Pinus monticola Dougl.), western redcedar and Pacific silver fir, respectively. Commercial thinning altered the species composition to 84.6, 13.8, and 1.6 % for Douglas-fir, western hemlock and western white pine, respectively. Western redcedar and Pacific silver fir, both represented by very low numbers (6 and 2 trees) before thinning, were eliminated in WL. Following thinning, the Shannon index of tree species diversity was reduced from 1.01 to 0.70 in FC and from 0.77 to 0.48 in WL (Table 1).

Commercial thinning changed diameter distributions in both study plots as thinning occurred mainly in diameter classes below 35 cm (Figures 1 and 2). Since all species other than Douglas-fir were found mainly in small diameter classes, these species were affected the most by the treatment. The properties of Douglas-fir diameter distribution were also modified: in FC, the mean DBH (\pm standard deviation) changed from 34.7 \pm 12.0 cm before thinning to 42.4 \pm 9.5 cm after thinning. In WL, the older study site, Douglas-fir diameter distribution was bimodal before thinning with peaks in 0–5 and 25–30 cm DBH classes (Figure 2). The individuals in the smallest diameter class were the product of natural regeneration. After thinning, the second peak occurred in 35-40 cm class and the mean DBH changed from 25.2 to 32.7 cm. However, the spread of observations remained the same in WL as standard deviations were 12.6 and 12.3 cm before and after thinning, respectively. Based on all species, after thinning there were representatives in all diameter classes in WL while the number of classes was reduced from 14 to 12 in FC.

Tree species genetic diversity

Before and after thinning estimates of heterozygosity parameters (average number of alleles per locus, percent polymorphic loci, and expected heterozygosities) for both study plots are presented in Table 2. In general, heterozygosity parameters did not differ significantly. However, thinning resulted in a loss of 8 and 7 alleles for FC and WL, respectively (Table 2). This loss of allelic variation represents only 7 and 6 % of the total number of alleles in FC and WL, respectively (Table 2). It is noteworthy that most of the allelic loss occurred in western hemlock (12 out of 15 alleles: 80 %) and western white pine (2 out of 15 alleles: 13 %). These two species do not represent the crop species and, as mentioned above, they were introduced to the plantation through natural regeneration. Only one allele (7 %) was lost from Douglas-fir in the FC plantation (Table 2).

Understorey vegetation diversity

In terms of species richness, response to treatment was similar in both plantations. The number of species fluctuated with sampling dates but showed a strong increasing linear trend ($r^2 = 0.62$ and 0.74 in WL and

Species		Week	s lake		Fairservice Creek				
	before thinning		after th	inning	before the	hinning	after thinning		
	trees · ha ⁻¹	m ² ·ha ⁻¹	trees • ha-1	m ² ·ha ⁻¹	trees · ha ⁻¹	m ² ·ha ⁻¹	trees ha-1	m ² ·ha ⁻¹	
Fd	980	61.07	416	39.83	452	47.83	252	37.34	
Hw	300	1.86	68	0.07	276	9.06	56	4.22	
Cw	24	0.02	0	0	152	2.79	24	0.42	
Pw	40	1.28	8	0.39					
Ba	8	0	0	0			·		
Total	1352	64.23	492	40.29	880	59.68	332	41.98	
н	0.77		0.48		1.01		0.7		

Table 1. Species composition, number of trees per hectare, basal area (m^2) per hectare and the Shannon diversity index (H) before and after commercial thinning for Weeks lake and Fairservice Creek (Fd = Douglas-fir, Hw = western hemlock, Cw = western redcedar, Pw = western white pine, Ba = Pacific silver fir).

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Table 2. Number of trees, number of loci, total number of alleles, number of alleles per locus (N_a) , proportion of
polymoprhic loci (PLP_{95}), expected heterozygosity (H_e), and allelic loss for western redcedar (Cw), western hemlock (Hw),
Douglas-fir (Fd), western white pine (Pw), and Pacific silver fir (Ba) before and after thinning in two Douglas-fir
plantations (Sd's re given in parentheses.

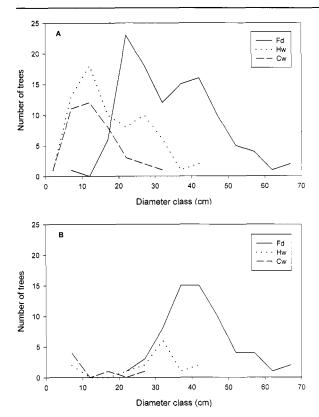
Plantation	Species	Thinning	# of trees	# of loci	# of alleles	N_a	<i>PLP</i> ₉₅	H_{e}	Allelic loss
Fairservice	Fd	Before	113	22	56	2.55(0.18)	54.55	0.153 (0.031)	-
Creek		After	63	22	55	2.50(0.19)	59.10	0.158(0.033)	1
	Hw	Before	69	20	31	1.55(0.15)	15.00	0.051(0.026)	_
		After	14	20	24	1.20(0.09)	15.00	0.043(0.027)	7
	Cw	Before	38	21	27	1.29(0.12)	19.05	0.068(0.039)	-
		After	6	21	27	1.29(0.12)	23.80	0.087(0.041)	-
Weeks Lake	Fd	Before	245	22	48	2.2(0.2)	54.5	0.164(0.035)	_
		After	104	22	48	2.2(0.2)	50.0	0.163(0.036)	-
	Hw	Before	75	15	23	1.5(0.2)	13.3	0.041(0.023)	_
		After	17	15	18	1.2(0.1)	20.0	0.045(0.026)	5
	Cw	Before	6	14	14	1.0(0.0)	0.00	0.000(0.000)	_
		After	0	na	na	na	na	na	na
	Pw	Before	10	15	19	1.3(0.1)	26.7	0.081(0.040)	_
		After	2	15	17	1.1(0.1)	13.3	0.067(0.045)	2
	Ва	Before	2	11	11	1.0(0.0)	00.0	0.000(0.000)	_
		After	0	na	na	na	na	na	na

FC, respectively) after commercial thinning (Figure 3). Nine new understorey species were found in WL after thinning: black raspberry (Rubus leucodermis Dougl.), prince's pine (Chimaphila umbellata (L.) Bart.), dandelion (Taraxacum Hall. spp.), Douglas-fir, western hemlock, western white pine, wall lettuce (Lactuca muralis (L.) Fresen.), fireweed (Epilobium angustifolium L.) and crisp starwort (Stellaria crispa Cham. & Schlecht.). In FC, 17 new species were found: bracken (Pteridium aquilinum (L.) Kuhn.), trailing blackberry (Rubus ursinus Cham. & Schlecht.), violet (Viola L. spp.), species from the Poaceae family, black raspberry, Menzies' pipsissewa (Chimaphila menziesii (R.Br.) Spreng.), prince's pine, dandelion, Douglas-fir, western hemlock, broad-leaved starflower (Trientalis latifolia Hook.), three-leaved foamflower (Tiarella trifoliata L.), wall lettuce, fireweed, sweet-scented bedstraw (Galium triflorum Michx.), red alder (Alnus rubra Bong.) and willow (Salix L. spp.). Species were regarded as new only if they were present on at least two sampling dates after thinning and were not found on any date in the year thinning took place. Two species were replaced: salmonberry (Rubus spectabilis Pursh) from FC and wild gooseberry (Ribes divaricatum Dougl.) from WL.

All new species were native except for wall lettuce and possibly dandelion that was not identified to species. Species were classified as native or exotic according to HITCHCOCK and CRONQUIST (1973).

After commercial thinning, species diversity based on the Shannon index (H) increased linearly in FC ($r^2 = 0.73$) (Figure 4) and the increase corresponded to the increase in species richness. On the other hand, H in WL did not change ($r^2 = 0.15$, P = 0.19) except for seasonal fluctuations (Figure 4). Likewise, species evenness (E_H) oscillated around mean values in both plantations over the course of the study. The species were more evenly distributed in terms of abundance in FC (mean $E_H = 0.65$) than in WL (mean $E_H = 0.34$).

Based on diversity orderings, species diversity decreased in both sites one year after thinning (Figures 5 and 6). The abundance of the most common species increased in WL and did not changed in FC. Two years after thinning, rare species increased in both sites causing an increase in diversity. Three years after thinning, diversity of rare and common species increased in FC. There is no comparable data for the same period in WL since the thinning took place one year later on that site.



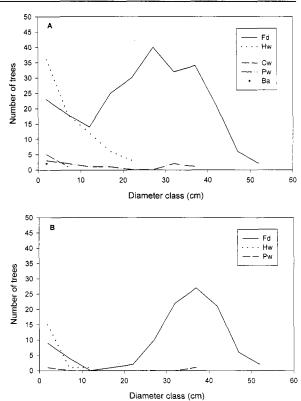


Figure 1. Diameter distribution for Douglas-fir (Fd), western hemlock (Hw) and western redcedar (Cw) in Fairservice Creek before thinning (A) and after thinning (B).

DISCUSSION

Stand structural diversity and tree species diversity

Commercial thinning performed in both plantations approximated thinning from "below" as trees were mostly, but not exclusively, cut in smaller diameter classes. As a result, stand diversity in terms of tree species abundance was reduced since all species other than Douglas-fir were present mainly in small diameter classes. As expected, Douglas-fir increased in abundance after the thinning; however, it did not reach its initial monoculture status. Tree species richness remained the same in FC and was reduced in WL due to the removal of western redcedar and Pacific silver fir. These two species were present in very low frequency and in the small diameter classes.

Tree species composition constitutes one element of stand diversity while structural diversity (the variety of tree sizes) represents another one. Because of the correlation between tree height and diameter, stand diameter diversity approximates stand spatial diversity, particularly its vertical component. Stand vertical diversity is important for wildlife composition and abundance. For example, MACARTHUR & MACAR-

Figure 2. Diameter distribution for Douglas-fir (Fd), western hemlock (Hw), western redcedar (Cw), western white pine (Pw) and Pacific silver fir (Ba) in Weeks Lake before thinning (A) and after thinning (B).

THUR (1961) found that diversity of bird species in deciduous forests was related to the vertical vegetation diversity rather than to the plant species diversity. BARBOUR et al. (1997) concluded that silvicultural practices, including thinning, can increase stand spatial diversity in Douglas-fir plantations in the Pacific Northwest while maintaining quality of wood products. In the present study, stand structure was simplified as a result of thinning; however, the reduction in stand structural diversity was relatively moderate. Even though over 60 % of trees were removed, only two small diameter classes were eliminated from FC and none from WL. The trees were cut mostly in small diameter classes resulting in an increase in the proportional abundance of trees in larger diameter classes. Large and older trees seem to be more important for survival of some wildlife species such as birds of prey, bark drillers and cavity dwellers than the abundance of small trees (e.g. EVANS & CONNER, 1979). It should also be noted that there was a large increase in numbers of seedlings of Douglas-fir (in WL) and western hemlock (in FC) in the second and third season following thinning.

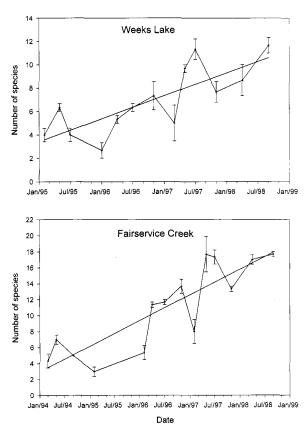


Figure 3. Species richness in Weeks Lake and Fairservice Creek (error bars represent standard errors based on 3 transects).

Tree species genetic diversity

Genetic diversity is essential for plantation health and survival. The results from the present study indicate that only one allele out of 56 present in the Douglas-fir FC plantation was lost (1.8%). This allele was rare and was present in the plantation with frequency that is less than 0.05. The value (i.e., selective advantage) of this rare allele is unknown at present. It should be stated that this population represents a plantation that is managed for fibre production and not as a regeneration source (i.e., seed production). The loss of alleles from production (i.e., seed orchards) and/or breeding populations as opposed to the loss of alleles from plantations is serious and requires proper management (see EL-KASSABY and RITLAND, 1996 a and b). Substantial losses of alleles were only observed for western hemlock on both study sites as well as western white pine in WL. The losses represent substantial reduction in genetic diversity. This was expected due to the fact that the thinning was initiated to increase the frequency of Douglas-fir, the crop tree species, in both sites. Expected heterozygosities for all species in both sites were not affected by thinning, indicating that the allelic loss

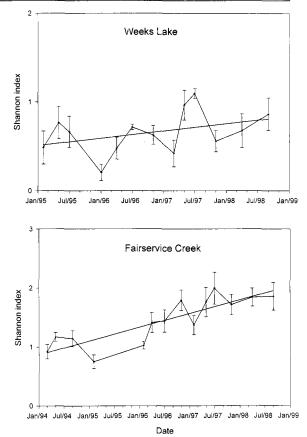


Figure 4. The Shannon diversity index in Weeks Lake and Fairservice Creek (error bars represent standard errors based on 3 transects).

was in the rare allele category (rare alleles do not contribute much to heterozygosity). Because most forest tree plantations are established from seed sources that are managed for maximizing genetic gain and diversity, thus a small reduction of genetic diversity during the course of plantation development is not expected to be of great concern.

Understorey vegetation diversity

Stand and ground vegetation structures are closely related (e.g. PITKÄNEN, 1997). Commercial thinning affects understorey vegetation by changing stand structure traits such as tree species composition and density, thus altering biophysical conditions of the site. In addition, mechanical damage to the habitat caused by the thinning operation can have a significant impact on ground vegetation diversity. However, disturbance due to thinning is usually highly heterogeneous across the stand. Depending on the initial stand traits and level of thinning, smaller or larger parts of the stand would not be much altered by thinning and their original vegetation will be preserved.

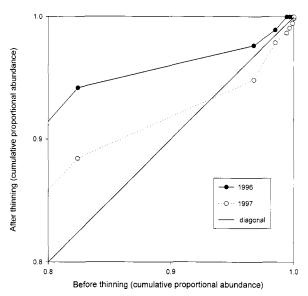


Figure 5. Comparative diversity profiles for Weeks Lake based on cumulative proportional abundance of plants before thinning (winter 1995) compared to cumulative proportional abundance of plants after thinning (winter 1996 and 1997). The upper right portion of the graph describes changes in rare species.

This study did not show detrimental effects of thinning on diversity of perennial plants in the understorey of two second growth Douglas-fir stands on southern Vancouver Island over the course of several years following the treatment. Salmonberry and wild gooseberry were replaced in WL and FC, respectively; however, their disappearance may have been accidental since both species were represented by few individuals only (2 and 3) before thinning. Both species disappeared in the year when thinning occurred suggesting mechanical damage.

Partial tree removal creates an opportunity for understorey vegetation expansion and colonization by new species in response to the altered biophysical conditions of the site. Established species expansion was evident one year after the treatment, particularly in WL where the dominant understorey plant (salal) increased in relative abundance from 82 to 94%. Species richness also increased significantly with time in both study sites. The newly arrived species represented a mixture of plants with respect to environmental requirements. Approximately 30% of the new species were plants with low to medium shade tolerance found usually in disturbed habitats (KLINKA et al., 1989). These included black raspberry, wall lettuce, fireweed, bracken, trailing blackberry and red alder. Since the bulk of the new species were with medium to high shade tolerance, it is likely that the increase in species richness will not be a short term. ALABACK & HERMAN

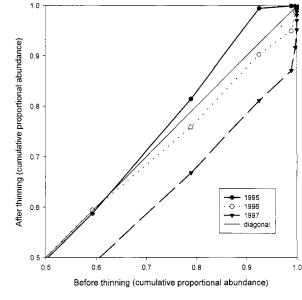


Figure 6. Comparative diversity profiles for Fairservice Creek based on cumulative proportional abundance of plants before thinning (winter 1994) compared to cumulative proportional abundance of plants after thinning (winter 1995, 1996 and 1997). The upper right portion of the graph describes changes in rare species.

(1988) found that 17 years after thinning of *Picea-Tsuga* forests in coastal Oregon, most species that colonized thinned plots were shade tolerant.

According to diversity profiles (based on winter sampling), species diversity decreased initially in both sites one year after thinning due to expansion of the most abundant established species. The Shannon index evaluated in winter before thinning was at 0.92 and 0.49 for FC and WL, respectively. One year after thinning, the value of the index decreased to 0.75 and 0.20 in FC and WL, respectively. HALPERN & SPIES (1995) also observed temporary decrease in understorey species diversity following disturbance such as logging in forests of the Pacific Northwest.

Although species richness increased with time in both study sites while the species evenness remained the same, the Shannon diversity index increased significantly over the entire course of the study in FC and remained unchanged in WL. The inconsistency can be explained by several factors related to the differences between the sites and to the intrinsic properties of the Shannon index. At the end of the study period, there were 18 species in FC compared to 11 species in WL even though both sites had almost the same number of species before the treatment and during the first year following thinning. Larger increase in the number of new plants in FC would correspond to the relatively larger increase in the value of the Shannon index since this index is more sensitive to the number of species is higher at higher species evenness. In FC, the value of evenness based on the Shannon index was almost twice the value of evenness found in WL. Moreover, the Shannon index is most sensitive to changes in species with relative abundance in the range of approximately 20-50% (CHAMBERS, 1983). In WL, no species were in that range during the entire study while in FC there were several species that had relative abundance between 20 and 50% at one or more sampling dates.

Different response to thinning found between the two sites with respect to the Shannon diversity index and the range of increase in species richness seem to be related to the initial biophysical conditions in the two sites. FC, the site that was apparently more diverse and nutrient rich responded more favourably to commercial thinning in terms of ground vegetation diversity than WL. WL had lower value of the Shannon index before thinning and was occupied with salal, a shrub characteristic of nitrogen-poor sites (KLINKA et al., 1989). On the other hand, FC seemed to be more fertile with respect to nitrogen: Oregon-grape, vanilla-leaf and sword fern, most abundant species on that site, grow usually in sites with medium (Oregon-grape) and high nitrogen content (vanilla-leaf and sword fern) (KLINKA et al., 1989). Another evidence of greater nutrient content in FC relates to the greater size of trees in FC despite that the FC stand was 16 years younger than WL stand.

Due to the increase in the number and abundance of understorey vegetation species, heterogeneity of forest habitat was likely greater after commercial thinning and that should have a positive impact on wildlife diversity. HAGAR et al. (1996) found that the abundance of breeding birds increased following commercial thinning of 40 to 55-year-old Douglas-fir stands in western Oregon. These species included some that are normally found in old growth forests (MCGARIGAL & MCCOMB. 1995). HAGAR et al. (1996) indicated that hardwoods cover is positively correlated with bird species richness. In the present study, an increase in number of alder and willow was observed in FC following thinning. In addition to birds, other groups of animals such as small mammals may also benefit from increased abundance of understorey vegetation (e.g. CAREY & JOHNSON, 1995).

In conclusion, commercial thinning of two planted Douglas fir stands on southern Vancouver Island had an impact on biodiversity in both plantations. Stand structural diversity was simplified due to the removal of a large number of smaller trees. Crop species genetic diversity was minimally affected by the treatment while non-crop tree species genetic diversities were greatly reduced. Noteworthy are the differences between the two stands in terms of the impact of commercial thinning on understorey vegetation. Understorey vegetation richness increased in both plantations at different rates and vegetation diversity estimated by the Shannon diversity index increased in one plantation and did not change in the other one.

LITERATURE CITED

- AGEE, J. K. & BISWELL, H. H. 1970: Some effects of thinning and fertilization on ponderosa pine and understory vegetation. *Journal of Forestry* **68**:709–711.
- ALABACK, P. B. & HERMAN, F. R. 1988: Long-term response of understorey vegetation to stand density in *Picea-Tsuga* forests. *Canadian Journal of Forest Research* 18:1522 –1530.
- ANDERSON, R. C., LOUCKS, O. L. & SWAIN, A. M. 1969: Herbaceous response to canopy cover, light intensity and throughfall precipitation in coniferous forests. *Ecology* 50:256–263.
- BARBOUR, R. J., JOHNSTON, S., HAYES, J. P. & TUCKER, G. F. 1997: Simulated stand characteristics and wood product yields from Douglas-fir plantations managed for ecosystem objectives. *Forest Ecology and Management* **91**:205 –219.
- BUONGIORNO, J., DAHIR, S., LU, H. C. & LIN, C. R. 1994: Tree size diversity and economic returns in uneven-aged forest stands. *Forest Science* **40**:83–103.
- CAREY, A. B. & JOHNSON, M. L. 1995: Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications* 5:336–352.
- CHELIAK, W. M. & PITEL, J. A. 1984: Techniques for starch gel electrophoresis of enzymes from forest tree species. Petawawa National Forestry Institute. Info, Rep., PI-X-42:1-49.
- CHAMBERS, J. C. 1983: Measuring species diversity on revegetated surface mines: an evaluation of techniques. Research Paper, Intermountain Forest and Range Experiment Station, USDA Forest Service. No. INT-322.
- CLAYTON, J. W. & TRETIAK, D. N. 1972: Amine-citrate buffers for pH control in starch gel electrophoresis. *Journal of Fisheries Research Border Canadian* 29:1169 –1172.
- CONKLE, M. T., HODGSKISS, P. D., NUNNALLY, L. B & HUNTER, S. C. 1982: Starch gel electrophoresis of conifer seeds: A laboratory manual. USDA, For. Serv. Gen. Tech. Rep. PSW-64.
- DURBIN, J. & WATSON, G. S. 1951: Testing for serial correlation in least square regression. *Biometrika* 38:159–177.
- EL-KASSABY, Y. A. & RITLAND, K. 1996a: Genetic variation in low elevation Douglas-fir of British Columbia and its relevance to gene conservation. *Biodiversity and Conser*vation 5:779–794.
- EL-KASSABY, Y. A. & RITLAND, K. 1996b: Impact of selection and breeding on the genetic diversity in Douglas-fir. *Biodiversity and Conservation* 5:795–813.
- EVANS, K. E. & CONNER, R. N. 1979: Snag management. In: Management of North Central and Northeastern forests for nongame birds. USDA For. Serv. Gen. Tech. Rep. NC–51, pp 214–225.
- FILDES, R. A. & HARRIS, H. 1966: Genetically determined

- variation of adenylate kinase in man. Nature 209:261-263.
- HAGAR, J. C., MCCOMB, W. C. & EMMINGHAM, W. H. 1996: Bird communities in commercially thinned and unthinned Douglas-fir stands of western Oregon. *Wildlife Society Bulletin* 24:353–366.
- HALPERN, C. B. & SPIES, T. A. 1995: Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications* 5:913–934.
- HANSEN, A. J., SPIES, T. A., SWANSON, F. J. & OHMANN, J. L. 1991: Conserving biodiversity in managed forests. *BioScience* 41:382–392.
- HAYES, J. P., CHAN, S. S., EMMINGHAM, W. H., TAPPEINER, J. C., KELLOGG, L. D. & BAILEY, J. D. 1997: Wildlife response to thinning young forests in the Pacific Northwest. *Journal of Forestry* 95:28–33.
- HERTEL, H. & KOHLSTOCK, N. 1994: Different genetic structures of two morphological types of Scots pine (*Pinus* sylvestris L.). Silvae Genetica 43:268–272.
- HITCHCOCK, C.L. & CRONQUIST, A. 1973: Flora of the Pacific Northwest. University of Washington Press, Seattle, Washington.
- HOSIUS, B. 1993: Is the genetic structure of a Norway spruce stand influenced by thinnings. *Forst und Holz* **48**:306 –308.
- HUNTER, M. L. 1990: Wildlife, forests, and forestry: Principles of managing forests for biological diversity. Prentice Hall; Englewood Cliffs, New Jersey.
- KLINKA, K., KRAJINA, V. J., CESKA, A. & SCAGEL, A. M. 1989: Indicator Plants of Coastal British Columbia. University of British Columbia Press, Vancouver, British Columbia.
- KONNERT, M. & SPIECKER, H. 1996: Does the felling of individual trees influence the genetic structure of stands. *Afz/Der Wald, Allgemeine Forst Zeitschrift fur Waldwirt*schaft und Umweltvorsorge **51**:1284–1291.
- KRUEGER, K. W. 1960: Behaviour of ground vegetation under a partially cut stand of Douglas-Fir. Res. Note Pacif. Nthwest. For. Range Exp. Sta. No. 198.
- LAUBER, U., ROTACH, P. & HUSSENDORFER, E. 1997: The influence of silvicultural interventions on the genetic structure of a young beech stand (*Fagus sylvatica L.*). Schweizerische Zeitschrift für Forstwesen 148:847–862
- LU, H. C. & BUONGIORNO, J. 1993: Long- and short-term effects of alternative cutting regimes on economic returns and ecological diversity in mixed-species forests. *Forest Ecology and Management* **58**:173–192.
- MACARTHUR, R. H. & MACARTHUR, J. W. 1961: On bird species diversity. *Ecology* 42:594–600.
- MAGURRAN, A.E. 1988: Ecological Diversity and Its Measurement. Princeton, N.J. Princeton University Press.

- MCGARIGAL, K. & MCCOMB, W. C. 1995: Relationship between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs* 65:235 –260.
- NIESE, J. N. & STRONG, T. F. 1992: Economic and tree diversity trade-offs in managed northern hardwoods. *Canadian Journal of Forest Research* 22:1807–1813.
- O'MALLEY, D. M., WHEELER, N. C. & GURIES, R. P. 1980: A manual for starch gel electrophoresis. Staff Paper Series, University of Wisconsin, Madison.
- PIELOU, E.C.1966: The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* 13:131–144.
- PITKÄNEN, S. 1997: Correlation between stand structure and ground vegetation: an analytical approach. *Plant Ecology* 131:109–126.
- POJAR, J., KLINKA, K. & MEIDINGER, D. V. 1987: Biogeoclimatic ecosystem classification in British Columbia. Forest Ecology and Management 22:119–154.
- RICE, P. M., TONEY, J. C., BEDUNAH, D. J. & CARLSON, C. E. 1997: Plant community diversity and growth form responses to herbicide applications for control of *Centaurea maculosa*. Journal of Applied Ecology 34:1397-1412.
- RIDGEWAY, G. J., SHERBURNE, S. W. & LEWIS, R. D. 1970: Polymorphism in the esterases of Atlantic herring. *Transactions of the American Fisheries Society* 99:147–151.
- SCHULTE, B. J. & BUONGIORNO, J. 1998: Effects of unevenaged silviculture on the stand structure, species composition, and economic returns of loblolly pine stands. *Forest Ecology and Management* 111:83–101.
- SICILIANO, M. J. & SHAW, C. R. 1976: Separation and visualization of enzymes on gels. *In:* Chromatographic and electrophoretic techniques (ed. I. Smith). Heinemann Medical Books, London. Vol. II: pp 185–209.
- SMITH, D. M. 1962: The Practice of Silviculture. John Wiley & Sons, N.Y.
- 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 Technology* 10:439–446.
- SAS. 1993: SAS/ETS user's guide: version 6. SAS Institute, Cary, N.C.
- SWINDEL, B. F., CONDE, L. F. & SMITH J. E. 1987: Index-free diversity orderings: concept, measurement, and observed response to clearcutting and site-preparation. *Forest Ecology and Management* 20:195–208.
- TAPPEINER, J. C. & ZASADA, J. C. 1993: Establishment of salmonberry, salal, vine maple, and bigleaf maple seedlings in the coastal forests of Oregon. *Canadian Journal* of Forest Research 23:1775–1780.