Long-term response of understory plant species to thinning and fertilization in a Douglas-fir plantation on southern Vancouver Island, British Columbia

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Abstract: The 27-year response of understory vegetation in a 51-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest to thinning and N fertilization treatments was examined in a silviculture experiment at Shawnigan Lake on southern Vancouver Island of British Columbia. The experiment was a two-way factorial design with three levels for each of thinning and N fertilization. No significant treatment effects on the number of either vascular or nonvascular species were detected. This was also true for the covers of the majority of understory species except salal (*Gaultheria shallon* Pursh) and Oregon beaked moss (*Kindbergia oregana* (Sull.) Ochyra). Heavy thinning led to high salal and Oregon beaked moss cover, whereas heavy fertilization resulted in lower cover of salal but had no effect on the cover of Oregon beaked moss. Although thinning had a marginal effect on the cover of canopy trees 27 years after treatment, the cover of the canopy trees had only minimal effects on understory vegetation. Conversely, no adverse effect of understory vegetation on canopy trees was found. This study suggested that after 27 years thinning and fertilization had little effect on understory vegetation whether in terms of species richness or vegetation cover. An effective way to conserve species diversity is to protect specific substrate types, e.g., tree trunks, stumps, and coarse woody debris. A commercial thinning was recommended to reduce the time of stem exclusion in similar type of forests.

Résumé : La réponse de la végétation de sous-étage après 27 ans suite à des traitements d'éclaircie et de fertilisation azotée a été évaluée dans le cadre d'une expérience sylvicole dans une forêt de douglas (*Pseudotsuga menziesii* (Mirb.) Franco) âgée de 51 ans et située au lac Shawnigan dans la partie sud de l'île de Vancouver en Colombie-Britannique. Le dispositif expérimental était un dispositif factoriel à deux facteurs avec trois niveaux d'éclaircie et de fertilisation azotée. Les traitements n'ont eu aucun effet significatif sur le nombre d'espèces vasculaires ou non vasculaires. Ceci était vrai également pour la couverture de la majorité des espèces de sous-étage excepté pour la gaulthérie shallon (*Gaultheria shallon* Pursh.) et l'eurhynchie de l'Oregon (*Kindbergia oregana* (Sull.) Ochyra). L'éclaircie forte a conduit à une importante couverture de gaulthérie shallon et d'eurhynchie de l'Oregon tandis qu'une fertilisation élevée a entraîné une plus faible couverture de gaulthérie shallon mais n'a pas eu d'effet sur la couverture d'eurhynchie de l'Oregon. Même si l'éclaircie a eu un effet marginal sur la couverture des arbres de la canopée 27 ans après le traitement, la couverture des arbres de la canopée a seulement eu un effet minimal sur la végétation de sous-étage. De la même façon, la végétation de sous-étage n'a pas eu d'effet néfaste sur les arbres de la canopée. Cette étude suggère qu'après 27 ans, l'éclaircie et la fertilisation azotée ont eu peu d'effets sur la végétation de sous-étage que ce soit en termes de richesse en espèces ou de couverture de la végétation. Une façon efficace de conserver la biodiversité consiste à protéger certains types de substrat, comme les troncs d'arbre, les souches et les débris ligneux grossiers. Une éclaircie commerciale a été recommandée pour réduire la durée de la période d'exclusion des tiges dans des forêts de même type.

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Introduction

A major concern in the management and conservation of the coastal forests in British Columbia is how, on the one hand, to maintain species diversity and ecological functions of the forests while, on the other hand, sustaining and increasing timber production and wood quality (Curtis and Carey 1996; Kremsater and Bunnell 1998). While overstory is the layer usually only composed of crop species, the understory is the primary component of floristic species diversity in this region. Although past silviculture practices almost exclusively aimed to promote the growth of crop species (Curtis and Carey 1996; Curtis et al. 1997), the notion of silviculture is now perceived as managing ecosystems, sustaining biodiversity, or managing forests as historical products (Kremsater and Bunnell 1998).

As a major component of species diversity, understory species play various roles in the coastal forests, e.g., they interfere with conifer establishment and seedling growth (Price et al. 1986; deMontigny and Weetman 1990), they provide habitat and food for wildlife (Mannan and Meslow 1984; Bunnell and Kremsater 1990; Carey and Johnson

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1995), and they affect nutrient cycling and regeneration (Fried et al. 1988; Trofymow et al. 1991). Given that silviculture and the growth of overstory can profoundly affect the composition and development of understory species (Alaback and Herman 1988; Stewart 1988; Bailey et al. 1998; Thomas et al. 1999), it is important to understand what are the relationships between overstory and undertory species and, more importantly, how silviculture regimes would affect these relationships.

Much knowledge about species diversity in the coastal forests was derived from the early seres of secondary succession in Douglas-fir or western hemlock stands that were left after harvesting or from natural disturbances (Schoonmaker and McKee 1988; Halpern and Spies 1995; Qian et al. 1997). Less is known about the effects of silviculture on understory vegetation, although some generalizations have been made by previous studies (Alaback and Herman 1988; Prescott et al. 1993; Klinka et al. 1996; Bailey et al. 1998; Thomas et al. 1999). One of these predicts that thinning of overstory Douglas-fir results in an increase in resource (e.g., light and nutrient) availability favouring the development of understory species, whereas N fertilization accelerates canopy closure resulting in reduced growth of understory vegetation. Another generalization predicts that, below a certain level of thinning intensity, species richness increases with the intensity of thinning, while fertilization might suppress species diversity because it promotes dominance of a few abundant species. These results were derived from relatively short-term observations, e.g., 17 years after thinning by Alaback and Herman (1988), and 12–16 years by Thomas et al. (1999). It is not clear whether these effects would still be evident in the longer term, e.g., after treated stands enter the stem exclusion stage.

In the early 1970s, as part of a series of thinning and fertilization experiments (Omule 1990), a large-scale experiment was conducted to evaluate the responses of 24-year-old second-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) to these treatments (Crown and Brett 1975) on southeastern Vancouver Island, British Columbia. The purpose of this experiment was to determine the mechanisms of response to thinning and fertilization and to develop effective and environmentally acceptable silviculture methods designed to increase wood yield. However, although more than 70 articles have been published on the effects of this experiment on growth and yield and nutrient responses of Douglas-fir (see review by Brix 1993), the response of understory plant species to the treatments has received limited attention. Stanek et al. (1979) investigated the growth response of salal (*Gaultheria shallon* Pursh) and bracken fern (*Pteridium aquilinum* (L.) Kuhn) to thinning and fertilization 6 years after treatment. In addition, Smith and Clark (1990) examined the effects of light penetration of the canopy on the leaf area index of salal in nearby untreated Douglas-fir stands. However, further knowledge is still needed to understand the long-term effect of thinning and fertilization on understory communities. This silviculture experiment provided a unique opportunity for such study.

The objectives of this study are to examine (*i*) the interactions among different vegetation layers, particularly the correlations between overstory and understory species; (*ii*) the effects of the treatments applied 27 years previously on the composition of understory plant species and their growth; and (*iii*) the implications of the experiment to the management of Douglas-fir forests.

Table 1. Stand density (stems/ha), basal area (m^2/ha), estimated leaf area index, and LAI-2000 readings for the four extreme treatments (T0F0, T0F2, T2F0, and T2F2) immediately following treatment (time = 0, age = 24) and 27 years after treatment.

Attribute	Time	Age (years)	T0F0	T0F2	T2F0	T2F2
Stems/ha	0	24	4852	4042	896	915
	27	51	3430	2349	896	902
Basal area	0	24	26.6	19.1	8.3	8.4
	27	51	54.1	51.1	33.1	43.9
LAI	0	24	5.20	3.65	1.90	1.94
	27	51	5.82	5.31	5.38	7.01
LAI-2000	27	51	4.06	4.38	3.32	3.86

Methods

The study site is located near Shawnigan Lake on southern Vancouver Island, approximately 30 km from Victoria, B.C. A detailed description of the study site and experimental design was given by Crown and Brett (1975). The size of the plantation is about 2 × 2 km and lies within the western variant of the dry maritime coastal western hemlock biogeoclimatic subzone (CWHxm), which is a very dry and low-nutrient site (Green and Klinka 1994) with a site index of 25 m at 50 years (Gardner 1990). The mean monthly temperature ranges from 0ºC in January to 18ºC in July. Mean annual precipitation is 1090 mm with nearly 80% of this falling between October and April. The thickness of the forest floor (L-H) averages 1.5 cm, and soils are coarse loamy Orthic Dystric Brunisols.

In the winter–spring of 1971 and 1972, three levels of thinning (control (T0), one third (T1), and two thirds (T2) of basal area removed) combined with three levels of N fertilization (control (F0), 224 (F1), and 448 (F2) kg N/ha as urea) in a 3 × 3 factorial design were applied to the 24-year-old Douglas-fir plantation with each treatment combination having two replicate plots established in each of the 2 years. Each treatment plot is 20 × 20 m surrounded by a 15 m wide treated buffer strip. Only the 1971 plots were used in this study, and the basal area, stand density (McWilliams and Thérien 1997), and estimated leaf area index (LAI; horizontally projected leaf area per unit of ground area) following treatment in 1971 at the start of the experiment and 27 years later are given in Table 1. LAI was estimated using regression equations developed from a biomass sampling 18 years after treatment (Mitchell et al. 1996) in which leaf biomass and leaf area were measured. These equations were then applied to the Shawnigan trees at age 24 and 51 to estimate LAI. A further estimation of LAI was done in 1998 using the LI-COR LAI-2000 canopy analyzer (LI-COR, Inc. 1990) for comparison.

In the summer of 1998, a vegetation survey was conducted to evaluate the effects of the treatments within the basic 3 × 3 design on understory plant species diversity. Two 5 × 5 m quadrats were set up in each of the 18 plots. Within each quadrat, vascular and nonvascular plants (excluding epiphytes) were identified to species (nomenclature sources: Hitchcock and Cronquist 1973; Vitt et al. 1988). Cover (percentage of ground covered by a population) was visually estimated for each species. The actual percent cover value was recorded for a species if its occurrence was ≥1%; otherwise, it was assigned 0.5%, if present. The presence–absence for each

Table 2. (A) Vascular and (B) nonvascular plant species recorded in the Douglas-fir experimental plantation at Shawnigan Lake on southern Vancouver Island, B.C.

(A) Vascular plants	
Canopy layer	**Herb layer**
Pseudotsuga menziesii	*Boschniakia hookeri*
Salix scouleriana	*Chimaphila umbellata*
Shrub – small tree layer	*Festuca occidentalis*
Gaultheria shallon	*Goodyera oblongifolia*
Mahonia nervosa	*Listera cordata*
Rosa gymnocarpa	*Polystichum munitum*
Pinus monticola	*Pteridium aquilinum*
Rubus ursinus	*Rubus ursinus*
Salix scouleriana	
Symphoricarpos albus	
Thuja plicata	
Tsuga heterophylla	
(B) Nonvascular plants	
Liverwort	**Lichen**
Frullania tamarisci ssp. *nisquallensis*	*Alectoria sarmentosa*
	Alectoria vancouverensis
Lepidozia reptans	*Cetraria orbata*
Lophocolea cuspidata	*Cladonia bellidiflora*
Lophocolea heterophylla	*Cladonia coniocraea*
Porella navicularis	*Cladonia macilenta*
Ptilidium californicum	*Cladonia* sp. (sterile)
Radula bolanderi	*Cladonia squamosa*
Scapania bolanderi	*Evernia prunastri*
Scapania umbrosa	*Hypogymnia enteromorpha*
Moss	*Hypogymnia inactiva*
Aulacomnium androgynum	*Hypogymnia physodes*
Buxbaumia piperi	Parmelia sulcata
Dicranoweisia cirrata	*Parmeliopsis hyperopta*
Dicranum fuscescens	*Platismatia glauca*
Dicranum scoparium	*Platismatia herrei*
Hylocomium splendens	*Usnea* sp.
Hypnum circinale	
Isothecium myosuroides	
Kindbergia oregana	
Neckera douglasii	
Orthotrichum consimile	
Orthotrichum lyellii	
Plagiothecium laetum	
Plagiothecium undulatum	
Pseudotaxiphyllum elegans	
Rhizomnium glabrescens	
Rhytidiadelphus loreus	
Rhytidiadelphus triquetrus	
Trachybryum megaptilum	

cryptogam species was also recorded, being stratified to substrate type (humus, coarse woody debris, stumps, and standing trunks).

The data from the two quadrats in each plot were combined to represent the plot. Two-way factorial analyses of variance (ANOVA) were conducted on both the number of species and the percent cover of each species group (tree, shrub, herb, and cryptogam). One-way ANOVA was also used to test for the differences in the number of cryptogam species on the four substrate types. Jaccard's index (Pielou 1984), based on presence–absence data, was used to measure the similarity in species composition among treatments and was calculated as the mean of the four pairwise plot comparisons within a treatment comparison.

To evaluate the possible effect of understory vegetation on the growth of overstory Douglas-fir, we also report results of a understory removal experiment that was conducted in the same site. From 1973 to 1990 one plot was treated repeatedly every year by monthly clipping all saplings, shrubs, and herbs for the purpose of evaluating the effect of understory on Douglas-fir growth. Clipping stopped in 1990. Since then, little understory has developed. A nearby paired plot was not clipped. Both plots were T2F2 and had very similar mensurational characteristics. Periodic diameter increments were measured between years 0, 3, 6, 9, 12, 15, 18, and 24 following thinning and fertilization treatment.

Results

The overstory on the study site, regardless of specific treatments, was dominated by Douglas-fir with remnant *Salix scouleriana* Barratt scattered in the canopy. The canopy of the plantation has been closed for several years, even though in the heavily thinned plots, two thirds of the basal area was initially removed. The understory shrub layer was dominated by salal, with Oregon grape (*Mahonia nervosa* Pursh) and bracken fern being subdominant, while the herb species were relatively depauperate throughout the plantation. Oregon beaked moss (*Kindbergia oregana* (Sull.) Ochyra) was the most abundant nonvascular species.

A total of 63 species (10 trees and shrubs, 8 herbs and 45 cryptogams) were recorded over the entire site (Table 2). There were no significant differences in the number of either vascular or nonvascular species among treatments (ANOVA, $p > 0.05$; Table 3). This was also true for species composition among different treatments (Table 4) as measured using Jaccard's similarity index. The similarities are generally low, which is typical in this region (M. Ryan, personal communication) and indicates the low percentage of species shared or the high variability in species composition among treatments.

The correlations between the cover of the four vegetation layers (tree, shrub, herb, and cryptogam) pooled across the treatments are shown in Table 5A. The cover of tree layer did not show significant correlation with any of the understory layers. In the understory, no significant correlations were found except between the shrub and cryptogam layers, which had a very strong negative association. The correlations between the dominant species in each of the four layers are shown in Table 5B. Again, the overstory Douglas-fir did not show any correlation with the cover of other species in understory. In the understory, salal and Oregon grape, and salal and Oregon beaked moss had strong negative correlations, whereas Oregon grape and Oregon beaked moss showed a significant positive correlation.

Although overstory cover was not correlated with the covers of understory species, 27 years after treatment thinning still had a marginally significant effect on the percent cover of canopy trees ($p = 0.078$; Fig. 1A). The cover decreased with the intensity of thinning, whereas fertilization had no effect on tree cover at this time. Canopy cover was mostly Douglas-fir, with contributions from other species being negligible.

Salal dominated the dense shrub layer, on average accounting for 85% of shrub cover. To avoid salal outweighing

Table 3. Number of vascular and nonvascular species classified by thinning and N fertilization treatments.

	Thinning			Fertilization		
	T0	T1	T2	F0	F1	F2
Vascular species	6.8 (1.0)	5.8 (0.8)	6.8 (1.7)	6.8 (1.3)	6.5 (1.4)	6.2 (1.2)
Cryptogam species	17.7 (4.5)	15.7 (4.0)	18.2 (1.5)	18.5 (4.1)	16.8 (1.5)	16.2 (4.4)

Note: The values are the mean of six replicates for each level of treatment, with SE given in parentheses. No significant differences ($p > 0.05$) in number of either vascular or nonvascular species for the two treatments were detected by a two-way analysis of variance.

Table 4. Similarity (Jaccard's index) in species composition among the plots of different (A) thinning and (B) N fertilization treatments.

(A) Thinning			
	T0	T1	T2
T0	0.444 (0.068)	0.459 (0.080)	0.454 (0.068)
T1		0.468 (0.085)	0.484 (0.062)
T2			0.465 (0.055)
(B) Fertilization			
	F0	F1	F2
F0	0.460 (0.088)	0.446 (0.065)	0.454 (0.077)
F1		0.444 (0.065)	0.483 (0.062)
F2			0.491 (0.047)

Note: Each treatment level had 6 replications, and thus the similarity values (SE are given in parentheses) are the average of the 15 combinations.

other shrubs, the effects of thinning and fertilization on the cover of salal and other shrub species were analyzed separately. Both thinning and fertilization had strong effects on the growth and development of salal (Figs. 1B and 1C), whereas neither treatment had any effect on the pooled cover of other shrub species (i.e., the sum of covers of shrubs excluding salal). The cover of salal monotonically increased with the intensity of thinning. The effect of N fertilization on salal growth was only evident in unthinned plots in which the cover of salal decreased with fertilization (Figs. 1C and 1D). Herb cover never exceeded 10% across plots and herbs were the least abundant species. No treatments had significant effects on herb cover.

Cryptogams were the richest group in the plantation with 45 species being found (Table 2). Oregon beaked moss was dominant, sometimes being the only species growing on humus and coarse woody debris substrates. ANOVA results showed that thinning had a strong effect on the development of Oregon beaked moss (Fig. 2A), whereas no effect of fertilization was found. The cover of Oregon beaked moss monotonically decreased with the intensity of thinning, contrary to the response of salal. Neither thinning nor fertilization had significant effects on the pooled cover of other nonvascular species (i.e., the sum of covers of nonvascular species excluding Oregon beaked moss). Although there was no difference in the number of cryptogam species among the treatments as shown earlier, there were significant differences in numbers among different substrates (Fig. 2B). Standing tree trunks hosted a significantly higher number of cryptogams than the other three substrate types. Coarse

Table 5. (A) Correlation coefficients for cover among four vegetation layers: tree, shrub, herb, and cryptogam. (B) Correlation coefficients for cover of five dominant or subdominant species: Douglas-fir, salal, Oregon grape, bracken fern, and Oregon beaked moss.

(A) Vegetation layers			
	Shrub	Herb	Cryptogam
Tree	–0.179	–0.053	0.177
Shrub		0.089	–0.907***
Herb			–0.016

(B) Dominant and subdominant species				
	Salal	Oregon grape	Bracken fern	Oregon beaked moss
Douglas-fir	0.050	0.142	0.017	0.072
Salal		–0.442***	0.041	–0.919***
Oregon grape			0.262	0.320*
Bracken fern				0.008

*$p < 0.05$.
***$p < 0.001$.

woody debris and stumps had an intermediate number of species, whereas humus had the fewest cryptogam species.

Table 6 shows the effect of understory vegetation on the DBH increments of Douglas-fir. Five of the seven increment periods failed to show any effects of understory removal on Douglas-fir growth, whereas diameter increments in the third and fourth periods (9 and 12 years after thinning) had significant effects. The trees consistently grew better in the plot where understory vegetation was present than in the plot with the removal of understory vegetation (Table 6), although only two periodic increments were significant.

Discussion

Despite a long history of silviculture research on Vancouver Island (Crown and Brett 1975; Curtis et al. 1997), few studies have addressed the effects of silvicultural treatments on understory plant species diversity, particularly the long-term effects (Prescott et al. 1993; Klinka et al. 1996). The profound effects of thinning and fertilization observed in previous studies (Bailey et al. 1998; Thomas et al. 1999) over a shorter term were not apparent in our study site 27 years after treatment. Except for salal and Oregon beaked moss, thinning had virtually no effect on understory cover, and the only effect of fertilization had was on salal cover in unthinned plots (Fig. 1C). More surprisingly, although there

Fig. 1. Effects of thinning and N fertilization on the percent cover of (A) canopy trees (mainly Douglas-fir) and (B–D) understory salal. Different letters in the figures indicate a significant statistical difference between different levels of a treatment. In Fig. 1A, tree cover between high and lower levels of thinning was only marginally different (p = 0.078).

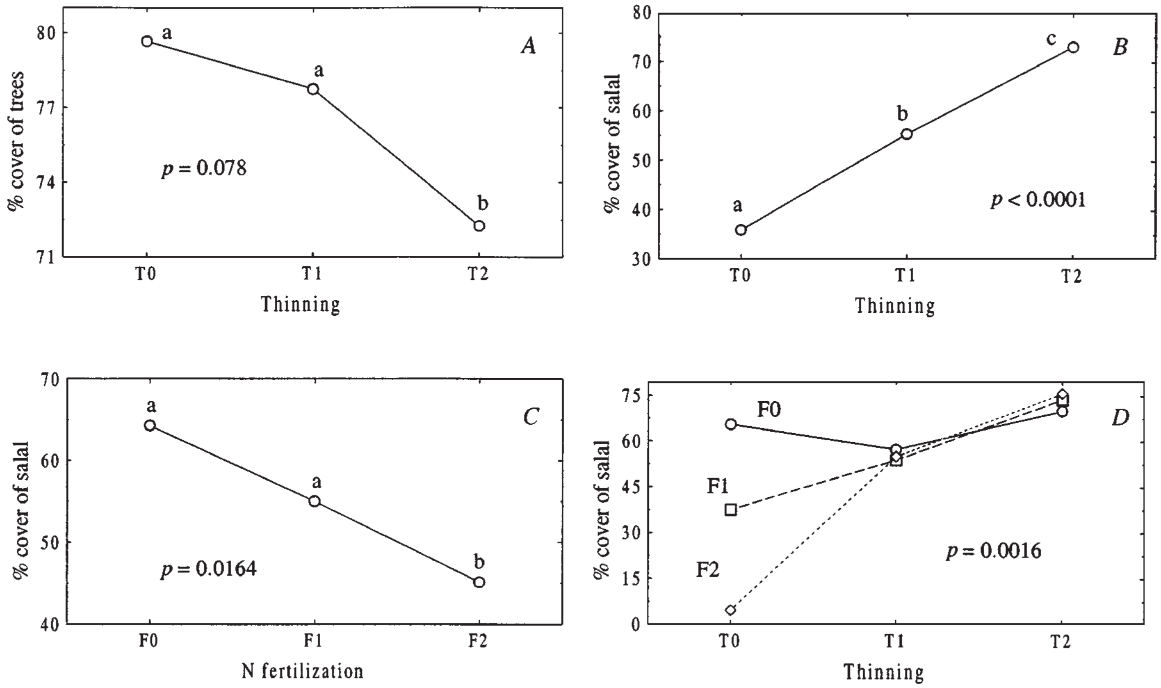
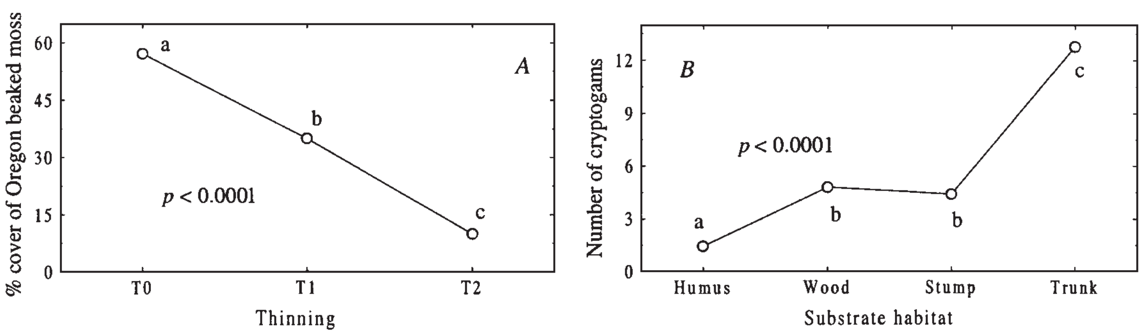


Fig. 2. (A) The effect of thinning treatment on the cover of Oregon beaked moss, the most dominant moss in the plantation. (B) The number of cryptogam species on different substrate habitats. Different letters in the figures indicate a significant statistical difference between different levels of a factor.



was still a marginal effect of thinning on tree cover (Fig. 1A), tree cover was not significantly correlated with any understory cover (Table 5), not even with salal that responded significantly to thinning (Fig. 1B). This result seems inconsistent with previous observations that showed strong negative correlations between overstory cover and understory vegetation (Klinka et al. 1996; Bailey et al. 1998). However, in our study site the canopies of overstory trees have already been closed, regardless of treatment. The marginal differences in canopy opening were not big enough to have discernible effects on the majority of understory species. However, salal is an efficient light user that can withstand different light conditions by producing sun and shade leaves (Smith 1991). It can even persist in dense mature stands where there is little aboveground biomass of salal (Bunnell 1990). Therefore, a small difference in light availability would probably produce a discernible salal response, explaining why salal still responded strongly to thinning and fertilization (Figs. 1B and 1C) but did not show a correlation with Douglas-fir (Table 5B). Although canopy cover can be a useful predictor of the cover of salal (Klinka et al. 1996), our results suggested that lack of correlation does not necessarily mean there is no difference in salal cover.

It is plausible that the strong negative association between salal and Oregon grape (Table 5B) was an outcome of competition for understory resources (e.g., light) between the two species, although a further addition or removal experiment for the two species is needed for direct evidence. The interpretation of the negative correlation between salal and Oregon beaked moss, however, is confounded with thinning. The negative correlation might simply be caused by the opposite responses of salal and Oregon beaked moss to thinning (Figs. 1B and 2A). A further ANOVA on the cover of Oregon beaked moss using salal cover as a covariate showed that the negative association between the two species was still very significant (partial correlation coefficient = –0.611,

Table 6. Periodic diameter increments and p values for unpaired t tests comparing the DBH increments of Douglas-fir when understory vegetation was present or removed.

Time (years)	Mean DBH increment		
	Nonremoval	Removal	p
3	4.109	4.015	0.552
6	2.793	2.573	0.066
9	2.591	2.135	0.001
12	1.884	1.635	0.021
15	1.315	1.279	0.657
18	1.081	0.988	0.197
24	1.612	1.532	0.498

$p < 0.001$) after removing the effect of thinning. Again, detailed field observations are necessary to further confirm whether the negative association is caused by competition or spatial segregation in microhabitat niches of the two species. The positive association between Oregon grape and Oregon beaked moss is probably due to their similar requirements for wet and shady microhabitats.

It has been predicted and usually observed that species richness is high prior to canopy closure, whereas when a stand reaches stem-exclusion stage, richness decreases because of the loss of early seral species from the stand (Oliver 1981; Halpern 1988). Contrary to the results of previous authors who found positive effects of light to moderate thinning on species richness based on relative short-term observations (Alaback and Herman 1988; Thomas et al. 1999), our study showed that after 27 years neither thinning nor fertilization had significant effects on species richness (Table 3). Our 51-year-old Douglas-fir stand is apparently now at the stem-exclusion stage that makes the understory depauperate of species, particularly herb species. This result might reflect the small size (about 2 × 2 km) of the whole plantation and, therefore, the dispersion of understory species throughout the plantation so that no species is restricted to a specific treatment.

Although in a young Douglas-fir stand the removal of understory vegetation would improve the growth of Douglas-fir by increasing photosynthetic rate (Price et al. 1986), our results showed that removal of understory vegetation had no benefit to Douglas-fir growth. No differences in soil moisture were observed between the plots of removal and nonremoval for the years measured between 1973 and 1990 (A.K. Mitchell, unpublished data). As a matter of fact, Douglas-fir seemed to grow slightly better with the presence of understory vegetation. This might be because, in the dry summer season, understory vegetation prevents evaporation of soil moisture. Another probable factor is that some of the applied fertilizer was immobilized in the understory vegetation and released several years later, becoming available for uptake by the trees (Trofymow et al. 1991). This would not occur in the plot where clipping was done. The analysis done on the two plots here is not strictly valid, as only one plot for each clipping treatment was included. The analysis is unduly liberal and included here simply to show possible trends.

In conclusion, several management implications can be summarized from this study.

(1) The Shawnigan Lake experiment showed that both thinning and fertilization can greatly improve productivity of Douglas-fir (Mitchell et al. 1996), and this positive effect can last for at least 24 years (McWilliams and Thérien 1997).

(2) Our results showed that, in the 51-year-old Douglas-fir stand 27 years after treatment, the effects of thinning and fertilization on understory species growth and diversity were minimal, only restricted to the few most abundant species, e.g., salal and Oregon beaked moss. Conversely, there was no evidence of any negative effect of understory vegetation on the growth of canopy trees. Therefore, removal of understory vegetation would probably not be beneficial to overstory trees if the plantation has already established.

(3) The fact that salal and Oregon beaked moss are the only two species having significant responses suggests that these two understory species are probably sensitive to the effects of light penetration, mediated by fertilization and thinning in the Douglas-fir plantation, and can be used as indicator species in monitoring the effects of thinning and fertilization on the ecosystem.

(4) Because the largest number of species are nonvascular and generally require specific substrates to grow, the presence of a species in a particular plot is largely dependent on whether suitable substrate is available and light conditions are favourable. If species diversity is the management goal, particular attention should be paid to protect various specific substrates, including tree trunks, coarse woody debris and stumps. This goal can be achieved by variable-density or so-called "biodiversity" thinning (Curtis and Carey 1996), which retains those substrate types where there is a large number of understory species.

(5) Based on other authors' research in a similar context and from the results of the Shawnigan Lake experiment, we expect that moderate thinning (e.g., up to two thirds of basal area removed) would increase understory species richness in the early stages prior to canopy closure, whereas at the stage of stem exclusion no adverse effect of thinning and fertilization on the species richness would be expected to occur.

These results suggested that short thinning rotation (e.g., less than 17 years, Alaback and Herman 1988; Thomas, et al. 1999) would have pronounced effect on the diversity and growth of understory species, but the effect should be small if the rotation length is as long as 27 years or longer. Therefore, to ensure species diversity and niche diversification in the similar type of Douglas-fir forests in the CWHxm on southern Vancouver Island, a feasible solution is a commercial thinning to minimize the time of the stem exclusion of these forests.

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