Salal Cedar Hemlock Integrated Research Program

Research Update #1: December 1996

Edited by

C.E. Prescott

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Cover photo: 14-year-old plantation of western red cedar on a cedar-hemlock (CH) cutover 2 years after application of fish-wood compost.

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SALAL CEDAR HEMLOCK INTEGRATED RESEARCH PROGRAM (SCHIRP)

Research Update #1: December 1996

Introduction

Cedar-hemlock (CH) cutovers in the Coastal Western Hemlock very wet maritime (CWHvm) biogeoclimatic subzone on northern Vancouver Island show poor regeneration about 8 years after clearcutting. The problem is indicated by foliar chlorosis and growth stagnation in planted Sitka spruce (*Picea stichensis* (Bong.) Carr.), and naturally regenerated western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Western redcedar (*Thuja plicata* Donn. ex D. Don) is less affected than the other species. These indications of nutrient deficiency on CH sites coincide with the vigorous reinvasion of the ericaceous shrub salal (*Gaultheria shallon* Pursh). Trees established on adjacent hemlock-amabilis fir (*Abies amabilis* (Dougl.) Forbes) (HA) cutovers do not experience this "growth check" (Weetman *et al.* 1989).

Prior to clearcutting, forests on CH sites are relatively open, uneven-aged old-growth stands with dense salal understories. The soils are typically undisturbed, compact, and imperfectly to moderately well-drained gleyed, humoferric podzols. In contrast, HA forests are dense, even-aged second-growth stands with minimal salal cover. Disturbed, friable humoferric podzols characterize these stands which originated from windthrow events in 1906 (Weetman *et al.* 1990). Lewis (1982) classified the two forest types as distinct phases of a single "salal-moss" (S1) ecosystem, and hypothesized that regeneration and site growth conditions typical of the HA phase could be achieved through silvicultural management of CH sites.

Foliar analyses indicated that conifers on CH cutovers were deficient in nitrogen and phosphorus. These low levels of N and P exist in CH sites prior to harvesting (Prescott *et al.* 1993), and are attributed to the immobilization of N in humus, resulting from excessive moisture, low soil faunal activity, cedar litter and tannins from salal. Additions of N and P fertilizers, in chemical forms (Weetman *et al.* 1989) or in organic wastes (McDonald *et al.* 1994), alleviate the chlorosis significantly improve conifer growth on CH cutovers. Following harvesting, the poor nutrient supply on CH sites is exacerbated by rapid reinvasion of salal. Salal competes with young conifers for water and nutrients, produces tannins which inhibit N mineralization and uptake (deMontigny and Weetman 1990), and interferes with the ectomycorrhizae of hemlock (Xiao 1986).

Results of research conducted prior to 1994 were summarized in the first synthesis report (Prescott and Weetman 1994). The purpose of this report is to update the synthesis, providing results of research conducted since that time. Studies presented are:

1) a trial comparing effects of species, planting density, scarification and fertilization at planting
2) a trial comparing salal eradication and fertilization
3) trials with sewage sludge and fish silage
4) additional fish silage fertilization trials
5) a trial with fish-wood compost and straw amendments
6) studies of N fixation and denitrification in CH and HA cutovers
7) studies of condensed tannins in salal and humus
8) studies of N cycling and fertilizer N fate with ^{15}N
9) studies of P forms in CH and HA forests and cutovers.

Influence of Density, Scarification and Fertilization at Planting on Growth of Cedar and Hemlock on CH and HA Sites

Jessica Pratt, Leandra Blevins and Cindy Prescott

Introduction

The current strategy for regenerating CH sites is to reach crown closure as soon as possible, thereby shading out the salal. Several silvicultural techniques might be applied to achieve this goal, alone or in combination. Planting trees at high densities should hasten crown closure, unless it results in slower growth of individual trees. Fertilization with N and P accelerates tree growth on CH sites, and typically increases crown size (Binkley 1986), which would further hasten crown closure. Scarification may also increase early growth rates by providing more planting spots and by mechanically disrupting the salal. Lewis (1982) suggested that mixing organic and mineral soil on CH sites by scarifying would also improve nutrient availability in a manner similar to that suggested for windthrow disturbance (Ugolini *et al.* 1990). The effects of these three silvicultural treatments on rates of growth of cedar and hemlock on CH and HA sites were compared in a large field trial. Planting density varied from 500 to 2500 stems/ha. Unlike previous trials in which fertilizer applied after growth rates had declined, trees in this trial were fertilized at the time of planting and 6 years later. Some of the plots at the highest density were also scarified prior to planting.

Methods

The trial was established in 1987 on a cutover that formerly supported both CH and HA forests. The area had been logged in 1986 and broadcast burned in the spring of 1987. There were 128 plots established, 64 on CH sites and 64 on HA sites. Each plot contained 64 trees; plot size varied with tree density. One-half (32) of the the plots on each site were planted with cedar, the other half with hemlock. One-half (16) of the plots of each species on each site were fertilized, the other half were not. Of these 16 plots, 4 plots were planted at 500 stems/ha and 4 at 1500 stems/ha. The remaining 8 were planted at 2500 stems/ha; 4 of these plots were scarified prior to planting.

Thirty-two plots were scarified in January 1988 with a 215 Cat Excavator backhoe with a 3-tyned rake attachment. Container stock seedlings (1-P415) of cedar and hemlock were planted in February 1988. Sixty-four seedlings were planted in each plot at spacings of 4.5, 2.6 or 2.0 m, corresponding to 500, 1500 and 2500 stems/ha. Sixty g of Nutricoat™ controlled-release fertilizer was applied and raked into the ground within a 15 cm radius of each tree in the fertilized plots. This provided 10 g N, 2.5 g P and 5 g K to each tree. Loading rates on an areal basis varied with planting density, with a maximum loading of 25 kg N, 6.25 kg P and 12.5 kg K /ha. Plots were refertilized in 1993; at this time N and P were broadcast to the entire plot at rates of 225 kg N and 75 kg P per hectare.

A subsample of 10 trees in each of the 64 plots planted at 2500 stems/ha were measured at the time of planting in February 1988. Average values for each species-by-site combination were used in the analyses. The height and root collar diameter of each of the 8,192 trees were remeasured in the fall or winter of 1988, 1989, 1990, 1992 and 1994.

Separate statistical analyses were conducted for each of the four species by site combinations (Cw on CH, Cw on HA, Hw on CH, Hw on HA). The effects of density and fertilization were tested with two-way ANOVA, excluding the scarified plots. Scarification and fertilization were compared using the values from the 2500 stems/ha plots only.

Results and Discussion

The effects of fertilizing at time of planting for the three tree densities are shown in Figure 1. Height responses are shown; the same trends were apparent in diameter and individual-tree volume responses. Cedar growth was similar in unfertilized plots on both CH and HA

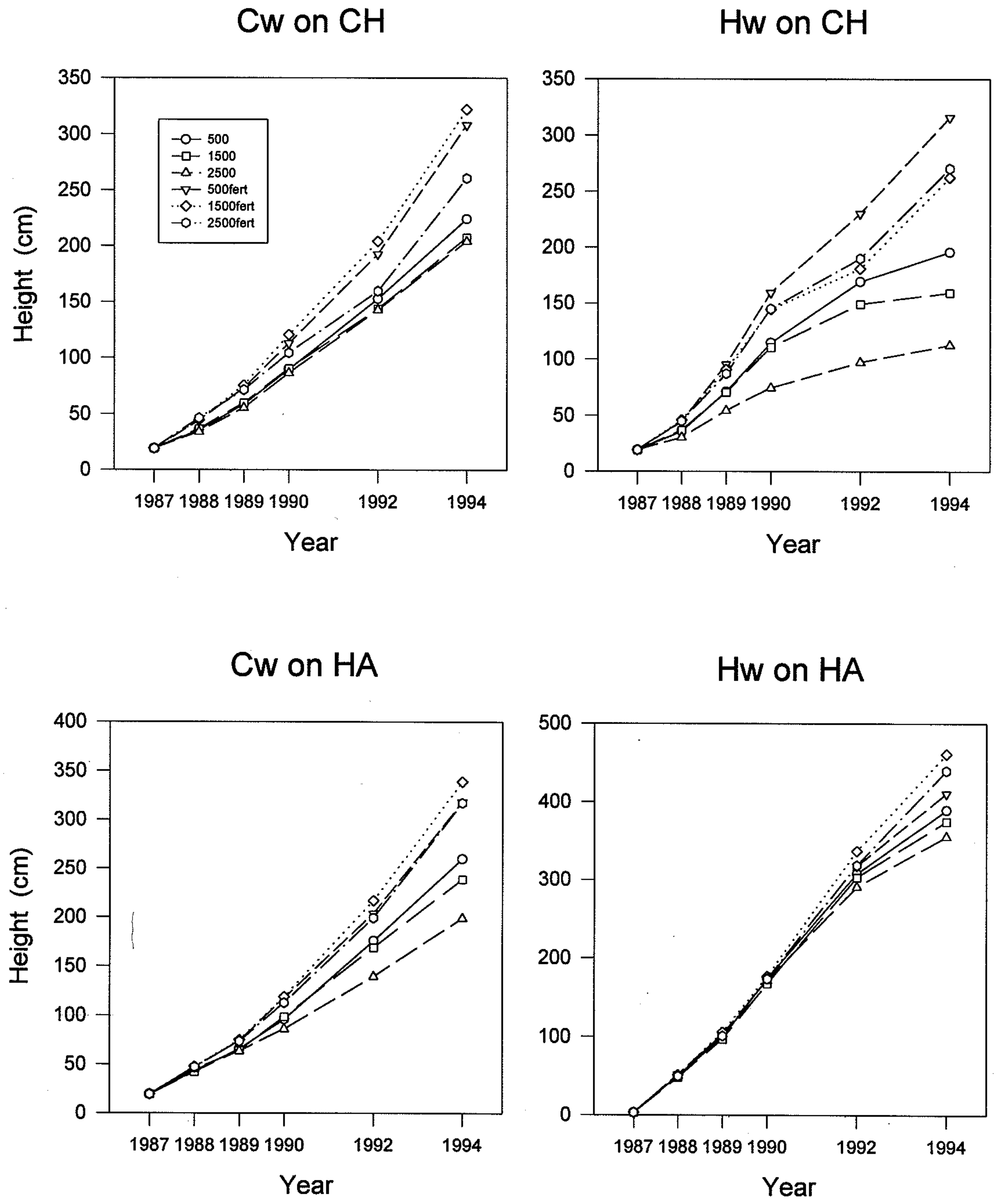


Figure 1. Height in cm of trees planted at densities of 500, 1500 and 2500 stems/ha with or without N+P fertilization at time of planting and in 1993.

sites, and it responded to fertlization similarly on both sites. Hemlock grew much more slowly on CH sites than HA sites, and responded much more to fertilization on CH sites. In both cedar and hemlock on both CH and HA sites, trees were larger in fertilized plots than in unfertilized plots of the same density. The similar growth of cedar and hemlock on fertilized CH sites contrasts with earlier studies in which N and P were applied 8-10 years after planting, in which hemlock growth was consistently greater than cedar. This suggests that cedar responds better when fertilized at time of planting than later. Greater response of cedar than hemlock to fertilization with teabags and briquettes at the time of planting has been observed on a salal-cedar site on northern Vancouver Island (S. Chambers, personal communication). In both of these trials, the fertilizer was placed very near the tree, in contrast to earlier trials in which it was broadcast across the plot. This would improve access to the fertilizer for the tree, and limit its uptake by salal, which may be particularly beneficial for cedar. Other trials have shown cedar to be particularly responsive to removal of salal (see next report), so cedar may also be more affected by increased growth of salal following broadcast fertilization. Therefore, the response of cedar may be attributable to the distribution of the fertilizer, rather than the timing. More research on the nutrition and rooting habits of cedar is necessary to better understand its response to fertilization at planting.

The signficant growth response to fertilization during the first 6 years was unexpected, given that this is considered to be the period of high nutrient availability following clearcutting. Earlier studies documented a gradual decline in N availability on CH cutovers during the first 8 years after clearcutting and slashburning (Prescott and Weetman 1994). Results from the fertilization at planting trial indicate that the elevated levels of N on CH sites early after disturbance are still insufficient for maximum conifer growth. Individual tree fertilization is preferable to broadcast fertilization at time of planting for two reasons. First, tree roots would not yet be extensive enough to capture nutrients applied more than 1 m from the stem, so much of the fertilizer would be wasted. Second, competing vegetation would respond more to broadcast fertilizer, which would reduce conifer responses.

Lewis (1982) suggested that the high productivity characteristic of HA sites could be achieved on CH sites through silvicultural intervention. In the current trial, this goal was at least temporarily achieved through fertilization at planting. Fertilized cedar on CH sites were larger than unfertilized cedar at corresponding densities on HA sites, indicating that fertilization at planting had improved growth of cedar trees on CH sites to a level comparable to HA sites. However, the fertilized hemlock on CH sites were not as large as unfertilized hemlock on HA sites.

Average tree sizes of both species planted at the highest density (2500 stems/ha) were smaller than those planted at the lower densities on both CH and HA sites. Responses to fertilization were also smaller in trees planted at the highest density. It is unlikely that competition with neighbouring trees would be significant in trees of this size. A more probable explanation is the lack of good planting sites on these cutovers which are characterized by mounds, depressions, airpockets in humus, and heavy slash accumulations. Many of the additional planting sites at the highest density were likely less suitable, resulting in poorer growth of many of the trees in this treatment. Growth and fertilization response was generally as good or better at densities of 1500 stems/ha compared to 500. Total stand volumes after 7 years were greatest at 2500 stems/ha, except in cedar on CH sites where volume was greatest at 1500 stems/ha (Figure 2).

Growth responses of both species planted at 2500 stems/ha to fertilization, scarification, or both, are shown in Figure 3. On HA sites, fertilization with or without scarification provided the greatest responses in both cedar and hemlock. Cedar appeared to be more responsive to fertilization than hemlock on HA sites. Responses to scarification were much smaller on HA sites. On CH sites, both species responded most to the combined treatment, and responses to either fertilization or to scarification alone were much smaller. Both treatments are therefore recommended to maximize growth on CH sites. Scarification is commonly carried out on CH sites as an alternative to slashburning; these results suggest that scarification may be beneficial in addition to slashburning. The additional effects of scarification are probably due to disruption of salal by this treatment, by removing the rhizomes. Salal resprouts rapidly after burning, which removes only the aboveground portions of the plant. Other trials in which salal has been removed manually have demonstrated prolonged growth responses of trees (see following report). An increase in nutrient availability following scarification is unlikely, since Keenan *et al.* (1994) found that N availability was not higher in mixed soil than in unmixed soil on these sites, and earlier trials

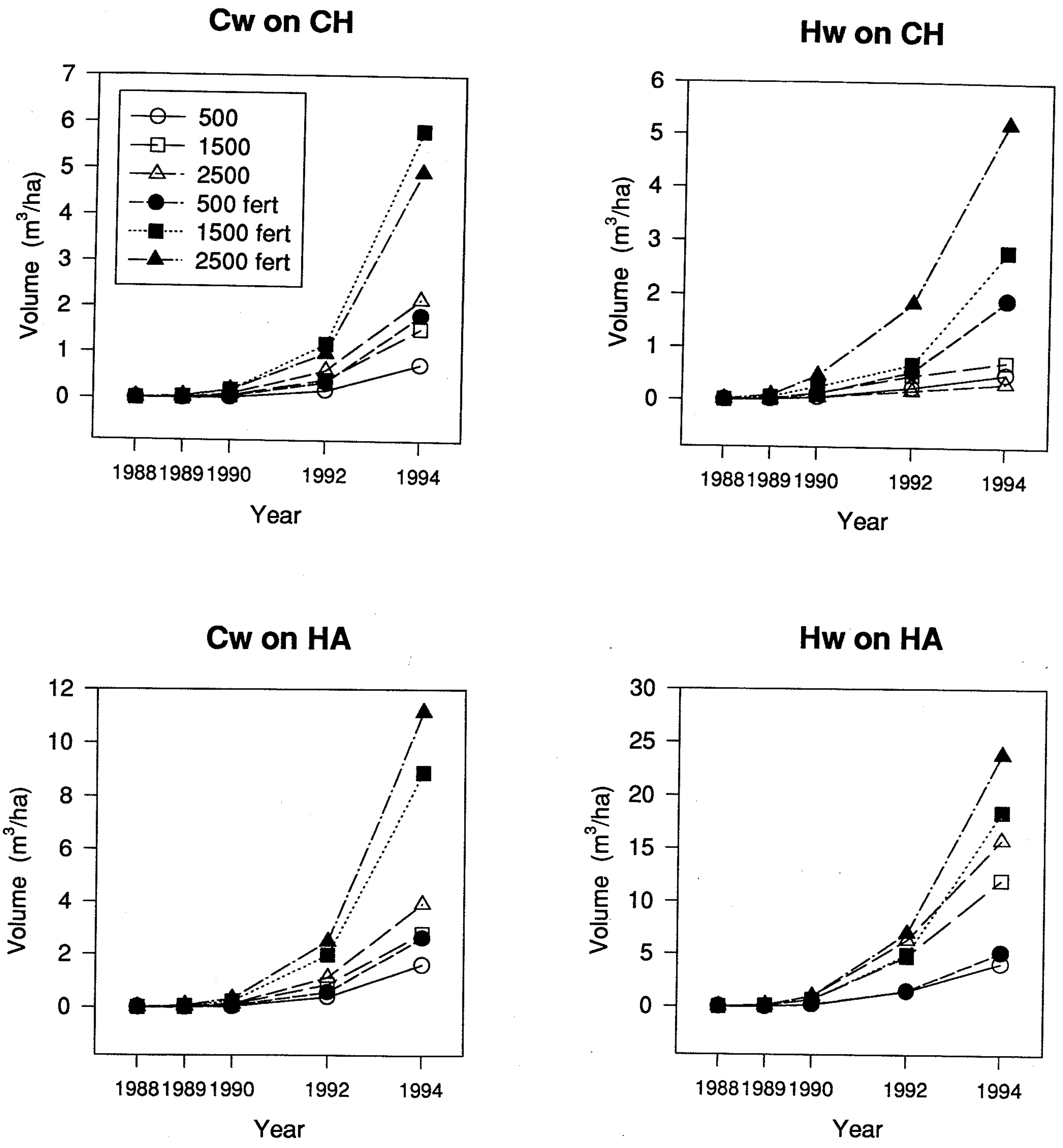


Figure 2. Volume in m^3/ha of trees planted at densities of 500, 1500 and 2500 stems/ha with or without N+P fertilization at time of planting and in 1993.

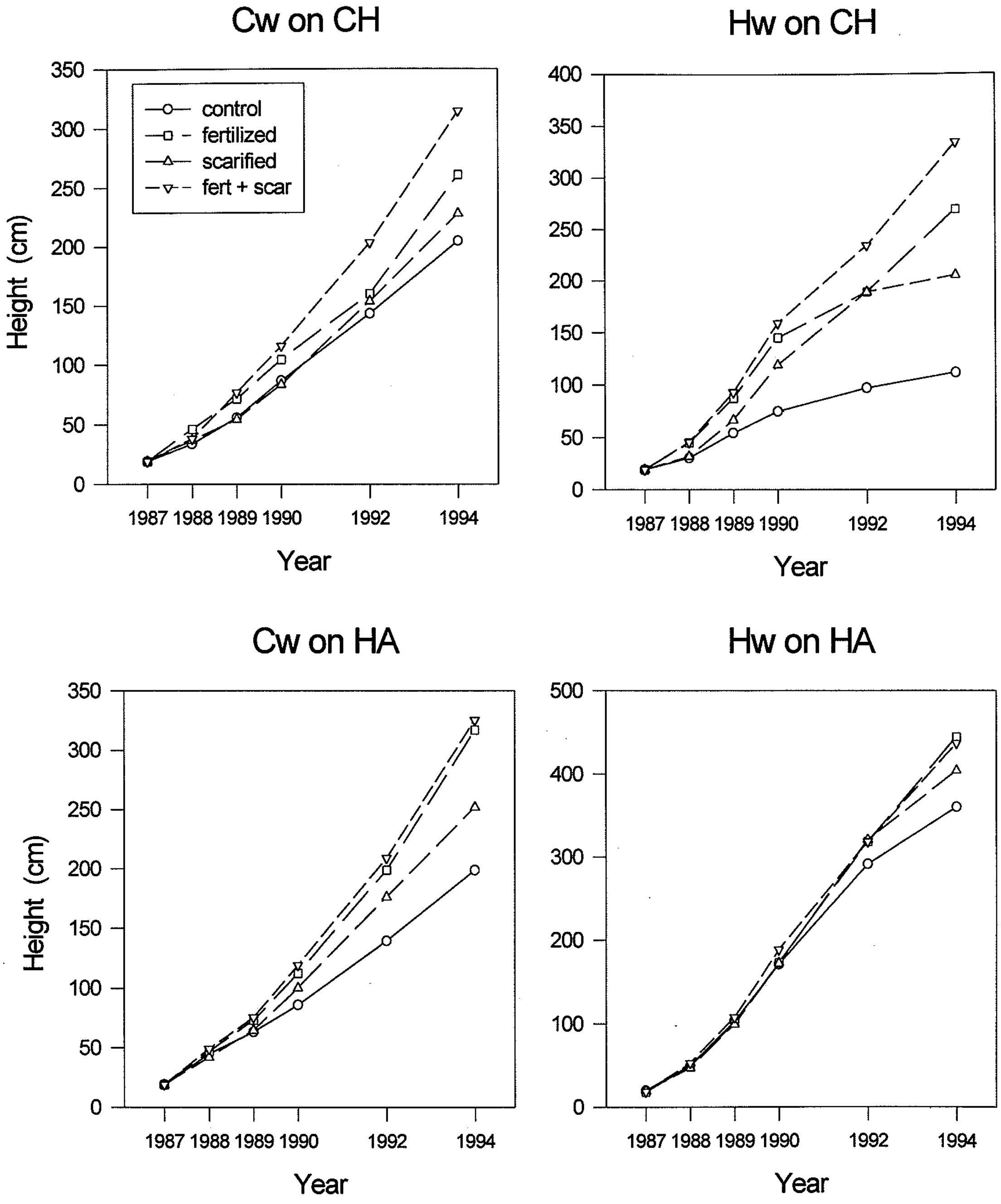


Figure 3. Height in cm of trees planted at 2500 stems/ha in plots that were scarified, fertilized at time of planting, both (fert + scar), or neither (control).

have indicated little response to scarification. Mechanical site preparation is used on other competitive sites as alternative to slashburning and herbicides to reduce competition from minor vegetation.

Rapid early growth of planted seedlings is essential on nutrient-poor, competitive sites such as CH cutovers. In this trial, mechanical site preparation in combination with individual tree fertilization at planting significantly accelerated crown closure on these sites. This combined treatment may be particularly effective on other sites dominated by ericaceous shrubs, such as *Kalmia* in eastern Canada or *Calluna* in the U.K. Increasing pressure to hasten early plantation growth to achieve "green-up", or to shorten rotation lengths to avoid local shortages in wood supply, may make these treatments economically attractive on other types of sites.

Fertilization and Salal Removal for Improving Conifer Regeneration on CH Sites

Jennifer Bennett

Introduction

A salal eradication research trial was established on CH sites in 1984 to test the efficacy of salal removal and N and P fertilization for controlling salal competition and improving the growth rates of conifers. It was hypothesized that reduced salal cover should result in both an increased nutrient availability to trees and a sustained higher level of productivity. Similarly, fertilization with N and P was hypothesized to reduce salal biomass by hastening crown closure and decreasing the amount of light in the understorey. Messier *et al.* (1989) demonstrated that salal biomass on CH sites was significantly reduced when the crown closure reached approximately 80%. The salal eradication trial was remeasured in 1995 to determine the duration and magnitude of changes in tree growth in response to the treatments, the effects of the treatments on salal cover, crown closure and nutrient availability, and whether crown closure alleviates growth problems through salal depression or improved nutrient availability. Questions asked included: have significant tree growth responses been achieved through salal removal and fertilization; are these responses sustained; do the dominant tree species vary in response to the treatments; have the treatments successfully advanced the stands towards crown closure, reduced salal cover and more efficient nutrient cycling; and have the treatments resulted in a significant alteration of the nutritional status of the soils and the trees?

Methods

The trial consisted of five replicate blocks located on five CH sites harvested and burned in either 1969, 1971, 1972 (2 sites) or 1975. Following burning, Sitka spruce seedlings were planted and western redcedar, western hemlock and shorepine (*Pinus contorta* var. *contorta*) regenerated naturally. The trial was established in 1984 and consisted of a $2 \times 3 \times 2$ factorial treatment system of: salal removal; N fertilization (250 kg N/ha of ammonium nitrate (NH_4NO_3) or urea); P fertilization (100 kg P/ha of triple superphoshate). In 1985 and 1989, Garlon 4E™ was applied to all treatment plots to inhibit salal re-establishment.

In this study, only four treatments in each of the five blocks were measured; control, salal removal, N (NH_4NO_3) and P fertilization, and combined (salal removal plus N and P fertilization) treatments. In each plot, the diameters, (at 1.3 m) of the 30 largest trees were measured to compare treatment responses. Height, dbh, age (at dbh), and annual radial increment of the 10 largest individuals of cedar, hemlock, and spruce were also measured to examine species-specific responses. The selected trees were representative of the harvestable component of each stand. Average crown closures and salal covers were visually estimated in each plot. All trees taller than 1.3m were counted to estimate stand densities, and in each plot one soil pit was dug to determine soil characteristics and aid ecosystem classification.

Five samples of the forest floor "F" layer horizon were collected randomly from each plot and were combined to produce one composite sample per plot. From each of the five composite samples, one 5 g (dry weight) sub-sample was analyzed for concentrations of total N, P and S. Nitrogen and P were analyzed with an Alpkem RFA 300 auto-analyzer, following sulphuric acid – hydrogen peroxide digestion (Parkinson and Allen 1975). Concentrations of total S were measured by combustion in a Leco furnace. A second sub-sample was dried at 70°C for 72 hours to determine the moisture content of each composite forest floor sample. A third 20 g (fresh weight) sub-sample was extracted with Bray's solution and concentrations of PO_4-P were determined using the auto-analyzer (McKeague 1978).

A fourth fresh sub-sample from each plot was incubated for 21 days at approximately 20°C. After incubation, concentrations of NH_4-N and NO_3-N were measured with the auto-analyzer following extraction with 50 mL of 2M KCl (Page *et al.* 1982).

In August, 1995, hemlock foliar litter was collected from 10 – 15 trees in each plot and was oven-dried for 72 hours at 70°C. These samples were then digested in sulphuric acid and hydrogen peroxide, and total N and P concentrations were determined using the auto-analyzer. Green hemlock foliage was collected from the upper crowns of five individuals in each plot during the initial stages of tree dormancy in September 1995. These samples were dried at 70°C for 48 hours and concentrations of total N, P and S were measured as described above. All analyses were conducted at the MacMillan Bloedel Woodland Services Laboratory in Nanaimo.

Statistical analyses

Differences in arithmetic mean tree diameters were initially tested using two-factor analysis of variance to assess the effects of treatment and block, and interactions between the two factors. The results showed that tree diameters (the 30 largest trees in each plot) from each block should be analyzed separately. One-way analyses of variance were then conducted on the tree diameters to establish significant differences in the treatments within each block.

The ages of the three tree species varied as a result of the different harvest years of the five blocks and the different times of establishment; spruce were planted and hemlock and cedar naturally regenerated. Therefore, a direct statistical comparison of the responses of the three species was not possible. Within-species covariance analyses were necessary to determine the influence of tree age as a covariant ($p < 0.0001$) of tree height and diameter. As a result, individual trees of each species were grouped into age classes composed of average ages that were not significantly different prior to comparing height and diameter responses to the treatments in each block. These comparisons were made on graphical and numerical bases.

The forest floor and the hemlock foliar nutrient concentrations from each block were combined by treatment and analyzed through one-way analysis of variance to establish any significant treatment effects on site nutrition. Annual radial growth increments were averaged and combined (all five blocks) to determine species-specific and treatment-specific diameter growth responses over time.

Results

The mean diameter of the 30 largest trees in each plot was significantly greater in the combined (fertilization plus salal removal) than in the control treatments (except in block 5) (Figure 4). Tree growth response to the salal removal and the fertilization treatments varied between blocks, which can be attributed to the differences in the species composition of the 30 largest trees in each of the blocks. To compare the diameter and height responses in the treatments, each species in each block was grouped into similar age classes. Blocks were compared independently; overall trends are presented in Table 1. Diameter and height response were highly

Table 1. Diameter and height of trees of each species in each treatment expressed as a percentage relative to the control.

	control (%)	fertilization (%)	salal removal (%)	combined (%)
Diameter				
spruce	100	143.4	124.2	200.2
hemlock	100	139.6	110.3	171.4
cedar	100	95.1	137.2	114.8
Height				
spruce	100	142.2	122.4	184.0
hemlock	100	132.3	111.3	159.0
cedar	100	104.9	126.5	113.8

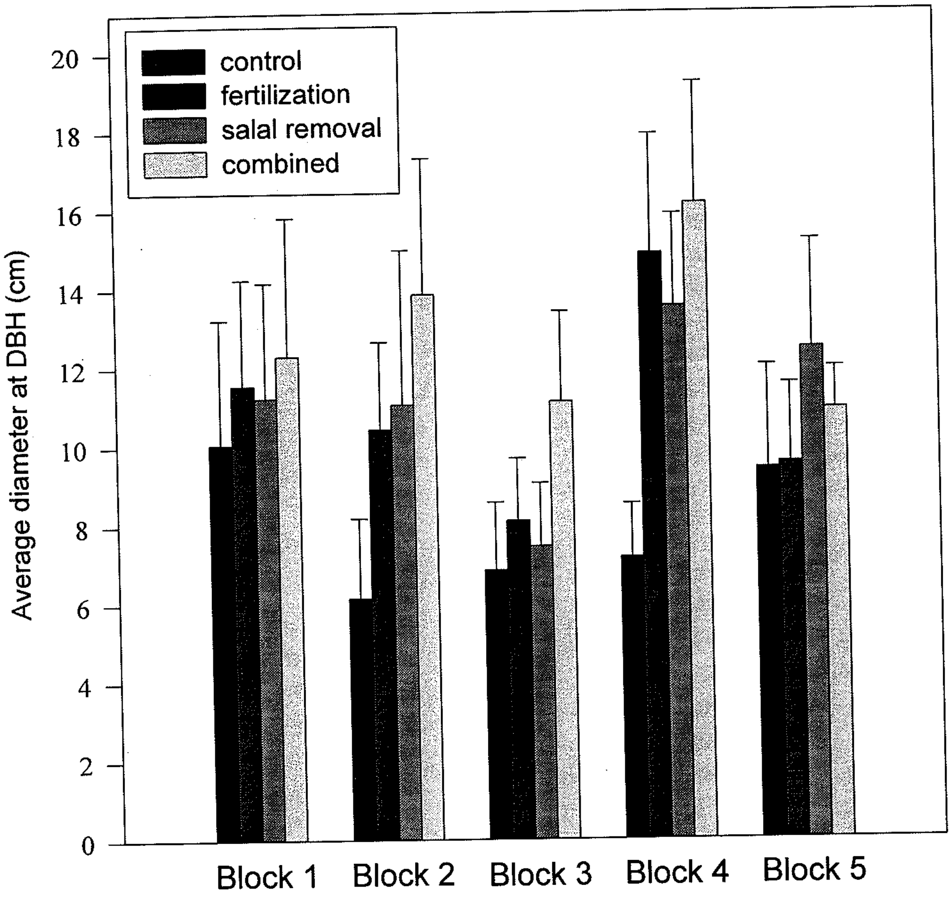
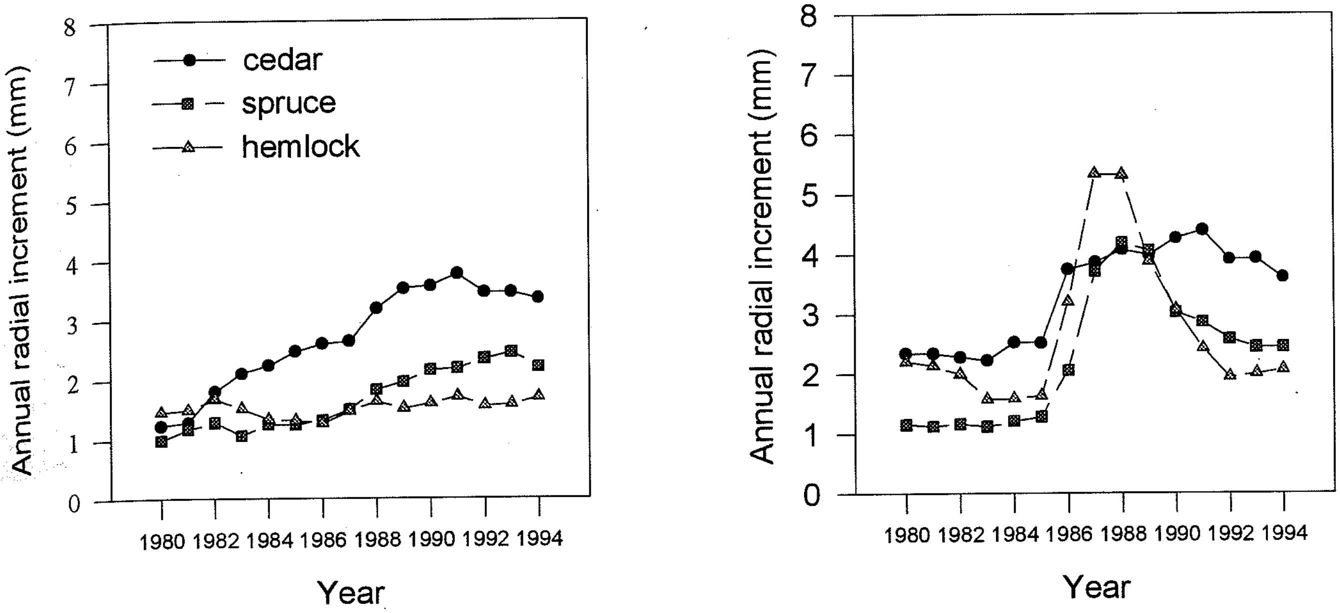


Figure 4. Average diameters of the 30 largest trees in each plot 10 years after fertilization, salal eradication or combined treatment.

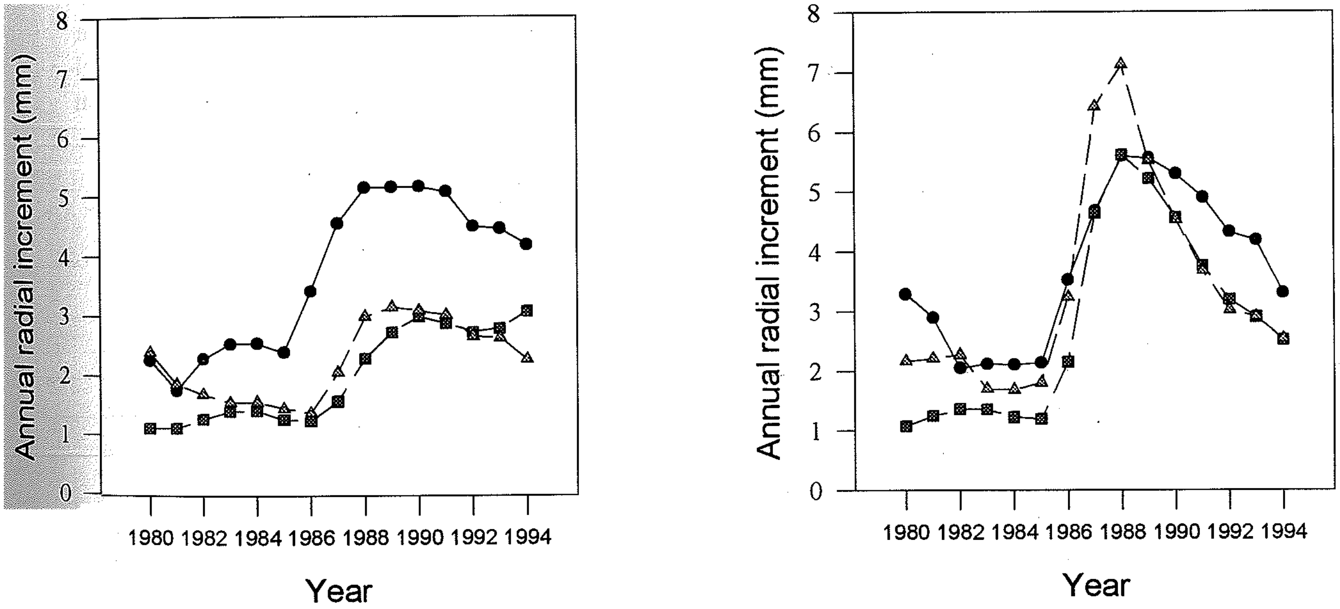
species-specific. Spruce and hemlock growth was greatest in.the combined treatments, followed by the fertilization treatments. Cedar growth was greatest in the salal removal and combined treatment plots.

The mean annual radial increments of each species over time are shown in Figure 5. In the control plots, cedar trees had the highest annual growth and the cedar radial increments generally increased through time. In the fertilization treatments, spruce and hemlock showed substantial increases in annual radial increments, but the increases declined within five years. Cedar did not show a large response to fertilization. Salal removal resulted in gradual and sustained increases in annual increment in all three species, however, cedar showed the greatest increases. In the combined treatments, patterns of annual radial increment growth of all three species suggested that the effects of the individual treatments may be additive, as indicated by the initial dramatic increase in annual growth (fertilization response) which was relatively sustained (salal removal response). The 1995 annual increments of hemlock and cedar in the combined treatments, however, did show a lower level of radial



Control

Fertilization



Salal removal

Combined (fertilization plus salal removal)

Figure 5. Annual radial increment of cedar, hemlock and spruce trees in plots receiving fertilization, salal removal or combined treatment in 1985.

growth than those in the salal removal plots. Over a ten-year period (1983-1993), changes in increment growth for all three species were greatest in the combined treatment followed by salal removal (Table 2). Of the three species, cedar, in the combined treatments, showed the greatest change in annual increment growth over the ten years.

Salal cover, as estimated in 1995, was lowest in the combined (5% cover) and salal removal (35% cover) treatments and highest in the fertilization (87% cover) and control (93% cover) treatments. A direct relationship between crown closure and salal cover was not found. In the fertilization treatments both were high, and in the combined treatments both were low.

Total N concentrations in the hemlock litter and foliage and total S concentrations in the green foliage did not differ significantly among treatments (Table 3). Total foliar P concentrations, however, were greater in the fertilization and combined treatments. Significantly higher total P concentrations were also found in the forest floors of the combined and fertilization treatments, but there were no differences in forest floor N or S concentrations (Table 4). Mineralized and nitrified N concentrations did not differ significantly, but a greater proportion of the mineralized N was nitrified in the salal removal treatment (Table 5). There were no significant differences in the amount of extractable P in the "F" layers of the three treatments and the control.

Discussion

In general, the heights and diameters of each tree species were consistently larger in the three treatments than in the controls. These responses, however, varied among the species. Similar to responses reported in previous trials (Prescott and Weetman 1994), spruce and hemlock showed the greatest response to N and P fertilization. Fertilization caused an immediate (within one year) response, but growth declined within five years of fertilization. This large response to fertilization shows that low nutrient availability limits the growth of these two species on CH sites and that they are more sensitive than cedar to low nutrient supply. Hemlock and spruce also responded to salal removal, but cedar showed the largest growth response to this treamtent. Salal removal resulted in gradual but sustained increases in cedar radial growth increment. This suggests that growth of cedar is inhibited more by the presence of salal than by a low N and P supply. For all three tree species, the removal of salal may reduce the competition for available N, to varying degrees, and result in sustained higher N availability.

Table 2. Average net annual radial increments of each species in each of the four treatments.

Treatment	Tree species	Average 1983 radial increment (mm × 10^{-2})	Average 1993 radial increment (mm × 10^{-2})	Difference in radial increment from 1983-1993 (mm × 10^{-2})
control	Cw	210	345	135
	Hw	139	245	106
	Ss	152	158	7
fertilization	Cw	223	393	169
	Hw	113	244	132
	Ss	158	200	42
salal removal	Cw	253	445	192
	Hw	139	278	139
	Ss	154	262	109
fertilization plus salal removal	Cw	212	419	207
	Hw	135	290	154
	Ss	170	291	120

Table 3. Concentrations of N, P and S in senesced and live foliage of hemlock in each treatment.

Treatment	Senesced Foliage		Live Foliage		
	% N	% P	% N	% P	% S
control	0.28 (0.02) a	0.03 (0.01) b	0.80 (0.15) a	0.09 (0.01) b	0.984 (0.012) a
fertilized	0.24 (0.06) a	0.15 (0.09) a	0.78 (0.13) a	0.23 (0.08) a	0.980 (0.010) a
salal removal	0.27 (0.02) a	0.03 (0.01) b	0.97 (0.12) a	0.09 (0.01) b	0.121 (0.026) a
fertilized + salal removal	0.26 (0.02) a	0.14 (0.05) a	0.78 (0.12) a	0.18 (0.06) ab	0.099 (0.006) a

Mean and standard deviation in brackets; values followed by the same letters are not significantly different.

Table 4. Concentrations of N, P and S in the forest floor "F" layers of each treatment.

Treatment	% N	% P	% S
control	1.03 (0.04) a	0.08 (0.01) b	0.12 (0.02) a
fertilized	1.15 (0.10) a	0.14 (0.01) a	0.12 (0.01) a
salal removal	1.07 (0.11) a	0.08 (0.01) b	0.11 (0.01) a
fertilized + salal removal	1.13 (0.62) a	0.12 (0.02) a	0.12 (0.01) a

Mean and standard deviation in brackets; values followed by the same letters are not significantly different.

Table 5. Extractable N (µg/g) after incubation and extractable P concentrations in the forest floor "F" layers of each treatment.

Treatment	Mineralized N ($NH_4 + NO_3$)	Nitrified ($N - NO_3$)	Proportion Nitrified ($NO_3 / NH_4 + NO_3$)	Extractable P
control	3.38 (1.23) a	1.78 (0.55) a	0.63 (0.36) ab	58.88 (5.81) a
fertilized	8.08 (6.72) a	2.24 (0.99) a	0.40 (0.22) b	64.02 (3.73) a
salal removal	3.04 (0.70) a	2.94 (0.79) a	0.96 (0.09) a	55.58 (7.37) a
fertilized + salal removal	3.10 (1.82) a	2.08 (1.11) a	0.80 (0.34) ab	58.96 (2.98) a

Mean and standard deviation in brackets; values followed by the same letters are not significantly different.

Crown closure was highest in the plots receiving the fertilization and combined treatments. This higher degree of closure probably resulted from the higher tree density in combination with the denser crowns in the fertilization treatments. Salal re-establishment was lowest in the combined treatment plots, likely a result of the reduced levels of light accompanying the increased canopy closure in this treatment. In the control plots, there was abundant salal and relatively open canopies. Unlike the combined treatment and the control, the fertilization and salal removal treatments did not follow the crown closure-salal cover inverse relationship. In the fertilized plots, high salal cover (87%) was sustained despite the increase canopy closure. The salal in these plots, however, had taller, lankier stalks and larger leaves, indicative of low light intensities (Messier *et al.* 1989). In the salal removal plots, both crown closure and salal cover were relatively low, as were the tree densities. Damage or stress to tree root systems during salal removal may have accounted for the low densities. Salal abundance was low despite the open canopy, suggesting that low light intensity is not the sole factor in determining salal re-establishment.

Foliar and forest floor nutrient analyses were used as indications of long-term changes in tree and site nutrient status resulting from the treatments. Concentrations of P in needle litter, green foliage and the forest floor were significantly higher in both the fertilized and combined treatments, suggesting that the single application of 100 kg P/ha resulted in a high site retention of P. Total N concentrations in both needle litter and green foliage indicated that no long-term changes in the N status of the trees had occurred as a result of the treatments.

Rates of mineralization and nitrification represent the amount of N potentially available to the trees. No patterns in response to the treatments were evident in measures of the mineralizable N, but the proportions of the two forms of mineralized N (NO_3 and NH_4) differed among the treatments. Forest floor NO_3 concentrations were the highest in the salal removal and combined treatments. Such increased NO_3 levels in the forest floor may have indirectly resulted from the removal of salal and the increases in nitrifier populations in the forest floor with reduced salal competition. Salal is able to access NH_4 and organic N (Xiao 1994), and with its extensive rhizome systems and mycorrhizal associations and may be competitively superior, keeping nitrifier populations (and tree growth) low. Furthermore, the ability of salal to use organic forms of N further "short-circuits" the N cycle, by reducing the amount of organic N available for mineralization (Chapin 1995). Removal of salal might therefore increase both tree growth and nitrification

The presence of salal appears to be the factor most limiting the growth of cedar. This growth limitation, however, does not appear to be solely due to competition for nutrients with salal, because fertilization did not cause a dramatic increase in cedar growth. The greater NO_3 proportions in the forest floor in the salal removal plots may be the factor accounting for the larger growth response of cedar. Cedar is generally associated with NO_3 – rich sites (Turner and Kranz 1985), and Krajina *et al.* (1972) demonstrated a preference of cedar for NO_3 in a seedling study. Cedar has also been shown to create and perpetuate conditions which favour higher nitrifier populations due to the high pH and base content of cedar litter (Prescott and Preston 1994, Turner and Kranz 1985). Other explanations for the relatively high growth performance of cedar when salal is removed are possible and warrant further research.

The changes in the proportions of available N (NO_3 and NH_4) in the forest floor of the salal removal treatments could also have influenced re-establishment of salal. Nitrate may be unavailable for salal use because like other ericaceous species, salal may not produce nitrate reductase (Smirnoff *et al.* 1984), and so may not be able to take up N in the NO_3 form. With a higher proportion of NO_3 in the forest floor following salal removal, salal may be at a competitive disadvantage with species that are able to synthesize nitrate reductase required for nitrate assimilation, and may not be able to re-establish vigorously. Higher NO_3 concentrations were not found in the fertilization treatments, and salal was abundant in these plots. The ability of salal to establish and maintain growth may, therefore be limited by both higher concentrations of forest floor NO_3 and reduced understorey light following crown closure.