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Understory competition effect on tree growth and biomass allocation on a coastal old-growth forest cutover site in British Columbia

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Abstract

We studied the effect of salal (*Gaultheria shallon* Pursh.) competition on height, diameter and biomass growth and biomass partitioning in coniferous trees planted to a recent clearcut site of old growth western red cedar-western hemlock (CH) forest on northern Vancouver Island, British Columbia. Tree species used were western red cedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Sitka spruce (*Picea sitchensis* (Bong.) Carr). Salal removal treatment was initiated at the time of planting in spring 1987. Plots were fertilized with 200 kg N ha^{-1} in spring 1991 and destructively sampled in fall 1992. Height growth from planted to 1989, in 1992 and total height growth were significantly greater in treated plots (salal removed) than in the control plots (salal remaining). Salal removal had a rather uniform impact on height growth for the three species tested. Total root collar diameter was 38% ($P < 0.1$), 88% ($P < 0.05$), and 65% ($P < 0.05$) greater in the treated plots than in the control plots, for red cedar, hemlock and spruce, respectively. Exclusion of understory vegetation had resulted in biomass increases of all the components (namely in the 1-year and 2-year foliage and branches and the older than 3-year components and various sized roots) we studied. Improved tree growth in the treated plots was attributed to the reduced uptake and immobilization of N and other nutrients by the competing understory. Below-ground understory was found to be quite persistent to surviving even after a prolonged period (6 years) of above-ground understory vegetation removal

Biomass allocation among the components studied was virtually unchanged by the presence of the competing understory, except in two instances. This result was quite different from most of the other reports on biomass partitioning under competition. Our hypothesis that salal competition for nutrients increases biomass partitioning to current year foliage and branch and roots was rejected. Unchanged partitioning is probably a way of response to nutrient deficiencies according to the resource depletion model of competition processes. Non-significantly higher biomass partitioning was observed in the 1-year

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foliar and branch and 0.25–1 cm root components. It was therefore possible that the 1991 fertilization alleviated the nutrient shortage problem which led to the rejection of the hypothesis.

Keywords: Understory competition; Height; Diameter growth; Biomass allocation; Salal; Resource depletion

1. Introduction

Understory vegetation affects and is affected by overstory vegetation and the conditions of the surrounding physical environment. Effects of environmental conditions and overstory vegetation on understory are well documented (Kimmins, 1987; Beatty, 1984). Under certain circumstances, understory vegetation is desirable, such as for wildlife habitat (Armleder and Dawson, 1992; Hoefer and Bratton, 1988) and for soil erosion control in erosion prone areas (Stewart and Forsling, 1931). More than often, understory vegetation is undesirable, especially in reforestation, because understory will compete for nutrients (Neary et al., 1990; Messier and Kimmins, 1990), water (Flint and Childs, 1987), and light (Flint and Childs, 1987; Brand and Janas, 1988) with overstory and seedlings. Sometimes understory vegetation may exert allelopathic interferences by chemicals released through above- or below-ground organs (Del Moral and Cates, 1971). Under those situations, understory vegetation control becomes a necessity for crop tree establishment in the early stages of reforestation.

A site specific example of regeneration failures caused by competing understory vegetation is the salal (*Gaultheria shallon* Pursh.) problem in the wetter Coastal Western Hemlock biogeoclimatic zone (CHWb) (Pojar et al., 1987) of coastal British Columbia. On old-growth western red cedar (*Thuja plicata* Donn ex D. Don)-western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)(CH) cutover sites, trees planted grew very well initially. Soon after the ericaceous evergreen shrub, salal, invaded into the sites (8–10 years after planting) the young plantation went into growth stagnation and the needles displayed chlorosis suggestive of nutrient deficiencies (Weetman et al., 1989a and Weetman et al., 1989b). This is of deep concern to the forest industry in British Columbia, because their allowable cut is going to be affected by declining second growth productivity and satisfactory regeneration is required by law.

Below-ground interference imposed by salal, which spreads vegetatively by means of rhizomes, either by competition for nutrients or by allelopathy was generally regarded as the cause for the growth stagnation (Messier, 1991; DeMontigny, 1992). While the exact mechanisms are still not clear, studies carried out on those sites and elsewhere do show that controlling the understory growth improved tree diameter and height (Messier, 1993) and volume (Deyoe and Dunsworth, 1988) growth. Messier (1992) investigated the effects of neutral shade and growing media on growth, biomass allocation and competitive ability of salal in a pot experiment; however, no study has been done to investigate the effect of understory competition on the biomass accumulation and allocation in various components, such as in foliar, branch, and various sized roots, of growing trees under field conditions on those salal-dominated sites. Biomass allocation information might be very useful in explaining the mechanisms by which understory affects crop tree growth.

Nilsson and Albrektson (1993) indicated that the allocation of carbon to stem wood production had high priority for trees under high competitive stress. In a study on planted black spruce (*Picea mariana* (Mill.) B.S.P.) in the Ontario Clay Belt, Munson and Timmer (1990) found similar trends in that seedlings responded to site nutrient stress by allocating more biomass to the stem and roots. Newton and Jolliffe (1993) reported a reversed trend for second growth black spruce stands in that bark and foliar mass proportions increased while stem and branch mass proportions declined with increasing density stress. Therefore biomass allocation priorities are often not absolute and overlapping (Oliver and Larson, 1990). In our study, we hypothesized that biomass partitioning to current year foliage and branch and roots would be increased in the control plots as a strategy to survive the strong competition from salal.

The objectives of this study were to examine the effect of understory removal on height and diameter growth and biomass accumulation and allocation among different years' growth of foliage and branch and roots of different sizes under field conditions. This work was a continuation of part of the salal removal experiment by Messier (1993).

2. Materials and methods

2.1. Study site

The study site is located on Block 4 of Tree Farm License (TFL) 25 near Port McNeill, on northern Vancouver Island, BC, Canada (50°36′N, 127°15′W). The ecosystem at the study site was classified as the wetter Coastal Western Hemlock biogeoclimatic subzone which comprises 98% of the Block (Lewis, 1982). The old-growth western red cedar-western hemlock forest is the climatic climax community consisting of a somewhat open western red cedar-western hemlock stand with a minor Pacific silver fir (*Abies amabilis*, Lewis, 1982) component. The site used for this study was clear-cut and burned before planting. After logging, the site was quickly and vigorously occupied by salal, responding to the extra light. Other species which often appear after logging, besides the dominant salal, include *Vaccinium* spp. , fireweed (*Epilobium angustifolium*), and mosses.

The CH phase ecosystem is situated on a gently undulating topography. The soil is a Ferro-Humic Podzol (Germain, 1985). A typical soil profile has the following horizons: LF layer, usually 10–25 cm in thickness, in the burned cutover sites (this horizon often reduces to less than 5 cm because of burning); a thick, mostly greater than 45 cm, humus layer; a thin Ae layer; Bhf; Bf (sometimes the bottom appears greyish, indicative of periodic reductions); followed by a BC or C horizon. Parent material is unconsolidated glacial moraine and fluvial outwash material (Lewis, 1982). Climatic conditions are as follows: annual precipitation 1730 mm, with most of it occurring in the winter months as rain. May, June, July and August are the most dry months; mean daily temperature varies from 2.4°C in January to 13.8°C in August.

2.2. Field trial setup

After clearcutting and slash burning of a CH phase ecosystem site, nursery-grown 'plug type' 1–0 seedlings of western red cedar, western hemlock, and Sitka spruce were planted at the start of the growing season in 1987. One set of seedlings were planted without the understory vegetation (treated). This was achieved by continuously removing the above-ground understory in the surrounding area with a diameter of 2 m. In this treatment, below-ground competition from adjacent vegetation was eliminated by periodically cutting around the circle to a depth of 40 cm (Messier, 1993). Another set of seedlings were grown under natural conditions, i.e., with competing understory vegetation (control). In the fall of 1990, in conjunction with a micro-plot level fertilization trial, four seedlings of each species from both treated and control treatments were trenched and plastic barriers placed around the trees with 1 m radius down to a depth of 50 cm. In April 1991, fertilizer was applied as ammonium sulphate at a rate of 200 kg N ha^{-1} to those microplots. Above-ground understory removal was carried out throughout the experiment. For the measurements described below, basal diameter and height growth were determined on four trees for each species. Biomass measurements for trees, understory and litter were based on two replicates.

2.3. Field measurements and sampling

Basal diameter (root collar diameter) and height of each tree were measured in early June 1991, right after the fertilizer application, on 21 May, and on 30 September 1992, before the final sampling. Two measurements were taken for basal diameter at two directions for each tree. The incremental height growth for the years 1992, 1991, and 1990 was measured before the destructive sampling. Half of the microplots (two replicates for each species by treatment combination) were destructively sampled in late October 1992. For each plot, the above-ground tree was cut at the root collar and put into a plastic bag. Tree roots were collected by excavating as much as possible of the root system. Understory vegetation was cut at the ground level and separated into salal and non-salal components. From each microplot, two 25 × 25 cm subplots were excavated by a 10 cm increment to a depth of 50 cm for understory root biomass quantification. Standing dead and litter were collected from each microplot.

2.4. Laboratory analysis

After the samples were transported to the laboratory, above-ground trees were separated into 1- and 2-year-old foliage and branches, and 3-year and older components. Tree roots were washed free of soil and separated into four groups: stump, roots > 1 cm, roots 0.25–1 cm, and roots < 0.25 cm. Understory roots were recovered from the soil samples without further separation. Because of the small quantities of roots obtained in the layers deeper than 10 cm, the understory roots were grouped into two samples for each profile: 0–20 cm and 20–50 cm. All the samples were then dried at 65°C. Western red cedar, an indeterminate species, exhibits morphology quite distinct from its coniferous associates in the Pinaceae, which makes it difficult to differentiate different years' growth using major branch whorls. We identified different years' growth for red cedar following the method proposed by Parker and Johnson (1987).

2.5. Statistical analysis

Homogeneity of variance and normality of distribution were checked before any further statistical analysis. Logarithmic (10) or square root transformations were performed wherever fit. Analysis of variance was performed on all experimental variables using the General Linear Models (GLM) procedure of the SAS package (Statistical Analysis Systems Institute Inc., 1985). The GLM statement LSMEANS was used to test the differences between means within each species and treatment.

3. Results and discussion

3.1. Tree height and basal diameter growth

Data for tree height growth in various periods and the total height on 1 October are presented in Fig. 1 for the three species studied. Statistical analysis (Table 1) showed that treatments had significant effect on height growth in 1992 ($P < 0.1$); however, no significant differences were found for height growth in summer 1992, or 1991 and 1990. Height growth between 1987 and 1989, and total height measured in early October 1992 were significantly greater in the treated plots than in the control plots, with $P = 0.0481$ and $P = 0.0096$, respectively (Fig. 1 and Table 1). No treatment by species interaction was observed for any of the parameters measured (Table 1), which means that treatment had a rather uniform effect on tree height growth for all the species studied.

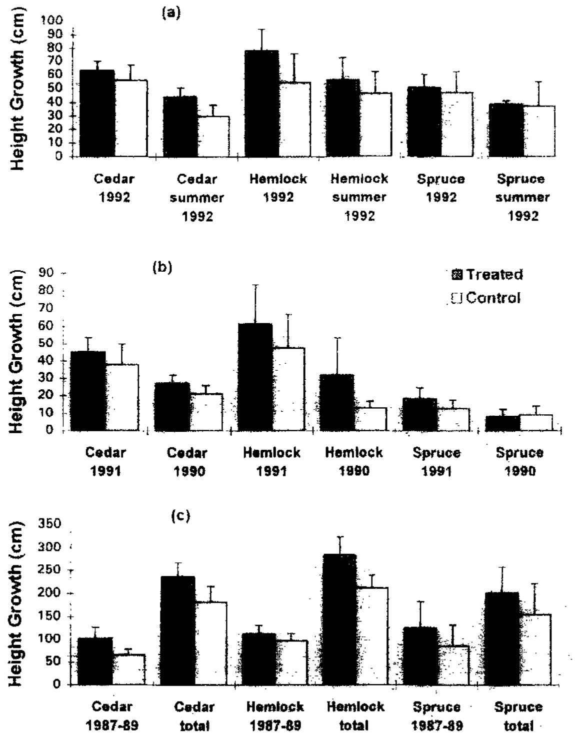

Fig. 1. Height growth of western red cedar, western hemlock and Sitka spruce in various periods. Vertical error bars represent standard deviations.

In a salal grubbing experiment reported by Weetman et al. (1989b), western red cedar plots that had salal removed tended to produce more height growth after 3 years of treatment. It was less obvious on western hemlock. The grubbing treatment increased relative foliar nitrogen concentrations for both cedar and hemlock in the first 2 years after treatment. In a similar study, the response in leader growth of plantation Sitka spruce was found to be immediate in fertilized salal-dominated plots (Weetman et al., 1989a). The annual height growth recovered matched the spruce growing on the salal free sites. It is therefore reasonable to conclude that the improved

Table 1

Analysis of variance [a] for the effect of understory competition and tree species on tree height and RCD growth

Variable	df	Height growth 1992	Height growth summer 1992	Height growth 1991	Height growth 1990	Height growth 1987–1989	Total height growth	Total RCD growth	RCD growth summer 1992
Treatment	1	+	ns	ns	ns	*	* *	* * *	*
Species	2	+	+	* * *	* * *	ns	*	ns	+
T × S	2	ns	ns	ns	ns	ns	ns	ns	ns

[a] The difference between means was significant at $^{+}P < 0.1$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; ns: non-significant;RCD: root collar diameter.

height growth in the plots with salal removal was the result of improved nitrogen availability.

The tree height growth rate increases obtained in 1991 and 1992 reflected the effect of fertilization in April 1991, although climatic conditions in different years may affect the height growth to some extent. As can be seen from Fig. 1a, most of the height growth was occurring in the summer months as was measured in 1992. When understory was removed from the plots, 72.1% and 75.4% of the annual growth occurred during the summer as compared with 85.3% and 78.9% when understory was present, for plots planted to hemlock and spruce, respectively. For plots planted to red cedar, it was 69.8% vs. 53.1%. This indicates that for hemlock and spruce, tree height growth tended to be spread over the year more evenly when the understory competition was removed, i.e., when competition exists, tree height growth was more severely impeded in the winter than in the summer. This may be explained by the fact that nutrients are more scarce in the winter because of slow mineralization under low temperature (Theodorou and Bowen, 1983) and high possibility of leaching loss under high precipitation (Zakharchenko, 1974; Kowalenko, 1989) in the winter. The reason for the reversed trend with red cedar was unknown. One of the red cedar trees in the treated plots had a height of 80 cm when measured on 1 October 1992. The height growth in the summer of 1992 was zero. This was obviously an outlier and was excluded from the subsequent calculations. The height growth calculations might be somewhat affected by this exclusion.

Red cedar and hemlock are indeterminate species (Weetman et al., 1989b), therefore height growth was benefited immediately after fertilization in 1991 (Fig. 1b). Sitka spruce as a determinate species, its current year's growth potential is determined by the growth condition in the year before. This was reflected by the increase in height growth for Sitka spruce in 1992, one year after the fertilizer application (Fig. 1a).

Understory removal also increased root collar diameter growth (Fig. 2). The total root collar diameter, when measured in early October 1992, was 38% ($P < 0.1$), 88% ($P < 0.05$), and 65% ($P < 0.05$) greater in the treated plots than in the control plots, for red cedar, hemlock and spruce, respectively. The growth of root collar diameter in the summer 1992 was 111% ($P < 0.05$) greater in the treated plots than in the control plots for red cedar, but was not significantly different for hemlock and spruce. The differences between species were generally not significant and no treatment by species interactions were found (Table 1).

Positive growth responses following understory vegetation removal were also found for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) on southern Vancouver Island (Green, 1990), and for Sitka spruce in heather (*Calluna vulgaris*, L.) dominated sites in

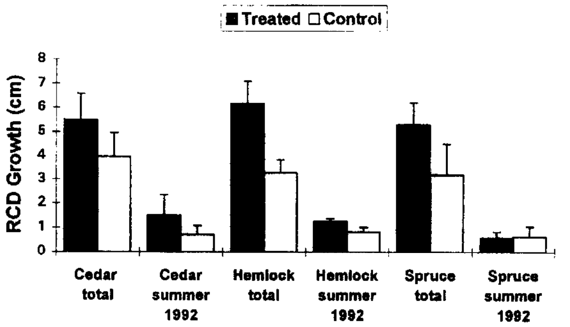

Fig. 2. Root collar diameter (RCD) growth in total and in summer 1992, for western red cedar, western hemlock and Sitka spruce. Vertical error bars represent standard deviations.

Scotland (Dickson and Savill, 1974). Messier's study (Messier, 1993) showed that understory vegetation removal had significantly increased total height and diameter increments in comparison with the control treatment in the first 3 years of field experiment. Since this study used Messier's field plots (Messier, 1993), it was interesting to note that increased height and diameter growth in the treated plots were sustained 6 years after seedling outplanting. In his study, Messier (1993) discovered that removal of understory vegetation increased resin ammonium nitrogen availability by 20–40% and resin phosphorus availability by 15–32% and estimated that 30–45% of the potentially available N was taken up annually by competing vegetation on CH sites. The reduced uptake and immobilization of nitrogen and other nutrients by the biomass of salal and other competing species in the treated plots apparently were the factors contributing to the improved tree height and diameter growth.

3.2. *Tree biomass accumulation*

The comparison of tree biomass growth between treated and control plots was plotted in Figs. 3 and 4. A prolonged exclusion of understory competing vegetation had resulted in a significant increase in biomass of all the components we studied (Table 2). Compared with the results in the height and root collar diameter growth, biomass seems to be a more reliable and sensitive measure of the effect of understory competition on tree growth, as more significant differences were detected. In effect, biomass growth reflects the growth along the entire stem (Brand and Magnussen, 1988) and the integration of the entire suite of physiological processes (Abrahamson and Caswell, 1982). Some significant interactions were found between treatments and species (Table 2). For example, the interaction for the 2-year foliage ($P <$ 0.01) was caused by the extremely low 2-year-old foliage biomass in the control hemlock plots. The current year biomass growth (Fig. 3a) showed that treatment had increased biomass growth from 1.6 (spruce branch) to 7.6 times (hemlock foliage) over the control. The greatest increase was attained with hemlock, the least with spruce, be it either branch or foliage components. Treatment effect on the biomass accumulation in 2-year-old foliage and branches and 3-year and older components had the same result and the magnitude of increases for the species was generally unchanged (Fig. 3b and c). For all the root components studied, the 'stump' and '> 1 cm roots' had the highest amounts of biomass in the treated plots. The differences in biomass accumulation between different root components were much smaller in the control plots (Fig. 4a and b). Salal removal gave an overall root biomass increase of 2.3 ($P =$ 0.4725); 7.6 ($P = 0.0065$); and 2.9 ($P = 0.0713$) times over control, for plots planted to red cedar, hemlock and spruce, respectively.

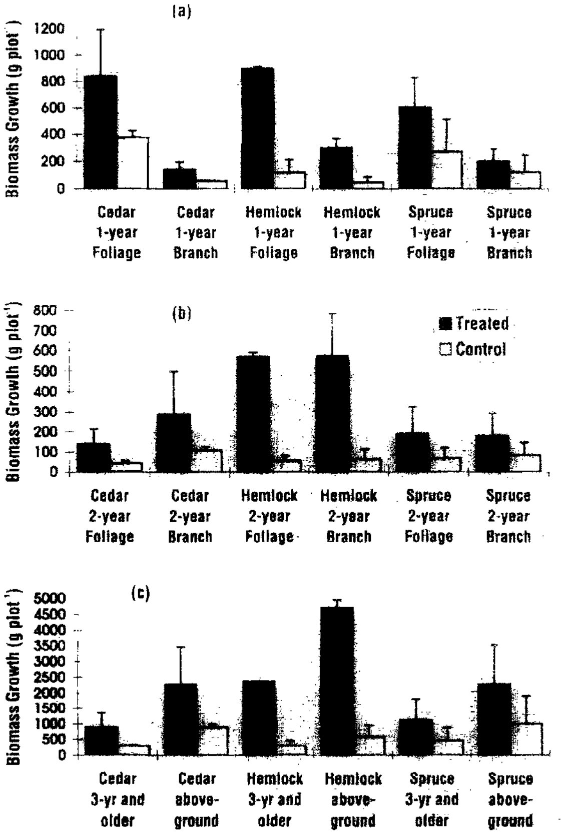

Fig. 3. Biomass accumulated at the final harvesting in various above-ground tree components. Vertical error bars represent standard deviations.

Fig. 5 shows the above- and below-ground biomass of the understory vegetation and standing dead salal and litter mass at the time of the final harvest. The above-ground understory biomass in the treated plots was kept at a minimum by repeated

Table 2
Analysis of variance [a] for the effect of understory competition and tree species on biomass accumulation of trees, understory and non-living components

Variable	df	1-year foliage	1-year branch	2-year foliage	2-year branch	3-year and up	AG tree	Stump	Roots > 1 cm
Treatment	1	* *	*	* * *	*	* *	* *	*	*
Species	2	ns	ns	* *	ns	+	ns	ns	ns
T × S	2	ns	ns	* *	ns	+	+	ns	ns

Variable	df	Roots 0.25–1 cm	Roots < 0.25 cm	USR 0–20 cm	USR 20–50 cm	Non-salal	Salal	Litter	Dead salal
Treatment	1	* *	* *	* * *	*	*	* * *	* * *	* *
Species	2	*	*	*	ns	*	* * *	*	ns
T × S	2	*	*	+	+	*	* * *	*	ns

[a] The difference between means was significant at + $P < 0.1$; * $P < 0.05$; * * $P < 0.01$; * * * $P < 0.001$; ns: non-significant. AG: above-ground; USR: understory roots.

clippings. The amount of above-ground understory vegetation harvested in the treated plots being the growth between the last cutting (16 July 1992) and the final harvest (30 September 1992). The above-ground understory biomass was as high as 1554, 2971, and 1373 g plot^{-1}, or 4947, 9457, and 4370 kg ha^{-1} for control plots planted to red cedar, hemlock and spruce, respectively (Fig. 5a). These data are in accordance with what Messier and Kimmins (1991) obtained on similar sites eight years after clearcutting and planting, while the below-ground understory biomass data was somewhat lower.

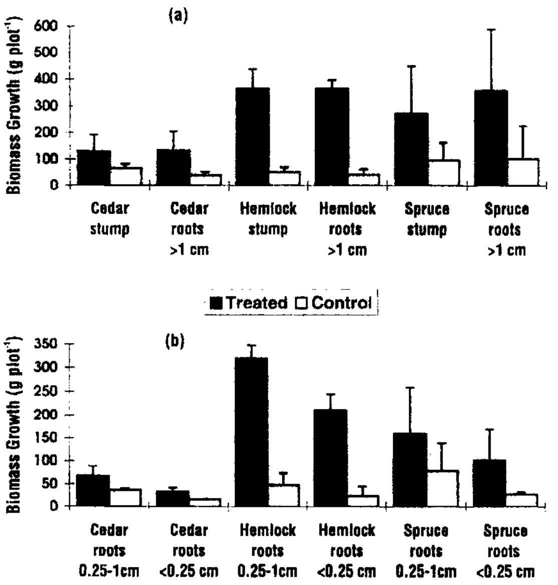

Fig. 4. Biomass accumulated at the final harvesting in various below-ground tree components. Vertical error bars represent standard deviations.

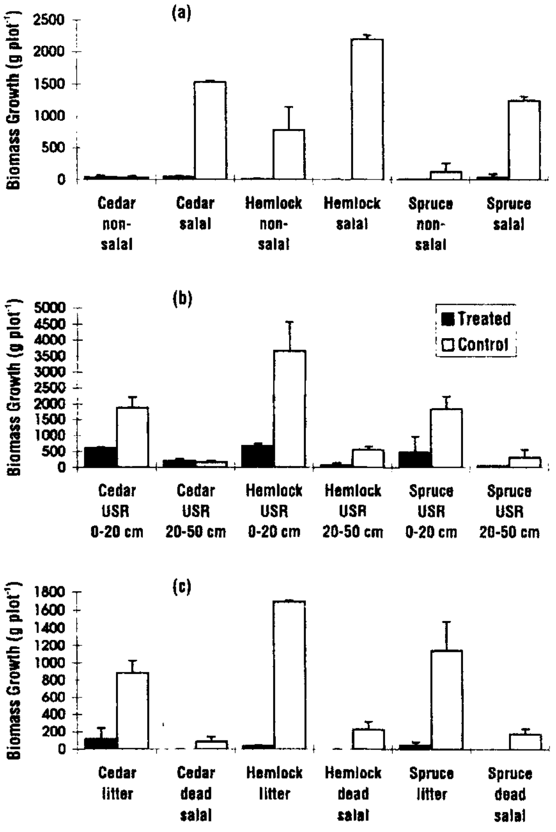

Fig. 5. Understory and dead salal and litter mass at the final harvesting. Vertical error bars represent standard deviations.

Interestingly, the below-ground biomass in the treated plots was very high (Fig. 5b) compared with what was on the above-ground which gave root/shoot ratios of 9.9, 98.5, and 10.8 for plots with red cedar, hemlock, and spruce, respectively, whereas the root/shoot ratios for the corresponding control plots were only 1.3, 1.4, and 1.6. This indicated that below-ground understory was quite persistent in surviving even after a prolonged period (6 years) of above-ground understory vegetation removal.

In a previously mentioned study on a similar site, above-ground salal biomass was 73% of total above-ground biomass 8 years after logging and burning (Messier and Kimmins, 1991). In our study, the above-ground salal biomass was 63%, 62% and 52% of the total above-ground biomass in the control plots planted to red cedar, hemlock and spruce, respectively, indicating that fertilization may have relatively improved the conifer seedling growth and had thus reduced the proportion of the above-ground salal biomass in the total above-ground biomass. Calculations showed that below-ground salal biomass was 91%, 71% and 79% of the total below-ground biomass for the respective control plots. The greater proportion of salal biomass in the total biomass below-ground than above-ground showed that the competition from salal for the limited resources is mainly from below-ground.

One of the consequences of uncurbed understory growth was the accumulation of litter mass in the control plots (Fig. 5c). The litter mass collected from the treated plots was primarily from the understory put back into the plots when it was clipped. Noticeable amounts of standing dead salal mass was also accumulated in the control plots, whilst there was none in the treated plots. The implication for this is that abundant understory growth will alter the resource allocation within the ecosystem and indirectly affect conifer growth, because nutrients immobilized in the litter and standing dead biomass will only become available through decomposition, which is a slow process (Fahey, 1983).

3.3. Tree biomass allocation

Although most of the traits of tree growth (e.g., height, diameter, and biomass in various fractions) were changed by the treatment, no statistically significant difference was found for the allocation of tree biomass among the various components, except for the hemlock 2-year branch and spruce < 0.25 cm roots, when biomass components were expressed as a percentage of the total tree biomass; nor were shoot/root ratios significantly different between treatments (Table 3). Therefore, our hypothesis proposed in the introduction is rejected based on these results. The results obtained here are different from those of Newton and Jolliffe (1993) (decrease in stem and branch and increase in foliar and bark mass proportion on increased density) and Nilsson and Albrektson (1993) (increased proportion of stem mass under high competitive stress).

When the competition is mainly for below-ground resources (nutrients), the resource depletion model of competition states that competition acts to reduce the relative growth rates of all individuals by the same proportion which results in an unchanged or lowered size inequality at higher densities after a given pe-

Table 3
Allocation (%) of biomass in various components of trees using total tree biomass as 100%

Treatment	1-year foliage	1-year branch	2-year foliage	2-year branch	3-year and up	Stump	Roots > 1 cm	Roots 0.25–1 cm	Roots < 0.25 cm	Shoot/root ratio
Cedar-T *	31.80a **	5.27a	5.23a	11.01a	33.00a	4.89a	5.02a	2.54a	1.24a	6.16a
Cedar-C	36.05a	5.59a	4.30a	10.45a	28.53a	6.36a	3.69a	3.53a	1.49a	5.71a
Hemlock-T	15.07a	5.00a	9.58a	9.64a	39.60a	6.09a	6.09a	5.38a	3.56a	3.74a
Hemlock-C	15.70a	6.45a	7.13b	8.48a	40.33a	6.86a	5.56a	6.42a	3.06a	3.47a
Spruce-T	18.94a	6.25a	5.95a	5.66a	35.12a	8.56a	11.24a	5.03a	3.24a	2.67a
Spruce-C	20.39a	9.43a	5.19a	6.45a	35.26a	7.41a	7.73a	6.05b	2.09a	3.20a

* T: treated; C: control. ** Same lowercase letters indicate no significant difference between treatment means within the same species of a component

riod of growth (Weiner and Thomas, 1986; Newton and Jolliffe, 1993). It would be reasonable to postulate that in order to have the size inequality unchanged or lowered at higher densities, the partitioning of dry matter in different components of a tree will be stable at different competition levels. If at higher densities the relative growth rates of all the individuals are not reduced by the same proportion, it would be more likely that plants will adopt different resource allocation strategies. In other words, when below-ground resources are the limiting factors, sometimes biomass allocation may be unchanged to arrive at proportional reductions in relative growth rate of various sized trees. In most reported cases biomass allocation strategies were somewhat altered by the competitive stresses imposed (Lieffers and Titus, 1989; Barclay et al., 1986; Munson and Timmer, 1990; Nilsson and Albrektson, 1993). In this study, the concurrent increases in height and root collar diameter in the treated plots, as was discussed earlier, also illustrated that the relative proportion of biomass allocation might be unchanged.

Table 3 indicated some statistically non-significant biomass partitioning for the three species: higher in current year foliar and branch components, lower in previous year foliar components (significant for hemlock), higher in the 0.25–1 cm roots (significant for spruce) in plots under salal competition than in plots without understory competition. Shoot/root ratios were also non-significantly lower in cedar and hemlock plots with salal. In the other components, the partitioning patterns were more irregular. The lower amount of biomass partitioned in the 2-year foliar component in plots with salal might be a result of greater transfer of nutrients to the current year components which resulted in lower photosynthetic efficiencies. Thus, another possibility is that the hypothesis is acceptable, but was falsely concealed by the fertilizer application in April 1991. The fertilization treatment had alleviated the nutrient shortage problem in the salal dominated plots in a short term, leading to non-significant differences in biomass allocation in different tree components, although biomass allocation was higher in the 1-year foliar, branch and 0.25–1 cm root components in the control plots than in the treated plots.

4. Conclusion

Plants with high competitive ability permit a high rate of acquisition of resources in productive, crowded vegetation. They have two important competitive characteristics (Grime, 1979): (i) the potential to produce a dense canopy of leaves and a large root surface area when growth condition is favorable; and (ii) the capacity to rapidly adjust morphogenetically both in the apportionment of photosynthate between root and shoot and in the size, morphology, and distribution of individual leaves and roots. One of our main study objects, salal, has all of these characteristics. It grows rapidly from extensive interconnected rhizomes, which persist for a long time even with the above-ground biomass eliminated (Bunnell, 1990; this study). It is capable of enhanced uptake of nutrients and water assisted by mycorrhizas. Salal competition poses considerable threat to the regeneration of coastal British Columbia forests.

It was evident from this study that salal competition reduces coniferous tree height and diameter growth and biomass accumulation. As is shown in this study, 6 years after planting, salal competition was still severely reducing tree growth. An extended study of the salal exclusion effect on tree growth is recommended to see when the growth rates of young coniferous trees in natural conditions (with salal competition) can catch up with that in the treated plots, if ever. No effective ways have been found yet to eliminate or control salal growth on an operational scale. Recently, Prescott et al. (1993) reported that repeated nitrogen fertilization to two salal dominated coastal Douglas-fir forests had reduced or completely eliminated above-ground salal growth. It would be interesting to conduct similar experiments on the salal dominated CH phase forests. If it works, there are two benefits to forest management: (a) salal competition could be reduced (at least to some extent) or even wiped out; and (b) tree nutrition and growth could be improved by repeated fertilization.

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