

The competitive role of *Gaultheria shallon* on planted western hemlock and western red cedar saplings on northern Vancouver Island

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Abstract

The presence of competing vegetation, particularly salal (*Gaultheria shallon* Pursh), was studied in relation to growth (measured as height and root collar diameter) of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red cedar (*Thuja plicata* Donn) saplings planted in cedar–hemlock (CH) and hemlock–amabilis fir (HA) phases of an ecosystem type on northern Vancouver Island in British Columbia, Canada. The leaf area indices (LAI) of several non-crop species were both negatively and positively correlated with cedar and hemlock height and root collar diameter, but the abundance of salal was mostly negatively correlated with conifer growth. On control CH, control HA, fertilized CH, and fertilized HA plots, salal LAI accounted for over 31%, 56%, 37%, and 31% respectively, of the variation in conifer growth. Scarification of the soil surface layers reduced the abundance of salal and it appeared to reduce the influence of salal on hemlock growth, perhaps because salal had only recently established on these sites. There was little evidence of a competitive effect of salal on cedar. However, fertilization and fertilization plus scarification significantly stimulated cedar growth, particularly when salal cover was sparse. Our results suggest that salal may compete with western hemlock, and to a lesser extent western red cedar, and that it may be an important cause of poor hemlock growth on CH cut-over sites.

Keywords: *Gaultheria shallon*; Salal; Hemlock; Cedar; Competition index

1. Introduction

Most of northern Vancouver Island in British Columbia, Canada, comprises the very wet maritime Coastal Western Hemlock biogeoclimatic subzone

(CWHvm) (Pojar et al., 1991). In the submontane variant of this subzone, the S1 ('salal-moss') ecosystem (Lewis, 1982) accounts for approximately 60% of the land area (Green et al., 1984), and is characterized by the presence of western red cedar (*Thuja plicata* Donn), western hemlock *Tsuga heterophylla* (Raf.) Sarg.), amabilis fir (*Abies amabilis* (Doubl.) Forbes), salal (*Gaultheria shallon* Pursh), and *Rhynchospora loreus* (Hedw.) Warnst.). Two phases

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Table 1
Layout of the experimental design of the SCHIRP site

| | | |
|---|----|---|
| (a) The design comprised 128 plots, with 64 trees per plot (Barker et al., 1991) | | |
| Site | 2 | (CH and HA) |
| Conifer | 2 | (western hemlock and western red cedar) |
| Planting density | 3 | (500, 1500, and 2500 trees ha ⁻¹) |
| Fertilization | 2 | (fertilized and unfertilized) |
| Replication | 4 | |
| Total | 96 | |
| (b) In addition to the above, scarified and scarified plus fertilized plots were established, but only on the highest planting density plots (2500 trees ha ⁻¹) | | |
| Site | 2 | (CH and HA) |
| Conifer | 2 | (western hemlock and western red cedar) |
| Planting density | 1 | (2500 trees ha ⁻¹) |
| Treatment | 2 | (scarified and fertilized plus scarified) |
| Replication | 4 | |
| Total | 32 | |

can be identified within the S1 ecosystem based on different stand histories, the cedar–hemlock phase (S1CH) and the hemlock–amabilis fir phase (S1HA) (Lewis, 1982), usually referred to as CH and HA, respectively. Typical forest stands on CH sites are dominated by old (i.e. over 200 years) western red cedar and western hemlock. These forests have an open canopy which may favor salal in the understory. Such forests are not affected by windthrow, and annual productivity is relatively low. In contrast, HA forest stands are younger (i.e. less than 100 years old) and are dominated by western hemlock and amabilis fir. These stands typically have a dense canopy and salal is only sparsely distributed on the forest floor. Annual productivity is high possibly due to repeated disturbance and soil mixing from windthrow.

After clearcutting, poor regeneration associated with slow growth and chlorosis of both planted and naturally regenerated conifer seedlings has been reported on CH sites (Weetman et al., 1989a). Salal is abundant in many parts of these cutovers and has been implicated as a possible cause of poor hemlock and cedar growth (Weetman et al., 1989b; Messier, 1991, 1993; deMontigny, 1992). In contrast, growth of planted and naturally regenerating conifer seedlings following clear-cutting and slashburning on HA sites is vigorous. Fireweed (*Epilobium angustifolium* L.) is abundant on HA sites, and salal does not form a dense ground cover.

Many studies have illustrated the competitive nature of salal on conifer saplings; however, competition has primarily been for water on sub-xeric sites (Long, 1977; Tan et al., 1978; Black et al., 1980; Vihaneck, 1985; Price et al., 1986; Fraser et al., 1993). Several authors have suggested that on CH sites salal has an inhibitory effect on conifer growth either by outcompeting saplings for soil resources (Weetman et al., 1989b; Messier, 1993), or through production of an allelopathic agent which inhibits mycorrhizal development, root development, or both (deMontigny, 1992). High productivity in HA sites has been suggested to be at least partly related to the dense regeneration of hemlock and fir which excludes salal, thereby eliminating competition and/or allelopathy. Furthermore, conifers associated with CH sites do not form dense stands and have an open canopy so salal can maintain a dense understory and

Table 2
The selected plots used in our experiment from the main SCHIRP study

| | | |
|------------------|----|---|
| Site | 2 | (CH and HA) |
| Conifer | 2 | (western hemlock and western red cedar) |
| Planting density | 1 | (2500 trees ha ⁻¹) |
| Treatment | 4 | (control, fertilized, scarified, fertilized plus scarified) |
| Replication | 4 | |
| Total | 64 | |

inhibit conifer seedling growth. Therefore, little ecological succession occurs on CH sites and these old cedar forests remain relatively stable.

The objectives of this study were to test the hypothesis that salal inhibits the growth of conifer saplings and to model competitive indices of the abundance of neighboring salal on the growth of planted 2-year-old western hemlock and western red cedar. We were also interested in determining how fertilization and scarification influenced the interactions between tree growth and the abundance and growth of salal.

2. Materials and methods

2.1. Study area

The study was conducted on northern Vancouver Island in the submontane variant of the CWHvm biogeoclimatic subzone (Lewis, 1982) approximately

20 km north of Port McNeill, B.C. (50°60'N, 127°35'W; 100 m elevation). The study site is part of Tree Farm License 25 Block 4 operated by Western Forest Products Ltd. Summers are typically cool and moist, and winters mild and wet as indicated by the following climatic data (average values from 1966 to 1992) collected at the Port Hardy Airport weather station located about 20 km north of the study area and 50 m above sea level. Mean annual rainfall is about 1700 mm, 65% of which falls between October and February. At least 50 mm of rain falls monthly from March to September, indicating that drought is absent from the deep mineral soils in all but exceptional years (Lewis, 1982). Mean daily temperature ranges from 13.7°C in July and August to 3.0°C in January and February. Owing to the frequent occurrence of fog in the summer and frontal clouds in the winter, exposure to direct sunlight is relatively low, ranging from an average of 6.4 h day⁻¹ in July to 1.5 h day⁻¹ in December. Soils have been described in detail by Germain (1985).

Table 3

List of naturally occurring species recorded within the study area on the CH and HA sites

| | Scientific name and authority | Abbrev. | Common name |
|-----|---|---------|------------------------|
| 1. | <i>Anaphalis margaritacea</i> (L.) B. & H. | Am | Pearly everlasting |
| 2. | <i>Blechnum spicant</i> (L.) Roth. | Bs | Deer fern |
| 3. | Bryophytes | B | |
| 4. | <i>Cornus canadensis</i> L. | Cc | Bunchberry |
| 5. | <i>Dryopteris expansa</i> (Presl) Fraser-Jenkins & Jeremy | De | Spiny wood fern |
| 6. | <i>Epilobium angustifolium</i> L. | Ea | Fireweed |
| 7. | <i>Equisetum sylvaticum</i> L. | Es | Horsetail |
| 8. | <i>Gaultheria shallon</i> Pursh | Gs | Salal |
| 9. | <i>Hypochoeris radicata</i> L. | Hr | Hairy cat's ear |
| 10. | <i>Lysichitum americanum</i> Hulten & St. John | La | Skunk cabbage |
| 11. | <i>Menaieseae ferruginea</i> Smith. | Mf | False azalea |
| 12. | <i>Mycelis muralis</i> (L.) Dumort. | Mm | Wall lettuce |
| 13. | <i>Pinus contorta</i> Dougl. | Pc | Lodgepole pine |
| 14. | Gramineae | G | Grass family |
| 15. | <i>Pteridium aquilinum</i> (L.) Kuhn. | Pa | Bracken fern |
| 16. | <i>Ribes laxiflorum</i> Pursh | Rl | Trailing black currant |
| 17. | <i>Rubus spectabilis</i> Pursh | Rs | Salmonberry |
| 18. | <i>Sambucus racemosa</i> L. | Sr | Elderberry |
| 19. | <i>Salix sitchensis</i> Sanson | Ss | Sitka willow |
| 20. | <i>Thuja plicata</i> Donn. | Tp | Western red cedar |
| 21. | <i>Tsuga heterophylla</i> (Raf.) Sarg. | Th | Western hemlock |
| 22. | <i>Vaccinium ovalifolium</i> Smith | V | Oval leaved blueberry |
| 23. | <i>Vaccinium parvifolium</i> Smith | V | Red huckleberry |

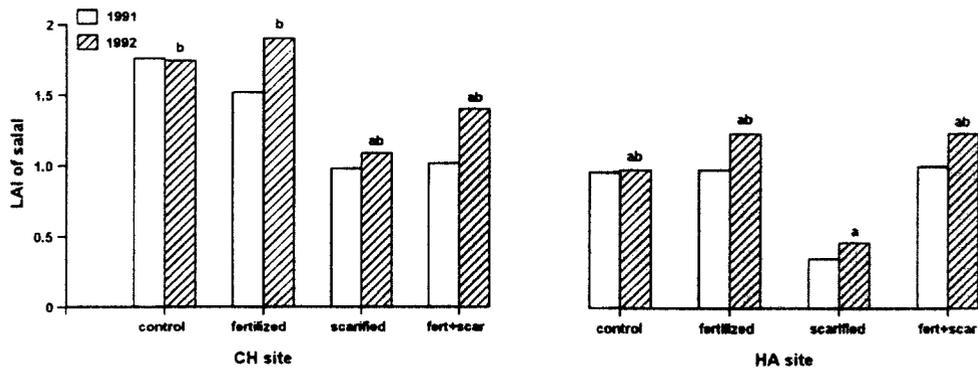
2.2. Field manipulations

The site was clear-cut logged in 1986, broadcast burned during the spring of 1987, and planted with western hemlock and western red cedar container grown, 1-year-old seedlings (PSB415), in 1988. The study site, which was established by Western Forest Products Ltd., comprises 128 plots with 64 seedlings per plot and is 97 ha. Western hemlock and western red cedar were not planted together; each plot is a single species stand. Table 1 outlines the layout of the experimental design. This experiment was designed to evaluate the effect of planting density, fertilization, site scarification, and some of their interactions on conifer seedling performance on CH and HA clear-cuts. The fertilization of the site was

done by adding 60 g of Nutriccoat controlled release fertilizer (Type 360: 16-10-10) to planting holes at the time of planting. Scarification was done in the spring of 1987 by a backhoe (215 Cat Excavator) with a three-tined rake attachment to remove salal rhizomes and to simulate windthrow by mixing the organic forest floor and the mineral soil.

Our study was initiated in 1990 when the trees had been in the field for 2 years, and indigenous vegetation had 3 years to develop after the site was burned. We restricted this study to the 64 plots with the highest planting density (2500 trees ha⁻¹) because only these plots were scarified (Table 2). To evaluate the influence of salal abundance on conifer performance, four conifers in each of the 64 plots were selected, each surrounded by approximately 0,

a.



b.

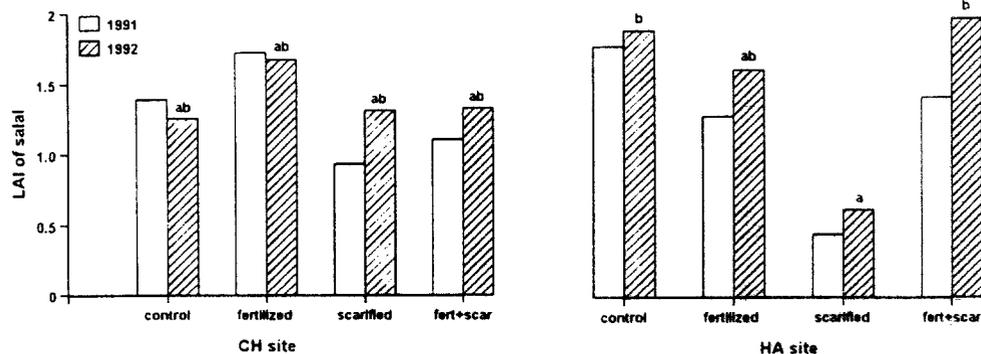


Fig. 1. Site \times treatment effects on salal LAI (number of leaf contacts per 50 points m⁻²), where western hemlock (a) and western red cedar (b) was planted, using three-way ANOVA. Tukey's Honestly Significant Difference test was applied to separate treatment means for 1992 data. Within a treatment, bars sharing the same letter are not significantly different ($P > 0.05$).

33, 66 and 100% salal cover. This resulted in the selection of a total of 255 trees (only three suitable hemlocks could be identified at one of the HA plots).

2.3. Data collection

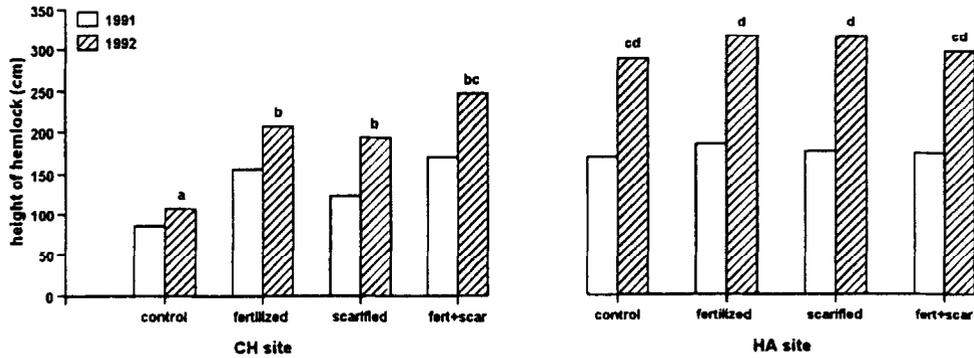
Around each selected conifer, a 1 m × 1 m quadrat was centred for measurement of the leaf area index (LAI) (i.e. leaf area per unit of land area; Kershaw and Looney, 1985) of neighboring vegetation during the summers of 1991 and 1992. The 1 m × 1 m quadrat frame was a grid with five lines on one side and ten lines on the adjacent side. For each of the 50 intersections of the lines, a plumb line was dropped. All leaves that were touched by the plumb line as it

descended to the ground were recorded (Table 3). The mean LAI was calculated for each species in each quadrat; therefore, the ‘unit’ of LAI presented in this paper is the number of leaf contacts per 50 points per square meter. Height and root collar diameter of the planted conifers were measured in 1990 and 1992 by Western Forest Products when trees had been in the field 2 years and 4 years, respectively.

2.4. Statistical analysis

Three-way ANOVAs were applied to salal leaf area index, conifer height and root collar diameter measured in 1992. The independent variables were site (CH and HA), fertilization (present and absent),

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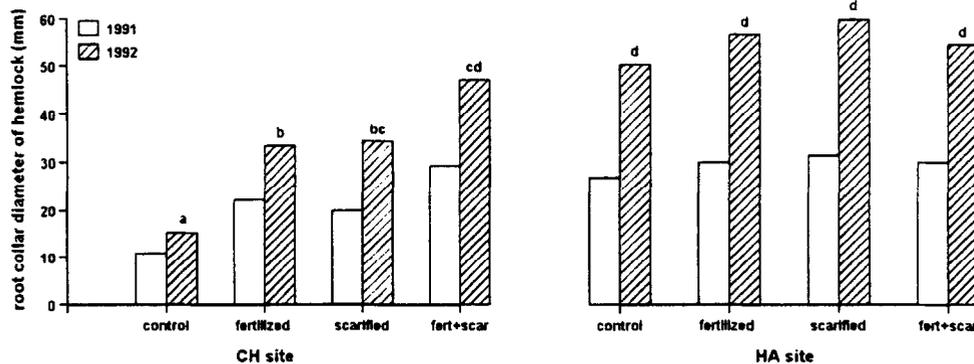


Fig. 2. Site × treatment effects on western hemlock height (a) and root collar diameter (b) using three-way ANOVA. Tukey’s Honestly Significant Difference test was applied to separate treatment means for 1992 data. Within a treatment, bars sharing the same letter are not significantly different ($P > 0.05$).

and scarification (present and absent). Data for western hemlock and western red cedar were analyzed separately using SYSTAT (Wilkinson, 1990). If data were heteroscedastic with a significance of $P < 0.1$ (Bartlett's test), logarithmic, arcsine, or square root transformations were done to normalize the variance. Tukey's Honestly Significant Difference test was used to separate treatment means.

Competition indices were calculated using non-linear regression models on the 1990–1992 2-year

growth increment of hemlock and cedar height and root collar diameter against salal LAI in 1991.

Stepwise multiple linear regression was applied to leaf area indices of all neighboring vegetation to determine which species were correlated with height and root collar diameter of western hemlock and western red cedar. LAI data from 1992 were used to determine the variation in conifer performance after 4 years in the field. Data for multiple linear regression models were tested for normality, homogeneity

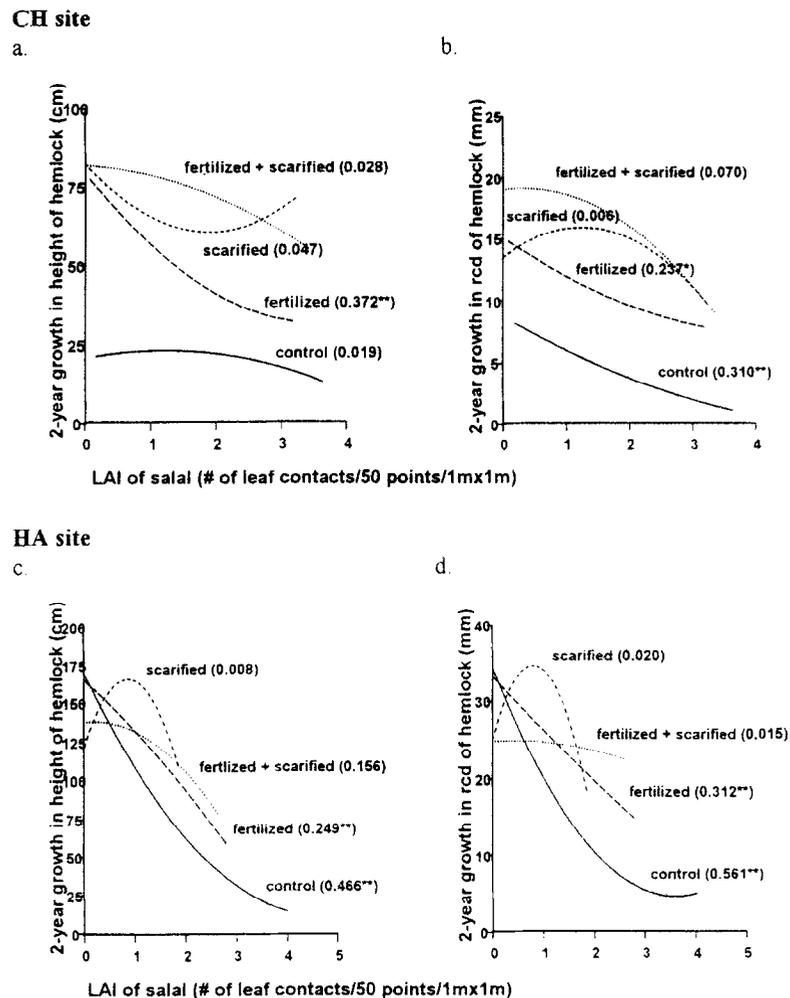


Fig. 3. The relationship between salal LAI and the 2 year growth increment (2–4 years after planting) of western hemlock height and root collar diameter (rcd) on CH ((a) and (b)) and on HA ((c) and (d)) sites within four treatments (control, fertilized, scarified, and fertilized plus scarified). Corrected R^2 values are presented in parentheses; * $P < 0.1$, ** $P < 0.05$.

of variance, and independence of errors before proceeding with analyses. No transformations were necessary.

3. Results

3.1. Treatment and site effects on *Gaultheria shallon*

Salal LAI in the western hemlock plots was greatest in control and fertilized plots on CH sites, i.e. scarification reduced LAI (Fig. 1(a)). Comparing the same treatment between sites, all treatments except fertilized plus scarified had a greater LAI of salal on CH sites. Scarified HA sites had the lowest salal LAI. The greatest increase in the growth of salal between 1991 and 1992 occurred on CH sites that were fertilized, whereas the LAI of salal barely increased between 1991 and 1992 in the control plots on both CH and HA sites.

The LAI of salal in the western red cedar plots (Fig. 1(b)) was generally higher than the LAI of salal in the western hemlock plots. Similar to the LAI of salal on western hemlock plots, there was little

growth of salal on either of the control plots. In contrast to the western hemlock plots, the LAI of salal on the western red cedar plots varied little between sites. Scarified HA sites had the lowest salal LAI.

3.2. Treatment and site effects and the correlation of the LAI of neighboring non-crop vegetation on western hemlock saplings

Hemlock height and root collar diameter showed similar treatment–response patterns (Fig. 2). Hemlock growing on control CH sites were significantly smaller than those on all other site × treatment combinations. Hemlock on CH sites were tallest on the fertilized plus scarified plots and attained intermediate heights on fertilized plots and scarified plots. This trend was not detected on HA sites. Other site differences were also evident such as those observed in height and root collar diameter of hemlock on fertilized and scarified sites. The greatest increases in height and root collar diameter occurred on the HA sites. There was very little growth in height or root collar diameter on control plots on CH sites.

Table 4

Summary of R^2 and P -values from multiple linear regression models of 4-year-old western hemlock against the LAI of neighboring vegetation in 1992. Underlined species have a negative correlation with the dependent variable

| Site | Treatment | Dependent variable ^a | Independent variables ^b | Sample size | R^2 | P -value |
|------|---------------|---------------------------------|--|-------------|-------|------------|
| CH | Control | Height | Mf, V, <u>Hr</u> , Mm | 16 | 0.706 | 0.006 |
| | | rcd | Mf, V, <u>Hr</u> , <u>Gs</u> , Mm | 16 | 0.823 | 0.002 |
| | Fertilization | Height | Mm, <u>Gs</u> , Tp | 16 | 0.537 | 0.023 |
| | | rcd | <u>Gs</u> , <u>V</u> , Ea | 16 | 0.742 | 0.001 |
| | Scarification | Height | <u>Cc</u> , <u>V</u> , Hr | 16 | 0.305 | 0.210 |
| | | rcd | <u>Bs</u> , <u>Cc</u> , V | 16 | 0.485 | 0.041 |
| | Fert. + scar. | Height | <u>V</u> , Mm | 16 | 0.252 | 0.152 |
| | | rcd | <u>V</u> , Mm, <u>Cc</u> , B | 16 | 0.661 | 0.012 |
| HA | Control | Height | <u>Gs</u> , <u>Rs</u> , <u>Bs</u> , <u>V</u> , <u>Sr</u> | 16 | 0.852 | 0.001 |
| | | rcd | <u>Gs</u> , <u>V</u> | 16 | 0.641 | 0.001 |
| | Fertilization | Height | Mm, <u>Bs</u> , De, Hr | 16 | 0.680 | 0.009 |
| | | rcd | Mm, Hr, <u>Ea</u> , <u>Bs</u> , De, Rs | 16 | 0.802 | 0.009 |
| | Scarification | Height | <u>B</u> , <u>Rs</u> , <u>Gs</u> | 15 | 0.519 | 0.039 |
| | | rcd | <u>B</u> | 15 | 0.458 | 0.006 |
| | Fert. + scar. | Height | R1 | 16 | 0.122 | 0.185 |
| | | rcd | <u>Rs</u> | 16 | 0.117 | 0.195 |

^a rcd, root collar diameter.

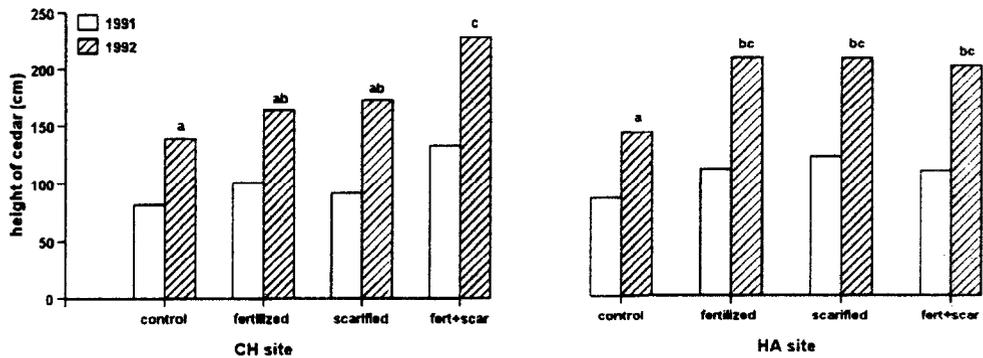
^b Listed in decreasing order of significance to the model. Abbreviations are listed in Table 3.

The non-linear regression models of the 2 year growth increment between 1990 and 1992 of the height and root collar diameter of western hemlock saplings showed similar trends (Fig. 3). In addition, a strong treatment effect was detected on CH sites. The abundance of salal appeared to have a greater influence on the root collar diameter of hemlock than on its height. The 2 year height and root collar diameter increments of hemlock growing on scarified plots showed little difference with increasing abundance of salal. Treatment effects were also detected in the 2 year growth increment of hemlock on HA sites, but they were not as pronounced as those on CH sites. However, the 2 year growth increment in hemlock height and root collar diameter on HA control plots showed the greatest response to increasing salal leaf area index of all conifer species \times site

\times treatment combinations. The 2 year increments in height and root collar diameter were approximately 175 cm and 35 mm, respectively, when salal was absent, but little growth in either variable occurred when salal was present with a LAI of over 3. Hemlock growing on fertilized HA sites also showed a significant decrease in 2 year increments with increasing abundance of salal, but 2 year hemlock growth rates on scarified and fertilized plus scarified plots were unaffected by salal.

Variation in hemlock height and root collar diameter was correlated, sometimes positive and sometimes negative, with the LAI of several neighboring species primarily on CH and HA control sites (Table 4), which suggests that fertilization and scarification reduced the influence of non-crop vegetation on hemlock growth. Of all neighboring species, salal

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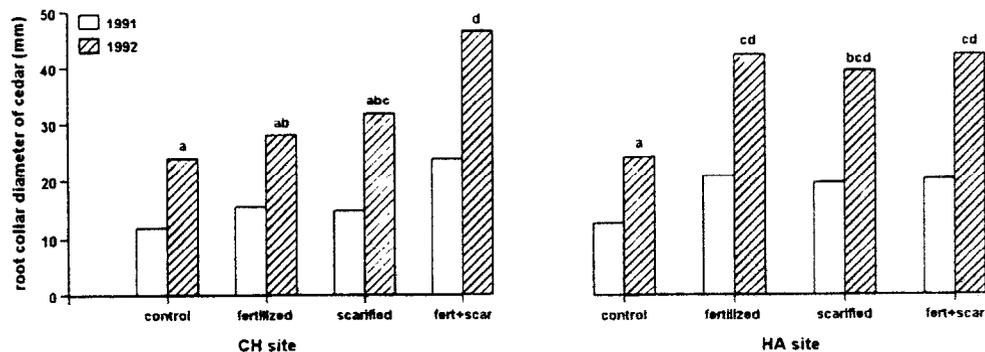


Fig. 4. Site \times treatment effects on western red cedar height (a) and root collar diameter (b) using three-way ANOVA. Tukey's Honestly Significant Difference test was applied to separate treatment means for 1992 data. Within a treatment, bars sharing the same letter are not significantly different ($P > 0.05$).

showed the most consistent negative correlation with hemlock growth, especially on control and fertilized CH sites, and on control HA sites.

3.3. Treatment and site effects and the correlation of the LAI of neighboring non-crop vegetation on western red cedar saplings

Cedar height and root collar diameter on fertilized plus scarified CH sites were generally greater than those associated with all other site × treatment combinations (Fig. 4). Fertilization plus scarification in-

creased height and root collar diameter of cedar on CH sites, but there was little difference in cedar size between the fertilized and scarified plots on the HA sites. There was no difference between CH and HA sites in height or root collar diameter of cedars growing on control plots. The 2 year growth increment of cedar height and root collar diameter was greatest on fertilized plus scarified CH sites and fertilized, scarified, and fertilized plus scarified HA sites.

There were few significant effects and no clear relationship between cedar growth rate between 1990

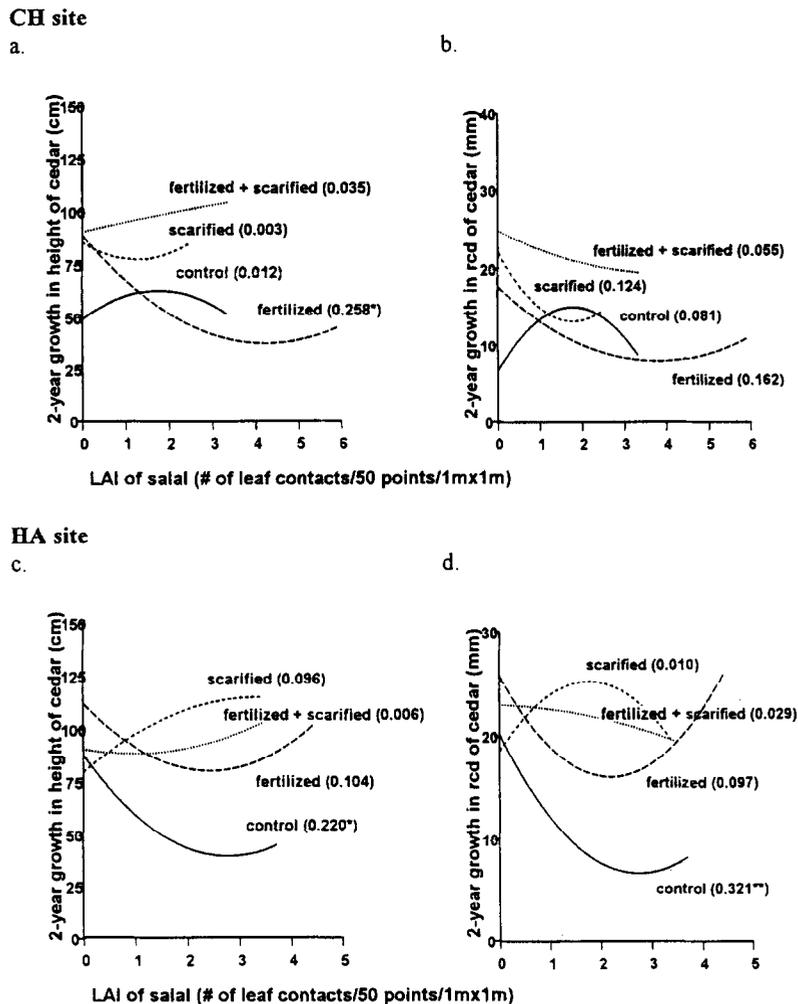


Fig. 5. The relationship between salal LAI and the 2 year growth increment (2–4 years after planting) of western red cedar height and root collar diameter (rcd) on CH ((a) and (b)) and on HA ((c) and (d)) sites within four treatments (control, fertilized, scarified, and fertilized plus scarified). Corrected R² values are presented in parentheses; * P < 0.1, ** P < 0.05.

Table 5

Summary of R^2 and P -values from multiple linear regression models of 4-year-old western red cedar against the LAI of neighboring vegetation in 1992. Underlined species have a negative correlation with the dependent variable

| Site | Treatment | Dependent variable ^a | Independent variables ^b | Sample size | R^2 | P -value |
|------|---------------|---------------------------------|---|-------------|-------|------------|
| CH | Control | Height | Ea, <u>Mm</u> , G, Hr, Cc, <u>Pa</u> , Gs | 16 | 0.720 | 0.077 |
| | | rcd | <u>G</u> , <u>Rs</u> , Cc | 16 | 0.511 | 0.031 |
| | Fertilization | Height | Mm, <u>Rs</u> , B, <u>Rl</u> , Hr | 16 | 0.833 | 0.001 |
| | | rcd | B, <u>Rs</u> , Mm | 16 | 0.700 | 0.002 |
| | Scarification | Height | <u>Rs</u> , <u>Rl</u> | 16 | 0.188 | 0.258 |
| | | rcd | <u>Rs</u> | 16 | 0.472 | 0.003 |
| | Fert. + scar. | Height | <u>B</u> | 16 | 0.332 | 0.037 |
| | | rcd | <u>Th</u> , <u>B</u> | 16 | 0.397 | 0.037 |
| HA | Control | Height | De, <u>Sr</u> , V | 16 | 0.679 | 0.003 |
| | | rcd | <u>Rs</u> , <u>Pa</u> , <u>G</u> | 16 | 0.713 | 0.001 |
| | Fertilization | Height | <u>Rl</u> , Ea, <u>Th</u> | 16 | 0.621 | 0.007 |
| | | rcd | <u>Rl</u> , <u>Th</u> , <u>Pa</u> | 16 | 0.738 | 0.001 |
| | Scarification | Height | <u>Es</u> , <u>V</u> , <u>Gs</u> , Ea, Am, De, B, <u>Bs</u> , Hr | 16 | 0.961 | 0.001 |
| | | rcd | <u>Ea</u> , <u>Gs</u> , <u>Es</u> , Hr, <u>V</u> , B, De, Am, <u>Bs</u> , <u>Sr</u> , <u>Rs</u> | 16 | 0.989 | 0.002 |
| | Fert. + scar. | Height | <u>Bs</u> , Ea, <u>Tp</u> , Hr, <u>Rl</u> | 16 | 0.710 | 0.016 |
| | | rcd | Ea, Hr, <u>Tp</u> , <u>Bs</u> | 16 | 0.729 | 0.004 |

^a rcd, root collar diameter.

^b Listed in decreasing order of significance to the model. Abbreviations are listed in Table 3.

and 1992 and salal LAI (Fig. 5). Cedar height and root collar diameter increments on control and fertilized plus scarified CH plots increased with increasing abundance of salal. The 2 year cedar growth rates were highest on fertilized plus scarified plots, but the greatest influence of salal abundance was detected on fertilized plots. When salal was absent, 2 year height and root collar diameter increments were approximately 90 cm, and 18 mm, respectively, while at a salal LAI of over 3, respective increments were reduced to 50 cm and 10 mm. Cedar grown on scarified CH plots was the least sensitive to salal abundance. On control HA sites, 2 year height and root collar diameter increments showed similar trends to cedar growing on fertilized CH sites. Cedar growing on treated plots within HA sites showed no influence to salal abundance.

The abundance of neighboring non-crop vegetation was significantly correlated, sometimes positive and sometimes negative, with the variation in height and root collar diameter of western red cedar saplings in most of the multiple linear regression models (Table 5). However, as observed with hemlock, cedar height and root collar diameter were best correlated with the LAI of neighboring species on control sites.

On control and scarified CH sites, and scarified HA sites, cedar growth showed a significant positive correlation with salal abundance.

4. Discussion

The primary objective of this study was to examine the influence of neighboring plant species, especially salal, on growth of western hemlock and western red cedar on CH and HA sites. Additional data on the microhabitat of the hemlock and cedar trees (soil nitrogen, soil phosphorus, soil carbon, soil moisture and soil coarse content) were not significantly correlated between CH and HA sites or treated plots; furthermore, they were not correlated with conifer performance (Fraser 1993). Therefore, abiotic factors will not be considered further. It was of particular interest to determine if our analyses provided evidence which supported the hypothesis that the presence of salal caused the poor conifer growth on CH sites. As observed previously by Bunnell (1990), we found that western hemlock and western red cedar responded differently to the abundance of

neighboring salal, as well as to fertilization and scarification treatments.

4.1. Western hemlock

To establish that salal is the primary cause of poor hemlock sapling growth on CH sites, three conditions must be satisfied. First, we must verify that conifer sapling performance is negatively correlated with the abundance of competing vegetation, particularly salal, on control sites. This condition was met by the western hemlock data. Hemlock height, and in particular, root collar diameter, showed a significant negative correlation with the LAI of neighboring vegetation on control CH and HA sites (Fig. 3 and Table 4), but the correlation was strongest on HA sites. Of all neighboring species, salal occurred in the multiple linear regression models most often (Table 4).

Second, if the presence of salal inhibits hemlock sapling growth, then treatments that reduce its abundance should result in enhanced conifer growth. Of the three treatments evaluated, site scarification had the greatest effect on salal abundance; salal LAI decreased by over 50% at both site types probably due to physical removal of rhizomes. The observation that growth of western hemlock saplings was enhanced on scarified CH sites compared to the control plots, but not HA sites (Figs. 3 and 4), is consistent with the salal hypothesis.

Third, if salal is a significant competitor for soil nutrients on CH sites, then fertilization and fertilization plus scarification treatments should also enhance hemlock growth. While these treatments had little effect on salal abundance (Fig. 1), western hemlock growth was enhanced significantly (Figs. 3 and 4). On control HA sites, growth of western hemlock was vigorous and soil treatment had no effect. However, the abundance of salal was negatively correlated to hemlock growth on fertilized CH and HA sites (Fig. 5), indicating that the level of fertilization used in this trial was not high enough to overcome the competitive influence of salal. Because soil water, carbon, and nutrient content were generally similar between sites and treatments, except for reduced phosphorus in scarified treatments (Fraser, 1993), these data support the hypothesis that salal contributes to poor hemlock growth on CH sites more

than abiotic factors owing to competition for nutrients.

4.2. Western red cedar

In contrast to the results with western hemlock, analyses of the western red cedar growth data resulted in little support for the salal hypothesis. The abundance of neighboring vegetation, including salal, was correlated significantly with the growth measurements of cedar on control CH sites, but correlations were positive (Table 5). On control HA sites, the root collar diameter increment between 1990 and 1992 was significantly negatively correlated with salal LAI (Fig. 5). However, salal was either not present in the multiple linear regression models or was positively correlated with cedar growth at most other HA sites. Therefore, the results for cedar do not support the salal hypothesis. Furthermore, scarification and fertilization plus scarification treatments enhanced cedar growth on both site types, but the abundance of salal showed a corresponding reduction only on HA sites. Bunnell (1990) also demonstrated that hemlock was more sensitive than cedar to the presence of salal.

If salal competes significantly for nutrients, then the conifer which is able to tolerate lower levels of nutrients would suffer the least in its presence (Tilman, 1988). Judging from our results, it would seem that cedar is able to tolerate resource depletion by salal better than hemlock. However, Krajina et al. (1982) have shown that western hemlock performs better than other conifers, including western red cedar, under conditions of nutrient deficiency. This apparent contradiction in comparison with our data may be explained if it is assumed that hemlock is more sensitive to any possible allelopathic effects salal may possess. Another explanation may be that there is a difference in the efficiency of the mycorrhizae associated with hemlock and cedar growing in CH and HA sites. Further studies are needed to determine why hemlock is more sensitive than cedar to the presence of salal.

4.3. Gaultheria shallon

To understand the role of salal on conifer plantations on northern Vancouver Island, it is essential to

consider the life history characteristics of salal. It is apparent from this study, and others (Bunnell, 1990; Messier and Kimmins, 1991) that salal can quickly colonize freshly logged sites and expand rapidly. Our study shows that scarification significantly reduced the abundance of salal even after 4 years. However, the growth of salal on CH sites between the fourth and the fifth year after the scarification treatment was quite high. If such growth continued, salal may become progressively more competitive with conifer saplings. On the other hand, this may not be a serious problem because the continued growth of the conifers should eventually shade out salal (Messier, 1992).

In conclusion, our results suggest that salal is a significant competitor with western hemlock, but not with western red cedar. Furthermore, there is evidence to show that salal may be an important cause of poor hemlock growth on CH cut-over sites. On control CH, control HA, fertilized CH, and fertilized HA plots, salal leaf area index accounted for over 31%, 56%, 37%, and 31% respectively, of the variation in hemlock growth. This shows that although competition between salal and hemlock appears to be strongest on CH sites (Messier, 1993), when salal is abundant on HA sites competition is evident. The comparative lack of salal on HA sites, combined with soils higher in nutrients, causes trees to grow better on HA sites. Scarification reduced the abundance of salal, thereby reducing the influence of salal on hemlock, perhaps because salal had only recently established on scarified sites. There was little evidence of a competitive effect of salal with cedar; however, fertilization and fertilization plus scarification stimulated cedar growth significantly, particularly when salal cover was sparse (i.e. LAI < 1). From a management perspective, fertilization in addition to site scarification would appear to be the best ameliorative treatment of hemlock and cedar plantations on CH cutovers.

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References

- Barker, J.E., Joyce, S., Bavis, P. and Dumont, B., 1991. I SCHIRP establishment trial. In: SCHIRP Newsletter, June 1991.
- Black, T.A., Tan, C.S. and Nnyamah, J.U., 1980. Transpiration rate of Douglas-fir trees in thinned and unthinned stands. *Can. J. Soil Sci.*, 60: 625–631.
- Bunnell, F.L., 1990. Reproduction of salal (*Gaultheria shallon*) under forest canopy. *Can. J. For. Res.*, 20: 91–100.
- DeMontigny, L.E., 1992. Evidence for allelopathy by salal (*Gaultheria shallon* Pursh) in conifer plantations on northern Vancouver Island. Ph.D. Thesis, University of British Columbia, Vancouver.
- Fraser, L.H., 1993. The influence of salal on planted hemlock and cedar saplings on northern Vancouver Island. M.Sc. Thesis, University of British Columbia, Vancouver.
- Fraser, L.H., Turkington, R. and Chanway, C.P., 1993. The biology of Canadian weeds. 101. *Gaultheria shallon* Pursh. *Can. J. Plant Sci.*, 73: 1233–1247.
- Germain, A., 1985. Fertilization of stagnated spruce plantations on northern Vancouver Island. M.Sc. Thesis, University of British Columbia, Vancouver.
- Green, R.N., Courtin, P.J., Klinka, K., Slaco, R.J. and Ray, C.A., 1984. Site diagnosis, tree species selection, and slashburning guidelines for the Vancouver Forest Region. Land Management Handbook 8. Ministry of Forests, Victoria, BC.
- Kershaw, K.A. and Looney, J.H.H., 1985. Quantitative and Dynamic Plant Ecology, 3rd edn. Edward Arnold, Baltimore, MD.
- Krajina, V.J., Klinka, K. and Worrall, J., 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. University of British Columbia Press, Vancouver.
- Lewis, T., 1982. Ecosystems of the Port McNeill block 4 of Tree Farm License 25. Int. Rep., Western Forest Products Ltd., Vancouver, BC.
- Long, J.N., 1977. Trends in plant species diversity associated with development in a series of *Pseudotsuga menziesii* / *Gaultheria shallon* stands. *Northwest Sci.*, 51: 119–130.
- Messier, C., 1991. Factors limiting early conifer growth in salal-dominated cutovers on northern Vancouver Island, British Columbia. Ph.D. Thesis, University of British Columbia, Vancouver, BC.
- Messier, C., 1992. Effects of neutral shade and growing media on growth, biomass allocation, and competitive ability of *Gaultheria shallon*. *Can. J. Bot.*, 70: 2271–2276.
- Messier, C., 1993. Factors limiting early growth of western-red cedar, western hemlock and Sitka spruce seedlings on erica-

- ceous-dominated clearcut sites in coastal British Columbia. *For. Ecol. Manage.*, 60(3–4): 181–206.
- Messier, C. and Kimmins, J.P., 1991. Above- and below-ground vegetation recovery in recently clearcut and burned sites dominated by *Gaultheria shallon* in coastal British Columbia. *For. Ecol. Manage.*, 46: 275–294.
- Pojar, J., Klinka, K. and Demarchi, D.A., 1991. Coastal western hemlock zone. In: D. Meidinger and J. Pojar (Editors), *Ecosystems of British Columbia*. Ministry of Forests, Victoria, BC, pp. 95–111.
- Price, J., Black, T.A. and Kelliher, F.M., 1986. Effects of salal understory removal on photosynthetic rate and stomatal conductance of young Douglas-fir trees. *Can. J. For. Res.*, 16: 90–97.
- Tan, C.S., Black, T.A. and Nnyamah, J.U., 1978. A simple diffusion model of transportation applied to a thinned Douglas-fir stand. *Ecology*, 59: 1221–1229.
- Tilman, D., 1988. Plant strategies and the dynamics and structure of plant communities. *Monographs in Population Biology* No. 26. Princeton University Press, NJ.
- Vihaneck, R.E., 1985. The effects of slashburning on the growth and nutrition of young Douglas-fir plantations in some dry, salal dominated ecosystems. M.Sc. Thesis, University of British Columbia, Vancouver.
- Weetman, G.F., Fournier, R., Barker, J., Schnorbus-Panozzo, E. and Germain, A., 1989a. Foliar analysis and response of fertilized chlorotic Sitka spruce plantations on salal-dominated cedar–hemlock cutovers on Vancouver Island. *Can. J. For. Res.*, 12: 1501–1511.
- Weetman, G.F., Fournier, R., Barker, J. and Schnorbus-Panozzo, E., 1989b. Foliar analysis and response of fertilized chlorotic western hemlock and western red cedar reproduction on salal-dominated cedar–hemlock cutovers on Vancouver Island. *Can. J. For. Res.*, 12: 1512–1520.
- Wilkinson, L., 1990. SYSTAT: The System for Statistics. Evanston, IL.