

**THE INFLUENCE OF SALAL  
ON PLANTED HEMLOCK AND CEDAR SAPLINGS  
ON NORTHERN VANCOUVER ISLAND**

by

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## **ABSTRACT**

Through correlation analyses between 2- and 4-year-old conifer performance (western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red cedar (*Thuja plicata* Donn ex D. Don)) and salal (*Gaultheria shallon* Pursh) leaf area index, and the effect of salal leaf area index on the 2-year growth increment of western red cedar and western hemlock, this study determines the influence of salal on poorly growing western red cedar and western hemlock plantations growing on clear-cut and burned old-growth western red cedar and western hemlock stands in the Coastal Western Hemlock biogeoclimatic zone. This study was set up on a pre-existing experimental site involving 8 site x treatment combinations: 2 sites (cedar-hemlock and hemlock-fir) and 4 treatments (control, fertilized, scarified, and fertilized plus scarified).

It is shown that increasing salal leaf area index reduces the growth of western hemlock more than western red cedar. When growing with western hemlock, it is inferred that salal is strongly competitive in control plots on CH sites, fertilized plots on CH sites, control plots on HA sites, and fertilized plots on HA sites. When growing with cedar, it is inferred that salal is weakly competitive on fertilized plots on CH sites, and control plots on HA sites. However, the negative influence of salal on western red cedar only occurred on 2-year-old trees, not 4-year-old trees, suggesting that the influence is waning. For hemlock, the opposite occurred. It is concluded that scarification is the best way to reduce the influence of salal on western hemlock and western red cedar.

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## INTRODUCTION

On northern Vancouver Island in the submontane variant of the CWHvm biogeoclimatic subzone (Green *et al.* 1984), poor regeneration, with associated slow growth and chlorosis has been reported in clear-cuts of western red cedar (*Thuja plicata* Conn ex D. Don) - western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forests (Weetman *et al.* 1989a). The complexity of the observed phenomena lead a group of scientists to adopt an integrated ecosystem-level approach to the problem. In 1985, the Salal-Cedar-Hemlock-Integrated-Research-Program was formed, or more simply the acronym SCHIRP. SCHIRP now involves many investigators from diverse fields including forestry, soil sciences and botany.

Salal (*Gaultheria shallon* Pursh) is abundant in many parts of these cutovers and has been shown to slow the growth of hemlock and cedar saplings (Weetman *et al.* 1989b; Messier 1991; deMontigny 1992). However, it is not known to what extent salal directly contributes to the poor plantation performance.

Competition among plants has been studied intensively over the past century because of its potential for influencing patterns of distribution and abundance. However, many papers that contend to observe competition have been shown by Connell (1983), Schoener (1983) and Underwood (1986) to be poorly designed and inconclusive. Furthermore, Goldberg and Barton (1992) observed that although many studies have shown that competition is happening, the majority do not show whether it has any major ecological and evolutionary consequence in nature. It is necessary, therefore, to conduct preliminary experiments in order to generate hypotheses which might predict the structure of plant communities before designing specific competition trials. My thesis examines the competitive influence of neighbouring non-crop species, particularly salal, on planted conifers. In order to generate hypotheses about the performance of planted conifers, a range of biotic and abiotic factors were measured.

## DESCRIPTION OF ECOSYSTEM

The large majority of northern Vancouver Island comprises the very-wet maritime Coastal Western Hemlock biogeoclimatic subzone (CHWvm), which is characterized by the species association of *Tsuga heterophylla*, *Thuja plicata*, *Abies amabilis*, *Gaultheria shallon*, *Rhytidiadelphus loreus*, and by a mean annual precipitation of 2787 mm (Pojar et al. 1991). Out of an approximate area of 32000 ha, Lewis (1982) has identified numerous ecosystems within the CWHvm biogeoclimatic subzone. The dominant ecosystem, occupying approximately 60% of the zone, Lewis termed the S1 ("salal-moss") ecosystem association: *Thuja plicata* - *Tsuga heterophylla* - *Abies amabilis* - *Gaultheria shallon* - *Rhytidiadelphus loreus*. Within this ecosystem, different stand history allows the identification of two phases of S1, the cedar-hemlock phase ( $S1^{CH}$ ) and the hemlock-amabilis fir phase ( $S1^{HA}$ ) (Lewis 1982). These will be referred to as CH and HA, respectively, in this thesis. Green et al. (1984) have classified the CH forest as  $CWHb_1(3)$ , and the HA forest as  $CWHb_1(4)$ .

The CH phase is characterized by "old-growth" forests dominated by large *Thuja plicata* Donn. (western red cedar), many with dead tops; poorly growing *Tsuga heterophylla* (Raf.) Sarg. (western hemlock); and a small number of very poorly growing *Abies amabilis* (Dougl.) Forbes (Pacific silver fir). Although accumulated tree biomass of CH sites is high, annual productivity is low. This ecosystem does not appear to have been disturbed by events such as catastrophic wind storms for at least 1000 years (Messier 1991). The canopy is open (i.e., not dense), thus permitting penetration of sunlight to understory vegetation. As a result, *Gaultheria shallon* Pursh (salal), *Vaccinium parvifolium* Howell (red huckleberry), and *V. alaskaense* Smith (Alaskan blueberry) form a fairly continuous and frequently dense understory. *Blechnum spicant* (L.) (deer fern), *Hylocomium splendens* (Hedw.) B.S.C. and

*Rhytidiadelphus loreus* (Hedw.) Warnst. grow sparsely under the *Gaultheria-Vaccinium* cover (Germain 1985).

CH sites have a compacted humus layer that is approximately 45 cm thick (Klinka *et al.* 1981). This layer is rich in decaying wood and overlies a moderately drained Ferro-Humic Podzol. For a description of the typical soil profile of CH forest see Table 1. The HA phase has a thin friable humus layer (10-40 cm)(Klinka *et al.* 1981). Compared to the HA sites, the humus layer in CH sites is higher in tannin content, higher in the ratio of carbohydrate to lignin, and has less advanced decomposition in the non-woody horizons (Preston 1992). Analysis of each of the LFH layers showed that CH forests have consistently lower availability of nitrogen and phosphorus (Prescott *et al.* 1992), and preliminary evidence suggests that the rates of nutrient cycling are higher in HA forests (Keenan and Kimmins 1992). Furthermore, Keenan and Kimmins (1992) determined that the nutrient quality of the litter in HA forests was higher than CH forests. HA forests have a higher abundance and biomass of soil fauna than CH forests, but the diversity is similar (Battigelli *et al.* 1992).

The HA phase is characterized by younger (i.e. < 100 years old) natural second growth western hemlock and Pacific silver fir. The average tree biomass of the HA sites is 1100 m<sup>3</sup>/ha/yr (J. Barker, pers. comm.) and the productivity of these forests is high, with tree growth up to 12 m<sup>3</sup>/ha/yr (Anonymous 1991). Unlike the CH forests, HA forests have experienced repeated catastrophic disturbance caused by high winds (Lewis 1982). The canopy is dense, excluding light and consequently almost all understory vegetation, including salal. Sparse *Vaccinium alaskaense*, *V. parvifolium*, *Blechnum spicant* L., *Polystichum munitum* (Kaulf.) Presl and *Tiarella trifoliata* L., and *Hylocomium splendens* (Hedw.) B.S.C. are present in the understory (Germain 1985). The HA phase is predominantly situated on upper slopes (Messier 1991). For a description of the typical soil profile of HA forests see Table 2. Table 3 summarizes



Table 1. Typical soil profile description of the CH ecosystem (adapted from Germain, 1985).

---

<u>Horizon</u>	<u>Depth (cm)</u>	<u>Description</u>
LF	25-22	Mixed coniferous and moss litter; loose consistency; many fine-roots and mycorrhizal hyphae; abrupt wavy boundary to,
H	22-0	black, dark reddish brown; highly decomposed organic matter; granular, slightly greasy in lower horizon; abundant roots of all sizes; abrupt, wavy boundary to,
Aeu	0-3	Grey to brown; sandy loam; medium subangular blocky; friable; few fine-roots; clear, broken boundary to,
Bhfu	3-18	Reddish brown, strong brown; sandy loam; weak medium subangular blocky; friable when moist; non-sticky and slightly plastic, wet: few to abundant fine- and medium-roots; abrupt wavy boundary to,
Bf	18-40	Strong brown, yellowish brown; gravelly sandy loam; weak medium subangular block; friable when moist; non-sticky and non-plastic, wet; few fine-roots; some medium to large roots; clear wavy boundary to,
Bfgj	40-60	Yellowish brown, brownish yellow; gravelly sandy loam, weak, medium and coarse subangular blocky, firm when moist; non-sticky and non-plastic, wet; very few roots; few faint mottles; abrupt wavy boundary to,
BCC	60+	Olive grey, strongly cemented to indurated gravelly sandy loam; no roots.

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Table 2. Typical soil profile description of the HA ecosystem (adapted from Germain, 1985).

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<u>Horizon</u>	<u>Depth (cm)</u>	<u>Description</u>
LF	60-55	Mixed coniferous, salal and moss litter; loose consistency; many fine-roots and mycorrhizal hyphae; abrupt wavy boundary to,
H	55-0	Reddish black, dark reddish brown; massive; greasy; abundant roots of all sizes; abrupt wavy boundary to,
Ae	0-4	Grey to brown; sandy loam; medium subangular blocky, friable; few fine and medium roots; clear, broken boundary to,
Bhf	4-19	Red, yellowish brown; sandy loam; weak medium subangular blocky; firm when moist; non-sticky and slightly plastic, wet; few fine-roots, few medium and coarse roots; abrupt wavy boundary to,
Bf	19-34	Yellowish red, yellowish brown; sandy loam; medium subangular block, firm when moist; non-sticky and non-plastic, wet; very few fine-roots, few medium and coarse roots; abrupt wavy boundary to,
Bfgj	34-55	Yellowish brown, gravelly sandy loam; weak, medium and coarse subangular blocky, extremely firm when moist; non-sticky and non-plastic; no roots; common faint mottles, seepage water present; abrupt wavy boundary to,
BCc	55+	Olive grey, strongly cemented to indurated gravelly sandy loam; no roots.

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Table 3. Summary of the attributes of CH and HA sites before and after clear-cutting and slashburning.

	<u>CH (cedar/hemlock)</u>	<u>HA (hemlock/fir)</u>
<b><u>BEFORE:</u></b>		
Dominant conifers	western red cedar and western hemlock	western hemlock and Pacific silver fir
Wind disturbance	absent	repeated catastrophic disturbance
Age of stand	"old-growth" > 200 years old	young < 100 years old.
Productivity of conifers	low	high
Canopy	open	dense
Salal abundance	plentiful	rare
<b><u>AFTER:</u></b>		
Natural regeneration of conifers	slow	prompt, dense, fast-growing
Performance of planted conifers	poor	good
Non-crop vegetation regeneration	plentiful salal, little fireweed	little salal, plentiful fireweed

the attributes of the CH and HA phases before and after deforestation and broadcast burning.

## **THE PROBLEM**

On HA sites, following clear-cutting and slashburning, tree growth from planted and naturally regenerated conifer seedlings is good. There is no sign of nutrient deficiencies. Fireweed (*Epilobium angustifolium*) is abundant and salal does not form a dense ground cover.

On CH sites, however, following clear-cutting and slashburning, tree growth from planted and naturally regenerated seedlings is often good for the first few years, but shortly thereafter trees become chlorotic, show signs of nutrient deficiencies, and often die. Salal re-establishes quickly on the clear-cuts and forms a dense ground cover.

## **HYPOTHESES CONCERNING ECOSYSTEM DIFFERENCES**

A number of hypotheses have been proposed to account for the differences in conifer growth and productivity between the CH and HA sites, four of which will be presented below. The first three hypotheses assume that the CH and HA sites are different seral stages of a single forest ecosystem association, the fourth does not. It is generally accepted that HA sites are the pioneer stage and CH sites are the climax stage (Lewis 1982).

## 1. The "disturbance hypothesis":

It is argued that areas frequently disturbed by catastrophic windstorms will regenerate to western hemlock and Pacific silver fir, as is observed on HA sites. Wind storms causes tree falls resulting in soil mixing which promotes a well-drained and aerated soil with active organic matter decomposition and nutrient cycling. Improved soils increase the growth rate of trees and help to produce dense stands which exclude salal by shading. In areas that are not affected by the windstorms i.e., CH sites, western hemlock and Pacific silver fir stands thin, allowing the regeneration of western red cedar. This improves the stand's ability to withstand windstorms because wind can pass through rather than strike against the forest stand.

## 2. The "salal hypothesis":

It is argued that salal (*Gaultheria shallon*) is a major competitor with conifer seedlings. There are two theories relevant to the salal hypothesis that SCHIRP is investigating. One theory proposes that salal suppresses the growth of conifer seedlings through an allelopathic agent which inhibits either mycorrhizal development, root development, or both (de Montigne 1992). This theory is related to observations of other ericaceous species in eastern Canada (Meades 1983) and the heathlands of Europe (Malcolm 1975) which have been attributed to growth problems of planted conifer seedlings after deforestation. The second theory suggests that salal is simply a better competitor than the conifer seedlings for soil nutrients in the CH clear-cuts. In either case, the reason for high productivity in HA sites following a major disturbance is that the dense regeneration of hemlock and fir excludes salal, thus eliminating either allelopathy, nutrient competition, or both. Because the CH stands are not dense, salal can maintain a dense understory, and inhibit most conifer seedling growth. Therefore, little ecological succession occurs at CH sites and the "old-growth" cedar forests remain relatively stable.

### **3. The "western red cedar hypothesis":**

Western red cedar, unlike western hemlock and Pacific silver fir, is highly resistant to decay due to the presence of a fungitoxic chemical (thujaplicin) and a chemical (thujic acid) which repels a variety of insects (Swan *et al.* 1987). Consequently, a forest-floor dominated by decomposing western red cedar will have a low mineralization potential and will immobilize nitrogen in the decomposer community, thus lowering the rate of nutrient cycling and nutrient availability. It has also been postulated that western red cedar is not a climax species, but a long-lived pioneer species that requires exposed mineral soil, or decaying cedar logs, and moderate levels of light to regenerate. Therefore, the conditions in windthrown HA sites are suitable for western red cedar, but because its initial growth is so slow, it is shaded out by the faster growing dense stands of western hemlock and Pacific silver fir. Because western red cedar is better able to regenerate on decaying cedar logs than western hemlock and Pacific silver fir, it can regenerate slowly in the CH sites.

### **4. The "site-difference hypothesis":**

This hypothesis proposes that HA and CH sites are not different seral stages in the same succession, but rather are two different plant associations determined by topography. HA sites are situated on knolls and upper slopes and are therefore more exposed to wind and better drained than the CH sites which are situated in lower areas.

In this study I focussed on the salal hypothesis. I made no attempt to make a distinction between the two salal theories but merely to test if the presence of salal suppresses cedar or hemlock growth. According to this hypothesis salal restricts conifer growth (particularly hemlock), therefore, the removal or absence of salal on the CH clear-cuts should promote the growth of an HA-type forest. Similarly, abundant growth of salal on the HA clear-cuts should promote the growth of a CH-type forest.

## LITERATURE REVIEW

### The biology of salal

*Gaultheria shallon* has slow initial growth for approximately the first 2 years, but once it is established it spreads vegetatively very rapidly by means of rhizomes (Messier 1991). The length and complexity of the rhizomes of an individual salal plant in an area dominated by salal has not been determined but Koch (1983) found new shoots up to 2m from the parent plant. Bunnell (1990) observed a strong tendency for daughter shoots to be clumped around the other shoot under sparse canopies, whereas daughter shoots were farther away from the oldest shoots under closed canopy. Salal accumulates considerable biomass in a growing season, but mainly through the expansion of rhizomes leading to the production of new shoots, not through significant increase in the height of preexisting shoots (Sabhasri 1961).

Salal's ability to respond to a continuum of understory light conditions by producing either sun leaves or shade leaves (Messier *et al.* 1989; Smith 1991) is important to its survival. Vales (1986) suggested that red and near infrared light enrichment may be an environmental trigger for stem elongation. Sabhasri (1961) found that salal stem elongation was highest under red light.

Individual shoots may survive for 10-15 years, but leaves are rarely older than four years before senescence (Haeussler and Coates 1986). Shoots will bear leaves only during the first few years (Koch 1983). Rhizomes have the potential to reproduce vegetatively indefinitely if there is sufficient light through the forest overstory (gaps and sunflecks or diffuse light conditions associated with denser stands) for above-ground stem and leaf growth. Bunnell (1990) found extensive mats of salal rhizomes between 80- 110 years old in conifer stands of the same age, even when above-ground salal densities were low. During winter, salal is virtually dormant and is very sensitive to frozen soils and frost (Sabhasri 1961).

Salal is at least a moderately shade tolerant species (Sabhasri 1961; Koch 1983) but its photosynthetic and respiration characteristics are consistent with a shade intolerant plant species (Sabhasri 1961). For an actively growing plant it was found that at low light intensities ( $50 \mu\text{molm}^{-2}\text{s}^{-1}$ ) respiration was greater than photosynthesis. Photosynthetic activity and seedling growth significantly increased with increased light intensities up to the maximum level tested ( $500 \mu\text{molm}^{-2}\text{s}^{-1}$ ) (Sabhasri 1961). Salal shade leaves are thought to have a lower light compensation point (Sabhasri 1961; Vales 1986). Maximum growth occurs under red light (Sabhasri 1961). Bunnell (1990) reported that the cost of flowering was shared across connected shoots of a plant, showing there is physiological integration between ramets.

The maximal growth of salal (roots, rhizomes, shoots and leaves) is between late April to August, peaking in early June. Vegetative buds burst in early April (Sabhasri 1961). Flowering can occur anytime between March and July depending on the area (Dimock *et al.* 1974). In Alaska, flowering occurs between March and June (Viereck and Little 1972). Near Vancouver, B.C., Pojar (1974) reported flowering between June 12 and July 4. In Washington state, flowering begins in the third week of June. Fruits ripen between August and October and remain on the stem until December (Dimock *et al.* 1974).

Largent *et al.* (1980) have reported that *G. shallon* can be associated with three different kinds of mycorrhizae: arbutoid, ericoid, and ectomycorrhizae. Three different fungal species have been identified, one is *Oidiodendron griseum* and the taxonomic position of the other two species are being studied (Xiao and Berch, 1992). This is the first report of *O. griseum* as an ericoid mycorrhizal fungus of *Gaultheria*.

*Gaultheria shallon* flowers are pollinated by insects, primarily bumblebees and flies (Pojar 1974). The fruit is a many-seeded capsule, and each inflorescence has 5-15 capsules. However, Bunnell (1990) found that salal will flower only when two conditions are met; on vigorous stems greater than four years old, and at a mean crown



completeness (a measure of forest canopy closure) less than 30%. Hebda (1982) found that *Gaultheria shallon* contributed less than 2% of the pollen and spore rain in areas dominated by salal, indicating how little salal flowers.

The fruits of salal remain on the stem until December and those seeds remaining are viable for up to one year following ripening (Dimock *et al.* 1974). Fruits have an average of 126 seeds each. When conditions are suitable for flowering, heavy crops of fruit are produced on a regular basis (Haeussler *et al.* 1990). Seeds are dispersed mainly by the animals which feed upon the fruit; black-tailed deer, Roosevelt elk, mountain beaver, ruffed grouse, blue grouse, and other small mammals and birds (Halverson 1986).

Seeds can remain viable for several years in cold, dry storage, but the viability of seeds under natural conditions is generally much reduced (Dimock *et al.* 1974). Sabhasri (1961) stored seeds at 4.4 °C for one year and found a decline in germination from 31% to 21%. Seeds do not require chilling (Haeussler *et al.* 1990) or stratification (McKeever, 1938) to induce germination. Successful germination requires moist, acidic sites under partial shade (Dimock *et al.* 1974) and light for eight hours or more per day is essential (McKeever 1938). In Washington, germination rates of 27-35% from fresh seed under lighted conditions were reported (Sabhasri 1961; Dimock *et al.* 1974). In British Columbia, Messier (pers. comm.) obtained germination rates of approximately 60% under the same conditions.

Despite the large quantity of seeds produced and the many seeds which germinate, seedling survival is very low (Haeussler *et al.* 1990). Sabhasri (1961) found that in Western Washington, seedling establishment is most successful in the understory of young Douglas- fir stands.

The most significant and effective form of colonization is through vegetative spread, both in open habitats and in deep shade. Once salal is present on a site, further expansion is almost exclusively by vegetative means (Sabhasri 1961; Koch 1983;

McGee 1988; Messier 1991) including layering and suckering from roots and stem bases. However, among the 54 naturally growing plants that Bunnell (1990) examined, no evidence of stem layering was found; rhizomes were the only means of producing new shoots. Bunnell (1990) forced stems into the organic mat and examined them one year later to find that they had grown adventitious roots, and concluded that layering must also occur naturally. He found, while monitoring the colonization of salal, that 85% of the space occupied by salal after nine years of growth was occupied during the first three years. Bunnell also discovered that the vegetative reproduction of ramets was negatively associated with age ( $r^2=0.95$ ) and no new shoots were produced after a plant reached nine years of age. Seed production may be significant in the initial colonization of a newly disturbed area (eg. wind storms, clear-cut), but considering that a plant must be at least four years old before it will flower, and that most colonization of an area occurs within the first three years, the vast majority of colonization occurs through vegetative spread. Bunnell (1990) found no seed production, only vegetative spread, at a mean crown completeness greater than 30%.

The rate of increase of salal populations depends largely on the stage of succession of the area. Messier (1991) proposed a general growth model based on the work of Messier (1991), Messier and Kimmins (1991), Messier *et al.* (1989), Vogt *et al.* (1987), and Vales (1986) (Fig. 1) of the development of salal over a 60-year period following a major disturbance (eg. clear-cutting and slashburning) of old-growth western red cedar and western hemlock forests on northern Vancouver Island. The development of the live fine-root, leaf, stem and rhizome biomass of salal has three different stages. Stage one is between 1-15 years and is characterized by a rapid growth rate of rhizomes and fine-roots, in particular, between 8-15 years. Stage two, approximately between 16-45 years, begins with a rapid decline in salal live fine-root biomass followed by a more gradual decrease in leaf and stem biomass. The decline of the population is caused by shading due to an increase in the overstory tree canopy.

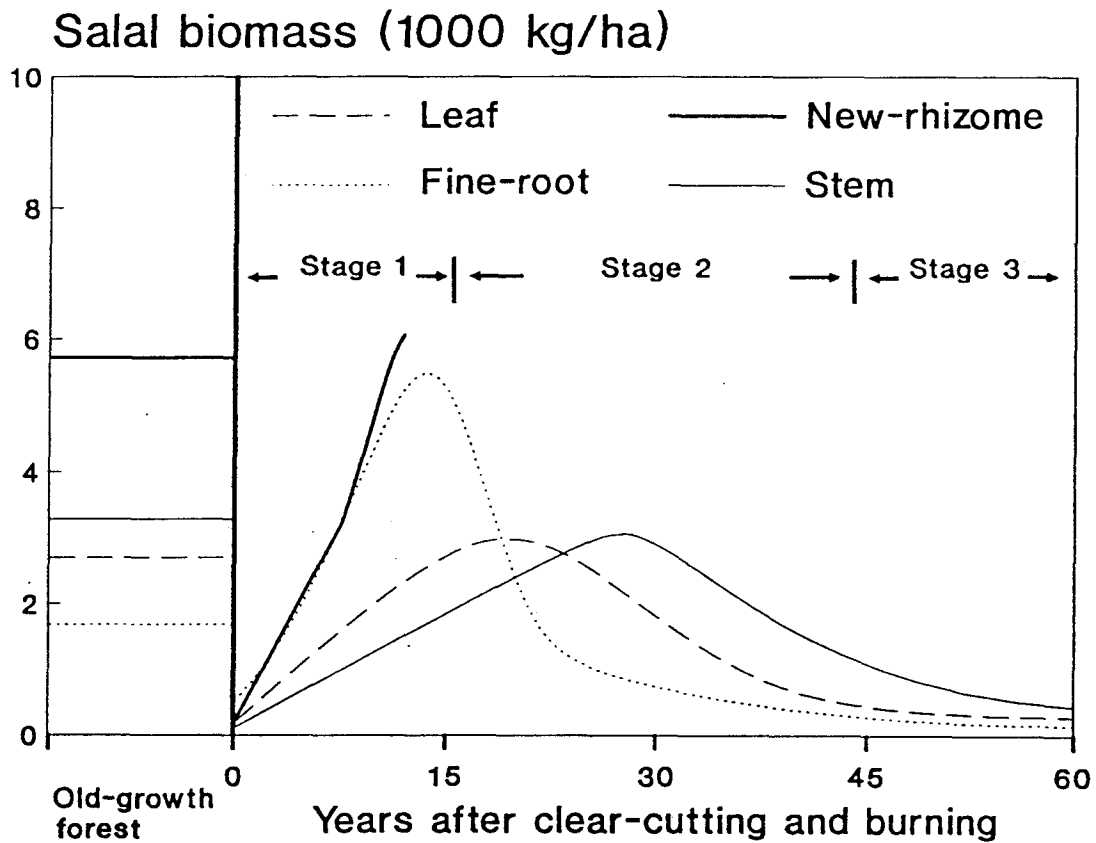


Figure 1. Hypothetical development of live-root, leaf, stem and rhizome abundance of *Gaultheria shallon* over a 60 year period following the clear-cutting and burning of old-growth forests of western red cedar and western hemlock on northern Vancouver Island (taken from Messier, 1991).

There are no data for rhizome biomass in the 10 to 60 year period, but it is believed to be high (Messier 1991). The final stage, occurring from 46 years until the next major disturbance, is the virtual exclusion of salal by the dense overstory canopy. However, it is not completely excluded and can quickly re-establish following a disturbance.

Much research effort has been focused on the competitive interactions of salal and coniferous tree species in low-elevation coastal British Columbia forests (Tan *et al.* 1978; Black *et al.* 1980; Price *et al.* 1986; Weetman *et al.* 1989a; Klinka *et al.* 1989a; Messier *et al.* 1990; Messier 1991). The competitive influence of salal on the seedlings of Douglas-fir, western hemlock, and Sitka spruce is believed to be much stronger than on western red cedar and lodgepole pine (Bunnell *et al.* 1990). Competition is most severe during the early stages of stand development (Long 1977) but may continue through the rotation, in particular, if the canopy is open enough to allow a well-developed understory of salal to persist (Stanek *et al.* 1979).

Young stands of Douglas-fir on sub-xeric sites are limited by soil water potential (Tan *et al.* 1977). At low values of soil water potential, the reduction in stomatal conductance is greater for Douglas-fir than for salal, indicating that salal transpiration would account for a higher proportion of total stand transpiration (Tan *et al.* 1978). Price *et al.* (1986), found that the removal of the salal understory of thinned 32-year-old Douglas-fir significantly increased rates of photosynthesis and tree growth due to an increase in the soil water potential. Other researchers have proposed that salal may be competing for nutrients in the Douglas-fir forests (Stanek *et al.* 1979; Haeussler and Coates 1986).

There is evidence to suggest that salal may also be competitive in moist ecosystems (Weetman *et al.* 1989b; Messier 1991). Two hypotheses have been proposed to account for this. First, is the resource exploitation hypothesis. Weetman *et al.* (1989a, 1989b) have shown that on northern Vancouver Island western red cedar and western hemlock cutovers that are dominated with salal are nutrient deficient.

Germain (1985) and Messier (1991) found that salal can have an impact on the nutrient budget of conifers. *Gaultheria shallon* forms ericoid, arbutoid and ectomycorrhizae (Largent *et al.* 1980), whereas western hemlock only form ectomycorrhizae, and western red cedar only form vesicular-arbuscular mycorrhizae; therefore, because salal might be more efficient at extracting nutrients such as nitrogen and phosphorous at low pH, and accessing nutrients in complex organic forms (Xiao, Cade-Menun and Berch pers. comm.). Parke *et al.* (1983) suggest that dense salal can lower soil temperatures causing reduced conifer growth by inhibiting root growth and mycorrhizal infection. The second hypothesis involves the possible allelopathic properties of salal. Del Moral and Cates (1971) did not find convincing evidence for allelopathy in salal, but Rose *et al.* (1983) have shown that allelochemicals in salal litter may inhibit seedling growth. It has been suggested that salal may have an allelopathic effect through the production of tannins and phenolic acids (de Montigny, 1992).

In general, salal is both resistant and resilient to many herbicides. The most successful herbicide in controlling salal is triclopyr ester (Garlon). Applying triclopyr ester at 4 kg a.i./ha reduced salal cover by 78% (Barker 1988). Combining diesel with triclopyr ester effectively controlled salal for three seasons in a Douglas-fir-salal ecosystem on the southeast coast of Vancouver Island (Dunsworth 1986). In an experiment conducted in a dry cedar-hemlock ecosystem, 4 kg a.i./ha triclopyr ester in diesel oil at 100 L/ha in early spring or late summer reduced salal cover by 60-90%. When using mineral oil as the carrier instead of diesel oil, salal cover was reduced by only 40% (Haeussler *et al.* 1990).

In all of the herbicidal tests to control salal, little is known about how the below-ground plant portion responds. D'Anjou (cited by Haeussler *et al.* 1990) showed that although above-ground parts of salal were well controlled by triclopyr ester, living roots (dry weight basis) still comprised 89% of that in untreated controls, indicating that roots continue to survive despite substantial foliar control.

Several studies have reported that salal will rapidly increase in cover and vigour following the removal or reduction of the forest canopy (Sabhasri 1961; Long and Turner 1975; Long 1977; Stanek *et al.* 1979; Black *et al.* 1980; Koch 1983; Gholz *et al.* 1985; Price *et al.* 1986; Vales and Bunnell 1988; Messier *et al.* 1989). Messier (1991) found that salal reestablishes relatively quickly below ground following clear-cutting and slashburning, but the above ground portion does not grow as rapidly and may take many years to become dominant.

Prescribed burning after logging can increase the growth of salal if the burn is light. Fire stimulates resprouting from roots and stem bases (Sabhasri 1961; Lafferty 1980). Only severe burns that penetrate sufficiently deep to kill the roots can reduce salal cover. Vihaneck (1985) reported that high severity burns on dry sites on eastern Vancouver Island decreased salal cover by 80% compared to adjacent unburned areas whereas low to moderate burns decreased cover by only 40%.

Fertilizer application, particularly nitrogen-rich fertilizer, increases both above and below-ground growth of salal (Sabhasri 1961; Anonymous 1970). However, in forest stands, applications of fertilizer that result in an increased tree canopy density may cause a decline in the vigour and cover of the salal understory due to shading (Long and Turner 1975; Stanek *et al.* 1979).

Salal readily forms new plants from cutting of the stem and the roots (Sabhasri 1961), so it can be expected that any form of soil disturbance that causes mechanical damage to the plant, but that does not physically remove it from the site, will stimulate resprouting. However, it has been reported by Muller (1989, cited in Haeussler *et al.* 1990) that heavy scarification on areas on Vancouver Island has resulted in very slow re-invasion of salal. R. Green (pers. comm.) has reported slow colonization of access logging roads in Cameron Valley, southern Vancouver Island. R. Green observed that if the organic layer is removed, exposing the mineral soil over a large area, salal will not quickly recolonize. He postulated that because areas of southern Vancouver Island

are very dry, salal rhizomes are particularly vulnerable to mortality caused by dessication following heavy scarification.

### **The salal hypothesis**

Central to the salal hypothesis is the assumption that the presence of salal, due to an as yet undetermined mechanism, markedly contributes to the decline of replanted forests on the CH sites. A number of studies have been conducted where the removal of salal improves the growth of neighbouring conifer seedlings (Weetman *et al.* 1989b; Messier 1991; Preston *et al.* 1992). However, although the evidence to support the idea that salal competition is central to conifer plantation stagnation at CH clear-cuts on Vancouver Island is compelling, it is nevertheless inconclusive.

A trial by Weetman *et al.* (1989b) was accomplished by manually "grubbing out" (removing with a pole-axe) the above-ground portion of salal, followed by a single application of the herbicide Garlon 4E (3.5 kg/ha) at the end of the second growing season to control re-establishment. Of the three conifer species tested (western red cedar, western hemlock, and Sitka spruce (*Picea sitchensis* (Bong.) Carr.), salal removal resulted in increased nitrogen uptake and a slight increase in height only in cedar. However, grubbing of the study sites to remove salal also caused mixing of the soil which possibly confounded the results and renders interpretation inconclusive. Furthermore, the study by Weetman *et al.* (1989b) was designed to determine simply if competition occurred. The occurrence of competition does not imply that it is central to the distribution and structure of plant communities (Goldberg and Barton 1991).

Messier (1991) studied the competitive effect of salal by planting Sitka spruce seedlings in the middle of 200 cm diameter patches from which all above-ground vegetation was continuously removed by clipping. Furthermore, below-ground competition from adjacent vegetation was eliminated by periodically trenching to a depth of 40 cm around the perimeter of these patches. Messier detected increased

growth of the Sitka spruce in the treated sites. However, Connell (1990) has criticized the practice of trenching because by severing the roots of competitors, the abundance of natural enemies (soil pathogens, root predators, etc.) in the vicinity of the roots of the target plants may be reduced and may lower the rate of attack on the plant. This may lead to an increase in the growth or survival of the target plant within trenched plots. This argument is supported by Gadgil and Gadgil (1971) who demonstrated that trenching on a pine plantation in New Zealand resulted in an increased rate of litter decomposition. They suggested that saprophytic fungal populations had increased in abundance or activity, or both, thus increasing nutrient availability. These effects would both result in what Connell refers to as "apparent" competition. To partially control for the "trenching effect", Messier (1991) should have set up an additional treatment where trenches were dug around seedlings without the above-ground portion of salal removed. The strength of Messier's (1991) conclusions is based on his measurements of the nitrogen that the above and below-ground portions of salal are able to immobilize in the first 8 years: approximately 9 kg/ha/year. This indicates a potential temporary loss of nitrogen to the system, but it is not proof that salal competes with conifer seedlings. It has been shown recently (Berch and Xiao, 1992) that salal is capable of growing only on organic forms of nitrogen due to its mycorrhizae. Therefore, the high rates of nitrogen that Messier (1991) reported being immobilized by salal may not have originally been in a form that was available to the conifers, regardless of whether salal was present or absent. The same may be true, and is currently under investigation (Berch and Cade-Menun 1992), for available phosphorus.

Preston *et al.* (1992) have preliminary results from a salal eradication and nitrogen fertilization experiment with western red cedar, western hemlock and Sitka spruce seedlings in which half of the plots salal was eradicated, and the remaining half were



control plots.  $(^{15}\text{NH}_4)_2\text{SO}_4$  was applied at 200 kg N/ha to all the plots. They report that after one growing season following salal removal a significant increase in tree height growth occurred for all the conifer species, especially western hemlock. However, salal removal did not significantly affect first year tree foliage nitrogen concentrations. Furthermore, tree foliage N-15 concentration was greater in the control plots than the salal eradicated plots. The researchers argued that this is a dilution effect caused by an increase in tree growth, and expect overall N-15 content in tree foliage to be greater in the salal eradicated plots.

In light of the research that has been done it seems reasonable to conclude that salal has a negative influence on the growth of conifers, but data are inconclusive. However, rigorous data are difficult to gather because manipulative field experiments often yield confounding effects. Therefore, it was necessary to investigate the influence of salal on conifer seedlings from a different perspective.

## OBJECTIVES

The specific objectives of my study were to:

1. quantify the relationship between leaf area index of salal and performance of neighbouring western hemlock and western red cedar saplings;
2. quantify the influence of leaf area index of other neighbouring species on western hemlock and western red cedar sapling performance;
3. relate abiotic environmental factors i.e., soil moisture, soil coarse content, soil carbon, soil total nitrogen, and soil total phosphorus to western hemlock, western red cedar and salal performance;
4. determine the effects of treatment: fertilization, scarification (i.e. manual removal of salal), and fertilization plus scarification; and site: CH and HA on western hemlock, western red cedar and salal growth and foliar nutrient concentration, as well as environmental variables.

## METHODS

### Study area

The study was conducted at the SCHIRP site located approximately 20 km north of Port McNeill situated on Block 4 of Tree Farm Licence 25 operated by Western Forest Products Ltd. on northern Vancouver Island, B.C., Canada ( $50^{\circ}60'/127^{\circ}35'$ ) (Fig.2). The SCHIRP site is in the submontane variant of the CWHvm biogeoclimatic subzone (Lewis 1982). The elevation of the site is approximately 100m above sea level. The summers are cool and moist and winters mild and wet. The following weather data were collected at the Port Hardy Airport weather station located about 20 km north of the study area at an elevation of 50m above sea level. The data represent an average from 1966-1992. The area receives approximately 1700 mm of rainfall annually, 65% occurring between October and February. From March to September no less than 50 mm of precipitation falls monthly, indicating that drought is absent from the deep mineral soils in all but exceptional years (Lewis 1982). The hours of direct sunlight vary from an average high of 6.4 h/day in July to an average low of 1.5 h/day in December. The frequent occurrence of fog in the summer and frontal clouds in the winter account for the low hours of direct sunlight. Mean daily temperature ranges from a high of  $13.7^{\circ}\text{C}$  in July/August to a low of  $3.0^{\circ}\text{C}$  in January/February.

### Field manipulations

The SCHIRP site was clear-cut logged in 1986, broadcast burned during the spring of 1987, and planted in 1988 (Barker *et al.* 1991). Therefore, the conifers were 2- and 4-years-old during the study period (1990 - 1992). At the time of the study, vegetation, including salal, had between 3- to 5-years to reinvade after broadcast burning in 1987.

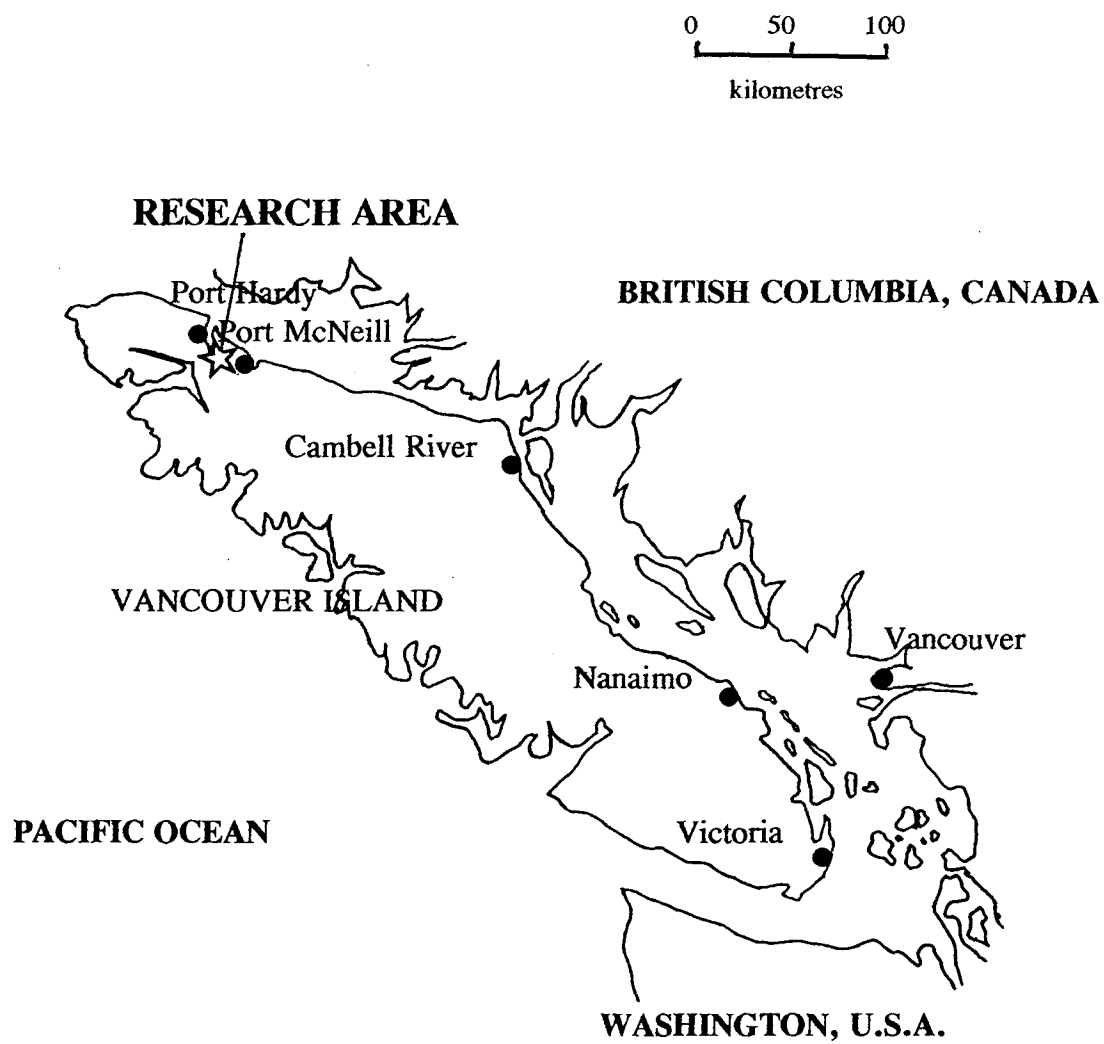


Figure 2. Study area - northern Vancouver Island.

The SCHIRP site has 128 plots, with 64 trees per plot, involving several treatments (Barker *et al.* 1991) (Fig.3):

2 ecosystems		- CH - HA
	x	
2 pure conifer stands		- western red cedar - western hemlock
	x	
3 densities		- 500 trees/ha - 1500 trees/ha - 2500 trees/ha
	x	
2 fertilities		- fertilized - unfertilized
	x	
4 replicates		

In addition, scarified and scarified plus fertilized plots were established, but only on the highest planting density plots of 2500 trees/ha.

2 ecosystems		- CH - HA
	x	
2 pure conifer stands		- western red cedar - western hemlock
	x	
2 treatments		- scarified - scarified plus fertilized
	x	
4 replicates		

Each tree was labelled and measured for height and root collar diameter in 1988, 1989, 1990 and 1992 by Western Forest Products.



Figure 3. SCHIRP site - experimental design. The 97 ha site is located on the Rupert 600 (R600) logging road. The site was clear-cut logged in 1986, burned in 1987, and planted in 1988. C=western red cedar, H=western hemlock, F=fertilized, S=scarified. (.....) represents the CH (cedar-hemlock) HA (hemlock-fir) boundary. Blocks 1-4 represent the four replications in the design, each block having both CH and HA sites. The smallest to largest boxes indicate planting densities of 2500, 1500, and 500 trees per hectare, respectively, with spacing between trees of 2.0 m, 2.63 m, and 4.5 m, respectively.

Table 4. Number of plots sampled from each site x treatment combination in the SCHIRP site at the highest planting density of 2500 trees/ha.

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**Western hemlock:**

<u>Treatment</u>	<u>CH site</u>	<u>HA site</u>
control	4	4
fertilized	4	4
scarified	4	4
fertilized + scarified	4	4

**Western red cedar:**

<u>Treatment</u>	<u>CH site</u>	<u>HA site</u>
control	4	4
fertilized	4	4
scarified	4	4
fertilized + scarified	4	4

Total = 64 plots

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Within the fertilized treatments, each tree was individually fertilized with 60g of Nutriccoat controlled release fertilizer (Type: 360 16-10-10). Scarification was done using a backhoe (215 Cat Excavator) with a 3-tynd rake attachment. The purpose of the scarification was to remove salal rhizomes and to simulate windthrow by mixing the organic forest floor and the mineral soil.

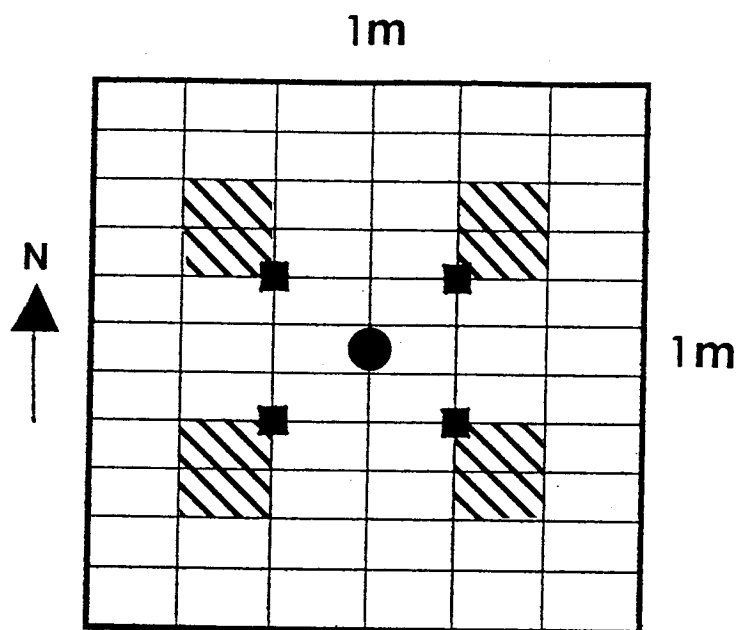
In my study, only the high density (2500 trees/ha) plots, represented by the smallest boxes in Figure 3, were used. It was reasoned that competition between planted conifers would be minimal at this early stage in growth at all densities and therefore the lower densities were not required. A total of 64 plots in the SCHIRP site were studied (Table 4).

## **Data collection**

During the summer of 1991, four conifer seedlings were selected from each of the 64 plots, except for one plot in which only three suitable conifers were found, for a total of 255 seedlings. The conifers were chosen based on the percent cover of salal surrounding them within a  $1\text{m}^2$  area. Four different abundances of salal were selected: approximately 0%, 33%, 66% and 100% salal cover. A  $1\text{m}^2$  quadrat was centered around each conifer on a direct north/south orientation. The same quadrats were measured over two summers (1991 and 1992). The following measurements were made on each of the quadrats:

i) vegetation measurements: During both summers, the leaf area index (leaf area per unit of land area) of all plant species present was measured using 50 systematically arranged points per quadrat (Fig. 4). A list of the plant species found on either CH or HA sites is presented in Table 5. At each point, the number of leaves from each species that passed through that point was counted. The mean leaf area per quadrat for





**Figure 4.** Diagram illustrating the methods used to measure leaf area index of non-crop vegetation, leaf litter of salal and soil variables. The conifer being measured is represented by ●. At each intersection of horizontal and vertical lines, the numbers of leaves of each species were counted for the leaf area index measurement. The areas represented by // were where the leaf litter of salal was collected. The solid boxes (■) were where the soil samples were collected.

Table 5. Species list of the naturally growing vegetation within the study area on the CH and HA sites.

	<u>Scientific name and authority</u>	<u>common name</u>
1.	<i>Anaphalis margaritaceae</i> (L.) B. & H.	pearly everlasting
2.	<i>Blechnum spicant</i> (L.) Roth.	deer fern
3.	<i>Bryophytes</i>	moss family
4.	<i>Cornus canadensis</i> L.	bunchberry
5.	<i>Dryopteris expansa</i> (Presl) Fraser-Jenkins & Jeremy	spiny wood fern
6.	<i>Epilobium angustifolium</i> L.	fireweed
7.	<i>Equisetum sylvaticum</i> L.	horsetail
8.	<i>Gaultheria shallon</i> Pursh	salal
9.	<i>Hypochoeris radicata</i> L.	hairy cat's ear
10.	<i>Lysichitum americanum</i> Hulten & St. John	skunk cabbage
11.	<i>Menziesia ferruginea</i> Smith.	false azalea
12.	<i>Mycelis muralis</i> (L.) Dumort.	wall lettuce
13.	<i>Pinus contorta</i> Dougl.	lodgepole pine
14.	<i>Poa</i> L.	grass family
15.	<i>Pteridium aquilinum</i> (L.) Kuhn.	bracken fern
16.	<i>Ribes laxiflorum</i> Pursh	trailing black currant
17.	<i>Rubus spectabilis</i> Pursh	salmonberry
18.	<i>Sambucus racemosa</i> L.	elderberry
19.	<i>Salix sitchensis</i> Sanson	sitka willow
20.	<i>Thuja plicata</i> Donn.	western red cedar
21.	<i>Tsuga heterophylla</i> (Raf.) Sarg.	western hemlock
22.	<i>Vaccinium ovalifolium</i> Smith	oval leaved blueberry
23.	<i>Vaccinium parvifolium</i> Smith	red huckleberry

each species was used for the analyses. Leaf area index is a measure of the photosynthetic potential of plants.

a) Conifer seedling performance as indicated by height and root collar diameter was measured on the 255 seedlings at 2-years-old and 4-years-old (1990 and 1992) by Western Forest Products. During a 3-day period in mid-July, 1992, four or five twigs each approximately 10-15cm long were clipped from each of the conifers for a foliar analysis. The samples were oven-dried at 28°C for 24 hours, and ground in a standard Braun coffee grinder. Concentrations of total nitrogen, phosphorus and potassium were measured from oven-dried samples on an autoanalyzer following sulphuric acid - hydrogen peroxide digestion (Parkinson and Allen 1975). A colour index of conifer trees was also scored in 1992 in order to determine a relationship between foliar nutrient concentration and colour index of conifers. It is well known that a plant with nutrient deficiency has different colour leaves than a healthy plant (Lavender and Walker 1979). A number was assigned to each of the conifers according to the colour of their needles: 1-indicated dark green, 2-light green, 3-yellow-green, and 4-yellow-brown.

b) *Gaultheria shallon* leaves were collected and analyzed for nitrogen, phosphorus, and potassium during the same time interval that conifer foliar analyses was conducted (mid-July, 1992). Between fifteen and twenty salal leaves greater than one year old were randomly selected from 48 of the 255 total number of quadrats. *Gaultheria shallon* leaves less than one year old have less cuticle thickness and colour than those greater than one year old. Older leaves had a thick waxy layer and were dark green in colour compared to the relatively thin, light green leaves less than one year old. Of the 48 quadrats, eight were randomly selected from each of three different treatments; control, fertilized, and scarified, on both the CH and HA sites. Concentrations of total nitrogen, phosphorus and potassium were measured from oven-

dried samples on an autoanalyzer following sulphuric acid - hydrogen peroxide digestion (Parkinson and Allen 1975).

c) *Gaultheria shallon* leaf litter was also collected from each of the 255 quadrats during the summer of 1992. The leaf litter was collected from four 10 cm<sup>2</sup> patches within each quadrat (Fig. 4). The leaf litter from each quadrat was combined, oven dried at 28°C for 48 hours and weighed. Because salal leaves live for an average of 4 years before shedding, a measurement of the abundance of salal leaf litter yielded an estimate of the length of time salal occupied the area immediately surrounding the conifers at these sites.

ii) Environmental measurements: Environmental variables were measured only during the summer of 1992. Soil samples from the rooting layers (humus layer and Ah layer) were collected from within each 1m<sup>2</sup> quadrat, and 4 subsamples from each quadrat were combined (Fig. 4). In the field, soils were put in a cooler during the day and transferred to a deep-freeze in the evening for storage where they remained frozen until analyzed. The following analyses were conducted for each of the samples: soil moisture, coarse soil content, total carbon, total nitrogen and available phosphorus.

After mixing the soil thoroughly, each of the soil samples was divided in half. Soil moisture was measured by weighing one half of each of the soil samples before and after oven drying at 27°C for 36 hours. Coarse soil content was measured by sieving the oven-dried soil through a 2mm sieve and weighing the portion of soil that could not filter through the sieve.

The remaining soil from each of the soil samples was air-dried for one week, and finely ground in a standard Braun coffee grinder in preparation for nitrogen, phosphorus and carbon analysis. A Leco analyzer was used to measure total carbon (Anonymous 1981). Total nitrogen and potassium was measured by initially digesting the soils. Because the soils were generally highly organic, 1g of soil was digested

using 1g of digestion mix ( $K_2SO_4$ ,  $CuSO_4 \cdot 5H_2O$ , and Se), and 10 ml  $H_2SO_4$ . Total nitrogen and potassium was measured by an autoanalyzer. To measure total phosphorus, samples were air-dried and extracted with Bray's solution (McKeague 1978) and analyzed on an autoanalyzer.

## **DATA ANALYSIS**

### **Site x treatment effects**

Three-way ANOVA's were applied to the soil variables, salal performance, and conifer performance. The independent variables were site (CH and HA); fertilization (present and absent); and scarification (present and absent). Western red cedar and western hemlock saplings were analyzed separately. SYSTAT (Wilkinson 1990) was used for all statistical procedures.

Bartlett's test for homogeneity of group variances was applied to each ANOVA. If the data were heteroscedastic with a significance of  $p < 0.10$  transformations were performed to meet the assumption of equal variances. Three transformations (Table 6) were applied: logarithmic ( $X' = \log X$ ), arcsine ( $P' = \arcsin P$ ), and square root ( $X' = \sqrt{X}$ ).

An appropriate means separation test for hypothesis generation is Fisher's protected least significant difference (LSD) (Saville 1990). This test was applied to each of the ANOVA's to separate treatment means ( $p < 0.05$ ).

### **Relationship between non-crop vegetation and conifer performance**

Stepwise multiple regression was applied to determine which vegetation variables (leaf area index) influenced height and root collar diameter of western red cedar and western hemlock saplings in each of the eight different site x treatment combinations: i.e. 2 ecosystems (CH and HA) x 4 treatments (control, fertilized,

Table 6. Transformations on western red cedar and western hemlock data in order to meet the assumption of equal variances for the analysis of variance. "-" represents that no transformation was necessary.

<b>Measurement Variables</b>	<b>Cedar</b>	<b>Hemlock</b>
Height of conifers (1990)	-	-
Root collar diameter of conifers (1992)	-	-
Height of conifers (1990)	log	-
Root collar diameter of conifers (1992)	log	-
Colour index of conifers	-	-
Foliar nitrogen of conifers	arcsine	-
Foliar phosphorus of conifers	-	log
Foliar potassium of conifers	arcsine	-
Leaf area index of salal (1991)	-	-
Leaf area index of salal (1992)	-	-
Salal leaf litter	log	square root
Foliar nitrogen of salal	-	-
Foliar phosphorus of salal	-	-
Foliar potassium of salal	-	-
Soil moisture	-	-
Soil coarse content	log	log
Soil total carbon	arcsine	arcsine
Soil total nitrogen	-	-
Soil total phosphorus	log	log

scarified, and fertilized plus scarified). Leaf area index data from 1991 were used to determine the variation in 2-year-old conifer performance measured in 1990. Ideally, conifer performance from 1991 should be used but the data were not available. Leaf area index data from 1992 were used to determine the variation in 4-year-old conifer performance measured in 1992. By decreasing the number of independent variables in the model, its predictive capability is enhanced. This is because the variance of the parameter estimates decreases. However, with the reduction of independent variables, bias may increase because the "true model" may have a higher dimension. The goal is to balance smaller variance against increased bias. Generally, variables within the models which displayed an absolute t-value less than 2.0, a p-value greater than 0.5, and tolerance values less than 0.1 were removed; the exceptions to this general rule were those variables that, when removed, the  $R^2$  and the analysis of variance p-value of the multiple regression model were reduced. Tolerance is a measure of correlation between variables and is calculated as 1 minus the square multiple correlation between a predictor and the other predictors included in the model. The multiple regression models were tested for normal distribution, homogeneity of variance, independent errors and to ensure that all the members of the population were described by the same linear model.

The primary emphasis of this study is to determine the influence of salal on conifer performance. Therefore, the individual  $R^2$  values of salal were calculated from the output of the multiple regression models to determine the variation of height and root collar diameter of the conifers by salal alone. The following method was used to calculate the  $R^2$  values of salal from the output of the multiple regression models (Zar 1984):

$$T^2 = F$$

$$F = \frac{\text{regression MS}}{\text{residual MS}}$$

$$\text{regression SS} = \text{residual SS} \times \text{df}$$

$$R^2 = \frac{\text{regression SS}}{\text{total SS}}$$

where; T=test statistic, F=test statistic, MS=mean square, SS=sum of squares.

This method is not a rigorous statistical test because the independent variables from a multiple regression model are not independent on their own. However it allows an estimate of the influence of salal alone on the height and root collar diameter of conifers.

### **The influence of the abundance of salal on the growth of conifers between 1990 and 1992.**

The growth increment of hemlock and cedar height and root collar diameter over two years were measured when the conifers were 2- and 4-years-old. The 2 year growth rates were separated by site (CH and HA) and treatment (control, fertilized, scarified, and fertilized plus scarified) for a total of 32 separate conditions: 2 conifers (hemlock and cedar) x 2 conifer performance variables (height and root collar diameter) x 2 sites (CH and HA) x 4 treatments (control, fertilized, scarified, and fertilized plus scarified). The growth rates of conifers were regressed against the leaf area index of salal for 1991, the mid-point of the 2-year time period, and the regression lines were compared.



## RESULTS

### Predictions

In order to accept the "salal hypothesis", a number of outcomes from the multiple regression models must occur. These predictions are made based on research conducted by SCHIRP researchers as to the response cedar and hemlock saplings have to the abundance of salal according to the "salal hypothesis". The following four paragraphs state the predictions. See Figure 5 for a summary of the predicted outcomes.

***Growth of hemlock on CH sites:*** According to Bunnell (1990), hemlock growth is more sensitive to the abundance of salal than cedar, therefore it is predicted that the abundance of salal will be negatively correlated with growth performance of hemlock on control and scarified plots to a greater degree than cedar. Scarification is meant to mimic the disturbance of the soil following trees felled in a windstorm and increase nutrient availability of the soil due to increased aeration and mineralization. Therefore, hemlock on scarified plots will grow marginally better than on control plots. Weetman (1989b) found that hemlock had a greater growth response to the addition of nitrogen and phosphorus than cedar. Furthermore, Weetman (1989b) found that after salal removal, increased nitrogen uptake was observed in cedar, not hemlock. Therefore salal abundance on fertilized, and fertilized plus scarified plots would show less influence on the growth of hemlock than cedar.

***Growth of hemlock on HA sites:*** It is predicted that salal abundance on control and scarified plots will be negatively correlated with hemlock growth. However, the growth of hemlock would be less sensitive to salal on HA sites compared to CH sites.

Salal abundance on fertilized, and fertilized plus scarified plots would show very little, if any, influence on the growth of hemlock.

***Growth of cedar on CH sites:*** It is predicted that salal abundance will be negatively correlated with height and root collar diameter of cedar on control and scarified plots, but that the correlation will not be strong because natural regeneration of cedar is better than hemlock on control CH sites (Weetman et al. 1989b). Because scarification may increase the available nutrients in the soil, cedar will grow better on scarified plots than control plots. On fertilized and fertilized plus scarified plots there may be a small negative correlation between cedar growth and salal abundance because the fertilization of the sites would diminish the effect of any resource depletion by salal. However, although tolerant of low nutrient soils, cedar grows rapidly in nutrient rich environments (Krajina *et al.*, 1982). Therefore cedar may be slightly inhibited by salal growth even when the site is fertilized.

***Growth of cedar on HA sites:*** It is predicted that the abundance of salal on control and scarified plots is negatively correlated with cedar growth but not as strongly as on CH sites. Salal abundance on fertilized and fertilized plus scarified plots will have very little negative influence, if any, on cedar growth but, similar to CH, fertilization will reduce the effect of salal, especially since HA sites are higher in nutrients compared to CH sites.

## HEMLOCK

### CH site

### HA site

treatment <sup>a</sup>	c	f	s	f+s		c	f	s	f+s
salal abundance	high	high	high	high		high	high	high	high
conifer response <sup>b</sup>	a	c	b	d		b	d	c	d

## CEDAR

### CH site

### HA site

treatment	c	f	s	f+s		c	f	s	f+s
salal abundance	high	high	high	high		high	high	high	high
conifer response	b	d	c	d		c	d	c	d

Figure 5. The predicted western hemlock and western red cedar response to high abundance of salal based on the salal hypothesis.

<sup>a</sup>c=control, f=fertilized, s=scarified.

<sup>b</sup>a=a 50% or more reduction in conifer growth compared to a conifer growing in optimum conditions, b=30-50% reduction in conifer growth compared to a conifer growing in optimum conditions, c=>0-30% reduction in conifer growth compared to a conifer growing in optimum conditions, d=no influence from salal.

## Site x treatment effect using 3-way ANOVA

### *western hemlock*

#### *a: Soil variables*

Generally, the soil moisture content was higher on CH sites than on HA sites (Fig. 6a), especially in control and in scarified sites. Also, the plots manipulated the most (fertilized plus scarified) on CH sites had the least soil moisture content. Although coarse content of soils increased with increasing field manipulation on CH sites, there was no significant difference (Fig. 6b). HA sites generally had a higher coarse soil content than CH sites, but fertilized HA sites were significantly greater than control CH, fertilized CH and scarified CH sites. Fertilized HA sites were also significantly greater than fertilized plus scarified HA sites. There was very little difference in the total carbon concentration of soils except that scarified HA sites had predictably lower total carbon than control HA sites (Fig. 6c). There was no difference in the total nitrogen concentration of the soil between the treatments on the HA sites (Fig. 6d). Interestingly, soils in control CH sites had a greater total nitrogen than both scarified CH sites and fertilized plus scarified CH sites. Also, soils of fertilized CH sites had a greater total nitrogen than scarified CH sites. An interesting pattern can be seen in the total phosphorus of soils (Fig. 6e); there was no difference between sites, however, soil from scarified plots in both CH and HA sites were significantly less than all other site x treatment combination except fertilized HA sites.

#### *b: salal performance*

The leaf area index of salal in 1991 (Fig. 7a) and 1992 (Fig. 7b), and the leaf litter of salal (Fig. 7c) all show similar patterns. Generally, control and fertilized plots on CH sites had a higher leaf area index and leaf litter than all other site x treatment combinations, i.e. scarification reduced leaf area index and leaf litter. Scarification on

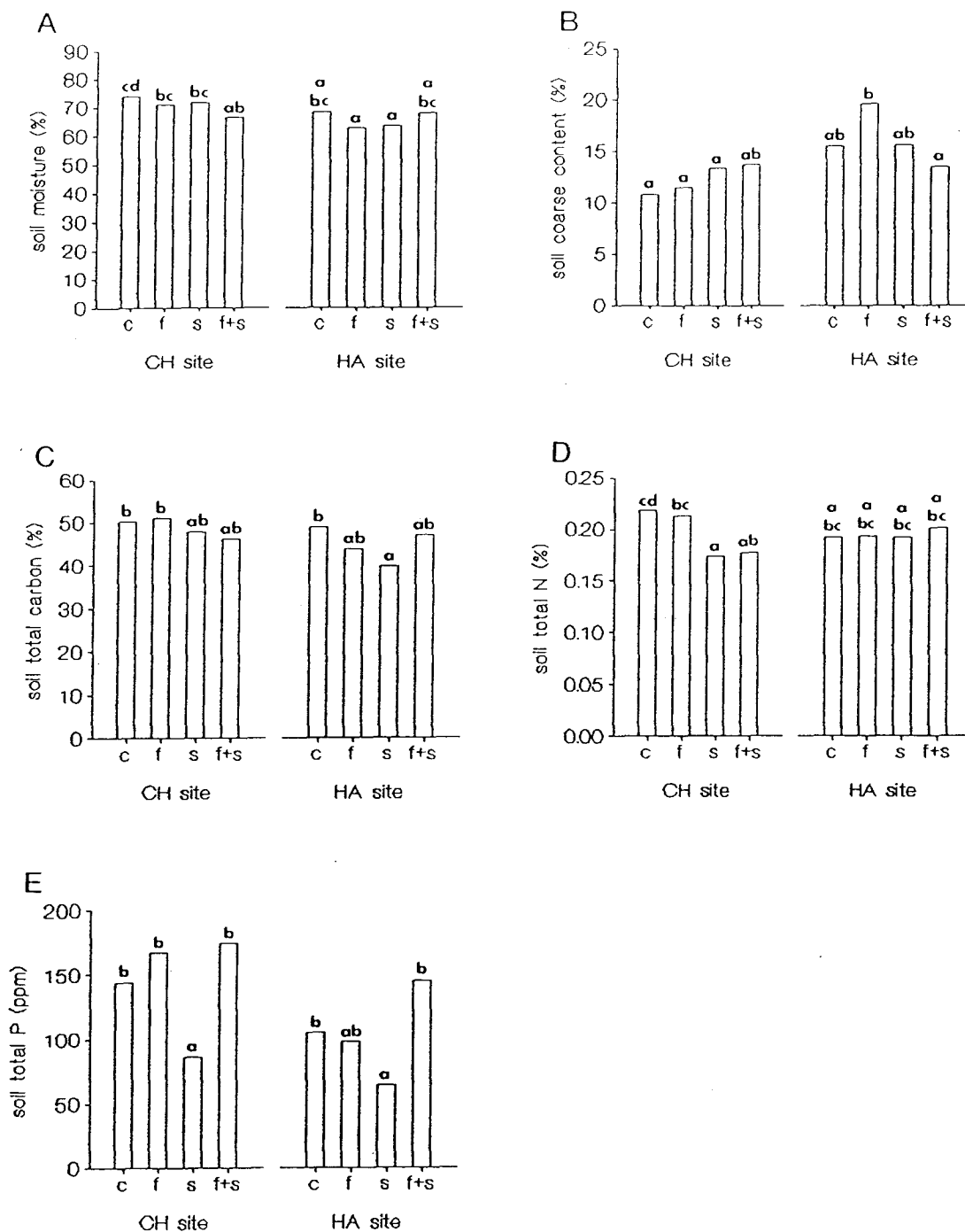


Figure 6. Site x treatment effect on soil variables (moisture, coarse content, total carbon, total nitrogen, and total phosphorus) where western hemlock was planted using 3-way ANOVA. Fisher's protected least significant difference was applied to separate treatment means. Within a group, bars sharing the same letter are not significantly different ( $p > 0.05$ ). On the x axis, c=control, f=fertilized, and s=scarified.

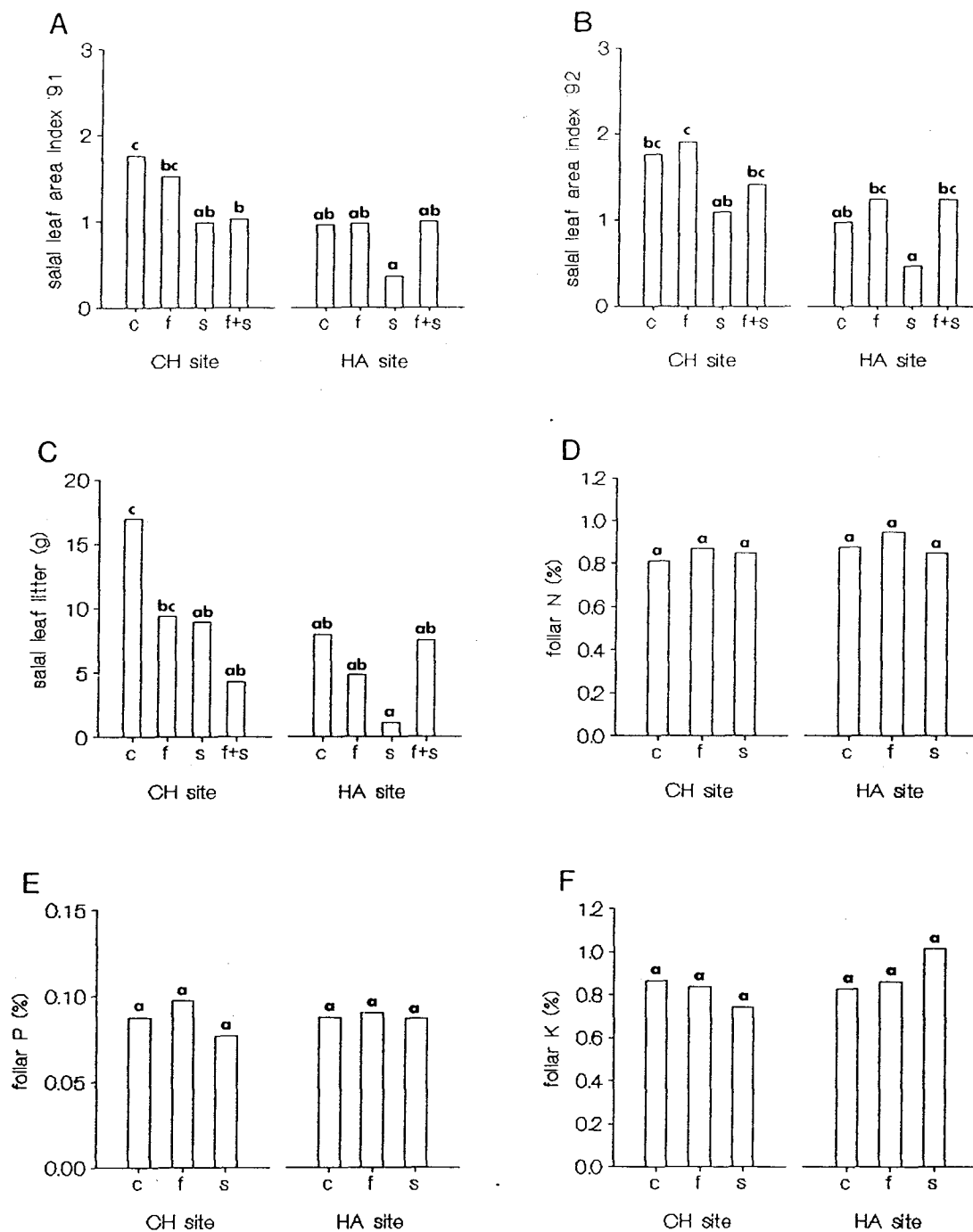


Figure 7. Site x treatment effects on salal performance (LAI, leaf litter, foliar nitrogen, foliar phosphorus, and foliar potassium) where western hemlock was planted using 3-way ANOVA. Fisher's protected least significant difference was applied to separate treatment means. Within a group, bars sharing the same letter are not significantly different ( $p > 0.05$ ). On the x axis, c=control, f=fertilized, and s=scarified.

HA sites showed that the lowest leaf area index and leaf litter values compared to all other site x treatment combinations. No significant differences were found between the treatments or sites of salal foliar nitrogen, phosphorus, or potassium concentrations at  $p < 0.05$  (Figures 7d,e,f), but foliar nitrogen concentration of salal on fertilized HA sites was greater ( $p < 0.10$ ) than control CH sites. Furthermore, foliar potassium concentration of salal on scarified HA sites was significantly greater than scarified CH sites.

*c: western hemlock performance*

Hemlock height (Fig. 8a) and root collar diameter (Fig. 8b) in 1990 showed similar patterns. Hemlock growing on control CH sites were significantly smaller, than all other site x treatment combinations. A treatment effect could be seen on CH sites where there was increasing height with increasing field manipulation, but this was not seen on HA sites. A noticeable site difference was evident, with height and root collar diameter of hemlock on fertilized CH sites and scarified CH sites being significantly smaller than fertilized HA sites and scarified HA sites, respectively. In 1992, the height (Fig. 8c) and root collar diameter (Fig. 8d) of 4-year-old hemlocks again showed similar patterns. The only significant difference between height and root collar diameter measurements of 2- and 4-year-old hemlocks is that the effect of scarification had increased height and root collar diameter at a greater rate on both CH and HA sites than the other treatments. Therefore 4-year-old hemlocks grown on scarified CH sites were not significantly shorter than 4-year-old hemlocks grown on fertilized CH sites, unlike 2-year-old hemlocks measured in 1990. Also, 4-year-old hemlocks grown on scarified HA sites were significantly taller than 4-year-old hemlocks grown on fertilized plus scarified CH sites, unlike 2-year-old hemlocks measured in 1990. Finally, unlike 1990, root collar diameter of hemlock on scarified HA sites was significantly greater than control HA sites.

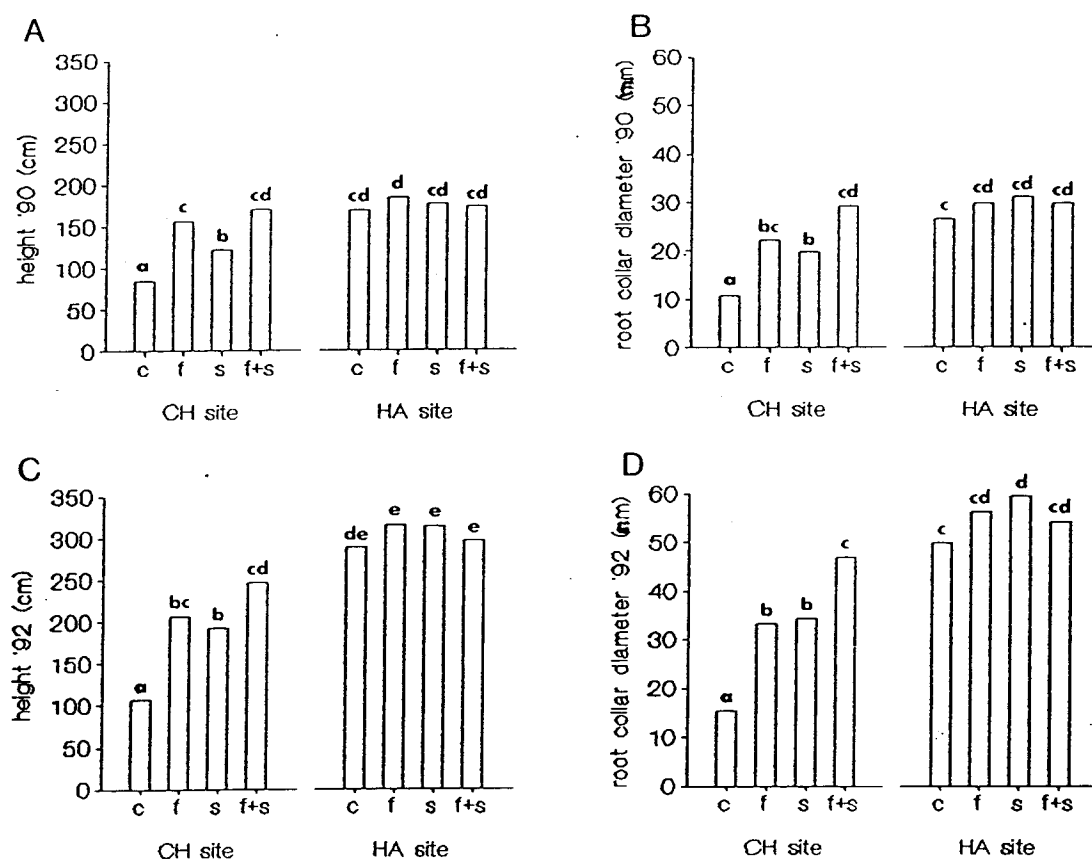


Figure 8. Site x treatment effects on western hemlock performance (height and root collar diameter) using 3-way ANOVA. Fisher's protected least significant difference was applied to separate treatment means. Within a group, bars sharing the same letter are not significantly different ( $p > 0.05$ ). On the x axis, c=control, f=fertilized, and s=scarified.



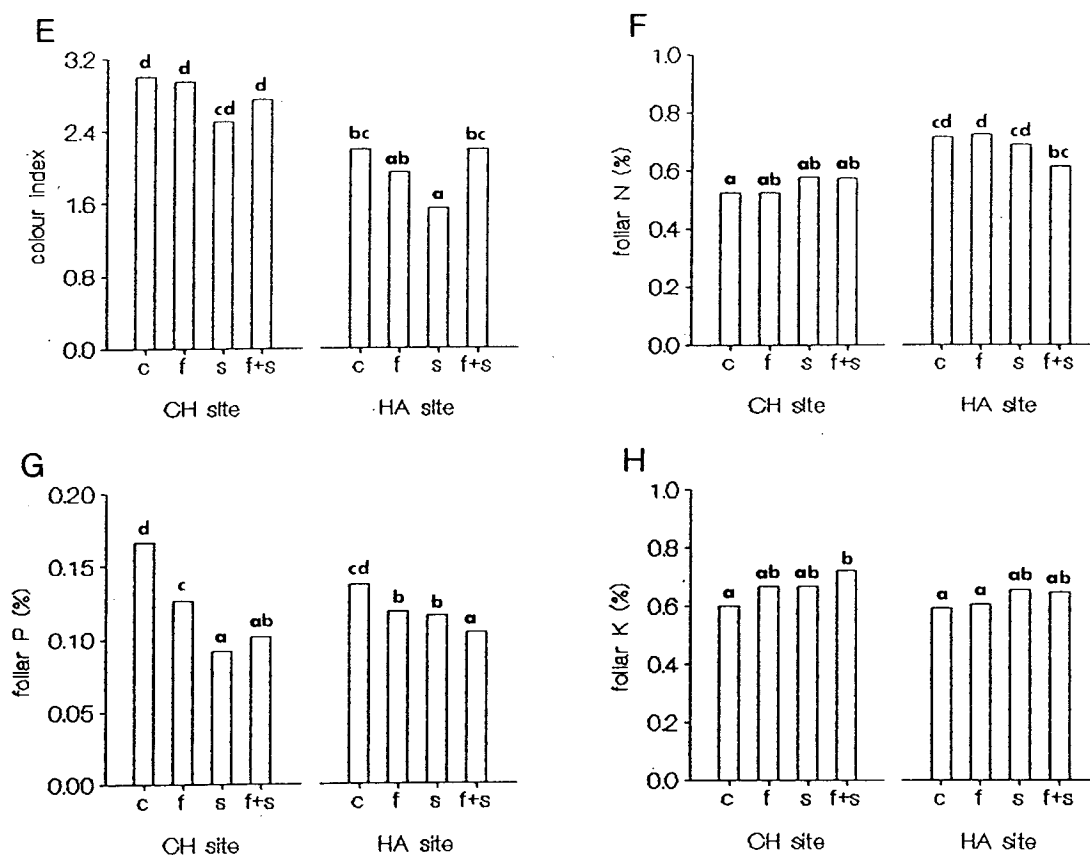


Figure 8 (cont.). Site x treatment effects on western hemlock performance (colour index, foliar nitrogen, foliar phosphorus, and foliar potassium) using 3-way ANOVA. Fisher's protected least significant difference was applied to separate treatment means. Within a group, bars sharing the same letter are not significantly different ( $p > 0.05$ ). On the x axis, c=control, f=fertilized, and s=scarified.

There was a distinct site difference in the colour index of hemlock (Fig. 8e). For each treatment, the colour index of hemlock was less on HA sites than on CH sites, i.e. hemlock grown on HA sites were greener. Furthermore, hemlock grown on scarified plots have a significantly lower colour index than those on control plots in each site. There was also a strong site difference in foliar nitrogen concentration (Fig. 8f), where hemlock grown on HA sites had higher concentrations than CH sites. The only condition in which hemlock grown on HA sites did not have a higher nitrogen concentration was fertilized plus scarified HA sites. The total foliar phosphorus concentration of hemlock varied little between CH and HA sites (Fig. 8g). However, foliar phosphorus concentration decreased with increasing field manipulation for both CH and HA sites. There was little variation in total foliar potassium concentration of hemlock between the site x treatment conditions (Fig. 8h). However, hemlock grown on the fertilized plus scarified treatment on the CH sites had a significantly higher foliar potassium concentration than hemlock grown on control CH sites.

### ***Western red cedar***

#### ***a: Soil variables***

Soil moisture did not vary significantly between treatments or sites (Figure 9a), and predictably, some fertilized sites had higher levels of nitrogen (HA on Fig. 9d) and phosphorus (CH and HA on Fig. 9e), although not always. The response of total carbon to the treatments was variable and showed no real pattern (Fig. 9c). Soil coarse content was greater on scarified sites compared to fertilized sites, but not control sites (Fig. 9b).

#### ***b: Salal performance***

In 1991, salal on scarified HA sites had a significantly lower mean leaf area index than all other treatments at both site types except for scarified CH sites (Fig.

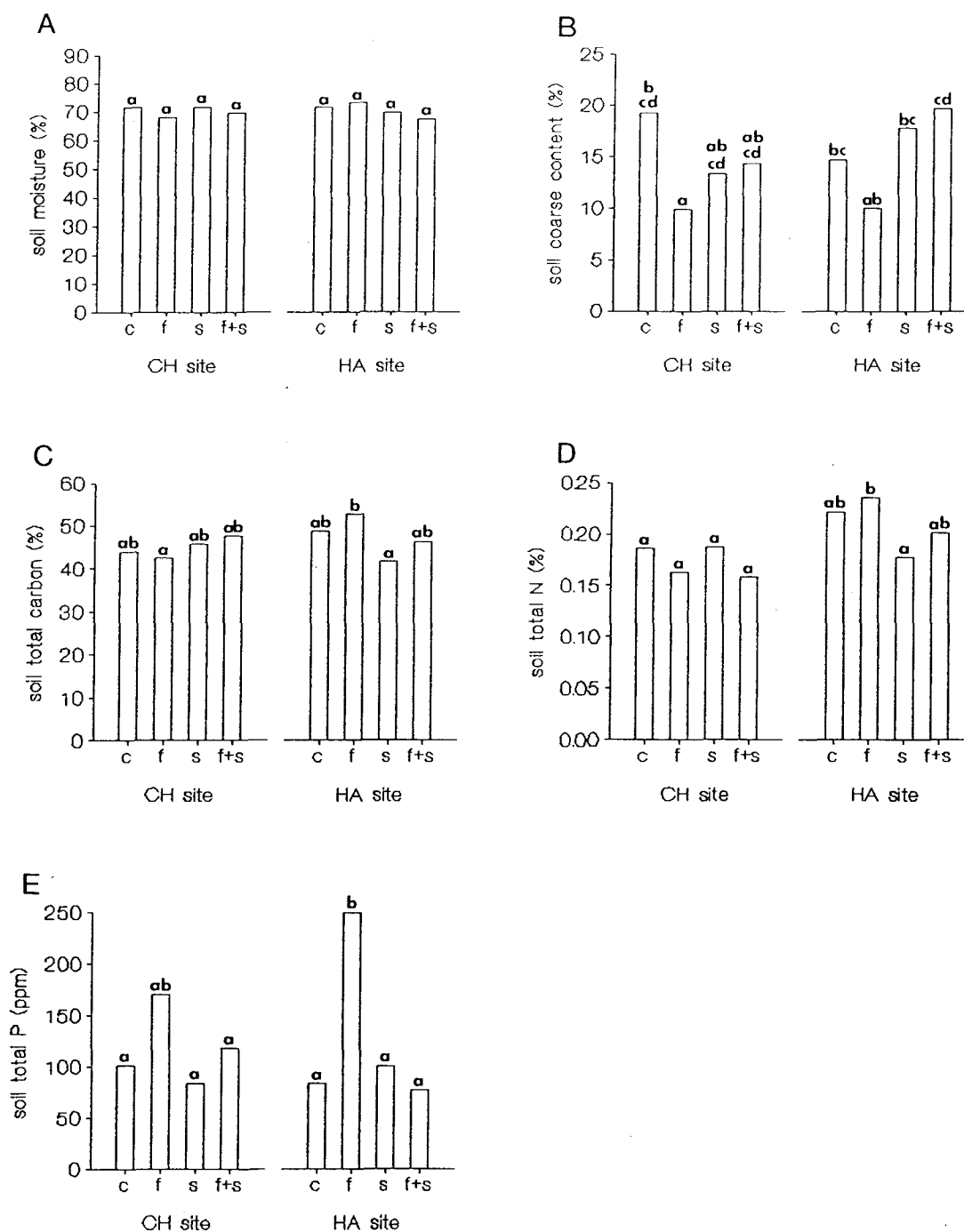


Figure 9. Site x treatment effects on soil variables (moisture, coarse content, total carbon, total nitrogen and total phosphorus) where western red cedar was planted using 3-way ANOVA. Fisher's protected least significant difference was applied to separate treatment means. Within a group, bars sharing the same letter are not significantly different ( $p > 0.05$ ). On the x axis, c=control, f=fertilized, and s=scarified.

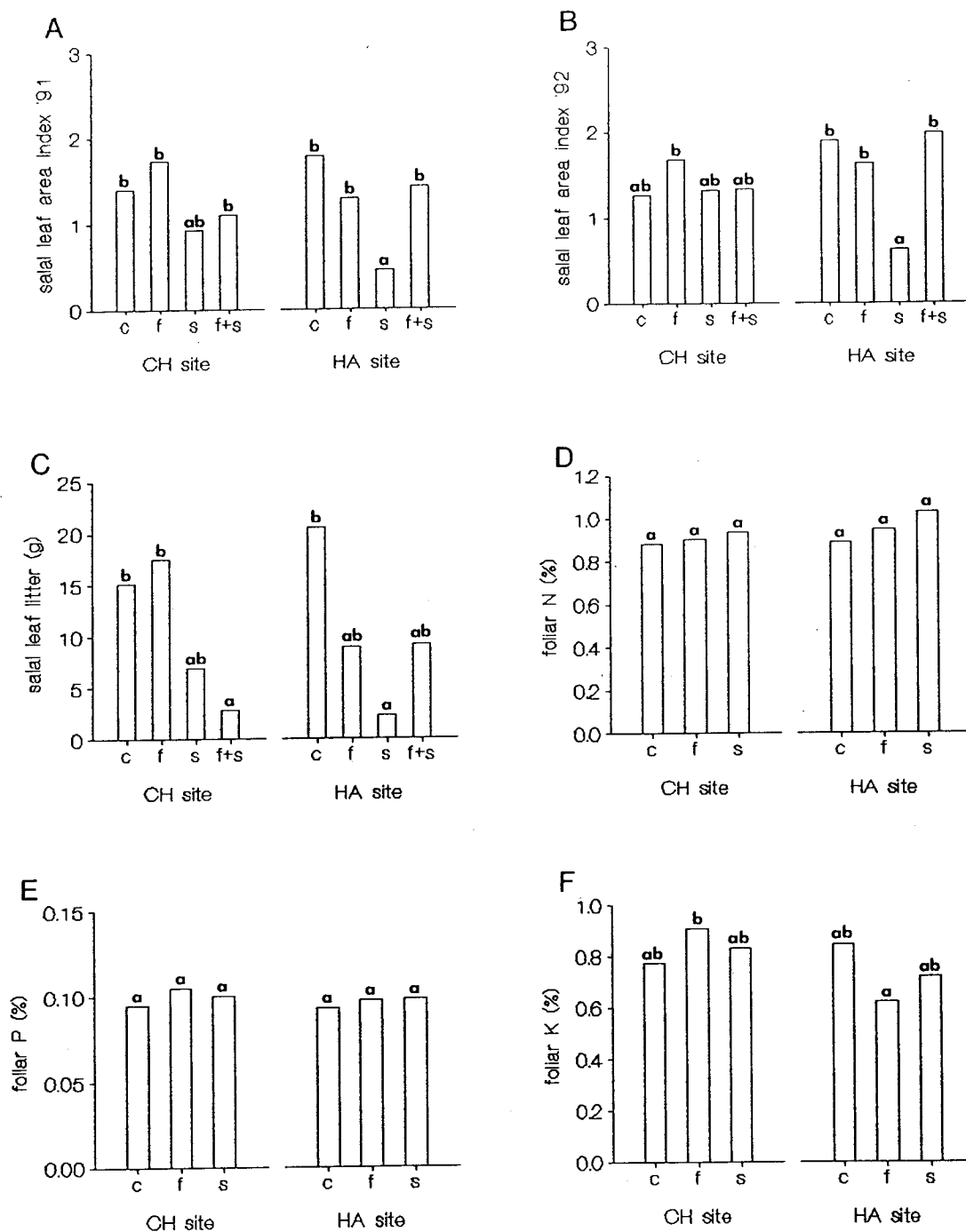


Figure 10. Site x treatment effects on salal performance (LAI, leaf litter, foliar nitrogen, foliar phosphorus, and foliar potassium) where western red cedar was planted using 3-way ANOVA. Fisher's protected least significant difference was applied to separate treatment means. Within a group, bars sharing the same letter are not significantly different ( $p > 0.05$ ). On the x axis, c=control, f=fertilized, and s=scarified.

10a). The highest mean leaf area index (1.8) was found on control HA sites. A similar, but less strong pattern was found in 1992 (Fig. 10b). Despite the large leaf area index of salal on fertilized plus scarified CH sites in both 1991 and 1992, salal leaf litter was lowest in those plots (Fig. 10c). There were no significant differences between treatments or sites in either the salal foliar nitrogen (Fig. 10d) or phosphorus concentrations (Fig. 10e). The mean foliar potassium concentration of salal on fertilized CH sites was significantly greater than that of salal at fertilized HA sites (Fig. 10f).

#### *c: Western red cedar performance*

2-year-old cedars height (Fig. 11a) and root collar diameter (Fig. 11b) measured in 1990 on fertilized plus scarified CH sites (132.9cm and 23.8mm, respectively) was mostly significantly greater than all other treatments in both sites. 4-year-old cedars height and root collar diameter measurements measured in 1992 showed that, predictably, fertilization and scarification significantly increased height in both CH and HA sites except for fertilized CH sites (Figures 11c and d). The added effect of fertilization plus scarification significantly increased height and root collar diameter of cedar on CH sites whereas on HA sites there was little difference in height and root collar diameter between field manipulations.

The colour index of cedar on CH sites showed little difference between treatments (Fig. 11e). However, on HA sites, colour index decreased with increasing field manipulation, i.e. cedar growing on fertilized plus scarified HA sites were significantly greener than control HA sites. Fertilization plus scarification increased foliar nitrogen and phosphorus of cedar in both CH and HA sites (Figures 11f and g). However, the only significant differences were that fertilized plus scarified CH sites had a higher foliar nitrogen than control CH and HA sites and fertilized CH sites. Also, fertilized plus scarified CH sites had a significantly higher foliar phosphorus than

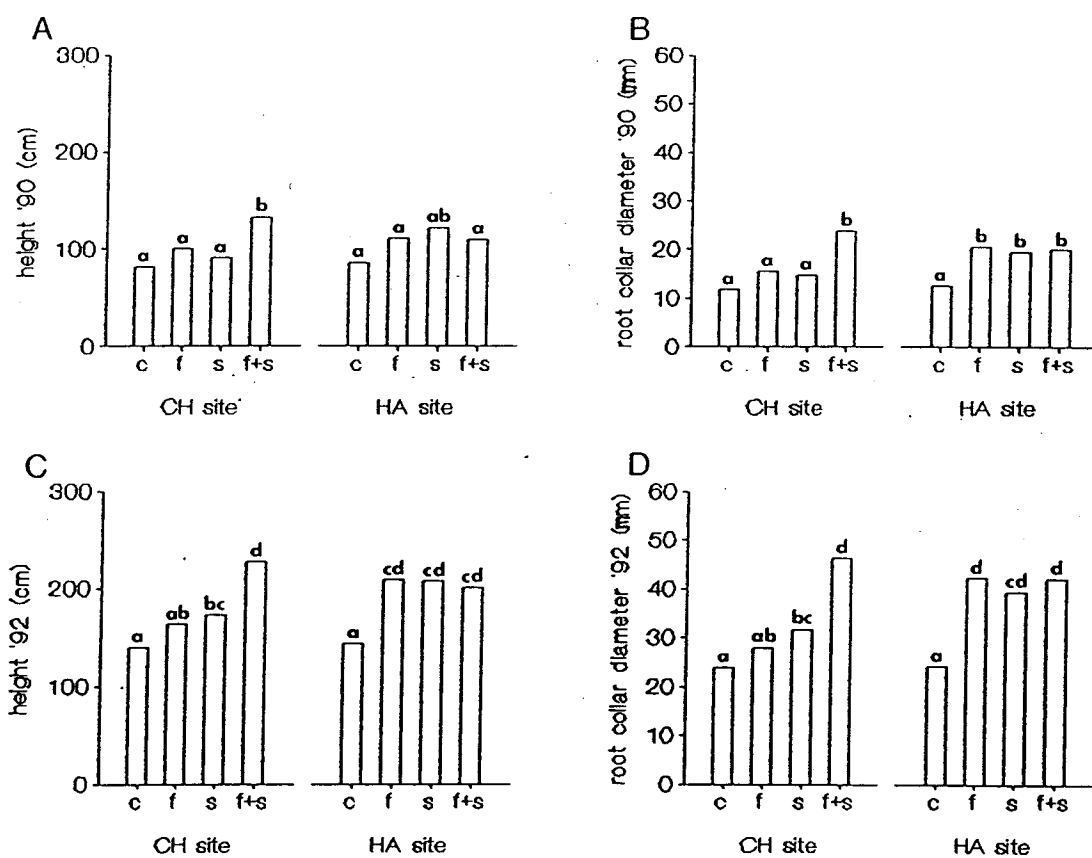


Figure 11. Site x treatment effects on western red cedar performance (height and root collar diameter) using 3-way ANOVA. Fisher's protected least significant difference was applied to separate treatment means. Within a group, bars sharing the same letter are not significantly different ( $p > 0.05$ ). On the x axis, c=control, f=fertilized, and s=scarified.

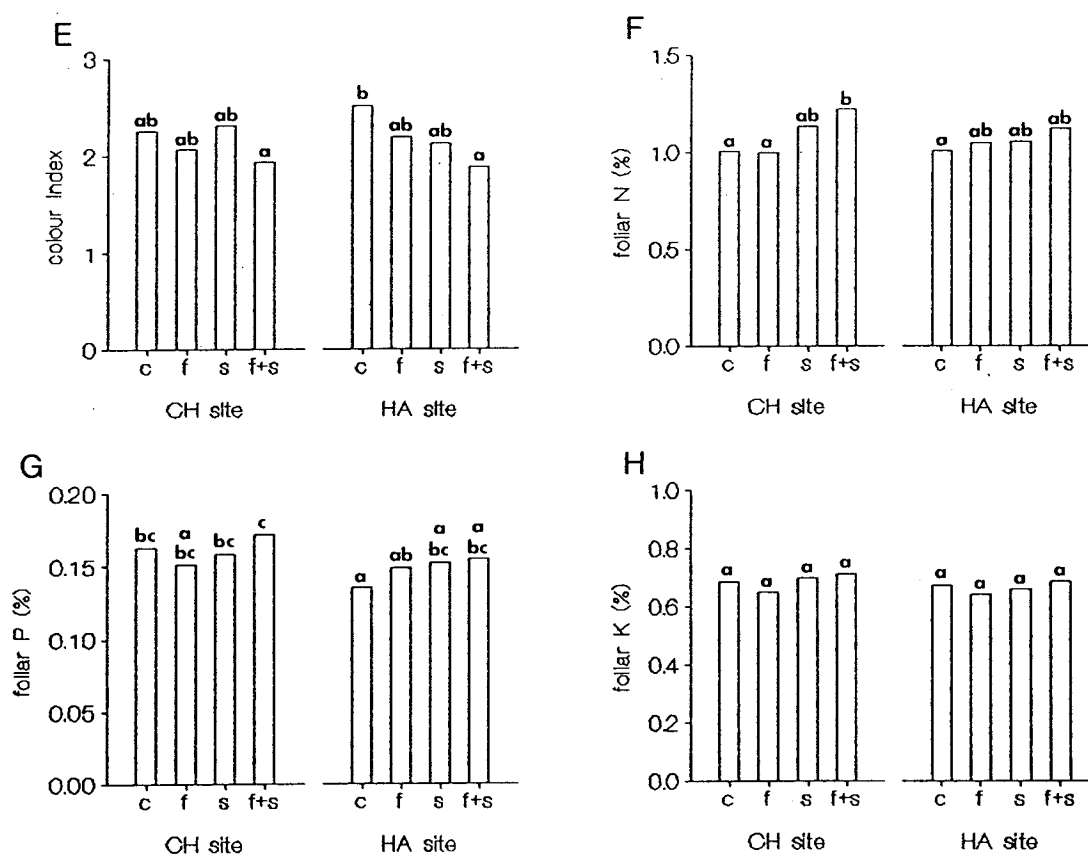


Figure 11 (cont.). Site x treatment effects on western red cedar performance (colour index, foliar nitrogen, foliar phosphorus, and foliar potassium) using 3-way ANOVA. Fisher's protected least significant difference was applied to separate treatment means. Within a group, bars sharing the same letter are not significantly different ( $p > 0.05$ ). On the x axis, c=control, f=fertilized, and s=scarified.

control HA sites. There were no significant differences in total foliar potassium concentration of cedar saplings between treatments at both sites (Fig. 11h).

## **Relationship between neighbouring non-crop vegetation and conifer growth using multiple regression.**

### ***WESTERN HEMLOCK***

#### ***Western hemlock saplings on control plots in CH sites:***

Over 67% of the variation in height (Table 7a) and over 56% of the variation in root collar diameter (Table 7b) of 2-year-old hemlocks were attributed to the presence of neighbours. *Hypochoeris radicata* and *G. shallon* were negatively correlated with height, while *B. spicant* and *E. angustifolium* were positively correlated. As with height, *G. shallon* was also negatively correlated with root collar diameter of hemlock, while *E. angustifolium* was positively correlated.

Over 70% of the variation in height (Table 7c) and over 82% of the variation in root collar diameter (Table 7d) of 4-year-old hemlocks were attributed to the presence of neighbours. Unlike the height model of 2-year-old hemlocks, *G. shallon* was no longer a significant variable. *Hypochoeris radicata* was still negatively correlated with height, while *A. margaritaceae*, *M. muralis*, and *Vaccinium* sp. were positively correlated with height. However, *M. muralis* was not significant in the model on its own. *Anaphalis margaritaceae*, *M. muralis*, and *Vaccinium* sp. were positively correlated with root collar diameter, while *H. radicata* and *G. shallon* were negatively correlated with root collar diameter.



Table 7. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western hemlock saplings on control plots in CH sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old hemlocks (1990)  
N=16; R=0.821;  $R^2=0.675$ ; adjusted  $R^2=0.556$

ANOVA p-value=0.010

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Epilobium angustifolium</i>	0.486	2.770	0.018
<i>Hypochoeris radicata</i>	-0.458	-2.553	0.027
<i>Gaultheria shallon</i>	-0.385	-2.010	0.070
<i>Blechnum spicant</i>	0.366	1.876	0.087

b. Dependent variable: root collar diameter of 2-year-old hemlocks (1990)

N=16; R=0.749;  $R^2=0.561$ ; adjusted  $R^2=0.493$

ANOVA p-value=0.005

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Gaultheria shallon</i>	-0.580	-3.118	0.008
<i>Epilobium angustifolium</i>	0.571	3.068	0.009

c. Dependent variable: height of 4-year-old hemlocks (1992)

N=16; R=0.840;  $R^2=0.706$ ; adjusted  $R^2=0.599$

ANOVA p-value=0.006

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Menziesia ferruginea</i>	7.833	4.670	0.001
<i>Vaccinium sp.</i>	3.751	4.510	0.001
<i>Hypochoeris radicata</i>	-8.056	-4.466	0.001
<i>Mycelis muralis</i>	0.282	1.699	0.117

d. Dependent variable: root collar diameter of 4-year-old hemlocks (1992)

N=16; R=0.907;  $R^2=0.823$ ; adjusted  $R^2=0.734$

ANOVA p-value=0.002

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Menziesia ferruginea</i>	6.770	4.947	0.001
<i>Vaccinium sp.</i>	3.257	4.806	0.001
<i>Hypochoeris radicata</i>	-6.963	-4.740	0.001
<i>Gaultheria shallon</i>	-0.447	-2.869	0.017
<i>Mycelis muralis</i>	0.353	2.474	0.033

std coef = standard partial coefficient

***Western hemlock saplings on control plots in HA sites:***

Only 21.7% of the variation in height of 2-year-old hemlock (Table 8a) was attributed to neighbours, but 81% of the variation in root collar diameter (Table 8b) of 2-year-old hemlocks were attributed to neighbours. The only variable in the height model was *G. shallon*, which was negatively correlated. The only variable positively correlated with root collar diameter of hemlock was *B. spicant*, all the other variables were negatively correlated.

Over 85% of the variation in height (Table 8c) and over 64% of the variation in root collar diameter (Table 8d) of 4-year-old hemlocks could be attributed to the presence of neighbours. All the variables, except for *B. spicant*, were negatively correlated with height of hemlock. Both variables in the root collar diameter model, *G. shallon* and *V. oxycoccus*, were negatively correlated with root collar diameter.

***Western hemlock saplings on fertilized plots in CH sites:***

Over 48% of the variation in height (Table 9a) and over 64% of the variation in root collar diameter (Table 9b) of 2-year-old hemlocks could be attributed to the presence of neighbours. *Cornus canadensis* was negatively correlated with height while *R. laxiflorum* and *R. spectabilis* showed positive correlations. *Cornus canadensis* was also negatively correlated with root collar diameter but, in contrast to the model for height, *R. laxiflorum* was negatively correlated with root collar diameter. *Gaultheria shallon*, which was removed from the height model because it was not significant, was negatively correlated with root collar diameter. *Epilobium angustifolium*, like *R. laxiflorum*, was positively correlated with root collar diameter.

Over 53% of the variation in height (Table 9c) and over 74% of the variation in root collar diameter (Table 9d) of 4-year-old hemlocks were attributed to the presence of neighbours. *Gaultheria shallon* showed a negative correlation to height of hemlock, while *M. muralis* and *T. plicata* were positively correlated. Similar to the height

Table 8. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western hemlock saplings on control plots in HA sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old hemlocks (1990)  
N=16; R=0.466;  $R^2=0.217$ ; adjusted  $R^2=0.161$

ANOVA p-value=0.069

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Gaultheria shallon</i>	-0.466	-1.969	0.069

b. Dependent variable: root collar diameter of 4-year-old hemlocks (1990)

N=16; R=0.900;  $R^2=0.810$ ; adjusted  $R^2=0.684$

ANOVA p-value=0.007

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Cornus canadensis</i>	-0.938	-4.253	0.002
<i>Dryopteris expansa</i>	-5.704	-4.105	0.003
<i>Blechnum spicant</i>	5.555	3.874	0.004
<i>Ribes laxiflorum</i>	-2.049	-3.793	0.004
<i>Gaultheria shallon</i>	-0.557	-3.612	0.006
<i>Hypochoeris radicata</i>	-0.423	-2.228	0.053

c. Dependent variable: height of 4-year-old hemlocks (1992)

N=16; R=0.923;  $R^2=0.852$ ; adjusted  $R^2=0.777$

ANOVA p-value=0.001

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Gaultheria shallon</i>	-0.638	-4.726	0.001
<i>Rubus spectabilis</i>	-1.016	-3.703	0.004
<i>Blechnum spicant</i>	1.000	3.393	0.007
<i>Vaccinium oxycoccus</i>	-0.448	-2.510	0.031
<i>Sambucus racemosa</i>	-0.301	-1.923	0.083

d. Dependent variable: root collar diameter of 4-year-old hemlocks (1992)

N=16; R=0.800;  $R^2=0.641$ ; adjusted  $R^2=0.585$

ANOVA p-value=0.001

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Gaultheria shallon</i>	-0.628	-3.739	0.002
<i>Vaccinium oxycoccus</i>	-0.413	-2.458	0.029

std coef = standard partial coefficient

Table 9. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western hemlock saplings on fertilized plots in CH sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old hemlocks (1990)  
N=16; R=0.694;  $R^2=0.482$ ; adjusted  $R^2=0.353$

ANOVA p-value=0.042

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Rubus spectabilis</i>	0.448	2.131	0.054
<i>Ribes laxiflorum</i>	0.434	2.067	0.061
<i>Cornus canadensis</i>	-0.371	-1.761	0.104

b. Dependent variable: root collar diameter of 2-year-old hemlocks (1990)

N=16; R=0.804;  $R^2=0.647$ ; adjusted  $R^2=0.519$

ANOVA p-value=0.015

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Cornus canadensis</i>	-0.871	-3.536	0.005
<i>Epilobium angustifolium</i>	1.692	3.345	0.007
<i>Ribes laxiflorum</i>	-1.397	-2.791	0.018
<i>Gaultheria shallon</i>	-0.507	-2.547	0.027

c. Dependent variable: height of 4-year-old hemlocks (1992)

N=16; R=0.732;  $R^2=0.537$ ; adjusted  $R^2=0.421$

ANOVA p-value=0.023

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Mycelis muralis</i>	0.470	2.307	0.040
<i>Gaultheria shallon</i>	-0.419	-2.036	0.064
<i>Thuja plicata</i>	0.384	1.910	0.080

d. Dependent variable: root collar diameter of 4-year-old hemlocks (1992)

N=16; R=0.861;  $R^2=0.742$ ; adjusted  $R^2=0.677$

ANOVA p-value=0.001

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Gaultheria shallon</i>	-0.674	-4.459	0.001
<i>Vaccinium sp.</i>	-0.748	-4.358	0.001
<i>Epilobium angustifolium</i>	0.638	3.777	0.003

std coef = standard partial coefficient

model, *G. shallon* was negatively correlated with root collar diameter, as was *Vaccinium sp.*, while *E. angustifolium* was positively correlated.

***Western hemlock saplings on fertilized plots in HA sites:***

About one-third of the variation in height (Table 10a) and over 55% of the variation in root collar diameter (Table 10b) of 2-year-old hemlocks were attributed to the presence of neighbouring non-crop vegetation. *Epilobium angustifolium* was negatively correlated with height and *M. muralis* was positively correlated. Similar to the height model, *E. angustifolium* was negatively correlated with root collar diameter and *M. muralis* was positively correlated with root collar diameter.

68% of the variation in height (Table 10c) and over 80% of the variation in root collar diameter (Table 10d) of 4-year-old hemlocks were attributed to the presence of neighbours. Of the four variables in the model *B. spicant* was the only one negatively correlated with height. However, *B. spicant* and *D. expansa* were significantly correlated with each other with tolerance values of 0.054 and 0.053, respectively. *Blechnum spicant* and *E. angustifolium* were both negatively correlated with root collar diameter, while *H. radicata*, *M. muralis*, *R. spectabilis*, and *D. expansa* were positively correlated with root collar diameter. As in the height model, *B. spicant* and *Dryopteris e.* were significantly correlated with each other with tolerance values of 0.054 and 0.052, respectively.

***Western hemlock saplings on scarified plots in CH sites:***

Only about one quarter of the variation in height (Table 11a) and root collar diameter (Table 11b) of 2-year-old hemlocks could be attributed to the presence of neighbouring non-crop vegetation. The height model was not statistically significant. The root collar diameter model was also not significant but is noteworthy that *G. shallon* was negatively correlated with root collar diameter.

Table 10. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western hemlock saplings on fertilized plots in HA sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old hemlocks (1990)  
N=16; R=0.594;  $R^2=0.353$ ; adjusted  $R^2=0.253$

ANOVA p-value=0.059

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Mycelis muralis</i>	0.691	2.619	0.021
<i>Epilobium angustifolium</i>	-0.472	-1.790	0.097

b. Dependent variable: root collar diameter of 2-year-old hemlocks (1990)

N=16; R=0.744;  $R^2=0.554$ ; adjusted  $R^2=0.486$

ANOVA p-value=0.005

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Epilobium angustifolium</i>	-0.849	-3.879	0.002
<i>Mycelis muralis</i>	0.649	2.963	0.011

c. Dependent variable: height of 4-year-old hemlocks (1992)

N=16; R=0.824;  $R^2=0.680$ ; adjusted  $R^2=0.563$

ANOVA p-value=0.009

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Mycelis muralis</i>	0.720	3.678	0.004
<i>Blechnum spicant</i>	-1.722	-2.342	0.039
<i>Dryopteris expansa</i>	1.418	1.906	0.083
<i>Hypochoeris radicata</i>	0.324	1.775	0.104

d. Dependent variable: root collar diameter of 4-year-old hemlocks (1992)

N=16; R=0.895;  $R^2=0.802$ ; adjusted  $R^2=0.669$

ANOVA p-value=0.009

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Mycelis muralis</i>	0.812	4.478	0.002
<i>Hypochoeris radiacata</i>	0.684	3.605	0.006
<i>Epilobium angustifolium</i>	-0.567	-2.832	0.020
<i>Blechnum spicant</i>	-1.704	-2.660	0.026
<i>Dryopteris expansa</i>	1.629	2.491	0.034
<i>Rubus spectabilis</i>	0.352	2.237	0.052

std coef = standard partial coefficient

Table 11. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western hemlock saplings on scarified plots in CH sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old hemlocks (1990)  
N=16; R=0.481;  $R^2=0.231$ ; adjusted  $R^2=0.039$

ANOVA p-value=0.350

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Rubus spectabilis</i>	-0.367	-1.444	0.174
<i>Vaccinium oxycoccus</i>	4.068	1.309	0.215
<i>Cornus canadensis</i>	-4.026	-1.295	0.220

b. Dependent variable: root collar diameter of 2-year-old hemlocks (1990)

N=16; R=0.498;  $R^2=0.248$ ; adjusted  $R^2=0.060$

ANOVA p-value=0.314

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Gaultheria shallon</i>	-0.364	-1.433	0.177
<i>Vaccinium oxycoccus</i>	3.901	1.272	0.228
<i>Cornus canadensis</i>	-3.810	-1.242	0.238

c. Dependent variable: height of 4-year-old hemlocks (1992)

N=16; R=0.552;  $R^2=0.305$ ; adjusted  $R^2=0.131$

ANOVA p-value=0.210

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Cornus canadensis</i>	-2.408	-1.969	0.072
<i>Vaccinium oxycoccus</i>	2.256	1.877	0.085
<i>Hypochoeris radicata</i>	0.447	1.707	0.114

d. Dependent variable: root collar diameter of 4-year-old hemlocks (1992)

N=16; R=0.696;  $R^2=0.485$ ; adjusted  $R^2=0.356$

ANOVA p-value=0.041

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Blechnum spicant</i>	-0.532	-2.559	0.025
<i>Cornus canadensis</i>	-2.353	-2.333	0.038
<i>Vaccinium oxycoccus</i>	2.191	2.174	0.050

std coef = standard partial coefficient

Over 30% of the variation in height (Table 11c) and over 48% of the variation in root collar diameter (Table 11d) of 4-year-old hemlocks could be attributed to the presence of neighbours. The height model was not significant. *Blechnum spicant* and *C. canadensis* were negatively correlated with root collar diameter, while *V. ovalifolium* was positively correlated. However, *V. ovalifolium* and *C. canadensis* were significantly correlated with each other with tolerance values of 0.042.

***Western hemlock saplings on scarified plots in HA sites:***

Over 45% of the variation in height (Table 12a) and over 35% of the variation in root collar diameter (Table 12b) of 2-year-old hemlocks could be accounted for by the presence of neighbours. *Epilobium angustifolium* was negatively correlated with height but *R. laxiflorum* showed a positive correlation. The only species variable in the root collar diameter model was *Epilobium angustifolium*, which was negatively correlated with root collar diameter.

Approximately one half of the variation in height (Table 12c) and over 67% of the variation in root collar diameter (Table 12d) of 4-year-old hemlocks could be attributed to the presence of neighbours. All the variables in the height model were negatively correlated, however *G. shallon* was not a significant variable on its own. The only species variable in the root collar diameter model was *Bryophyte sp.*, which was negatively correlated.

***Western hemlock saplings on fertilized plus scarified plots in CH sites:***

Only 13.2% of the variation in height (Table 13a) and 18.4% of the variation in root collar diameter (Table 13b) of 2-year-old hemlocks were attributed to neighbouring non-crop vegetation. Both variables in the height model, *Cornus canadensis* and *Sambucus racemosa*, were negatively correlated, however, the model was not significant. *Blechnum spicant* was positively correlated with root collar



Table 12. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western hemlock saplings on scarified plots in HA sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old hemlocks (1990)  
N=16; R=0.678;  $R^2=0.459$ ; adjusted  $R^2=0.369$

ANOVA p-value=0.025

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Epilobium angustifolium</i>	-0.498	-2.316	0.039
<i>Ribes laxiflorum</i>	0.385	1.791	0.098

b. Dependent variable: root collar diameter of 2-year-old hemlocks (1990)

N=16; R=0.597;  $R^2=0.356$ ; adjusted  $R^2=0.306$

ANOVA p-value=0.019

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Epilobium angustifolium</i>	-0.597	-2.680	0.019

c. Dependent variable: height of 4-year-old hemlocks (1992)

N=16; R=0.721;  $R^2=0.519$ ; adjusted  $R^2=0.388$

ANOVA p-value=0.039

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Bryophyte sp.</i>	-0.518	-2.325	0.040
<i>Rubus spectabilis</i>	-0.448	-1.987	0.072
<i>Gaultheria shallon</i>	-0.314	-1.395	0.191

d. Dependent variable: root collar diameter of 4-year-old hemlocks (1992)

N=16; R=0.676;  $R^2=0.458$ ; adjusted  $R^2=0.416$

ANOVA p-value=0.006

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Bryophyte sp.</i>	-0.676	-3.311	0.006

std coef = standard partial coefficient

Table 13. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western hemlock saplings on fertilized plus scarified plots in CH sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old hemlocks (1990)  
N=16; R=0.363;  $R^2=0.132$ ; adjusted  $R^2=0.000$

ANOVA p-value=0.400

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Sambucus racemosa</i>	-0.282	-1.085	0.298
<i>Cornus canadensis</i>	-0.262	-1.007	0.332

b. Dependent variable: root collar diameter of 2-year-old hemlocks (1990)

N=16; R=0.428;  $R^2=0.184$ ; adjusted  $R^2=0.058$

ANOVA p-value=0.268

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Blechnum spicant</i>	0.390	1.490	0.160
<i>Mycelis muralis</i>	-0.323	-1.234	0.239

c. Dependent variable: height of 4-year-old hemlocks (1992)

N=16; R=0.502;  $R^2=0.252$ ; adjusted  $R^2=0.137$

ANOVA p-value=0.152

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Vaccinium oxycoccus</i>	-3.215	-2.012	0.065
<i>Mycelis muralis</i>	3.040	1.902	0.080

d. Dependent variable: root collar diameter of 4-year-old hemlocks (1992)

N=16; R=0.813;  $R^2=0.661$ ; adjusted  $R^2=0.537$

ANOVA p-value=0.012

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Vaccinium oxycoccus</i>	-4.104	-3.367	0.006
<i>Mycelis muralis</i>	3.881	3.170	0.009
<i>Cornus canadensis</i>	0.463	2.474	0.031
<i>Bryophyte sp.</i>	0.396	2.193	0.051

std coef = standard partial coefficient

diameter, while *M. muralis* was negatively correlated. However, like the model for height, both variables were not significant.

Approximately one-quarter of the variation in height (Table 13c) and over 66% of the variation in root collar diameter (Table 13d) of 4-year-old hemlocks were attributed to the presence of neighboring non-crop vegetation. *Cornus canadensis* was negatively correlated with height but *M. muralis* was positively correlated. However, the model was not significant. *Vaccinium ovalifolium* was negatively correlated with root collar diameter, while *M. muralis*, *C. canadensis*, and *Bryophyte sp.* were positively correlated. However, *R. laxiflorum* and *M. muralis* were correlated with each other with tolerance values of 0.021.

***Western hemlock saplings on fertilized plus scarified plots in HA sites:***

Over 40% of the variation in height (Table 14a) and over 29% of the variation in root collar diameter (Table 14b) of 2-year-old hemlocks could be accountable for by the presence of neighbours. Although two of the variables, *E. angustifolium* and *M. muralis* were significant in the height model, the p-value for the entire model was not significant. *Mycelis muralis*, the only species variable in the root collar diameter model, was negatively correlated.

Only approximately one-tenth of the variation in height (Table 14c) and root collar diameter (Table 14d) of 4-year-old hemlocks were attributed to neighbours, but neither of the models was significant.

Table 14. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western hemlock saplings on fertilized plus scarified plots in HA sites measured in 1991 and 1992, respectively.

a. Dependent variable: height of 2-year-old hemlocks (1990)  
N=16; R=0.634;  $R^2=0.402$ ; adjusted  $R^2=0.185$

ANOVA p-value=0.190

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Epilobium angustifolium</i>	1.736	2.530	0.028
<i>Mycelis muralis</i>	-1.372	-2.144	0.055
<i>Blechnum spicant</i>	0.569	1.561	0.147
<i>Rubus spectabilis</i>	-0.538	-1.341	0.207

b. Dependent variable: root collar diameter of 2-year-old hemlocks (1990)

N=16; R=0.544;  $R^2=0.296$ ; adjusted  $R^2=0.246$

ANOVA p-value=0.029

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Mycelis muralis</i>	-0.544	-2.426	0.029

c. Dependent variable: height of 4-year-old hemlocks (1992)

N=16; R=0.349;  $R^2=0.122$ ; adjusted  $R^2=0.059$

ANOVA p-value=0.185

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Ribes laxiflorum</i>	0.349	1.394	0.185

d. Dependent variable: root collar diameter of 4-year-old hemlocks (1992)

N=16; R=0.342;  $R^2=0.117$ ; adjusted  $R^2=0.054$

ANOVA p-value=0.195

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Rubus spectabilis</i>	-0.342	-1.361	0.195

std coef = standard partial coefficient

## **WESTERN RED CEDAR**

### ***Western red cedar saplings on control plots in CH sites:***

The models for height (Table 15a) and root collar diameter (Table 15b) of 2-year-old cedars in 1990 were similar, however, *G. shallon* and *R. sylvaticus* were included in the height model but not in the root collar diameter model. Over 72% of the variation in height and over 59% of the variation in root collar diameter was attributed to the abundance of neighbours. Although *G. shallon* was included in the height model, it was positively associated with the height of cedars. None of the variables were negatively correlated with height or root collar diameter. *Cornus canadensis* accounted for the most variation in the height ( $T=3.064$ ) and the root collar diameter model ( $T=3.456$ ).

72.0% of the variation in height (Table 15c) and over 51% of the variation in root collar diameter (Table 15d) of 4-year-old cedars were attributed to neighbours. Although *G. shallon* was included in the height model it was not significant. *Pteridium aquilinum* and *Mycelis muralis* were negatively associated with height, while *E. angustifolium*, *C. canadensis*, *Poa* sp., *H. radicata* and *G. shallon* were positively associated. Unlike height, the abundance of *Poa* sp. was negatively associated with root collar diameter.

### ***Western red cedar saplings on control plots in HA sites:***

Over 86% of the variation in height (Table 16a) and over 93% of the variation in root collar diameter (Table 16b) of 2-year-old cedars were attributed to neighbours (Tables 16a,b). *Gaultheria shallon*, *D. expansa* and *Vaccinium* sp. were negatively correlated with height, but the influence of *Vaccinium* sp. was not statistically significant. In contrast, *H. radicata* and *B. spicant* were positively correlated with height. Similar to the height model, *H. radicata*, *B. spicant*, and *E. angustifolium* were positively correlated with root collar diameter, but *Dryopteris e.*, *R. spectabilis*,

**Table 15.** Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2-and 4-year-old western red cedar saplings on control plots in CH sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old cedars (1990)  
N=16; R=0.849;  $R^2=0.721$ ; adjusted  $R^2=0.536$

ANOVA p-value=0.034

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Cornus canadensis</i>	0.599	3.064	0.013
<i>Hypochoeris radicata</i>	0.555	2.887	0.018
<i>Epilobium angustifolium</i>	0.485	2.300	0.047
<i>Gaultheria shallon</i>	0.478	2.256	0.050
<i>Blechnum spicant</i>	0.510	1.989	0.078
<i>Rubus spectabilis</i>	0.358	1.666	0.130

b. Dependent variable: root collar diameter of 2-year-old cedars (1990)

N=16; R=0.773;  $R^2=0.597$ ; adjusted  $R^2=0.451$

ANOVA p-value=0.029

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Cornus canadensis</i>	0.729	3.456	0.005
<i>Hypochoeris radicata</i>	0.527	2.634	0.023
<i>Epilobium angustifolium</i>	0.432	1.957	0.081
<i>Blechnum spicant</i>	0.404	1.924	0.081

c. Dependent variable: height of 4-year-old cedars (1992)

N=16; R=0.848;  $R^2=0.720$ ; adjusted  $R^2=0.474$

ANOVA p-value=0.077

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Epilobium angustifolium</i>	0.979	3.632	0.007
<i>Mycelis muralis</i>	-0.747	-2.834	0.022
<i>Poa sp.</i>	1.733	2.755	0.025
<i>Hypochoeris radicata</i>	0.623	2.735	0.026
<i>Cornus canadensis</i>	0.626	2.647	0.029
<i>Pteridium aquilinum</i>	-1.127	-2.135	0.065
<i>Gaultheria shallon</i>	0.506	1.844	0.102

d. Dependent variable: root collar diameter of 4-year-old cedars (1992)

N=16; R=0.715;  $R^2=0.511$ ; adjusted  $R^2=0.388$

ANOVA p-value=0.031

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Poa sp.</i>	-0.843	-2.846	0.015
<i>Rubus spectabilis</i>	0.827	2.757	0.017
<i>Cornus canadensis</i>	0.407	1.948	0.075

std coef = standard partial coefficient

Table 16. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western red cedar saplings on control plots in HA sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old cedars (1990)  
N=16; R=0.930;  $R^2=0.866$ ; adjusted  $R^2=0.799$

ANOVA p-value=0.000

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Blechnum spicant</i>	0.851	4.856	0.001
<i>Hypochoeris radicata</i>	0.976	2.959	0.014
<i>Gaultheria shallon</i>	-0.356	-2.421	0.036
<i>Dryopteris expansa</i>	-0.404	-2.408	0.037
<i>Vaccinium sp.</i>	-0.351	-1.105	0.295

b. Dependent variable: root collar diameter of 2-year-old cedars (1990)

N=16; R=0.968;  $R^2=0.936$ ; adjusted  $R^2=0.894$

ANOVA p-value=0.000

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Blechnum spicant</i>	1.481	5.001	0.001
<i>Hypochoeris radicata</i>	0.468	4.315	0.002
<i>Rubus spectabilis</i>	-1.035	-3.349	0.009
<i>Epilobium angustifolium</i>	0.455	1.991	0.078
<i>Dryopteris expansa</i>	-0.405	-1.913	0.088
<i>Gaultheria shallon</i>	-0.189	-1.402	0.194

c. Dependent variable: height of 4-year-old cedars (1992)

N=16; R=0.824;  $R^2=0.679$ ; adjusted  $R^2=0.598$

ANOVA p-value=0.003

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Dryopteris expansa</i>	11.289	4.081	0.002
<i>Sambucus racemosa</i>	-10.916	-3.949	0.002
<i>Vaccinium sp.</i>	0.473	2.842	0.015

d. Dependent variable: root collar diameter of 4-year-old cedars (1992)

N=16; R=0.844;  $R^2=0.713$ ; adjusted  $R^2=0.641$

ANOVA p-value=0.001

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Rubus spectabilis</i>	0.767	4.870	0.000
<i>Pteridium aquilinum</i>	1.795	3.037	0.010
<i>Poa sp.</i>	-1.526	-2.593	0.024

std coef = standard partial coefficient

and *G. shallon* were negatively correlated. However, the influence of *G. shallon* was not statistically significant.

Over 67% of the variation in height (Table 16c) and over 71% of the variation in root collar diameter (Table 16d) of 4-year-old cedars could be attributed to the presence of neighbours. *Sambucus racemosa* was negatively correlated with height while *Vaccinium sp.* and *D. expansa* were positively correlated. However, *S. racemosa* and *D. expansa* were highly correlated with each other as indicated by tolerance levels of 0.004 and 0.003, respectively. Similar to the height model, *S. racemosa* was negatively correlated with root collar diameter, but *P. aquilinum* and *H. radicata* were positively correlated. Also similar to the height model, *S. racemosa* and *P. aquilinum* were significantly correlated with a tolerance of 0.069 and 0.068, respectively.

***Western red cedar saplings on fertilized plots in CH sites:***

Only 19.0% of the variation in height (Table 17a) of 2-year-old cedars were attributed to neighbouring non-crop vegetation, but over 74% of the variation in root collar diameter (Table 17b) of 2-year-old cedar was attributed to neighbours. *Gaultheria shallon* was negatively correlated with root collar diameter, and accounted for most of the observed variation ( $T=-3.930$ ). *Rubus spectabilis*, *B. spicant*, and *H. radicata* were also negatively correlated with root collar diameter. In contrast, *P. aquilinum*, *E. angustifolium*, and *C. canadensis* were positively correlated with root collar diameter.

Over 83% of the variation in height (Table 17c) and 70% of the variation in root collar diameter (Table 17d) of 4-year-old cedars were attributed to the presence of neighbours. *Rubus spectabilis* and *R. laxiflorum* were negatively correlated with height, while *H. radicata*, *M. muralis*, and *Bryophyte sp.* showed positive correlations. However, *H. radicata* and *R. laxiflorum* were not significant to  $p>0.05$  on their own,



Table 17. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western red cedar saplings on fertilized plots in CH sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old cedars (1990)

N=16; R=0.436;  $R^2=0.190$ ; adjusted  $R^2=0.000$

ANOVA p-value=0.453

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Blechnum spicant</i>	0.327	1.227	0.243
<i>Vaccinium oxycoccus</i>	0.321	1.185	0.259
<i>Gaultheria shallon</i>	-0.134	-0.491	0.632

b. Dependent variable: root collar diameter of 2-year-old cedars (1990)

N=16; R=0.865;  $R^2=0.748$ ; adjusted  $R^2=0.528$

ANOVA p-value=0.054

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Gaultheria shallon</i>	-1.271	-3.930	0.004
<i>Pteridium aquilinum</i>	1.285	3.438	0.009
<i>Rubus spectabilis</i>	-0.581	-2.881	0.020
<i>Blechnum spicant</i>	-1.100	-2.876	0.021
<i>Cornus canadensis</i>	0.554	2.250	0.055
<i>Epilobium angustifolium</i>	0.671	2.166	0.062
<i>Hypochoeris radicata</i>	-0.413	-1.858	0.100

c. Dependent variable: height of 4-year-old cedars (1992)

N=16; R=0.912;  $R^2=0.833$ ; adjusted  $R^2=0.749$

ANOVA p-value=0.001

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Mycelis muralis</i>	0.764	5.370	0.000
<i>Rubus spectabilis</i>	-0.809	-5.282	0.000
<i>Bryophyte sp.</i>	0.637	4.237	0.002
<i>Ribes laxiflorum</i>	-0.360	-2.019	0.071
<i>Hypochoeris radicata</i>	0.340	1.901	0.087

d. Dependent variable: root collar diameter of 4-year-old cedars (1992)

N=16; R=0.837;  $R^2=0.700$ ; adjusted  $R^2=0.625$

ANOVA p-value=0.002

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Bryophyte sp.</i>	0.755	4.248	0.001
<i>Rubus spectabilis</i>	-0.786	-4.204	0.001
<i>Mycelis muralis</i>	0.607	3.530	0.004

std coef = standard partial coefficient

but they were significant to  $p > 0.10$ . As with height, root collar diameter was also negatively correlated with the presence of *R. spectabilis*, and positively correlated with *M. muralis* and *Bryophyte sp.*

***Western red cedar saplings on fertilized plots in HA sites:***

Over 52% of the variation in height (Table 18a) and over 59% of the variation in root collar diameter (Table 18b) of 2-year-old cedars were attributed to the presence of neighbours. *Pteridium aquilinum* and *Dryopteris expansa* were negatively correlated with height while *R. laxiflorum* and *M. muralis* were positively correlated with height. However, both *P. aquilinum* and *D. expansa* were not significant in the model on their own. *Pteridium aquilinum* and *Vaccinium sp.* were negatively correlated with root collar diameter but both were not significant in the model on their own, while *R. laxiflorum* was positively correlated with root collar diameter.

Over 62% of the variation in height (Table 18c) and over 73% of the variation in root collar diameter (Table 18d) of 4-year-old cedars could be attributed to neighbours. Although *T. heterophylla* was negatively correlated with height, it was not significant in the model on its own. *Epilobium angustifolium* and *R. laxiflorum* were both positively correlated with height. *Tsuga heterophylla* and *P. aquilinum* were negatively correlated with root collar diameter but the effect of *P. aquilinum* on its own was not significant in the model. *Ribes laxiflorum* was positively correlated with root collar diameter as it was for all height and root collar diameter measurements of cedar saplings on fertilized plots in HA sites (Tables 18a,b,c,d).

***Western red cedar saplings on scarified plots in CH sites:***

Over 47% of the variation in height (Table 19a) and only about one third of the variation in root collar diameter (Table 19b) of 2-year-old cedars were attributed to neighbouring non-crop vegetation. *Blechnum spicant* and *Vaccinium sp.* were

Table 18. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western red cedar saplings on fertilized plots in HA sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old cedars (1990)

N=16; R=0.724;  $R^2=0.525$ ; adjusted  $R^2=0.352$

ANOVA p-value=0.065

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Ribes laxiflorus</i>	0.767	3.051	0.011
<i>Mycelis muralis</i>	0.606	2.094	0.060
<i>Pteridium aquilinum</i>	-0.410	-1.750	0.108
<i>Dryopteris expansa</i>	-0.442	-1.485	0.166

b. Dependent variable: root collar diameter of 2-year-old cedars (1990)

N=16; R=0.773;  $R^2=0.598$ ; adjusted  $R^2=0.498$

ANOVA p-value=0.010

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Ribes laxiflorum</i>	0.679	3.667	0.003
<i>Pteridium aquilinum</i>	-0.237	-1.277	0.226
<i>Vaccinium sp.</i>	-0.184	-0.998	0.338

c. Dependent variable: height of 4-year-old cedars (1992)

N=16; R=0.788;  $R^2=0.621$ ; adjusted  $R^2=0.526$

ANOVA p-value=0.007

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Ribes laxiflorum</i>	0.516	2.851	0.015
<i>Epilobium angustifolium</i>	0.361	1.887	0.084
<i>Tsuga heterophylla</i>	-0.297	-1.533	0.151

d. Dependent variable: root collar diameter of 4-year-old cedars (1992)

N=16; R=0.859;  $R^2=0.738$ ; adjusted  $R^2=0.673$

ANOVA p-value=0.001

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Ribes laxiflorum</i>	0.641	4.237	0.001
<i>Tsuga heterophylla</i>	-0.293	-1.880	0.085
<i>Pteridium aquilinum</i>	-0.269	-1.731	0.109

std coef = standard partial coefficient

Table 19. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western red cedar saplings on scarified plots in CH sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old cedars (1990)  
N=16; R=0.687;  $R^2=0.472$ ; adjusted  $R^2=0.340$

ANOVA p-value=0.047

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Rubus spectabilis</i>	2.772	2.982	0.011
<i>Blechnum spicant</i>	-1.403	-2.885	0.014
<i>Vaccinium sp.</i>	-2.213	-2.587	0.024

b. Dependent variable: root collar diameter of 2-year-old cedars (1990)

N=16; R=0.566;  $R^2=0.321$ ; adjusted  $R^2=0.151$

ANOVA p-value=0.185

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Blechnum spicant</i>	-0.560	-1.990	0.070
<i>Rubus spectabilis</i>	0.529	1.938	0.076
<i>Gaultheria shallon</i>	0.397	1.521	0.154

c. Dependent variable: height of 4-year-old cedars (1992)

N=16; R=0.434;  $R^2=0.188$ ; adjusted  $R^2=0.063$

ANOVA p-value=0.258

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Rubus spectabilis</i>	0.380	1.519	0.153
<i>Ribes laxiflorum</i>	-0.185	-0.739	0.473

d. Dependent variable: root collar diameter of 4-year-old cedars (1992)

N=16; R=0.687;  $R^2=0.472$ ; adjusted  $R^2=0.435$

ANOVA p-value=0.003

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Rubus spectabilis</i>	0.687	3.539	0.003

std coef = standard partial coefficient

negatively correlated with height but *R. spectabilis* was positively correlated with height. *Gaultheria shallon* was positively correlated with root collar diameter but the model was not statistically significant.

Only 18.8% of the variation in height (Table 19c) of 4-year-old cedar was attributed to neighbours, but over 47% of the variation in root collar diameter (Table 19d) of 4-year-old cedars were attributed to neighbours. *Rubus spectabilis* was positively correlated and *R. laxiflorum* was negatively correlated with height, however the model was not significant. *Rubus spectabilis*, the only variable in the root collar diameter model, was positively correlated.

***Western red cedar saplings on scarified plots in HA sites:***

Over 35% of the variation in height (Table 20a) and approximately one half of the variation in root collar diameter (Table 20b) of 2-year-old cedars were attributed to the presence of neighbours. *Gaultheria shallon* and *Rubus spectabilis* were positively correlated with cedar height. Also, *Anaphalis margaritaceae* and *G. shallon* were positively correlated with root collar diameter, but the influence of *G. shallon* was not significant in the root collar diameter model on its own.

Over 96% of the variation in height (Table 20c) and over 98% of the variation in root collar diameter (Table 20d) of 4-year-old cedars were attributed to the presence of neighbours. Although much of the variation is accounted for, the large number of variables included in the model make it difficult to determine the principle variables. There was little difference between the models except that the root collar diameter model included two more variables, *S. racemosa* and *R. spectabilis*, which were negatively and positively correlated, respectively. It is important to note that *G. shallon* was positively correlated with height and root collar diameter.

Table 20. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western red cedar saplings on scarified plots in HA sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old cedars (1990)  
N=16; R=0.598;  $R^2=0.357$ ; adjusted  $R^2=0.258$

ANOVA p-value=0.057

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Rubus spectabilis</i>	0.513	2.259	0.042
<i>Gaultheria shallon</i>	0.425	1.875	0.083

b. Dependent variable: root collar diameter of 2-year-old cedars (1990)

N=16; R=0.693;  $R^2=0.481$ ; adjusted  $R^2=0.401$

ANOVA p-value=0.014

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Anaphalis margaritaceae</i>	0.611	3.053	0.009
<i>Gaultheria shallon</i>	0.341	1.707	0.111

c. Dependent variable: height of 4-year-old cedars (1992)

N=16; R=0.980;  $R^2=0.961$ ; adjusted  $R^2=0.903$

ANOVA p-value=0.001

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Equisetum sylvaticum</i>	-0.814	-6.500	0.001
<i>Vaccinium sp.</i>	-0.502	-5.670	0.001
<i>Gaultheria shallon</i>	0.616	5.077	0.002
<i>Epilobium angustifolium</i>	-0.958	-3.985	0.007
<i>Anaphalis margaritaceae</i>	0.485	3.957	0.007
<i>Dryopteris expansa</i>	0.523	3.611	0.011
<i>Bryophyte sp.</i>	0.330	2.900	0.027
<i>Blechnum spicant</i>	-0.335	-2.777	0.032
<i>Hypochoeris radicata</i>	0.622	2.564	0.043

d. Dependent variable: root collar diameter of 4-year-old cedars (1992)

N=16; R=0.994;  $R^2=0.989$ ; adjusted  $R^2=0.959$

ANOVA p-value=0.002

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Epilobium angustifolium</i>	-1.630	-10.085	0.001
<i>Gaultheria shallon</i>	0.815	9.519	0.001
<i>Equisetum sylvaticum</i>	-0.766	-8.819	0.001
<i>Hypochoeris radicata</i>	1.308	7.267	0.002
<i>Vaccinium sp.</i>	-0.388	-6.548	0.003
<i>Bryophyte sp.</i>	0.527	6.222	0.003
<i>Dryopteris expansa</i>	0.478	5.049	0.007
<i>Anaphalis margaritaceae</i>	0.759	4.818	0.009
<i>Blechnum spicant</i>	-0.606	-4.668	0.010
<i>Sambucus racemosa</i>	-0.624	-4.320	0.012
<i>Rubus spectabilis</i>	0.379	3.787	0.019

***Western red cedar saplings on fertilized + scarified plots in CH sites:***

Only 20.2% of the variation in height (Table 21a) and 9.5% of the variation in root collar diameter (Table 21b) of 2-year-old cedars could be attributed to neighbouring non-crop vegetation. Both models were not statistically significant.

Over 33% of the variation in height (Table 21c) and over 39% of the variation in root collar diameter (Table 21d) of 4-year-old cedars were attributed to neighbours. *Bryophyte sp.*, the only species associated with height of cedar, was negatively correlated. *Bryophyte sp.* was also negatively correlated with root collar diameter but *T. heterophylla* was positively correlated.

***Western red cedar saplings on fertilized + scarified plots in HA sites:***

Approximately three-quarters of the variation in height (Table 22a) and over 63% of the variation in root collar diameter (Table 22b) of 2-year-old cedars could be attributed to the presence of neighbours. All four variables included in the height model were positively correlated with height. As with the height model all the species except *Mycelis a.* were positively correlated with root collar diameter of cedar. However, the effect of *B. spicant* and *E. angustifolium* on their own were not significant in the model.

71% of the variation in height (Table 22c) and over 72% of the variation in root collar diameter (Table 22d) of 4-year-old cedars could be attributed to the presence of neighbours. *Hypochoeris radicata*, *B. spicant*, and *E. angustifolium* were positively correlated with height, while *R. laxiflorum* and *Thuja plicata* showed a negative correlation. Similar to the height model, *H. radicata*, *B. spicant*, and *E. angustifolium* were positively correlated with root collar diameter, while *T. plicata* was negatively correlated.

Table 21. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western red cedar saplings on fertilized plus scarified plots in CH sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old cedars (1990)

N=16; R=0.449;  $R^2=0.202$ ; adjusted  $R^2=0.079$

ANOVA p-value=0.231

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Cornus canadensis</i>	-0.710	-1.769	0.100
<i>Hypochoeris radicata</i>	0.657	1.635	0.126

b. Dependent variable: root collar diameter of 2-year-old cedars (1990)

N=16; R=0.308;  $R^2=0.095$ ; adjusted  $R^2=0.030$

ANOVA p-value=0.246

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Epilobium angustifolium</i>	-0.308	-1.210	0.246

c. Dependent variable: height of 4-year-old cedars (1992)

N=16; R=0.576;  $R^2=0.332$ ; adjusted  $R^2=0.285$

ANOVA p-value=0.019

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Bryophyte sp.</i>	-0.576	-2.640	0.019

d. Dependent variable: root collar diameter of 4-year-old cedars (1992)

N=16; R=0.630;  $R^2=0.397$ ; adjusted  $R^2=0.304$

ANOVA p-value=0.037

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Tsuga heterophylla</i>	0.582	2.515	0.026
<i>Bryophyte sp.</i>	-0.533	-2.307	0.038

std coef = standard partial coefficient



Table 22. Multiple regression models determining the correlation between the leaf area index of neighbouring species and the growth of 2- and 4-year-old western red cedar saplings on fertilized plus scarified plots in HA sites measured in 1990 and 1992, respectively.

a. Dependent variable: height of 2-year-old cedars (1990)  
N=16; R=0.858;  $R^2=0.735$ ; adjusted  $R^2=0.639$

ANOVA p-value=0.003

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Blechnum spicant</i>	0.642	4.082	0.002
<i>Epilobium angustifolium</i>	0.444	2.741	0.019
<i>Pinus contorta</i>	0.353	2.236	0.047
<i>Hypochoeris radicata</i>	0.352	2.190	0.051

b. Dependent variable: root collar diameter of 2-year-old cedars (1990)

N=16; R=0.795;  $R^2=0.631$ ; adjusted  $R^2=0.386$

ANOVA p-value=0.098

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Hypochoeris radicata</i>	1.392	3.077	0.013
<i>Mycelis muralis</i>	-2.528	-2.465	0.036
<i>Ribes laxiflorum</i>	2.116	2.297	0.047
<i>Rubus spectabilis</i>	0.936	1.894	0.091
<i>Blechnum spicant</i>	0.369	1.788	0.107
<i>Epilobium angustifolium</i>	0.362	1.654	0.132

c. Dependent variable: height of 4-year-old cedars (1992)

N=16; R=0.843;  $R^2=0.710$ ; adjusted  $R^2=0.565$

ANOVA p-value=0.016

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Blechnum spicant</i>	0.431	2.455	0.034
<i>Epilobium angustifolium</i>	0.440	2.452	0.034
<i>Thuja plicata</i>	-2.991	-2.145	0.058
<i>Hypochoeris radicata</i>	2.966	2.119	0.060
<i>Ribes laxiflorum</i>	-0.353	-2.049	0.068

d. Dependent variable: root collar diameter of 4-year-old cedars (1992)

N=16; R=0.854;  $R^2=0.729$ ; adjusted  $R^2=0.630$

ANOVA p-value=0.004

<u>Independent variables</u>	<u>std coef</u>	<u>T</u>	<u>P-value</u>
<i>Epilobium angustifolium</i>	0.417	2.770	0.028
<i>Hypochoeris radicata</i>	5.421	-2.553	0.001
<i>Thuja plicata</i>	-5.396	-2.010	0.001
<i>Blechnum spicant</i>	0.411	1.876	0.027

std coef = standard partial coefficient

## **Relationship between salal leaf area index and conifer growth using the multiple regression models.**

Tables 23 and 24 summarize the influence of the leaf area index of salal on height and root collar diameter of 2- and 4-year-old western hemlock and western red cedar, respectively, measured in 1990 and 1992.

Height and root collar diameter of 2- and 4-year-old hemlock was significantly negatively correlated with salal abundance on control CH sites, fertilized CH sites, and control HA sites. The greatest influence from salal on hemlock was on the root collar diameter of 4-year-old hemlock on fertilized CH sites,  $R^2=0.428$ . From 1990 to 1992, the influence of salal appeared to diminish on control CH sites but increased on fertilized CH sites and control HA sites.

Height and root collar diameter of 2-year-old cedars were significantly negatively correlated with the abundance of salal on control HA sites and fertilized CH sites, but not 4-year-old cedars. Cedar performance was significantly positively correlated with salal abundance on control CH sites, scarified CH sites, and scarified HA sites.

Table 23. Summary of the correlations between the leaf area index of salal and western hemlock height and root collar diameter using the multiple regression models. "np" means salal is not present in model. "+" and "-" mean that salal is positively and negatively correlated with hemlock growth, respectively.

	<u>correlation</u>	<u>R<sup>2</sup></u>	<u>p</u>
<i>CH control sites:</i>			
1990 (height)	-	0.119	0.070
1990 (root collar diameter)	-	0.328	0.008
1992 (height)	np	np	np
1992 (root collar diameter)	-	0.146	0.017
<i>HA control sites:</i>			
1990 (height)	-	0.217	0.069
1990 (root collar diameter)	-	0.275	0.006
1992 (height)	-	0.332	0.001
1992 (root collar diameter)	-	0.387	0.002
<i>CH fertilized sites:</i>			
1990 (height)	np	np	np
1990 (root collar diameter)	-	0.208	0.027
1992 (height)	-	0.160	0.064
1992 (root collar diameter)	-	0.428	0.001
<i>HA fertilized sites:</i>			
1990 (height)	np	np	np
1990 (root collar diameter)	np	np	np
1992 (height)	np	np	np
1992 (root collar diameter)	np	np	np
<i>CH scarified sites:</i>			
1990 (height)	np	np	np
1990 (root collar diameter)	-	0.129	0.177
1992 (height)	np	np	np
1992 (root collar diameter)	np	np	np
<i>HA scarified sites:</i>			
1990 (height)	np	np	np
1990 (root collar diameter)	np	np	np
1992 (height)	-	0.085	0.191
1992 (root collar diameter)	np	np	np
<i>CH fertilized plus scarified sites:</i>			
1990 (height)	np	np	np
1990 (root collar diameter)	np	np	np
1992 (height)	np	np	np
1992 (root collar diameter)	np	np	np
<i>HA fertilized plus scarified sites:</i>			
1990 (height)	np	np	np
1990 (root collar diameter)	np	np	np
1992 (height)	np	np	np
1992 (root collar diameter)	np	np	np

Table 24. Summary of the correlations between the leaf area index of salal and western red cedar height and root collar diameter using the multiple regression models. "np" means salal is not present in model. "+" and "-" mean that salal is positively and negatively correlated with cedar growth, respectively.

	<u>correlation</u>	<u>R<sup>2</sup></u>	<u>p</u>
<i>CH control sites:</i>			
1990 (height)	+	0.158	0.050
1990 (root collar diameter)	np	np	np
1992 (height)	+	0.119	0.102
1992 (root collar diameter)	np	np	np
<i>HA control sites:</i>			
1990 (height)	-	0.079	0.036
1990 (root collar diameter)	-	0.014	0.194
1992 (height)	np	np	np
1992 (root collar diameter)	np	np	np
<i>CH fertilized sites:</i>			
1990 (height)	-	0.016	0.632
1990 (root collar diameter)	-	0.486	0.004
1992 (height)	np	np	np
1992 (root collar diameter)	np	np	np
<i>HA fertilized sites:</i>			
1990 (height)	np	np	np
1990 (root collar diameter)	np	np	np
1992 (height)	np	np	np
1992 (root collar diameter)	np	np	np
<i>CH scarified sites:</i>			
1990 (height)	np	np	np
1990 (root collar diameter)	+	0.131	0.154
1992 (height)	np	np	np
1992 (root collar diameter)	np	np	np
<i>HA scarified sites:</i>			
1990 (height)	+	0.174	0.083
1990 (root collar diameter)	+	0.116	0.111
1992 (height)	+	0.167	0.002
1992 (root collar diameter)	+	0.249	0.001
<i>CH fertilized plus scarified sites:</i>			
1990 (height)	np	np	np
1990 (root collar diameter)	np	np	np
1992 (height)	np	np	np
1992 (root collar diameter)	np	np	np
<i>HA fertilized plus scarified sites:</i>			
1990 (height)	np	np	np
1990 (root collar diameter)	np	np	np
1992 (height)	np	np	np
1992 (root collar diameter)	np	np	np

**Relationship between soil variables and conifer growth, and soil variables and salal growth using multiple regression.**

Tables 25, 26, and 27 summarize the multiple regression models determining the correlation between soil variables and 4-year-old hemlock height and root collar diameter, 4-year-old cedar height and root collar diameter, and salal leaf area index, respectively. The complete multiple regression models including the standard coefficients of the independent variables are not presented because the models were generally not significant. Some general trends found in the models were that increased height and root collar diameter of western hemlock and western red cedar were associated with high soil moisture and total nitrogen. Also, higher percentages of total carbon were associated with poor growth of hemlock and cedar. Soil coarse content and total phosphorus showed no trends.

Increasing salal leaf area index was associated with increasing soil total phosphorus on CH and HA scarified sites. Otherwise, there was no significant correlation between salal leaf area index and the other soil variables (moisture, coarse content, total nitrogen, and total potassium).

Table 25. Summary of correlations between soil variables (moisture, coarse content, total carbon, total nitrogen, and total phosphorus) and the growth of 4-year-old western hemlock saplings measured in 1992 using the multiple regression models.

SITE	TREATMENT	PERFORMANCE VARIABLE	N	R	R <sup>2</sup>	P-value
CH	CONTROL	HEIGHT	16	0.361	0.131	0.902
CH	CONTROL	RCD	16	0.348	0.121	0.916
CH	FERTILIZED	HEIGHT	16	0.501	0.251	0.655
CH	FERTILIZED	RCD	16	0.428	0.183	0.805
CH	SCARIFIED	HEIGHT	16	0.512	0.262	0.630
CH	SCARIFIED	RCD	16	0.606	0.367	0.392
CH	FERTILIZED + SCARIFIED	HEIGHT	16	0.177	0.031	0.996
CH	FERTILIZED + SCARIFIED	RCD	16	0.731	0.535	0.123
HA	CONTROL	HEIGHT	16	0.570	0.324	0.485
HA	CONTROL	RCD	16	0.595	0.355	0.419
HA	FERTILIZED	HEIGHT	16	0.755	0.570	0.089
HA	FERTILIZED	RCD	16	0.706	0.498	0.167
HA	SCARIFIED	HEIGHT	15	0.666	0.444	0.299
HA	SCARIFIED	RCD	15	0.666	0.444	0.300
HA	FERTILIZED + SCARIFIED	HEIGHT	16	0.647	0.419	0.291
HA	FERTILIZED +SCARIFIED	RCD	16	0.579	0.335	0.461

N=number of hemlock included in the model.

RCD = root collar diameter.

Table 26. Summary of the correlations between soil variables (moisture, coarse content, total carbon, total nitrogen, and total phosphorus) and the growth of 4-year-old western red cedar saplings measured in 1992 using the multiple regression models.

SITE	TREATMENT	PERFORMANCE VARIABLE	N	R	R <sup>2</sup>	P-value
CH	CONTROL	HEIGHT	16	0.729	0.531	0.128
CH	CONTROL	RCD	16	0.609	0.371	0.383
CH	FERTILIZED	HEIGHT	16	0.538	0.289	0.566
CH	FERTILIZED	RCD	16	0.509	0.259	0.637
CH	SCARIFIED	HEIGHT	16	0.576	0.332	0.469
CH	SCARIFIED	RCD	16	0.515	0.265	0.469
CH	FERTILIZED + SCARIFIED	HEIGHT	16	0.459	0.211	0.747
CH	FERTILIZED + SCARIFIED	RCD	16	0.448	0.201	0.769
HA	CONTROL	HEIGHT	16	0.473	0.224	0.717
HA	CONTROL	RCD	16	0.402	0.161	0.848
HA	FERTILIZED	HEIGHT	16	0.731	0.534	0.124
HA	FERTILIZED	RCD	16	0.753	0.567	0.092
HA	SCARIFIED	HEIGHT	16	0.409	0.167	0.837
HA	SCARIFIED	RCD	16	0.547	0.299	0.542
HA	FERTILIZED + SCARIFIED	HEIGHT	16	0.729	0.531	0.127
HA	FERTILIZED +SCARIFIED	RCD	16	0.710	0.504	0.159

N=number of hemlock included in the model.

RCD = root collar diameter.

Table 27. Summary of the correlations between soil variables (moisture, coarse content, total carbon, total nitrogen, and total phosphorus) and the leaf area index of salal using the multiple regression models.

SITE	TREATMENT	N	R	R <sup>2</sup>	P-value
CH	CONTROL	32	0.537	0.288	0.097
CH	FERTILIZED	32	0.494	0.244	0.175
CH	SCARIFIED	32	0.567	0.321	0.059
CH	FERTILIZED + SCARIFIED	32	0.502	0.252	0.157
HA	CONTROL	32	0.358	0.128	0.585
HA	FERTILIZED	32	0.403	0.162	0.434
HA	SCARIFIED	31	0.681	0.464	0.006
HA	FERTILIZED + SCARIFIED	32	0.351	0.123	0.607

N=number of independent leaf area index measurements taken for each multiple regression model.



## **The influence of the abundance of salal on the growth of conifers between 1990 and 1992**

### ***western hemlock***

Height increase (Fig. 12a) and root collar diameter increase (Fig. 12b) of hemlock between 1990 and 1992 in most cases was reduced with increasing amounts of salal (Table 23).

The growth rate of hemlock height and root collar diameter on CH sites showed a strong treatment effect. Hemlock growing on control plots had the lowest growth rate, followed by fertilized plots, scarified plots, and fertilized plus scarified plots. Salal had a greater influence on the root collar diameter of hemlock than on its height. The slopes of the three root collar diameter regressions (Fig. 12b) were similar, indicating that salal had a similar influence in each of the treatments. The growth rate of the height and root collar diameter of hemlock growing on scarified plots showed little difference with increasing abundance of salal.

Similar to CH sites, the growth rate of hemlock height and root collar diameter on HA sites showed a treatment effect but it was not as strong. The two year growth increment of height and root collar diameter of hemlock growing on control plots showed the greatest response to increasing salal leaf area index than any other site x treatment combination for both hemlock and cedar. The growth rate of height and root collar diameter when salal was absent was approximately 170 cm/2yr, and 33 mm/2yr, respectively, while at a leaf area index of 3, the growth rate was close to 0 for both height and root collar diameter. Hemlock growing on fertilized plots also showed a significant decrease with increasing abundance of salal. The growth rate of hemlock growing on scarified and fertilized plus scarified plots showed no significant influence to increasing abundance of salal.

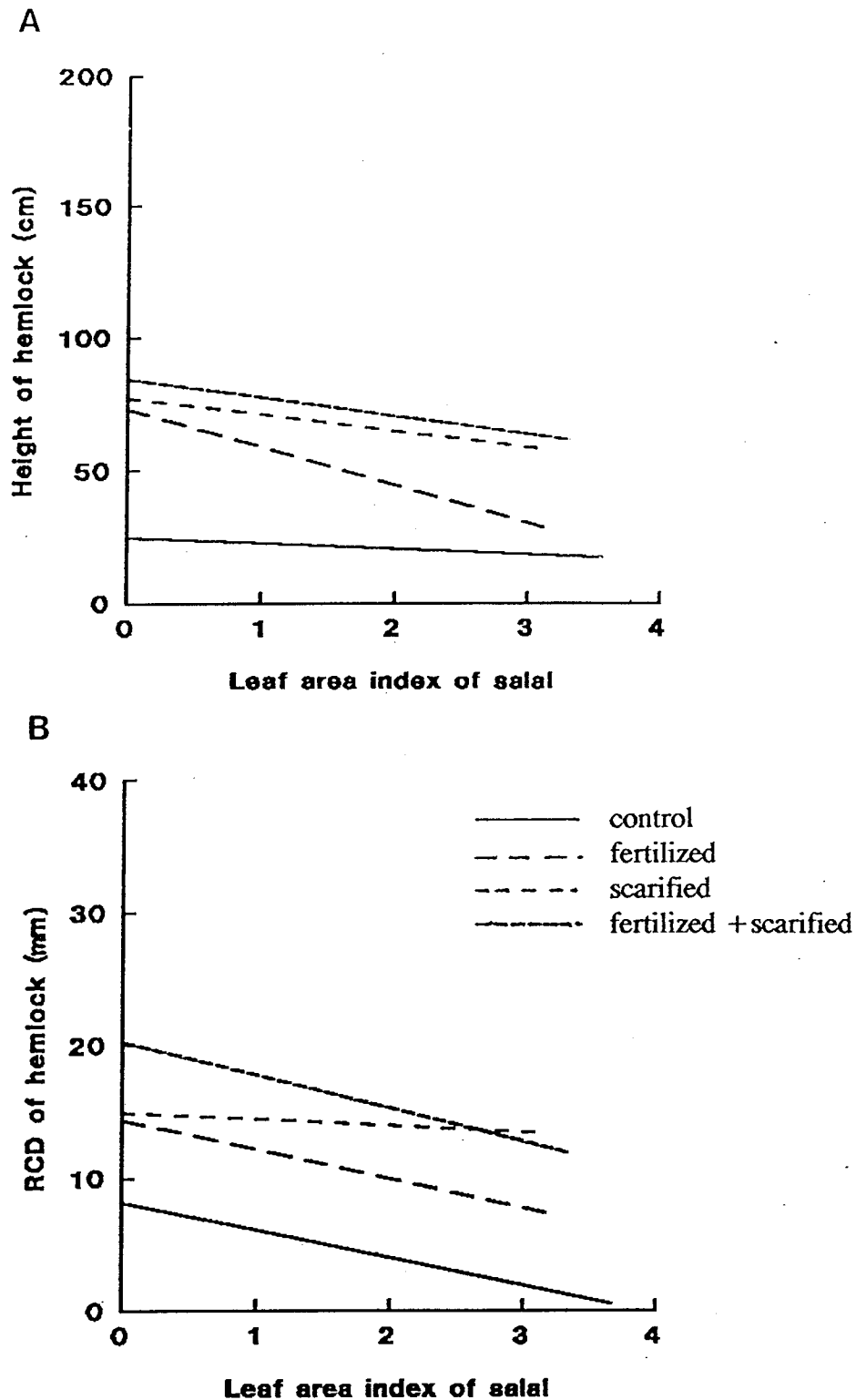


Figure 12. The relationship between salal LAI measured in 1991 and the 2-year growth increment of western hemlock height and root collar diameter (between 2- and 4-years after planting) on CH sites within four different treatments (control, fertilized, scarified, and fertilized plus scarified). The regression lines for each treatment extend to the maximum salal LAI measured.

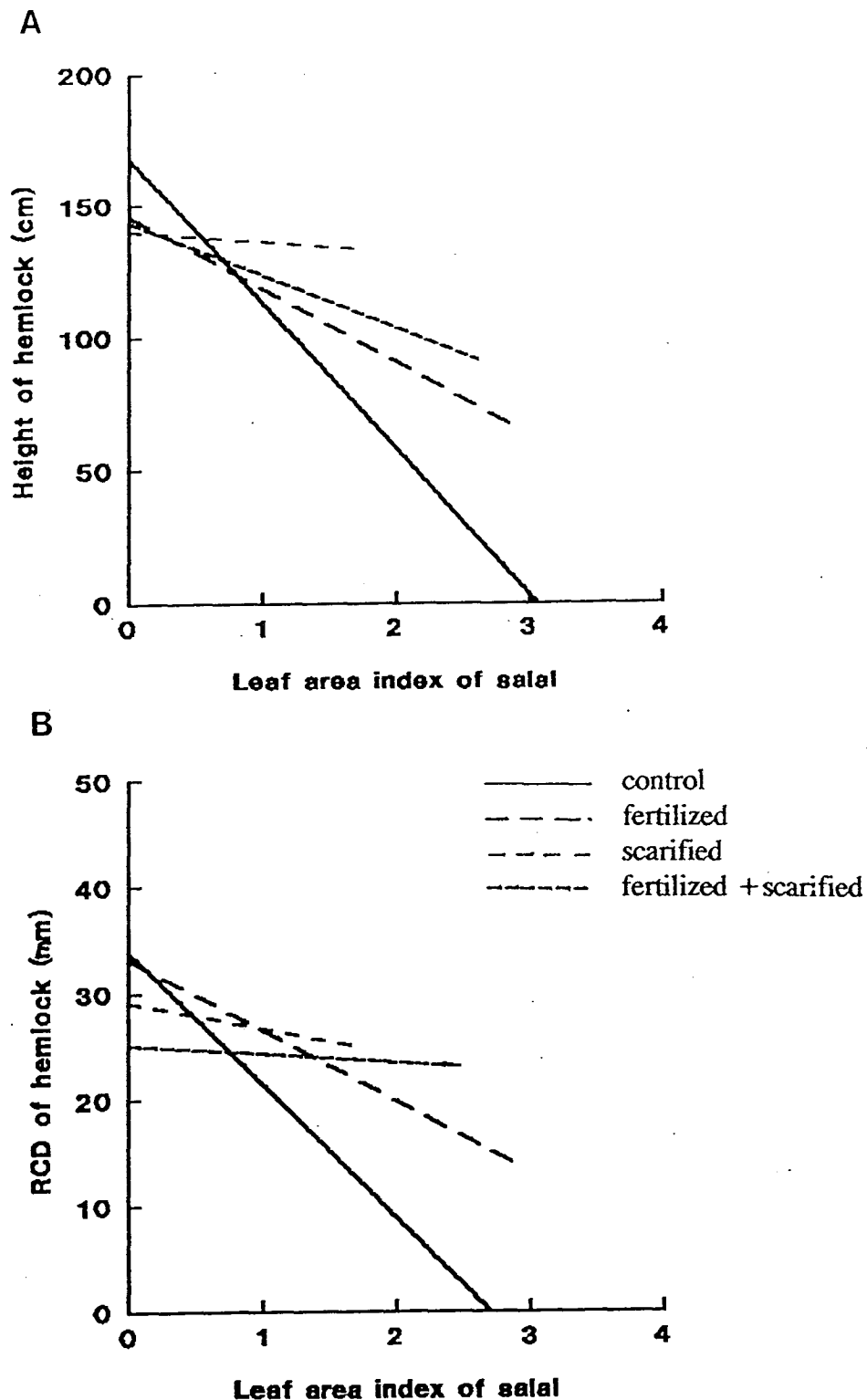


Figure 13. The relationship between salal LAI measured in 1991 and the 2-year growth increment of western hemlock height and root collar diameter (between 2- and 4-years after planting) on HA sites within four different treatments (control, fertilized, scarified, and fertilized plus scarified). The regression lines for each treatment extend to the maximum salal LAI measured.

Table 28. Summary of the  $R^2$  values of the growth of western hemlock and western red cedar between 1990 and 1992 against the leaf area index of salal for each site x treatment combination.

	$R^2$	P-value
<u>Hemlock Height on CH sites</u>		
control	0.021	0.591
fertilized	0.354	0.015
scarified	0.042	0.444
fertilized + scarified	0.029	0.527
<u>Hemlock Root Collar Diameter on CH sites</u>		
control	0.310	0.025
fertilized	0.232	0.059
scarified	0.006	0.774
fertilized + scarified	0.077	0.299
<u>Hemlock Height on HA sites</u>		
control	0.445	0.005
fertilized	0.256	0.045
scarified	0.009	0.744
fertilized + scarified	0.162	0.122
<u>Hemlock Root Collar Diameter on HA sites</u>		
control	0.503	0.002
fertilized	0.314	0.024
scarified	0.022	0.600
fertilized + scarified	0.015	0.654
<u>Cedar Height on CH sites</u>		
control	0.013	0.669
fertilized	0.214	0.071
scarified	0.003	0.832
fertilized + scarified	0.035	0.488
<u>Cedar Root Collar Diameter on CH sites</u>		
control	0.081	0.285
fertilized	0.162	0.122
scarified	0.124	0.182
fertilized + scarified	0.055	0.381
<u>Cedar Height on HA sites</u>		
control	0.201	0.081
fertilized	0.094	0.248
scarified	0.099	0.235
fertilized + scarified	0.006	0.770
<u>Cedar Root Collar Diameter on HA sites</u>		
control	0.286	0.033
fertilized	0.081	0.285
scarified	0.011	0.697
fertilized + scarified	0.030	0.524

*western red cedar*

The relationship between the growth rate of cedar and the leaf area index of salal was far less clear than with hemlock and salal (Figs. 14, 15; Table 24). Furthermore, there were fewer  $R^2$  values with a P-value  $< 0.1$  than hemlock.

The growth rate of height and root collar diameter of cedar growing on control plots in CH sites increased with increasing abundance of salal. The same can be said for the growth rate of height of cedar growing on fertilized plus scarified plots in CH sites. The growth rate of the height and root collar diameter of cedar was greatest on fertilized plus scarified plots. The growth rate of height and root collar diameter of cedar grown on fertilized plots showed the greatest influence to increasing abundance of salal. When salal was absent, the growth rate of height and root collar diameter was approximately 75 cm/2yr, and 15 mm/2yr, respectively, while at a salal leaf area index of 6, the growth rate of height and root collar diameter was approximately 40 cm/2yr, and 7mm/2yr, respectively. Cedar grown on scarified plots showed the least change in growth rate with the change in salal abundance.

The growth rate of cedar growing on HA sites differed considerably from cedar growing on CH sites. Instead of an increasing growth rate with increasing abundance of salal, cedar growing on control plots on HA sites showed a decreasing growth rate. Furthermore, instead of a decreasing growth rate with increasing abundance of salal, cedar growing on scarified plots on HA sites showed an increasing growth rate. The growth rate of cedar growing on fertilized, scarified and fertilized plus scarified plots were all roughly equal, and they were all greater than the growth rate of cedar growing on control plots.

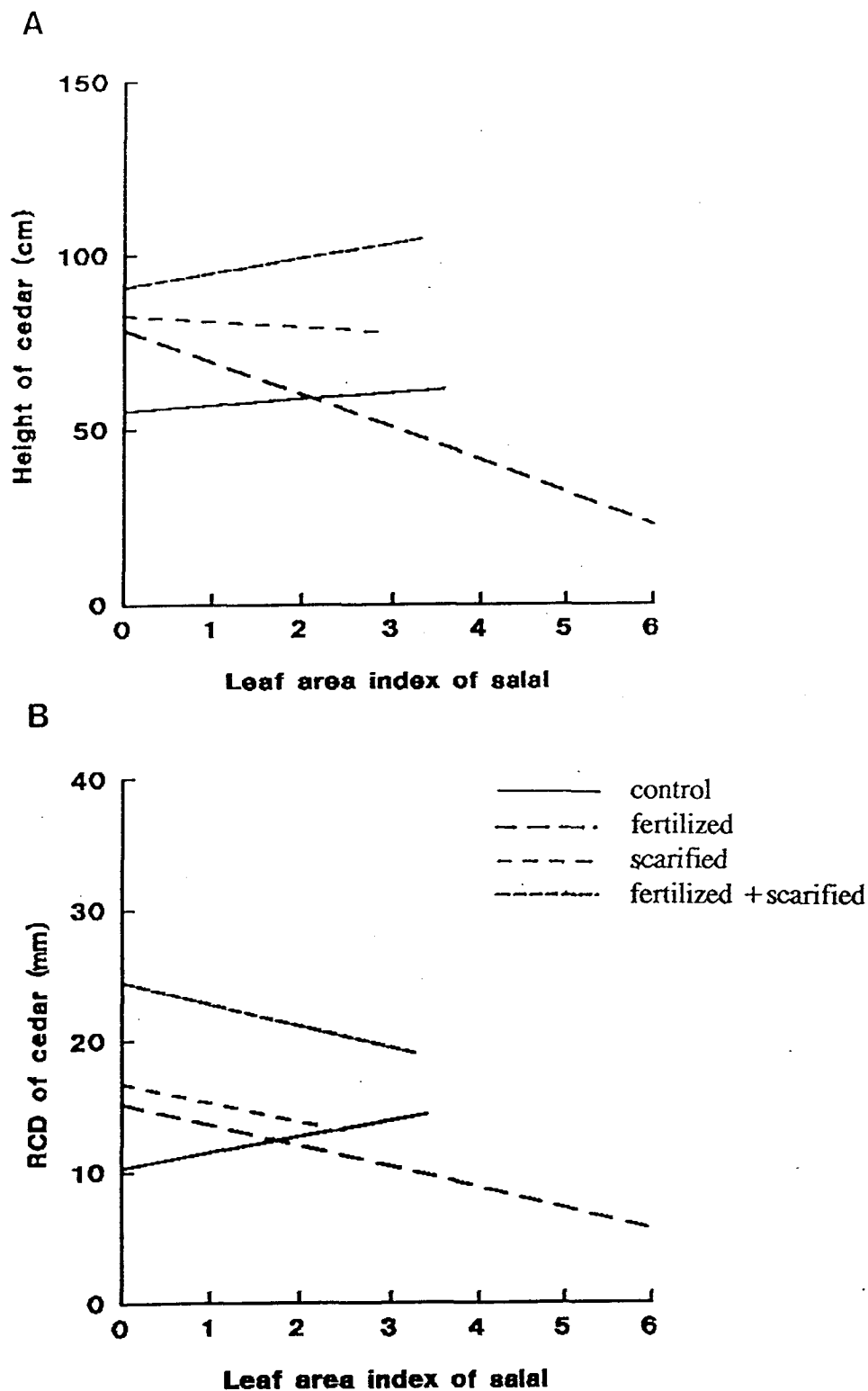
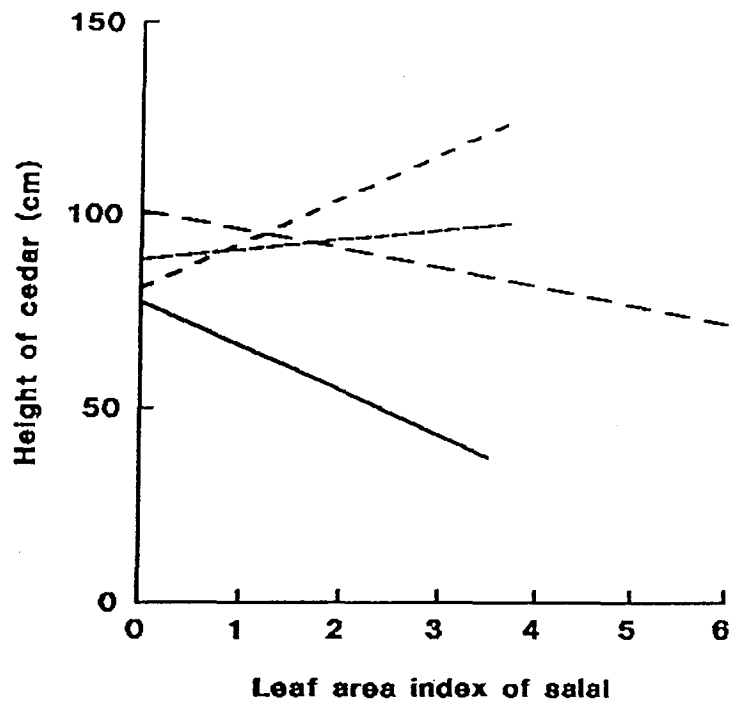


Figure 14. The relationship between salal LAI measured in 1991 and the 2-year growth increment of western red cedar height and root collar diameter (between 2- and 4-years after planting) on CH sites within four different treatments (control, fertilized, scarified, and fertilized plus scarified). The regression lines for each treatment extend to the maximum salal LAI measured.

A

90



B

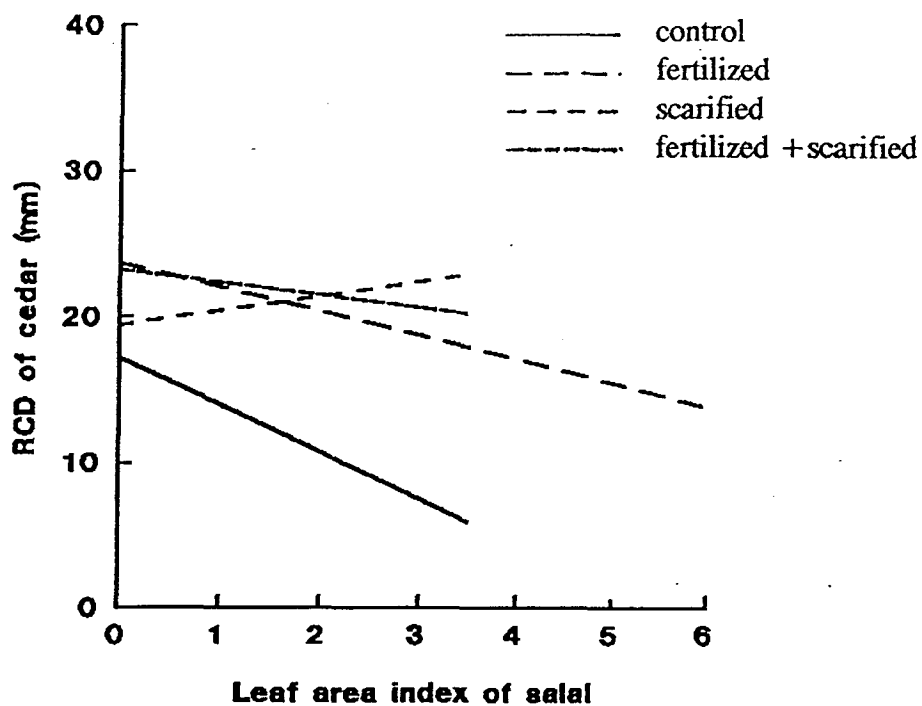


Figure 15. The relationship between salal LAI measured in 1991 and the 2-year growth increment of western red cedar height and root collar diameter (between 2- and 4-years after planting) on HA sites within four different treatments (control, fertilized, scarified, and fertilized plus scarified). The regression lines for each treatment extend to the maximum salal LAI measured.

## DISCUSSION

### **Were the predictions of the salal hypothesis met?**

The influence of salal on growth of trees can be assessed in two ways. First, correlation and regressions between conifer growth and salal abundance at any one point in time. These, of course, can only lead to speculative interpretations and do not allow a direct assessment of the impact of the presence of salal on growth of trees. Secondly, and more realistically, we can correlate the abundance of salal and the tree height and root collar diameter increments from 1990 to 1992. A number of predictions about the influence of salal on conifer growth were presented earlier in this thesis based on the salal hypothesis. To support the salal hypothesis alone, all of these predictions must be met. Figure 16 summarizes the major findings of this study to determine if the salal hypothesis is supported.

***Growth of hemlock on CH sites:*** The results of this study corroborate many of the predictions for hemlock growing on CH sites. Hemlock was more sensitive to salal than cedar, and hemlock growth was reduced with increasing abundance of salal on control plots. However, scarification reduced the influence of salal on hemlock considerably, and salal growing on fertilized CH sites reduced the performance of hemlock.

***Growth of hemlock on HA sites:*** The greatest reduction in hemlock growth by the abundance of salal occurred on control HA sites. The salal hypothesis predicts that salal would be competitive on control HA sites, but it does not predict that the strongest competition would occur here. Scarification on HA sites, like CH sites, reduced the influence of the abundance of salal considerably on hemlock growth, which is contrary to the prediction. As predicted, fertilization of HA sites, contrary to CH sites, also reduced the influence of salal on the growth of hemlock.



***Growth of cedar on CH sites:*** Unexpectedly, cedar growth seemed to be encouraged by salal on control CH sites and scarified CH sites. This of course is directly opposite to the prediction. Furthermore, cedar growth was reduced by salal on fertilized CH sites which is also contrary to the prediction.

***Growth of cedar on HA sites:*** As predicted, cedar growth was reduced by salal on control HA sites, but the correlation was stronger than control CH sites. Cedar growing on scarified HA sites seemed to be encouraged by salal which is directly opposite to the prediction. As predicted, cedar growing on fertilized HA sites were not influenced by salal.

The predictions of the salal hypothesis were not all met. Therefore, the presence of salal cannot be accepted as the principal factor contributing to the poor growth of conifers on CH sites. However, salal clearly does have some impact on conifers, especially hemlock, and lends at least partial support to the hypothesis.

## HEMLOCK

### CH site

### HA site

#### **predictions:**

treatment <sup>a</sup>	c	f	s	f+s		c	f	s	f+s
salal abundance	high	high	high	high		high	high	high	high
conifer response <sup>b</sup>	a	c	b	d		b	d	c	d

#### **observed:**

treatment	c	f	s	f+s		c	f	s	f+s
salal abundance	high	high	high	high		high	high	high	high
conifer response	a*	a	d	d*		a	a	d	d*

## CEDAR

### CH site

### HA site

#### **predictions:**

treatment	c	f	s	f+s		c	f	s	f+s
salal abundance	high	high	high	high		high	high	high	high
conifer response	b	d	c	d		c	d	c	d

#### **observed:**

treatment	c	f	s	f+s		c	f	s	f+s
salal abundance	high	high	high	high		high	high	high	high
conifer response	+	b	+	d*		b	d*	+	d*

Figure 16. The predicted outcomes compared to the observed outcomes of western hemlock and western red cedar response to high abundance of salal based on the salal hypothesis.

<sup>a</sup>c=control, f=fertilized, s=scarified.

<sup>b</sup>a=a 50% or more reduction in conifer growth compared to a conifer growing in optimum conditions, b=30-50% reduction in conifer growth compared to a conifer growing in optimum conditions, c=>0-30% reduction in conifer growth compared to a conifer growing in optimum conditions, d=no influence from salal.

\* = the prediction was the same as the observed.

+ = an increase in conifer growth with increasing salal abundance.

## **Gaultheria shallon as a competitor of conifers**

### ***Relationship between salal leaf area index and conifer performance using multiple regression***

Western red cedar and western hemlock responded differently to the abundance of salal indicating that there is a species effect, with cedar less sensitive to salal than hemlock, which supports the general view (Bunnell 1990).

A strong case can be made for the competitive influence of salal on hemlock. With increasing leaf area index of salal, both height and root collar diameter of hemlock was reduced in control plots on CH and HA sites and on fertilized plots on CH sites. Salal on scarified plots generally had no influence on the height and root collar diameter of hemlock. It is possible that the minimal influence of salal on scarified plots was because scarification effectively removed most of the salal rhizomes. Therefore, salal would have to establish by seed propagation on scarified sites which is a slow method of colonization for salal because salal does not readily produce seeds, and the percentage of successful seed germination is low (Fraser et al. 1993). Because salal is slower at establishing it may not be exerting much of an influence on conifer growth at the time of this study. The leaf litter of salal was much less on scarified sites than other treatments which is an indication that salal was recently established. Leaf litter may be considered a relative measure of the age of salal, i.e. a large leaf litter means salal has been established for a long time. The areas which were fertilized did not show any big differences in leaf area index or leaf litter of salal from those areas which were not fertilized. This indicates that any effect of salal on the resources did not affect the performance of hemlock in fertilized, high-nutrient soils. To explain the negative correlation of salal and hemlock in fertilized CH sites, it must be assumed that these sites are still comparatively low in nutrients. However, the measurements of soil total nitrogen do not reflect this assumption. This may be explained by the fact that the

sites were fertilized 4 years ago, therefore, any available nitrogen from the fertilization treatment has probably been incorporated by other plants or lost from the system. Also, total nitrogen is an imperfect measurement which doesn't account for the entire nitrogen cycle. Based on what is known about the soil properties of CH and HA sites (Lewis 1982; Messier 1991; Prescott *et al.* 1993) it seems evident that HA sites have a higher nutrient availability than CH sites.

There is evidence in this study that increasing leaf area index of salal reduced the growth of western red cedar under certain conditions. However, control plots on CH sites showed that the abundance of salal was positively correlated with both the height and root collar diameter of 2-year-old cedars measured in 1990, which rejects the salal hypothesis. Also, the root collar diameter of 2-year-old cedars growing in scarified plots on CH sites, and both height and root collar diameter of 2- and 4-year-old cedars growing in scarified plots on HA sites showed a positive correlation with salal. This also rejects the salal hypothesis. Scarified plots on HA sites had the lowest leaf area index and leaf litter during 1991 and 1992, therefore not only was salal sparse, but the minimal leaf litter suggests that it had only recently been established within the area. This may account for the observed anomaly where the abundance of salal seemed to increase cedar growth.

Evidence for the competitive influence of salal on 2-year-old cedars height and root collar diameter was found in control plots on HA sites and fertilized plots on CH sites. Salal had a greater negative influence on control plots on HA sites than fertilized plots on CH sites. This agrees with the salal hypothesis but because of the other results the hypothesis is rejected for cedar. The fertilized plots on CH sites and the control plots on HA sites had the two highest mean leaf area index for 1991 and the highest salal leaf litter. Both sites may be considered as nutrient medium because HA sites have higher concentrations of available soil nutrients than CH sites (Prescott *et al.* 1993), and in this case, the CH sites were fertilized. Nutrient medium soils appear to

be conducive to good salal growth, and abundant levels of salal on nutrient medium soils were competitive with cedar. The abundance of salal was not correlated with cedar growth during the 1992 measurements which may mean that salal is competitive only during the first few years following clear-cutting and slashburning. Messier (1991) projected that the expansion of salal will cease between 10 and 20 years after clear-cutting and slashburning. Until that time, Messier suggested that salal would continue exerting a large effect on the nutrient resources. There is no evidence of a negative effect of salal on cedar growth after 7 years following clear-cutting and slashburning in this study, which suggests that the growth of cedar is not influenced by a possible depletion of resources by salal after 7 years. This may be due to the tolerance of western red cedar to limited resources (Gregory 1957), even though they may require very high nutrient levels for optimum nutrition (Krajina 1969), or that the expansion of salal has ceased. However, western hemlock is tolerant of equally low levels of nutrients, in fact, it has been shown that western hemlock survives any deficiency treatment better than any other conifer (Krajina *et al.* 1982).

***The influence of the abundance of salal on the growth of conifers from 1990 to 1992***

The 2-year growth increment of hemlock was reduced by the presence of salal to a much greater extent than cedar. The rate of height increase of hemlock on CH sites did not vary much with increasing abundance of salal. For hemlock growing on control CH sites, presumably there was such a large deficit of nutrients that hemlocks did poorly regardless of the abundance of salal. Scarification of CH sites may have increased the fertility of the sites and delayed the establishment of salal, therefore, although hemlocks may have had abundant salal growing nearby, the salal was recently established and not exerting a strong influence. The 2-year growth rate of hemlock growing on fertilized plots were influenced the most by salal abundance. This shows

that although the rate of height increase of hemlock can be increased with the fertilization of CH sites, the presence of salal will reduce the rate. Root collar diameter may be a more accurate estimate of biomass of hemlock than height. Hemlock is faster growing than cedar and allocates more biomass to leader growth, characteristic of a shade-tolerant species (Packee 1990). This may explain why root collar diameter was more sensitive to the abundance of salal than height. The only condition in which the abundance of salal had no influence on the rate of root collar diameter increase of hemlock was on scarified CH sites, presumably because scarification increased the fertility of the sites and delayed the establishment of salal.

Western hemlock was more sensitive to the abundance of salal on HA sites than on CH sites. The greatest influence that salal had on the growth rates of height and root collar diameter increase of hemlock was found on control plots on HA sites. HA sites have higher levels of available nutrients than CH sites (Weetman *et al.* 1989b; Prescott *et al.* 1993). This shows that salal is more strongly competitive with hemlock when there are relatively more available nutrients. With fertilization and scarification the rate of height and root collar diameter increase of hemlock when salal was absent was approximately the same as control plots. However, the rate of height and root collar diameter increase of hemlock planted on plots which had been scarified were more resistant to increasing leaf area index of salal. Hemlock height and root collar diameter growth rate were reduced with increasing leaf area index of salal on fertilized HA sites. This was a different response than the results from the multiple regression models. Therefore, salal is a serious competitor with hemlock under specific field conditions: control CH sites, fertilized CH sites, control HA sites, and fertilized HA sites.

There is very little evidence to suggest that salal is competitive with western red cedar. There were only two significantly negative relationships between the growth rate of cedar and the leaf area index of salal: height of cedar on fertilized CH plots and

on fertilized HA plots. Unlike hemlock, the height of cedar was more sensitive to the abundance of salal than root collar diameter, i.e. cedar allocates more biomass to root collar diameter. Scarification eliminates any negative influence from salal presumably by delaying its establishment. Unless the leaf area index of salal is kept below 1, it would not be beneficial to fertilize CH sites to improve the growth rate of cedar.

### **The influence of the leaf area index of non-crop species other than salal on conifer growth**

The multiple regression models of the leaf area index of all non-crop species were more effective at predicting cedar and hemlock growth on control and fertilized plots than on scarification plots and fertilization plus scarification plots. The disturbance caused by scarification may have delayed the establishment and propagation of non-crop species, therefore delaying the onset of competition effects. It is possible that competition from non-crop species on scarified plots will never significantly hinder the growth of conifers because after 4 years of growth the conifers may be large enough to inhibit the establishment of non-crop species through shading.

Generally, the non-crop species which were correlated with height of hemlock and cedar were also correlated with root collar diameter during the same year and under the same conditions. However, the multiple regression models for root collar diameter more often had a higher  $R^2$  value than height, particularly for hemlock. Hemlock allocates more biomass to leader growth than cedar, and although a hemlock may be relatively high, it may not have a correspondingly large root collar diameter. In this case, root collar diameter on hemlock may be a more accurate measurement of competition than height because it is more sensitive to limitation of resources.

For only three species could generalities be made about their relationship with the conifers over all of the site x treatments conditions.

The abundance of *Epilobium angustifolium* is an indicator of nutrient-rich soils (Klinka *et al.* 1989b), and generally, the abundance of *E. angustifolium* was positively correlated with conifer growth. However, conifer growth on some of the sites that were scarified was negatively correlated with *E. angustifolium*, especially hemlock growth. Scarification increased the abundance of *E. angustifolium*, thus increasing its influence on conifer growth. The fact that the abundance of *E. angustifolium* was negatively correlated with hemlock growth on fertilized HA sites indicates that hemlock is more sensitive to competition from *E. angustifolium* than cedar.

The abundance of *Hypochoeris radicata*, an indicator of exposed mineral soil (Klinka *et al.* 1989b), was positively correlated with cedar growth in practically every condition where it was significant in the multiple regression models. Hemlock growth was predominantly negatively correlated with the abundance of *H. radicata*. Therefore, it is likely that cedar grows well on exposed mineral soil whereas hemlock grows better with a high amount of organic matter. This is consistent with research conducted on sites suitable for the development of cedar (Minore 1990) and hemlock (Packee 1990) seedlings.

The abundance of *Cornus canadensis*, an indicator of nitrogen-poor soils (Klinka *et al.* 1989b), was predominantly positively correlated with the growth of cedar where it was included in the multiple regression models. In contrast, the abundance of *C. canadensis* was predominantly negatively correlated with the growth of hemlock. The fact that cedar was positively correlated with *C. canadensis*, an indicator of nitrogen-poor soils, suggests that cedar can tolerate low nutrient environments and that it is not negatively influenced by *C. canadensis*. It is interesting to note that *C. canadensis* was more abundant where cedar was planted compared to hemlock. There is a strong association between the abundance of *C. canadensis* and cedar growth.



It is evident that not only is hemlock more sensitive to salal than cedar, hemlock is also generally more sensitive to the abundance of non-crop vegetation and to nitrogen-poor soils. The abundance of *Blechnum spicant* and *Mycelis muralis*, indicators of low and high soil nitrogen, respectively, (Klinka *et al.* 1989b), are exceptions, where, at least for control plots, they were positively correlated with hemlock growth. The abundance of *Blechnum spicant* and *Mycelis muralis* were also positively correlated with cedar growth.

### **Abiotic environmental factors influence on salal leaf area index and conifer growth using multiple regression**

The soil variables (soil moisture, soil coarse content, soil total carbon, soil total nitrogen, and soil total phosphorus) were poor predictors of conifer growth, and equally poor at predicting salal abundance. Generally, high levels of soil total nitrogen and soil total moisture were positively correlated with hemlock and cedar growth, and high levels of soil total carbon were negatively correlated with hemlock and cedar growth. This corroborates the known requirements for good hemlock and cedar growth (Burns 1990). The influence of soil coarse content and soil total phosphorus on hemlock and cedar growth was variable and indeterminate. The only soil variable that showed any significance in predicting salal leaf area index was total phosphorus. Increasing soil total phosphorus was correlated with increasing salal leaf litter on scarified CH and HA sites. This indicates that phosphorus is limiting salal growth. It has been shown that salal can obtain access to organic nitrogen (Xiao and Berch 1993), therefore, phosphorus, not nitrogen, may be the limiting nutrient to salal growth. If this is true, nitrogen fertilization alone may be a preferable treatment for improving conifer growth by limiting salal growth.

The reason for the lack of correlation between soil variables and conifer performance are numerous. Although it is relatively easy to determine the total quantity of nutrients present in a soil sample, only a small fraction of the total pools are available for nutrient uptake by plants each year and nutrient availability varies temporally. Therefore, measurements of total nutrients may not relate well to the quantities available to plants. It would be more beneficial to determine the rate at which nutrients are cycled each year than to know the total quantity of nutrients within an ecosystem. Furthermore, nutrient availability varies spatially, with more nutrients in the upper profile. This coincides with the maximum occurrence of fine-root growth. But, in some cases, nutrient supplies from deeper than 50 cm are important (Binkley 1986). It is not surprising that fertilized plots generally had no greater levels of soil total nutrients than control plots because the sites were fertilized 4 years before the analysis. Therefore, most of the nutrients from the fertilizer treatment would be incorporated by plants or leached out of the system.

### **Site x treatment effect using 3-way ANOVA**

#### ***Salal performance:***

The growth of salal was analyzed separately according to the neighbouring conifer. Generally, there was no difference in salal growth whether in association with cedar or with hemlock. However, in control plots in HA sites there was more salal leaf litter and a higher salal LAI with cedar than with hemlock. It would seem that hemlock suppresses salal growth to a greater degree than cedar or that the soil type that encourages hemlock discourages salal, or perhaps that cedar facilitates salal growth. Not surprisingly, scarification decreased leaf area index and leaf litter of salal. However, the greatest increase in leaf area index of salal from 1991 to 1992 occurred on the scarified plots. This indicates that salal had expanded its above-ground growth to

near its maximum potential on control and fertilized plots by 1991, i.e. 4 years after establishment. This agrees with Bunnell's (1990) findings that 85% of the space occupied by salal after nine years of growth was occupied during the first three years. On scarified plots, salal appears to be still expanding, indicating that scarification delays the establishment of salal, therefore reducing the influence salal may have on conifers. The fact that salal showed little difference in foliar nutrients between site x treatment combinations indicates that salal is tolerant of low nutrient environments or that it does not have the capacity to retain high levels of nutrients in its foliage when grown on high nutrient environments. However, this does not mean that salal does not increase its uptake of nutrients in high nutrient environments. In higher nutrient environments it is likely that salal will turn over its leaves at a faster rate, increasing leaf litter.

***Western hemlock performance:***

There was a strong site effect where the growth of hemlock was greater on HA sites, probably due to the greater availability of nutrients. A treatment effect was observed on CH sites, where fertilization and scarification increased the growth of hemlock. Nutrients do not appear to be limiting hemlock growth on HA sites. Fertilization and scarification decreased foliar nitrogen and foliar potassium, however the concentration of nitrogen and potassium may decrease with increasing total biomass of the hemlocks. Therefore, the net concentration of nitrogen and potassium of the hemlock in the treated plots may be equal to, or even greater than, the control plots.

***Western red cedar performance:***

The site effect on western red cedar was not as obvious as for western hemlock. Cedar growth on control plots on CH and HA sites were similar. But fertilization and scarification increased the growth of cedar more on HA sites than CH sites. The effect

of scarification increased dramatically from 1990 to 1992, surpassing the effect of fertilization. Therefore, the effects of soil mixing is delayed but, perhaps, ultimately preferable because there is very little competition from non-crop species. By the time non-crop species can establish, shading from the conifers will suppress growth. On HA sites, treatment had little effect on height, root collar diameter, colour index, and foliar nitrogen compared to the control plots. This indicates that cedar growing on control plots on CH sites are nutrient deficient to a greater degree than control plots on HA sites. This supports the findings that HA sites are higher in nutrients than CH sites (Weetman *et al.* 1989b; Prescott and McDonald 1992). This also shows that cedar are slower growing species than hemlock. Cedar had higher foliar nitrogen, phosphorus, and potassium concentrations than hemlock. Perhaps on a net foliar nutrient basis, hemlock may be higher because they are taller. In any case, slower growth and accumulation of nutrients of cedar may be one reason why salal had minimal influence on cedar performance.

#### ***Soil variables:***

Soil moisture did not differ between site x treatment combinations. This suggests that soil moisture does not limit conifer growth, which Messier (1991) also reported. Soil total carbon also did not differ between site x treatment combinations, but Messier (1991) found that HA soils were lower in soil total carbon than CH soils. The coarse content of soils on HA sites where hemlock were grown were higher than the soils on CH sites. A higher coarse content is conducive to a well-drained soil and increased mineralization of nutrients (Binkley 1986), therefore increasing the growth potential of the conifers. Soils where cedar were grown did not show the same pattern in coarse content as where hemlock was grown. This may mean that there is a difference in the degree to which the growth of hemlock and cedar alter the soil structure, or that the disturbance of the soil caused by windthrow alters the soil

structure. Fertilization and scarification had varying effects on nutrient availability of the soil. For the soils where hemlock was growing, fertilization had no effect on total nitrogen or phosphorus. This may be due to the fact that the soils were fertilized four years before the analysis and hemlock and neighbouring vegetation have incorporated all of the available nutrients. Scarification, on the other hand, seemed to reduce the total soil phosphorus. For the soils where cedar was growing, fertilization increased the total nitrogen and phosphorus, which could mean that cedar is slower at extracting nutrients than hemlock.

### **Competition theory related to salal**

Based on the growth of salal, and the sites where the abundance of salal reduced conifer growth, salal may be termed a "competitive - stress-tolerant" strategist (Grime 1977, 1979). Much attention has been centered on Grime's theories (Harper 1982; Grubb 1985; Loehle 1988; Grace 1990; Turkington *et al.* 1993) as they predict the response of plants under different environmental conditions. Grime's theory is based on the life history characteristics of a plant's established phase depending on the degrees of "stress" (phenomena which restrict photosynthetic production) and "disturbance" (partial or total destruction of plant biomass) to which they are adapted. According to this classification, those plants adapted to low levels of both disturbance and stress are referred to as "competitive," those adapted to low disturbance and high stress are "stress-tolerant," and those adapted to high disturbance and low stress are "ruderal." In this study, low levels of both disturbance and stress are fertilized plots, low disturbance and high stress are control plots, high disturbance and low stress are scarified, and fertilized plus scarified plots. One of the most important characteristics of this classification is the maximum relative growth rate (RGR<sub>max</sub>). Plants with a

high RGR<sub>max</sub> are better able to utilize nutrients in a high nutrient environment and are therefore the best competitors. Good competitors develop biomass rapidly, allocating little energy to sexual reproduction, in order to dominate both above- and below-ground resources.

The relative growth rate of salal is high when nutrients are high which is evident by the high abundance of salal on the higher nutrient sites. This suggests that salal has a high RGR<sub>max</sub> which is indicative of a competitor-type strategist. Only after approximately 4 years will salal flower (Fraser *et al.* 1993). The delay in sexual reproduction allows for the expansion of salal both above- and below-ground (Messier, 1991). Although salal is able to persist in low-nutrient conditions (Fraser *et al.* 1993), the limited distribution range of salal indicates that it does not have a wide tolerance. Scarification, i.e. disturbance, significantly reduced the leaf area index and leaf litter of salal and effectively eliminated the negative influence of salal on conifer performance. In this case, salal is not a strong "ruderal" strategist. However, salal does resprout from severed rhizomes and lightly burnt stems (Fraser *et al.* 1993), therefore, conferring limited "ruderal" strategist traits. Based on salal's characteristics, Grime would predict that salal would be competitively dominant in nutrient rich, undisturbed soils, which holds true for this study.

## SUMMARY AND CONCLUSIONS

This study shows that the presence of salal reduces the growth of western hemlock more than western red cedar. Both the correlations of salal abundance on hemlock height and root collar diameter from the multiple regression models, and the influence of salal on height and root collar diameter growth from 1990 to 1992 show that salal abundance is strongly associated with poor hemlock growth. The multiple regression models show that in control plots on CH sites, control plots on HA sites, and fertilized plots on CH sites salal could account for over 32%, 38%, and 42% of the variation in conifer performance, respectively. The analysis of the 2-year growth of hemlocks between 1990 and 1992 show that salal reduces hemlock growth rate in control plots on CH sites, fertilized plots on CH sites, control plots on HA sites and fertilized plots on HA sites. Scarification appears to reduce the influence of salal on hemlock, perhaps because salal present on scarified plots are recently established and are not exerting a strong nutrient drain on the system. When growing with cedar, salal appears to be weakly competitive in control plots on HA sites, fertilized plots on CH sites and fertilized plots on HA sites. However, this negative association of salal on cedar only occurred on 2-year-old trees, not 4-year-old trees, suggesting that the influence is waning. For hemlock, the influence of salal was greatest on 4-year-old saplings, suggesting that the influence of salal is increasing.

Foliar nitrogen, phosphorus, and potassium concentrations were greater for cedar than hemlock, indicating that cedar utilizes nutrients more effectively. This may account for the minimal influence of salal on cedar performance.

Soil variables showed no strong trends for predicting the performance of hemlock or cedar. There is some evidence to suggest that salal is limited by phosphorus.

### **Management implications for hemlock and cedar growing on CH sites**

It is important to recognize the difference between the influence of salal on cedar and hemlock growing on CH sites because cedar and hemlock require different treatments to control against the competitive influence of salal. Fertilization, scarification and fertilization plus scarification increases the growth rate of hemlock on CH sites. However, with increasing abundance of salal, the growth rate of hemlock on fertilized sites is reduced rapidly compared to hemlock on scarified and fertilized plus scarified sites. Therefore, scarification or fertilization plus scarification is the recommended treatment. Cedar increases its growth rate with increasing abundance of salal on control CH sites. Therefore, no treatment is necessary to control against the competitive influence of salal. However, it is shown that fertilization, scarification and fertilization plus scarification increases the performance of cedar, especially when the leaf area index of salal is below 1. Fertilization would not be recommended as a treatment because with salal leaf area index over approximately 1, there is a significant decrease in the growth rate of salal, i.e. fertilization increases the competitiveness of salal. The recommended treatment would be either no treatment, or fertilization plus scarification.

More research needs to be conducted on the effect of phosphorus on salal. If phosphorus is a limiting nutrient for salal, a fertilization treatment of nitrogen alone would not encourage salal growth but would increase conifer growth and quickly shade out any salal.



## **Future research**

This research has revealed the need for additional studies to improve our understanding of the influence of salal on the growth of cedar and hemlock saplings following clear-cut logging and slashburning of CH sites on northern Vancouver Island. The following 5 suggestions outline the most important studies needed:

1. A manipulative replacement series experiment in a controlled environment to determine the point when the abundance of salal inhibits hemlock and cedar growth.
2. Age effect of salal on the growth of hemlock and cedar.
3. Fertilization trials to determine the nutrient requirements of salal and whether it is limited by phosphorus.
4. Long-term effects of scarification on salal growth in association with hemlock and cedar growth.
5. Determine why cedar appears to be more resistant to the influence of salal than hemlock.

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