Factors Limiting Coniferous Seedling Growth in Recently Clearcut Sites Dominated by *Gaultheria shallon* in the CWHvm Subzone
Factors Limiting Coniferous Seedling Growth in Recently Clearcut Sites Dominated by *Gaultheria shallon* in the CWHvm Subzone

by

Christian Messier and James P. (Hamish) Kimmins

Department of Forest Sciences
University of British Columbia
Vancouver, B.C.

March 1990
Funding for this publication was provided by the Canada-British Columbia Forest Resource Development Agreement - a five year (1985-90) $300 million program cost-shared equally by the federal and provincial governments.

Canadian Cataloguing in Publication Data
Messier, Christian, 1961-

Factors limiting coniferous seedling growth in recently clearcut sites dominated by Gaultheria shallon in the CWhvm subzone

(FRDA report, ISSN 0835-0752 ; 149)

Issued under Canada-BC Forest Resource Development Agreement.
Co-published by B.C. Ministry of Forests.
"Canada/BC Economic & Regional Development Agreement."
Includes bibliographical references: p.
ISBN 0-7726-1235-8


SD397.C7M47 1990 634.975 C91-092023-0

©1990 Government of Canada,
Province of British Columbia

This is a joint publication of Forestry Canada and the British Columbia Ministry of Forests.

Produced and distributed by the Ministry of Forests, Research Branch.

For additional copies and/or further information about the Canada-British Columbia Forest Resource Development Agreement, contact:

Forestry Canada or B.C. Ministry of Forests
Pacific Forestry Centre Research Branch
506 West Burnside Road 31 Bastion Square
Victoria, B.C. V8Z 1M5 Victoria, B.C. V8W 3E7
(604) 388-0600 (604) 387-6719
SUMMARY

Nutritional stress has been reported in planted and naturally regenerated conifers growing in association with an ericaceous species, salal (*Gaultheria shallon*), in clearcuts previously occupied by old-growth western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) (CH site). No such stress was apparent in clearcuts previously occupied by natural second-growth western hemlock and amabilis fir (*Abies amabilis*) stands (HA site) that developed following windthrow in 1907.

In the spring of 1987, a series of field experiments was initiated to investigate some of the major ecological processes affecting the growth of conifers on recently clearcut CH and HA sites; and to investigate some silvicultural solutions to the poor conifer growth on the clearcut CH sites. The approach taken was to study several of the factors that were considered to be key determinants at the broad ecosystem level. The research included studies of: 1) below- and above-ground vegetation recovery, soil nutrient availability, and soil microenvironmental modifications following logging and slashburning; 2) interference by salal; 3) coniferous seedling growth on clearcut CH and HA sites under several different experimental conditions; 4) the effects of microsite variation on seedling growth within clearcut CH sites; 5) the effect of light intensity on salal growth, acclimation, survival and competitive ability; and 6) the effects of mechanical site preparation on seedling growth on clearcut CH and HA sites.

Results show that the regrowth of the non-crop vegetation can potentially immobilize between 30 and 45% of the available N annually on CH sites for the first 8 years. Western redcedar responded the least to any treatment that increased or decreased nutrient availability. Western redcedar and western hemlock were the best-growing species on CH and HA sites, respectively. Slow release fertilizer increased growth only for the first 2 years after application.

Low levels of nutrient availability and intensive occupation of the below-ground environment by rhizomes and fine roots of salal were found to be the main factors associated with poor seedling growth on clearcut CH sites. Mechanical site preparation on such sites slowed down the recovery of salal, but decreased the overall nutrient availability for the first 2 years (the duration of the study so far), so that no major gain in seedling growth was achieved by the treatment. No difference in total percent mycorrhizal infection was found between conifer seedlings growing with and without salal. Small depressions constitute good planting microsites for western redcedar. Our results suggest that the below-ground competitive ability of salal is greatly reduced with the closing of the overstory tree canopy.
ACKNOWLEDGEMENTS

We wish to thank K.J. Mackenzie, E. Morton, S. Williams, T. Honer, C. Trethewey, R. Oran, A. Quinde, H. Granander, J. Glaubitz, R. Keenan, L. Ruddick, G. Glover, and P. Warnes for skilled assistance with the field and laboratory work. Thanks are due to A. Ruth for the mycorrhizal work and M. Tsze for the laboratory work. Drs. T. Ballard, F. Bunneil, K. Klinka, and G. Weetman provided much appreciated advice throughout the study. We are especially grateful to B. Dumont, M. Watkinson, S. Joyce, and P. Bavis for their helpful discussion and continual support and encouragement throughout the study. Western Forest Products Ltd. kindly provided lodging facilities and a multitude of other services without which it would have been very difficult to complete the project. This research was supported through Forest Resource Development Agreement (FRDA) contract 2.31, and National Sciences and Engineering Research Council of Canada and B.C. Science Council GREAT scholarships awarded to C. Messier.
TABLE OF CONTENTS

SUMMARY .................................................................................................................. iii

ACKNOWLEDGEMENTS ......................................................................................... iv

1 INTRODUCTION .................................................................................................. 1
   1.1 Review of the Problem .................................................................................. 1
   1.2 Study Objectives ......................................................................................... 4

2 STUDY AREA AND ECOSYSTEM DESCRIPTION ............................................. 4

3 STUDY OF VEGETATION AND SOIL RECOVERY FOLLOWING CLEARCUTTING AND
   SLASHBURNING .................................................................................................. 5
   3.1 Materials and Methods ................................................................................ 5
   3.2 Results .......................................................................................................... 6

4 STUDY OF SEEDLING GROWTH IN FIELD EXPERIMENTS ............................ 10
   4.1 Materials and Methods ................................................................................ 10
   4.2 Results .......................................................................................................... 12

5 STUDY OF SALAL GROWTH, ACCLIMATION, SURVIVAL, AND COMPETITIVE ABILITY .... 14
   5.1 Materials and Methods ................................................................................ 15
   5.2 Results .......................................................................................................... 15

6 STUDY OF MECHANICAL SITE PREPARATION .................................................. 18
   6.1 Materials and Methods ................................................................................ 18
   6.2 Results .......................................................................................................... 19

7 STUDY OF MICROTOPOGRAPHIC INFLUENCES ON SOIL PROPERTIES AND
   SEEDLING GROWTH .......................................................................................... 21
   7.1 Materials and Methods ................................................................................ 21
   7.2 Results .......................................................................................................... 21

8 DISCUSSION ........................................................................................................ 22
   8.1 Ecological Processes after Harvesting in Salal-Dominated Ecosystems on Northern
       Vancouver Island ............................................................................................. 22
   8.2 Operational Significance and Recommendations ........................................... 25

9 LITERATURE CITED .......................................................................................... 26

TABLES

1 Soil nutrient status compared for 2- to 4-year post-burning clearcut CH (2-4+B CH) and HA
   (2-4+B HA) sites and 8- to 10-year post-burning clearcut CH (8-10+B CH) sites .................. 9

2 Characteristics of tree overstory and salal understory between the four conifer plots studied.... 16
3 Global PPFD and percentage of full sunlight measured directly above the salal understory within four western redcedar/western hemlock plots and a clearing under clear and overcast sky conditions................................................................. 17

4 Comparisons of some important soil properties on scarified and non-scarified clearcut CH and HA sites the second year following clearcutting and slashburning......................................................... 20

FIGURES

1 View of the CH and HA forest ecosystems before (upper half, left and right, respectively) and 10 years after logging and slashburning (lower half). ................................................................. 1

2 View of a 16-year-old Sitka spruce plantation established on the CH forest ecosystem. .................. 3

3 Planted 9-year-old western redcedar growing on clearcut CH sites. ............................................. 3

4 Above- and below-ground biomass and percentage cover of (A) salal plus Vaccinium and (B) fireweed plus bunchberry vegetation groups on clearcut CH sites burned 2, 4 and 8 years previously. ........................................................................ 7

5 Total amount of nitrogen and phosphorus contained in above- and below-ground biomass of non-crop vegetation on clearcut CH sites burned 2, 4 and 8 years previously. ...................... 7

6 Above-ground biomass and percentage cover of fireweed and salal on clearcut HA sites burned 2 and 4 years previously. ................................................................................................................ 8

7 Mean soil temperatures for the 1987-1989 period at 3, 10 and 25 cm depth based on combined data from clearcut CH and HA sites. ........................................................................................................ 8

8 Vegetation-removed treatment applied to western redcedar growing on clearcut CH sites burned 2-4 years previously. .................................................................................................................. 11

9 Total height increment after three growing seasons of Sitka spruce, western hemlock and western redcedar for the three types of site and the vegetation-not-removed and vegetation-removed treatments. ..................................................................................... 13

10 Comparison of annual height increment of Sitka spruce seedlings between the three treatments on the 2-4+B CH sites for the first 3 years after planting. ................................................................. 14

11 Salal leaf area and thickness under seven different coniferous canopy closures and resulting light environments. .................................................................................................................. 16

12 Effect of decreasing light intensity on salal carbon allocation to leaves and fine roots. ................. 17

13 Effect of scarification on the early recovery of salal (Sal), fireweed (Fw), and other non-crop species (Oth) on clearcut CH and HA sites for the first 2 years following logging and slashburning. .................................................................................. 19

14 Comparisons of the height increment in 1989 of western hemlock and western redcedar between scarified and non-scarified clearcut CH and HA sites. ......................................................... 20

15 Comparisons of the height and diameter increments in 1989 of planted 3-year-old western hemlock (A) and western redcedar (B) seedlings between top, mid-top, mid, mid-bottom and bottom microtopographic positions within 4-year-old post-burning clearcut CH sites. ......................................................... 22

16 Fine root biomass, % cover, and basal area of salal and Douglas-fir in 11- to 12-year-old (open canopy) and 35- to 70-year-old (closed canopy) stands. ................................................................. 24

17 Hypothetical relationships between the leaf and fine root biomass of salal under developing stands. ................................................................................................................................. 24
1 INTRODUCTION

1.1 Review of the Problem

In the windward, submontane, wetter variant of the wet subzone (CWH-vm) of the Coastal Western Hemlock biogeoclimatic zone on northern Vancouver Island (Green et al. 1984), two very different kinds of forest occur side by side on what is believed to be a single ecosystem association.¹

The first of these two forest ecosystems, the undisturbed old-growth western redcedar-western hemlock ecosystem (hereafter called the CH) occurs extensively on the east and west side of northern Vancouver Island, and is characterized by open stands of western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) (Figure 1). This forest ecosystem is believed to account for as much as 100 000 ha of coastal forests in British Columbia (Weetman et al. 1990c).

The second forest ecosystem, the western hemlock-amabilis fir ecosystem (hereafter called the HA), occurs on sites that have apparently been subjected to periodic massive disturbance by windthrow. The HA ecosystem, which is characterized by closed stands of western hemlock and amabilis fir (*Abies amabilis*) (Figure 1), occurs as scattered patches in a matrix of the CH ecosystem. Forest ecosystems intermediate between the HA and CH can be found, which Lewis² suggests indicates the potential for the HA ecosystem to develop into the CH ecosystem given enough time without windthrow or other catastrophic disturbance.

![Image of forest ecosystem]

**Figure 1.** View of the CH and HA forest ecosystems before (upper half, left and right, respectively) and 10 years after logging and slashburning (lower half). Note the difference in stand structure before logging and in tree growth after logging between the two forest ecosystems.

---


² Ibid.
Slow growth of planted and naturally regenerated conifer stands on clearcut salal-dominated CH sites following logging or slashburning has raised questions about the factors that may be limiting the growth of these young stands. One such question relates to approximately 1500 ha of Sitka spruce (Picea sitchensis) plantations established by Western Forest Product (WFP) between 1966 and 1976 on clearcut CH sites on TFL 25 near Port McNeill, northern Vancouver Island. These plantations are now experiencing severe growth stagnation and nutritional stress (Figure 2). Barker et al. (1987) showed that the growth of these plantations started to decline 5–8 years following planting. This decline is coincident with the re-establishment and complete occupation of the site by salal (Gaultheria shallon Pursh) (Weetman and Fournier 1986). Below-ground antagonistic interferences by salal (through competition for nutrients or allelopathy) have been suggested as an explanation for the poor growth of Sitka spruce (Germain 1985; Weetman et al. 1990a). The allelopathy hypothesis followed the observation that the stagnation symptoms of the Sitka spruce on salal-dominated sites on northern Vancouver Island were similar to those exhibited by Sitka spruce growing on sites dominated by heather (Calluna vulgaris) in Scotland (G.F. Weetman, pers. comm.). Because stagnated spruce in both cases are growing well above the ericaceous cover, competition for light has been ruled out. Fertilization with N and P alleviates stagnation symptoms, but only for about 6 years (Germain 1985). Germain (1985) stated that several repeated fertilizations may be necessary to get sufficient canopy closure to suppress the salal understory. It is not known, however, what coniferous overstory canopy closure and resultant light environment is required to shade out salal.

The early research on the CH growth stagnation problem revealed that both seedlings and saplings of western redcedar growing on clearcut CH sites are performing better than those of Sitka spruce and western hemlock. Recent studies conducted by Weetman et al. (1990 a, b) showed that the annual height increment of 10- to 16-year-old natural western redcedar (33 cm/year) was greater than that of planted 16-year-old Sitka spruce (12 cm/year) or natural 10- to 16-year-old western hemlock (13 cm/year) during 1985, 1986, and 1987.

The same studies also showed that the complete removal of salal from 1984 to 1987 by manual and hericidal means (Garlon®) significantly (P<0.05) improved the annual height increment of the natural western redcedar (50 cm/year), but not of Sitka spruce (18.5 cm/year) and western hemlock (20 cm/year). Fertilization with 250 kg N ha⁻¹ as ammonium nitrate or urea and 100 kg P ha⁻¹ as triple superphosphate had a significant positive effect on the annual height increment of western redcedar (47 cm/year), Sitka spruce (36 cm/year), and western hemlock (52 cm/year). Western redcedar has been the preferred species on clearcut CH sites in the last 10 years, and has achieved a satisfactory annual height growth of 25–30 cm per year (Figure 3). Friberg reported an average annual height increment of 39 cm for natural 25-year-old western redcedar saplings growing on a CH site.

There is a striking difference in tree growth and site productivity between adjacent clearcut CH and HA sites, HA sites being more productive than CH sites. The current explanation for this difference is that periodic windthrow has improved the physical and chemical properties of the soils on the more wind-prone HA ecosystem. Germain (1985) found better soil nutrient status on HA than on CH ecosystems. Repeated windthrows are also believed to be responsible for the improved productivity on some sites in coastal Alaska (B. Borrmann, pers. comm.). If these explanations were correct, scarification techniques that emulate windthrow events on better-drained CH sites may induce a series of reactions that could eventually lead to improved site productivity. Although such scarification is expensive, the potential long-term improvement in site productivity may justify the investment: the HA ecosystem has a mean annual volume increment of 12 m³/ha compared to 5 m³/ha for the CH ecosystem (Barker et al. 1986).

---


5 Lewis, 1982.
FIGURE 2. View of a 16-year-old Sitka spruce plantation established on the CH forest ecosystem. Note the extremely slow height growth for the last 5–8 years.

FIGURE 3. Planted 9-year-old western redcedar growing on clearcut CH sites. Note that the average height increment is approximately 30 cm per year.
1.2 Study Objectives

This study investigated some of the major ecological processes controlling early conifer growth on recently clearcut and slashburned CH and HA sites. Attention was directed to the below-ground factors that may limit coniferous seedling productivity in the salal-dominated CH forest ecosystem. The report is structured around five specific objectives:

1. To quantify the changes in the soil temperature, moisture and nutrient status, and the above- and below-ground biomass of the non-crop vegetation on clearcut CH sites burned 2–10 years previously, and on clearcut HA sites burned 2–4 years previously.

2. To investigate, using field and pot experiments, the effects of salal, slow release fertilizer, the time since burning, and forest ecosystems (CH versus HA) on the growth and mycorrhizal infection of Sitka spruce, western hemlock and western redcedar.

3. To investigate, using field and pot experiments, the effects of different light intensities on the growth, acclimation, survival and competitive ability of salal.

4. To investigate the effects of mechanical site preparation (i.e., mixing of organic matter and mineral soil) on soil nutrient status, soil temperature and moisture, and seedling growth, and on the rate of recovery of salal and fireweed biomass in recently clearcut CH and HA sites.

5. To investigate the effects of small topographical variations within clearcut CH sites on a variety of soil factors, on the non-crop species such as salal and fireweed, and on western redcedar and western hemlock growth.

2 STUDY AREA AND ECOSYSTEM DESCRIPTION

The study area is located in Block 4 of TFL 25 between Port McNeill and Port Hardy in the CWHvm biogeoclimatic subzone (Green et al. 1984) on northern Vancouver Island, B.C. (50° 60’/127° 35’). The area receives approximately 1700 mm of rain annually, with 65% of the precipitation occurring between October and February. Rainfall during the growing season is thought to be sufficient to prevent any soil moisture deficit. Mean daily temperature ranges from a low of 3.0°C in January/February to a high of 13.7°C in July/August. All weather data were obtained from the Port Hardy Airport weather station located within 15 km of the study area.

The CH ecosystem represents the climatic climax community and consists of open western redcedar/ western hemlock stands. This ecosystem has not been disturbed for several thousand years. The open canopy allows light to penetrate the tree cover which promotes the growth of a dense understory of salal and Vaccinium parvifolium, and V. alaskaense. Only sparse herbs (Blechnum spicant) and mosses (Hylocomium splendens and Rhytiidium boreale) are found under the Gaultheria-Vaccinium cover (Germain 1985). This forest ecosystem has a thick (20–60 cm), compacted lignin sulfur (Klinka et al. 1981) humus layer overlying a moderately well to somewhat imperfectly drained ferro-humic podzol. Western hemlock and western redcedar germinants are found mainly on rotten logs. Following logging or logging and slashburning, the CH ecosystem is quickly reinvaded by salal. Natural regeneration following logging is slow and sparse and consists mainly of western redcedar and western hemlock seedlings.

The HA ecosystem occurs on sites that are subjected to periodic catastrophic windthrow, and it is characterized by closed stands of western hemlock and amabilis fir. Salal is virtually absent from the understory. Only some sparse Vaccinium alaskaense, and V. parvifolium, herbs (Blechnum spicant, Polystichum munitum and Tiarella trifoliata) and moss (Hylocomium splendens) are present in the understory (Germain 1985). This forest ecosystem is usually situated on upper slopes, and has a thin (10–15 cm) friable

---

6 Lewis, 1982.
humimor (Klinka et al. 1981) humus layer overlying a well-drained ferro-humic podzol. Western hemlock and amabilis fir germinants are found in abundance on the forest floor and on rotten logs, but western redcedar does not appear to germinate. Natural regeneration after disturbance is rapid and dense, consisting mainly of western hemlock. Following logging or logging and slashburning, fireweed (Epilobium angustifolium) invades, rapidly creating a dense cover. Transitions between these two forest ecosystems are often abrupt and are not necessarily related to obvious topographic features.

3 STUDY OF VEGETATION AND SOIL RECOVERY FOLLOWING CLEARCUTTING AND SLASHBURNING

The removal of a forest canopy at the time of harvesting drastically alters a variety of ecosystem processes. Understanding these alterations and their effects on plant growth (both crop and non-crop species) is a prerequisite to the practice of sound, efficient and sustainable forestry.

The characteristic increase in nutrient availability following harvesting is one of the major changes caused by clearcutting. This flush of nutrients (called “assart effect”) has been measured on a variety of sites throughout North America (e.g., Binkley 1984; Martin 1985; Krause and Ramlal 1986; David 1987). David (1987) identified four main factors likely to be responsible for this flush of nutrients: 1) input of readily decomposable above- and below-ground dead organic matter; 2) changes in soil temperature and moisture regimes which favour an increase in microbial numbers and activity, and the associated decomposition; 3) reduction in the uptake of nutrients and water by the vegetation and their increased availability to micro-organisms and planted seedlings, and; 4) reduction in the mycorrhizal inhibition of decomposition (Gadgil and Gadgil 1975, 1978). One major consequence of the increased decomposition following harvesting is a decrease in the organic matter accumulated in the forest floor (Covington 1981; Martin 1985). Feller (1982) showed that slashburning following harvesting further increased nutrient availability.

Whatever the factors involved, this flush of nutrients often permits a rapid regrowth of the vegetation after forest removal. This revegetation varies according to the intensity of the disturbance (Dyreness 1971) and quality of the site (Boring et al. 1981; Hamilton and Yearsley 1988). In some cases, recovery is extremely rapid. Marks (1974), for example, estimated that it took only 4 years for pin cherry (Prunus pensylvanica) to occupy a site fully following clearcutting in hardwood forests in northeast United States. Once the flush of nutrients ends and the above- and below-ground environment is fully occupied by non-crop species, the growth of crop species can be significantly reduced or precluded altogether.

3.1 Materials and Methods

Field experiment

Study area and experimental design

Field studies were initiated in the summer of 1987 on 2- and 8-year post-burning clearcut CH sites and on 2-year post-burning clearcut HA sites near Port McNeill, northern Vancouver Island. These studies were continued for 2 years. Two cutovers of each site type in the Si ecosystem association7 were selected, for a total of six study areas. Three 15 x 30 m plots were established on each study area.

The experiment was designed as completely randomized plots in which the cutovers were nested within the sites. The Tukey HSD multiple comparison test was used to compare the treatment means.

7 Lewis, 1982.
Above- and below-ground biomass and nutrient content

Twenty-four 1-m² plots were clipped and 12 root cores were sampled to assess the above- and below-ground biomass (oven-dry weight), respectively, of salal, Vaccinium spp., fireweed, and bunchberry (Cornus canadensis) on the clearcut CH sites. Only above-ground biomass was assessed on the clearcut HA sites.

Plant nutrient concentrations for each species and plant component were either measured with standard analytical techniques; or estimated from values obtained from the literature (Sabhasri 1961; Klinka 1976) or from values obtained from other studies in the area (Weetman and Fournier, pers. comm.).

Soil chemistry, organic matter content, nutrient availability and relative decomposition rates

Thirty-six forest floor samples were taken at depths of 0–8 cm and 8–25 cm. Standard soil analyses were used to determine soil pH, total N and P, mineralizable (anaerobic incubation) and extractable N, extractable P, organic matter content, carbon content, soil moisture content and microbial activity (assessed in the laboratory using the CO₂ evolution method of Singh and Gupta [1977]). Soil ammonium, nitrate and phosphate availability and decomposition rate used the ion-exchange resin bag and confined cellulose disc methods, respectively (Binkley 1984). These data were used to define differences in the soil nutrient status among different depths and sites, and to give a measure of the change in nutrient availability over time on the clearcut CH site.

Soil microclimate

Soil temperature was measured with dial soil thermometers and soil moisture with quick draw soil tensiometers at depths of 3, 10 and 25 cm on all sites between 11:00 am and 1:00 pm 1–3 days every month from May to July and in November and February of each year of the study (1987-1989, inclusive).

Potted seedling bioassays

In March 1988, seedlings were potted near the research sites to serve as a bioassay of the variation in forest floor fertility from the chronosequence of clearcut CH sites. Sitka spruce and western redcedar 1-0 plug seedlings were established in pots (20 x 40 x 20 cm) containing forest floor material taken from 0–8 and 8–20 cm depths on 1-, 3- and 9-year post-burning clearcut CH sites. The experiment was analysed as a 3 x 2 factorial in a completely randomized design. Orthogonal contrasts were used to compare the treatment means. After each growing season (end of 1988 and 1989), the height and diameter increments of the coniferous seedlings were measured.

3.2 Results

Field experiment

Vegetation recovery

Figure 4 shows the above- and below-ground biomass at different percentage cover of salal plus Vaccinium spp. (A) and fireweed plus bunchberry (B) vegetation groups following logging and slashburning on clearcut CH sites. Species were grouped because of the difficulty in distinguishing fine roots among species. Salal was the main species both above- and below-ground, making up to 90% of the total above-ground biomass on the site logged and slashburned 8-years previously. In all cases, the below-ground biomass (i.e., fine roots and rhizomes) of the non-crop vegetation was greater than the above-ground biomass.

Figure 5 shows the estimated total nitrogen and phosphorus contained in the living biomass of the non-crop vegetation on clearcut CH sites logged and slashburned 2, 4 and 8 years previously. Average annual immobilization is estimated at about 9 and 0.9 kg/ha of nitrogen and phosphorus,
respectively, during the first 8 years. This nutrient immobilization does not occur under mature forest stands because the non-crop vegetation biomass is fairly stable, and no net annual immobilization occurs.

Figure 6 illustrates the above-ground biomass of the non-crop vegetation on clearcut HA sites 2 and 4 years after logging and slashburning. After 2 years, fireweed was the main species present. After 4 years, however, salal made up 41% of the cover and 55% of the total biomass. The above-ground biomass of fireweed remained unchanged from 2 to 4 years. No below-ground biomass assessment was made on clearcut HA sites.

![Salal-Vaccinium group](image1)

![Fireweed-bunchberry group](image2)

FIGURE 4. Above- and below-ground biomass and percentage cover of (A) salal plus Vaccinium and (B) fireweed plus bunchberry vegetation groups on clearcut CH sites burned 2, 4 and 8 years previously. The vertical bars represent one standard error.

![N (kg/ha) vs P (kg/ha)](image3)

FIGURE 5. Total amount of nitrogen and phosphorus contained in above- and below-ground biomass of non-crop vegetation on clearcut CH sites burned 2, 4 and 8 years previously.
FIGURE 6. Above-ground biomass and percentage cover of fireweed and salal on clearcut HA sites burned 2 and 4 years previously. The vertical bars represent one standard error.

Soil temperature and moisture

Soil moisture deficits were not detected on any site during the summers 1987 and 1988. Furthermore, no difference in soil water potential or gravimetric soil moisture down to 25 cm depth was found between the different types and ages of site studied. All soil water potential measurements were below 0.021 MPa, which indicated near field capacity conditions.

Figure 7 presents mean soil temperatures measured at several depths between 11:00 am and 3:00 pm on clearcut CH and HA sites near Port McNeill from 1987 to 1989. In general, soil temperature was a few degrees (1–4°C) higher: 1) on clearcut HA sites burned 2–4 years before than on clearcut CH sites burned 2–4 years before; and 2) on clearcut CH sites burned 2–4 years before rather than 8–10 years before. The differences were the greatest at the 3 cm depth and the least at the 25 cm depth.

FIGURE 7. Mean soil temperatures for the 1987-1989 period at 3, 10 and 25 cm depth based on combined data from clearcut CH and HA sites.
**Soil nutrient status**

Soil nutrient status for the three types of sites is summarized in Table 1. Soil pH and microbial activity were similar across all site types; and the 8–25 cm depth always had lower pH and microbial activity than the 0–8 cm depth.

**TABLE 1.** Soil nutrient status compared for 2- to 4-year post-burning clearcut CH (2–4+B CH) and HA (2–4+B HA) sites and 8- to 10-year post-burning clearcut CH (8–10+B CH) sites. Numbers in rows followed by the same lowercase letter are not significantly (P > 0.05) different between sites and depths. Values in parentheses are one standard error.

<table>
<thead>
<tr>
<th>Sites</th>
<th>2–4+B CH</th>
<th>8–10+B CH</th>
<th>2–4+B HA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0–8</td>
<td>8–25</td>
<td>0–8</td>
</tr>
<tr>
<td><strong>pH</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.47 b</td>
<td>4.03 a</td>
<td>4.33 b</td>
</tr>
<tr>
<td></td>
<td>(0.10)</td>
<td>(0.07)</td>
<td>(0.04)</td>
</tr>
<tr>
<td><strong>Microbial activity</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(mg/g per 24 hr)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.56 b</td>
<td>0.38 a</td>
<td>0.59 b</td>
</tr>
<tr>
<td></td>
<td>(0.05)</td>
<td>(0.04)</td>
<td>(0.04)</td>
</tr>
<tr>
<td><strong>Total N</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(%)</td>
<td>1.25 c</td>
<td>0.95 a</td>
<td>1.10 b</td>
</tr>
<tr>
<td></td>
<td>(0.05)</td>
<td>(0.03)</td>
<td>(0.06)</td>
</tr>
<tr>
<td><strong>C/N ratio</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>45.3 a</td>
<td>59.8 b</td>
<td>58.0 b</td>
</tr>
<tr>
<td></td>
<td>(1.9)</td>
<td>(2.5)</td>
<td>(5.2)</td>
</tr>
<tr>
<td><strong>Mineralizable NH₄⁺</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(ppm)</td>
<td>0.37 c</td>
<td>0.24 b</td>
<td>0.28 b</td>
</tr>
<tr>
<td></td>
<td>(0.03)</td>
<td>(0.02)</td>
<td>(0.02)</td>
</tr>
<tr>
<td><strong>Extractable NH₄⁺</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(ppm)</td>
<td>0.14 b</td>
<td>0.13 b</td>
<td>0.05 a</td>
</tr>
<tr>
<td></td>
<td>(0.01)</td>
<td>(0.02)</td>
<td>(0.01)</td>
</tr>
<tr>
<td><strong>Available PO₄⁻</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(ppm)</td>
<td>0.220 d</td>
<td>0.043 c</td>
<td>0.005 b</td>
</tr>
<tr>
<td></td>
<td>(0.056)</td>
<td>(0.016)</td>
<td>(0.001)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Depths (cm)</th>
<th>8</th>
<th>20</th>
<th>8</th>
<th>20</th>
<th>8</th>
<th>20</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Resin NH₄⁺</strong></td>
<td>(mg/a)</td>
<td>0.472 a</td>
<td>0.469 a</td>
<td>0.580 b</td>
<td>0.632 b</td>
<td>0.873 c</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.015)</td>
<td>(0.011)</td>
<td>(0.035)</td>
<td>(0.027)</td>
<td>(0.019)</td>
</tr>
<tr>
<td><strong>Resin NO₃⁻</strong></td>
<td>(mg/g)</td>
<td>0.047 a</td>
<td>0.047 a</td>
<td>0.045 a</td>
<td>0.042 a</td>
<td>0.043 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.002)</td>
<td>(0.001)</td>
<td>(0.002)</td>
<td>(0.002)</td>
<td>(0.001)</td>
</tr>
<tr>
<td><strong>Resin PO₄⁻</strong></td>
<td>(mg/g)</td>
<td>0.160 c</td>
<td>0.165 c</td>
<td>0.053 b</td>
<td>0.025 a</td>
<td>0.124 c</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.030)</td>
<td>(0.027)</td>
<td>(0.002)</td>
<td>(0.006)</td>
<td>(0.02)</td>
</tr>
<tr>
<td><strong>Decomposition rate</strong></td>
<td>(%)</td>
<td>25.9 b</td>
<td>19.7 a</td>
<td>27.3 b</td>
<td>19.7 a</td>
<td>65.0 d</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(4.0)</td>
<td>(3.8)</td>
<td>(4.7)</td>
<td>(4.3)</td>
<td>(6.1)</td>
</tr>
</tbody>
</table>

Some striking differences in soil nutrient parameters are evident between the different types of site. Of note were the significantly (P<0.05) greater extractable NH₄⁺, mineralizable NH₄⁺, available PO₄⁻, and resin NH₄⁺ in the 2- to 4-year post-burning clearcut CH sites than in the 8- to 10-year post-burning clearcut CH sites. The HA sites had significantly (P<0.05) greater extractable NH₄⁺, available PO₄⁻ (for the 8–25 cm depth only), resin NH₄⁺, and relative decomposition rate than the 2- to 4-year post-burning clearcut CH sites. Soil nutrient availability was generally lower for the 8–25 cm depth than for the 0–8 cm depth. The higher relative decomposition rate of the cellulose on the clearcut HA sites was associated with a greater observed micro- and meso-faunal activity. Results from the total N, extractable and mineralizable NH₄⁺, and the resin NH₄⁺ between the 2- to 4- and 8- to 10-year post-burning clearcut CH sites are contradictory. Further work is required to explain these findings.
Potted seedling bioassay

Sitka spruce and western redcedar were grown in pots containing forest floor taken from three CH sites (1-, 3- and 9-year post-burning clearcut CH sites) at two depths (0–8 and 8–25 cm). Sitka spruce over the two growing seasons grew significantly more (P<0.01) in the 1- and 3-year post-burning clearcut CH material than in the 9-year post-burning clearcut CH material, and in soil from the 0–8 cm depth than from the 8–25 cm depth. No significant difference (P=0.37) in western redcedar growth in the three different soils was found, but growth was significantly (P=0.001) lower on material from the 8–25 cm depth than from the 0–8 cm depth. The results for Sitka spruce are consistent with the overall differences in the soil nutrient status reported in Table 1 between the 2–4+B CH and 8–10+B CH sites and between the 0–8 and 8–25 cm depths.

4 STUDY OF SEEDLING GROWTH IN FIELD EXPERIMENTS

Logging and slashburning practices are known to increase resource availability temporarily (Binkley 1984; Krause and Ramil 1986; David 1987), and this often allows crop trees to grow well for the first few years after forest removal (Martin 1985). In some cases, the termination of the flush of nutrients and the full occupancy of the above- and below-ground environment by non-crop vegetation may coincide.

Non-crop vegetation interferes with crop trees through competition for water (Price et al. 1986; Flint and Childs 1987; Petersen et al. 1988), nutrients (Carter et al. 1984; Cole and Newton 1986; Elliot and White 1987), and light (Brand 1986; Brand and Janas 1988); through the modification of soil characteristics (Damman 1971; Read 1984); and through direct allelopathic effects (Del Moral and Cates 1971; Hanson and Dixon 1987; Mallik 1987; Cote and Thibault 1988). All of these factors interfere with the uptake of resources by crop trees. In some cases, however, non-crop vegetation may benefit crop trees through, for example, nitrogen accretion (Binkley 1981) and the reduction of evapotranspiration (Conard and Radosевич 1982).

Salal, a common ericaceous shrub which thrives on poor to medium sites in many low and some mid-elevational coastal forests in British Columbia (Klinka et al. 1989), competes with crop trees in all phases of stand development, and deters the establishment and growth of commercial tree species in both naturally and artificially regenerated stands. A good review on the autecology of salal can be found in Haeussler and Coates (1986). On dry sites, salal depletes soil water to levels that seriously hinder photosynthesis of crop trees (Price et al. 1986). On moist sites, it may compete for nutrients or produce compounds that inhibit nutrient availability to conifers (Germain 1986; Messier et al. 1988). Production by ericaceous shrubs of compounds which interfere directly or indirectly with coniferous seedling growth has been reported from Scotland (Calluna vulgaris: Handleby 1963; Robinson, 1972; Read 1984) and eastern Canada (Kalmia angustifolia: Mallik 1987; Mallik and Newton 1988).

4.1 Materials and Methods

Field seedling experiment

Study area

This experiment was conducted on the same sites as for the study of vegetation and soil recovery following clearcutting and slashburning (see Section 3.1).

Coniferous seedling data

Several hundred nursery-grown western redcedar, Sitka spruce, and western hemlock PSB 1-0 seedlings were planted in April 1987 on each of the three types of sites (i.e., 2- and 8-year post-burning clearcut CH sites and 2-year post-burning clearcut HA sites) near Port McNeill. Eight-year post-burning clearcut HA sites were not investigated because by that age, clearcut HA sites are densely revegetated with 3–5 m tall western hemlock.
The experiment was a 3 x 3 x 3 nested-factorial using a completely randomized design. Orthogonal contrasts were used to compare the treatment means. The three main factors were: 1) three coniferous species (western redcedar, Sitka spruce and western hemlock), 2) three sites (2- to 4- and 8- to 10-year post-burning clearcut CH sites, and 2- to 4-year post-burning clearcut HA sites), and 3) three planting treatments. The treatments included: seedlings planted without any additional treatment (i.e., the vegetation-not-removed treatment); seedlings planted and supplied with 40 g of a 14-14-14 NPK slow release fertilizer (Osmocote®, Sierra Chemical Company, California) placed at a depth of 10 cm in four holes equally spaced at a distance of 10 cm from the seedlings (i.e., the fertilized treatment); and seedlings planted in the middle of 200 cm diameter patches from which all above-ground vegetation was continuously removed by clipping, and from which below-ground competition was continuously cut around the patches to a depth of 40 cm (i.e., vegetation-removed treatment: Figure 8).

The height and diameter of each seedling were evaluated just after planting, and at the end of 1987, 1988 and 1989 growing seasons. In addition, the effect of the vegetation-not-removed treatment and vegetation-removed treatment on mycorrhizal infection was examined in 1989 using seedlings from clearcut CH sites burned 2-4 years previously.

Potted seedling experiments were undertaken. The results are reported in Messier (1990) but were not applicable for operational forestry.

![Figure 8](image)

**FIGURE 8.** Vegetation-removed treatment applied to western redcedar growing on clearcut CH sites burned 2–4 years previously. Note that all the vegetation has been removed from an area 1 m in radius all around the seedling.

**Soil data**

Nutrient availability (measured with ion-exchange resin bags), relative decomposition rate (measured with confined cellulose discs), soil moisture (measured with soil tensiometers), and soil temperature (measured with dial soil thermometers) were compared between the vegetation-not-removed and the vegetation-removed treatments on all six study areas.
4.2 Results

Field seedling experiment

Total height increment of Sitka spruce, western redcedar and western hemlock 3 years after planting for the three types of site and two treatments is shown in Figure 9. The following general observations can be made and are significant at $P<0.05$:

1. The removal of the non-crop vegetation significantly increased growth for all species on all types of sites. The response was generally greater on 2–4+B CH and 8–10+B CH than on 2–4+B HA sites.

2. Western hemlock benefited most from the vegetation-removed treatment; western redcedar responded least.

3. In the vegetation-not-removed treatment on 2–4+B CH and 8–10+B CH sites, western redcedar grew the best and performed better than western hemlock or Sitka spruce in the vegetation-removed treatment on 8–10+B CH sites. However, western redcedar grew less than western hemlock and Sitka spruce for both treatments on the 2–4+B HA sites and for the vegetation-removed treatment on 2–4+B CH. This suggests that western redcedar was the least affected by the presence of salal, and that its growth was insensitive to site age or phase.

4. Western hemlock grew better than the other two species both with and without vegetation removal on the HA sites and in the vegetation-removed treatment on the 2–4+B CH sites.

5. Growth for western hemlock and Sitka spruce species was the least on the 8–10+B CH and the greatest on the 2–4+B HA sites.

No significant difference ($P=0.56$) in total percent mycorrhizal infection was found between the vegetation-not-removed and the vegetation-removed treatments on the 2–4+B CH sites. For both treatments, the percent mycorrhizal infection on western hemlock, Sitka spruce and western redcedar was greater than 95%.

The rate of cellulose decomposition between the vegetation-removed and vegetation-not-removed treatments was also not significantly different ($P=0.62$) on the three types of site. There was, however, significantly more available ammonium ($P=0.02$) and phosphate ($P=0.007$) for the vegetation-removed than vegetation-not-removed treatments for the three types of site.

The rooting pattern of the three coniferous species varied markedly. Western hemlock and Sitka spruce produced long lateral roots (up to 2.5 m long) close to the surface; western redcedar produced shorter roots (up to 0.8 m long), but these were more evenly distributed in the forest floor.
FIGURE 9. Total height increment after three growing seasons of Sitka spruce, western hemlock and western redcedar for the three types of site and the vegetation-not-removed and vegetation-removed treatments. The growth difference within each species and type of site shows the interference effects of the non-crop vegetation. The site effects are shown by the growth differences between the three types of site within each species where the interference effects of the non-crop vegetation was removed (i.e., for the vegetation-removed treatment). The vertical bars are one standard error of the mean.

Slow release fertilizer applied immediately after planting resulted in a significant (P<0.01) increase in the growth of the seedlings on CH sites for the first 2 years only. During the third year, the growth was slower on the vegetation-removed treatment and similar to that on the vegetation-not-removed treatment (Figure 10). Associated with this reduced growth in the third year were symptoms of nutrient deficiency (yellowing of all foliage, reduction in size of new foliage, and reduced leader growth). Slow release fertilizer did not significantly increase (P>0.05) growth on the 2–4+8 HA sites, and no symptoms of nutrient deficiency were apparent in the third year.
5 STUDY OF SALAL GROWTH, ACCLIMATION, SURVIVAL, AND COMPETITIVE ABILITY

Many plants are able to grow and survive at low light intensities because they can acclimate or adjust to shade. Plant characteristics responsible for shade tolerance (or shade acclimation) include: responsiveness of stomata to sunflecks, genetic control of anatomical changes in leaves, changes in chlorophyll-protein ratios, activity of enzymes involved in chemical processes in chloroplasts, slow respiration rates, efficient photosynthetic rates at low light intensities, and various metabolic changes (Kramer and Kozlowski 1979). One of the major mechanisms by which plants adjust to low light levels, however, is by allocating proportionately more carbon to the shoots than to the roots (Chapin et al. 1987).

To grow, plants have to produce more carbohydrates through photosynthesis than they use through respiration. The light level at which photosynthesis equals respiration represents the light compensation point for a particular plant. According to Perry et al. (1969), plants adapted to grow in shade reach this light compensation point at around 0.5% of full sunlight, whereas plants adapted to grow in full sunlight reach the light compensation point at around 1.5%. This light compensation point is measured at the leaf level, however, and the minimum light requirement for the whole plant is usually slightly higher. Other factors such as diseases and competition also contribute to make the minimum light requirement for the survival and growth of plants somewhat higher than the actual light compensation point. Because different plant species respond differently to these factors, the species exhibit very different minimum light requirements.

Most quantitative studies of light requirements of forest trees and shrubs have been conducted in a greenhouse or a growth chamber (e.g., Kwasiga and Grace 1986; Minore 1988). The only information usually available to describe the minimum light requirements of forest trees and shrubs growing in their natural habitats is based on a subjective classification system of shade tolerant, mid-tolerant, intolerant (e.g., Spurr and Barnes 1980; Krajina et al. 1982). Very few studies have tried to quantify the minimum light requirement for survival of forest trees and shrubs growing naturally under a forest canopy.
5.1 Materials and Methods

Field experiment

Study area and experimental design

This component of the study was conducted in an area which had been clearcut logged in 1951 and left to regenerate naturally without any slashburning, and in an adjacent old-growth forest. The overstory consisted of a mixture of western redcedar, western hemlock, Sitka spruce and amabilis fir. Three 315-m² plots in the young stand and one 2800-m² plot in the old-growth stand were established, varying in species composition, density (stems/ha), and overstory canopy closure. The data for each category of measurement were analyzed by a one-way ANOVA. The Tukey HSD multiple comparison test was used to compare the treatment means.

Light measurements

For each of the four plots, light measurements (Photosynthetic Photon Flux Density: PPFD = 400–700 nm) were made directly above the understory layer of salal. Measurements were made during July, August and September of 1987 and 1988 between the hours of 11:00 am and 2:00 pm PST using a 1 m long LI-191 line quantum sensor (LI-COR, Inc., Lincoln, Nebraska). They were taken on clear sky (90–100% clear) and overcast sky (100% overcast) conditions for each of 1987 and 1988. For the open plots (plots 1 and 2), light measurements were divided between those taken between the trees (in the gaps) and directly under the trees. Light measurements were also made in an adjacent clearcut just before and after each series of in-plot measurements to determine full sunlight intensity.

Salal leaf morphology

Salal leaves were sampled at the same height above the ground as the light measurements in each of the four stands and in an adjacent 3-year-old clearing. The leaves were measured for area and thickness, and these characteristics were related to the light environment experienced by the leaves.

Potted experiment

Nursery-grown Sitka spruce and western redcedar seedlings (1-0 plug type) and salal plants were grown as a mixture of two species in a ratio of 3:5 (conifer: salal) in pots (20 x 40 x 20 cm) containing forest floor taken from 3-year post-burning clearcut CH and HA sites. In each pot, five salal plants were established on one half and three coniferous seedlings on the other half. The half of the pot occupied by salal was subjected to one of four shading treatments: 1) no shade, 2) 30% (two layers), 3) 10% (four layers) and 4) 5% (five layers) of full sunlight intensity (PPFD). The experiment was a 2 x 2 x 4 factorial (2 soil materials x 2 species x 4 light intensities) in a completely randomized design. Orthogonal contrasts were used to compare the treatment means.

The coniferous seedlings and salal plants were established in the pots in March 1988 and harvested in October 1989 after two complete growing seasons. At the time of harvest, the above- and below-ground biomass of coniferous seedlings and salal plants and the height and diameter increment of the coniferous seedlings were measured.

5.2 Results

Field experiment

Table 2 outlines the characteristics of the tree overstory and salal understory for the four coniferous stands investigated. Irradiance (Global PPFD and percentage of full sunlight) measured directly above the salal cover in the four conifer plots and between overcast and clear sky conditions is summarized in Table 3. Salal cover and density decreased (Table 2), salal height increased.
(Table 2), and salal leaves underwent major morphological modification (Figure 11) as tree canopy cover increased (Table 2) and as light intensity decreased (Table 3). Under plots 1 and 2, the average light levels varied from 2 to 38% of full sunlight (Table 3), and salal was dense and abundant. Salal was very tall and had large leaves under plot 3, where light levels averaged between 1.8 and 3.3% of full sunlight (Table 3). Only dead salal stems and few small salal leaves resprounting from old rhizomes were found under plot 4, indicating that salal was shaded out. The average light level recorded under plot 4 was very low, varying from 0.3 to 1.2% of full sunlight (Table 3).

![Leaf area (cm²)/leaf](image)

![Leaf thickness (mm)](image)

**FIGURE 11.** Salal leaf area and thickness under seven different coniferous canopy closures and resulting light environments. A description of the different plots and resulting light environments is given in Tables 3 and 4, respectively. Vertical bars are one standard error.

**TABLE 2.** Characteristics of tree overstory and salal understory between the four conifer plots studied. All plots were in the CH phase.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Plot 1</th>
<th>Plot 2</th>
<th>Plot 3</th>
<th>Plot 4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tree overstory</td>
<td>Salal understory</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age (yr)</td>
<td>36 old-growth</td>
<td>36</td>
<td>36</td>
<td>36</td>
</tr>
<tr>
<td>Densities (stems/ha)</td>
<td>12 400</td>
<td>490</td>
<td>20 200</td>
<td>6400</td>
</tr>
<tr>
<td>Species composition (%)^a</td>
<td>H52C45S3</td>
<td>H65C29F6</td>
<td>C64H27S9</td>
<td>H65C29F6</td>
</tr>
<tr>
<td>Basal area (m²)</td>
<td>11.4</td>
<td>185</td>
<td>64.4</td>
<td>51</td>
</tr>
<tr>
<td>Tree cover (%)</td>
<td>40</td>
<td>60</td>
<td>80</td>
<td>95</td>
</tr>
<tr>
<td>Height (m)</td>
<td>Avg. 3.8</td>
<td>30</td>
<td>6.4</td>
<td>12.1</td>
</tr>
<tr>
<td></td>
<td>Range 1.2-6.5</td>
<td>4.5-45</td>
<td>1.5-9.2</td>
<td>6.2-17.9</td>
</tr>
<tr>
<td>Diameter (cm)</td>
<td>Avg. 2.73</td>
<td>40.4</td>
<td>5.49</td>
<td>8.81</td>
</tr>
<tr>
<td></td>
<td>Range 0.3-9.8</td>
<td>2.0-225.0</td>
<td>0.6-15.2</td>
<td>2.9-25.3</td>
</tr>
<tr>
<td>Salal cover (%)</td>
<td>90</td>
<td>85</td>
<td>60</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Height (m)</td>
<td>1.9</td>
<td>2.2</td>
<td>4.3</td>
<td>3.5^b</td>
</tr>
<tr>
<td>Densities (stems/ha)</td>
<td>205 000</td>
<td>150 000</td>
<td>44 600</td>
<td>3500^b</td>
</tr>
</tbody>
</table>

^a H: western hemlock; C: western redcedar; S: Sitka spruce; F: amabilis fir.

^b Values from dead salal stems.
TABLE 3. Global PPFD and percentage of full sunlight measured directly above the salal understory within four western redcedar/western hemlock plots and a clearing under clear and overcast sky conditions. The values are averages of point measurements made between 11:00 am and 2:00 pm, and combine both direct and diffuse light.

<table>
<thead>
<tr>
<th></th>
<th>Clearing (CL)</th>
<th>1A in gaps</th>
<th>1B under trees</th>
<th>2A in gaps</th>
<th>2B under trees</th>
<th>3 under trees</th>
<th>4 under trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Global PPFD (μmol m⁻² s⁻¹)</td>
<td>1473.0</td>
<td>560.9 a</td>
<td>72.7 b</td>
<td>379.6 a</td>
<td>332 c</td>
<td>27.2 c</td>
<td>4.5 d</td>
</tr>
<tr>
<td>% of full sunlight</td>
<td>100.0</td>
<td>38.0</td>
<td>4.9</td>
<td>25.7</td>
<td>2.3</td>
<td>1.8</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Global PPFD (μmol m⁻² s⁻¹) | 338.6          | 79.3 a      | 34.1 b         | 90.4 a     | 33.2 b         | 11.1 c        | 3.9 d         | 324.6 |
| % of full sunlight | 100.0                | 23.4        | 10.1           | 26.7       | 9.8            | 3.3           | 1.2           |

NOTE: Numbers in rows followed by the same lowercase letter are not significantly different (P>0.05) between plots. A description of the plots is given in Table 2. Numbers between parentheses represent the coefficient of variation as a percentage.

Potted experiment

Coniferous seedling growth

Both Sitka spruce and western redcedar grew slightly but significantly (P=0.005) better as the light intensity reaching salal decreased. Because of the small amount of salal below-ground biomass produced in the pots compared to that in the field, these results should be interpreted with caution. Both species grew significantly (P=0.001) better in the soil taken from the 2–4+6 HA than CH sites.

Effect of light intensity on salal growth

Salal responded dramatically to the different shading treatments. Both salal leaf and fine root biomass decreased as the light intensity decreased. The decline in fine root biomass was much more rapid than that in leaf biomass, resulting in a dramatic increase in the leaf/fine root biomass ratio with the decline in light intensity (Figure 12).

![Figure 12](attachment:image.png)

**Figure 12.** Effect of decreasing light intensity on salal carbon allocation to leaves and fine roots. Vertical bars represent one standard error.
6 STUDY OF MECHANICAL SITE PREPARATION

The development of thick mor organic horizons at the surface of acidic forest soils can potentially tie up large amounts of nutrients (Ross and Malcolm 1988). Such accumulations of organic matter are caused by slow rates of decomposition which can result from one or more of: 1) the physical and chemical nature of the litter; 2) the environmental conditions (i.e., soil temperature, moisture and aeration) of the forest floor; and 3) the kind, number, and activity of micro-organisms present in the soil (Singh and Gupta 1977). By modifying at least one of these factors, site preparation applied in forestry can stimulate soil organic decomposition and nutrient mobilization.

Many different methods of mechanical site preparation have been used, ranging from simple mixing of horizons to complete elimination of the organic layer (often referred to as scalping). Whatever the method used, mechanical site preparation generally results in early increases in coniferous growth (Thomson and Neustein 1973; Pehl and Bailey 1983; Burger and Pritchett 1988). This is thought to be due to any combination of the following factors: 1) an increase in the volume of soil available for rooting (Ross and Malcolm 1982); 2) improved aeration and drainage in the soil (Read et al. 1973; Ross and Malcolm 1982); 3) stimulation of nutrient mobilization (Krause and Ramjal 1986; Burger and Pritchett 1988); 4) suppression of non-crop vegetation (Malcolm 1975; Pehl and Bailey 1983; Burger and Pritchett 1988); and 5) provision of a more suitable planting site for seedlings (Ross and Malcolm 1982).

6.1 Materials and Methods

Study area and experimental design

The experimental area was located between Port McNeill and Port Hardy, and had been logged in 1986 and slashburned in the spring of 1987. The experiment design was a 2 x 2 x 2 factorial in a completely randomized design, and consisted of 32 plots (16 x 16 m in size) randomly located within a 97-ha clearcut that included several patches of CH and HA sites. The three main factors investigated were: 1) CH and HA phases, 2) non-scarified and scarified sites, and 3) western hemlock and western redcedar. The sites were scarified in January 1988 with a backhoe (215 Cat excavator) with a three-tined rake (70–100 cm teeth long) attachment. The objectives of the scarification were to remove the salal rhizomes, to simulate windthrow by mixing the organic matter and mineral soil, and to remove or redistribute slash to facilitate planting. Within each treatment, four plots were planted with western hemlock and four plots with western redcedar.

Coniferous seedling measurements

Western redcedar and western hemlock height and root collar diameter were measured at the end of the first (1988) and second (1989) growing seasons.

Soil data

Soil samples (taken from the upper 20 cm), ion-exchange resin bags and confined cellulose discs were analyzed in the laboratory in June 1988 and 1989 to determine the effects of each treatment on the soil nutrient status and relative decomposition rate. The same soil analyses as described in Section 3.1 were carried out. Soil temperature and moisture were measured at 10 and 25 cm soil depth between 11:00 am and 2:00 pm each month from July to September and in November 1988 and 1989.

Non-crop vegetation measurements

The above-ground biomass of the non-crop vegetation was assessed in July 1988 and 1989. The procedure described in Section 3.1 was used.
6.2 Results

Vegetation regrowth

Site preparation had a major impact on the recovery of the non-crop vegetation during the first 2 years. Salal above-ground biomass decreased on both clearcut CH and HA sites, whereas fireweed increased (Figure 13). After 2 years, salal above-ground biomass in the scarified treatment was only 25% of the non-scarified treatment on the clearcut CH sites, and 3% on the clearcut HA sites. The regrowth of salal on the scarified clearcut CH sites was rapid, going from 8 kg/ha in the first year to 312 kg/ha in the second year. On the non-scarified clearcut CH sites, salal above-ground biomass went from 532 kg/ha the first year to 1354 kg/ha the second year.

![Graph showing above-ground biomass](image)

**FIGURE 13.** Effect of scarification on the early recovery of salal (Sal), fireweed (Fw), and other non-crop species (Oth) on clearcut CH and HA sites for the first 2 years following logging and slashburning.

Soil measurements

Scarification increased soil temperature slightly (by 0.5–2.0°C) on both clearcut CH and HA sites, especially at 3 cm. Soil temperatures were in the range reported in Figure 7. Scarification had no observable effect on soil water potential throughout the summer of 1989.

The soil nutrient status 2 years after scarification is reported for scarified and non-scarified CH and HA clearcuts (Table 4). On clearcut CH sites, scarification significantly (P<0.05) decreased microbial activity, mineralizable NH₄+, available PO₄³⁻, resin NH₄+ and PO₄⁻, and relative decomposition rate. On the clearcut HA sites, scarification significantly (P<0.05) decreased mineralizable NH₄+, extractable NH₄+, available PO₄⁻, and resin NH₄+ and PO₄⁻, but increased resin NO₃⁻ and relative decomposition rate.

Seedling growth

Height increment was significantly increased by scarification, except for western redcedar on the CH site (Figure 14). In 1989, height increment was significantly (P=0.003) greater on HA than CH sites for both species, but the difference was small for western redcedar. Western hemlock grew significantly (P=0.001) faster than western redcedar on both types of site, but the differences were greater on clearcut HA sites.
FIGURE 14. Comparisons of the height increment in 1989 of western hemlock and western redcedar between scarified and non-scarified clearcut CH and HA sites. The vertical bars represent one standard error of the mean.

TABLE 4. Comparisons of some important soil properties on scarified and non-scarified clearcut CH and HA sites the second year following clearcutting and slashburning. Values in parentheses are one standard error. Values within each row with different lowercase letters are statistically different at $P<0.05$.

<table>
<thead>
<tr>
<th></th>
<th>2+BCH Non-scarified</th>
<th>2+BCH Scarified</th>
<th>2+BHA Non-scarified</th>
<th>2+BHA Scarified</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>4.45 a (0.10)</td>
<td>4.45 a (0.12)</td>
<td>4.28 a (0.07)</td>
<td>4.50 a (0.10)</td>
</tr>
<tr>
<td>Microbial activity (mg CO$_2$/g per 24 hr)</td>
<td>0.77 b (0.07)</td>
<td>0.54 a (0.05)</td>
<td>0.66 b (0.03)</td>
<td>0.70 b (0.03)</td>
</tr>
<tr>
<td>Mineralizable NH$_4^+$ (ppm)</td>
<td>0.13 c (0.01)</td>
<td>0.09 b (0.01)</td>
<td>0.19 a (0.02)</td>
<td>0.14 c (0.02)</td>
</tr>
<tr>
<td>Extractable NH$_4^+$ (ppm)</td>
<td>0.05 a (0.005)</td>
<td>0.04 a (0.01)</td>
<td>0.09 b (0.01)</td>
<td>0.05 a (0.01)</td>
</tr>
<tr>
<td>Available PO$_4^-$ (ppm)</td>
<td>0.06 b (0.01)</td>
<td>0.01 a (0.003)</td>
<td>0.10 c (0.02)</td>
<td>0.02 a (0.01)</td>
</tr>
<tr>
<td>Resin NH$_4^+$ (mg/g)</td>
<td>0.45 a (0.05)</td>
<td>0.57 ab (0.09)</td>
<td>0.90 c (0.08)</td>
<td>0.69 b (0.09)</td>
</tr>
<tr>
<td>Resin NO$_3^-$ (mg/g)</td>
<td>0.005 b (0.001)</td>
<td>0.004 ab (0.001)</td>
<td>0.003 b (0.000)</td>
<td>0.008 c (0.001)</td>
</tr>
<tr>
<td>Resin PO$_4^-$ (mg/g)</td>
<td>0.35 b (0.04)</td>
<td>0.21 a (0.05)</td>
<td>0.35 b (0.04)</td>
<td>0.19 a (0.03)</td>
</tr>
<tr>
<td>Decomposition rate (%)</td>
<td>0.25 b (0.03)</td>
<td>0.15 a (0.02)</td>
<td>0.17 a (0.02)</td>
<td>0.25 b (0.03)</td>
</tr>
</tbody>
</table>

* Average of two depths, 8 and 20 cm.
7 STUDY OF MICROTOPOGRAPHIC INFLUENCES ON SOIL PROPERTIES AND SEEDLING GROWTH

Microelevation and microscale chemical properties of the forest soil are often highly variable (Beatty and Stone 1986). This fine scale (microsite is measured in square metre and metre scales) heterogeneity has often been ignored in site research, which has focused on larger scale (macrosite is measured in hectare and 100-m scales) gradients in the environment (Beatty 1984).

Microenvironmental heterogeneity of the forest floor has been attributed to tree falls (Beatty and Stone 1986), mounds and pits (Ruel et al. 1988), decaying wood (Quesnel and Lavkulich 1981; Sidle and Shaw 1983), variations in overstory canopy species composition (Beatty 1984; Turner and Franz 1986), litter depths (Sydes and Grime 1981), and soil properties (Dwyer and Merriam 1981; Sidle and Shaw 1983). Better tree growth has been related to nutrient-richer soil microsites (Adams 1974; Husted 1982).

7.1 Materials and Methods

Study area

The experiment was conducted in the same 2- to 4-year post-burning clearcut CH sites that are described in Section 4.

Coniferous seedling measurements

Western redcedar and western hemlock seedlings in the vegetation-not-removed treatment in Section 4 were also used in this study. The height and diameter increments of each seedling were used as biindicators of the relative quality of the microsite.

Non-crop vegetation and microtopographic measurements

The percentage cover of fireweed and salal in 1-m² plots centred around each seedling, and the microtopographic position (top, mid-top, mid, mid-bottom, and bottom of small mounds) of each seedling was estimated in July 1989. Top and bottom positions were situated at least 0.5 m above and below the level ground (i.e., mid-positions).

Soil variables

Four equally spaced soil cores were collected from a 0–15 cm depth in the soil within 20 cm around each seedling at the end of October 1989 and bulked to form one soil sample per seedling. Soil analyses to assess nutrient status were carried out as described in Section 3. Ion-exchange resin bags and confined cellulose discs were buried around each seedling to estimate the nutrient availability and relative rate of decomposition, respectively, in the seedling’s root environment.

In October 1989, the soil surrounding each seedling was excavated and the substrate in which the seedlings roots were located was described.

Experimental design and statistical analyses

The experiment was a completely randomized design in which the cutovers were nested within the sites. The Tukey’s HSD multiple comparison test was used to compare the treatment means.

7.2 Results

Western redcedar growth increased from the top to the bottom microtopographic positions (Figure 15B). No similar trend was evident for western hemlock (Figure 15A). Of all the other variables measured (i.e., salal cover, fireweed cover, pH, moisture, resin ammonium, nitrate and phosphorus, and cellulose decomposition), only fireweed percentage cover showed the same significant trend as western redcedar growth.
FIGURE 15. Comparisons of the height and diameter increments in 1989 of planted 3-year-old western hemlock (A) and western redcedar (B) seedlings between top, mid-top, mid, mid-bottom and bottom microtopographic positions within 4-year-old post-burning clearcut CH sites. The vertical bars represent one standard error of the means.

8 DISCUSSION

8.1 Ecological Processes after Harvesting in Salal-Dominated Ecosystems on Northern Vancouver Island

Many of the differences in ecosystem processes between clearcut CH and HA sites on northern Vancouver Island result from the conditions in the forest before harvesting. The old-growth CH forest ecosystem has a thick accumulation of organic matter on the forest floor, of which decaying western redcedar (believed to decay relatively slowly) forms a substantial proportion. At the same time, the open canopy of the CH forest ecosystem allows light to penetrate the understory promoting the development of a dense salal cover. Light intensity in gaps averages 25% of full sunlight, but it may reach up to 80% under large gaps. The resulting dense cover of salal may contribute to the thick accumulation of organic matter on the forest floor because salal litter decomposes slowly (DeCatazaro and Kimmens 1985) and it may release compounds that reduce the rate of decomposition in the forest floor. These conditions may produce a poor substrate for tree growth.

By comparison, the windthrown HA forest ecosystem has a relatively small accumulation of organic matter, composed mainly of decaying western hemlock and amabilis fir. Decomposition of the organic matter, including the decaying wood, appears to be more rapid than in the CH forest ecosystem. Very little understory vegetation is present in the HA forest; low light intensity (2–5% of full sunlight: C. Messier, pers. comm.) probably precludes the growth of most plants. The forest floor is consequently made up mainly from above- and below-ground litter of western hemlock and amabilis fir. The apparently more rapid decomposition and nutrient cycling in this forest ecosystem type create conditions which favour rapid tree growth.

After the logging and slashburning of the CH forest ecosystem, salal re-establishes itself quickly, mainly by resprouting from rhizomes already present. During the first 2 years after harvesting, few new rhizomes are produced and new growth is in fine roots and shoots (Figure 4A). Salal appears to exploit fully the above- and below-ground environment it already occupies before it produces new rhizomes. By 8 years after logging and slashburning, however, salal has usually developed a large biomass of rhizome (Figure 4A). Above-ground salal biomass remains fairly constant from 4 to 8 years after logging and slashburning, although some increase comes from fine roots and rhizomes (Figure 4A). Other non-crop species also invade clearcut CH sites (Figure 4B). Fireweed, for example, invades quickly and increases
biomass only slightly after 2 years. On the other hand, bunchberry colonizes the sites more slowly and increases gradually even after 2 years (Figure 4B).

Weetman et al. (1990c) estimated that, on average, 20–30 kg of nitrogen per hectare are available annually for plant uptake on these poor to medium clearcut CH sites following logging and slashburning. We estimate in this study that 9 kg of nitrogen per hectare can be immobilized annually in the biomass of the non-crop vegetation for at least the first 8 years (Figure 5). Therefore, the regrowth of the non-crop vegetation can potentially immobilize between 30 and 45% of the available N on these sites every year. This immobilization may explain most of the differences in coniferous growth between the vegetation-not-removed and vegetation-removed treatments (see Figure 9) on clearcut CH sites.

Weetman et al. (1990 a and b) have also suggested that the release of chemicals by salal into the root environment of the coniferous seedlings may inhibit the normal mycorrhizal infection of tree roots, and consequently the uptake of nutrient ions. However, we found no evidence of this type of interference. Furthermore, a greenhouse bioassay in another study failed to find any evidence that the presence of salal reduced the ability of Sitka spruce, western hemlock or western redcedar to take up nutrient ions (McDonald 1989).

Coniferous seedlings planted on clearcut CH sites 8–10 years after burning grew less than seedlings planted on sites 2–4 years after burning (Figure 9). Growth of Sitka spruce in pots was also lower in forest floor taken from clearcut CH sites burned 9 years previously than from clearcut CH sites burned 1 or 3 years previously. Soil fertility declined from 2 to 10 years after logging and slashburning (see Table 1). Germain (1985) and Weetman et al. (1990c), working on similar sites, reported a similar decrease in nutrient availability 3–4 years after logging and slashburning. This decline in nutrient availability is believed to impose a nutritional stress on these coniferous species, in addition to the stress caused by salal competition.

Field and potted bioassays showed that western hemlock and Sitka spruce — and to a lesser extent western redcedar — grew better on clearcut and slashburned HA than on CH sites, both with or without non-crop vegetation. Large differences in the soil nutrient status were found between these CH and HA sites (Table 1), but no differences in soil moisture tension and only very small differences in soil temperature (i.e., maximum 2°C). The variation in coniferous seedling growth between these two forest ecosystem types following logging and slashburning thus appears to be explained by variations in nutrient availability.

The nutritional stress reported in 8- to 14-year-old coniferous plantations growing on clearcut and slashburned CH sites on northern Vancouver Island (Germain 1985; Weetman et al. 1990a, 1990b) appears to be the result of 1) inherently low soil fertility in cutover originating from the old-growth CH forest 2) salal competition for scarce nutrients and their subsequent immobilization in salal biomass, and 3) reduced site fertility caused by the termination of the flush of nutrients that occurs in the immediate post-logging and slashburning period (see Messier and Kimmins, 1990, for more information). The CH forest ecosystem does not appear to cycle enough nutrients to sustain satisfactory tree growth. This is especially true for a nutrient-demanding species such as Sitka spruce (Miller and Miller 1987).

As conifers grow and develop on clearcut CH sites, the overstory tree canopy slowly closes and reduces the light intensity reaching understory salal. This reduction in light intensity causes changes in salal’s (as shown in Table 2) above-ground biomass (Vales 1986), leaf morphology (Figure 11), and biomass distribution (Figures 12 and 16). The hypothetical changes in the fine root and leaf biomass of salal over time following the removal of the tree canopy are shown in Figure 17. The biomass increases and resulting nutrient immobilization in salal fine roots and leaves comes to a stop and then declines. The proportion of biomass being allocated to the fine roots also decreases as the tree canopy closes. Eventually, as the light level in the understory falls between 2 and 5% of full sunlight, salal disappears almost completely (see Messier et al. 1989 for more information). Presumably, as the biomass of salal declines, especially the fine root biomass, competition for nutrients also declines.
FIGURE 16. Fine root biomass, % cover, and basal area of salal and Douglas-fir in 11- to 12-year-old (open canopy) and 35- to 70-year-old (closed canopy) stands. Notice the sharp decline in salal fine root biomass from open to closed Douglas-fir canopies (after Vogt et al. 1987).

FIGURE 17. Hypothetical relationships between the leaf and fine root biomass of salal under developing stands. The arrow indicates the tree cover and light conditions at which salal is shaded out. These relationships were developed from Figures 4, 12, and 16 and from data from Vales (1986).
8.2 Operational Significance and Recommendations

This research has looked at some of the major ecological processes controlling early conifer growth and has investigated some possible silvicultural solutions for managing the salal-dominated CH forest ecosystem type. The following recommendations can be made:

1. Western redcedar and western hemlock are the recommended species on clearcut and slashburned CH and HA sites, respectively, if neither fertilization, nor scarification treatments are applied.

2. Any delay in planting will hinder tree growth because salal re-establishes very quickly (especially below-ground) following harvesting, and because the flush of nutrients induced by logging and slashburning disappears.

3. Treatments that reduce salal regrowth will improve the early growth of western hemlock and Sitka spruce, and to a lesser extent western redcedar.

4. The intensity of competition by salal should decline after canopy closure because: 1) the biomass and nutrient accumulation by salal ceases following closure; and 2) salal allocates proportionately more biomass to its leaves than to its fine roots as the light intensity in the understory decreases, which further reduces its ability to compete for nutrients.

5. One should be cautious before implementing any silvicultural treatment to promote the growth of western redcedar on CH sites. Western redcedar did not show any major response to treatments that either reduced or increased nutrient availability. However, Weetman et al. (1990b) have found older western redcedar to respond to fertilization.

6. Salal is most abundant on nutrient-poor to -medium sites where slow tree growth can be expected regardless of the presence or absence of salal. Such slow growth may therefore be a reflection of the site as much as or more than the presence of salal.

7. Salal competition for nutrients, and reduced site fertility over time on clearcut and slashburned CH sites, appear to be the major causes of reduced growth of Sitka spruce. However, the nutritional stress observed in currently stagnated 8- to 14-year-old Sitka spruce plantations may be reduced after tree canopy closure because of the reduction in salal biomass and competition for nutrients. This hypothesis is now being studied by other researchers.

8. The rotation-length effect on tree growth of early reduction (due to salal) or improvement (due to silvicultural treatments) is difficult to predict unless these effects are sustained over time. Short-term gains or losses in tree growth will not necessarily lead to a major difference in harvestable volume at the end of the rotation period. Rotation-length, ecosystem-level management simulation models that can account for the effects of the rotation-length dynamics of nutrients, light competition, and stand dynamics are required for such an assessment (e.g., FORCYCTE-11: Kimmins 1988).

9. Light to moderate slashburning does little to decrease the amount of salal rhizomes in areas with thick forest floor accumulation because of the lack of growing season moisture deficits. However, such slashburning does eliminate above-ground salal biomass and facilitate planting, apparently without compromising the fertility of the site. More research is needed, however, to ascertain the economic consequences of slashburning.

10. The upper layer (0–8 cm) seems to be the most fertile part of the forest floor on CH sites. Consequently, very hot slashburns are not recommended, because they have the potential to eliminate this rich upper layer.

11. Tree canopy closure greater than 85% that reduces below-canopy light intensities to 2–5% are needed to shade out salal completely. However, it is not necessary to achieve such low light intensities to reduce the negative impact of salal, because below-ground salal biomass declines markedly below 10% full sunlight.
12. The mixing of organic material and mineral soil by mechanical site preparation did not improve the soil nutrient status during the first 2 years of post-treatment. However, it did reduce salal regrowth, and resulted in increased growth of western hemlock seedlings.

13. Slow release fertilizer applied immediately after planting improved seedling growth for the first 2 years only. During the third year, most of the fertilized western hemlock and Sitka spruce and many of the western redcedar seedlings showed signs of nutritional stress and reduced aboveground growth. Similar results were obtained for Douglas-fir seedlings growing in the CDF (B. Green, pers. comm.). These conditions are believed to be caused by a re-allocation of resources to root production following the end of nutrient release from the fertilizer pellets, or by an alteration in mycorrhizal infection of the roots caused by the nutrient-rich conditions created by fertilization. A good review on the effects of fertilization at time of planting can be found in Brockley (1988).

14. On mesic CH sites, small depressions (i.e., the bottom of microtopographic positions) can constitute good microsites for western redcedar, although it is not yet clear why this is so. Small depressions tend to be colder and moister, offering protection against the sun and the wind. They are also richer in some nutrients and higher in pH, although neither of the last two factors was significantly different (P=0.1). These microsites were also more likely to be occupied by fireweed, perhaps a reflection of somewhat better nutritional conditions.

9 LITERATURE CITED


Krajina, V.J., K. Klinka, and J. Worrall. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Univ. B.C., Fac. For., Vancouver, B.C.


