Forest Ecology and Management, 60 (1993) 181-206
Elsevier Science Publishers B.V., Amsterdam

Factors limiting early growth of western redcedar, western hemlock and Sitka spruce seedlings on ericaceous-dominated clearcut sites in coastal British Columbia

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(Accepted 5 April 1993)

Abstract

A 3 year field and pot study was conducted to determine the effects of several biotic and abiotic factors on the early growth of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata*, Donn) and Sitka spruce (*Picea sitchensis*, Bong. Carr.) seedlings established on 2- and 8-year-old clearcut sites previously occupied by old-growth western hemlock and western redcedar forests (referred to as younger and older CH, respectively), and on adjacent 2-year-old clearcut sites previously occupied by second-growth western hemlock and amabilis fir (*Amabilis amabilis* (Dougl.) Forbes) forests (referred to as younger HA) in coastal British Columbia. The objective of the study was to determine which factors are associated with the poor growth characteristic of the salal (*Gaultheria shallon*, Pursh) dominated CH clearcut sites.

No soil moisture deficits were measured on any of the three types of clearcut sites at any time of year. The best seeding growth was on the younger HA sites followed by the younger CH sites and then the older CH sites. The better growth on the younger HA sites was associated with a higher availability of N and P in the first 20 cm depth of the forest floor. No differences in matric soil water potential and pH, and only small differences in soil temperature were measured between the three types of clearcut sites. Complete removal of the competing vegetation on the younger and older CH sites resulted in an increase in conifer seedling growth and in the availability of N (22–40%) and P (15–32%); however, it did not affect cellulose decomposition and matric soil water potential, and increased soil temperature only slightly. Both western hemlock and Sitka spruce seedlings were very responsive to differences in nutrient availability measured between types of clearcut sites and planting treatments. In contrast, western redcedar was not responsive. All three conifer species had very high mycorrhizal colonization on the younger CH sites, and this was not altered by the removal of the competing vegetation (mainly salal).

These results suggest that the nutritional stress and poor growth of conifers on salal-dominated CH clearcut sites in coastal British Columbia can be explained by: (1) inherently low forest floor nutrient

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availability; (2) competition between salal and conifer seedlings for scarce nutrients and nutrient immobilization in salal; (3) declining nutrient availability a few years after clearcutting and slashburning.

Introduction

The implementation of successful regeneration programs requires, among other things, identification of the factors that limit plantation establishment and growth. Factors in the environment that may limit plant growth can be divided between those that can be affected by other plants, and those that are more or less intrinsic to the sites. Competing vegetation often interferes with the growth of conifers directly through resource competition (i.e. light, moisture and nutrients) and chemical inhibition (i.e. allelopathy), or indirectly by modifying the environment in a way that is detrimental to the conifers (Weidenhamer et al., 1989). All of these effects have the potential to interfere with the normal uptake of resources by conifers. Numerous examples for each of these possible types of interference exist in forestry: competition for water (Price et al., 1986; Flint and Childs, 1987; Petersen et al., 1988), nutrients (Eissenstat and Mitchell, 1983; Neary et al., 1990), and light (Brand, 1986; Brand and Janas, 1988); modification of the environment (Damman, 1971; Read, 1984; Coates et al., 1991); and direct allelopathic interferences (Rose et al., 1983; Mallik, 1987; Hanson and Dixon, 1987; Dote and Thibault, 1988). Clearcutting and slashburning practices are known to increase resource availability temporarily (Binkley, 1984; Krause and Ramlal, 1986; David, 1987), and this often allows crop trees to grow very well for the first few years following forest removal (Martin, 1985). However, in some cases, both the termination of the flush of nutrients and the full occupancy of the above- and below-ground environment by competing vegetation that occurs a few years after clearcutting can limit the duration of this period of good growth.

In a previous paper, Messier and Kimmins (1990b) discussed some possible causes for the N and P deficiencies reported by Weetman et al. (1989a) in Sitka spruce (*Picea sitchensis*, Bong. Carr.) seedlings and saplings growing on clearcut sites originating from old-growth western redcedar (*Thuja plicata*, Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands (hereafter referred to as CH) in coastal British Columbia. Similar deficiencies are also found in western hemlock, and to a lesser extent in western redcedar seedlings and saplings growing on the same sites (Weetman et al., 1989b). Interestingly, growth of these same conifer species is much better on adjacent cutovers originating from second-growth western hemlock and amabilis fir (*Amabilis amabilis*, (Dougl.) Forbes) stands (hereafter referred to as HA) that have been subjected to periodic massive disturbance by windthrow. Trees on these HA clearcut sites do not show any sign of nutritional stress.

Below-ground antagonistic interference by salal (*Gaultheria shallon*, Pursh; an ericaceous species), either by competition for nutrients or allelopathy, has been suggested as an explanation for the poor growth of these conifers on CH clearcut sites (Germain, 1985; Weetman et al., 1989a,b; DeMontigny, 1991), but neither of these mechanisms have been quantified. Competition for light has been ruled out as a possible antagonistic factor, because stagnated conifers are growing well above the competing vegetation.

The main objective of this study was to compare the early growth of western hemlock, western redcedar and Sitka spruce seedlings under contrasting sites and treatment conditions to determine which factors are associated with the poor conifer growth on CH clearcut sites. Three principal hypotheses were successfully tested:

(1) that salal competes with the conifer trees for nutrients on CH clearcut sites;

(2) that the poorer conifer growth found on CH than HA clearcut sites is related to a lower overall soil nutrient status;

(3) that the reduction in tree growth occurring 5–8 years after clearcutting on CH sites is related to a reduction in soil nutrient availability following the early flush of nutrients.

Materials and methods

Study area

The study area is located in the submontane variant of the CWHvm biogeoclimatic subzone (Pojar et al., 1987) on northern Vancouver Island, B.C., Canada (50°60′ N, 127°35′ W). The area is characterized as having a gently undulating topography (Suquash lowlands) which rarely exceeds 300 m in elevation. The surface material consists of deep (1 m in many places) unconsolidated fluvioglacial sediments. This surface material is underlain by Cretaceous sedimentary rocks. The annual rainfall is approximately 1700 mm, with 65% of the precipitation occurring between October and February. Although there is less rainfall in the summer than in the winter months, rainfall during the growing season is thought to be sufficient to prevent any soil moisture deficit (Lewis, 1982). The number of hours of sunshine per day varies from an average high of 6.4 in July to an average low of 1.5 in December; these low values reflect the frequent occurrence of fog in the summer and frontal clouds in the winter. 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 at an elevation of 50 m. These data represent an average for the last 36 years.

The research was conducted on clearcut sites that originated as either old-growth western hemlock and western redcedar (CH) forests or as second-growth western hemlock and amabilis fir (HA) forests. These two forest ecosystems have been classified by Lewis (1982). The CH forest ecosystem occurs extensively on the east side of northern Vancouver Island, on the west side of Vancouver Island and on the west side of the mainland, and is characterized by open stands of western redcedar and western hemlock. This ecosystem has apparently not been catastrophically 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, *Vaccinium parvifolium*, Howell and *Vaccinium alaskaense*, Smith. Only sparse ferns (*Blechnum spicant* (L.)) and mosses (*Hylocomium splendens* (Hedw.) B.S.C. and *Rhytidiadelphus loreus* (Hedw.) Warnst.) are found under the salal–*Vaccinium* cover (Germain, 1985). This forest ecosystem has a thick (20–60 cm, but mostly more than 45 cm), compacted humus layer rich in decaying wood (Lignohumimor; Klinka et al., 1981) overlying a moderately well to somewhat imperfectly drained Ferro-Humic Podzol. Western hemlock and western redcedar germinants are found in abundance, mainly on large western redcedar decaying logs, but the stand structure suggests that few of these survive more than a few years. Following clearcutting or clearcutting and slashburning, the CH ecosystem is quickly reinvaded by salal from rhizomes that are present in the old-growth CH forest (Messier and Kimmins, 1991). Natural regeneration of conifers following disturbance is slow and sparse and consists mainly of western redcedar and western hemlock seedlings.

The HA forest ecosystem occurs on sites that are subjected to periodic catastrophic windthrow, and is characterized by closed stands of western hemlock and amabilis fir. Only some sparse salal, *V. alaskaense*, and *V. parvifolium*, ferns (*Blechnum spicant*), herbs (*Polystichum munitum* (Kaulf) Presl and *Tiarella trifolitia* L.), and mosses (*Hylocomium splendens*) are present in the understory (Germain, 1985). This forest ecosystem is frequently situated on upper slopes, and has a relatively thin (10–40 cm) friable humus layer (Humimor; Klinka et al., 1981) overlying a moderately well drained Ferro-Humic Podzol. Western hemlock and amabilis fir germinants are found in abundance on the forest floor and on rotten logs. Western redcedar either does not germinate or germinants do not become established under the HA ecosystem canopy. Following clearcutting or clearcutting and slashburning, this ecosystem is rapidly invaded by a dense cover of fireweed (*Epilobium angustifolium* L.). Natural regeneration after disturbance is rapid and dense, consisting mainly of western hemlock. Transitions between the CH and HA forest ecosystems on the landscape are often abrupt and are not always related to obvious topographic features.

Field studies were started in the summer of 1987 on CH and HA clearcut sites that were situated on upper slope positions. Two ages of sites were chosen for the CH forest ecosystem (2 and 8 years after clearcutting and slashburning), but only 2 years after clearcutting and slashburning was chosen for the HA forest ecosystem. Experiments could not be established on HA clearcut sites where clearcutting and slashburning had not occurred for 8 years or more because of dense 3–5 m tall western hemlock regeneration. Two different cutovers 8–12 ha in size and 2–5 km apart were selected for each of the three types of clearcut sites. The 2-year-old HA cutovers were adjacent to the 2-year-old CH cutovers, whereas the 8-year-old CH cutovers were some 4–8 km away. All study cutovers were selected based on their homogeneity and similarity: similar slope position, aspect, surface material, forest floor thickness, soil characteristics, severity of burn, and tree species composition prior to disturbance as determined by the stumps. It was assumed that the 2- and 8-year-old CH clearcut sites had similar ecological attributes prior to disturbance, that they received a similar degree of disturbance, and that they share a similar post-disturbance stand history (Cole and Van Miegroet, 1989).

Field seedling bioassays

Nursery-grown 'plug type' 1-0 seedlings of western redcedar, western hemlock, and Sitka spruce were planted in April 1987 on each of the two cutovers of each of the three types of clearcut sites, for a total of 648 seedlings. These seedlings were left to grow for three growing seasons until the CH sites were 4 and 10 years old (hereafter referred to as younger and older CH sites, respectively) and 4 years old on the HA sites (hereafter referred to as younger HA sites).

The experiment was a $3 \times 3 \times 2$ nested-factorial using a completely randomized design in which two cutovers were nested within each type of clearcut site. The three main factors investigated were:

(1) three coniferous species (western redcedar, western hemlock, and Sitka spruce);
(2) three types of clearcut site (younger CH, older CH and younger HA sites);
(3) two planting treatments: (a) seedlings planted without any additional treatment except for the elimination of light competition (control treatment) and (b) 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 from adjacent vegetation was eliminated by periodically cutting around the patches to a depth of 40 cm (vegetation-removed treatment). The vegetation surrounding the seedlings in both planting treatments was clipped down periodically to eliminate competition for light. This was done to emulate the natural field conditions in which conifer saplings are growing above a dense understory of competing vegetation.

The height and basal diameter of each seedling were measured just after planting in the spring of 1987, and at the end of the 1987, 1988 and 1989 growing seasons. Orthogonal and non-orthogonal contrasts were used to compare the treatment means. For the contrasts that were non-orthogonal, the H' error was used instead of the H error (Sokal and Rohlf, 1981). The H' error was obtained by the following equation

$$H' = 1 - (1 - H)^{1/k}$$

where k represents degrees of freedom.

Log- or square-root-transformed values were used when the variances were not homogeneous using Bartlett's test. Both transformed and untransformed data were checked for homogeneity of variances and normality of distribution. Only the untransformed means are presented, but the statistics of some of the means were performed on transformed means.

The effect of competing vegetation of mainly salal on the degree of mycorrhizal colonization of the three conifer species was evaluated in 1989 on a subsample of eight seedlings taken from each of the control and vegetation-removed treatments on the younger CH sites. The fine roots, which were obtained by carefully excavating as much as possible of the root system, were kept at 3°C until analyzed. The root system of each seedling was cut in 5 cm sections and thoroughly mixed before taking three subsamples for analyses. A t-test was carried out to compare the frequency of each of the mycorrhizal types between the two planting treatments for each conifer species.

The roots were prepared for the determination of mycorrhizal colonization using the following method. The roots were soaked and heated (80–90°C) for 3 h in 10% KOH, bleached in a mixture of water, 30% H_2O_2 and ammonia for 2 h, and then acidified in 85% lactic acid for 20 min. Finally, the roots were stained in a mixture of 85% lactic acid, glycosol, water and trypan blue.

Each root sample was divided into three subsamples and the percentage colonization by mycorrhizal fungi was assessed by observing the stained root system using a dissecting microscope. The mycorrhizal status of Western hemlock and Sitka spruce was assessed by calculating the percentage of root tips that were non-mycorrhizal and those that were colonized by each of the four following ectomycorrhizal types.

(1) *Cenococcum geophilum* (Cg): tips with black hyphae forming Hartig net, hyphae mostly 4–5 μm wide, mantle when present with radiate pattern.
(2) Brown (B): tips with brown hyphae forming Hartig net, hyphae mostly 2 μm wide, mantle with jigsaw pattern.
(3) *Thelophora terrestris* (Tt): tips without brown hyphae, stele of the root obscured, Hartig net present, hyploid cystidia few to abundant, 80–130 μm long $\times$ 3 μm wide at clamped base, with radial taper to 1.5 μm at the tip.
(4) Others (O): all others.

The non-mycorrhizal (NM) tips were those without brown hyphae and hartig net, and with the stele of the root clearly visible. Western redcedar mycorrhizal status was assessed by calculating the proportion of root length colonized by vesicular–arbuscular (VA) mycorrhizae using the gridline intersect method (Kormanik and McGraw, 1982).

The above- and below-ground biomass of six randomly chosen seedlings in the control treatment for each of the three conifer species was compared after three growing seasons between the younger CH and HA sites. The experiment was a 3×2 factorial using a completely randomized design in which three conifer species were compared between the two types of clearcut sites. The above-ground biomass was obtained by clipping each seedling at the forest floor level, and the below-ground biomass was obtained by manually removing the growth medium (mainly organic matter) surrounding the roots of each seedling.

Soil nutrient status and microenvironment

Eighteen forest floor cores (7.4 cm in diameter) were taken in 1988 from depths of 0–8 cm and 8–20 cm on each of the two cutovers on each of the younger CH and HA, and older CH sites. These three types of clearcut sites were 3 years, 9 years, and 3 years old at the time of sampling, respectively. The fresh samples were stored at 3°C for less than 1 week prior to being passed through a 2 mm sieve before analysis. A subsample was oven-dried at 70°C for 24 h to determine the moisture content. All the results are reported on an oven-dry basis.

Forest floor pH was determined in distilled water with a glass electrode using a soil:water ratio of 1:4 (g:ml). Total N and P were measured by digesting 0.2 g (oven-dry mass) of forest floor material overnight with a mixture of potassium sulfate, sulfuric acid and selenium in a block digester. Extractable N was determined by extracting and shaking 5 g (fresh mass) of forest floor material with 100 ml 2 M KCl solution for 1 h. Available P was determined by extracting and shaking 5 g (fresh mass) of forest floor material with 100 ml 0.01 M HCl solution for 5 min. Mineralizable N was determined by extracting 5 g (fresh mass) of forest floor material with 100 ml 2 M KCl solution following anaerobic incubation in 25 ml of distilled water at 30°C for 7 days. The digest solutions were then analyzed for N and P using a Technicon AutoAnalyser II (Technicon Instrument Corp., Tarrytown, NY). Soil organic matter was determined by loss on ignition (24 h at 500°C), and carbon content calculated by dividing the organic matter content by 1.723 (Armson, 1979).

In early May 1988, 24 ion-exchange resin bags and cellulose disks were buried for 4 months at depths of 8 and 20 cm in the forest floor on all three types of clearcut sites near planted seedlings for the control and at depth of 8 cm for the vegetation-removed treatments to compare the relative levels of soil ammonium, nitrate and phosphate availability and relative decomposition rate in the seedling root environment. The resin bags were prepared of mixed cation (21 g of 68% moisture Amberlite IRC-50 C.P. RCOO-H-) and anion (29 g of 65% moisture Amberlite IRC-45 C.P. RNH_3^+OH-) exchange resin enclosed in stocking bags, and the cellulose disks were composed of 4.25 cm diameter Whatman No. 1 enclosed in 1 mm nylon mesh bags. The resin mixture bags had cation and anion exchange capacities of approximately 33 $mmol_c$ each. To prevent microbial growth on the resin, approximately 4% of the exchange capacity of the resin was loaded with mercuric chloride ($HgCl_2$). After 2 months, the resin was removed from the bags, air-dried, shaken with 200 ml 1 M KCl for 1 h, and the extract analyzed for NH_4^+-N, NO_3^--N, and PO_4^--P as described above. The cellulose disks were cleaned in distilled water, dried at 70°C for 24 h, and their loss of mass determined.

Ten soil temperature measurements using dial soil thermometers were made intermittently at depths of 3, 10, and 25 cm and ten soil moisture measurements using quick draw soil tensiometers (Soil Moisture Equipment, Washington, DC) were made intermittently at depths of 10 and 25 cm on each of the three types of clearcut site for the control and vegetation-removed treatments. Both measurements were made between 11:00 and 14:00 h twice every month from May to September in both 1987 and 1988.

The experiment was a nested factorial using a completely randomized design in which two cutovers were nested within each type of clearcut site. The main factors were: (1) three types of clearcut site; (2) two or three soil depths; (3) two planting treatments.

Orthogonal and non-orthogonal contrasts were used to compare the treatment means. Log- or square-root-transformed values were used when the variances were not homogeneous using Bartlett's test.

All these soil and microenvironmental measurements were designed to compare the soil nutrient status and microenvironment between the three types of clearcut site and between the control and the vegetation-removed planting treatments.

Above- and below-ground biomass of competing vegetation

The below- and above-ground biomass of the competing vegetation was measured on each cutover by taking six root cores (7.4 cm in diameter) at the beginning of June 1988, and by clipping 12 1 m^2 quadrants at the end of July 1988, respectively. The below-ground biomass was sorted by hand into different diameter sizes (0–1, 1–2, 2–5, and over 5 mm), and two species groups. Salal and *Vaccinium* spp. were combined in a single group and bunchberry (*Cornus canadensis*, L.) and fireweed in another group, owing to the difficulty in distinguishing between the fine roots of individual species within these two groups. No below-ground biomass assessment was made for the younger HA sites. The above-ground biomass collected from each quadrant was separated by species and between leaf and non-leaf components. A thorough description of the methodology can be found in Messier and Kimmins (1991). A one-way analysis of variance was carried out to compare the different biomass components measured between the three types of clearcut sites. The Tukey HSD multiple comparison test was used to compare the treatment means. Log- or square-root transformed values were used when the variances were not homogeneous using Bartlett's test.

Pot seedling bioassays

In March 1988, a pot experiment was initiated in an open area near the research sites. This experiment was designed to evaluate the effect of salal on Sitka spruce and western redcedar seedling growth and mycorrhizal infection, and to compare the growth of Sitka spruce and western redcedar between the three types of clearcut site in a more controlled environment. Nursery-grown Sitka spruce and western redcedar seedlings (1-0 plug type) and salal plants were established at two different conifer:salal plant ratios (4:6 and 4:0) in pots $20 \times 40 \times 20$ cm in size. Three types of growth media were used: the upper 8 cm of the forest floor from the same younger CH and HA sites and older CH sites as for the field experiment. The experiment was a $3 \times 2 \times 2$ factorial (three types of clearcut site × two salal–conifer combinations × two conifer species) using a completely randomized design. There were three pots per treatment, for a total of 36 pots. Orthogonal contrasts were used to compare the treatment means within each growing season. Salal plants were established as rhizomes 10 cm in length with at least two healthy buds.

The growth medium for each type of clearcut site was thoroughly mixed and all rhizomes and most fine and medium roots were removed prior to filling the pots. All pots were maintained in full sunlight, and the soil was held near saturation. At the end of each of the 1988 and 1989 growing seasons, the height and basal diameter of all conifers were measured. The degree of mycorrhizal colonization of Sitka spruce and western redcedar was determined at the end of the 1989 growing season as for the field seedlings.

Results

Competing vegetation, forest floor nutrient status and microenvironment

There were considerable differences in the amount of competing vegetation among the three types of clearcut sites (Table 1). In 1989, both of the younger and older CH sites were dominated by salal, whereas the younger HA sites had both fireweed and salal in almost equal amounts. Fireweed biomass did

Table 1
Comparison of oven-dry biomass (kg ha^{-1}) of competing vegetation between the three types of clearcut site in 1989

Species	Type of clearcut sites		
	Younger HA	Younger CH	Older CH
Above-ground biomass			
Vaccinium spp.	21[a]	54[a]	375[b]
Gaultheria shallon	1950[a]	3626[b]	4078[b]
Cornus canadensis	0	26[a]	406[b]
Epilobium angustifolium	1910[b]	293[a]	169[a]
Total	3881[a]	3999[a]	5028[b]
Below-ground biomass			
Gaultheria–Vaccinium	–[1]	3561[a]	10079[b]
Epilobium–Cornus	–	549[a]	1336[b]
Total	–	4110[a]	11415[b]

[1]Not sampled.
Note: CH type, cutovers originating from an old-growth western hemlock and western redcedar forest; HA type, cutovers originating from a second-growth western hemlock and amabilis fir forest.
Values in rows with the same superscript are not statistically ($P>0.05$) different between types of clearcut sites.

not change much from 1987 to 1989 in the younger HA sites, whereas during the same period, salal biomass increased more than six-fold, from 300 to 1950 kg ha^{-1}. The older CH sites had significantly ($P<0.01$) more above-ground competing vegetation biomass than the younger CH and HA sites, and the older CH sites had significantly ($P<0.01$) more below-ground biomass than the younger CH sites. No below-ground biomass data were available for the younger HA sites.

Because no statistical difference ($P>0.1$) were found between the cutovers within each type of clearcut site for most soil variables, the soil values from the two cutovers within each type of clearcut site were combined. No significant (all $P>0.1$) interactions were found between the three types of clearcut site and two depths for each of the soil variables measured. The orthogonal contrasts showed that the younger CH sites had a significantly ($P<0.01$) higher total N, extractable PO_4^--P, mineralizable NH_4^+-N, and resin PO_4^--P in both the 0–8 and 8–25 cm depths than the older CH sites (Table 2). The younger HA sites had a significantly ($P<0.01$) higher extractable PO_4^--P (at 8–25 cm depth only), extractable NH_4^+-N and rate of cellulose decomposition in both the 0–8 and 8–25 cm depths than the younger CH sites (Table 2). Only small differences in soil temperature were found among the three types of clearcut sites at depths of 3, 10 and 25 cm between 11:00 and 14:00 h for ten dates between May to September in 1987 and 1988; Table 3 reports the soil temperature for three dates in 1988 only. No soil moisture deficit was

Table 2
Comparisons of forest floor nutrient status and *P*-values between three types of clearcut site and two soil depths. Values in parentheses are one standard error of the mean

	Younger CH		Older CH		Younger HA		ANOVA (*P*-value)	
	0–8 cm	8–25 cm	0–8 cm	8–25 cm	0–8 cm	8–25 cm	Site type	Depth
pH	4.47	4.03	4.33	3.91	4.49	4.09	0.021	0.000
	(0.10)	(0.07)	(0.04)	(0.03)	(0.08)	(0.06)		
Total N	1.25	0.95	1.10	0.84	1.05	0.86	0.009	0.000
(%)	(0.05)	(0.03)	(0.06)	(0.03)	(0.06)	(0.06)		
C/N ratio	45.3	59.8	58.0	68.3	53.1	60.2	0.034	0.000
	(1.9)	(2.5)	(5.2)	(3.4)	(3.2)	(4.5)		
Mineralizable	0.37	0.24	0.28	0.17	0.37	0.25	0.005	0.000
NH_4^+-N (ppm)	(0.03)	(0.02)	(0.02)	(0.01)	(0.02)	(0.02)		
Extractable	0.14	0.13	0.05	0.05	0.19	0.22	0.001	0.640
NH_4^+-N (ppm)	(0.01)	(0.02)	(0.01)	(0.01)	(0.03)	(0.02)		
Extractable	0.224	0.043	0.005	0.001	0.191	0.182	0.000	0.000
PO_4^--P (ppm)	(0.056)	(0.016)	(0.001)	(0.000)	(0.061)	(0.053)		
	Depth (cm)							
	8	20	8	20	8	20		
Resin NH_4^+-N	0.472	0.469	0.580	0.632	0.873	0.829	0.000	0.512
($mg\,g^{-1}$)	(0.015)	(0.011)	(0.035)	(0.027)	(0.019)	(0.023)		
Resin NO_3^--N	0.047	0.047	0.045	0.042	0.043	0.040	0.532	0.812
($mg\,g^{-1}$)	(0.002)	(0.001)	(0.002)	(0.002)	(0.001)	(0.001)		
Resin PO_4^--P	0.160	0.165	0.053	0.025	0.124	0.062	0.000	0.072
($mg\,g^{-1}$)	(0.030)	(0.027)	(0.002)	(0.006)	(0.020)	(0.012)		
Decomposition rate	25.9	19.7	27.3	19.7	65.0	45.0	0.000	0.009
Cellulose (%)	(4.0)	(3.8)	(4.7)	(4.3)	(6.1)	(7.1)		

Note: see Table 1 for definitions of CH and HA types.

Table 3
Comparison of soil temperatures (°C) between the three types of clearcut site at depths of 3, 10, and 25 cm between 11:00 and 14:00 h in 1988: C, control treatment; VR, vegetation-removed treatment. Values in parentheses are one standard error of the mean

Sampling date and sky conditions	Planting treatment	Type of clearcut site								
		Younger HA			Younger CH			Older CH		
		3 cm	10 cm	25 cm	3 cm	10 cm	25 cm	3 cm	10 cm	25 cm
25 June 1988 (partly cloudy)	C	18.8 (1.4)	16.2 (0.6)	11.9 (0.6)	18.8 (2.0)	15.6 (0.8)	11.8 (0.5)	18.2 (0.9)	15.5 (0.6)	13.4 (0.3)
	VR	21.6 (1.5)	17.6 (0.8)	12.2 (0.3)	21.0 (1.8)	15.7 (0.6)	12.0 (0.4)	23.0 (0.9)	17.6 (1.1)	12.1 (0.5)
15 August 1988 (rainy)	C	14.5 (0.3)	15.3 (0.3)	14.5 (0.2)	14.9 (0.4)	14.9 (0.2)	13.7 (0.2)	14.2 (0.5)	14.8 (0.3)	13.5 (0.2)
	VR	15.9 (0.1)	16.0 (0.1)	15.1 (0.2)	14.9 (0.6)	15.6 (0.2)	14.0 (0.2)	14.5 (0.3)	15.1 (0.2)	13.8 (0.2)
12 September 1988 (sunny)	C	21.8 (1.1)	16.4 (0.6)	13.1 (0.2)	17.4 (0.9)	14.3 (0.7)	12.4 (0.2)	17.1 (0.9)	13.6 (0.6)	11.1 (0.3)
	VR	25.3 (1.1)	17.6 (0.8)	13.9 (0.1)	20.3 (0.8)	15.1 (0.8)	12.4 (0.3)	20.9 (0.9)	15.0 (0.8)	11.9 (0.3)

Note: see Table 1 for definitions of CH and HA types.

measured in any type of clearcut site and any treatment in either year, as matric soil water potential values were always above -0.021 MPa.

The removal of the competing vegetation increased the availability of resin NH_4^+-N by 22–40% and resin PO_4^--P by 15–32% on all three types of clearcut site, but did not affect the availability of resin NO_3^--N and the rate of cellulose decomposition (Table 4). Soil temperature was generally 1–3°C higher on the vegetation-removed than control treatments, and these differences were significant ($P<0.05$) mainly at the 3 cm depth (Table 3).

Figure 1 illustrates the total height and diameter increments of western redcedar, western hemlock and Sitka spruce seedlings after three growing seasons between the two planting treatments and three types of clearcut site. Statistically significant ($P<0.001$) differences were found between the three types of clearcut site, two planting treatments and three conifer species (Table 5). All of the interactions between types of clearcut site, conifer species and planting treatments were significant at $P<0.01$, but only the interaction between types of clearcut site and conifer species was important (i.e. contributed more than 5% to the total sum of squares of all the factors and interactions). This latter interaction indicated that western redcedar was much less

Table 4
Comparisons of nutrient availability and cellulose decomposition rate between the control (C) and vegetation-removed (VR) treatments for the three types of clearcut site. Values in parentheses are one standard error of the mean

Factor	Planting treatment	Type of clearcut site		
		Younger CH	Older CH	Younger HA
Resin NH_4^+-N ($mg\ g^{-1}$)	C	0.472^a (0.015)	0.580^a (0.035)	0.873^a (0.019)
	VR	0.598^b (0.024)	0.812^b (0.055)	1.065^b (0.034)
Resin NO_3^--N ($mg\ g^{-1}$)	C	0.047^a (0.002)	0.045^a (0.002)	0.043^a (0.002)
	VR	0.053^a (0.004)	0.046^a (0.004)	0.049^b (0.003)
Resin PO_4^--P ($mg\ g^{-1}$)	C	0.160^a (0.030)	0.053^a (0.002)	0.124^a (0.020)
	VR	0.211^b (0.022)	0.061^b (0.004)	0.165^a (0.024)
Decomposition rate Cellulose (%)	C	25.9^a (4.0)	27.3^a (4.7)	65.0^a (6.1)
	VR	22.6^a (5.1)	29.3^a (4.5)	73.4^a (9.2)

Note: see Table 1 for definitions of CH and HA types.
Values in rows with the same superscript are not statistically ($P>0.05$) different between treatments.

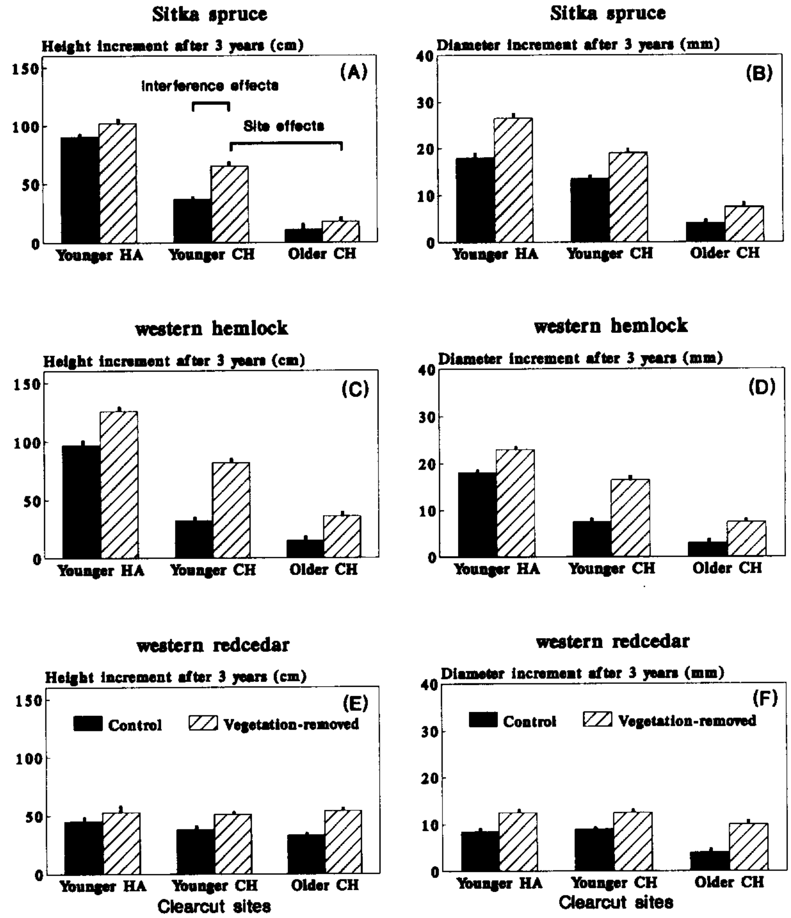

Fig. 1. Total height and diameter increments of western hemlock, Sitka spruce and western redcedar seedlings after three growing seasons: comparison between the two planting treatments and three clearcut sites. The vertical bars show one standard error of the mean with $n=30$–36.

affected than Sitka spruce and western hemlock by the differences found between the three types of clearcut site.

The other statistically significant, but less important, interactions indicate that:

(1) western redcedar total height and diameter increments were less affected by the removal of the competing vegetation than were western hemlock and Sitka spruce (species × treatments);

(2) the three conifer species responded differently to the two different planting treatments on the younger HA sites than on the younger and older CH sites (sites × treatments);

(3) the differences in western redcedar total height and diameter increments

Table 5
ANOVA summary table showing variance ratios (F), P-values and error mean square for total height and diameter increments after three growing seasons of western hemlock (Hw), western redcedar (Cw) and Sitka spruce (Ss) between the two planting treatments and three types of clearcut site

Source	Total height increment after three growing seasons			Total diameter increment after three growing seasons		
	d.f.	F-ratio	P	d.f.	F-ratio	P
Cut 1 (younger HA)	1	1.34	0.248	1	0.56	0.453
Cut 2 (younger CH)	1	0.02	0.895	1	2.93	0.088
Cut 3 older CH)	1	4.63	0.032	1	2.66	0.103
Site type (S)	2	600.30	0.000	2	635.92	0.000
Younger HA vs. younger CH			0.000			0.000
Younger CH vs. older CH			0.000			0.000
Treatment (T)	1	144.23	0.000	1	228.08	0.000
Species (Sp)	2	23.36	0.000	2	42.73	0.000
Cw vs. Ss+Hw			0.000			0.000
Ss vs. Hw			0.002			0.000
S×T	2	6.85	0.000	2	4.03	0.003
Sp×T	2	5.98	0.000	2	5.05	0.001
S×Sp	4	67.57	0.000	4	48.49	0.000
S×Sp×T	4	7.45	0.000	4	7.50	0.000
Cut1×T	1	0.48	0.615	1	1.03	0.360
Cut2×T	1	4.34	0.013	1	7.50	0.000
Cut3×T	1	2.64	0.073	1	2.59	0.077
Cut1×Sp	2	1.40	0.247	2	0.17	0.849
Cut2×Sp	2	3.93	0.019	2	4.72	0.009
Cut3×Sp	2	1.96	0.141	2	2.16	0.116
Cut1×T×Sp	2	1.48	0.204	2	1.55	0.187
Cut2×T×Sp	2	1.58	0.178	2	0.97	0.422
Cut3×T×Sp	2	0.67	0.613	2	0.19	0.945
Error mean square	622	8.70		622	1.53	

Note: see Table 1 for definitions of CH and HA types.

between planting treatments and types of clearcut site differed from those of western hemlock and Sitka spruce (sites×treatments×species).

The interactions between cutovers and the main treatments were either statistically non-significant ($P>0.05$) or, if significant, not important (i.e. small sum of squares).

Both total height and diameter increments were found to be significantly ($P<0.001$) greater on the younger HA than CH sites, and on the younger CH than the older CH sites. The vegetation-removed treatment significantly ($P<0.001$) increased total height and diameter increments in comparison with the control treatment. Western redcedar total height and diameter increments were significantly ($P<0.001$) lower than those of Sitka spruce and western hemlock. Sitka spruce diameter increment was significantly

($P<0.001$) greater than that of western hemlock, whereas western hemlock height increment was significantly ($P=0.002$) greater than that of Sitka spruce. No significant ($P>0.05$) difference was obtained between cutovers within each type of clearcut site, except between the cutovers in the older CH sites, in which case a small significant difference was found for the total height increment (Table 5).

The general pattern of growth differences obtained between types of clearcut site, planting treatments and species were very similar for both total height and diameter increments, and therefore the same general conclusion can be drawn from either of these two growth variables.

The percentage mortality of seedlings 3 years after planting was less than 2 for all three species on all types of clearcut site and for both planting treatments, except for western hemlock and Sitka spruce on the control treatment on the older CH sites, where it was 8 and 10, respectively. An inspection made at the end of the fourth growing season showed that the mortality of western hemlock and Sitka spruce on the older CH sites for the control treatment had increased to 70%. In comparison, the mortality for other planting treatments varied between 2 and 6%.

Root and shoot dry weight and shoot:root ratios of seedlings excavated at the end of the third growing season for the control treatment on the younger CH and HA sites are shown in Table 6. On the younger CH sites, Sitka spruce had the highest shoot and root dry weight and lowest shoot:root ratio of all three species; western hemlock had the highest and lowest values, respectively, on the younger HA sites. Western redcedar had a significantly ($P<0.001$) lower shoot and root dry weight and a higher shoot:root ratio than western hemlock and Sitka spruce on both younger CH and HA sites. The three conifer species had a significantly ($P<0.001$) higher root and shoot

Table 6
Comparison of the shoot and root dry weights (g) and shoot:root ratio 3 years after planting of western redcedar, western hemlock and Sitka spruce seedlings for the control treatment between the younger CH and HA sites. Values in parentheses are one standard error of the mean

Site	Component	Species		
		Western hemlock	Western redcedar	Sitka spruce
Younger CH	Root	15.1 (4.2)	6.6 (1.9)	31.2 (8.2)
	Shoot	40.2 (12.7)	22.5 (6.9)	68.5 (21.2)
	Shoot:root ratio	2.54 (0.14)	3.52 (0.36)	2.04 (0.15)
Younger HA	Root	66.1 (17.2)	9.6 (1.1)	58.1 (8.7)
	Shoot	211.1 (61)	37.7 (5.6)	189.1 (19.7)
	Shoot:Root ratio	3.26 (0.35)	3.96 (0.46)	3.45 (0.33)

Note: see Table 1 for definitions of CH and HA types.

dry weight and shoot:root ratio on the younger HA than CH sites. Western hemlock and Sitka spruce seedlings produced long lateral roots (up to 2.5 m in length compared with mean seedling total height of 85 cm) in the top 5 cm of the forest floor on the younger CH sites, whereas western redcedar produced shorter roots (up to 0.8 m in length compared with mean seedling total height of 80 cm), but these were found be deeper in the forest floor than the roots of the western hemlock and Sitka spruce.

Four types of mycorrhizal fungi were identified on western hemlock and Sitka spruce seedlings growing on the younger CH sites sampled in 1989 (Table 7). No statistically significant ($P > 0.05$) difference in percentage mycorrhizal colonization was obtained for western hemlock between the two planting treatments for any of the mycorrhizal types identified. However, a significantly higher ($P = 0.005$) and lower ($P = 0.02$) percentage mycorrhizal infection was found on Sitka spruce roots on the control compared with the vegetation-removed treatments for the types *Cenococcum geophilum* and *Telephora terrestris*, respectively. For both planting treatments and both conifer species, the total percentage mycorrhizal colonization was greater than 90.

No significant ($P = 0.874$) difference in percentage mycorrhizal colonization was found on western redcedar growing in the younger CH sites in 1989 between the control and vegetation-removed treatments. For both planting treatments the total percentage mycorrhizal colonization was greater than 95.

Table 7
Percentage, mycorrhizal colonization on western hemlock and Sitka spruce root tips growing in the field on the younger CH[1] sites between the control and vegetation-removed treatments. Values in parentheses are one standard error of the mean

Species	Treatment	Type of mycorrhizal fungi[2]					
		NM	CG	B	TT	Other	Total
Western hemlock	Control	8.0^a	25.0^a	25.7^a	16.3^a	25.0^a	92.0^a
		(4.9)	(4.5)	(12.2)	(8.9)	(6.1)	(4.9)
	Vegetation-removed	1.7^a	37.0^a	5.0^a	29.3^a	26.7^a	98.0^a
		(0.3)	(11.8)	(2.0)	(11.8)	(7.3)	(0.4)
Sitka spruce	Control	0.7^a	12.3^b	7.0^a	68^a	12^a	99.3^a
		(0.2)	(2.9)	(2.9)	(6.1)	(4.9)	(0.5)
	Vegetation-removed	0.5^a	0.8^a	2.5^a	87.3^b	8.9^a	99.5^a
		(0.2)	(0.2)	(0.3)	(2.7)	(2.2)	(0.4)

[1]See Table 1 for definition of younger CH site.
[2]NM, non-mycorrhizae; CG, *Cenococcum geophilum*; B, Brown types; TT, *Thelophora terrestris*; Other, all others.
Values in columns with the same superscript are not statistically ($P > 0.05$) different between treatments.

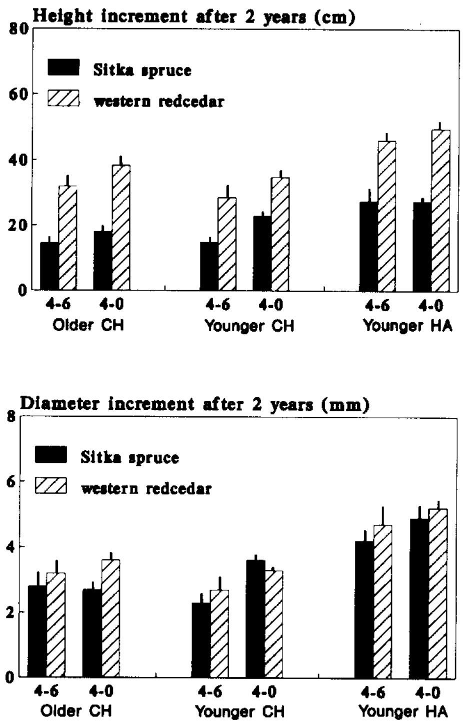

Fig. 2. Comparison of height and diameter increments after two growing seasons of Sitka spruce and western redcedar seedlings grown in the forest floor, taken from the younger CH and HA and older CH sites for the conifer:salal 4:6 and 4:0 combinations. The vertical bars are one standard error of the mean with $n=3$.

Pot seedling growth

No statistically significant differences ($P>0.15$) in height and diameter growth (Fig. 2) and mycorrhizal infection were found between the conifer:salal 4:6 and 4:0 combinations for Sitka spruce and western redcedar grown in the forest floor taken from the three types of clearcut site. The same four types of mycorrhizal fungi were identified on Sitka spruce roots in the pot experiment for all three growing media as in the field on the younger CH sites. The height and diameter increments of both conifer species were statistically ($P<0.001$) higher in the forest floor taken from the younger HA than CH sites, whereas no significant differences were found between the younger and older CH sites (Fig. 2).

Discussion

Factors limiting conifer growth on CH clearcut sites

The large differences in early growth of western redcedar, western hemlock and Sitka spruce seedlings between types of clearcut site (Fig. 1) were associated with large differences in the amount of competing vegetation (Table 1) and forest floor nutrient status (Table 2). Large growth differences existed between types of clearcut site, even when the effect of the competing vegetation was removed (Fig. 1). Therefore, in Fig. 1, the growth differences found within each species and type of clearcut site between the control and vegetation-removed treatments shows the interference effects, whereas the growth differences found between types of clearcut site within each species for the vegetation-removed treatment show the site effects.

Interference effects

All three types of clearcut site investigated had a substantial amount of competing vegetation surrounding the conifer seedlings. On both the younger and older CH sites, salal was the dominant competing vegetation, whereas on the younger HA sites both salal and fireweed were abundant. The removal of the competing vegetation around individual confer seedlings was found to increase conifer seedling growth (Fig. 1), especially for western hemlock and Sitka spruce on the two types of CH sites. Similar growth responses following the removal of salal were found for Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings growing in cutovers in southern Vancouver Island (Green, 1990), and for Sitka spruce seedlings growing in heather (*Calluna vulgaris*, L.; another ericaceous species) dominated cutovers in Scotland (Dickson and Savill, 1974). However, none of the three conifer species responded very well to the removal of the competing vegetation on the younger HA sites. This lack of growth response on the younger HA sites suggests that the competing vegetation did not deplete the nutrient resource to a level at which competition could occur. This explanation is substantiated by the greater availability of N and P found on the younger HA sites compared with the other two types of CH sites, and by the very small conifer growth response obtained by the application of fertilizer at planting on the younger HA sites for both western hemlock and Sitka spruce (Messier and Kimmins, 1990a).

The vegetation-removed treatment increased the availability of N and P by 22–40% and 15–32%, respectively, for all three types of site, increased the soil temperature slightly, and did not affect the rate of cellulose decomposition (Tables 3 and 4). Competition for water was apparently non-existent owing to the regular rainfall and fog which occurred throughout the growing season. Competition for light was not a factor in this study because all seedlings were growing in full sunlight conditions. The amount of N available annually for plant uptake on the nutrient poor CH sites following clearcutting and slashburning has been estimated by Weetman et al. (1990) to be between 20 and 30 kg ha^{-1}. Messier and Kimmins (1990b) calculated that approximately 9 kg N ha^{-1} $year^{-1}$ is tied up in the living tissue of the competing vegetation on CH sites during the first 8 years following clearcutting and slashburning; this constitutes between 30 and 45% of the estimate of Weetman et al. (1990) of the potentially available N on these CH clearcut sites. Therefore, the uptake and immobilization of nitrogen and other nutrients in expanding salal biomass and other competing species provides an explanation for some of the large differences in conifer growth found between the control and vegetation-removed treatments on the two types of CH clearcut sites (Fig. 1). Competition for nutrients, although often mentioned as a possible factor of competition, has rarely been isolated as the main cause of conifer growth suppression. However, two recent studies (Eissenstat and Mitchell, 1983; Neary et al., 1990) have found competition for nutrients to be the main factors affecting conifer growth.

Mycorrhizae are known to enhance nutrient uptake in trees (Perry et al., 1987). Walker (1987) reported that such enhancement has been shown experimentally in Sitka spruce for phosphate, nitrate, ammonium, potassium and simple organic nitrogenous compounds. A few studies have reported evidence of allelopathic potential of shrubby species on mycorrhizal colonization of tree species (Handley, 1963; Robinson, 1972; Côté and Thibault, 1988). Handley reported that poor growth of Sitka spruce on sites covered by heather in Scotland was associated with a lack of mycorrhizal development. Laboratory studies showed that extracts from mycorrhizal heather roots inhibited the growth of mycorrhizal fungi known to be associated with Sitka spruce (Robinson, 1972). Based on the latter two studies and on field observations in coastal British Columbia, it has been hypothesized (Germain, 1985; Weetman et al., 1989a,b) that the release of chemicals by salal into the root environment of conifer seedlings might inhibit the normal mycorrhizal infection of their roots, and consequently the normal uptake of nutrient ions. Neither the field seedling bioassay nor the pot experiment, where Sitka spruce, western redcedar and western hemlock seedlings were growing with and without salal, showed any difference in the total percentage mycorrhizal infection. A greenhouse bioassay by McDonald (1989) did not show any evidence that the presence of salal reduced the ability of Sitka spruce, western hemlock or western redcedar to take up nutrient ions.

Site effects

The growth of all three conifer species was greater on the younger HA than younger CH sites which was in turn greater than on the older CH sites, both with and without the presence of competing vegetation (Fig. 1); similar results were found in the pot experiment between the younger HA and CH sites (Fig. 2). Forest floor nutrient availability was generally greatest in the order younger HA > younger CH > older CH sites (Table 2), whereas no difference in matric soil water potential and only small differences in soil temperature were found between the three types of clearcut site (Table 3).

Consequently, the differences in conifer seedling growth between the younger CH and HA sites can be explained partly by differences in forest floor nutrient availability intrinsic to these two types of clearcut sites. The differences in forest floor nutrient availability found between the CH and HA clearcut sites are probably the result of conditions prevailing prior to clearcutting and slashburning (Germain, 1985; Messier and Kimmins, 1990a; Prescott et al., 1993). However, the very different nature of the vegetation found on the younger HA compared with the younger CH sites (Table 1) following clearcutting and slashburning could also be of importance in explaining the large differences in early conifer growth measured between these two types of clearcut sites. Fireweed is an annual plant that produces an easy-to-decompose litter every year, whereas salal is a perennial plant that produces leaves that decompose relatively slowly (DeCatanzaro and Kimmins, 1985). Moreover, salal keeps its leaves for more than 6 years when growing under canopy (F. Bunnell, personal communication, 1991). The phenological and functional differences between these two competing species may contribute somewhat to the differences in nutrient availability measured between the two types of clearcut sites in the first few years following clearcutting and slashburning. The yearly input of easily decomposable leaves of fireweed on the younger HA sites supplies an excellent source of carbohydrates and nutrients for the microfauna and flora. It was visually noticed that a greater level of micro and mesofaunal activity was associated with the higher rate of decomposition of the cellulose disks on the younger HA sites. In contrast, very little input of fresh leaves occurred on the younger CH sites during the first 4 years, and very little sign of microfaunal activity was observed on the cellulose disks on this type of site. The functional differences in the competing species invading these two forest ecosystems following clearcutting and slashburning may also contribute to some of the differences in forest floor nutrient availability found between CH and HA clearcut sites.

The lower rate of conifer growth found on the older compared with the younger CH sites with the effect of the competing vegetation removed, can be explained by a decrease in nutrient availability found over time following clearcutting and slashburning (Table 2). Germain (1985), working on similar CH cutovers nearby, also reported a decrease in nutrient availability 3–4 years following clearcutting and slashburning. Decline in nutrient availability a few years following the removal of a forest cover has been reported in several studies (Covington, 1981; Binkley, 1984; Martin, 1985; Krause and Ramlal, 1986; David, 1987). The high percentage mortality of planted western hemlock and Sitka spruce seedlings observed on the control treatment on the older CH sites during the third and fourth years after planting is suggested to be related to the severe nutritional stress on the older CH sites with no control of competition.

These differences in nutrient availability found between the three types of clearcut site (i.e. site effects) are responsible for some of the differences in conifer seedling growth in addition to that caused by competing vegetation (i.e. interference effects) (Fig. 1).

Conifer species

The better height growth measured for western redcedar compared with western hemlock and Sitka spruce on both types of CH sites for the control treatment agrees with the observations of Curran and Dunsworth (1988) for the same three conifer species growing on similar nutrient-poor clearcut sites on the west side of Vancouver Island. Several possible mechanisms may explain the relatively good growth of western redcedar on CH clearcut sites. First, the slightly better height growth of western redcedar on the younger CH sites was achieved with two to three times less root and shoot biomass than western hemlock and Sitka spruce (Table 6). This means that western redcedar seedlings needed to take up less nutrients to achieve a certain height growth than Sitka spruce and western hemlock. A similar explanation was suggested by Miller and Miller (1987) to explain the differences in early growth between Sitka spruce, Corsican pine, and Scots pine on nutrient-poor clearcut sites in Britain. Secondly, the deeper rooting habit of western redcedar fine roots observed in the field in this study may allow this species to obtain nutrients not available to the more shallow rooting Sitka spruce and western hemlock seedlings. Finally, a report by Ryan et al. (1986) found western redcedar to be more tolerant of nutrient solutions of low pH which contain relatively high levels of Al ions than western hemlock and particularly Sitka spruce. This greater tolerance of western redcedar to acidic conditions might also confer a growth advantage on the acidic CH clearcut sites. This latter possibility is questionable, however, since both western hemlock and Sitka spruce grew very well on the younger HA site which was found to have a pH value similar to those found on the CH sites (Table 2).

Western hemlock and Sitka spruce responded more than western redcedar to all treatments and types of clearcut site that affected forest floor nutrient availability. Omule (1988) also found very little difference in height growth between 25-year-old western redcedar growing in nutrient-poor sites compared with those growing on nutrient-medium sites on the west coast of southern Vancouver island. These two sites are ecologically similar to the CH and HA sites reported in this study. The inability of western redcedar to substantially increase its growth on the nutrient richer younger HA sites in the field experiment further suggests that on these acidic, ammonium-dominated sites, western redcedar seedlings do not respond very well to an increase in nutrient availability (Messier and Kimmins, 1992). These results suggest that early silvicultural treatments to increase N and P availability on such sites will tend to favor western hemlock and Sitka spruce over western redcedar.

Conclusion

The results of this study indicate that the nutritional stress and poor growth reported in young conifer plantations growing on salal-dominated CH clear-cut sites in coastal British Columbia are the consequences of the combined effects of inherently low forest floor fertility, salal competition for scarce nutrients and their subsequent immobilization in salal biomass, and reduced forest floor nutrient availability caused by the termination of the increase of available nutrients that occurs for a few years after clearcutting and slash-burning. The low availability of nutrients in the forest floor 5–8 years following clearcutting and slashburning and the uptake and immobilization of a large amount of nutrients in salal biomass occurring on CH clearcut sites does not appear to leave enough nutrients to support rapid tree growth. This is especially true for a nutrient-demanding species such as Sitka spruce (Miller and Miller, 1987). These results cannot completely rule out the involvement of allelochemicals or a mycorrhizal effect, but demonstrate that the observed growth stress can be accounted for without appeal to these mechanisms. These findings lead to the more fundamental question of what processes are controlling nutrient availability and how these might be manipulated through silviculture treatments to increase conifer seedling performance in CH clear-cut sites.

Acknowledgments

We wish to thank S. Williams, P. Warnes, E. Morton, C. Trethewey, T. Honer, and M. Tze for invaluable technical help and P. Puttonen and J.P. Kimmins for commenting on the manuscript. Western Forest Products Ltd. kindly provided lodging facilities. This research was supported through a Forest Resource Development Agreement contract 2.31 and a Natural Sciences and Engineering Research Council of Canada and Graduate Research Engineering and Technology (B.C.) scholarships.

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