Voluntary paper

NUTRITIONAL STRESS IN *PICEA SITCHENSIS* PLANTATIONS IN COASTAL BRITISH COLUMBIA: THE EFFECTS OF *GAULTHERIA SHALLON* AND DECLINING SITE FERTILITY

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Abstract. Examples of nutritional stress in conifer seedlings caused by competing ericaceous species (e.g. Calluna and Kalmia), have been reported in several parts of the world. Nutritional stress (primarily N deficiency) has been reported in Sitka spruce (Picea sitchensis) plantations growing in association with an ericaceous species, salal (Gaultheria shallon), in coastal British Columbia. Nutritional interference by salal was investigated on a chronosequence of sites up to 10 yr after clearcutting and slashburning. No direct evidence for an allelopathic contribution to the N stress was obtained. However, the rapid accumulation of salal fine roots and rhizomes, and the nutrients contained therein, provides a partial explanation for the observed stress symptoms. Soil analyses and seedling bioassays demonstrated a reduction in fertility in the period 8 to 10 yr after clearcutting and slashburning in comparison to the period 2 to 4 yr, which is believed to impose further nutritional stress on Sitka spruce. It is concluded that the nutritional stress in these Sitka spruce plantations is caused by a combination of (1) salal competition for nutrients and their subsequent immobilization in salal biomass, and (2) declining site fertility caused by the termination of the flush of nutrients (the "assart period") that occurs in the immediate post-clearcutting and slashburning period. Sustaining good growth of plantations under such circumstances will require site nutrient management as well as vegetation management.

Résumé. Plusieurs examples de stress nutritif chez les semis de conifères, causé par les végétaux de la famille des éricacées (*e.g. Calluna* et *Kalmia*), ont été reportés de par le monde. Un stress nutritif (principalement une déficience en azote) a été reporté pour des plantations d' épinette de Sitka (*Picea sitchensis*) croissant sur la côte ouest de la Colombie Britannique en association avec une espèce de la famille des éricacées, salal (*Gaultheria shallon*). L'interférence nutritive induite par salal a été étudiée le long d'une chronoséquence jusqu'a 10 ans après la coupe et le brûlage controlé. Aucune évidence d'intèférence d'ordre allélopathique par salal fut obtenue. Cependant, l'accumulation rapide et abondante de racine de salal, accompagnée d'une immobilisation des éléments nutritifs dans la biomasse de salal, offrent une explication adéquate pour une partie du stress nutritif reporté. Autant les analyses de sol que les essais avec les semis d'épinette de Sitka indiquent une diminution de fertilité entre 8 et 10 ans après la coupe et le brûlage controlé comparativement à 2 et 4 ans, ce qui ajoute au stress nutritif de l'épinette de Sitka. Les auteurs conluent que le stress nutritif reporté chez les plantations d'épinette de Sitka est causé par l'effet combiné (1) de la compétition par salal pour les éléments nutritifs et leurs immobilisations subséquentes dans la biomasse de salal, et (2) du déclin de la fertilité du site causé par la terminaison de l'influe d'éléments nutritifs associés avec la coupe et le brûlage controlé. Le maintien d'une croissance adéquate de ces plantations exige une intervention au niveau du site et de la végétation indésirable.

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1. Introduction

During the 1970s and 1980s, Sitka spruce (*Picea sitchensis*, Bong. Carr.) was planted extensively on northern Vancouver Island (B.C., Canada) to regenerate slashburned clearcuts previously occupied by old-growth *Thuja plicata*, Donn, *Tsuga heterophylla*, Raf. Sarg., and an ericaceous understory shrub salal (*Gaultheria shallon*, Pursh [CH sites]). The planted Sitka spruce grew well initially on these sites, but experienced nutritional stress and reduced growth 8 to 14 yr after planting (Germain, 1985; Weetman *et al.*, 1990a,b). Accompanying the onset of the nutritional stress was the reestablishment of a complete ground cover of salal, and it has been suggested that there is a causal connection between these two temporally synchronous events (Weetman *et al.*, 1990a,b). Other ericaceous species have been implicated in nutritional stress in conifer plantations (Mallik, 1987; Robinson, 1972; Handley, 1963; Rose *et al.*, 1983).

Three hypotheses to explain this nutritional stress were tested in the study reported in this paper: (1) that salal competition for N can provide an adequate explanation for the observed nutritional stress; (2) that salal inhibits the availability of nutrients to seedlings by interfering with their mycorrhizae; and (3) that the fertility of these CH sites declines after 8 yr following clearcutting and slashburning due to the termination of the flush of nutrients (or "assart effect") associated with this disturbance. A series of pot and field experiments was carried out to test these hypotheses.

2. Materials and Methods[1]

2.1 Study area and research sites

The study area was located in the Coastal Western Hemlock biogeoclimatic zone (Green *et al.*, 1984) on northern Vancouver Island, B.C., Canada (50°60'N/127°35'W) on a landscape unit described by Lewis (1982) as the undisturbed old-growth phase of the western redcedar (*Thuja plicata*, Donn)/western hemlock (*Tsuga heterophylla*, Raf. Sarg.) ecosystem type. The study area is characterized as having a gently undulating topography which rarely exceeds 300 m in elevation. It receives approximately 1700 mm of rain annually. Although the summer months experience less rainfall than the winter months, growing season rainfall is thought to be sufficient to prevent any soil moisture deficit (Lewis, 1982). Mean daily temperature ranges from a low of 3.0°C in Jan/Feb to a high of 13.7°C in July/Aug. Following clearcutting and slashburning, this CH ecosystem type experiences rapid reinvasion by salal from rhizomes that are present in the old-growth forest. Salal will dominate such clearcuts as long as it is not shaded out by the developing overstory. The CH ecosystem has a thick (30 to 100 cm), compacted humus layer rich in decaying wood (mostly western redcedar) over a moderately-well to somewhat imperfectly drained ferro-humic podzol.

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[1] Space limitations prevent detailed descriptions of the methods used. These are presented in Messier (in preparation).

Two "ages" of site were chosen for the study: 2 and 8 years post-burning. For each site age, two differenct cutovers were chosen based on their homogeneity: similar slope position, aspect and intensity of burn. All four cutovers were considered representative of the CH phase ecosystem. This kind of chronosequence research assumes that all the cutovers share a similar post-disturbance stand history and had similar ecological attributes prior to disturbance. The assumption is realistic for this study because of the uniformity of the CH ecosystem and the great care taken in the selection of the study sites.

2.2 Field seedling bioassays

Several hundred nursery grown "plug type" 1-0 seedlings of Sitka spruce were planted in April 1987 on each of three plots for each of two cutovers for each of two site ages and left to grow for three growing seasons (*i.e.* until the sites were 4 and 10 yr post-burning). The experiment was a 2 x 2 nested-factorial experiment using a completely randomized design with six plots of 5 to 6 seedlings per treatment. The two main factors were as follows: (1) two site ages (2 to 4 and 8 to 10 yr post-burning CH sites), and (2) two planting treatments nested within plots and cutovers. In treatment 1, seedlings were planted without additional treatment (control); in treatment 2, seedlings were planted in the middle of 200 cm diameter patches from which all above-ground vegetation was continuously removed by clipping and from which the belowground competition was periodically reduced by cutting to a depth of 40 cm in the forest floor around patches.

The height and diameter of each seedling was evaluated just after planting and at the end of each growing season, except for the diameter which was remeasured only for the last two growing seasons. In addition, the degree of mycorrhizal infection was evaluated on a subsample of seedlings from each planting treatment on the 2 to 4 yr post-burning CH site when this site was 4 yr post-burning.

2.3 Pot seedling bioassays

In March 1988 two pot experiments were initiated in an open area near the research sites.

The first experiment was designed to evaluate the effect of different densities of salal on Sitka spruce seedling growth and mycorrhizal infection. Seedlings of Sitka spruce and salal were planted at different densities (4:6, 4:0, 3:2, and 2:4 spruce-salal, respectively) in pots 20 x 40 x 20 cm in size. Two types of growth media, taken from the upper 8 cm of the forest floor, from 3 and 9 yr post-burning CH sites were used. The experiment was 2 x 4 factorial using a completely randomized design. Salal plants were established as 10 cm long rhizomes with at least two healthy buds.

In the second experiment, the soil fertility along a chronosequence of CH sites was assessed in the absence of salal using Sitka spruce seedlings as a bioassay. Sitka spruce 1 to 0 plug seedlings were established in pots with forest floor material taken from three CH sites (1, 3, and 9 yr post-burning) and from two depths (0 to 8 cm and 8 to 20 cm). The experiment was a 2 x 3 factorial using a completely randomized design.

The growth medium for each experiment was thoroughly mixed and all rhizomes and most fine and medium roots were removed prior to filling two pots per treatment. All pots were maintained in full sunlight, and the soil near field capacity.

At the end of each growing season, the height and diameter increments of the Sitka spruce were measured and pot averages calculated. The degree of mycorrhizal infection of the Sitka spurce was determined for the 4:0 and 4:6 spruce-salal combinations of the first experiment at the end of the experiment.

2.4 Vegetation of biomass and nutrient content

The competing vegetation root and rhizome biomass was assessed on 2, 4 and 8 yr post-burning CH sites down to a depth of 45 cm by taking ten soil cores (7.4 cm in diameter) per site in June of 1987 (two cutovers of each of 2 and 8 yr post-burning sites) and in June of 1989 (two cutovers of 4 yr post-burning site on the same cutovers as the 2 yr post-burning site, but 2 yr later). For each core, the belowground biomass was sorted into two different sizes (fine-roots: < 2 mm and rhizomes: > 2 mm) and two species groups (*Gaultheria-Vaccinium* and *Epilobium-Cornus*). Distinction between the two groups was possible due to their different root morphologies. Roots were visually separated into live and dead categories based upon their color, texture and resilience. The roots were oven-dried at 70°C for 24 hr and weighed.

The aboveground biomass was assessed on the same sites by clipping twenty-four 1 m^2 plots per site in mid-July (*i.e.* at the peak of the vegetation season). The biomass was then separated by species into leaf and stem + reproductive components, oven-dried at 70°C for 24 hr and weighed.

The nutrient concentrations for each species and biomass component were either measured in the laboratory or estimated from the literature (Klinka, 1976; Sabhasri, 1961; Weetman and Fournier, pers. comm.). The nutrient concentrations of salal roots measured in the laboratory agreed with those reported by Sabhasri (1961).

2.5 Soil properties and microenvironment

The experiment was a 2 x 2 nested-factorial using a completely randomized design. The two main factors were as follows: (1) two sites (3 and 9 yr post-burning), and (2) two soil depths nested within the cutovers (two cutovers per site age). Twenty-four forest floor cores were taken in 1988 on each of 3 and 9 yr post-burning CH sites from depths of 0 to 8 and 8 to 20 cm. Forest floor pH, mineralizable N (anaerobic incubation), extractable and total N, available and total P, microbial activity (assessed in the laboratory using CO_2 evolution method), and organic matter content were measured using standard soil analyses. Twenty-four bags of mixed cation and anion exchange resin and confined cellulose discs were used to assess soil ammonium, nitrate and phosphate availability and relative decomposition rate, respectively.

Soil temperature (using dial soil thermometers) and moisture (using quick draw soil tensiometers) were measured at depths of 3, 10 and 25 cm on all sites and all planting treatments between 11:00 and 1:00 p.m. every month from May to July of 1987 to 1989.

3. Results

3.1 Field seedling bioassays

Figure 1 compares the annual height and diameter increments of Sitka spruce seedlings over the first three growing seasons after planting for the 2 to 4 and 8 to 10 yr post-burning CH sites and for the two planting treatments. From the analyses of variance carried over all growth variables, the following general statements can be made: (1) the growth was significantly greater on the 2 to 4 than on the 8 to 10 yr post-burning CH sites; (2) there were not statistical differences ($P > 0.1$) between the two cutovers within each site age and between the plots within each cutover; and (3) there were no significant ($P > 0.05$) interactions between site ages and planting treatments. Salal removal (planting treatment 2) increased growth during the second and third post-treatment years on the 2 to 4 yr post-burning site, but only during the third post-treatment year on the 8 to 10 yr post-burning site. No statistical difference ($P = 0.856$) in total percent mycorrhizal infection was found between the two planting treatments on the 2 to 4 yr post-burning site. For both planting treatments, the percent mycorrhizal infection on spruce roots was greater than 98%. There was, however, statistically more ($P = 0.002$) % infection by *Cenococcum geophilum* on the control (13%) than on the salal removal (1%) treatments.

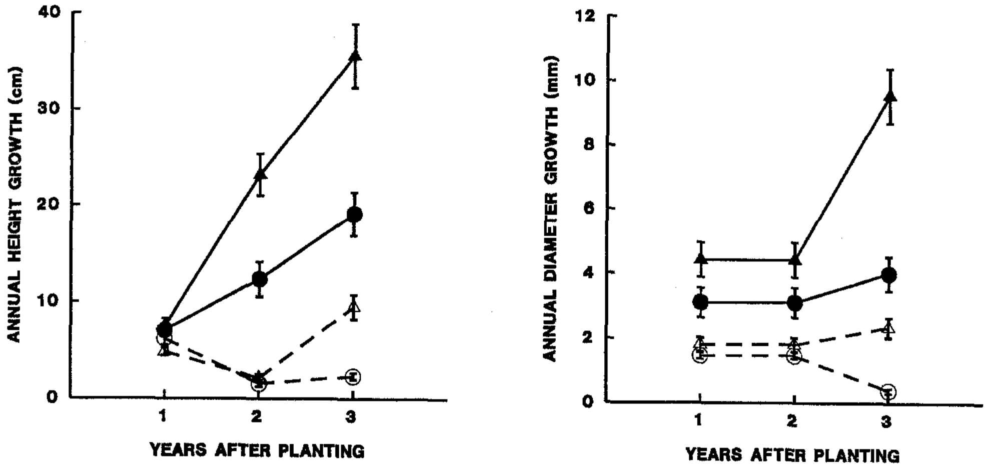

Figure 1. Sitka spruce annual height and diameter increments on 2 to 4 (filled symbols and continuous lines) and 8 to 10 (open symbols and dotted lines) year post-burning CH sites using two treatments: control (- ● ○ -), and vegetation removal (- ▲ △ -). The annual diameter growth shown for each of the first 2 yr after planting was calculated as the average value over the first 2 yr. Vertical bars are one standard error.

3.2 Vegetation biomass and nutrient content

There was 2,130 kg ha^{-1} of oven-dry total live belowground biomass (fine roots and rhizomes) in the 2 yr post-burning CH site, of which 1,690 kg ha^{-1} was live fine-roots (< 2 mm). Although the aboveground vegetation was very sporadic 2 yr after burning, live roots were found in all core samples at every depth. These early values increased to 4,545 kg ha^{-1} of total live belowground biomass and 2,250 kg ha^{-1} of live fine-root in the 4 yr post-burning site. There was 11,980 kg ha^{-1} of total live belowground biomass in the 8 yr post-burning CH site, of which 5,560 kg ha^{-1} was live fine-roots. The aboveground biomass of the competing vegetation was 1,310, 3,630 and 5,260 kg ha^{-1} on the 2, 4 and 8 yr post-burning sites, respectively. On all sites, the *Gaultheria-Vaccinium* group (of which *Gaultheria* was the dominant species) comprised between 80 and 95% of the total live biomass. No statistical difference ($P > 0.15$) was found between cutovers within each site age.

Figure 2 shows the increase in the amount of N and P within the competing vegetation across the chronosequence. On average, approximately 9 and 0.8 kg ha^{-1} of N and P, respectively, are tied up in the competing vegetation annually over the 2 to 8 yr post-clearcutting and slashburning period. In comparison to the aboveground, the proportion of N and P tied up in the belowground biomass increases with time with clearcutting and slashburning due to the increase in the production of live salal rhizome (> 2 mm).

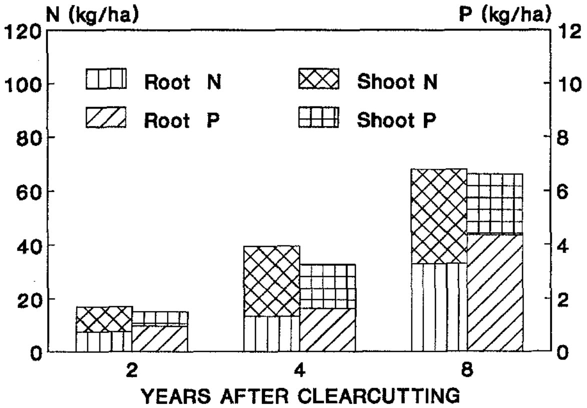

Figure 2. Total amount of N and P contained in aboveground and belowground biomass of competing vegetation on 2, 4 and 8 yr post-burning CH sites.

3.3 Soil properties and microenvironment

Table I compares the soil properties of 3 and 9 yr post-burning CH sites.

Table I

Comparison of some of the soil properties between 3 and 9 yr post-burning CH sites (3 + B CH and 9 + B CH, respectively). Values in parentheses are one standard error.

	3+B CH		9+B CH		ANOVA (P-value)	
	Depths				Factors	
	0-8 cm	8-25 cm	0-8 cm	8-25 cm	Sites	Depth
pH	4.47	4.03	4.33	3.91	0.156	0.000
	(0.10)	(0.07)	(0.04)	(0.03)		
C/N ratio	45.2	60.7	58.3	68.5	0.024	0.000
	(1.7)	(2.5)	(5.4)	(3.4)		
CO_2 evolution	0.56	0.38	0.59	0.33	0.874	0.000
(g CO_2/g/24 hr)	(0.05)	(0.04)	(0.04)	(0.02)		
Total N (%)	1.25	0.95	1.10	0.84	0.010	0.000
	(0.05)	(0.03)	(0.06)	(0.03)		
Total P (%)	0.068	0.045	0.063	0.042	0.082	0.000
	(0.017)	(0.013)	(0.017)	(0.012)		
Extractable	0.14	0.13	0.05	0.05	0.000	0.560
NH_4^+ (ppm)	(0.01)	(0.02)	(0.01)	(0.01)		
Mineralizable	0.37	0.24	0.28	0.17	0.006	0.000
NH_4^+ (ppm)	(0.03)	(0.02)	(0.02)	(0.01)		
Available PO_4^-	0.220	0.043	0.005	0.001	0.000	0.000
(ppm)	(0.056)	(0.016)	(0.000)	(0.000)		

	Depths				Factors	
	8 cm	20 cm	8 cm	20 cm	Sites	Depth
Resin NH_4^+	0.472	0.469	0.580	0.632	0.000	0.463
(mg g^{-1})	(0.015)	(0.011)	(0.035)	(0.027)		
Resin NO_3-	0.047	0.047	0.045	0.042	0.657	0.743
(mg g^{-1})	(0.002)	(0.001)	(0.002)	(0.002)		
Resin PO_4-	0.160	0.165	0.053	0.025	0.000	0.132
(mg g^{-1})	(0.030)	(0.027)	(0.011)	(0.006)		
Cellulose	25.9	19.7	27.3	19.7		
decomposition (%)	(4.0)	(3.8)	(4.7)	(4.3)	0.823	0.010

Because no statistical difference ($P > 0.1$) was found between the cutovers within each site age for most soil variables, the soil values from the two cutovers within each site age were combined. The statistical P-values for the comparison between the two site ages and two depths for each of the soil variables are shown in Table I. With the exception of resin NH_4^+, pH, and CO_2 evolution, all soil variables indicated greater fertility on the 3 than on the 9 yr post-burning sites. Similarly, with the exception of extractable NH_4^+ and all resin variables, all soil variables indicated a decline in fertility between the upper and lower sampling depths. There was an unexplainable contradiction between the results from the extractable and mineralizable NH4+ and the resin NH_4^+. Further work is required to explain this contradiction.

No soil moisture deficit (*i.e.* all soil water potential values were below 0.021 MPa) was observed throughout the summers of 1987 and 1988 on any site and for any planting treatment. Furthermore, no difference in soil water potential or gravimetric soil moisture was measured between site ages and between planting treatments. Soil temperature was generally a few degrees (1 to 3°C) higher on the 2 to 4 than on the 8 to 10 yr post-burning sites, and on the vegetation removal treatment as compared to the control treatment. The differences were statistically significant ($P < 0.01$) mainly at the 3 cm depth.

3.4 Pot seedling bioassays

No statistical difference in height and diameter growth and total mycorrhizal infection (both in terms of total percent colonization and proportion of colonization by different types of mycorrhizal fungi) was found between the spruce-salal 4-6 and 4-0 combinations for the first pot experiment. However, Sitka spruce height and diameter growth for the spruce-salal 4-0 combination was statistically lower ($P < 0.01$) than Sitka spruce growth for the 3-2 or 2-4 combinations. It was observed that on average one Sitka spruce seedling produced two to three times more biomass (aboveground and belowground) over the two growing seasons than two salal plants. Therefore, the Sitka spruce seedlings from the 3-2 and 2-4 spruce-salal combinations suffered from less competition than the Sitka spruce from the 4-0 spruce-salal combination.

In the second pot experiment, statistically greater height and diameter growth ($P < 0.01$) were found in the growth medium from the 1 and 3 yr post-burning sites than from the 9 yr post-burning site. Statistically lower growth ($P < 0.01$) was also obtained from the 8 to 20 cm depth substrate than the 0 to 8 cm depth substrate for all site ages. These results confirm those obtained in the field (Table I).

4. Discussion

The results of the field seedling bioassay indicate that the growth of Sitka spruce was improved markedly by the removal of the competing vegetation of mainly salal. Moreover, the needles of the seedlings where the competing vegetation had been removed were markedly greener than the needles on the control seedlings, suggesting increased nutrient uptake. Weetman *et al.* (1990a,b) showed that Sitka spruce growing on such CH sites are deficient in both N and P, and that the application of fertilizer alleviates the nutritional stress. Our results show that salal interferes with the uptake of an adequate supply of nutrients by Sitka spruce, and this occurs early after planting. No moisture deficit was found on these sites throughout the year, and therefore competition for water was ruled out as a possible factor.

On average, the amount of N available annually for plant uptake on these poor sites following clearcutting and slashburning has been estimated by Weetman *et al.* (1990b) to be between 20 and 30 kg ha^{-1}. This value is likely to decrease with time since clearcutting and slashburning. This figure is in the lower part of the range of annual N uptake requirements for conifer stands (6.5 to 88 kg N ha^{-1} yr^{-1}) reported by Cole and Rapp (1981). From Figure 2, it was calculated that approximately 9 kg ha^{-1} of N yr^{-1} is tied up in living tissue of the competing vegetation; this constitutes between 30 and 45% of the potentially available N on the site. This immobilization of N in salal biomass can explain much of the differences in growth between the two planting treatments reported in Figure 1. It is believed that the development of competing vegetation biomass will continue for some years beyond 8 yr before it reaches its maximum development. Sabhasri (1961), for example, estimated the salal biomass under a 120 yr old *Pseudostuga menziessi* (Mirb.) Franco stand at 35,000 kg, almost twice the maximum amount found in this study. No data on total salal biomass are available for older CH stands that are similar to the 2 to 10 yr old ones reported here.

Sitka spruce growth was significantly lower on the 8 to 10 than 2 to 4 yr post-burning CH sites for both treatments (Figure 1). The pot experiment showed that in the absence of competing vegetation the growth of Sitka spruce was lower on soil from 9 yr post-burning sites than from either 1 or 3 yr post-burning sites. Table I shows a decline in soil fertility from 3 to 9 yr after burning on these sites. Germain (1985), working on similar sites, reported the post-distrubance "assart" flush of nutrients to last less than 5 yr. This initial increase in soil fertility following forest harvesting follwed by a decline a few years later is a well known phenomenon (Covington, 1981; Krause and Ramlal, 1986). This decline in fertility 8 to 10 yr after clearcutting and slashburning is believed to impose some nutritional stress on Sitka spruce in addition to that caused by salal competition.

It has also been hypothesized (Weetman *et al.*, 1990 a, b; Germain, 1985) that the release of chemicals by salal into the root environment of Sitka spruce inhibits the normal mycorrhizal infection of the spruce roots, and consequently the normal uptake of nutrient ions. Neither the field seedling bioassay nor the pot experiment, where Sitka spruce seedlings were growing with and without salal, showed any difference in the total percent mycorrhizal infection. Furthermore, in comparison to the salal-free 4-0 spruce-salal combinations, the Sitka spruce growing in the 3-2 and 2-4 spruce-salal combination in the first pot experiment did not show any sign of dramatic growth reduction due to the presence of salal. The intraspecific interference by Sitka spruce appeared to be more significant than the interspecific interference by salal. Finally, a greenhouse bioassay in another study failed to find evidence that the presence of salal reduced Sitka spruce ability to take up nutrient ions (McDonald, 1989).

These results indicate that most of the nutritional stress in Sitka spruce plantations on northern Vancouver Island can be explained by a combination of: (1) salal competition for nutrients and their subsequent immobilization in salal biomass, and (2) declining site fertility following the flush of nutrients associated with clearcutting and slashburning. The hypothesis regarding the inhibition by salal of the mycorrhizal infection of Sitka spruce roots was not verified.

Sitka spruce is considered a nutrient demanding species (Germain, 1985), especially prior to canopy closure (Miller and Miller, 1987), and there are insufficient nutrients on these salal-dominated CH sites to sustain rapid growth. The advent of canopy closure conditions resulting in a stabilization or reduction in salal biomass, and a consequent reduction in nutrient competition, may reduce the nutritional stress observed in currently stagnated 8 to 14 yr old Sitka spruce plantations. This hypothesis is now under investigation by other researchers.

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