Causes and amelioration of nutrient deficiencies in cutovers of cedar-hemlock forests in coastal British Columbia

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Poor growth of conifer regeneration occurred on sites formerly occupied by old-growth cedar-hemlock (CH) forests in coastal British Columbia, 5–8 years after clearcutting and slashburning. Symptoms included chlorotic foliage and growth check of Sitka spruce, western hemlock, western red cedar and amabilis fir, coincident with the expansion of the ericaceous shrub, salal, on the cutovers. Fertilization trials identified N and P deficiencies as the cause of the growth check of conifers, and additions of 300 kg N ha⁻¹ and 100 kg P ha⁻¹ significantly improved tree growth rates. Equivalent growth responses were achieved with additions of sewage sludge and fish silage. Burning, cultivating, liming, higher planting densities or herbicide application, were less effective in promoting conifer growth. The nutrient deficiencies in conifers on CH cutovers were the result of two factors: low nutrient availability in soil and humus, and competition and interference from salal. Salal immobilized substantial amounts of N in biomass and an in vitro study suggested it was able to use organic forms of N through its mycorrhizal fungi. The mycorrhizae of salal also interfered with those of hemlock, which further reduced their ability to take up nutrients. High concentrations of phenolic acids were associated with salal, which interfere with mineralization and uptake of N. The low availability of N and P in CH cutovers originated in forest floors of the old-growth forests prior to clearcutting. Nutrient availability was low in all layers of the forest floor in CH forests, and this appeared to result from three main factors. First, cedar litter contains less N and more decay-resistant material than other species, and produces forest floors with low rates of N mineralization. Second, the forest floors in CH forests are wetter and have less soil fauna than in HA forests, leading to incomplete decomposition and mineralization of N. Third, the salal understorey in CH forests interferes with mineralization of N through the production of tannins.

Key words: growth check, fertilization, herbicide, ericaceous shrub, sewage sludge, mycorrhizae, allelopathy, nitrogen availability, nutrient cycling, NMR analysis

Une faible croissance de la régénération résineuse a été observée sur les sites anciennement couverts par de vieilles forêts de cèdres et de pruches (CP) de la région côtière de la Colombie-Britannique, 5 à 8 années après la coupe à blanc et le brûlage des résidus. Les symptômes observés comprendraient le feuillage chlorosé et l'hypertrophie de la croissance chez l'épinette de Sitka, la pruche de l'ouest, le cèdre rouge de l'ouest, le sapin gracile, la coïncidence avec la progression d'un éricacée arbus-tif, le salal sur les parterres de coupe. Des essais de fertilisation ont identifié des carences en N et en P comme étant la cause de l'hypertrophie de la croissance des conifères, et l'apport de 300 kg/ha de N et de 100 kg/ha de P a significativement amélioré le taux de croissance des arbres. Des réactions équivalentes de croissance ont été atteintes par l'apport de boues résiduelles de traitement des eaux et de résidus de transformation de poisson. Le brûlage, la préparation du sol, l'apport de chaux, des densités plus élevées de plantation, se sont avérés moins efficaces pour accroître la croissance des résineux. Les carences en éléments nutritifs des conifères des parterres CP sont le résultat de deux facteurs: la faible disponibilité des éléments nutritifs dans le sol et l'humus, ainsi que la compétition et l'interférence causées par le salal. Le salal immobilisait de grandes quantités de N dans la biomasse et une étude in vitro suggérait qu'il était capable d'utiliser des formes organiques de N par l'entremise de champignons mycorrhiziens. Les mycorrhizes du salal interféraient également avec celles de la pruche, ce qui réduisait d'autant plus la capacité d'intégrer les éléments nutritifs. De fortes concentrations d'acides phénoliques ont été associées avec le salal, ce qui empêche la minéralisation et l'intégration de N. La faible disponibilité de N et de P dans les parterres de CP provenait des sols forestiers des vieilles forêts avant même la coupe. La disponibilité des éléments nutritifs était faible dans tous les couches du sol forestier des forêts de CP, et cela semblait être le résultat de trois principaux facteurs. En premier lieu, la litière de cèdre contient moins de N et plus de substances résistantes à la décomposition que les autres espèces, et entraînait la formation de sols forestiers ayant de faibles taux de N minéralisé. En second lieu, les sols forestiers des forêts de CP étaient plus humides et comportaient moins d'éléments de la faune pédologique que dans les autres forêts, provoquant ainsi une décomposition et une minéralisation incomplète de N. En troisième lieu, le couvert de salal dans les forêts de CP interrompt la minéralisation de N par la production de tanins.

Mots clés: hypertrophie de la croissance, fertilisation, phytocide, éricacée arbus-tif, boues résiduelles, mycorrhizes, allélopathie, disponibilité de l'azote, cycle des éléments nutritifs, analyse de l'azote minéralisée

Introduction

This report presents an overview of the findings of the Salal Cedar Hemlock Integrated Research Program (SCHIRP), which are described in more detail by Prescott and Weetman (1994). The objective of this decade-long research effort was to determine the underlying causes of poor growth of regenerating

western red cedar (*Thuja plicata* Donn.), western hemlock [*Tsuga heterophylla* (Raf. Sarge), amabilis fir (*Abies amabilis* Dougl.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) on cutovers of coastal old-growth cedar-hemlock forests invaded by salal. Logging of coastal old-growth cedar-hemlock (CH) forests during the 1960s generated substantial areas of cutovers which regenerated very slowly with cedar and hemlock. To achieve more rapid regeneration, sites were slashburned to reduce slash accumulations and the heavy cover of the ericaceous shrub, salal (*Gaultheria shallon* Pursh), and planted with Sitka spruce. The spruce plantations grew well initially, but by age six to eight years, they showed signs of severe nutrient defi-

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ciency and growth rates declined markedly. Cedar appeared to be less influenced by the nutritional problems on these sites and consequently cedar was planted thereafter. However, growth check and associated chlorosis were apparent in all species five to eight years after clearcutting and slashburning, coincident with the expansion of salal on CH sites. The problem did not occur on adjacent sites formerly occupied by second-growth forests of hemlock and amabilis fir (HA).

Research was conducted to determine silvicultural practices to alleviate the growth problem, and to understand the fundamental cause of the poor nutrition of trees. Initial field trials demonstrated deficiencies of N and P as the cause of poor growth. Subsequent studies examined the decline in N and P availability following clearcutting and burning, and the role of salal in contributing to poor conifer growth. The cause of poor nutrient supply was investigated by comparing nutrient cycling in old-growth CH forests with second-growth forests of HA which do not have low nutrient supply after clearcutting.

Study Area

The study area is on northern Vancouver Island, between the towns of Port Hardy and Port McNeill, BC (50° 60' N lat., 127° 35' W long.) at elevations of less than 300 m. The area is within the very wet maritime subzone of the Coastal Western Hemlock (CWH) biogeoclimatic zone (Pojar *et al.* 1991), and has a maritime climate with mild winters and cool moist summers. Mean annual precipitation is about 1700 mm, 65% of which occurs between October and February, and almost all is rain. Mean annual temperature is 7.9°C, and daily averages range from 2°C in January to 14°C in August. The surface geological material is deep unconsolidated morainal and fluvial outwash material overlying sedimentary and volcanic bedrock.

The distribution of forest vegetation across this area varies with topography, geological substrate, and the type and frequency of natural disturbance. Wildfire is uncommon, and the predominant natural disturbance is windthrow. The forests are largely composed of western red cedar, western hemlock and amabilis fir, with some Sitka spruce on the outer coast and lodgepole pine (*Pinus contorta* var. *contorta* Dougl.) on poorly drained sites. On well-drained to somewhat imperfectly-drained middle or upper slope situations, the forests occur in two distinct types: 1) old-growth CH forests dominated by western red cedar up to 1000 years old with a small component of western hemlock, and 2) second-growth HA forests dominated by western hemlock and amabilis fir, that are even-aged and originated following a windstorm in 1906. Lewis (1982) could not distinguish between the two forest types on the basis of topography or mineral soil characteristics, and included them in the same ecosystem association. He further hypothesized that HA forests were a seral stage of CH forests. Both types have deep mor forest floors, generally of greater depth in the CH than the HA type (Germain 1985). Soils are duric or orthic Humo-Ferric Podzols.

Silvicultural Trials

Experiments were established in CH cutovers to test the effectiveness of a variety of treatments for improving the growth of conifers. Treatments included fertilization, scarification, weed control, planting density manipulation, burning and liming. The strategy was similar to that applied to the problem of "heather

check" in the U.K. and Ireland (Carey 1977; Taylor 1987), namely to increase tree growth leading to crown closure and shading out of salal (Messier *et al.* 1989). It is hoped that once nutrient competition from salal is reduced, tree growth will be sustained.

Fertilization Trials

Single-tree screening trials were conducted on Sitka spruce and western red cedar on CH sites five to eight years after planting (Weetman *et al.* 1989a, 1989b). Numerous combinations of N, P and K were applied in the spring to circular plots of 5 m radius centered on the test tree. Fertilizer combinations were generally replicated five times. The first-year response data were analyzed using foliar vector analysis. The results indicated that the growth of both species was limited by N and P but not by K. The growth limitation of spruce was much greater than that of cedar. Fertilizer doses of 200–300 kg N ha⁻¹ and 50–100 kg P ha⁻¹ were identified as optimum treatments.

In the conventional plot trials, square plots (25 or 30 m on a side) of pure spruce, cedar or western hemlock were hand-fertilized five to eight years after planting (Weetman *et al.* 1989a, 1989b; Thompson and Weetman 1992a). Spruce plots received one of six treatments (all numbers are kg ha⁻¹): 0N, 0P (control); 100N + 50P; 200N + 50P; 300N + 50P; 300N + 150P; or 300N + 50P + 91K plus a micronutrient mix. Cedar and hemlock plots received one of 12 treatments; 0, 100, 200 or 300 N, combined with 0 P, 100 P, or 100 P plus micro-nutrients. Each treatment was replicated three times to give 18 plots of spruce and 36 plots each of cedar and hemlock. The results indicated that growth of all three species was limited by N and P deficiencies. The growth limitation was greatest for spruce and least for cedar. For spruce, the greatest growth rates were recorded in the 300N + 150P and 300N + 50P + micronutrient treatments. For cedar and hemlock, the greatest growth response was in the 200 or 300N plus 100 P (with or without micronutrients) treatments. The growth response was greatest in the second to fourth years following fertilization of spruce and hemlock, but it continued for at least seven years in all three species (Fig. 1). Combined data from these experiments indicated a strong correlation between relative growth rate and foliar N concentrations (Fig. 2). Fertilization with N and P significantly accelerated crown closure (% of ground area shaded by crowns) (Fig. 3). Six years following treatment with 300 kg N ha⁻¹ plus P, crown closure exceeded 70%, while crown closure averaged 30% in control plots.

Operational fertilization experiments were conducted in 1986 in four 50 ha trials in CH cutovers (Thompson and Weetman 1992a). Fertilizer was applied by helicopter at 300 kg N ha⁻¹ plus 100 kg P ha⁻¹ to cedar, and 225 kg N ha⁻¹ plus 75 kg P ha⁻¹ to spruce. Twenty-six circular plots were established, 4 to 12 m in radius (smaller plots in denser stands). Most plots contained spruce, cedar and hemlock. For all three species, operational fertilization significantly increased growth rates. The growth response to fertilization was greatest for spruce, very large for hemlock and modest for cedar.

To determine the efficiency of fertilization, ¹⁵N-labelled ammonium sulphate fertilizer was applied to single tree plots of Sitka spruce, western red cedar and western hemlock on a CH cutover (Chang *et al.* in press). Salal was manually removed from half of the plots. Total ¹⁵N recovery in the plant-soil system after two growing seasons was 54–83%. Most of the

Fig. 1. Height increment of spruce, cedar and hemlock on coastal cedar-hemlock cutovers after fertilization with N, P, K and micronutrients.

Fig. 2. Relationship between height growth and foliar % N of conifers on CH cutovers.

^{15}N recovered was immobilized in the soil (62–83%). In the plots with salal, 20–31% of the ^{15}N was immobilized in understorey vegetation, and only 2–5% was in the trees. In the plots from which salal had been removed, 8–18% of the ^{15}N was in the trees and only 2–5% was in the understorey.

Fig. 3. Crown closure (%) of conifers in fertilized plots on CH cutovers.

Control of salal prior to fertilization was recommended to increase the efficiency of fertilizer use by trees.

An assessment of the economics of operational fertilization of CH cutovers (Thompson and Weetman 1992b) yielded the following conclusions: 1) hemlock fertilization is financially justified, 2) spruce fertilization is financially justified, provided that insect problems do not significantly reduce yield or wood quality, 3) cedar fertilization is financially justified if: (a) prices for cedar logs rise at a faster rate than prices for most other species; (b) fertilization releases stands from growth check for longer than five years or (c) cedar stands include at least 10% hemlock or 25% spruce, and 4) fertilization is financially justified at a discount rate of 3% when it reduces the rotation by five years and at a discount rate of 5% when it reduces the rotation by at least 10 years. Since most plantations established on CH cutovers have a significant component of ingrown hemlock and a response period of at least seven years, fertilization of young plantations with 300 kg N ha^{-1} and 100 kg P ha^{-1} can be expected to yield significant financial gains.

Fertilization, Scarification and Planting Density Trials

Two experiments with cedar and hemlock at the time of planting were conducted on both CH and HA cutovers (Thompson and Weetman 1992a). The first experiment compared fertilization with no treatment, for hemlock and cedar planted on CH and HA cutovers at densities of 500, 1500 and 2500 stems ha^{-1} . Each treatment plot contained 64 seedlings and treatments were replicated four times, for a total of 96 plots. On an area basis, the fertilizer dose varied with planting density: 25 kg N ha^{-1} , $6.25 \text{ kg P ha}^{-1}$ and $12.5 \text{ kg K ha}^{-1}$ at 2500 stems ha^{-1} , 60% as much at 1500 stems ha^{-1} and 20% as much at 500 stems ha^{-1} . In the second experiment, the treatments were fertilization and scarification, with density constant at 2500 stems ha^{-1} . Each treatment combination was replicated four times for a total of 64 plots. The fertilizer dose was 10 g N, 2.5 g P and 5 g K per tree. Soil was scarified with a backhoe to a depth of 0.5 m; this treatment also removed salal.

Height growth after five years differed between species and between CH and HA sites. Hemlock on HA sites was unaffected by treatment and grew more rapidly than hemlock on CH sites or cedar on either site type. Untreated hemlock on CH sites grew the least, particularly at the highest planting

density. Hemlock on CH sites was very responsive to both fertilization and scarification. Cedar growth differed little between site type or planting density. Both scarification and fertilization resulted in modest increases in growth on either site. Foliar N concentration was strongly correlated with growth of both species. Mixing of soil mineral and organic horizons through scarification did not increase nutrient availability (Keenan *et al.* 1994), indicating that decomposition of humus was limited more by its poor quality than by soil microclimate.

Organic Fertilization Trials

Two trials were established in plantations on CH cutovers to test the efficacy of a variety of organic wastes for improving the growth and nutrition of trees. In the first trial (Weetman *et al.* 1993), the response of nine-year-old cedar, hemlock and amabilis fir in plots treated with municipal sewage sludge from Vancouver was compared with response in plots treated with N + P fertilizer and untreated controls. Sewage sludge was applied at 500 kg N ha⁻¹ and 133 kg P ha⁻¹; fertilizer was applied at 225 kg N ha⁻¹ as ammonium nitrate and 75 kg P ha⁻¹ as triple super phosphate. The higher loadings of sewage sludge were designed to compensate for much of the N and P being bound in organic matter. The trial was replicated in three blocks, each of which contained four 15 × 15 m plots of each tree species. During the first growing season, height growth of trees in plots of all three species treated with sludge or inorganic fertilizer was two to three times that in control plots. Nitrogen concentrations in foliage were also two to three times those in control plots, and were highest in N + P fertilized plots. After three years, growth was still enhanced in trees of all three species fertilized with sewage sludge or N + P (Brown 1994).

In the second trial (McDonald *et al.* 1994) in a nine-year-old cedar plantation on the same CH cutover, several organic wastes were applied: sewage sludge, sewage sludged mixed with pulp sludge, fish silage mixed with wood ash, silage and ash mixed with pulp sludge, wood ash alone, and inorganic N + P fertilizer. Organic wastes were applied at about 500 kg N ha⁻¹; N + P fertilizer was applied at 225 kg N ha⁻¹ and 75 kg P ha⁻¹. All of the additions except wood ash increased height and diameter of cedar trees (Fig. 4). The greatest height growth during the three years after treatment was in the N + P fertilized plots, followed by the plots treated with silage and sewage sludge. Mixing with pulp sludge reduced the response to sludge or silage. Wood ash alone suppressed tree growth. During the third growing season, height and diameter increment remained high in the plots treated with fish silage (with and without pulp sludge), but declined in other treatments (Brown 1994).

Burning, Cultivation and Weed Control

A trial was established in 1982 to evaluate the effects of burning, cultivation and weed control on growth of hemlock, amabilis fir and cedar on CH sites (Barker, unpublished data). Treatments were burned, unburned × cultivated, uncultivated × weed control, no weed control. Plots were cultivated to 0.75 m depth using a rake attachment to a backhoe. Plots receiving weed control (salal suppression) were sprayed with Garlon 4E at 2.5 kg active ingredient ha⁻¹. Cedar, hemlock and amabilis fir were planted in 7 × 7 tree blocks at 2.8 m spacing. Foliar samples were collected three growing seasons

Fig. 4. Diameter growth of cedar trees on CH cutovers treated with organic wastes. Each value is the mean of 25 trees.

after planting and concentrations of N and P were measured. Height and root collar diameter were measured after four growing seasons. Live salal cover was measured prior to treatment and after three growing seasons.

Growth, survival and foliar P concentrations of all three species were greater in burned plots. Cedar and amabilis fir had significantly higher foliar N concentrations on burned sites, but hemlock had lower foliar N concentrations on burned sites. Burning resulted in elevated foliar P concentrations in all three species and significantly higher rates of growth and survival. Cultivation increased tree growth on unburned sites, probably as a result of salal removal. Foliar N concentrations in amabilis were greater on cultivated sites; foliar P concentrations in cedar were lower on burned sites. The herbicide damaged

seedling foliage and did not kill the salal which resprouted from rhizomes following treatment. All three treatments reduced salal from 30–34% cover in control plots to 19% by burning, 27% by cultivation, and 18% by herbicide application. Averaging all species and treatment combinations, relative growth rate was increased 42% by burning, 12% by cultivation, and 2% by weed control.

Salal Eradication

An experiment was initiated in 1984 to examine the effects of salal removal and fertilization on spruce, cedar and hemlock trees on CH sites (Weetman *et al.* 1989a, 1989b). The experimental design was $2 \times 3 \times 2$ factorial: (S0, S1) $\times$ (N0, N1, N2) $\times$ (P0, P1), where S0 = intact salal, S1 = salal removed, N0 = control, N1 = 250 kg N ha⁻¹ as ammonium nitrate, N2 = 250 kg N ha⁻¹ as urea, P0 = control and P1 = 100 kg P ha⁻¹ as triple superphosphate. Fertilizers were applied in April 1985. Salal was manually removed in 1985 from thirty 25 $\times$ 25 m ha plots and left *in situ*. Intact salal roots were treated with Garlon 4E (3.5 kg active ingredient ha⁻¹) at the end of the second growing season to prevent resprouting. The effects of salal removal on conifer height and diameter increment were assessed after three growing seasons.

Foliar N concentrations for all three species in salal removal plots were significantly higher than in control plots, but foliar P concentrations were unaffected by salal removal. Three-year height increments for spruce, hemlock and cedar were greater in plots from which salal was removed. Cedar response was more closely related to salal removal, while hemlock response was more closely related to fertilization.

Lime and Starch Amendments

The possibility that rates of N mineralization in CH humus could be stimulated by adding available carbon in potato starch or by raising the pH by adding lime, was addressed in field and laboratory experiments (Prescott and McDonald 1994). Lime was applied to a CH cutover at a rate of 2500 kg ha⁻¹, and fertilizer was applied at 275 kg N ha⁻¹ as urea and 75 kg P ha⁻¹ as triple superphosphate, in a randomized complete block design in 1989. There were three 30 $\times$ 30 m plots of each treatment: control, limed, fertilized, and limed plus fertilized. Four years after application, trees in fertilized plots had longer leaders and were greener in colour, but there were no visual effects of the lime additions. The effects of lime and N + P fertilizer were also tested in a greenhouse bioassay. Seedlings of cedar, hemlock and Sitka spruce were grown in pots of CH humus to which lime and fertilizer had been applied at rates approximating 5000 kg lime ha⁻¹, 225 kg N ha⁻¹ and 75 kg P ha⁻¹. After 1.5 years, the biomass of seedlings of all three species was significantly greater in pots that received fertilizer (with or without lime), but there was no effect of lime.

In a field trial on a CH cutover, potato starch was added combined with N fertilizer. Four years later, the trees that received fertilizers had longer leaders and greener foliage, but there were no visual effects of starch addition. The effects of starch and glucose additions were also tested in a laboratory incubation. Five-gram samples of humus (H and Hw) from a CH cutover were amended with 354 mg of potato starch and incubated in the lab for 36 days. There was no effect of the starch addition on the rates of net N mineralization or CO₂ evolution in H or

Hw samples. Addition of glucose, a simpler C compound, stimulated microbial activity and decreased N availability in CH humus. These experiments indicated that additions of starch or lime would not improve rates of N mineralization in humus in CH cutovers.

Response to Clearcutting

The origin of the growth check of conifers on CH cutovers was investigated by comparing nutrient availability on CH and HA sites and across a chronosequence of CH sites. Allelopathic effects and mycorrhizal interactions of salal and conifers were examined to determine if they play a role in the dominance of salal on CH sites.

Soil Nutrient Availability

Weetman *et al.* (1990) found that extractable and mineralizable N generally declined on CH sites from year 1 to year 8 after burning. Messier (1993) compared CH sites two and eight years after burning, and reported declines in total N and extractable P, and a decrease in P retained in ion-exchange resin bags. HA sites two years after burning had higher rates of cellulose decomposition than two-year post-burning CH sites, but lower total N. Cade-Menun (1995) examined P availability in soil from CH cutovers immediately, five years and 10 years after clearcutting and burning. There was a flush of available (Bray-extractable) P immediately after burning, which declined during the next 10 years, and a decline in total P during the 10 years. Foliar nutrient concentrations of salal and fireweed also declined over time in CH cutovers; N declined steadily over the eight years, whereas P and K reached minimum values within two or three years.

Seedling growth performance was used as a bioassay of soil fertility on different aged cutovers and different site types (CH and HA) in several experiments. Messier (1993) planted one-year-old nursery-grown seedlings of hemlock, cedar, and Sitka spruce on HA sites two years after burning, and on CH sites two and eight years after burning. Light competition was prevented by clipping back the competing vegetation. Height and diameter growth of western red cedar was not affected by time since burning on the CH site (two–eight years), or by differences between CH and HA sites on the two-year post-burning sites. In contrast, growth of hemlock and Sitka spruce were greatest on the HA site, followed by the young CH site, and least on the oldest CH site. Spruce and cedar seedlings were grown for two growing seasons in pots containing forest floor material from the same sites used in the field bioassay. The greatest height and diameter growth during the two growing seasons was in forest floors from two-year HA sites. These results confirmed the field seedling bioassay results, suggesting that nutrient availability is in the order two-year post-burning HA > two-year CH > eight-year CH, and that cedar is relatively insensitive to nutrient availability.

A greenhouse trial was conducted to monitor soil P availability in a CH chronosequence (McDonald, unpublished data). Seedlings of Sitka spruce and western red cedar were grown for one year in pots containing soils from a chronosequence of CH cutovers, one year, four years and eight years after burning, and from an old-growth CH forest. The above- and belowground biomass, nutrient concentrations and P-32 uptake of each seedling were measured. Estimates of the size of the labile P pool were made by isotopically exchange-

Fig. 5. P-32 uptake by seedlings grown in soils from an old-growth CH forest and from 1-, 4- and 8-year post-burning CH sites.

Fig. 6. P sorption and isotopically exchangeable P (I.E.P.) in soils from an old-growth CH forest and from 1-, 4- and 8-year post-burning CH sites.

able P (I.E.P.). The P-retention capacity of the soil was estimated by adding P solutions. The results are summarized (Figs. 5 and 6). Seedlings grown in the one- and four-year post-burning soils took up the most P-32. Seedlings grown in the eight-year post-burning soils took up the least P-32, in spite of a greater demand, as reflected in lower foliar P concentrations and less biomass production. The eight-year post-burning soil also had the greatest capacity to fix P and the smallest labile pool. This suggests the P deficiency in CH cutovers arises at least partly through fixation of P in these soils.

The C and N contents of the microbial biomass in a chronosequence of CH sites (three and 10 years after burning, and old-growth) were measured in fumigation experiments in the laboratory (Chang *et al.* 1995). Microbial C and N content were greater in the old-growth forest than in the cutovers. The least extractable N and the greatest microbial C:N ratio were in the 10-year cutover. The results of these studies support the hypothesis that a significant component of the growth problem on CH sites is a rapid decline in soil nutrient availability during the decade following harvesting and burning.

The Role of Salal

Several experiments were conducted to determine the role of salal in contributing to growth check of conifers on CH cutovers. Messier and Kimmins (1990, 1991) estimated the biomass and nutrient content of competing vegetation in a CH chronosequence two, four and eight years after clearcutting and slashburning. Between two and eight years, the above- and below-ground biomass and N and P contents of competing vegetation increased exponentially. At least 70% of the biomass at each time was salal. By eight years, the biomass of competing vegetation averaged about 17,000 kg ha⁻¹, which contained about 70 kg N ha⁻¹ and 7 kg P ha⁻¹.

In the field trial with cedar, hemlock and spruce seedlings on two-year HA and two- and eight-year CH sites, Messier (1993) included a vegetation-removal treatment. A 200 cm patch around each seedling was kept free of competing vegetation by continuously clipping aboveground parts and trenching to 40 cm around the perimeter. After three growing seasons, the height and diameter of seedlings of all three species on all sites were greater in the vegetation-removed plots. Cedar grew more

slowly and was less affected by removal of competing vegetation than were spruce and hemlock. Removal of competing vegetation also increased soil temperatures by 1–3°C and the availability of N and P in resin bags.

Allelopathic effects of salal were assessed by deMontigny (1992). Tannins, thought to be either a procyanidin or a procyanidin and prodelphinidin mixture, were identified in the leaves, roots, flowers, berries and litter of salal using C-13 NMR. Tannins are known to reduce the biodegradability and humification of organic matter. Phenolic acid concentrations in humus from CH forests were significantly higher in syringic, p-coumaric and ferulic acids, all of which have inhibited root ion uptake in laboratory experiments. In a laboratory bioassay, phenolic acid solutions at field concentrations, and a 5% solution of salal flower and berry (unbuffered) significantly reduced the germination of Sitka spruce and cedar seeds. Seedlings of spruce, cedar and hemlock watered with the salal leachate solution had significantly lower biomass than the control seedlings after 12 weeks. Root samples of mature cedar and hemlock were placed into the treatment solutions augmented with a P-32 labelled phosphorus solution. The phenolic acid solution reduced P uptake by cedar and hemlock to 36% and 69% (respectively) of that of controls. The salal leachate solution had an even more pronounced effect, reducing P uptake by cedar and hemlock to 15% and 9% (respectively) of that of controls.

Mycorrhizal Interactions of Salal, Cedar and Hemlock

A greenhouse trial was conducted to examine the influence of salal on growth and mycorrhizal colonization of cedar seedlings (Husted, unpublished data). One-year-old nursery stock cedar seedlings were planted in pots containing humus from an eight-year post-burning CH cutover. The four treatments were: 1) one cedar per pot, 2) two cedars per pot, 3) one cedar and one salal seedling per pot, and 4) one cedar and one salal with root systems separated by a wooden divider. After two growing seasons, relative growth rate and N and P contents were reduced in cedars grown in competition with cedar or salal. Colonization of cedar roots with mycorrhizal (VAM) fungi was reduced by 10% in pots containing salal compared to pots containing either one or two cedars. In partitioned pots, VAM colonization was similar in all treatments. These results

suggested that the presence of salal roots reduced mycorrhizal colonization and nutrient uptake by cedar seedlings.

Additional studies were conducted to determine: 1) the forms of salal mycorrhizae, 2) if mycorrhizae enable salal to use organic N, and 3) if salal mycorrhizae are antagonistic to those of hemlock (Xiao 1994). Salal formed typical ericoid mycorrhizae, characterized by a web of hyaline hyphae on the surfaces of root hairs and crowded hyphal complexes inside the outer layer of cortical cells (Xiao and Berch 1993). The ability of the four species of ericoid mycorrhizal fungi, isolated from salal roots, to use different forms of organic N was tested in pure culture or in association with salal. The organic forms of N applied were glutamine (an amino acid), glutathione (a peptide), and bovine serum albumin (BSA, a protein). The mycorrhizal plants of salal inoculated by all four fungi had higher colonization rate on glutathione or BSA than on ammonium or glutamine. The ericoid mycorrhiza formation of salal was suppressed by application of ammonium and simple organic N, and favoured by more complex organic N. Interactions between species of four ericoid mycorrhizal fungi and three ectomycorrhizal fungi of western hemlock were examined in pure culture. All three ectomycorrhizal fungi were inhibited by ericoid mycorrhizal fungi, but none of the four ericoid mycorrhizal fungi were inhibited by any of the ectomycorrhizal fungi.

These studies demonstrated that salal competes with conifers for nutrients and interferes with nutrient uptake by producing tannins and phenolic acids. Mycorrhizal fungi of salal also contribute to its dominance on CH sites by providing access to organic forms of N and by reducing the growth of hemlock seedlings through inhibition of their mycorrhizal fungi.

The Forests

Studies of the two forest types, CH and HA were undertaken to determine: 1) if the low N and P supply in CH cutovers was present in old-growth CH forests, and 2) the origins of differences in N and P availability between the two forest types.

Possible origins of the differences in N availability that were investigated were: 1) more N is bound in humus and woody debris in CH forest floors so that less N is cycling and available;

2) decomposition of litter is slower in CH forests, resulting in slow rates of N mineralization; 3) the lack of disturbance by windthrow in CH forests has led to the development of conditions such as poor soil drainage and aeration which inhibit mineralization of N; 4) the forests occupy different sites with respect to soil, climate and topography, which create differences in N and P cycling.

Measurements of nutrient availability in CH and HA forest floors demonstrated that lower N and P availability in CH forest floors existed prior to clearcutting (Prescott *et al.* 1993). All layers of CH forest floors had lower concentrations of total and extractable N and mineralized less N during 40-day aerobic incubations in the laboratory. Total and extractable P was lower only in the litter layer of CH forest floors. Seedlings of cedar, Sitka spruce, hemlock, and amabilis fir grown from seed in forest floor material from CH forests grew more slowly and took up less N and P than did seedlings grown in HA forest floor material during a one-year greenhouse experiment (Fig. 7). Analysis of P forms by P-31 solution NMR spectroscopy indicated that concentrations of total and available P were lower in CH forest floors, and there was less polyphos-

Fig. 7. N content of seedlings of cedar, spruce, hemlock and amabilis fir grown for 1 year in forest floor F layer material from CH and HA forests.

phate and more phosphate in CH forest floors (Cade-Menun 1995).

There was little evidence to support the hypothesis that more N and P were immobilized in detritus in CH forests, since the total amounts of N and P in CWD and forest floors were similar in the two forest types: (2.18 Mg N ha⁻¹ in CH, 2.05 in HA; 142 kg P ha⁻¹ in CH, 118.5 in HA) (Keenan *et al.* 1993). However, there was relatively more N in the humus (H) layer in CH forests and less in the F layer, so the N may be less available in CH forests. The greater mass of humus in CH forests may be the result of their greater age, or less complete decomposition, as discussed below.

Less N was returned in aboveground litter in CH forests (14.2 kg N ha⁻¹) than in HA forests (35.9), as a result of lower mass and N concentrations in foliar litter (Keenan *et al.*, in press). There was greater internal recycling within the trees, which resulted from very efficient use of N by cedar, and from more efficient use of N by hemlock growing in CH forests. This is probably a response to low N availability and could also create a positive feedback that would exacerbate the low N availability in CH forest floors.

Decomposition rates of standard litter substrates were similar in the two forest types, and rates of CO₂ evolution from each forest floor layer during lab incubations were similar to or greater than those in HA forests (Prescott *et al.* 1995a). These findings suggest that the decomposition potential of the two sites is similar. The lower N availability despite similar rates of litter decay may be attributable to the tannins, which bind proteins and immobilize N. There was evidence for tannins in the CH forest floor C-13 NMR spectrum, as indicated by a peak at 145 ppm (deMontigny *et al.* 1993). The dipolar-dephased CH spectrum also had higher intensity at 108 ppm, another feature diagnostic of tannins. This tannin may be associated with salal; C-13 NMR spectra of salal components indicated high levels of tannin.

The presence of cedar in CH forests could also contribute to low N availability. In a modeling study (Keenan *et al.* 1995),

there was lower N availability in forest floors in simulated cedar forests, than in hemlock forests. In trials at the UBC Research Forest (Prescott and Preston 1994), and in Ireland (Prescott *et al.* 1995b), low rates of N mineralization were measured in forest floors in cedar plantations, compared with adjacent plantations of other species including hemlock and firs. The relatively low concentrations of N and high concentrations of waxes and lipids in cedar litter may be responsible for slower N mineralization in cedar forests.

There was evidence that moisture levels in CH humus and soil were greater than in HA forests, and this may have resulted in conditions that inhibit decomposition and nutrient cycling in CH forests. Moisture contents of samples of humus and mineral soils were usually greater in CH forests, and sensors placed in the humus recorded consistently higher moisture levels in CH forests. Mineral soil in many of the CH forests studied was more compacted and cemented layers were continuous and shallower than in HA forests (deMontigny 1992). This could lead to poorer drainage of humus, as indicated by the occurrence of hydromors in CH forests. There was a lower biomass of fauna and greater representation by aquatic animals such as copepods and brachiopods in CH humus, also indicative of wetter conditions (Battigelli *et al.* 1994). The high moisture and smaller faunal biomass could result in less complete decomposition in CH humus. This was suggested by the higher concentrations of lipids and carbohydrates in C-13 NMR spectra of CH forest floors and the poorer lignin biodegradation (acid:aldehyde ratio) in CH forest floors (Prescott *et al.* 1995a). The poorer drainage in CH humus may be attributed to the lack of soil disturbance by windthrow, or the tendency for the CH forests studied to be on lower topographic positions.

Conclusions

The growth check in conifer regeneration in cutovers of cedar-hemlock forests is a consequence of inadequate supplies of N and P. The low nutrient supply originates in the forest floor of the old-growth cedar-hemlock forests, prior to cutting (Fig. 8). Several factors appear to contribute to low nutrient availability in CH forest floors, and their relative importance is not clear. Cedar litter, tannins associated with salal, and greater soil water lead to incomplete decomposition and low N availability in CH forest floors. Under these conditions, there is more efficient use of nutrients by trees, and less nutrients recycled in litter, which further reduces nutrient availability in the forest floor. These conditions develop over several centuries without severe disturbance, and may be most prevalent on lower slope positions.

After clearcutting there is an assart effect causing a temporary improvement in N and P availability for growth of regeneration (Fig. 9). During this period, salal resprouts from rhizomes, immobilizing nutrients in biomass and causing growth check in conifers through N and P competition, mycorrhizal antagonisms and release of tannins. The growth check of the conifers can best be relieved by fertilization with additions of 300 kg N ha⁻¹ and 100 kg P ha⁻¹, or fish silage or sewage sludge. With this treatment, it is hoped that crown closure will be reached after a few years, shading the salal and leading to sustained improvement in the growth rates of conifers.

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Fig. 8. Development of low nutrient supply in old-growth CH forests.

Fig. 9. Strategy for improving conifer growth on CH cutovers.

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