Increases in tree growth and nutrient supply still apparent 10 to 13 years following fertilization and vegetation control of salal-dominated cedar–hemlock stands on Vancouver Island[1]

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Abstract: Cedar–hemlock forests on Vancouver Island are primarily nitrogen limited and characterized by an understory dominated by the ericaceous shrub salal (*Gaultheria shallon* Pursh.). In 1984, an experiment was established on regenerating cedar–hemlock forests to determine the effects of nitrogen and phosphorus (N + P) fertilization and vegetation control on conifer growth. It was hypothesized that these treatments would not only stimulate tree growth, but also improve nutrient supply, stand productivity, and site quality. To test this hypothesis, tree height growth, canopy closure, salal biomass, foliar and forest floor N and P concentrations, and seedling growth on forest floor were measured 10–13 years after treatment. Both salal control and fertilization increased tree growth and canopy cover, and reduced salal biomass. However, only fertilized plots showed changes in site quality measurable 10–13 years following N + P application. Hemlock foliar P concentrations, forest floor total N and P levels, and hemlock height increments were higher in these plots. Forest floors from the fertilized plots also supported greater growth of conifer seedlings. These results suggest that sustained changes to site quality may be achieved with N + P fertilization of cedar–hemlock forests.

Résumé : Sur l'île de Vancouver, l'azote est le principal facteur limitant dans les forêts de thuya et de pruche qui sont caractérisées par la domination d'une éricacée arbustive, le salal (*Gaultheria shallon* Pursh.). Une expérience a été établie en 1984 dans des forêts de thuya et de pruche en régénération pour déterminer les effets de la fertilisation avec de l'azote et du phosphore (N + P) et de la maîtrise de la végétation sur la croissance des conifères. On assumait que ces traitements allaient non seulement stimuler la croissance des arbres mais également améliorer la disponibilité des nutriments, la productivité des peuplements et la qualité de station. Pour tester cette hypothèse, nous avons mesuré la croissance en hauteur des arbres, la fermeture du couvert, la biomasse du salal, la concentration de N et P dans la couverture morte et la croissance des semis 10 à 13 ans après le traitement. Tant le traitement témoin avec le salal que la fertilisation ont augmenté la croissance des arbres et la fermeture du couvert et réduit la biomasse du salal. Cependant, seules les parcelles fertilisées ont montré des changements mesurables dans la qualité de station 10 à 13 ans après l'application de N + P. La concentration de P dans le feuillage de la pruche, la quantité totale de N et P dans la couverture morte et l'accroissement en hauteur de la pruche étaient plus élevés dans ces parcelles. La couverture morte supportait également un plus forte croissance des semis de conifère dans les parcelles fertilisées. Ces résultats indiquent qu'il est possible d'obtenir une amélioration durable de la qualité de station par la fertilisation avec N + P dans les forêts de thuya et de pruche.

[Traduit par la Rédaction]

Introduction

Nitrogen (N) is the primary nutrient limiting tree growth and productivity in many forested systems (Miller 1988; Chapin et al. 1993; Killam 1994). Consequently, forest managers often try to increase the availability of N to trees and, where possible, alleviate N deficiency throughout the life of the stand. To achieve these objectives, a variety of treatments including fertilization and vegetation control are used (Smith et al. 1997; Allen 2001). Fertilizers are applied to increase the pool size of available N, whereas control of competing vegetation is thought to redistribute the N pool to the target trees.

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Tree growth is usually increased following vegetation control (Oppenheimer et al. 1989; Snowden and Khanna 1989; Glover and Zutter 1993), although in some systems, growth is not affected (Russell 1961; Cain 1985). When a growth response does occur, it is typically short-lived, and this response is thought to be a result of a temporary increase in the availability of nutrients such as N to the trees. Site N capital and the total amount of available N are not altered (Snowden and Khanna 1989). Resources that would have been absorbed by the competing vegetation are just redirected to the trees. Thus, site quality, defined as the capacity of the forest floor and soil to support tree growth, is unchanged, and the amount of N may be insufficient and still limit growth. The trees therefore resume pretreatment growth rates. Significantly higher net nitrification rates in soils 5 years after being treated with herbicide have been reported in some systems (Li et al. 2003), suggesting that changes in N cycling can be achieved with vegetation control. However, these changes are described, in part, by increased soil temperature and reduced soil moisture (Li et al. 2003) and may also be caused by soil microbe responses to reduced carbon inputs following vegetation removal (Hart et al. 1994). Therefore, the elevated net N cycling rates may also be temporary and return to those previously found on site once the system is revegetated and the canopies expand.

Similar to vegetation control, the application of N fertilizer commonly increases tree growth, and the elevated growth rates are also typically short-lived. Trees often resume pretreatment growth within 5–10 years of fertilization (Miller 1981; Ballard 1984). However, unlike vegetation control, it has been suggested that fertilization can more permanently alter site quality and cause sustained increases in tree growth. By applying a single large dose of N or repeated applications of lower N doses that in summation are large relative to soil N capital, the capacity of the soil to immobilize the added N is overcome, thereby increasing N availability and site quality (Miller 1981, 1988; Snowden and Khanna 1989; Prescott et al. 1993). Additions of 470 kg N/ha and greater have been reported to elevate tree growth and nutrient availability in a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) plantation (Binkley and Read 1985; Strader and Binkley 1989) and in a jack pine (*Pinus banksiana* Lamb.) forest (Prescott et al. 1995), and these effects were still measurable 15–23 years following fertilization. Similarly, the use of organic fertilizers can also increase site quality by including other nutrients and organic carbon with the fertilizer application (Prescott et al. 1993). Six years after the application of municipal sewage sludge in coastal Washington, volume growth of Douglas-fir was elevated by 42–53%, and the increased growth was expected to continue for several more years (Cole et al. 1984). Thus, it does appear that certain N fertilizer regimes can cause changes in site quality and stand productivity that persist beyond the typical 5- to 10-year treatment response.

Fertilizer studies have established that N is the most limiting nutrient to the growth of western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) regenerating on cedar–hemlock cutovers on northern Vancouver Island, British Columbia (Weetman et al. 1989*a*, 1989*b*). Within 5–7 years of clear-cutting and burning these sites, the regenerating conifers' growth slows, and the trees develop foliar chlorosis (Weetman et al. 1989*b*). Reestablishment of the ericaceous shrub salal understory coincides with the appearance of the foliar chlorosis, and it has been suggested that competition from salal exacerbates the poor N availability (Weetman et al. 1990). Salal resprouts vegetatively from rhizomes in the soil and forms a very extensive network of rhizomes (Huffman et al. 1993) and very fine roots (Xiao 1994). Within 8 years of clear-cutting a hemlock forest in Oregon, the reestablished salal understory had more than 300 stems·m^{-2} above ground and greater than 170 m·m^{-2} of rhizomes below ground (Huffman et al. 1993). In addition the shrub is believed to indirectly degrade site quality through the production and release of tannins that immobilize N and reduce N mineralization (Preston 1999). Xiao (1994) also showed that ericoid mycorrhizal fungi inhibit the growth of fungi that form ectomycorrhizal associations with hemlock roots, suggesting a possible reduction in the ability of the conifer to take up N. Therefore, the shrub has the ability to be a very effective competitor.

To ameliorate the poor N availability and improve conifer growth in cedar–hemlock forests, a main management objective is to accelerate crown closure of the conifers and shade out salal. Messier et al. (1989) showed that aboveground salal biomass is significantly reduced when light levels in the understory are less than 1.8% of photosynthetic photon flux density measured in the open under clear-sky conditions. Thus, it is hypothesized that with increased crown closure, salal biomass will be reduced, resulting in an alleviation of competition for nutrients, increased rates of N cycling and availability, and improved site quality and stand productivity. Sustained increases in conifer growth would be the outcome owing to the larger pools of available N. To test this hypothesis, a fertilization – salal control experiment (previously referred to as "salal grubbing and fertilization" (Weetman et al. 1989*a*, 1989*b*) and "silviculture trial" (Bradley et al. 2000)) was installed in 1984 on recently cleared and burned cedar–hemlock sites. The study was established as a factorial design to compare the treatment combinations of salal control and N + P fertilization. To determine whether fertilization or salal control (applied singly or in combination) had increased tree growth, reduced salal cover, and resulted in changes in site quality, the study was revisited in 1995–1999.

Tree heights were measured to determine tree growth responses to the treatments, and tree canopy cover and salal foliar biomass were measured to estimate the relationship between crown closure and salal biomass. To establish a sustained increase in the ability of the sites to support tree growth, 3-year height increments of the dominant cedar, hemlock, and spruce were measured 10–13 years after study installation. To detect improvements in nutrient supply 10 and 12 years after study establishment, N and P concentrations in foliage and forest floors and seedling growth in forest floors from each treatment were determined.

Methods

Site description

The fertilization – salal control experiment was established on five cleared and burned cedar–hemlock sites on

Table 1. Total stand and individual tree species densities (stems·ha^{-1}) in the fertilization – salal control experiment, as measured in 1995.

	Treatment			
	Untreated	Fertilization	Salal control	Fertilization + salal control
Hemlock	1104 (221)	1408 (177)	1024 (177)	1416 (264)
Spruce	752 (124)	968 (125)	992 (151)	896 (245)
Cedar	1112 (233)	1048 (173)	1120 (194)	912 (277)
Total	3088 (226)	3560 (202)	3216 (86)	3312 (162)

Note: Values are means of five values with standard errors in parentheses.

Western Forest Products Ltd. Tree Farm License 6 on northern Vancouver Island. These sites are located within the very wet maritime Coastal Western Hemlock (CWHvm) biogeoclimatic subzone (Green and Klinka 1994) and receive an average annual precipitation of 1700 mm, 65% of which falls between October and February. The mean annual temperature is 7.9°C, with daily averages ranging from 2.4°C (January) to 13°C (August) (Prescott and Weetman 1994).

The five cedar–hemlock sites were harvested and burned in 1971 (two sites), 1973 (two sites), and 1974 (one site) and planted with Sitka spruce seedlings. Cedar, hemlock, and small amounts of shore pine (*Pinus contorta* Dougl. ex Loud. var. *contorta*) regenerated naturally to produce the stands measured in 1995 (Table 1). At the time of measurement, the understory vegetation was composed of salal, *Vaccinium* spp., false azalea (*Menziesia ferruginea* Smith), salmonberry (*Rubus spectabilis* Pursh), bunchberry (*Cornus canadensis* L.), and moss (*Hylocomium splendens* (Hedw.) B.S.G., *Kindbergia oregana* (Sull.) Ochyra, and *Rhytidiadelphus loreus* (Hedw.) Warnst.). Forest floors were thick with well-developed H horizons (Humimors) or large amounts of decomposing wood in the H horizon (Lignomors) (Green et al. 1993). The soils were Duric or Orthic Humo-Ferric Podzols (Prescott and Weetman 1994), and the soil parent materials were sandy loam glacial tills with smaller areas of glacial fluvial, fluvial terrace, or finer-textured saprolites (Lewis 1985).

The fertilization – salal control experiment was established in 1984 as a randomized complete block design, blocked by site, and consisted of a 3 × 2 × 2 factorial of N fertilization (ammonium nitrate, urea, or no fertilizer), P fertilization (triple superphosphate or no fertilizer), and salal control (controlled and not controlled). In the present study, only the 2 × 2 factorial of salal control and N (ammonium nitrate) + P fertilization were assessed. This fertilization regime was chosen because previous studies established that tree growth responses to urea and ammonium nitrate additions to cedar–hemlock sites were not significantly different, and that N and P applied together produced the largest growth response (Weetman et al. 1989*a*). In the salal control treatment, all aboveground salal biomass was cut in July–August 1984 and left on site, and rhizomes and root systems were pulled from the forest floor and soil. Resprouting of the residual rhizomes was inhibited by the application of Garlon 4E at the end of the 1985 and 1989 growing seasons with diesel and water carriers, respectively. The fertilizer treatment (250 kg N·ha^{-1} and 100 kg P·ha^{-1}) was applied manually in April 1985.

Tree responses

In 1995, one circular measurement plot with a radius of 8.9 m (0.025 ha) was established in the center of each treatment plot. To determine tree growth responses and a sustained increase in the ability of the site to support tree growth, the heights of the 10 dominant trees of each species were evaluated within each measurement plot in 1995 and 1998. Tree dominance was established by tree diameter (measured at 1.3 m) and canopy position. In plots with closed crowns, the trees with the largest diameters and present in the dominant canopy layer were selected. In the plots not yet reaching canopy closure, the trees with the largest diameters were measured. Only the heights of the dominant trees of each species were assessed because height growth of dominant trees is assumed to be density independent (Smith et al. 1997) and therefore will not be influenced by the differences in tree establishment and total and individual species stand densities. From these measurements and tree heights measured when the experiment was installed (1984), height growth since treatment application (1998–1984 measurements) and 3-year height increments (1998–1995 measurements) were calculated. Because data for spruce heights in 1984 were missing for one of the blocks, four blocks were used to calculate spruce height growth since treatment application.

Canopy cover and salal abundance

Five systematically located 0.75-m^2 subplots were established in each measurement plot in 1999. Percent canopy cover above the centre of each subplot was estimated with a concave spherical densiometer. Salal leaves within each subplot were collected and dried to a constant mass at 70°C.

Forest floor and foliar N and P concentrations

In August 1995, samples of the forest floor F layer (Green et al. 1993) were collected from five random locations within each measurement plot and were combined to produce one composite sample per measurement plot. From each of the 20 composite samples, a 5-g (dry mass) subsample was analyzed for total N and P concentration with an Alpkem RFA 300 auto-analyzer, following sulphuric acid – hydrogen peroxide digestion (Parkinson and Allen 1975). A second 20-g subsample was extracted with a medium strength Bray's solution (Byers 1978), and PO_4–P concentrations were measured with the auto-analyzer. A third subsample was dried at 70°C to constant mass to determine sample moisture content.

To provide an indication of the nutrient availability to the conifers, both senesced but unabcised foliage (hereafter referred to as “senesced foliage”) and live foliage (hereafter referred to as “green foliage”) were collected from hemlock trees in each measurement plot (Prescott et al. 1992). In August 1995, senesced foliage was gathered from 10–15 trees in each plot, and in September 1995, green foliage was collected from the upper crowns of five hemlock trees in each plot. All foliar samples were composited by foliar type and measurement plot and dried to constant mass at 70°C. Total N and P concentrations in the green and senesced hemlock foliage were determined as described above. All analyses were conducted at the MacMillan Bloedel Woodland Services Laboratory in Nanaimo, British Columbia.

Bioassay of nutrient supply

A seedling bioassay was conducted using forest floor F layer (Green et al. 1993) gathered from the 20 study plots. In June 1997, forest floor was collected from five random locations within each measurement plot, composited by plot, and passed through a shredder–mulcher to break up roots and create a homogeneous growth medium. Each forest floor substrate was then divided into ten 2.6-L plastic pots, and each pot was planted with six cedar or hemlock seeds (five pots per species). After germination, the seedlings were culled to leave three plants in each pot. The pots were randomly arranged on a table within a glass greenhouse at The University of British Columbia. The locations of the pots on the table were changed after 2 months to minimize the influences of microsite differences in greenhouse conditions on seedling growth. The seedlings were exposed to natural lighting conditions, were watered as needed, and experienced 24-h temperatures ranging from 11 to 41°C. In September 1997, after one growing season, the seedlings were harvested, rinsed with tap water, and dried to constant mass at 70°C.

Statistical analyses

Differences among treatment responses for tree height growth, 10- to 13-year height increment, foliar nutrient concentration, percent canopy cover, salal leaf biomass, and cedar and hemlock seedling dry masses were determined with analysis of variance (ANOVA) for a 2 × 2 factorial randomized complete block design using the general linear model (GLM) procedure.

The correlation between salal leaf biomass and percent canopy cover was determined using Spearman’s correlation analysis. All analyses were conducted with SAS (SAS Institute Inc. 1993) and used a significance level of 0.05.

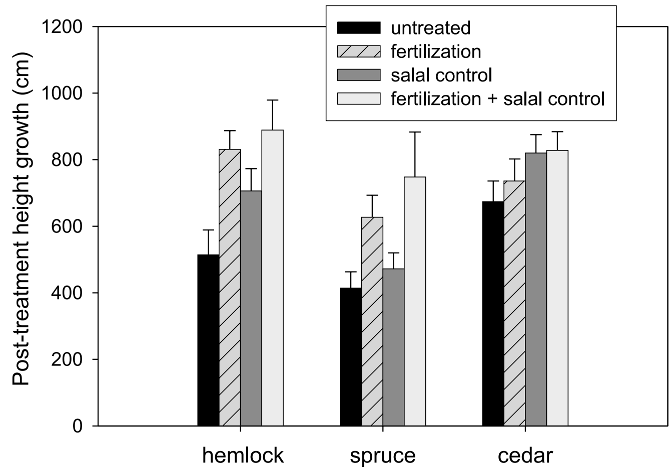
Results

Tree responses

Fertilization and salal control significantly increased dominant tree height growth, although the responses of the species to the individual treatments varied (Fig. 1; Table 2). The heights of hemlock and spruce were larger in the plots that were fertilized, whereas salal control significantly increased the cedar heights.

Only the 10- to 13-year height increments of hemlock were significantly influenced by fertilization (Fig. 2; Table 2).

Fig. 1. Height growth of cedar, hemlock, and spruce following treatment application in the fertilization – salal control experiment. Values are means, and error bars are standard errors; n = 5.



Canopy cover and salal abundance

Percent canopy cover and salal foliar biomass were significantly affected by both treatments (Tables 3 and 4). Canopy cover was highest in plots receiving salal control and fertilization, whereas salal foliar biomass was significantly reduced in the plots receiving the two treatments. The combined treatment plots had the greatest canopy cover and lowest salal biomass.

There was a significant negative correlation between canopy cover and salal foliar biomass (Fig. 3). With the exception of one fertilized plot, all treated plots had approximately 80% or greater canopy cover. Plots receiving both the salal control and fertilization treatments had greater than 90% canopy cover.

Forest floor and foliar N and P concentrations

Concentrations of N and P in the forest floors (F layer) and foliage 10 years after treatment are presented in Table 3. The N concentrations in the forest floors of the plots that were fertilized were significantly higher than those in the unfertilized plots (Table 4). Fertilization had the opposite effect on N concentrations in green hemlock foliage with the fertilized trees having lower N levels than the trees that were not fertilized. In the plots receiving salal control, the foliar N concentrations were higher than in the controls. The N concentrations in the senesced hemlock foliage were not significantly affected by the treatments.

Concentrations of P in the senesced and green hemlock foliage and the forest floors were all still significantly elevated 10 years after fertilization (Tables 3 and 4). Although the differences were not significant, mean extractable P concentrations in the forest floor were also higher in the plots that were fertilized.

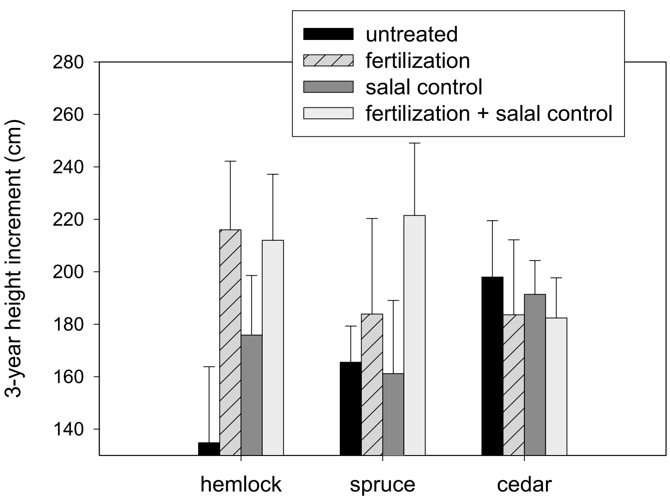
Bioassay of nutrient supply

The hemlock and cedar seedlings grown on forest floor from the plots that had been fertilized 10 years earlier were significantly larger (Tables 3 and 4).

Table 2. *P* values for the 2 × 2 factorial analysis of variance of hemlock, spruce, and cedar height growth (since treatment application) and 3-year height increments (10–13 years after treatment application) in the fertilization – salal control experiment.

	Treatment		
	Fertilization	Salal control	Fertilization × salal control
Hemlock			
Post-treatment height growth	0.006	0.111	0.200
3-year height increment	0.043	0.496	0.409
Spruce			
Post-treatment height growth	0.010	0.265	0.687
3-year height increment	0.188	0.568	0.473
Cedar			
Post-treatment height growth	0.509	0.038	0.609
3-year height increment	0.534	0.837	0.885

Fig. 2. Three-year height increments of cedar, hemlock, and spruce in the fertilization – salal control experiment 10–13 years after treatment application. Values are means, and error bars are standard errors; n = 5.



Discussion

When considered on a whole-plot level, both salal control and N + P fertilization significantly increased tree height growth, indicating that the two treatments can at least temporarily alleviate nutrient limitations and the competitive influences of salal on conifer growth in cedar–hemlock forests. When the species' responses to the treatments are evaluated separately, however, it becomes apparent that in these mixed species stands, hemlock and spruce showed the greatest responses to fertilization, whereas salal control favoured the growth of cedar.

Previous measurements from the current study and results from other studies on cedar–hemlock sites have shown that all three species respond positively to both removal of salal and N + P fertilization. Three years after treatment, cedar, hemlock, and spruce heights were higher in the N + P fertilized than in the unfertilized plots of the fertilization – salal control experiment (Weetman 1989*b*). Similarly, in single-species plots, Weetman et al. (1989*a*, 1989*b*) also found 146, 494, and 618% increases in cedar, hemlock, and spruce heights, respectively, relative to untreated plots 4 years after the application of 200 kg N·ha^{-1} and 50 kg P·ha^{-1}. Thus, all three species typically do show fertilizer responses at least 4 years after treatment. Likewise, cedar, hemlock, and spruce also have been found to respond to salal control. Although only cedar showed a strong response to salal control in the fertilization – salal control experiment 3 years after treatment, Chang (1996) found the growth of 6-year-old trees of each species to be significantly larger when surrounding salal had been removed at the time of planting. Fraser et al. (1995) also found that the growth of hemlock saplings was negatively correlated with salal leaf area index on a cedar–hemlock site 3 years following site clearing and burning.

It is not known why the results from the fertilization – salal control experiment 13 years after treatment are inconsistent with earlier measurements of this trial and results from other studies. However, it must be acknowledged that the fertilization – salal control experiment and other studies had different establishment conditions and measurement timings. The fertilization – salal control experiment assessed treatment responses in mixed stands, whereas the others examined single-species plots. In addition, measurements in the above outlined studies were taken up to 6 years following treatment, whereas the results reported here are based on 10- to 13-year treatment responses. Thus the reactions of cedar, hemlock, and spruce to N + P fertilization and salal control may differ in mixed stands and change during the development of mixed stands. More work is necessary to test this hypothesis.

Fertilization and salal control also significantly increased conifer crown cover and reduced salal abundance. With accelerated crown development following treatment application, shade in the understory increased and may have reduced salal abundance and vigor in the treated plots. Interestingly, fertilization was as effective as salal control in decreasing the amount of salal biomass, with reduced amounts of light in the understory resulting from expanded crowns probably being at least, in part, responsible. Thus, within 14 years of application, both treatments achieved the manage-

Table 3. Salal foliar biomass, percent canopy cover, N and P concentrations in senesced and green hemlock foliage and forest floor, extractable P concentrations in the forest floor, and dry masses of cedar and hemlock seedlings from the pot bioassay.

	Treatment			
	Untreated	Fertilization	Salal control	Fertilization + salal control
Salal foliar biomass (kg·ha^{-1})	2238 (488)	978 (319)	644 (229)	147 (52)
Canopy cover (%)	57 (8)	85 (6)	86 (3)	94 (1)
N (%)				
Senesced foliage	0.25 (0.03)	0.27 (0.01)	0.27 (0.01)	0.26 (0.01)
Green foliage	0.80 (0.07)	0.78 (0.06)	0.97 (0.05)	0.78 (0.05)
Forest floor	1.03 (0.02)	1.15 (0.04)	1.07 (0.05)	1.13 (0.03)
P (%)				
Senesced foliage	0.04 (0.01)	0.09 (0.02)	0.06 (0.03)	0.11 (0.03)
Green foliage	0.09 (0.01)	0.23 (0.04)	0.09 (0.01)	0.18 (0.03)
Forest floor	0.08 (0.004)	0.14 (0.01)	0.08 (0.003)	0.12 (0.01)
Forest floor extractable P (mg P·g forest floor^{-1})	0.059 (0.003)	0.065 (0.002)	0.056 (0.003)	0.059 (0.001)
Seedling dry mass (g)				
Cedar	55.8 (8.1)	150.3 (22.8)	52.8 (10.3)	92.9 (17.6)
Hemlock	57.5 (5.2)	132.4 (17.8)	53.3 (12.5)	86.8 (23.5)

Note: Values are means of five values with standard errors in parentheses.

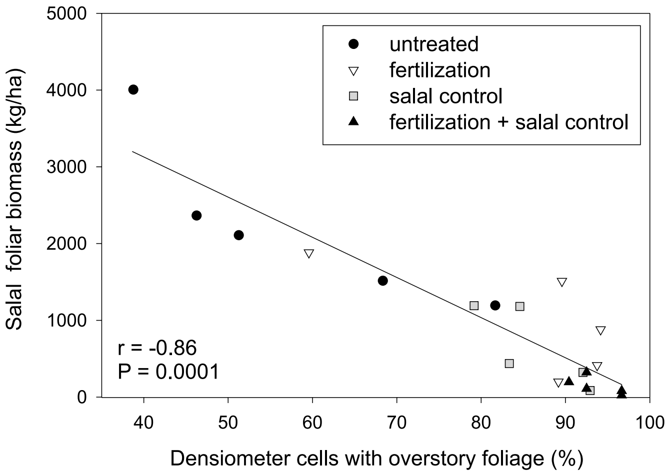
Table 4. *P* values for the 2 × 2 factorial analysis of variance of salal foliar biomass, canopy cover 14 years after treatment, nutrient concentrations in forest floor and senesced and green hemlock foliage 10 years after treatment, and total seedling biomass of seedlings grown in forest floor collected from each treatment 12 years after treatment.

	Treatment		
	Fertilization	Salal control	Fertilization × salal control
Salal foliar biomass (kg·ha^{-1})	0.012	0.002	0.223
Canopy cover (%)	0.009	0.006	0.096
N (%)			
Senesced foliage	0.643	0.894	0.272
Green foliage	0.014	0.040	0.044
Forest floor	0.008	0.837	0.284
P (%)			
Senesced foliage	0.036	0.420	0.915
Green foliage	0.000	0.237	0.204
Forest floor	0.000	0.160	0.254
Forest floor extractable P (mg P·g forest floor^{-1})	0.066	0.070	0.568
Seedling dry mass (g)			
Cedar	0.008	0.099	0.238
Hemlock	0.004	0.168	0.215

ment objective of increased crown closure and reduced salal biomass.

A sustained increase in the capacity of the forest floor and soil to supply nutrients and support tree growth also appears to have been achieved 10–13 years after treatment application. However, only fertilization induced such effects. Forest floor from the plots that were fertilized had significantly higher total N and P concentrations, and forest floor harvested 12 years after treatment application supported greater seedling growth. In addition, green and senesced hemlock foliage also had higher P concentrations, and 10- to 13-year height growth of hemlock was greater in the fertilized than in the unfertilized plots. The consistent trend in these results suggests that changes in site quality have been achieved through N + P fertilization to cedar–hemlock sites and have persisted for at least 13 years following treatment. Measurements of microbial activity in the forest floors from the fertilization – salal control experiment in 1997 also support this conclusion. Bradley et al. (2000) found that the fertilized plots had significantly higher gross N cycling rates and

Fig. 3. The relationship between crown closure and salal foliar biomass in the fertilization – salal control experiment. Each point is the mean of five measurements from each plot. The correlation coefficient (*r*) and probability (*P*) value are given.



larger pools of available N, as determined by both aerobic and anaerobic incubations.

In contrast, the influences of salal control on tree growth and measures of site quality could not be detected 10–13 years after the removal of the ericaceous shrub. Seedling growth in the forest floors from the salal control plots was similar to that found in the untreated forest floors, and the 10- to 13-year height growth of the conifers was not influenced by salal control either. Thus, vegetation control did not appear to make lasting changes to the quality of cedar–hemlock sites. Nutrient availability was probably temporarily increased, as indicated by the significantly larger cedar heights, but nutrient cycling and the ability of the forest floors and soils to supply N and P to the trees were not altered. Bradley et al. (2000) also found that gross N mineralization in forests floor from salal control plots did not differ from the rates measured in the untreated plots 13 years after treatment application, further supporting the hypothesis that N supply was only temporarily elevated by the treatment.

Stand responses to treatments such as fertilization and vegetation control can be classified as type A, B, or C based on the degree to which the imposed treatment alters resource availability (Morris and Lowery 1988). The A-type response occurs when more permanent increases in nutrient supply, site quality, and carrying capacity have been achieved, resulting in continued gains in tree height over untreated stands for the duration of stand development. In contrast, B- and C-type responses are the result of short-term increases in resource availability, with trees either maintaining (B-type) or losing (C-type) the gains in height by rotation age. When trees exhibit the B-type response, resources on site are temporarily increased, whereas in systems with C-type responses, site resources are only allocated to the trees earlier than would have occurred without silvicultural treatment. Based on the height measurements from the fertilization – salal control experiment 10–13 years after treatment, it appears that N + P fertilization of cedar–hemlock sites may produce changes in nutrient availability, therefore inducing a type-A response in hemlock. If such is the case, regenerating cedar–hemlock forests that are fertilized with N + P may shift to being dominated by hemlock. Conversely, salal control did not appear to have a sustained effect on tree growth or site quality in the cedar–hemlock forests, and therefore it will result in a type B or C response. To determine if N + P fertilization of cedar–hemlock forests results in a permanent increase in site quality, and therefore a true type-A response, the fertilization – salal control experiment will be monitored until the end of the rotation.

The apparent sustained improvement in site quality and nutrient supply following a single application of N + P to cedar–hemlock sites that are primarily N limited challenges or offers a new addition to the conventional N fertilization hypothesis. According to this hypothesis large doses or repeated applications of N are necessary to improve site quality. Only 250 kg N·ha^{-1} was applied in the fertilization – salal control experiment, representing 4% of the total N present in cedar–hemlock forest floors and upper 10 cm of mineral soil (Bennett et al. 2002), yet changes in site quality appear to have been achieved. The mechanism responsible for the potential changes to the quality of cedar–hemlock sites with N + P fertilizer application is unclear, but may be a result of the inclusion of P in the fertilizer treatment or the influence of N + P fertilization on the ericaceous salal understory.

In previous studies examining the effects of fertilization on conifer growth on cedar–hemlock sites, the application of N or N + P increased heights and diameters, whereas P alone did not cause significant increases in growth (Weetman et al. 1989*a*, 1989*b*; Prescott and Weetman 1994). Based on these results, the growth of cedar, hemlock, and spruce on cedar–hemlock sites is believed to be primarily limited by N, followed by P. Phosphorus fertilization on sites that are P limited, however, often results in sustained improvements in tree growth and P availability (Flinn et al. 1979; Turner and Lambert 1988), and the inclusion of P on sites that are predominantly limited by N availability may induce a similar response. Such a phenomenon has been reported in several studies. Amateis et al. (2000) reported elevated height growth in loblolly pine (*Pinus taeda* L.) 10 years following the application of N and P to plantation forests in the southeastern United States. Perhaps the inclusion of P in the N fertilization of cedar–hemlock forests also causes a sustained increase in site quality and conifer growth. It is unknown how the combined addition of N and P would improve site quality and stand productivity, but Pastor et al. (1984) found that P content in litter was strongly correlated with net N mineralization in soils from a mixed forest, suggesting that increased P levels may stimulate N cycling and availability.

Alternatively, the apparently sustained changes in cedar–hemlock site quality with fertilization may be a function of the influences of N + P additions on the salal understory. As previously mentioned, ericaceous shrubs are thought to degrade site quality through the release of tannins and immobilization of N in recalcitrant compounds (Preston 1999). Nitrogen mineralization and availability is therefore probably decreased when Ericaceae represent a large component of the understory. However, the addition of N + P fertilizer may not only reduce salal biomass but may also somehow lessen or counteract the degrading influences of salal on site quality. One such way may be through a reduction in tannin concentrations in salal foliage. Bradley et al. (2000) found that salal foliage from the plots that had been fertilized had significantly lower concentrations of condensed tannins. Several of the studies reporting changes in N availability and tree growth in response to N fertilization were also established on sites with ericaceous shrubs accounting for a large proportion of the understory. In jack pine (*Pinus banksiana* Lamb.) forests with understories of *Kalmia angustifolia* L. and *Vaccinium angustifolium* Ait., Prescott et al. (1995) found higher rates of net N mineralization in fertilized than nonfertilized plots 22 years after N application. Similarly, net mineralization (Strader and Binkley 1989) and volume growth (Miller and Tarrant 1983) 22 and 15 years, respectively, after fertilization were higher in the N-fertilized than nonfertilized plots of a Douglas-fir forest with a salal understory (D. Binkley, personal communication). Thus, the sustained changes in site quality following fertilization may, in part, be a result of the presence of ericaceous shrubs. Fertilizer additions may alter the ability of the shrub to influence nutrient cycling and resource availability.

Although the breadth of measurements conducted on the fertilization – salal control experiment could not elucidate the mechanism responsible, the results suggest a change in site quality and stand productivity following the single addition of low doses of N + P fertilizers to cedar–hemlock sites. Not only were the 10- to 13-year height increments of hemlock greater on the fertilized than unfertilized plots, but the quality of the forest floors receiving N + P also improved in that they could support greater seedling growth 12 years after fertilizer application. In contrast, salal control only temporarily stimulated tree growth, probably through increased nutrient availability. The increase was short-lived and did not change site quality. Based on the potential sustained influences of N + P fertilization on salal-dominated cedar–hemlock sites, further research into the response mechanisms is warranted, and the systems should be monitored to determine the duration of fertilizer response.

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