

Understorey competition affects tree growth and fate of fertilizer-applied ^{15}N in a Coastal British Columbia plantation forest: 6-year results

Scott X. Chang and Caroline M. Preston

Abstract: Growth of planted seedlings in cutovers dominated by salal (*Gaultheria shallon* Pursh) is poor largely because of low N availability and understorey competition. In this paper, the response of tree growth and fertilizer recovery to understorey competition was studied. The trees were four years old when $(^{15}\text{NH}_4)_2\text{SO}_4$ (200 kg N/ha, 3.38004% enrichment) was applied in 1991 to single-tree plots, with either understorey removed from (treated) or left (control) in the plots. Half of the plots were either sampled after two (1992) or six (1996) growing seasons. Understorey competition continued to significantly reduce height and diameter growth between 1992 and 1996, except diameter growth for western redcedar (*Thuja plicata* Donn.). Nitrogen and ^{15}N concentration in both tree and understorey components decreased from 1992 to 1996 and N concentration in 1-year-old foliage in 1996 (but not in 1992) was significantly lower in the control than in the treated plots, indicating that the site was low in N supply and the effect of fertilizer application on tissue N concentration did not last for 6 years. Results strongly indicated that the trees or understorey vegetation had no net uptake of fertilizer N beyond the second growing season. Understorey vegetation components played a significant role in the uptake and recycling of fertilizer N in this forest ecosystem.

Résumé : La croissance de semis plantés dans des coupes à blanc dominées par le salal (*Gaultheria shallon* Pursh) est faible surtout à cause de la faible disponibilité de N et de la compétition en sous-étage. Les effets de la compétition en sous-étage sur la croissance des arbres et la récupération du fertilisant ont été étudiés. Des parcelles composées d'arbres individuels âgés de quatre ans ont été fertilisées avec $(^{15}\text{NH}_4)_2\text{SO}_4$ à raison de 200 kg N/ha, soit un apport de 3,38004%. La végétation de sous-étage a été laissée dans les parcelles témoins et enlevée dans les parcelles traitées. La moitié des parcelles ont été échantillonnées après deux ans (1992) et l'autre moitié après six ans (1996). La compétition en sous-étage a continué à réduire significativement la croissance en hauteur et en diamètre entre 1992 et 1996, à l'exception de la croissance en diamètre du thuya géant (*Thuja plicata* Donn.). La concentration en azote et en ^{15}N dans les arbres et la végétation de sous-bois a diminué de 1992 à 1996. En 1996 (mais non en 1992), la concentration de N dans le feuillage d'un an était significativement plus faible dans les parcelles témoins que dans les parcelles traitées. Ces résultats indiquent que le site était pauvre en N et que l'effet de la fertilisation sur la concentration de N dans les tissus n'a pas duré six ans. Les résultats montrent clairement que ni les arbres ni la végétation de sous-étage n'a eu un prélèvement net de fertilisant azoté au-delà de la deuxième saison de croissance. Les composantes de la végétation de sous-étage ont joué un rôle important dans le prélèvement et le recyclage du fertilisant azoté dans cet écosystème forestier.

[Traduit par la Rédaction]

Introduction

Poor growth of regenerating western redcedar (*Thuja plicata* Donn.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) has long been observed on cutovers of coastal old-growth cedar-hemlock (CH) forests, following the invasion of the sites by an ericaceous shrub, salal (*Gaultheria shallon* Pursh) (Weetman et al. 1989a, 1989b). Poor growth was generally a consequence of inadequate supply of N and P in the forest

floor of the original old-growth CH forest (Prescott et al. 1996). The low nutrient availability in the CH forest floor was caused by several factors, including high tannin contents in salal and incomplete decomposition of litter that reduces nutrient recycling (Prescott et al. 1996; Preston 1999).

The low N availability problem was aggravated by the invasion of the site by salal (Messier 1993), as a substantial portion of the available N can be found in non-crop vegetation (Messier 1991). Interference of competing weeds on N uptake by crop trees has been found on many other sites. Woods et al. (1992) reported that 68% of the applied fertilizer was found in annual weeds in young radiata pine (*Pinus radiata* D. Don) plantations on a sandy Podzol in southeastern South Australia. Preston et al. (1990) reported comparable or higher recovery of ^{15}N in understorey in the 1-year study of 11-year-old lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) and 13-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in British Columbia. In forests where water availability was not limiting, the effect of

Received September 1, 1999. Accepted April 11, 2000.

S.X. Chang.¹ Department of Forestry, P.O. Box 8008, North Carolina State University, Raleigh, NC 27695-8008, U.S.A.

C.M. Preston. Pacific Forestry Centre, Natural Resources Canada, Canadian Forest Service, 506 West Burnside Road, Victoria, BC V8Z 1M5, Canada.

¹Corresponding author. e-mail: sxchang@unity.ncsu.edu

weed control in improving nutrient supply to slash (*Pinus elliottii* Engelm.) and loblolly pines (*Pinus taeda* L.) has been found to equal that of applying large amounts of fertilizer (Neary et al. 1990).

Salal, a perennial evergreen plant species, is much more aggressive and persistent on the site than most annual weeds (Chang et al. 1996b). To correct nutrient deficiency on the CH forest cutover sites, N was applied; however, our understanding of the effectiveness of such a practice was poor. There have been few publications on the effect of weed competition on the efficiency of fertilizer N applied to forest ecosystems; much information has come from agroforestry studies, where proper management of understorey species (pasture or annual crops) can tremendously affect the success of a specific crop–tree or pasture–tree combination and intensively managed pine plantations (Nambiar and Nethercott 1987; Niehm et al. 1992; Smethurst and Nambiar 1989; Nambiar and Sands 1993; Clinton and Mead 1994). There has also been little study of fertilizer recovery beyond 1 or 2 years. In an 8-year study, Preston and Mead (1994) found no additional uptake of ^{15}N compared with 1 year.

An experiment was initiated in fall 1990 on 4-year-old western redcedar, western hemlock, and Sitka spruce trees planted on CH cutover sites to investigate the effect of weed (mainly salal) competition on tree growth and fertilizer N use efficiency, using the ^{15}N tracer technique. Two-year results were reported in Chang et al. (1996a); 6-year results are reported here. The specific objectives of this paper were (i) to quantify the growth response of trees to weed competition 6 years after the fertilizer application; (ii) to evaluate the long-term fate of applied fertilizer N, particularly to determine if there was any new fertilizer N being taken up by the trees from years 3 to 6; and (iii) to examine the internal cycling of labeled fertilizer N in tree components.

Materials and methods

The site

The research site was located on Tree Farm License (TFL) 25 on lands of Western Forest Products Ltd. near Port McNeill (50°36'N 127°15'W) in the very wet maritime subzone of the Western Hemlock Biogeoclimatic zone (Pojar et al. 1991) on northern Vancouver Island, British Columbia. The original vegetation cover before clear-cutting and slash burning in 1985 was a very old forest of western redcedar and western hemlock. Understorey on the site at the time the experiment was installed was dominated by salal, with lesser amounts of fireweed (*Epilobium angustifolium* L.), deer fern (*Blechnum spicant* (L.) Roth), blueberry (*Vaccinium* spp.), bunchberry (*Cornus canadensis* L.), and sometimes a moss layer.

The site is characterized by a gently undulating topography, a thick humus (H) layer that usually exceeds 0.45 m, and large quantities of fallen logs on the surface of the forest floor and decomposed or partially decomposed woody debris in the humus layer (Keenan et al. 1993). The average bulk density of the sampled plots was 0.20, 0.26, 0.33, 0.45, and 0.55 $\text{Mg}\cdot\text{m}^{-3}$ in the 0–0.1, 0.1–0.2, 0.2–0.3, 0.3–0.4, and 0.4–0.5 m soil depth, respectively. This illustrates that the 0–0.3 m depth of the soil profile is primarily humus (H) and the 0.3–0.5 m depth has some mineral soil component. The underlying Ferro-Humic Podzol was moderately well to somewhat imperfectly drained. The area receives an annual precipitation of 1700 mm, most of which is received during the winter

period. Mean daily temperatures vary from 3.0°C in January–February to 13.7°C in July–August (Lewis 1982).

Field experiment and sampling

Trees for the study were selected from those planted in April 1987 in a previous study of the effects of fertilization and salal removal (Messier 1993). Trees were selected from those that had not received fertilizer but including those that had been subject to removal of aboveground competing vegetation (which was mainly salal). Salal removal was maintained in Messier's study by periodic aboveground clipping and cutting around the microplots to 0.4 m depth.

Single-tree microplots (1 m radius) were established in the fall of 1990 when the trees were 4 years old, and they were trenched and separated from the bulk soil using plastic sheeting to a depth of 0.5 m, which was beyond the rooting depth. A completely randomized factorial design was used for the experiment. The experiment consisted of three species (western redcedar, western hemlock, and Sitka spruce) and two treatments: no understorey removal (control) and aboveground understorey removal (treated), with four replications. A total of 24 microplots were established (3 species \times 2 treatments \times 4 replicates).

Nitrogen-15 labeled $(\text{NH}_4)_2\text{SO}_4$ (3.38044 atom% ^{15}N enrichment) was applied on April 16, 1991, at a rate of 200 $\text{kg N}\cdot\text{ha}^{-1}$ to all 24 microplots. For each plot, the fertilizer was evenly applied from a large watering can in a total of 4 L water. As the top humus layer (0–0.1 m) has a water holding capacity of over 300%, the penetration of added water should not have exceeded 0.01–0.02 m at the time of application. There was some regrowth of salal and other understorey species on the treated plots; in particular, salal continued to resprout from its network of rhizomes despite several years of suppression. Removal of understorey vegetation in the treated plots was maintained, throughout the duration of the experiment, by periodic clipping and the small amounts of material were placed on the surface of the plot.

Two of the four replications were randomly sampled in October 1992, at the end of the second growing season after fertilizer application. Results from that study were reported in Chang et al. (1996a). Half of the plots were left to grow and were sampled in September 1996. The procedure for the 1996 destructive sampling was very similar to that of the 1992 sampling. The aboveground understorey vegetation and litter were collected first, then the aboveground tree was cut at ground level. Two randomly located soil pits (0.25 \times 0.25 m) were excavated to a depth of 0.5-m in intervals of 0.1 m. After the soil pits were sampled, tree roots in the microplots were carefully excavated using hand tools to recover as many visible roots as possible from the entire microplot to a depth of 0.5 m. This generally included excavating all roots greater than 1 mm in diameter.

Laboratory and statistical analyses

Soil samples from each 0.1 m thick layer of a pit were weighed in the laboratory and then soil water content was measured to determine the bulk density of each soil layer. Visible roots were removed from the soil samples. A proportionate (by weight) subsample was taken from each of the two samples from the same depth of a microplot, mixed, and air-dried. The samples were oven-dried before performing total N and ^{15}N analysis.

After the biomass samples were brought into the laboratory, the aboveground tree was separated into (i) 1-year-old (current-year) and >1-year-old needles; (ii) 1-year-old and >1-year-old branches; and (iii) stem. The belowground tree was not further divided. The aboveground understorey vegetation was separated into salal and non-salal. The non-salal component comprised mainly deer fern, blueberry, and bunchberry. The belowground understorey roots were not further divided. Roots picked from the soil samples were

separated into tree roots and understorey roots and were converted to per plot basis. Tree roots picked from the soil samples were used to correct the tree root biomass for each plot by scaling up the biomass recovered in the soil pits to per plot basis. Plant materials were dried at 65°C and weighed, coarsely ground, and then subsampled for fine grinding to pass a 40-mesh screen.

Plant samples were analyzed for total N by the semi-micro-Kjeldahl method (Bremner and Mulvaney 1982), with the exception that mercuric oxide was used as the catalyst. The distillates were collected in boric acid – ethanol, acidified, and dried at 70°C. The ammonium N was converted to dinitrogen gas using the Rittenberg reaction with alkaline lithium hypobromite, and analyzed for ¹⁵N enrichment using a Vacuum Generators Sira 9 mass spectrometer (Preston et al. 1990). Soil samples were dried and ground to 50 µm in a Siebtechnik mill. Total N and ¹⁵N enrichment were determined following the method used for plant sample analysis.

For statistical analysis, data sets were checked first for homogeneity of variance and normality of distribution. Logarithmic transformation was performed on the following measurements to bring the data sets to normal distribution and homogeneity: biomass of >1-year-old foliage, total N concentration in aboveground tree components except the >1-year-old branches, aboveground salal biomass, biomass of aboveground other understorey vegetation, and litter. However, means were reported on untransformed data. Analyses of variance were performed on all experimental variables using the general linear models (GLM) procedure of the SAS package (SAS Institute Inc. 1989). Diameter and height growth was first analyzed using diameter in 1992 as a covariate. The covariate was not significant; therefore, the final analysis followed a completely randomized factorial design. In cases where the effect of year (1992 vs. 1996) was tested, year was treated as a third factor in the factorial design. Group means of independent variables were compared between treatments for each species by Scheffé's multiple range test, for each component considered.

Results

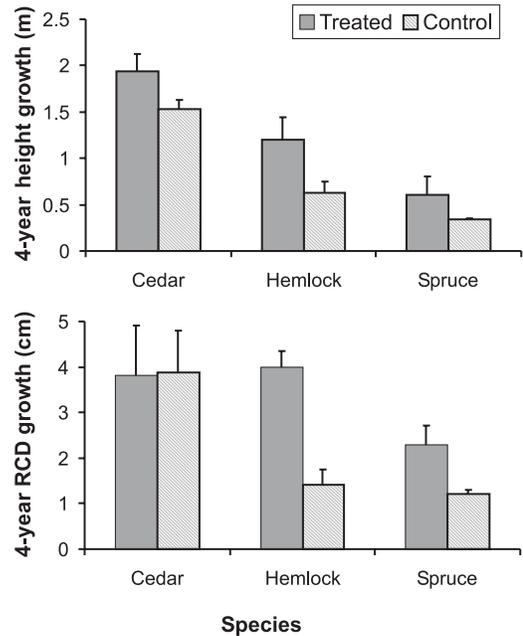
Growth trends

If the sizes of trees sampled in 1992 and those left for the 1996 sampling were initially (in October 1992) different, then comparison between the data sets from the two samplings would be difficult. Analysis of the data sets revealed that sizes of trees at the end of the 1992 growing season for the two groups (groups of trees for the 1992 vs. 1996 sampling) were not significantly different in height and root collar diameter (RCD), neither were there any significant interactions among group, species, and treatment (data not shown).

Height growth (increment) from October 1992 to September 1996 continued to be significantly affected by understorey vegetation control for all three species, but RCD growth was only affected by treatment for hemlock and spruce (Fig. 1). Differences among species were significant (ANOVA values not shown), with redcedar growing the fastest in both height and diameter and spruce the slowest, regardless of the treatment (Fig. 1). On average, spruce and hemlock grew only 27 and 53%, for height, and 46 and 71%, for RCD, respectively, as fast as redcedar in the 4-year period.

Tree biomass harvested in September 1996 was significantly affected by understorey competition in each component, except the 1-year-old foliage and 1-year-old branches (Fig. 2, Table 1). The effect of understorey competition on

Fig. 1. Height and root collar diameter (RCD) growth of western redcedar, western hemlock, and Sitka spruce in a 4-year period (October 1992 to September 1996). Error bars are SE.



tree biomass was much greater on spruce and hemlock than on redcedar, as indicated by the difference in biomass between the treated and control. The majority of the biomass was accumulated in the foliage and branches >1 year old, and in the stem and roots (Fig. 2). Although there were significant species × treatment interactions for foliar and branch biomass of the >1-year-old components (Table 1), there was no change of ranking between the control and treated plots for each species (Fig. 2). Total tree biomass was significantly affected by the treatment by species interaction and by treatment. Analysis of the interaction term showed that treatment effect on total tree biomass was only significant for hemlock (data not shown). Biomass of aboveground salal, root, and litter was significantly greater in the control than in the treated plots (Fig. 3). No treatment effect was found for biomass of the other understorey species components.

Nitrogen trends in biomass

Nitrogen concentration in the various tree components was much higher in the 1992 than in the 1996 sampling (Fig. 4, $p < 0.001$, ANOVA values not shown). No treatment effect on N concentration was found for any of the tree components in either sampling except for the 1-year-old foliage in the 1996 sampling, where foliar N concentration was significantly higher in the treated than in the control plots. Nitrogen concentration in the 1-year-old components (both foliage and branches) showed a decreasing trend from redcedar to hemlock to spruce; in the other components, differences among species were not significant. In the 1996 samples, N concentration in the 1-year-old foliage was below the critical levels established for these species (Ballard and Carter 1985) regardless of species and treatment.

Nitrogen-15 abundance (%) in the various tree components also decreased from 1992 to 1996 (Fig. 5, $p < 0.001$,

Table 1. Analysis of variance (F values) for the effect of understorey competition and tree species on components of tree biomass.

Variable	df	1-year foliage	1-year branch	>1-year foliage	>1-year branch	Stem	Root
Species (S)	2	8.97*	8.64*	1.56	2.94	1.31	2.34
Treatment (T)	1	1.41	2.73	59.26**	29.41**	7.18*	14.76**
S × T	2	1.27	1.17	8.09*	5.56*	2.87	2.98

* $p < 0.05$.

** $p < 0.01$.

Fig. 2. Tree biomass harvested in September 1996. Error bars are SE. CT, treated redcedar; CC, control redcedar; HT, treated hemlock; HC, control hemlock; ST, treated spruce; SC, control spruce; F, foliage; B, branches.

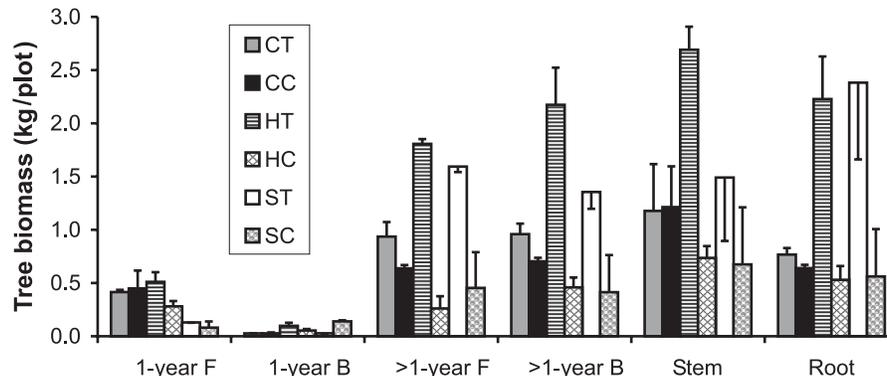
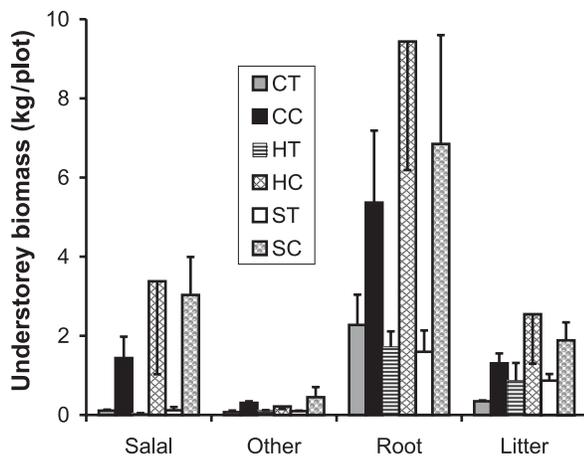


Fig. 3. Understorey biomass harvested in September 1996. Error bars are SE. Abbreviations are as in Fig. 2.



ANOVA data not shown); however, in all tree components studied, ^{15}N abundance levels in 1996 were greater than the natural abundance level (0.3663%). Because of the dilution effect (see Chang et al. 1996a for a detailed discussion), no significant treatment effect was found for ^{15}N abundance in tree components, except in roots in the 1996 sampling (data not shown); there were no species × treatment interaction for any of the components studied. In the 1992 samples, ^{15}N abundance tended to be highest in spruce and lowest in redcedar; this trend did not exist in the 1996 samples.

Figures 6 and 7 show that both N concentration and ^{15}N abundance in understorey vegetation decreased from 1992 to 1996 ($p < 0.001$, ANOVA data not shown), regardless of treatment and the type of component studied. In both 1992 and 1996, with a few exceptions, N concentration was

higher ($p < 0.05$, ANOVA values not shown) in the treated than in the control plots, but ^{15}N abundance was higher ($p < 0.05$, ANOVA values not shown) in the control than in the treated plots (Figs. 6 and 7).

Nitrogen trends in soil

Preliminary analysis showed that there was no species or species × treatment or species × treatment × depth effect on soil N concentration or ^{15}N abundance; therefore, the species data were combined to analyze for the treatment and depth effects. Soil N concentration appeared to be higher in the control than in the treated plots throughout the soil profile in both 1992 and 1996 (Fig. 8); however, the difference between the treatments in 1992 was not statistically significant, because of the large soil variability. The only significant effect found in 1992 was the depth effect ($p < 0.001$). In 1996, however, both depth and treatment significantly affected soil N concentration in the profile, without a significant depth × treatment interaction.

The inherent soil variability did not seem to affect the uniform labeling of ^{15}N -enriched material to the soil, shown by the small standard error bars for soil ^{15}N enrichments (Fig. 9). Again in 1992 there were significant differences only among the depths. In the 1996 sampling, there was significant treatment, depth, and treatment × depth interaction; at this sampling, a significant treatment effect was found only at the 0–0.1 m depth. For the treated plots, soil ^{15}N abundance was significantly higher in the surface layer than in the other layers, and in the control plots, soil ^{15}N abundance varied as follows: 0–0.1 > 0.1–0.2 > 0.2–0.5 m depth.

Recovery of ^{15}N

From 5.1 to 11.9% of the applied fertilizer was recovered in the trees in the treated plots, compared with 2.2 to 2.5%

Fig. 4. Effect of understorey removal and tree species on N concentration in tree components in 1992 and 1996. Error bars are SE. Abbreviations are as in Fig. 2.

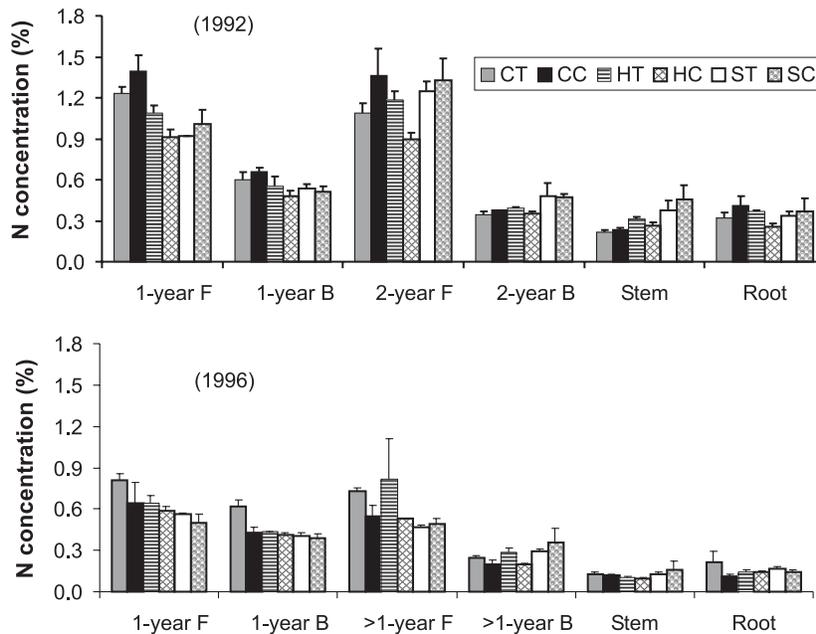
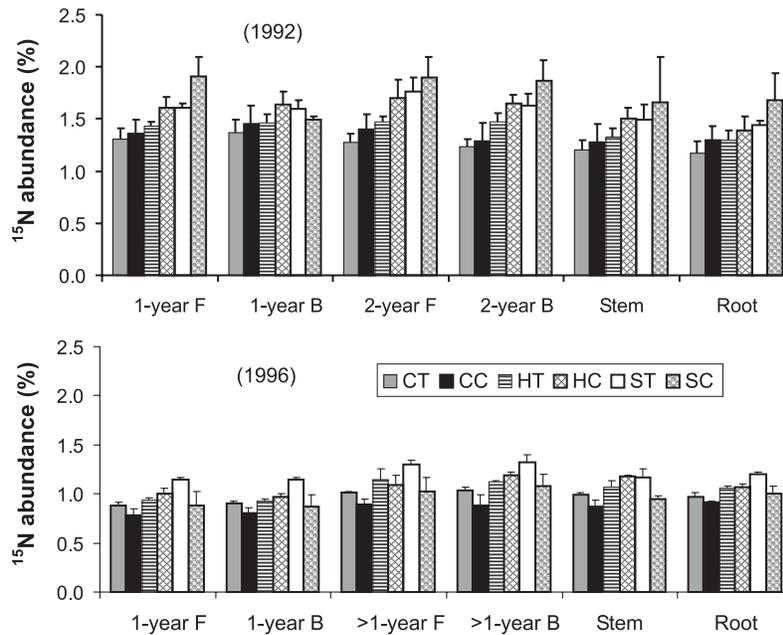


Fig. 5. Effect of understorey removal and tree species on ¹⁵N abundance in tree components in 1992 and 1996. Error bars are SE. Abbreviations are as in Fig. 2.



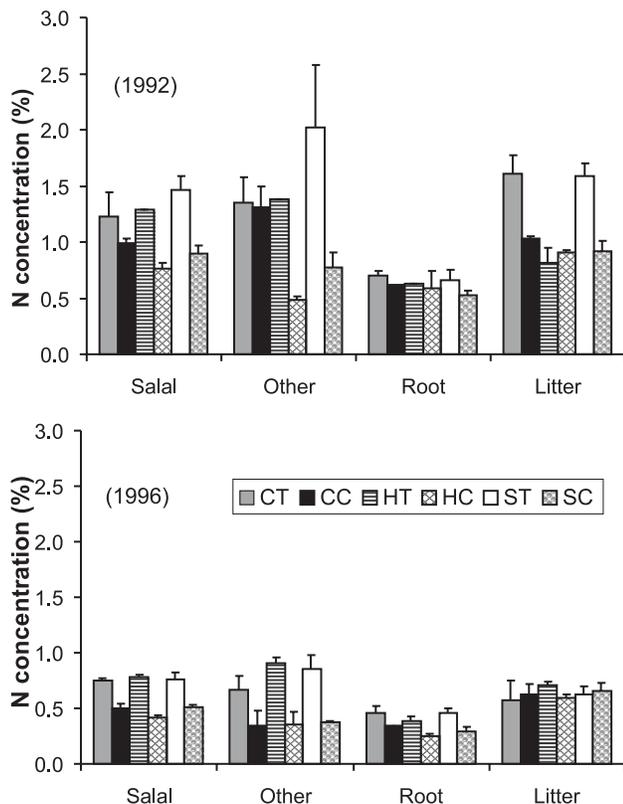
in the control plots (Table 2); in contrast, from 1.8 to 2.4% of the applied fertilizer was recovered in the understorey vegetation in the treated plots, compared with 6.0 to 8.8% in the control plots (Table 2). There was no treatment × species interaction or species effect for any of the independent variables studied, and treatment effect was significant for all but one (soil) independent variable studied. Understorey removal resulted in significantly greater fertilizer N recovery rates in tree components but lead to a significantly lower total recovery for the soil–plant system at the end of the sixth growing season after fertilizer application. The majority of

the fertilizer N was found in the soil compartment, from 47.4 to 63.2% and from 67.1 to 68.8%, in the treated and control plots, respectively. Analysis showed that total fertilizer N recovery in the soil profile (0–0.5 m) did not significantly change from 1992 to 1996 ($p = 0.0944$, ANOVA values not shown).

Discussion

Weed control is often essential for successful plantation establishment and for maintaining an adequate level of tree

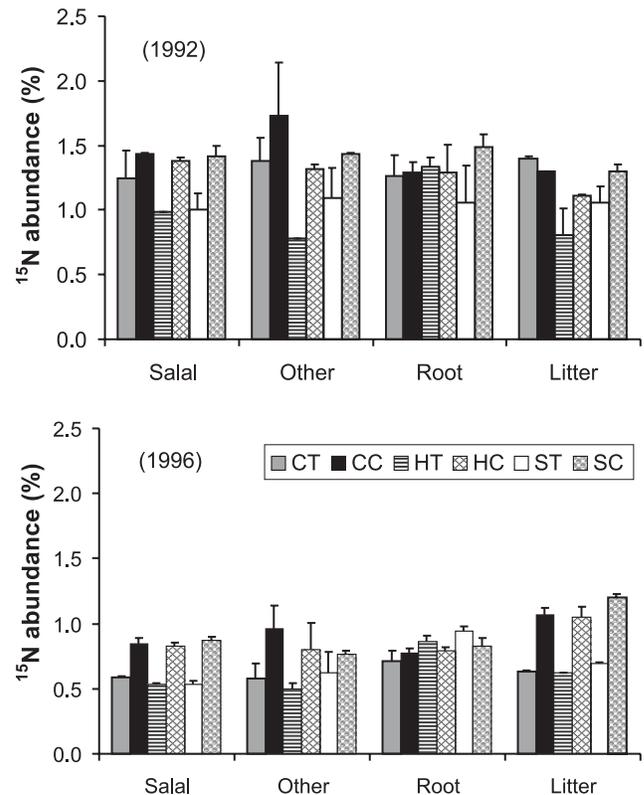
Fig. 6. Effect of understorey removal and tree species on N concentration in understorey vegetation components in 1992 and 1996. Error bars are SE. Abbreviations are as in Fig. 2.



nutrition as weeds may compete with trees for light (Knox et al. 1995), nutrients, water (Knox et al. 1995; Berendse 1982; Morris et al. 1993), or other limiting resources. The site studied in this paper had low soil nutrient availability owing primarily to the characteristics of the forest floor in the old-growth forest before harvesting (Prescott et al. 1996). For such a site, the benefit of removing the competing weeds was still apparent 10 growing seasons after planting or six growing seasons after the plots were installed, except for RCD growth in redcedar (Fig. 1). Western hemlock seemed to be the most responsive species to weed control, consistent with an earlier report (Chang et al. 1996b). Results showed that western redcedar grew best in the last 4 years and was less affected by weed competition (Fig. 1), indicating that redcedar may be more adapted to the site with low nutrient supply. However, a longer term monitoring of the species is required to make a more conclusive conclusion. Trends in biomass growth were similar to those in height and diameter growth (Fig. 2); however, in this case it was not possible to calculate the biomass increment from October 1992 to September 1996, as the data presented are the total biomass at the time of harvesting in 1996, except for the 1-year-old foliage and branches, which represented the growth in a single year of these two components.

The significant reduction in the 1-year-old foliage and branch biomass and the reduction in N concentration in these components from 1992 to 1996 signified that a severe nutrient deficiency was starting to set in. Nitrogen concentrations in the 1-year-old foliar samples were marginal for

Fig. 7. Effect of understorey removal and tree species on ^{15}N abundance in understorey vegetation components in 1992 and 1996. Error bars are SE. Abbreviations are as in Fig. 2.



redcedar and marginal to deficient for hemlock and spruce in 1992; in 1996, the levels in 1-year-old foliage were very severely deficient for all species and both treatments according to the recommendations of Ballard and Carter (1985). The higher foliar N concentrations in the 1-year-old (1996) foliar and branch samples in the treated than in the control plots ($p < 0.05$) indicated that weed removal somewhat improved the nutritional status of the trees in the treated plots, consistent with many other reports (cf. Nambiar and Sands 1993). However, weed control alone was not enough to elevate the foliar N concentration to adequate levels for any of the species studied, reflecting the nature of the soil with low N supply. The reduction in N concentration in the old tree components from 1992 to 1996 was caused by internal transfer from old to new tissues and a dilution effect by biomass growth when there was limited N supply from the forest floor and mineral soil.

The trend in ^{15}N abundance was similar to that of total N. Nitrogen-15 abundance in all tree components studied decreased from 1992 to 1996, regardless of species and treatment. Nitrogen-15 abundance in the current-year (1996) growth was greater than the natural abundance level (0.3663%), showing the strong ability of new growth to obtain N from old tissues through retranslocation (Mead and Preston 1994); differences between the treated and control plots were not significant at the 1992 nor at the 1996 sampling. However, as has been illustrated in the earlier paper, the ^{15}N content in tree components in 1992 was significantly greater in the treated than in the control plots (Chang et al.

Fig. 8. Effect of understorey removal on soil total N concentration in the soil profile in 1992 and 1996. Error bars are SE.

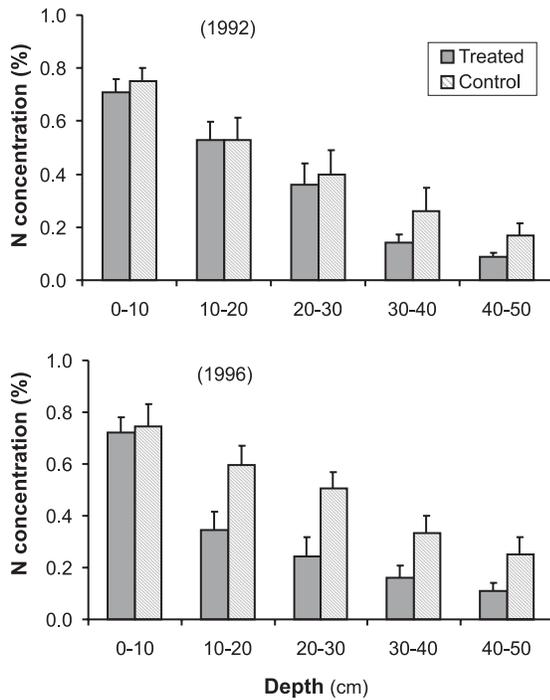
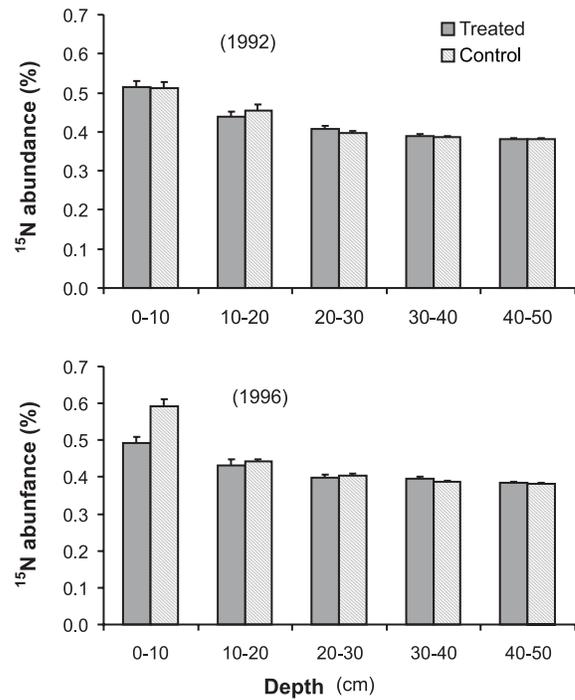


Fig. 9. Effect of understorey removal on bulk soil ^{15}N abundance in the soil profile in 1992 and 1996. Error bars are SE.



1996a), because of greater tree biomass growth in the treated plots; in the 1996 sampling, this was reflected by the greater recovery rate in tree biomass in the treated plots (Table 2). The greater N concentration in the aboveground understorey components in the treated than in the control plots (Fig. 6) showed that the new growth (in the treated plots, understorey vegetation was clipped periodically) benefitted from the lower competition in this soil with low N supply. The reversed trend in ^{15}N abundance (Fig. 7) showed that fertilizer ^{15}N was preserved and recycled in these perennial shrubs.

Mead and Preston (1994), in studying the distribution and retranslocation of ^{15}N fertilizer in young lodgepole pine trees, showed that, although total N concentration increased from the oldest to the most recently formed foliage, ^{15}N concentrations in tree components of different ages were relatively stable owing to two processes: (i) the translocation of ^{15}N -enriched N from old tissues to new growth and (ii) the continued uptake of N from the soil; this fraction of N had ^{15}N at close to background levels. This finding is supported by data from the present study, where ^{15}N abundance was much more uniform than total N concentration in different tree components, in both 1992 and 1996 (Figs. 4 and 5). Because we did not find net ^{15}N uptake from the soil by the trees, we attributed ^{15}N found in the new (1996) growth solely from retranslocation (Mead and Preston 1994). Thus, we are able to calculate the amount of N retranslocated to the new growth as outlined below.

Since ^{15}N concentrations in different tree components were kept relatively uniform in both 1992 and 1996, we can assume that N translocation occurred in all tree components (Mead and Preston 1994; Millard and Proe 1992). Otherwise, we would have seen ^{15}N concentrated in a particular tree component. Because there was no net increase in ^{15}N re-

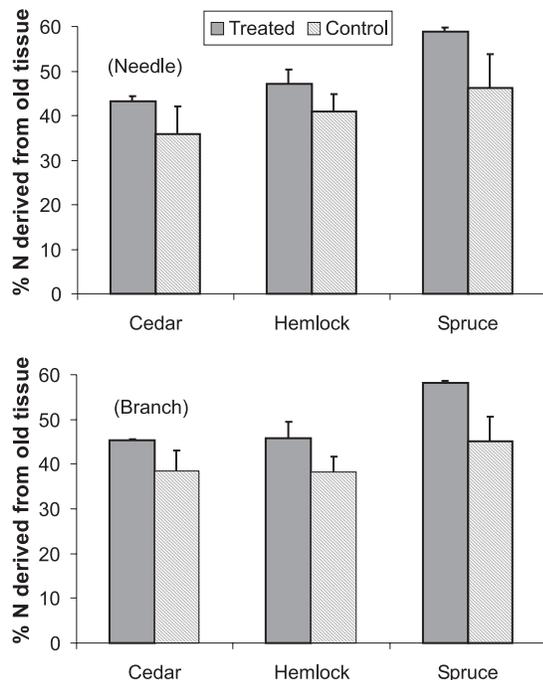
covery in tree root systems from 1992 to 1996 (Table 2; Chang et al. 1996a), we assume that ^{15}N in old root tissues was primarily transferred to new root growth. We did not separate stems into different ages and are thus unable to construct the ^{15}N concentration changes in stems over time. For the purpose of simplification, we assume that ^{15}N transferred from old stem tissues was primarily used for new stem growth. Thus, the ^{15}N found in new foliage and branches would largely be from old foliage and branch tissues. We stress that these are approximations only for the purpose of conducting the exercise below; the real scenario of N retranslocation is much more complicated. These assumptions are supported by at least two points of evidence: (i) Nambiar and Fife (1991) showed that, in several radiata pine experiments, there was a strong linear relationship between N content of current + 1-year-old needles in spring and the amount of N retranslocated from the needles during the following growing season; and (ii) our data showed that the proportion of root, stemwood, and the sum of 1- and 2-year-old foliage and branch biomass as a percentage of total tree biomass did not change from 1992 to 1996; therefore, we can reasonably expect the proportional distribution in 1995 to be similar to that in 1996. In other words, it is possible to maintain the ^{15}N concentration relatively constant in the tree components by just retranslocating ^{15}N from old needles and branches to new needles and branches, and so forth, if the components always grow proportionately. The ability of trees to maintain a stable biomass partitioning is also illustrated by Chang et al. (1996b), where they found that biomass allocation among the components was virtually unchanged by understorey competition.

Thus, using a mass-balance approach, the foliage and branch ^{15}N concentration in 1995 was reconstructed and used to calculate the percentage of N in current-year tissues

Table 2. Percent recovery of fertilizer N six growing seasons after application.

Component	Cedar		Hemlock		Spruce	
	Treated	Control	Treated	Control	Treated	Control
Aboveground tree	4.61 _a (0.43)	2.30 _b (0.28)	10.75 (2.82)	1.88 (0.58)	6.85 (0.40)	1.91 (1.57)
Tree root	0.52 _a (0.19)	0.20 _b (0.03)	1.19 (0.31)	0.27 (0.06)	1.77 (0.65)	0.25 (0.20)
Total tree	5.13 _a (0.62)	2.51 _b (0.31)	11.94 (3.12)	2.16 (0.63)	8.62 (0.25)	2.16 (1.77)
Aboveground understorey	0.15 _a (0.06)	2.11 _b (0.81)	0.09 (0.04)	3.54 (2.30)	0.17 (0.09)	4.47 (1.56)
Understorey root	1.90 _a (0.86)	3.85 _b (0.98)	1.71 (0.37)	4.65 (0.21)	2.26 (1.04)	4.28 (1.01)
Total understorey	2.05 _a (0.92)	5.96 _b (1.78)	1.80 (0.33)	8.19 (2.51)	2.43 (1.13)	8.75 (2.57)
Litter	0.26 _a (0.06)	3.17 _b (1.27)	0.84 (0.46)	5.46 (2.72)	0.89 (0.18)	5.24 (0.38)
Soil	63.24 _a (21.01)	68.83 _a (1.99)	47.36 (7.61)	68.46 (16.22)	48.47 (7.52)	67.12 (4.70)
Total	70.69 _a (21.37)	80.47 _b (4.74)	61.95 (9.95)	84.28 (11.62)	60.41 (5.97)	83.27 (3.53)

Note: Values in parentheses are SEs. There was no treatment \times species interaction for any of the independent variables studied. The treatment effect applies to the means across the species. Values with different letters are significantly different.

Fig. 10. Percentage of N in the 1996 growth of foliage and branches derived from old foliar and branch tissues. Error bars are SE.

derived from old foliar and branch tissues using the approach of Mead and Preston (1994). Calculation showed that, for the 1996 growth, both foliage and branches acquired a large proportion (ranging from 30 to 60%) of their N from old tissues (Fig. 10). Sitka spruce consistently had a greater percentage of the N requirement transferred from old tissues. A greater percentage of the N required for foliar and

branch growth ($p < 0.05$, data not shown) was met by retranslocation in the treated than in the control plots, reflecting more ^{15}N -fertilizer recovered in 1992 in the treated plots (Chang et al. 1996a) and available for retranslocation. Nambiar and Fife (1991) suggested that the larger the nutrient pool, or uptake, with the plant, the greater the amount available for retranslocation. The greater percentage of internal N retranslocation should have helped sustain the higher growth rate in the treated plots (Fig. 1).

The apparently higher soil N concentration in the control than in the treated plots cannot be fully explained. There was no significant presence of N-fixing plant species in the understorey and presence of understorey cover should not have caused a significant increase in asymbiotic N fixation, a source of N that generally contributes very little of the N needed by the plants in undisturbed old-growth forests in the area (Cushon and Feller 1989; Heath et al. 1988). Therefore, there was no apparent N source that could have contributed significant amounts of N to increase the soil N concentration in the control plots. However, the higher ^{15}N abundance in the surface humus layer of control than in treated can be explained as a result of accumulation of litter on the surface of the forest floor, as both tree and understorey plants had higher ^{15}N abundance levels than the soil layers (Figs. 5, 7, and 9). In 1992, although there was litter accumulated at the soil surface in the control plots, little of the litter had been decomposed and incorporated into the surface soil (that is the F (partially decomposed litter) and H (humus) layers). The soil ^{15}N abundance level changed very little from 1992 to 1996, illustrating that the ^{15}N immobilized in the soil was very stable.

Six years after ^{15}N -labeled fertilizer N was applied, the majority of the ^{15}N was still retained in the soil. This is consistent with results from many other similar studies (Koopmans et al. 1996; Buchmann et al. 1996; Preston et al.

1990; Nõmmik and Larsson 1989). Contrasting to the finding in Koopmans et al. (1996), who studied sites with high rates of N deposition, the retention of ^{15}N in the organic layers (primarily humus layer, see the materials and methods section) in this study was quite stable as no obvious decrease of ^{15}N recovery rate in the soil was found. A greenhouse study following on the 1992 sampling showed that residual ^{15}N in the studied soil, after being labeled for one growing season, was no more available than that had been labeled for 3 years (Chang et al. 1999), an indication that fertilizer-applied N was quickly immobilized and stabilized after application. Short-term (most studies) and long-term (Preston and Mead 1994) retention in the soil may also be very different. Preston and Mead (1994) showed loss between 1 and 8 years, although short-term soil recovery was quite high. This study showed no loss of soil ^{15}N between 2 and 6 years ($p = 0.0944$), maybe due to the input of ^{15}N -labeled litter, and possibly due to the fact that the organic horizons are deep, and have high input of tannins, which may help to retain N (especially in the control plots) by changing N release patterns or slowing decomposition rates (Northup et al. 1995, 1998; Preston 1999). It is interesting to note that ^{15}N recoveries in this organic soil were very similar to other studies where mineral soil and thin organic horizons were the norm (see Preston et al. 1990 and references cited therein). One might have expected the recovery to be higher in the humus layers with very high C/N ratios. This reflected the fact that, although N immobilization in the soil is quick, a portion of the fertilizer-applied N is always lost soon after applied.

The effect of weed competition on fertilizer N use efficiency was significant for every independent variable examined, except for N immobilized in soil (Table 2). The general trend for species differences in 1996 was the same as in the 1992 sampling, with the highest tree recovery rate in hemlock in the treated plots and the lowest also in hemlock in the control plots. Compared with the 1992 sampling, the declining ^{15}N recovery rate in the vegetation components could have been caused by the recycling of N from vegetation to litter and then to the soil through litter decomposition (Mead and Preston 1994). This is reflected in the increase of ^{15}N recovered in the soil from 1992 to 1996, especially in the control plots, where litter accumulation was much higher than in the treated plots. This results in a greater percentage of the fertilizer N being recovered in the soil-plant system of the control than in the treated plots, showing that a greater fertilizer N recovery by vegetation may help retain more N in the ecosystem. The role of weeds for N retention in ecosystems has been observed in conventional fertilization studies (Smethurst and Nambiar 1989; Woods et al. 1992).

Since ^{15}N -fertilizer recovered in tree biomass was somewhat lower in 1996 than in 1992 (Table 2; Chang et al. 1996a), it strongly indicated that, from 1992 to 1996, there was no net uptake of ^{15}N from the soil by the trees, regardless of the species. This result is consistent with Mead and Preston (1994) and Preston and Mead (1994). There was no new uptake of ^{15}N by understory species either as indicated by the lower ^{15}N recovery rate by understory vegetation in 1996 than in 1992, although the biomass of understory vegetation was higher in 1996. The lower ^{15}N recoveries in the

1996 standing biomass reflected what was cycled back to the soil primarily through litter fall.

Conclusions

Trees or the understory vegetation did not accumulate any more fertilizer-applied N after the first two growing seasons following fertilizer application. Fertilizer N that had been immobilized by the soil and vegetation in the first 2 years was quite resilient and was not subject to significant losses. The site had very low intrinsic N availability as 10 years after planting, or 6 years after fertilizer application, foliar N was at very severely deficient levels. Salal invasion aggravated the nutrient deficiency problem of the site, especially at the early stage of stand development. Weed competition was a major cause for low fertilizer use efficiency by trees and poor tree growth; growth response was significant to weed removal 10 years after planting and weed control. Thus, weed control is strongly recommended for stand establishment and before investment in fertilization is made. However, understory vegetation may play a role in helping to retain N in the system.

Acknowledgements

Funding for this study was provided by a Natural Sciences and Engineering Research Council of Canada grant for the Salal-Cedar-Hemlock Integrated Research Project with contributions from Western Forest Products Ltd., MacMillan Bloedel Ltd., and Fletcher Challenge Ltd. Kevin McCullough made a major contribution to field sampling and sample analysis. Thanks are extended to the three anonymous reviewers for their helpful comments.

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