Effect of understory competition on distribution and recovery of ^{15}N applied to a western red cedar – western hemlock clear-cut site

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Abstract: Fertilizer labeled with ^{15}N was used to study the fate of N in forest soil–plant systems with (control) and without competition (treated) from an ericaceous evergreen shrub, salal (*Gaultheria shallon* Pursh), on a western red cedar (*Thuja plicata* Donn ex D. Don) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) clear-cut site on northern Vancouver Island. Fertilizer was applied in April 1991 at 200 kg N·ha^{-1} as $(NH_4)_2SO_4$ (3.38044% ^{15}N enrichment) to single-tree plots of 1 m radius. Four-year-old western red cedar, western hemlock, and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) were used and the plots were destructively sampled after two growing seasons (October 1992). The distribution of ^{15}N within trees was virtually unaffected by the treatment but displayed differences among species. The majority of the ^{15}N in a tree was found in the current-year needles. Because of the dilution effect, ^{15}N abundances in the above ground tree components were not different between treatments but ^{15}N contents were significantly increased by salal removal. The pattern of and treatment effect on total N distribution were similar to those of ^{15}N. Total recovery by trees of applied ^{15}N was 7.7, 17.8, and 10.3% in the treated plots planted with cedar, hemlock, and spruce, respectively. The corresponding values for the control plots were 4.1, 2.0, and 4.9%. Understory in the control plots immobilized 14.8, 24.6, and 13.5% of the applied N for plots planted with the respective species. Total recoveries in soil and vegetation ranged from 57 to 87%, of which 59 to 82% was recovered in the soil compartments. Results clearly showed that trees competed poorly with the understory vegetation for the applied fertilizer N.

Résumé : Un fertilisant azoté marqué avec ^{15}N a été utilisé afin d'étudier le devenir de N dans des systèmes sol forestier–plante avec (témoin) ou sans compétition (traité) d'une éricacée arbustive à feuilles persistantes, la gaulthérie « shallon » (*Gaultheria shallon* Pursh), sur un site coupé à blanc de cèdre de l'Ouest (*Thuja plicata* Donn ex D. Don) – pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) du Nord de l'île de Vancouver. Le fertilisant a été appliqué en avril 1991 au taux de 200 kg N·ha^{-1} sous forme de $(NH_4)_2SO_4$ (taux d'enrichissement de 3,38044% de ^{15}N) à des parcelles de 1 m de rayon constituées d'un seul arbre. Des tiges de 4 ans de cèdre de l'Ouest, de pruche de l'Ouest et d'épinette de Sitka (*Picea sitchensis* (Bong.) Carrière) ont été utilisées et les parcelles ont été complètement échantillonnées en octobre 1992, après deux saisons de croissance. La distribution de ^{15}N dans les arbres n'a pas été affectée par le traitement mais a présenté des différences entre les espèces. Le ^{15}N présent dans les arbres a surtout été retracé dans les aiguilles de l'année courante. À cause de l'effet de dilution, l'abondance de ^{15}N dans les composantes épigées des arbres n'était pas différente entre les traitements mais le contenu de ^{15}N était significativement augmenté par l'éradication de la gaulthérie. Le patron et l'effet du traitement sur la distribution de N total étaient similaires à ceus de ^{15}N. Le recouvrement total par l'arbre de ^{15}N appliqué atteignait respectivement 7,7, 17,8 et 10,3% dans les parcelles traitées et plantées avec le cèdre, la pruche et l'épinette. Les valeurs correspondantes pour les parcelles témoins étaient de 4,1, 2,0 et 4,9%. La sous-végétation dans les parcelles témoins a immobilisé 14,8, 24,6 et 13,5% de N appliqué pour les parcelles plantées avec les espèces respectives. Le recouvrement total dans le sol et la végétation a varié de 57 à 87%, duquel 59 à 82% se retrouvait dans les compartiments du sol. Les résultats indiquent clairement que les arbres ont piètrement compétitionné avec la végétation du sous-bois pour utiliser le fertilisant azoté qui avait été ajouté.
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Introduction

Nitrogen is often the factor limiting growth of temperate and boreal coniferous forests (Wollum and Davey 1975). Although increased research activities have led to an improved understanding of N dynamics in forest ecosystems, interpretation and evaluation of N status in forest soils are still difficult because mechanisms of N cycling and availability in forest soils remain poorly understood and site specific (Binkley and Hart 1989).

A site-specific problem in the wetter Coastal Western Hemlock biogeoclimatic zone of coastal British Columbia is the growth stagnation and regeneration failure observed on large areas of old-growth western red cedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (CH) clear-cut sites. Initially, the trees (western red cedar and western hemlock) planted on the clear-cut sites grew normally, but as an ericaceous evergreen shrub, salal (*Gaultheria shallon* Pursh), invaded the sites, the young plantation went into growth stagnation. The annual leader growth was reduced and the needles displayed chlorosis, suggestive of N and P deficiencies (Prescott and Weetman 1994).

Nutritional deficiency (mainly N) has been identified as one of the factors leading to young conifer tree growth stagnation on the CH sites (Messier 1993; Prescott et al. 1993*a*). The rapid regrowth of salal (both above- and below-ground) after clear-cutting and slash-burning (Messier and Kimmins 1991) and its vigorous competition for scarce nutrients (Messier 1993) exert further adverse effects on tree growth performance. According to Messier (1991), 30–45% of the available N on CH clear-cut sites could be found in the noncrop vegetation. Fertilization is the most commonly used method to overcome nutrient deficiency problems in forestry. However, N application may also encourage abundant growth of salal and other understory vegetation before crown closure, thus increasing understory competition for nutrients and other resources. If a large proportion of the applied fertilizer N is immobilized by noncrop understory vegetation, then the efficiency of fertilization in releasing growth stagnation is reduced, which could lead to the failure of fertilization programs in reaching the desired silvicultural objectives.

Fertilizer N recovery has been studied using the ^{15}N tracer technique in Sitka spruce (*Picea sitchensis* (Bong.) Carrière) (Hulm and Killham 1990), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) (Melin and Nômmik 1988), slash pine (*Pinus elliottii* Engelm.) (Mead and Pritchett 1975*a*, 1975*b*), lodgepole pine (*Pinus contorta* Dougl. ex. Loud. var. *latifolia* Engelm.) (Preston et al. 1990), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Heilman et al. 1982; Preston et al. 1990), and some other tree species. These studies indicated that recovery of N in trees was generally low (10–25%). However, no reports were found on western hemlock and western red cedar forests.

The research cooperative of the Salal–Cedar–Hemlock Integrated Research Program (SCHIRP, Prescott and Weetman 1994) provided an excellent opportunity to study the effect of understory vegetation competition on tree N fertilizer use efficiency and total and applied N distribution in the soil–vegetation system. The objectives of the present study were (1) to study the distribution of ^{15}N in the plant–soil system; (2) to determine the effect of salal competition on the uptake of fertilizer N by trees; (3) to test whether different tree species have different capacities to compete with understory vegetation for N supply.

Table 1. Selected soil properties of the study site.

Depth (cm)	pH*	Organic C ($g \cdot kg^{-1}$)	Nitrogen		C/N ratio	Bulk density ($Mg \cdot m^{-3}$)
			$g \cdot kg^{-1}$	$kg \cdot ha^{-1}$		
0–10	3.00	464.6	7.30	1291	63.7	0.177
10–20	3.11	376.5	5.31	1167	70.9	0.220
20–30	3.40	291.0	3.79	1301	76.7	0.343
30–40	3.92	114.3	2.01	1167	57.0	0.582
40–50	4.30	62.5	1.32	958	47.5	0.728

*Measured in 1:1 (v/v) 0.01 M $CaCl_2$.

Materials and methods

Study area

This study was carried out on Tree Farm Licence (TFL) 25 near Port McNeill (50°36′N, 127°15′W) in the wetter Coastal Western Hemlock biogeoclimatic zone (Pojar et al. 1987) on northern Vancouver Island. This area receives an annual precipitation of 1700 mm, most of which is received during winter. Mean daily temperatures vary from 3.0°C in January–February to 13.7°C in July–August (Lewis 1982).

The research area is characterized by a gently undulating topography. There is a thick (typically >45 cm) humus layer (with a large proportion of deeply decomposed woody material) overlying a moderately well to somewhat imperfectly drained Ferro-Humic Podzol. Selected soil properties for the various depths sampled are given in Table 1.

The study was conducted on a CH clear-cut site that was burned after clear-cutting and then planted with three tree species. Understory on the site was dominated by salal, with lesser amounts of fireweed (*Epilobium angustifolium*), deer fern (*Blechnum spicant*), blueberry (*Vaccinium* spp.), bunchberry (*Cornus canadensis*), and sometimes a moss layer. 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.

Field experiment

This experiment was established as a completely randomized factorial design, with three species (western red cedar, western hemlock, and Sitka spruce) and two treatments (no understory removal (control) and aboveground understory removal (treated)). Each treatment and species combination was replicated four times.

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 50 cm, which was beyond the rooting depth. A total of 24 microplots were established (3 species ×

2 treatments × 4 replicates). ^{15}N-labeled $(NH_4)_2SO_4$ (3.38044% ^{15}N enrichment) was applied on April 16, 1991, at a rate of 200 kg N·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 topsoil layer (0–10 cm) has a water holding capacity of over 300%, the penetration of added water should not have exceeded 1–2 cm at the time of application. There was some regrowth of salal and other understory species on the treated plots; in particular, salal continued to resprout from its network of rhizomes despite several years of suppression. Removal of understory vegetation was maintained in the treated plots by periodic clipping, and the small amounts of material were placed on the surface of the plot.

Destructive sampling took place in October 1992, two growing seasons after fertilizer application. Half of the 24 microplots were randomly selected and destructively sampled (3 species × 2 treatments × 2 replicates). Half of the plots were left to grow for another few years for a longer term ^{15}N uptake study. For the destructive sampling, first the aboveground understory vegetation was cut at ground level. Next, the litter and standing dead biomass (mostly salal) were collected. Then the aboveground tree was removed from the plot. Two randomly located soil pits (25 by 25 cm) were excavated to a depth of 50 cm in intervals of 10 cm. After the soil pits were finished, the tree roots in the microplots were carefully excavated using hand tools to recover visible roots as much as possible from the entire plot.

Soil samples in each plastic bag (from a 10 cm thick layer of a pit) were weighed in the laboratory. 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 for total N and ^{15}N analysis.

After the biomass samples were brought into the laboratory, the aboveground tree was separated into (1) needles (current year and 1 year old) and (2) branches (current year, 1 year old, and ≥2 years old. There were few ≥2-year-old needles and therefore they were not separated from the ≥2-year-old branches. The belowground tree was separated into stump, small roots (<0.25 cm in diameter), medium roots (0.25–1.0 cm), and large roots (>1.0 cm). The aboveground understory vegetation was separated into salal and nonsalal. The nonsalal component comprised mainly fireweed, deer fern, blueberry, and bunchberry. The belowground understory roots were divided into two layers: 0–20 and 20–50 cm. Roots picked from the soil samples were separated into tree roots and understory 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. A further separation of the understory roots into salal and nonsalal was not possible. Plant materials were dried at 65°C. All the plant components were weighed (dry weight), coarsely ground, and then subsampled for fine grinding.

Laboratory analyses

After the plant samples were ground to pass a No. 40 sieve (0.425 mm), they were analyzed for total N by the semimicro-Kjeldahl method described by Bremner and Mulvaney (1982), except that mercuric oxide was used as the catalyst. The distillates, collected in boric acid – ethanol, were dried at 70°C. The ammonium N was converted to dinitrogen gas using the Rittenberg reaction with alkaline lithium hypobromite, and analyzed for ^{15}N enrichment using a Vacuum Generators Sira 9 mass spectrometer (Preston et al. 1990).

Field-moist soil samples were air dried and ground to pass a No. 18 sieve (2 mm diameter), and were then oven-dried at 65°C and ground to 50 μm in a Siebteknik mill. Total N was analyzed by the semimicro-Kjeldahl method and ^{15}N enrichment by mass spectrometer, following the methods used for plant sample analysis. The pH for soil samples was measured in 1:1 (v/v) 0.01 M $CaCl_2$ solutions. Total C concentrations of soil samples were determined using a LECO CR-12 C analyzer (model 781-600, Leco Corporation 1981).

Statistical analyses

Homogeneity of variances and normality of distributions of data sets were checked before any statistical analysis. Data that were not homogeneous (recovery of ^{15}N in understory roots) were sine transformed prior to analysis. However, means were reported on untransformed data. Analyses of variance (ANOVA) were performed on all experimental variables using the general linear models (GLM) procedure of the SAS package (SAS Institute Inc. 1985). Group means of independent variables were compared between treatments for each species by Scheffé's multiple range test, for each component considered.

Results

^{15}N distribution within trees

The distribution of ^{15}N in tree components is shown in Table 2. Within the trees, the largest proportions of ^{15}N recovered were found in the current-year needles of the three species, irrespective of treatment. The second largest proportion of the ^{15}N recovery was in the ≥2-year-old branches, followed by 1-year-old needles, except for ^{15}N in the treated western hemlock plots. From 49 to 74% of the ^{15}N recovered in the trees was found in the needles. Between 84 and 94% of the ^{15}N in the trees was found in the aboveground tree components, while 6 to 16% was in belowground tree components, including the stump.

Based on ANOVA results (data not shown), no significant treatment × species interactions were found on ^{15}N distribution for all of the components studied. No significant difference was induced by salal-removal treatment for ^{15}N distribution in all of the tree components studied (Table 2). Tree species significantly affected the distribution of ^{15}N in current-year needles ($F = 77.99$, $p = 0.0001$), 1-year-old needles ($F = 30.39$, $p = 0.0007$), ≥2-year-old branches ($F = 14.30$, $p = 0.0052$), stumps ($F = 5.28$, $p = 0.0476$), and coarse ($F = 5.53$, $p = 0.043$) and medium ($F = 24.86$, $p = 0.0012$) roots. The distribution of ^{15}N in various components was quite similar for hemlock and spruce under the same treatment (except for the 1-year-old needles), while the data for western red cedar were quite different from those of hemlock and spruce, for the tree components with significant treatment × species interaction.

^{15}N distribution within understory

When understory ^{15}N contents were expressed as a percentage of total understory ^{15}N, there were dramatic differences in the distribution of ^{15}N in understory components between treatments with and without understory removal (Table 3). ANOVA results (data not shown) showed that there were no treatment × species interactions for all of the components studied, except for the aboveground nonsalal component. Significantly larger proportions of ^{15}N were in the aboveground salal biomass in the control plots than in the treated plots. This was expected, since in the control plots there was abundant understory growth,

Table 2. Within-tree distribution (whole tree as 100%) of applied ^{15}N by tree component after two growing seasons.

	Cedar		Hemlock		Spruce	
Component	Control	Treated	Control	Treated	Control	Treated
Needles						
Current-year	66.55	64.27*Ans*	32.10	30.70*B*	37.29	35.19*B*
	(0.80)	(1.03)	(4.48)	(0.41)	(5.44)	(0.78)
1-year-old	7.89	8.74*Ans*	17.18	22.35*B*	13.62	15.11*C*
	(0.04)	(0.61)	(1.19)	(2.42)	(0.72)	(2.19)
Branches						
Current-year	5.37	5.58*Ans*	7.09	5.47*A*	6.56	6.50*A*
	(0.32)	(0.58)	(0.77)	(1.49)	(2.78)	(0.38)
1-year-old	4.80	5.31*Ans*	6.99	7.34*A*	5.99	5.03*A*
	(0.16)	(1.24)	(0.88)	(2.02)	(0.02)	(0.40)
≥2-year-old	8.08	10.07*Ans*	25.02	21.34*B*	23.33	22.56*B*
	(0.42)	(0.64)	(4.58)	(0.76)	(5.10)	(2.57)
Stump	1.98	1.54*Ans*	2.49	1.78*AB*	3.72	3.16*B*
	(0.16)	(0.07)	(0.37)	(0.33)	(1.20)	(0.26)
Roots						
>1 cm	1.14	1.57*Ans*	2.71	2.35*AB*	2.02	4.09*B*
	(0.12)	(0.17)	(0.33)	(0.19)	(1.11)	(0.49)
0.25–1 cm	1.74	1.05*Ans*	4.02	3.74*B*	3.98	3.51*B*
	(0.33)	(0.01)	(0.62)	(0.56)	(0.23)	(0.30)
<0.25 cm	2.49	1.89*Ans*	2.43	4.96*A*	3.50	4.87*A*
	(0.04)	(0.96)	(0.96)	(0.15)	(2.10)	(0.90)

Note: Values in parentheses are SEs of the means. For Tables 2, 3, and 5, values followed by the same letters indicate no species effect (at $p = 0.05$ level) on the treatment or the treatment means [(control + treated)/2]. When there was no significant treatment × species interaction, A–C were used, and when there was a significant treatment × species interaction, D, d, E, and e were used. ns, no significant treatment effect on the species or the species means ($p > 0.05$). When there were no significant treatment × species interactions, ns (or * in Tables 3 and 5) refers to all three species.

while in the treated plots there was very limited understory (aboveground) regrowth after repeated removal. Treatment × species interaction was significant ($F = 5.87$, $p = 0.0386$) for ^{15}N distribution in the aboveground nonsalal component. ^{15}N distribution in the aboveground nonsalal components was variable, with a larger proportion in the treated plots than in the control plots for cedar ($p < 0.05$), larger proportion in the control plots than in the treated plots for hemlock ($p < 0.05$), and no difference between treatments for spruce. A much greater proportion of the ^{15}N was found in the understory roots in the treated plots than in the control plots. No effect of tree species on ^{15}N distribution in the understory components was found.

^{15}N distribution within the soil–plant system

Figure 1 shows that when the ^{15}N content in the soil–plant system was expressed as a percentage of total ^{15}N recovered, significantly greater proportions of ^{15}N were in the tree components in the treated plots than in the control plots without understory removal ($p < 0.05$); the relationship was reversed for the proportion of ^{15}N in the understory ($p < 0.05$). Greater proportions of ^{15}N were found in the litter and standing dead components in the control plots than in the treated plots ($p < 0.05$), while the reverse was found for ^{15}N distribution in the soil ($p < 0.05$). Neither species effect nor treatment × species interaction were found to be significant for ^{15}N distribution in the soil–plant system (data not shown).

^{15}N contents in aboveground tree components

^{15}N abundance and contents in the aboveground tree components and their ANOVA table are presented in Table 4. Salal-removal treatment apparently reduced (nonsignificantly) ^{15}N abundance in the aboveground tree components, regardless of species (Table 4), with the exception of spruce current-year branches. This obviously was a dilution effect, where the greater ^{15}N uptake could not compensate for the greater biomass accumulation in the treated plots. Species exhibited significant differences in ^{15}N abundance in some of the components (current-year and 1-year-old foliage, and 1-year-old branches), but treatment effects were not significant in any of the components. When ^{15}N was expressed as milligrams per plot, salal removal significantly increased the storage of ^{15}N in all of the aboveground tree components (Table 4). The treatment × species interaction was significant for ^{15}N content in 1-year-old needles and ≥2-year-old branches. For those two components, treatment effects were found to be significant ($p <$

Table 3. Distribution (as % of total ^{15}N in understory) of applied ^{15}N in understory components after two growing seasons, based on untransformed data.

	Cedar		Hemlock		Spruce	
Component	Control	Treated	Control	Treated	Control	Treated
Aboveground salal	57.37 (0.56)	6.74*A** (0.66)	41.65 (16.65)	0.17*A* (0.17)	46.03 (7.67)	12.97*A* (10.66)
Aboveground nonsalal	1.19*D* (0.86)	6.97*d*ns (3.45)	7.67*D* (0.69)	0.64*d** (0.64)	3.61*D* (2.39)	6.04*d*ns (1.83)
Root 0–20 cm	39.42 (2.32)	73.80*A** (0.64)	44.65 (14.27)	93.56*A* (5.01)	48.20 (3.96)	67.96*A* (1.82)
Root 20–50 cm	2.03 (0.91)	12.49*A*ns (4.75)	6.04 (3.08)	5.64*A* (4.20)	2.17 (1.32)	13.03*A* (10.65)
Total understory	100	100	100	100	100	100

Note: Values in parentheses are SEs of means. See Table 2 for an explanation of the statistical analyses. *Significant treatment effect on species means ($p < 0.05$). In this table and in Table 5, lowercase letters were used for the "Treated" treatment comparisons and uppercase letters were used for the "Control" comparisons when there was a significant treatment × species interaction.

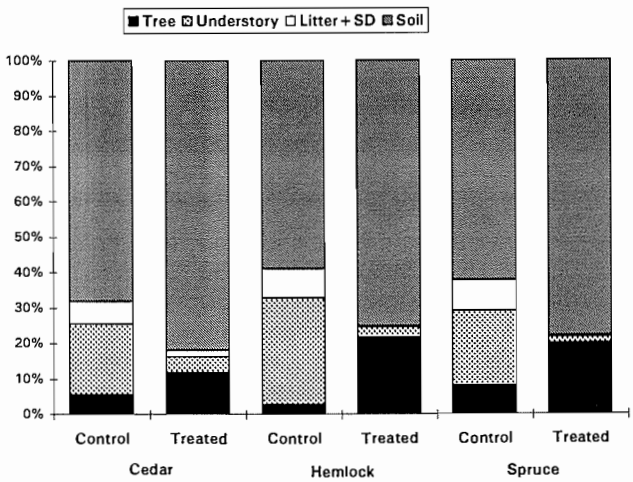
0.05) only for western hemlock. Differences between species in ^{15}N storage (mg/plot) were found for 1-year-old needles and ≥2-year-old branches.

Recovery of ^{15}N

From 7.7 to 17.8% of the applied fertilizer was recovered in the trees in the treated plots, compared with only 2 to 5% in the control plots (Table 4). Treatment × species interaction was significant for ^{15}N recoveries in aboveground trees, tree roots, and total trees. Treatment effects on ^{15}N recoveries in above- and below-ground tree and total tree components were significant for hemlock ($p < 0.05$). Differences in ^{15}N recovery among species were observed only between cedar and hemlock for the understory removal treatment. Treatment × species interaction was also significant for ^{15}N recovery in aboveground understory ($F = 11.68$, $p = 0.0085$). Understory removal reduced ^{15}N recovery in the above-ground understory compartment for every species studied. However, differences between species only existed between hemlock and spruce for the control treatment. There were no interactions between treatment and species for ^{15}N recovery in understory root and in the litter + standing dead compartments. Understory removal reduced the amount of ^{15}N recovered in those compartments ($p < 0.05$). The significantly higher amount of ^{15}N recovered in the above- and below-ground understory and litter + standing dead in the control compared with the treated, regardless of the tree species, was due to the manipulation of the understory in the experiment.

The greatest total recovery of applied ^{15}N in the soil–plant system was in the treated hemlock plots (87.3%), while the least was in the treated spruce plots (56.8%, Table 5). After two growing seasons, most of the recovered ^{15}N was in the soil component. Total recovery of ^{15}N in the soil was as high as 66.8% of added N in the treated hemlock plots. There was no significant effect from treatment, species, and treatment × species interaction for total recovery and recovery in the soil.

Fig. 1. Distribution of ^{15}N in the soil–plant systems expressed as a percentage of total applied ^{15}N recoveries. SD, standing dead. Litter is total plant litter (tree + understory).



Discussion

N distribution within biomass

With two exceptions, understory competition did not affect the proportionate distribution of ^{15}N within the trees. Values for ^{15}N abundance in above- (Table 4) and below-ground tree components (data not given) were also not significantly affected by the salal removal. The detailed analysis of biomass changes at this site (Chang et al. 1996) showed that understory removal resulted in biomass increases in all tree components, without any effect on their distribution within trees. Tree height and basal diameter also responded positively to understory removal. Therefore, we conclude that the pattern of ^{15}N distribution was determined by the distribution pattern of biomass in various tree components, or the resource depletion model (Newton and Jolliffe 1993).

Table 4. Effect of understory removal and tree species on ^{15}N abundance and contents in aboveground tree component and analysis of variance.

	N as	Current-year foliage	Current-year branch	1-year-old foliage	1-year-old branch	≥2-year-old branch
Cedar						
Control	%	1.36	1.45	1.40	1.29	1.28
	mg/plot	70.33	5.57	8.28	5.19	8.84
Treated	%	1.31	1.36	1.28	1.24	1.20
	mg/plot	130.29	10.91	18.23	11.53	21.59
Hemlock						
Control	%	1.61	1.63	1.71	1.65	1.51
	mg/plot	16.29	3.53	7.97	3.49	11.47
Treated	%	1.43	1.46	1.48	1.47	1.33
	mg/plot	139.67	25.07	99.64	33.59	99.23
Spruce						
Control	%	1.91	1.49	1.90	1.87	1.66
	mg/plot	45.52	9.22	15.43	6.97	26.53
Treated	%	1.61	1.59	1.76	1.63	1.50
	mg/plot	88.26	16.22	38.80	12.43	57.05
			ANOVA (*F* value)			
Species (2)	%	6.72*	0.96	5.76*	7.25*	1.29
	mg/plot	1.99	0.96	16.16**	2.25	26.67***
Treatment (1)	%	3.47	0.34	1.92	2.25	0.63
	mg/plot	29.20**	9.23*	49.50***	10.78**	91.55***
Species ×	%	0.58	0.80	0.08	0.30	0.03
treatment (2)	mg/plot	3.09	1.92	18.26**	3.60	24.59**

Note: Degrees of freedom for treatment, species, and species × treatment are given in parentheses.
*$p < 0.05$
**$p < 0.01$
***$p < 0.001$.

This model states that competition acts to reduce the relative growth rates of all individuals by the same proportion if the competition is mainly for belowground resources (nutrients). Thus, not only N distribution within trees, but also plant N content and ^{15}N recovery, were largely determined by biomass changes following understory removal treatment.

The distribution of ^{15}N (and also total N, data not shown) in the tree components was comparable to that reported by Preston et al. (1990) in studies on 11-year-old lodgepole pine stands and 13-year-old Douglas-fir stands at two forest sites in British Columbia. The distribution of ^{15}N followed that of total N very closely, indicating either a proportionate uptake of applied N and native N by tree components or a rapid turnover and redistribution of ^{15}N within the tree (Mead and Preston 1994). Internal N cycling from old tissues to new growth was suggested by Mead and Pritchett (1975*a*) and Nômmik and Larsson (1989). The finding that most of the ^{15}N in the trees was in the current-year needles is consistent with other reports (Melin et al. 1983; Nambiar and Bowen 1986; Melin and Nômmik 1988).

After several years of understory removal, one would expect the aboveground understory biomass and hence ^{15}N content to be zero in the treated plots. However, salal is a very persistent plant (Prescott et al. 1993*b*) that resprouts quickly after the aboveground biomass is clipped. Therefore, some understory biomass and N were recovered in the treated plots at the time of the final harvesting. The understory removal treatment greatly altered the distribution of ^{15}N in the understory components. For example, a greater amount of ^{15}N accumulated in the understory, standing dead biomass, and litter layer in the control than in the treated plots because of greater standing dead and litter mass produced in the former than in the latter. As for the trees, a similar distribution of ^{15}N and total N was found in the understory, as the distribution of ^{15}N and total N in understory was also largely determined by biomass distribution.

Competition of salal for N

Preston et al. (1990) studied the fate of ^{15}N-labeled fertilizer applied on snow at two forest sites and found that understory vegetation reduced uptake of fertilizer N by crop trees. In a lodgepole pine stand, tree uptake ranged from 1.9 to 10.1%, while understory uptake ranged from 2.4 to 3.4%. However, in a Douglas-fir stand, understory took up more fertilizer N (10.8%) than the tree (5.5%). In the present study, total ^{15}N recovery by trees was 4.1, 2.0, and 4.9% in control plots planted with western red cedar, western hemlock, and Sitka spruce, respectively. The corresponding values for the treated plots were 7.7, 17.8, and 10.3%. These generally low values reveal that fertilization

Table 5. Recovery of fertilizer N in the soil–plant system after two growing seasons.

	Cedar		Hemlock		Spruce	
Component	Control	Treated	Control	Treated	Control	Treated
Aboveground tree	3.78*D* (0.50)	7.2*d*ns (1.31)	1.72*D* (0.62)	15.54*d** (1.28)	4.27*D* (1.68)	8.60*d*ns (1.99)
Tree root	0.30*D* (0.05)	0.45*d*ns (0.01)	0.23*D* (0.08)	2.29*e** (0.21)	0.60*D* (0.12)	1.65*d*ens (0.60)
Total tree	4.08*D* (0.55)	7.65*d*ns (1.32)	1.95*D* (0.70)	17.83*d** (1.49)	4.86*D* (1.80)	10.25*d*ns (2.59)
Aboveground understory	8.66*DE* (0.27)	0.41*d** (0.08)	10.82*D* (0.56)	0.25*d** (0.25)	6.72*E* (0.88)	0.55*d** (0.16)
Understory root	6.15 (0.55)	2.65*A** (0.42)	13.75 (8.06)	2.34*A* (0.54)	6.78 (0.55)	0.84*A* (0.18)
Litter + standing dead	4.79 (0.33)	1.07*A** (0.86)	6.45 (0.15)	0.08*A* (0.05)	5.86 (2.32)	0.25*A* (0.13)
Soil	50.68 (0.85)	56.20*A*ns (10.72)	46.85 (0.33)	66.81*A* (18.91)	40.69 (7.07)	44.88*A* (13.11)
Total	74.35 (0.79)	67.97*A*ns (8.89)	79.81 (6.98)	87.30*A* (16.60)	64.90 (7.91)	56.76*A* (10.67)

Note: Values in parentheses are SEs of the means. See Tables 2 and 3 for an explanation of the statistical analyses.

of those stands has low efficiency, which is not unique to this site. ^{15}N recovery in understory was far greater than that in the trees in the control plots. Both litter and standing dead biomass originated from understory biomass. If the ^{15}N recovered in the litter and standing dead biomass is added to that of the understory, it reveals that ^{15}N-labeled fertilizer immobilized by understory vegetation was 4.8, 15.9, and 3.3 times as much as that taken up by trees in the control plots.

The effect of understory competition on the ^{15}N recovery in trees was the focus of two recent publications (Clinton and Mead 1994*a*, 1994*b*). They studied the ^{15}N uptake by trees under simulated grazing, complete removal of pasture, and rank ryegrass (*Lolium perenne* L.) – cocksfoot (*Dactylis glomerata* L.) – clover (*Trifolium repens* L.) pasture and found that (1) removing pasture competition doubled tree ^{15}N; (2) pasture was a major competitor for N because of its greater root biomass and root density; and (3) there were no significant treatment differences in ^{15}N recovery in the 0–20 cm depth of soil. Some of the findings from the present study were similar: (1) removal of salal competition doubled tree ^{15}N uptake by cedar and spruce, and increased ^{15}N uptake by hemlock more than 8 times; (2) salal was a persistent competitor for ^{15}N, i.e., 6 years after understory removal, from 1.4 to 3.1% of the applied ^{15}N was recovered in the understory of treated plots; (3) removal of salal understory increased ^{15}N incorporation into soil (0–50 cm, nonsignificant); (4) total recovery tended to be higher in the plots with understory present, because the understory took up more applied N shortly after application, thus reducing N loss from the system by leaching or other mechanisms; and (5) the accumulation of ^{15}N in the understory biomass, litter, and standing dead material greatly reduced the availability of fertilizer N to crop trees.

There have been no studies to indicate whether N tied up in the salal biomass or litter would be more easily available to trees, through mineralization, than that immobilized in the soil organic matter; however, in the short term, incorporation of N in salal biomass reduces its availability to crop trees. It is unlikely that N immobilized by salal would be turned over very quickly because of the persistent survival of salal even under adverse conditions and because of low rates of salal litter decomposition. For example, 6 years after aboveground salal removal was initiated, recovery of understory root biomass was from 523 to 800 g/plot (Chang et al. 1996).

Uptake of ^{15}N by understory vegetation (excluding litter and standing dead biomass) was 14.8, 24.6, and 13.5% of the total applied, for control plots planted with cedar, hemlock, and spruce, respectively. Those data were in the upper range of ^{15}N usually found in understory (Preston et al. 1990). In the plots where salal was repeatedly removed, from 80 to 99% of the ^{15}N recovered in understory was in the understory roots, because of the strong regrowth capacity of the salal rhizomes. Results clearly showed that trees competed poorly with the understory vegetation for the fertilizer N applied. The large amount of ^{15}N stored in the soil (mostly in organic form) that was immobilized largely through microbial processes demonstrated that trees also competed poorly with the soil microbial biomass for the applied N.

The retention and recovery of ^{15}N in the soil profile are affected by a combination of physical, chemical, and biological factors (Overrein 1972). Among the different treatment by species combinations, the physical and chemical factors being the same because the experiment in this study was conducted on the same site, biological factors were mainly what affected the final ^{15}N recovery in the soil. The presence of abundant understory vegetation in

the control plots perhaps resulted in more ^{15}N being taken up initially by plants in the plot and might also have encouraged remineralization (because plants can increase substrate availability to soil microorganisms, Fisher and Gosz 1986) and uptake by plants of the ^{15}N immobilized by the soil organic matter, thus reducing the amount of ^{15}N recovered in the soil.

N budget

There have been few studies on forest ecosystems that provided complete balance sheets for applied fertilizer N, whether using conventional methods or the ^{15}N tracer technique (Melin and Nômmik 1988). The total recovery in the soil–plant system in this study ranged from 57 to 87% of the total applied. The part that was not accounted for was presumably lost from the system. The most probable possibility for N loss might be leaching loss. Other mechanisms for N loss include transport of N out of the plots by roots extending beyond the plot boundaries, litter falling outside of the plots, or litter being carried by wind (Heilman et al. 1982). The heterogeneous nature of the soil causes sampling errors that may lead to under- or over-estimation of ^{15}N recovery in the soil–plant systems. Nitrification, and thus denitrification and volatilization loss, were probably minimal, as this soil has very low pH (Björkman et al. 1967; Melin et al. 1983).

Conclusions

Western hemlock and Sitka spruce seem to be more responsive to removal of competing vegetation than western red cedar in terms of applied ^{15}N uptake by above- and belowground tree components. Based on the limited data obtained in this study, we propose that if N fertilization after understory control is possible, western hemlock and Sitka spruce stands should have the priority. However, if fertilization is to be carried out without pretreatment for controlling understory vegetation, western red cedar stands should have the priority. In the control plots, understory took up more ^{15}N than trees, indicating that salal was a persistent competitor for ^{15}N and that N availability was reduced by immobilization by understory biomass. Fertilization on those CH clear-cut sites brings a practical problem: on the one hand, young plantations around 8–10 years old experience nutrient deficiencies and growth stagnation and are in need of external nutrient additions; on the other hand, fertilization on those young plantations has a low efficiency. Despite low fertilizer recovery efficiencies, fertilization of those sites has been shown to be effective in improving plantation growth.

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References

Binkley, D., and Hart, S.C. 1989. The components of nitrogen availability assessments in forest soils. Adv. Soil Sci. **10**: 57–112.

Björkman, E., Lundeberg, G., and Nômmik, H. 1967. Distribution and balance of ^{15}N labeled fertilizer nitrogen applied to young pine trees (*Pinus sylvestris* L.). Stud. For. Suec. **48**: 1–15.

Bremner, J.M., and Mulvaney, C.S. 1982. Nitrogen–total. *In* Methods of soil analysis. Part 2. Chemical and microbiological properties. *Edited by* A.L. Page. Agronomy, **9**(2): 595–624.

Chang, S.X., Weetman, G.F., and Preston, C.M. 1996. Understory competition effect on tree growth and biomass allocation on a coastal old-growth forest cutover site in British Columbia. For. Ecol. Manage. In press.

Clinton, P.W., and Mead, D.J. 1994*a*. Competition for nitrogen between *Pinus radiata* and pasture. I. Recovery of ^{15}N after one growing season. Can. J. For. Res. **24**: 882–888.

Clinton, P.W., and Mead, D.J. 1994*b*. Competition for nitrogen between *Pinus radiata* and pasture. II. Trends in plant and soil processes. Can. J. For. Res. **24**: 889–896.

Fisher, F.M., and Gosz, J.R. 1986. Effects of plants on net mineralization of nitrogen in forest soil microcosms. Biol. Fertil. Soils, **2**: 43–50.

Heilman, P.E., Dao, T.H., Cheng, H.H., Webster, S.R., and Christensen, L. 1982. Comparison of fall and spring applications of ^{15}N-labeled urea to Douglas-fir: II. Fertilizer nitrogen recovery in trees and soil after 2 years. Soil Sci. Soc. Am. J. **46**: 1300–1304.

Hulm, S.C., and Killham, K. 1990. Response over two growing seasons of a Sitka spruce stand to ^{15}N-urea fertilizer. Plant Soil, **124**: 65–72.

Lewis, T. 1982. Ecosystems of the Port McNeill Block 4 of Tree Farm Licence 25. Internal Report, Western Forest Products Ltd., Vancouver, B.C.

Mead, D.J., and Preston, C.M. 1994. Distribution and retranslocation of ^{15}N in lodgepole pine over eight growing seasons. Tree Physiol. **14**: 389–402.

Mead, D.J., and Pritchett, W.L. 1975*a*. Fertilizer movement in a Slash pine ecosystem. I. Uptake of N and P and N movement in the soil. Plant Soil, **43**: 451–465.

Mead, D.J., and Pritchett, W.L. 1975*b*. Fertilizer movement in a slash pine ecosystem. II. N distribution after two growing seasons. Plant Soil, **43**: 467–478.

Melin, J., and Nômmik, H. 1988. Fertilizer nitrogen distribution in a *Pinus sylvestris*/*Picea abies* ecosystem, central Sweden. Scand. J. For. Res. **3**: 3–15.

Melin, J., Nômmik, H., Lohm, U., and Flower-Ellis, J. 1983. Fertilizer nitrogen budget in a Scots pine ecosystem attained by using root-isolated plots and ^{15}N tracer technique. Plant Soil, **74**: 249–263.

Messier, C. 1991. Factors limiting early conifer growth in salal-dominated cutovers in northern Vancouver Island, British Columbia. Ph.D. thesis, University of British Columbia, Faculty of Forestry, Vancouver.

Messier, C. 1993. Factors limiting early growth of western red cedar, western hemlock and Sitka spruce seedlings on ericaceous-dominated clearcut sites in coastal British Columbia. For. Ecol. Manage. **60**: 181–206.

Messier, C., and Kimmins, J.P. 1991. Above- and below-ground vegetation recovery in recently clearcut and burned sites dominated by *Gaultheria shallon* in coastal British Columbia. For. Ecol. Manage. **46**: 275–294.

Nambiar, E.K.S., and Bowen, G.D. 1986. Uptake, distribution and retranslocation of nitrogen by *Pinus radiata* from ^{15}N-labeled fertilizer applied to podzolized sandy soil. For. Ecol. Manage. **15**: 269–284.

Newton, P.F., and Jolliffe, P.A. 1993. Above-ground dry matter partitioning, size variation, and competitive processes within second-growth black spruce stands. Can. J. For. Res. **23**: 1917–1929.

Nômmik, H., and Larsson, K. 1989. Assessment of fertilizer nitrogen accumulation in *Pinus sylvestris* trees and retention in soil by ^{15}N recovery technique. Scand. J. For. Res. **4**: 427–442.

Overrein, L.N. 1972. Isotope studies on nitrogen in forest soil. II. Distribution and recovery of ^{15}N-labeled fertilizer nitrogen in a 40-month lysimeter investigation. Norwegian Forest Research Institute, As, Norway. Medd. Nor. Skogforsoksves. **122**: 308–324.

Pojar, J., Klinka, K., and Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manage. **22**: 119–154.

Prescott, C.E., and Weetman, G.F. 1994. Salal cedar hemlock integrated research program: a synthesis. Faculty of Forestry, University of British Columbia, Vancouver.

Prescott, C.E., McDonald, M.A., and Weetman, G.F. 1993*a*. Availability of N and P in the forest floor of adjacent stands of western red cedar – western hemlock and western hemlock – amabilis fir on northern Vancouver Island. Can. J. For. Res. **23**: 605–610.

Prescott, C.E., Coward, L.P., Weetman, G.F., and Gessel, S.P. 1993*b*. Effects of repeated nitrogen fertilization on the ericaceous shrub, salal (*Gaultheria shallon*), in two coastal Douglas-fir forests. For. Ecol. Manage. **61**: 45–60.

Preston, C.M., Marshall, V.G., McCullough, K., and Mead, D.J. 1990. Fate of ^{15}N-labeled fertilizer applied to snow at two forest sites in British Columbia. Can. J. For. Res. **20**: 1583–1592.

SAS Institute Inc. 1985. SAS procedures guide for personal computers, version 6 edition. SAS Institute Inc. Cary, N.C.

Wollum, A.G., and Davey, C.B. 1975. Nitrogen accumulation, transformation and transport in forest soils. For. Soils For. Manage. Proc. North Am. For. Soils Conf. 4th 1973. pp. 67–106.