

# Factors contributing to the superior growth and N nutrition of 11-year-old lodgepole pine compared with Sitka spruce on a N-poor cedar–hemlock cutover<sup>1</sup>

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**Abstract:** We tested several hypotheses to explain the superior growth and nitrogen (N) status of lodgepole pine (*Pinus contorta* Dougl. ex Laws. var. *contorta*) compared with Sitka spruce (*Picea sitchensis* (Bong.) Carrière) on a N-poor site by comparing N distribution, N retranslocation, rooting distribution, and mycorrhizal fungi in plots of 11-year-old trees on a cedar–hemlock cutover. Aboveground N content was nine times greater in pine than in spruce of the same age, and thus, we conclude that pine acquired more N during the 11 years than spruce. Greater N acquisition by pine was not related to rooting depth, as both species rooted primarily in the residual forest floor. There were differences in mycorrhizal fungal associates: a high proportion of pine roots were infected with *Suillus*-like fungi. Pine produced more aboveground biomass per unit N (388 compared with 292 g·g<sup>-1</sup> in spruce) and distributed more N to young foliage. Nitrogen retranslocation efficiency (based on foliar N contents in July and October) was higher in pine (50–52%) than in spruce (24–36%). These characteristics all appear to contribute to pine's abilities to both acquire more N and use it more efficiently and, thus, outperform spruce on this N-poor site.

**Résumé :** Nous avons testé plusieurs hypothèses pour expliquer pourquoi le pin lodgepole (*Pinus contorta* Dougl. ex Laws. var. *contorta*) a une meilleure croissance et un meilleur bilan de l'azote (N) que l'épinette de Sitka (*Picea sitchensis* (Bong.) Carrière) sur un site pauvre en N. Des parcelles ont été établies dans un peuplement de cèdre et de pruche coupé à blanc où les arbres étaient âgés de 11 ans afin de comparer la distribution de N, la translocation de N, la distribution des racines et les champignons mycorrhiziens. Le contenu en azote épigé était neuf fois plus élevé chez le pin que chez l'épinette du même âge. Par conséquent, nous concluons que le pin a emmagasiné plus de N que l'épinette au cours des onze années de croissance. La plus forte accumulation de N par le pin n'était pas liée à la profondeur de l'enracinement car le système racinaire des deux espèces se développait principalement dans la couverture morte résiduelle. Les champignons mycorrhiziens associés aux deux espèces étaient différents. Une forte proportion des racines de pin étaient infectées par des champignons apparentés à *Suillus*. Le pin produisait plus de biomasse épigée par unité de N (388 comparativement à 292 g·g<sup>-1</sup> pour l'épinette) et distribuait davantage de N vers le jeune feuillage. L'efficacité de la translocation de N, basée sur le contenu en N en juillet et octobre, était plus élevée chez le pin (50–52%) que chez l'épinette (24–36%). Ces caractéristiques semblent toutes contribuer à l'acquisition de plus de N et à son utilisation plus efficace par le pin qui décline l'épinette sur ce site pauvre.

[Traduit par la Rédaction]

## Introduction

On cutover cedar–hemlock sites on northern Vancouver Island, growth of regenerating conifers (Sitka spruce, *Picea sitchensis* (Bong.) Carrière; western redcedar, *Thuja plicata* Donn ex D. Don; and western hemlock, *Tsuga heterophylla*

(Raf.) Sarg.) is poor, with trees exhibiting symptoms of N deficiency including chlorotic foliage and near cessation of growth. These sites have low nitrogen (N) and phosphorus (P) availability and low N mineralization rates; large accumulations of humus and coarse woody debris; and are dominated by an ericaceous shrub, salal (*Gaultheria shallon* Pursh) (Prescott et al. 1993). Lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *contorta*) is a minor component of the old-growth forests in this area, particularly on the wetter sites, and occurs occasionally on the cutovers. In contrast to the very chlorotic foliage of the other conifers, pine foliage is always dark green. This observation led us to speculate that pine may be better able to access and utilize N on these very N-poor sites. A nurse trial with mixtures of Sitka spruce and lodgepole pine established on a cedar–hemlock cutover in 1988 provided an opportunity to compare the growth and N content of the two species on a cedar–hemlock site. We also explored the mechanisms by

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which pine achieves superior growth and N status, such as retranslocation and mycorrhizal associates.

Plant species from infertile soils typically have high nutrient-use efficiency (NUE) and, therefore, produce more biomass per unit of nutrient acquired (Chapin 1980; Aerts 1995). Plants also conserve nutrients and reduce their dependence on the soil resources through retranslocation of nutrients at time of senescence. Until recently, nutrient retranslocation was believed to be an adaptation for sites with low nutrient supply (Bowen 1980) and, thus, was expected to be more intense under low nutrient conditions. However, other studies have indicated that efficiency of N withdrawal and retranslocation are unaffected by soil fertility (Chapin and Moilanen 1991; Fahey and Birk 1991) but are controlled by internal factors, primarily growth rate (Nambiar and Fife 1987). Greater root:shoot ratios have been reported on sites with low availability of nutrients, especially N (Chapin 1980; Keyes and Grier 1981). The mycorrhizal fungi associated with a tree species influence its nutrition, as mycorrhizal fungi differ in their ability to capture, store, and transfer N to the host (Abuzinadah et al. 1986). Infection with specific ectomycorrhizal fungi allows some species to obtain N from organic sources (Finlay et al. 1992; Kielland 1994), and this may be particularly important on N-poor sites (Northup et al. 1995).

In this study, we first confirmed that lodgepole pine had more N in aboveground biomass than Sitka spruce by measuring aboveground biomass and N content of 11-year-old trees on a cedar–hemlock cutover. We then explored the mechanisms by which lodgepole pine might acquire more N by examining rooting depth and mycorrhizal fungal associates. Finally, we examined whether lodgepole pine used N more efficiently than Sitka spruce in biomass production by measuring NUE, aboveground distribution, and retranslocation of N from senescing foliage.

## Materials and methods

### Study area

The trial is located in the submontane variant of the Coastal Western Hemlock very wet maritime (CWHvm) biogeoclimatic subzone (Pojar et al. 1987) on northern Vancouver Island, British Columbia, Canada (50°59'N, 127°24'W). The area has gently undulating topography, which rarely exceeds 300 m in elevation. The soils are well-drained to poorly drained Ferro-Humic Podzols on unconsolidated fluvio-glacial sediments. Annual precipitation is 1700 mm, with 65% of the precipitation occurring between October and February. Mean daily temperatures range from 3.0°C in January to 13.7°C in July (Prescott et al. 1993).

Old-growth cedar–hemlock forests have a dense understorey of salal, *Vaccinium parvifolium* Howell, *Vaccinium alaskaense* Smith, ferns (*Blechnum spicant* (L.)), and mosses (*Hylocomium splendens* (Hedw.) B.S.C. and *Rhytidiadelphus loreus* (Hedw.) Warnst.) (Messier 1993). They have a thick (usually about 45 cm) compacted humus layer, containing abundant decaying wood (Keenan et al. 1993). Following clear-cutting and slash burning, cedar–hemlock sites are quickly reinvaded by salal (Messier and Kimmis 1991). Natural regeneration of conifers following disturbance is slow and sparse and consists primarily of western redcedar and western hemlock (Messier 1993).

A nursing mixture trial was established in March 1988 after clear-cutting (1984–1985) and slash burning (1987) an old-growth cedar–hemlock forest. Three species combinations were compared:

pure Sitka spruce, Sitka spruce mixed with lodgepole pine, and Sitka spruce mixed with western white pine (*Pinus monticola* Dougl. ex D. Don). There were three plots of each species combination at each of three densities: 2-m spacing (4337 trees/ha), 2.6-m spacing (2566 trees/ha), and 3-m spacing (1927 trees/ha). There was a total of 27 plots, and all 9 plots of a given density were within a single block. One-year-old containerized planting stock of each species was used. The pine seedlings were planted between each spruce in an intimate mixture in a 7 × 7 grid, resulting in 85 trees per plot. One additional plot of each species (Sitka spruce, lodgepole pine, and western white pine) was planted at the same time, adjacent to the nursing mixture trial. We used the pure spruce and lodgepole pine plots for estimating biomass, N content, and mycorrhizal fungal communities of the two species. The entire experiment covered an area of about 1 ha, and there were no buffers between the plots. The ground vegetation was dominated by salal, *Cornus canadensis* L., *Pteridium aquilinum* (L.) Kuhn, and *Blechnum spicant*. Soil moisture ratings based on the composition of the ground vegetation (Klinka et al. 1989) ranged from moist (17 plots) to wet (7 plots) to very wet (3 plots).

We used the nine plots (3 densities × 3 species) of mixed Sitka spruce and lodgepole pine from the nursing mixture trial for analysis of growth of the two species. The total height of all trees in the nine mixed plots were measured in December 1997 (10 growing seasons after planting).

### N content

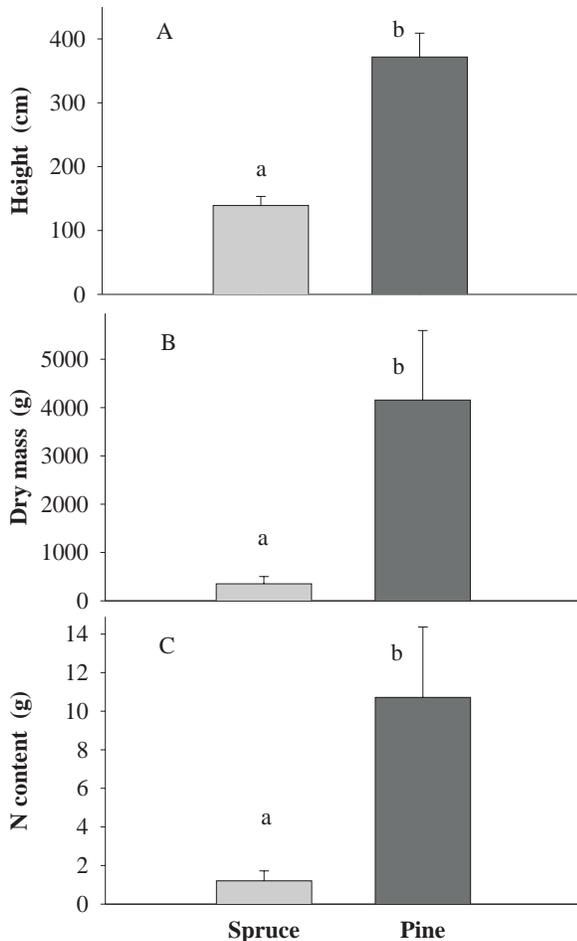
Ten 11-year-old trees from each of the pure plots of lodgepole pine and Sitka spruce were destructively harvested in mid-July 1998. The 10 trees of each species were selected to represent their frequency distribution in each of five height classes of lodgepole pine (120–620 cm) and six height classes of Sitka spruce (40–290 cm) in the mixed plots. Height, diameter at breast height (DBH), and root collar diameter (RCD) measurements of all sample trees were recorded before felling. Aboveground biomass was sampled in mid-July when current foliage elongation should be complete and prior to peak litter fall.

Trees were cut at the soil surface, and aboveground portions were transported whole to the laboratory at the University of British Columbia where they were separated into three different aboveground components: stem, branches, and foliage. The foliage was further separated into age-classes. All parts were oven-dried at 70°C to a constant mass, and the dry mass of each biomass component was determined. Three representative samples of the branch and stem components and one sample of each needle age-class were ground separately in a Wiley mill to <2 mm. The N concentration of each sample was determined using Caro's acid digest (wet oxidation with sulphuric acid and hydrogen peroxide digest) (Lavkulich 1981), followed by colorimetric analysis of N on an AlpKem autoanalyzer. Total N content of each component was calculated by multiplying the dry mass of each component by the N concentration. All plant parts were summed to estimate the total aboveground dry mass and N content of each tree.

Regression equations were generated relating the dry masses and N contents of the sample trees from the pure plots to independent variables including height, diameter, basal area, and volume. Volume was estimated using the volume of a cylinder equation ( $V = \pi r^2 h$ ). Backward-elimination procedures were used to determine the best model (Dowdy and Wearden 1991). Volume was most closely related ( $r^2 > 0.82$ ) to the dependent variables (total biomass and total N). Student's *t* test was used to test the differences between regression lines of the two species (Zar 1984, pp. 292–299). These equations were then used to estimate the average aboveground biomass and N content of lodgepole pine and Sitka spruce trees in each mixed plot in the nursing mixture trial.

Total height and estimated aboveground biomass and N contents of pine and spruce in the mixed plots were compared using two-

**Fig. 1.** Mean height (A), aboveground dry mass (B), and aboveground N content (C) of 11-year-old lodgepole pine and Sitka spruce trees in the nursing mixture trial on a cedar–hemlock cutover ( $n = 6$ ). Error bars are 1 SD. Different letters indicate significant ( $P < 0.001$ ) differences between the two species.



way analysis of variance ( $n = 3$ ), testing effects of species, density, and interactions. Tukey's honestly significant test was used to test the difference between pairs of means. Variation in N concentrations among the different age-classes of foliage was analyzed using the Kruskal–Wallis test, because the age-classes were not independent, being from a continuous population. Unless otherwise stated, significant differences are at  $P < 0.05$ . All statistical analyses were performed using SAS software (version 6.2, SAS Institute Inc. Cary, N.C.).

### Rooting distribution

The distribution of the main rooting zone of pine and spruce was estimated in three holes dug in the extra spruce plot and the extra pine plot, and in each of the nine plots of pure spruce and nine plots of mixed spruce and lodgepole pine.

### Mycorrhizal fungal associates

A field assessment of the mycorrhizal fungal community associated with the roots of the pine and spruce trees was conducted in mid-July 1999 (when the trees were 12 years old). Thirty cores of forest floor ( $7 \times 15$  cm) were sampled from the centre of each of the pure pine and spruce plots. The cores were taken approximately 50 cm from the base of 15 randomly selected trees in each plot (two cores per tree). The 30 cores per plot were randomly

bulked into 10 samples, put into plastic bags, and kept cold while being transported back to the laboratory. Samples were kept moist and cold in a refrigerator until analysed in September 1999.

At the time of assessment, the forest floor cores were soaked for a few hours to loosen the roots, which were then gently washed in tap water. Root systems were cut into 2-cm sections and randomly selected until 200 active mycorrhizal and nonmycorrhizal root tips were counted. Root tips were classified as active if they were turgid with a pale apex, except for certain mycorrhizae, such as *Cenococcum* mycorrhizae, which were turgid and black in colour. Mycorrhizal roots were observed under a dissecting microscope at  $40\times$  magnification and under a compound microscope at  $400\times$  (and sometimes  $1000\times$  oil immersion), either as whole mounts (entire root tip) or a mantle peel (only the fungus). Mycorrhizal roots were classified according to the detailed procedure of Goodman et al. (1996). Characteristics including colour, branching, and texture of the ectomycorrhiza (described under  $40\times$  magnification); features of the extramatrical hyphae; mantle pattern; presence of cystidia and mycelial strands; and reaction to specific chemicals (examined under  $400$  or  $1000\times$  magnification) were used to separate the active mycorrhizae into different morphological categories. These were then compared with published descriptions (Ingleby et al. 1990; Goodman et al. 1996) for identification. Mycorrhizae formed by different fungal genera can usually be separated by morphological methods (Hagerman et al. 1999).

### Nitrogen-use efficiency

Biomass and N content data collected from the 20 pine and spruce trees sampled in the pure plots were used to calculate NUE, which is defined as the dry mass produced (g) per unit of N absorbed (g).

### Retranslocation efficiency

Brown, senesced foliage was collected from each age-class of pine and spruce needles prior to abscission in early October 1998, bulked, dried, and analyzed for N as previously described. The mass of 100 needles was determined for senesced needles (all age-classes bulked) and each age-class of green needles. Values for senesced foliage were compared with the measures of N content of foliage of each age-class using the following formula:

$$\text{Retranslocation \%} = [(C_1 - C_2) / C_1] \times 100$$

where  $C_1$  is the N content of green needles (sampled in mid-July) and  $C_2$  is the N content of senesced needles (sampled in October) (Mälkönen 1974; Nambiar and Fife 1991). Because the total mass of senesced needles was not determined, nutrient content was based on the mass of 100 needles. There were differences both between and within species in the age-class of needles that senesced. Of the 10 pine trees sampled, 2-year-old needles senesced in three trees, 3-year-old needles in two trees, and 4-year-old needles in five trees. Of the 10 spruce trees sampled, senescence occurred in 4-year-old needles in nine trees and in  $\geq 5$ -year-old needles in one tree. Retranslocation of N was calculated separately for each age-class of needles of each species. Although N is not readily leached from needles (Chapin and Kedrowski 1983), leaching losses were estimated by soaking senesced needles in water for 24 h on a shaker table to determine the soluble N content (Fahey and Birk 1991). The solution was filtered through Whatman No. 42 filter paper and the extracts were analyzed colorimetrically for ammonium and nitrate on the Alpkem autoanalyzer.

### Results

The mean total height of lodgepole pine in the mixed plots was 371 compared with 140 cm for Sitka spruce (Fig. 1A). The mean estimated aboveground biomass of pine

trees was about 12 times greater than that of spruce (Fig. 1B). Pine trees also contained about nine times more N than spruce in aboveground biomass (Fig. 1C). These species differences were all significant ( $P < 0.0001$ ).

The root systems of both species were largely confined to the residual forest floor from the previous forest, with the greatest concentration of fine roots in the upper 10–15 cm. The depth of the forest floor in the extra pine plot ranged from 15 to 49 cm, whereas in the extra spruce plot it ranged from 8 to 18 cm. The forest floors in the three mixed pine–spruce plots were significantly ( $P < 0.01$ ) deeper (26 cm) than in the three pure spruce plots (14 cm). The deeper forest floor in pine and mixed pine–spruce plots appeared to be a consequence of the floor being less dense and better aerated, rather than having greater mass.

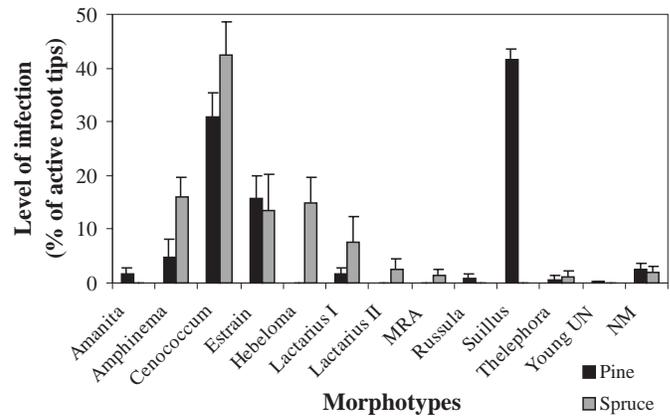
There were some differences in mycorrhizal fungi on roots of pine and spruce collected from the extra plots of the two species. Nine distinct mycorrhizal types were identified on pine root systems and eight on spruce, five of which were common to both species (Appendix Table A1). The level of mycorrhizal infection for both species was  $98 \pm 2.5\%$  (mean  $\pm$  SD). The most common types observed on pine were *Suillus*-like, *Cenococcum*-like, and E-strain, whereas on spruce the dominant types were *Cenococcum*-like, *Amphinema*-like, *Hebeloma*-like, and E-strain (Fig. 2). *Amanita*-like, *Suillus*-like, and *Russula*-like types were only found on pine. *Hebeloma*-like, *Lactarius*-like II, and MRA were unique to spruce.

Pine trees were more efficient with N, producing a mean of 388 g of aboveground biomass per gram of N, compared with 292 g for spruce. Pine trees also had higher foliar NUE (Fig. 3). This was not achieved through lower N concentrations in the pine foliage. In fact, pine had higher N concentrations in current foliage ( $1.1 \pm 0.2\%$ ) than Sitka spruce ( $0.6 \pm 0.1\%$ ). Rather, pine produced more wood per mass of foliage (Fig. 4). Pine had a greater proportion of dry mass in the stem and branches compared with spruce, and consequently, the proportional distribution of dry mass to foliage was significantly ( $P < 0.05$ ) lower for lodgepole pine (23%) than for spruce (44%). The proportional distribution of total N content among the three aboveground components (stem, branches, and foliage) was similar in both species. It thus appears that pine produced more biomass with less N by producing less foliage (i.e., pine had greater foliar efficiency). Pine also retranslocated a greater proportion of N from needles prior to senescence (50–52% compared with 24–36% in spruce; Table 1). Nitrogen concentration in senesced foliage was similar in both species and was  $0.40 \pm 0.05\%$  in pine and  $0.41 \pm 0.08\%$  in spruce. Nitrogen losses during laboratory leaching of needles were negligible for both species.

## Discussion

The vastly greater aboveground biomass and N content of lodgepole pine compared with Sitka spruce on the cedar–hemlock cutover is consistent with the prevalence of pines on N-poor sites (Miller et al. 1979) and the notion that pine is conservative with N (Prescott et al. 1989; Binkley and Giardina 1998). It is also consistent with the suggestion that Sitka spruce is a nutrient- or site-demanding species (Miller

**Fig. 2.** Mean percentage of active root tips infected by morphological types on 12-year-old lodgepole pine and Sitka spruce trees on a cedar–hemlock cutover. Error bars are 1 SE ( $n = 10$ ). Young UN, young unknown type; NM, nonmycorrhizal.

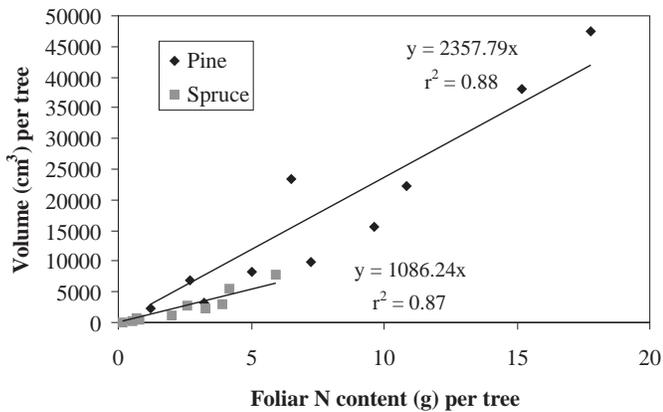


1995). On nutrient-poor peatlands and heathlands in Britain and Ireland, lodgepole pine has little requirement for fertilizer other than P (Carey and Hendrick 1986), while Sitka spruce requires high P and potassium (K) application and repeated applications of N (Dickson and Savill 1974).

We could not definitively demonstrate that lodgepole pine had greater total N content, because root biomass was not measured in the field. However, several lines of evidence suggest that it is unlikely that the root biomass of pine was sufficiently small to offset its greater aboveground biomass relative to spruce. Carey et al. (1984) found similar root masses of Sitka spruce and lodgepole pine growing on a peaty site in Ireland. McKay and Malcolm (1988) found greater fine-root biomass in the forest floor in pure spruce stands compared with mixed pine and spruce stands, but the difference was not sufficient to compensate for the lower aboveground biomass production in pure spruce plots. The nutrient capital of fine roots was also slightly greater in pure spruce than in mixed plots but was insignificant compared with the large difference in nutrient contents of the aboveground components. Waring et al. (1998) examined coarse-root production for a wide range of species and concluded that estimates were fairly conservative and generally amounted to less than 20% of aboveground production. Therefore, it is unlikely the much larger aboveground biomass of pine on the cedar–hemlock site was offset by smaller belowground biomass. We conclude that lodgepole pine had greater total N content and, thus, had acquired more N than Sitka spruce while growing for 11 years on the cedar–hemlock cutover.

Differences in rooting distribution might allow lodgepole pine access to more pools of N in the soil profile. Sitka spruce is considered to be a shallow rooting species, and lodgepole pine is a deeper rooting species; however, rooting depth varies greatly with soil conditions, especially in spruce (Coutts and Philipson 1987). Yeatman (1955) found that three pine species rooted to greater depths than spruce on poor upland heath in Britain and attributed the differences to the conditions in the wet peat layer. Lodgepole pine was found to root to twice the depth of spruce on a peaty gley (Everard et al. 1970) and deep peat (Booth and Mayhead

**Fig. 3.** Volume production for a given foliar N content in 11-year-old lodgepole pine and Sitka spruce trees from a cedar–hemlock cutover. The slopes of the two regression lines are significantly ( $P < 0.05$ ) different based on Student's  $t$  test.

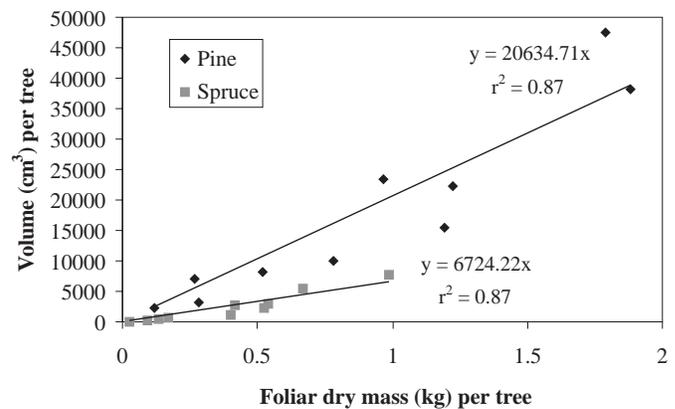


1972, cited in Ray and Schweizer 1994). However, on the cedar–hemlock site, the rooting distribution of the two species was similar, being confined almost entirely to the residual forest floor from the previous forest. Roots of either species were rarely found in the highly compacted, gleyed mineral soil, although some spruce roots were found in the upper few centimetres of the mineral soil. The greater depth and lower density of forest floor in lodgepole pine and mixed pine–spruce plots may be related to the ability of lodgepole pine to dry out peat (Farrell and O'Hare 1974), thus improving aeration. Thus differences in rooting distribution do not appear to explain the superior growth of lodgepole pine on this site.

Pine might be able to access more N by having a greater intensity of mycorrhizal colonization, or through associations with mycorrhizal fungi that are especially effective at N absorption. Total colonization of the pine and spruce roots was very high, averaging 98%. A few morphological types accounted for the majority of root tips: *Cenococcum*-like and E-strain (on both species), *Suillus*-like (on pine), and *Hebeloma*-like and *Amphinema*-like (on spruce). The differences in ectomycorrhizae that we observed would be expected to cause some differences in nutrient uptake between the two tree species, because ectomycorrhizal fungi differ in their ability to use protein and transfer the assimilated N to the host plant (Abuzinadah et al. 1986). Some ectomycorrhizal fungi are able to utilize peptides, proteins, and some amino acids as N sources (Abuzinadah and Read 1986; Finlay et al. 1992; Turnbull et al. 1995), and some produce an acid carboxy proteinase that allows them to absorb N from insoluble components of humus (Abuzinadah and Read 1986). Mycorrhizal lodgepole pine had higher growth rates on a protein source than on ammonium (Abuzinadah et al. 1986), and *Suillus bovinus* (Fr.) O. Kuntze has been identified as a "protein fungus" based on its ability to grow on protein (Abuzinadah and Read 1986). In our trial, the *Suillus*-like mycorrhizae found on more than 40% of the pine root systems (but absent on the spruce root systems) may provide the pines access to additional organic N.

Lodgepole pine used N more efficiently than Sitka spruce for biomass production, which is in keeping with the find-

**Fig. 4.** Volume production for a given foliar dry mass in 11-year-old lodgepole pine and Sitka spruce trees from a cedar–hemlock cutover. The slopes of the two regression lines are significantly ( $P < 0.01$ ) different based on Student's  $t$  test.



ings of Birk and Vitousek (1986) and Prescott et al. (1989). Spruce trees initially grow slowly, because they are unable to produce a large photosynthetic surface quickly, as a result of possessing small, thick needles that contain a relatively large dry mass per unit projected area (Cannell 1987). The smaller projected area per unit mass of Sitka spruce needles suggests that spruce needles require more resources for construction than pine needles. Young spruce typically have a much larger foliar biomass compared with pines of similar growth rates (Miller and Miller 1987). These differences in total foliage mass relate not to the amount of foliage formed in a current year but, rather, to the amount of older foliage accumulated (leaf longevity) (Miller and Miller 1987). Sitka spruce in the current study retained more age-classes of needles than pine. Why spruce retains so much foliage on infertile sites for so little apparent growth advantage is not clear. Greenway et al. (1992) working with black spruce (*Picea mariana* (Mill.) BSP) found no evidence to support the hypothesis that older needles serve as a nutrient source in nutrient-poor conditions or as a nutrient storage site in conditions of excess nutrient availability. It may just be that the genetic characteristics of Sitka spruce limit its ability to grow on N-poor sites. Because foliage is rich in N compared with other tissues, the larger foliar biomass of spruce would create a high N demand, further limiting its ability to grow on N-poor sites.

In contrast, pine produced more wood volume with less foliar biomass. Lodgepole pine also had higher N concentrations in young foliage than Sitka spruce, and a greater proportion of its foliage in young age-classes. This would enhance photosynthesis, which is strongly affected by N availability, with the entire process being reduced under conditions of N limitation (Lambers et al. 1998). Thus, lodgepole pine may be using N more efficiently by concentrating its N in young needles, thus enabling high photosynthetic rates under conditions of low N availability.

Lodgepole pine and Sitka spruce had similar retranslocation proficiency values (terminal concentration in senesced needles) (Killingbeck 1996) (pine, 0.40% N; spruce, 0.41% N). These concentrations are close to the maximum potential retranslocation of N in woody perennials

**Table 1.** Dry mass, N concentration, and retranslocation of N (100 needle basis) in foliage of 11-year-old lodgepole pine and Sitka spruce on a cedar–hemlock cutover.

Needle age (years)	Lodgepole pine				Sitka spruce			
	Dry mass (g/100 needles)	N concentration (% oven-dried mass)	N content (mg/100 needles)	Retranslocation (%) <sup>a</sup>	Dry mass (g/100 needles)	N concentration (% oven-dried mass)	N content (mg/100 needles)	Retranslocation (%) <sup>a</sup>
Current	0.480	1.08	5.19	—	0.281	0.60	1.69	—
1	1.017	0.97	9.75	—	0.332	0.58	1.95	—
2	1.256	0.79	9.97	52 (3) <sup>b</sup>	0.353	0.60	2.14	—
3	1.395	0.69	9.94	52 (2) <sup>b</sup>	0.298	0.58	1.75	—
4	1.469	0.63	9.50	50 (5) <sup>b</sup>	0.301	0.60	1.78	36 (9) <sup>b</sup>
5+ <sup>c</sup>	—	—	—	—	0.235	0.63	1.48	24 (1) <sup>b</sup>
Senesced	1.240	0.40	4.74	—	0.261	0.41	1.13	—

<sup>a</sup>Retranslocation (%) = ((N content of green needles in age-class – N content in senesced)/N content of green needles in age-class) × 100.

<sup>b</sup>Values in parentheses are the numbers of sample trees in age-class of foliage with needles that senesced.

<sup>c</sup>5+, needles of age 5 and older combined.

(0.3% N; Killingbeck 1996). However, pine had greater retranslocation efficiency (percent reduction between green and senesced needles). Retranslocation appears to be driven by shoot growth rather than nutrient supply in the soil (Nambiar and Fife 1987; Millard and Proe 1992). Therefore, the rapid growth of lodgepole pine relative to Sitka spruce on this site may contribute to its higher N retranslocation efficiency. The combination of larger foliar biomass, higher foliar N concentration, and greater N retranslocation would allow lodgepole pine to have more N available for new shoot growth. This all points to a continuing divergence of lodgepole pine and Sitka spruce growth on this site.

## Conclusions

This study confirmed that lodgepole pine had substantially more N in aboveground biomass than Sitka spruce of the same age on a N-poor cedar–hemlock cutover. Lodgepole pine had different mycorrhizal fungal associates, which may contribute to greater N acquisition by lodgepole pine. Lodgepole pine was also more efficient with N than Sitka spruce, producing more biomass per unit of N. This was achieved through having proportionally less foliage, greater N concentrations in young foliage, and greater N retranslocation efficiency. Lodgepole pine appears to be a highly suitable species for timber production on these infertile sites.

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## References

- Abuzinadah, R.A., and Read, D.J. 1986. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. I. Utilization of proteins and peptides by ectomycorrhizal fungi. *New Phytol.* **103**: 481–493.
- Abuzinadah, R.A., Finlay, R.D., and Read, D.J. 1986. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants II. Utilization of protein by mycorrhizal plants of *Pinus contorta*. *New Phytol.* **103**: 495–506.
- Aerts, R. 1995. The advantages of being evergreen. *Trends Ecol. Evol.* **10**: 402–407.
- Binkley, D., and Giardina, C. 1998. Why do tree species affect soils? The warp and woof of tree–soil interactions. *Biogeochemistry*, **42**: 89–106.
- Birk, E.M., and Vitousek, P.M. 1986. Nitrogen availability and nitrogen use efficiency in loblolly pine stands. *Ecology*, **67**: 69–79.
- Booth, T.C., and Mayhead, G.J. 1972. Report on forest research. Her Majesty's Stationery Office, London.
- Bowen, G.D. 1980. Coping with low nutrients. *In* *Biology of Australian plants*. Edited by J.S. Pate and A.J. McComb. University of Western Australia Press, Perth, Australia. pp. 33–64.
- Cannell, M.G.R. 1987. Photosynthesis, foliage development and productivity of Sitka spruce. *Proc. R. Soc. Edinburgh*, **93B**: 61–73.
- Carey, M.L., and Hendrick, E. 1986. Lodgepole pine in the Republic of Ireland. I. Site types, ground preparation and nutrition. *For. Ecol. Manage.* **15**: 301–317.
- Carey, M.L., McCarthy, R.G., and Hendrick, E. 1984. Nutrient budgets in young Sitka spruce and lodgepole pine on a raised bog. *In* *Proceedings of the 7th International Peat Congress*, Dublin. Vol. 3. The Irish National Peat Committee, Dublin. pp. 207–218.
- Chapin, F.S., III. 1980. The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* **11**: 233–260.

- Chapin, F.S., III, and Kedrowski, R.A. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology*, **64**: 376–391.
- Chapin, F.S., III, and Moilanen, L. 1991. Nutritional controls over nitrogen and phosphorus resorption from Alaskan birch. *Ecology*, **72**: 709–715.
- Coutts, M.P., and Philipson, J.J. 1987. Structure and physiology of Sitka spruce roots. *Proc. R. Soc. Edinburgh*, **93B**: 131–144.
- Dickson, D.A., and Savill, P.S. 1974. Early growth of *Picea sitchensis* (Bong.) Carr. on deep oligotrophic peat in Northern Ireland. *Forestry*, **47**: 17–26.
- Dowdy, S., and Wearden, S. 1991. *Statistics for research*. 2nd ed. John Wiley & Sons, New York.
- Everard, J.E., Neustein, S.A., and Taylor, G.G.M. 1970. Crop stability. *For. Comm. Rep. For. Res. Her Majesty's Stationery Office*, London. pp. 96–97.
- Fahey, T.J., and Birk, E. 1991. Measuring internal distribution and resorption. *In Techniques and approaches in forest tree ecophysiology. Edited by J.P. Lassoie and T.M. Hinckley*. CRC Press, Boca Raton, Fla. pp. 225–245.
- Farrell, E.P., and O'Hare, P.J. 1974. Depth of water-table in a *Picea sitchensis* fertilizer experiment on blanket peat. *Ir. For.* **31**: 36–45.
- Finlay, R.D., Forstegård, Å., and Sonnerfeldt, A.M. 1992. Utilization of organic and inorganic nitrogen sources by ectomycorrhizal plants. II. The uptake and distribution of phosphorus by mycelial strands interconnecting host plants. *New Phytol.* **104**: 157–165.
- Goodman, D.M., Durall, D.M., Trofymow, J.A., and Berch, S.M. (Editors). 1996. *A manual of concise descriptions of North American ectomycorrhizae including microscopic and molecular characterization*. Mycologue Publications, Sidney, B.C.
- Greenway, K.J., MacDonald, S.E., and Lieffers, V.J. 1992. Is long-lived foliage in *Picea mariana* an adaptation to nutrient-poor conditions? *Oecologia*, **91**: 184–191.
- Hagerman, S.M., Jones, M.D., Bradfield, G.E., Gillespie, M., and Durall, D.M. 1999. Effects of clear-cut logging on the diversity and persistence of ectomycorrhizae at a subalpine forest. *Can. J. For. Res.* **29**: 124–218.
- Ingleby, K., Mason, P.A., Last, F.T., and Fleming, L.V. 1990. Identification of ectomycorrhizae. *Her Majesty's Stationery Office*, London. *Inst. Terr. Ecol. Res. Publ.* 5.
- Keenan, R.J., Prescott, C.E., and Kimmins, J.P. 1993. Mass and nutrient content of woody debris and forest floor in western red cedar and western hemlock forests on northern Vancouver Island. *Can. J. For. Res.* **23**: 1052–1059.
- Keyes, M.R., and Grier, C. 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Can. J. For. Res.* **11**: 599–605.
- Kielland, K. 1994. Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecology*, **75**: 2373–2383.
- Killingbeck, K.T. 1996. Nutrients in senesced leaves: key to the search for potential resorption and resorption efficiency. *Ecology*, **77**: 1716–1727.
- Klinka, K., Krajina, V.J., Ceska, A., and Scagel, A.M. 1989. *Indicator plants of coastal British Columbia*. University of British Columbia Press, Vancouver.
- Lambers, H., Chapin, F.S., III, and Pons, T.L. 1998. *Plant physiological ecology*. Springer-Verlag, New York.
- Lavkulich, L. 1981. Total nitrogen determination—colorimetric by autoanalyzer—for soils and plant material. *In Methods manual. Edited by L. Lavkulich*. Pedology Laboratory, Department of Soil Science, University of British Columbia, Vancouver. pp. 32–36.
- Mälkönen, E. 1974. Annual primary production and nutrient cycle in some Scots pine stands. *Commun. Inst. For. Fenn.* **84**: 1–87.
- McKay, H.M., and Malcolm, D.C. 1988. A comparison of fine root component of a pure and mixed coniferous stand. *Can. J. For. Res.* **18**: 1416–1426.
- 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.
- Millard, P., and Proe, M.F. 1992. Storage and internal cycling of nitrogen in relation to seasonal growth of Sitka spruce. *Tree Physiol.* **10**: 33–43.
- Miller, H.G. 1995. The influence of stand development on nutrient demand, growth and allocation. *Plant Soil*, **168–169**: 225–232.
- Miller, H.G., and Miller, J.D. 1987. Nutritional requirements of Sitka spruce. *Proc. R. Soc. Edinburgh*, **93B**: 75–83.
- Miller, H.G., Cooper, J.M., Miller, J.D., and Pauline, O.J.L. 1979. Nutrient cycles in pine and their adaptations to poor soils. *Can. J. For. Res.* **9**: 19–26.
- Nambiar, E.K.S., and Fife, D.N. 1987. Growth and nutrient retranslocation in needles of radiata pine in relation to nitrogen supply. *Ann. Bot. (London)*, **60**: 914–916.
- Nambiar, E.K.S., and Fife, D.N. 1991. Nutrient retranslocation in temperate conifers. *Tree Physiol.* **9**: 185–207.
- Northup, R.R., Yu, Z., Dahlgren, R.A., and Vogt, K.A. 1995. Polyphenol control of nitrogen release from pine litter. *Nature (London)*, **377**: 227–229.
- Pojar, J., Klinka, K., and Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. *For. Ecol. Manage.* **22**: 119–154.
- Prescott, C.E., Corbin, J.P., and Parkinson, D. 1989. Biomass, productivity, and nutrient-use-efficiency of aboveground vegetation in four Rocky Mountain coniferous forests. *Can. J. For. Res.* **19**: 309–317.
- Prescott, C.E., McDonald, M.A., and Weetman, G.F. 1993. Availability of N and P in the forest floors of adjacent stands of western red cedar – western hemlock – amabilis fir forests on northern Vancouver Island. *Can. J. For. Res.* **23**: 606–610.
- Ray, D., and Schweizer, S. 1994. A study of the oxygen regime and rooting depth in deep peat under plantations of Sitka spruce and lodgepole pine. *Soil Use Manage.* **10**: 129–136.
- Turnbull, M.H., Goodall, R., and Stewart, G.R. 1995. The impact of mycorrhizal colonization upon nitrogen source, utilization and metabolism in seedlings of *Eucalyptus grandis* Hill ex. Maiden and *Eucalyptus maculata* Hook. *Plant Cell Environ.* **18**: 1386–1394.
- Waring, R.H., Landsberg, J.J., and Williams, M. 1998. Net primary production of forests: a constant fraction of gross primary production? *Tree Physiol.* **18**: 129–134.
- Yeatman, C.W. 1955. *Tree root development on upland heaths*. Her Majesty's Stationery Office, London. *For. Comm. Bull. No.* 21.
- Zar, J.H. 1984. *Biostatistical analysis*. 2nd ed. Prentice Hall Inc., Englewood Cliffs, N.J.

**Table A1.** Key identification features of each of the morphotypes observed on 12-year-old lodgepole pine (PI) and Sitka spruce (Ss) trees growing on a cedar–hemlock cutover.

Macroscopic description	Mantle type(s)	Emanating hyphae	Mycelial strands	Cystidia	Host species
<b><i>Amanita muscaria</i>-like (KB 120)</b>					
Short stubby, dense cluster, white velvet look, thick mantle	Thick, outer: pseudo-parenchymatous, 10–12 µm, uneven mantle edge	Absent	Absent	Absent	PI
<b><i>Amphinema</i>-like (KB 80)</b>					
Light brown, orange, with wefts of yellow emanating hyphae	Outer: felt prosenchyma, 4 µm Inner: net synenchyma Stain yellow in KOH	Common, some verrucose, clamps, yellow in KOH	Strands and hyphae similar	Absent	PI, Ss
<b><i>Cenococcum geophilum</i>-like (KB 10)</b>					
Black, rough mycorrhiza with abundant black emanating hyphae	Outer: thick, net synenchyma 5 µm, “stained glass” pattern	Smooth, 4 µm, no clamps	Absent	Absent	PI, Ss
<b>E-strain (KB 30)</b>					
Light brown, orange with white tip, smooth and shiny	Felt or net prosenchyma, 4–7 µm	Rare, no clamps, smooth to verrucose ornamentation	Absent	Absent	PI, Ss
<b><i>Hebeloma</i>-like (KB 100)</b>					
Yellow–brown, cottony	Outer: felt prosenchyma, 3–4 µm Inner: net synenchyma	Common, 3–5 µm, verrucose, hemispherical clamps	Absent	Absent	Ss
<b><i>Lactarius</i>-like I (resembles <i>L. glycosmus</i>-like (Ingleby et al. 1990)) (KB 110)</b>					
Monopodial pinnate, not branched, woolly, long white hyphae	Outer: net synenchyma, 2–3 µm Matrix: granular Inner: interlocking irregular synenchyma Toluidine blue: pink	Common, 5 µm, clear contents	Loose, verrucose some granular, clamps	Absent	PI, Ss
<b><i>Lactarius</i>-like II (resembles <i>L. rubrilacteus</i>-like (Ingleby et al. 1990)) (KB 180)</b>					
Older tips, teal; young tips, tan; finely grainy	Outer: net prosenchyma or net synenchyma Inner: net synenchyma or interlocking irregular synenchyma	Absent	Loose, 4 µm, no ornamentation, clamps	Absent	Ss
<b>MRA-like (<i>Mycelium radicans atrovirens</i>) (KB 20)</b>					
Brown, rough mycorrhiza with whitish tip	Outer: felt prosenchyma, 3–4 µm Inner: net synenchyma, 2–3 µm	Rare, slightly verrucose ornamentation, no clamps	Absent	Absent	Ss
<b><i>Russula</i>-like (KB 60)</b>					
Dichotomous branching, cream or beige, velvety, white cystidia visible	Outer: net and felt prosenchyma, 4–5 µm, yellowish orange	Absent	Absent	Common, awl type, clear colour, length ~30 µm, granular, no septa	PI
<b><i>Suillus</i>-like (KB 40)</b>					
Coralloid branching, whitish brown, very furry	Outer: felt prosenchyma, 3–4 µm, globular	Common, globular and large ornamentation, purplish colour, granular	Absent	Absent	PI
<b><i>Thelephora</i>-like (KB 70)</b>					
Whitish–fawn, smooth, velvety	Outer: felt prosenchyma, 3–4 µm Inner: net synenchyma, 4–5 µm	Absent	Absent	Common, awl shaped, length ~180 µm, clear colour, basal clamps	PI, Ss
<b>Unknown 1 (KB 130)</b>					
Orange–yellow, smooth, beaded, matte	Outer: felt prosenchyma	Length: 15–20 µm, granular, no clamps	Absent	Absent	PI