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Above- and below-ground growth of white spruce seedlings with roots divided into different substrates with or without controlled-release fertilizer

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Abstract

Thirty-two one-year-old white spruce *(Picea glauca* (Moench) Voss) seedlings were grown outdoors for one season in 35 L pots buried in the soil. The pots were vertically split in half. One compartment (mineral) was filled with loamy sand. The bottom of the other compartment (organic) was filled with 10 cm sand topped with 15 cm of organic substrates. Two seedling types (16 seedlings each), (i) polystyroblock-grown and (ii) peat-board grown with mechanical root pruning had their root systems split approximately in half into each of the vertical compartments. Controlled-release (26-12-6 N-P-K) fertilizer was added to one or to none (control) of the compartments. Above- ground growth was positively affected by fertilizer placed in either soil compartment. Nutrient content of the foliage was greater in fertilized than in unfertilized seedlings; N and P concentrations were significantly increased. Bud reflushing occurred frequently in fertilized seedlings. Unfertilized container-grown seedlings had the fewest roots in either soil compartment. Unfertilized mechanically-pruned seedlings had significantly greater root length, root surface area, and more root tips in mineral than in organic compartments. They also had more P in current- year leaves than did unfertilized container-grown seedlings. Fertilizer added to mineral compartments significantly affected root growth in these compartments only, whereas when added to organic compartments it affected root growth in both compartments. Root systems of the two seedling types were differently affected by fertilizer: in mechanically-pruned seedlings, the number of roots was reduced but their length and diameter increased; in container-grown seedlings, root proliferation was stimulated and this increased total root length and root surface area. Five ectomycorrhizal-morphotypes were identified. E-strain was the most abundant. Except for *Cenococcum*, all morphotypes were present in nursery stock prior to planting. Changes in distribution of morphotypes after planting appeared related to root health condition rather than to applied fertilizer.

Introduction

Slow growth (growth check) during the first post- planting years has been reported for various forest species including P. *glauca* and its hybrids with P *engelmannii* Parry Engelm. (Burdett et al. 1984; Mullin, 1964; Sutton, 1972; Vyse, 1981). Growth check occurs even on sites where resource supply does not appear to be growth limiting (Hallsby, 1995). A positive effect of the presence of surface organic matter on growth of planted seedlings has been recognized (McMinn, 1982) and site preparation treatments that mix organic soil into the planting microsite have been successfully tried (Hallsby, 1995; McMinn, 1982; Sutton, 1993). Methods of organic matter treatment that would optimize seedling establishment are yet to be

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Developed (Hallsby, 1995). However, Balisky et al. (1995) considered the forest floor as an appropriate rooting medium for planted tree seedlings; They proposed that root morphologies and planting strategies would have to be site-specifically modified to promote the development of roots into the organic/mineral soil interface. These authors suggested that planting into microsites consisting of rotten wood or duff might be advantageous to seedling establishment while planting into mineral soil could be det~imenta1. This still remains controversial.

Organic horizons of forest soils are an important reservoir of mineral nutrients, especially of nitrogen Jurgensen et al. (1997). Adding fertilizer to organic matter may increase its decomposition rates (Salonius, 1972). Several types of controlled-release fertilizers are now available. In colder climatic zones and at high elevations, tree planting can be limited by long-Lasting snow cover and short growing season. It is uncertain whether conifer seedlings can substantially benefit from controlled-release fertilizer when planted late in the season. Growth performance of seedlings treated with fertilizer at planting was inconsistent in British Columbia (Anonymous, 1995) but some trials showed promising results (van den Driessche, 1988). The identification of causes for inconsistent growth performance of fertilizer-treated seedlings from various types of planting stock was recommended (Anonymous, 1995).

Mycorrhizal associations between fungi and roots of conifer species are common and are believed to be important and beneficial to the growth of forest trees. Organic soil substrates well support organisms favorable to trees, including mycorrhizal fungi (Jurgensen et al., 1997) but it is not known whether roots located in mineral and organic soils differ in their ability to form mycorrhizae with different species of fungi. Decreased colonization of conifer roots by mycorrhizal fungi with increasing rates of fertilizer release has been reported (e.g. Crowley et al., 1986; Gagnon et al., 1995). However, little is known about effects of fertilizer applications on the abundance and composition of mycorrhizae on conifer roots located in different soil substrates.

The objectives of this study were to evaluate (i) above-ground growth responses to controlled-release fertilizer under short (late planting) growing season, (ii) differences in above and below-ground growth responses to the placement of the fertilizer package in either the mineral or organic soil compartments, compared to unfertilized controls, (iii) the development or root system portions divided into different types of soil and as influenced by the applied fertilizer, (iv) the effect of fertilizer treatments on seedlings nutritional status, (v) the influence of soil types and fertilizer treatments on the composition and abundance of ectomycorhizal morphotopes on roots of studied seedlings, and (vi) compare the above listed responses between two different types of white spruce planting stock.

Materials and methods

Plant material

A single white spruce seed source of central British Columbia origin was sown in mid-March 1996 into (I) PSB 415B styroblocks@[1] and (2) Vapo[2] peat trays. The PSB container cavities are 149 mm deep, 35 mm in diameter, the plants are spaced approximately 45x45 mm. The Vapo peat boards are 80 mm thick and are held in plastic trays designed for crosswise cutting of the peat boards. The trays have perforated bottoms but no lateral restrictions to root growth. Plants are spaced 50 x 50 mm (Parviainen and Tervo, 1989). The peat boards were heat-sterilized and calcinated at manufacture. Both stock types were grown at Red Rock Research Station in Prince George, British Columbia in the same greenhouse and the same watering and fertilizing regime until late September 1996. Vapo seedlings were mechanically pruned during nursery growth three times (last time one week before lifting to separate individual seedlings) using an electric knife run through slots in the sides of the plastic tray containing the peat boards. About four hundred seedlings of each stock type were lifted in October 1996, and stored frozen (-2 °C) until June 1997.

Divided-root system experiment

On June 16, 1997, sixteen seedlings of heights in the range of 110-140 mm and root collar diameters between 2.2-2.8 mm) were selected from each stock type. Roots were gently washed and each seedling was individually planted into a 33 L plastic pot (with bottom drainage holes) divided vertically in half (Figure 1) by a sheet of aluminum sealed to the pot with silicone caulk. A small notch was cut in the middle of

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[1] **Beaver Plastic Limited, Edmonton, Alberta.** [2] **Kekkilii *aY,* Vapo Group, Tuusula, Finland.**

Table 1. Soil nutrient elements in the three types of root growth media used in the divided-root experiment with white spruce seedlings

Element	Units	Nursery-bed soil (mineral compartment)	Soil organic mix	Masonry sand (Bottom of organic compartment)
Total C	%	0.86	9.94	0.19
Total N	%	0.05	0.19	0.01
N(NH4+)	ppm	0.32	1.21	0.25
N(NO3-)	ppm	6.90	0.44	2.31
C/N ratio		18.97	52.99	15.88
Available P	ppm	162.2	111.4	59.7
Exchangeable K	cmol+/kg	0.19	0.45	0.21
Exchangeable Al	cmol+/kg	0.03	0.01	0.06
Exchangeable Na	cmol+/kg	0.02	0.01	
Exchangeable Fe	cmol+/kg	0	0	
Exchangeable Mg	cmol+/kg	1.05	1.74	1.39
Exchangeable Ca	cmol+/kg	2.76	10.47	3.25
Exchangeable Mn	cmol+/kg	0.01	0	0
S	%	0.0055	0.0199	0.0036
Effective CEC*	cmol+/kg	4.10	12.8	4.90
pH		6.10	6.93	7.38

*Effective exchangeable cations (CEC) are expressed as the sum of seven cations (Ca, Mg, K, Mn. Fe. Al, and Na).
% = percent of dry weight.

the top edge of the aluminum sheet to allow placing a seedling with its root collar below the soil surface. Each seedling had its roots split approximately in half into each of the two compartments separated by the metal sheet. Tap roots in both stock types had been air-pruned during nursery growth and were not treated any different than other roots while dividing the root systems. In each pot, one compartment (the mineral compartment) contained non-sterilized loamy sand taken from the nursery bed. The second compartment (organic compartment) had the bottom 10 cm filled with non-sterilized masonry sand (to improve drainage) topped with 15 cm of commercially available organic mix containing compost, peat, and decomposing ground bark.3 Samples of the soil media were taken for chemical analysis (Table I).

Seedlings of each stock type were then randomly assigned to one of three fertilizer treatments: 6 pots to the control treatment (no fertilizer added), 5 pots to fertilizer into the organic compartment, and 5 to the fertilizer into the mineral compartment. One fertilizer-containing package4 (9 g; 26.33% total N, 12.00% phosphate, and 6.02% soluble potash) in polyurethane-coated granules providing 24.9% coated slow-release N, 5.27% coated slow-release P, 5.13% slowly available soluble K, and 6.01% S (combined)) was placed 2 cm away from the outermost roots at the depth of about 12 cm in each fertilized compartment. The rate of fertilizer release is temperature dependent and at soil temperatures typical for the central interior of British Columbia the fertilizer would be slowly released over up to 3 growing seasons (N .C. Anderson, Reforestation Technologies International, person. comm., 1999). The 32 pots were buried to their rims into the soil of the nursery bed, watered only once after planting, then left at ambient outdoor conditions until the end of the growing season. The pots were frequently checked and germinating weeds removed.

Seedling measurements and ectomycorrhizae assessment

Seedlings were removed from pots on October 2, 1997 and their shoots and roots were separated at the root collar. Shoots were individually packaged and labeled for identification. Subsamples of foliage from the nursery year and current year shoots were taken for scanning and determination of projected leaf sur-

3 **The Answer Garden Products, Ltd., Abbotsford, B.C., Canada.** 4 **Reforestation Technologies International, Salinas, California, USA.**

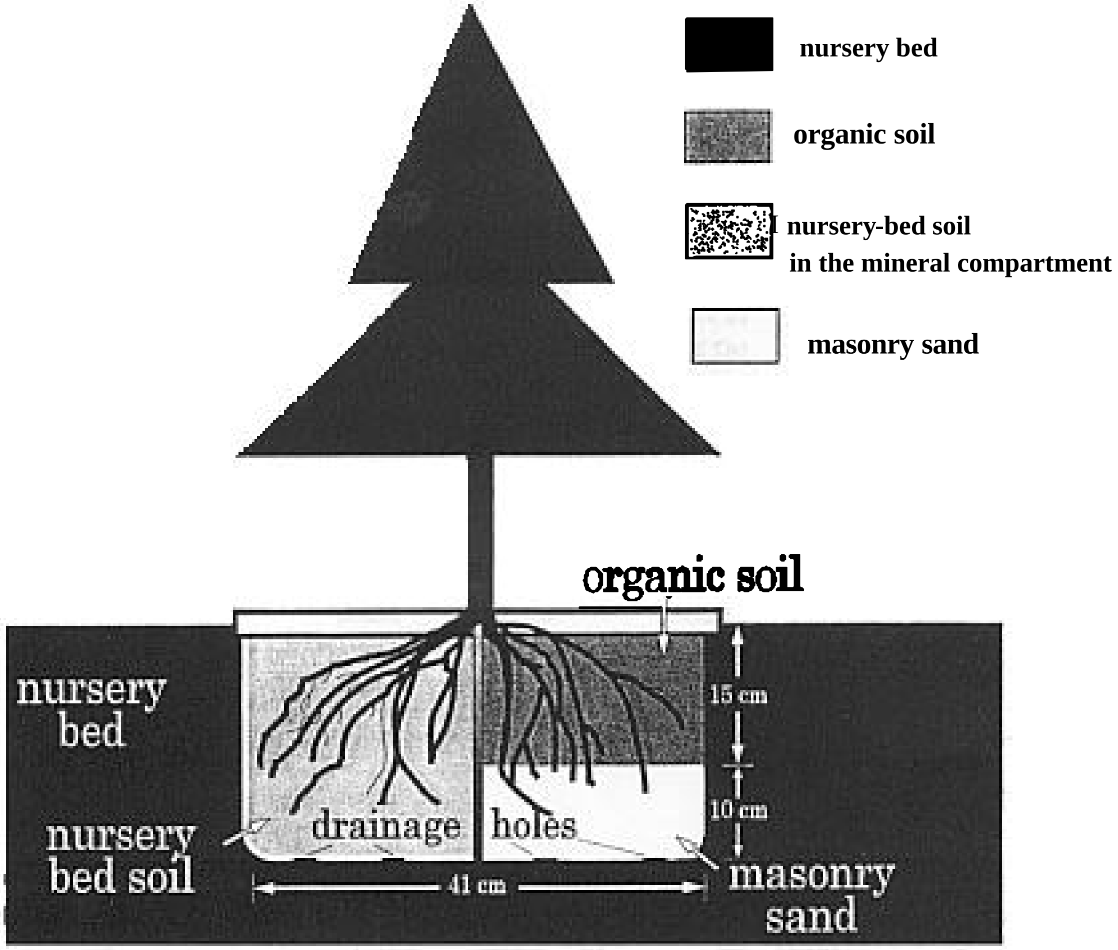

Figure I. Schematic drawing (not to scale) of the arrangement of soil substrates in pots used in the divided-root experiment.

face area,[5] then the subsamples were dried to constant weight and the relationship between projected leaf area and dry weight was determined for each year- portion of each seedling. The remaining foliage and stems were also dried to constant weight and determined separately so the total projected area of each year of growth of each seedling could be calculated from the ratios derived from the subsampled foliage. The subsamples and the rest of the foliage were then combined and sent for nutrient analysis to the analyticallaboratory of the British Columbia Ministry of Forests (BCMoF). Roots from different pot compartments were separated and. individually labeled. The roots were gently washed to remove adhering soil. Roots from each pot compartment were subdivided to smaller portions to reduce overlapping, scanned on the Hewlett-Packard C2521 B scanner and digitally analyzed.[6] Immediately after scanning, the roots were packed in plastic bags and sent to the University of Northern British Columbia (Prince George Campus) for ectomycorrhizae assessment. Entire root-system portions from each split compartment were examined to determine mycorrhizal status. Characterization and confirmation of each type of ectomycorrhiza was done using bright field optics. Macroscopic characteristics and abundance counts were done using a dissection microscope; to confirm mantle, emanating hyphae, Hartig net and rhizomorph features, frequent root squash mounts were prepared and examined under a compound microscope (Massicotte, 1994). An abund- ance estimate of each ectomycorrhiza was made for all laterals and for each entire split root system (64 in total). Split root system abundance measures were statistcally analyzed for E-strain fungi only as the dis- tribution and/or low abundance of other fungi did not allow for statistical comparisons.

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[5] **WinNeedle software, Regent Instruments, Quebec City,** Qc, **Canada.**

[6] **WinRhizo software, Regent Instruments.**

Samples of the three soil types filling the pot compartments as well as foliage collected from the trees grown with split roots were analyzed at the BCMoF analytical laboratory. The procedures were based on methods described by Carter (1993) and Kalra and Maynard (1991). For plant tissue elements, ground tissue samples were strong acid/microwave digested and analyzed with ARL 3560 ICP spectrometer. Plant tissue nitrogen and carbon were determined by combustion analysis on the Fisons NA-1500 NCS elemental analyzer. Soil exchangeable cations were determined by a 0.1 *M* barium chloride extraction. Available ammonium-N and nitrate-N were extracted from soil samples with 2 *N* KCI and measured with the Technicon colorimetric auto-analyzer. Available P was determined by the Bray-Pl extraction method followed by colorimetric analysis for orthophosphate on the UV-visible spectrophotometer. Finely-ground soil subsamples were used to determine total N and C with Fisons NA -1500 NCS elemental analyzer and sulfur with the Leco SC-132 sulfur elemental analyzer. Soil pH was determined on a 1: 1 water slurry except for the organic substrate where 1: 2 water slurry was used.

Experimental.design and statistical analysis

The experiment used a completely randomized design and all variables not separated by pot compartments or years of growth (foliage only) were analyzed by one- way ANOVA using SAS 6.97 statistical package. The mean square (MS) of a tree nested in fertilizer treatment and stock type were used as an error term for testing effects of all sources. For variables determined by pot compartment (e.g. root length in each compartment) the design was treated as a split-plot with fertilizer treatment and stock type being the crossed main plot factors and the compartment the split-plot factor. The same was done' for foliage nutrient con- tent analysis, with foliage year of origin being the split-plot factor. Effects of the stock type, fertilizer treatment and the interaction between these two were tested with MS of a tree nested in stock type and fertilizer treatment. All other effects were tested with MS of the compartment (or the year for foliage) nested in 'all higher factors. The same model was used when analyzing root length and root surface area distribution by multivariate analysis of variance (MANOVA). Diagnostic statistics were performed using the Univariate Procedure of SAS. No data transformations were necessary.

Results

Ambient air temperature and rainfall during the period the experiment

Mean air temperatures (1.2 m above ground) at the Environment Canada meteorological station (Prince George airport) located in the proximity of the re- search station were: 13.6 °C, 15.7 °C, 15.9 °C, and 11.5 °C, for June, July, August, and September, 1997, respectively. Total precipiation and the number of days with measurable precipitation (in brackets) were: 55.2 mm (8), 73.0 mm (19), 38.2 mm (11), and 49.0 mm (14) for June 16-30, July, August, and September, respectively.

Shoot growth

At planting, Vapo seedlings were taller *(p=O.O2)* (mean height 133 mm) and thicker *(p=O.O2)* at the stem base (mean diameter 2.7 mm) than PSB seed- lings (113 mm and 2.4 mm, respectively). At the end of the 1997 growing season, planting stock had no significant effect on seedling height, stem diameter, or any other morphological variable listed in Table 2. Only the fertilizer treatment significantly affected the final 1997 seedling height *(p0.0001*), the height increment *(p=0.001)*, the final 1997 stem-base diameter (p=0.0001) and its increment (p=0.0001), total dry weight of stems *(p=0.04)*, dry weight of the 1997 leaves *(p=0.02)*, projected area of the 1997 leaves *(p=0.04)* and dry weight of the root system (both pot compartments combined) (p=0.0001). Means of all impacted variables were always greater in fertilizer- treated seedlings than in untreated controls. However, pot compartment choice for placement of fertilizer did not affect shoot growth (Table 2). In summary, fertilized seedlings had more shoot growth than un- fertilized seedlings. Almost half of the seedlings in pots re flushed buds in mid-summer but only two were from unfertilized plants -both of PSB stock type. Among the dozen fertilized plants that reflushed, eight received fertilizer into the mineral compartments and both stock types were equally represented.

Root growth

Unfertilized PSB seedlings developed comparatively few root tips in either soil (Figure 2). Unfertilized Vapo seedlings had copious root tips in the mineral soil and few in the organic soil (Figure 2). Fertilizing PSB seedlings in mineral compartments stimulated

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7 The SAS Institute, Cary, N.C., USA.

Table 2. Morphological characteristics (least square means) of seedlings grown with their root systems split into organic and mineral compartments with or without slow release fertilizer

	Fertilizer placement		
	None	**In** mineral	**In** organic
Variable			
Height (mm)	182b	230a	228a
1997 height increment (mm) Stem-base diameter	65b	l09a	97a
(mm)	4.09b	5.96a	'5.8Ia
1997 stem diameter increment (mm) Dry weight	1.43b	3.42a	3.27a
(g) of:			
all leaves*	2.08a	3.043	2.84a
all stems	1.57b	2.36a	2.57a
new (1997) leaves	1.06b	2.083	1.77a
root system (compartments combined) New	1.02b	1.963	2.01a
(1997) leaves projected surface area (mm2)	6136b	111323	9334a

* 1996 (nursery-grown) + 1997 foliage.

Note: Means of the same variable followed by the same letters are not significantly different from each other at ()(= 0.05.

root proliferation in these compartments only. Fertilizer placed into organic compartments significantly stimulated root proliferation in this compartment in both types of planting stock. Fertilizing Vapo seed- lings in either compartment significantly reduced root tip numbers in the mineral soil. In both stock types, fertilizing mineral compartments had no marked effect on root numbers in organic compartments (Figure 2). The differences in root tip numbers between the stock types, pot compartments, and fertilizer treatments resulted in a significant three-way interaction of these three factors (Table 3).

Root length and root surface area were analyzed using the same analytical model as for root tip numbers. Surprisingly, results of these ANOVAs did not show a significant three-way interaction effect on root length (p=O.17) and root surface area *(p=O.22)*. How- ever, pair-wise comparisons of least square means of different three-way combinations indicated that such interaction effect should be expected for both these variables. Because of this discrepancy, least square means of all three-way combinations are shown for root length (Figure 3) and root surface area (Figure 4). Significantly different means for both variables were separated on the basis of calculated least significant differences.

Root length and root surface area of unfertilized PSB seedlings were comparatively low in both compartments (Figures 3-4). Fertilizing PSB seedlings in mineral compartments increased root tip number, root length, and root surface area in these compartments only (Figures 2-4). Fertilizing organic compartments increased the length and surface area of PSB roots in both compartments, compared to unfertilized seed- lings (Figures 3-4). Root length and root surface area of unfertilized Vapo seedlings were much greater in mineral than in organic compartments; although root number of fertilized Vapo seedlings declined in fertilized mineral compartments (Figure 2), root length was not reduced and root surface area significantly increased (Figures 3-4). Vapo seedlings responded to 1crtilizing mineral compartments by elongating and thickening their roots and reducing root proliferation. In spite of this reduction, there were still more roots than in unfertilized organic compartments of Vapo or PSB seedlings. Fertilizing organic compartments of Vapo seedlings stimulated root proliferation in these compartments and increased the length and surface area of the roots (Figures 2-4). Responses of roots in mineral compartments to fertilizing organic compartments were different in the two stock types. In PSB, root tip numbers rose correspondingly in both compartments (Figure 2). Root length and root surface area in mineral compartments also increased (Figures 3-4). In Vapo, root numbers in mineral compartments declined the same as in response to their direct fertilizing but root length and surface area did not change, compared to unfertilized seedlings (Figures 2-4).

Table 3. Results of analysis of variance on root tip numbers of white spruce seedlings grown with root systems divided into organic and mineral compartments with or without controlled-release fertilizer

Source	DF	MS	F	p>F	Error term
STK	1	3662099	0.7	0.4255	MS Tree (STK Fert)
Fen	2	2312R947	4.1	0.0275	MS Tree (STK Fert)
STK*Fen	2	62611690.	11.2	0.0003	MS Tree (STK Fert)
Tree (STK Fen)	26	5585536	1.6	0.1033	MS Error
Comp	I	70123100	20.8	0.0001	MS Error
Comp*STK	2	29650960	8.8	0.0064	MS Error
Comp * Fert	2	20380424	6.0	0.0070	MS Error
Comp*Fen*STK	2	14244234	4.2	0.0259	MS Error
Error	26	3378566			

STK = planting stock, Fert = fertilizer treatment, Comp = divided-pot compartment, DF = degrees of freedom, MS = mean square.

Experimental effects on radial growth of roots were further examined by MANOVA using root length and root surface area distribution divided into three root diameter classes: (I) less than 0.4 mm, (2) 0.4 to 0.8 mm, inclusive, and (3) more than 0.8 mm. Outcomes were similar for both root length and root surface area and differed little whether absolute values or percents were analyzed. Roots and root parts thinner than 0.4 mm constituted more than half of the total length of root systems, regardless of the stock type, compartment, and fertilizer treatment. Roots thicker than 0.4 mm were significant contributors to the root system surface area (not shown). Differences to root surface area distribution due to fertilizer treatments were more conspicuous than the differences in the distribution of root length. Both stock types, when un- fertilized, had the greatest percent of their root length and root surface area in the smallest root diameter class, especially so in the Vapo seedlings. Fertilizer application shifted more root length and root surface area to the two greater root diameter classes in both stock types, but more so in Vapo than in PSB seedlings and more in mineral than in organic compartments.

Soil nutrients, foliage nutrient concentration, and nutrient content

The organic soil had a higher C/N ratio than did either of the two mineral substrates (Table I). It had more N in the form of ammonia whereas the two sands had more N in nitrate. The total exchangeable cations was greater in the organic mix than in the mineral substrates. The nursery-bed soil (mineral compartment) had more available phosphorus than either the organic mix or the sand used for filling the bottom of the organic compartment, possibly due to prior use of the nursery bed for seedling production and related fertilizer applications. All three soil substrates had close to neutral pH (Table I).

Regardless of foliage age and fertilizer treatment, concentrations of macronutrients and micronutrients in leaves of seedlings in the divided-root experiment were adequate according to Chapin and Van Cleve (1989). Concentrations of macroelements contained in the fertilizer were highest in leaves of fertilized plants, regardless of which compartment was fertilized. However, differences existed among N, P, and K concentrations in foliage of different age, and/or between the stock types. N concentration following fertilizing was increased by approximately two-fold in nursery foliage and by 2.5 times in new, current- year foliage, compared to unfertilized seedlings that had 1.1% (percent of dry weight) N concentration, regardless of leaf age. This was reflected in foliage N content (concentration x dry weight) as shown in Table 4. Significant interaction effects between fertilizer treatment and foliage age were detected for N concentration *(p=0.000* I) and N content *(p=0.0076).* No significant differences were found between stock types.

Unfertilized PSB seedlings had low P concentration (0.12%) compared to unfertilized Vapo seedlings (0.28%) *(p=0.02).* Vapo seedlings had P concentrations similar to that of fertilized seedlings (Table 4). Fertilized and unfertilized Vapo seedlings had significantly greater concentration of K (0.71 % and 0.82%, respectively) than unfertilized PSB seedlings (0.52%) but not fertilized PSB seedlings (0.75%). Different age

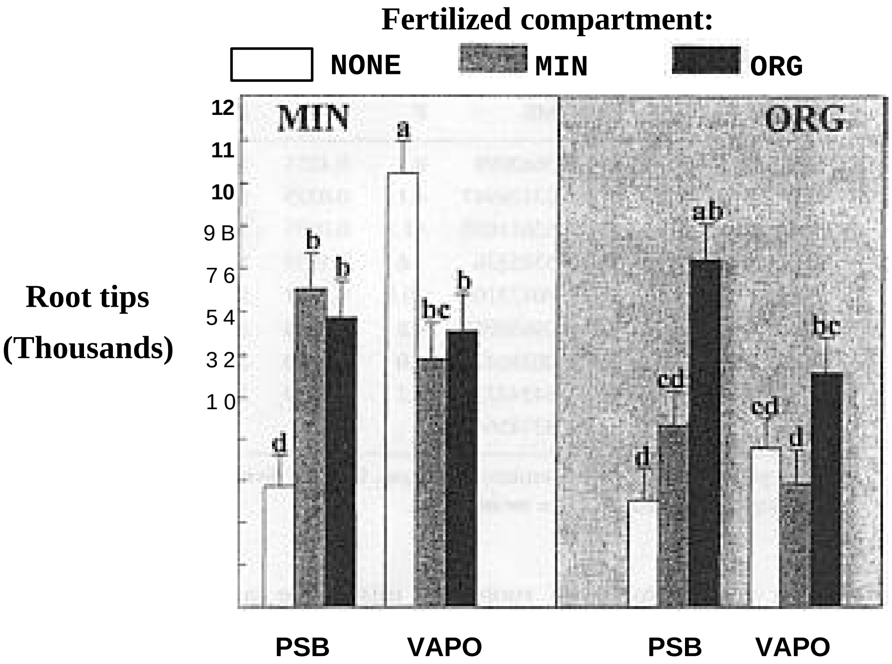

Figure 2. Mean numbers of root tips (Figure 2), aggregate root lengths (Figure 3), and root surface areas (Figure 4) of white spruce seedling root system portions present in compartments of different soil types and with or without controlled-release fertilizer. The clear panels on the left show responses of root system portions located in mineral compartments whereas the shaded panels on the right show responses of roots in organic compartments. Bars marked with the same letters show means not significantly different from each other (across both panels) at *a* = 0.05.

leaves of Vapo seedlings had similar K concentrations while new leaves of PSB seedlings had 0.13% higher K concentration than nursery foliage. These differences caused interaction effects of stock type with fertilizer treatment *(p=0.0005)* and stock type with foliage age *(p=0.02)* on the concentration of K. Contents of K in foliage are shown in Table 4.

Concentrations of other elements were lower in new leaves than in nursery leaves but their contents were greater in new foliage due to its greater biomass (Table 4). Iron, whose content was also much lower in new than in nursery leaves (not shown), was an exception.

Ectomycorrhizae and root condition assessment

Except for *Cenococcum,* all morphotypes found on roots from the divided-root experiment were present in nursery stock prior to planting. *Thelephora* was the most abundant morphotype that colonized PSB seedlings during nursery growth. *Amphinema* and *Mycelium radicis atrovirens* (MRA) were common on PSB seedlings but E-strain occurred at low levels. In contrast, E-strain was the most abundant nursery morphotype on Vapo seedlings, which also had moderately abundant *Thelephora. Emphysema* and MRA did not occur on Vapo roots prior to outplanting.

Five ectomycorrhizal morphotypes were characterized on roots and a small number of roots on two seedlings were colonized by unidentified fungi. The most abundant ectomycorrhiza was E-strain. It was absent on the entire root system of only one seedling. Generally, E-strain was less abundant on seedlings with poorer root systems (those systems with many roots that were shrivelled, darkened, or with damaged rhizodermal layers) and these occurred more often in PSB, especially in unfertilized seedlings. E-strain abundance was analyzed by ANOVA and significant effects of the pot compartment (p=O.OI) and of stock type *(p=O.OOO* I) were found. More roots were colonized by E-strain in mineral (75%) than in organic (61%) compartments and in Vapo (85%) than in PSB (51%) seedlings.

Amphinema was the second most common ectomycorrhiza, although much less abundant than E-strain. It occurred in 42 of 64 pot compartments, more frequently in PSB (29 compartments) than in Vapo seedlings, and more abundantly in PSB than in Vapo (17.8% versus 1.9% of colonized root tips, respectively). *Thelephora* and MRA occurred at similar lower levels, rarely occupying more than 5% *(Thelephora)* or 1% (MRA) of roots. Both appeared to associate more frequently with older roots, such as those in the root

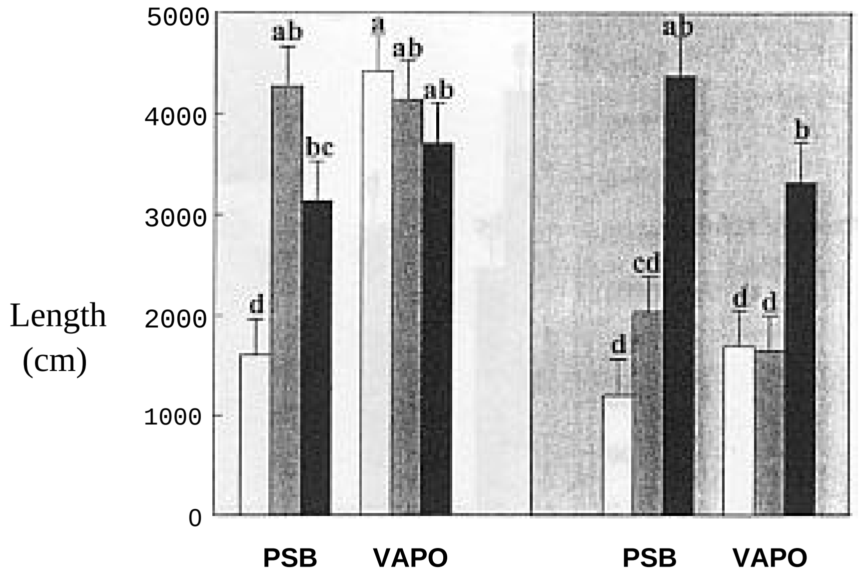

Figure 3.

collar area. MRA also seemed to associate with root systems in poorer condition, often those on which E- strain levels were low. *Thelephora* occurred in 56 of 64 compartments. MRA occurred in both soil types but in 29 PSB compartments compared to only 14 Vapo. *Cenococcum* occurred at very low levels, often on less than 1% of the root system. It occurred on roots of six PSB and seven Vapo seedlings and in all but two seedlings only in the mineral compartment.

Percent of non-colonized or lightly colonized root tips was greater in organic (22%) than in mineral (6%) compartments. This difference occurred in PSB (32% and 7% for organic and mineral compartments, respectively) but not in Vapo seedlings (approximately 10% for each compartment.

Discussion

Controlled-release fertilizer stimulated growth of white spruce seedlings of both stock types in spite of late planting. Austin and Strand (1960), Rothacher and Franklin (1964), and Carlson and Preisig (1981) obtained similar results with different fertilizer formulas and with different conifers. Our study covered only the first growing season and may not indicate long-term trends in growth performance of fertilized seedlings. One reason for inconsistency of planting stock performance treated with slow release fertilizer (Anonymous, 1995) may be the variation among different trials in fertilizer formulas, stock types, and site, especially soil characteristics.

Frequent bud reflushing in potted seedlings might have resulted from the confinement of the soil in pots causing concentration of fertilizer around the roots. Most of the reflushing occurred in seedlings with fertilized mineral compartments. Differences between the compartments in moisture fluctuation would not be surprising and these could modify the timing or rates of fertilizer release. The contribution of lammas growth to the current-year shoot extension was so minimal that it was not separately measured. Coutts and Philipson (1976) showed a negligible effect of high N concentration on shoot elongation from the first flush of growth of Sitka spruce seedlings, but a very significant effect on shoot growth from the second flush. However, their fertilizer application treatments were different (not a controlled-release fertilizer) than in our study and a long, constant photoperiod they used apparently sustained shoot elongation after the second flush. The controlled-release fertilizer used in our study stimulated shoot elongation enough to cause numerous bud flushes in mid-summer but not enough to sustain the resultant shoot elongation under ambient, decreasing day length. Bud reflushing may result in delayed maturation of shoot tips causing their succulence and concerns have been expressed about a potential predisposition of shoots in fertilizer-treated seedlings to frost and desiccation injury (Brockley, 1988). Yet, *Picea glauca* treated with the same controlled-release fertilizer as the one used in this study suffered significantly less winter damage

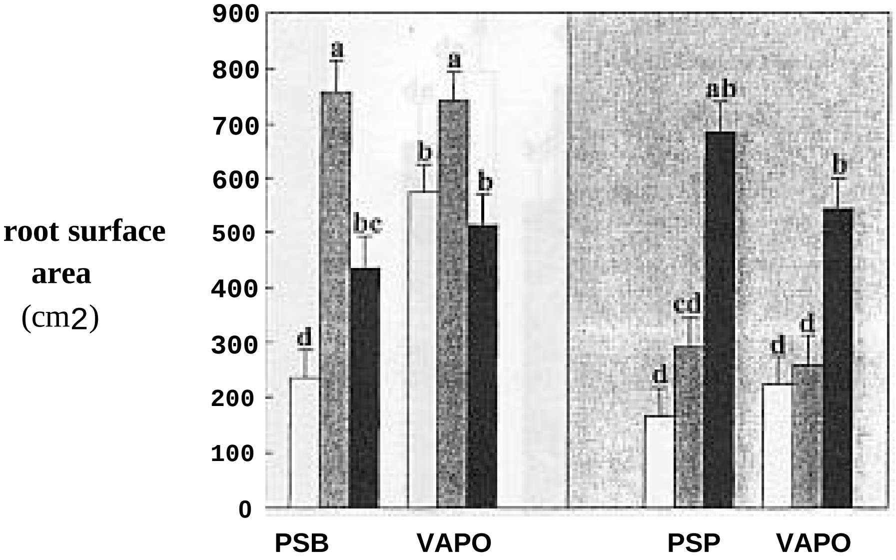

Figure 4.

attributed to desiccation than did unfertilized seedlings (Krasowski, 1998).

The study reported here accounted only for nutrients in the foliage at the end of the experiment and not for nutrient uptake, translocation, and losses due to leaching. Nevertheless, total nutrient pools of all elements other than apparently unavailable Fe were greater in fertilized than in unfertilized seedlings. Nutrient pools reflect the plant's nutrient uptake (Chapin and Van Cleve, 1989) which must have been greater in fertilized than in unfertilized plants. Only N accumulated in fertilized plants at a level that significantly increased its concentration in leaves. However, fertilizer N was supplied in much greater proportion than P and K.

The most striking difference between root growth of unfertilized PSB and Vapo seedlings was the great proliferation of roots of the latter in mineral compartments. Vapo seedlings had significantly higher percent of their roots colonized by mycorrhizal fungi than did PSB seedlings they also had fewer roots in poor condition. A reduced root colonization by E-strain fungus was particularly common in unfertilized PSB seed- lings. These factors could affect nutrient uptake and be the cause of the observed differences in P and K con- tents between the two stock types. While the growth of both stock types benefited from the applied controlled- release fertilizer, it appears that the fertilizer was much more critical to the improved growth of PSB than Vapo roots.

Studies on Sitka spruce (Coutts and Philipson, 1976; Philipson and Coutts, 1977) showed that nutrueints, particularly N, stimulated radial growth of roots in direct contact with fertilizer. There was little growth stimulation of unfertilized portions of Sitka spruce roots even though the supplied nutrients were apparently translocated to these roots. In white spruce seedlings examined in this study, fertilizer had a localized effect on root proliferation, elongation, and radial growth mainly when placed into mineral compartments. When applied to organic compartments, the fertilizer effect was no longer localized but the growth of roots was differently affected in the two stock types. Localized proliferation of roots could be viewed as an adaptive mechanism of root systems allowing them to exploit local concentrations of nutrients in the soil (Drew, 1975; Drew and Saker, 1975; Robinson, 1994; van Vuuren et al., 1996). This would explain responses of PSB seedlings to fertilizer addition and the response of Vapo seedlings to fertilizing the organic compartments. In the absence of localized nutritional stimulus in the soil, root proliferation and root growth of white spruce seedlings depended on the soil type and on properties of root systems resulting from different nursery cultures. Based on results of this trial and on results obtained by Coutts and Philipson (1976) and Philipson and Coutts (1977), it might be expected that the symmetry of root systems treated with localized supply of fertilizer could be altered. However, Carlson and Preisig (1981) re- ported no such alterations in Douglas fir supplied with slow-release fertilizer at planting.

Difference~ in root growth between the two unfertilized stock types in mineral soil were not reflected

Table 4. Nutrient content of white spruce seedling foliage of plants from the Divided root experiment

Fertilizer treatment		None		In Mineral		In organic	
Foliage produced in		1996	1997	1996	1997	1996	1997
Element	Units						
C	g x 10-1	0.5244b	0.5193b	0.4581b	1.064a	0.540b	0.941a
Ca	g x 10-1	0.0090ab	0.0051b	0.0083ab	0.0122a	0.0108a	0.0130a
K	g x 10-1	0.0072b	0.0071b	0.0060b	0.0162a	0.0081b	0.0161a
Mg	g x 10-1	0.0020b	0.0016b	0.0019b	0.0030a	0.0020b	0.0022ab
Mn	g x 10-6	438.8cd	245.4d	494.6bc	843.7a	563.3bc	800.6ab
N	g x 10-1	0.0076c	0.0076c	0.0176b	0.0512a	0.0121bc	0.0532a
P	g x 10-1	0.0021b	0.0023b	0.0022b	0.0058a	0.0030b	0.0060a
S	g x 10-1	0..03b	0.0011b	0.0017b	0.0031a	0.0021ab	0.0029a
Foliage dry Weight	g x 10-1	1.02c	1.06c	0.96c	2.07a	1.10c	1.77b

Note: Means of the same variable followed by the same letters are not significantly different from each other at (X = 0.05.

in corresponding differences to the shoot growth of these stock types. However, in another portion of these studies (Krasowski, 1998) shoots and roots of Vapo seedlings grew significantly more than in PSB seedlings, without ferilizer but over a month-longer growing season. The poor root growth in organic soil was reversed by adding fertilizer. Stimulation of all as- pects of root growth in the organic soil must have been mediated by the addition of at least one of the elements contained in the fertilizer. We did not use natural forest soils in this experiment but its results suggest that ad- ditional studies on different types of forest soils are needed before the recommendations for planting con- ifer seedlings with roots located in organic layers of the forest floor (Balisky et al., 1995) could be broadly accepted. At least in some organic soils, root prolif- eration during the seedling-establishment phase could be enhanced by applying slow release fertilizer, es- pecially when container-grown seedlings are planted. Seedlings planted in organic soil and not supplied with fertilizer may have underdeveloped root systems.

Coutts (1982) reported stimulation of root growth in wet soil but poor growth and dying of some roots in dry soils. These responses were independent of the soil type (sandy loam or peat were used). Our study was intentionally conducted under ambient con- ditons without supplemental irrigation and differences in moisture fluctuation between the mineral and or- ganic soils were likely, especially in August which was the driest month during the study period. Surface organic soil may dry excessively on warm days (Sutton, 1991) and this may have occurred in our study. However, the stimulation of root growth in organic compartments by fertilizer suggests that nutrient im- mobilization rather than low soil moisture limited root growth in these compartments.

The differences in the composition and abundance of ectomycorrhizae appeared to be related more to root health status than to the different root-growth media and fertilizer treatments. Since root assessment re- vealed more poor and dying roots in unfertilized than in fertilized seedlings and in PSB than Vapo seedlings, interaction effects involving stock type and fertilizer treatment on ectomycorrhizae composition could be indirect. It is not known why PSB seedlings had more shriveled and dying roots than Vapo. In unfer- tilized PSB seedlings, the proliferation of lateral roots appeared suppressed. This was con!!;istent with obser- vations made in other studies. Excavated root systems of white spruce PSB seedlings often resembled the expansion of their nursery configuration (Krasowski et al., 1996). These root systems had numerous long, vertically oriented laterals, and fewer branches than 'fibrous' root systems of Vapo seedlings. .

Dahlberg (1990) found no evidence that the pres- ence of organic layer in forest soils could affect the establishment and development of ectomycorrhizae in planted seedlings. In our study, the only mycorrhizal fungus that seemed to prefer one type of soil was *Cenococcum.* It was more common in roots located in mineral than in organic soil, even though its abundance was extremely low. Since organic compartments had sand in their bottom portions, it is possible that the two occ~rrences of *Cenococcum* in organic compartments were in sand rather than in organic soil. Inoculation of Sitka spruce seedlings with *Cenococcum* did not improve growth of seedlings planted on clearcuts ill Alaska (Loopstra et al. 1988; Shaw et al., 1987). Resident fungi provided better nutritional benefits to the host plants than inoculated species of three fungi, including *Cenococcum* (Sidle and Shaw, 1987).

Controlled-release fertilizer used in this study did not reduce colonization of roots by mycorrhizal fungi. Reductions in the degree of root colonization by fungi could be related to the suppression of fungal develop- ment by high, toxic concentrations of fertilizer salts in the soil (Maronek et al., 1981, 1982). This was not evident in the current study indicating that there was no toxic effect of the applied fertilizer on my- corrhizal fungi. *Thelephora,* a common morphotype during nursery growth, was partly replaced by other fungi after planting. Low levels of *Amphinema* and MRA on roots of Vapo may reflect the absence of these fungi on nursery roots of this stock type. The fact that seedlings came from greenhouse culture and were growing outdoors for only one season may account for the absence of other mycorrhizal fungi. The apparent reverse relationship between the abundance of E-strain on healthy root systems and MRA on poorer root sys- tems is interesting. Numerous reports have proposed that MRA may display semi-pathogenic behaviour on weak or senescent roots (De la Bastide and Kendrick, 1990; Haug et al., 1988; Livingston and Blaschke 1984).

Successful planting of white spruce seedlings and its future growth may depend on the attributes of seed- ling's root system and on the soil substrate in which these roots are placed. Results of this study are not readily transferable to n,!tural field situatuations with real forest floors. The organic materials of forest floors vary in their physical and chemical properites but ususally have lower pH and C:N ratio than the or- ganic mix used in this study (P. Sanbom, soil scientist, Prince George Forest Region, person. comm., 1998). Also, the organic material used in this study was ho- mogenized and lacked the natural vertical and lateral variability of forest floors. Nevertheless, this study indicated that slow release fertilizer can improve the growth of shoots and roots of white spruce seedlings in spite of the short growing season resulting from late planting. It also showed that root growth of different types of white spruce planting stock differed in rela- tion to the type of the growing medium and in response to the application of controlled-release fertilizer. Test- ing the effectiveness of controlled-release fertilizer on growth of shoots and roots of trees planted into natural and varied forest soils would be a logical expansion of the reported study.

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References

Anonymous 1995 Gromax TM and fertilization at time of planting: a provincial summary of operational and research experience. Regeneration Note #7 , Forest Renewal Section, Silviculture Practices Branch, British Columbia Ministry of Forests.

Austin R C and Strand R F 19()() The use {If slowly soluble fcrtilizer.o; in forest planting in the Pacific Northwest. J. For. 58, 619-627.

Balisky A C, Salonius P, Walli C and Brinkman D 1995 Seedling roots and forest floor: misplaced and neglected aspects of British Columbia's reforestation effort? For. Chron. 71, 59-65.

Burdett A N, Herring L J and Thompson C J 1984 Early growth of planted spruce. Can. J. For. Res. 14, 644-651.

Br(JCkley R P 1988 The effects of fertilization on the early growth of planted seedlings: a problem analysis. Forest Resource Develop- ment Agreement (FRDA). Rep<)rt lA:) **II,** Forestry Canada, British Columbia Ministry of Forests joint publication, Victoria B.C. pp. 16.

Carlson W C and Preisig L 1981 Effects of controlled-release fertil- izers on the shoot and root development of Douglas-fir seedlings. Can. J. For. Res. 11,230-242.

Carter M. 1993. Soil sampling and methods of analysis. Canadian Society of Soil Science. 1993.

Chapin F S III and Van Cleve K 1989 Approaches to studying nutri- ent uptake, use and loss in plants. *In* Plant Physiological Ecology, Eds R W Pearcy, J Ehleringer, HA Mooney and P W Rundel. pp. 185-207. Chapman and Hall, New York.

Coutts M P 1982 Growth of Sitka spruce seedlings with roots di- vided between soils of unequal matric potential. New Phytol 92, 49-61.

Coutts M P and Philipson J J 1976 The influence of mineral nutrition on the root development of trees I. The growth of Sitka spruce with divided root systems J. Exp. Bot. 27, I 102-1111.

Crowley D E, Maronek D M and Hendrix J W 1986. Effect of slow release fertilizers on formation of mycorrhizae and growth of container grown pine seedlings. .J..Envin)n. Hort. 4, 97-101.

Dahlberg A 1990 Effect of soil humus cover on the establishment and development of mycorrhiza on containerized *Pinus sylvestris* L. and *Pinus contorta ssp. latifolia* Engelm. after outplanting. Scand. J. For. Res. 5, 103–112.

De la Bastide P Y and Kendrick B 1990 The *in vitro* effects of benomyl on disease tolerance, ectomycorrhiza formation, and growth of white pine *Pinus strobus* seedlings. Can. J. Bot. 68, 444–448.

Drew M C 1975 Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. New Phytol. 75, 479–90.

Drew M C and Saker L R 1975 Nutrient supply and the growth of the seminal root system in barley. J. Exp. Bot. 26(90), 79–90.

Gagnon J, Langlois C G, Bouchard D and Le Tacon F 1995 Growth and ectomycorrhizal formation of container-grown Douglas-fir seedlings inoculated with *Laccaria bicolor* under four levels of nitrogen fertilization. Can. J. For. Res. 25, 1953–1961.

Hallsby G 1995 Field performance of outplanted Norway spruce: effects of organic matter amendments and site preparation. Can. J. For. Res. 25, 1356–1367.

Haug I, Weber G and Oberwinkler F 1988 Intracellular infection by fungi in mycorrhizae of damaged spruce trees. Eur. J. For. Path. 18, 112–120.

Jurgensen M F, Harvey A E, Graham R T, Page-Dumroese D S, Tonn J R, Larsen M J and Jain T B 1997 Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of inland nortwest forests. For. Sci. 43, 234–251.

Kalra Y P and Maynard D G 1991 Methods Manual for Forest Soil and Plant Analysis. Forestry Canada Information Report NOR-X-319.

Krasowski M J 1998. The development of roots and root systems in white spruce (*Picea glauca* ([Moench] Voss) seedlings and the influence of cultural treatments on root morphology, anatomy and the capacity to conduct water. Ph.D. dissertation, University of Victoria, Victoria, B.C. 273 p.

Krasowski M J, Letchford T, Caputa A, Bergerud W A, Ott P K, 1996 The susceptibility of white spruce seedlings to overwinter injury and their post-injury field responses. New Forests 12, 261–278.

Livingston W H and Blaschke H 1984 Deterioration of mycorrhizal short roots and occurrence of *Mycelium radicis atrovirens* on declining Norway spruce in Bavaria. Eur. J. For. Path. 14, 340–348.

Loopstra E M, Shaw C D III and Sidle R C 1988 Ectomycorrhizal inoculation fails to improve performance of Sitka Spruce seedlings on clearcuts in southeastern Alaska. West. J. Appl. For. 43, 110–112.

Maronek D M, Hendrix J W and Stevens C D 1981 Fertility-mycorrhizal interactions in production of containerized pine oak seedlings. Scientia Horticulturae 15, 283–289.

Maronek D M, Hendrix J W and Cornelius P L 1982 Slow-release fertilizers for optimizing mycorrhizal development in container-grown pine seedlings inoculated with *Pisolithus tinctorius*. HortScience 107, 1104–1110.

Massicotte H B 1994 Characterization of ectomycorrhizal morphotypes. *In* Practical Methods in Mycorrhiza Research. Eds M Brundrett, L Melville and L Peterson, Chap 11, pp. 88–94. Mycologue Publications.

McMinn R G 1982 Ecology of site preparation to improve performance of planted white spruce in northern latitudes. *In* Forest regeneration at high latitudes: experiences from northern British Columbia. USDA For. Serv. Proc. Northwest For. Range Exp. Stn. Misc. Rep. 82–1 pp. 25–32.

Mullin R E 1964 Reduction in growth of white spruce after outplanting. For. Chron. 40, 488–494.

Parviainen J and Tervo L 1989 A new approach for production of containerised coniferous seedlings using peat sheets coupled with root pruning. Forestry 62 (suppl.), 87–94.

Philipson J J and Coutts M P 1977 The influence of mineral nutrition on the root development of trees. II. The effect of specific nutrient elements on the growth of individual roots of Sitka spruce. J. Exp. Bot. 28, 864–871

Robinson D 1994 The responses of plants to non-uniform supplies of nutrients. New Phytol. 127, 635–674.

Rothacher J S and Franklin J F 1964 Fertilizer pellets improve growth of planted Douglas-fir on an unfavorable site. U.S. For. Serv. Tree Plant. Notes 67, 9–11.

Salonius P O 1972 Microbial response to fertilizer treatments in organic forest soils. Soil Sci. 114, 12–19.

Shaw C G III, Sidle R C and Harris A S 1987 Evaluation of planting sites common to a southeast Alaska clear-cut. III. Effects of microsite type and ectomycorrhizal inoculation on growth and survival of Sitka spruce seedlings. Can. J. For. Res. 17, 334–339.

Sidle R C and Shaw C G III 1987 Evaluation of planting sites common to a southeast Alaska clear-cut. IV. Nutrient levels in Ectomycorrhizal Sitka spruce seedlings. Can. J. For. Res. 17, 340–345.

Sutton R F 1972 Constraints on the growth of young white spruce. *In* White spruce the ecology of northern resource. Ed. R G McMinn, Can. For. Serv. North. For. Res. Cent. Inf. Rep. Nor-X-40. pp. 24–39.

Sutton, R F 1991 Soil properties and root development in forest trees: A review Forestry Canada, Ont. Region, Sault Ste. Marie, ON. Inf. Rep. O-X-413, 42 p.

Sutton R F 1993 Mounding site preparation: a review of European and North American experience. New For. 7, 151–192

van den Driessche R 1988 Response of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) to some different fertilizers applied at planting. New For. 2, 89–100.

van Vuuren M M I, Robinson D and Griffiths B S 1996 Nutrient inflow and root proliferation during the exploitation of a temporally and spatially discrete sources of nitrogen in soil. Plant Soil 178, 185–192.

Vyse A 1981 Growth of young spruce plantations in interior British Columbia. For. Chron. 57, 174–180.