Growth and nutrient dynamics of western hemlock with conventional or exponential greenhouse fertilization and planting in different fertility conditions

B.J. Hawkins, D. Burgess, and A.K. Mitchell

Abstract: In many northern forests, low nutrient availability constrains growth of young trees. We tested the efficacy of exponential nutrient application to load western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) seedlings with nutrients to enhance field performance. Seedlings were grown with conventional, constant-rate fertilization (100 mg N·L^{-1}) or with exponentially increasing fertilization at rates of 2% and 3% per day in a greenhouse. Growth and nutrient allocation were characterized. Seedlings from the three greenhouse treatments were then planted in an outdoor nursery experiment for 2 years with NPK fertilizer applied at 10, 25, or 100 mg N·L^{-1}, and in a 3-year field experiment with and without slow-release fertilizer. Seedling height, biomass, and nutrient concentration did not differ greatly among exponential or constant-rate fertilization treatments in the greenhouse. The influence of postplanting fertility, both in the nursery and in the field, outweighed the effect of greenhouse exponential nutrient application. In the outdoor nursery, seedlings from all greenhouse treatments showed increased growth with higher rates of fertilization. In the field, there were no differences in growth among seedlings from the three greenhouse treatments, but fertilization at planting increased growth. The capacity for nutrient loading in container-grown western hemlock was likely exceeded because large quantities of N were applied in all treatments.

Résumé : Dans plusieurs forêts nordiques, la faible disponibilité en nutriments constitue une contrainte pour la croissance des jeunes arbres. Les auteurs ont testé l'efficacité d'une application exponentielle de nutriments pour saturer en nutriments des semis de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) de façon à améliorer leur performance sur le terrain. Les semis ont été cultivés de façon conventionnelle avec un taux de fertilisation constant (100 mg N·L^{-1}) ou avec une fertilisation augmentant de façon exponentielle à des taux de 2 % ou 3 % par jour dans une serre. La croissance et l'allocation des nutriments ont été caractérisées. Les semis des trois traitements en serre ont ensuite été plantés à l'extérieur dans le cadre d'une expérience en pépinière d'une durée de deux ans avec une fertilisation NPK appliquée à des taux de 10, 25 ou 100 mg N·L^{-1}, ou dans le cadre d'une expérience sur le terrain d'une durée de trois ans avec ou sans application d'un fertilisant à décomposition lente. Les traitements de fertilisation à taux constant ou augmentant de façon exponentielle à l'étape de l'étude en serre n'ont pas eu beaucoup d'effet sur la hauteur, la biomasse et la concentration en nutriments des semis. L'influence de la fertilité après la plantation, tant en pépinière que sur le terrain, a dépassé l'effet de l'application exponentielle de nutriments en serre. En pépinière, les semis issus de tous les traitements en serre ont augmenté leur croissance parallèlement à l'augmentation du taux de fertilisation. Sur le terrain, aucune différence de croissance n'a été observée entre les semis des trois traitements en serre, mais la fertilisation après la plantation a augmenté leur croissance. La capacité de saturation en nutriments des semis de pruche de l'Ouest produits en récipients a probablement été dépassée parce que tous les traitements impliquaient de fortes quantités d'azote.

[Traduit par la Rédaction]

Introduction

In many temperate regions, tree seedling growth is constrained because of low nutrient availability (Millard 1996) or competition for nutrients from other vegetation (Grossnickle 2000). Fertilization has improved nutrient availability and conifer seedling growth in several studies in coastal British Columbia (Arnott and Burdett 1988; Weetman et al. 1989; Prescott et al. 1996) and elsewhere in the Pacific Northwest (Carlson 1981; Radwan et al. 1990; Radwan 1992). Broad-

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cast fertilization has proven unsatisfactory in some cases because it stimulates the growth of competing species (McDonald et al. 1994).

Individual tree fertilization at the time of planting can improve seedling growth, but this method is not consistently effective unless competing species are controlled (Brockley 1988). A more efficient way to fertilize seedlings may be to load them with nutrients in the greenhouse. This technique was used with success in eastern Canada, where nutrient-loaded seedlings exhibit better growth than conventionally fertilized seedlings, especially on weed-prone sites (Timmer 1997). Nutrient loading promoted luxury consumption of nutrients and increased nutrient reserves in seedlings. These reserves contributed to improved field performance through increased nutrient retranslocation, new root production, and earlier bud break (Timmer 1997). Greater root:shoot ratio and improved stomatal control of nutrient-loaded plants also contributed to better performance (Timmer and Miller 1991; Imo and Timmer 1992). Nutrient loading may be accomplished through late-season fertilization, high fertilization rates over the entire growing season, or exponential fertilization at high rates (Timmer 1997).

Exponential nutrient loading theory originated in tree seedling nutrition studies in Sweden (Ingestad and Lund 1986; Ingestad 1987). Ingestad (1987) demonstrated that maximum seedling growth occurs when nutrients are applied at a high, exponentially increasing rate matched to maximum plant relative growth rate. Exponential fertilization increases nutrient additions as seedling requirements increase during the period of exponential growth. This results in constant rather than variable internal plant nutrient concentrations when plants increase in size but nutrient supply remains constant. Exponential nutrient loading, where nutrients are supplied at an exponentially increasing rate exceeding seedling growth rate, may be superior to conventional, constant-rate nutrient loading because the danger of nutrient toxicity for young seedlings is minimized and nutrients are accumulated to higher levels (Timmer 1997).

Ideally, nutrient-loaded seedlings have higher internal nutrient concentrations when planted and thus will have the potential for superior growth and an advantage over competing vegetation, relative to conventionally fertilized seedlings. This was accomplished in several earlier field and controlled environment studies (Malik and Timmer 1995, 1996). Nutrient-loaded conifer seedlings can have greater growth and nutrient uptake after outplanting, particularly on nutrient-deficient sites (Timmer and Munson 1991). The effect of nutrient loading on growth and survival may not always be positive (van den Driessche 1991) because higher nutrient levels in seedlings may increase their susceptibility to moisture stress, frost damage, and herbivory (Brown et al. 1996).

Many studies have demonstrated that, given the same quantity of nutrients, exponential nutrient loading enables seedlings to accumulate greater internal nutrient stores than constant-rate fertilization (Timmer et al. 1991; Miller and Timmer 1997; Quoreshi and Timmer 1998; Xu and Timmer 1998; Qu et al. 2003). Despite the demonstrated potential of exponential nutrient loading, there has been little investigation of this technique applied to Pacific Northwest conifers. In most previous studies, nutrients were applied at lower rates than are used in British Columbia nurseries. Earlier studies were conducted mainly with determinate conifer species such as *Pinus resinosa* (Timmer and Armstrong 1987), *Picea glauca*, and *Picea mariana* (Burgess 1990) that stop growth in mid-summer, set bud, and then accumulate nutrient reserves through the late summer and early autumn. Relatively fast-growing, indeterminate conifers such as western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) that continue to initiate leaves and grow as long as the environment is favorable may react differently to exponential nutrient additions by increasing height growth, for example, as well as accumulating nutrients.

In an earlier comparison of the effects of different rates of exponential nutrient addition on the seedling development of two Pacific Northwest conifers, Burgess (1991) found that indeterminate western hemlock responded more favorably to exponential fertilization than did determinate *Pseudotsuga menziesii*. Western hemlock achieved the greatest growth rate and nitrogen (N) uptake efficiency when fertilized at a 6% or 4% exponentially increasing rate, respectively, while constant-rate fertilization produced the greatest N uptake efficiency in *Pseudotsuga menziesii*, and growth was similar in constant-rate and 6% treatments (Burgess 1991). Western hemlock was thus considered to be a promising species for exponential fertilization, but Burgess (1991) concluded that further research was required to determine optimum nutrient levels for different site types.

Our objective was to build on the work of Burgess (1991) and to study growth and nutrient dynamics of western hemlock seedlings subject to conventional fertilization and two rates of exponential fertilization in the greenhouse, over a second and third growing season in different conditions of fertility, both in an outdoor nursery and in the field. The outdoor nursery experiment was designed to evaluate the effects of exponential fertilization on nutrient retranslocation across a wide range of nutrient availabilities. The field experiment was intended to compare the performance of seedlings fertilized conventionally with that of seedlings fertilized exponentially under operational field conditions. In both nursery and field experiments, seedlings were grown in different soil fertilities to test for greenhouse fertilizer treatment × growing site fertility interactions. We hypothesized that exponential nutrient loading at the highest rate would produce seedlings with greater nutrient reserves for retranslocation and thus greater growth after planting, particularly in conditions of low nutrient availability.

Materials and methods

This study comprised a greenhouse nutrient-loading experiment followed by an outdoor nursery experiment and a field planting experiment. Timelines, treatments, and sampling schedules were summarized (Table 1). Details of seedling culture and experimental procedures are described next.

Greenhouse pretreatment phase (5 March – 28 April 1999)

Western hemlock seed from a local source (Mesachie Lake, 48°46′N, 124°10′W, 599 m a.s.l.) was moist stratified at 4 °C for 3 weeks. Over 7000 seeds were sown into Styroblock®

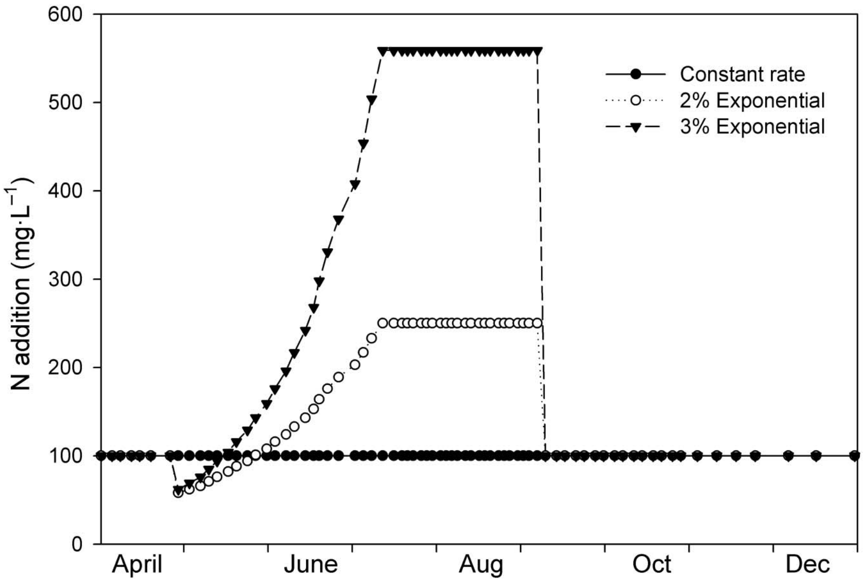
Table 1. Schedule of treatments and measurements for nutrient-loading study with western hemlock.

(A) Greenhouse nutrient-loading experiment.		
Pretreatment phase		
1999	5 Mar.	Sowing
	2 Apr.	Pretreatment (100 mg $N \cdot L^{-1}$)
Nutrient-loading phase		
1999	29 Apr.	Begin nutrient treatments (weekly height measurements)
		Constant rate (twice a week 100 mg $N \cdot L^{-1}$)
		2% per day (twice a week)
		3% per day (twice a week)
	12 July	Maximum treatment levels
		Conventional (twice a w eek 100 mg $N \cdot L^{-1}$)
		2% (twice a week 250 mg $N \cdot L^{-1}$)
		3% (twice a week 559 mg $N \cdot L^{-1}$)
	1 Sept.	Harvest 1 (H1): biomass and NPK allocation
	4 Sept.	End treatments
Hardening phase		
1999	6 Sept.	Hardening treatment (8-h day length)
		Nutrient treatment; all: once a week 100 mg $N \cdot L^{-1}$
	5 Jan.	Harvest 2 (H2): biomass and NPK allocation
Storage phase		
2000	17 Jan.	Lift and store
	6 May	Out of storage — Harvest 3 (H3): biomass and NPK allocation
(B) Outdoor nursery experiment.		
2000	1 May	Begin treatments
		10 mg $N \cdot L^{-1}$
		25 mg $N \cdot L^{-1}$
		100 mg $N \cdot L^{-1}$
		Biweekly height measurements
	15 Aug.	Height, diameter, and biomass and NPK allocation
		1999 leaf, stem, root
		2000 shoot, root
2001	7 Jan.	Height, diameter, and biomass and N allocation
		1999 + 2000 leaf, stem, root
	30 June	Height, diameter, and biomass and N allocation
		1999 leaf, stem, root
		2000 leaf, stem
		2000 + 2001 root
		2001 shoot
	16 Aug.	Height, diameter, and biomass and N allocation
		1999 + 2000 leaf, stem
		2001 shoot
(C) Field experiment.		
2000	4 May	Planting treatments
		Fertilized or not fertilized
	15 Sept.	First-year height, diameter, N, P, K, S, Ca, Mg, Mn
2001	15 Sept.	Second-year height, diameter, N, P, K
2002	15 Sept.	Second-year height, diameter

Note: Greenhouse nutrient-loading experiment: April–September 1999; outdoor nursery experiment: May 2000 – September 2001; field experiment: May 2000 – September 2002).

410A trays (Beaver Plastics Ltd., Edmonton, Alberta) in a greenhouse at the Pacific Forestry Centre, Victoria, British Columbia, in early March 1999. The 80-cm^3 cavities were filled with a 2:1 peat:vermiculite mix with 4.7 kg dolomite lime·m^{-3} added to raise the medium pH to 5.0 and to supply Ca and Mg. The cavities were covered with grit after sow-

Fig. 1. Nitrogen (N) addition on each fertilization date for three greenhouse nutrient treatments from 1 April to 31 December 1999.



ing. All seedlings were irrigated to saturation with nutrient solution containing 100 mg N·L^{-1} (Plant Prod® 20–20–20 All-Purpose Fertilizer, Brampton, Ontario) twice a week from 2 to 26 April 1999 (5.5 mg N per seedling).

Greenhouse nutrient-loading experiment (29 April – 4 September 1999)

Three nutrient treatments were applied from 29 April to 6 September 1999 in the greenhouse. There were approximately 780 seedlings in three replicates of each nutrient treatment. The three nutrient treatments were conventional fertilization, 2% exponential fertilization, and 3% exponential fertilization (Fig. 1). In conventional fertilization, the operational standard of 100 mg N·L^{-1} (514 µS·cm^{-1}) solution was applied throughout. The 2% exponential fertilization treatment began with 58 mg N·L^{-1} (332 µS·cm^{-1}) solution in the first application. The concentration was then increased at an exponentially increasing rate of 2% per day to a maximum of 250 mg N·L^{-1} (1167 µS·cm^{-1}), which was maintained from 12 July to 6 September. The 3% exponential fertilization treatment began with 62 mg N·L^{-1} (349 µS·cm^{-1}) solution. It was increased at an exponentially increasing rate of 3% per day to a maximum of 559 mg N·L^{-1} (2511 µS·cm^{-1}) from 12 July to 6 September. The exponential function used to calculated nutrient additions was

$$N_t = N_s(e^{rt} - 1) - N_{(t-1)}$$

where N_t is the amount of N to be added at time t for a given relative addition rate r; N_s is the initial quantity of N in the seedlings at the initiation of the treatment, and $N_{(t-1)}$ is the cumulative amount of N added, up to and including the last fertilizer addition (Ingestad and Lund 1979).

The chosen rates of exponential nutrient addition were a compromise between maximizing growth rate and avoiding nutrient toxicity. In past studies, maximum growth rate of western hemlock seedlings was 4.7% (Burgess 1991), but at that rate of nutrient addition the nutrient solution would have become too concentrated. The amount of nutrients added is based on the initial N content of the seedlings; thus, in fast-growing western hemlock, the initial N addition is relatively large. An exponential increase in nutrient concentration could then become toxic. The concern over nutrient toxicity led to a cap on exponential addition after 10.5 weeks.

In all treatments, seedling containers were irrigated to saturation with nutrient solution twice per week. On average, 11 mL of solution was added to each cavity as measured by the volume of liquid captured in several containers with equivalent-opening diameters placed adjacent to seedling containers in the path of the spray boom. Conductivity of the applied fertilizer solutions and of leachate collected from under the seedling containers was measured at each fertilizer application. Seedling foliage was rinsed with one pass of water after fertilization.

Hardening phase (6 September 1999 – 17 January 2000)

To induce bud set and hardening, day length was reduced to 8 h using blackout curtains beginning on 7 September. Between 9 September and 30 December, seedlings from all greenhouse nutrient treatments received 21 applications of nutrient solution containing 100 mg N·L^{-1}. By 30 December, the total quantity of N added to each seedling in the control, 2%, and 3% treatments was 83, 134, and 236 mg, respectively.

Cold storage phase (17 January – 6 May 2000)

Operationally, seedlings are usually lifted and cold stored to insure that chilling requirements are met. Seedlings from the three greenhouse nutrient treatments were lifted on 17–18 January 2000 and placed in cold storage at –2 °C.

Experimental measures (nutrient loading, hardening, and storage phases)

During greenhouse culture, seedling heights and diameters were measured every 2 weeks (n = 24 per treatment and replicate). Biomass was determined from destructive samples

(n = 16 per treatment and replicate) made (*i*) at the end of the nutrient-loading phase (Harvest 1 (H1): 1 September 1999), (*ii*) at the end of the hardening phase prior to lifting for cold storage (Harvest 2 (H2): 5 January 2000), and (*iii*) when the trees were taken out of cold storage for planting (Harvest 3 (H3: 6 May 2000). Roots were washed free of soil, and seedlings were divided into root, stem, and foliage components, which were dried for 48 h at 70 °C and weighed. Individual tree biomass data were analysed in a nested analysis of variance (ANOVA) (three replicates within three nutrition treatments) with the general linear model

$$Y_{ijkl} = \mu + A_i + B_{j(i)} + \varepsilon_{k(ij)}$$

where levels of factors were as follows: nutrient treatment (i = 1, 2, 3), replicate (j = 1, 2, 3), and seedling (k = 1, 2,…, 16). Treatment means were differentiated by Tukey's studentized range test using tree within replicate as the error term (SAS Institute Inc. 1989).

Seedlings were sampled (bulked samples from six trees per treatment and replicate) at H1, H2, and H3 and partitioned for root, stem, and foliage nutrient analysis (N, phosphorus (P), potassium (K)), determined by the combustion technique (modified Dumas) on a LECO FP 228 nitrogen determinator (Sweeney and Rexroad 1987). Data from bulked samples (n = 1 per treatment and replicate) were analysed in a nested ANOVA (three replicates within three nutrition treatments), and treatment means differentiated by Tukey's studentized range test.

Soil samples were taken at H1, H2, and H3 from each treatment and replicate (n = 1) and analysed for total N (%N), NH_4, NO_3 (Sweeney and Rexroad 1987), available P (micrograms per gram) (Bray and Kurtz 1945), and pH (Kalra and Maynard 1991).

Outdoor nursery experiment (8 May 2000 – 16 August 2001)

On 8–11 May 2000, 270 seedlings averaging 14.5 cm height and 3.1 mm root-collar diameter (±1 SD) were selected from each greenhouse nutrient treatment. Seedlings were transplanted into 3-L pots containing an 8:5 (*v*/*v*) mixture of peat and sand to which 3.1 kg coarse dolomite lime·m^{-3} was added. Pots were placed in an outdoor nursery compound at the Pacific Forestry Centre.

The 270 seedlings from each greenhouse nutrient treatment were divided among three replicates of three fertility treatments; thus there were 30 seedlings per greenhouse treatment, nutrient treatment, nursery fertility treatment, and replicate. The nursery fertility treatments were 10, 25 and 100 mg N·L^{-1} (Green Valley 20–20–20). Pots were fertilized with nutrient solution to saturation once per week from late May to the end of August 2000. Pots were also irrigated with water, if needed, to prevent drying.

Twenty-five seedlings per replicate were measured every 2 weeks for height growth in 2000. Four seedlings per replicate were harvested as follows: in early August 2000, after shoot extension; in early January 2001, during the dormant season; in late June 2001, immediately after shoot extension; and in mid-August 2001. Harvested seedlings were measured for height and root-collar diameter and divided into needles, stems, and roots by age-class (Table 1). Each seedling part was oven-dried and weighed, and then parts were bulked by replicate for analysis of N, P, and K as described previously.

Biomass and nutrient data from harvests in 2000 and 2001 were analyzed with a 3 × 3 factorial ANOVA (SAS Institute Inc. 1989). The general linear model was

$$Y_{ijkl} = \mu + A_i + B_j + AB_{ij} + C_{k(ij)} + \varepsilon_{l(ijk)}$$

where levels of factors were as follows: greenhouse nutrient treatment (i = 1, 2, 3), nursery fertility treatment (j = 1, 2, 3), replicate (k = 1, 2, 3), and seedling (l = 1, 2, 3, 4). Replicate was used as the error term to test the main effects and their interaction. Percent nutrient concentration data were arcsin square-root transformed prior to analysis. Means were compared using Tukey's studentized range test.

Field experiment (8 May 2000 – 15 September 2002)

Between 26 April and 4 May 2000, 1536 seedlings from the three greenhouse nutrient treatments were planted on a site near Jordan River, British Columbia (48°33′N, 124°03′W, 700 m a.s.l.). The site was clear-cut in 1999 and was considered of low productivity (Western Forest Products Ltd. Silvicultural Prescription). Four blocks were set up on the site, each containing 384 seedlings divided among the 3 greenhouse nutrient treatments × 2 field fertilization treatments. The field fertilization treatments included (*i*) an unfertilized control and (*ii*) seedlings fertilized at the time of planting with a 9 g forest blend (26–12–6) Silva Pak placed 2.5 cm from the seedling and 2.5 cm below the surface upslope from the seedling.

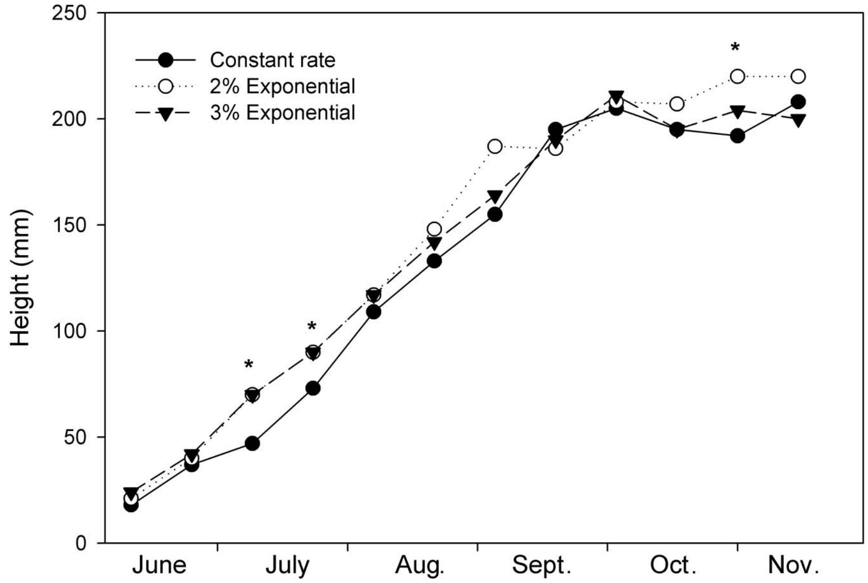
The 3 greenhouse nutrient treatments × 2 field fertilization treatments made up the six field treatments. Each block was divided into six plots, and the six treatments were randomly allocated. Sixty-four seedlings were planted in each plot in an 8 × 8 arrangement at 3-m spacing. The interior 16 seedlings per plot (4 × 4) were measured for height and root-collar diameter immediately after planting and in September 2000, 2001, and 2002. Some seedlings were subject to browsing damage from deer, and these were not included in the analysis. Current foliage of a sample of seedlings outside the interior core were harvested for analysis of foliar N, P, K, Ca, Mg, Mn, Al, and S concentration in September 2000 and for N, P, and K concentration in 2001. Three bulked samples from about 20 plants per treatment per block were collected in 2000, and one bulked sample was collected in 2001.

Growth and nutrient data were analyzed with a one-way randomized block design (SAS Institute Inc. 1989). The general linear model for analysis of variance was

$$Y_{ijkl} = \mu + B_i + F_j + BF_{ij} + \varepsilon_{l(ij)}$$

where levels of factors were as follows: block (i = 1, 2, 3, 4), nutrient treatment × field fertilizer treatment (j = 1, 2,…, 6), and seedling (l = 1, 2,…, 16). F_j was considered a fixed factor, thus the error term used to test this effect was BF_{ij}. Orthogonal contrasts were used to compare among greenhouse nutrient treatments and between field fertilizer treatments. Percent nutrient concentration data were arcsin square-root transformed prior to analysis.

Fig. 2. Height of western hemlock seedlings in three greenhouse nutrient treatments in 1999. SE hidden by symbols. "*" indicates dates on which seedling heights differed significantly ($P < 0.05$) among treatments.



Results

Greenhouse nutrient-loading experiment

Differences in height among seedlings from the three greenhouse treatments were small, and by the time of lifting for cold storage (H2) there were no significant differences in seedling height among the greenhouse nutrient treatments (Fig. 2). There was no apparent effect of the treatments on the duration of shoot growth.

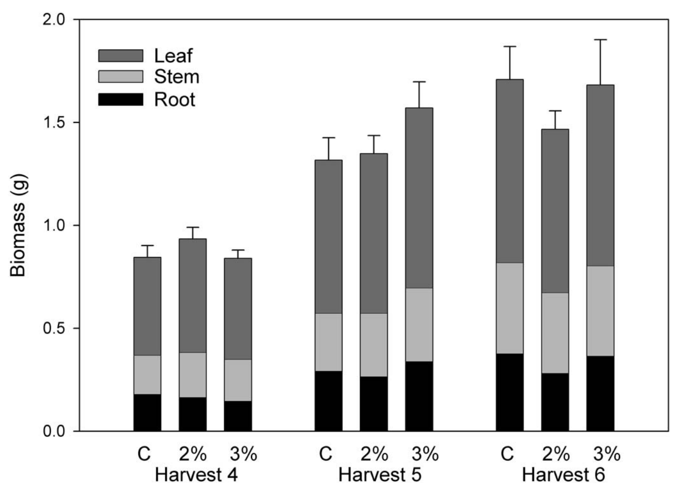
Nutrient treatment had no significant effect on seedling biomass or any of its components (root, stem, leaf) after the exponential fertilization phase (H1), after hardening (H2), or after cold storage (H3) (Fig. 3). Root:shoot ratio was not significantly different among the nutrient treatments on any of the harvest dates.

At the end of the exponential fertilization phase (H1), N concentration in roots, stems, and leaves was greater in 3% seedlings than 2% or constant-rate seedlings (Bonferroni adjusted $P < 0.004$) (Table 2). Thereafter, N levels increased slightly in roots, stems, and leaves of constant rate and 2% seedlings, so there were no significant differences in N concentrations in any of the seedling parts at H2 or H3 (Table 2).

Applying a nutrient solution containing N, P, and K at exponentially increasing rates did not result in nutrient loading of P or K. Concentrations of P were highest in root tissue from the constant-rate treatment at H1, the end of the exponential fertilization phase (Table 2). After the hardening phase (H2) and at the end of cold storage (H3), foliar and root P concentrations were stable across the three nutrient treatments (Table 2). Root K concentrations were lowest in the 2% and 3% treatments at the end of the exponential fertilization phase (H1) (Table 2). Foliar K concentrations did not differ significantly among nutrient treatments or among harvest dates (Table 2).

To confirm that exponential fertilization increased levels of available nutrients for seedlings, chemical analyses of the growing medium at H1 showed average soil N concentration in the constant-rate, 2%, and 3% treatments to be 0.67% ± 0.01%, 0.88% ± 0.01%, and 1.18% ± 0.02%, respectively. Soil P concentrations were 0.02%, 0.04%, and 0.06%, respectively. Once seedlings entered the hardening phase with equal nutrient additions in all treatments, soil nutrients converged. At H2, soil N concentrations ranged from 0.83% ± 0.04% in the 3% treatment to 0.73% ± 0.02% in the constant-rate treatment. Available P ranged from 0.025% to 0.022%.

Fig. 3. Biomass of western hemlock seedling components at the end of the nutrient-loading treatments (H1, 1 September 1999), prior to cold storage at the end of the hardening phase (H2, 15 January 2000), and after cold storage (H3, 6 May 2000) under a constant-rate nutrient application (C) and under 2% and 3% exponential nutrient application rates. Means (±SE) within biomass components are not significantly different ($P < 0.05$).



Outdoor nursery experiment

Height of exponentially fertilized seedlings in the outdoor

Table 2. Mean N, P, and K concentrations (%) (±SE in parentheses, $n = 3$) in roots, stems, and leaves of western hemlock seedlings grown with nutrients added at a constant (C), 2%, or 3% addition rate at the end of the exponential feeding stage (H1), prior to lifting for cold storage (H2), and after cold storage (H3).

	Root			Stem			Leaf		
Harvest	C	2%	3%	C	2%	3%	C	2%	3%
Nitrogen									
H1	1.54	1.71	**2.14**	0.96	0.95	**1.34**	2.32	2.30	**2.75**
	(0.1)	(0.08)	(0.02)	(0.05)	(0.05)	(0.06)	(0.19)	(0.05)	(0.07)
H2	1.77	1.87	1.85	1.15	1.10	1.18	2.2	2.40	2.39
	(0.08)	(0.07)	(0.04)	(0.06)	(0.06)	(0.04)	(0.09)	(0.04)	(0.05)
H3	2.08	2.08	1.95	1.20	1.17	1.48	2.41	2.30	2.68
	(0.07)	(0.07)	(0.16)	(0.05)	(0.04)	(0.15)	(0.08)	(0.03)	(0.08)
Phosphorus									
H1	**0.67**	0.49	0.40	0.28	0.24	0.28	0.44	0.34	0.41
	(0.01)	(0.04)	(0.01)	(0.02)	(0.004)	(0.009)	(0.01)	(0.02)	(0.007)
H2	0.39	0.34	0.31	0.15	0.14	0.14	0.43	0.40	0.36
	(0.02)	(0.01)	(0.01)	(0.005)	(0.003)	(0.005)	(0.01)	(0.01)	(0.01)
H3	0.37	0.34	0.32	0.24	0.23	0.22	0.42	0.37	0.35
	(0.01)	(0.02)	(0.02)	(0.009)	(0.03)	(0.02)	(0.01)	(0.01)	(0.004)
Potassium									
H1	**1.30**	0.91	0.64	1.43	1.39	1.46	1.49	1.45	1.55
	(0.08)	(0.04)	(0.01)	(0.08)	(0.03)	(0.04)	(0.004)	(0.05)	(0.05)
H2	0.66	0.57	0.57	0.46	0.46	0.43	1.40	1.39	1.31
	(0.05)	(0.02)	(0.01)	(0.01)	(0.003)	(0.02)	(0.02)	(0.02)	(0.05)
H3	0.59	0.61	0.54	0.80	0.84	0.81	1.34	1.35	1.29
	(0.01)	(0.02)	(0.01)	(0.02)	(0.05)	(0.03)	(0.04)	(0.05)	(0.03)

Note: Numbers in bold indicate values that are significantly different within a plant part and harvest.

nursery was significantly ($P < 0.05$) greater than that of constant-rate seedlings until June 2001, when 2%, 3%, and constant-rate seedlings averaged 47.3 ± 2.5, 45.5 ± 2.5, and 42.4 ± 2.0 cm in height, respectively. Seedling root-collar diameter in the 3% treatment was consistently, but not significantly, greater than diameter of seedlings in the other treatments during the same time period.

Near the end of the first growing season in August 2000, mean biomass of seedlings in 3%, 2%, and constant-rate treatments was 9.95 ± 0.35, 9.39 ± 0.36, and 8.76 ± 0.43 g, respectively ($P = 0.09$). By January 2001 there were no longer significant differences in total biomass among greenhouse nutrient treatments.

Examining seedling components showed that biomass and N contents of leaves and stems in the outdoor nursery were not significantly affected by greenhouse nutrient treatment; however, root biomass and N content were affected. In August 2000 and June 2001, N content of roots formed in 2000 and 2001 was significantly greater ($P < 0.02$) in exponentially fertilized seedlings (Fig. 4). N content of leaves formed in 1999 and 2000 decreased as the plants increased in size, which was assumed to be evidence of retranslocation of N to newly formed tissues. Percent N retranslocation was generally highest in the constant-rate nutrient treatment (Table 3A).

Growth of all seedling components increased with higher fertility in the nursery (Fig. 5). In August 2000, after 2 months of fertilization, only new stem biomass was significantly affected, but by January 2001 increased levels of fertilization significantly increased biomass of all seedling components except the 1999 leaves. By June and August 2001, biomass of all seedling components increased with fertilization (Fig. 5).

N concentrations in all seedling components increased significantly with increasing fertility, thus N contents also increased (Fig. 6). The effects of greenhouse nutrient treatments were overwhelmed by the effect of nursery fertility treatment. Even in the lowest fertility treatment, seedling N content increased with time (Fig. 6). The 2 mg difference in N content between constant-rate and 3% seedlings in May 2000 (Fig. 4) was small compared to the 99 mg increase in N content between May and August 2000 in the 10 $mg \cdot L^{-1}$ treatment (Fig. 6). Seedling P and K concentrations generally increased with fertility treatment except in June 2001, when P and K concentrations of the new needle flush were lowest in the high-fertility treatments (data not shown).

Trends in both the quantity and percentage of N retranslocated differed among the nursery fertility treatments. Retranslocation from first-year (1999) needles was greatest in the 2000 growing season in the low-fertility treatment (10 $mg \cdot L^{-1}$), but in the 2001 growing season, retranslocation from leaves formed both in 1999 and 2000 was greatest in the high-fertility treatment (100 $mg \cdot L^{-1}$) (Table 3B). P and K retranslocation from 1999 leaves in the three fertility treat-

Fig. 4. Nitrogen (N) content of western hemlock seedling components in the outdoor nursery experiment averaged for constant-rate, 2%, and 3% greenhouse nutrient treatments in May 2000, August 2000, January 2001, and June 2001. Values below the zero line indicate root N content. Values above the zero line indicate shoot N content.

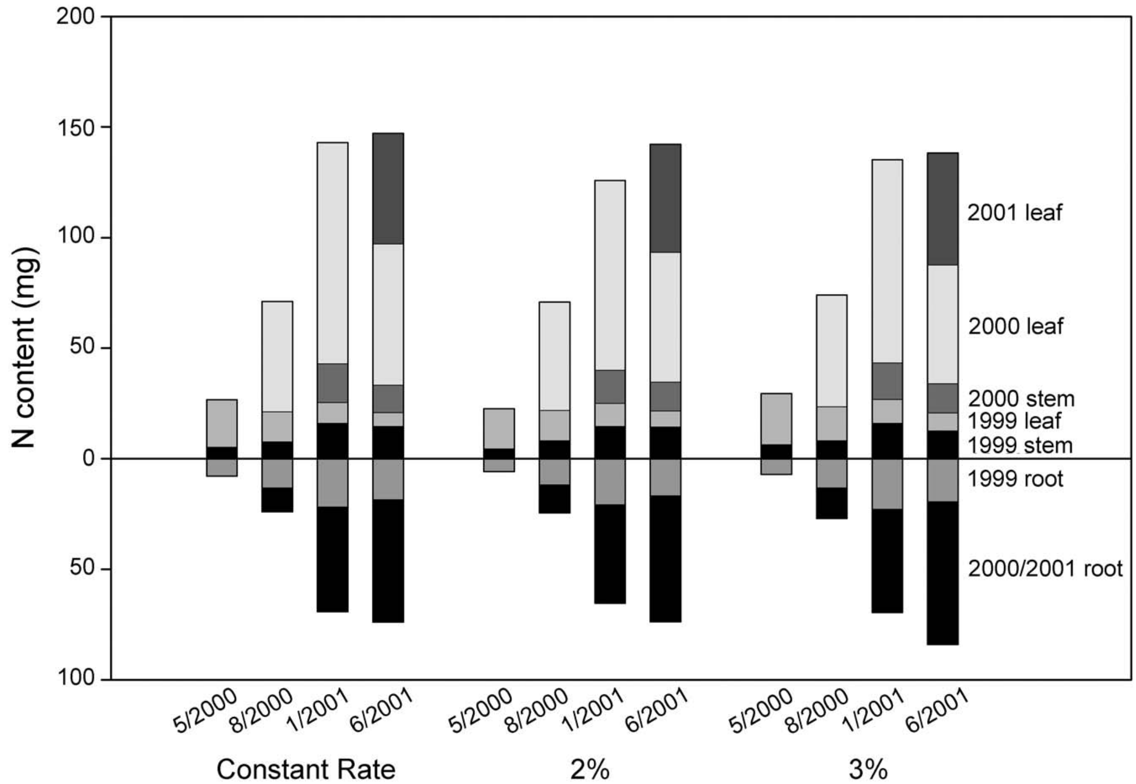


Table 3. Seasonal nitrogen retranslocation in western hemlock seedlings in the outdoor nursery experiment averaged for (A) greenhouse nutrient treatments or (B) nursery fertility treatments.

(A) Greenhouse nutrient treatment.

	Constant		2%		3%	
Season*	N (mg)	N (%)	N (mg)	N (%)	N (mg)	N (%)
1999 leaves						
Summer 2000	7.6	36	4.7	25	7.7	33
Autumn 2000	4.2	30	3.3	26	4.1	25
Spring 2001	2.9	30	3.4	24	3.9	30
2000 leaves						
Spring 2001	35.9	25	29.1	22	30.4	16

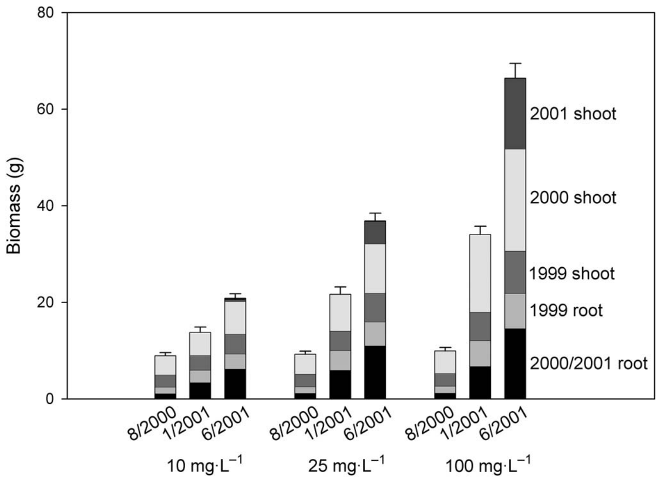
(B) Nursery fertility treatment.

	10 mg·L^{-1}		25 mg·L^{-1}		100 mg·L^{-1}	
Season	N (mg)	N (%)	N (mg)	N (%)	N (mg)	N (%)
1999 leaves						
Summer 2000	8.9	42	7.9	37	3.2	15
Autumn 2000	5.2	41	2.4	18	4.0	21
Spring 2001	1.1	15	3.0	26	6.1	44
2000 leaves						
Spring 2001	0.6	2	9.7	18	85.2	44

Note: Retranslocation from leaves formed in 1999 and 2000 was calculated and is presented as the decrease in mean N content (milligrams) and the percent decrease in N content from the previous harvest (%).

*Summer 2000: May–August 2000; autumn 2000: August 2000 – January 2001; spring 2001: January–June 2001.

Fig. 5. Biomass of western hemlock seedling components in three fertility treatments (10, 25 and 100 mg N·L^{-1}, in the outdoor nursery experiment in August 2000, January 2001, and June 2001.



ments showed a similar pattern to N (data not shown). There was little to no retranslocation of P or K from leaves formed in 2000.

Field experiment

In the field there were no significant interactions of greenhouse nutrient treatment and field fertilizer treatment for any morphological or physiological parameters. Three years after outplanting (September 2002), the greenhouse nutrient treatments did not differ significantly in their effect on total height or height increment of seedlings (Table 4). Root-collar diameter was significantly ($P < 0.05$) greater in the 3% nutrient treatment than in the 2% and constant-rate treatments (Table 4). Seedlings fertilized at the time of planting had significantly ($P < 0.01$) greater total height, annual height increment, and root-collar diameter than did unfertilized seedlings three growing seasons after planting (Table 4).

One growing season after planting (September 2000), N concentration in 3% seedlings was 1.69% ± 0.12%, significantly greater ($P < 0.04$) than in 2% (1.49% ± 0.12%) or constant-rate (1.53% ± 0.13%) seedlings. Ca and S concentrations were also higher, on average, in 3% seedlings (data not shown). Seedlings receiving fertilizer at the time of planting had significantly ($P < 0.001$) greater N concentrations than did unfertilized seedlings (2.10% ± 0.06% and 1.04% ± 0.03%, respectively). Other elements did not differ significantly among field fertilization treatments.

Two years after planting (September 2001), neither greenhouse nutrient treatment nor fertilizer at planting had a significant effect on nutrient concentration of new foliage. Foliar N concentrations averaged 1.51% ± 0.03%. Concentrations of P and K were greatest in seedlings that were not fertilized at planting (data not shown).

Discussion

Greenhouse nutrient-loading experiment

Exponential nutrient loading of first-year western hemlock

Table 4. Mean total height, mean annual height increment, and root-collar diameter of western hemlock seedlings three growing seasons after planting in the field experiment, averaged for greenhouse nutrient treatments or field planting with (F1) or without (F0) fertilizer.

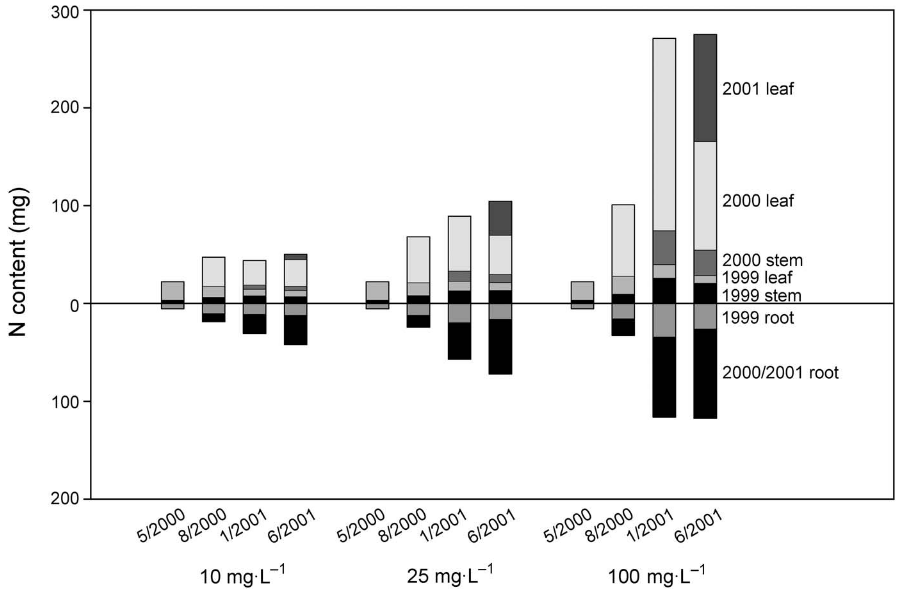
	Height (cm)	Height increment (cm)	Root-collar diameter (mm)
Greenhouse nutrient treatment			
Constant	73.3±2.0a	27.0±1.1a	9.2±0.3a
2%	67.9±1.8a	27.1±1.1a	9.0±0.3a
3%	74.4±1.9a	30.2±1.2a	10.4±0.3a
Field fertilization treatment			
F0	67.3±1.4a	26.6±1.0a	8.4±0.2a
F1	76.0±1.6b	29.7±1.2b	10.7±0.2b

Note: Means (±SE) followed by the same letter are not significantly different within a treatment.

seedlings in the greenhouse resulted in minor improvements in growth and nutrient status. Immediately after the exponential fertilization phase (H1), plant N concentrations were elevated in 3% seedlings, but this did not result in significantly greater height or biomass (Table 2, Fig. 3). At that time, constant-rate, 2%, and 3% seedlings had received 58, 108, and 211 mg N, respectively. The differences in N concentrations among treatments declined during the hardening phase, when all seedlings were supplied with 100 mg N·L^{-1}. At the end of the hardening period (H2), constant-rate, 2%, and 3% treatments had received a total of 83, 134, and 236 mg N per seedling, but these differences translated into only a slight increase in total biomass in 3% seedlings (Fig. 3) and plant N concentrations in 2% and 3% seedlings (Table 2). The convergence of N concentrations during a hardening phase, when all treatments are supplied with uniform quantities of N, was also observed in *Picea mariana*, although exponentially fertilized seedlings provided with the greatest quantity of N were always larger (Table 5, study *c*) (Boivin et al. 2002).

The trend of smaller plant size but greater N concentration in exponential seedlings compared to constant-rate seedlings given the same quantity of N was seen in other studies (Table 5, studies *a*, *b*, *o*, *p*). What is surprising about our study is that the much greater quantities of N applied to the exponentially fertilized western hemlock seedlings did not greatly increase their size or N concentration. Our study applied much higher quantities of N to individual seedlings compared to studies with conifers from eastern North America (Table 5, studies *a*–*j*), and we surmise that at these high levels of fertilization, even constant-rate seedlings had more N than could be taken up by the given root volume, and thus seedling growth and N concentrations were near a maximum in all treatments. This is supported by the high foliar N concentrations in seedlings from all greenhouse treatments (Table 2). Foliar N concentrations greater than 2% were achieved only at a 6% exponential addition rate in an earlier study with western hemlock (Burgess 1991). If we applied sufficient or excess nutrients in all treatments, it would account for the uniform seedling size and N content across all treatments and the declining efficiency of uptake from 41%

Fig. 6. Nitrogen (N) content of western hemlock seedling components in the outdoor nursery experiment averaged for 10, 25, and 100 mg·L^{-1} nursery fertility treatments in May 2000, August 2000, January 2001, and June 2001. Values below the zero line indicate root N content. Values above the zero line indicate shoot N content.



to 21% to 15.5% of applied N in constant-rate, 2%, and 3% treatments, respectively.

Outdoor nursery experiment

In two subsequent growing seasons in an outdoor nursery, western hemlock seedlings from the 3% greenhouse treatment had significantly greater height and root growth than did 2% or constant-rate seedlings. Seedling height in the 3% treatment was 7% greater in August 2000 and 10% greater in August 2001 than height of constant-rate seedlings. Although differences in biomass were not statistically significant among greenhouse nutrient treatments, mean biomass of seedlings in the 3% treatment was 13% greater than that of seedlings in the constant-rate treatment in August 2000 and 8% greater in June 2001.

We did not observe a greater effect of exponential greenhouse fertilization in low-fertility conditions in either the outdoor nursery experiment or the field. This contrasts with studies by Xu and Timmer (1998, 1999), who conducted exponential nutrient loading with Chinese fir (*Cunninghamia lanceolata*), an indeterminate species like western hemlock. Chinese fir seedlings provided with 15 or 45 mg N at exponentially increasing rates had 42% greater biomass on soils of low fertility (Table 5, study *m*), but only 8% greater biomass on high-fertility soils. Seedlings in all our treatments received greater quantities of N in the greenhouse than did the Chinese fir seedlings, however, and our seedlings were 50% larger. Significant improvements in growth due to exponential fertilization do not always occur in other pot trials with low-fertility soils (e.g., Timmer et al. 1991) (Table 5, study *a*).

Exponential nutrient loading of western hemlock seedlings in the greenhouse did not result in a significant increase in nutrient reserves for retranslocation in the following growing seasons relative to the constant-rate seedlings. Foliar N content was slightly higher in the 3% treatment at the end of cold storage, but this difference was not significant. There were only small differences in retranslocation noted among the nutrient treatments in the outdoor nursery (Table 3). In all nursery treatments, the additional N available for retranslocation in the 3% treatment seedlings was a small fraction of N taken up in the second growing season.

Whole-plant N concentrations were high in western hemlock seedlings from all greenhouse nutrient treatments. An adequate whole-plant N concentration for western hemlock was reported at 1.87% (van den Driessche 1976), and maximum whole-plant N concentration of western hemlock seedlings provided free access to nutrients in hydroponic culture was 1.9% (Brown et al. 1996). In our study, whole-plant N concentrations ranged from 2.0% in the 2% treatment to 2.26% in the 3% treatment at the time of planting; thus, there appears to have been a large pool of N available for retranslocation in all treatments. Whole-plant N concentrations in all treatments were greater than those of 22-week-old Chinese fir exponentially fertilized with 15 mg N per seedling; thus, we did not observe the development of N deficiency in constant-rate seedlings observed in Chinese fir seedlings (Table 5, study *m*).

In 2000, when fertility treatments were applied in the outdoor nursery experiment, N application in the 10 mg·L^{-1} treatment was insufficient to supply the demands of growing shoots and N was retranslocated from older leaves. In the 100 mg·L^{-1} fertility treatment, however, high external N supply reduced the demand for internal sources of N and rates of retranslocation were relatively low. In 2001, when no N was supplied, we suggest N reserves in 10 mg·L^{-1} plants were already depleted, therefore N retranslocation was low. In 100 mg·L^{-1} plants, N reserves were still available, thus retranslocation was greater from 1- and 2-year-old leaves of these plants. Greater quantities of new shoot N retranslocated from internal sources when seedlings are planted on soils of

Table 5. Biomass and nitrogen (N) concentration of seedlings of conifer species subject to conventional (C) or exponential (E) fertilization in the nursery at the end of the nursery fertilization period and after one growing season in low-fertility bioassays or field sites.

		Nursery			Field (second growing season)		
Fertilization	N (mg/tree)	Biomass (mg)	N (%)	Regime	Biomass (mg)	N (%)	Additional information
(*a*) *Picea mariana* (Timmer et al. 1991)							
C	10	536*	1.95*	70-cm^3 containers; 20–20–20 fertilizer†; weekly nutrient additions for 12 weeks	2 260	1.19	Outdoor soil bioassay OG11 – *Ledum*
E	10	415*	2.62*		—	—	
ModE	10	332*	2.49*		2 570	1.25	
C	20	619*	2.42*		2 960	1.11	
E	20	596*	2.95*		—	—	
ModE	20	377*	2.49*		3 260	1.08	
(*b*) *Picea mariana* (Quoreshi and Timmer 1998, 2000)							
C	12.5	594	1.24	110-cm^3 containers; 20–10–20 fertilizer; weekly nutrient additions for 18 weeks; nonmycorrhizal seedlings	1 528*	1.14*	Greenhouse soil bioassay, hardwood–*Alnus* site
E	12.5	495	1.70		1 528*	1.23*	
E	25	634	1.76		1 805*	1.18*	
E	50	685	1.95		2 361*	1.27*	
(*c*) *Picea mariana* (Boivin et al. 2002)							
C	14.7	221	2.04	40-cm^3 containers; 20–20–20 fertilizer; weekly nutrient additions for 15 weeks	600	2.62	After 14 additional weeks in nursery, 12 mg N applied to all treatments
C	41.2	287	2.54		790	2.10	
E	38.7	318	2.62		795	2.47	
E	57.6	286	2.91		810	2.88	
(*d*) *Picea mariana* (Miller and Timmer 1997)							
C	15	234*	2.05*	40-cm^3 containers; 20–20–20 fertilizer; weekly nutrient additions for 14 weeks	436*	1.30*	After 106-day hardening treatment, no fertilizer
C	40	286*	2.52*		618*	1.32*	
E	40	318*	2.61*		650*	1.47*	
E	60	286*	2.91*		689*	2.37*	
(*e*) *Picea mariana* (Malik and Timmer 1998)							
C	10	990	1.33	40-cm^3 containers; 20–20–20 fertilizer; weekly nutrient additions for 18 weeks; measured at time of planting	1 864*	1.00*	No herbicide, OG10 site
E	32	1030	2.24		2 734*	1.29*	
E	64	1110	2.41		3 230*	1.31*	
(*f*) *Picea mariana* (Imo and Timmer 2001, 2002)							
C	10	810	1.50	40-cm^3 containers; 20–20–20 fertilizer; weekly nutrient additions for 22 weeks	2 700	1.33	Values for greenhouse soil bioassay OG4, feathermoss–weedy
E	64	810	3.05		4 300	1.18	
C	10	810	1.50		735*	1.30*	Mixedwood–herb, untreated
E	64	810	3.05		1 647*	1.33*	
(*g*) *Picea mariana* (Salifu and Timmer 2003)							
—	0	34	2.04	40-cm^3 containers; 20–20–20 fertilizer; weekly nutrients for 15 weeks			
C	10	400	1.50				
E	30	459	2.44				
E	65	472	3.18				
E	80	390	3.32				
(*h*) *Picea mariana* (Malik and Timmer 1995, 1996)							
C	10	990	1.36	40-cm^3 containers; 20–20–20 fertilizer; constant feed	2 170	1.06	Greenhouse soil bioassays OG7, no herbicide
C	32	970	2.04		2 550	1.17	
C	10	990	1.36		2 100	1.38	Mixedwood OG7, no herbicide
C	32	970	2.04		2 420	1.54	
(*i*) *Pinus resinosa* (Timmer and Armstrong 1987)							
C	39	227	2.68	70-cm^3 containers; 100:13:65 (N–P–K); semiweekly nutrient additions for 12 weeks			
E	9.75	266	2.10				
E	19.5	269	2.22				
E	39	270	2.48				

Table 5 (*concluded*).

		Nursery			Field (second growing season)		
Fertilization	N (mg/tree)	Biomass (mg)	N (%)	Regime	Biomass (mg)	N (%)	Additional information
(*j*) *Pinus resinosa* (Miller and Timmer 1994)							
E	25	1029	1.73	70-cm^3 containers; 20–20–20 fertilizer; weekly nutrient additions for 12 weeks; well watered			
E	75	1382	2.66				
(*k*) *Pseudotsuga menziesii* (Burgess 1991)							
C	27.07	1040	1.43	62-cm^3 cavities; 100:13:65 (N–P–K); semiweekly nutrient additions for 18 weeks; measured after 10-week treatment			
E	9.98	720	0.64				
E	12.28	800	0.75				
E	26.28	850	1.42				
E	83.05	1150	2.21				
(*l*) *Tsuga heterophylla* (Burgess 1991)							
C	27.07	350	1.74	62-cm^3 cavities; 100:13: 65 (N–P–K); semiweekly nutrient additions for 18 weeks; measured after 10-week treatment			
E	9.33	230	0.75				
E	10.35	260	0.76				
E	16.51	370	1.33				
E	41.48	540	1.72				
(*m*) *Cunninghamia lanceolata* (Xu and Timmer 1998, 1999)							
—	0	386*	0.7*	110-cm^3 cavities; 20–20–20 fetilizer; weekly nutrient additions for 20 weeks	—	—	Measured after 150 days growth with 0 mg N
C	15	743*	1.26*		11 600	0.80	
E	15	910*	1.84*		—	—	
E	45	951*	3.12*		16 500	0.85	
E	75	892*	3.21*		—	—	
(*n*) *Larix kampferi* (Qu et al. 2003)							
C	10	289	0.91	287-cm^3 cavities; 15–15–15 fertilizer; weekly nutrient additions for 12 weeks			
E	10	293	1.31				
E	20	326	1.64				
E	40	421	2.10				
(*o*) *Larix gmelinii* × *Larix kampferi* (Qu et al. 2003)							
C	10	233	0.76	287-cm^3 cavities; 15–15–15 fertilizer; weekly nutrient additions for 12 weeks			
E	10	231	1.15				
E	20	260	1.39				
E	40	416	1.52				
(*p*) *Picea glauca* (McAlister and Timmer 1998)							
—	0	36	2.22	Bare-root seedling nursery; NH_4NO_3 (year 1) and $NH_4H_2PO_4$ (year 2, 3); broadcast granular fertilizer at 15- to 20-day intervals; measured after 1 year in nursery	7 700	0.74	145 days after planting (year 4)
C	86.5‡	59	2.48		16 800	0.73	
C	173.5‡	65	2.83		22 900	0.81	
E	173.5‡	61	2.93		23 600	0.90	

Note: ModE, modified exponential with increased nutrients at the start of the fertilization period.
*Estimated from figures.
†20–20–20 fertilizer = $N–P_2O_5–K_2O$ = 20N:45P:80K.
‡Calculated from total rates of N addition/ha over 3 years in the nursery divided by 750 seedlings·m^{-3}.

very low fertility have also been observed in Chinese fir (Xu and Timmer 1999) and black spruce (Salifu and Timmer 2001). We observed a similar trend for P and K that was not seen in black spruce (Salifu and Timmer 2001). In Douglas-fir (*Pseudotsuga menziesii*) and western redcedar (*Thuja plicata*), retranslocation of N, P, and K were all greater when seedlings were grown at low rather than high rates of nutrient application (Hawkins and Henry 1999).

Field experiment

In the field experiment, 3% seedlings had significantly greater foliar N concentrations at the end of the first growing season after outplanting. At the end of the third growing season, 3% seedlings had approximately 10% greater root-collar diameter and height increment than did 2% or constant-rate seedlings. Greater root-collar diameter of 3% seedlings may have indicated greater root biomass as observed in the nursery experiment, where the allocation of biomass to new roots was improved by exponential fertilization.

The effect of postplanting fertilization with approximately 2.3 g N per seedling far outweighed the effects of greenhouse nutrient treatments. Xu and Timmer (1999) concluded that nutrient loading of Chinese fir in the greenhouse was more effective in promoting biomass production than postplanting fertilization when they compared the effect of equivalent additions of N applied via nutrient loading or in granular form after planting.

Many studies have shown that, compared to seedlings fertilized at a constant rate, higher levels of N applied exponentially during greenhouse culture enhance early growth of black spruce (*Picea mariana*) and red pine (*Pinus resinosa*) seedlings transplanted to forest soils (Table 5, studies *a*, *b*, *e*, *f*). Although nutrient loading of seedlings at a constant rate also improves subsequent growth (Table 5, study *h*), exponential nutrient loading allows plants to develop tolerance to high nutrient concentrations and can result in a steady-state accumulation of internal nutrients to even higher levels (Timmer 1997). These nutrients can then be retranslocated to new growth. Exponential fertilization may also result in a more stable shoot:root balance (Timmer 1997) and greater mycorrhizal development (Quoreshi and Timmer 1998).

Although the total quantities of N added in our experiment were much greater than those in most nutrient-loading studies (Table 5, studies *a*–*o*), our growth results are consistent with results from other conifer species. After 1 year in the field, 3% seedlings had a 10% higher foliar N concentration than constant-rate seedlings, and after three field growing seasons, 3% seedlings had a 12% greater height increment. One growing season after outplanting, black spruce seedlings given 10 mg N in exponentially increasing doses had a 1%–5% increase in height, a 9%–18% increase in shoot biomass, and a 1%–5% increase in N concentration depending on site, compared to seedlings fertilized with 10 mg N at a constant rate. Seedlings receiving 20 mg N exponentially had a 1%–7% increase in height, a 4%–12% increase in shoot biomass, and a 0%–4% increase in N concentration relative to constant-rate trees (Table 5, study *a*) (Timmer et al. 1991). These improvements were attributed to stable internal nutrient accumulation, lower shoot:root mass ratios, and fertilizer concentrations and supply patterns more closely matched to natural conditions (Timmer et al. 1991, Timmer 1997). In another study with the same species on a low-fertility site, seedlings supplied with 12.5 mg N at a constant or exponential rate showed no difference in biomass, but exponentially fertilized seedlings did show an elevated N concentration (Table 5, study *b*) (Quoreshi and Timmer 2000). *Picea glauca* bare-root seedlings with 173.5 mg N per seedling applied at a constant rate or exponentially over 3 years had 3% greater biomass and 11% higher N concentration in exponentially fertilized seedlings one growing season after outplanting (Table 5, study *p*) (McAlister and Timmer 1998). This is the only study we have found that applied a similar quantity of N as that in our study, but it was extended over 3 years.

Summary

In our experiments with western hemlock, the influence of postplanting fertility conditions, both in the nursery and in the field, far outweighed the effect of nutrient loading in the greenhouse. We did not observe the substantial increase in size or N concentration in response to exponential fertilization often observed in other species (Table 5, studies *a*–*g*, *i*, *l*, *m*–*o*) and saw little evidence of increased nutrient retranslocation in exponentially fertilized seedlings. The small response to exponential fertilization in our study could be attributed to a number of causes:

(*i*) Indeterminate western hemlock continued growth later into the hardening period, diluting internal nutrient reserves in exponentially fertilized seedlings. We do not believe this occurred, because exponentially fertilized seedlings did not have much greater height or biomass than did constant-rate seedlings, as would be expected with a prolonged growing season.

(*ii*) Extra fertilizer added to exponentially fertilized seedlings was lost through overflow or leaching. Because seedlings were fertilized at least twice per week during the growing season, significantly greater concentrations of nutrients must have surrounded roots of exponentially fertilized seedlings from the end of May to the beginning of September (Fig. 1). Even if some of the extra nutrients were lost, exponentially fertilized seedlings should still have had an opportunity for greater nutrient uptake.

(*iii*) Hemlock does not respond to high rates of nutrient addition. Although productivity of immature stands of western hemlock is not always correlated with nutrient availability (Kayahara et al. 1995), seedlings of this species do respond to high rates of nutrient addition. In a constant-rate fertilization experiment, western hemlock seedlings receiving 10, 100, or 250 mg $N \cdot L^{-1}$ in solution over three growing seasons had significantly increased biomass and foliar N concentration with increasing N addition (Hawkins et al. 2000). In an earlier study of exponential fertilization, western hemlock seedlings grown with a 6% nutrient addition rate had significantly greater fresh biomass than that of constant-rate or 4% seedlings after 10 weeks of treatment (Table 5, study *l*). After 4 additional weeks of treatment, both 6% and 4% seedlings had significantly greater fresh biomass and foliar N concentration than that of constant-rate seedlings. By that time, 6%, 4%, and constant-rate seedlings had received approximately 222.5, 50.6, and 35 mg N, respectively (calculated from Burgess 1991), a significantly greater spread than in our experiment. Our constant-rate seedlings received 66% more N by the end of the nutrient-loading phase than those of Burgess (1991). We believe this explains the similar size and N concentrations in constant-rate and exponentially fertilized seedlings in our experiment.

(*iv*) When N is applied to western hemlock seedlings at a constant, high rate, the resulting seedlings are equally competitive with seedlings fertilized exponentially. Conventional British Columbia nursery fertilization practices aim for a target of 2.0%–2.6% foliar N, depending on species, and can apply 80–125 mg N per seedling (D. Swain, S. Kiiskila, PRT Ltd., personal communication, 2002). This is much more N than the 10–30 mg N per seedling applied in some nurseries in eastern Canada (Table 5, studies *a*–*j*). Higher N loadings in British Columbia are achieved, in part, by a longer period of fertilization lasting 31 weeks or more, compared to the 18–

22 weeks described in other papers (Table 5, studies *b*, *e*, *f*). Standard container sizes in British Columbia are also slightly larger (80 cm^3) than those in many of the nutrient-loading experiments done by others (Table 5, studies *c*–*l*). A larger container holds a larger volume of nutrient solution, which likely increases the quantity of N available to each seedling between feedings. While slow-growing species such as black spruce might experience nutrient toxicity if nutrients were applied at the rates standard in British Columbia forest nurseries, Salifu and Timmer (2003) showed that 65 mg N per seedling, a rate three times the Ontario nursery standard, produces optimum growth in black spruce.

We have demonstrated that applying fertilizer at a constant rate can produce western hemlock seedlings that are equally competitive with exponentially fertilized seedlings. Future studies of the exponential nutrient-loading technique with species from the Pacific Northwest should explore whether seedlings of equivalent quality can be produced with lower quantities of N applied exponentially. The response of seedlings of determinate and indeterminate species grown with 50 and 80 mg N applied at a constant rate and exponentially should be compared. Exponential treatments should begin earlier, when seedling initial nutrient content is lower, allowing a longer treatment time before solution nutrient concentrations become too high. This may indicate ways in which seedling nurseries in British Columbia could apply fertilizer more efficiently and economically.

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