Growth and foliar nutrition of juvenile western hemlock and western redcedar plantations on low- and medium-productivity sites on northern Vancouver Island: response to fertilization and planting density

R.W. Negrave, C.E. Prescott, and J.E. Barker

Abstract: A factorial trial was established to examine the effects of planting density and fertilization on the growth of western redcedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) on nutrient-poor (CH) sites and nutrient-medium (HA) sites. Two levels of NPK fertilization were crossed with three levels of planting density (500, 1500, and 2500 stems/ha). Fifteen years after establishment and 10 years after the last fertilizer application, height, individual stem volume increment, stand volume, 5 year periodic annual increment (PAI), and 5 year periodic height increment were all increased by fertilization. Fertilization of CH sites increased annual stand volume increment by 753%–2552% and 122%–209% for hemlock and cedar, respectively; fertilization of HA sites increased PAI by 94%–264%. Volume growth response to fertilization was greater on HA than on CH sites. Increasing stand density reduced height growth on CH sites but not on HA sites. These results suggest that competition for nutrients can be a significant growth-limiting factor even before canopy closure occurs and that treatment of ericaceous sites may not be justified by productivity increases.

Résumé : Un dispositif factoriel a été mis en place pour étudier les effets de la densité de plantation et de la fertilisation sur la croissance du thuya géant (*Thuja plicata* Donn ex D. Don) et de la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) établis sur des stations pauvres (CH) et modérément riches (HA) en nutriments. Deux niveaux de fertilisation en NPK ont été appliqués dans chacun des trois niveaux de densité de plantation (500, 1500 et 2500 tiges/ha). Quinze ans après l'établissement et 10 ans après l'application de la dernière fertilisation, la hauteur, l'accroissement en volume des tiges individuelles, le volume du peuplement, l'accroissement annuel périodique quinquennal (AAP) et l'accroissement périodique quinquennal en hauteur ont tous augmenté à cause de la fertilisation. La fertilisation des stations CH a augmenté l'accroissement annuel en volume du peuplement de 753 % à 2552 % pour la pruche et de 122 % à 209 % pour le thuya. La fertilisation des stations HA a augmenté l'AAP de 94 % à 264 %. À la suite de la fertilisation, la réaction de la croissance en volume des stations HA a été supérieure à celle des stations CH. L'augmentation de la densité des peuplements a réduit la croissance en hauteur sur les stations CH, mais pas sur les stations HA. Ces résultats indiquent que la compétition pour les nutriments peut être un facteur important pour limiter la croissance des arbres avant même que survienne la fermeture de la canopée. De plus, il est possible que le traitement des stations à éricacées ne soit pas justifié par des augmentations de la productivité.

[Traduit par la Rédaction]

Introduction

Reforestation of sites dominated by ericaceous shrubs such as heather (*Calluna vulgaris* (L.) Hull), sheep laurel (*Kalmia angustifolia* L.), and salal (*Gaultheria shallon* Pursh) can be particularly challenging (Mallik 2003). In addition to strongly competing for soil nutrients, ericaceous shrubs, through the production of polyphenolic compounds, can interfere with mineralization of nitrogen (N) and "short-circuit" the N cycle to the detriment of the young trees. On northern and western Vancouver Island, conifer plantations established on salal-dominated sites formerly occupied by old-growth western redcedar (*Thuja plicata* Donn ex D. Don) aand western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) stands (CH sites) typically experience growth check 5–8 years after establishment. In contrast, plantations established on adjacent sites formerly occupied by even-aged stands of western hemlock and amabilis fir (*Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes) sites (HA sites), and where salal is less abundant, continue to grow well (Weetman et al. 1990). Early field fertilization trials indicated that tree growth on CH sites could be substantially accelerated by fertilization with N and phosphorus (P) (Weetman et al. 1989). This observation prompted con-

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sideration of a possible silvicultural option for improving productivity of CH sites — planting at high planting densities and fertilizing with N and P. It was thought that this would promote rapid crown closure, which would eliminate the salal and lead to increased nutrient availability and sustained increases in conifer growth. It was hoped that a treatment could be defined that would promote stand development of CH sites similar to that observed on adjacent HA sites.

A factorial trial was established in 1988 to test this silvicultural hypothesis by examining the effects of a range of planting densities in combination with fertilization on the growth of western redcedar and western hemlock on both CH and HA sites. The trial was twinned on HA sites to provide a direct comparison with HA sites and to determine if stand development on HA sites could also be improved through these treatments. Tree size, stand volume, and mortality were examined 15 years after trial establishment to detect cumulative effects of the treatments on tree growth and stand productivity. Annual tree growth rate and periodic annual increment (PAI) between 1997 and 2002 were examined to better determine whether fertilization increased growth 5–10 years after application. Foliar nutrient concentrations were also measured 10 years after the last fertilizer application to determine whether there has been a sustained effect of treatments on nutrient availability and tree nutrition. If the initial hypothesis was correct, we would expect to find the following in the high-density fertilized plots: greater tree height, stand volume, and height growth in the 1997–2002 period; lower individual stem volume growth but greater PAI; and sustained higher foliar concentrations of N and P.

Materials and methods

Study sites

The study site was on northern Vancouver Island, between Port Hardy and Port McNeill (50°60′N, 127°35′W) in the Submontane Very Wet Maritime variant of the Coastal Western Hemlock Biogeoclimatic, or CWHvm1, zone (Green and Klinka 1994). The study site was approximately 50 m a.s.l. in undulating terrain with wetlands located in depressions. Surface materials consist of unconsolidated glacial moraine and fluvial outwash deposits that range from blankets to shallow veneers with exposed bedrock. Mineral soil texture ranged from silty clay loams to fine sand with high coarse fragment contents. Folisols and organic soils of wetland origin are also common on the study site.

The area receives approximately 1900 mm of precipitation annually, most of which falls as rain. Growing season soil moisture deficits typically do not occur (Lewis 1992). Daily mean temperatures range from 3.3 °C in January to 14.1 °C in August. A relatively high percentage of the annual solar radiation is received as diffuse radiation (McKay and Morris 1985), reflecting overcast conditions throughout the year and frequent summer fog. Direct sunlight exposure ranges from 1.5 h/day in December to 6.4 h/day in July. Global solar radiation incident of a horizontal surface averages 10.212 $MJ \cdot m^{-2} \cdot day^{-1}$ and ranges from a low of 2.043 $MJ \cdot m^{-2} \cdot day^{-1}$ in December to 18.935 $MJ \cdot m^{-2} \cdot day^{-1}$ in July (McKay and Morris 1985).

The experiment was conducted on two common CWHvm1 forest types. The HA sites are occupied by stands composed of western hemlock and amabilis fir. The CH sites are occupied by stands dominated by western redcedar with lesser amounts of western hemlock and amabilis fir.

The CH sites support old-growth forests that include large trees up to 1000 years in age (Keenan 1993). Diameter-class distributions suggest that these are self-replacing climax forests. Canopies in these stands are irregular with frequent gaps, and the understory is consequently well developed and dominated by salal. The HA sites in this study are second-growth forests that mostly originated from a major windstorm in 1906 (Prescott and Weetman 1994). These forests are more uniform in structure and are composed of younger trees, mostly from 70 to 100 years old but with a range of 30 to 160 years. Canopies in HA forests are uniform and dense with little light penetration to the forest floor. Thus, the understory is sparse in HA forests. It is generally thought that forests on HA sites are cyclically destroyed and regenerated by catastrophic windthrow events (Lewis 1992), whereas CH sites are less prone to windthrow and, thus, maintain themselves indefinitely.

Both CH and HA sites are typically found on well to imperfectly drained Humo-Ferric Podzols and are loamy in texture (Lewis 1992; de Montigny 1992; Green and Klinka 1994). However, soils on CH sites often have compacted B horizons and typically include Duric horizons or other root-restricting features in their profiles (Lewis 1992; de Montigny 1992). Soils on HA sites are typically more friable and aerated than on CH sites and show frequent evidence of mixing owing to windthrow. Root-restricting layers are thin and discontinuous on HA sites. Mineral soils on CH sites have lower N concentrations and greater carbon (C) / N ratios than soils on HA sites.

Forest floor layers on HA sites tend to be thin and friable compared with those on CH sites. In general, forest floors on CH sites have a greater total mass, less F-layer material, but more coarse woody material (Keenan et al. 1993). Humus form and soil fauna composition suggest that forest floors on CH sites are wetter than those on HA sites (Battigelli 1992; Prescott and Weetman 1994).

Nitrogen and P availability is lower on CH sites than on HA sites, and the reasons for this phenomenon remain obscure. The presence of compacted and concreted soils combined with the tendency for CH sites to be found at lower topographic positions may best explain this situation. The wetter nature of CH humus and soil above concreted layers and resulting reduction of biological activity may be responsible for the lower N and P availability that characterizes these sites (Prescott and Weetman 1994; Prescott et al. 1996).

Experimental design and treatments

Ninety-six square treatment plots, each containing 64 sample trees were established in 1987. Plot size and tree spacing varied with density. Trees in the 500 stems/ha plots were planted 4.5 m apart, resulting in a central (core) measurement area of 36 m × 36 m and a total plot size of 54 m × 54 m, including a buffer zone. Buffer zones were planted at the same spacing as the core areas they surrounded. The 1500 stems/ha treatment had a tree spacing of 2.6 m, a core measurement area of 21 m × 21 m and a total area plot size of 32 m × 32 m. Between-tree spacing was 2 m in the 2500 stems/ha treatment, with a 16 m × 16 m core measurement area and total plot size of 36 m × 36 m. The 500 and 1500 stems/ha treatments each had four rows of buffer trees on each side, whereas the 2500 stems/ha treatment has 10 rows of buffer trees.

Treatments were arranged in a fully crossed factorial combination with two levels of fertility (fertilized and unfertilized) and three levels of density (500, 1500, and 2500 stems/ha). The 2 × 3 combination of fertilizer or no fertilizer by densities was applied to each of redcedar and hemlock and duplicated on both CH and HA sites. The CH and HA sites used in this study were scattered throughout a 3 km^2 area in close proximity to each other. Each fertilization–density–species combination was randomly assigned within four blocks on each site, with a single treatment level replicate per block. Thus, a total of 48 plots examined 12 treatments with 4 replications per treatment level. The area where the experiment occurred sloped down from a ridge and was bisected by a series of watercourses and blanket bogs. The blocks were roughly arranged to include both CH and HA areas. The randomized block design was compromised somewhat to accommodate the large size of some of the 500 stems/ha plots.

Fertilized plots received a 60 g dressing of Nutricote® controlled-release fertilizer at time of planting. The fertilizer was raked into 15 cm radius areas around each seedling and provided 10 g of N, 2.5 g of P, and 5 g of potassium (K) to each seedling. Total application rates per hectare varied with density. All fertilized plots were refertilized before the beginning of the growing season in 1993 with a broadcast application of 225 kg/ha of N and 100 kg/ha of P as urea (46:0:0, N:P:K) and triple superphosphate (0:45:0, N:P:K).

Measurements

Height and diameter of each living sample tree within core measurement areas were measured after the completion of growth in late fall of 1988, 1989, 1990, 1992, 1994, 1997, and 2002. Height was recorded to the nearest centimetre. Diameter was measured 1.3 m above the root collar (breast height) in 1997 and 2002. Tree volumes were calculated using standard British Columbia Forest Service taper equations (Kozak 1988).

Samples of current-year foliage were collected from the upper crowns of trees within each plot. Foliage was collected after the cessation of growth in the fall of 2002. Samples of current-year foliage were collected from the upper crowns of about 60 trees in each plot and combined into one composite sample per plot. Composite samples were dried to constant mass at 70 °C and ground. Nutrient concentrations were determined following sulphuric acid – hydrogen peroxide digestion (Parkinson and Allen 1975). Nitrogen and P concentrations were determined colorimetrically on a Technicon autoanalyzer. Concentrations of K, calcium (Ca), magnesium (Mg), manganese (Mn), and aluminum (Al) were determined by atomic absorption spectrometry; copper (Cu), zinc (Zn), and iron (Fe) concentrations were determined through dry-ashing and subsequent analysis with atomic absorption spectrometry. Boron (B) concentration was determined colorimetrically with the azomithine-H method. Total sulphur (S) concentration was determined using a LECO sulfur analyzer. Available sulphate–sulphur (SO_4-S) concentration was determined using 0.01 N HCl extractions and determined colorimetrically in a hydroiodic acid – bismuth reducible distillate. All analyses were conducted at Pacific Soils Analysis Incorporated, Richmond, British Columbia.

Statistical analysis

A general linear model approach (PROC Mixed in SAS, SAS Institute Inc., Cary, North Carolina) was used to examine the cumulative effect of treatments on stand and tree growth after 15 years of stand development on each site and on current foliar nutrient concentrations. A mixed-effects model was used for each site type with species, fertilization, and density tested as fixed effects and block included as a random effect. A randomized complete block design with a 2 × 3 × 2 factorial combination of treatment levels was used: cedar or hemlock; 500, 1500, or 2500 stems/ha; and fertilized or unfertilized. Tukey's honestly significant difference test was used to separate differences in treatment levels and interactions. The following variables were analyzed: tree height, stand volume, cumulative mortality; PAI for 1997–2002; mean single-stem volume increment for 1997–2002; and foliar nutrient concentration (N, P, K, S, Ca, Mg, Mn, Cu, Al, Fe, B, and available SO_4-S). The single-stem volume increment variable was selected in preference to diameter or diameter increment as a measure of intraspecific competition. Covariate analysis of 1997–2002 incremental height growth was calculated using tree height in 1992 (before broadcast fertilization) to determine effects of the second fertilization application on height growth. Separate covariate analyses were conducted for each tree species using a mixed-effects model with two levels: fertilization and site. Blocks were analyzed as a random effect. This modification of the design was necessary to find an appropriate homogenous-slopes model for the covariate analysis. Logarithmic transformations were used to homogenize variances where necessary to meet regression assumptions. The correlation between foliar nutrient concentration and recent tree growth, using mean annual height increment for the 1997–2002 period, was determined using Pearson correlation analysis. All statistical analyses were conducted using SAS version 8.2 (SAS Institute Inc., Cary, North Carolina) with a significance level of $p < 0.05$ used for hypothesis testing.

Results

Height

Fertilization increased the height growth of cedar and hemlock stands on both CH and HA sites (Fig. 1 and Tables 1 and 2). Fertilization increased the mean height of hemlock on CH sites by 86%–162% and cedar by 33%–48%. Unfertilized cedar had significantly greater mean height than unfertilized hemlock on CH sites; however, hemlock responded more strongly to fertilization, and no significant differences for height existed between fertilized cedar and hemlock on CH sites. The gains in height with fertilization on CH sites at 500, 1500 and 2500 stems/ha, respectively, were 1.79, 2.20, and 1.64 m for cedar and 4.41,

Fig. 1. Height development of western redcedar (Cw) stands on (*a*) HA (nutrient medium) and (*b*) CH (nutrient poor) sites and western hemlock (Hw) stands on (*c*) HA sites and (*d*) CH sites.

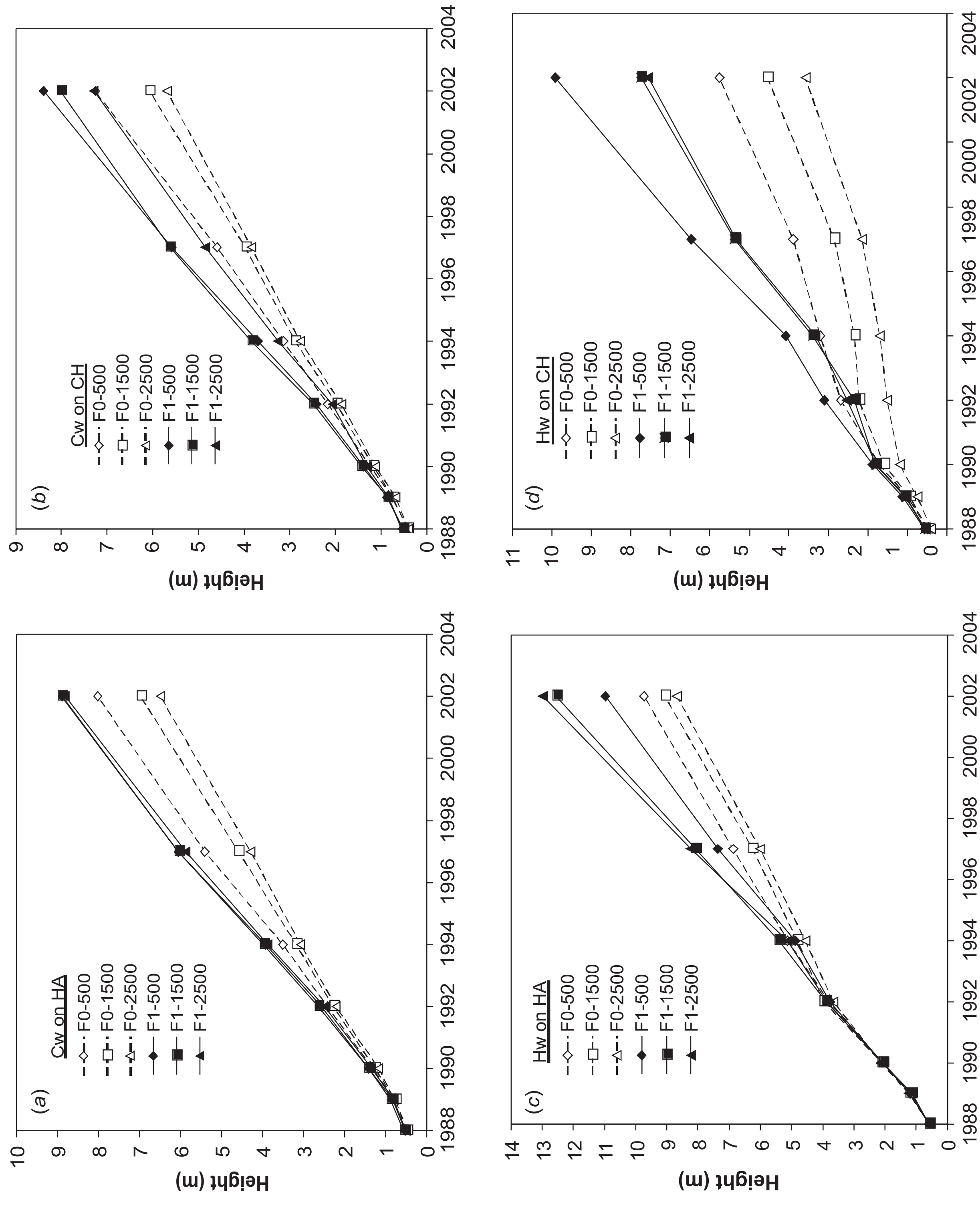


Table 1. Size (2002), growth (1997–2002), and mortality (to 2002) variables.

Species[a]	Fertilization[b]	Stand density (stems/ha)	Height (m)	Stand volume (m^3/ha)	Mortality (%)	Height increment (m/year)	Stem volume increment (dm^3/year)	Periodic annual increment (m^3·ha^{-1}·year^{-1})
CH sites								
Cw	F0	500	5.36 (0.59)	10.39 (3.41)	0.8 (1.6)	0.39 (0.05)	3.38 (1.20)	1.65 (0.57)
Cw	F0	1500	4.53 (0.55)	15.17 (6.73)	0.4 (0.8)	0.31 (0.04)	1.54 (0.68)	2.27 (0.97)
Cw	F0	2500	4.08 (0.33)	17.49 (3.51)	0.4 (0.8)	0.24 (0.04)	1.00 (0.24)	2.50 (0.62)
Cw	F1	500	7.15 (0.49)	25.27 (5.35)	4.3 (3.5)	0.48 (0.04)	7.78 (1.57)	3.67 (0.74)
Cw	F1	1500	6.73 (0.61)	54.47 (17.05)	0.8 (0.9)	0.39 (0.05)	4.79 (1.43)	7.03 (2.15)
Cw	F1	2500	5.72 (1.05)	51.79 (23.74)	2.3 (2.7)	0.37 (0.07)	2.90 (1.27)	7.10 (3.17)
Hw	F0	500	3.65 (0.26)	1.63 (0.58)	6.3 (4.4)	0.20 (0.05)	0.55 (0.15)	0.25 (0.08)
Hw	F0	1500	3.17 (0.29)	2.28 (1.01)	5.9 (3.9)	0.20 (0.03)	0.27 (0.10)	0.38 (0.15)
Hw	F0	2500	2.27 (0.19)	1.03 (0.28)	3.1 (2.2)	0.10 (0.03)	0.08 (0.02)	0.19 (0.05)
Hw	F1	500	8.06 (1.21)	21.13 (8.38)	8.2 (3.7)	0.53 (0.12)	6.97 (2.73)	3.13 (1.24)
Hw	F1	1500	5.92 (1.01)	22.23 (9.43)	6.3 (6.1)	0.33 (0.11)	2.33 (0.98)	3.24 (1.44)
Hw	F1	2500	5.95 (1.35)	36.74 (24.21)	2.3 (2.7)	0.32 (0.14)	2.07 (1.39)	5.04 (3.45)
HA sites								
Cw	F0	500	5.85 (1.24)	13.87 (7.11)	5.5 (4.7)	0.35 (0.06)	4.14 (1.85)	1.90 (0.85)
Cw	F0	1500	5.08 (0.84)	22.01 (9.12)	1.6 (1.3)	0.32 (0.07)	2.14 (0.83)	3.11 (1.22)
Cw	F0	2500	4.23 (1.75)	30.22 (30.79)	1.6 (1.3)	0.21 (0.15)	1.70 (1.63)	4.19 (4.01)
Cw	F1	500	7.29 (0.99)	26.87 (10.53)	7.4 (8.1)	0.47 (0.07)	8.28 (3.38)	3.68 (1.38)
Cw	F1	1500	7.66 (1.17)	85.63 (33.51)	3.5 (4.5)	0.49 (0.10)	8.22 (3.51)	11.48 (4.63)
Cw	F1	2500	7.27 (0.78)	114.07 (34.18)	3.1 (2.9)	0.46 (0.03)	6.36 (1.89)	15.14 (4.21)
Hw	F0	500	7.65 (1.99)	19.36 (14.00)	5.5 (2.7)	0.46 (0.12)	5.83 (4.12)	2.71 (1.94)
Hw	F0	1500	7.12 (2.67)	40.82 (34.55)	7.0 (6.6)	0.43 (0.23)	4.29 (4.01)	5.61 (4.91)
Hw	F0	2500	7.04 (3.45)	61.69 (63.27)	7.4 (5.6)	0.44 (0.27)	3.83 (3.85)	8.59 (8.74)
Hw	F1	500	9.65 (0.63)	39.61 (6.83)	16.4 (13.6)	0.61 (0.05)	13.51 (2.52)	5.39 (0.96)
Hw	F1	1500	11.68 (0.73)	148.75 (29.26)	12.9 (9.0)	0.81 (0.09)	15.95 (2.98)	20.48 (4.27)
Hw	F1	2500	11.61 (1.16)	190.40 (59.13)	8.6 (0.9)	0.83 (0.09)	11.27 (3.01)	25.56 (6.98)

Note: CH site, nutrient poor conditions; HA site, nutrient medium conditions.Values are means with SEs given in parentheses.

[a] Cw, western redcedar; Hw, western hemlock.

[b] F0, unfertilized; F1, fertilized.

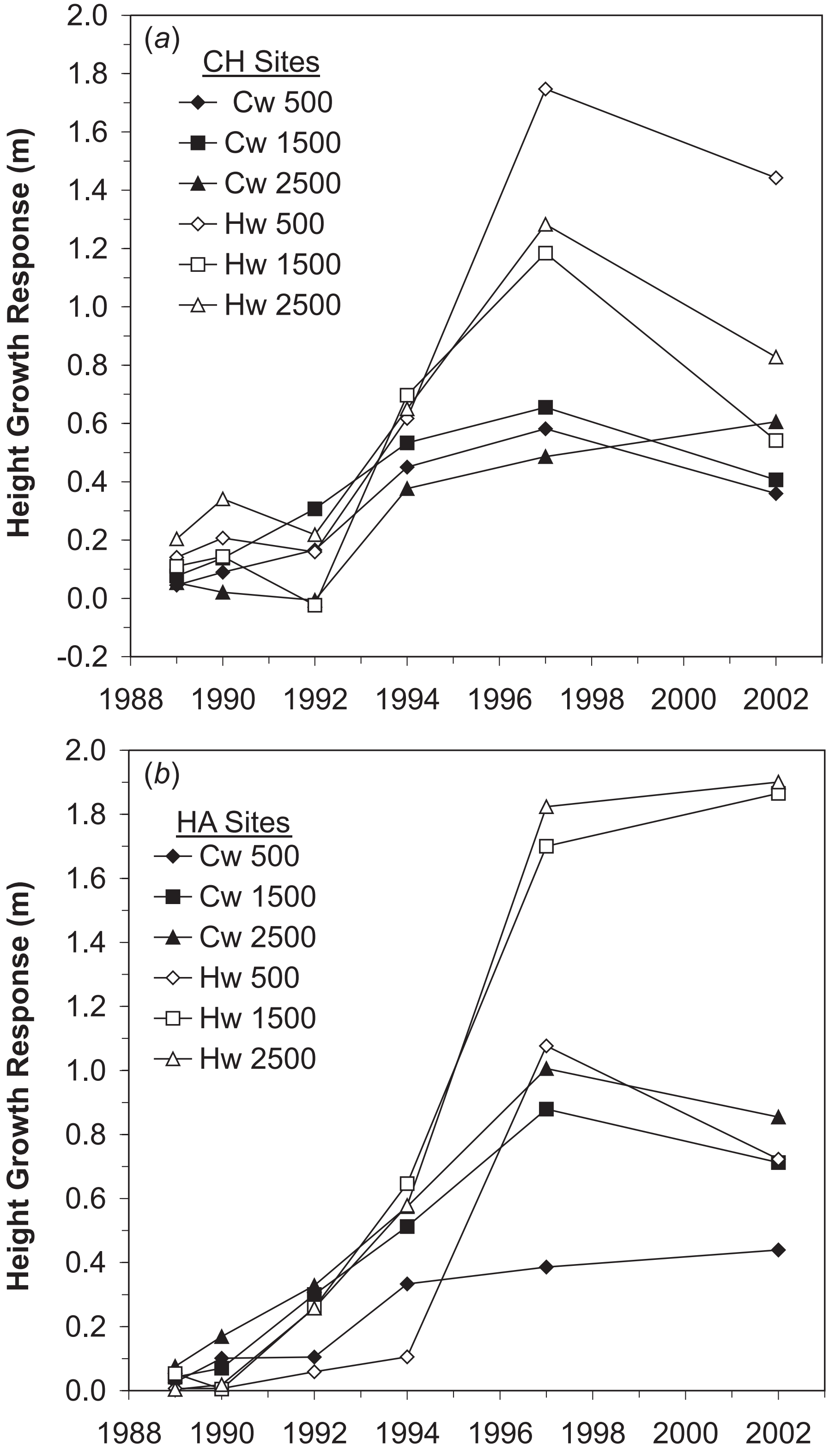
Table 2. Analysis of size, growth, and mortality variables (*p* values).

Source of variation	df$_n$[a]	Height	Stand volume	Mortality	Stem volume increment	Periodic annual increment
CH sites						
Species (S)	1	<0.0001*	<0.0001*	0.0002*	<0.0001*	<0.0001*
Planting density (D)	2	<0.0001*	0.0185*	0.0536	<0.0001*	0.0332*
Fertilization (F)	1	<0.0001*	<0.0001*	0.1859	<0.0001*	<0.0001*
S × D	2	0.2240	0.1134	0.1674	0.1639	0.2166
S × F	1	<0.0001*	<0.0001*	0.4413	<0.0001*	<0.0001*
D × F	2	0.2827	0.1425	0.5182	0.1833	0.1781
S × D × F	2	0.0619	0.0238*	0.8300	0.0659	0.0626
HA sites						
S	1	<0.0001*	0.0277*	0.0027*	0.0120*	0.0240*
D	2	0.5055	<0.0001*	0.2737	<0.0001*	<0.0001*
F	1	<0.0001*	<0.0001*	0.0371*	0.0472*	<0.0001*
S × D	2	0.5189	0.9392	0.8081	0.9350	0.9321
S × F	1	0.6978	0.6352	0.2525	0.4909	0.5533
D × F	2	0.1189	0.1789	0.5145	0.2369	0.1716
S × D × F	2	0.9164	0.9781	0.5675	0.9478	0.9642

Note: Values with an asterisk (*) are significant at $p < 0.05$ for the *F* test. CH site, nutrient poor conditions; HA site, nutrient medium conditions.

[a] df$_n$, numerator degrees of freedom.

Fig. 2. Height response of western redcedar and hemlock to fertilization of (*a*) CH (nutrient poor) and (*b*) HA (nutrient medium) sites.



2.75, and 3.68 m for hemlock. On HA sites, fertilization significantly increased the mean height of cedar by 25%–72% and of hemlock by 26%–65%. The gains in height with fertilization on HA sites at 500, 1500, and 2500 stems/ha, respectively, were 1.44, 2.58, and 3.04 m for cedar and 2.00 m, 3.56, and 4.57 m for hemlock.

Increasing stand density decreased mean height growth of both species on CH sites (Table 2). Increasing density significantly reduced height growth in the order 500 stems/ha >1500 stems/ha > 2500 stems/ha. Density did not affect height on HA sites (Table 2); however, hemlock was significantly taller than cedar on these sites.

Height growth response to fertilization over time was calculated by subtracting the mean incremental height growth of unfertilized treatments from fertilized treatments for successive measurement years and presented graphically (Fig. 2). On CH sites, a negative response to fertilization at planting is indicated for cedar at 2500 stems/ha and hemlock at 1500 stems/ha for the 1990–1992 period. Fertilization early in 1993 stimulated height response that reached a maximum in 1997 before declining. Exceptions to this were cedar at 2500 stems/ha on the CH site, cedar at 500 stems/ha on the HA site, and the 1500 and 2500 stems/ha hemlock treatments on the HA site. All fertilized treatments showed a positive response after the 2002 growing season (10 growing seasons after fertilization), although hemlock response was generally greater than cedar on both sites.

Covariate analysis indicated that the pregrowing season fertilizer application in 1993 increased 1997–2002 incremental height growth of both cedar and hemlock (Table 3) compared with the unfertilized treatments. The mean height of trees in 1992 was significant as a covariate ($p < 0.0001$) for both cedar and hemlock. No significant site differences were present and neither was the site × fertilization interaction significant.

Stand volume

Fertilization increased stand volumes on both CH and HA sites (Tables 1, 2, and 4). On CH sites, unfertilized cedar volume was greater than unfertilized hemlock. Unfertilized cedar stands had 537%–1598% greater volume than hemlock on CH sites, and the difference increased with density. On CH sites, fertilization significantly increased cedar stand volume by 259% for the 1500 stems/ha treatment and 196% for the 2500 stems/ha treatment. There was a 143% increase in cedar volume with fertilization in the 500 stems/ha treatment, but this was not significant. Fertilization increased hemlock stand volumes at all densities. Increases were 1196%, 875%, and 3467% for the 500, 1500, and 2500 stems/ha treatments, respectively. The mean volumes of fertilized cedar stands were greater than those of hemlock, but the difference was significant only for the 1500 stems/ha treatment, where it was 145% greater than hemlock. Volume gain with fertilization on CH sites at 500, 1500, and 2500 stems/ha, respectively, was 14.9, 39.3, and 34.3 m^3 for cedar and 19.5, 20.0, and 35.7 m^3 for hemlock.

On HA sites, hemlock volumes were 40%–104% greater than that of cedar. Fertilization increased volumes on HA sites by 93%–289%. Statistically, the 500 stems/ha treatment had a lower volume than the two denser treatments, which did not differ. The density increase from 500 to 2500 stems/ha increased volume by 118%–381%. Volume gains with fertilization on HA sites at 500, 1500, and 2500 stems/ha, respectively, were 13.0, 63.6, and 83.9 m^3 for cedar and 20.3, 107.9, and 128.7 m^3 for hemlock. However, unlike CH sites, the density × fertility interaction was not statistically significant on HA sites.

The PAI (1997–2002) was increased by fertilization on both sites (Tables 1 and 2). On CH sites, fertilization significantly increased the PAI of both cedar and hemlock. The PAI of cedar was statistically greater than that of hemlock on both fertilized and unfertilized treatments. Although the proportional increase of PAI was greater in hemlock than in cedar on CH sites, 753%–2552% compared with 122%–209%, the absolute increase was similar in both species ranging from 2.02 to 4.85 m^3·ha^{-1}·year^{-1}. The greatest growth for cedar was on the fertilized treatment at 1500 stems/ha (7.03 m^3·ha^{-1}·year^{-1}), whereas that for hemlock was the fertilized treatment at 2500 stems/ha (5.04 m^3·ha^{-1}·year^{-1}).

Table 3. Covariate analysis of 1997–2002 height increments.

Source	df$_n$^{a}	Western redcedar	Western hemlock
Height 1992	1	<0.0001*	<0.0001*
Site (S)	1	0.6128	0.5704
Fertilization (F)	1	0.0095*	<0.0001*
S × F	1	0.4898	0.2077

Note: Values with an asterisk (*) are significant at $p < 0.05$ for the F test.
[a] df$_n$, numerator degrees of freedom.

Table 4. Comparison of 2002 stand volumes among the treatments on CH sites (nutrient poor conditions).

Treatment^a	Stand volume (m^3/ha)
Cw–F0–500	10.39 (3.41)b
Hw–F0–500	1.63 (10.58)a
Cw–F0–1500	15.17 (6.73)bc
Hw–F0–1500	2.28 (1.01)a
Cw–F0–2500	17.49 (3.51)bc
Hw–F0–2500	1.03 (0.28)a
Cw–F1–500	25.27 (5.35)bcde
Hw–F1–500	21.13 (8.38)bcd
Cw–F1–1500	54.47 (17.05)e
Hw–F1–1500	22.23 (1.23)bcd
Cw–F1–2500	51.79 (23.74)de
Hw–F1–2500	36.74 (24.21)cde

Note: Values followed by the same letter do not differ significantly ($p > 0.05$).
[a] Cw, western redcedar; Hw, western hemlock; F0, unfertilized; and F1, fertilized. Tree densities (500, 1500, and 2500 stems/ha) are also given.

On HA sites, the PAI of hemlock was significantly greater than that of cedar (Tables 1 and 2). Fertilization significantly increased PAI similarly for both species by 94%–264% on HA sites. PAI reached a maximum of 5.56 m^3·ha^{-1}·year^{-1} on fertilized HA sites at 2500 stems/ha. The best cedar growth was 15.14 m^3·ha^{-1}·year^{-1}, also on fertilized HA sites at 2500 stems/ha. PAI gains with fertilization on CH sites at 500, 1500 and 2500 stems/ha, respectively, were 2.0, 4.8, and 4.6 m^3·ha^{-1}·year^{-1} for cedar and 2.9, 2.9, and 4.9 m^3·ha^{-1}·year^{-1} for hemlock.

Density increased PAI significantly (Tables 1 and 2) with the 500 stems/ha treatments having the lowest PAI on both CH and HA sites for both species. PAI was greatest in the 1500 stems/ha treatment on CH sites and the 2500 stems/ha treatment on HA sites.

The mean single-stem volume increment (1997–2002) was increased by fertilization on both sites (Tables 1 and 2). On CH sites, significant differences also existed for species and annual stem growth increased in the order unfertilized hemlock < unfertilized cedar < fertilized hemlock < fertilized cedar. The mean stem growth was greater in hem-

Table 5. Foliar nutrient concentrations.

Species	Fertilization	Planting density (stems/ha)	N (%)	P (%)	K (%)	S (%)	Ca (%)	Mg (%)
CH sites								
Cw	F0	500	1.09 (0.06)	0.15 (0.01)	0.59 (0.06)	0.10 (0.01)	0.73 (0.10)	0.13 (0.01)
Cw	F0	1500	0.97 (0.04)	0.16 (0.02)	0.53 (0.04)	0.09 (0.01)	0.69 (0.05)	0.13 (0.01)
Cw	F0	2500	1.06 (0.13)	0.15 (0.02)	0.48 (0.02)	0.09 (0.00)	0.71 (0.07)	0.13 (0.01)
Cw	F1	500	1.06 (0.08)	0.17 (0.01)	0.53 (0.04)	0.10 (0.00)	0.79 (0.08)	0.13 (0.01)
Cw	F1	1500	0.97 (0.11)	0.16 (0.01)	0.46 (0.06)	0.09 (0.01)	0.85 (0.09)	0.11 (0.01)
Cw	F1	2500	0.98 (0.03)	0.16 (0.01)	0.46 (0.10)	0.09 (0.01)	0.86 (0.09)	0.12 (0.02)
Hw	F0	500	0.79 (0.07)	0.09 (0.02)	0.62 (0.10)	0.08 (0.01)	0.24 (0.02)	0.09 (0.01)
Hw	F0	1500	0.76 (0.02)	0.11 (0.03)	0.68 (0.08)	0.08 (0.01)	0.22 (0.02)	0.08 (0.01)
Hw	F0	2500	0.78 (0.05)	0.10 (0.01)	0.66 (0.04)	0.09 (0.01)	0.23 (0.03)	0.08 (0.01)
Hw	F1	500	0.78 (0.02)	0.19 (0.02)	0.63 (0.11)	0.08 (0.00)	0.25 (0.04)	0.09 (0.00)
Hw	F1	1500	0.71 (0.05)	0.18 (0.03)	0.61 (0.04)	0.08 (0.00)	0.24 (0.05)	0.11 (0.02)
Hw	F1	2500	0.74 (0.09)	0.20 (0.04)	0.58 (0.04)	0.08 (0.00)	0.27 (0.06)	0.11 (0.02)
HA sites								
Cw	F0	500	1.02 (0.06)	0.16 (0.03)	0.47 (0.08)	0.09 (0.00)	0.83 (0.05)	0.11 (0.02)
Cw	F0	1500	1.02 (0.02)	0.16 (0.01)	0.50 (0.04)	0.09 (0.01)	0.83 (0.13)	0.13 (0.01)
Cw	F0	2500	0.99 (0.06)	0.17 (0.01)	0.55 (0.07)	0.09 (0.01)	0.86 (0.10)	0.12 (0.00)
Cw	F1	500	1.11 (0.12)	0.18 (0.02)	0.41 (0.08)	0.09 (0.01)	1.05 (0.07)	0.11 (0.02)
Cw	F1	1500	1.18 (0.15)	0.18 (0.01)	0.51 (0.03)	0.09 (0.01)	0.98 (0.09)	0.11 (0.01)
Cw	F1	2500	1.12 (0.05)	0.19 (0.02)	0.50 (0.06)	0.09 (0.01)	0.99 (0.05)	0.12 (0.01)
Hw	F0	500	0.92 (0.11)	0.11 (0.01)	0.65 (0.10)	0.10 (0.02)	0.22 (0.03)	0.09 (0.01)
Hw	F0	1500	0.86 (0.15)	0.09 (0.01)	0.56 (0.04)	0.10 (0.01)	0.22 (0.04)	0.09 (0.02)
Hw	F0	2500	0.92 (0.19)	0.10 (0.02)	0.54 (0.09)	0.10 (0.02)	0.29 (0.11)	0.09 (0.03)
Hw	F1	500	0.79 (0.04)	0.19 (0.04)	0.55 (0.04)	0.08 (0.00)	0.23 (0.05)	0.12 (0.01)
Hw	F1	1500	1.01 (0.04)	0.18 (0.02)	0.47 (0.03)	0.10 (0.01)	0.42 (0.11)	0.12 (0.04)
Hw	F1	2500	1.06 (0.09)	0.18 (0.05)	0.49 (0.14)	0.11 (0.01)	0.44 (0.12)	0.11 (0.01)

Note: CH site, nutrient poor conditions; HA site, nutrient medium conditions; Cw, western redcedar; Hw, western hemlock; F0, unfertilized; and F1,

lock than in cedar on the HA site. Increasing density significantly reduced the single-stem volume increment, although this was more pronounced on CH sites. The stem volume increment significantly decreased in the order 500 stems/ha > 1500 stems/ha > 2500 stems/ha on CH sites. On HA sites, the stem volume increment was significantly less for the 2500 stems/ha treatment compared with the 500 stems/ha treatment.

Mortality

Despite the effects of planting density on growth, density-dependent mortality was not evident on these sites (Tables 1 and 2). Mortality was significantly greater in hemlock than in cedar: up to 687% greater on CH and 269% on HA sites. Fertilization significantly increased mortality on HA sites: a 35%–94% increase for cedar and a 16%–198% increase for hemlock. In general, mortality was about twice as great on HA sites compared with CH sites. Total cumulative mortality was still low, ranging from less than 1% on unfertilized CH to 16% for fertilized hemlock on HA sites. In the latter case, there appeared to be a reverse association between density and mortality.

Foliar nutrient concentrations

Fertilization increased foliar N concentration on HA but not CH sites (Tables 5 and 6). Foliar N concentrations for unfertilized hemlock on CH sites were lower than previously noted in the literature (Radwan and DeBell 1980, 1989; Radwan et al. 1984, 1991; Radwan and Harrington 1986; Weetman et al. 1989; Bennett et al. 2003; Kranabetter et al. 2003). Regardless of treatment, both species were very severely to severely N deficient on both site types (Ballard and Carter 1986). A significant correlation ($p < 0.05$) existed between foliar N concentration and mean annual height growth for the 1997–2002 period for both cedar and hemlock on CH sites ($r^2 = 0.29$ and $r^2 = 0.21$, respectively; Table 7) and HA sites ($r^2 = 0.72$ and $r^2 = 0.55$).

Fertilization increased foliar P in both species on both sites (Tables 5 and 6) but more so in hemlock. Unfertilized hemlock on both sites was either severely or moderately deficient in P (Ballard and Carter 1986). Unfertilized cedar was slightly P deficient, except in the 2500 stems/ha treatment on HA sites, where P was adequate. Fertilization increased hemlock P status to slightly deficient and cedar's status to adequate, except in the two highest density treatments on CH, which remained slightly deficient. Significant correlations between foliar P concentration and growth existed for both cedar and hemlock on the CH site ($r^2 = 0.62$ and $r^2 = 0.62$, respectively, Table 7) and hemlock on the HA site ($r^2 = 0.59$).

Fertilization decreased foliar K levels on both sites (Tables 5 and 6). The P status of both cedar and hemlock in all sites and treatments was slightly to moderately deficient (Ballard and Carter 1986). Fertilization also reduced foliar Mn and B levels in hemlock on the CH site. The Ca concentration was increased by fertilization on HA sites and in ce-

Fe (ppm)	Cu (ppm)	Zn (ppm)	Mn (ppm)	Al (ppm)	B (ppm)	SO_4-S (ppm)
40.51 (12.77)	3.38 (0.27)	12.29 (0.66)	337.37 (115.41)	38.49 (3.90)	9.72 (0.55)	131.03 (17.20)
37.82 (4.47)	3.37 (0.65)	12.69 (1.04)	254.24 (62.81)	40.50 (6.41)	9.98 (1.13)	117.05 (27.03)
33.77 (2.77)	3.24 (0.77)	10.81 (1.59)	494.42 (109.46)	40.51 (6.53)	9.27 (0.46)	109.65 (19.97)
45.99 (10.10)	3.39 (0.30)	13.26 (1.36)	318.45 (114.12)	38.57 (13.74)	10.21 (0.94)	149.35 (25.35)
33.54 (2.64)	3.62 (0.81)	12.21 (1.80)	385.52 (270.53)	48.26 (6.23)	10.18 (0.21)	133.44 (23.01)
29.34 (5.32)	3.47 (0.31)	12.80 (1.13)	270.99 (46.05)	30.00 (3.96)	9.97 (1.04)	145.50 (29.25)
45.37 (13.75)	12.98 (10.76)	9.08 (3.10)	2375.31 (391.13)	281.75 (99.05)	25.07 (2.78)	240.00 (56.27)
38.84 (6.91)	5.16 (2.79)	6.85 (0.85)	2143.26 (599.01)	260.06 (78.87)	24.58 (3.56)	265.86 (66.76)
40.22 (7.48)	3.51 (0.52)	6.36 (0.88)	2408.74 (290.92)	194.79 (21.82)	24.34 (0.92)	309.94 (44.16)
49.33 (14.99)	25.72 (40.39)	11.82 (10.50)	2049.31 (315.28)	360.07 (99.75)	22.78 (1.56)	243.85 (39.41)
37.63 (10.06)	3.89 (1.23)	6.35 (1.54)	1718.70 (584.23)	260.84 (55.53)	23.65 (3.27)	273.01 (56.28)
37.68 (6.42)	3.64 (0.40)	6.76 (0.72)	1768.04 (666.87)	290.73 (59.14)	22.78 (2.18)	255.20 (40.05)
37.68 (6.22)	4.04 (0.93)	12.12 (2.12)	324.85 (112.56)	36.33 (10.48)	10.95 (1.43)	145.95 (21.95)
44.40 (9.24)	3.36 (0.26)	12.64 (0.68)	405.32 (131.26)	38.35 (7.82)	10.22 (0.96)	129.68 (22.40)
41.66 (13.51)	3.36 (0.27)	12.76 (0.45)	264.84 (73.84)	32.24 (0.23)	9.55 (0.97)	148.11 (25.75)
36.34 (8.01)	3.64 (0.28)	12.92 (0.36)	439.86 (127.05)	36.36 (8.13)	11.87 (1.40)	125.67 (49.44)
43.32 (9.70)	4.61 (0.71)	15.05 (2.87)	319.87 (84.92)	40.63 (6.51)	12.53 (2.71)	109.92 (47.99)
37.84 (11.72)	4.59 (0.73)	14.32 (2.17)	343.00 (84.91)	34.47 (8.00)	12.98 (3.45)	100.59 (27.69)
46.85 (9.30)	4.69 (2.04)	6.64 (1.04)	1854.21 (738.32)	370.83 (54.04)	20.96 (3.03)	261.76 (73.01)
40.28 (8.45)	4.93 (2.89)	7.28 (1.70)	1763.33 (523.27)	281.00 (61.17)	21.88 (3.46)	290.36 (32.10)
42.84 (9.83)	4.80 (2.40)	7.79 (2.35)	2229.50 (254.59)	284.02 (85.41)	19.71 (5.21)	257.87 (65.28)
42.72 (8.53)	3.50 (0.90)	5.82 (1.38)	1354.56 (323.68)	396.98 (84.47)	19.94 (3.63)	171.11 (52.90)
40.21 (5.00)	5.97 (2.90)	9.20 (1.02)	2067.60 (454.04)	456.91 (115.09)	17.99 (3.18)	196.41 (38.99)
41.78 (14.75)	4.18 (0.73)	9.13 (2.68)	1660.90 (440.12)	391.98 (75.63)	15.16 (1.15)	276.79 (47.92)

fertilized. Values are means with SEs given in parentheses.

dar on CH sites (Tables 5 and 6). Fertilization also increased the concentration of foliar Mg in hemlock on both sites. Fertilization of HA sites increased foliar Zn concentrations in both species and Al concentration in hemlock. Growth of both cedar and hemlock was strongly correlated with foliar Ca concentration on HA sites (r^2 = 0.52 and r^2 = 0.69, respectively).

Discussion

Continued enhancement of tree and stand growth by the addition of N and P fertilizer 10 years after treatment is suggested by (*i*) significant increases in 1997–2002 incremental height growth in fertilized stands, (*ii*) significant correlations between foliar P and 1997–2002 height growth on both sites and between foliar N and periodic growth on HA sites, (*iii*) greater foliar P concentration in fertilized stands on both sites, and (*iv*) greater foliar N concentration on HA sites. Our results are in agreement with those of Bennett et al. (2003) and Blevins et al. (2006), who reported long-term increased growth of hemlock and cedar on CH sites associated with P and N fertilization, respectively. Our results suggest that the response of hemlock and cedar to fertilization with P and N is not just restricted to CH sites. The long-term response to fertilizer N (on HA sites) was not expected. The strong correlation of hemlock growth to N concentration on the HA site suggests that hemlock was able to respond to increased availability of N because its P requirements were met. Although hemlock P requirements may also have been met on the CH site, lack of N availability prevented further growth response. This is further support to the suggestion (Bennett et al. 2003; Blevins et al. 2006) that P nutrition is pivotal for hemlock growth and explains previous contradictory results for N fertilization of hemlock. Continued increased growth of fertilized stands is consistent with results showing elevated growth rates from a single application for up to 30–50 years (Nohrstedt 2001; Jandl et al. 2002), particularly with applications of triple superphosphate (Turner et al. 2002).

A likely mechanism for continued growth following fertilization on CH sites is elevated nutrient supply rate. A single application of fertilizer containing N and P elevated the soil supply of available N and P on CH sites 10–13 years after treatment (Bradley et al. 2000; Bennett et al. 2003). Fertilization also resulted in significantly increased growth and foliar P concentration of dominant hemlock compared with unfertilized stands (Bennett et al. 2003). The lack of fertilization effect on foliar N concentration and continued elevation of foliar P in this study suggests that N availability is no longer elevated on fertilized CH sites, but higher P availability persists. However, the generally greater correlation between foliar P concentration and growth than between foliar N and growth suggests that P may be the more limiting resource on CH sites. In contrast, the closer correlation between foliar N concentration and growth rate suggests that N may be the more limiting nutrient on HA sites.

Table 6. Analysis of foliar nutrient concentrations: *p* values.

Source of variation	df_n^a	N	P	K	S	Ca	Mg	Zn	Fe	Cu	Mn	Al	B	SO_4-S
CH Sites														
Species (S)	1	<0.0001*	0.0301	<0.0001*	0.0003*	<0.0001*	<0.0001*	<0.0001*	0.0242*	0.1025	<0.0001*	<0.0001*	<0.0001*	<0.0001*
Planting density (D)	2	0.0207*	0.9074	0.1841	0.1594	0.7160	0.8876	0.0912	0.0005*	0.1242	0.5023	0.0996	0.2313	0.6178
Fertilization (F)	1	0.0767	<0.0001*	0.0245*	0.7708	0.0004*	0.0110*	0.3737	0.8002	0.5598	0.0219	0.0680	0.5603	0.7022
S × D	2	0.6286	0.5610	0.1482	0.0281*	0.8856	0.4933	0.2812	0.5997	0.1218	0.5583	0.1050	0.2949	0.1560
S × F	1	0.9001	<0.0001*	0.9388	0.4835	0.0109*	<0.0001*	0.9797	0.7752	0.5916	0.0483	0.0603	0.0017*	0.1098
D × F	2	0.5992	0.2941	0.6569	0.9836	0.3888	0.3913	0.5843	0.1896	0.6665	0.4723	0.5289	0.9265	0.6998
S × D × F	2	0.7191	0.6968	0.4151	0.6092	0.6404	0.0503	0.7683	0.8864	0.6478	0.8876	0.2987	0.2898	0.2899
HA sites														
S	1	<0.0001*	<0.0001*	0.0192*	0.3055	<0.0001*	0.0062*	<0.0001*	0.4377	0.0724	<0.0001*	<0.0001*	<0.0001*	<0.0001*
D	2	0.1056	0.6925	0.8645	0.3526	0.0809	0.5907	0.0072*	0.9366	0.3136	0.4299	0.4697	0.7281	0.4315
F	1	0.0018*	<0.0001*	0.0116*	0.8987	<0.0001*	0.0220*	0.0129*	0.5068	0.5902	0.2799	0.0036*	0.2969	0.0021*
S × D	2	0.1085	0.1108	0.0036	0.0612	0.0203*	0.5330	0.5651	0.2781	0.4430	0.2090	0.5814	0.9973	0.1363
S × F	1	0.1652	<0.0001*	0.3315	0.6961	0.3520	0.0035*	0.4055	0.9548	0.2439	0.1540	0.0046*	0.0617	0.3110
D × F	2	0.0167	0.9676	0.7472	0.0803	0.5609	0.6581	0.1600	0.9455	0.1572	0.3052	0.1943	0.9036	0.3092
S × D × F	2	0.1761	0.9793	0.6035	0.2766	0.0529	0.6106	0.8030	0.9210	0.6964	0.0680	0.2134	0.8105	0.0478*

Note: CH site, nutrient poor conditions; and HA site, nutrient medium conditions. Values with an asterisk are significant at $p < 0.05$ for the *F* test.

[a] df_n, numerator degrees of freedom.

Table 7. Pearson correlation analysis of 1997–2002 height growth with foliar nutrient concentrations of N, P, and Ca.

		CH sites		HA sites	
Nutrient	Variable	Cw	Hw	Cw	Hw
N	R^2	0.288	0.205	0.716	0.552
	p	0.1093*	0.2601	<0.0001*	0.0011*
P	R^2	0.618	0.623	0.309	0.591
	p	0.0002*	0.0001*	0.0850	0.0004*
Ca	R^2	0.251	0.0719	0.516	0.693
	p	0.1661	0.6960	0.0025*	<0.0001*

Note: CH site, nutrient poor conditions; HA site, nutrient medium conditions; Cw, western redcedar; and Hw, western hemlock. Values with an asterisk are significant at $p < 0.05$ for the *F* test.

The smaller PAI for hemlock than for cedar on CH suggests that hemlock growth response is tapering off on CH sites. Indeed, fertilized hemlock trees on CH sites were visually chlorotic by fall 2002. Cedar is now the more productive species and shows a stronger response to fertilization. Cedar is also the more valuable of the two species. Growing cedar rather than hemlock appears to be better justified on CH sites. This is contrary to conclusions based on short-term results of this trial (Blevins and Prescott 2002) and demonstrates the value of long-term field trials for supporting silvicultural decisions.

The surprisingly strong and more sustained volume response of conifers on HA sites to fertilization suggests that investments in fertilization, for both hemlock and cedar, are likely more financially justifiable on HA rather than on CH sites. Although cedar has not typically been grown on HA sites, cedar growth, in terms of volume development and PAI, was approximately double on HA compared with CH sites. It makes little sense to invest in fertilization of CH stands when their productivity is much lower than that of HA stands. We suggest that the most appropriate management strategy for CH sites is to plant cedar at a modest density (≤1500 stems/ha) and reserve fertilizer investments for the HA sites.

These stands have not yet closed canopy, but interspecific competition for soil nutrients has already limited single-stem growth on CH sites more than on HA sites and reduced height growth on CH sites. These observations are likely explained by the inherently lower soil nutrient supply capacity of CH sites versus HA sites (Weetman et al. 1990; Prescott et al. 1996). On CH sites, higher planting densities would reduce the small pool of available soil nutrients sooner than would lower planting densities. The greater nutrient availability on HA sites has resulted in lower density stress and weak development of competition. The reduction in height growth with increasing density on CH sites was unexpected, because it is almost axiomatic in forestry that height growth is insensitive to density (e.g., Oliver and Larson 1996). Our results suggest that this assumption does not hold true where soil nutrient supply is a significant factor controlling stand development. The lack of density-dependent mortality on CH sites, especially when fertilized, and the fact that they had not yet closed canopy (treatments with the greatest reduction in growth due to density were also the shortest and most open) suggests that stands there are not differentiating as a result of competition for light but that competition is dominantly symmetric (Weiner 1985, 1986; Lieffers and Titus 1989). Symmetric competition develops in response to limitations in soil resources (Weiner 1985, 1986; Lieffers and Titus 1989; Nambiar and Sands 1993) and is likely to occur sooner in denser plantings, because the aggregate nutrient demand of the stand is greater than in less dense stands. Moisture stress is not an issue in these stands, because growing-season soil moisture deficits do not occur in this area (Messier 1993). Planting density reduced tree size development and resulted in symmetric competition in other studies (e.g., Nilsson 1994).

The generally stronger initial growth response of hemlock than cedar to fertilizer application may be explained by species rooting characteristics. Cedar tends to root more deeply within the soil profile than hemlock (Bennett et al. 2002; Wang et al. 2002), which may give hemlock an initial advantage in acquiring surface-applied fertilizer nutrients. It may also explain the declining growth of the denser plantings of hemlock on CH sites with time as nutrients of fertilizer origin are incorporated into biomass of trees, taken up by understory vegetation, and leaked to soil pools, thus becoming more limiting. Growth begins to slow because the hemlock cannot access nutrients located deeper in the soil profile; conversely, cedar, with its ability to root and access nutrient pools deeper in the soil, does not experience such an apparent decline in growth. The greater flood tolerance of cedar (Krajina et al. 1982) may also partly explain its generally greater growth on CH sites, which experience fluctuating water tables. The ability to tolerate saturated soils may allow cedar to access nutrients deeper in saturated soils than can hemlock.

The lack of a density or density × fertilization interaction effects on mortality suggests that fertilization did not increase density-dependent mortality. Fertilized stands in this experiment were more uniform (Negrave 2004) than the unfertilized one, which suggests that fertilization did not increase competition for light and differentiation but merely reduced symmetric competition for nutrients. The higher mortality on HA sites may be due to root pathogens. *Armillaria* spp. fruiting bodies were noted on the stump of a tree at the study site, and some mortality in the HA areas was clumped, which is characteristic of root pathogen centres. Higher nutrient levels may increase development of *Armillaria* (Singh 1983), but the effects of fertilization on *Armillaria* development and consequent mortality remain unclear (e.g., Rykowski 1983; Filip et al. 2002).

The long-term increase in foliar P concentration of fertilized conifers on both CH and HA sites is consistent with earlier findings for hemlock on CH sites (Bennett et al. 2003). The elevated N concentrations on HA sites 10 years after the last fertilization is consistent with long-term increases in N availability previously reported for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) and jack pine (*Pinus banksiana* Lamb.) forests (Binkley and Reid 1985; Strader and Binkley 1989; Prescott et al. 1995), although these studies had larger application rates than ours. Our observed long-term reductions in Mn and B concentrations in hemlock on fertilized CH sites contradicts Weetman et al. (1989), who noted a substantial increase in foliar Mn and B concentrations in hemlock associated with N and P fertilization on a CH site one growing season after treatment. Presumably, the fertilization initially increased uptake of Mn and B, but foliar concentrations were diluted by subsequent growth. Zhang and Allen (1996) noted increased foliar concentrations of Ca but decreased concentrations of Mg associated with N fertilization of loblolly pine (*Pinus taeda* L.). Increased availability of Ca, Mg, Mn, and B likely resulted from organic matter mobilization following urea application and subsequent changes in soil pH due to ureolysis and nitrification (Otchere-Boateng and Ballard 1978, 1981). A long-term increase in foliar Mg concentration by fertilization has not previously been noted in either hemlock or cedar. This is surprising, because dilution of foliar Mg with increased growth is the anticipated response.

The initial hypothesis that high planting density combined with fertilization would accelerate crown closure and increase CH site productivity to that of HA sites by displacing salal and increasing nutrient availability is not supported by our results. Although fertilization increased conifer growth in our trial, it also increased salal growth by about the same proportion on CH sites (Negrave 2004), and increasing conifer density tended to reduce growth. In a different trial on CH sites in which stand densities were much higher than ours (3100–3600 stems/ha), Bennett et al. (2003) found that fertilization continued to increase growth of hemlock, but not cedar, 13 years after N and P application. Salal abundance was not reduced by the fertilization in this case. Increasing stand density did not increase height growth and actually decreased heights on CH sites. Increasing stand density did not increase stand volumes on CH sites, and the density effect on PAI was inconsistent. Neither did stand density significantly affect nutrient availability. Strategies for improving productivity of heather sites in the British Isles include planting at higher densities (similar to those in Bennett et al. 2003). However, because of the small diameters of these trees, density management will be necessary to produce commercial-sized trees unless an extended rotation is accepted. Density management is a standard treatment in the United Kingdom but is rare in British Columbia, especially on low sites. Thus, any strategy to increase the productivity of CH sites that employs high planting densities is unlikely in British Columbia.

Productivity of ericaceous sites in other areas has been increased through silvicultural treatments to allow the production of commercial tree crops. The combination of ploughing and fertilization, with the option of herbicide application on some sites, has increased production of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) in Britain (Taylor and Tabbush 1990). Scarification and, to a lesser extent, fertilization, increased site quality of sheep laurel sites in eastern Canada (Thiffault et al. 2004). Although our results along with those of Bennett et al. (2003) and Blevins et al. (2006) indicate that silvicultural treatments may increase productivity of CH sites, the responses and the economic return on these expenditures is probably minor compared with the results that can be achieved on HA sites. The long-term results of our silvicultural trials indicate that the optimal strategy for regenerating CH sites is to plant cedar at intermediate densities, whereas the optimal strategy for HA sites is to also plant cedar and fertilize.

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