Growth and nutritional responses of western hemlock to fertilization: A review

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Abstract

Western hemlock (*Tsuga heterophylla*) dominates coastal forests of British Columbia. Current age-class distributions may reduce wood supply in the near term. Fertilization might improve growth and supply, but hemlock is considered unresponsive or erratic in its response. This paper reviews how hemlock has responded to fertilization in past studies and discusses some of the difficulties in interpreting those responses.

Topics include (1) nutrient deficiencies (2) experimental designs used, and growth and nutritional responses measured, (3) relationships between nutrient availability and growth of hemlock and associated conifers, and fertilization effects as influenced (4) by site and (5) by tree and stand characteristics. Few generalizations can be drawn from the literature. Phosphorus (P) additions may enhance response to additions of nitrogen (N), although P-deficient stands remain difficult to identify without measuring a response to P fertilization. For older (mid-rotation) stands, it is not possible to separate possible effects of stand age, stand density, and site and treatment applied (e.g., N-only versus N+P) on response to fertilization. There is a need to better define constraints on growth responses (nutrients, moisture, light) to fertilization in mid-rotation stands on key site types. Field experiments should be initiated to better define the relationships among stand age, stand density, stem growth, stand productivity, and stand leaf area, and to determine how these parameters may be influenced by nutrient availability. New experiments should apply more nutrients than N alone and should be designed to better characterize how nutrient supply and stand nutrient demand change with stand development.

KEYWORDS: *western hemlock,* Tsuga heterophylla, *fertilization, growth, nitrogen, phosphorus*

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The Issue

Western hemlock (*Tsuga heterophylla*) is the most commercially important tree species in coastal British Columbia, comprising 34% and 25% of the annual harvest (Crown land) in the Vancouver and Prince Rupert forest regions, respectively, from 1994 to 1999.[1] Hemlock is most common and exhibits its greatest growth in the low-elevation Coastal Western Hemlock (CWH) biogeoclimatic zone, but also occurs in drier and higher elevation subzones (e.g., Peterson *et al.* 1998). Hemlock is a climax species, establishing early or late in succession (Franklin 1988). The main silvicultural system is clearcutting, followed by planting or natural regeneration. Rotation lengths for second-growth hemlock are 60–80 years (A. van Niejenhuis, Western Forest Products, pers. comm., 2003). Harvested wood is used for pulp, plywood, and lumber (Jozsa *et al.* 1998; Miller 1999).

Many hemlock-dominated forest management units in coastal British Columbia have unbalanced age-class distributions, which may lead to near-term reductions in wood supply (Pearse 2001). Markets for hemlock lumber have been depressed since the mid-1990s (Piros 2001), but demands to preserve remaining old-growth coastal rainforest and the costs of logging on the coast are increasing. Understanding limits to growth of immature hemlock in accessible stands is increasingly important.

A low availability of mineral nutrients often limits forest growth. Appropriate fertilization can increase the amount and value of wood produced in a given area more economically than do other silvicultural treatments (McWilliams and Carter 1998), and might increase the productivity and supply of hemlock. However, growth responses of western hemlock stands to fertilization have long been considered unpredictable (Weetman *et al.* 1992). Because of this uncertainty, operational fertilization of hemlock-dominated stands in British Columbia is currently recommended only for young stands on sites rich in decaying wood in the CWHvh subzone or on salal-prone sites in the CWHvm1 subzone (B.C. Ministry of Forests 1995).

This paper reviews past and ongoing studies documenting how stem growth of hemlock has responded to fertilization, and suggests gaps in knowledge that make predictions of hemlock growth response to fertilization difficult. It follows other published reviews (Weetman

et al. 1992; Brix 1993b); many of the topics included were raised at a workshop on hemlock fertilization.[2]

Fertilization of coastal forests in the Pacific Northwest and southwestern British Columbia has generally meant fertilizing Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) forests with N, as urea. Relationships between site characteristics and the growth of coastal Douglas-fir were recognized early in the 20th century (Isaac and Hopkins 1937) and fertilization with N often increased the growth of Douglas-fir (Gessel and Walker 1956; Heilman and Gessel 1963; Knight 1963; Crossin *et al.* 1966). Widespread research trials were established in the 1960s–1970s in Oregon and Washington (Regional Forest Nutrition Research Project, RFNRP) and coastal British Columbia (EP703) to evaluate the long-term effects of thinning and fertilization with N as urea. N was added at rates of 0, 224, or 448 kg/ha in RFNRP and 0, 225, 450, 675, and 900 kg N/ha in EP703. Based on these studies, single applications of N at 224 kg/ha were estimated, over 10 years, to increase gross volumes by 22–25 m^3/ha in unthinned stands and by 27–32 m^3/ha in thinned stands (Chappell *et al.* 1992). These substantial responses by Douglas-fir to N fertilization have been corroborated by other long-term studies (Omule 1990; Brix 1993a; Weetman *et al.* 1997) and by shorter-term studies relating response to site characteristics (Miller *et al.* 1989; Carter *et al.* 1998). Growth of Douglas-fir has generally not increased when elements other than N were added alone or in combination with N (Gessel *et al.* 1981; Weetman *et al.* 1997; Carter *et al.* 1998). The size of response, frequency of stands that respond to N alone, and value of Douglas-fir have led to widespread fertilization of coastal Douglas-fir forests with urea.

Nutritional requirements and fertilization responses of hemlock have been examined in a number of studies (Table 1). Early studies were those of Smith *et al.* (1968) at the University of British Columbia Research Forest, RFNRP, EP703, and studies initiated by Weyerhaeuser and Crown Zellerbach in Oregon and Washington (Webster *et al.* 1976). Hemlock stands were a minor component of the RFNRP (34 installations, compared with 114 of Douglas-fir) and EP703 (24 installations, compared with 61 of Douglas-fir). Early studies examined responses of hemlock in mid-rotation to N fertilization. More recently, responses of young (5–8 year old) hemlock to fertilization with N, P, and other elements on cutovers of old-growth cedar–hemlock (CH) sites and of more productive second-growth hemlock–amabilis fir (HA) sites were examined on

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TABLE 1. Summary of hemlock stand fertilization trials.

Study ID	Location	# Install	Yr	Fert treatment*	Age/duration	Var	% response	Design notes
RFNRP[a]	Wa, Ore	34	1969	227, 455 kg N/ha	<10–>35 (U)/7 10–>40 (T)/7	D	4 (–25 to +38) 6 (–33 to +54)	2 plots/trt; 0.04 ha/plot
Weyerhaeuser[b]	WC PS	16 7	1970	100, 300, 500 lbs N/acre	? /4 ? /4	B	0 25	Trt not replicated within site; plot size unknown
Crown-Zellerbach[b]	OC OC WV	?		150, 300 lbs N/acre 100, 200 lbs N/acre 100, 200 lbs N/acre	? /4–6 ? /5 ? /6	D B	1, 12 0, –27 63, 64	?
EP703[c]	SWBC	9	1971	225, 450 kg N/ha	30–65/9	B	–4 (U); 21 (HT)	2 plots/trt; 60 trees/plot pre-thin
Radwan et al. (1991)	WC	1	1982	224 kg N/ha; 100, 300, 500 kg P/ha	25/4	B	0.7 (–11 to +7)	3 plots/trt; 0.02 ha and 8 meas trees/plot
SCHIRP hemlock plot fertilization demo trial[d,e]	NVI	1	1987	100, 200, 300 kg N; 100 kg P/ha w/ or w/o micronutr-refert 1997	5–8/14	V**	233u–209s***	0.06–0.09 ha and 60–70 trees/plot
SCHIRP fert. × planting density × scarification trial[e]	NVI-CH NVI-HA	1 1	1988	10 g N, 2.5 g P, 5 g K/tree at plant; 225 kg N, 75 kg P/ha at year 6	0, 5/10	V**	2757u–690s (CH site); 173u–106s (HA site)***	Densities of 500, 1000, or 2000 trees/ha; only 2500 trees/ha received scarification trt
de Montigny and de Jong (1998)	QCI	1	1991	225 kg N; 100 kg P/ha	21–25 /5	B	23–29	2 plots/trt; 0.12 ha/plot
Carter et al. (2001)	SWBC	44	1990	N225, N225, P100 blend	15–40/3	B	Up to 90	2 plots/trt; 0.04 ha and 6 meas trees/plot
White (2000)	SWBC	8	1995	224 kg N; 100, 500 kg P/ha w/ w/o other	19–42(?)/3	B	11–73	6 single-tree plots/trt in 4 responsive and 4 unresponsive sites of Carter et al. (2001)
van den Driessche et al. (2002a, 2000b, unpubl. manuscript)	NVI	3	1999	N100, N200; w/ w/o P, K, S	11–18/3	V	4–18	3 plots/trt; > 0.09 ha and 50 or 81 measured trees /plot
Beese et al. (2001)	WVI	1	1996	7.3 g N, 3.1 g P/tree	0/5	V	575 (F), 1325 (F+V)	3 plots/trt; 121 or 169 meas trees/plot

[a] Olson et al. (1981); [b] Webster et al. (1976); [c] Omule and Britton (1991); [d] Weetman et al. (1989); [e] Blevins and Prescott (2002).

* All fertilization studies include unfertilized control; ** Estimated from diameter and height data on SCHIRP Web site; *** Response in absence (u) or presence (s) of scarification.

Abbreviations: Study ID – RFNRP, Regional Forest Nutrition Research Project; SCHIRP, Salal Cedar Hemlock Integrated Research Project. Location – Wa, Washington; Ore, Oregon; WC, Washington coast; PS, Puget Sound lowland; OC, Oregon coast; WV, Willamette Valley; SWBC, Southwestern BC; NVI, Northern Vancouver Island; QCI, Queen Charlotte Islands; WVI, Western Vancouver Island. # Install – number of installations in study. Yr – year established. Age – U, unthinned; T, thinned; HT, heavily thinned. Variable (Var) – D, diameter; B, basal area; V, volume.

northern Vancouver Island (Weetman *et al.* 1989; Prescott and Weetman 1994; Blevins and Prescott 2002) and responses of mid-rotation hemlock to N, P, and other elements have been examined on other sites (White 2000; Carter *et al.* 2001; van den Driessche *et al.* 2002a, 2002b, unpubl. manuscript). Young spaced stands on CH sites are now operationally fertilized, with 11 653 ha aerially fertilized with 225 kg N/ha and 75 kg P/ha from 1989 to 2001 (A. van Niejenhuis, Western Forest Products, pers. comm., 2001). It is unknown to what extent responses observed to date on CH and HA sites apply to other sites, and under what conditions older stands will respond to fertilization.

How Variable Is the Growth Response of Hemlock to Fertilization?

In the RFNRP, 10 of 26 unthinned hemlock installations had diameter growth responses >10% (basal area increase of ca. 20%) over 7 years to both rates of N addition. Increases averaged 4% across sites (equivalent to a basal area increase of 8%), to a maximum of 54% (Olson *et al.* 1981). In comparison, 75% of unthinned Douglas-fir stands had volume growth increases of >10%; percentage increases in basal area may have been greater than percentage increases in volume (Miller *et al.* 1986). Consequently, while the frequency of stands responding may have been less in hemlock than in Douglas-fir, the reported data for unthinned stands are not directly comparable. Average basal area increases of fertilized unthinned hemlock through 7 years (8%) were less than those of Douglas-fir through 8 years (19%, estimated from Stegemoller and Chappell 1990). Hemlock clearly responded some of the time to N fertilization, but probably less frequently and with smaller average responses than did Douglas-fir. In EP703, N fertilization increased volume in 76% of Douglas-fir stands and 60% of the hemlock stands (Chappell *et al.* 1992). Comparisons are hampered by inconsistent height measurements (Darling and Omule 1989; Omule and Britton 1991) and the small number of hemlock installations (9 of 16) that had both fertilizer treatments and control plots (Stone 1994). In those 9 installations, N additions increased basal area by >10% in 2 of 4 unthinned stands and in all 5 thinned stands (Omule and Britton 1991).[3] Fertilizing Douglas-fir with 225 kg N/ha increased stand basal area by 5–7% in unthinned and thinned stands (Omule 1990). In EP703, it is unclear that hemlock was less responsive to N fertilization than was Douglas-fir.

The reported range of responses by hemlock to fertilization is wide, perhaps because studies have covered a broad range of experimental designs, treatments, responses measured, sites, tree ages, tree sizes, and stand densities.

Hemlock can respond to fertilization, although it often does not. It is unclear to what extent lesser average relative stem growth responses to fertilization in hemlock, compared with Douglas-fir, were due to differences in physiology or to the sites on which each was examined. The reported range of responses by hemlock to fertilization is wide, perhaps because studies have covered a broad range of experimental designs, treatments, responses measured, sites, tree ages, tree sizes, and stand densities (Table 1). These factors, along with comparisons of growth responses to nutrient availability by hemlock and associated conifers, are discussed below.

Why Has Hemlock Varied So Much in Its Growth Response to Fertilization?

Can Experimental Design Affect Results?

Experimental design can affect the results of fertilization experiments and their interpretation through choice of plot sizes, treatments selected, and replication. In assessing stand nutritional requirements, it is necessary to identify what elements are deficient and, ultimately, to add the limiting elements at sufficient rates and over large enough areas so that effects can be assessed at a stand level.

Exploratory studies employing many single- or few-tree plots, and combined with growth measurements over a relatively short period, are often used to identify what elements are deficient; such trials have been used to study hemlock fertilization responses (Weetman *et al.* 1989; White 2000). Advantages of such an approach are that many treatments can be assessed with considerable replication in small and variable stands and at lower cost than if larger plots were employed. Deficiencies identified by such trials have been confirmed in larger plot studies (Weetman *et al.* 1989). Treatment effects may be

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[3] Based on relation between mean absolute and relative responses derived from Chappell *et al.* (1992).

less apparent in smaller plots than in larger plots if added nutrients are captured by adjacent unfertilized trees (Cellier and Correll 1984); treatments may be less long-lived, and, if few trees are treated, the possibility increases that responses may be unrepresentative of the whole stand. Dominant trees may be in more fertile microsites and respond less to fertilization; alternatively, growth responses by dominants might further suppress subordinates (Webster *et al.* 1976). Large plots (e.g., Blevins and Prescott 2002) are ultimately needed to assess long-term effects of fertilization on hemlock stand development and mortality.

Are Elements Other Than N Deficient?

Aside from N, P seems most likely to limit the growth of hemlock. Evidence for P deficiencies comes from studies where P alone was added to potted seedlings in soils from stands in coastal Washington (Heilman and Ekuan 1980; Radwan *et al.* 1991; Radwan 1992) and from field studies in which growth responses to N+P were greater than to N alone (Weetman *et al.* 1989; White 2000; White *et al.* 2000; Carter *et al.* 2001; van den Driessche *et al.* 2002a, 2002b, unpubl. manuscript). Effects of adding P alone were reported from three sites: an 18-year-old stand on Vancouver Island (van den Driessche *et al.* 2002b, unpubl. manuscript) and 25- and 34-year-old stands in coastal Washington (Radwan *et al.* 1991); P alone did not increase growth in those studies.

Aside from N, P seems most likely to limit the growth of hemlock.

Deficiencies of elements other than P have not been conclusively shown to restrict growth responses of hemlock to N fertilization, although foliar SO_4-S concentrations were decreased by N-only fertilization, compared with controls (43 vs. 198 mg/kg; Carter *et al.* 2001). However, fertilization with NPKS, compared with NP, did not increase growth (van den Driessche *et al.* 2002a, 2002b, unpubl. manuscript).

Where P has been applied after planting in field experiments, maximum rates applied have varied, ranging from 100 (Weetman *et al.* 1989; Carter *et al.* 2001; van den Driessche *et al.* 2002a) to 200 (van den Driessche *et al.* 2002b, unpubl. manuscript) to 500 kg P/ha (White *et al.*

2000). Fertilization with N+P (100 kg P/ha) did not increase height growth of hemlock, but N+P (500 kg/ha) did (White *et al.* 2000) and foliar P concentrations increased with P rate. Hence, the growth of hemlock was enhanced in the last study by P additions at rates far higher than typically applied.

Do Responses Vary with the Type of Fertilizer Added?

Use of urea (46-0-0) as an N source has been suggested to contribute to the erratic responses of hemlock to N-only fertilization. The hypothesis is that hydrolysis of urea raises soil solution pH (Nason and Myrold 1992) to levels that damage fine roots and mycorrhizae, which are concentrated near the soil surface (Bennett *et al.* 2002). This may decrease elemental uptake and reduce growth. In one study, sulphur-coated urea increased hemlock

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growth more and decreased foliar concentrations of P, K, and S less than did urea (Radwan and DeBell 1989). In another study, fertilization of young hemlock with urea decreased uptake and foliar concentrations of P, Ca, Mg, Mn, Fe, and B (Gill and Lavender 1983a), but did not affect above-ground growth. Concentrations decreased most in the stand that responded the least to urea applications in a previous study. However, fertilization with urea did not decrease mycorrhizal abundance in hemlock roots in the longer term (Gill and Lavender 1983b; Kernaghan *et al.* 1995).

In a comparative study of N fertilizers in a 28-year-old hemlock stand, growth was increased similarly by urea, ammonium nitrate, ammonium sulphate, and calcium nitrate (Radwan *et al.* 1984). In a study of potted seedlings in sandy loam soil, shoot mass did not differ between urea and 11 other N sources (Radwan and DeBell 1980). Thus far, there is little evidence that urea is less effective than other N sources at promoting growth of hemlock.

TABLE 2. Critical foliar elemental concentrations for hemlock (adapted from Carter 1992).

Element	Concentration[a]			
	Very severely deficient	Moderate–severe deficiency	Slight–moderate deficiency	Adequate
N	<10.0	10.0–12.0	12.0–13.5	>13.5
P	<1.1	1.1–1.5	1.5–2.5	>2.5
K	<4.0	4.0–4.5	4.5–6.5	>6.5
Ca	<0.6	0.6–0.8	0.8–1.0	>1.0
Mg	<0.6	0.6–0.8	0.8–1.0	>0.10
S	?	?	?	?
		Probable deficiency	Possible deficiency	Adequate
Fe		< 5	25–50	>50
B		<5	5–12	>20
Cu		<1	1–3	>3
Zn		<10	10–15	>15
Mn		4–15	15–25	>25

[a] Concentrations for N, P, K, Ca, Mg, in g/kg; concentrations for remaining elements in mg/kg and are not specific for hemlock.

Effects of different inorganic P sources on hemlock have not been examined. Most studies have applied P as triple-super phosphate (0-45-0); P has also been applied as ammonium phosphate (van den Driessche *et al.* 2002a, 2002b, unpubl. manuscript).

The effects of organic and inorganic fertilizers on growth of hemlock have been compared. Fertilization increased height growth of hemlock, but responses did not differ between municipal biosolids and inorganic N and P (Weetman *et al.* 1993; Prescott and Brown 1998), even though the biosolids contained twice as much N.

Identifying Elemental Deficiencies in Hemlock

Assessments of stand nutritional status are important for inferring which stands will likely respond to nutrient additions and in interpreting why stands may not have responded to nutrient additions. Foliar elemental concentrations (Table 2) are commonly used as an index of tree nutritional status. Analyses can be expensive, but the cost may be small relative to installing, maintaining, and measuring growth in a large field experiment. Most recent studies of hemlock responses to fertilization incorporated foliar analyses as part of the response measurements, although some did not.

The choice of tissue, the timing of sampling, and the form in which the element is measured may affect whether a deficiency is identified. In studies of hemlock and other conifers, current-year foliage has generally been analyzed, but deficiencies of mobile elements (N and P) may be more evident in older needles (e.g., van den Driessche 1984). Urea fertilization decreased P concentrations in 2- to 3-year-old and immature current-year needles of hemlock, but not in current-year mature needles (Gill and Lavender 1983a). However, elemental concentrations in older needles have not since been examined as a diagnostic tool in hemlock. Vector analysis, which assesses responses in current-year needle mass *and* elemental concentrations to infer nutritional status, has been applied in hemlock studies (Weetman *et al.* 1989; Carter *et al.* 2001). Application of vector analysis is problematic, because hemlock exhibits indeterminate shoot growth. Consequently, both needle mass and needle numbers may increase during the growing season following fertilization. Weetman *et al.* (1989) found that needle mass per 1000 needles was more highly correlated with 3-year height growth than was needle mass per unit shoot length. Carter *et al.* (2001) confined sampling to proximal needles on the shoot (i.e., those most likely to be pre-formed). Only two of six sites showing increased first-season individual needle mass also had significant increases in 3-year basal area.

Concentrations of specific forms of elements (e.g., N as arginine; P as orthophosphate; S as sulphate) may be a more sensitive indicator of tree nutrient status than are total concentrations (Ballard and Carter 1986; White 2000). It is not yet clear whether measurements of specific elemental forms are a better predictor of growth response to fertilization.

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Have Growth Measurements in Hemlock Fertilization Studies Been Sufficient to Detect Responses to Fertilization?

An ongoing problem in forest fertilization experiments (not specific to hemlock) is accurately estimating response (i.e., determining how the treated sample would have grown if not fertilized) (McWilliams and Burk 1994). Pre-treatment heights and diameters are often used as covariates to increase the sensitivity of detecting fertilization effects (Cellier and Correll 1984); regression approaches using pre- and post-fertilization diameter increment data have also been applied in studies of hemlock (Olson *et al.* 1981; White *et al.* 2000; Carter *et al.* 2001). Olson *et al.* (1981) demonstrated that responses based on the latter approach may differ greatly from responses based on plot mean comparisons.

Radial responses to fertilization are normally measured at breast height (DBH, 1.3 m). If diameter increment varies along the stem, changes in DBH may not accurately estimate changes in mean stem diameter. Relationships between crown development and diameter growth along the stem have been examined in hemlock from the RFNRP trials (Kershaw and Maguire 2000). Cross-sectional area increment reached a maximum at quadratic mean foliage height and decreased below that point, with increment tending to be lower at breast height than at the base of the live crown. Fertilization increased DBH less than diameter in the mid-upper stem in radiata pine (*Pinus radiata*) (Whyte and Mead 1976; Barker 1978), and Scots pine (*Pinus sylvestris*) (Valinger 1992). In Douglas-fir, N fertilization increased diameter more at breast height than higher along the stem after 3 years (Brix and Ebell 1969), but did not differentially affect diameter growth along the stem over a longer period (Thomson and Barclay 1984).

Nutrient availability may affect wood density. Although wood density has been examined in hemlock (Jozsa *et al.* 1998), effects of fertilization on wood density have not. In Douglas-fir, N fertilization increased DBH by 60% and decreased specific gravity by 12% (Brix and Ebell 1969). In radiata pine, mean wood density at 15 and 20 years decreased 8% as foliar N increased from 0.8 to 1.2 g/kg; wood density at 6–7 years decreased 18% as foliar N increased from 8 to 1.4 g/kg (Beets *et al.* 2001). In an optimal nutrition study, fertilization increased radial growth of Norway spruce (*Picea abies*) three-fold and decreased wood density by about 20%, largely by increasing earlywood increment (Makinen *et al.* 2002). In hemlock, ring widths were negatively correlated with wood density in 90-year-old trees, particularly in juvenile wood; relative densities increased with the proportion of the ring as latewood (Jozsa *et al.* 1998).

This finding suggests that if fertilization increased diameter increment in hemlock, it might decrease ring density and increase the proportion of the ring as earlywood.

Do Growth and Growth Response of Hemlock to Fertilization Vary with Measures of Site Fertility?

Understanding how the growth of hemlock relates to site characteristics is important for predicting which stands will be responsive to fertilization.

Site index (SI) of hemlock increased with N availability and foliar N concentration (Radwan and DeBell 1980; Kayahara *et al.* 1995). In southwestern British Columbia, the increase in SI with foliar N was asymptotic. Maximum SI occurred at about 10 g N/kg, a concentration considered deficient for Douglas-fir (Ballard and Carter 1986). In Washington, SI increased linearly with foliar N as N increased from 10.4 to 13.6 g N/kg (Radwan and DeBell 1980). Likewise, height increment increased linearly with foliar N, P, and S as N increased from 8 to 15 mg/g, P increased from 1.0 to 2.9 mg/g, and S increased from 0.6 to 1.3 mg/g (Kranabetter *et al.* 2003).

Site index may underestimate potential productivity gains with increasing soil fertility (Kayahara *et al.* 1995). Hemlock site index was often less than that of Douglas-fir on comparable soils, but yield was 33–101% greater (Steinbrenner 1976), a consequence of greater stocking and greater volume per tree at a common diameter and height (Wiley 1976). Maximum height growth occurred at lower foliar N concentrations than required for maximum diameter growth in Corsican pine (*Pinus nigra* var. *maritima*) (Miller *et al.* 1981) and young hemlock (van den Driessche *et al.* 2002b, unpubl. manuscript). Fertilization often has greater effects on diameter and basal area than on height.

Fertilization at planting at a density of 2500 trees/ha, followed by refertilization at year 6, increased volume after 10 years by 2757% (fertilized only) and 5314% (scarified and fertilized) in the less fertile CH site and 156% in the more fertile HA site (Blevins and Prescott 2002). However, absolute increases in volume with fertilization were greater (48.7 vs. 37.2 m^3/ha) in the more productive HA sites.

In spaced sapling stands (11–18 years old), the stand growing on the rich–very rich site (Green and Klinka 1994) had greater 3-year volume response to N+P than did stands on the poor–medium sites (van den Driessche *et al.* 2002a, 2002b, unpubl. manuscript); the two stands that responded were at lower elevations than was the

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unresponsive stand. In somewhat older stands (11–39 years old), growth response to fertilization with N+P and other elements was unrelated to measures of soil nutrient availability (Carter *et al.* 2001). Pre-treatment foliar P concentrations were lower in responsive than in unresponsive stands. Diameter responses to N addition in 10- to 40-year-old hemlock stands, though not correlated with site index, were correlated with (Bray-2) extractable P in the forest floor and with the ratios of extractable P:mineralizable N and extractable P:total N in mineral soil (Radwan and Shumway 1983).

In 34- to 63-year-old stands in the CWHvm1 subzone, basal area response to N fertilization was greater in stands on fresh–moist sites than in moderately dry sites when unthinned; thinned stands responded on both fresh–moist and moderately dry sites in the CWHvm1 subzone (Omule and Britton 1991). It is unclear whether smaller responses on drier sites were due directly to moisture stress, or associated with reduced nutrient uptake under drier conditions; nonetheless, thinning apparently alleviated the limiting factor. The role of moisture stress in constraining growth responses to fertilization by hemlock is unknown.

An ability to characterize soil nutrient availability would help in predicting hemlock growth responses to fertilization. Estimates of available N and P are typically of mineral forms determined in various extracts. For example, available mineral P has been determined in hemlock soils following extraction with Bray-1, Bray-2, Mehlich-1, Mehlich-2 reagents, sodium bicarbonate, and sodium and ammonium acetate (Heilman and Ekuan 1980; Radwan *et al.* 1985, 1991; Kayahara *et al.* 1995; van den Driessche *et al.* 2002a, 2002b, unpubl. manuscript). In a comparison of extractants, available P values were correlated with each other, but response to N fertilization was best correlated with Bray-1, Bray-2, sodium bicarbonate, and Mehlich-1 extractable P (Radwan *et al.* 1985), suggesting that reduced P availability limited growth response to N fertilization on those sites.

However, if most soil N and P exists in organic form, and if organic forms are accessible to the plant, assays of mineral forms may underestimate N and P availability. In hemlock-dominated stands, the proportion of soil P in organic forms can be high. Bray-P was a smaller proportion of total P and the proportion of P in organic forms (monoesters, diesters, phosphonate) was greater (44% vs. 9%) in hemlock stands than in Douglas-fir–dominated stands (Preston and Trofymow 2000). Soil on a CH site may have had a smaller proportion of sodium hydroxide-extracted P as orthophosphate and a greater proportion

as orthophosphate diesters than did soil on the HA site (Cade-Menun *et al.* 2000). Plants in organic soils may produce extracellular phosphatases and make organic P available in quantities sufficient to satisfy P requirements (Kroehler and Linkins 1991). Depletion of P in the rhizosphere of Norway spruce seedlings was confined to soil organic P and correlated with acid phosphatase activity (Haussling and Marschner 1989). Western redcedar (*Thuja plicata*) seedlings grew in response to additions of organic P sources and the response was associated with acid phosphatase activity (Cade-Menun and Berch 1997).

Nitrogen is generally thought to be assimilated in mineral form (Marschner 1995). However, mycorrhizal trees can assimilate organic N, although the relative importance of organic and inorganic N is not known (Nasholm and Persson 2001). It is unknown to what extent hemlock accesses organic sources of N and P.

Is Hemlock Less Responsive to Increases in Nutrient Availability Than Its Coniferous Associates?

Although the RFNRP studies indicated that hemlock responded less, on average, to N fertilization than did Douglas-fir, little evidence suggests that hemlock is less responsive to changes in nutrient availability than are its coniferous associates when compared under identical conditions.

Little evidence suggests that hemlock is less responsive to changes in nutrient availability than are its coniferous associates when compared under identical conditions.

In field studies, SI of hemlock and Sitka spruce (*Picea sitchensis*) increased similarly across parent materials differing in fertility, but on a given parent material, SI of hemlock was more variable than that of Sitka spruce (Kranabetter *et al.* 2003). On a rich–very rich site (CWHxm 05) on Vancouver Island, volume growth increased with N+P fertilization as much or more in 11-year-old hemlock as in intermixed Douglas-fir. However, response to N alone was less in hemlock than in fir (van den Driessche *et al.* 2002a, unpubl. manuscript). Fertilization of a 17-year-old mixed stand of hemlock

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and Douglas-fir with N increased heights in both species; fertilization with N+P (500 kg P/ha) increased the height of hemlock, but not Douglas-fir (White *et al.* 2000). Hemlock and Douglas-fir may therefore differ in response to P additions on some sites. On northern Vancouver Island, volume response (relative and absolute) through 10 years to fertilization at planting and again at year 6 was greater in hemlock than in redcedar on a CH site; absolute increase in volume was also greater in hemlock than in cedar on the more productive HA site (Blevins and Prescott 2002). When unfertilized, 14-year-old hemlock trees were taller than amabilis fir, but shorter than western redcedar; however, fertilization increased height growth the most in hemlock (Prescott and Brown 1998).

In potted seedling studies, hemlock grew less than did: (1) Douglas-fir under comparable rates of nutrient addition (Burgess 1991); (2) western redcedar and Sitka spruce in solution culture at comparable N addition rates (Brown *et al.* 1996b); and (3) Douglas-fir, western redcedar, and Sitka spruce when grown in combinations of forest soil, compost, inorganic fertilizer, and sewage sludge (Bledsoe and Zasoski 1981). Lower maximum growth rates of hemlock seedlings were associated with lower maximum whole-plant N uptake and tissue N concentration, less increase in shoot:root ratios with increasing N supply, and a reduced allocation of assimilated N to photosynthetic proteins (Brown *et al.* 1996a, 1996b). Under comparable conditions, potential growth rates of hemlock may be less than those of other conifers at the young seedling stage, but there is little evidence of such differences in older trees.

How Do Stem Growth Responses to Fertilization Vary with Tree or Stand Characteristics?

Significant stem growth responses to fertilization by young hemlock have often been reported (Weetman *et al.* 1989; van den Driessche 1997; Blevins and Prescott 2002). Fertilization at planting increased 5-year volumes on a western Vancouver Island site (Beese *et al.* 2001) and increased 2-year biomass in higher-elevation *Vaccinium*-dominated sites (Titus *et al.* 2002). In the last two studies, response to fertilization during the measurement periods was enhanced by control of competing understory vegetation, but the effect of vegetation control alone was smaller than that of fertilization alone. Vegetation control, as scarification, did not enhance response to fertilization in an HA site, but did in a CH site (Blevins and Prescott 2002). In the CH site, fertilization, but not vegetation control, also increased N cycling rates (Bradley *et al.* 2000). Responses by young hemlock indicate that time to free-to-grow in hemlock can be reduced by appropriate fertilization.

In older hemlock stands (those which have reached canopy closure), stem growth increases with fertilization have also been reported (see above). It is unclear how responses have been influenced by stand characteristics such as age and stand density, compared with effects related to site or to the treatment (e.g., N-only applied). Such effects may be confounded in previous studies. Having said that, relative growth responses to N only were greater in 15- to 24-year-old stands compared with younger and older stands when unthinned, and were greater in 10- to 20-year-old stands than in 21- to 40-year-old stands when thinned (Olson *et al.* 1981), possibly suggesting an age effect on response. Growth response to fertilization across 44 sites was not associated with stand age or density in 11- to 39-year-old spaced hemlock stands (densities 550–900 stems/ha) (Carter *et al.* 2001), but that study was not specifically designed to assess the effects of age and density on response. Effects of N fertilization were greater in thinned than in unthinned stands (Webster *et al.* 1976; Omule and Britton 1991), but interactions of thinning and N+P fertilization were not significant (de Montigny and de Jong 1998). On sites where N fertilization increased diameters in thinned stands, it also increased diameters in unthinned stands (Olson *et al.* 1981).

Mid- or late-rotation hemlock stands should respond to fertilization if growth is more constrained by insufficient supplies of nutrients than by insufficient moisture or light. The relative importance of constraints imposed by availability of nutrients, moisture, and light is unknown for hemlock. Tree requirements for nutrients are highest when canopy closure occurs; after the canopy is fully formed, retranslocation from senescing foliage provides an increasing proportion of nutrients for new growth (Miller 1986). That proportion has not been quantified for mid- or late-rotation hemlock, but seems important for estimating stand nutrient demand (from soil) and predicting growth response to fertilization. Likewise, the extent to which insufficient moisture and light constrain growth in closed-canopy hemlock stands is unknown, but such knowledge might indicate where and when thinning would enhance stem growth responses to fertilization.

Stem growth responses of mid- and late-rotation hemlock to fertilization might be better understood (and become more predictable) if attention was paid to stand characteristics such as stand leaf area (leaf area index, LAI) that integrate stand age, tree size, and stand density, rather than stem growth alone. LAI may be useful to examine because: (1) it is closely related to stand growth

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(Waring 1983; Vose and Swank 1990), which integrates average individual tree size and stem density; (2) stem growth responses to fertilization are due largely to increases in leaf area (Brix 1981) and may be minimal above a certain LAI (Waring 1983; Vose and Allen 1988); and (3) LAI is closely related to light interception, soil water availability, and stand water use. LAI can be measured relatively quickly and non-destructively. It is not currently known how stem growth varies with LAI in shade-tolerant hemlock, but the relationship could be tested as part of experiments designed to compare the effects of stand density at a given stand age and effects of age at given stand densities on key sites. Such experiments would also provide a basis for assessing how supplies of nutrients, moisture, and light constrain the growth of hemlock.

Ultimately, it is essential to be able to model the growth responses of hemlock to fertilization if fertilization is to be thoroughly evaluated as a silvicultural tool for hemlock management. Fortunately, an appropriate model already exists and is in use in British Columbia. The Tree and Stand Simulator (TASS; Mitchell 1975) is a distance-dependent growth and yield model that simulates the interaction of crowns in three-dimensional space. The size of each crown determines the amount of stemwood increment (Goudie 1999). In general, TASS is used in economic assessments of silvicultural treatments and to support timber supply analyses. TASS has been used to model effects of stand density on crown characteristics, stem growth, and wood quality in hemlock (Goudie 1999), but fertilization responses of hemlock have not yet been modelled, largely because response data are lacking. Therefore, it seems prudent in new studies of hemlock growth responses to fertilization to collect crown data compatible with TASS.

Summary

Hemlock growth responses to fertilization cannot yet be accurately predicted across a variety of stands and sites. Though variable, growth responses have been significant in many studies. Hemlock is sufficiently important in coastal forestry to justify additional study of its nutrition and growth responses to fertilization. There is not only a need for additional well-designed empirical trials on key sites, but for more fundamental process-oriented studies that improve our understanding of constraints to hemlock growth. The latter should lead to better predictions of stem growth response to fertilization in different sites and stands. Such studies need to be coordinated among industry and private, government, and university researchers.

Hemlock growth responses to fertilization cannot yet be accurately predicted across a variety of stands and sites.

Nitrogen has the greatest effect of elements added singly. Phosphorus (P) additions may enhance response to additions of nitrogen (N). This has been most conclusively shown for young stands growing on cutovers of old-growth cedar–hemlock (CH) within the CWHvm1 subzone. Following fertilization, foliar N concentrations decreased after a few years, but foliar P concentrations remained elevated 11 years after fertilization (Blevins and Prescott 2002), suggesting that the effects of P additions might persist longer than those of N. Elsewhere, additions of P have sometimes improved responses of hemlock to N fertilization. Fertilization with N+P, compared with N alone, increases fertilization costs (Carter *et al.* 2001), so it is important to better identify on which sites trees are likely to be limited by P when fertilized with N, and to verify whether rates of P addition less than currently used (75–100 kg/ha) increase growth satisfactorily.

Nitrogen has the greatest effect of elements added singly.

There is a need to better understand how stand age, stand density, and tree size affect stem growth responses to fertilization and, ultimately, to model these responses. Such effects could be examined by varying density in stands of different ages and by comparing the effects of age at constant densities on well-characterized and key site types. Measurements of leaf area index, in conjunction with studies of fertilization effects on growth in relation to stand development, might give new insight into patterns of stem growth response. If appropriately designed, such studies could provide a basis for better understanding of the relative importance of nutrients, moisture, and light in controlling growth. Collection of crown data compatible with TASS will allow growth responses to fertilization to be modelled; this, in turn, will allow better assessments of the potential for fertilization to increase wood supply in hemlock-dominated forests.

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