

Nutrition management of cedar and hemlock plantations in coastal British Columbia

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Abstract Recent re-measurements of silvicultural trials in conifer plantations on nutrient-poor cedar-hemlock (CH) cutovers on northern Vancouver Island have confirmed co-limitation by nitrogen and phosphorus. Repeated fertilization increased volumes of both cedar and hemlock on CH sites (at 2,500 stems ha⁻¹) by about 100 m³ ha⁻¹ relative to unfertilized plots 22 years following initial fertilization, and increased the productivity of regenerating conifers to a level approximating that of neighbouring hemlock-amabilis fir (HA) sites. More surprising was the response to fertilization on the more-productive HA sites. After 22 years, cedar in fertilized HA plots had produced an extra 180 m³ ha⁻¹ compared to unfertilized HA plots, while hemlock had produced an extra 250 m³ ha⁻¹ in fertilized plots (at 2,500 stems ha⁻¹). Thus, contrary to expectations, the greatest volume responses of both hemlock and cedar to fertilization occurred on the good (HA) sites rather than on the poor (CH) sites. Ecological studies of CH and HA sites supported the hypothesis that the poor nutrient supply and productivity of CH sites is a long-term consequence of excessive moisture, and that the two site types bracket a critical ecological threshold of moisture, aeration and redox.

Keywords Silviculture · Fertilization · Productivity · Nitrogen · Phosphorus · Moisture · Redox

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Introduction

Nutritional management of forested sites depends on research that addresses the two principle questions: what nutrients are limiting, and what is the fundamental cause of the poor nutrient supply? With this information, a site-specific fertilization regime can be tailored and fertilization can be augmented with other silvicultural practices that address the underlying cause of the poor nutrient supply. In this paper we provide an overview of such a research program, the Salal Cedar Hemlock Integrated Research Program (SCHIRP), describe some of the key research findings over a period of three decades, and present recent findings from long-term silvicultural trials and ecological studies that address these two fundamental aspects of forest nutrition management.

Diagnosis of nutrient deficiencies and responses to fertilization

Overview of early SCHIRP silvicultural trials

The SCHIRP Program was initiated in 1985 to address a challenging forest regeneration situation on northern Vancouver Island, British Columbia. Following clearcut-harvesting and slash-burning, growth of planted and naturally regenerated conifers was initially good, but declined precipitously within 5–8 years, coincident with obvious yellowing of foliage. Interestingly, the growth check appeared on cutovers of old-growth forests of western redcedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (here-after referred to as cedar-hemlock or ‘CH’ sites), but not on adjacent cutovers of second-growth forests of hemlock and amabilis fir (*Abies amabilis* (Dougl.) Forbes) (HA sites). Fertilization screening trials confirmed deficiencies of nitrogen (N) and phosphorus (P) in conifers on CH sites (Weetman et al. 1989a, b) and long-term trials confirmed co-limitation of growth of regenerating conifers by N and P (Blevins and van Niejenhuis 2003). Analyses of foliage, litter and forest floors indicated that P supply remained elevated following fertilization such that a single application of P was sufficient, but that additional applications of N would be necessary at least until crown closure (Bennett et al. 2003). Subsequent field trials demonstrated the potential for large growth responses with addition of organic wastes such as municipal biosolids, fish-wood waste compost and fish silage to CH sites (McDonald et al. 1994, Prescott and Zabek 1997, Prescott and Blevins 2005). Although it had been assumed that nutrient supply was adequate during the first few years after planting, significant responses to fertilization-at-planting were demonstrated in field trials. On the basis of early results of these field fertilization trials the major licensee in the area, Western Forest Products Inc., initiated a program of operational fertilization of CH cutovers. Current operational practice for CH sites is planting at 1,000–1,400 stems ha⁻¹ with fertilizer ‘tea-bags’, fertilization with 200 kg N ha⁻¹ and 75 kg P ha⁻¹ at free-growing, and 200 kg N ha⁻¹ 7–10 years later. However, recent analyses of tree-growth responses in one long-term trial (The SCHIRP Installation) are causing foresters to re-think current silvicultural prescriptions for both CH and HA sites.

The SCHIRP installation

The SCHIRP Installation was initiated in 1989, to determine the optimal combination of tree species, planting density and fertilization for conifer regeneration on both CH and HA sites. The study sites were initially logged in 1986, broadcast-burned in 1987 and planted in late 1987 and early 1988. Ninety-six plots were assembled in a 3-km² area; 48 on CH

sites and 48 on HA sites. Each plot contained 64 core sample trees of either western hemlock or western redcedar surrounded by at least two rows of buffer trees. In the 500-sph plots, trees were planted 4.5 m apart, resulting in a central (core) measurement area of 36×36 m and a total plot size of 54×54 m, including a buffer zone. The 1,500 stems ha^{-1} treatment had a tree spacing of 2.6 m, a core measurement area of 21×21 m and a total area plot size of 32×32 m. In the 2,500 stems ha^{-1} treatment, between-tree spacing was 2 m, with a 16×16 m core measurement area and total plot size of 36×36 m. Buffer zones were planted at the same spacing as the core areas they surrounded. The 500- and 1,500-sph treatments had four rows of buffer trees on each side while the 2,500-sph treatment has 10 rows of buffer trees.

The experiment was arranged in a fully crossed factorial combination: two species (hemlock or cedar), three density levels (500, 1,500 and 2,500 stems ha^{-1}), and two fertilization treatments (control or fertilized). Each site type (CH or HA) was divided into four blocks, and each of the 12 possible combinations of species-density-fertility was randomly located within each block. Fertilizer was applied at time of planting with each seedling receiving 60 g of slow-release Nutricote[®], which provided 10 g of N, 2.5 g of P and 5 g of K per seedling. Five growing seasons later (early 1993), 225 kg ha^{-1} of N (urea) and 75 kg ha^{-1} of P (triple superphosphate) was applied by hand in a simulated broadcast application. An additional 225 kg ha^{-1} of N (urea) was applied in a simulated broadcast application in 2004 (after 15 growing seasons). Height of each living sample tree within core measurement areas in each plot were measured after the completion of growth in late fall of 1988, 1989, 1990, 1992, 1994, 1997, 2002 and 2009. Diameter (dbh) was measured in 1997, 2002 and 2009. Tree volumes were calculated using standard British Columbia Forest Service taper equations (Kozak 1988).

After 15 years (2002; Negrave et al. 2007), fertilization had increased stand-volume periodic annual increment (PAI) on CH sites by 753–2,552 and 122–209 % for hemlock and cedar, respectively. The greatest growth of cedar was in the fertilized treatment at 1,500 stems ha^{-1} ($7.0 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$); that of hemlock was in the fertilized treatment at 2,500 stems ha^{-1} ($5.0 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$). Fertilization also increased volume growth of both species on HA sites, by 94–264 %, with maximum PAI of hemlock ($25.6 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) and cedar ($15.1 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$) occurring on fertilized HA sites at 2,500 stems ha^{-1} . The surprisingly strong and sustained volume response of both species to fertilization on HA sites prompted Negrave et al. (2007) to suggest that fertilizer dollars might be better invested on HA sites rather than CH sites.

22-year growth responses in the SCHIRP installation

Height and volume data from the 22-year re-measurements of the SCHIRP Installation were analyzed using a mixed-effects model (general linear model PROC Mixed in SAS) for each combination within: two species (hemlock or cedar); three types of density (500, 1,500 and 2,500 stems ha^{-1}); and two types of fertility (control or fertilized). Block was incorporated as a random effect in the model. Repeated-measures analysis was applied with time and time-treatment interactions included as factors in the ANOVA. Significant levels within treatments and their interactions were compared by adjusting the least square means for Tukey's Honestly Significant Difference test. This model was applied to the following variables: tree height, stand volume, PAI 1997–2002 and PAI 2003–2009. A natural logarithmic transformation was applied to all variables to homogenize the variances. Tukey's Honestly Significant Difference test was used to analyze the correlation between PAI 1997–2002 and PAI 2003–2009 within single treatments. Significant levels

were set at $\alpha = 0.05$; SAS version 8.2 (SAS Institute Inc., Cary, North Carolina) was used for all analyses.

After 22 growing seasons, average height and volume were greater in fertilized plots throughout all densities, species and sites compared to the respective unfertilized treatments (Table S-1). On CH sites, significantly different growth responses of western redcedar and western hemlock to fertilization were evident in the height and volume data (Table 1; Fig. 1) and in the PAI of height and volume for both periods (1997–2002 and 2003–2009; except height during the second period) (Table 2). Although hemlock trees were initially much smaller than cedar trees on CH control sites; the response of hemlock to fertilizer was much greater than cedars, so that by 2009 volumes of fertilized hemlock

Table 1 Mixed model analyses of average height and volume on CH and HA sites

Treatment	NDF	DDF	F	p
CH sites				
<i>Height</i>				
Spp	1	33	28.17	<.0001*
Fert	1	33	437.23	<.0001*
Den	2	33	35.1	<.0001*
Den × Spp	2	33	1.72	0.1941
Spp × Fert	1	33	53.71	<.0001*
Den × Fert	2	33	4.64	0.0167*
Den × Spp × Fert	2	33	2.06	0.143
<i>Volume</i>				
Spp	1	33	111.73	<.0001*
Fert	1	33	544.6	<.0001*
Den	2	33	5.63	0.0079*
Den × Spp	2	33	0.63	0.5404
Spp × Fert	1	33	48.09	<.0001*
Den × Fert	2	33	2.65	0.0853
Den × Spp × Fert	2	33	3.07	0.0598
HA sites				
<i>Height</i>				
Spp	1	33	50.52	<.0001*
Fert	1	33	68.46	<.0001*
Den	2	33	0.25	0.784
Den × Spp	2	33	0.95	0.3962
Spp × Fert	1	33	2.68	0.111
Den × Fert	2	33	3.2	0.0535
Den × Spp × Fert	2	33	0.2	0.8162
<i>Volume</i>				
Spp	1	33	23.67	<.0001*
Fert	1	33	95.02	<.0001*
Den	2	33	31.93	<.0001*
Den × Spp	2	33	2.42	0.1042
Spp × Fert	1	33	3.76	0.0611
Den × Fert	2	33	12.13	<.0001*
Den × Spp × Fert	2	33	0.59	0.561

NDF numerator degrees of freedom, DDF denominator degrees of freedom, Spp species, Fert fertilization, Den density

* p value <0.05

Table 2 Mixed model analyses of periodic annual increment in height and volume on CH sites during each measurement period (1997–2002 and 2003–2009)

Treatment	NDF	DDF	F	p
<i>PAI-H (1997–2002)</i>				
Spp	1	33	24.13	<.0001*
Fert	1	33	52.49	<.0001*
Den	2	33	18.16	<.0001*
Den × Spp	2	33	0.5	0.6086
Spp × Fert	1	33	8.23	0.0071*
Den × Fert	2	33	1.58	0.2205
Den × Spp × Fert	2	33	1.46	0.2472
<i>PAI-H (2003–2009)</i>				
Spp	1	33	1.19	0.2825
Fert	1	33	319.95	<.0001*
Den	2	33	16.68	<.0001*
Den × Spp	2	33	0.7	0.5049
Spp × Fert	1	33	23.73	<.0001*
Den × Fert	2	33	8.91	0.0008*
Den × Spp × Fert	2	33	0.16	0.8518
<i>PAI-V (1997–2002)</i>				
Spp	1	33	107.28	<.0001*
Fert	1	33	277.31	<.0001*
Den	2	33	3.47	0.043*
Den × Spp	2	33	1.22	0.3076
Spp × Fert	1	33	50.13	<.0001*
Den × Fert	2	33	1.64	0.2088
Den × Spp × Fert	2	33	2.86	0.0712
<i>PAI-V (2003–2009)</i>				
Spp	1	33	85.78	<.0001*
Fert	1	33	601.53	<.0001*
Den	2	33	5	0.0127*
Den × Spp	2	33	0.42	0.6592
Spp × Fert	1	33	34.7	<.0001*
Den × Fert	2	33	2.72	0.0806
Den × Spp × Fert	2	33	2.12	0.1362

NDF Numerator degrees of freedom, DDF denominator degrees of freedom, Spp species, Fert fertilization, Den density

* p value <0.05

exceeded those of unfertilized cedar and were approaching those of fertilized cedar (Fig. 1). Notably, the volume of fertilized hemlock on CH sites was approaching that of unfertilized hemlock on HA sites (Table S-1; Fig. 2).

On HA sites, average total height and volume (Table 1), and PAI of height and volume during both periods (1997–2002 and 2003–2009) (Table 3) significantly differed between the two species. Independent of fertilization and stand density, hemlock had much higher total average height and volume and PAI of height and volume than did cedar on HA sites (Tables S-1, S-2).

There was a significant interaction between fertilization and stand density on total height on CH sites but not on HA sites (Table 1). For PAI of height there was no significant interaction between fertilization and stand density on either CH and HA sites during the early (1997–2002) period, but during the second period there was a significant interaction at both sites (Tables 2, 3). Stand volumes at the higher stand densities (1,500 and 2,500 stems ha⁻¹)

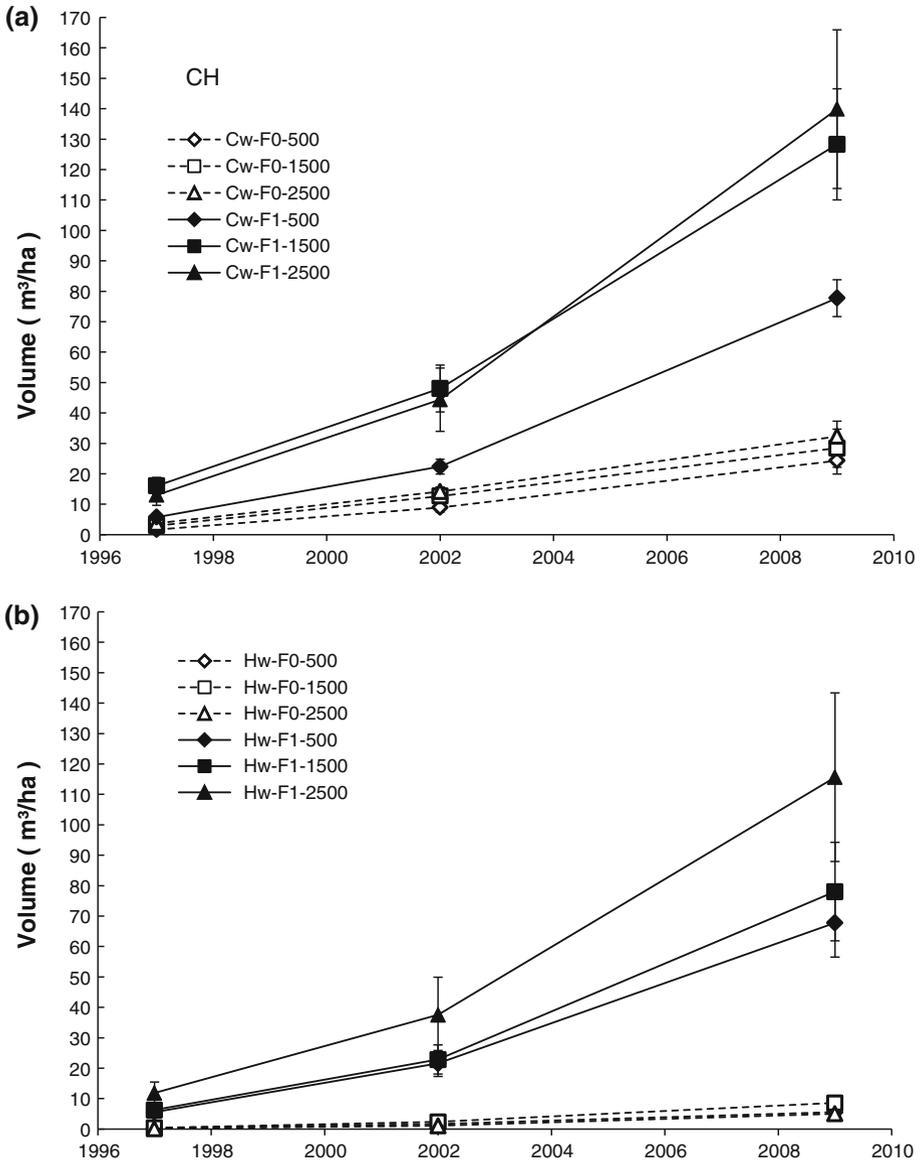


Fig. 1 Stand volume development in each treatment on CH sites, 1997–2009 (10–22 years after initial fertilization in 1987). **a** western red cedar (Cw); **b** western hemlock (Hw); F0 control, F1 fertilized; planting densities are 500, 1,500 and 2,500 stems ha^{-1} . Error bars are standard error of mean of 4 plots per treatment

were substantially greater than those at the lowest (500 stems ha^{-1}) density after fertilization (Figs. 1, 2). This was most apparent in the 2009 measurements and on HA sites. On HA sites there were significant interactions between stand density and fertilization for average total volume (Table 1), but no significant interactions for PAI of volume during either period (Table 3). On CH sites, there were no significant interactions between stand density and fertilization on average total volume or PAI of volume (Tables 1, 2).

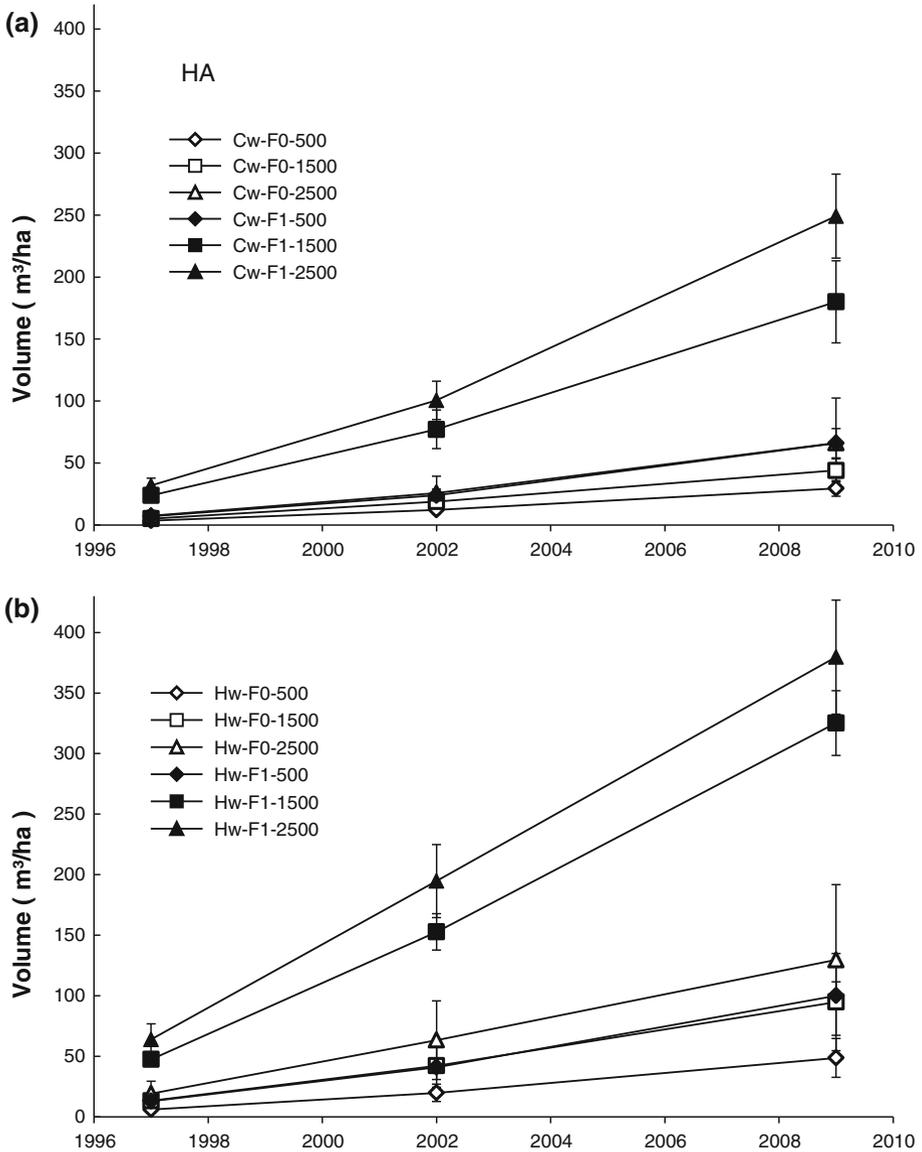


Fig. 2 Stand volume development in each treatment on HA sites, 1997–2009 (10–22 years after initial fertilization in 1987). **a** western red cedar (Cw); **b** western hemlock (Hw); F0 control, F1 fertilized; planting densities are 500, 1,500 and 2,500 stems ha⁻¹. Error bars are standard error of mean of 4 plots per treatment

Revisiting silvicultural prescriptions for CH sites

The initial goal of fertilization and other silvicultural interventions on CH sites was to increase productivity of regenerating conifers to a level approximating that of neighbouring HA sites. The data from this trial indicate that this objective can be accomplished by planting at high density and repeatedly fertilizing CH sites. Repeated fertilization

Table 3 Mixed model analyses of periodic annual increment in height and volume on HA sites during each measurement period (1997–2002 and 2003–2009)

Treatment	NDF	DDF	F	p
<i>PAI-H (1997–2002)</i>				
Spp	1	33	24.17	<.0001*
Fert	1	33	43.61	<.0001*
Den	2	33	0.25	0.7835
Den × Spp	2	33	1.22	0.3084
Spp × Fert	1	33	2.65	0.1128
Den × Fert	2	33	2.51	0.0966
Den × Spp × Fert	2	33	0.31	0.7332
<i>PAI-H (2003–2009)</i>				
Spp	1	33	20.76	<.0001*
Fert	1	33	62.58	<.0001*
Den	2	33	0.03	0.9734
Den × Spp	2	33	1.13	0.3355
Spp × Fert	1	33	0.06	0.8035
Den × Fert	2	33	3.46	0.0431*
Den × Spp × Fert	2	33	0.08	0.9279
<i>PAI-V (1997–2002)</i>				
Spp	1	33	9.58	0.004*
Fert	1	33	50.85	<.0001*
Den	2	33	12.88	<.0001*
Den × Spp	2	33	0.08	0.9204
Spp × Fert	1	33	0.23	0.6356
Den × Fert	2	33	1.85	0.1734
Den × Spp × Fert	2	33	0.04	0.962
<i>PAI-V (2003–2009)</i>				
Spp	1	33	7.46	0.01*
Fert	1	33	69.53	<.0001*
Den	2	33	12.01	0.0001*
Den × Spp	2	33	0.14	0.8668
Spp × Fert	1	33	0.05	0.8225
Den × Fert	2	33	1.8	0.1808
Den × Spp × Fert	2	33	0.08	0.9271

NDF numerator degrees of freedom, DDF denominator degrees of freedom, Spp species, Fert fertilization, Den density

* p value <0.05

increased volumes of both cedar and hemlock on CH sites (at 2,500 stems ha⁻¹) by about 100 m³ ha⁻¹ relative to unfertilized plots 22 years following initial fertilization (Table S-1). More surprising was the response to fertilization on HA sites. After 22 years, cedar in fertilized HA plots had produced an extra 180 m³ ha⁻¹ compared to unfertilized HA plots, while hemlock had produced an extra 250 m³ ha⁻¹ in fertilized plots (at 2,500 stems ha⁻¹). The greatest stand volume after 22 years was fertilized hemlock planted at 2,500 stems ha⁻¹ on HA sites (380 m ha⁻¹). In contrast, the greatest volume on CH sites was for cedar planted at 2,500 stems ha⁻¹ (140 m³ ha⁻¹). Thus, contrary to expectations, the long-term results of this trial indicate that the greatest volume responses of both hemlock and cedar to fertilization occur on the good (HA) sites rather than on the poor (CH) sites.

Ecological studies of the underlying cause of the poor nutrient supply on CH sites

Overview of early studies

Additional silvicultural trials and ecological studies had been initiated on CH sites to determine if other silvicultural treatments would address the underlying cause of the poor nutrient supply on CH sites, and so provide an alternative to repeated applications of fertilizer. A number of possible causes were identified, based on comparison of CH sites with neighbouring HA sites in which nutrient supply and productivity were high. One of the most obvious differences between the two site-types was the abundance of the ericaceous shrub, salal (*Gaultheria shallon* Pursch.), which was abundant in CH forests and assumed near-complete coverage of CH cutovers. In contrast, HA forests had sparse understory vegetation and cutovers contained a mix of salal and herbs such as fireweed (*Chamerion angustifolium* (L.) Scop.). In addition to competition, it was thought that salal, like other ericaceous shrubs, could interfere with nutrient supply by causing immobilization of nitrogen into phenolic compounds, and could have allelopathic effects on nearby conifer seedlings. Although almost-complete eradication of salal in a field trial on CH cutovers did result in improved growth of conifers, nutrient addition was still required to significantly improve tree growth (Bennett et al. 2004). Likewise, tremendous tree growth responses to nutrient addition despite enhanced growth of salal also indicated that competitive, nutritional or allelopathic effects of salal were not the fundamental cause of the poor conifer growth on CH sites (Prescott and Sajedi 2008, Mallik and Prescott 2001).

Could the absence of windthrow disturbance of CH forests (in contrast to second-growth HA forests) be responsible for the poor nutrient supply? The role of repeated windthrow in countering effects of paludification had been suggested in similar forests in coastal Alaska (Bormann et al. 1995). Field trials were installed employing soil scarification to mimic the soil disturbance afforded by windthrow events, to determine if this would promote a sustained increase in nutrient availability on CH cutovers. However neither the long-term effects of scarification on tree growth nor short-term effects of mixing soil and humus indicated beneficial effects of soil mixing on nutrient availability (Keenan et al. 1994).

HA and CH forests were considered to be successional phases of the same ecosystem type, so it was hypothesized that the low nutrient supply in old-growth CH forests could develop over time through progressive immobilization of nutrients in humus. However, no evidence (such as transitional forests or cedar regeneration in old HA forests) could be found in support of the hypothesis that HA forests developed through succession into CH forests, with associated immobilization of nutrients into humus. Finally, no evidence could be found in comparative effects of coastal conifer species on soil nutrient availability that the presence of cedar contributed to the low nutrient supply in CH forests (Prescott et al. 2000, Prescott 2010).

The excess moisture hypothesis

Although initially classified as having similar soils and occurring on the same site-type (Lewis 1982), indications of a fundamental difference among CH and HA sites began to accumulate during the course of the above studies. These observations included: the presence of shore pine (*Pinus contorta* Dougl. ex Laws. var. *contorta*), usually associated with forested bogs, on CH sites (Bothwell et al. 2001), identification of aquatic insects (copepods) in CH humus layers (Battigelli et al. 1994), and greater frequency of hydromors and gleyed horizons (indicative of frequently saturated soils) on CH sites (deMontigny

et al. 1993). Samples of forest-floor layers from CH sites tended to have moisture contents just above 80 % (wet-weight basis) and lower rates of N mineralization than those from HA sites, which were just below 80 % (Prescott, personal observation). Together these observations suggested that excessive moisture could be the fundamental cause of the low nutrient supply and poor conifer growth on CH sites. Given the high precipitation in this area (1,800 mm year⁻¹) any factor that impeded drainage could lead to conditions of excess moisture and associated saturation and anoxia, which would interfere with nutrient mineralization.

The excess moisture hypothesis was first tested through measurements along topographical gradients from HA forests through CH forests and to the wetter forested bog ecosystems to determine if there was evidence of a difference in soil aeration along this gradient, and if this was reflected in activity levels of various enzymes involved in decomposition of organic matter. Seven stands of CH, HA and forested bog ecosystems were selected in July and October 2004. At each site, 10 iron rods were inserted into the soil at random locations. Rust formation on the rods was assessed periodically; the depth of the rust indicating the extent of aerobic conditions in the soil. At the same time, 10 samples of the forest floor from each site were removed and gravimetric moisture content was measured following oven-drying at 70 °C for 48 h. Forest floor material from five CH, HA and forested bog sites was collected for assessment of enzyme activity.

A rapid microplate enzyme assay system (Sinsabaugh et al. 2003) was used to compare the key enzymes (β glucosidase, cellobiohydrolase, phenol oxidase and peroxidase) involved in carbon cycling in soil. For β glucosidase and cellobiohydrolase, 0.02 g of thawed soil samples were added to 100 ml of 50 mM, pH 5.0, acetate buffer and homogenized for 1 min at maximum speed using a Kinematic Polytron. 200- μ l aliquots were dispensed into a black, 96-well microplate; 16 replicate wells per sample. 50 μ l of 200 μ M substrate solution (4-MUB- β -D-glucoside or 4-MUB- β -D-cellobioside) was added to each sample well. Soil background fluorescence was measured using 50 μ l of acetate buffer with 200 μ l of soil sample. Negative control wells included 200 μ l of acetate buffer with 50 μ l of substrate solution. Quench standard wells contained 200 μ l sample suspension plus 50 μ l of standard (10 μ M 4-methylumbelliferone). Positive control wells received 200 μ l acetate buffer with 50 μ l of standard. A standard curve was generated with each soil type to assess quench. Plates were incubated at 20 °C for 3 h and activity was measured using a microplate fluorimeter with 360 nm excitation and 460 nm emission filters. After correcting for controls, quenching and substrate background activities were expressed in units of nmol h⁻¹ g⁻¹. For the phenol oxidase and peroxidase assays a colorimetric method was performed using L-3,4-dihydroxy-phenyl-alanine (L-DOPA) (Sinsabaugh et al. 1992). 1.0 g soil was placed in a 125-mL screw-cap Nalgene bottle and thoroughly homogenized in 50–60 mL of 50-mM acetate buffer, pH 5. 200- μ L aliquots of each sample were dispensed into eight replicates of each microplate well. 50 μ L of DOPA solution 25 (mM) was then added to each well. The peroxidase plates were prepared in the same way, except that each well also received 10 μ L of 0.3 % H₂O₂. Substrate and sample blanks were included. The contents of the microplate were mixed then incubated at 20 °C for 16 h. Absorbance was read using a microplate spectrophotometer at 460 nm.

There was a clear difference in aeration status among the three forest types, as indicated by the proportion of the iron bars which had not rusted during placement in the soil (Fig. 3a). In HA forests, <10 % of the rods was not rusted (i.e. indicative of anoxic conditions); in CH forests the proportion was mostly between 10 and 60 %; in forested bog forests, between 40 and 90 % of the rod indicated anoxic conditions. Examining only the

portion of the rod that was in the forest floor (Fig. 3b), indicated similar moisture patterns, with anoxic conditions indicated in the order forested bog > CH > HA.

Gravimetric moisture content data of forest floors (Fig. 4) supported earlier observations: in July, only cedar- skunk cabbage forests were >80 % water, but in October many of the CH forest floors were as well. HA forest floors were almost always <80 % water. The great range in moisture contents of the CH forests indicates that some CH sites are considerably wetter than others.

The activities of some of the enzymes (phenol oxidase, β-glucosidase) were consistent with our expectation of higher enzyme activity in HA and least in forested bogs (Fig. 5), but other enzymes did not show this pattern (data not shown). The pH of the forest floors were similar (4 to 4.5); thus differences in enzyme activities cannot be attributed to differences in pH.

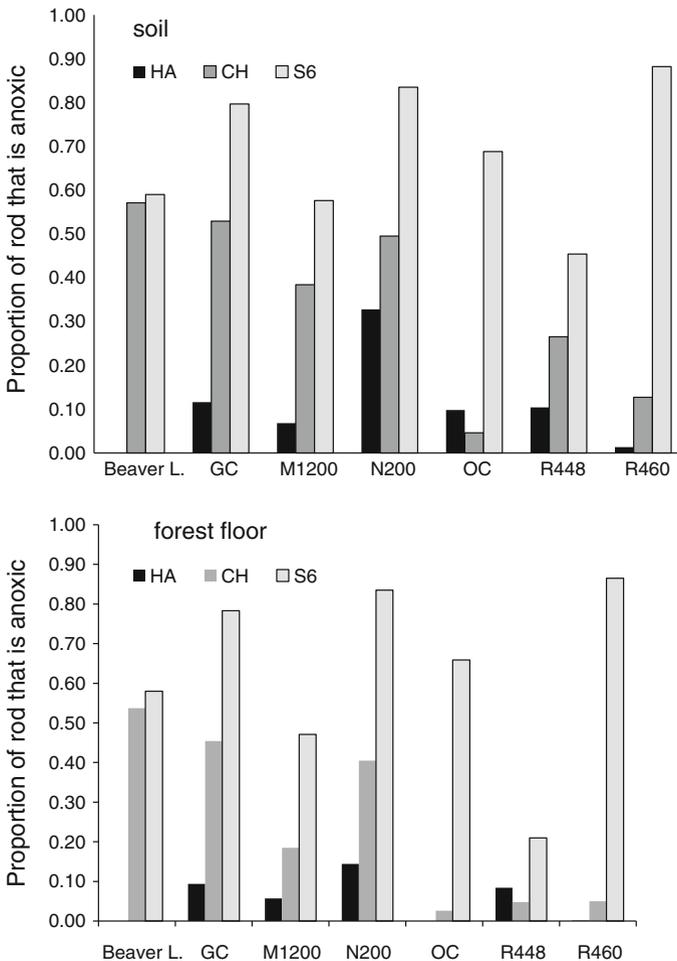


Fig. 3 Proportion of total iron rod length that indicated anoxic conditions in mineral soil (upper figure) and forest floor (lower figure) in HA forests, CH forests and S6 (forested bog) ecosystems located along a topographical gradient at 7 locations

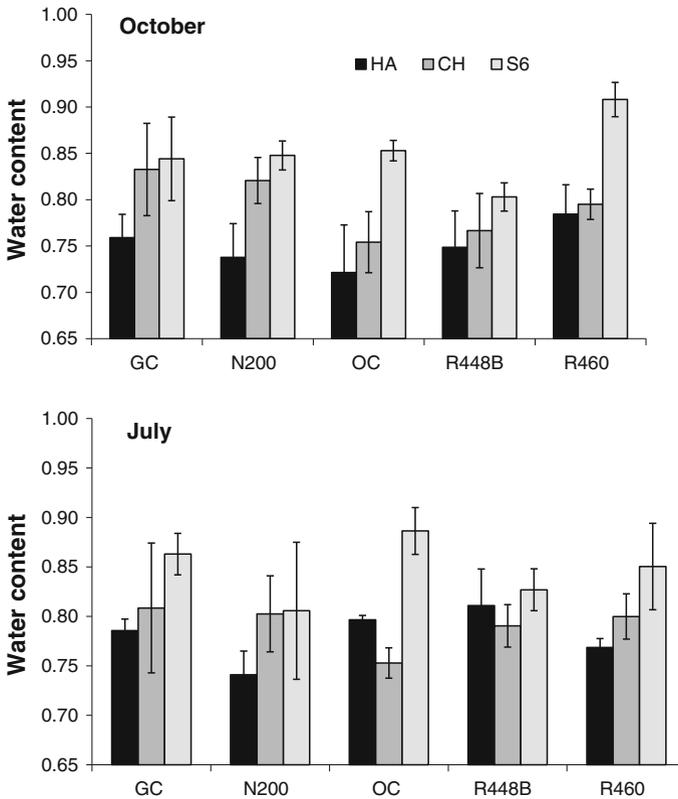


Fig. 4 Water content (proportion of fresh weight) of forest floor material from forests, CH forests and S6 (forested bog) ecosystems located along a topographical gradient at 5 locations

Greater frequency of anoxic conditions and shallower aerated depth on CH sites relative to HA sites was confirmed in a later study comparing 5 CH and 5 HA sites (Sajedi et al. 2012). Measurements of moisture content and redox confirmed that forest floors were significantly wetter in CH compared to HA forests, and had lower redox values, most of which were below the 300 level considered to be a critical threshold for anoxic conditions (Sajedi et al. 2012). Ordination of soil characteristics indicated that HA soils were relatively homogeneous and characterized by high oxidic depth, redox potential and % sand, while CH soils separated into three distinct groups: one much like HA soils, a second characterized by very low redox and shallow oxidic depth, and intermediate soils with high silt and clay, saturated but with redox like HA soils (Fig. 6). This was consistent with the earlier studies of aeration on CH sites, and indicated that there is a range of ‘CH-ness’. It also demonstrated that soil texture or presence of a pan layer could cause moisture to accumulate to excess conditions, resolving the question of why CH sites occasionally occur at higher slope positions.

Ecological development of different nutritional conditions on CH and HA sites

The current hypothesis for the development of distinct site-types despite similar parent material and climate is shown in Fig. 7. Where drainage is adequate, organic matter is efficiently decomposed and nutrient supply is high, and forests of hemlock and amabilis fir

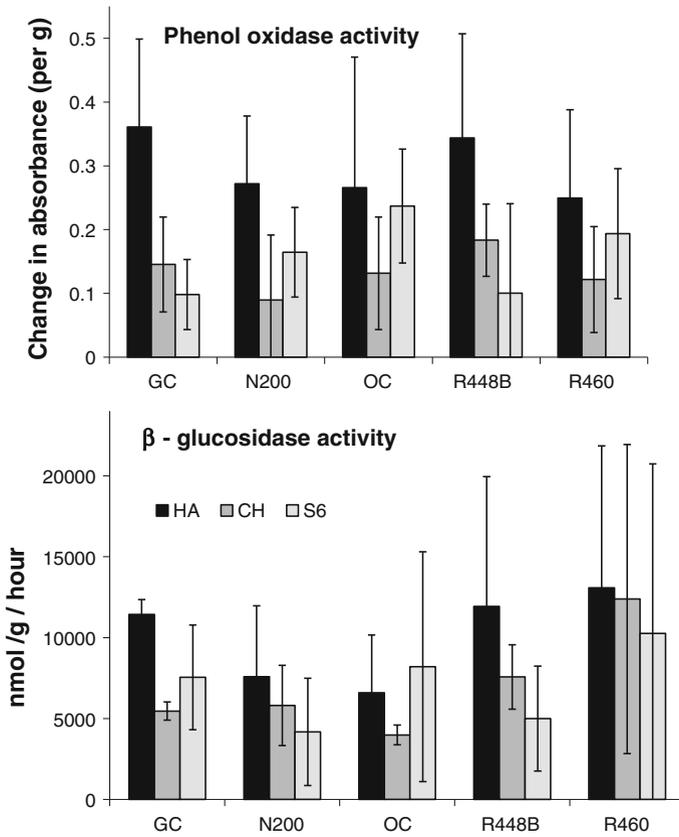


Fig. 5 Activity of the enzyme phenol oxidase in forest floors in HA forests, CH forests and S6 (forested bog) ecosystems located along a topographical gradient at 5 locations

predominate, reflecting the ability of these species to grow quickly when conditions are good. Where drainage is restricted (whether through slope position, fine-textured soil or presence of a pan layer), the soils are saturated for substantial parts of the year. Anoxic conditions occur in much of the soil profile, including the forest floor, and mineralization processes are impeded. Over centuries, nutrients (especially N and P) become progressively immobilized within the humus, and nutrient availability declines. Cedar, by virtue of its ability to grow in wet soils, becomes competitive, as does salal, due to its ability to thrive under conditions of low nutrient availability. Plants in this ecosystem have low concentrations of nutrients in their foliage, hence litter, and higher concentrations of recalcitrant compounds, which further reduce nutrient mineralization rates. These positive feedbacks with vegetation and litter chemistry exacerbate the low nutrient supply and cause progressive divergence of the sites into distinct plant communities, despite their close proximity and similar soils.

If, as the evidence suggests, excessive moisture is the fundamental cause of the low productivity of CH sites, the silvicultural treatment most likely to bring about a sustained enhancement of tree growth is drainage. A drainage trial was established in this area, but in a forested bog ecosystem, and growth of cedars was indeed, markedly improved within 15 m of each ditch. A drainage trial in a CH cutover would be instructive to determine if

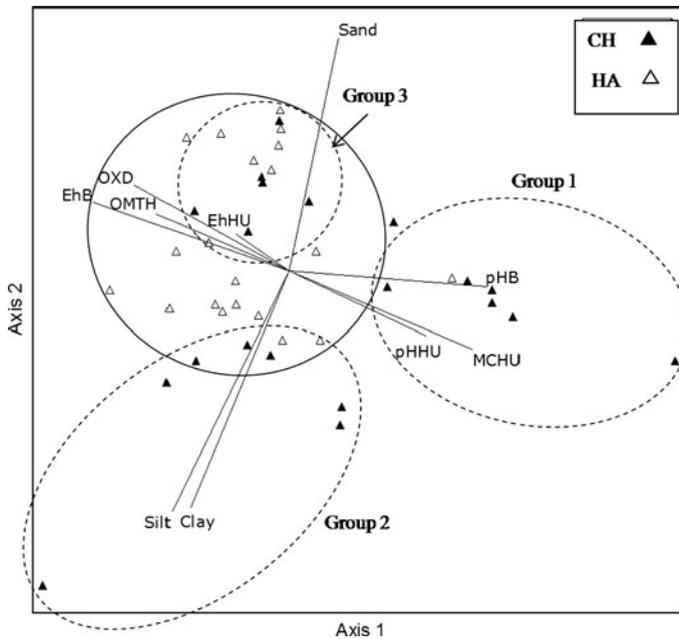


Fig. 6 Ordination diagram of principal component analysis (PCA) of soil characteristics in CH and HA forests, demonstrating the similarity of soils on HA sites but distinct differences in characteristics of soils on CH sites. From Sajedi et al. (2012)

this treatment could provide the original goal of turning CH sites into HA sites. However, the economics of this treatment, the ecological consequences, and the social acceptability of site conversion would need to be addressed before this would be given serious consideration as a silvicultural option for regeneration of CH sites. In the absence of site conversion, repeated fertilization with N and P remains the best treatment to improve the productivity of regenerating conifers on CH sites.

On the need for long-term research

Unravelling the complex ecological interactions underlying the differences in nutrient supply on these sites required a concerted and sustained research effort. Although initial observations and early results from silvicultural trials indicated that the abundance of salal was the primary cause of nutritional deficiencies in conifers, sustained research provided several lines of evidence that salal was a symptom and not a cause of the problem. Likewise, excess moisture was initially ruled out as a cause of the differences in nutrient supply given the very subtle differences in slope position of the two site types, but accumulated evidence from ecological studies and silvicultural trials led to this hypothesis being considered. Finally, the discovery of the unexpectedly high response to fertilization on the rich (HA) sites was the serendipitous result of a curiosity-driven decision to replicate treatments on HA sites in the SCHIRP Installation. While quick fixes may be implemented based on diagnoses of nutrient deficiencies, the most effective and sustainable management requires that foresters develop a sound understanding of the sites they are managing—an understanding that transcends site classification. It will not be lost on the

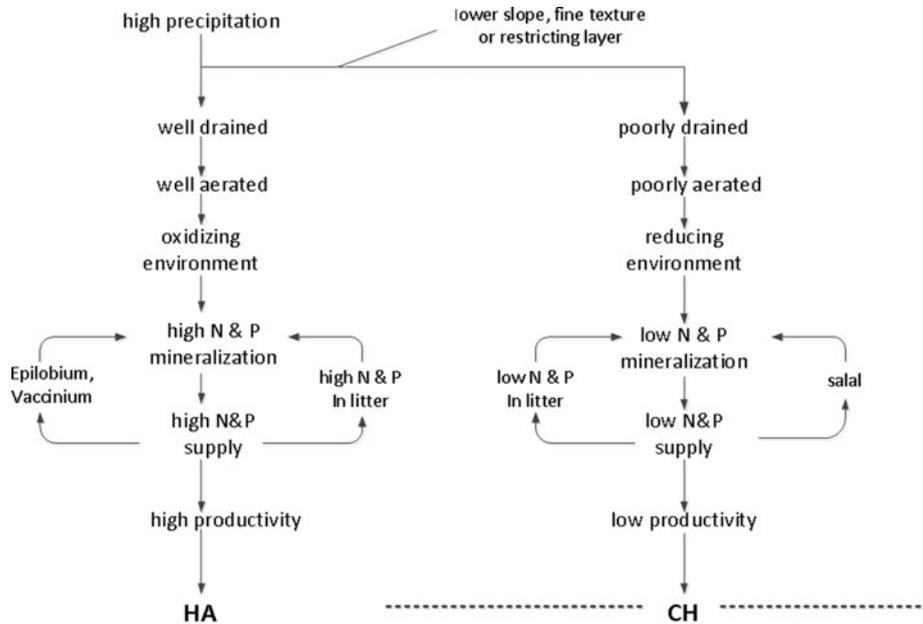


Fig. 7 Conceptual diagram of processes through which small differences in slope position or soil properties can, under conditions of high precipitation ($1,800 \text{ mm year}^{-1}$), lead to low N and P supply and low productivity on CH sites. Positive feedbacks through litter nutrient content and vegetation community composition are indicated. *Dashed line* indicates range of possible conditions within the CH site type

astute reader that the current ecological understanding and associated silvicultural prescription for CH sites would have been in place much sooner if thinking and research options had not been constrained by the belief that the sites were the same, based on their ecological classification. These sites have now been re-classified to reflect their distinct nutritional status, productivity and management challenges.

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