Three-year growth response of young Douglas-fir to nitrogen, calcium, phosphorus, and blended fertilizers in Oregon and Washington

Three-year growth response of young Douglas-fir to nitrogen, calcium, phosphorus, and blended fertilizers in Oregon and Washington

Douglas B. Mainwaring [a,*], Douglas A. Maguire [a], Steven S. Perakis [b]

[a] Department of Forest Engineering, Resources & Management, Oregon State University, Corvallis, OR 97331, United States
[b] US Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, OR 97331, United States

ABSTRACT

Studies of nutrient limitation in Douglas-fir forests of the Pacific Northwest focus predominantly on nitrogen, yet many stands demonstrate negligible or even negative growth response to nitrogen fertilization. To understand what nutrients other than nitrogen may limit forest productivity in this region, we tested six fertilizer treatments for their ability to increase stem volume growth response of dominant and co-dominant trees in young Douglas-fir plantations across a range of foliar and soil chemistry in western Oregon and Washington. We evaluated responses to single applications of urea, lime, calcium chloride, or monosodium phosphate at 16 sites, and to two site-specific nutrients blends at 12 of these sites. Across sites, the average stem volume growth increased marginally with urea, lime, and phosphorus fertilization. Fertilization responses generally aligned with plant and soil indicators of nutrient limitation. Response to nitrogen addition was greatest on soils with low total nitrogen and high exchangeable calcium concentrations. Responses to lime and calcium chloride additions were greatest at sites with low foliar calcium and low soil pH. Response to phosphorus addition was greatest on sites with low foliar phosphorus and high soil pH. Blended fertilizers yielded only marginal growth increases at one site, with no consistent effect across sites. Overall, our results highlight that calcium and phosphorus can be important growth limiting nutrients on specific sites in nitrogen-rich Douglas-fir forests of the Pacific Northwest.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

Nitrogen (N) is widely considered to be the most common growth limiting nutrient in terrestrial ecosystems worldwide, particularly in temperate forests (LeBauer and Treseder, 2008). In the Pacific Northwest, USA, field experiments in both natural and planted second growth forests demonstrate widespread N limitation of growth in Douglas-fir, the most abundant and commercially important conifer in the region (Miller and Pienaar, 1973; Peterson et al., 1984; Stegemoeller and Chappell, 1990). Consequently, N fertilization is widespread in commercial forests of the region, with nearly 40,000 ha of timberland fertilized annually in Oregon through the 1990s (http://www.oregon.gov/ODF/STATE_FORESTS/FRP/annual_reports.shtml). The magnitude of Douglas-fir growth response to N fertilization can depend on a number of factors, such as intrinsic site productivity (Edmonds and Hsiang, 1987; Miller et al., 1989), site N availability (Hopmans and Chappell, 1994; Peterson et al., 1984), degree of crown closure (Barclay and Brix, 1985), and the combination of crown size and foliar density (Brix and Ebell, 1969; Brix, 1983).

Douglas-fir response to N fertilization varies regionally across the Pacific Northwest, and in some cases, such as the coastal forest province, up to one-third of stands can show negligible and even negative growth responses to N fertilization (Peterson and Hazard, 1990). Some of these forest stands nevertheless continue to receive N fertilization due to a lack of methodology for identifying specific stands that are responsive to N and other nutrient(s) that may limit forest growth. In addition, historically the economic returns of fertilizing N-limited forests generally outweighed costs of occasionally fertilizing non-responsive stands. Improved nutrient management thus has the potential to increase the cost efficiency of fertilization for timber production, particularly as fertilization costs have risen. Improved N management can also reduce undesirable foliar nutrient imbalances (Mohren et al., 1986), pest and pathogen outbreaks (Turner and Lambert, 1986), soil fluxes of nitrous oxide and methane greenhouse gases (Castro et al., 1994) and nitrate leaching to waterways (Bisson et al., 1992), while improving soil carbon stabilization and storage (Swanston et al., 2004). Interactions between excess N and reduced

* Corresponding author. Tel.: +1 541 737 8107.
  E-mail address: doug.mainwaring@oregonstate.edu (D.B. Mainwaring).

growth due to pathogen susceptibility may be particularly important in coastal Douglas-fir forests. The endemic foliar fungal pathogen *Phaeocryptopus gaeumannii* (i.e., Swiss needle cast, or SNC) that is associated with excess foliar N in Douglas-fir (El-Hajj et al., 2004) has caused an estimated growth loss of 400,000 m^3 annually in 10–30 year old plantations in north coastal Oregon (Maguire et al., 2011).

Forest soils of the Pacific Northwest coastal region are among the most N-rich worldwide due to long-term disturbance cycles that promote early-successional biological N$_2$-fixation and soil N accretion by red alder (Perakis et al., 2011). Where such N-rich soils are planted to Douglas-fir, rates of soil available N supply can exceed plant N demands (Perakis and Sinkhorn, 2011), suggesting that other nutritional factors may limit Douglas-fir growth. Biogeochemical theory predicts that as N accumulates and geological parent materials weather, phosphorus (P) can be depleted from available forms and limit plant growth (Walker and Syers, 1976; Vitousek, 2004). Indeed, P is thought to be co-limiting with N in many ecosystems worldwide (Elser et al., 2007); in the Pacific Northwest, additions of P can improve growth of Douglas-fir seedlings when P is added alone (Heilman and Ekuan, 1980; Porada, 1987) and of young trees when added in combination with N (Gessel et al., 1979). High soil N that promotes nitrification and nitrate leaching in Douglas-fir forests also decreases soil pH (Perakis and Sinkhorn, 2011), which may reduce soil P availability by enhancing sorption onto iron-oxides (Haynes, 1982). Finally, high soil aluminum (Al) associated with andic soil properties in the region (Meurisse, 1976) may further decrease soil P availability (Johnson et al., 1986).

High N availability in soils may also lead more directly to the depletion of available base cations such as calcium (Ca) and magnesium (Mg) due to elevated nitrification, soil acidification, and coupled nitrate and base cation leaching loss (Aber et al., 1989; Perakis et al., 2013). In naturally N-rich Douglas-fir forests of the Oregon Coast Range, Ca is more likely than Mg to be deficient, as indicated by nutrient availability patterns in plants and soils, and contrasting patterns of Ca and Mg supply in atmospheric deposition relative to plant nutrient demands (Perakis et al., 2006). High nitrification and base cation depletion that lower soil pH also increase the solubility of potentially toxic elements such as Al and manganese (Mn) in these soils (Perakis et al., 2013). These processes may make it difficult to discern between base cation deficiency versus metal toxicity as factors limiting tree growth (Rengel, 1992; Cronan et al., 1989; Shortle and Smith, 1988). Studies on young Douglas-fir seedlings have shown that, under conditions of high Al concentration in the growing media, addition of Ca resulted in both increases in root development and root Ca concentration (Ryan et al., 1986; Porada, 1987). High Al also affects Douglas-fir root morphology (Curt et al., 2001) and inhibits Ca, P, Mg, Fe, and Zn uptake. Field experiments that manipulate Ca availability independent of pH are needed to discern effects of low Ca from elevated Al in high N soils.

We here report initial results of the "Beyond N" (BN) field experiments intended to advance our understanding of nutrients that may limit Douglas-fir growth on high-N forest soils of the Pacific Northwest. We focused our growth response measurements on tree stem volume growth which is of interest to commercial forestry in the region, and compared this to foliar and soil chemical factors to elucidate the nutritional deficiencies underlying the observed stem growth responses. We used novel fertilization compounds for this work, because forest fertilization experiments typically add nutrients in widely-available commercial formulations that can add other potentially growth limiting nutrients and/or alter soil pH in ways that confound hypothesized nutrient limitation patterns (e.g., Barron et al., 2009). We added P as monosodium phosphate, to minimize potentially confounding results stemming from application of P with N (i.e., as mono- and di-ammonium phosphate) or with Ca (i.e., triple super phosphate), a challenge commonly encountered when interpreting results of most operational fertilizer trials. Furthermore, sodium is the most abundant cation in precipitation in this coastal region, so the amount added in monosodium phosphate should be inconsequential. We added Ca separately as the neutral salt CaCl$_2$ and also as CaCO$_3$ (i.e., lime) to discern between potential effects of Ca as a nutrient versus an inducer of a pH shift, and because chloride is the most abundant anion in precipitation in this region. Finally, we also added nutrients in the form of two nutrient-blends formulated to address site-specific nutrient conditions, as assessed by soil chemistry in the first approach and by foliar chemistry in the second, and to provide information on full growth potential when nutrient limitation was relaxed. The specific objectives of this analysis were to determine if: (1) stem volume growth responds to any of six nutrient amendments designed to ameliorate possible nutrient limitations in Douglas-fir and (2) stem volume growth response can be predicted from initial soil and/or foliar chemistry.

2. Methods

2.1. Study sites

Sixteen study sites were distributed across a range in elevation, aspect, and needle retention classes in the Oregon and Washington Coast Ranges and west slope of the Cascade Mountains (43.28–46.60°N and 122.05–124.25°W; Fig. 1). Target stands were mid-rotation (av. = 19.1 years of age) Douglas-fir plantations of operational density (av. = 800 trees ha^{-1}) that had received no previous thinning or fertilization within the previous 10 years (Table 1).

Because identifying Douglas-fir stands that will respond to N fertilization has traditionally been very difficult (e.g.,Peterson and Hazard, 1990), the scope of inference was best described as the population of young Douglas-fir plantations that had not been previously fertilized. However, the wide range in initial foliar chemistry (Table 1), soil chemistry (Tables 2 and 3), soil taxonomic
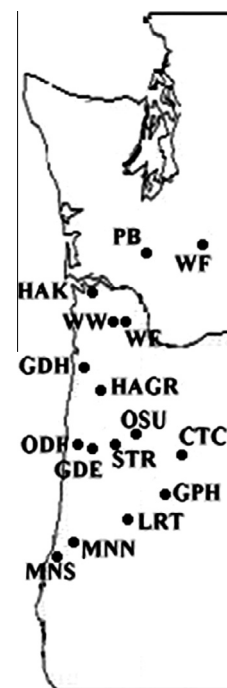
Fig. 1. Locations of the 16 "Beyond N" fertilizer trials in Oregon and Washington.

Table 1
Average tree and stand attributes for the 16 installations comprising the Douglas-fir "Beyond N" fertilization trials.

Plot	Quadratic mean dbh (cm)	Ht. (m)	Crown ratio	Foliage retention (yrs)	BH age (years)	Site Index (m @ 50 yrs)	Fol. N (%)	Fol. P (%)	Fol. Ca (%)	DF density (trees/ha)	DF basal area (m²/ha)	Soil taxonomic class
CTC	27.9	23.1	0.57	3.38	23.0	41.8	1.30	0.145	0.540	977	35.4	Fine, mixed, active, mesic Typic Palehumults
GDE	39.1	28.1	0.51	2.77	27.1	46.0	1.46	0.115	0.205	512	43.4	Fine, mixed, active, mesic Typic Haplohumults
GDH	29.2	21.1	0.64	1.62	19.8	41.3	1.43	0.115	0.185	724	32.6	Fine, Isotic, Mesic Andic Humudepts
GPH	23.4	17.2	0.64	3.64	15.0	47.5	1.26	0.150	0.530	921	24.9	Fine, mixed, active, mesic Xeric Haplohumults
HAGR	27.2	16.6	0.75	2.22	15.9	46.5	1.51	0.140	0.310	683	27.9	Fine, isotic, mesic Andic Humudepts
HAK	32.0	23.9	0.60	2.36	21.8	46.9	1.31	0.135	0.295	630	37.3	Medial, mixed, mesic Humic Haploxerands
LRT	36.8	22.6	0.65	3.35	21.1	43.1	1.24	0.175	0.540	435	36.3	Fine, mixed, superactive, mesic Aquultic Haploxeralfs
MNN	27.4	17.8	0.70	2.22	13.3	54.1	1.42	0.110	0.205	782	31.4	Fine-loamy, isotic, mesic Typic Humudepts
MNS	29.5	20.9	0.61	2.66	20.0	46.6	1.43	0.110	0.300	768	33.9	Fine-silty, isotic, isomesic Andic Humudepts
ODF	25.9	16.9	0.69	2.34	14.7	48.9	1.56	0.135	0.290	877	30.2	Fine-loamy, mixed, mesic Andic Haplumbrepts; medial over loamy, ferrihydritic over isotic, mesic Alic Hapludands
OSU	25.9	18.0	0.67	3.31	14.8	46.9	1.27	0.179	0.608	819	32.6	Fine-loamy, mixed, active, mesic Aquultic Haploxeralfs; fine-loamy, mixed, active, mesic Ultic Haploxeralfs; fine, mixed, superactive, mesic Aquultic Haploxeralfs
PB	26.4	21.5	0.47	3.41	20.4	45.1	1.30	0.175	0.455	1186	36.5	Fine, mixed, active, mesic Xeric Palehumults
STR	29.2	20.2	0.65	2.71	17.7	48.7	1.27	0.175	0.490	754	35.8	Fine, mixed, active, mesic Typic Haplohumults
WE	19.6	12.9	0.71	2.13	13.0	44.1	1.44	0.190	0.520	1544	31.4	Fine-loamy, mixed, mesic dystric eutochrepts; fine-loamy, mixed, mesic Umbric Dystrochrepts
WF	35.1	20.2	0.79	3.65	20.0	42.7	1.23	0.170	0.415	476	39.7	Cindery over medial Typic
WW	29.5	23.0	0.59	2.28	28.4	36.2	1.19	0.210	0.350	708	35.4	Cinders over medial TypicCryorthods

Table 2
Soil pH, CEC, and macronutrients at the 16 sites comprising the Douglas-fir "Beyond N" fertilization trials.

Site	pH	CEC (meq/100 g)	C (%)	N (%)	P (mg/kg)	K (meq/100 g)	Ca (meq/100 g)	Mg (meq/100 g)	Na (meq/100 g)	S (%)
CTC	5.39	53.09	6.564	0.313	0.971	1.320	16.786	5.423	0.176	0.021
GDE	4.84	44.21	10.045	0.595	8.624	0.654	1.544	0.920	0.233	0.048
GDH	4.69	53.90	11.294	0.589	0.440	0.327	0.566	0.544	0.229	0.054
GPH	5.90	25.34	4.233	0.191	13.595	0.886	8.910	2.202	0.117	0.011
HAGR	5.01	54.44	9.104	0.486	1.186	0.664	2.816	1.932	0.270	0.038
HAK	5.08	51.51	11.437	0.556	5.157	0.389	1.297	0.686	0.271	0.044
LR	5.81	25.12	3.118	0.161	8.830	0.888	6.146	2.227	0.144	0.010
MAC	6.26	25.67	3.131	0.205	21.559	1.151	13.281	2.540	0.148	0.012
MNN	4.58	50.21	12.221	0.782	2.114	0.581	0.762	0.538	0.235	0.060
MNS	5.25	41.69	8.709	0.454	1.914	0.697	2.569	1.456	0.243	0.034
ODF	4.93	42.04	9.255	0.486	2.653	0.682	1.711	1.449	0.198	0.043
PB	5.84	21.56	5.783	0.253	17.443	0.442	3.597	0.857	0.169	0.016
STR	5.38	32.82	5.050	0.282	15.049	1.013	6.019	2.827	0.182	0.018
WE	6.06	19.53	3.290	0.179	46.133	0.607	6.770	1.532	0.126	0.008
WF	5.00	23.07	7.193	0.215	13.286	0.229	2.279	0.617	0.111	0.021
WW	5.65	29.76	4.347	0.186	22.672	0.918	7.940	2.522	0.160	0.010
Mean	5.35	37.12	7.173	0.371	11.352	0.715	5.187	1.767	0.188	0.028

Table 3
Soil micronutrients at the 16 sites comprising the Douglas-fir "Beyond N" fertilization trials.

Site	B (mg/kg)	Cu (mg/kg)	Mn (mg/kg)	Zn (mg/kg)	Mo (mg/kg)	Fe (mg/kg)
CTC	0.4	1.0	22.4	0.7	<0.1	
GDE	0.4	0.5	2.3	0.7	<0.1	78.0
GDH	0.7	0.1	3.5	0.1	<0.1	
GPH						
HAGR	0.4	0.6	6.5	0.3	<0.1	166.0
HAK	0.3	0.4	3.7	0.6		111.7
LR						
MAC	0.2	1.6	38.0	1.0	<0.1	221.0
MNN	0.4	0.6	4.7	0.4	<0.1	
MNS	0.3	0.7	3.4	0.6	<0.1	
ODF	0.5	0.4	2.9	0.5	<0.1	127.0
PB	0.3	1.5	38.0	1.7		86.3
STR	0.3	0.5	8.7	0.8	<0.1	157.0
WE						
WF	0.2	1.5	29.4	2.0	<0.1	210.8
WW						
Mean	0.366	0.778	13.613	0.776	<0.1	144.725

classification (Table 1), and observed growth responses strongly suggested that the scope of inference likely represented the population of managed Douglas-fir stands of similar age and stand density in western Oregon and Washington.

Sites received either seven treatments (twelve sites) or only five of the seven treatments (four additional sites) (Table 1). The five treatments common to all 16 sites included the following amendments and rates: (1) untreated control (no fertilization), (2) nitrogen (225 kg N ha^{-1} as urea), (3) calcium (1020 kg Ca ha^{-1} as CaCO$_3$ lime (prilled, 34% Ca^{2+}), intended to provide Ca and increase soil pH), (4) calcium (105 kg Ca ha^{-1} as CaCl$_2$, intended to provide Ca but with minimal influence on soil pH) and (5) phosphorus (580 kg P ha^{-1} as monosodium phosphate). Twelve of the 16 sites also received two site-specific blends. The Kinsey blend was based on an analysis of soil chemistry and targeted to achieve a specific base cation saturation ratio (65% Ca, 15% Mg and 3.5% K; Albrecht, 1975), and attaining this ratio typically necessitated nutrient additions for two consecutive years. Because the Kinsey regime is tailored to soil chemistry at each site, nutrients additions varied by site, and called for addition of N, P, S, B, Cu, and Ca (as lime) on all 12 sites; dolomitic lime on 11 of the sites; Zn and Fe on nine of the sites; Mg on eight of the sites; K on six of the sites; and Mn on one of the sites (Table 4). The Fenn prescription entailed a single application of a blended fertilizer to bring foliar nutrient concentrations above deficiency levels defined by Walker and Gessel (1991) with modifications based on operational trials implemented by the late George Fenn (forest landowner from Elkton, Oregon). The Fenn blend called for addition of N on all 12 sites; K, Mg, and S on 11 sites; Ca on ten sites; and Zn on two sites (Table 5).

Treatments were ground applied on fixed-area plots (0.01 ha; radius = 5.67 m) centered on an undamaged, dominant or co-dominant "measurement" tree. Tree spacing at our sites averaged 3.53 m, so that the fertilizer addition typically encompassed the stems of multiple trees adjacent to the target measurement tree. Suitable measurement trees were selected on a 20 m grid, skipping grid points if no suitable subject tree was available. Treatments were randomly assigned to ten plots per treatment per site, and fertilizer was applied during February–April 2007, in a single

application typical of most commercial forest fertilizations. The Kinsey treatment was designed as a two-year regime, with non-lime materials applied during February–April 2007 and lime applied in February of 2008.

2.2. Measurements

The following dimensions were recorded from January to March of 2007 for all measurement trees located at the center of each treatment plot: diameter at breast height (dbh at 1.4 m, measured to nearest 0.1 cm), tree height (nearest 0.1 m), height to lowest live branch (nearest 0.1 m), breast-height sapwood width (from cores) (nearest 1 mm), and diameter at 5.5 m above ground level (nearest 0.1 cm). All other trees within the fixed-area treatment plot were also measured for initial dbh (nearest 0.1 cm) and plot basal area was computed as a measure of local stand density. To standardize foliage sampling, the southernmost branch in the fifth whorl from the tip of the tree was identified. The largest 4-yr-old lateral was removed from this branch on each tree for chemical analysis of foliage and estimation of foliage retention. Foliage retention, commonly used as an index of SNC severity (Maguire et al., 2011), was calculated as the sum of the proportion of retained needles within each needle age class. The samples for foliar chemistry were a composite sample of 2006 foliage (formed in the growing-season prior to fertilization treatments) from each of the plot measurement trees receiving the same treatment at a given site.

Two soil cores of surface mineral soil (0–10 cm, diameter = 7.5 cm) were collected from opposite sides of each plot measurement tree at approximately 1 m from the stem, then composited by treatment within sites, and subsampled for chemical analysis.

All measurements were repeated in the fall of 2009, after the end of the third growing season since treatment.

2.3. Chemical analysis

Chemical analysis was performed by the Central Analytical Laboratory at Oregon State University. All foliar samples were dried at 65 °C and ground to pass a 20 mesh sieve. Total nitrogen was

Table 4
Rates of application for materials included in the Kinsey fertilization regimes.

Material	WF	CTC	HAGR	STR	GDE	GDH	PB	OSU	ODF	MNN	MNS	HAK	Mean
Fertilizer application rates (kg/ha)													
Mono-ammonium phosphate	255	255	255	255	255	255	255	255	255	255	255	255	234
K$_2$SO$_4$	204	509	127			127	178	433					132
Sulfur	97	107	92	97	92	97	97	97	92	87	97	81	94
Boron	15	15	15	15	10		15	15	10		5	7	10
ZnSO$_4$	20		20	20	15	20	10	10	20	20			13
CuSO$_4$	20	10	10	20	31	20	20	20	25	25	25	25	21
FeSO$_4$		407	331	407	407		407	433	407	407	407	407	301
Potassium magnesium sulfate	407		305			305	764		407	330	407	407	278
MnSO$_4$							102						9
MgSO$_4$					305								25
Calcium lime	356	4939	1935	2851	1222	1222	967	2138	2291	967	2291	1527	1892
Dolomitic lime	1222	4226	2749	2546	3055	3157			2189	3259	1731	2138	2627
Elemental application rates (kg/ha)													
N	134	31	31	0	31	31	31	31	31	31	31	31	28
P	69	69	69	0	69	69	69	69	69	69	69	69	63
K	166	228	113	0	0	113	220	194	74	60	74	74	110
S	224	279	250	97	261	209	381	265	269	247	269	255	250
Ca	391	2760	1310	1615	1103	1124	367	812	1328	1049	1232	1027	1268
Mg	204	549	391	331	459	444	84	0	329	460	270	323	320
Mn	0	0	0	0	0	29	0	0	0	0	0	0	3
B	2	2	2	2	1	0	2	2	1	0	1	1	2
Zn	7	0	7	7	5	7	4	4	7	7	0	0	5
Cu	5	2	2	5	7	5	5	5	6	6	6	6	5
Fe	0	85	70	0	85	0	85	91	85	85	85	85	63

Table 5
Materials and rates of application for blended Fenn fertilizers.

Material	WF	CTC	HAGR	STR	GDE	GDH	PB	OSU	ODF	MNN	MNS	HAK	Mean
Material Fertilizer application rates (kg/ha)													
ESN (slow release N)	534	33	190	155	334	334	190	67	67	601	785	190	290
Potassium magnesium sulfate	637		382	382	764	764	382	255	255	448	240	382	408
Gypsum			280	117	700	700	280	351	351	84	534	280	306
Ammonium sulfate		467	47				47					47	51
ZnSO$_4$										307	157		39
Elemental application rates (kg/ha)													
N	203	111	82	59	127	127	82	25	25	228	298	82	121
K	117	0	70	70	140	140	70	47	47	82	44	70	75
S	140	112	148	106	301	301	148	123	123	176	185	148	168
Ca	0	0	64	27	161	161	64	81	81	19	123	64	70
Mg	70	0	42	42	84	84	42	28	28	49	26	42	45
Zn	0	0	0	0	0	0	0	0	0	124	64	0	17

determined by a dry combustion LECO CNS-2000 analyzer. For all other elements, 0.5 g ground samples were dry-ashed at 550 °C for 10 h, then extracted with 10 mL of a 5% HNO$_3$ solution overnight. The supernatant solutions were analyzed by a Perkin Elmer Optima 3000DV ICP optical emission spectrometer.

Soil pH was determined electrometrically from the supernatant of a 1:2 soil:water mixture (McLean, 1982). Soil extractable P was determined using a dilute acid–fluoride method (Bray-1 P). Soil exchangeable Ca (sCa) was extracted with unbuffered 1 M ammonium acetate and analyzed by atomic absorption spectrophotometer. Total soil nitrogen (sN) was determined using elemental analysis. All soil nutrient concentrations were expressed on a dry mass basis determined at 105 °C for 48 h. We expressed soil exchangeable Ca data as % Ca by mass (i.e., 100∗g Ca$_{exch}$/g soil) when evaluating growth responses as a function of soil Ca status. Soil Ca:N ratio (sCa/sN) was the ratio of Ca$_{exch}$ to total soil N. Cation exchange capacity (CEC) was determined using an ammonium acetate extraction followed by spectrophotometric analysis.

2.4. Analysis

Fertilizer treatment effects on three-year stem volume growth (Bruce and Demars, 1974) were tested by analysis of covariance under a generalized randomized complete block design (Quinn and Keough, 2002). This analysis was performed as a mixed-effects regression analysis to correct for several tree covariates relating to initial tree size and local stand density. These covariates included diameter, height, crown ratio (ratio of live crown length to total height, expressed as %), crown base sapwood area, foliage retention, and plot-level basal area. Sapwood area at breast height was computed by assuming a circular stem cross-section and by estimating diameter inside bark at breast height from dbh (Larsen and Hann, 1985). Sapwood area at crown base was then estimated from an existing regional sapwood taper function (Maguire and Batista, 1996). Tests were considered statistically significant at α = 0.05, and variables were included in the final regression models at this same α-level. Tests were considered marginally significant if $0.05 < p < 0.10$.

Treatment effects on volume growth were first tested at the regional level. Any significant effects were further explored by testing separately for differences in volume growth among treatments. The basic statistical model was as follows:

$$\ln(Y_{ijk}) = \mu + \theta_i + \tau_j + (\theta\tau)_{ij} + \alpha_1 \ln(D^2H_{ijk}) + \alpha_2 \ln(BA_{ijk}) + \varepsilon_{ijk} \quad (1)$$

where $\ln(\cdot)$, natural logarithm; Y_{ijk}, stem volume growth for kth tree receiving jth treatment in ith block; μ, mean response; θ_i, random effect of block (site) i; i = 1, 2,... 16; τ_j, fixed effect of treatment j;

j = 1, 2,...,7; $(\theta\tau)_{ij}$, block x treatment interaction effects; D^2H, covariate representing size of kth tree receiving jth treatment in ith block, where D is initial diameter at breast height (cm) and H is initial height (m); BA, covariate representing local stand density around kth tree receiving jth treatment in ith block, where BA is basal area (m^2 ha^{-1}); α_1–α_2, parameters to be estimated from the data and representing effect of tree covariates D^2H and BA; ε_{ijk}, random error for the ith tree from the jth treatment in the ith block, with $\varepsilon_{ijk} \sim N(0, \sigma_\varepsilon^2)$.

All 16 sites were included to test for urea, lime, calcium chloride, and phosphorus fertilization effects, and 12 sites were available for testing the Kinsey regime and Fenn blend.

Replication within sites allowed testing of site x treatment interactions and identification of site-specific treatment effects. Site-specific effects were tested with a statistical model consistent with Eq. (1) but with the random site effect and its interactions removed.

Because we expected response to fertilization to vary continuously over gradients in initial site and stand conditions, the test of discrete treatment effects in model (1) was considered a coarse initial assessment that would require refinement to link initial conditions to magnitude of growth response. This refinement was essentially a test of the hypothesis that volume growth response can be predicted from initial soil and/or foliar chemistry. A second set of analyses was therefore performed by replacing site or block effects with attributes that characterized each site, e.g., site index, soil variables, and foliar nutrient concentrations. After identifying the most promising site-level predictors through literature review and several all-subsets regression analysis within SAS PROC REG (SAS Institute Inc. 2009), various linear and non-linear statistical models were fitted to predict site-level volume growth response from covariates describing initial site conditions.

3. Results

3.1. Initial nutrient concentrations

The range of nutrient concentrations in soil and foliage illustrated the wide variability in initial conditions among the 16 study sites (Table 1). For example, foliar N ranged from 1.19% to 1.56%, foliar Ca ranged from 0.185% to 0.608%, and foliar P ranged from 0.11% to 0.21%. As in most fertilization studies, available soil N was unknown, but total soil N concentration ranged from 0.16% to 0.83%, bracketing the range of surface soil N values that scale linearly to *in situ* annual net N mineralization in Douglas-fir stands (Perakis and Sinkhorn, 2011). Soil pH ranged from 4.74 to 6.46, and soil Ca$_{exch}$ ranged from 19.53 to 54.44 meq/100 g.

3.2. Regional treatment effects on volume growth

The regional volume growth analysis that considered all sites as a single population with covariates (full model (1)) yielded an insignificant treatment effect ($p = 0.26$), and a significant block x treatment interaction ($p = 0.01$), indicating that after adjusting for tree size and stand density, responses to treatment were site-specific rather than general across the region. Multiple comparisons indicated that stem volume growth differed only marginally among treatments for urea ($p = 0.069$), lime ($p = 0.051$) and phosphorus ($p = 0.10$). For urea, lime, and phosphorus, these marginal responses corresponded to an average volume growth increase of 3.7%, 4.0%, and 3.3%, respectively (Fig. 2).

Site-specific analysis of covariance (model (1) with no block effects or block interactions) indicated that volume growth increases were significant following N treatment at two sites (CTC, WW), calcium chloride treatment at one site (WE), and phosphorus treatment at one site (MNS). In addition, three sites demonstrated a marginally significant increase in volume growth following phosphorus treatment (CTC, ODF, WE), and one site following the Kinsey regime (CTC) (Table 6).

3.3. Influence of initial site and stand conditions on volume growth

Variables for predicting volume growth response of measurement trees included tree attributes, site factors (e.g., site index), and variables representing various initial soil and foliar nutrient concentrations. The variables selected for predicting volume growth response varied by treatment (Table 7).

A large amount of the variation in regional volume response to N fertilization was explained by the soil calcium to nitrogen ratio (sCa/sN) in the following statistical model ($R^2 = 0.91$, MSE = 0.0106):

$$\ln(VOLGR) = a_0 + a_1 \ln(D^2H) + a_2 \ln(SI) + a_3(pH) + a_4 \ln(fCa) \\ + a_5 \ln(sCaN) + a_6(I_U) + a_7 I_U * \ln(sCaN) \qquad (2)$$

where VOLGR, predicted periodic annual volume increment for individual tree (dm^3 yr^{-1}); SI, site index (m at 50 years, (Bruce, 1981)); pH, initial soil pH; fCa, initial foliar calcium concentration (%); sCaN, initial ratio of soil calcium (sCa) to soil nitrogen (sN); I_U, urea fertilization indicator variable (1 if urea fertilized; 0 otherwise); a_0–a_7, parameters estimated from the data and all other variables are defined above.

After accounting for initial tree size (D^2H), site index, soil pH, and foliar calcium concentration, growth response to nitrogen
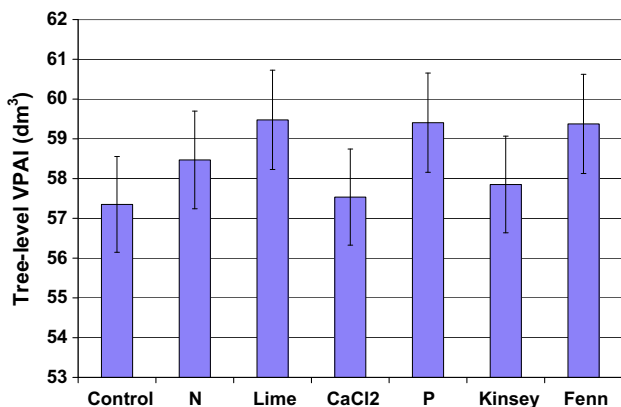
Fig. 2. Mean periodic annual volume increment (VPAI) of measurement trees for the three-year growth period immediately following fertilization on the 12 sites receiving all seven fertilization treatments (after adjusting for D^2H and plot basal area). Error bars are the standard error for each treatment within the ANCOVA.

Table 6

Three-year volume growth response (%; [treatment−control]/control) of measurement trees to fertilizer treatments, including site-specific multiple comparison tests from ANCOVA ($p < 0.05$ (**); $0.05 < p < 0.10$ (*)).

	N	Lime	CaCl$_2$	Phos	Kinsey	Fenn
CTC	*__35.0__	15.8	15.0	*__18.3__	*__16.1__	1.4
GDE	9.1	2.6	12.3	−7.1	3.1	14.4
GDH	−11.7	2.4	0.5	−12.0	−3.6	−9.4
GPH	6.4	3.5	7.9	7.5		
HAGR	−3.2	1.8	−12.0	1.2	−2.0	−2.7
HAK	−2.6	−4.3	3.6	−4.0	−3.1	1.6
LRT	−0.1	−0.9	−5.9	−1.7		
MNN	−7.4	9.6	7.3	−0.1	−11.1	2.4
MNS	6.7	12.6	−9.7	**__17.5__	5.9	9.0
ODF	0.8	−0.3	−3.1	*__12.0__	8.4	10.0
OSU	0.5	6.8	7.4	6.4	5.8	8.1
PB	−6.6	−0.1	3.0	4.2	−3.1	1.8
STR	1.3	−8.6	−6.6	5.2	−8.0	−5.4
WE	10.3	13.3	**__20.8__	*__14.8__		
WF	4.0	−4.7	−8.0	−4.5	−2.0	6.1
WW	**__26.3__	9.4	8.2	−4.2		

Table 7

Significant block-level variables and their corresponding parameter estimates for predicting three-year response of Douglas-fir volume growth (proportion of control treatment) to fertilization.

Treatment	Parameter	Predictor	Parameter estimate	Standard error
Nitrogen	a_0	Intercept	1.36321	1.05515
	a_1	D^2H	0.49565	0.04181
	a_2	ln(SI)	1.27235	0.27537
	a_3	pH	−0.19103	0.07241
	a_4	ln(fCa)	0.48655	0.12307
	a_5	ln(sCaN)	−0.08443	0.04377
	a_6	I_U	0.13831	0.05423
	a_7	$I_U * \ln(sCaN)$	0.04652	0.02564
Lime	b_{31}	Constant	14.5030	16.8966
	b_{32}	D^2H	0.4743	0.0416
	b_{33}	SI	1.0601	0.2726
	b_{34}	fCa	0.5971	0.1282
	b_{35}	sCaN	−0.0822	0.0327
	b_{36}	pH	−0.2609	0.0920
	b_{37}	I_C	−1.9140	0.7703
	b_{38}	$I_C * fCa$	−0.37	0.1406
	b_{39}	$I_C * pH$	0.2969	0.1237
Calcium chloride	b_{41}	Constant	26.4773	34.7495
	b_{42}	D^2H	0.4759	0.0447
	b_{43}	SI	0.8535	0.3265
	b_{44}	fCa	0.7144	0.1444
	b_{45}	sCaN	−0.1350	0.0425
	b_{46}	pH	−0.2211	0.0980
	b_{47}	I_C	−1.7936	0.7596
	b_{48}	$I_C * fCa$	−0.3312	0.1417
	b_{49}	$I_C * pH$	0.2829	0.1220
Phosphorus	c_1	Constant	0.0444	0.0617
	c_2	D^2H	0.4375	0.0509
	c_3	SI	1.9562	0.3401
	c_4	fP	10.9373	3.6542
	c_5	$fP * pH$	−1.3531	0.5472
	c_6	I_P	−5.2574	1.9862
	c_7	$I_P * pH$	1.0577	0.3913
	c_8	$I_P * fP$	29.0023	13.6814
	c_9	$I_P * fP * pH$	−5.8157	2.6090

fertilization was negligible if the soil Ca/N ratio was $\leqslant 0.06$. At sites with higher soil Ca/N ratio, the expected maximum volume growth response was ~17% (Fig. 3).

Volume growth response to both lime and CaCl$_2$ application was positively correlated with initial soil pH ($p = 0.025$ and 0.029, respectively) and negatively correlated with initial foliar calcium concentration ($p = 0.015$ and 0.028, respectively) (Figs. 4 and
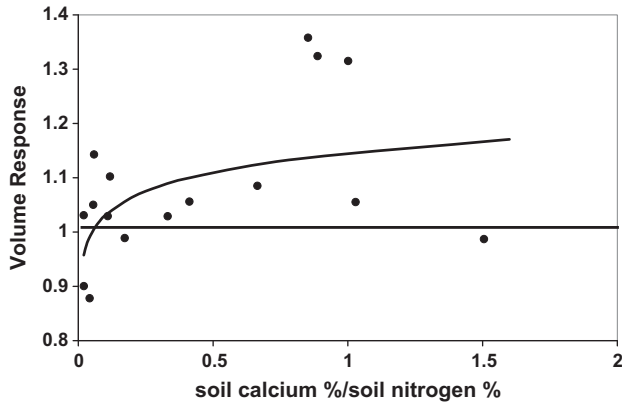
Fig. 3. Mean volume growth response of measurement trees (proportion of control mean) for three-year period immediately following nitrogen fertilization as a function of initial soil exchangeable calcium (g) to total nitrogen (g) ratio (R^2 = 0.71).
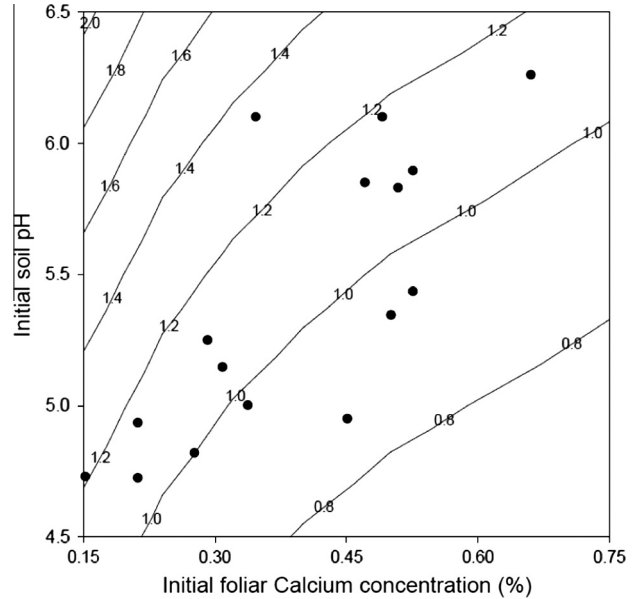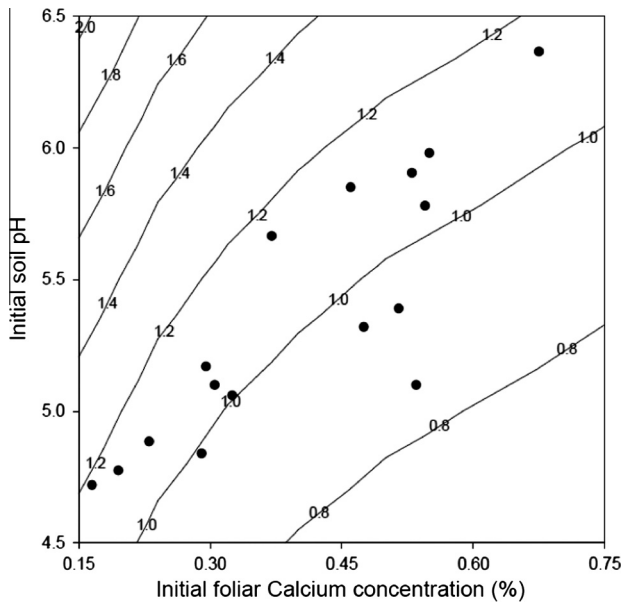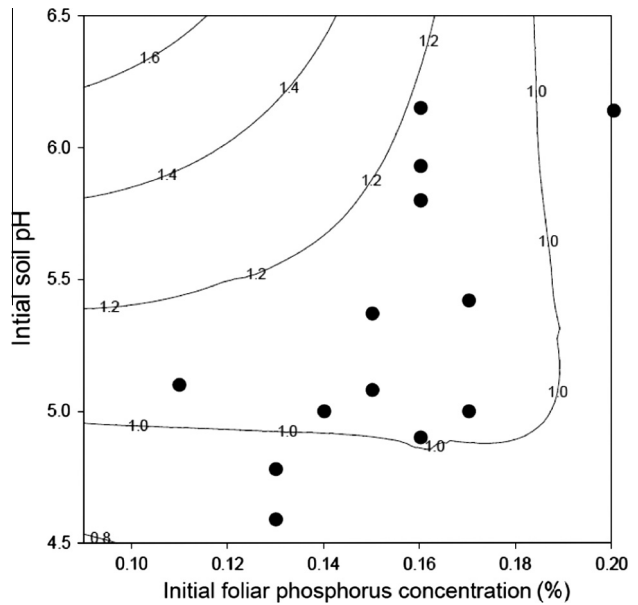

Fig. 4. Mean volume growth response of measurement trees (proportion of control mean) for the three-year period immediately following lime fertilization as a function of initial soil pH and foliar calcium concentration (R^2 = 0.91).

Fig. 5. Mean volume growth response of measurement trees (proportion of control mean) for the three-year period immediately following $CaCl_2$ fertilization as a function of initial soil pH and foliar calcium concentration.

Fig. 6. Mean volume growth response of measurement trees (proportion of control mean) for the three-year period immediately following phosphorus fertilization as a function of foliar phosphorus concentration.

5). The following model described the volume growth response surface (R^2 = 0.90, 0.90 and MSE = 277.9, 304.3, respectively):

$$\text{VOLGR} = (b_{j1}) * (D^2H)^{bj2} * \text{SI}^{bj3} * \text{fCa}^{bj4} * \text{sCaN}^{bj5}$$
$$* \exp\left((b_{j6}^* pH) + (I_C * (b_{j7} + b_{j8} \ln(fCa) + b_{j9} * pH))\right) \quad (3)$$

where I_C, Ca fertilization indicator variable (1 if Ca fertilized; otherwise 0); b_{j0}–b_{j8}, parameters estimated from the data for the jth treatment ($j = 3$ for lime, $j = 4$ for $CaCl_2$) and all other variables are defined above.

Response of stem volume growth to P fertilization was related to initial foliar P concentration ($p < 0.0001$) and the interaction between foliar P and soil pH ($p = 0.016$), as described by the following model (R^2 = 0.86, and MSE = 419.2):

$$\text{VOLGR} = c_1(D^2H)^{c2} * \text{SI}^{c3} * \exp[(c_4 + c_5 pH) * fP]$$
$$* \exp[I_P * (c_6 + c_7 pH + c_8 fP + c_9 pH * fP)] \quad (4)$$

where fP, initial foliar phosphorus (%); I_P, fertilization indicator variable (1 if fertilized; 0 otherwise); c_1–c_9, parameters estimated from the data and all other variable are defined above.

Growth response to P fertilization increased with decreasing foliar P at high soil pH, but this effect was damped at low soil pH (Fig. 6). Growth response fell to negligible levels as foliage P concentration exceeded 0.18%, regardless of soil pH (Fig. 6).

Growth responses to the Kinsey regime and Fenn blend were not significantly related to initial soil pH or to initial soil or foliar concentrations of any added nutrients.

4. Discussion

In previous N fertilization studies in western Oregon and Washington, growth responses of Douglas-fir averaged about 4

m³ ha⁻¹ yr⁻¹ for the first four-year growth period following application (Peterson and Hazard, 1990). Volume growth responded significantly to N fertilization on the sites described here as part of the BN study, despite the fact that many sites had relatively high foliar and soil N concentrations. Douglas-fir foliar N of 1.35% is considered the threshold for N sufficiency (Carter, 1992). However, nine of our 16 sites had foliar N below this threshold, including the only two sites that responded significantly to N-fertilization (WW: foliar N = 1.19%, and CTC: foliar N = 1.30%). While foliar N often predicts response to N fertilization (Van Den Driessche, 1979; Hopmans and Chappell, 1994; Carter et al., 1998), there is significant variation in this response, perhaps because N concentration does not incorporate other metrics of plant performance, such as leaf area index (LAI), total canopy N (Brix, 1983; Vose and Allen, 1988; Albaugh et al., 1998), availability of other essential elements, or possible interactions with soil water availability. The possible influence of these other factors may explain why only two of the nine sites in this study having a foliar N below 1.35% exhibited a significant positive response to N addition. Most notably from our analysis, response to N fertilization depended on soil Ca:N ratio rather than either soil or foliar N alone (Fig. 3).

The lack of response of one-third of coastal Oregon forests to N fertilization (Peterson and Hazard, 1990), combined with evidence for low Ca availability relative to other macronutrients and the positive response to lime application, raises the possibility that Ca may limit Douglas-fir growth when N is abundant (Perakis et al., 2006). Soil N in this region reaches very high levels compared to many forests worldwide, and is highest near the coast (Perakis et al., 2011). In turn, high N accumulation promotes N mineralization and nitrification in excess of plant requirements, leading to soil acidification, coupled nitrate and calcium leaching, and long-term calcium depletion (Perakis and Sinkhorn, 2011; Perakis et al., 2013). Likewise, in the BN study sites, we also observed an inverse relationship between soil Ca and soil N, with sites further from the coast (>30 km) having relatively low soil N concentrations (averaging 0.23%, stdev = 0.07, $n = 9$). Prior work in this region also suggests that our sampling focus on surface 0–10 cm soil is likely effective at discerning N availability differences among sites, as soil % N in the top 10 cm significantly predicts *in situ* annual net N mineralization ($r^2 = 0.87$) and total soil N pools to 100 cm depth in the Coast Range ($r^2 = 0.77$, Perakis et al., 2011), and N content in the top 10 cm of soil significantly predicts N content to 100 cm depth in a range of forests across the Pacific Northwest ($r^2 = 0.88$, $n = 80$; Remillard, 2000). These correlations suggest that a lack of deep soil sampling in the current study is unlikely to explain why surface N concentrations failed to predict growth response to N fertilization. Other causes, such as potential differences in soil mass (i.e., soil N stocks), N mineralization rate, consequent N availability per unit total soil N, availability of soil Ca, or other factors for which soil Ca:N might serve as a surrogate, may be important when considering soil N concentration as a predictor growth response to N fertilization.

Previous studies with Douglas-fir seedlings have shown a positive growth response to liming (Heilman and Ekuan, 1973; Littke and Zabowski, 2007). We found that at a given pH, sites with low foliar Ca displayed a greater volume growth response to Ca fertilization. Likewise, for a given foliar Ca concentration, average growth response to Ca addition increased with soil pH. Because Ca availability generally increases with soil pH, the low Ca concentration at a relatively high pH suggests sites with inherently low soil Ca availability, where non-acidic Mg, K, or Na base cations comprise a larger proportion of the exchange complex. In contrast, increased volume growth response to lime addition at low soil pH and low foliar Ca may be related less to Ca deficiency and more to mitigation of Al toxicity, as shown by Porada (1987) in Douglas-fir

seedlings, particularly given the similarity in symptoms (Rengel, 1992).

While volume growth response to Ca fertilization was positive regardless of its form of application (as CaCO₃ lime, or CaCl₂), the long-term effects of the different Ca treatments are not likely to remain the same. Three years after fertilization, the most obvious difference among Ca applications was between the lime and Kinsey treatments. Both treatments added large amounts of Ca (Kinsey average: 1268 kg Ca/ha; lime: 1020 kg Ca/ha). The lack of a discernable growth response to the Kinsey regime may be due in part to the one year delay in Ca application, but also in part to low statistical power associated with the smaller number of treated sites. Calcium is not a metabolic nutrient involved in photosynthesis and respiration, and remedial Ca additions can take more than 4 years to significantly increase diameter growth (Long et al., 1997; Battles et al., 2013). This potential response lag suggests that longer-term monitoring may be needed to detect treatment differences in response to Ca addition. Nevertheless, short term growth may be improved with Ca applications where deficiencies exist, and its application in forms other than lime may be operationally preferable due to the smaller quantity of material required.

The responsiveness of trees with high foliar Ca to Ca fertilization was unexpected. The lowest foliar Ca concentration found in the BN dataset was 0.14%, suggesting a slight to moderate deficiency by Ballard's and Carter's (1986) standards and a clear deficiency by Carter's (1992) and Walker's and Gessel's (1991) standards, although these standards were partially based on seedling studies. Calcium is relatively immobile in plants and especially in conifers (Marschner, 1995; Vergutz et al., 2012), and in mature trees reaches higher concentrations in older foliage deep in the crown (Lavender and Carmichael, 1966; Mainwaring and Maguire, 2008); in fact, Ca concentration within a tree can average 65% greater in 4-yr foliage than in 1-yr foliage, and for a given age class can average 40% greater near crown base than at the top of the tree (Mainwaring and Maguire, 2008). Foliage samples for the BN study were collected from young needles relatively high in the crown where Ca concentrations are expected to be lowest. Any practical use of foliar Ca as a diagnostic for Ca fertilization needs to account for the age and position of sampled foliage, preferably by exact replication of these methods or potentially through calibration to a standard crown position (Mainwaring and Maguire, 2008).

Increased growth of Douglas-fir with added P is common for seedlings (Heilman and Ekuan, 1980; Van Den Driessche, 1984; Radwan et al., 1991) but generally not for larger trees (Radwan et al., 1991). We found that the growth response to P fertilization at a given pH increased as foliar P decreased, though positive responses were limited to sites with soil pH > 5 (Fig. 6). These findings clarify the lack of response observed in Radwan et al. (1991), who studied sites with soil pH < 5 and initial foliar P concentration (0.12%) below the P deficiency threshold (P = 0.15%, Ballard and Carter, 1986). A similar lack of stem growth response to P fertilization was recorded for N- and P-fertilized trees in the Washington Cascades (Steinbrenner, 1981), but initial foliar P and soil pH were not provided. Phosphorus is widely known to decline in availability as soil pH decreases (Brady, 1990), and results from our study indicated that large additions of P (580 kg P/ha) were not sufficient to overcome low P availability at low soil pH. In contrast, lower rates of P addition as triple super-phosphate (200 kg P/ha) to three high N soils with pH 4.4–5.5 within our study area did increase Bray-1 P from 4-to 40-fold for 2 years, though plant responses were not assessed (Van Huysen et al., in prep). Finally, organic forms of soil P increase significantly with soil N in Douglas-fir forests, and may represent an important reservoir for plant available P in low-pH soils (Perakis et al., 2013). Additional work on soil P dynamics and its relationships to plant P availability in N-rich, low-pH soils of the Douglas-fir region is warranted.

We expected that the Kinsey nutrient regime and Fenn blend, both of which supplied multiple nutrients tailored to site-specific assessments and subsequently inferred requirements, would provide an upper ceiling of potential nutrient limitation to Douglas-fir growth in our study. The lack of clear growth response to these treatments, coupled with the small growth responses overall to single-nutrient treatments, may be explained by the short-term nature of our study, omission of key micronutrients, antagonism among nutrients, or general lack of strong nutrient limitation on at least those sites with relatively high N and high organic matter content. In addition, these blended nutrient treatments are relatively expensive due to the chemical analyses required to develop site-specific prescriptions, mixing of relatively small amounts of prescribed compounds, and application of large quantities of material per unit area. Our BN study suggested that these blends are not advisable as economic alternatives to more targeted nutrient additions.

Whether three years is a long enough period of time for plant absorption of nutrients and subsequent response to treatment may be questioned. The fate of applied nitrogen within Douglas-fir stands of varying ages appears consistent: trees generally absorb up to 30% of N within the first two growing seasons (Nason and Myrold, 1992). Chemical analyses of foliar nutrients for this study have shown significant increases in N after one and three years following N application, significant increase in foliar P three years after P application, though no change in foliar calcium. Although a sustained or delayed response was thought possible, there has been no sign of a regional tree response to N, P, or Ca application following a subsequent six-year remeasurement (Mainwaring et al., unpublished data).

One regional factor that has been implicated in delayed treatment response to thinning is the SNC-induced reduction in foliage retention (Mainwaring et al., 2005). Foliage retention with or without its interaction with a treatment indicator was generally not a significant covariate in the regression models. Any parameter estimates that were significantly different from zero almost always indicated greater growth with lower initial foliage retention. This trend was consistent with a decline in foliage longevity along gradients of increasing inherent fertility (Li et al., 2006; Pensa et al., 2007), and after N fertilization (Brix, 1981; Balster and Marshall, 2000). Because foliar loss due to SNC occurs where soil nitrogen is particularly high, it is difficult to separate the effects of fertility and SNC on low foliage retention within the target population. Nitrogen fertilization has been shown to elevate leaf area index of responding Douglas-fir stands (Brix, 1981), and low leaf area index has even been used as a diagnostic for prescribing fertilization in loblolly pine (Fox et al., 2007). Presence of SNC on many of the Beyond N sites probably negated the potential efficacy of foliage retention as a predictor of response to fertilization, despite the fact that in severely impacted SNC stands foliage retention is positively correlated with total foliage area (Weiskittel and Maguire, 2006). The poor performance of foliage retention probably also follows from the above-mentioned inverse relationship to total leaf mass (Brix, 1981). This relationship, in combination with strong negative correlations between foliage retention and foliage N concentrations in regions impacted by SNC, argue strongly against N fertilization to either boost productivity or ameliorate SNC. Sites with low soil Ca:N ratio can display more severe SNC symptoms (Maguire et al., 2000). Of the two sites exhibiting a positive volume growth response to nitrogen treatment, one had moderately low foliage retention in 2006 (2.28 yrs), suggesting significant impacts from SNC. However, the two-year-old needles from this site showed little evidence of stomatal occlusion by pseudothecia (Mainwaring, pers. obs.), so the low foliage retention may have been related to the high water table and poor drainage class of the soil (Bond-Lamberty et al., 2002).

5. Conclusions

(1) Across the sixteen sites used for this study, a marginally significant increase in 3-yr volume growth was apparent after treatment with urea, lime, and phosphorus, though these average regional responses were driven by significant responses on a small number of the sites.

(2) Predicted volume growth responses depended on initial site-level covariates. The most efficient returns from N fertilization would be obtained on sites where the soil Ca: N ratio exceeds 0.5. Calcium fertilization can be effective for increasing the growth of Douglas-fir in stands where there is low foliar calcium for a given level of pH. The efficacy of Ca added as $CaCl_2$ suggested that, in stands meeting this criterion, a short term response may be possible by adding Ca in chemical forms with lower weight and associated application costs than traditional applications of Ca as lime.

(3) Phosphorus fertilization can be effective in increasing the growth of Douglas-fir stands with low foliar P (<0.18%) on soils with pH greater than 5. The relationship between P response and pH suggested that P fertilizers containing Ca (e.g., soft rock phosphate) may be most promising.

(4) The response to fertilizers was not dependent on SNC severity. Results suggested that Douglas-fir did not generally respond to these fertilizers where soils are high in N, low in Ca, or low in pH, all common characteristics of the soils where SNC has been especially problematic.

(5) The positive correlations found between initial soil pH and growth response to fertilization suggested that treatments capable of increasing soil pH may offer the greatest promise for boosting growth in Douglas-fir. Because increasing soil pH through lime application is a slow process, additional time will be necessary to determine its efficacy both as a single application and as part of the Kinsey treatment regime.

References

Aber, J.D., Nadelhoffer, J.K., Steudler, P.A., Melillo, J.M., 1989. Nitrogen saturation in northern forest ecosystems. BioScience 39, 378–386.

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., King, J.S., 1998. Leaf area and above-and belowground growth responses of loblolly pine to nutrient and water additions. Forest Sci. 44, 317–328.

Albrecht, W.A. 1975. The Albrecht papers. vol. 1: Foundation concepts. Acres USA, Kansas City.

Ballard, T.M., Carter, R.E. 1986. Evaluating forest stand nutrient status. B.C. Min. Forests, Victoria, Land Management Rep. 20. pp. 60.

Balster, N.J., Marshall, J.D., 2000. Decreased needle longevity of fertilized Douglas-fir and grand fir in the northern Rockies. Tree Phys. 20, 1191–1197.

Barclay, H.J., Brix, H. 1985. Fertilization and thinning effects on a Douglas-fir ecosystem as Shawnigan Lake: 12-year growth response. In: Canadian Forestry Serv, Pacific Forestry Centre, Infor Rpt BC-X-271, Victoria, BC.

Barron, A.R., Wurzburger, N., Bellenger, J.P., Wright, S.J., Kraepiel, A.M., Hedin, L.O., 2009. Molybdenum limitation of asymbiotic nitrogen fixation in tropical forest soils. Nat. Geosci. 2, 42–45.

Battles, J.J., Fahey, T.J., Driscoll, C.T., Blum, J.D., Johnson, C.E., 2013. Restoring soil calcium reverses forest decline. Environ. Sci. Technol. Lett.. http://dx.doi.org/10.1021/ez400033d.

Bisson, P.A., Ice, G.G., Perrin, C.J., Bilby, R.E., 1992. Effects of forest fertilization on water quality and aquatic resources in the Douglas-fir region. In: Chappel, H.N., Weetman, G.F., Miller, R.E. (Eds.), Forest Fertilization: Sustaining and Improving Nutrition and Growth of Western Forests. Institute of Forest Resources No. 73, College of Forest Resources, University of Washington, Seattle, WA, pp. 179–193.

Bond-Lamberty, B., Wang, C., Gower, S.T., 2002. Leaf area dynamics of a boreal black spruce fire chronosequence. Tree Phys. 22, 993–1001.

Brady, N.C., 1990. The Nature and Properties of Soils. MacMillan Publishing Co., New York, p. 621.

Brix, H., 1981. Effects of thinning and nitrogen fertilization on branch and foliage production in Douglas-fir. Can. J. Forest Res. 11, 502–511.

Brix, H., 1983. Effects of thinning and nitrogen fertilization on growth of Douglas-fir: relative contribution of foliage quantity and efficiency. Can. J. Forest Res. 13, 167–175.

Brix, H., Ebell, L.F., 1969. Effects of nitrogen fertilization on growth, leaf area, and photosynthesis rate in Douglas-fir. Forest Sci. 15, 189–196.

Bruce, D., 1981. Consistent height-growth and growth-rate estimates for remeasured plots. Forest Sci. 27, 711–725.

Bruce, D., DeMars, D.J. 1974. Volume equations for second-growth Douglas-fir. USDA-Forest Service Research Note PNW-239.

Carter, R.E., 1992. Diagnosis and interpretation of forest stand nutrient status. In: Chappell, H.N., Weetman, G.F., Miller, R.E. (Eds.), Proceedings from Forest Fertilization Symposium: Sustaining & Improving Nutrition & Growth of Western Forests. Institute of forest resources Contrib. 73. Univ. of Washington, Seattle, pp. 90–97.

Carter, R.E., McWilliams, E.R.G., Klinka, K., 1998. Predicting response of Coastal Douglas-fir to fertilizer treatments. Forest. Ecol. Manag. 107, 275–289.

Castro, M.S., Peterjohn, W.T., Melillo, J.M., Steudler, P.A., Gholz, H.L., Lewis, D., 1994. Effects of nitrogen fertilization on the fluxes of N_2O, CH_4, and CO_2 from soils in a slash pine plantation. Can. J. Forest Res. 24, 9–13.

Cronan, C.S., April, R., Bartlett, R., Bloom, P., Driscoll, C., Gherini, S., Henderson, G., Joslin, J., Kelly, J.M., Newton, R., Parnell, R., Patterson, H., Raynal, D., Schaedle, M., Schodield, C., Sucoff, E., Tepper, H., Thornton, F., 1989. Aluminum toxicity in forest exposed to acidic deposition: the ALBIOS results. Water Air Soil Pollut. 48 (181), 192.

Curt, T., Lucot, E., Bouchaud, M., 2001. Douglas-fir root biomass and rooting profile in relation to soils in a mid-elevation area (Beaujolais Mounts, France). Plant Soil 233, 109–125.

Edmonds, R.L., Hsiang, T., 1987. Forest floor and soil influence on response of Douglas-fir to urea. Soil Sci. Am. J. 51, 1332–1337.

El-Hajj, Z., Kavanagh, K., Rose, C., Kanaan-Atallah, Z., 2004. Nitrogen and carbon dynamics of a foliar biotrophic fungal parasite in fertilized Douglas-fir. New Phytol. 163, 139–147.

Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary production in freshwater, marine, and terrestrial ecosystems. Ecol. Lett. 10, 1135–1142.

Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R., Carlson, C.A., 2007. Tree nutrition and forest fertilization of pine plantations in the southern United States. S. J. Appl. Forest. 31, 5–11.

Gessel, S.P., Steinbrenner, E.C., Miller, R.E., 1979. Response of Northwest forests to elements other than nitrogen. In: Gessel, S.P., Kenady, R.M., Atkinson, W.A. (Eds.), Proceedings of the Forest Fertilization Conference. Institute of Forest Resources No. 40, College of Forest Resources, University of Washington, Seattle, WA, pp. 140–149.

Haynes, R.J., 1982. Effects of liming on phosphate availability in acid soils, a critical review. Plant Soil 68, 289–309.

Heilman, P.E., Ekuan, G., 1973. Response of Douglas-fir and western hemlock seedlings to lime. Forest Sci. 19, 220–224.

Heilman, P.E., Ekuan, G., 1980. Phosphorus response of western hemlock seedlings on Pacific coastal soils from Washington. Soil Sci. Soc. Am. J. 44, 392–395.

Hopmans, P., Chappell, H.N., 1994. Growth response of young, thinned Douglas-fir stands to nitrogen fertilizer in relation to soil properties and tree nutrition. Can. J. Forest Res. 24, 1684–1688.

Johnson, D.W., Cole, D.W., Van Miegroet, H., Horng, F.W., 1986. Factors affecting anion movement and retention in four forest soils. Soil Sci. Soc. Am. J. 50, 776–783.

Larsen, D.R., Hann, D.W. 1985. Equations for predicting diameter and squared diameter inside bark at breast height for six major conifers of Southwest Oregon. In: Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA. Research Note 77. pp. 4.

Lavender, D.P., Carmichael, R.L., 1966. Effect of three variables on mineral concentrations in Douglas-fir needles. Forest Sci. 12, 441–446.

LeBauer, D.S., Treseder, K.K., 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89, 371–379.

Li, M.-H., Kräuchi, N., Dobbertin, M., 2006. Biomass distribution of different-aged needles in young and old Pinus cembra trees at highland and lowland sites. Trees 20, 611–618.

Littke, K., Zabowski, D., 2007. Calcium uptake, portioning, and sinuous growth in Douglas-fir seedlings. Forest Sci. 53, 692–700.

Long, R.P., Horsley, S.B., Lilja, P.R., 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. Can. J. Forest Res. 27, 1560–1573.

Maguire, D.A., Batista, J.L.F., 1996. Sapwood taper models and implied sapwood volume and foliage profiles for coastal Douglas-fir. Can. J. Forest Res. 26, 849–863.

Maguire, D.A., Mainwaring, D.B., Kanaskie, A., 2011. Ten-year growth and mortality in young Douglas-fir stands experiencing a range in Swiss needle cast severity. Can. J. Forest Res. 41, 2064–2076.

Maguire, D., Waring, R., Cromack, K., Boyle, J., 2000. Trends in soil and foliar nutrients across a range in Swiss needle cast severity. In: Filip, G. (Ed.), Swiss Needle Cast Cooperative Annual Report 2000. Oregon State University, Corvallis, Oregon, USA, College of Forestry, pp. 79–84.

Mainwaring, D., Maguire, D., 2008. Within-crown variability of foliar nutrients in coastal Douglas-fir. In: Shaw, D., Woolley, T. (Eds.), Swiss Needle Cast Cooperative Annual Report 2008. College of Forestry, Oregon State University, Corvallis, Oregon, USA, pp. 49–57.

Mainwaring, D.B., Maguire, D.A., Kanaskie, A., Brandt, J., 2005. Growth responses to commercial thinning in Douglas-fir stands with varying severity of Swiss needle cast in Oregon, USA. Can. J. Forest Res. 35, 2394–2402.

Marschner, H., 1995. Mineral Nutrition of Higher Plants, second ed. Academic Press, Boston, MA.

McLean, E.O. 1982. Soil pH and lime requirement. In: Page, A.L., Keeney, D.R. (Eds), Methods of Soil Analysis, Part 2. Agron. Monogr. 9, Am. Soc. Agron., Madison, Wisc. pp. 199–223.

Meurisse, R.T., 1976. Some chemical and other properties of western hemlock soils in Oregon: their relationship to productivity. In: Atkinson, W.A., Zasoski, R.J. (Eds.), Western Hemlock Management Conference. University of Washington, Seattle, WA, pp. 49–55.

Miller, R.E., McNabb, D.H., Hazard, J., 1989. Predicting Douglas-fir growth and response to nitrogen fertilization in western Oregon. Soil Sci. Soc. Am. J. 53, 1552–1560.

Miller, R.E., Pienaar, L.V. 1973. Seven-year response of 35-yr old Douglas-fir to nitrogen fertilizer. USDA Forest Service Res. Pap. PNW-165. pp. 24.

Mohren, G.M.J., Van Den Burg, J., Burger, F.W., 1986. Phosphorus deficiency induced by nitrogen input in Douglas-fir in the Netherlands. Plant Soil 95, 191–200.

Nason, G.E., Myrold, D.D., 1992. Nitrogen fertilizers, fates and environmental effects in forests. In: Chapell, H.N., Weetman, G.F., Miller, R.E. (Eds.), Forest Fertilization, Sustaining and Improving Nutrition and Growth of Western Forests, College of Forest Resources, Contribution #73. University of Washington, Seattle, pp. 67–81.

Pensa, M., Liblik, V., Jalkanen, R., 2007. Variation in Scots pine needle longevity and nutrient conservation in different habitats and latitudes. Can. J. Forest Res. 37, 1599–1604.

Perakis, S.S., Sinkhorn, E.R., 2011. Biogeochemistry of a temperate forest nitrogen gradient. Ecology 92, 1481–1491.

Perakis, S.S., Sinkhorn, E.R., Compton, J.E., 2011. $\delta^{15}N$ constraints on long-term nitrogen balances in temperate forests. Oecologia 167, 793–807.

Perakis, S.S., Sinkhorn, E.R., Catricala, C.E., Bullen, T.D., Fitzpatrick, J., Hynicka, J.D., Cromack Jr., K., 2013. Forest calcium depletion and biotic retention along a soil nitrogen gradient. Ecol. Appl. 23, 1947–1961.

Perakis, S.S., Maguire, D.A., Bullen, T.D., Cromack, K., Waring, R.H., Boyle, J.R., 2006. Coupled nitrogen and calcium cycles in forests of the Oregon coast range. Ecosystems 9, 63–74.

Peterson, C.E., Hazard, J.W., 1990. Regional variation in growth response of coastal Douglas-fir to nitrogen fertilizer in the Pacific Northwest. Forest Sci. 36, 625–640.

Peterson, C.E., Ryan, P.J., Gessel, S.P., 1984. Response of northwest Douglas-fir stands to urea: correlation with forest soil properties. Soil Sci. Soc. Am J. 48, 162–169.

Porada, H.J. 1987. The effect of aluminum on the growth and mineral composition of Douglas-fir and western hemlock. Ph.D. Dissertation, University of Washington, Seattle.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.

Radwan, M.A., Shumway, J.S., DeBell, D.S., Kraft, J.M., 1991. Variance in response of pole-size trees and seedlings of Douglas-fir and western hemlock to nitrogen and phosphorus fertilizers. Can. J. Forest Res. 21, 1431–1438.

Remillard, S.M. 2000. Soil carbon and nitrogen in old-growth forests in western Oregon and Washington. MS Thesis, Oregon State University. Corvallis, OR.

Rengel, Z., 1992. Role of calcium in aluminium toxicity. New Phytol. 121, 499–513.

Ryan, P.J., Gessel, S.P., Zasoski, R.J., 1986. I. acid tolerance of Pacific Northwest conifers in solution culture. I. Effect of high aluminum concentration and solution acidity. Plant Soil 96, 239–257.

SAS Institute, 2009. SAS/STAT(R) 9.2 User's Guide, second ed. SAS Institute Inc., Cary, NC.

Shortle, W.C., Smith, K.T., 1988. Aluminum-induced calcium deficiency syndrome in declining red spruce. Science 240, 1017–1018.

Stegemoeller, K.A., Chappell, H.N., 1990. Growth response of unthinned and thinned Douglas-fir stands to single and multiple applications of nitrogen. Can. J. Forest Res. 20, 343–349.

Steinbrenner, E.C., 1981. Growth response of young Douglas-fir to repeated application of nitrogen and phosphorus. Soil Soc. Am. J. 45, 953–955.

Swanston, C.W., Homann, P.S., Caldwell, B.A., Myrold, D.D., Ganio, L., Sollins, P., 2004. Long-term effects of elevated nitrogen on forest soil organic matter stability. Biogeochemistry 70, 229–252.

Turner, J., Lambert, M.J., 1986. Nutrition and nutritional relationships of *Pinus radiata*. Annu. Rev. Ecol. Syst. 17, 325–350.

Van Den Driessche, R., 1979. Estimating potential response to fertilizer based on tree tissue and litter analysis. In: Gessel, S.P., Kenady, R.M., Atkinson, W.A. (Eds.), Forest fertilization conference. Inst Forest Res Contrib. 40, Univ. Wash, Seattle, pp. 214–220, 275 p.

Van Den Driessche, R., 1984. Response of Douglas fir seedlings to phosphorus fertilization and influence of temperature on this response. Plant Soil 80, 155–169.

Van Huysen, T.L., Perakis, S.S., Harmon, M.E. 2014. Phosphorus effects on soil properties and litter decomposition in nitrogen-rich forests. (In prep).

Vergutz, L., Manzoni, S., Porporato, A., Novais, R.F., Jackson, R.B., 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecol. Monogr. 82, 205–220. http://dx.doi.org/10.1890/11-0416.1.

Vitousek, P.M., 2004. Nutrient Cycling and Limitation: Hawai'i as a Model System. Princeton University Press, Princeton, NJ.

Vose, J.M., Allen, H.L., 1988. Leaf area, stemwood growth, and nutrition relationships in loblolly pine. Forest Sci. 34, 547–563.

Walker, R.B., Gessel, S.P. 1991. Mineral deficiencies of coastal Northwest conifers. Institute of Forest Resources, School of Forestry, University of Washington, Seattle, WA. Contribution No. 70. pp. 63.

Walker, T.W., Syers, J.K., 1976. The fate of phosphorus during pedogenesis. Geoderma 15, 1–19.

Weiskittel, A.R., Maguire, D.A., 2006. Response of Douglas-fir leaf area index and litterfall dynamics to Swiss needle cast in north coastal Oregon, USA. Ann. Forest Sci. 64, 1–10.