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Utility of in situ ion-exchange membranes to assess nutrient availability, productivity, and fertilizer response of coastal Douglas-fir of the Pacific Northwest

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Abstract

Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] is the predominant forest plantation species in the Pacific Northwest (PNW), with site productivity and fertilizer response influenced by climate and soil variations. This study investigates the utility of in situ 12-week supply measurements of nitrogen (N), calcium (Ca), and phosphorus (P) to ion-exchange resins (specifically Plant Root Simulator [PRS] probes) to estimate carbon (C):N ratios, soil nutrient contents (0–1 m), foliar nutrient concentrations, Douglas-fir productivity (site index and basal area mean annual increment), and fertilizer volume response. PRS nutrient supply rates were correlated with N, Ca, and P soil nutrient contents (0–1 m), C:N ratios, and foliar nutrient concentrations. Low PRS NO₃ supply rates (<25 mg N·m⁻²·burial period⁻¹) were correlated with lower Douglas-fir productivity and greater fertilizer volume response. PRS NO₃ supply rates performed as well as total soil N contents and foliar N concentrations at estimating volume growth response to fertilizer. Twelve weeks after fertilization, PRS NO₃, NH₄, and Ca supply rates were significantly elevated compared to the unfertilized treatment. This research found that PRS probes were an effective in situ tool and are recommended for understanding N, Ca, and P nutrient availabilities, site productivity, and fertilizer response in Douglas-fir plantations and for developing fertilizer prescriptions.

1 | INTRODUCTION

Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] is native to the Pacific Northwest (PNW) and is the predominant forest plantation species throughout the region (Franklin & Dyrness, 1988). Douglas-fir productivity varies across the PNW (18–55 m at 50 years) due to differences in climate and distinct soil types (Littke et al., 2016; Miller et al., 1989; Steinbrenner, 1979). The maritime climate in the PNW yields a dry and

warm summer climate, but this varies due to distance from the Pacific Coast, by elevation, and latitudinally (Franklin & Dyrness, 1988). There are substantial disparities in soil quality throughout the region due to geologic parent material, soil depths, textures, and soil nutrient concentrations (Carter et al., 1998; James et al., 2014; Kruckeberg, 1991; Littke et al., 2011; Littke, Harrison, Zabowski, Briggs, et al., 2014; Miller et al., 1989; Steinbrenner, 1979; Turner et al., 1979).

Over the course of more than four decades, fertilization has been integrated into the intensive management practices of Douglas-fir plantations across the region (Chappell et al., 1991). This approach aims to accelerate growth rates

Abbreviations: DBH, diameter at breast height; MAI, mean annual increment; PNW, Pacific Northwest; PRS, Plant Root Simulator.

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and reduce the time needed for rotation. Nitrogen (N) has been identified as the nutrient most limiting site productivity in the coastal PNW, but other nutrients, such as calcium (Ca) and phosphorus (P), can be limiting as well (Gessel et al., 1981; Mainwaring et al., 2014; Perakis et al., 2006; Radwan & Shumway, 1984). Urea (46–0–0) serves as the predominant N fertilizer in the area because of its high N content, which facilitates efficient application by helicopter. Urea has demonstrated growth-enhancing effects of up to $13 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ (mean of $4 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) in approximately 70% of Douglas-fir plantations in the coastal PNW (Hanley et al., 2006; Peterson et al., 1984). Previous research has established connections between soil and foliar N levels and the response to fertilization in the coastal PNW, underscoring the significance of N as the most limiting nutrient and a predictor of inherent forest productivity. For instance, indicators such as the carbon (C):N ratio of forest floor and soil, soil mineralizable N, total soil N content, and foliar N concentration have all demonstrated correlations with response to N fertilization (Carter et al., 1998; Edmonds & Hsiang, 1987; Hopmans & Chappell, 1994; Littke, Harrison, Zabowski, Ciol, et al., 2014; Peterson et al., 1984; Shumway & Atkinson, 1978; Sucre et al., 2008; Turner et al., 1988). Geologic parent material has also been shown to affect N fertilization response in the coastal PNW due to distinct combinations of soil forming factors (specifically climate, relief, and time), affecting water and N availability and tree growth (Littke, 2012). The ability to identify forests with low soil N availability holds vital importance in managing forest plantations to enhance and sustain forest productivity (Powers et al., 2005).

Although N has been the most studied nutrient in coastal PNW forests, it is important to understand the availability of and interactions with other soil nutrients. Coastal PNW soils with high N enrichment have been identified as having low soil exchangeable Ca contents ($<1000 \text{ kg Ca} \cdot \text{ha}^{-1}$ to 1 m soil depth) due to excessive leaching of Ca over time, which results in a greater use by trees of atmospheric Ca than weatherable mineral Ca (Hynicka et al., 2016; Perakis et al., 2006, 2013; Van Miegroet & Cole, 1984). Calcium deficiencies could be accelerated by excessive N fertilization, which causes increases in soil N concentrations, N mineralization, and N leaching yet decreases soil pH and potentially increases Ca leaching (Davis et al., 2012; Fox, 2004; Nason, 1989). Due to the potential for urea fertilization to induce Ca limitations, the effect of urea-supplied N on Ca and other nutrients should be investigated under differing levels of N availability across the coastal PNW. In support of the interaction between Ca and urea fertilization, Mainwaring et al. (2014) found greater urea fertilization response on Douglas-fir stands with low soil total N and high soil exchangeable Ca concentrations in the coastal PNW.

Mainwaring et al. (2014) also found greater response to P fertilization on sites with low foliar P concentration and high

Core Ideas

- Plant Root Simulator (PRS) ion-exchange resins estimated N, Ca, and P availability in Douglas-fir forests.
- Soils with low PRS NO_3 resulted in lower Douglas-fir site index and basal area mean annual increment.
- Greater fertilizer response of Douglas-fir was found on soils with low PRS NO_3 and soil total N.
- Urea fertilization increased PRS NO_3 , NH_4 , and Ca supply rates after 12 weeks.
- In a subset of installations, PRS NO_3 and NH_4 were reduced to control levels after 32 weeks.

soil pH. On northern Vancouver Island, BC, N and P fertilization of western hemlock [*Tsuga heterophylla* (Raf.)] and western redcedar (*Thuja plicata* Donn ex D. Don) has resulted in large responses of $4.5 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ over 22 years (Prescott et al., 2013). An interaction between N and P in coastal PNW western hemlock forests has been suggested due to greater response to urea fertilization on forest floors with high extractable P contents, although this relationship was not found in Douglas-fir (Shumway & Atkinson, 1978). However, in other regional studies of Douglas-fir and western hemlock, no measurable or marginal response was found due to forest P fertilization (alone and/or combined with other nutrients) (Gessel et al., 1981; Radwan et al., 1991). Soils close to the Pacific Ocean have been found to be low in P due to colder, wetter climates, which results in lower levels of available and inorganic P and greater levels of organic P (Kranabetter, Sholinder, et al., 2020; Preston & Trofymow, 2000; Radwan et al., 1985). While P limitations are not expected to be an issue due to the young geologic age soil parent materials of the coastal PNW (Johnson et al., 2003; Littke et al., 2011), the historic replacement of coastal climax Sitka spruce [*Picea sitchensis* (Bong.) Carr.] and western hemlock forests with Douglas-fir plantations has resulted in an increased population on coastal soils with high soil N and low soil P that have been less responsive to N fertilization (Franklin & Dyrness, 1988; Munger, 1940; Radwan & DeBell, 1980; Webster et al., 1976).

Previously established, extensive nutrition studies in the coastal PNW to determine nutrient limitations have primarily sampled forest floor and soil C:N ratios, total soil N contents, and exchangeable soil cation contents (Edmonds & Hsiang, 1986; James et al., 2014; Littke, Harrison, Zabowski, Briggs, et al., 2014; Miller et al., 1989; Perakis & Sinkhorn, 2011) with a smaller subset of soils measured for mineralizable N, mineral N fractions (NO_3 and NH_4), exchangeable Ca, and

extractable soil P (Carter et al., 1998; Hynicka et al., 2016; James et al., 2016; Mainwaring et al., 2014; Perakis et al., 2013; Shumway & Atkinson, 1978; Sucre et al., 2008). Collecting soil nutrition data is time consuming and expensive given soil microsite variability and the extensive area of forest cover, especially in the coastal PNW. Foliar nutrient sampling is commonly used as an estimate of soil nutrient availability based on the uptake of available nutrients, yet it is difficult on large trees and restricted by some forestry companies due to the potentially dangerous use of firearms or ladders to remove current foliage (Ballard & Carter, 1986; Carter et al., 1998; Littke, Harrison, Zabowski, Briggs, et al., 2014; Mainwaring et al., 2014). Ion-exchange resins, such as Plant Root Simulator (PRS) (Western Ag Innovations) probes, have been used to measure soil nutrient supply rates in different biomes around the world (Ochoa-Hueso et al., 2023) and for assessing soil fertility in agricultural systems (Dick & Culman, 2016; Qian & Schoenau, 2002). In forests, ion-exchange resins have been used to determine N availability, changes in N availability post-fertilization, and effects of harvest intensity and vegetation control (Hangs et al., 2004; Harrison & Maynard, 2014; Hope, 2009; Lewandowski et al., 2016; Littke et al., 2020; Yan et al., 2012). Laboratory and in situ incubations of ion-exchange resins have been found to differ due to on-site factors such as climate and soil water availability, but in situ ion-exchange resin nutrient availability estimates should be more related to plant root nutrient availability than controlled laboratory incubations or single point-in-time nutrient extraction samples (Binkley & Matson, 1983). Because previous research has shown that fertilization increased soil total N, inorganic N, and N mineralization both in the short and long term in coastal PNW soils, there is the potential to capture changes in N, Ca, and P supply rates after urea fertilization over time according to background nutrient availabilities and climate and water availability during the growing season (Fox, 2004; Mead et al., 2008; Nason, 1989).

The objectives of this study were to (1) assess the ability of PRS probes deployed in situ to evaluate soil nutrient availability, site productivity, and urea fertilizer response of Douglas-fir forests, (2) understand the change in regional in situ PRS nutrient supply rates 12 weeks after urea fertilization, and (3) determine, in a subset of installations, if there are differences between fall and spring unfertilized PRS nutrient supply rates and immediate (0–12 weeks) and subsequent (20–32 weeks) post-fertilization samples. We tested the following hypotheses: (1) PRS N, Ca, and P nutrient supply rates can improve estimates of soil nutrient availability, site productivity, and fertilizer response of Douglas-fir forests compared to traditional laboratory nutrient extraction techniques, and (2) urea fertilization will result in a significant change in PRS N, Ca, and P nutrient supplies 0–12 and 20–32 weeks after fertilization.

2 | METHODS

2.1 | Installation design

The most extensive collection of Douglas-fir fertilization sites in the coastal PNW originated from the efforts of the Regional Forest Nutrition Research Project (RFNRP) in the 1960s and 1970s (Stegemoeller et al., 1990), which facilitated the assessment of per-unit-area tree growth responses to fertilizer additions. However, the results of plot-based fertilization studies, like the RFNRP study, can be confounded by spatial variation in soil and initial stocking differences between fertilized plots and unfertilized control plots. To address these discrepancies in initial plot characteristics, previous research by Peterson et al. (1984) and Miller et al. (1989) utilized stand characteristics like relative density, site index, age, and basal area to normalize tree growth results between fertilized and control plots. More recently, paired-tree fertilization studies, where individual trees were paired based on similar site and tree measurement variables, have been established to determine response to fertilization based on similar starting conditions, yet paired-tree studies do not yield response per unit area (Littke, Harrison, Zabowski, & Briggs, 2014; Miller et al., 1996). In this study, issues with traditional plot-based and paired-tree fertilization studies were addressed by establishing a series of paired-plot installations randomly located across the coastal PNW on Stand Management Cooperative (SMC) member ownership. The SMC is composed of 12 forest landowners comprising 200,000 ha across the coastal PNW and is based in the University of Washington.

To obtain a representative sample of industrial timberlands across the coastal PNW, six zones were designated in the range of coastal Douglas-fir in western Oregon, Washington, and British Columbia (BC) (Figure 1). The four Oregon and Washington zones were delineated by soil parent material characteristics and physiographic attributes (Littke et al., 2011; USGS, 1946). Washington West contained mostly glacial and sedimentary parent materials in the Puget Trough, Olympic Mountains, and the Washington section of the Oregon Coast Range, while the Washington East encompassed mainly igneous parent materials in the Northern Cascade Mountains and the Washington portion of the Middle Cascade Mountains. In Oregon, the Oregon West region included sedimentary and igneous parent materials in Oregon portions of the Oregon Coast Range and the Klamath Mountains, and the Oregon East region covered mainly igneous parent materials in the Oregon Middle Cascade Mountains. For Washington and Oregon zones, installations were allocated according to the proportion of the industrial forestland area within each zone (Washington West [$n = 10$], Washington East [$n = 6$], Oregon West [$n = 10$], and Oregon East [$n = 6$]) for a total of 32 paired-plot installations (Rogers et al., 2016). The two

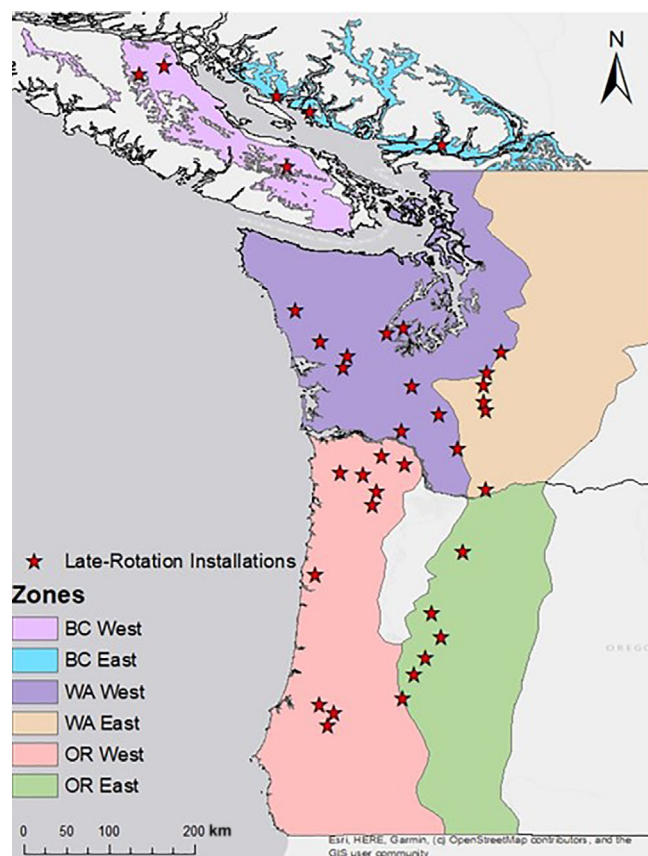


FIGURE 1 Thirty-eight Stand Management Cooperative late-rotation study installations by state or province zone.

zones in BC were designated as industrial forestland productive for Douglas-fir on Vancouver Island and the BC mainland selected from the following subzones: CWHdm, coastal western hemlock (CWH) dry maritime; CWHds1, dry submarine; CWHmm1 and CWHmm2, moist maritime; CWHms1, moist submarine; CWHxm1 and CWHxm2, very dry maritime (Green & Klinka, 1994). Three installations were allocated to each BC zone (Vancouver Island or mainland) for a total of six installations in BC (Figure 1).

Latitude and longitude coordinates were randomly chosen within the boundaries of the forested area within each zone and buffered with a radius of 5.4 km to create a set of search areas. Within each zone, search areas were randomly prioritized. Candidate stands meeting the installation criteria were then randomly selected within each search area. To be eligible, stands must have been “late-rotation,” within 8–10 years of planned harvest (total stand age 28–64 years), and must have had at least 75% of the basal area in Douglas-fir, with at least 85% of the basal area being conifer. Stands could have been thinned, or not, in the current rotation or previously fertilized, as long as fertilization occurred more than 6 years prior to establishment.

Thirty-eight paired-plot installations were established between 2015 and 2018 (Figure 1; Table S1). At each instal-

lation, four or five temporary circular plots between 0.1 and 0.2 ha, based on stand density, were established, such that each plot contained around 75 trees. Trees in the plots were identified by species and initially measured for diameter at breast height (DBH) (1.37 m), for the purposes of selecting the two most similar plots at each location, according to diameter distribution and basal area. The final paired-plots were within $\pm 10\%$ for basal area and $\pm 10\%$ for quadratic mean diameter. One plot at each location was selected at random to receive nitrogen fertilizer, as urea, hand-applied at a rate of $224 \text{ kg N}\cdot\text{ha}^{-1}$. All measurement plots were surrounded by a minimum of 10-m treated (or untreated) buffer using best practices (rainy weather conditions and uniform fertilizer application). Fertilization was carried out in March–April (spring sampling) in Washington and Oregon installations and in November (fall sampling) in BC installations due to the preference for fall fertilization by the British Columbia Ministry of Forests (Dave Goldie, personal communication, 2017).

2.2 | Tree measurements

Within the two paired-plots, all live Douglas-fir trees $>5 \text{ cm}$ DBH were measured for species, DBH, and general conditions. A subset of trees (42 trees per plot) were measured for total height (HT) and height-to-live-crown (HLC). The plots were remeasured after the fourth growing season from treatment in the fall or winter for DBH, HT, HLC, and tree status. Unmeasured HT and HLC were estimated using CIP-SANON (version 4.2; Oregon State University) (Mainwaring et al., 2022) using the equation form of Krumland and Wensel (1988). Volume per tree was calculated using a taper equation for Douglas-fir trees (Poudel et al., 2018). King’s site index (King, 1966) was calculated using the average height of the 192 largest DBH Douglas-fir trees per hectare equivalent in each plot. Cumulative growth rate was measured as basal area mean annual increment (MAI), which is the mean tree basal area divided by tree breast height age at the time of establishment per plot.

Because there was no measurable effect of fertilization on mortality (mean fertilized mortality was $60 \pm 16 \text{ trees}\cdot\text{ha}^{-1}$ and mean control mortality was $52 \pm 12 \text{ trees}\cdot\text{ha}^{-1}$), dead trees at 4 years were removed from fertilizer area response calculations. To further limit the effect of initial stand condition differences between control and fertilized plots, a linear regression between control volume per tree (m^3) at year 0 (TVOL0) and control volume per tree at Year 4 (TVOL4) (m^3) was calculated for each installation (i) (McWilliams & Burk, 1994):

$$\text{Control TVOL4}_i = \beta_0 + \beta_1 \times \text{Control TVOL0}_i. \quad (1)$$

Equation (1) was used to estimate control-calibrated 4-year volume per tree on the fertilized plot in each installation. Four-year fertilizer response per tree was calculated as the percent difference between mean actual fertilized plot tree volume at 4 years (FertTVOL₄) and mean control-calibrated fertilized plot tree volume at 4 years (CCTVOL) over the difference between CCTVOL₄ and fertilized plot tree volume at establishment (FertTVOL₀):

Tree fertilizer volume response per installation

$$= \frac{[\text{mean}(\text{Fert TVOL}_i) - \text{mean}(\text{CC TVOL}_i)]}{\text{mean}(\text{CC TVOL}_i - \text{Fert TVOL}_0)} \times 100. \quad (2)$$

Fertilizer response per area at each installation was determined by the difference between the sum of tree volume in the fertilized plot and the sum of control-calibrated tree volume in the fertilized plot:

Area fertilizer volume response per installation

$$= \frac{(\sum \text{Fert TVOL}_i) - (\sum \text{CCTVOL}_i)}{\frac{\text{plot acres}}{4 \text{ years}}}. \quad (3)$$

2.3 | Climate and soil nutrition

Average mean annual air temperature and precipitation through the ClimateNA program were determined for each installation for the 4 years postfertilization (2016–2019 [$n = 2$], 2017–2020 [$n = 10$], 2018–2021 [$n = 22$], and 2019–2022 [$n = 4$] based on fertilization date) (version 7.41; University of British Columbia) (Wang et al., 2016) (Table 1). Average yearly precipitation as snow for 4 years post-fertilization was also assessed using ClimateNA for each installation (Table 1). Soil parent materials consisted of glacial outwash, glacial till, sedimentary, igneous, and volcanic ash, and soil orders included Entisols, Inceptisols, Andisols, and Ultisols (Soil Survey Staff, n.d.).

Pretreatment soil nutrients were sampled on both paired-plots. Three forest floor samples of known area were composited per plot. Near the center of each plot, one soil pit was sampled to a depth of 1 m vertically at depths of 0–0.15, 0.15–0.3, 0.3–0.5, 0.5–0.7, and 0.7–1 m using hammer cores ranging from 5 to 7.6 cm in diameter for bulk density and soil nutrient analysis. The wider hammer core (7.6-cm diameter) was used on rocky soils, and the thinner hammer core (5-cm diameter) was used on clayey soils without rocks. If rocks were too large to be included in the hammer cores for volume assessment, a bulk sample including soil and rocks was taken to determine percent weight and volume of rocks (assuming a particle density of 2.65 g cm^{-3}). Forest floor and

soil samples were air-dried for at least 2 days. Cored and bulk mineral soils were sieved to 4.75 mm, and forest floor samples were ground. Soils were sieved to 4.75 mm because 2–4.75 mm samples from coastal PNW soils have been found to contain 80% of the soil mass and 60% of the soil C content of the <2 mm fraction for soil depths of 0–1 m (Holub & Hatten, 2019). All samples were weighed to determine the bulk density of fine soil (<4.75 mm) relative to total volume. When bulk samples were taken, the cored sample total volume was adjusted to account for the percent volume of rocks from the bulk sample. A subsample from each depth was dried at 105°C for 2 days to determine moisture content. Forest floor and soil samples were analyzed for total C and N using a CHN analyzer (CHN Analyzer 2400; PerkinElmer, Inc.). Available NO_3 and NH_4 were extracted with 2.0 M potassium chloride and analyzed using a O-I Analytical 500 auto analyzer (O-I Analytical) (Magill & Aber, 2000). Exchangeable cations (Ca, Mg, K) were extracted from forest floor and mineral soil samples using 1.0 M ammonium chloride (Skinner et al., 2001). Mineral soil P was analyzed using the Bray-1 method (Bray & Kurtz, 1945). Total forest floor nutrients were analyzed using EPA Method 3050b (U.S. EPA, 1996). Exchangeable cations, Bray P, and total nutrients were analyzed on an ICP-AES (ThermoFisher Scientific Co). Total N, exchangeable Ca, and Bray P contents were determined for each sampling depth by nutrient concentration, depth, and fine-soil bulk density and summed to a depth of 1 m. Soil nutrient contents to 1 m were used over shallow soil (0–0.15 m) due to the large amount of total and available N and exchangeable Ca below 0.15 m in coastal PNW soils below 15 cm (James et al., 2014, 2016; Sucre et al., 2008). In the current study, 69% of total soil N, 84% of exchangeable Ca, and 68% of Bray P soil contents were found below 15 cm, and 50%, 70%, and 50%, respectively, were found below 30 cm.

Four sets of anion and cation PRS probes (Western Ag Innovations) were installed in each plot at each installation. Probes were installed in the four cardinal directions from the plot center to capture any differences within a plot. At each installation point, a small soil pit was dug on the downhill side more than 1 m away from a plot tree. One set of anion and cation probes were installed horizontally at 5-cm mineral soil depth, orientated vertically widthwise to avoid water pooling. The goal of using only shallow soil PRS probes was the simplicity of the method and is based on previously found negative linear correlations between forest floor and surface soil C:N ratios and total soil N contents (to 1 m) and foliar N concentrations (Littke, Harrison, Zabowski, Briggs, et al., 2014). The shallow soil PRS probe sampling in this study was tested as an index of total site nutrition, without the additional effort required to monitor deep soil with PRS probes or soil sampling or challenging foliage collections. Probes were installed during fertilization or no treatment (March–April [spring]) in Washington and Oregon and removed after 12 weeks to capture PRS nutrient supply rates during the

TABLE 1 Mean, minimum, and maximum climate, soil nutrients, Plant Root Simulator (PRS), foliar nutrient concentrations, site productivity, and fertilizer response variables with codes and units for late-rotation Douglas-fir installations.

Variable	Code	Units	<i>n</i>	Mean	Median	Min	Max
Latitude	LAT	Degrees	38	46.3	46.4	43.2	50.1
Longitude	LONG	Degrees	38	−123.2	−123.1	−125.8	−122.0
Elevation	ELEV	m	38	384	332	61	975
Mean annual temperature	MAT	°C	38	10.1	10.3	7.8	11.6
Mean annual precipitation	MAP	mm	38	1900	1805	1263	3555
Precipitation as snow	PAS	mm	38	92	72	23	292
Forest floor C:N ratio	FFCN	No unit	38	38	35	25	66
Surface soil C:N ratio (0–0.15 m)	SSCN	No unit	38	25	23	15	46
Surface soil pH (0–0.15 m)	SSpH	No unit	38	5.1	5.2	3.8	5.9
Soil total N (0–1 m)	SOILN	kg N·ha ^{−1}	38	8162	7699	1444	20,561
Soil available NO ₃ (0–1 m)	SOILNO3	kg NO ₃ ·ha ^{−1}	38	16.3	10.1	1.7	148.6
Soil available NH ₄ (0–1 m)	SOILNH4	kg NH ₄ ·ha ^{−1}	38	42.2	30.6	2.9	300.7
Soil exchangeable Ca (0–1 m)	SOILCa	kg Ca·ha ^{−1}	38	5959	1334	166	59,211
Soil bray P (0–1 m)	SOILP	kg P·ha ^{−1}	38	79	50	5	446
PRS NO ₃ –N	PRSN03	mg N·m ^{−2} ·burial period ^{−1}	38	74	22	1	453
PRS NH ₄ –N	PRSNH4	mg N·m ^{−2} ·burial period ^{−1}	38	3.2	2.2	0.1	12.7
PRS Ca	PRSCa	mg Ca·m ^{−2} ·burial period ^{−1}	38	956	876	46	2765
PRS P	PRSP	mg P·m ^{−2} ·burial period ^{−1}	38	2.5	2.2	0.4	9.1
Foliar N	FOLN	%	37 ^a	1.24	1.24	0.74	1.73
Foliar Ca	FOLCa	%	37 ^a	0.66	0.65	0.29	1.24
Foliar P	FOLP	%	37 ^a	0.18	0.16	0.09	0.41
Total age	AGE	Years	38	36	35	28	64
Douglas-fir stand density	DFTPH	Trees·ha ^{−1}	38	669	608	274	2180
King's site index	SIKING	m at 50 years	38	42	44	27	50
Basal area mean annual increment	BAMAI	cm ² ·year ^{−1}	38	24.5	25.0	3.5	38.9
Fertilizer response per tree	FertRespTree	%	34 ^a	11.9	5.8	−20.1	86.3
Fertilizer response per area	FertRespArea	m ³ ·ha ^{−1} ·year ^{−1}	34 ^a	2.2	1.5	−4.3	9.1

^aFour installations were damaged by windstorms or fire prior to 4-year measurements and were dropped for fertilizer response analysis. One of these installations was damaged prior to foliar sampling.

start of the Douglas-fir growing season where climate and soil moisture are optimal for growth (Beedlow et al., 2007; Brix, 1972). In BC, PRS probes were installed in November (fall) for 12 weeks to measure the PRS nutrient supply rates after soil sampling and immediate effects of fertilization. The six installations in BC received an additional PRS probe installation for 12 weeks in the spring in control and fertilization plots (20–32 weeks after fertilization). PRS probes were rinsed clean of soil particles using deionized water, composited by plot, and sent to the manufacturer for analysis of NO₃, NH₄, Ca, K, Mg, P, S, and micronutrients. PRS probe data are presented as the amount of nutrient accumulated per unit area of membrane over the burial period (84 days). All 0- to 12-week control PRS nutrient supply rates (installed in spring in Washington and Oregon and fall in BC) were used to compare with soil and foliar nutrients, site productivity, and fertilizer

response because they were installed at the same time as soil sampling.

Two growing seasons after establishment, foliar samples were taken from control plots at each installation. One branch was removed from four trees per plot, either using a shot gun, climbing the tree, or picking up recently senesced foliage when the other two options were prohibited. Foliage was sampled from branches including the last 3 years of growth. Foliar sampling differed from traditional methods of current foliar sampling (Ballard & Carter, 1986) because they were sampled for a foliar nutrient biomass assessment. Foliar samples were dried at 65°C for 2 days and ground. Foliar samples were analyzed for total C and N using a CHN analyzer. Total metals were extracted using EPA Method 3050b (U.S. EPA, 1996) and analyzed on an ICP-AES (ThermoFisher Scientific Co.). A subsample of five installations showed no difference

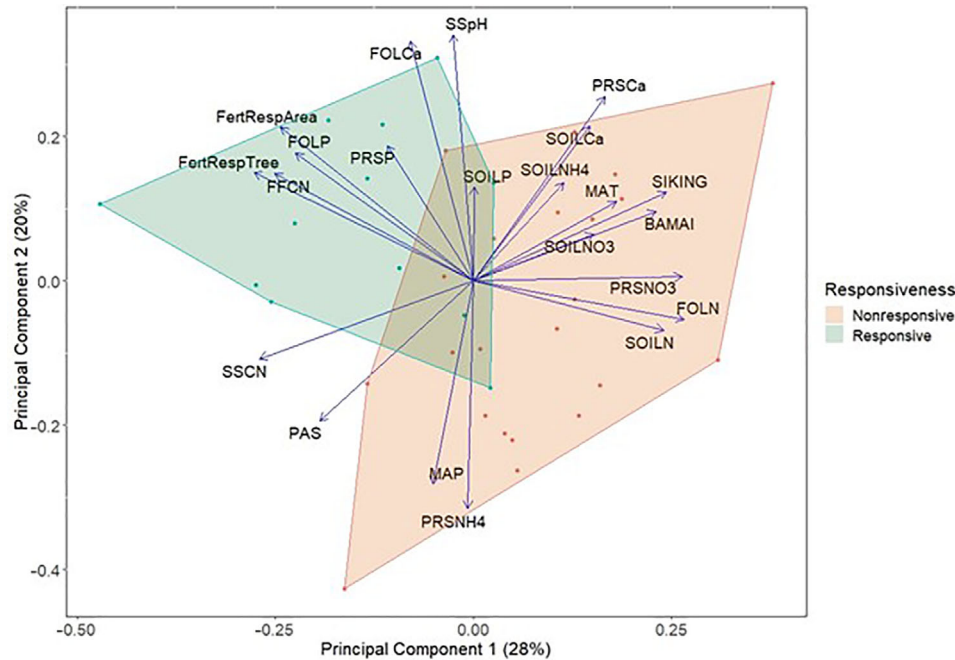


FIGURE 2 The first two principal components according to climate (mean of 4 years post-fertilization), soil nutrient contents, Plant Root Simulator (PRS) nutrient supplies, foliar nutrient concentrations, site productivity, and fertilizer response variables. Variable codes are explained in Table 1. Responsiveness is described as significantly different measured and control-calibrated volume growth per tree for each installation ($p < 0.10$).

in foliar N concentration between current and the last 2 years of foliage (data not shown). Expected differences between current and older foliage will be discussed where appropriate.

2.4 | Statistical methods

Relationships between climate, nutrient availability, PRS probe nutrient supply, site productivity, and Douglas-fir fertilizer response variables were visualized using principal component analysis (PCA). Each variable was normalized using the “scale” function in R such that each variable had a mean value of zero and a standard deviation of 1 (R version 4.3.1.; The R Foundation for Statistical Computing). The “prcomp” function in R was used to calculate principal components and the proportion of variance explained by each component. A biplot was graphed using the “autoplot” function in the ggplot2 package (Wickham, 2016).

The focus of this manuscript was to analyze the individual estimation ability of PRS N, Ca, and P nutrient supply rates for soil and foliar N, Ca, and P, site productivity, and fertilizer response. Future publications will focus on combining predictor variables to improve prediction of these dependent variables. Linear and nonlinear equations were fit if significant ($\alpha < 0.10$) between PRS nutrient supply rates and soil and foliar nutrient availability, site productivity, and fertilizer response variables. Significant differences ($\alpha < 0.10$) between control and fertilized PRS nutrient supply (0–12 weeks in

Washington and Oregon, and 0–12 and 20–32 weeks in BC) were accessed through a Mann–Whitney U test in R using the “wilcox.test” function. *Post hoc* significant differences were determined using Tukey’s HSD test ($\alpha < 0.10$). Significant fertilization responsiveness was determined using a one-sample t -test on the difference between fertilized volume growth at 4 years and control-calibrated volume growth at 4 years within each installation ($\alpha < 0.10$).

3 | RESULTS

3.1 | Principal component analysis

Results from the PCA confirmed that PRS nutrient supply rates were associated with soil and foliar nutrient extractions, site productivity measurements, and Douglas-fir fertilizer response (Figure 2). The PCA indicated that fertilizer responsiveness showed a clear separation in space on the first principal component. Nonresponsive and responsive installations were positively and negatively, respectively, associated with the first principal component. The first principal component showed a positive relationship between high total soil N content, PRS NO_3 , foliar N concentration, site index, and basal area MAI and a negative relationship with precipitation as snow, forest floor and surface soil C:N ratio, foliar P concentration, and fertilizer volume response per tree and area (Figure 2). The second principal component did not

separate fertilization responsiveness groups but was positively related to surface soil pH, soil exchangeable Ca content, PRS Ca and P nutrient supply rates, foliar Ca and P concentration, and fertilizer volume response per tree and area. Mean annual precipitation, precipitation as snow, and PRS NH_4 supply rate were negatively associated with the second principal component.

3.2 | Nutrient availability

PRS nutrient supply rates were correlated with soil nutrient contents and foliar nutrient concentrations. There were positive logarithmic relationships between PRS NO_3 supply rate and soil total N content and foliar N concentration (Table 2). Installations with low PRS NO_3 supply rate ($<25 \text{ mg N}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$), which was half of the total installations, contained lower soil total N ($6427 \text{ kg N}\cdot\text{ha}^{-1} \pm 739 \text{ SE}$) compared to installations with high PRS NO_3 supply rate ($>25 \text{ mg N}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$) ($9898 \text{ kg N}\cdot\text{ha}^{-1} \pm 875 \text{ SE}$) (Figure 3A). Similarly, foliar N concentrations were lower at low PRS NO_3 supply rates ($1.11\% \text{ N} \pm 0.04 \text{ SE}$ compared to $1.37\% \text{ N} \pm 0.05 \text{ SE}$). Forest floor and surface soil C:N ratios were also greater at low PRS NO_3 supply rates ($42 \pm 2 \text{ SE}$ vs. $35 \pm 1 \text{ SE}$ and $30 \pm 2 \text{ SE}$ vs. $21 \pm 1 \text{ SE}$, respectively) (Table 2). PRS NH_4 supply rates were not associated with soil or foliar N variables yet were correlated with Ca availability variables such as surface soil pH, soil Ca content, and foliar Ca concentration (Table 2). The sum of PRS NO_3 and NH_4 supply rates did not improve the prediction of N availability over PRS NO_3 supply rates alone (data not shown).

Soil exchangeable Ca content (0–1 m) was highly correlated with PRS Ca supply rate (Table 2). High soil exchangeable Ca contents were detected at PRS Ca supply rates over $1500 \text{ mg Ca}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$ ($17,007 \text{ kg Ca}\cdot\text{ha}^{-1} \pm 1934 \text{ SE}$ compared to $3013 \text{ kg Ca}\cdot\text{ha}^{-1} \pm 1846 \text{ SE}$) (Figure 3B). Soil exchangeable Ca content was also slightly correlated with surface soil pH and soil total N content (0–1 m). Foliar Ca concentration was positively linearly correlated to PRS Ca supply rate. All installations below 0.4% foliar Ca concentration (last 3 years of foliage) were found at PRS Ca supply rates below $1000 \text{ mg Ca}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$ and with low surface soil pH (<5) (data not shown). Conversely, installations with PRS Ca supply rates below $1000 \text{ mg Ca}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$ and high soil pH (>5) tended to have greater foliar Ca concentrations (up to 0.98% Ca). While pH was not recorded from PRS sampling, low soil pH (<5) was best estimated using PRS NH_4 supply rates greater than $3 \text{ mg N}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$ (Table 2). Foliar Ca concentration was better predicted using mean annual precipitation, surface soil pH, and soil exchangeable Ca content (0–1 m) than PRS Ca supply rate (Table 2).

PRS P supply rates estimated foliar P concentrations better than soil extractable P (Table 2). According to the positive linear relationship between PRS P and foliar P (Figure 3C), the lowest foliar P concentrations were found at PRS P supply rates below $2 \text{ mg P}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$, although higher foliar P concentrations were also found at this range. Installations with low PRS P and adequate foliar P ($>0.15\% \text{ P}$) tended to have lower foliar N concentrations ($<1.3\% \text{ N}$) due to a negative linear correlation between foliar N and foliar P ($R^2 = 0.32$; data not shown). Soil Bray P content was related to the positive logarithm of PRS P supply rate but was not estimated significantly by any other forest floor, soil, or foliar variables, nor was it correlated with foliar P concentration (Figure 3C; Table 2). While there were no significant correlations between mean annual precipitation and soil, foliar, and PRS P, there was an observation that lower P concentrations or contents ($<73 \text{ kg P}\cdot\text{ha}^{-1}$ in soil, $<1.6 \text{ mg P}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$, and $<0.20\% \text{ foliar P}$) were found on installations with greater than 2300 mm annual precipitation (data not shown).

3.3 | Site productivity and fertilizer response

PRS NO_3 supply rate was positively related to measures of Douglas-fir productivity and negatively related to Douglas-fir fertilizer response (Table 3). Site index and basal area MAI were related to the positive logarithm of PRS NO_3 supply rate (Figure 4A). Installations with low PRS NO_3 ($<25 \text{ mg N}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$) had on average a Douglas-fir site index of $39.7 \text{ m} \pm 1.4 \text{ SE}$ at 50 years, while installations with high PRS NO_3 supply rates averaged $45.2 \text{ m} \pm 0.6 \text{ SE}$ at 50 years. Similarly, installations with low PRS NO_3 supply rates had lower basal area MAI ($21.1 \text{ cm}^2\cdot\text{year}^{-1} \pm 2 \text{ SE}$ vs. $27.9 \text{ cm}^2\cdot\text{year}^{-1} \pm 1.5 \text{ SE}$). Soil total N content was more highly correlated with Douglas-fir site index than PRS NO_3 supply rate, but both had the same significance level (Table 3). PRS NO_3 supply rate performed better for estimating basal area MAI than all soil and foliar nutrients, but foliar N concentration was the best estimator of basal area MAI compared to other soil and foliar nutrients (Table 3).

Fertilizer volume response per tree was negatively correlated with the logarithm of PRS NO_3 supply rate (Figure 4B; Table 3). Installations with low PRS NO_3 supply rates responded more strongly to fertilization ($19.5\% \pm 6.5 \text{ SE}$) than installations with high PRS NO_3 supply rates ($4.4\% \pm 3.2 \text{ SE}$). Total soil N and foliar P concentration resulted in greater correlations with fertilizer response per tree compared to PRS NO_3 supply rate but was within the same significance range (Table 3). There was also a negative logarithmic relationship between PRS NO_3 supply rate and fertilizer volume response per area. Installations with low PRS NO_3 supply rates had greater fertilizer volume

TABLE 2 Linear and nonlinear equations between Plant Root Simulator (PRS) nutrient supply rates, forest floor, soil, and foliar nutrient availability variables from control plots.

Independent Variables		Dependent Variables		
		FFCN	SSCN	SSpH
MAT/MAP	NS			
PRSN03	NS			
PRSNH4	NS			
PRSCa	NS			
PRSP	NS			
FFCN	NS			
SSCN	NS			
SSpH	NS			

(Continues)

TABLE 2 (Continued)

Independent Variables	Dependent Variables		
	FFCN	SSpH	SSCN
SOILN		NS	
SOILCa			
SOILP			

Note: Cells with NS were nonsignificant. Blank cells were duplicate tests. Variable codes and units are explained in Table 1. R^2 values are in parentheses. *Significant at the 0.05 probability level. **Significant at the 0.01 probability level. ***Significant at the 0.001 probability level.

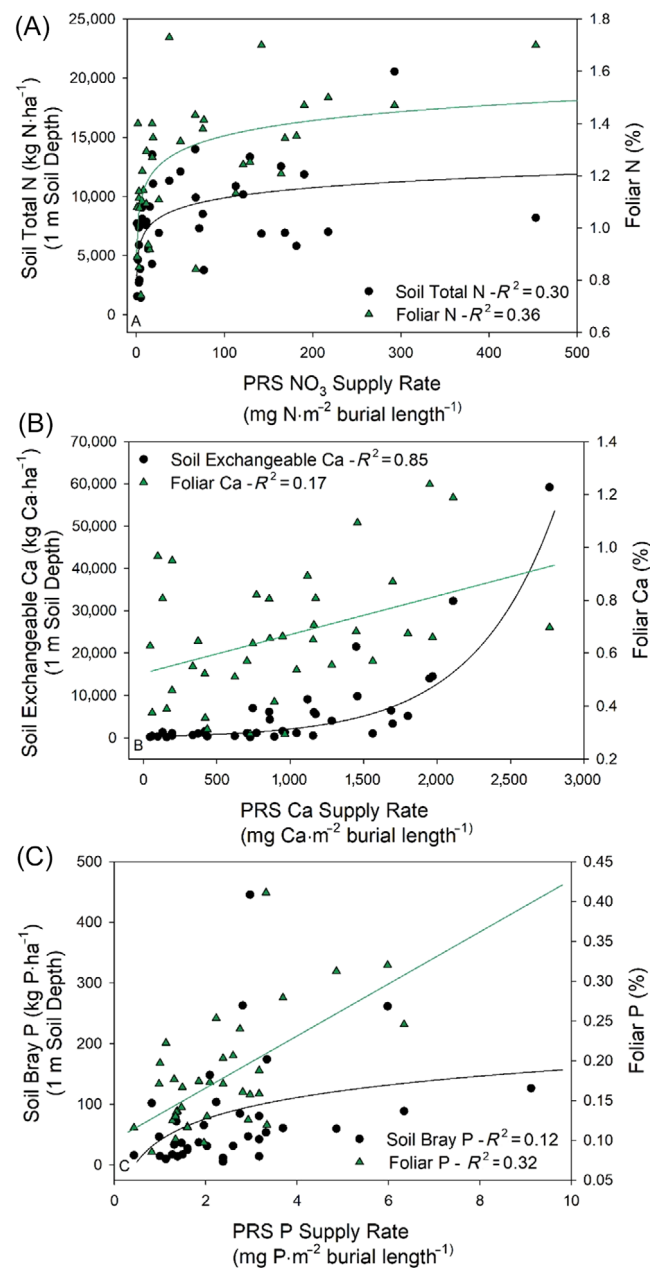


FIGURE 3 Relationships between control plot Plant Root Simulator (PRS) NO₃ (A), Ca (B), and P (C) and soil nutrient contents (left y-axis) and foliar nutrient concentrations (right y-axis) with R^2 values. Equations for regression lines are available in Table 2.

response per area ($3.2 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1} \pm 0.9 \text{ SE}$ compared to $1.2 \text{ m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1} \pm 0.7 \text{ SE}$). Forest floor C:N ratio and foliar N and P concentration showed greater correlations and lower p -values for estimating fertilizer volume response per area than PRS NO₃ supply rate (Table 3).

Fertilizer volume response per tree and per area was positively correlated, with inconsistencies caused by lower-than-expected area response on two installations that were highly responsive to fertilization (per tree) with low growth per tree ($0.023 \text{ m}^3 \cdot \text{tree}^{-1} \cdot \text{year}^{-1}$ vs. the mean of

TABLE 3 Linear and nonlinear relationships between control plot Plant Root Simulator (PRS), forest floor, soil, and foliar nutrient availability variables and site productivity and fertilizer response variables.

Independent Variables	Dependent Variables			
	SIKING=	BAMAI=	FertRespTree=	FertRespArea=
MAT/MAP	$2.09 \times MAT$ +21.64 ($R^2 = 0.12$)*	$-0.005 \times MAP$ +35.03 ($R^2 = 0.12$)*	$76.98 \times \ln(MAT)$ +188.72 ($R^2 = 0.13$)*	
PRSNO3	$1.64 \times \ln(PRSNO3)$ +37.20 ($R^2 = 0.25$)*	$2.48 \times \ln(PRSNO3)$ +16.46 ($R^2 = 0.23$)**	$-6.99 \times \ln(PRSNO3)$ +34.76 ($R^2 = 0.31$)*	$-0.97 \times \ln(PRSNO3)$ +5.38 ($R^2 = 0.25$)*
PRSCa	$0.003 \times PRSCa$ +39.64 ($R^2 = 0.11$)*	NS	NS	NS
FFCN	$-0.21 \times FFCN$ +50.67 ($R^2 = 0.13$)*	$-0.31 \times FFCN$ +36.41 ($R^2 = 0.11$)*	$1.1 \times FFCN$ -30.4 ($R^2 = 0.26$)*	$0.19 \times FFCN$ -5.02 ($R^2 = 0.32$)*
SSCN	$-0.37 \times SSCN$ +51.63 ($R^2 = 0.24$)*	$-0.48 \times SSCN$ +36.33 ($R^2 = 0.16$)**	$1.53 \times SSCN$ -26.4 ($R^2 = 0.28$)*	$0.20 \times SSCN$ -2.69 ($R^2 = 0.19$)*
SOILN	$5.49 \times \ln(SOILN)$ - 6.2 ($R^2 = 0.35$)*	$6.3 \times \ln(SOILN)$ -31.44 ($R^2 = 0.16$)**	$-23.22 \times \ln(SOILN)$ -217.71 ($R^2 = 0.40$)*	$-2.79 \times \ln(SOILN)$ +26.97 ($R^2 = 0.24$)*
SOILNO3	$2.65 \times \ln(SOILNO3)$ - 36.43 ($R^2 = 0.21$)*	NS	$-8.62 \times \ln(SOILNO3)$ +32.03 ($R^2 = 0.15$)*	NS
SOILNH4	$3.07 \times \ln(SOILNH4)$ - 32.42 ($R^2 = 0.29$)*	NS	NS	NS
SOILCa	$1.41 \times \ln(SOILCa)$ +31.81 ($R^2 = 0.14$)*	NS	NS	NS
FOLN	$9.61 \times \ln(FOLN)$ +40.58 ($R^2 = 0.11$)*	$15.53 \times FOLN$ +5.28 ($R^2 = 0.17$)*	$-53.4 \times FOLN$ +78.21 ($R^2 = 0.30$)*	$-8.27 \times FOLN$ +12.48 ($R^2 = 0.30$)*
FOLCa	NS	NS	$46.59 \times FOLCa$ -17.88 ($R^2 = 0.19$)*	$8.16 \times FOLCa$ -3.01 ($R^2 = 0.24$)*
FOLP	NS	NS	$228.07 \times FOLP$ -26.3 ($R^2 = 0.38$)*	$34.92 \times FOLP$ -3.66 ($R^2 = 0.37$)*
SIKING		$1.14 \times SIKING$ -25.23 ($R^2 = 0.55$)*	$-1.38 \times SIKING$ +70.48 ($R^2 = 0.12$)*	NS
BAMAI			$-0.9 \times BAMAI$ +34.21 ($R^2 = 0.12$)*	NS

Note: Variable codes and units are explained in Table 1. Cells with NS are nonsignificant. R^2 values are in parentheses.

*Significant at the 0.05 probability level. **Significant at the 0.01 probability level. ***Significant at the 0.001 probability level.

0.05 m³·tree⁻¹·year⁻¹) and moderate stand density (629 and 459 trees·ha⁻¹ vs. the mean of 669 trees·ha⁻¹) (Table 1; Figure 5). Other low-productivity installations with lower growth per tree (0.008 and 0.012 m³·tree⁻¹·year⁻¹) resulted in closer to expected area response due to high stand densities (1661 and 2180 trees·ha⁻¹).

3.4 | Fertilization effects on nutrient supply rate

Urea fertilization significantly increased PRS NO₃, NH₄, and Ca supply rates 12 weeks after treatment (Table 4). Fertilized plots contained PRS NO₃ supply rates that were about

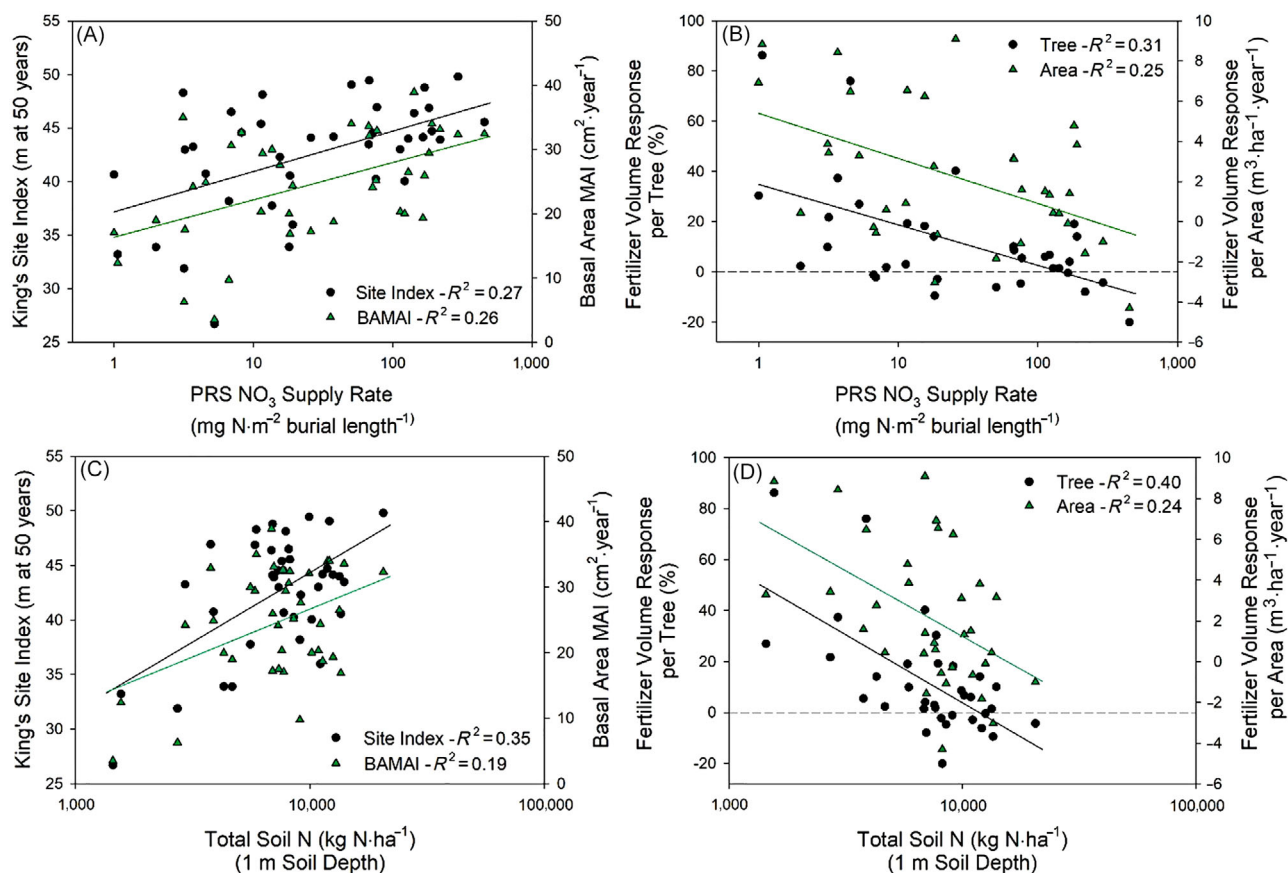


FIGURE 4 Relationships between control plot Plant Root Simulator (PRS) NO_3 supply rate and total soil N (1 m soil depth) and King's Douglas-fir site index (King, 1966) and basal area mean annual increment (A and C) and fertilizer volume response per tree and per area (B and D) with R^2 values. Regression equations are available in Table 3.

TABLE 4 Mean Plant Root Simulator (PRS) nutrient supply rates during the 0–12 weeks (all installations; $n = 34$) and 20–32 weeks (BC only; $n = 6$) after establishment or urea fertilization ($224 \text{ kg N} \cdot \text{ha}^{-1}$).

Nutrient	Mean PRS nutrient supply ($\text{mg} \cdot \text{m}^{-2} \cdot \text{burial period}^{-1}$) ^a				<i>p</i> -value
	Control (0–12 weeks)	Fertilized (0–12 weeks)	Control (20–32 weeks)	Fertilized (20–32 weeks)	
$\text{NO}_3\text{-N}$ (all)	74 ± 16 a	707 ± 76 b			<0.001
$\text{NO}_3\text{-N}$ (BC only)	139 ± 72 a	531 ± 190 b	79 ± 42 a	204 ± 78 ab	0.04
$\text{NH}_4\text{-N}$ (all)	3.2 ± 0.5 a	139.5 ± 35.1 b			<0.001
$\text{NH}_4\text{-N}$ (BC only)	4 ± 1 a	432 ± 149 b	3.2 ± 2 a	74 ± 44 a	0.002
Ca (all)	956 ± 108 a	1264 ± 120 b			0.06
Ca (BC only)	983 ± 238	1121 ± 365	627 ± 105	599 ± 183	0.35
P (all)	2.5 ± 0.3	2.4 ± 0.3			0.27
P (BC only)	2.3 ± 0.5	2.8 ± 1.5	4.4 ± 2.1	2.6 ± 0.9	0.72

Note: Significant treatment differences are in bold ($\alpha < 0.10$) and different lowercase letters within each row indicate significant differences according to Tukey's HSD test.

^aTreatment means $\pm$ SE.

10 times higher than control plots after 12 weeks. PRS NO_3 supply rates in control and fertilized plots were related to forest floor and surface soil C:N ratios by power equations (Figure 6A,B). Control PRS NO_3 supply rates were consistently low at high forest floor C:N (>40) and surface soil C:N

(>25) ratios, and increases in fertilized PRS NO_3 supply rates were lowest at high C:N ratios.

PRS NH_4 supply rates were 44 times greater in fertilized plots than in control plots (Table 4). Control PRS NH_4 supply rates showed a negative linear relationship with surface

TABLE 5 Linear and nonlinear relationships between forest floor and soil C:N and pH and Plant Root Simulator (PRS) nutrient supply rate with (Fert) and without fertilizer (Control).

Independent Variables	Dependent Variables					
	Control PRSNO3=	Fert PRSNO3=	Control PRSNH4=	Fert PRSNH4	Control PRSCa=	Fert PRSCa=
FFCN	5.57E08 $\times FFCN^{-4.68}$ ($R^2 = 0.58$)***	1.34E07 $\times FFCN^{-2.87}$ ($R^2 = 0.19$)*	NS		NS	NS
SSCN	8.40E06 $\times SSCN^{-4.02}$ ($R^2 = 0.25$)***	7.99E06 $\times SSCN^{-3.07}$ ($R^2 = 0.24$)***	0.13 $\times$ SSCN +0.14 ($R^2 = 0.06$)	8.5 $\times$ SSCN -85.24 ($R^2 = 0.11$)*	-39.53 $\times$ SSCN +1928.36 ($R^2 = 0.17$)**	-33.44 $\times$ SSCN +2148.55 ($R^2 = 0.16$)**
SSpH	NS	NS	22.73 $\times$ SSpH +22.73 ($R^2 = 0.41$)***	NS	951 $\times$ SSpH ² - 8669 $\times$ SSpH + 20208 ($R^2 = 0.38$)***	870 $\times$ SSpH ² - 7634 $\times$ SSpH + 17480 ($R^2 = 0.38$)***

Note: Variable codes and units are explained in Table 1. Cells with NS are nonsignificant. R^2 values are in parentheses.

*Significant at the 0.05 probability level. **Significant at the 0.01 probability level. ***Significant at the 0.001 probability level.

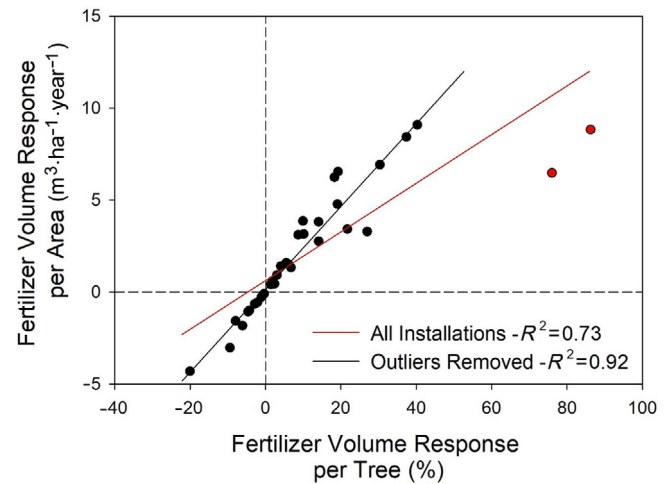


FIGURE 5 Linear relationships between fertilizer volume response per tree (%) (FertRespTree) and fertilizer volume response per area ($\text{m}^3 \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$) (FertRespArea). The equations presented are: all installations (FertRespArea = $0.13 \times \text{FertRespTree} + 0.63$) and two outliers removed (FertRespArea = $0.23 \times \text{FertRespTree} + 0.15$).

soil pH (Figure 6C), but there was no effect of pH on fertilized PRS NH_4 supply rates (data not shown). Fertilization increased PRS Ca supply rates by 32% over control plots (Table 4). The increase in PRS Ca supply rate was greatest at surface soil pH values over 4.5 (Figure 6D). There was no effect of fertilization on PRS P supply rates.

In installations with fall fertilization (BC only) ($n = 6$), PRS NO_3 supply rates were greatest in the fall fertilization sampling (0–12 weeks after fertilization) compared to the fall and spring control samplings (Figure 6A,B; Table 4). There were no significant differences between PRS NO_3 supply rates in the control samplings and the spring after fertilization sampling (20–32 weeks post-fertilization). The fall fertilization sampling contained greater PRS NH_4 supply rates than the fall and spring control treatments and the fertilized treatment spring sampling (Table 4). There were no significant effects of treatment or sampling time on PRS Ca and P supply rate in the BC installations (Table 4).

4 | DISCUSSION

PRS NO_3 supply rates in unfertilized plots effectively estimated N availability of coastal PNW Douglas-fir forests. Total soil N, C:N ratios, and foliar N were best estimated by PRS NO_3 supply rates instead of NH_4 supply rates. Net and gross N mineralization rates have been previously found to increase with decreasing forest floor and soil C:N ratios and increasing total soil N (Högberg et al., 2006; Krana-better, Mckeown, et al., 2020; Perakis & Sinkhorn, 2011). Interestingly, the mean forest floor and surface soil C:N ratios (38 and 25, respectively) in this study were previously

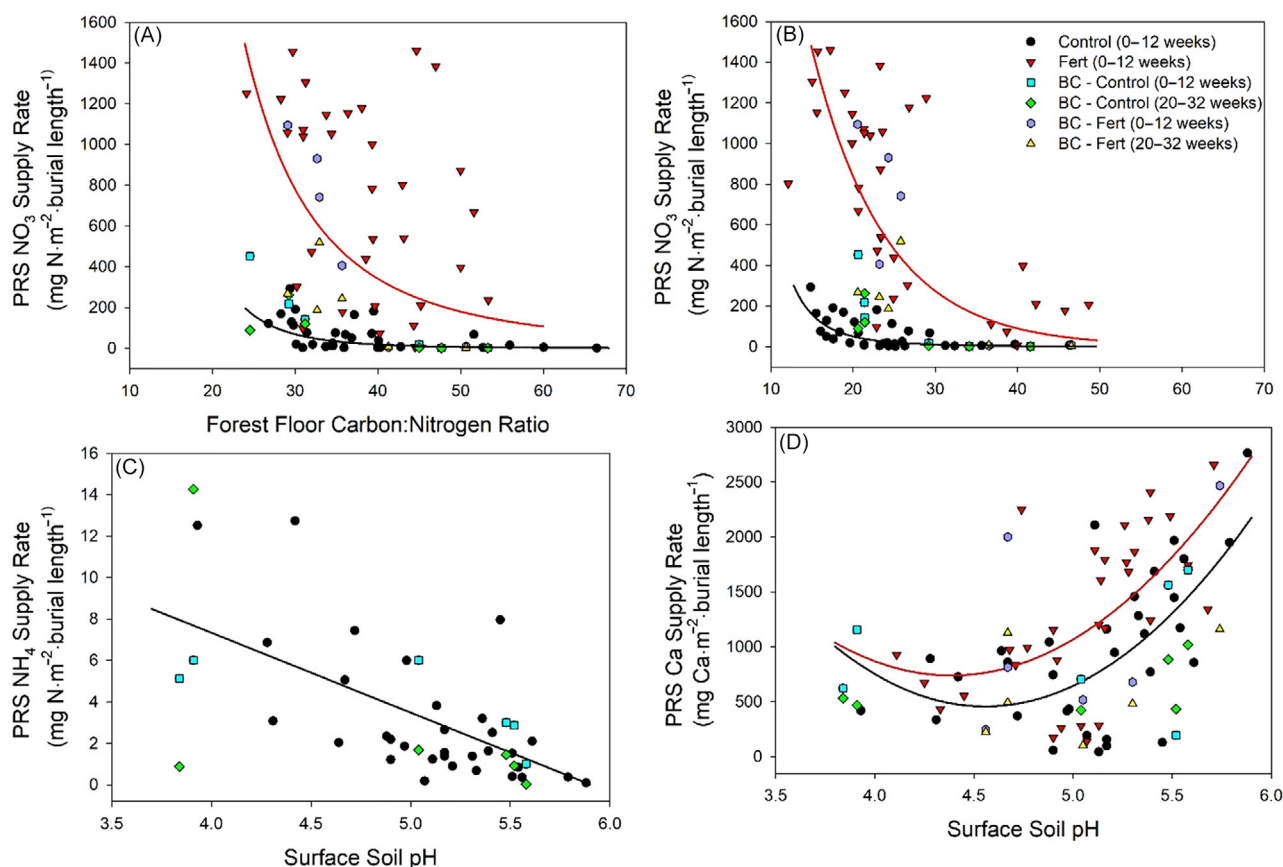


FIGURE 6 Relationships between pre-treatment forest floor C:N ratio (A) and surface soil C:N ratio (B) by control and fertilized (0–12 weeks) Plant Root Simulator (PRS) NO₃ supply rate and pre-treatment surface soil pH by PRS NH₄ (C) and Ca (D). Pre-treatment values were taken separately from control or fertilized plots for comparison with post-treatment values. Data from BC are shown separately for 0- to 12-week (fall installation) and 20- to 32-week (spring installation) samplings. Regression equations are based on 0- to 12-week Washington and Oregon (spring installation) and 0- to 12-week BC (fall installation) data and are available in Table 5.

found to be close to the range of C:N ratios indicating fertilizer response in Douglas-fir (greater response over C:N of 40 and 25, respectively) (Littke, Harrison, Zabowski, Ciol, et al., 2014). The importance of NO₃ over NH₄ is expected because it is the more mobile form of inorganic N and found at higher concentrations in coastal PNW soils yet is more susceptible to leaching compared to NH₄ (Devine et al., 2012; Perakis et al., 2013; Strahm et al., 2005). However, in colder climate spruce and pine forests, PRS NH₄ supply rates were found to be higher than PRS NO₃ supply rates (Harrison & Maynard, 2014). In this study, installations with the coldest mean annual temperatures (<9.1°C) contained equal or lower PRS NO₃ supply rates compared to PRS NH₄ supply rates (data not shown). Similarly, the lowest PRS NO₃ supply rates were found at elevations over 450 m (38 vs. 96 mg N·m⁻²·burial period⁻¹) except for one installation with 292 mg N·m⁻²·burial period⁻¹ at 597 m elevation (data not shown). The finding that NO₃ is limiting in colder climates is supported by previous research that found greater Douglas-fir urea fertilization response on stands with high elevations (>400 m) and colder April and December temperatures (Littke et al., 2017).

Low PRS NO₃ supply rates (<25 mg N·m⁻²·burial period⁻¹) were associated with lower site productivity of Douglas-fir, which is supported by previous research findings of decreasing site productivity with lower N availability (Carter & Klinka, 1990; Kabzems & Klinka, 1987; Littke et al., 2016; Miller et al., 1989). However, not all installations with low PRS supply rate had low site index (eight of 19 installations above the mean site index of 42 m) or basal area MAI (six of 19 above the mean BAMAI of 24.5 cm²·year⁻¹). These installations tended to contain greater total soil N contents and lower C:N ratios than installations with low site productivity, suggesting that they had adequate N availability with little excess NO₃ (data not shown) (Nason et al., 1990).

Many installations with low PRS NO₃ supply rates also responded well to urea fertilization, which supports previous findings that tree growth can be increased on coastal PNW Douglas-fir plantations with low N availability (Carter et al., 1998; Edmonds & Hsiang, 1986; Littke, Harrison, Zabowski, Ciol, et al., 2014; Miller et al., 1989; Sucre et al., 2008). However, some installations with low PRS NO₃ supply rates, which were broadly distributed across the region and geologic parent materials, responded marginally or did

not respond to urea fertilization (7/19 installations). All seven non-responding installations with low PRS NO_3 supply rates contained a combination of low foliar P concentration, low PRS Ca supply rates, or high site index. Five installations contained slightly deficient foliar P ($<0.15\%$ P) (Ballard & Carter, 1986), which suggests a secondary P limitation. Six non-responding installations had low PRS Ca supply rates, which could suggest a negative effect of fertilization on Ca availability (Fox, 2004). Three of these installations had high site index, suggesting that NO_3 supply rates were at adequate levels and that the maximum site productivity had been reached (Nason et al., 1990). Nonetheless, the findings from this study support the use of in situ PRS probes as a useful strategy for determining Douglas-fir forests most likely responsive to urea fertilization as well as detecting forests with other nutrient limitations where urea fertilization might not be effective.

While N is the nutrient mainly identified as limiting in coastal PNW Douglas-fir stands (Chappell et al., 1991), Ca and P fertilizations have been found to yield growth responses in the coastal PNW (Mainwaring et al., 2014). In this study, soil exchangeable Ca content to 1-m soil depth was strongly estimated using PRS Ca nutrient supply. A lesser relationship was found between foliar Ca and PRS Ca nutrient supply. One reason for the marginally significant relationship between PRS Ca supply rates and foliar Ca in this study was that foliage was sampled from the last 3 years of branches. To prevent Ca toxicity, Ca accumulates in Douglas-fir foliage over time as plant-unavailable Ca pectate and Ca oxalate, which could make up over half of the Ca concentration in foliage over 0.4% Ca (Littke & Zabowski, 2007). Also, lime fertilization response of Douglas-fir was greatest at foliar Ca concentrations below 0.4% Ca (from 1-year-old foliage) (Mainwaring et al., 2014). In the coastal PNW, soil and foliar Ca have been found to be negatively associated with soil N due to N enrichment increasing Ca leaching over time (Hynicka et al., 2016; Perakis et al., 2006, 2013). Specifically, foliar Ca in coastal or sedimentary and high N-basaltic soils was sourced primarily from the atmosphere instead of weathering from parent materials due to N enrichment depleting exchangeable Ca.

While P limitations and fertilization are common in many forest systems outside of the PNW (Elser et al., 2007; Fox et al., 2007; Mohren et al., 1986; Renou-Wilson & Farrell, 2007), P nutrition of coastal PNW Douglas-fir forests has been studied less frequently (Gessel et al., 1981; Kranabetter, Sholinder, et al., 2020; Mainwaring et al., 2014; Perakis et al., 2013; Radwan & Shumway, 1984). In this study, PRS P supply rates had a better correlation with foliar P concentrations than with soil extractable P. Due to the lack of correlation between soil Bray P content and foliar P ($R^2 = 0.006$), it is likely that a sequential extraction might have improved the understanding of available soil P on these installations (Debruler et al., 2019). It is also possible that the horizontal placement of the PRS probes at 5-cm depth in the mineral soil did not capture the greater P availability in the forest floor (Huang & Schoe-

nau, 1997). While highly variable on the low range, PRS P supply rates over $3.5 \text{ mg P}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$ could identify Douglas-fir stands that were not limited in P due to high foliar P concentrations. The interaction between N and P availability in the coastal PNW is complex due to the type of soil P (organic or inorganic), soil pH, and amount of precipitation. Soil organic P has been found to increase with increasing soil C and N concentrations, yet foliar P was correlated with inorganic P only (Kranabetter, Sholinder, et al., 2020; Perakis et al., 2013). Further complicating the understanding of P availability, ectomycorrhizal species have been found to optimally allocate exoenzymes to increase P availability in P-limited, high-precipitation, podzolized soils (Meeds et al., 2021). The installations with the highest precipitation levels ($>2300 \text{ mm}$ mean annual precipitation) in this study were found to have consistently low soil P contents, PRS P supply rates, and foliar P concentrations, but there were no linear or nonlinear relationships between mean annual precipitation and P availability variables. Installations with greater foliar P concentrations (and lower foliar N due to the negative linear correlation with foliar P) responded better to urea fertilization in this study, while installations with low foliar N ($<1.3\%$ N) and foliar P ($<0.15\%$ P) did not respond to fertilization. These findings suggest that P limitations may be inhibiting growth response to urea fertilization in some coastal PNW forests, which is supported by western hemlock response to combined N and P fertilization on northern Vancouver Island, BC (Blevins et al., 2006; Prescott et al., 2013; Radwan et al., 1991) and Douglas-fir response to P fertilization on P-limited soils with high pH (>5.0) (Mainwaring et al., 2014).

Nitrogen fertilization as urea resulted in a large increase in PRS NO_3 ($40\times$ greater) and NH_4 ($90\times$ greater) supply rates and a marginal increase in PRS Ca ($2\times$ greater) during the 12 weeks after fertilization. The finding that post-fertilization PRS NO_3 supply rates were lower due to high pre-treatment surface-soil C:N ratios suggests that there was less excess NO_3 available after fertilization in these soils. Some of the added N from fertilization was likely immobilized in soils with high C:N ratios, which might have limited the fertilization effect on these installations (Chang et al., 1997; Mead et al., 2008; Nason, 1989). Alternatively, the added N from fertilization could have been taken up quickly by the N-limited Douglas-fir or understory plants (Chang & Preston, 2000; Nason et al., 1990). Nine weeks after fertilization of a Douglas-fir study on Vancouver Island, BC, ^{15}N -labeled urea resulted in an increase of $6\text{--}24 \text{ kg N}\cdot\text{ha}^{-1}$ in Douglas-fir foliage, with $80\text{--}100 \text{ kg N}\cdot\text{ha}^{-1}$ being immobilized in the soil (Nason, 1989). Data from the fall-season-fertilized BC installations showed a drop in PRS NO_3 and NH_4 supply rates from 20 to 32 weeks compared to 0–12 weeks postfertilization. PRS NO_3 supply rates were depleted by about half 32 weeks after fertilization, while PRS NH_4 supply rates had returned to control levels. In a spring and fall urea fertilization study in British Columbia, fall fertilization increased short-term

uptake efficiency of Douglas-fir compared to spring fertilization due to greater fall rainfall increasing contact with the tree roots (Nason et al., 1990). However, there were no differences in fertilizer use efficiency in this study after 10 years (Mead et al., 2008). Therefore, the decrease in PRS N supply rates observed after 20 weeks in the BC fall fertilization suggests that the fertilizer-added N was incorporated into the forest floor, soil, and trees and not lost to leaching.

Installations with high pre-treatment NO_3 supply rates and excessive PRS NO_3 supply rates post-fertilization have the potential for increased leaching of NO_3 along with other nutrients (Aber et al., 1998; Perakis & Sinkhorn, 2011, 2013; Perakis et al., 2006). In this study, PRS Ca supply rates increased 12 weeks post-fertilization likely due to replacement of Ca on cation-exchange sites with fertilizer-added NH_4 . This mobilized Ca would be more available to the ion-exchange resins as well as to plants, but also more susceptible to leaching along with excess NO_3 from fertilization (Davis et al., 2012). Repeated urea fertilization has been found to decrease soil pH as well as exchangeable Ca and Mg in Douglas-fir soils (Fox, 2004). A similar loss of base cations from N-enriched soils has been found when comparing stands of N-fixing red alder to Douglas-fir (Van Miegroet & Cole, 1984). This is of particular concern in soils with long-term losses of base cations due to N enrichment and intensive harvesting and/or competing vegetation control (Hynicka et al., 2016; Littke et al., 2020; Perakis et al., 2006, 2013). However, in soils with adequate base cation availability, a single, operational rate of urea fertilization (as was used in this study) is not likely to cause significant base cation losses.

5 | CONCLUSIONS

PRS NO_3 supply rates performed as well as or better than previously established nutrient extractions for assessing N availability, site productivity, and fertilizer response of PNW Douglas-fir. Calcium and P availability was also estimated by PRS Ca and P supply rate, respectively. Low PRS NO_3 supply rates ($<25 \text{ mg N}\cdot\text{m}^{-2}\cdot\text{burial period}^{-1}$) were associated with low site index and basal area MAI and high urea fertilizer volume response per tree and per area. Urea fertilization increased PRS NO_3 , NH_4 , and Ca supply rates over 12 weeks after fertilization compared to untreated soils. Increases in post-treatment NO_3 and NH_4 supply rates were greatest at low surface soil C:N ratios. Temporary increases in Ca supply rates were found after fertilization in this study, but excess enrichment of N in soils with low exchangeable base cations could result in leaching losses over time.

Soil nutrient extractions represent the time and conditions at which the sample was taken, while the in situ PRS nutrient supply rates assess the cumulative effects of climate and water availability on current soil nutrient availability. This study demonstrated that in situ PRS supply rates are an effective

management tool and are recommended for assessing nutrient availability, site productivity, and response to fertilization in coastal PNW Douglas-fir soils compared to standard soil and foliar nutrient samples, which can be expensive and difficult to obtain.

AUTHOR CONTRIBUTIONS

Kim Littke: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; validation; visualization; writing—original draft; writing—review and editing. **Scott Holub:** Conceptualization; formal analysis; investigation; methodology; writing—review and editing. **Eric Bremer:** Resources; writing—review and editing. **Eric Turnblom:** Conceptualization; funding acquisition; project administration; resources; supervision; writing—review and editing.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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