Assessing the effects of fertilization on Douglas-fir growth responses and edaphic variables in the Pacific Northwest

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Abstract

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Douglas-fir (*Pseudotsuga menziesii var. menziesii.*) is an important commercial tree species in the coastal Pacific Northwest (PNW), and its biomass is also regarded as a significant forest carbon (C) sink. Productivity of Douglas-fir varies regionally due to nutrient availability (especially nitrogen). Nitrogen (N) fertilization can improve Douglas-fir productivity, but knowledge gaps remain in the mechanisms affecting growth response to fertilization, as well as in the effects of this management practice to the soil nutrient condition itself in the long term due to the complex interactions between environmental variables. This study leveraged a paired-tree fertilization study to examine the growth response of Douglas-

fir to soil nutrient availability and fertilization, plus the effects of the fertilization on the edaphic variables ten to thirteen years after the N input. The objectives of this study were to 1) Predict Douglas-fir growth responses after N fertilization in the PNW; 2) Examine changes in soil nutrient availability ten to thirteen years after fertilization. In this study, N fertilization was applied across 15 sampled Douglas-fir installations throughout coastal Oregon and Washington State, and basal area and ring area responses to the fertilization were analyzed along with the initial and current soil macronutrient levels measured with Probes. Results of this study show that 1) multiple factors affect the long-term response of Douglas-fir growth to one-time N fertilization; 2) the levels of soil cation availability and surface C:N ratio affect response extent; 3) the level of initial N content determines the responding patterns; 4) N fertilization has limited long-term effect on soil nutrient availability; 5) stand-level understanding of edaphic and geoclimatic conditions should contribute to better outcomes of N fertilization in the PNW. Our findings provide critical references for accurately assessing the long-term effects of N fertilization on Douglas-fir productivity and the ecosystem services of plantation forests such as carbon sequestration.

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Abstract

1. Introduction

1.1 Soil Physical and Biological Characteristics, and Plant Growth

Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] is a native species to the Pacific Northwest (PNW), and a crucial commercial species for wood products. Due to its economic value and ability to adapt to the varying soil and climate characteristics throughout the region, Douglas-fir is the dominant forest plantation species in the PNW (Franklin and Dyrness 1988), and is considered to be a globally important carbon sink (Ishii et al., 2017; Briegel et al., 2020). However, variability in regional climate and soil conditions impact the productivity of Douglas-fir (Steinbrenner, 1979). Soil nutrient availability and moisture-holding capacity is variable across the region; temperature fluctuations, together with precipitation patterns, further interact with soil characteristics, directly influencing growth rates and timber quality, therefore, creating site-specific challenges in Douglas-fir management (Steinbrenner, 1979; Miller et al., 1989; Littke et al., 2018). Littke et al. (2016, 2024) further emphasized the role of soil chemistry, particularly nitrogen (N) availability and carbon-to-nitrogen ratios in the forest floor, as critical predictors of Douglas-fir growth; low nitrate (NO_3) supply rates in soils were associated with reduced Douglas-fir biomass productivity (C sequestration capacity) and greater response to N fertilization.

Soil nutrient availability and moisture-holding capacity, which are critical determinants of Douglas-fir growth, exhibit considerable spatial variability across the PNW. These variations are influenced by factors such as soil texture, organic matter content, and climatic conditions, which collectively shape site productivity and management responses, as Figure 1 illustrates.

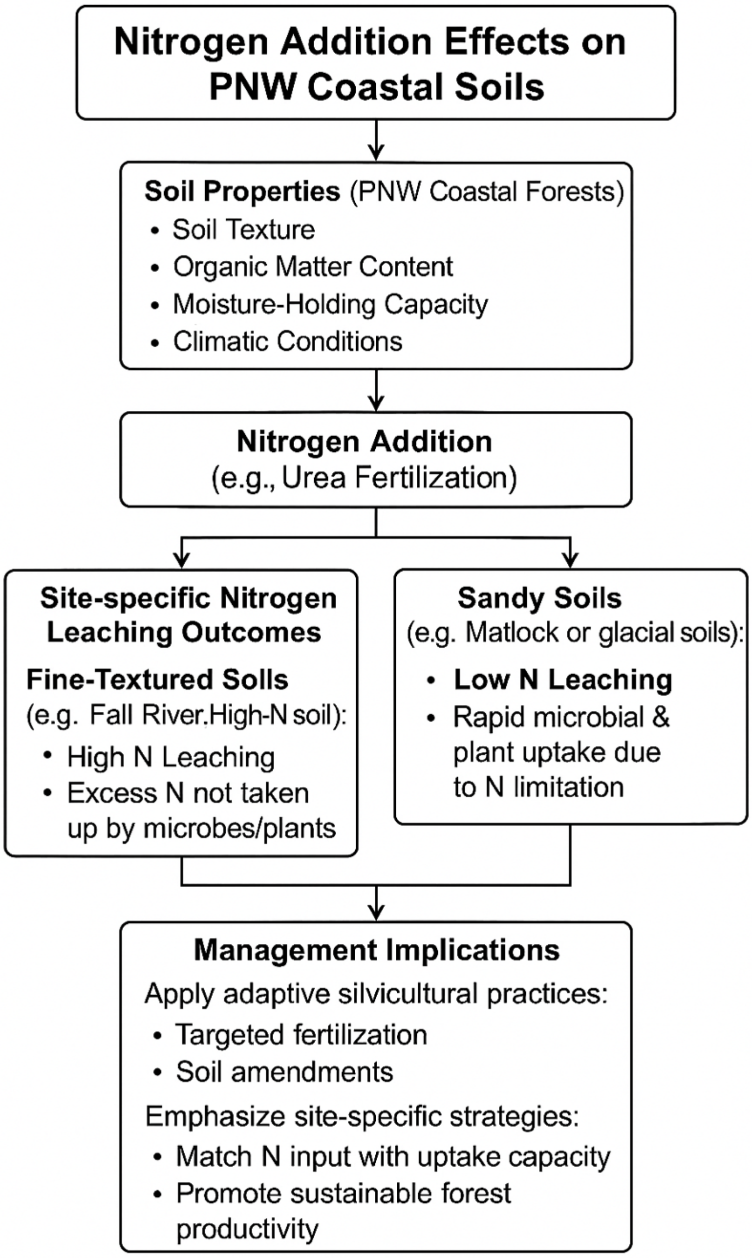

Figure 1. Nitrogen Addition Effects on PNW Coastal Soils

Contrary to common assumptions, nutrient-rich, fine-textured soils tend to experience higher N leaching, as excess N is not immediately taken up by vegetation and microbes (Devine et al., 2012). For example, at one of this study's experimental installations, Fall River, high-N loamy soil exhibited significantly greater leaching, compared to another installation, Matlock, with a low-N sandy soil following harvest (Devine et al., 2012). Similarly, Flint et al. (2008)

demonstrated that sandy glacial soils showed minimal N leaching after urea fertilization, as available N was rapidly absorbed by microbes and vegetation due to nutrient limitations. Adaptive silvicultural practices, such as targeted fertilization and soil amendments, are crucial for addressing the challenges posed by variable nutrient and moisture conditions. Understanding site-specific soil characteristics allows for the optimization of fertilization efficiency and water conservation strategies, ensuring sustainable forest management practices (Cook et al., 2024).

The PNW has a maritime climate, characterized by wet winters and dry summers, and its local site characteristics (e.g., latitude, elevation, slope, aspect) can be highly variable (Franklin & Dyrness, 1988). As a result of these climate and topographical trends and in concert with other soil formation factors (e.g., parent material, biota), there is significant regional variability in soil conditions. In the coastal PNW, which is the focus of this study, the soils developed from Eocene to Holocene geologic formations, reflecting a range of parent materials, weathering intensities, and organic matter accumulation processes (Kruckeberg, 1991). These differences in soil formation history have led to variations in soil structure, nutrient concentrations, and site productivity, as soils with higher weathering intensity and finer textures often retain more nutrients and moisture, supporting greater forest growth, while younger or coarser soils may be more prone to nutrient leaching and water limitations (Steinbrenner, 1979, Turner et al., 1979, Littke et al., 2011). These factors create distinct soil features which control everything from water movement to nutrient availability, significantly impacting plant growth and eventual harvest yields (Miller et al., 1989; Littke et al., 2014a; Littke et al., 2016; Littke et al., 2018).

In the PNW, N has been identified as the most limiting nutrient for productivity in conifer forests (Miller et al., 1989, Carter and Klinka, 1990). The predominant N fertilizer in the region is urea (46-0-0) (Harrison et al., 2016; Littke et al., 2014b), due to its high N content and the fact that it allows for efficient helicopter application (Peterson et al., 1984). Variables influencing N availability, such as the understory C:N ratio, are important predictors of Douglas-fir response to urea fertilization (Peterson et al., 1984). Specifically, in a soil with moderate pH like those in this study region, higher soil C content is often associated with an accumulation of soil organic matter (OM), particularly in forms with varying decomposition rates. The availability of OM to microbes and plants depends on its chemical composition and decomposition stage, rather than total soil C alone (Sollins et al., 2006). This accumulation of organic matter can contribute to soil structure improvement, increase water retention capacity, and enhance nutrient availability through mineralization processes (Six et al., 2004; Littke et al., 2024). Meanwhile, in soils with high C:N ratios, soil microbes tend to immobilize available N while decomposing excess carbon, a process known as microbial N immobilization (Littke et al., 2024). This reduces N availability for plant uptake, potentially leading to N deficiency for the trees (Kirkby et al., 2011). Fertilizer efficiency is, therefore, often related to the initial soil C:N ratio at the sites, though the potential for improved productivity or need for nutrient input is site-dependent and associated with geoclimatic variables such as temperature and precipitation (Littke et al., 2014c; Harrison et al., 2016), as will be discussed in the following sections of this paper.

Soils of the PNW are very diverse and contain all soil orders except gelisols and oxisols. Dominant orders include Inceptisols, Entisols, Ultisols, and Andisols (Hipple, 2011; NRCS, 2022). Andisols, particularly common in areas influenced by volcanic activity such as the Cascade Range, are notable for their characteristic physical properties including high porosity, good water retention, and fertility. These soils often contain elevated levels of phosphorus (P), potassium (K), and magnesium (Mg) due to volcanic ash deposition, which makes them suitable for forest productivity (Shoji et al., 1993; Brady and Weil, 2004). In contrast, soils derived from glacial deposits, which are common in regions shaped by Pleistocene glaciations, including the northern PNW, tend to show heterogeneity ranging from poorly drained, clay-rich valley bottom soils to well-drained sandy loams on terraces or ridges. Such variability in texture often leads to differences in water retention and fertility across the landscape (Brady and Weil, 2004; NRCS, 2022). For example, sandy loams may exhibit rapid drainage, but their nutrient leaching potential depends on initial nutrient content and biological demand. While nutrient-rich, fine-textured soils (e.g., high-N loamy to clayey soils) are more prone to N leaching due to excess nutrients not being immediately taken up, low-N, coarse-textured soils tend to have minimal leaching as available N is rapidly absorbed by microbes, understory vegetation, or trees (Flint et al., 2008; Devine et al., 2012). Thus, while sandy loams drain quickly, their leaching behavior varies based on site nutrient availability and microbial competition.

Besides texture, soil temperature and moisture regimes are also key regulators of both physical properties and biological processes in the soils. Soil temperature influences rates of microbial metabolism, thus affecting organic matter decomposition and nutrient cycling rates (Lloyd and Taylor, 1994). Cooler soil temperatures in higher-elevation or coastal regions could slow down these processes, leading to the accumulation of organic matter and the formation of rich, humus-based soil horizons, whereas warmer soils tend to exhibit faster organic matter decomposition, which may deplete soil carbon stocks more quickly (Gallo et al., 2023). Soil moisture, particularly in the summer, could be a critical constraint on tree growth in the PNW (Carter and Klinka, 1990; Hanson and Weltzin, 2004). While the coastal PNW benefits from maritime influences that moderate drought stress, inland regions may still experience comparable more pronounced water deficits during the summer months (Littke et al., 2018). This stress might be exacerbated in coarse-textured soils with low water-holding capacity where summer droughts could reduce nutrient uptake efficiency, limit microbial activity, and restrict tree root scavenging impacting forest productivity by impairing photosynthesis and carbon allocation (Hanson and Weltzin 2004; Waring and Running, 2007).

The biological characteristics of soils further influence stand productivity by mediating nutrient availability and cycling. Soil microbial communities play a central role in the mineralization of organic matter, releasing essential nutrients such as N, P, and sulfur (S) that are critical for plant growth (Brady and Weil, 2004; Paul, 2014). Symbiotic relationships with mycorrhizal fungi especially enhance tree nutrient acquisition by extending root surface area and accessing nutrients otherwise unavailable in mineral-bound or organic forms (Kranabetter et al., 2013; Paul, 2014). The abundance and activity of soil microorganisms are directly linked to soil moisture and temperature regimes, with microbial processes slowing considerably during dry summers or cold winters (Lloyd and Taylor, 1994; Gallo et al., 2023). Soil fauna, such as earthworms and arthropods, could also contribute to soil aeration, organic matter decomposition, and nutrient cycling through their physical activity (Brussaard, 1997). In well-structured soils, these biological processes promote soil aggregation and porosity, therefore enhancing root penetration and access to water and nutrients; conversely, in compacted or degraded soils, which may result from heavy machinery use or erosion, biological activity could be hindered, and root growth be limited, thus impairing the overall plant productivity (Amaranthus et al., 1996; Brady and Weil, 2004).

Overall, the combination of diverse soil-forming processes, temperature and moisture regimes, and biological activity creates a highly variable soil landscape in the PNW. Understanding these interactions is critical for managing soil health and ensuring sustainable forest productivity, particularly under the challenges of climate variability and increasing summer drought frequency.

1.2 Soil Chemical Properties, Nutrient Interactions, and Effects on Douglas-fir Growth

The cycling of elements in the soil are interconnected processes, with N serving as a central regulator of the cycles for other essential nutrients (Siah et al. 2023) . In coastal PNW soils with naturally high N levels, reductions in soil Ca and Mg availability have been observed, which may limit optimal Douglas-fir growth and nutrient uptake efficiency (Perakis et al., 2006). N enters the soil in highly soluble and readily available forms such as ammonium (NH_4) or nitrate (NO_3). However, NO_3 is prone to leaching, particularly in well-drained soils, which can result in both nutrient losses and disruptions to charge balance within the soil solution. This NO_3^- loss also results in the co-leaching of exchangeable cations such as Ca, Mg, and K, which are essential for tree growth and health (Otchere-Boateng, 1976; Fox, 2004; Sergent et al., 2014). When N is introduced into the system via fertilization, it typically enters in the form of urea or ammonium-based fertilizers, which release ammonium ions upon hydrolysis. In well-aerated soils, ammonium is converted to nitrate through microbial nitrification, a process that releases hydrogen ions into the soil and decreases soil pH, causing soil acidification. The extent of such pH decrease depends on the nitrification potential of the soil, which varies based on factors such as soil texture, organic matter content, microbial activity, and initial soil pH (Otchere-Boateng, 1976; Brady and Weil, 2004). And the acidification, in turn, decreases the availability of key nutrients like Ca, Mg, and phosphorous while increasing the solubility of toxic metals such as Al, which can inhibit root growth and nutrient uptake (Otchere-Boateng, 1976). For instance, Mainwaring et al. (2014) noted that sites with low exchangeable Ca exhibited reduced urea fertilization responses, underscoring the importance of maintaining balanced soil chemistry to avoid nutrient imbalances caused by acidification. Nitrogen availability also alters the uptake of other nutrients through both antagonistic and stimulatory interactions. Excess N can promote cation leaching, reducing Ca, Mg, and P availability; conversely, higher N supply can stimulate plant physiological demand for P, thereby increasing

P uptake efficiency (Siah et al., 2023). These complex interactions can be partially visualized in a Mulder's Chart (Figure 2) below, which illustrates key nutrient relationships, although it does not capture all potential interactions in forest soils.

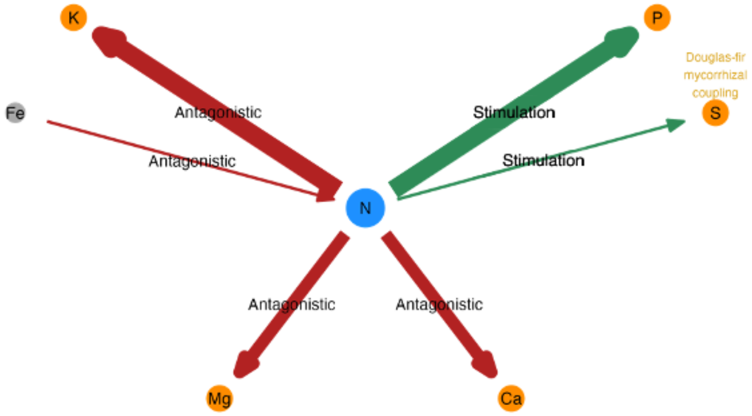

Figure 2. Antagonistic and Stimulation relationships between some soil nutrients

Soil Ca availability might be co-limiting the response of Douglas-fir to N fertilization, especially in the areas with high N availability. Studies have shown that, over time, soils with N enrichment are often associated with low exchangeable Ca levels, likely due to low soil pH and increased leaching and nutrient competition (Perakis et al., 2006 and 2013). For example, coastal PNW soils typically have high N availability but are often low in Ca; in contrast, Cascade soils are generally more Ca-rich but may lack sufficient N (Perakis et al., 2006 and 2013; Mainwaring, et al., 2014). Glacial soils, due to their limited weathering and young development stage, may be deficient in both nutrients. These regional contrasts underscore the need to consider specific soil nutrient profiles when evaluating fertilization strategies. Mainwaring et al. (2014) found that Douglas-fir stands with low soil Ca levels exhibited minimal growth response to N fertilization, highlighting the importance of Ca in supporting tree growth. In soils with low pH, Ca availability is decreased, and Al toxicity is increased (Littke et al., 2024 and 2025).

Soil chemical properties, such as cation exchange capacity (CEC) and pH, play pivotal roles in determining nutrient availability. Exchangeable cations, including Ca, Mg, and K require charge balance in soil solution. The presence of anions such as NO_3 enhances nutrient mobility but can also lead to cation leaching, particularly in acidic soils where CEC is reduced (Cole et al., 1975; Johnson and Cole, 1980; James et al., 2016; Littke et al., 2025). For example, soils in coastal plantations often show Ca deficiencies due to excessive leaching, especially in areas subjected to frequent fertilization (Perakis et al., 2013). The effect of nutrient availability on Douglas-fir growth is therefore a combination of macronutrients rather than being solely dependent on one of them, e.g. N.

A summary of Ca and P roles, deficiencies, and soil availability factors is provided in Table 1. Phosphorus availability is another key factor influencing Douglas-fir responses to N fertilization. Phosphorus plays a critical role in energy transfer, root development, and overall tree metabolism, yet its availability in soils is highly dependent on soil pH, parent material, and the weathering processes that release P into plant-available forms (Brady and Weil, 2004). Sites with low foliar P or limited extractable soil P may show limited responses to N fertilization, as increased tree growth can outpace the P supply; in contrast, high extractable P contents may mitigate these limitations, allowing for improved synergy between N and P uptake (Radwan et al., 1991; Littke et al., 2024). Nitrogen fertilization not only directly enhances N availability for photosynthesis and metabolic functions, but also promotes synergistic interactions with P in plant metabolism (Güsewell, 2004; Smith and Smith, 2011). Increased N availability could stimulate biomass production and accelerate root growth, enhancing plant access to P reserves in the soil (Siah et al., 2023). However, urea fertilization was associated with lower Douglas-fir foliar P in a recent study (Littke et al., 2025).

Table 1. Some effects of nutrient availability on Douglas-fir growth and how they may be affected by soil characteristics

Nutrient	Function in Douglas-fir	Deficiency Effects	Availability Factors
Nitrogen	Photosynthesis and protein synthesis	Reduced growth and chlorosis	Organic matter content, microbial activity
	Biomass accumulation	Poor foliage development	Soil temperature, moisture, leaching
Calcium	Cell wall integrity	Stem deformities	Soil pH & CEC
	Lignin biosynthesis	Reduced wood quality	Base cation leaching
Phosphorus	Energy transfer	Limited root growth	Soil parent material
	Root development	Reduced tree metabolism	Weathering & pH control

Collectively, these interactions highlight the need for a holistic approach to nutrient management in Douglas-fir plantations. The interplay of N, P, Ca, and other essential elements within the soil chemical framework determines the long-term sustainability of forest productivity, and fertilization management must therefore account for these interactions, ensuring that N inputs are balanced with other nutrients, to support optimal tree growth and soil health.

1.3 Soil Nitrogen Fertilization in the PNW

In the coastal PNW, N fertilization has been a critical component of Douglas-fir plantation management for decades. Currently, approximately 1.5% of Douglas-fir plantations are fertilized each year, and estimates indicate that approximately 250,000 acres of Douglas-fir plantations have been fertilized since 1990 (Briggs, 2007; Littke et al., 2014b). This widespread practice emerged as a response to nutrient limitations in intensively managed forest systems, where N is often the primary factor limiting productivity (Chappell et al., 1991).

Over the past decades, N fertilization has been part of common Douglas-fir plantation management practices across the region to help reduce the rotation time between harvests (Chappell et al., 1991). Studies have shown that N-fertilized plantations typically exhibit faster growth rates, larger area growth as well as increased tree heights compared with the unfertilized stands; this accelerated growth has therefore contributed to shorter rotation periods, which improved the economic returns of forestry management (Peterson & Hazard, 1990; Mainwaring et al., 2014).

While N fertilization initially increases soil N availability, its long-term retention is influenced by multiple factors, including initial soil N levels, vegetation uptake, and microbial activity, rather than soil drainage alone. As discussed above, studies including Devine et al. (2012) and Flint et al. (2008) highlighted the importance of site-specific N dynamics in assessing fertilization strategies. Future studies should account for the interactions between initial soil N status, vegetation composition, and hydrological conditions to optimize fertilization efficiency and minimize environmental impacts.

1.4 Soil Carbon Impact on Fertilization Success

Soil C:N ratios are widely recognized as an indicator of N availability and play critical roles in determining the success of fertilization strategies in forest ecosystems. These ratios reflect the balance between organic carbon inputs, such as litter and soil organic matter, and N cycling processes, including decomposition, mineralization, and immobilization (Brady and Weil, 2004). While a low C:N ratio usually reflects higher N availability for plant uptake, a high C:N ratio could indicate slower decomposition and nutrient release due to the presence of recalcitrant organic materials, or potential N immobilization due to poor litter quality or slow decomposition and mineralization.

The volume growth response of Douglas-fir to N fertilization has been found to be positively correlated with the C:N ratios of both the forest floor and the surface soil horizons (Peterson et al. 1984, Edmonds and Hsiang 1987; Miller et al. 1989; Littke et al., 2024). Several studies have demonstrated that positive volume growth responses are more commonly observed when the forest floor C:N ratio exceeds approximately 40:1, and when the mineral soil C:N ratio (particularly in the surface A horizon) exceeds 25:1 (Littke et al., 2014c). These thresholds suggest that sites with higher C:N ratios are more likely to benefit from fertilization, presumably due to greater N limitation and microbial competition for N. Nevertheless, soils with very high C:N ratios may initially exhibit limited availability of nitrate (NO_3) following fertilization. Littke et al. (2024) found that sites with high forest floor and surface soil C:N ratios showed little NO_3 accumulation immediately after N application, indicating strong microbial immobilization or low nitrification potential. However, delayed growth responses have been observed in high C:N sites, with significant increases in ring width not appearing until the second year after fertilization (White et al., 1988; Otchere-Boateng, 1976; Littke, unpublished data). This delayed response is hypothesized to result from the time required to build up an active nitrifying microbial community capable of processing the added N into nitrate. Therefore, identifying the forest floor and A horizon C:N ratios are important in N fertilization as these ratios could be major predictors for assessing the responses in the PNW (Peterson et al. 1984; Littke et al. 2014c, 2017, 2024). Deeper soil horizons (B and C horizons) also have shown predictive values, though relatively limited effects due to their lower organic matter content and reduced biological activity (Edmonds and Hsiang, 1987; Miller et al., 1989). This vertical stratification emphasizes the need for targeted sampling of not only the surface organic layers, but various soil horizons when developing site-specific fertilization prescriptions. While this research emphasizes surface horizons, further research may be warranted to evaluate whether deeper soil horizons also play a role in regulating N dynamics and tree growth response following fertilization.

1.5 Project Objectives and Hypotheses

Despite decades of research on the fertilization of coastal PNW Douglas-fir, there remains a need for further exploration of long-term growth responses and site-specific factors. However, earlier studies focused on plot-based fertilization installations (Peterson et al., 1984; Miller et al., 1989), which typically have little replication and thus are difficult to expand beyond single locations as plot variability could overshadow the effect of the fertilization itself (Littke et al., 2014b). An alternative method is single-tree fertilization. In this method, individual trees at a single site are selected to be fertilized while the others remain untreated. However, it is difficult to scale the results of the single-tree studies to per acre estimates, and whether the pre-treatment characteristics of the treated vs control trees are similar may be unsure (Mainwaring et al., 2014). Paired-tree studies, the approach employed in this study, aim to mitigate some of these challenges. This method selects pairs of trees with similar pre-treatment characteristics, such as DBH, live crown height, and site conditions, to reduce variability caused by natural site heterogeneity. By minimizing pre-existing differences, paired-tree studies allow for more accurate comparisons between fertilized and control trees, improving statistical confidence (Littke et al., 2014b; Zhu et al., 2021). Despite these advantages, it is important to note that paired-tree studies, like single-tree studies, cannot be directly scaled to stand-level estimates. However, they remain a cost-effective alternative to large-scale plot-based installations and can provide insights that may inform broader forest management strategies.

The carbon sequestration function of forest plantations has garnered increasing global attention (Ishii et al., 2017). In addition to providing economic timber, Douglas-fir plantations may also offer future revenue opportunities through carbon trading mechanisms (Isaac-Renton et al., 2025). A key contributor to this potential is the aboveground biomass of Douglas-fir, which constitutes a major component of its carbon sink capacity. However, due to limited understanding of the long-term impacts of fertilization and other management practices on Douglas-fir growth, current models estimating aboveground biomass remain subject to considerable uncertainty. As discussed above, long-term responses to fertilization are influenced by a variety of factors, including soil nutrient levels, physico-chemical properties, and geoclimatic conditions. Therefore, identifying the key factors that govern the long-term growth response of Douglas-fir to nitrogen fertilization is crucial for both optimizing fertilization strategies and accurately assessing carbon sequestration potential.

To better understand Douglas-fir N fertilization responses, a series of paired-tree installations were established between 2008 and 2011 by the University of Washington Stand Management Cooperative (SMC), a coalition of 12 forest landowners comprising 200,000 ha across the coastal PNW. Built on previous findings from these installations (described in Section 2.1 below) (Littke et al. 2014b), the objective of this study is to predict the Douglas-fir growth responses to N fertilization in the Pacific Northwest, as well as the influence of fertilization on the site soils. Specifically, this study aims to:

1. Examine the relationships between baseline soil and stand conditions as well as post-treatment Douglas-fir growth responses.
2. Investigate the effect of baseline edaphic properties on PRS nutrient supply rates.
3. Determine if PRS-measured nutrient supply rates in control and fertilized plots are associated with observed Douglas-fir growth response .

Null hypotheses pertaining to the objectives considered in this study are:

1. Baseline soil and stand conditions do not affect the post-treatment Douglas-fir growth responses in the study region.
2. Baseline soil nutrient properties have no relation with the PRS nutrient supply rates.
3. Growth response categories do not correspond to significant differences in PRS nutrient supply rates across control and fertilized plots.

2. Materials and Methods

2.1 Study Site and Study Design

Between 2008 and 2011, the SMC established paired-tree fertilization plots in 71 Douglas-fir installations (Figure 3) across the Pacific Northwest (Littke et al. 2014b). Each installation contained 48 tree plots of 5 m diameter circles established on 15 m grids, from which 12-20 tree-pairs were selected to ensure similar DBH and live crown lengths within each pair (Figure 4). A one-time urea fertilization was applied to one tree from each pair at 224 kg N ha^{-1}. A subset of 15 of the paired-tree fertilization installations were selected for soil nutrient level measurement with *in situ* cation and anion exchange membranes (Plant Root Simulator™ probes (PRS), Western Ag, Saskatoon, Canada). The installations were located along a range of latitudes and longitudes on the west side of the Cascades in the PNW, covering various elevations and mean annual precipitations, though mean annual temperature differs little among the installations. King's site index, a measurement of potential site productivity expressed as the height of dominant or co-dominant trees at age 50, calculated following the method described in Littke et al. (2014c), also differ among the selected installations, as well as soil N and Ca contents (Table 2). Table 2.1 lists the main site characteristics of the 15 installations. The selection was made based on coverage of different growth response groups. The 15 installations cover five each from the non-responding, temporarily responding (0-2-year response), and 4-year responding installations based on previous work (Littke et al., 2014b). The non-response group exhibited no significant Douglas-fir basal area growth response to the N addition. The temporary-response group exhibited 0-2 years of basal area growth response with no cumulative response from 0-4 years. In the long-term response group, tree basal area growth was boosted by the fertilization event for at least four years. In addition to these installation-level attributes, all subsequent analyses employed a standardized set of 18 stand and environmental variables encompassing climate (MAP, MAT), geography (LAT, LONG, ELEV), site quality (SI), soil physical status (AWS) and chemical properties of the forest floor and mineral soil (FFCN, SOILN, SOILCN) as well as nutrient-supply rates measured with PRS™ probes for the macro- and micronutrients N, P, K, Ca, S, Zn and Al. Full names, abbreviations, measurement units, and descriptive statistics (mean, minimum and maximum across the 15 installations) for each variable are provided in Table 3. This stand-alone table is intended to give readers a quick reference for interpreting abbreviated labels in subsequent figures, most notably the PCA biplot (Figure 5), and to document the underlying data range used in the GLM modelling.

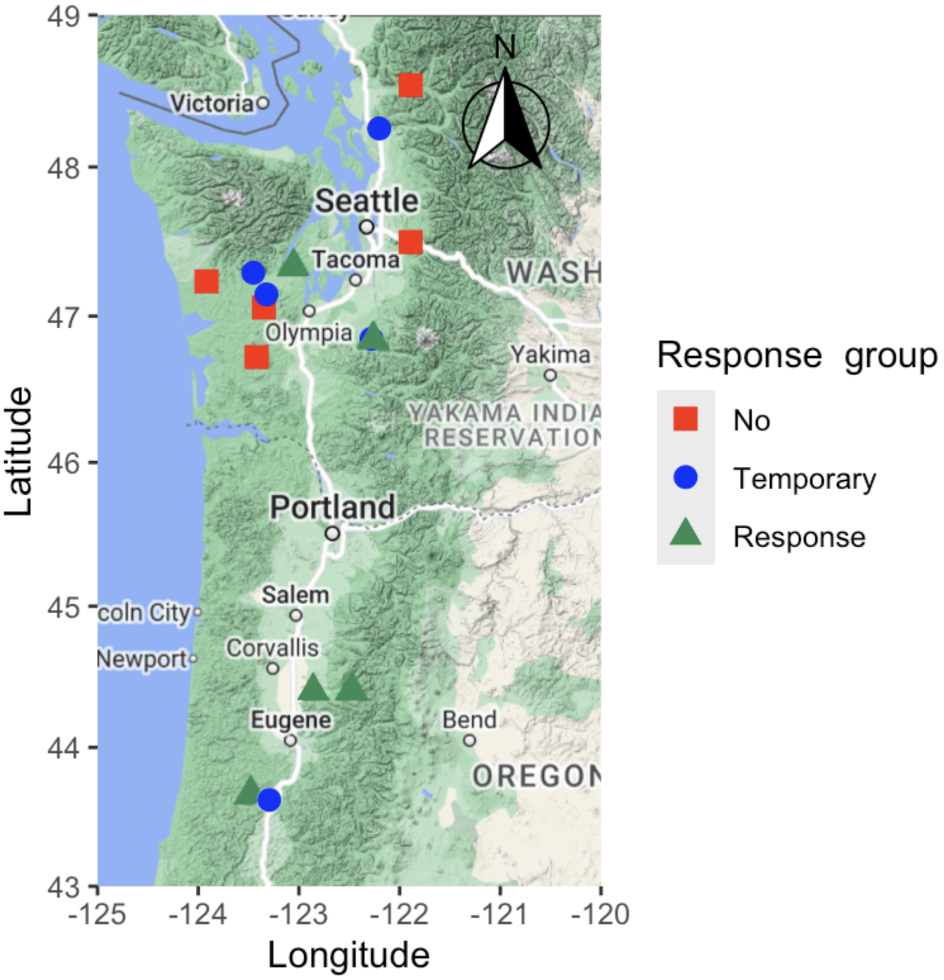

Figure 3. Map of candidate installations, from SMC paired-tree fertilization study (Littke et al., 2014c)

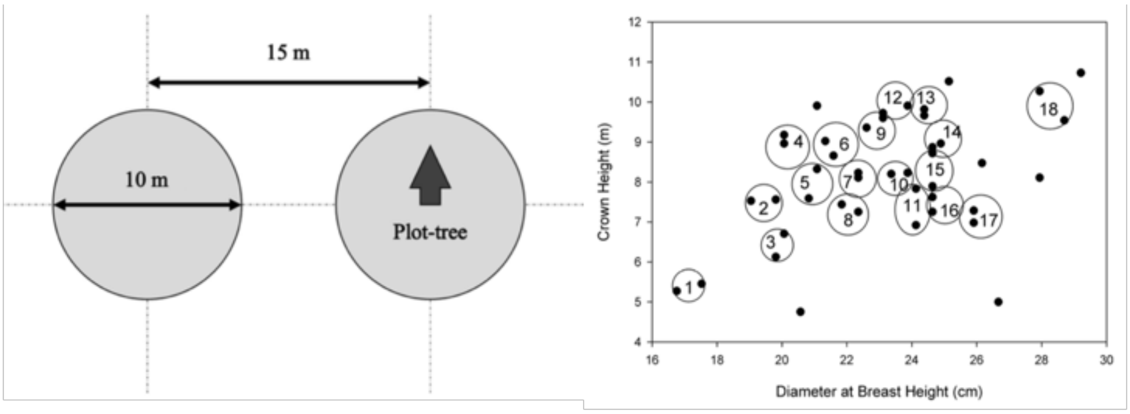

Figure 4. 15 m grid plot setup (left) and example of pair selection by most similar DBH and crown height (right, circles indicate selected pairs) (Littke et al., 2014b)

Table 2. Study site location and selected installation features

INST	Name	Response	Latitude	Longitude	Elev (m)	MAT (ºC)	MAP (mm)	King's SI (m 50 yr)	Soil N (kg ha^{-1})	Forest Floor C:N	Soil Ca (kg ha^{-1})
824	Oppelt Rd	No	47.058	-123.349	91	10.5	2,225	45	10796	20	745
836	Rabbit Creek	Temporary	47.293	-123.452	213	10.0	3,448	49	16534	40	1164
838	Star Lake	Temporary	47.147	-123.323	110	10.4	2,506	40	3660	32	207
839	Russell Ranch	No	48.541	-121.889	137	10.3	1,760	45	3701	35	1341
841	Cascadia	Response	44.405	-122.475	427	11.1	1,789	43	15842	42	3849
842	Scott Mt	Response	44.402	-122.859	549	11.2	1,538	43	15443	33	2470
843	Devore Mt	Temporary	43.611	-123.304	282	11.8	1,178	40	23462	45	1469
844	Brush Cr	Response	43.663	-123.479	183	12.0	1,243	44	15613	34	22568
848	McKinley	Temporary	48.255	-122.202	91	10.5	1,423	45	9235	29	22120
855	Bucklake	Temporary	46.846	-122.280	356	10.3	1,196	45	6710	31	3769
856	Murphy	Response	46.843	-122.263	455	10.0	1,398	40	9283	33	31191
871	Echo Glen	No	47.499	-121.891	262	10.0	2,026	47	17894	21	158
881	Humptulips	No	47.235	-123.918	61	9.9	2,961	46	9113	27	392
883	Alderbrook	Response	47.334	-123.056	159	10.6	2,076	34	1337	38	680
888	Fall River	No	46.722	-123.420	317	9.6	2,426	47	12870	51	230

Notes:
INST = installation ID; Response = plot response type (No, Temporary, or long-term Response, based on tree growth performance after fertilization);
Elev = elevation (m); MAT = mean annual temperature (°C); MAP = mean annual precipitation (mm);
King’s SI = site index, defined as the height of dominant or co-dominant trees at age 50 (King, 1966);
Soil N = total N (kg ha^{-1}, 0–1 m); Soil Ca = exchangeable calcium (kg ha^{-1}, 0–1 m).
Climate data (2008–2020) were estimated using the ClimateNA program (Wang et al., 2016).

Table 3. Variable definitions and descriptive statistics

Variable	Abbreviation	Unit	Mean	Min	Max
Latitude	LAT	° N	46.5	43.6	48.5
Longitude	LONG	° W	-122.9	-123.9	-121.9
Elevation	ELEV	m	246.3	61.0	549.0
Mean Annual Temperature (2008–2020)	MAT	°C	10.5	10.0	12.0
Mean Annual Precipitation (2008–2020)	MAP	mm yr^{-1}	2004.5	1212.0	3507.0
Site Index (King's)	SI	m @ age 50	43.5	34.0	49.0
Forest floor C:N ratio	FFCN	–	34.1	20.0	51.0
Surface Soil C:N ratio	SOILCN	–	17.3	9.0	41.0
Total Soil N (0–100 cm)	SOILN	kg ha^{-1}	11432.9	1337.0	23462.0
Available Water Supply (0-100 cm)	AWS	mm	151.5	64.3	280.0
PRS Nitrate Supply Rate	NO3_Con	µg N 10 cm^{-2} 12 wk^{-1}	44.6	1.1	158.2
PRS Ammonium Supply Rate	NH4_Con	µg N 10 cm^{-2} 12 wk^{-1}	5.5	1.5	10.0
PRS Calcium Supply Rate	PRS_Ca	µg Ca 10 cm^{-2} 12 wk^{-1}	893.3	211.0	1964.0
PRS Potassium Supply Rate	PRS_K	µg K 10 cm^{-2} 12 wk^{-1}	196.8	64.0	347.0
PRS Phosphorus Supply Rate	PRS_P	µg P 10 cm^{-2} 12 wk^{-1}	2.7	0.9	6.7
PRS Zinc Supply Rate	PRS_Zn	µg Zn 10 cm^{-2} 12 wk^{-1}	1.2	0.4	2.4
PRS Sulfur Supply Rate	PRS_S	µg S 10 cm^{-2} 12 wk^{-1}	11.9	5.2	18.5
PRS Aluminum Supply Rate	PRS_Al	µg Al 10 cm^{-2} 12 wk^{-1}	29.3	6.4	87.1

Climate data (2008–2020) were estimated using the ClimateNA program (Wang et al., 2016);
King's SI = site index, defined as the height of dominant or co-dominant trees at age 50 (King, 1966);
Available water supply from 0-100 cm (Soil Survey Staff, 2025).

2.2 Field Methods

Within each installation, each tree was measured for pretreatment diameter at breast height (DBH), height (HT), and height to live crown (HLC), with additional observations on environmental factors such as the presence of alder and canopy openings, in order to pair the study trees. The study focused on dominant or co-dominant trees to ensure consistent growth comparisons across treatments. (Littke et al., 2014b).

Before the fertilization, forest floor and soils were sampled for physical and nutrient level analysis at the center of the installation (Littke et al. 2014c). All samples were air-dried for at least 48 hours and weighed for bulk density calculations. A subsample from each soil depth was dried at 105°C for two days to measure moisture content. Soil total C and N contents were determined using a CHN analyzer (CHN Analyzer 2400; PerkinElmer, Inc). The exchangeable cations (Ca, Mg, K) were extracted from soil samples using 1.0 M NH4Cl and analyzed with an inductively coupled plasma mass spectrometer (ICP-MS) following the procedure described in Littke et al. (2024), which in turn follows the method of Skinner et al. (2001). All extractions and analyses were conducted as part of the original study and data were used without modification. In fall 2020, 11-12 years after the fertilization, four randomly selected paired-tree plots (four control and four fertilized trees) were instrumented with one set of anion and cation Plant Root Simulator^{TM} (PRS) probes (Western Ag, Saskatoon, Saskatchewan, Canada) at 5 cm depth in the spring and removed after 12 weeks. Probes were installed by making horizontal slots in the mineral soil surface 5 cm below the forest floor using a garden knife. Each probe was inserted horizontally into the slot, with its broad surface oriented vertically (i.e., the long dimension lying perpendicular to the soil surface) to prevent water-pooling. Probes were within a 1 m radius of fertilized trees and locations selected to avoid compacted soils on tracks and major roots/debris from trees. The probes were installed facing the upper slope, so that water flows naturally along them, and spaced 1-inch apart. When collected, PRS probes were rinsed with DI water, composited by plot, and analyzed by Western Ag. General methodology includes membrane elution using 0.5 mol/L HCl with subsequent analyses for ammonium and nitrate (colorimetrically determined using automated flow injection analysis with a FIAlyzer (FIAlab Inc, USA) as well as Ca, K, Mg, P, S, Al, Fe, Mn, Cu, Zn, B, Al, Pb, and Cd (inductively coupled plasma optical emission spectrometry (ICP-OES) with an Optima ICP-OES 8300 analyzer (PerkinElmer Inc., USA)) (Western Ag Innovations; Hangs et al., 2002). As stated, soil characteristics such as pH, C:N ratios, N and base cations were measured using samples collected prior to fertilization, while nutrient availability (e.g., PRS_K, PRS_Zn) was assessed using the PRS probes 11-12 years after.

2.3 Analysis and Statistical Methods

All analyses were performed in R version 4.3.1 (R Core Team, 2023). Throughout the analysis, the studied installations were classified into three categories - responding, temporarily responding, and non-responding - calculated as the percent difference in average basal area growth between fertilized and control trees at each installation according to 0-2, 2-4, and 0-4 year response (Littke et al. 2014b). To address the first objective of this study (whether pre-treatment soil and stand conditions affect the post-treatment Douglas-fir growth responses), fertilization basal area responses were analyzed using principal component analysis (PCA), generalized linear models (GLM), and random forest in relation to pre-treatment stand and soil variables. PCA was conducted using the stats package (R Core Team, 2023); GLMs were fitted using the MASS package (Venables and Ripley, 2002); and random forest analysis was performed with the randomForest package (Liaw and Wiener, 2002). Partial dependence plots were generated via the pdp package (Greenwell, 2017) to visualize marginal effects of predictor variables in random forest models. The caret package (Kuhn, 2023) was used to conduct model tuning and cross-validation. To reduce the influence of multicollinearity and identify the most predictive variables, we used a two-step feature selection approach: a preliminary correlation matrix screening to remove highly collinear predictors, followed by random forest analysis to rank variable importance in predicting 4-year basal area response. Two importance metrics were used: the percent increase in mean squared error (%IncMSE) and the increase in node purity (IncNodePurity).Variable collinearity was examined using correlation matrices visualized via corrplot (Wei and Simko, 2021). The parametric models were chosen for easier incorporation into other common growth and yield models, and the random forest model was meant to detect hidden relationships in the data.

For the second objective of this study (examining whether post-fertilization PRS nutrient supply rates have any relation with the pre-fertilization baseline edaphic properties), post-treatment PRS supply rates were compared with the pre-treatment soil variables using PCA (as described above) and linear regression, grouped by the control and fertilized plots and by the different fertilization response groups. This study also explored correlations between PRS nutrient supply rates and the different growth response groups.

To assess the suitability of parametric tests, we conducted Shapiro-Wilk tests for normality on all available combinations of nutrient type, treatment (Control or Fertilized), and response group (No, Temporary, Response). Among the 66 tested groups, the vast majority showed no significant deviation from normality ($p > 0.05$), suggesting that the rate data are approximately normally distributed. Only a few groups, such as NO_3 under control treatment, exhibited strong deviations ($p < 0.01$), and several others showed marginal non-normality ($0.01 < p < 0.05$).

To evaluate whether PRS nutrient supply rates varied systematically among response types (non-responding, temporarily responding, and responding), we applied linear mixed effects models to each nutrient. These models tested the fixed effects of Response Type, Treatment (Control vs. Fertilized), and their interaction, while accounting for variability among installations as a random effect. For each of the 11 nutrients measured via Plant Root Simulator (PRS) probes—nitrate (NO_3), ammonium (NH_4), calcium (Ca), magnesium (Mg), potassium (K), P, iron (Fe), manganese (Mn), zinc (Zn), sulfur (S), and aluminum (Al). We used the following model:

$$Nutrient_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + u_k + \epsilon_{ijk}$$

where α_i is the fixed effect of Response Type (i = No, Temporary, Response), β_j is the fixed effect of Treatment ($_j$ = Control, Fertilized), $(\alpha\beta)_{ij}$ is the fixed interaction term between response type and treatment, u_k is the random intercept for Installation (k=1,...,15), and ϵ_{ijk} is the residual error. These models were implemented using the nlme::lme() function in R, with nutrient supply rates as the response variable, and installation treated as a random effect (Pinheiro et al. 2023). All nutrients were analyzed individually. Fixed effects significance was evaluated using Type III ANOVA via the anova() function, followed by post-hoc comparisons using emmeans (Lenth, 2023) and multcomp (Hothorn et al., 2008). Compact letter displays (CLDs) for post-hoc groupings were generated using packages multcompView (Graves et al., 2024) and agricolae (de Mendiburu, 2023). For ordination and clustering of soil nutrient profiles, we used non-metric multidimensional scaling (NMDS) and hierarchical clustering with the vegan (Oksanen et al., 2025), labdsv (Roberts, 2023), and dendextend (Galili, 2015) packages. Decision trees via package rpart (Therneau & Atkinson, 2025) were explored to identify key thresholds for response classification.

For general data visualization, the ggplot2 (Wickham, 2016) and ggbiplot (Vu and Friendly, 2024) packages were used to create statistical analysis result plots, while ggmap (Kahle and Wickham, 2013) and ggspatial (Dunnington, 2023) were used for spatial data mapping. Data cleaning, transformation, and modeling preparation steps were performed using packages dplyr (Wickham et al., 2015), tidyr (Wickham et al., 2024), purrr (Henry & Wickham, 2020), and broom.mixed (Bolker & Robinson, 2024) for tidy model outputs, enabling seamless integration with reporting workflows.

3. Results

3.1 Modelling Growth Responses

Principal component analysis (PCA) results comparing pre-fertilization site and soil conditions to Douglas-fir growth response to N fertilization showed that the first two principal components (PC1 and PC2) together explained approximately 45.2% of the total variance (24.9% and 20.3%, respectively, Figure 5). PC1 was largely associated with climatic and spatial gradients, including mean annual precipitation (MAP), latitude, and elevation (ELEV), while PC2 was more strongly influenced by soil nutrient and organic matter variables, such as forest floor C:N ratio (FFCN), available water storage (AWS), and nutrient supply rates (e.g., PRS_K, PRS_Zn). Several variables identified as significant predictors in the GLM (e.g., PRS_Al, PRS_K, PRS_Zn, AWS, FFCN, ELEV) also contributed strongly to separation in PCA space, reinforcing their role in determining fertilization response potential. Although the response groups (No, Temporary, Response) show partial overlap in the PCA biplot, there is a visual tendency for responding installations to be more associated with nutrient availability indicators, such as higher C:N ratios (FFCN), higher K and Zn supply rates (PRS_K, PRS_Zn), and greater AWS, while non-responding installations appear closer to higher aluminum availability (PRS_Al). These trends, while suggestive, are exploratory and not statistically confirmed by the PCA alone. Temperature (MAT) and site index (SI) loadings point along upper right - bottom left quadrants of the biplot, suggesting they may contribute to variation along PC1 or PC2. However, their influence on response classification is less distinct visually and may require further targeted analysis to confirm their role. Temporary responding installations occupy an intermediate space in the PCA biplot, suggesting that they share some traits with both the non-responding and the responding installations.

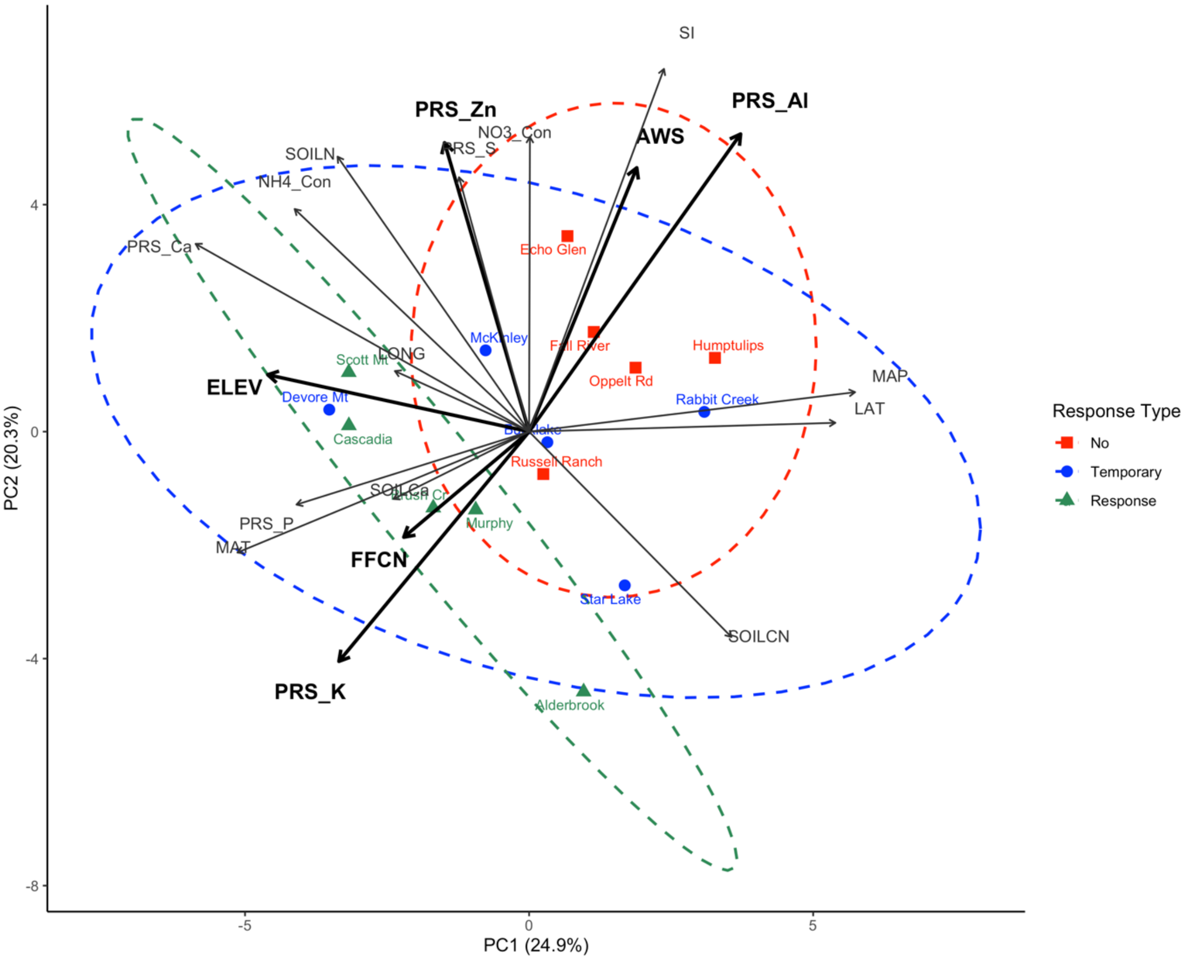

Figure 5. PCA biplot for the tree growth response versus stand characteristics. Points represent individual installations grouped by fertilization response type: non-responding (red squares), temporarily responding (blue circles), and consistently responding (green triangles). Ellipses indicate 95% confidence regions for each group. Arrows represent the loadings of environmental variables on the first two principal components. Bold arrows highlight variables identified as significant predictors in the GLM ($p \leq 0.05$). Nutrient levels are the PRS probe supply rates from the control trees.

The random forest model identified a consistent set of variables associated with the four-year basal area response (FBAR4) to fertilization. Across both importance metrics, percent increase in mean squared error (%IncMSE) and increase in node purity (IncNodePurity), the top-ranked predictors included site index (SI), PRS aluminum supply (PRS_Al), forest floor C:N ratio (FFCN), and PRS potassium supply (PRS_K), along with available water storage (AWS), elevation (ELEV), and PRS zinc supply (PRS_Zn) (Figure 6).

These variables were repeatedly associated with higher model sensitivity and improved node splitting performance, suggesting that both site productivity indicators (e.g., SI, ELEV) and nutrient-related metrics (e.g., PRS_K, PRS_Al, PRS_Zn, FFCN) play a central role in modulating fertilization outcomes. Notably, SI ranked highest under both importance metrics, reinforcing its strong association with fertilization response across diverse sites.

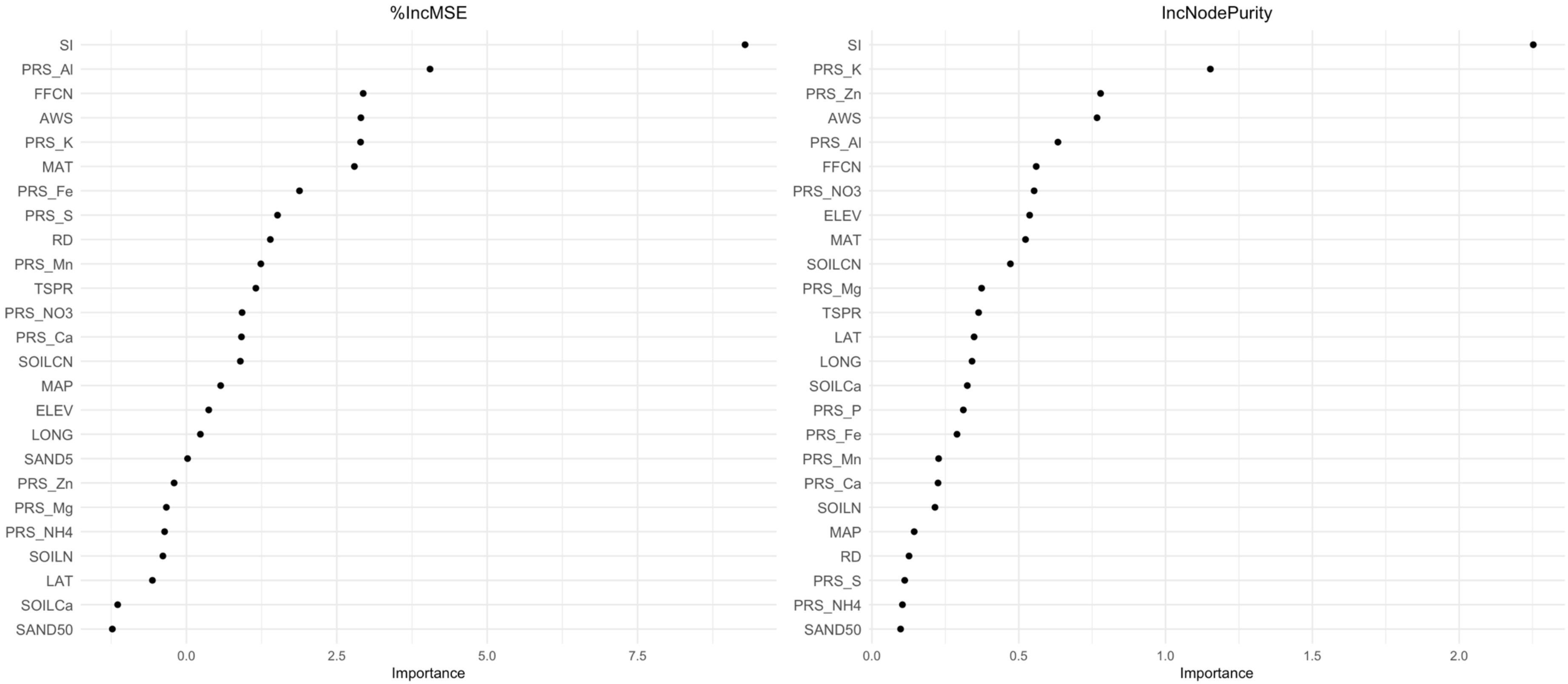

Figure 6. Variable importance rankings from random forest regression predicting 4-year basal area response (FBAR4)

Left: Importance measured by percent increase in mean squared error (%IncMSE); Right: Importance measured by increase in node purity (IncNodePurity). Higher values indicate greater predictive contribution. Variables consistently ranked among the top predictors across both metrics include site index (SI), PRS aluminum supply (PRS_Al), forest floor carbon-to-nitrogen ratio (FFCN), and PRS potassium supply (PRS_K).

The final GLM retained four variables: PRS Al supply rates, forest floor C:N ratio, PRS K supply rates, AWS, elevation, and PRS Zn supply rates (Table 4, $p < 0.05$). All PRS supply rates were from control plots. The model achieved a residual deviance of 0.766 (7 degrees of freedom) and an AIC of 15.95. Specifically, forest floor C:N ratios, PRS K supply rates, and elevation were positively associated with growth response, while PRS Al, PRS Zn, and AWS were negatively related to growth response. These relationships are illustrated in Figure 7, which shows linear trends between individual predictors and FBAR4 across sites. For example, installations with higher PRS K supply tended to exhibit stronger positive basal area responses (Figure 7b), whereas higher PRS Al or PRS Zn supply rates were associated with reduced or even negative responses (Figure 7c, 7d). These contrasting patterns underscore the dual role of nutrients as both facilitators and potential inhibitors of treatment effectiveness, depending on their chemical form and site context.

Table 4. Generalized Linear Regression model results for the unfertilized plots

Variable	**Estimate**	**Std. Error**	**t value**	**Pr(>|t|)**	**Significance**
PRS_Al	0.67	0.17	3.90	0.0059	**
FFCN	0.59	0.11	5.20	0.0013	**
PRS_K	0.66	0.14	4.83	0.0019	**
AWS	-0.30	0.12	-2.48	0.042	*
ELEV	0.33	0.096	3.43	0.011	*
PRS_Zn	-0.53	0.10	-5.24	0.0012	**

Site characteristics against the 4-year basal area growth response. "**" indicates p-values ≤ 0.01, "*" indicates p-values between 0.01 and 0.05, "." indicates p-values between 0.05 and 0.1. Abbreviations: PRS aluminum supply rates (PRS_Al), forest floor C:N ratio (FFCN), PRS potassium supply rates (PRS_K), available water storage (AWS), elevation (ELEV), and PRS zinc supply rates (PRS_Zn).

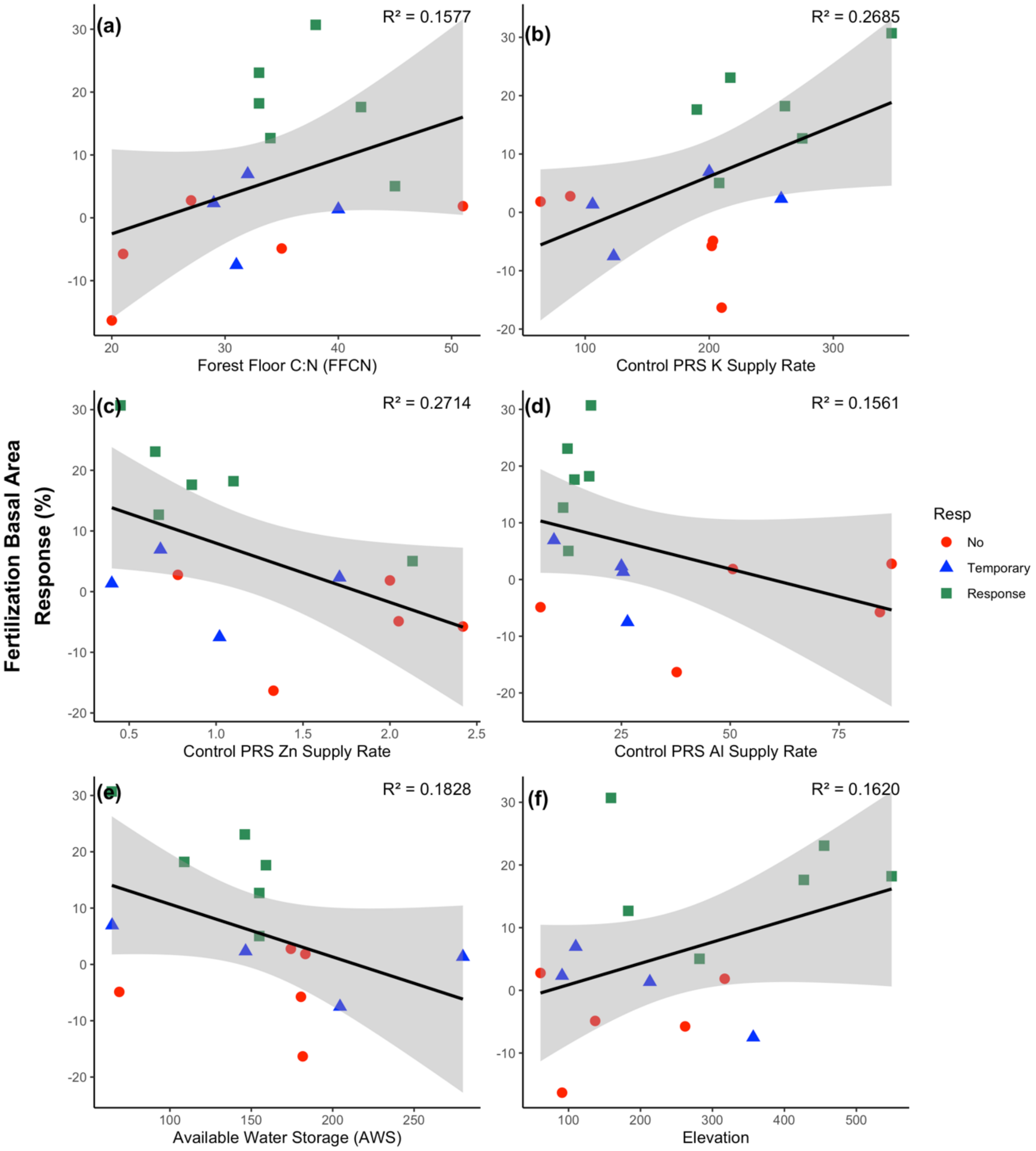

Figure 7. Relationships between pre-fertilization forest floor C:N (a), PRS K supply rate (b), PRS Zn supply rate (c), PRS Al supply rate (d), available water storage (e), elevation (f), and the four-year basal area response to fertilization (%). Red, blue, and green lines indicate the distribution of non-responding, temporarily responding, and responding installations, respectively. Gray shades by the regression lines indicate the 95% confidence intervals. The y-axis refers to fertilization basal area response four years after treatment.

Potential interactions between fertilization response type and the top predictors were evaluated to test whether site-specific factors influenced treatment outcomes differently across response groups. Interaction terms for forest floor C:N ratios and PRS K supply rates were added to the GLM but showed no statistically significant effects. In both cases, the main effects remained relatively stable, and no evidence emerged for differential slopes among response categories. Given the lack of evidence for differential effects and the limited sample size (n = 15), further tests on interactions for PRS Zn and Al supply rates were not tested. Including additional interaction terms would substantially reduce degrees of freedom and increase the risk of overfitting, without prior indication of group-specific trends. Including further interaction terms would reduce degrees of freedom and increase the risk of overfitting without a priori evidence of group-specific trends. Therefore, the simpler additive model without interactions was retained for interpretation. Despite the small sample and associated limitations in statistical power, the results support a consistent effect of several site and soil factors across all response types. Specifically, forest floor C:N ratio, base cation availability, and PRS Al supply appear to influence fertilization outcomes in a broadly similar way across installations, regardless of their categorical response classification.

3.2 PRS Nutrient Supply Rate Patterns

Across all nutrients measured on control and fertilized plots, few showed significant variation by response group or treatment. PRS Al supply rate was the only nutrient to differ significantly among response categories ($p = 0.018$), with lower values generally associated with consistently responding sites, regardless of fertilization status. Several other elements, including Mn, Ca, and Zn, showed weak trends toward response-based differences ($p < 0.2$), though these did not reach statistical significance. Neither fertilization treatment nor its interaction with response group had a significant effect on PRS nutrient supply rates for any element. Overall, nutrient levels following fertilization remained highly variable and overlapped substantially across response types and treatments, indicating that the underlying nutrient availability patterns were relatively stable and not strongly altered by the fertilizer application (Figure 8). These findings support earlier interpretations from the GLM (Table 4), in which PRS Al, K, and Zn supply rates measured under control conditions were significant predictors of 4-year basal area response. In particular, the consistent differences in Al supply rates observed post-fertilization align with its role as a potential soil constraint on growth response (Figure 7).

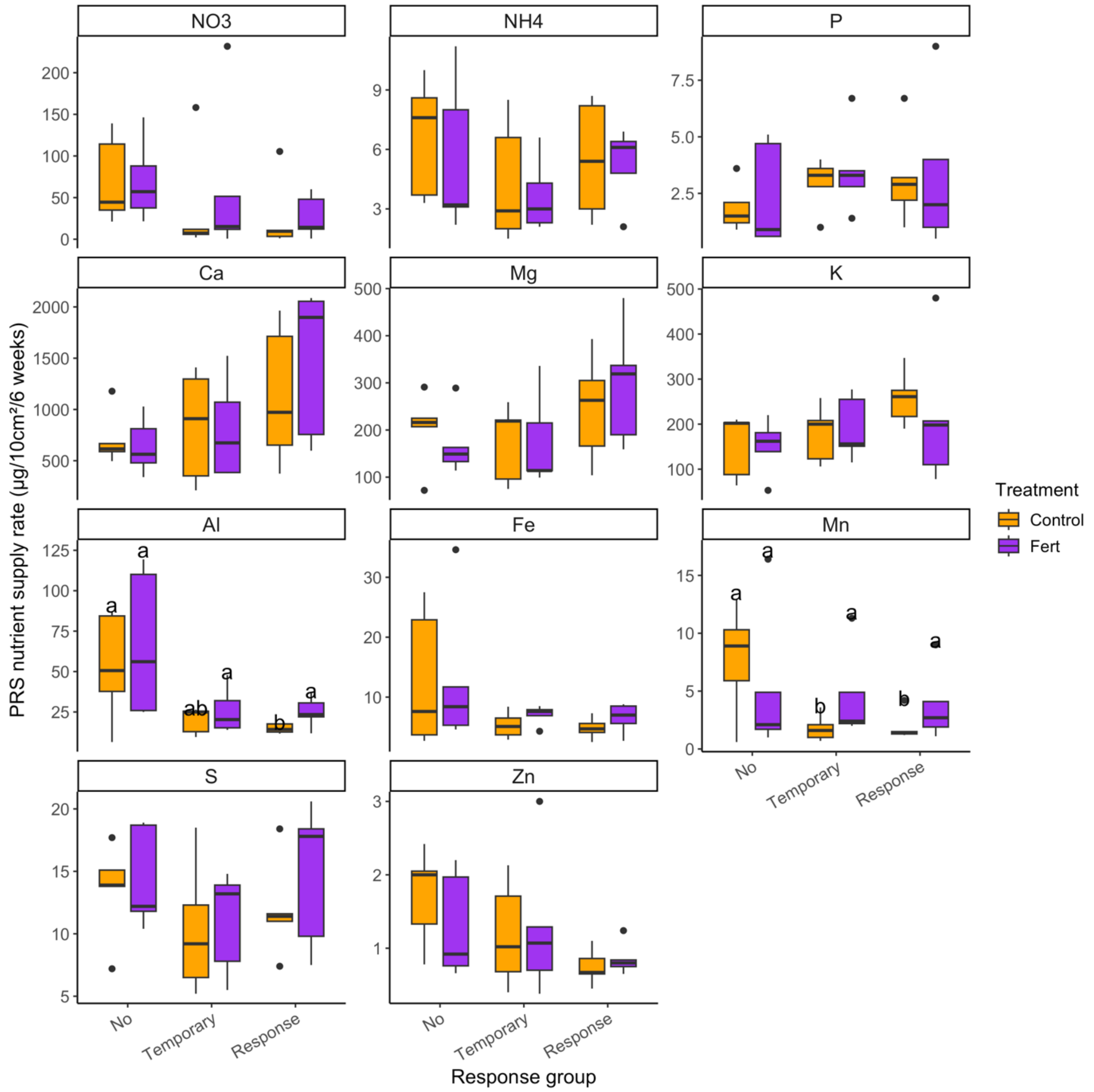

Figure 8. Comparisons of PRS nutrient supply rates across plant growth response types, shown separately for control and fertilized treatments. Boxplots represent nutrient supply rates for each nutrient, grouped by post-fertilization growth response type (No, Temporary, and Response), with control (orange) and fertilized (purple) treatments shown side-by-side for each group. Horizontal lines indicate medians; dots represent outliers. Lower-cased letters represent statistical significance from Tukey's HSD tests ($p < 0.05$).

4. Discussion

4.1 Impacts of Soil N and N-nutrient Interactions on Tree Growth Response

While N availability is a recognized driver of Douglas-fir productivity in the PNW, our multivariate and regression analyses reveal that growth response to N fertilization is co-modulated by a suite of specific soil nutrient availabilities and site factors. Consistent across Principal Component Analysis, Random Forest regression, and Generalized Linear Modeling, key predictors of the four-year basal area response included forest floor C:N ratio, PRS aluminum Al, K, Zn, available water storage, elevation, and site index. This underscores that fertilization outcomes are governed by complex interactions beyond baseline N deficiency alone.

Among these predictors, our GLM identified a strong positive association between forest floor C:N ratio and growth response. This finding aligns with established ecological theory and the diverse edaphic context of PNW forests. The region is renowned for its immense conifer forests, and the forest productivity across this region is related to the diversity of soil types (Carpenter et al. 2014). Specifically, within PNW forests, soil N availability strongly influences tree growth; sites with high soil N availability combined with adequate moisture typically support stands exhibiting high productivity (Perakis & Sinkhorn, 2011). At high elevation sites, colder climates suppress microbial activity, slowing N cycling rates and limiting site productivity; this is evidenced by high forest floor C:N ratios indicating slow decomposition and low N release (Slesak et al., 2010). Conversely, productivity challenges often arise in sites characterized by young, excessively drained glacial soils, which limit the retention of nutrients and moisture essential for sustained tree growth (Homann et al., 1995). Although low native N availability has often been considered a limiting factor for tree growth in the PNW forests, fertilization outcomes can vary depending on other soil and site characteristics (Chappell et al., 1991). For example, glacial soils, which tend to be well-drained and occur at lower elevations, may exhibit rapid N cycling and uptake, resulting in weak or inconsistent growth responses despite low baseline N levels (Littke et al., 2012; Littke et al., 2017). Consequently, factors beyond simple N deficiency often govern forest growth responses in the PNW. At sites where N is not the limiting nutrient, the input of additional N will have a limited effect on Douglas-fir growth (Rothe et al., 2002; Fisher and Binkley, 2000; Kenk and Fischer, 1988).

Specifically, the mechanism linking high C:N ratios to positive response, as shown in our results, involves microbial N dynamics. High C:N ratios, especially >40 in the forest floor or >25 in mineral soil, indicate conditions where microbes may immobilize added N, making it temporarily unavailable to trees (Vitousek & Matson, 1985; Melillo et al., 1982; Littke et al., 2014c); in contrast, lower C:N ratios suggest that added N is more readily mineralized and accessible for plant uptake. If the added N exceeds the microbial or plant uptake capacity, NO_3 may leach out of the system. Thus, C:N ratios serve as important indicators of both microbial demand and the potential effectiveness of fertilization, as observed in other temperate forest systems (Aber et al., 1998; Booth et al., 2005), but are not the only soil factor influencing fertilizer response. Our results confirm that under high C:N ratio conditions, Douglas-fir stands exhibited significantly stronger basal area growth increases following N fertilization (Edmonds and Hsiang, 1986; Miller et al., 1989; Littke et al., 2014c). This suggests that added N effectively alleviated a primary N limitation in sites characterized by high organic matter C:N. Conversely, sites with lower C:N ratios likely have faster N cycling and higher inherent N availability; consequently, added N may be less critical for growth or more susceptible to losses through leaching if it exceeds plant and microbial uptake capacity (Littke et al., 2024). Thus, C:N ratios serve as a robust empirical indicator in our study for predicting the potential effectiveness of N fertilization in these Douglas-fir stands, consistent with observations in other temperate forests.

However, the influence of C:N does not operate in isolation. Beyond C:N ratio, our analyses identified aluminum (Al) availability as a critical constraint on fertilization response. The GLM revealed a significant negative relationship between PRS Al supply and the four-year basal area response; this finding was reinforced by Random Forest, which ranked PRS Al highly in both importance metrics. Notably, PRS Al was the only nutrient measured that showed a statistically significant difference among response groups, with consistently responding installations exhibiting lower Al supply rates compared to non-responding installations, regardless of fertilization treatment. This underscores the potential role of Al toxicity in limiting Douglas-fir growth response. Elevated Al solubility, typically associated with acidic soil conditions, can directly damage root systems, impairing nutrient and water uptake (Brady and Weil, 2004). Importantly, our PRS data indicate that higher inherent soil Al availability (measured in control plots) is associated with reduced fertilization benefits, suggesting that initial site conditions, rather than solely fertilizer-induced acidification, are a key determinant of Al-related constraints. This aligns with observations that control plots of non-responding sites already had higher PRS Al levels. A long-term analysis of urea fertilization effects on PRS nutrient supplies at the Fall River Long-Term Soil Producitivity site found that urea application further increased PRS Al supply rates for two years after fertilization. These results suggest that fertilizing with urea in soils with high Al rates could lead to further, although temporary, increases in Al toxicity due to lower soil pH (Littke et al., 2025).

In contrast to Al, K availability emerged as a positive modulator of response. The GLM identified PRS K supply rate as a significant positive predictor of fertilizer basal area response, suggesting that adequate K nutrition supports the tree's ability to utilize added N effectively, potentially through roles in enzyme activation, osmoregulation, and protein synthesis. Meanwhile, although the PCA visually associated responding sites with higher K, PRS K supply rates themselves did not differ significantly among response groups. This indicates that the relative sufficiency of K within the broader nutrient context, rather than an absolute threshold, may be more important for facilitating a positive response.

The role of Zn in fertilizer response presented a complex picture. The GLM showed a significant negative relationship between PRS Zn supply and growth response, a trend also captured by the Random Forest. This negative effect is noteworthy as Zn is an essential micronutrient. This may be due to the Zn toxicity at very high availability levels, though PRS values were likely within typical ranges; Zn interactions inducing imbalances with other micronutrients (e.g., Cu, Fe); or an association with sites exhibiting only temporary responses. Like K, PRS Zn supply rates did not show significant differences among response groups, highlighting the complexity of its interaction with fertilization outcomes. The observation that urea fertilization can transiently increase micronutrient availability (Littke et al., 2025) raises the possibility that short-term Zn mobilization might contribute to the temporary response pattern observed in some installations, although this remains speculative and requires further investigation.

PRS P supply was not a significant predictor in the GLM, and no significant differences in PRS supply rates for P, Ca, or Mg were found among response groups. This suggests that, within the range of conditions sampled in this study, P availability (as measured by PRS probes) was not a primary co-limiting factor explaining the variation in N fertilization response. This finding might be related to lack of foliar P data, as Littke et al. (2024) has found a positive correlation between foliar P levels and fertilization response and noted a negative correlation between foliar P and N; foliar P concentration data may have provided more evidence in the co-limitation of growth response due to P availability and would be a helpful addition for future research. In our case, logistical constraints precluded foliar sampling across these installations. While element ratios (e.g., N:P) can indicate microbial nutrient limitations (Saggar et al., 1998; Güsewell, 2004; Heuck et al., 2015), our data did not reveal a significant link between P constraints inferred from such ratios and the observed growth responses. The multivariate separation of response groups in PCA, despite the lack of significant univariate differences for most individual nutrients (except Al), points towards the importance of overall nutrient balance and sufficiency. Responding sites appear to occupy a position in the PCA space characterized by relatively adequate levels of base cations (e.g. K, Ca, Mg) and P, coupled with lower inherent Al availability and higher forest floor C:N ratios - indicating N limitation. This balanced sufficiency, particularly for adequate K and low Al, alongside N limitation, likely creates conditions where added N can be effectively utilized for growth.

4.2 Fertilization Effect on Long-term Soil Nutrient Contents

Our study provides evidence that a single operational application of urea fertilizer has minimal lasting effects on soil nutrient availability in these Douglas-fir stands. Measurements using PRS probes 11-12 years post-fertilization showed no significant differences in the supply rates of base cations (e.g. Ca, Mg, K), Al, or other measured nutrients between control and fertilized plots. Furthermore, nutrient levels showed substantial overlap across response groups and treatments, indicating a return to background conditions. This key finding suggests that concerns regarding long-term soil acidification and cation loss driven by N fertilization (Fox, 2004; Littke et al., 2025), while valid for scenarios of repeated application, are not supported for this single application event within the period studied.

While nitrogen fertilization inevitably influences ecosystem nutrient cycling, our results align with observations that operational-scale, single applications have limited persistent chemical impacts. Nitrogen use efficiency (NUE) - the proportion of applied N taken up by trees - is a critical factor. Studies suggest that typical NUE values for forest fertilization range from 30% to 50% depending on site conditions, species, and application method (Biernat et al., 2020; Harrison et al., 2011). The apparent dissipation of fertilization effects on soil nutrients in our study after 11-12 years suggests that N not initially taken up by trees or immobilized was likely lost from the system, via leaching, volatilization, or denitrification, or cycled without causing measurable long-term shifts in the availability of other nutrients measured by PRS.

The potential for N leaching, a major environmental concern (Camargo & Alonso, 2006), also appears context dependent. Our finding of negligible long-term nutrient changes is consistent with Flint (2008), who reported low N leaching losses following urea application in coarse-textured glacial soils under Douglas-fir, a soil type represented within our study installations. This suggests that sites similar to those in our study and those on glacial outwash soils may possess characteristics (e.g., texture, vegetation uptake capacity) that promote better retention or rapid processing of applied N compared to finer-textured or more saturated soils.

Therefore, our data support the ecological sustainability of strategic, single applications of urea fertilizer in Douglas-fir management. The lack of significant long-term alterations to soil nutrient availability (as captured by PRS) 11-12 years post-application indicates that economic gains from growth response can potentially be achieved without measurable drawbacks to the measured soil nutrient status in these ecosystems. Management should, however, remain cognizant of site-specific factors influencing N retention and potential leaching risks identified in other soil types.

4.3 Additional Environmental Factors Affecting Fertilization Response

While this study was designed to explore the relationship between soil characteristics, especially its nutrient levels, on the Douglas-fir fertilization responses, the results suggested that other non-edaphic variables may also exert influence on growth outcomes. In particular, site index (SI) also emerged as the strongest single predictor in Random Forest models, and PCA associated lower SI values with responding stands; while elevation emerged as a significant factor in the GLM, and longitude also stood out in the PCA result, likely due to their associations with regional climate, including temperature, precipitation, and the timing and form of those precipitation events. These results demonstrate that site location within the complex topography of the PNW fundamentally shapes the growth response to N fertilization through its control over temperature and precipitation regimes.

The finding that SI strongly predicts fertilization response suggests that stands growing on inherently lower productivity sites (indicated by lower SI) - often characterized by factors like cooler temperatures (higher elevation), slower N cycling, and potentially poorer soils - derive the greatest benefit from N fertilization, likely because N is a primary growth constraint. Sites index thus appears to integrate multiple site limitations, including climatic and edaphic factors influencing N availability. Our results support its use as a practical, high-level indicator for predicting fertilization response potential across diverse PNW landscapes.

Elevation, by shaping site microclimate through temperature gradients, atmospheric pressure, and growing season length, plays a complex role in determining fertilization outcomes. Higher elevation sites in the Pacific Northwest tend to be cooler and wetter, which can enhance soil moisture retention and reduce heat stress. However, these colder temperatures can also suppress microbial activity and slow N mineralization, thereby limiting the availability of plant-accessible N despite favorable moisture conditions. This trade-off may explain why responding installations in this study clustered with higher elevation and lower temperature indicators in the PCA, suggesting that low-temperature inhibition of N cycling explains growth response to added N. Conversely, lower elevations may experience warmer temperatures that enhance N mineralization and cycling, potentially diminishing the observable benefit from additional N fertilization. While some low-elevation sites have fine-textured soils with good water holding capacity and relatively high N availability, others, such as glacial soils in the Puget region, remain nutrient-poor and water-limited, suggesting that the expected response to N fertilization is limited by water availability and nutrients besides N.

Longitude, on the other hand, may indirectly influence Douglas-fir growth by capturing regional climatic patterns associated with proximity to coastal or inland weather systems. Coastal locations in the PNW are often characterized by sedimentary parent materials and associated soils that tend to exhibit higher NO_3 and Al availability. Our analyses showed responding installations tended to be located further inland (higher longitude values). In the PNW, regional mountain systems - including the Olympics, Coast Range, and Cascades - play a major role in shaping precipitation patterns. Sites located further inland, particularly those between the coast and the Cascade Range, experience more pronounced seasonal variation in temperature and precipitation. These inland sites often undergo drier growing seasons, which can promote higher nutrient mineralization rates and enhance overall stand productivity. In contrast, coastal sites typically receive greater annual rainfall, leading to increased nutrient leaching, particularly of P (Kranabetter et al., 2020). As a result, these wetter sites often exhibit high N availability but lower Ca, Mg, and P availability, along with the aforementioned higher PRS NO3 and Al levels associated with sedimentary soils, which may limit tree growth response to additional N fertilization. The longitudinal gradient observed in our study (higher response inland) may therefore reflect not only the climatic transition but also a shift away from coastal soil conditions typified by elevated PRS NO_3 and Al. This climatic and edaphic imbalance helps explain the lower fertilization responses observed in coastal installations.

Many of these stands demonstrated less physiological stress under warming conditions, evidenced by smaller reductions in stomatal conductance with rising temperatures (Littke, unpublished data). This suggests that water availability was not a limiting factor in that region. Littke et al. (2024) similarly noted that coastal sites with high precipitation often show reduced P availability, and potentially higher Al solubility, further supporting the idea that P limitation and potentially Al phytotoxicity may constrain growth in these systems despite N enrichment. Taken together, these findings support the positive correlation observed between longitude and growth response and point to the importance of regional climatic and edaphic gradients in modulating fertilization effectiveness.

These results underscore the need to account for both edaphic and non-edaphic factors, including elevation, longitude, and site-specific climatic conditions, when evaluating the effectiveness of N fertilization in Douglas-fir forests. Prior studies have similarly identified elevation, seasonal temperature and precipitation, and water supply as strong predictors of fertilization response (Littke et al. 2014c), and our findings further confirm the influence of climate and elevation on site-level nutrient dynamics and tree growth outcomes. Parent material diversity across the PNW undoubtedly underpins much of the regional soil variability (e.g., Ca-rich Cascade igneous parent materials vs. Ca-poor coastal sedimentary parent materials), influencing baseline nutrient availability as discussed previously (Hynicka et al., 2016). While not explicitly modeled as a separate variable here, its influence is captured indirectly through the soil nutrient measurements and site index that proved significant in fertilizer response models. Ultimately, the interplay between parent material (driving soil genesis), topography (modulating climate), and climate itself (controlling temperature and precipitation) creates the complex spatial patterns in fertilization response elucidated by our analysis results.

5. Conclusions

Though fertilization is a common practice in PNW Douglas-fir forests, urea application at these coastal PNW sites had a limited effect on soil nutrients ten years after treatment. The growth responses of Douglas-fir to a one-time fertilizer application are influenced by multiple factors. Our findings suggest that soil cation availability and forest floor and surface soil C:N ratios play a crucial role in determining the extent of the response. Specifically, sites with high cation levels, high C:N ratios, and low Al experienced more pronounced and prolonged growth responses, whereas N-rich sites exhibited no response. Sites that responded temporarily to fertilization contained intermediate soil nutrient availability compared to responding and non-responding sites. The only significant difference between sites that continued response and temporary responders was that responding sites contained less PRS Al. Soil nutrient availability was found to significantly affect both the magnitude and duration of the response, highlighting the importance of soil nutrient and environmental conditions to target responding stands. Despite the focus on soil chemistry in this study, our results indicate that elevation and longitude, which affect temperature and precipitation, could be major predictors to fertilizer growth response. Our results highlight the importance of climate, soil, and site characteristics to provide further details on N fertilization impacts on both the Douglas-fir growth and the soil nutrition levels in the short-to-long term in the Pacific Northwest. Data suggest that fertilization could be a helpful management strategy at sites with low N availability and otherwise adequate soil cation nutrition. At sites with rich native N, managing other essential nutrients may be more efficient and economic than inputting additional N. These findings suggest the importance of targeted N additions for closing productivity gaps while leaving the soil resource intact. Future research should establish a coordinated network of long-term experimental sites across key environmental gradients, e.g., elevation, longitude, parent material, in the PNW. This network should specifically test diverse fertilization regimes, such as varying N doses, formulations, application frequencies, and potential nutrient combinations like N+P, to evaluate their effectiveness under contrasting site conditions. Integrating intensive field monitoring of tree physiology, soil nutrient dynamics, and climatic variables with multifactorial modeling approaches will be essential to reduce the uncertainties in assessing both the long-term economic effects of management practices such as N fertilization on Douglas-fir tree growth and the ecosystem services of planted forestry such as carbon sequestration potential.

Appendices:

A.1 List of Figures

A.2 List of Tables

A.3 References

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