The Effects of Biogeoclimatic Properties on Water and Nitrogen Availability and Douglas-Fir Growth and Fertilizer Response in the Pacific Northwest

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Abstract

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Coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the predominant plantation species of the western Pacific Northwest, although soil and climate characteristics vary throughout the region. This study investigated the effects of water and nitrogen availability on Douglas-fir growth throughout the region. Sixty Douglas-fir plots were established from Vancouver Island, BC to southern Oregon. Biogeoclimatic properties and fertilizer response were investigated according to soil nutrient regimes (SNRs) and soil parent materials alone (SPMs) and split by state and province (RSPMs). The effects of climate, site, and soil properties were investigated on soil water, soil nitrogen (N), and foliar variables using boosted regression trees and generalized additive models. Soil water availability was affected by soil depth and texture and influenced total soil N content and needle area. Sedimentary SPMs and very rich SNRs were identified as the most productive due to fine textured soils with greater water and N availabilities, which resulted in greater site index values and low fertilizer response. Glacial SPMs and medium SNRs had the lowest soil productivity due to coarse-textured soils with low water and N contents. Height:DBH ratio was greatest on stands with glacial SPMs yielding greater than expected site index values. Low spring temperatures and low water availability led to high forest floor C:N ratios, which then led to lower foliar nitrogen concentrations. Forest floor C:N ratios and fertilizer response were higher on igneous SPMs and British Columbia glacial RSPMs. These studies highlighted the effects of soil water and N availability on Douglas-fir growth and fertilizer response throughout the region.

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CHAPTER 1. SOIL WATER AND NITROGEN AVAILABILITY EFFECTS ON FORESTS

1.1 INTRODUCTION

Water and nitrogen are consistently the most limiting factors to the growth of forests in the Pacific Northwest as well as the world (Hanson and Weltzin 2000; LeBauer and Treseder 2008). The limitations of water and nitrogen (N) in forests are demonstrated through thinning and fertilization management schemes that are aimed at increasing water and N availability.

Soil texture, soil depth, and climate are the biggest predictors of soil water availability. A coarse-textured soil will allow easy access of roots to water, but will have fast soil water drainage, while clayey soils will have slower drainage, but will increase resistance to root water uptake. Soil depth affects how much water is stored in forest soils during dry periods. Climate, including precipitation, snow, and temperature, determines how often soil water is replenished, while vegetative cover, soil depth, and soil texture determine how fast it is depleted. The role of water availability in forests depends on the frequency of droughts during the growing season and how well trees are adapted to dealing with low soil water availability.

Forestry plantations tend to be concentrated on land that is mountainous or otherwise not suitable for agricultural production, which suggests that this land is lacking some aspect of a productive agricultural soil. Steep, rocky and/or young soils are commonly used for forest plantations and these soils have poor water holding capacities and are deficient in nutrients (Heilman and Gessel 1963; Steinbrenner 1979). The most common limiting nutrient in forests throughout the world is N (LeBauer and Treseder 2008). Fertilization practices have been developed to cope with low N availabilities and stimulate tree growth (Keeney 1980).

Interactions between water and N availabilities are difficult to examine because soils with high nitrogen availabilities tend to have higher water availabilities (Kabzems and Klinka 1987a). To understand the single and interactive effects of water and N, it is important to consider background water and nitrogen availabilities as well as those achieved with thinning, irrigation or fertilization. Thinning or irrigation will, in general, increase water availability in forests while leaving nitrogen at background levels (Brix 1972). Fertilization can improve soil N availability, but background water availability may still be an issue (Brix 1972). The singular and interaction effects of water and N on forest systems will be examined in this chapter.

1.2 LITERATURE REVIEW

Water and N availabilities affect all aspects of forest systems (Figure 1.1). The belowground processes that are affected by water and N are roots, forest floor, and soil, which then affect water and N uptake. Photosynthesis and evapotranspiration are cellular processes that are directly affected by water and N availability. The major aboveground processes in forests that are influenced by water and N are overstory foliage growth, stem growth, radial growth, and understory growth. Aboveground forest processes are all interconnected to produce a forest system that is dependent upon water and N availabilities.

1.2.1 Roots

When altering water and N availability in forest stands, it is important to understand belowground effects. Temporary changes in water and N availabilities might cause greater transpiration from increased foliage growth and/or a decrease in root biomass allocation (Brooks et al. 2009), but if the changes in water and N availabilities are not long term, foliage loss and root turnover will result in decreased water and nutrient uptake. Therefore, it is important to know the starting root biomass and how it is changed through forest management.

Root structure can be determined by the amount of water available during root growth. Dry soil can yield sparse roots because soil strength and physical resistance limit root growth (Kozlowski 1949). However, assuming that root growth is not hindered by extremely dry soil, species' root growth can react differently to water stress depending on the water-stress tolerance of the species. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) roots grow deeper into the soil in drier soils than in wet soils, but ponderosa pine grows deep roots under both situations (Steinbrenner and Rediske 1964). The preference of ponderosa pine for deep roots is a water stress tolerance mechanism to access deep-water reserves during dry summers.

When fertilizer is added to forest soils, root biomass decreases through shorter fine-root longevity due to increased decomposition, greater herbivory, and higher respiration costs (Hendricks et al. 1993; Eissenstat et al. 2000; Hendricks et al. 2000; Gough et al. 2004; Hobbie and Colpaert 2004). Increased turnover of roots will keep fertilizer-derived-N cycling in fertilized soils. Fertilizer additions tend to mirror high-productivity sites such that biomass is preferentially allocated aboveground. However, the effects of fertilization on roots will dissipate if N availability or cycling returns to pre-fertilization levels.

Roots are the first stop during water and N uptake and are, therefore, highly affected by water and nutrient concentrations. Low-productivity stands tend to have lower soil water and N availability than high-productivity stands (Kabzems and Klinka 1987b). To deal with low availabilities, root biomass allocation is greater on low-productivity sites, but root turnover is also greater due to difficult soil conditions (Keyes and Grier 1981). Even though root turnover will also be increased under high N conditions, stands with low water and N availability will retain higher root biomass allocation than those with high availabilities.

Root layout can also change according to water and N availabilities such that a highly-branched root system is necessary for diffusion of limiting water and nutrients, while a simple unbranched root system is sufficient for mass flow of available water and nutrients (Ballard and Cole 1974). A highly-branched root system will allow access to pockets of available water and N in poor soils. The differences in root layout support root biomass allocation differences according to water and N availability.

However, when water and N have been added to stands, changes in root biomass are variable (Axelsson and Axelsson 1986; Gower et al. 1992; Raison and Myers 1992; de Visser et al. 1994) because root biomass changes depend on the background water and nutrient limitations of the stand. If root growth had previously been limited by soil structure, an increase in water availability will increase root biomass; under non-restrictive conditions, increased water and N availability will most likely decrease root biomass allocation because of an increased mass flow of water and N.

1.2.2 Nitrogen Uptake

Uptake of N differs by the form of N that is being used. Nitrate is taken up through mass flow, while ammonium is taken up through diffusion (Bowen 1984). Nitrate does not interact strongly with soil colloids, which means an increase in concentration in dry soil, but a high probability of leaching in wet soil. Because ammonium is associated with soil exchange sites, low water availabilities can decrease ammonium uptake. If low water availability over time has yielded an extensive root system, trees will be able to access N in dry soils (Bowen 1984), but, if low water availability is sudden, a decrease in N uptake will occur through decreased root absorption due to decreased foliar assimilation and suberization of roots (Bowen and Cartwright 1977).

Uptake of N by roots depends on the availability of N in the soil. A high rate of mineralization is necessary for accessing organically-bound N, which dominates in the soil horizons that contain the majority of the roots (Khanna and Ulrich 1984). A high cation exchange capacity is also necessary for holding and accessing soil ammonium. Although stands with high N availabilities have smaller root systems relative to aboveground biomass, elevated enzyme synthesis allows greater root uptake of N per unit fine-root mass over stands with low N availabilities.

Mycorrhizae are also necessary for nutrient and water uptake especially in low-productivity soils. Mycorrhizae have been found to increase water use efficiency in colonized seedlings (Hobbie and Colpaert 2004). Also, mycorrhizae can increase root N uptake by absorbing nutrients that might be leached from the soil, extracting unavailable soil N, and absorbing organic N compounds (Harley 1969; Fisher and Stone 1969; Bowen 1973).

Water availability is tightly coupled with N uptake. In a coarse, low nutrient soil in Washington, N uptake through mass flow was found to be much lower than uptake through diffusion and dispersion (Ballard and Cole 1974), whereas mass flow would be the main source of water and N in a soil with high water and N availabilities. This is supported by the fact that thinning and fertilization have been found to increase N uptake in radiata pine (Carlyle 1998) and that N fertilization would be most effective during years of high water availabilities (Brix 1972; Carter et al. 1998). Because water and N availabilities are normally tied together, an increase in N availability under conditions of low water will increase diffusion uptake of N, but an increase in water availability with fertilization will increase mass flow to roots and will accentuate N uptake over fertilization alone.

1.2.3 Water Uptake

Similar to the effects of water on N uptake, N availability is strongly linked to water uptake and use. Improved N availability has been linked to greater water use efficiency (Gessel et al. 1990; Hobbie and Colpaert 2004; Jassal et al. 2010). Water uptake under improved N conditions can be increased because roots with high nutrients have increased hydraulic conductance (Sands and Mulligan 1990) and faster recovery of leaf water potential (Myers and Talsma 1992).

At low soil available water, soil water concentration was the biggest contributor to needle water potential, but, at higher soil water availabilities, foliage N concentration and soil temperature were the most important in needle water potential (Myers and Talsma 1992). Improved stomatal control of water loss in fertilized trees kept higher pre-dawn and midday water potentials over unfertilized trees (Myers and Talsma 1992).

Therefore, the interactions between water and N uptake are strongly coupled. An increase in N availability in the soil will increase root N uptake, but will also increase water uptake through root hydraulic conductance, mycorrhizal colonization, and stomatal control. However, fertilization might also cause excessive soil water uptake if a large foliage mass is produced that cannot be supported by available soil water (Brooks and Coulombe 2009). Therefore, while there is a secondary increase in water uptake due to increased N nutrition, water uptake must be kept in balance with N uptake or the advantages of fertilization will not be realized.

1.2.4 Forest Floor and Soil

Water and N availabilities along with air temperatures have a large impact on how the forest floor accumulates organic matter and decomposes (Zhang et al. 2010). Low soil water availability can cause an accumulation in the forest floor due to an increase in litterfall, an inhibition of soil biotic activity, increased immobilization, and decreased soil and ecosystem respiration (Spurr and Barnes 1980; Joslin et al. 2000; Jassal et al. 2007), which can be seen on dry sites as a thicker forest floor. During times of high water availability in the forest floor, however, microbial activity has been found to increase, which would increase N availability through increased mineralization, decomposition, and respiration of the forest floor and soil (Tietema et al. 1992; Joslin et al. 2000; Wilson and Maguire 2009; Raat et al. 2010).

Fertilization is expected to increase decomposition through an increase in litter mass and quality (lower C:N ratio) (Heilman and Gessel 1963), root turnover, and root consumption by soil fauna (Hendricks et al. 2000). However, if no increases in N availability through fertilization are found, then decomposition will not change (Prescott et al. 1993).

Conversely, decomposition of recalcitrant organic matter was decreased in forest floors with high anthropogenic N deposition due to the inhibition of extracellular enzymes (Sinsabaugh et al. 2002). Decreasing anthropogenic N deposition increased the microbial biomass through increased immobilization and N cycling rates and increased urease activity through increased decomposition of microorganisms and roots (Enowashu et al. 2009).

The variability in N effects on forest floor decomposition is due to differences between fertilization and anthropogenic N. Fertilization may increase forest floor decomposition and cycling shortly after application, but the effect will decline over time. Anthropogenic N deposition is a long-term input of N that distinctly changes the chemistry of the forest floor and soil.

The interactions of varying water and N availabilities on forest floor and soil are less well understood. Water or N additions both increase microbial biomass N, while N addition alone increased net N mineralization and water did not (Hungate et al. 2007). The combination of increased water and N availabilities should have the effect of stimulating microbes in the forest floor and soil, which will increase N availability in the short-term.

1.2.5 Stem Volume Growth

Tree stem volume growth strategies follow available summer moisture (Spurr and Barnes 1980). All trees stop shoot extension during times of water stress, but some trees (pines of the southeast US) can flush again if water becomes available. Shoot growth termination is caused by decreased photosynthetic production due to stomatal constriction in an attempt to control water loss (Spurr and Barnes 1980).

As with species’ stem growth tolerances to water stress, tree species react differently to N availabilities. Species that are tolerant of low N soils will grow poorly on low N soils, but will show a limited response to increased N availability (Mitchell and Chandler 1939). Conversely, species that require high amounts of available N will respond well to increased N availability, but will grow very poorly at low N availabilities.

It is possible that species that are adapted to low N availabilities are growing on soils with low water availabilities and cannot respond to increased N because the next most limiting factor is water. Similarly, low N levels are the least detrimental to growth during drought conditions, while high N levels can be harmful to growth and survival during drought conditions due to supporting a larger foliage area and higher root turnover (Pharis and Kramer 1964; Brooks and Coulombe 2009). On the other hand, species that are adapted to high N availabilities may not respond to increased N because the sites that they occupy may contain too much N to be impacted through fertilization (Carter et al. 1998). The implications of species’ N availability tolerances must be understood when changing N availability through fertilizer because adding N may trigger water or other nutrient limitations.

1.2.6 Ring Growth

Increasing water and N availability has been shown to increase tree stem diameter. Specifically, the combination of irrigation or thinning and fertilization has increased the production of earlywood (Brix 1972; Brix and Mitchell 1980) more than irrigation and fertilization alone. The increase in earlywood was not related to an increase in period of tracheid production, but was due to an increase in tracheid growth rate (Brix and Mitchell 1980). When investigated separately, thinning and fertilization increased earlywood growth, but fertilization decreased latewood percentage.

Thinning can increase soil water availability to surviving trees (Brix and Mitchell 1986), which could prolong the earlywood growth period in dry soils. However, thinning treatments, high July precipitation, and adequate soil water led to increased latewood growth in Douglas-fir (Beedlow et al. 2007; Kantavichai et al. 2010). Decreases in earlywood and latewood growth due to low water availability have been traced to decreases in tracheid formation due to soil water stress in Douglas-fir (Brix and Mitchell 1980; Kantavichai et al. 2010). The effect of water availability on earlywood and latewood growth depends on the time at which water availability is increased; an increase in spring water availability might stimulate earlywood growth, while an increase in summer water availability might extend latewood growth (Kennedy 1961).

Nitrogen uptake and foliar N concentrations have been related to basal area increment in radiata pine (Carlyle 1998). In particular, fertilization alone has been shown to increase earlywood growth rate, increase earlywood wall thickness, and decrease latewood thickness (Cahill and Briggs 1992). However, biosolids application has been found to increase earlywood and latewood production in Douglas-fir (Kantavichai et al. 2010), but the ring latewood percentage was decreased. The effects of fertilization on earlywood growth might be due to increased foliar photosynthetic efficiency, metabolic activity, and hormone supplies to the cambium (Brix and Mitchell 1980).

The effects of water and N availabilities on earlywood and latewood growth have been covered by the above sources, but an in-depth examination of site-to-site variability is lacking. Brix (1972) and Brix and Mitchell (1980) found that earlywood and latewood growth were increased and latewood percentage was decreased through fertilization and thinning more than they were alone. This change in radial growth shows the combined physiological effects of increasing water and N availability in low productivity stands.

1.2.7 Photosynthesis

Total photosynthesis depends on tree leaf area, but while leaf area varies in the long-term due to water and N availabilities, photosynthesis rate exhibits a short-term response to availabilities. Water stress effects on photosynthesis are a response to protect the tree from further water stresses. Specifically, photosynthesis decreases during water stress may be due to stomatal closing, decreased enzyme activity, and permeability of CO_2 through dehydration of membranes, cell walls, and cuticles (Crafts 1968). An example of water stress effects on photosynthesis are shown through a decrease in production of photosynthates in stands with high leaf area during dry years, but an increase in production of photosynthates according to leaf area during wet years (McMurtie et al. 1990).

The effect of N on photosynthesis in the literature can be separated into background N availabilities and changes in N due to fertilization. Increasing concentrations of foliar N led to increased maximum assimilation rate, maximum electron transfer rate, maximum carboxylation rate, and leaf chlorophyll, but Rubisco activation rate and the amount of N invested in Rubisco decreased with higher foliar N concentrations (Ripullone et al. 2003; Manter et al. 2005). Therefore, the efficiency of photosynthesis is increased with increasing foliar N concentrations.

Fertilization has been found to increase (Brix 1971; Murthy et al. 1996; Gough et al. 2004) or not affect (Brix and Ebell 1969; McMurtrie et al. 1990) photosynthesis in the literature. Gough et al. (2004) found that the effect of fertilization would last only 100 days after application. Similar to foliage with high N concentrations, fertilized foliage had an increased rate of electron transport, carboxylation capacity, and respiration over control foliage (Gough et al. 2004; Jassal et al. 2010). Contrary to foliage with high N concentrations, fertilization effects on photosynthesis are short-lived, which explains the findings of no response in some studies.

The response of photosynthesis to fertilization is dependent upon adequate water supply just as water-mediated photosynthesis response is related to foliar N status. Because inherent photosynthesis and Rubisco capacities are dependent on the most limiting environmental factor, photosynthesis levels will follow limiting factors unless they are altered. For example, fertilization has increased absolute rates of photosynthesis, but only until water stress became too high (Brix 1972). The net effect of irrigation and fertilization is an increase in photosynthesis more than irrigation and fertilization alone if water or N were limiting (McMurtrie et al. 1990). Water and N availabilities have a negative effect on photosynthesis rates through seasonal water deficits and limitations to photosynthetic mechanisms.

1.2.8 Evapotranspiration

Evapotranspiration of forests is increased due to high soil water availability (Sands and Mulligan 1990; Murthy et al. 1996; Jassal et al. 2009). The balance between stomatal acceptance of CO_2 for production of photosynthetic assimilates and stomatal water loss depends on how much water is available for uptake. The amount of foliage produced will therefore be balanced between the two processes (Grier and Running 1977).

Water and N availabilities have a strong effect on photosynthesis and water availability and climate control evapotranspiration, but the effect of N availability on evapotranspiration is less understood. Investigations of fertilization have found no effect on evapotranspiration (Jassal et al 2009; Jassal et al. 2010) or soil water potential (Brix and Mitchell 1986). In the second case, fertilization caused an increase in foliar area, but did not cause a faster depletion of soil water, which is hypothesized to be through greater stomatal control of water loss in fertilized foliage (Brix and Mitchell 1986).

The effects of interactions between water and N availabilities on evapotranspiration most likely mirror mechanisms that are covered by photosynthesis and water uptake studies. Like photosynthesis, changes in stomatal conductance due to fertilization are probably short-term, but long-term increases in leaf area might lead to earlier water deficits (Brooks and Coulombe 2009).

1.2.9 Overstory Foliage

Water and N availabilities have been thought to be the limiting factors to forest leaf area (Allen et al. 1990). Similarly, leaf area index has been increased by fertilization and irrigation in radiata pine and Douglas-fir (Brix 1972; Linder et al. 1987). More specifically, number of needles, needle thickness, and needle area were increased by an increase in water and N availability (Brix 1972; Linder et al. 1987; Raison and Myers 1992).

One way to compare water availability effects on overstory foliage is to compare leaf area indexes over different communities. Waring et al. (1978) found that leaf areas decreased on sites with low soil moisture and high evaporative demand. Conversely, leaf area was greatest in areas with high precipitation (Grier and Running 1977). Water limitations are represented by low soil available water, which causes stomatal closure, lower photosynthesis, and higher respiration rates (Waring et al. 1978). Within different species, those best suited to water stress have small, hairy and/or blue-gray leaves with a small surface-area to volume ratio (Sands and Mulligan 1990). Therefore, the inherent water availabilities in different forest communities are determining what species occupy the community, but water availability is limiting the total leaf area that the community can hold irrespective of species (Grier and Running 1977).

Photosynthetic increases are a short-term response to fertilization, but that short increase can increase foliage size and area, which stimulates tree growth (Gough et al. 2004). Many studies have linked increased N availability to greater foliage growth or area (Brix 1972; Linder et al. 1987; Raison and Myers 1992; Gough et al. 2004; Wilson and Maguire 2009), but the relative increase in foliage is due to the availability of water. One example is fertilized radiata pine, which had an increase in foliage due to fertilization during a wet year (Linder et al. 1987). The new foliage caused a rapid depletion of soil water the next year because of the extra transpiring foliage and could not take advantage of the increased N availability. However, fertilization can increase water availability through increasing leaf area and interception, which shades out understory and creates more water for overstory tree roots (Turner and Lambert 1987).

An increase in overstory foliage area through fertilization is, therefore, dependent on the availability of water. If fertilization causes an increase in foliar area, then more photosynthetic assimilates can be produced, which can lead to increased growth throughout the tree. Increased water availability through thinning or irrigation will stimulate stomatal conductance and N uptake, which will increase foliage size and decrease litterfall (Brix 1972; Gower et al. 1992). Because of these relationships, an increase in water availability (to a point) is the safest way to stimulate foliage growth, while increased N availability can yield large foliage growth only if water is available.

1.2.10 Understory Growth

Understory species are a strong competitor for water, N, light, and space with overstory trees. Water conservation techniques for understory species include maintaining a large photosynthesizing area, high photosynthesis efficiency per unit leaf area, low respiration rates per unit leaf area, controlled water loss, absorbing water efficiently, using photosynthate for growth, and forming an extensive root system (Spurr and Barnes 1980). Understory cover has been shown to increase as foliar N decreases (Barclay and Hall 1986), which is due to decreases in leaf area index as foliar N concentration decreases.

Understory species have been used to predict soil water and nutrient regimes in British Columbia, England, and Germany because of their innate growth preferences (Green et al. 1989; Wilson et al. 2001). The interactions of light, water, and N availabilities determine the presence and type of understory species that the site can support. However, the availability of light in forests is directly related to water and N availability through overstory foliage growth; low water and N availability will keep overstory foliar growth low and allow an understory cover that will directly compete for resources.

1.3 DISCUSSION

There are many individual effects and interactions between water and N availabilities on forest systems (Figure 1.1). The effects of water and N availabilities on ecosystem processes can be thought of in tiers. For example, changes to the first tier affect the subsequent tiers.

1.3.1 First Tier Pools and Processes

Aboveground, root, and soil and forest floor pools and processes represent the first-tier effects of soil water and N availability (Figure 1.1). Aboveground processes include changes to the photosynthetic system, stomatal control, and hormones. High N availability increases the chlorophyll content of foliage, carboxylation rate, and electron transfer rate, but decreases Rubisco production rate with the effect of increasing photosynthetic efficiency in foliage. Water availability controls foliar enzyme activity, permeability to CO_2, and growth hormones which affect growth in other parts of the tree. Stomatal conductance is affected by both water and N because it is directly related to water availability in the soil, but stomatal control is increased through high N availability. High water and N availability will increase aboveground processes, while low availabilities will decrease aboveground processes. Increasing water or N through thinning, irrigation or fertilization will increase the first tier aboveground processes that are involved in photosynthesis, while low availabilities will decrease these processes.

Rooting structure is changed due to water and N availability. Root depth and branching are both decreased due to the accessibility of water and N through mass flow. Similarly, mycorrhizal colonization is decreased under conditions of high availabilities because mycorrhizae become unnecessary to access nutrients. Root turnover can be increased due to high N concentrations in the soil or through difficult soil conditions in soils with low water. However, since the amount of belowground productivity is greater in low productivity stands (Keyes and Grier 1981) there is a net negative effect of water and N on root turnover. Root conductance is increased through high N availability, which can increase water uptake. The net effect of water and N on root pools and processes such as root conductance, root branching, root depth, and mycorrhizal colonization are opposite to those of aboveground processes. Root processes increase under low water and N availabilities through necessity and decrease under improved water and/or N because of luxury.

The important first-tier soil pools and processes affecting soil water and N availability include forest floor C:N ratios, soil microbes pools, and the rate of mineralization/immobilization and mass flow/diffusion in the soil. Litter quality, as represented by C:N ratios, improves under high N availability because foliage contains more N and is easily decomposed by soil microbes, which are also stimulated by high water and N availabilities. Because of the increased amount of soil microbes and improved litter quality, immobilization is decreased and mineralization is increased due to improved water and N availability. Because of the increases in N availability stated above, mass flow will dominate because of the ease of water and N uptake, while diffusion will be minimal because nutritional demands can be met through mass flow. Forest floor and soil processes will be increased the most under high water and N, while smaller increases will be seen when only one is increased and the largest decrease in forest floor and soil process under low water and N.

1.3.2 Second Tier Pools and Processes

The second tier processes are directly affected by the first tier pools and processes and directly affect third and fourth tiers (Figure 1.1). The second tier mechanisms that will be discussed are photosynthesis, water and N uptake. Water and N uptake are affected by many belowground mechanisms that involve root growth, soil microbes, and the availability of water and N in the soil, but are also affected by tree water uptake through stomatal conductance. Increasing water or N uptake through fertilization, irrigation or thinning will stimulate the unaffected uptake process, but may also strain limitations because of increased growth. There is also a feedback of increased water and N uptake that then stimulates the photosynthetic system as well.

Photosynthesis is the engine of the tree and, therefore, is affected by almost every process that is involved with water and N uptake. The largest changes to the photosynthetic system are due to high water and N availabilities. Irrigation, thinning or fertilization will increase photosynthesis, but will be limited by water or N uptake.

1.3.3 Third Tier Pools and Processes

The third tier processes are affected by the changes in first and second tier process due to water and N availabilities (Figure 1.1). Tracheid growth rate is affected directly through changes in growth hormones and indirectly through photosynthesis, which causes a change in earlywood and latewood growth and ratio depending on availabilities. Stomatal conductance directly affects evapotranspiration through water availability and stomatal control. Litterfall is directly affected by photosynthesis and water availability due to foliage carbon balance. Root and microbial respiration is highly dependent on water and N availabilities due to changes in root turnover (Eissenstat et al., 2000) and soil microbe activity (Raat et al., 2010). Root turnover, litter quality, soil microbes, and soil water and N availability affect forest floor and soil decomposition.

In the simplified diagrams, tracheid growth rate is increased the most through greater water and N availability, but tracheid growth rate is also stimulated by increases in water and/or N. Litterfall is decreased by greater water and N availability, but increased by low water and N availability and fertilization. Decomposition is greatly affected by high or low water and N availabilities, but stimulated by water or N additions.

1.3.4 Fourth Tier Pools and Processes

The most visible effects of water and N availabilities are seen in the fourth tier, which consists of foliage biomass, stem biomass, root biomass, understory biomass, and forest floor biomass (Figure 1.1). These processes are a culmination of the effects from all of the above tiers and are therefore affected by both water and N at all times.

Starting from the ground up, root biomass is affected directly by root structural and turnover responses to water and N availabilities and indirectly through respiration, decomposition, and foliage biomass. Root biomass is lowest under high water and N availabilities because of luxury consumption through mass flow and highest under low water and N availabilities because expanded root growth is necessary to locate and uptake water and nutrients through diffusion. Adding water or N to a forest will decrease root biomass through increased root turnover after fertilization or decreasing the need for deep rooting after thinning.

Forest floor biomass is also affected by root and microbial respiration and decomposition as well as litterfall, which are all mediated by lower tier mechanisms. A lack of water and N will slow decomposition of the forest floor retaining otherwise available nutrients. Supplementing water or N to the stand will decrease forest floor biomass by improving soil microbial growth, but a system with adequate water and N levels will contain the lowest forest floor biomass due to higher decomposition rates.

Aboveground foliar biomass, according to water and N availability, is strongly dependent upon the impacts of photosynthetic assimilation. While the photosynthetic system can be quickly altered due to water and N availabilities, foliar biomass is a long-term response is changing availabilities. Increasing water or N availability will support more foliar growth of overstory trees unless one is severely limiting. Foliar biomass then acts as a feedback mechanism to the other fourth tier processes except forest floor biomass by determining the supply of assimilates throughout the tree or determining understory light availability.

Water and N availability stimulate growth hormones and assimilation, which influences tree stem biomass growth. When foliage biomass is increased through greater water and N availability there is also a feedback of increased photosynthetic assimilation that will further increase stem biomass (Landsberg and Waring 1997). Similar to foliage, stem biomass will react more to both high water and N availabilities than to an increase in one.

Understory species are dependent on the same mechanisms as overstory species, yet are at a disadvantage for light availability. In the context of this process model, understory biomass is influenced the same as overstory biomass, but responds negatively to overstory biomass changes. An increase in overstory foliage would therefore decrease understory growth through lowered light availability. Low water and N availabilities support the growth of understory the most because overstory foliage growth is kept low. An increase in water availability through irrigation or thinning in a low N forest might stimulate understory growth because overstory foliage growth cannot respond without an increase in N.

1.3.5 Models

The many first tier processes have a strong effect on all fourth tier processes due to water and N availabilities. However, the importance of each process depends on deficits or luxury of water and N. If availabilities are increased through irrigation, thinning or fertilization, a limiting process may only be changed to the next most limiting factor.

In a forest with low water and N availabilities (Figure 1.2), soil and forest floor processes will dominate. The lack of available water and N will produce a large root system to improve uptake while aboveground processes are hindered. Second tier processes such as photosynthesis, water uptake, and N uptake will be limited through high immobilization rates and a dependence on diffusion. Litterfall and decomposition are the third tier processes that are most affected by a lack of water and N. Litterfall is elevated to decrease use of assimilates and water loss by foliage. Decomposition is slowed due to high immobilization rates and a decrease in soil microbes. The above processes can increase understory biomass, root biomass, and forest floor biomass while decreasing foliage, stem, and radial biomass. Root biomass is stimulated through the root processes discussed earlier. Forest floor biomass is increased through decreased decomposition and increased litterfall. High litterfall rates further decrease overstory foliage biomass with a feedback effect of decreasing stem biomass. Understory species will outcompete the overstory trees for water and N because understory species have smaller requirements.

An increase in water through thinning or irrigation would drastically change the above processes (Figure 1.3). Soil and forest floor processes will be increased through mass flow, soil microbes, and mineralization rates, which will decrease root allocation while increasing water uptake. Nitrogen uptake will also be increased through increased water availability feedbacks. Aboveground processes and therefore photosynthesis will be stimulated through high water availability and improved N availability. The increase in water will then affect third tier processes by decreasing litterfall, increasing decomposition, and increasing tracheid growth. Litterfall will decrease because improved stomatal conductance will allow higher photosynthesis rates and support more foliar biomass, which will then stimulate stem biomass. Understory biomass will be stimulated due to increased water availability especially if the stand is thinned due to higher light availability unless the overstory foliage can reestablish canopy closure. The increase in water and N will decrease root growth allocation and forest floor biomass.

Changes in forest processes due to fertilization are similar to those through thinning or irrigation (Figure 1.4). Correspondingly, forest floor, soil, and aboveground processes are increased through fertilization, while root processes are decreased. Nitrogen uptake is increased through fertilization, which can increase water uptake through improved stomatal control.

Photosynthesis will also increase due to increased aboveground processes and improved uptake. Tracheid growth rate and decomposition will increase and root growth and forest floor biomass will decrease as in improved water conditions. One difference between increasing water or N is litterfall; fertilization may cause more litterfall than in improved water conditions because the larger foliar mass produced after fertilization could cause water deficits, which would increase litterfall. The increased foliar mass after fertilization will have feedback increases to stem biomass as water availability increases. However, understory biomass will be decreased due to fertilization because the increased overstory foliar biomass will shade-out the understory.

The greatest aboveground biomass will be seen under high water and N (Figure 1.5). Soil and forest floor processes, aboveground processes, water uptake, N uptake, photosynthesis, and foliar growth will be the dominating processes and will increase more from water or N improvements than either alone. Root processes are minimal in high water and N conditions because of the accessibility of mass flow and available N. Large overstory foliar biomass is retained because litterfall is negligible in systems with high water and N. Understory biomass, root biomass, and forest floor biomass will be lowest in this system because of the large overstory, aboveground biomass allocation, and decomposition, respectively.

1.3.6 Comparisons

This model describes the effects of water and N on aboveground and belowground forest components similar to the SHAWN model proposed by Barclay and Hall (1986). SHAWN is a mechanistic model that was based on the extensive data collected from thinning and fertilization studies at Shawnigan Lake (Barclay and Hall 1986). The water and N model proposed in this review is based on the trends in the SHAWN model, but also incorporates research from Douglas-fir over the Pacific Northwest with the addition of other conifer species including radiata pine and ponderosa pine. Using information from different climates, soils, species, and management techniques, the model from this study reviews the effects of water and N on forest processes and will allow forest managers to interpret the effect of different availabilities on tree biomass allocation.

1.4 CONCLUSIONS

Among the processes above, the most important initial response to water and N is in the forest floor and soil because that is where availabilities are determined through the balance of diffusion and mass flow and immobilization and mineralization. Photosynthesis rate is the most important secondary response because it is controlled by all first tier processes in all systems and affects the larger third and fourth tier processes. Litterfall is the most important third tier process because it signifies the ability of the tree to produce and sustain foliage. Overstory foliar biomass is the most important fourth tier pool because it is largely affected by changes in first, second, and third tier processes and is important for stimulating stem growth and outcompeting understory species. High water and N availabilities will yield greater aboveground processes and pools, while low availabilities will necessitate greater belowground pools and processes. After reviewing the literature on water and N availabilities in forests, there is little research on the effects of different climates and soils on soil water and N availability and the response of tree growth to these differences. The mechanisms identified in this paper will be used to identify the interactions of water and N on Douglas-fir growth throughout the Pacific Northwest.

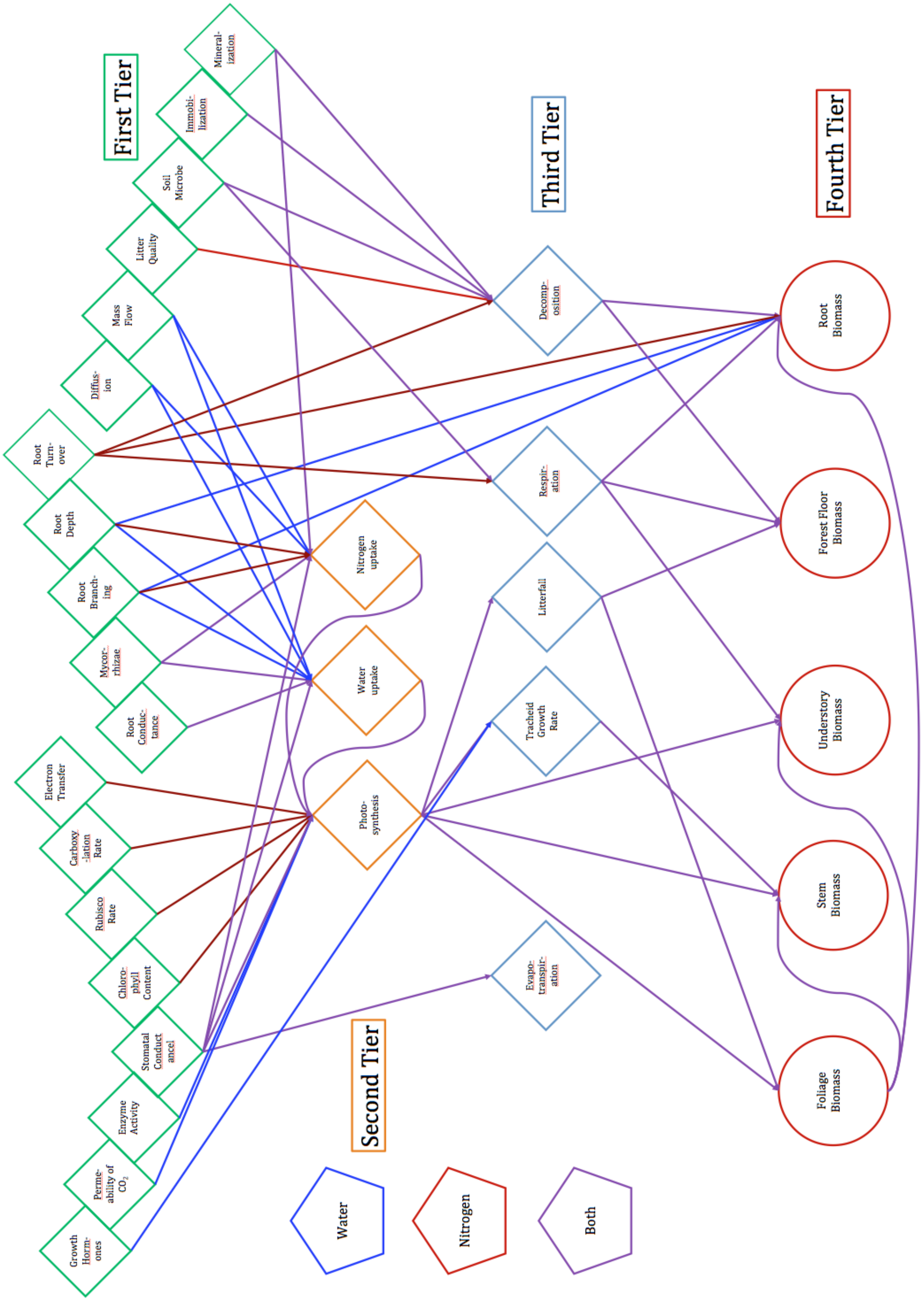


Figure 1.1. This figure shows the effect of water and nitrogen availability on forest ecosystem pools and processes. The arrows coming from the text boxes show that water (blue), nitrogen (red) or both (purple) are affecting the pool or process. An arrow to the top of the box shows that the above pool or process is affecting it.

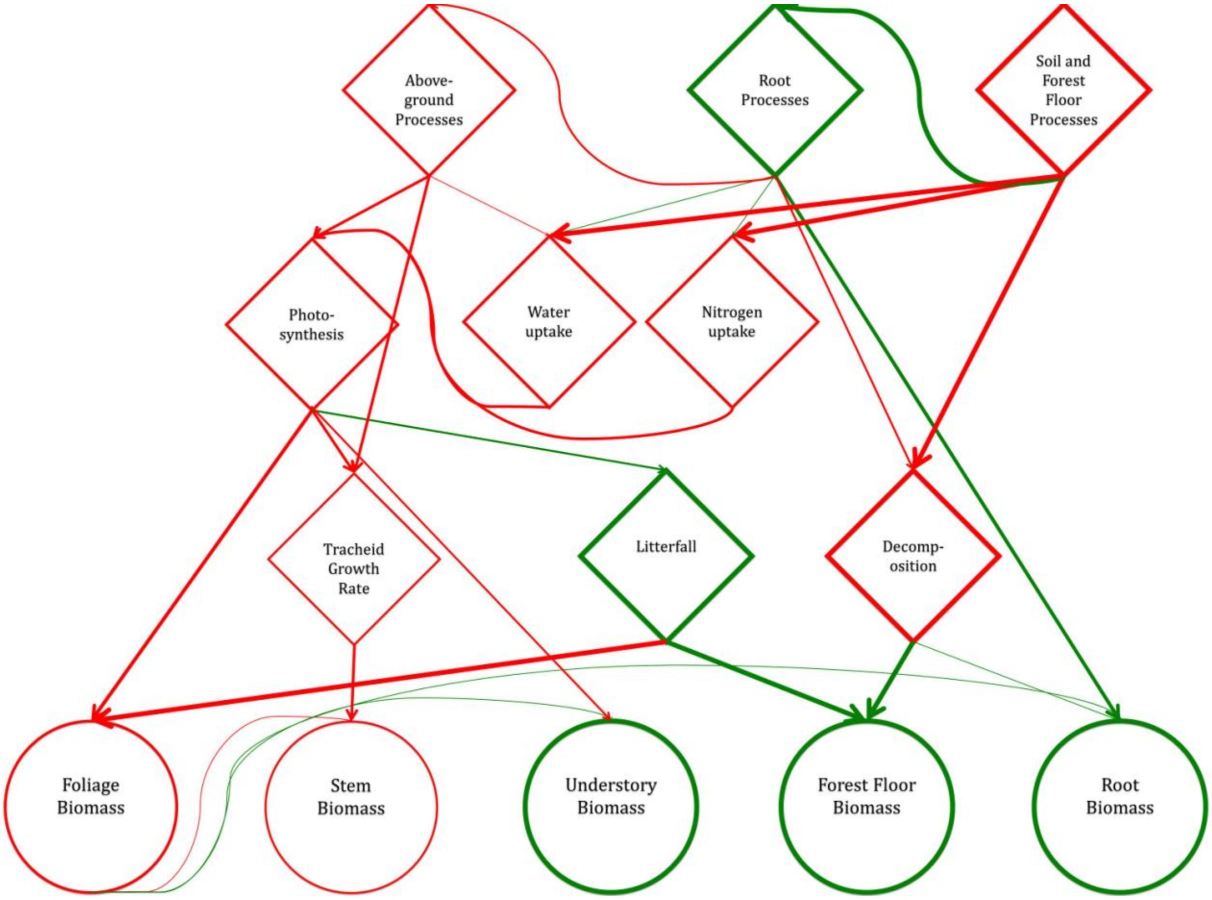


Figure 1.2. The effect of low water and nitrogen availability on simplified ecosystem processes. The color of the text boxes and arrows show the net change due to water or nitrogen availability. The thickness of the textboxes and arrows displays the level of change in the process in the different systems as caused by low water and nitrogen availability.

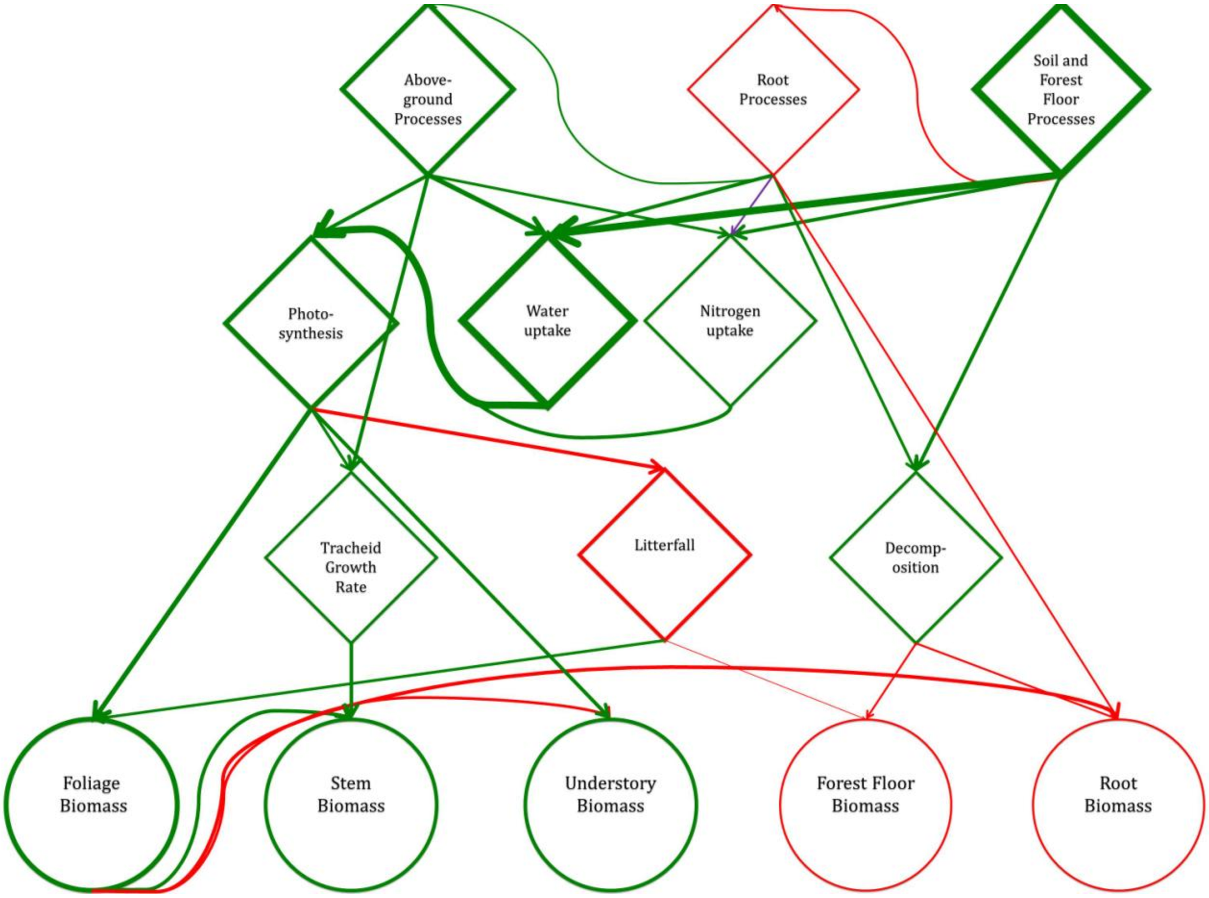


Figure 1.3. The effect of improved water availability due to thinning or irrigation on a forest ecosystem with low water and nitrogen availability. The color of the text boxes and arrows show the net change due to water or nitrogen availability. The thickness of the textboxes and arrows displays the level of change in the process in the different systems as caused by low water and nitrogen availability.

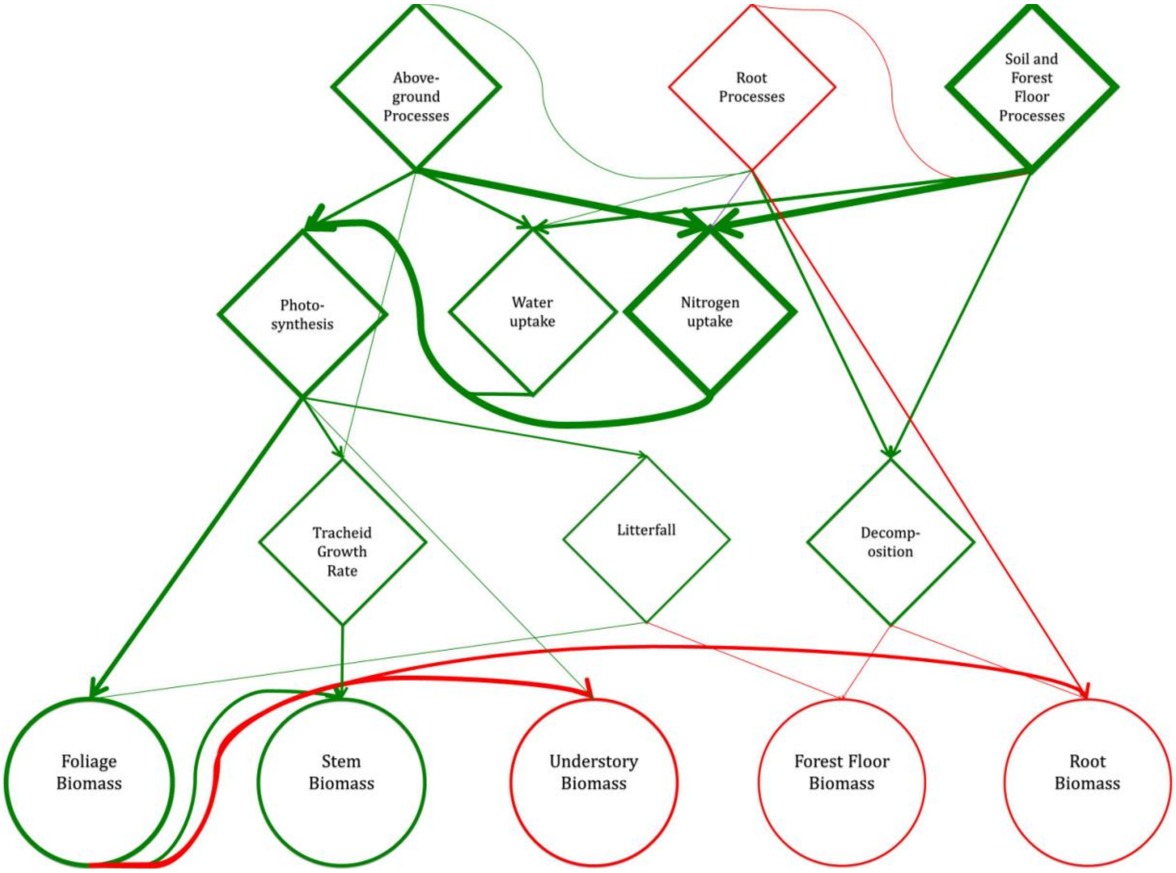


Figure 1.4. The effect of improved nitrogen availability due to fertilization on a forest ecosystem with low water and nitrogen availability. The color of the text boxes and arrows show the net change due to water or nitrogen availability. The thickness of the textboxes and arrows displays the level of change in the process in the different systems as caused by low water and nitrogen availability.

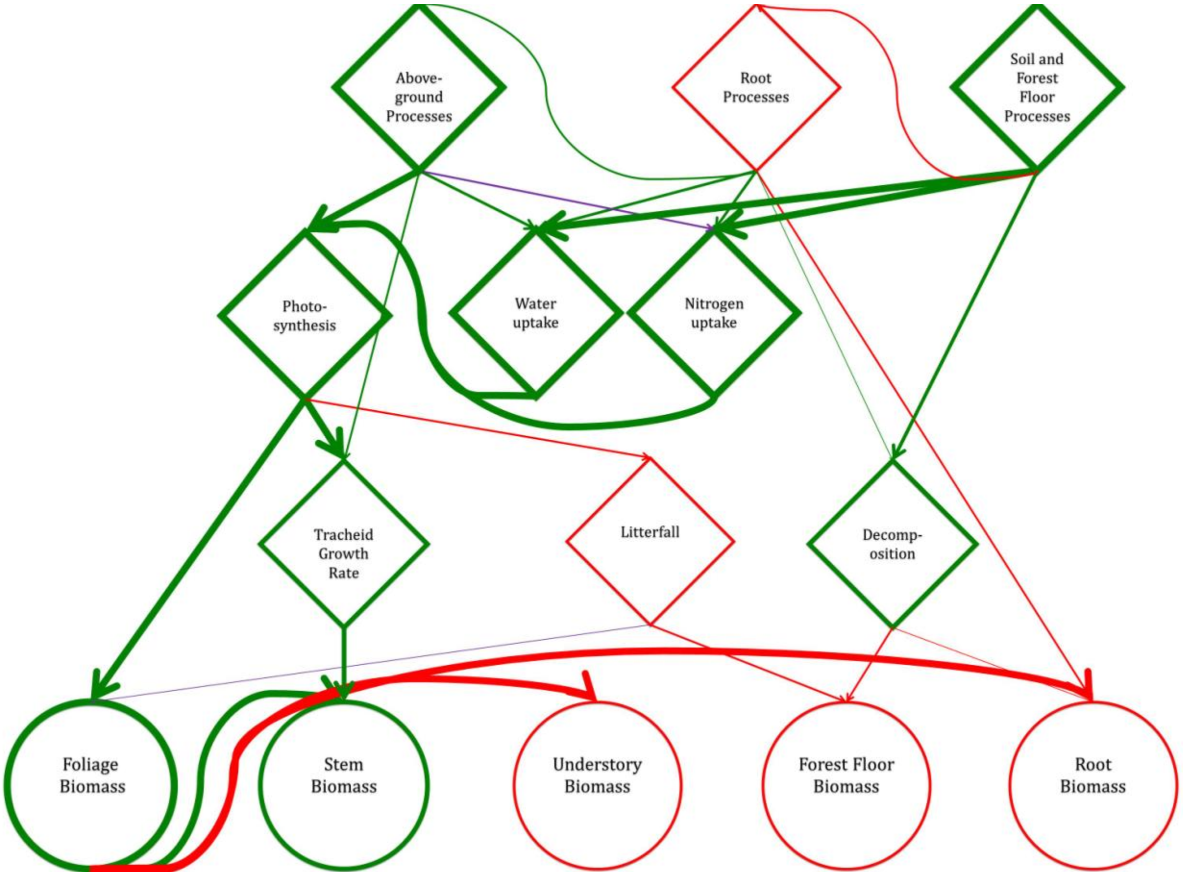


Figure 1.5. The effect of high water and nitrogen availability on simplified forest ecosystem processes. The color of the text boxes and arrows show the net change due to water or nitrogen availability. The thickness of the textboxes and arrows displays the level of change in the process in the different systems as caused by low water and nitrogen availability.

CHAPTER 2: UNDERSTANDING SOIL NUTRIENTS AND CHARACTERISTICS IN THE PACIFIC NORTHWEST THROUGH PARENT MATERIAL ORIGIN AND SOIL NUTRIENT REGIMES

2.1 ABSTRACT

A convenient method is necessary for assessing the availability of soil nitrogen in plantation Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in the Pacific Northwest. The objective of this research was to use soil parent materials (SPMs) and soil nutrient regimes (SNRs) to determine the most efficient method to characterize soil nitrogen availability in Douglas-fir stands. It was hypothesized that SPMs and SNRs would effectively separate stands with distinctive climate, site, and soil characteristics and forest floor and soil carbon and nitrogen reserves. At sixty Douglas-fir stands, SPMs and SNRs were determined and soil particle percentages, soil depth, and forest floor and soil nitrogen and carbon contents were measured to a depth of one-meter. Soils of sedimentary origin and very rich and rich SNRs contained greater nitrogen and carbon contents than those from glacial and igneous origins and medium SNRs. Sedimentary SPMs and very rich SNRs were developed from older parent materials and had significantly greater soil depths and finer textures than those from glacial SPMs and medium SNRs. SNRs and SPMs are recommended as good estimators of soil nutrient pools and soil characteristics in Douglas-fir plantation forests of the Pacific Northwest.

2.2 INTRODUCTION

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is native to the Pacific Northwest and is the most-commonly utilized forest plantation species across the region (Franklin and Dyrness 1988). It grows on many of the diverse soil types found in the Pacific Northwest, but with varying levels of productivity (Steinbrenner, 1979; Kabzems and Klinka, 1987b). Previous observations of correlations between soil nitrogen (N) and growth response to fertilization in the Pacific Northwest suggest that N tends to be limiting and is predictive of inherent forest productivity. For example, forest floor and soil carbon to nitrogen (C:N) ratio (Peterson et al. 1984), soil mineralizable N (Shumway and Atkinson 1978), and total soil N content (Hopmans and Chappell 1994) have all been used to predict response to N fertilization with some success.

An ability to locate forests with low soil N contents is important for forest plantation management in order to improve and sustain forest productivity (Powers et al., 2005). Soil parent materials (SPMs) and soil nutrient regimes (SNRs) have been used in the past to assess soil nutrient availability and other soil characteristics (Steinbrenner 1979; Turner et al. 1979; Turner and Lambert, 1986; Kabzems and Klinka 1987a; Courtin et al. 1988).

The dominant SPMs of the Pacific Northwest are formed from marine encroachment, glacial advance and retreat, and ancient and recent volcanic activity occurring over 50 million years (Kruckeberg 1991). Soil parent materials have been shown to have a major influence on soil characteristics like depth and texture (Steinbrenner 1979) and Turner et al. (1979) found that total soil N contents were highly variable between SPMs in the Douglas-fir region. Similarly, in radiata pine (*Pinus radiata* D.Don) plantations in Australia, volcanic, metamorphic, sedimentary, and unconsolidated parent materials were found to have different soil chemical deficiencies and soil N concentrations (Turner and Lambert, 1986). Also, use of SPMs differentiated site index, a productivity indicator using projected tree height, of radiata pine in New Zealand (Watt et al. 2009).

Soil nutrient regimes were developed to understand available soil nutrition (mainly N) and site productivity through easily determined soil factors or understory vegetation (Krajina 1969; Green and Klinka et al. 1994; Pyatt 1995). There are five classes of SNRs that range from very poor SNRs with low available N to very rich SNRs with rapid decomposition and high available N (Green and Klinka et al. 1994). In British Columbia, SNRs can differentiate stands with different soil N contents and Douglas-fir site index values (Kabzems and Klinka 1987a; Kabzems and Klinka 1987b; Courtin et al. 1988).

The objectives of this research were to use SPMs and SNRs to characterize soil nutrient and water availability in Douglas-fir plantation forests throughout the coastal Pacific Northwest region through climate, soil characteristics, and soil nutrients. The research was conducted as part of a larger research project on forest productivity. We tested the following hypotheses: 1) forest stands with different SPMs and SNRs have distinctive geologic ages, slopes, elevations, and climate, 2) soil characteristics such as depth and texture are distinct among different SPMs and SNRs, 3) forest floor and soil C and N reserves are predictable throughout the Pacific Northwest according to SPMs and SNRs, and 4) Soil parent materials differentiate forest stands with distinct site and soil characteristics better than SNRs.

2.3 MATERIALS AND METHODS

2.3.1 Plot Installation

Beginning in 2008, the Stand Management Cooperative, a collective of forest product companies, colleges, and government agencies, installed paired-tree trials in 60 Douglas-fir plantations extending from northern Vancouver Island to southern Oregon to characterize site and soil characteristics that might predict Douglas-fir growth (Figure 2.1). Installations were established over three years on a range of latitudes, elevations, slopes, and position on slope based on availability from government agencies and forest product companies (Table 2.1). Installations contained predominantly plantation Douglas-fir trees and covered 1.1-ha.

2.3.2 Soil Parent Material

Parent material was determined from a combination of USGS geologic maps (U.S.G.S. 2010a; U.S.G.S. 2010b), NRCS soil series descriptions (Soil Survey Staff 2010), and soil pit observations. The age of SPMs were estimated from USGS geologic maps (U.S.G.S. 2010a; U.S.G.S. 2010b). Glacial SPMs are characterized by glacial activity within the last 14,000 years and are composed of tills or outwash (Kruckeberg 1991). The glacial soils in this study cover many soil series that were classified as Inceptisols, Andisols, and one Alfisol. Sedimentary SPMs consisted of sandstone, siltstone, shale, and marine sediments that formed soils that were classified in the Inceptisol, Alfisol, and Ultisol soil orders. Igneous SPMs were formed from basalt, flow breccias, pumice, and ash. The soil orders of the igneous soils in this study are Inceptisols, Andisols, Spodosols, Alfisols, and Ultisols. Because some soils contained remnants of more than one SPM, the most dominant SPM was chosen. For example, many glacial SPMs in the Washington Cascade Mountains received volcanic ash inputs, but were labeled as glacial because of their soil composition at depth.

2.3.3 Soil Sampling

Soil samples were taken from the center of each installation, but avoided the primary rooting systems of the trees. One soil pit per installation was excavated down to one-meter or until reaching a compacted layer and horizonation was determined (Soil Survey Manual 1993). Bulk density samples were taken for each horizon by the core or clod method, depending on soil texture and hardness (Blake and Hartge 1986). For the core method, one or two 8.5 cm diameter cores per horizon were taken with a sharpened pipe that was hammered horizontally into the undisturbed soil face. Samples collected with the corer were also used for nutrient analysis. Clod samples were taken when the soil was too hard for the core method (Blake and Hartge 1986). For each horizon, multiple clods were chipped off of the undisturbed soil face and bagged. When clods were taken, a separate nutrient sample was retrieved.

Core and nutrient samples were air-dried and sieved to 2-mm. Subsamples of each horizon were removed from the <2-mm fraction for separate nutrient and dry weight analyses. For determination of bulk density using the clod method, three representative clods of each horizon were chosen to access volume using the methods of Blake and Hartge (1986). The volume and weight of the clods were used to determine average horizon bulk density. Bulk density was calculated for both core and clod samples as the weight of <2-mm soil over the total volume of the sample. Mineral soil mass was estimated by multiplying the <2-mm fraction of soil mass by the bulk density and depth of the soil horizon.

2.3.4 Nutrient Analysis

One forest floor sample was excavated per installation above the soil pit from a 0.5-m^2 area to the top of the mineral soil horizon. Forest floor samples were oven-dried to constant weight at 65^0 C and a 20-40-g subsample was removed for nutrient analysis. Any rocks and mineral soil were separated from the organic matter and used to estimate total weight of the forest floor without rocks and mineral soil.

Mineral soil samples were pre-ground by hand with a mortar and pestle, while forest floor were fine-ground to 100-mesh in a Wiley Mill. Both samples were analyzed for total carbon and nitrogen using a Perkin-Elmer CHN Analyzer (Model 2400, Norwalk, CT). Per-hectare soil C and N contents were calculated from nutrient concentration and mineral soil mass. Forest floor C and N contents were determined by nutrient concentrations and dry weight per area.

2.3.5 Soil Characteristics

Soil nutrient regimes were determined using the “Key to Soil Nutrient Regimes” from Green and Klinka (1994). Five soil nutrient regimes (very poor, poor, medium, rich, and very rich) have been classified in British Columbia based on soil depth, texture, wetness, color, and forest floor type. These soil and forest floor variables were determined for each installation through visual inspection of the soil and forest floor and soil nutrient regime was determined.

Soil texture was measured with the hydrometer method (Gee and Bauder 1986) on samples taken at 5-cm and 50-cm depths in the soil profile. The soil texture depths were chosen because they allowed a comparison of rooting zone soil textures that could be compared across all of the installations because soil horizonation was highly variable.

Soil effective depth and depth of the A horizon were determined to compare to Steinbrenner’s (1979) soil classification study. Effective depth is the depth of the soil profile minus the volume of rocks and gravel. Depth of A horizon is the total depth of all A, AB, and BA horizons in the soil profile if they were present.

2.3.6 Climate

Summer precipitation and Hargreaves climatic moisture deficit was estimated using data from ClimateWNA (Wang et al. 2010). The average summer (June, July, and August) precipitation from 1990-2009 was determined for each installation. Annual climatic moisture deficit (1990-2009) is measured as the difference between monthly evaporation and precipitation (Wang et al. 2010).

2.3.7 Statistics

A one-way ANOVA with an alpha of 0.10 was used to test differences between climate, site characteristics, soil characteristics, and soil nutrients by SPMs and SNRs (R Studio, Version 0.95.89, 2011). Multiple pairwise comparisons of means were made using the Tukey test.

2.4 RESULTS

Of the 60 stands investigated in this study, 27 were determined to be of glacial origin, 14 of igneous origin, and 19 of sedimentary origin. SPMs, as determined by soil and geologic maps, were in agreement with soil pit observations for all but 3% of the installations. The SNRs found in this study were medium, rich, and very rich; no soils keyed to poor or very poor. Half of the soils in this study keyed to the rich SNR.

2.4.1 Site Characteristics

SPMs formed over significantly different time periods ($p<0.001$, Table 2.1). Sedimentary and igneous SPMs were deposited over 20-30 million years ago, while glacial SPMs were deposited less than 13,000 years ago. Igneous SPMs were found at the highest elevations while glacial SPMs were at the lowest elevations ($p<0.001$). Percent slope, however, was not significantly different between parent materials ($p=0.277$).

Parent material ages were significantly different between SNRs (Table 2.1); very rich SNR parent materials were significantly older than those from the medium and rich SNRs ($p<0.001$). However, slope and elevation were not significantly different between SNRs ($p=0.169$ and $p=0.841$, respectively).

Average summer precipitation (total of June, July, and August from 1990-2009) was significantly higher in glacial SPM installations than in sedimentary SPM installations ($p=0.003$, Table 2.1). Rich SNR installations received significantly higher summer precipitation than very rich SNR installations ($p<0.001$). Climatic moisture deficit was significantly greater on sites with sedimentary SPMs than those with glacial SPMs (p=0.005). Very rich SNR sites received greater climatic moisture deficits than those with medium or rich SNRs (p=0.003).

2.4.2 Soil Characteristics

Soil effective depth and depth of the A horizon were significantly different by SPMs and SNRs (Table 2.1). Sedimentary SPMs had significantly greater effective depths than igneous and glacial SPMs ($p<0.001$). Similarly, effective depth was significantly different between all three SNRs ($p<0.001$). Soil A horizon depth was significantly lower in glacial SPMs than in igneous and sedimentary SPMs (*p*=0.003). The very rich SNR soils contained greater A horizon depths than the rich and medium SNR soils (*p*=0.002).

Soil texture differences were also found between soils of sedimentary, glacial, and igneous SPMs. Clay particle percentage at the 5-cm soil depth was significantly greater in igneous and sedimentary SPM soils than in glacial SPM soils (*p*=0.005, Figure 2.2A). At 50-cm, all SPM soils contained significantly different clay percentages (*p*<0.001). Sand particle percentage at 5-cm was significantly greater in glacial SPM soils than in sedimentary and igneous SPM soils (*p*<0.001). At 50-cm, sand percentage was significantly different between all SPMs (*p*<0.001).

Like SPMs, SNRs separated soils with different textures. The very rich SNRs contained significantly lower sand percentage at 5-cm and 50-cm than the medium and rich SNRs (*p*<0.001, Figure 2.2B). At 5-cm and 50-cm, clay percentages were significantly different between all SNRs (*p*<0.001).

2.4.3 Soil Nitrogen and Carbon

Mineral soil total nitrogen and carbon varied by SPM throughout the study area (Table 2.1). Soils derived from sedimentary SPMs contained significantly greater N in the mineral soil to one-meter depth (or to the depth of the compacted layer) than those of igneous or glacial SPMs (*p*<0.001). Soils derived of sedimentary SPMs also contained significantly greater C in the mineral soil than those of igneous and glacial SPMs (*p*=0.005).

Mineral soil N contents were 3 and 1.6 times greater in the very rich SNR than in the medium and rich SNRs, respectively (*p*<0.001, Table 2.1). The same relationship was found in soil C contents between medium, rich, and very rich SNRs with the rich SNR containing 2 times more mineral soil C than the medium SNR and the very rich SNR containing 4.8 times more than the medium SNR (*p*<0.001).

SNRs were also able to separate soils with different C and N contents within each different SPM. Within glacial soils, medium and rich SNRs contained significantly different C (*p*=0.007) and N (*p*=0.016); only one soil keyed to the very rich SNR (Figures 2.3A and 2.3B). Igneous soils were keyed as medium, rich, and very rich SNRs. The very rich SNR igneous soils contained significantly greater soil N contents than medium and rich SNRs (*p*=0.011), while the very rich SNR igneous soils only contained greater C content than the medium SNR soils (*p*=0.009). All but three of the sedimentary soils keyed to the very rich SNR. There was no significant difference between soil N and N in rich and very rich SNR sedimentary soils (*p*=0.648 and *p*=0.268, respectively).

Forest floor N and C contents were not significantly different by SPM and were a relatively small percentage of total soil C and N to one-meter soil depth (*p*=0.420 and *p*=0.102, respectively, data not shown). Forest floor C:N ratios were significantly higher in soils of igneous origin than in soils of glacial or sedimentary origin (*p*=0.019, Table 2.1), yet forest floor C:N ratios were not differentiated by SNRs (*p*=0.374). Mineral surface soil C:N ratios were not significantly different between SPMs (*p*=0.155), but were separated by SNRs (*p*=0.013). Whole soil profile C:N ratios were significantly greater in glacial SPM soils than in igneous and sedimentary SPMs (*p*=0.015). The very rich SNR soils had significantly lower whole soil profile C:N ratios than rich and medium SNRs (*p*=0.035).

2.5 DISCUSSION

2.5.1 Site Characteristics

Soil parent materials and SNRs were differentiated by many site characteristics including parent material age, which is very important in the Pacific Northwest because there is a wide variation from 11,000 to 40 million years. Soil parent materials, therefore, represent not only differences in mineral formulation, but differences in time since geologic deposition, which affects rock weathering and soil development. The effect of parent material age is also supported by the differences found in SNRs.

Soils of igneous descent were found at the highest elevations, which is due to their presence in the Cascade Mountain Range. A higher average elevation on igneous sites is evidenced by lower average year-round temperatures and greater precipitation as snow (data not shown, Wang et al 2012) compared to the low elevation sedimentary and glacial SPM soils (Table 2.1). However, there was no difference in elevation between medium, rich, and very rich SNRs, which implies that the difference in climate due to elevation may not be directly related to soil nutrient development. Slope was slightly higher on medium SNRs, though not significantly, which suggests that, at some sites, poor soil quality (as determined by SNRs) is due to erosion while other sites have poor soil quality for other reasons such as recent glaciation.

Distinct summer precipitation totals and climatic moisture deficits between SPMs and SNRs suggest that climate, as well as differences in parent material types and ages, has a strong effect on soil development (Table 2.1). Therefore, soil development patterns in this region are influenced directly by SPMs, but also by covariation between SPMs and other soil forming factors like climate and slope.

2.5.2 Soil Characteristics

Effective soil depth is an important factor in soils because it describes the amount of soil available to roots, which is important for soil nutrient and water holding capacity. Similarly, the depth of the A horizon determines the development of the organic-mineral horizon and extent of this nutrient-rich horizon. Previously, glacial SPM soils have been found to contain lower effective depth and A horizon depth than in residual (sedimentary and igneous SPM) soils (Steinbrenner 1979). Effective depth and depth of A horizon have also been positively correlated with Douglas-fir site index in the Pacific Northwest (Steinbrenner 1979; Miller et al. 1989). Therefore, in this study, it is expected that the ranges of effective depth and depth of A horizon within SPMs and SNRs will correspond with forest productivities. The effects of these soil characteristics on forest productivities in this study will be measured in the future.

Soil texture, specifically the percentages of clay and sand in the soil, determines how water is stored in the soil after rainfall and how quickly it is depleted through root uptake or gravity (Rawls et al. 1982; Warren et al. 2005). Glacial SPMs and medium SNRs contained high sand contents at both depths and adequate summer precipitation, which suggests that these soils allow easy uptake of water by roots, but experience rapid drainage. Sedimentary SPMs and very rich SNRs experienced the lowest summer precipitation and greatest climatic moisture deficits, but the clay to clay loam texture of these soils suggests a much higher soil water holding capacity than the sandy clay loam and sandy loam soils of the glacial SPMs and medium SNRs (Rawls et al. 1982). Igneous SPMs and rich SNRs had clay loam and sandy clay loam soil textures (respectively), high summer precipitation, and moderate climatic moisture deficits, which suggests that these soils may have the highest summer soil water availability. A high soil water holding capacity is necessary for the productive growth of Douglas-fir in the dry summer months of the Pacific Northwest (Carter and Klinka 1990).

2.5.3 Soil Nitrogen and Carbon

The three contrasting SPMs, in which the soils in this regional study formed, produced distinct mineral soil N and C contents due to the time and climate since the parent materials were formed and/or deposited. For instance, the sedimentary SPMs in this study were laid down over a 6 million year period, while igneous parent materials were deposited over a 21 million year period and in some cases were covered with ash and pumice more recently (U.S.G.S. 2010a; U.S.G.S. 2010b). In contrast, the glacial soils were laid down as glacially-resistant rocks between 11,000-14,000 years ago (Kruckeberg 1991).

Differences in soil N content have been found previously between SPMs in the Pacific Northwest (Turner et al. 1979; Kabzems and Klinka 1987a) and elsewhere (Turner and Lambert, 1986), but high variability has been observed. The glacial, igneous, and sedimentary SPMs in this study formed from distinctly different rock types, ages, elevations, and climates. Because of these differences a chronosequence or lithosequence cannot be investigated with these sites. However, identifying SPMs appears to be a convenient method to examine how site and soil characteristics relate to soil nutrition and therefore site productivity in the Pacific Norhwest. The actual effects of SPMs on forest productivity will be measured and reported for this study when it becomes available.

Soil nutrient regimes (Green and Klinka 1994) effectively determined soil N and C contents in these Pacific Northwest soils. Soil nutrient regimes have been used in British Columbia forestry for decades to explain soil nutrients (Kabzems and Klinka 1987a) and site productivity (Kabzems and Klinka 1987b). Soil nutrient regimes use visual and textural characteristics that are typical of soils with high nutrient availability that can be easily determined from a mapped soil series or soil pit. Based on the results of this study, SNRs are an alternative to the SPM classifications to understand soil nutrition and site productivity throughout the Pacific Northwest. Forest productivity as determined by SNRs will be examined for this study in the future.

Soil parent materials were able to separate forest floor and whole-soil C:N ratios, while SNRs separated mineral surface soil and whole-soil C:N ratios. Identification of forest floor C:N ratios and surface soil C:N ratios is important because these ratios have been found to be predictors of Douglas-fir fertilizer response in the Pacific Northwest (Peterson et al. 1984; Miller et al. 1989).

2.5.4 Comparisons

These Douglas-fir plantations have experienced up to two previous harvests, yet many soils still hold large pools of total soil C and N to a depth of one-meter. The fact that SPMs and SNRs differentiate soil N and C contents suggests that foresters can easily estimate forest soil nutrient reserves with either of these two methods. With this information, stands that are nutrient limited can potentially be identified and steps can be taken to retain nutrients on the site though management techniques that conserve soil nutrients or to increase nutrients through fertilization.

Although SPMs and SNRs both separated soil N and C contents, all three SNRs were separated while igneous and glacial SPMs could not be separated. The lowest soil N contents were found in the medium SNR (4,726 kg N/ha). The ability to locate soils with low nitrogen contents is important because soils that contain less than 4,500 kg N/ha have been identified as containing inadequate soil N for tree uptake (Heilman and Gessel 1963).

While SNRs are more efficient at separating soils with different C and N contents, SPMs are more easily identified with a basic understanding of geology and the use of soil or geology maps. Soil nutrient regimes require an examination of the landscape and soil of a site, which can make distinguishing SNRs difficult over a large landscape, but valuable at a smaller spatial scale such as a tree farm. Soil nutrient differences within each SPM, however, can be separated using SNRs to improve the estimation of Douglas-fir plantation soil nutrient reserves.

2.6 CONCLUSIONS

Distinct climates, site characteristics, soil characteristics, and soil N and C contents are represented within the different SPMs and SNRs in the Pacific Northwest. Within this region, data from this study could be applied to forests with similar SPMs and SNRs to understand soil characteristics such as effective depth, depth of A horizon, carbon to nitrogen ratios, soil texture, and soil carbon and nitrogen contents to improve a forest manager’s understanding of water holding capacity, soil nutrient reserves, harvest impacts, and fertilizer growth response.

Table 2.1. Stand Management Cooperative paired-tree fertilization installation site and soil characteristics averages (in bold) and standard error (in parentheses) by soil parent material and soil nutrient regime. Parent materials and soil nutrient regimes with different lowercase letters are significantly different ($p<0.10$).

Soil Parent Material	Average Summer Precipitation (mm)*	Climatic Moisture Deficit (mm)*	Geologic Age[†]	Slope (%)	Elevation (m)	Effective Depth[‡] (cm)	Depth of A horizon[‡] (cm)	Nitrogen (kg N ha^{-1})	Carbon (Mg C ha^{-1})	Forest Floor C:N Ratio	Surface Soil C:N Ratio	Soil Profile C:N Ratio
Glacial	**152** (8) a	**248** (13) a	**12370** (385) a	**12** (3)	**176** (18) a	**63** (4) a	**17** (2) a	**7327** (929) a	**125** (16) a	**32** (2) a	**22** (1)	**19** (1) a
Igneous	**134** (13) ab	**295** (35) ab	**22 million** (3 million) b	**17** (3)	**612** (74) c	**74** (6) a	**28** (4) b	**9483** (1253) a	**137** (14) a	**40** (3) b	**21** (1)	**16** (1) b
Sedimentary	**105** (9) b	**350** (26) b	**38 million** (1 million) c	**16** (3)	**341** (44) b	**95** (2) b	**30** (3) b	**13254** (1064) b	**196** (14) b	**30** (2) a	**19** (1)	**15** (1) b
Soil Nutrient Regime[§]	Average Summer Precipitation (mm)*	Climatic Moisture Deficit (mm)*	Geologic Age[†]	Slope (%)	Elevation (m)	Effective Depth[‡] (cm)	Depth of A horizon[‡] (cm)	Nitrogen (kg N ha^{-1})	Carbon (Mg C ha^{-1})	Forest Floor C:N Ratio	Surface Soil C:N Ratio	Soil Profile C:N Ratio
Medium	**129** (7) ab	**264** (11) a	**8 million** (4 million) a	**20** (6)	**317** (65)	**54** (7) a	**18** (4) a	**4726** (799) a	**71** (9) a	**37** (3)	**23** (2) a	**18** (2) ab
Rich	**153** (9) a	**258** (19) a	**11 million** (3 million) a	**11** (2)	**349** (55)	**73** (4) b	**20** (2) a	**8799** (813) b	**148** (13) b	**33** (2)	**21** (1) a	**18** (1) a
Very Rich	**103** (9) b	**359** (25) b	**35 million** (2 million) b	**15** (3)	**307** (39)	**94** (1) c	**33** (3) b	**14025** (1045) c	**201** (14) c	**32** (2)	**19** (1) b	**15** (1) b

*Average June, July, and August precipitation (1990-2009) and climatic moisture deficit from ClimateWNA (Wang et al 2010)

[†] Determined from U.S.G.S. Geologic Maps (U.S.G.S. 2010a; U.S.G.S. 2010b)

[‡] As defined by Steinbrenner (1979)

[§] According to Green and Klinka (1994)

Figure 2.1. Location of Stand Management Cooperative paired-tree installations in the Pacific Northwest by soil parent material type. Markers designate soil parent material type: glacial (dark shading with dot), igneous (dark shading no dot), and sedimentary (light shading no dot). Image courtesy of Google (2011).

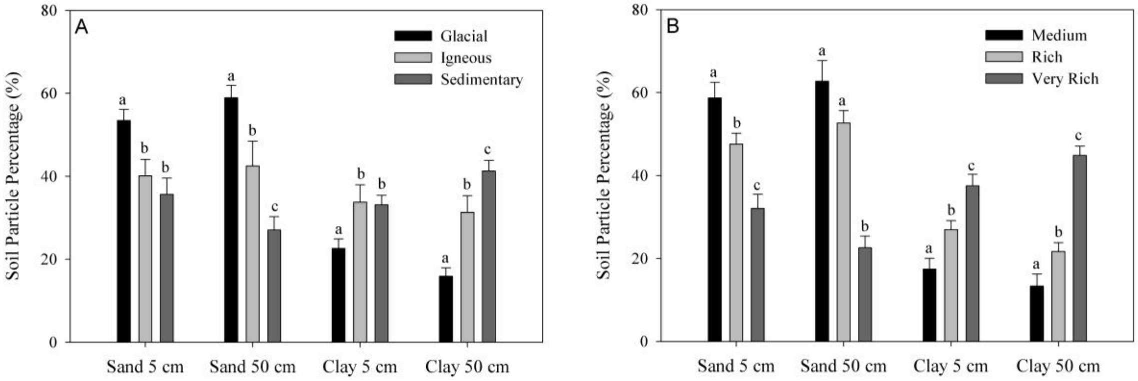


Figure 2.2. Soil particle percentages of Stand Management Cooperative paired-tree fertilization installation soils by particle size (sand or clay), depth (5 or 50 cm), and soil parent material (A) or soil nutrient regime (B, Green and Klinka, 1994) with standard error. Bars with different lowercase letters are significantly different ($p<0.10$) within each soil particle and depth type.

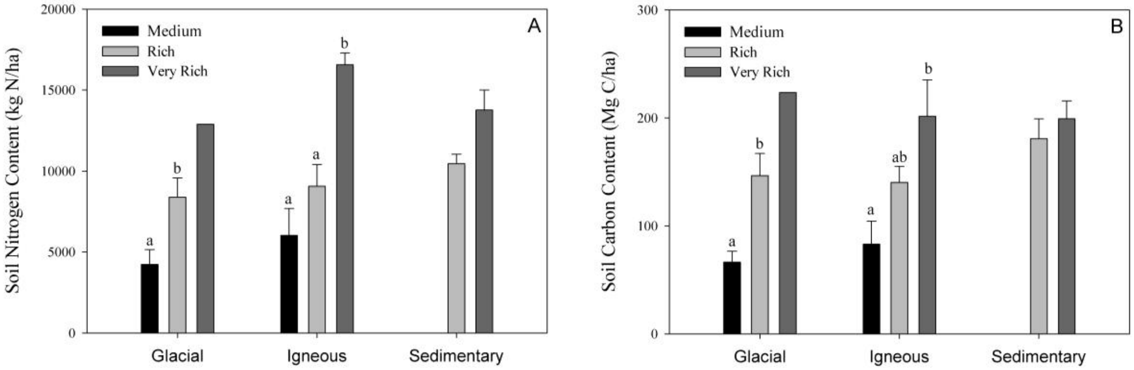


Figure 2.3. Soil nitrogen (kg N/ha) (A) and carbon (Mg C/ha) (B) contents in the Stand Management Cooperative paired-tree fertilization installations by soil parent material and soil nutrient regimes with standard error. Bars with different lowercase letters are significantly different ($p<0.10$) within soil parent material type. Bars with no error bars represent single data points.

CHAPTER 3. DOUGLAS-FIR SITE AND SOIL PRODUCTIVITY AND NITROGEN FERTILIZER RESPONSE ACCORDING TO DIFFERENCES IN SOIL PARENT MATERIALS AND CLIMATES IN THE PACIFIC NORTHWEST

3.1 ABSTRACT

Soil parent materials (SPMs) within the Pacific Northwest are known to result in distinctly different soil characteristics and nitrogen availability, but it is not well known how differences in SPMs and regional climates effect the growth of coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Seasonal climate, soil texture and depth, and soil water and nitrogen availability and Douglas-fir foliar, site index, growth rate, and fertilizer response properties were examined on sixty coastal Douglas-fir research plantations. Evaluations included using soil parent materials (SPMs: glacial, igneous, sedimentary) alone and split by region (RSPMs) (British Columbia, Washington, and Oregon), which provide a finer-scaled examination on the effects of climate, to determine trends in biogeoclimatic properties. Glacial SPMs received greater summer precipitation than sedimentary SPMs. Sedimentary SPMs had the highest summer soil water and soil nitrogen (N) contents, while northern glacial SPMs had the lowest soil water and N contents. Glacial SPMs were identified as having the lowest soil productivity and lowest foliar N concentration and needle areas yet had high site index estimations, height:DBH ratios, and volume mean annual increments, which suggests an effect of stockability on tree growth allocation. Periodic annual increments were not different by SPMs, but growth percent appeared to be affected by the different stand ages of SPMs. Igneous SPMs and British Columbia glacial RSPMs were identified as having the lowest seasonal temperatures, which led to higher forest floor C:N ratios and greater fertilizer response, due to low mineralization and decomposition rates. Soil and site productivity were not exclusively related in Douglas-fir forests due to the effects of climate on N availability and stockability on tree growth.

3.2 INTRODUCTION

The coastal Pacific Northwest has a wide variety of soils and varying climates, yet supports one primary plantation tree species, coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). However, Douglas-fir plantation productivity varies greatly throughout the region due to different site and soil properties (Steinbrenner 1979; Edmonds and Hsiang 1987; Miller et al. 1989).

Two reasons soil characteristics differ throughout the region are the variety of soil parent materials (SPMs) and climates (Steinbrenner 1979; Franklin and Dyrness 1988; Chapter 2). Three common categories of parent materials formed over very different geologic ages: sedimentary SPMs formed around 38 million years ago, igneous SPMs about 22 million years ago, and glaciers deposited new parent materials around 12,000 years ago (Kruckeberg 1991; Chapter 2). Partly due to these parent material age differences, glacial soils have been found to have coarser soil textures and less soil nitrogen (N) than sedimentary soils, while igneous soils have properties that are moderate between glacial and sedimentary soils (Steinbrenner 1979; Chapter 2).

Additionally, the coastal Pacific Northwest covers a large latitudinal range (42°N-50°N), resulting in large climatic differences throughout the region and the proximity of the Pacific Ocean, Coast Range, and the Cascade Mountains strongly affect local climate (Franklin and Dyrness 1988). Because parent materials are found in areas of the Pacific Northwest with different landscapes and latitudes they receive different summer precipitation and moisture deficits; for example, sedimentary SPMs generally receive less summer precipitation and have higher moisture deficits than glacial SPMs (Chapter 2).

Because distinct climate, site, and soil properties were found on different SPMs (Steinbrenner 1979; Chapter 2), it is likely that Douglas-fir growth will be different on SPMs. The latitudinal extent of the Pacific Northwest is likely causing differences in temperature and precipitation that could be affecting the weathering of soils from different parent materials in the different states and provinces of the region (British Columbia, Washington, and Oregon) (RSPMs).

The objective of this research was to use SPMs and RSPMs to 1) characterize biogeoclimatic properties and fertilizer response in Douglas-fir plantation forests throughout the coastal Pacific Northwest region. We tested the following hypotheses: 1) Douglas-fir stands on different SPMs and RSPMs have distinct climates, soil texture, forest floor and soil N pools, 2) SPMs and RSPMs can differentiate forest productivity according to foliar properties, site index, growth rate, and fertilizer response, and 3) RSPMs describe areas with different biogeoclimatic properties and fertilizer response better than SPMs due to the additional effects of climate.

3.3 MATERIALS AND METHODS

The Stand Management Cooperative, a cooperative of forest product companies, universities, and government agencies, installed paired-tree plots in 60 Douglas-fir plantations beginning in 2008. Plots were installed in the region from northern Vancouver Island to southern Oregon to characterize site and soil characteristics that might predict Douglas-fir fertilizer response (Figure 3.1). Based on availability from government agencies and forest product companies, plots were established over three years on a range of latitudes, elevations, slopes, and position on slope (Chapter 2). Plots covered an area of 1.1-ha and contained predominantly plantation Douglas-fir trees.

Paired-tree plots were established with 48 dominant and co-dominant selected Douglas-fir on a 15-meter grid during the winter seasons of 2007-2009 (Figure 3.2A). Pre-treatment diameter at breast height (DBH), total height, height to live crown, and any unusual environmental factors (presence of alder, canopy openings, etc) were measured for each plot-tree. Selected plot-tree pre-treatment dimensions ranged between 18-33 cm in DBH and 11-26 meter height. Twelve to twenty pairs of plot-trees were chosen according to similar DBHs and crown length, which is the difference between height and height to live crown (Figure 3.3). One plot-tree from each pair was randomly chosen to be fertilized with 224-kg N ha^{-1} in the spring. The treatment area around each plot-tree was a 78.5-m^2 circle (Figure 3.2B).

3.3.1 Climate and Soil Characteristics

A combination of United States Geological Survey maps (U.S.G.S. 2010a; U.S.G.S. 2010b), Natural Resources Conservation Services (NRCS) soil series descriptions (Soil Survey Staff 2010), and soil pit observations were used to characterize SPMs, which are described in detail in Chapter 2. Three basic SPMs (glacial (GLA), igneous (IGN), and sedimentary (SED)) were determined from the mapped and described sources (Table 3.1). Soil parent materials were divided into RSPMs depending on which state or province they were located (British Columbia (BC), Washington (WA), and Oregon (OR) (Table 3.1). Analysis of sand and clay contents, effective soil and A horizon depths, N and C contents, and C:N ratios were previously described in Chapter 2 (Table 2.1). Effective depth is defined as the depth of the soil to one-meter minus the volume of rocks. A horizon depth is defined as the sum of A, AB, and BA horizons for each soil (Steinbrenner 1979).

For the years of 1990-2009, seasonal air temperature and precipitation were determined for each plot through the ClimateWNA program (Version 6.62, University of British Columbia, Vancouver, BC) (Wang et al. 2012). Yearly seasonal air temperature and precipitation were averaged for each plot (Table 3.2).

Daily volumetric soil water content (%) at 5-cm and 50-cm depth in the mineral soil was measured using Decagon soil moisture sensors (EC-5 Soil Moisture Sensors, Decagon Devices, Pullman, WA). Soil moisture pits were dug to 60-cm depth and sensors were installed on the uphill site of the pit into the undisturbed soil face. Because soil moisture sensors were installed over different time periods, only soil moisture data from the spring and summer of 2010 were used to keep the effect of climate on soil moisture the same on each plot. The lowest summer volumetric soil water content (%) from soil moisture sensors at 5-cm and 50-cm were defined as lowest soil moisture at 5-cm and 50-cm (Table 3.3). If there were soil moisture sampling errors in 2010, the average of the lowest summer volumetric soil water content from 2009 and 2011 were used. The difference between field capacity and lowest soil moisture content multiplied by the amount of soil not filled with rocks was defined as an index of plant available water (Equation 1, Table 3.3):

$$Plant\ Available\ Water\ (mm) = \left(Field\ capacity\ (\%) - Lowest\ soil\ moisture\ (\%)\right) * 100\ mm\ (soil) * (1 - Rock\ volume\ (\%)) \quad (1)$$

Field capacity was recorded in the spring as the average volumetric soil water content held in the soil 2 days after a rain event. Rock volume was determined from the oven-dry weight and density of soil rocks using a pycnometer for small rocks and wax-dipped displacement of large rocks. Two 10-cm soil depths surrounding the soil moisture sensors (0-10 cm and 45-55 cm) were used to classify plant available water in the soil around the soil moisture sensors. Lowest soil moisture and plant available water at 5-cm and 50-cm were used to describe summer soil water availability at each plot.

3.3.2 Foliage and Tree Characteristics

Six unfertilized plot-trees were randomly chosen for foliar analysis from the 12-20 unfertilized plot-trees per plot. During the fall season two-years after plot installations, foliar samples were taken from the upper crowns of six plot-trees by cutting or shooting. Branch and foliar samples were stored at 3^{o} C until ready for analysis. Foliage was removed from branches and an equal number of average-sized current-year needles were selected from each tree for a total of 100 needles per plot for needle area analysis. The wet weight of 100 needles was recorded and the needles were placed on a clear sheet without overlapping for needle area analysis. Needle area was defined as the projected area of 100 needles (Table 3.3). Needle sheets were sent through a leaf area meter (Leaf Area Meter LI-3100, Li-Cor Biosciences, Lincoln, NE) five times and the measured areas were averaged to determine needle area for each plot. The remaining foliage was combined and dried at 65 ^{o} C for two days. The dried foliage was ground to 1-mm in a Wiley Mill and analyzed for N concentration (CHN Analyzer 2400, PerkinElmer Inc., Waltham, CT) (Table 3.3).

Breast height age was measured as the average plot tree breast height age (1.3-m) of five trees per installation at the time of plot establishment (2008-2011). King's site index (King 1966) was calculated using the average height of the ten trees with the greatest diameters at breast height from the 40 selected plot-tree Douglas-fir in that installation (Hanson et al. 2002) (Table 3.4). Nigh's site index (Nigh 1997) was calculated using the average height of the plot-tree Douglas-fir with the top three greatest diameters at breast height for each installation of 40 trees (Table 3.4). To determine Flewelling's site index, the mean height of the 24-40 plot trees and total tree age was measured and entered into the DFSITE program (Flewelling et al. 2001) (Table 3.4).

Average height (m) and DBH (m) of plot-trees at the time of plot installation were converted to height:DBH ratio (Table 3.4). The basal area growth of plot-trees was divided by breast height age to determine basal area mean annual increment (MAI) for each plot (Table 3.4).

Volume MAI was determined from the average plot-tree volume determined from the equations of Bruce and DeMars (1974) divided by stand age at breast height (Table 3.4).

Two-year fertilization response was measured during the fall two years after application. The two-year change in diameter at breast height and total height were recorded for each plot-tree. Average control plot-tree basal area and height growth after two years were recorded and converted to periodic annual increment (PAI). Volume at the start of the study and after two growing seasons was determined from the equations of Bruce and DeMars (1974) and converted to average control plot-tree volume PAI. The average plot-tree two-year percent change in growth at each plot was determined as the percent change in control-tree basal area, height, and volume measurements before and after plot installation. Control-tree basal area, height, and volume PAI and percent growth were compared across all plots to determine the current growth rate of non-treated trees (Table 3.5).

The average two-year basal area, height, and volume growth differences between fertilized and control paired-trees were recorded for each plot to determine fertilizer growth response (Table 3.5). Fertilizer percent response was measured as the average percent difference in basal area, height, and volume growth between paired fertilized and control trees at each plot (Edmonds and Hsiang 1987) (Table 3.5).

3.3.3 Statistics

Annual and seasonal climate, soil textures, soil water, and soil N characteristics were compared for each SPM and RSPM through a one-way ANOVA in the R Statistical Software (R version 4.13.0, R Development Core Team 2011). Plot-averaged Douglas-fir stand variables, foliar properties, productivity variables, growth rates, and fertilizer response values were also compared by SPMs and RSPMs using a one-way ANOVA in the R Statistical Software (R version 4.13.0, R Development Core Team 2011). Significant differences between climate, soil, and tree characteristics were determined using an alpha of 0.10. For each significant ANOVA test, a Tukey honest significant difference test was used in the R Statistical Software (R version 4.13.0, R Development Core Team 2011) to determine which SPMs and RSPMs were significantly different at an alpha of 0.10.

3.4 RESULTS

3.4.1 Climate and Site Characteristics

A wide range in seasonal precipitation and temperatures occurred over the last 20 years on sites with different SPMs and located in different regions (states and provinces) (Table 3.1). However, spring and autumn precipitation and summer temperatures were not significantly different between SPMs and RSPMs ($p>0.10$, data not shown). Glacial and sedimentary SPMs experienced significantly different winter and summer precipitation; glacial SPMs had the lowest winter precipitation while sedimentary SPMs had the lowest summer precipitation. Igneous SPMs had significantly lower winter, spring, and autumn temperatures than sedimentary SPMs.

Some climatic differences were found between soil parent materials in different regions (Table 3.1). Oregon plots had significantly lower summer precipitation regardless of SPMs. Washington glacial RSPMs had significantly higher winter, spring, and autumn temperatures than BC glacial RSPMs and were closer in temperature to OR sedimentary RSPMs. Washington sedimentary RSPMs had significantly lower autumn temperatures than OR sedimentary RSPMs.

Significantly different site characteristics were found on distinct SPMs and RSPMs (Table 3.1). Igneous SPMs had the highest elevations while glacial SPMs had the lowest elevations. Slope was not found to be significantly different by SPMs, but BC glacial RSPMs had greater slopes than WA glacial and WA sedimentary RSPMs.

3.4.2 Soil, Water, and Nitrogen Characteristics

Distinct differences in soil characteristics were also found between SPMs and RSPMs (Table 3.2). Glacial SPMs had significantly lower clay contents and higher sand contents at 5-cm and 50-cm than sedimentary SPMs. However, when considering RSPMs, WA glacial soils had lower sand contents and higher clay contents than BC glacial soils. Sedimentary SPMs had finer soil textures at 50-cm and greater effective soil depths than igneous and glacial SPMs, but only glacial SPMs had thinner A horizon depths than igneous and sedimentary SPMs.

Soil water and N contents were found to be significantly different between SPMs and RSPMs due to differences in soil characteristics and climate (Table 3.3). Sedimentary SPMs held a greater amount of summer soil moisture (5-cm and 50-cm) and had higher plant available water (5-cm) than glacial SPMs. In RSPMs, BC glacial soils held the lowest amount of summer soil moisture (5-cm and 50-cm) compared to the finer textured OR igneous and sedimentary soils. However, OR igneous RSPMs had less plant available water at 5-cm depth than OR sedimentary RSPMs. Plant available water at 50-cm was not significantly different by SPM or RSPM (data not shown).

Glacial SPMs, especially those in BC, had lower total soil N contents than other SPMs (Table 3.3). Mineral surface soil C:N ratios were higher in BC glacial RSPMs than in WA glacial and all other RSPMs. Soil parent materials and RSPMs yielded inconsistencies in forest floor C:N ratio differences; igneous SPMs had significantly higher forest floor C:N ratio than glacial and sedimentary SPMs, while BC glacial and OR igneous RSPMs had the highest forest floor C:N ratios.

3.4.3 Douglas-fir Characteristics

Sedimentary SPMs were found to have a lower stand age than the rest of the installations, which was due to stand selection based on canopy closure and is partially related to the site productivity of SPMs and RSPMs (Table 3.2). Specifically, OR sedimentary RSPMs had a lower stand age than glacial SPMs and WA igneous RSPMs. Stand density was also different between SPMs and RSPMs. Glacial SPMs had lower Douglas-fir stand density than sedimentary SPMs, but there were no significant differences between RSPMs. When all tree species stand density was measured, only BC glacial RSPMs contained higher stand densities than WA igneous RSPMs.

Foliar N concentrations and needle areas were significantly lower in trees growing on glacial SPMs than sedimentary SPMs (Table 3.4). However, investigation of RSPMs showed that foliar N concentrations and needle areas were much lower on BC glacial plots than on WA glacial plots.

Glacial SPMs had significantly greater height:DBH ratios than igneous and sedimentary SPM plots (Table 3.4). However, when RSPMs were examined, BC and WA glacial plots were only significantly greater than OR sedimentary plots. All three site index equations designated igneous SPMs as having the lowest site index. Specifically, OR igneous RSPMs were found to have significantly lower site index estimations than WA sedimentary RSPMs. Basal area MAI (15-20 year age range) were not significantly different by SPM or RSPM (data not shown), but volume MAI (15-20 year age range) were found to be lower in sedimentary SPMs than glacial

SPMs. Oregon igneous RSPMs were identified as having significantly lower volume mean annual increment than WA igneous RSPMs.

3.4.4 Two-year Growth Rate and Fertilizer Response

Soil parent materials and RSPMs could not be used to separate average plot-tree basal area PAI (data not shown). However, when split by RSPMs, BC glacial RSPMs had significantly lower height PAI (15-20 year age range) than most RSPMs while OR igneous RSPMs had a significantly lower volume PAI than WA igneous RSPMs (Table 3.5). Glacial SPMs were consistently lower in two-year basal area, height, and volume growth percent. Oregon sedimentary RSPMs had greater two-year height growth percent than WA sedimentary RSPMs.

Igneous SPMs responded to fertilization significantly more than sedimentary and glacial SPMs (Table 3.5). Fertilizer height and volume growth response could not be separated by RSPMs, but OR igneous plots were found to have greater fertilizer basal area growth response than WA glacial installations. Fertilizer basal area and volume percent response were also greater in igneous SPMs than on glacial SPMs. Oregon igneous RSPMs had significantly greater basal area and volume percent response than WA glacial RSPMs.

3.4.5 Climate, Soil, and Douglas-fir Relationships

There were many correlations between climate and soil characteristics and soil water, soil N, and foliar properties (Table 3.6). Total soil N contents were positively related to seasonal temperatures, soil depth, and lowest soil moisture; surface soil C:N ratios were negatively related to these properties. Lowest soil moisture, which represents soil water-holding capacity, and total soil N content were greatest on soils with finer textures. Foliar N was negatively related to surface soil and forest floor C:N ratios, but needle area was not strongly correlated with any climate, soil, soil water, and soil N characteristics.

Douglas-fir site index values were greatest with warmer winter temperatures and lower surface soil and forest floor C:N ratios (Table 3.6). Height:DBH ratios were positively related to stand age, but there was also a negative influence of needle area on height:DBH ratio. Basal area and volume MAI were both negatively influenced by Douglas-fir stand density, but only volume MAI was positively correlated with stand age. Basal area, height, and volume PAI were positively related to basal area MAI. Stand age and height:DBH ratios were the best predictors of basal area, height, and volume growth percent yet there were also positive relationships between soil depth, soil N, and needle area on growth percent. Basal area and volume fertilizer response were greatest due to high forest floor and surface soil C:N ratios, but there were no linear relationships between climate and soil properties and fertilizer height response.

3.5 DISCUSSION

Classification of plots using SPMs and RSPMs defined stands with different climates and soil and site productivities throughout the Pacific Northwest. Although there were significant differences between soil and site properties between SPMs, splitting SPMs by region identified differences within each parent material due to climate.

3.5.1 Climate and Soil Characteristics

Distinct summer precipitation between SPMs and RSPMs were related to latitudinal differences (R^2=0.40, data not shown). Franklin and Dyrness (1988) and Krajina (1959) have previously identified biogeoclimatic regions of the Pacific Northwest with differences in climate and soils. The RSPMs used in this study roughly followed these physiographic regions. The BC glacial stands represent the coastal western hemlock very dry maritime subzone (Green and Klinka 1994). Some of the variation in the WA glacial stands in this study could be due to the combination of the northern Cascades, Puget Trough, and Olympic Peninsula regions (Franklin and Dyrness 1988). Washington igneous sites were concentrated in the southern Washington Cascade region. Sedimentary sites in WA and OR were found in the Coast Range zone and OR igneous sites were split between the western and high Cascades. However, not all SPMs were found grouped together because some sedimentary SPMs were found in the Washington Cascade region and some igneous SPMs were found in the Coast Range zone (Figure 3.1). Therefore, classification by SPM and region (states and province) are mostly designating areas with distinct effects of topography, geology, and climate on site and soil productivity in the Pacific Northwest.

Water availability, using plant available water and lowest soil moisture measurements, was affected by the different soil textures and depths found in SPMs and RSPMs even though they experienced different climates (Tables 3.2 and 3.3). Shallow soil depths and low clay contents led to lower summer soil moisture in glacial SPMs than sedimentary SPMs with BC glacial RSPMs affected the most (Rawls et al. 1982; Warren et al. 2005). Soil water-holding capacity is important because Douglas-fir can continue producing earlywood during the dry summer months on soils that retain available moisture further into the summer (Domec and Gartner 2002; Beedlow et al. 2007; Kantavichai et al. 2010).

Differences between climates, soil textures and depths, and soil water availability in SPMs and RSPMs combined to affect soil N availability throughout the region. Soil N contents and availability have been found to be strongly affected by soil texture and water holding capacity (Kabzems and Klinka 1987a; Klinka and Carter 1990; Prescott et al. 2000), which is supported in this study by the positive correlations between total soil N content and sand content, clay content, and lowest soil moisture at 50-cm (Table 3.6). Accordingly, glacial SPMs had lower total soil N contents than igneous and sedimentary SPMs (Table 3.3). One explanation for the differences in soil N contents between SPMs is the time since geologic deposition of parent materials. Sedimentary parent materials were deposited around 38 million years ago, which yielded more time for parent material weathering and soil development than in igneous and glacial parent materials (deposited 22 million years ago and 12 thousand years ago, respectively) (Kruckeberg 1991; Chapter 2).

However, forest floor C:N ratios did not follow the same trends as total soil N and surface soil C:N ratio (Table 3.3). Instead, igneous SPMs and BC glacial RPSMs had the highest forest floor C:N ratios, which is associated with cooler winter and spring air temperatures in these regions. Low winter and spring temperatures decrease the amount of forest floor flora and microbes that can assist in summer decomposition (Zhang et al. 2010). Forest floor C:N ratios have been found to be predictive of fertilizer response in the Pacific Northwest because it is indicative of organic matter decomposition, mineralization, and plant N availability (Peterson et al. 1984; Edmonds and Hsiang 1987; Prescott et al. 2000).

3.5.2 Douglas-fir Productivity and Fertilizer Response

As a result of the many differences in climate and soils throughout the Pacific Northwest, Douglas-fir site index values have been found to be increased with greater soil moisture and N availability (Miller et al. 1989; Carter and Klinka 1990; Klinka and Carter 1990). However, in this study, site index estimations were high on plots with glacial SPMs, which had the lowest soil moisture and N contents (Tables 3.3 and 3.4).

These high site index values in glacial SPMs were related to significantly greater height:DBH ratios in glacial SPMs than in igneous and sedimentary SPMs (Table 3.4). In other studies, height:DBH ratios have been found to be strongly related to stand density and age (Reukema and Smith 1987; Peracca and O'Hara 2008). While height:DBH ratios were positively correlated with age (Table 3.6) in this study, there was no strong effect of stand density on height:DBH ratio ($R^2<0.01$; data not shown). Instead, height:DBH ratios were negatively related to needle area, which suggests that height:DBH ratios are related to soil water-holding capacity (Grier and Running 1977; Waring et al. 1978). One possible factor in the relationship between foliar properties and height:DBH ratios is the difficulty in accessing upper-canopy foliage in tall trees, but there was a stronger negative correlation between needle area and height:DBH ratio than height alone ($R^2=0.25$ and $R^2=0.10$, respectively; data not shown). Volume MAI of SPMs also followed the trend of height:DBH ratios; glacial SPMs had greater volume MAI than sedimentary SPMs (Table 3.4).

Another explanation for greater height:DBH ratios in glacial SPMs could be due to the difference in stockability of these SPMs due to distinct biogeoclimatic properties. Stockability is defined as the amount and size of trees that a stand can hold based on site productivity (Hall 1983; DeBell et al. 1989). When the average plot stem DBH and heights were mapped according to the stand management graph by Drew and Flewelling (1979), all glacial SPMs were found within the ranges of canopy closure and competition mortality, but the sedimentary and igneous SPMs were mostly under the crown closure line even though stem DBH were within the same range (18-36 cm) (data not shown). This suggests that lower soil water-holding capacity and soil N contents have caused a lower stockability on glacial SPMs compared to sedimentary SPMs with greater water and N availability. Height growth allocation may be greater on glacial SPMs due to the effect of a lower stockability on competition-based height:DBH ratios. Because sedimentary SPMs had lower height:DBH ratios and a greater stockability, more trees could be planted on these soils to increase competition-based height growth. The higher forest floor C:N ratios and lower site index values on igneous soils suggests an negative impact of plant-available N on height growth and increasing stand density would decrease plant-available N.

Another possible explanation of greater height:DBH ratios on glacial SPMs is the strong relationship between soil water availability and earlywood ring growth (Domec and Gartner 2002; Beedlow et al. 2007; Kantavichai et al. 2010). In the dry summer of 2009, the average earlywood basal area growth on 28 plots was positively associated with the date of the first soil depletion event, which is described as the first sharp drop in soil moisture during the summer before refilling with moisture (R^2=0.30, data not shown). The plots that experienced the latest soil drying (September) and grew the greatest amount of earlywood were located in Oregon and received the lowest summer precipitation, while the plots that dried down the earliest (July) and formed the least earlywood were glacial soils with the greatest summer precipitation (Table 3.2; data not shown). Less earlywood growth on glacial SPMs could lead to lower basal area growth, which might shift allocation of assimilates to vertical stem growth. Interestingly, in the wet summers of 2010 and 2011 all plots dried down in the same month (August) and this relationship was not observed.

The climate and soil differences by SPMs were not able to separate differences in basal area, height, or volume periodic annual increments, but growth percent differences were found between SPMs and RSPMs (Table 3.5). Periodic annual increments were also slightly negatively correlated with all species and Douglas-fir stand density (Table 3.6) yet only volume PAI was slightly positively correlated with age. Stand density and age were not used as covariates in this analysis because they were significantly different according to SPM and RSPM (Table 3.2). Stand age at the time of plot establishment was greater in glacial and igneous SPMs because stands took longer to reach canopy closure due to lower soil water and N availability, respectively, than in sedimentary SPMs. Accordingly, greater understory competition on low productivity soils probably led to lower seedling survival of Douglas-fir on glacial SPMs (Devine et al. 2011). This is supported by greater all species stand density in BC glacial RSPMs, which had the lowest soil productivity. Extensive salal (*Gaultheria shallon* Pursh) understories were also found on the poorest glacial SPMs in BC and WA (data not shown). Glacial SPMs also had the lowest basal area, height, and volume growth percent, which is due to the strong effect of stand age on growth percent.

Fertilizer response was greatest in igneous SPMs, but the greatest response to fertilizer was found with OR igneous RSPMs (Table 3.5). Igneous SPMs (and BC glacial RSPMs) also had the highest forest floor C:N ratios, which has been indicative of fertilizer response in the past (Peterson et al. 1984; Edmonds and Hsiang 1987). Fertilizer basal area and volume percent response were also positively correlated with forest floor C:N ratio (Table 3.6), but there was no relationship with forest floor C:N ratios and fertilizer height percent response. Although low plant-available N due to high forest floor C:N ratios appears to be indicative of fertilizer response (Peterson et al. 1984; Edmonds and Hsiang 1987), the finding that igneous SPMs and BC glacial RSPMs responded strongly to fertilization suggests that regional soil parent materials should be used as a selection criteria for fertilization.

3.5.3 Soil Parent Materials by Region

Separation by SPMs resulted in stands with distinct site and soil productivities, but there were some differences within SPMs according to region (Tables 3.2-3.5). It appears that distinct climates and soil characteristics are the causative factors of regional differences in site and soil productivity between SPMs. For example, glacial stands in BC have lower seasonal temperatures and clay contents than glacial stands in WA, which resulted in greater forest floor C:N ratios and therefore greater fertilizer response. However, lower summer precipitation in igneous and sedimentary stands in OR did not yield lower water and N availability and Douglas-fir growth than in WA stands. These findings support the interaction of climate and soils for predicting regional differences in site and soil productivity. Regional soil parent materials are recommended over SPMs alone for determining biogeoclimatic properties and fertilizer response of Douglas-fir forests of the Pacific Northwest due to the combination of climate, site, and soil characteristics that are covered.

3.5.4 Regional Glacial SPMs

Recent glaciation has limited the amount of time for soil development compared to sedimentary and igneous SPMs (Kruckeberg 1991; Chapter 2). Accordingly, glacial SPMs had coarser soil textures than other SPMs, which led to lower soil water-holding capacities in these soils (Table 3.2). However, since glacial SPMs received the highest amount of summer precipitation, soil moisture was replenished frequently throughout the summer. When split regionally, though, BC glacial RSPMs contained more coarse fragments than WA glacial RSPMs. This difference in soil textures suggests that soil water availability is less limiting in WA glacial than BC glacial RSPMs.

Glacial SPMs also had lower soil N availability due to lower total soil N contents than other SPMs (Table 3.3). Furthermore, BC glacial RSPMs may have lower plant-available N because there are higher forest floor and surface soil C:N ratios due to lower winter and spring temperatures than in WA glacial RSPMs (Table 3.2). For example, among all plots, winter and spring temperatures were found to be slightly negatively correlated with mineral surface soil C:N ratios (Table 3.6). The combination of coarse soils, low air temperatures, low soil water holding capacity, and low soil N availability suggest that BC glacial soils have the lowest soil productivity, which is supported by these sites having the lowest foliar N concentrations and smallest needle areas.

In the past, site index values have been found to be lower on Douglas-fir growing on glacial soils than on residual (sedimentary and igneous) soils (Steinbrenner 1979). However, Douglas-fir productivity variables do not follow this trend because site index values, basal area MAI, and volume MAI measurements were not different in BC glacial RSPMs compared to the other RSPMs (Table 3.4). Instead, glacial SPMs had some of the highest site index estimations and volume MAI because height:DBH ratios were greatest in glacial SPMs compared to igneous and sedimentary SPMs.

Glacial stands have high site index values, but WA glacial RSPMs have the second highest site index values while BC glacial RSPMs have the second lowest site index values. The difference in site index between WA and BC glacial RSPMs appears to be caused by the difference in forest floor C:N ratios between stands in WA and BC (28 and 45 C:N, respectively) (Table 3.3). Forest floor C:N ratios were negatively correlated with site index values (Table 3.6) because they are indicative of plant-available N due to rates of mineralization and decomposition (Peterson et al. 1984; Prescott et al. 2000). Washington glacial RSPMs have the lowest forest floor C:N ratios of all RSPMs indicating high N cycling in the forest floor even though total soil N contents are low (8,300 kg N/ha). Accordingly, the RSPMs with the lowest forest floor C:N ratios (WA glacial and all sedimentary stands) have the highest King’s site index values (Table 3.4). These findings support the use of forest floor C:N ratios as an indicator of the N availability of these forests over the use of total soil N contents.

Washington glacial RSPMs did not respond highly to N fertilization (Table 3.5). The high volume MAI and PAI of glacial SPMs suggest that they have been growing as well or better than other stands in the region and additional growth may not be available through N fertilization. British Columbia glacial RSPMs tended to respond better to fertilization than stands in WA, although not significantly better, which further supports the suggestion that there is lower N availability due to the high forest floor and surface soil C:N ratios in BC glacial soils.

3.5.5 Regional Igneous SPMs

Igneous SPMs were characterized as having lower seasonal temperatures than other SPMs (Table 3.2), which is expected because igneous SPMs were located near the Cascade Mountain Range and had the highest elevations (Chapter 2). Regional soil parent materials, however, identified WA igneous stands as receiving much greater summer precipitation than OR igneous stands.

Igneous parent materials are younger than sedimentary parent materials but generally much older than glacial parent materials. Igneous rocks and ash have been weathering for approximately 22 million years forming well-developed soils (Chapter 2). Washington and OR igneous RSPMs had clay loam soil textures that were moderate both in clay and sand contents compared to glacial and sedimentary SPMs and provided adequate soil water availability.

Forest floor C:N ratios were found to be high in igneous SPMs, which suggests that, similar to BC glacial RSPMs, there are limitations in forest floor decomposition in igneous soils due to lower seasonal air temperatures (Table 3.2). Foliar N concentrations in igneous SPMs were also affected by high forest floor C:N ratios because, across all plots, foliar N concentrations were negatively related to forest floor C:N ratio (Table 3.6). Needle areas were not affected by high forest floor C:N ratio, however, because some of the largest needle areas were found on igneous SPMs (Table 3.4).

Igneous SPMs had the lowest site index values even though they were found to have adequate soil water availability (Tables 3.3 and 3.4). These low site index values can be partially tied to lower height:DBH ratios in igneous SPMs than in glacial SPMs even though stand ages were not significantly different. Specifically, OR igneous RSPMs had the lowest site index values and volume mean and periodic annual increments of all RSPMs, but only volume mean and periodic annual increments were different between WA and OR igneous stands (Tables 3.4 and 3.5). Basal area and volume growth percent, however, were higher in igneous stands than in glacial stands, which may be due to the smaller volumes of igneous stands at the time of fertilization.

Igneous SPMs consistently responded to fertilization with greater basal area and volume response in fertilized trees (Table 3.5). In particular, Oregon igneous RSPMs had greater fertilizer absolute and relative basal area, height, and volume response than other SPMs. The finding that most igneous SPMs responded to fertilization is important because fertilization can be focused on these areas. High forest floor C:N ratios have also been indicative of fertilizer response in the past (Peterson et al. 1984; Edmonds and Hsiang 1987).

3.5.6 Regional Sedimentary SPMs

Douglas-fir growing on sedimentary SPMs throughout the Pacific Northwest experienced the highest winter precipitation and seasonal temperatures and the lowest summer precipitation (Table 3.2). Oregon sedimentary RSPMs received lower summer precipitation than WA sedimentary RSPMs, which in turn had lower summer precipitation than other stands in WA. The clay loam (5-cm) and clay (50-cm) soils found in sedimentary SPMs retained soil moisture keeping water availability high even though summer precipitation was low (Tables 3.2 and 3.3). Sedimentary SPMs had the highest total soil N contents, lowest forest floor and surface soil C:N ratios, highest foliar N concentrations, and largest needle areas, which are probably due to the combination of older, more-developed soils, warmer seasonal temperatures, finer soil textures, and higher soil water availability than other SPMs (Steinbrenner 1979; Kruckeberg 1991; Chapter 2).

Stands on sedimentary SPMs had some of the highest site index values even though the lowest height:DBH ratios were found on sedimentary SPMs (Table 3.4). Stand age might be a cause of low height:DBH ratios because the sedimentary stands were significantly younger stands than the other SPMs (Table 3.2). Stand ages were different among SPMs because the higher productivity sedimentary SPMs stands reached canopy closure earlier (a selection criteria for these plots) than the lower productivity stands (Devine et al. 2011).

Even with some of the highest site index values, sedimentary SPMs had a lower volume MAI than igneous and glacial SPMs, but there was no difference in volume PAI (Tables 3.4 and 3.5). Also, due to a younger stand age, sedimentary SPMs had the greatest basal area, height, and volume growth percent. Specifically, OR sedimentary stands had the greatest growth percent of all RSPMs with significantly greater height growth percent in OR sedimentary stands than in WA sedimentary stands.

Similar to glacial SPMs, sedimentary SPMs did not respond well to fertilization (Table 3.5). Nitrogen fertilizer response tends to be lower in highly productive stands because of greater availability of soil N (Miller et al. 1989; Shumway and Olson 1992; Carter et al. 1998). Nevertheless, fertilizer response of high productivity sites is variable and high productivity sites with greater soil water availability have responded to fertilization (Carter et al. 1998). Some sedimentary plots were observed to respond to fertilization, but a link with soil water availability could not be found. Instead, forest floor C:N ratio tended to be the best predictor of fertilizer response in sedimentary plots, where forest floor C:N ratios above 35 yielded a greater than 10% fertilizer volume response, while there was large response variability at sites with a forest floor C:N below 35 (data not shown).

3.6 CONCLUSIONS

Soil parent materials alone and split regionally defined areas with unique climates, site characteristics, and soils with varying textures, depths, water availability, and N availability. Glacial and sedimentary SPMs had different climates with sedimentary SPMs having higher winter precipitation and glacial SPMs having the higher summer precipitation. Overall, sedimentary SPMs had the greatest soil productivity based on soil water and N availability, while glacial SPMs, especially those in BC, had the lowest productivity soils according to soil water holding capacity and soil N contents. Igneous SPMs had moderate soil textures and depths when compared to sedimentary and glacial SPMs, but also had the lowest seasonal air temperatures and highest forest floor C:N ratios. Foliar N concentrations and needle areas were highest in sedimentary SPMs.

Soil productivity of SPMs did not directly translate to tree growth measurements. Glacial SPMs had higher site index values than igneous SPMs due to greater height:DBH ratios, which led to glacial SPMs having the highest volume MAI of all of the SPMs. Differences in height:DBH ratios and site index values appear to be due to differences in stand ages, stockability, and plant-available N between SPMs and RSPMs. There were no differences between PAI and SPMs, but BC glacial stands and OR igneous stands were found to have the lowest height and volume PAI, respectively. Igneous SPMs, especially those in Oregon, responded the best to N fertilization due to higher forest floor C:N ratios. Soil parent materials alone or split regionally in the Pacific Northwest were found to define areas with a distinct mix of climates, soil and site productivities, and N fertilizer response.

Table 3.1. Climate and site properties with means (bold) and standard error (SE) for soil parent materials and regional soil parent materials. Significant differences were defined using p-values from one-way ANOVA. Properties labeled by different lowercase letters within soil parent materials and regional soil parent materials are significantly different (α<0.1).

Properties	Statistics	Soil Parent Material Glacial (GLA)	 Igneous (IGN)	 Sedimentary (SED)	Regional Soil Parent Material British Columbia Glacial (BCGLA)	 Washington Glacial (WAGLA)	 Washington Igneous (WAIGN)	 Oregon Igneous (ORIGN)	 Washington Sedimentary (WASED)	 Oregon Sedimentary (ORSED)
Annual Precipitation*	Mean	**1660**	**1760**	**1820**	**1750**	**1630**	**1970**	**1470**	**1840**	**1790**
	SE	100	140	130	250	110	200	160	160	220
	Sig.	a	a	a	a	a	a	a	a	a
	p-value		0.61				0.51			
Winter Precipitation* (mm)	Mean	**640**	**720**	**800**	**670**	**630**	**790**	**620**	**810**	**800**
	SE	40	70	60	80	50	100	70	80	90
	Sig.	a	ab	b	a	a	a	a	a	a
	p-value		0.09				0.25			
Summer Precipitation* (mm)	Mean	**150**	**130**	**110**	**160**	**150**	**170**	**90**	**140**	**80**
	SE	10	10	10	30	10	10	10	10	10
	Sig.	b	ab	a	b	b	b	a	b	a
	p-value		<0.01				<0.01			
Annual Temperature* (C)	Mean	**10.3**	**9.8**	**10.6**	**9.3**	**10.5**	**9.6**	**10.0**	**10.1**	**11.0**
	SE	0.1	0.3	0.2	0.1	0.1	0.4	0.6	0.2	0.4
	Sig.	ab	a	b	a	bc	ab	ab	abc	c
	p-value		0.05				<0.01			
Winter Temperature* (C)	Mean	**4.3**	**3.4**	**4.7**	**3.1**	**4.6**	**3.3**	**3.6**	**4.1**	**5.3**
	SE	0.2	0.4	0.3	0.2	0.1	0.5	0.7	0.2	0.4
	Sig.	b	a	b	a	bc	a	ab	abc	c
	p-value		0.01				<0.01			
Spring Temperature* (C)	Mean	**9.4**	**8.6**	**9.6**	**8.2**	**9.8**	**8.5**	**8.6**	**9.3**	**9.8**
	SE	0.1	0.4	0.3	0.1	0.1	0.4	0.7	0.3	0.4
	Sig.	b	a	b	a	bc	ab	abc	abc	c
	p-value		0.02				<0.01			
Autumn Temperature* (C)	Mean	**10.5**	**10.4**	**11.1**	**9.5**	**10.8**	**10.1**	**10.8**	**10.5**	**11.7**
	SE	0.1	0.3	0.2	0.2	0.1	0.3	0.4	0.2	0.3
	Sig.	ab	a	b	a	bc	ab	b	b	c
	p-value		0.03				<0.01			
Elevation (m)	Mean	**180**	**610**	**340**	**190**	**170**	**550**	**690**	**320**	**360**
	SE	20	70	40	30	20	80	140	60	60
	Sig.	a	c	b	a	a	bc	c	ab	ab
	p-value		<0.01				<0.01			
Slope (%)	Mean	**12**	**17**	**16**	**28**	**7**	**19**	**15**	**12**	**19**
	SE	3.0	3.0	3.0	8.0	2.0	6.0	2.0	4.0	4.0
	Sig.	a	a	a	b	a	ab	ab	a	ab
	p-value		0.40				<0.01			

* Wang et al (2012)

Table 3.2. Field-measured stand and soil properties with means (bold) and standard error (SE) for soil parent materials and regional soil parent materials as defined in Table 3.1. Significant differences were defined using p-values from one-way ANOVA. Properties labeled by different lowercase letters within soil parent materials and regional soil parent materials are significantly different (α<0.1).

Properties	Statistics	Soil Parent Material			Regional Soil Parent Material					
		GLA	IGN	SED	BCGLA	WAGLA	WAIGN	ORIGN	WASED	ORSED
Stand Age (years)	Mean	**19**	**19**	**16**	**21**	**19**	**20**	**17**	**17**	**15**
	SE	0.5	1.1	0.6	1.3	0.5	1.4	1.4	0.9	0.9
	Sig.	b	b	a	c	bc	bc	ab	ab	a
	p-value	<0.01			<0.01					
All-species Stand Density (trees ha^{-1})	Mean	**930**	**910**	**980**	**1120**	**880**	**850**	**990**	**1060**	**920**
	SE	40	60	40	90	40	80	100	70	50
	Sig.	a	a	a	b	ab	a	ab	ab	ab
	p-value	0.57			0.05					
Douglas-fir Stand Density (trees ha^{-1})	Mean	**750**	**800**	**870**	**800**	**730**	**740**	**870**	**890**	**860**
	SE	30	50	30	60	30	70	60	40	40
	Sig.	a	ab	b	a	a	a	a	a	a
	p-value	0.02			0.04					
Sand Content at 5-cm (%)	Mean	**53**	**40**	**36**	**70**	**49**	**45**	**34**	**37**	**34**
	SE	2.6	3.9	4.0	2.4	2.5	5.8	4.3	7.5	3.8
	Sig.	b	a	a	b	a	a	a	a	a
	p-value	<0.01			<0.01					
Sand Content at 50-cm (%)	Mean	**59**	**43**	**27**	**73**	**55**	**42**	**44**	**30**	**25**
	SE	3.0	6.0	3.2	2.8	3.3	7.7	10.3	5.9	3.1
	Sig.	c	b	a	c	bc	ab	ab	a	a
	p-value	<0.01			<0.01					
Clay Content at 5-cm (%)	Mean	**23**	**34**	**33**	**6**	**27**	**30**	**39**	**32**	**34**
	SE	2.3	4.1	2.3	0.9	1.8	5.2	6.7	4.0	2.7
	Sig.	a	b	b	a	b	b	b	b	b
	p-value	0.01			<0.01					
Clay Content at 50-cm (%)	Mean	**16**	**31**	**41**	**4**	**19**	**31**	**32**	**39**	**43**
	SE	2.1	4.0	2.5	1.2	2.1	5.2	6.8	4.2	3.1
	Sig.	a	b	c	a	b	bc	bc	c	c
	p-value	<0.01			<0.01					
Effective Depth* (cm)	Mean	**63**	**74**	**95**	**46**	**68**	**72**	**77**	**95**	**96**
	SE	4.0	6.0	2.0	9.0	4.0	8.0	9.0	3.0	3.0
	Sig.	a	a	b	a	ab	b	bc	c	c
	p-value	<0.01			<0.01					
A Horizon Depth* (cm)	Mean	**17**	**28**	**30**	**12**	**18**	**24**	**32**	**31**	**30**
	SE	2.0	4.0	3.0	4.0	3.0	4.0	9.0	5.0	4.0
	Sig.	a	b	b	a	ab	ab	b	b	b
	p-value	0.03			0.02					

*Steinbrenner (1979)

Table 3.3. Soil water and nitrogen properties with means (bold) and standard error (SE) for soil parent materials and regional soil parent materials as defined in Table 3.1. Significant differences were defined using p-values from one-way ANOVA. Properties labeled by different lowercase letters within soil parent materials and regional soil parent materials are significantly different (α<0.1).

Properties	Statistics	Soil Parent Material			Regional Soil Parent Material					
		GLA	IGN	SED	BCGLA	WAGLA	WAIGN	ORIGN	WASED	ORSED
Lowest Volumetric Water Content at 5-cm (%)	Mean	**7.9**	**10.9**	**11.6**	**4.7**	**8.9**	**8.8**	**13.7**	**10.8**	**12.3**
	SE	1.2	1.4	0.9	1.7	1.4	1.9	1.5	0.8	1.6
	Sig.	a	ab	b	a	ab	ab	b	ab	b
	p-value	0.06			0.04					
Lowest Volumetric Water Content at 50-cm (%)	Mean	**11.6**	**16.6**	**18.8**	**4.9**	**13.5**	**14.4**	**19.5**	**18.3**	**19.3**
	SE	1.5	2.2	1.6	1.2	1.7	3.6	1.7	2.3	2.5
	Sig.	a	ab	b	a	ab	ab	b	b	b
	p-value	0.01			<0.01					
Plant Available Water at 5-cm (mm)	Mean	**10.3**	**11.2**	**13.8**	**8.1**	**10.9**	**12.2**	**9.9**	**12.3**	**15.2**
	SE	0.6	1.4	1.0	1.2	0.6	2.2	1.3	1.4	1.3
	Sig.	a	ab	b	a	ab	ab	a	ab	b
	p-value	0.02			0.01					
Total Soil N Content (kg N ha^{-1})	Mean	**7,300**	**9,500**	**13,300**	**4,000**	**8,300**	**8,900**	**10,300**	**11,500**	**14,800**
	SE	900	1,300	1,100	2,100	1,000	1,800	1,800	1,200	1,600
	Sig.	a	b	b	a	ab	abc	bc	bc	c
	p-value	<0.01			<0.01					
Mineral Surface Soil C:N Ratio	Mean	**22**	**21**	**19**	**27**	**20**	**21**	**21**	**20**	**19**
	SE	1.0	1.2	0.8	3.3	0.6	1.2	2.4	0.7	1.4
	Sig.	a	a	a	b	a	a	a	a	a
	p-value	0.16			0.01					
Forest Floor C:N Ratio	Mean	**32**	**40**	**30**	**45**	**28**	**35**	**46**	**29**	**31**
	SE	2.1	2.7	2.1	5.6	1.3	1.9	4.8	1.9	3.6
	Sig.	a	b	a	b	a	ab	b	a	a
	p-value	0.02			<0.01					

Table 3.4. Douglas-fir foliar, site index, height:DBH ratio, and cumulative growth properties with means (bold) and standard error (SE) for soil parent materials and regional soil parent materials as defined in Table 3.1. Significant differences were defined using p-values from one-way ANOVA. Properties labeled by different lowercase letters within soil parent materials and regional soil parent materials are significantly different (α<0.1).

Properties	Statistics	Soil Parent Material			Regional Soil Parent Material					
		GLA	IGN	SED	BCGLA	WAGLA	WAIGN	ORIGN	WASED	ORSED
Foliar N Concentration (%)	Mean	**1.26**	**1.28**	**1.36**	**1.19**	**1.29**	**1.32**	**1.23**	**1.33**	**1.39**
	SE	0.03	0.03	0.03	0.10	0.03	0.04	0.04	0.03	0.05
	Sig.	a	ab	b	a	ab	ab	ab	ab	b
	p-value	0.06			0.07					
Needle Area (cm^2 per 100 needles)	Mean	**32**	**38**	**37**	**26**	**34**	**37**	**39**	**36**	**38**
	SE	1.0	1.5	0.9	1.1	0.9	1.3	3.2	1.5	1.0
	Sig.	a	b	b	a	b	b	b	b	b
	p-value	<0.01			<0.01					
King's Site Index* (m at 50 years)	Mean	**44**	**41**	**44**	**40**	**45**	**42**	**40**	**45**	**43**
	SE	0.9	0.8	0.7	2.1	0.9	1.0	1.0	1.1	0.7
	Sig.	b	a	b	ab	b	ab	a	b	ab
	p-value	0.04			0.01					
Nigh's Site Index[†] (m at 50 years)	Mean	**44**	**41**	**43**	**42**	**44**	**42**	**40**	**44**	**43**
	SE	0.8	0.8	0.6	2.3	0.8	0.8	1.4	1.0	0.6
	Sig.	b	a	ab	ab	ab	ab	a	b	ab
	p-value	0.07			0.11					
Flewelling's Site Index[‡] (m at 30 years)	Mean	**25**	**23**	**26**	**24**	**25**	**24**	**22**	**27**	**26**
	SE	0.5	0.9	0.8	1.3	0.5	1.1	1.6	1.0	1.2
	Sig.	ab	a	b	ab	ab	ab	a	b	ab
	p-value	0.01			0.04					
Height:DBH Ratio	Mean	**78**	**73**	**71**	**79**	**77**	**74**	**71**	**75**	**68**
	SE	1.3	1.4	1.7	1.7	1.6	1.8	2.2	2.3	2.0
	Sig.	b	a	a	b	b	ab	ab	ab	a
	p-value	0.01			0.01					
Volume Mean Annual Increment (cm^3 year^{-1})	Mean	**22,400**	**18,900**	**17,800**	**20,200**	**23,000**	**22,600**	**14,100**	**18,700**	**16,900**
	SE	1,200	2,200	1,000	2,700	1,400	3,100	1,500	1,200	1,600
	Sig.	b	ab	a	ab	b	b	a	ab	ab
	p-value	0.04			0.02					

* King (1966) † Nigh (1997) ‡ Flewelling et al. (2001)

Table 3.5. Two-year Douglas-fir growth rate and fertilizer response properties with means (bold) and standard error (SE) for soil parent materials and regional soil parent materials as defined in Table 3.1. Growth rate is defined as two-year periodic annual increment and percent growth. Fertilizer response is defined as two-year individual-tree absolute and relative growth differences between fertilized and control trees. Significant differences were defined using p-values from one-way ANOVA. Properties labeled by different lowercase letters within soil parent materials and regional soil parent materials are significantly different ($\alpha<0.1$).

Properties	Statistics	Soil Parent Material			Regional Soil Parent Material					
		GLA	IGN	SED	BCGLA	WAGLA	WAIGN	ORIGN	WASED	ORSED
Height Periodic Annual Increment (cm year^{-1})	Mean	**97**	**103**	**100**	**70**	**105**	**107**	**99**	**90**	**108**
	SE	4.7	5.5	4.0	11.4	3.6	6.8	9.6	3.5	5.8
	Sig.	a	a	a	a	b	b	b	ab	b
	p-value	0.66			<0.01					
Volume Periodic Annual Increment (cm^3 year^{-1})	Mean	**50,600**	**50,200**	**43,200**	**40,900**	**53,400**	**59,300**	**38,100**	**41,300**	**45,000**
	SE	3,300	5,800	2,400	6,300	3,700	8,500	4,000	2,300	4,200
	Sig.	a	a	a	ab	ab	b	a	ab	ab
	p-value	0.30			<0.01					
Basal Area Growth Percent (%)	Mean	**12.6**	**16.3**	**18.1**	**11.8**	**12.8**	**14.6**	**18.6**	**15.6**	**20.3**
	SE	0.7	1.5	1.5	1.8	0.8	1.6	2.7	1.5	2.3
	Sig.	a	b	b	a	ab	abc	bc	abc	c
	p-value	<0.01			<0.01					
Height Growth Percent (%)	Mean	**10.1**	**12.2**	**12.9**	**7.5**	**10.9**	**11.3**	**13.4**	**10.8**	**14.8**
	SE	0.5	0.8	0.9	1.0	0.4	0.6	1.5	0.8	1.2
	Sig.	a	ab	b	a	ab	b	bc	ab	c
	p-value	0.01			<0.01					
Volume Growth Percent (%)	Mean	**24.0**	**30.4**	**33.4**	**20.1**	**25.1**	**27.4**	**34.3**	**28.0**	**38.3**
	SE	1.2	2.4	2.6	2.9	1.3	2.3	4.5	2.4	3.9
	Sig.	a	b	b	a	ab	ab	bc	abc	c
	p-value	<0.01			<0.01					
Fertilizer Basal Area Growth Response (cm^2)	Mean	**3.0**	**11.2**	**6.2**	**7.3**	**1.8**	**8.1**	**15.5**	**4.0**	**8.3**
	SE	1.5	3.0	2.5	3.5	1.6	4.8	2.0	3.4	3.8
	Sig.	a	b	ab	ab	a	ab	b	ab	ab
	p-value	0.04			0.06					
Fertilizer Volume Growth Response (cm^3)	Mean	**4,000**	**12,600**	**5,300**	**6,500**	**3,300**	**12,500**	**12,600**	**3,500**	**6,900**
	SE	1,600	1,600	2,000	4,200	1,700	2,100	2,500	2,900	2,800
	Sig.	a	b	a	a	a	a	a	a	a
	p-value	0.01			0.04					
Fertilizer Basal Area Percent Response (%)	Mean	**7.1**	**19.0**	**8.4**	**18.8**	**3.8**	**15.4**	**23.9**	**5.8**	**10.7**
	SE	3.2	3.9	3.4	8.8	3.0	6.1	3.6	5.2	4.6
	Sig.	a	b	ab	ab	a	ab	b	ab	ab
	p-value	0.06			0.05					
Fertilizer Volume Percent Response (%)	Mean	**5.5**	**15**	**5.6**	**11.2**	**3.9**	**13.5**	**17.1**	**5**	**6.6**
	SE	2.1	2.5	2.0	6.0	2.0	3.7	3.3	3.2	2.6
	Sig.	a	b	a	ab	a	ab	b	ab	ab
	p-value	0.01			0.04					

Table 3.6. Important linear relationships (R^2) between climate and soil characteristics on soil water, soil N, and foliar properties (top table) and climate, soil, soil N, and foliar characteristics on Douglas-fir growth properties (bottom table). Negative correlations are in bold font.

Soil and Foliar Properties	Winter Temperature	Spring Temperature	Autumn Temperature	Sand Content 50-cm	Clay Content 5-cm	Clay Content 50-cm	Effective Depth	A Horizon Depth	Lowest Soil Moisture 5-cm	Lowest Soil Moisture 50-cm	Plant Available Water 50-cm	Surface Soil C:N Ratio	Forest Floor C:N Ratio
Lowest Soil Moisture 5-cm					0.25	0.20	0.25						
Lowest Soil Moisture 50-cm				**0.34**	0.29	0.39	0.34	0.24	0.31				
Total Soil N Content	0.27		0.24	**0.32**	0.23	0.35	0.44	0.25	0.38	0.55	0.21		
Surface Soil C:N Ratio	**0.28**	**0.30**	**0.32**				**0.21**	**0.25**		**0.24**			
Forest Floor C:N Ratio												0.36	
Foliar N Concentration												**0.25**	**0.30**

Douglas-fir Growth Properties	Winter Temperature	Summer Precipitation	A Horizon Depth	Total Soil N Content	Surface Soil C:N Ratio	Forest Floor C:N Ratio	Needle Area	All-species Stand Density	Douglas-fir Stand Density	Stand Age	Height:DBH Ratio	Basal Area MAI	Volume MAI
King's Site Index						**0.27**							
Flewelling's Site Index	0.32				**0.29**	**0.22**							
Height:DBH Ratio							**0.27**			0.33			
Basal Area MAI									**0.27**				
Volume MAI									**0.35**	0.26			
Basal area PAI											**0.31**	0.22	
Height PAI					**0.26**							0.22	
Volume PAI								**0.26**	**0.45**			0.54	0.60
Basal Area Growth Percent		**0.26**								**0.50**	**0.39**		**0.36**
Height Growth Percent			0.23	0.22	**0.23**		0.29			**0.45**	**0.44**		
Volume Growth Percent		**0.24**	0.20				0.25			**0.53**	**0.45**		**0.28**
Fertilizer Basal Area Response						0.21							
Fertilizer Basal Area Response (%)						0.28							
Fertilizer Volume Response (%)					0.24	0.29							

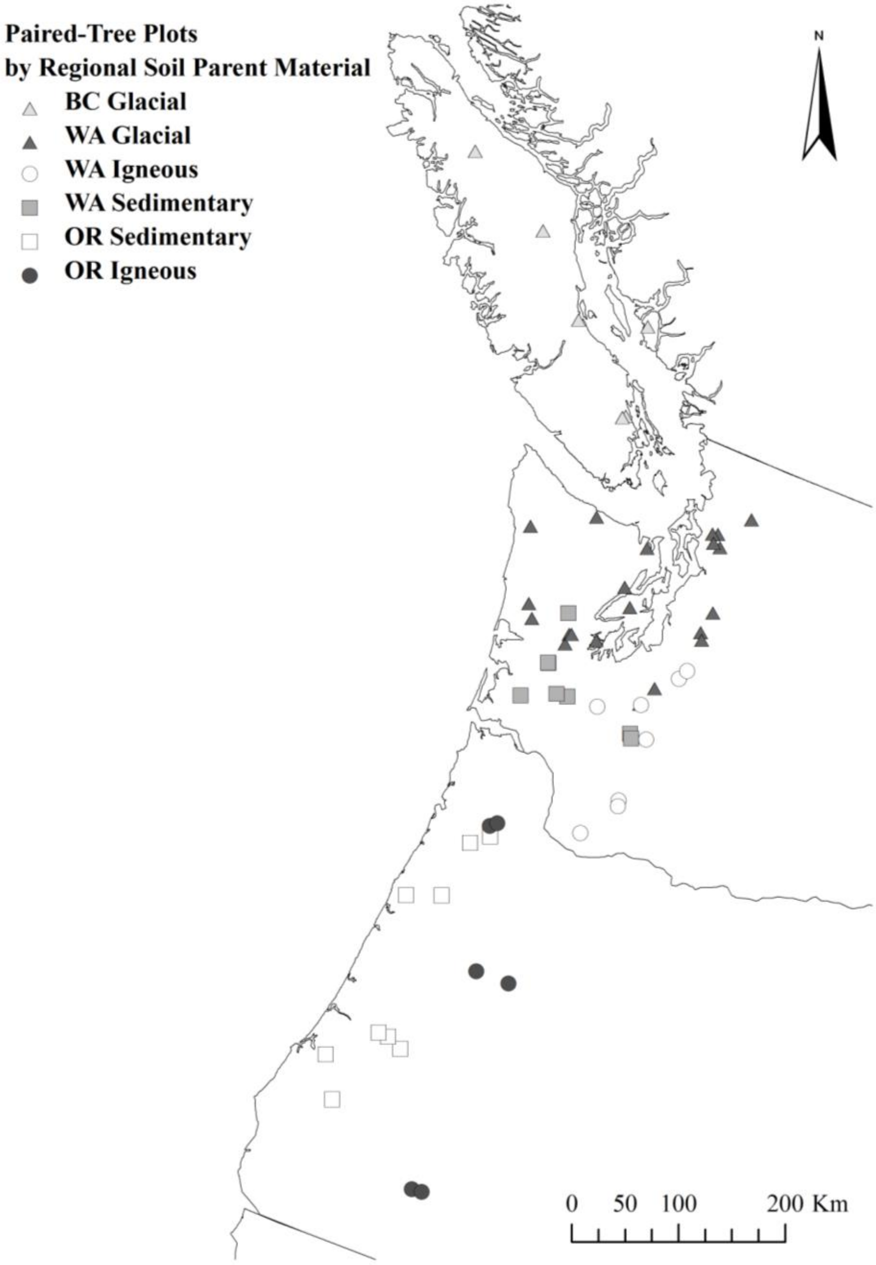


Figure 3.1. Location of Stand Management Cooperative paired-tree plots in the Pacific Northwest by regional soil parent material type. Soil parent material types are designated by symbols representing each plot. States and provinces are labeled as follows: British Columbia (BC), Oregon (OR), and Washington (WA). Maps were sourced from ESRI® Data and Maps.

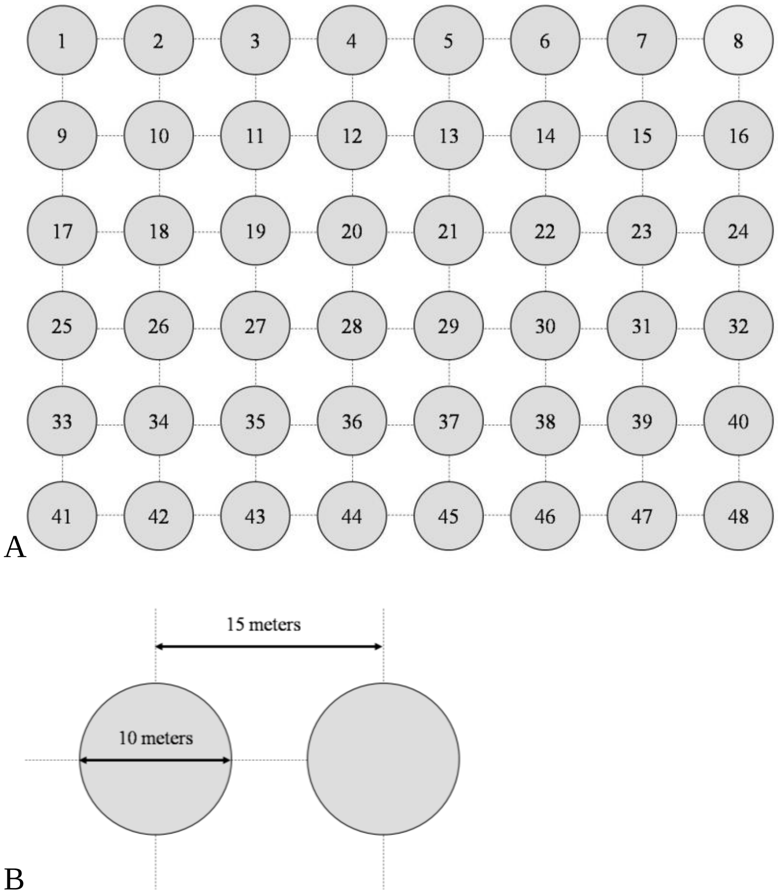


Figure 3.2. Stand Management Cooperative paired-tree plot layout of 48 Douglas-fir (A) on a 15 meter grid (B). The center of each circle represents a selected Douglas-fir tree. The circle represents the treatment (fertilization or no fertilization) area (81 m^2).

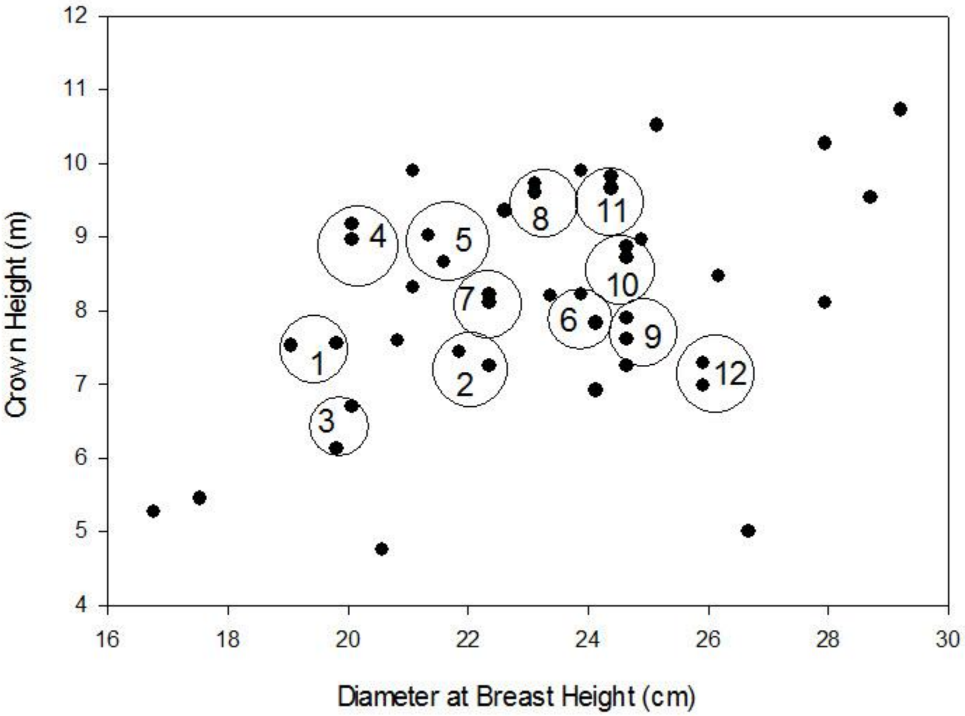


Figure 3.3. This graph shows an example of pairing selected plot-trees by most similar diameter at breast height (cm) and crown height (m). Numbered circles demonstrate the chosen paired-trees.

CHAPTER 4. EFFECTS OF CLIMATE, SITE, AND SOIL CHARACTERISTICS ON WATER AND NITROGEN AVAILABILITY IN DOUGLAS-FIR PLANTATIONS

4.1 ABSTRACT

Soil water and nitrogen (N) availability are used for modeling Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) growth in the Pacific Northwest, but the interactions of soil water and N are not well understood in the region. The objectives of this study were to determine the best predictors of soil water and N availability and their effect on foliar properties using mapped and field-measured climate, site, and soil factors for sixty Douglas-fir plots from northern Vancouver Island to southern Oregon. Boosted regression trees (BRT) and generalized additive models (GAM) were used to determine the best predictors of soil water, soil N, and foliar properties using mapped, field-measured, and combined data sources. Models produced by BRT and GAM contained common predictors and there were no significant differences in deviance explained and adjusted R^2 by model type and data source. Soil water availability was positively influenced by clay content, organic matter content, and soil depth. Total soil N and surface soil carbon:nitrogen (C:N) ratios were related to soil water-holding capacity, plant available water, and soil depth. Forest floor ratio C:N ratios were greatest in Oregon igneous, Washington igneous, and British Columbia glacial plots due to climate limitations on decomposition. Foliar N concentrations were affected by plant-available N, while needle area was affected by soil water-holding capacity. Soil and water-holding properties were the most important variables from mapped sources. This study showed that BRT and GAM can produce useful models to describe soil water, soil N, and foliar properties according to mapped and field-measured climate, site, and soil factors.

4.2 INTRODUCTION

Forest modeling is currently being employed throughout many environments around the world to better understand tree growth and other ecosystem processes. A change from empirical to process-based and hybrid modeling has necessitated prediction of climate and soil water and nitrogen (N) availability as it pertains to tree growth (Schwalm and Ek 2001). For example, the 3-PG model uses estimates of monthly climate data, soil water-holding capacity, and a fertility rating to help predict tree physiology and growth (Landsberg and Waring, 1997).

Climate models such as DAYMET (http://www.daymet.org) and ClimateWNA (Wang et al. 2012) are used in forest modeling to estimate the effects of climate on evapotranspiration. These climate effects can then be combined with projected soil water holding capacity (Soil Survey Staff 2010) through a modified Thornthwaite’s equation to estimate the difference between potential and actual evapotranspiration (Lutz et al. 2010). Similarly, using DAYMET in the Douglas-fir Hybrid Growth Simulation model, Weiskittel et al. (2010) effectively modeled summer soil water availability. Before these climate models were available, soil moisture regimes (Krajina 1969) were designated for British Columbia forests according to slope position, water table, and soil characteristics (Green and Klinka 1994) to define stands with different productivities (Klinka and Carter 1990).

While summer soil water availability is a common limitation in forest growth (Hanson and Weltzin 2000), nitrogen has been recognized as the most limiting nutrient in forests throughout the world (LeBauer and Treseder 2008). The 3-PG model has been used throughout the world to estimate forest site properties according to a fertility rating between 0 and 1 instead of actual nutrition values because information on nutrient availability is limited (Landsberg and Waring 1997). In British Columbia and England, soil nutrient regimes were developed to understand available soil nutrition (mainly N) through easily determined soil factors or understory vegetation (Krajina 1969; Green and Klinka 1994; Pyatt 1995). Total soil N content has been used in numerous studies because it is an approximation of soil nitrogen availability that is relatively easy to sample. While total soil N does not take into account available-N (NO_3 and NH_4) and N-uptake by plants, it has been related to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) site index (Edmonds and Chappell 1994), volume growth (Miller et al. 1989), and fertilizer response (Sucre et al. 2008). Forest floor and surface soil horizon carbon to N (C:N) ratios have also been used to describe stand N availability because they account for the accessibility of N in microbial decomposition (Prescott et al. 2000). Accordingly, Douglas-fir volume growth response after N fertilization has been found to be positively correlated with forest floor C:N ratio (Peterson et al. 1984; Edmonds and Hsiang, 1987) and surface soil C:N ratio (Miller et al. 1989; Gessel et al. 1990).

Foliar properties, such as foliar N concentration and leaf area, have also been used in the past to indicate stand productivity as affected by climate and water and N availability. Douglas-fir foliar N concentrations have been found to be representative of forest soil water and N availability (Klinka and Carter 1990) and to increase with N fertilization (Brix 1972). Accordingly, Douglas-fir foliar N has been positively related to basal area increment (Turner et al. 1988) and negatively related to N fertilizer response (Turner et al. 1988; Hopmans and Chappell 1994). Throughout the Pacific Northwest, larger leaf areas have been found in areas with temperate air temperatures and sufficient soil moisture (Waring et al. 1978), higher precipitation, a more positive summer water balance (Grier and Running 1977), and after N fertilization and irrigation treatments (Brix 1972; Gower et al 1992). Consequently, leaf area index, the common measurement of needle area in forests, has been found to be related to N fertilizer growth response in loblolly pine (*Pinus taeda* L.) (Vose and Allen 1988).

In the Pacific Northwest, Douglas-fir plantations grow on a wide variety of soil properties such as soil texture, depth, and N contents due to varying parent material origins, climates (precipitation and air temperatures), and topography (Steinbrenner 1979; Chapter 2). Such differences can cause diverse soil water and nitrogen availabilities, which in turn affect Douglas-fir foliar characteristics and tree growth throughout the region (Steinbrenner 1979; Carter and Klinka 1990; Klinka and Carter 1990). A better understanding of soil water and N availabilities can improve Pacific Northwest forest plantation productivity (if deficiencies are found) by using management techniques that optimize water and N availability, such as planting density, thinning, and N fertilization. Tree growth models could also be improved with a more detailed understanding of what effects soil water and N availabilities throughout the Pacific Northwest.

The objectives of this paper were to: 1) find mapped and measured climate, site, and soil properties that best determine field-measured soil water, N, and foliar properties and 2) determine if boosted regression trees (BRT) are adequate for describing forest soil water, nitrogen, and foliar characteristics compared to generalized additive models (GAM). Boosted regression trees and GAM are non-linear statistical models that will be used to assess the best mapped and measured predictors of soil water, N, and foliar characteristics in this study. Mapped variables are defined as those that can be assessed from online or mapped resources, while field-measured variables were determined directly on plots in this study and generally not available as widely-mapped resources.

The following hypotheses were tested: 1) field-measured climate, site, and soil characteristics contribute significantly to models that predict summer soil water, soil N, and foliar properties over mapped variables alone, 2) BRT models perform as well as GAM models for explaining the biogeochemical effects of climate, site, and soil properties on forest soil water, nitrogen, and foliar characteristics.

4.3 MATERIALS AND METHODS

To test these hypotheses, 60 1.1-ha plots were established in plantation Douglas-fir forests in the Pacific Northwest. All plots were at or near canopy closure (11-27 breast height age) and had similar spacing (750 trees-per-ha) to control for differences in age and density. The study covers Douglas-fir plantation forests owned by forest product companies, universities, and government agencies from northern Vancouver Island, British Columbia to southern Oregon (Figure 4.1). Plots varied in elevation, slope, and landform, but were typical of many plantation sites throughout the Pacific Northwest (Table 4.1). Plots were composed of 48 plot-trees with an 81-m^2 treatment area around each plot-tree on a 15-m grid as part of a fertilization study. Site quality and forest productivity also varied considerably amount the sixty sites (King's site index of 32-55 meters at 50-years) (Chapter 3) (King 1966).

4.3.1 Climate Variables

Average monthly and seasonal air temperature and precipitation (1990-2009) were determined for each installation through the ClimateWNA program (Version 6.62, University of British Columbia, Vancouver, BC) (Wang et al. 2012) (Table 4.1). Average yearly above-canopy growing degree days (greater than 5^{o} C) and precipitation as snow for 1990-2009 were also assessed using ClimateWNA for each plot.

Air temperature sensors (iButton hygrochron DS1923-F5, Maxim Integrated Products Inc., Sunnyvale, CA) were placed 10-cm above the forest floor at each plot. In 2010, daily average growing-season air temperatures were measured on each plot. Under-canopy growing degree days were determined when daily air temperature was greater than 5^{o} C as the total of the difference between average daily air temperature and 5^{o} C (Table 4.1). Under-canopy growing days were counted as the total number of under-canopy growing degree days in 2010 to measure the number of growing-season days for each plot.

4.3.2 Site Variables

Site variables were measured for each plot as latitude, longitude, slope, elevation, and aspect (Table 4.1). Enhanced vegetation index (EVI) and normalized difference vegetation index (NDVI) were recorded for each plot using MODIS/Terra data (1x1 degree resolution) and accessed through the Monsoon Asia Integrated Regional Study (NASA, 2011). The EVI is an estimate of the greenness of the measured area and is sensitive to high biomass regions (NASA, 2011). The NDVI is the difference between near-infrared radiation and visible wavelength radiation over the sum of the two radiation measurements (NASA, 2011). Both vegetation indices were recorded as the maximum monthly reading for 2010.

Plots were classified by their regional latitude location (north, central, and south) in each state or province (British Columbia, Washington, and Oregon) to determine if there were regional differences between plots (Table 4.1 and Figure 4.1). Soil parent material was determined using geologic maps (U.S.G.S. 2010a; U.S.G.S. 2010b), soil series descriptions (Soil Survey Staff 2010), and soil pit observations and were split into glacial, sedimentary, and igneous by region (state or province) to determine if there were parent material effects on soil water, nitrogen, and foliar properties (Chapters 2 and 3).

4.3.3 Soil Variables

Soil sand, clay, and organic matter contents to 100-cm depth were recorded from the Natural Resources Conservation Service soil surveys (Soil Survey Staff 2010) to determine the accuracy of mapped soil variables (Table 4.1). In addition, soil characteristics were measured at a central location on each plot. One soil pit was sampled to a maximum of one-meter depth of mineral soil or to the depth of a compacted horizon. Bulk density samples were taken by the core or clod method, depending on soil texture and hardness (Blake and Hartge 1986). One forest floor sample was removed from an undisturbed, measured area above the soil pit. Soil samples were dried, sieved to 2-mm, and ground; forest floor samples were dried and ground to 1-mm in a Wiley Mill.

For each plot, effective soil depth (depth of the soil minus rock volume) and depth of the A horizon were determined according to Steinbrenner (1979) (Table 4.1). Soil texture was measured as sand or clay content using the hydrometer method (Gee and Bauder 1986) on samples taken at 5-cm and 50-cm depths in the soil profile. These depths for soil texture measurement were chosen because they match soil moisture sampling depths and allowed a comparison of rooting zone soil textures that could be compared across all of the plots.

4.3.4 Soil Water Variables

Hargreaves' climatic moisture deficit is calculated by ClimateWNA as the sum of the monthly difference between modeled evaporation and precipitation (average of 1990-2009) (Wang et al. 2012). Summer heat:moisture index was determined over the same period as the mean warmest monthly temperature divided by the mean summer precipitation (Wang et al. 2012). Available water-holding capacity and available water supply to 100-cm depth were taken from the NRCS database for each mapped soil (Soil Survey Staff 2010). Climate data from ClimateWNA (Wang et al. 2012) and available water-holding capacity (Soil Survey Staff 2010) were combined with site characteristics (latitude, slope, and aspect) to determine climatic water deficit, which is the sum of the monthly difference between potential and actual evapotranspiration, through a modified Thornthwaite's equation (Lutz et al. 2010). Mapped soil water availability variables for each plot were described using climatic moisture deficit, summer heat:moisture index, climatic water deficit, available water-holding capacity, and available water supply (Table 4.1).

Decagon soil moisture sensors were used to measure daily soil water availability at 5-cm and 50-cm depth in the mineral soil (EC-5 Soil Moisture Sensors, Decagon Devices, Pullman, WA). Sensors were installed into the undisturbed soil face on the uphill side of the pit. Soil moisture data from 2010 were used because almost all of the plots had soil moisture data for that year. Lowest soil moisture was defined as the lowest summer volumetric soil water content (%)

from soil moisture sensors at 5-cm and 50-cm. If there was no soil moisture data for 2010, lowest soil moisture data from 2009 and 2011 were averaged. At 5-cm and 50-cm, plant available water was measured as the difference between field capacity and lowest soil moisture content multiplied by the volume of soil not filled with rocks:

$$Plant\ Available\ Water\ (mm) = \left(Field\ capacity\ (\%) - Lowest\ soil\ moisture\ (\%)\right) * 100\ mm\ (soil) * (1 - Rock\ volume\ (\%)) \qquad (1)$$

Field capacity was measured as the volumetric soil water content (%) two days after a rain event in the spring and winter season. Rock volume (%) was determined from the total weight of soil rock and rock density using a pycnometer for small rocks and wax-dipped displacement of large rocks. Lowest soil moisture and plant available water were used to describe summer soil water availability at each plot (Table 4.2).

4.3.5 Soil Nitrogen and Foliar Variables

Soil was sampled by horizon for C and N concentration and bulk density. All samples were analyzed for C and N concentration using a CHN analyzer (CHN Analyzer 2400, PerkinElmer Inc., Waltham, CT). Total soil nitrogen content to one-meter was determined from the combination of soil horizon nutrient concentrations, depths, and bulk densities (Table 4.2). Forest floor and mineral surface soil horizon C:N ratio were determined from C and N concentrations (Table 4.2).

Current-year foliage samples were cut or shot from the upper crowns of six trees during the fall season two years after plot installation. The six foliar sample trees were randomly chosen from the 12-20 unfertilized plot-trees per plot. Foliar samples were stored at 3^{o} C until ready for analysis. Foliage was plucked from branches when still at field moisture. An equal number of average-sized current-year needles were selected from each plot tree for a total of 100 needles per plot for needle area analysis. The 100 needle weight of the wet needles was recorded and then the needles were placed on a clear sheet without overlapping. A leaf area meter (Leaf Area Meter LI-3100, Li-Cor Biosciences, Lincoln, NE) was used to measure the projected area of 100 needles (Table 4.2). The remaining foliage was combined and dried at 65° C for two days. The dried foliage was ground to 1-mm in a Wiley Mill and analyzed for N concentration (CHN Analyzer 2400, PerkinElmer Inc., Waltham, CT) (Table 4.2).

4.3.6 Statistics

Two non-linear statistical models were used to assess the best predictors of soil water, N, and foliar properties (response variables) in this study. Models for estimating soil water, soil N, and foliar properties (Table 4.2) from mapped and field-measured climate, site, and soil variables (predictor variables) (Table 4.1) were developed using BRT and GAM. All predictors plus field-measured soil water variables were used as predictors in soil N models. In the foliar models, field-measured soil water and N as well as all other variables were used as predictors.

Boosted regression trees and GAM have been used in the past to describe species' distributions (Yee and Mitchell 1991; Leathwick et al 2006; Elith et al. 2008), soil bulk density (Martin et al. 2009), tree form (Robinson et al. 2011), and site index (Aertsen et al. 2010). Boosted regression trees and GAM modeling techniques have performed equally well when compared using the same data, but have produced a different combination of predictors in previous studies (Leathwick et al. 2006; Aertsen et al. 2010).

Boosted regression trees and GAM models allow the user to select the distribution family that best represents the data. All response variables were tested for normality so that a Gaussian distribution could be used in the analyses if appropriate. A Q-Q plot in the R Statistical Software (R version 13.0) was produced to assess normality and to determine the proper transformation. All response variables showed a normal distribution except forest floor C:N ratio, which was transformed using a log function.

Boosted regression tree modeling is a combination of regression trees and machine learning. This method is described in detail by Elith et al. (2008). Each model starts with one simple regression-tree that explains the most deviance of the response variable. Each successive regression-tree is formulated to describe the unexplained deviance in the previous regression-tree. A learning rate is imposed on each regression-tree to slow the model forming process and to decrease the influence of each regression-tree. When the successive models cannot explain more response variable deviance, a final model is produced stagewise so that the predictor variable influence and effects are combined from all models. To use BRT correctly, Elith et al. (2008) recommends using a learning rate that returns around 1000 trees and a stochastic sampling of the data for each tree.

Boosted regression tree models were produced using the step function in the R Statistical Software (R version 13.0, R Development Core Team 2011) and the package "dismo" (Hijmans et al. 2011) with parameters recommended in Elith et al. (2008). Parameters were set for the step function to produce between 1000-1500 trees for each model with the following parameters: tree complexity (1), bag fraction (0.75), learning rate (0.001-0.05), and a Gaussian probability distribution. Boosted regression tree models return the relative influence (%) of each predictor used in the model for a total of 100%.

Mapped, field-measured, and a combination of mapped and measured data source models were produced for each dependent variable. Initially, the best ten predictors were selected from each of the mapped and measured models. Then, one predictor variable was removed from the model at a time until the six best predictor variables remained. Less than six predictors were kept in the model if a variable had a smaller relative influence than the other predictors and did not increase the deviance explained by the model when it was removed. The six retained mapped and measured predictors were input into the combined model and the six best predictors were retained to form the combined model. Partial dependence plots with smoothing were produced for each variable using the "dismo" package (Hijmans et al. 2011). The partial dependence plots show the effect of each predictor variable on the response variable keeping all other predictors at their average. The effect of predictors on the response variables in the partial dependence plots are shown as fitted functions, which are the difference between modeled response values and the mean response value. Ranges of predictor variables with a fitted function values above zero were identified as yielding a higher than average response.

Generalized additive models produce non-linear estimations of response effects through model-produced smoothing splines. In many cases, this method is preferentially used over generalized linear models when the shape of each response curve is unknown because it can be detected by the model instead of being fitted by the researcher (Wood 2001). The smoothing splines can excessively fit the data, but this "wiggliness" can be controlled through limiting degrees of freedom to avoid overfitting. It has been recommended to keep each predictor variable at two degrees of freedom (Aertsen et al. 2010), which allows splines to be designated anywhere from a straight line to a parabolic shape and often fits observed relationships well.

Separate GAM models were produced for each response variable according to mapped variables for January-June temperature, July-December temperature, January-June precipitation, July-December precipitation, seasonal temperature, seasonal precipitation, soil texture and water availability, and site variables (8 total models) using the R package “mgcv” (Wood 2010) and a Gaussian probability distribution in the R Statistical Software (R version 13.0, R Development Core Team 2011). The significance of independent variables in GAM was determined at a p-value of 0.10. All mapped GAM models were combined and irrelevant predictors were dropped to determine the best model using six or less mapped variables. The same procedure was completed with the measured variable GAM models. The best predictor variables from the mapped and measured models for each response variable were combined to produce six or less predictors for the combined model. Generalized additive model plots were produced as partial dependence plots to show the effect of predictor variables on response variables. The smooth curve designated by the GAM model is represented in each graph. Fitted functions are the same as described in BRT models and the predictor range that yielded fitted functions above 0 were identified as above average.

The model statistics from mapped, measured, and combined data sources were compared within and between the two modeling types (BRT and GAM). Model strength was assessed through deviance explained, adjusted R^2, and root mean square error (RMSE) (Aertsen et al. 2010). Deviance explained and adjusted R^2 were on the same scale for every model and were pooled by model type (BRT and GAM) and data source (mapped, measured, and combined) and significant differences between them were analyzed through a two-way ANOVA and the Tukey honestly significant difference test in the R Statistical Software (R version 13.0, R Development Core Team 2011). This test will examine if BRT or GAM are better for explaining soil water, soil N, and foliar properties and which data source is best.

4.4 RESULTS

4.4.1 Soil Water Variables

Lowest soil moisture at 5-cm (LOW5) was best explained by the GAM model based on combined data sources while the BRT model based on combined data sources was the second best based on model statistics (Table 4.3). Clay content (5-cm) and effective depth were the most important predictors of LOW5 because they were used in both of the combined data source models (Table 4.4); both predictors had a positive relationship with LOW5. The BRT model based on combined data sources was the preferred model for describing lowest soil moisture at 50-cm (LOW50) (Figure 4.2, Table 4.3); LOW50 increased with increasing effective depth, clay content (50-cm), and A horizon depth (Table 4.4). Effective depth and clay percentage were the principal measured variables in predicting LOW5 and LOW50 in the BRT and GAM models. There were no mapped predictors that were common between the lowest soil moisture models, but mapped variables from the NRCS were found in both models.

The models based on mapped data were the preferred models for describing plant available water at 5-cm (PAW5) (Table 4.3). There were no variables used in common in the BRT and GAM models based on mapped data, but higher available water supply and mid-range April precipitation led to greater PAW5 (Table 4.4). Plant available water at 50-cm (PAW50) was best explained by the BRT model from combined data sources relative to all other models (Table 4.3). Regional latitude was the most important predictor, with northern Washington and central Oregon categorized as having the highest PAW50 (Table 4.4). Conversely, no GAM models performed well for explaining PAW50. The preferred BRT and GAM models for PAW50 both included the negative effect of sand content (50-cm) and the positive influence of effective depth. Boosted regression trees consistently modeled PAW5 and PAW50 better than GAM models. No predictors were selected in common between the best models of PAW5 and PAW50.

4.4.2 Soil Nitrogen Variables

The GAM models based on measured and combined predictors best explained total soil N content (SOILN) over all models, but the GAM model based on measured predictors had the best model statistics (Figure 4.3, Table 4.3). The BRT models based on measured and combined variables also performed well for explaining SOILN. Lowest soil moisture at 5-cm and 50-cm and effective depth were the essential predictors of SOILN because they were selected in both the GAM and BRT models based on measured variables (Table 4.5).

A combination of mapped and measured variables was best for explaining mineral surface soil horizon C:N ratio (SSCN) in the BRT and GAM models (Table 4.3). Shallow A horizon depths and lower LOW50 were the most important variables for predicting SSCN in the combined BRT and GAM models (Table 4.5). Mapped NRCS organic matter content, clay content, and available water supply also contributed to the combined BRT model.

The GAM model for forest floor C:N (FFCN) ratio based on combined variables performed better than all other FFCN models (Table 4.3). Using just BRT models, FFCN was best explained by the model based on combined variables. Regional soil parent material was the most influential predictor in this model and showed that installations on igneous parent materials in Oregon and glacial parent materials in British Columbia had the highest FFCN (Table 4.5). Only PAW5 was selected in the two preferred models for FFCN, but February and spring temperatures were also used in both models.

4.4.3 Foliar Variables

The BRT model based on combined data sources performed the best of all models for explaining foliar N concentration (FOLN) (Table 4.3). The GAM models performed poorly for explaining FOLN, but the GAM model based on measured variables had the best model statistics. The preferred BRT and GAM models both included the positive influence of effective depth and the negative effect of FFCN on FOLN (Table 4.5).

None of the models performed well for explaining needle area (NDLAREA), but the best model was the GAM model based on combined data (Table 4.3). In the BRT models, NDLAREA was best explained by measured variables. Clay content at 50-cm was the most important predictor of NDLAREA because it was selected in both of the preferred models; however, the GAM model suggested a decrease in NDLAREA above 60% clay content, while the BRT model predicted an increase in NDLAREA with increasing clay content (Table 4.5).

4.4.4 Model Test

Imposing a conventional α-level (e.g., 0.10), there were no significant differences between deviance explained and adjusted R^2 according to model type (p=0.880 and p=0.370, respectively) or data source (p=0.202 and p=0.234, respectively). Very weak statistical evidence (moderate p-value) suggested that BRT models had higher adjusted R^2 values than the GAM models. Similarly, very weak statistical evidence (moderate p-values) indicated that the models from combined data sources performed the best with the greatest deviance explained and adjusted R^2 values, while the mapped models had the lowest deviance explained and adjusted R^2 values.

4.5 DISCUSSION

4.5.1 Soil Water Availability

The lowest soil moisture content reached during the growing season is important in forests because it incorporates the water-holding capacity of the soil, precipitation inputs during the growing season, and evapotranspiration of soil water during the summer. Due to the wide range of soil textures and summer climates, there was a wide range of lowest soil moisture throughout the range of Douglas-fir in this study (Table 4.2). As expected, installations with the shallowest soil depths and lowest clay and organic matter contents reached the lowest soil moisture in the summer (Rawls et al. 1982; Warren et al. 2005). However, with inspection of the temporal changes in soil moisture during the summer, the installations with the lowest soil moistures did not remain at a minimum level for long before moisture was replenished by precipitation; the summer of 2010 had periodic mid-summer rain (data not shown). However, in an extended dry summer, these installations would most likely have drought limitations to tree growth (Case and Peterson 2005). Mapped soil texture and organic matter contents were moderately effective for predicting lowest soil moisture, but to better identify installations with limiting soil moisture it will be necessary to directly measure soil texture and depth.

Summer plant available water is similar to lowest soil moisture because it is dependent upon the water-holding capacity of the soil, but it is also influenced by the soil rock content. With the rock content of these soils ranging from 0% to 73% (data not shown) and soil textures ranging from loamy sand to clay, a wide range of plant available water was found throughout these plots (Table 4.2). Silt loam soils have been previously identified to have the highest water-holding capacity (Rawls et al. 1982). In this study, the greatest amount of plant available water was found in plots with greater soil depth, available water supply, and clay content as well as a lower sand content (Table 4.4). The combination of mapped and measured variables selected in plant available water models supports the impact of actual soil depth and texture data on plant available water (Rawls et al. 1982; Warren et al. 2005), while demonstrating the relevance of available water supply data as mapped by the NRCS. Also, those installations with higher autumn temperatures had favorable plant available water, which followed a trend of increasing autumn temperatures along with finer textured soils with decreasing latitude in the Pacific Northwest ($Autumn\ Temperature\ (°C) = -0.3 * latitude + 23$, R^2=0.25, RMSE=0.8).

Many of the plant available water predictor variables are similar to those in the lowest soil moisture models, but there is a greater effect of mapped variables on plant available water suggesting that sites with favorable plant available water could be predicted from the selected mapped predictors. Also, selected predictor variables were different between lowest soil moisture and plant available water models at 5-cm and 50-cm. Therefore, the field-measured lowest soil moisture and plant available water variables described plots with distinct summer soil water availability at depth, while addressing water-holding capacity and soil water availability differently.

4.5.2 Soil Nitrogen Availability

Total soil N content and surface soil C:N ratio were strongly related to measured soil texture, depth, and water availability (Table 4.5). However, the relationship between total soil N content and surface soil C:N ratio were inversely related to these predictors because total soil N content is positively related to soil N availability while surface soil C:N ratio is negative related to N availability (Kabzems and Klinka 1987a; Miller et al. 1989). Measured soil water variables were important for describing total soil N content and surface soil C:N ratio, which supports the use of lowest soil moisture and plant available water for describing soil water availability. Therefore, the combination of fine soil textures and deeper soils and the subsequent high water-holding capacity in these soils are characteristics that are associated with yielding a soil with high N availability. Previously, soil mineralizable N was found to be significantly higher on sites with moist soil moisture regimes and rich or very rich soil nutrient regimes (Klinka and Carter 1990), which are characterized as having the deepest soils and the finest particle sizes (Green and Klinka 1994).

Forest floor C:N ratios were not thoroughly explained by the field-measured soil variables which predicted total soil N contents and surface soil C:N ratios. Instead, mapped and measured climate variables were important for predicting forest floor C:N ratio. Regional soil parent materials were the most important predictor of forest floor C:N ratio with the highest C:N ratios found with igneous and British Columbia glacial parent materials ($p<0.01$). Those regions having similarly high forest floor C:N ratio are the farthest apart in the Pacific Northwest and are experiencing similar yet different limitations in N cycling. Forest floor decomposition is inhibited due to consistently lower winter and spring temperatures in British Columbia and igneous plots than the rest of the region (Chapter 3) (Zhang et al. 2010). Conversely, summer precipitation decreases with latitude yielding the lowest amount of precipitation in southern Oregon ($Summer\ Precipitation\ =\ 17 * latitude - 656$, $R^2=0.40$, RMSE=37), which could be causing a limitation in water availability that is decreasing decomposition of the forest floor. This suggests that parent material classifications are identifying areas with different climates, which probably have more effect on the forest floor than the soil parent materials. However, it further supports the use of parent materials as an efficient method of classifying areas with different climates and soil characteristics (Steinbrenner 1979; Chapters 2 and 3).

Currently, there are no convenient methods of predicting soil nitrogen availability in forests. The soil characteristics identified as indicative of total soil N content in this study could help improve estimations of Douglas-fir site index (Edmonds and Chappell 1994), volume growth (Miller et al. 1989), and N fertilizer response (Sucre et al. 2008). Because field-measured soil properties were necessary for predicting total soil N content, an understanding of actual soil textures and water availability is essential to determine sites with critical N availabilities that could be affecting tree growth. The importance of forest floor and surface soil C:N ratio in predicting Douglas-fir N fertilizer volume growth response supports their use in describing forest N availability (Peterson et al. 1984; Edmonds and Hsiang, 1987; Miller et al. 1989; Gessel et al. 1990). Also, the finding that climate and soil characteristics from mapped sources are important for predicting forest floor and surface soil C:N ratios greatly improves the potential for more accurate prediction of N fertilizer growth response over the region.

4.5.3 Foliar Properties

Needle area and foliar N concentration were both greater on plots with higher plant available water (Table 4.5). This result is consistent with previous findings that greater foliar N concentrations and greater foliar mass (100 needles) occur on sites with moist soil moisture regimes (Kabzems and Klinka 1987b; Klinka and Carter 1990). Foliar N concentration was also positively related to soil depth and surface soil C:N ratio, while needle area was positively related to finer soil textures. The difference in predictor variables between foliar properties demonstrates that foliar N concentration is more strongly affected by soil nitrogen availability, while needle area is affected more by soil water availability. These relationships are supported by a greater effect of N fertilization on foliar N concentration than needle area and a larger influence of irrigation on needle area than foliar N concentration (Brix 1972).

Unfortunately, the best models in this study failed to describe needle area and foliar N concentration as well as the field-measured soil water and N properties (Table 4.5). However, the best predictors of these foliage characteristics were identified for the Pacific Northwest and may find application in some situations. The models formulated in this study for needle area and foliar N concentration further support their use to predict water and nitrogen availability in the Pacific Northwest because foliar properties are representative of the uptake of available water and N in the soil (Grier and Running 1977; Waring et al. 1978; Klinka and Carter 1990). Also, foliar samples are easier to collect than actual soil water and N and can therefore be used to understand their effects on tree growth. Specifically, foliar N concentrations have been found to be indicative of basal area periodic annual increment (Turner et al 1988) and N fertilizer response (Turner et al 1988; Hopmans and Chappell 1994; Carter et al. 1998).

4.5.4 Mapped Variables

Soil texture and water availability variables as mapped by the Natural Resources Conservation Service (Soil Survey Staff 2010) were the strongest predictors of lowest soil moisture, plant available water, total soil N content, surface soil C:N ratio, foliar N concentration, and needle area in the BRT models based on mapped variables only (data not shown). A strong relationship between mapped soil series characteristics and actual soil characteristics can therefore be concluded. In fact, sand and clay contents at 50-cm were linearly correlated with NRCS sand and clay contents (R^2=0.30 and R^2=0.40, respectively). However, almost all BRT models based on mapped variables were significantly improved with the addition of measured variables, specifically soil texture, depth, and water availability. The high performance of the models based on combined data sources underscores the importance of understanding actual soil physical properties and soil water availability in addition to mapped climate, site, and soil variables.

Climate variables were selected in all models based on either mapped only or combined data sources. Because average air temperatures and precipitation (1990-2009) were used in the study, the current effects of climate variables on soil water, soil nitrogen, and foliage were assessed in these models. Twenty years of climate data was chosen because it covered the majority of the years that trees have occupied the stands used in this study. The effects of yearly climate are also complicated by the fact that the plots used in this study were installed over three years. Moreover, climate data from ClimateWNA was not available for years after 2009 (Wang et al. 2011). However, if air temperature and precipitation change significantly over an extended period of time due to climate change, the climate variables used in these models could be used to project changes in soil water availability under the soil characteristics covered in this study.

Some of the relationships between climate variables and soil water and N availability and foliar properties are due to climate differences throughout the range of the study. For example, spring and autumn temperatures and summer precipitation, which were frequently used in the models based on mapped and combined data, were found to be significantly different by regional latitude category and regional soil parent material (Chapter 3). Accordingly, latitude and longitude occurred in many mapped models along with other site characteristics. Therefore, throughout the Pacific Northwest, monthly and seasonal air temperatures and precipitation are useful in a spatial and temporal context.

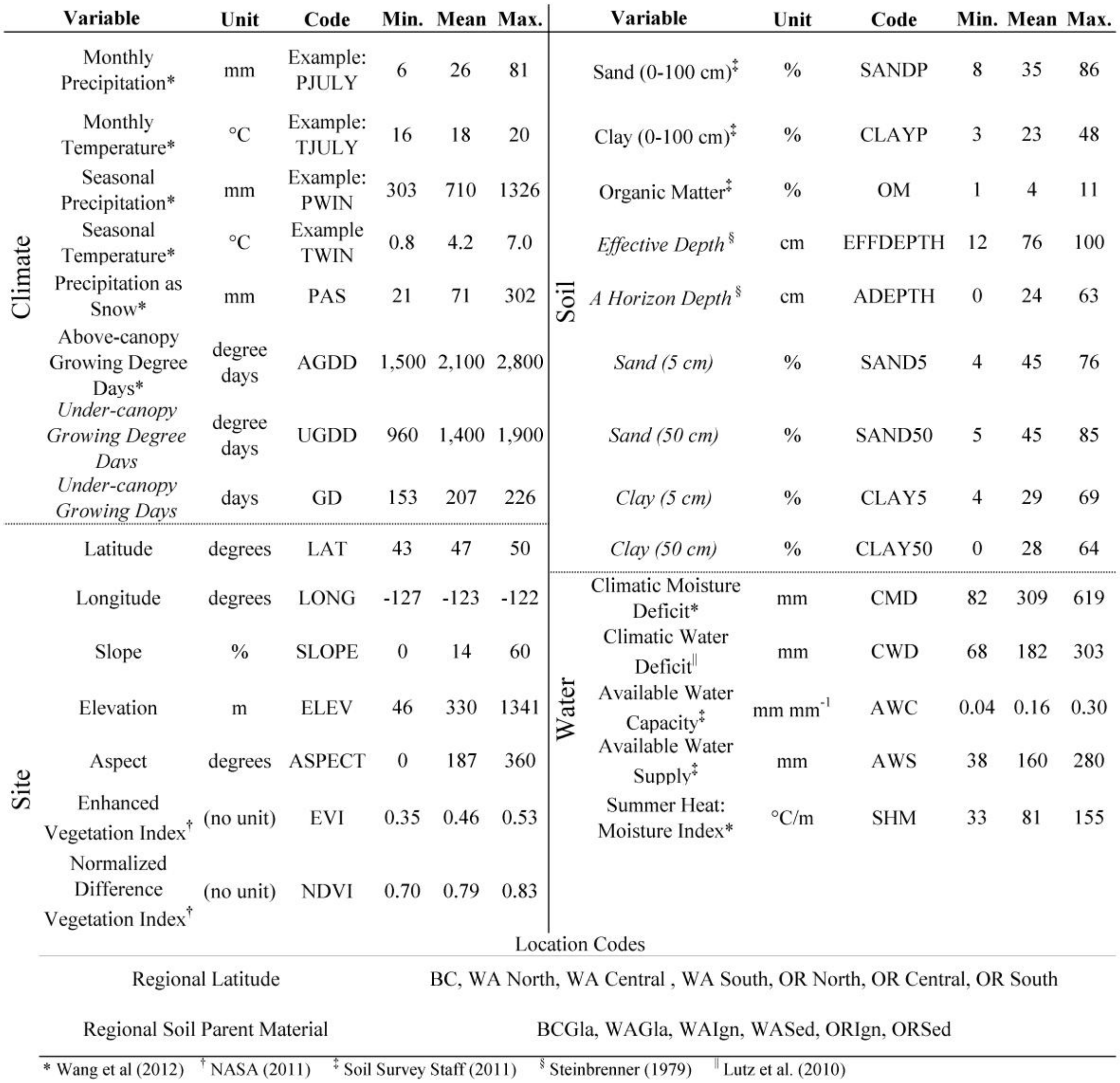
4.5.5 Model Types

The BRT models based on combined data sources performed as well as GAM models based on combined data sources for soil moisture, soil N, and foliar properties. In the BRT models, the addition of mapped and measured variables produced strong models that defined sites with varying water availability, nitrogen availability, and foliar properties. Some differences were found between model statistics of BRT and GAM models from the same data source; BRT models performed worse than GAM in some models because there was a strong relationship between a predictor and response variable and the overall model strength declined because other predictors were kept out of the model in favor of the strongest predictor. One example was the performance of the needle area BRT model based on combined data where mapped NRCS soil variables overwhelmed the otherwise superior measured model (Table 4.3). Some weak GAM models where formed when predictor variables performed well in their own models, but one of the predictors became insignificant when they were combined. In this case, the GAM model only contained one or two predictor variable(s) as in the case of foliar N concentration model based on combined data sources (Table 4.5).

4.6 CONCLUSIONS

Soil water and N availability differed greatly over the range of coastal Douglas-fir in the Pacific Northwest due to biogeoclimatic variables. Field-measured soil characteristics, especially soil texture and depth, were strongly related to soil water availability. Soil N content and surface soil C:N ratio were also related to field-measured soil texture and depth as well as soil water availability, while forest floor C:N ratio was affected to a greater degree by climate variables. Needle areas were greater in plots with greater water-holding capacity and foliar N concentration was positively related to plant available water and nitrogen availability. The interrelationships between field-measured climate, site, soil, soil water and N availabilities, and foliar properties support their potential value in future models to understand the effects of soil water and N availability on Douglas-fir growth. Mapped climate, site, and soil variables affected soil water, soil N, and foliar properties, but performed better when supplementing models that included measured variables than when used alone. Boosted regression trees performed as well as GAM models with some shared predictors. Both modeling techniques described the biogeoclimatic relationships between climate, site, soil, soil water, soil N, and foliar properties in the Pacific Northwest.

Table 4.1. Independent variables, units, and codes sorted by type (climate, site, soil, and water). Measured variables are in italics and the remaining variables were from mapped or modeled sources. The minimum, mean, and maximum values are reported for each variable from the 60 plots in the Stand Management Cooperative Paired-tree Study. Location codes are mapped in Figure 4.1.



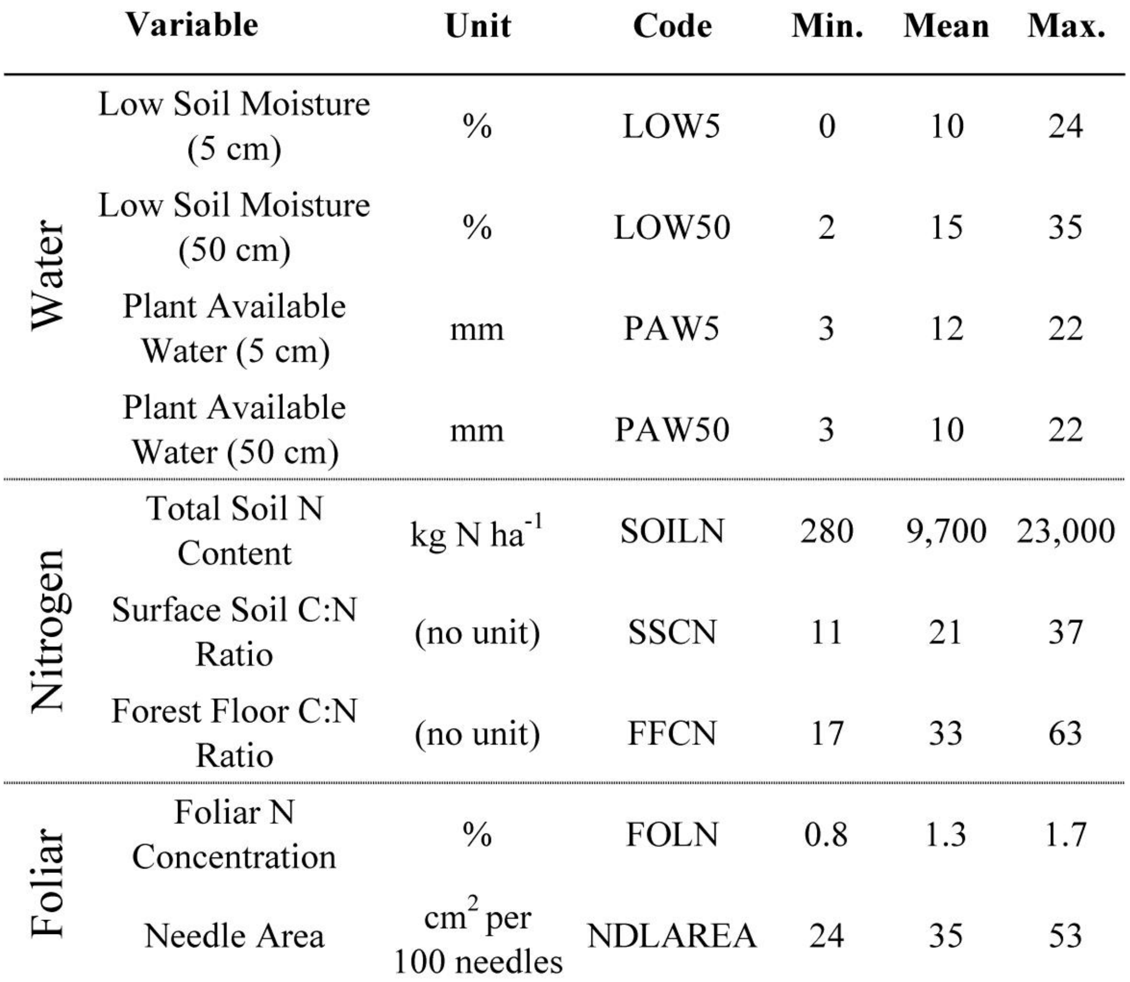
	Variable	Unit	Code	Min.	Mean	Max.		Variable	Unit	Code	Min.	Mean	Max.
Climate	Monthly Precipitation*	mm	Example: PJULY	6	26	81	Soil	Sand (0-100 cm)[‡]	%	SANDP	8	35	86
	Monthly Temperature*	°C	Example: TJULY	16	18	20		Clay (0-100 cm)[‡]	%	CLAYP	3	23	48
	Seasonal Precipitation*	mm	Example: PWIN	303	710	1326		Organic Matter[‡]	%	OM	1	4	11
	Seasonal Temperature*	°C	Example TWIN	0.8	4.2	7.0		*Effective Depth*[§]	cm	EFFDEPTH	12	76	100
	Precipitation as Snow*	mm	PAS	21	71	302		*A Horizon Depth*[§]	cm	ADEPTH	0	24	63
	Above-canopy Growing Degree Days*	degree days	AGDD	1,500	2,100	2,800		*Sand (5 cm)*	%	SAND5	4	45	76
	Under-canopy Growing Degree Days	degree days	UGDD	960	1,400	1,900		*Sand (50 cm)*	%	SAND50	5	45	85
	Under-canopy Growing Days	days	GD	153	207	226		*Clay (5 cm)*	%	CLAY5	4	29	69
Site	Latitude	degrees	LAT	43	47	50		*Clay (50 cm)*	%	CLAY50	0	28	64
	Longitude	degrees	LONG	-127	-123	-122	Water	Climatic Moisture Deficit*	mm	CMD	82	309	619
	Slope	%	SLOPE	0	14	60		Climatic Water Deficit[‖]	mm	CWD	68	182	303
	Elevation	m	ELEV	46	330	1341		Available Water Capacity[‡]	mm mm^{-1}	AWC	0.04	0.16	0.30
	Aspect	degrees	ASPECT	0	187	360		Available Water Supply[‡]	mm	AWS	38	160	280
	Enhanced Vegetation Index[†]	(no unit)	EVI	0.35	0.46	0.53		Summer Heat: Moisture Index*	°C/m	SHM	33	81	155
	Normalized Difference Vegetation Index[†]	(no unit)	NDVI	0.70	0.79	0.83							

Location Codes

Regional Latitude	BC, WA North, WA Central , WA South, OR North, OR Central, OR South
Regional Soil Parent Material	BCGla, WAGla, WAIgn, WASed, ORIgn, ORSed

* Wang et al (2012) [†] NASA (2011) [‡] Soil Survey Staff (2011) [§] Steinbrenner (1979) [‖] Lutz et al. (2010)

Table 4.2. Dependent variables, units, and codes sorted by type (water, nitrogen, and foliage). The minimum, mean, and maximum values are reported for each variable from the 60 plots in the Stand Management Cooperative Paired-tree Study.

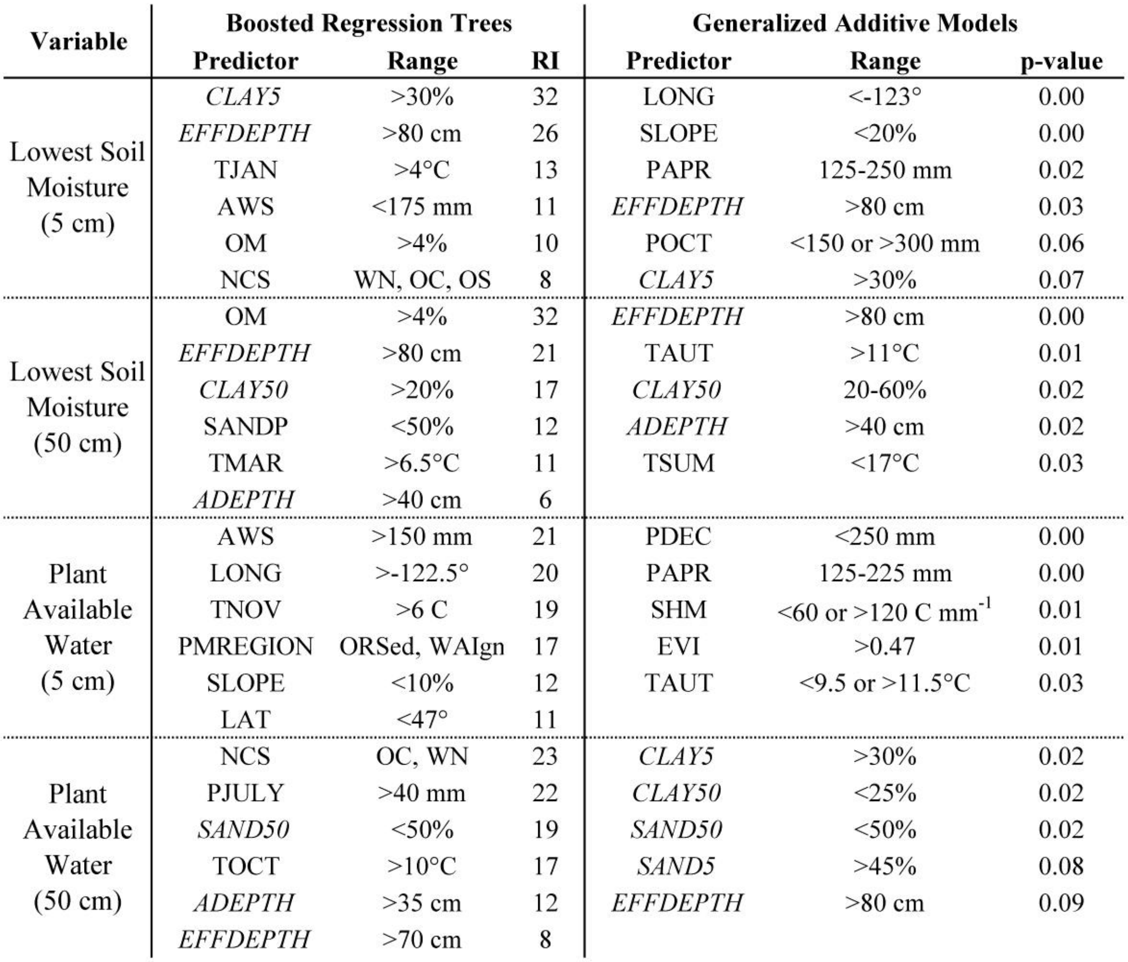


	Variable	Unit	Code	Min.	Mean	Max.
Water	Low Soil Moisture (5 cm)	%	LOW5	0	10	24
	Low Soil Moisture (50 cm)	%	LOW50	2	15	35
	Plant Available Water (5 cm)	mm	PAW5	3	12	22
	Plant Available Water (50 cm)	mm	PAW50	3	10	22
Nitrogen	Total Soil N Content	kg N ha^{-1}	SOILN	280	9,700	23,000
	Surface Soil C:N Ratio	(no unit)	SSCN	11	21	37
	Forest Floor C:N Ratio	(no unit)	FFCN	17	33	63
Foliar	Foliar N Concentration	%	FOLN	0.8	1.3	1.7
	Needle Area	cm^2 per 100 needles	NDLAREA	24	35	53

Table 4.3. Comparison of model type (boosted regression trees and generalized additive models) and data source (mapped, measured, and combined) statistics for measured soil water, nitrogen, and foliar variables. Deviance explained (DE) (%), adjusted R^2 (AR2), and root mean square error (RMSE) are stated for each model. Statistics were compared between data sources within each model type and between all models for each variable, which are separated by dotted lines. The preferred models for each variable are identified as having the best model statistics within each model type (bold). The best model statistics between all models for each variable are underlined. The preferred models for each model type and variable are described in detail in Tables 4.4 and 4.5.

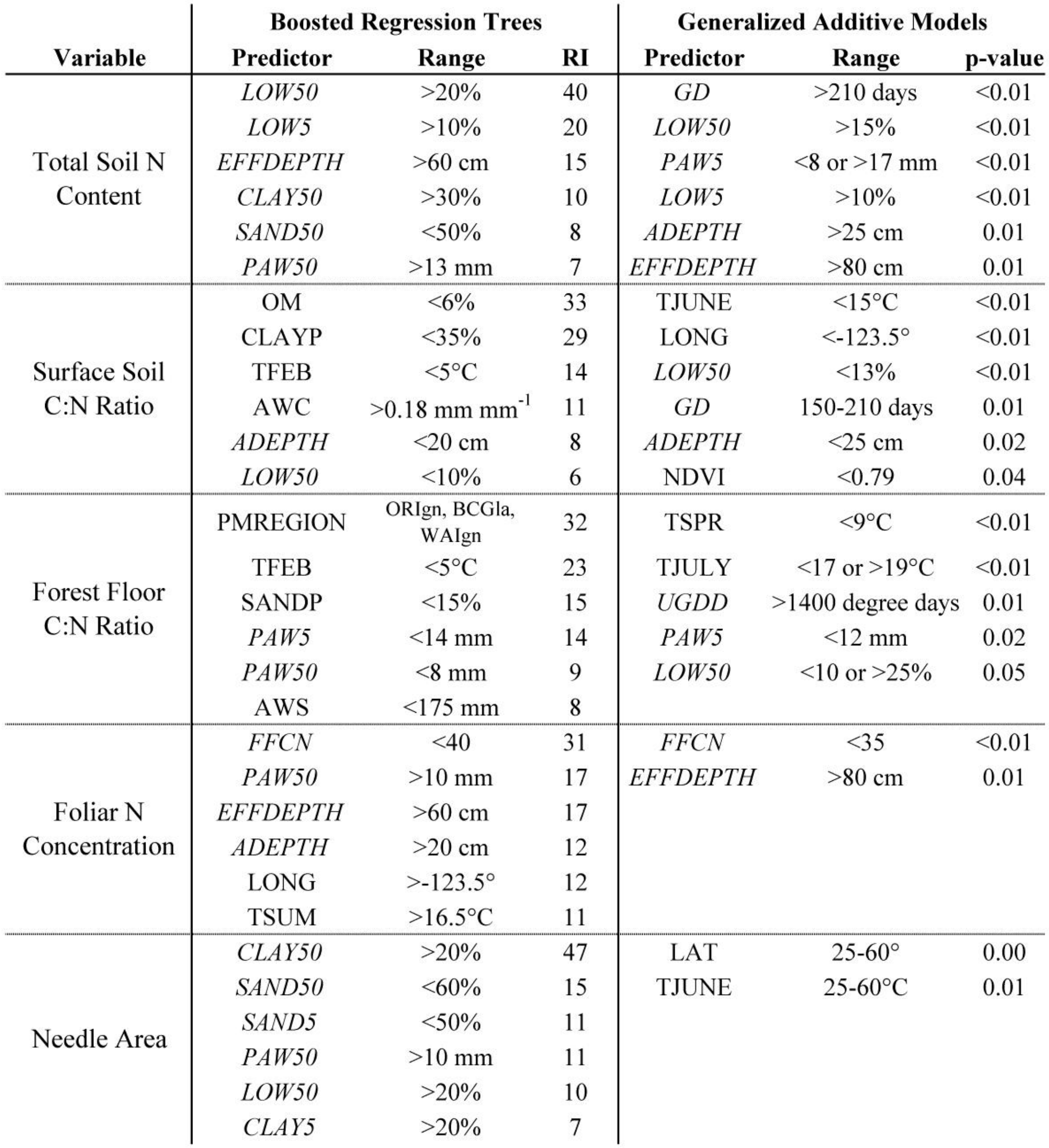
Variable	Statistic	Boosted Regression Trees			Generalized Additive Models		
		Mapped	Measured	Combined	Mapped	Measured	Combined
Lowest Soil Moisture (5-cm)	DE	22	42	**55**	47	35	**57**
	AR2	0.26	0.41	**0.54**	0.43	0.32	**0.51**
	RMSE	4.86	4.20	**3.67**	4.02	4.45	**3.60**
Lowest Soil Moistur (50-cm)	DE	47	65	**81**	42	60	**64**
	AR2	0.46	0.62	**0.79**	0.39	0.56	**0.60**
	RMSE	5.94	4.84	**3.57**	6.18	5.15	**4.90**
Plant Available Water (5-cm)	DE	**65**	32	51	**44**	33	31
	AR2	**0.63**	0.33	0.50	**0.39**	0.28	0.28
	RMSE	**2.47**	3.43	2.92	**3.13**	3.42	3.45
Plant Available Water (50-cm)	DE	42	18	**53**	7	**24**	14
	AR2	0.45	0.17	**0.54**	0.06	**0.17**	0.11
	RMSE	2.99	3.56	**2.70**	3.79	**3.43**	3.66
Total Soil N Content	DE	25	**73**	73	56	**80**	77
	AR2	0.33	**0.74**	0.61	0.52	**0.77**	0.75
	RMSE	4579	**2726**	2737	3289	**2379**	2509
Surface Soil C:N Ratio	DE	55	70	**72**	66	54	**72**
	AR2	0.54	0.69	**0.71**	0.63	0.49	**0.68**
	RMSE	3.01	2.46	**2.38**	2.62	3.06	**2.40**
Forest Floor C:N Ratio	DE	47	51	**58**	43	40	**56**
	AR2	0.46	0.51	**0.56**	0.38	0.36	**0.51**
	RMSE	0.22	0.21	**0.20**	0.23	0.23	**0.20**
Foliar N Concentration	DE	35	48	**55**	23	**37**	28
	AR2	0.38	0.47	**0.53**	0.19	**0.34**	0.24
	RMSE	0.140	0.101	**0.094**	0.123	**0.111**	0.119
Needle Area	DE	2	**29**	4	37	38	**42**
	AR2	0.00	**0.28**	0.11	0.35	0.34	**0.40**
	RMSE	5.31	**5.15**	5.27	4.27	4.23	**4.08**

Table 4.4. The preferred boosted regression tree and generalized additive models for lowest soil moisture (5 and 50 cm) and plant available water (5 and 50 cm) based on statistics in Table 4.3. Predictor variables in boosted regression tree models are sorted by highest relative influence (RI) and generalized additive models are sorted by lowest p-value. Table 4.1 describes the predictor codes. The range of the predictive variable designates the range at which the response variable has an above average value (see Figures 4.2 and 4.3 for an example). Measured variables are in italics.



Variable	**Boosted Regression Trees**			**Generalized Additive Models**		
	Predictor	**Range**	**RI**	**Predictor**	**Range**	**p-value**
Lowest Soil Moisture (5 cm)	*CLAY5*	>30%	32	LONG	<-123°	0.00
	EFFDEPTH	>80 cm	26	SLOPE	<20%	0.00
	TJAN	>4°C	13	PAPR	125-250 mm	0.02
	AWS	<175 mm	11	*EFFDEPTH*	>80 cm	0.03
	OM	>4%	10	POCT	<150 or >300 mm	0.06
	NCS	WN, OC, OS	8	*CLAY5*	>30%	0.07
Lowest Soil Moisture (50 cm)	OM	>4%	32	*EFFDEPTH*	>80 cm	0.00
	EFFDEPTH	>80 cm	21	TAUT	>11°C	0.01
	CLAY50	>20%	17	*CLAY50*	20-60%	0.02
	SANDP	<50%	12	*ADEPTH*	>40 cm	0.02
	TMAR	>6.5°C	11	TSUM	<17°C	0.03
	ADEPTH	>40 cm	6			
Plant Available Water (5 cm)	AWS	>150 mm	21	PDEC	<250 mm	0.00
	LONG	>-122.5°	20	PAPR	125-225 mm	0.00
	TNOV	>6 C	19	SHM	<60 or >120 C mm^{-1}	0.01
	PMREGION	ORSed, WAIgn	17	EVI	>0.47	0.01
	SLOPE	<10%	12	TAUT	<9.5 or >11.5°C	0.03
	LAT	<47°	11			
Plant Available Water (50 cm)	NCS	OC, WN	23	*CLAY5*	>30%	0.02
	PJULY	>40 mm	22	*CLAY50*	<25%	0.02
	SAND50	<50%	19	*SAND50*	<50%	0.02
	TOCT	>10°C	17	*SAND5*	>45%	0.08
	ADEPTH	>35 cm	12	*EFFDEPTH*	>80 cm	0.09
	EFFDEPTH	>70 cm	8			

Table 4.5. Boosted regression tree and generalized additive models for total soil nitrogen content, surface soil C:N ratio, forest floor C:N ratio, foliar N concentration, and needle area based on statistics in Table 4.3. See Table 4.4 caption for table information.



	Boosted Regression Trees			**Generalized Additive Models**		
Variable	**Predictor**	**Range**	**RI**	**Predictor**	**Range**	**p-value**
Total Soil N Content	*LOW50*	>20%	40	*GD*	>210 days	<0.01
	LOW5	>10%	20	*LOW50*	>15%	<0.01
	EFFDEPTH	>60 cm	15	*PAW5*	<8 or >17 mm	<0.01
	CLAY50	>30%	10	*LOW5*	>10%	<0.01
	SAND50	<50%	8	*ADEPTH*	>25 cm	0.01
	PAW50	>13 mm	7	*EFFDEPTH*	>80 cm	0.01
Surface Soil C:N Ratio	OM	<6%	33	TJUNE	<15°C	<0.01
	CLAYP	<35%	29	LONG	<-123.5°	<0.01
	TFEB	<5°C	14	*LOW50*	<13%	<0.01
	AWC	>0.18 mm mm^{-1}	11	*GD*	150-210 days	0.01
	ADEPTH	<20 cm	8	*ADEPTH*	<25 cm	0.02
	LOW50	<10%	6	NDVI	<0.79	0.04
Forest Floor C:N Ratio	PMREGION	ORIgn, BCGla, WAIgn	32	TSPR	<9°C	<0.01
	TFEB	<5°C	23	TJULY	<17 or >19°C	<0.01
	SANDP	<15%	15	*UGDD*	>1400 degree days	0.01
	PAW5	<14 mm	14	*PAW5*	<12 mm	0.02
	PAW50	<8 mm	9	*LOW50*	<10 or >25%	0.05
	AWS	<175 mm	8			
Foliar N Concentration	*FFCN*	<40	31	*FFCN*	<35	<0.01
	PAW50	>10 mm	17	*EFFDEPTH*	>80 cm	0.01
	EFFDEPTH	>60 cm	17			
	ADEPTH	>20 cm	12			
	LONG	>-123.5°	12			
	TSUM	>16.5°C	11			
Needle Area	*CLAY50*	>20%	47	LAT	25-60°	0.00
	SAND50	<60%	15	TJUNE	25-60°C	0.01
	SAND5	<50%	11			
	PAW50	>10 mm	11			
	LOW50	>20%	10			
	CLAY5	>20%	7			

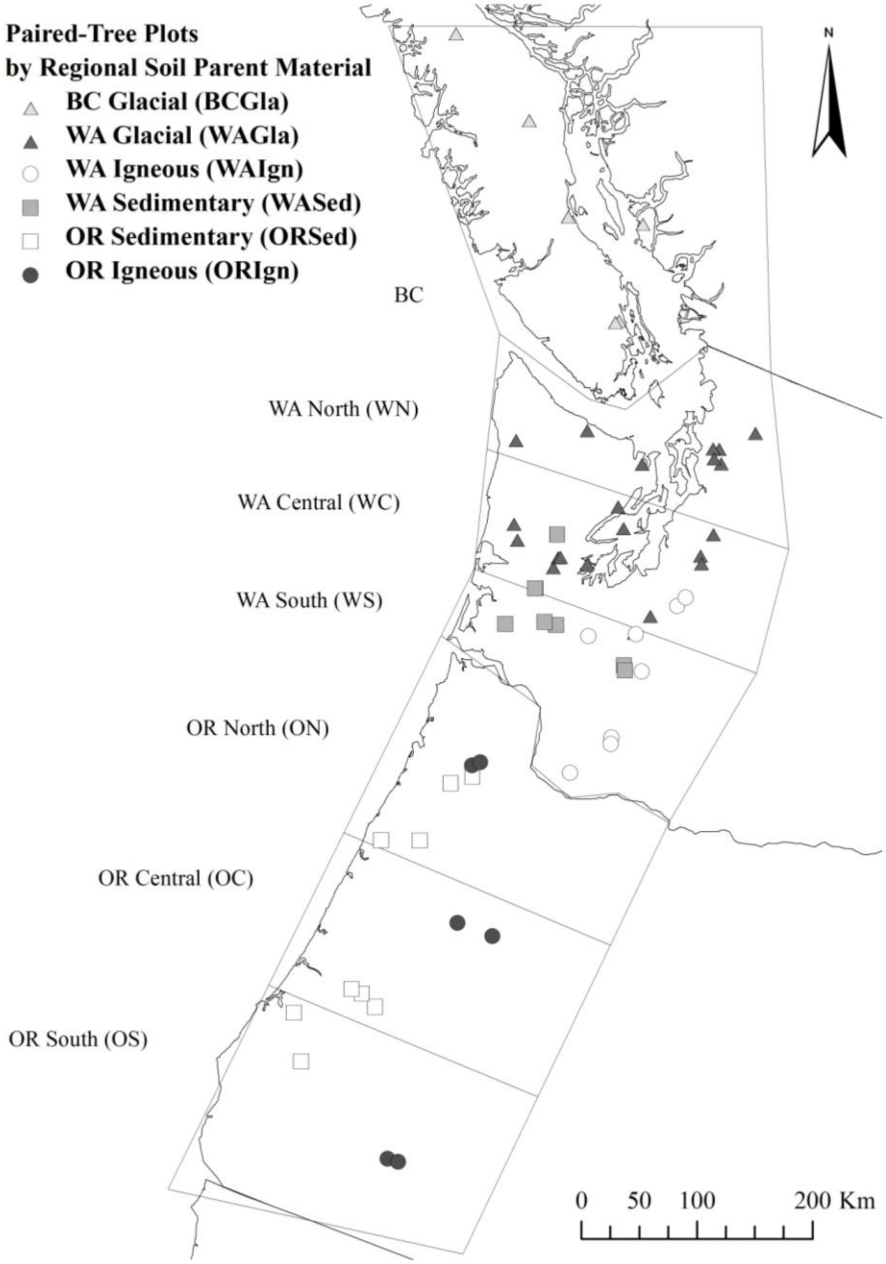


Figure 4.1. Location of Stand Management Cooperative Type V plots in the Pacific Northwest by soil parent material type and region. Soil parent material types are designated by symbols representing each plot. Regional latitudes are represented by polygons with the label to the left of each polygon. States and province are labeled as follows: British Columbia (BC), Oregon (OR), and Washington (WA). Maps were sourced from ESRI® Data and Maps.

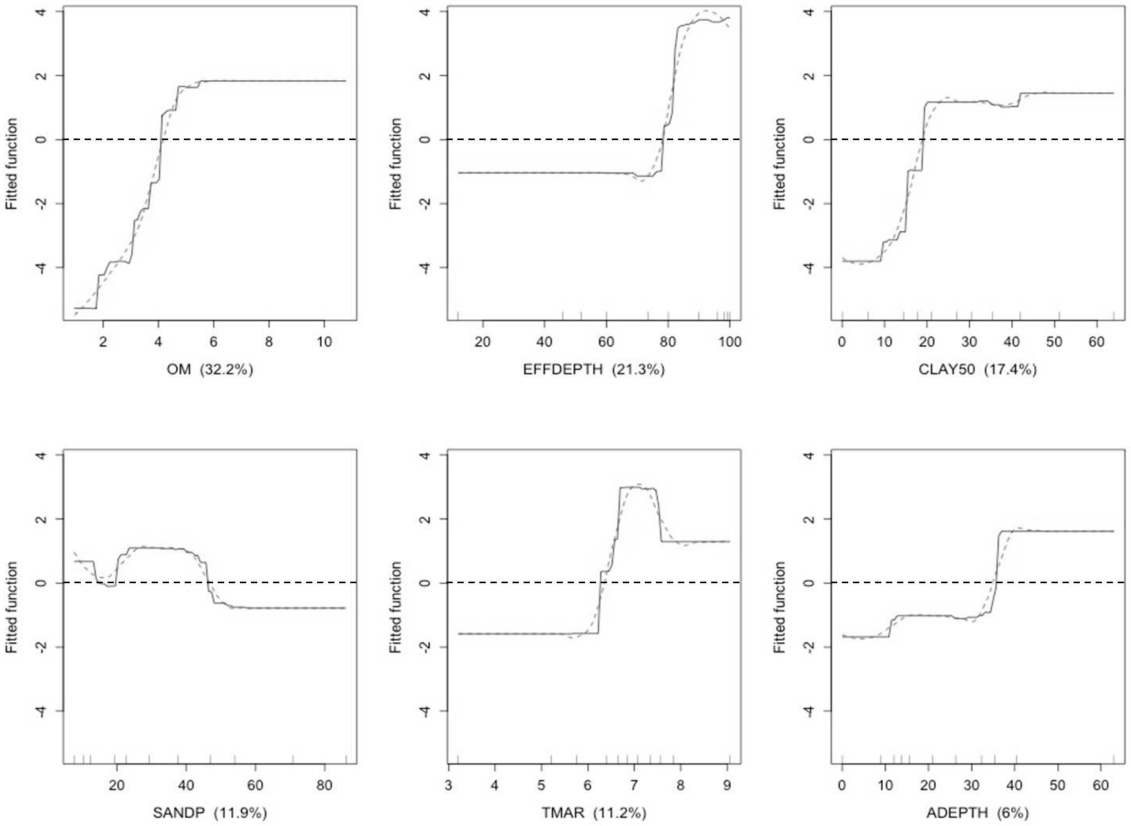


Figure 4.2. This grouping of graphs represents the preferred boosted regression tree model for lowest soil moisture (50 cm). Each graph represents the fitted function (solid line) and the smoothed line (gray dashed line) of lowest soil moisture according to the x-axis (predictor) variable keeping all other predictor variables average. The fitted function is the difference between the actual y-axis (response) value and the mean response value. Mean responses are denoted by black dashed lines. The predictor variable definitions can be found in Table 4.1. The relative influence of the predictor variable on lowest soil moisture is in parentheses below each graph. The rug graph represents the range of each predictor in deciles.

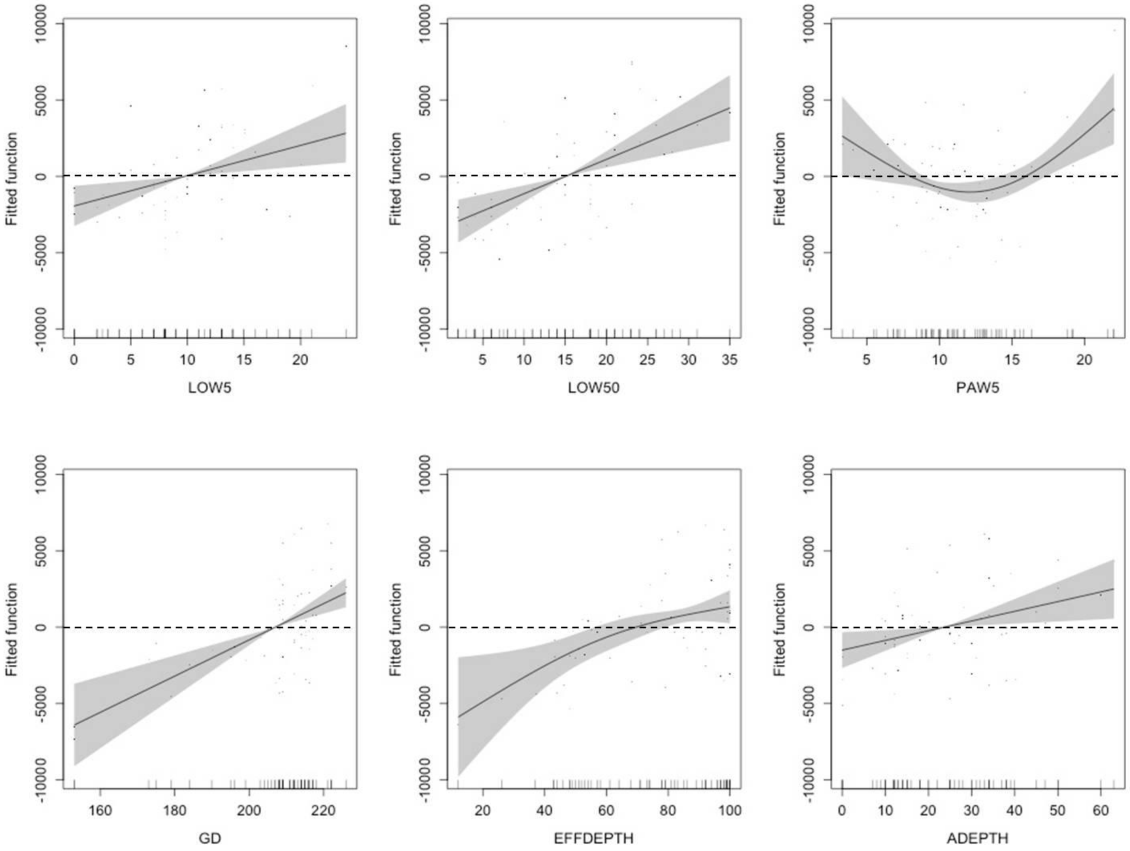


Figure 4.3. Generalized additive model graphs for total soil N content using measured predictor variables. Each graph shows the fitted function residuals (dots) with upper and lower standard error (±2) smooth estimates (shaded area). The fitted function (black line) is the difference between the actual y-axis (response) value and the mean response value. Mean responses are denoted by black dashed lines. The x-axis (predictor) variable definitions can be found in Tables 4.1 and 4.2. The rug graph represents the data range of each predictor variable.

CHAPTER 5. CONCLUSIONS

Douglas-fir plantations throughout the Pacific Northwest have distinct climate, site, and soil conditions. Soil parent materials (SPMs) and regional soil parent materials (RSPMs) identified areas with distinctly different site and soil productivity and fertilizer response. Soil nutrient regimes also identified soils with distinct soil carbon (C) and nitrogen (N) contents. Glacial SPMs, especially those in British Columbia, had the lowest soil productivity, but had higher site index values and volume mean annual increments due to greater height:DBH ratios. Sedimentary SPMs received the lowest summer precipitation yet had deeper, finer soils than the other SPMs, which led to the greatest summer soil moisture availability and soil nitrogen availability. Greater soil productivity in sedimentary SPMs led to higher site index values and growth percent, but volume mean annual increments were the lowest in sedimentary SPMs. Younger stand ages due to earlier canopy closure with sedimentary SPMs appears to be affecting height:DBH ratio and growth percent measurements between SPMs. Igneous SPMs were identified as having the lowest plant-available N due to high forest floor C:N ratios, which led to greater fertilizer response on these plots.

Lowest soil moisture, representing soil water-holding capacity, and plant available water are greatest on soils that are deeper and have higher clay and lower sand contents (Figure 5.1). Soil N availability increased with greater summer soil moisture, plant available water, soil depth, and clay content. Needle area and foliar N concentration were highest on plots with greater soil water holding capacity, but foliar N concentration was also greater on plots with higher soil N availability and deeper soils. Boosted regression trees (BRT) and generalized additive models (GAM) tended to describe soil water and nitrogen availabilities and foliar properties better using the combination of mapped and measured data sources. Mapped soil and water availability characteristics from the Natural Resource Conservation Service (NRCS) were the most important variables from mapped data sources for describing soil water, N, and foliar properties. Overall, the BRT models using combined data sources performed well for describing soil water and nitrogen availability and foliar properties of plantation Douglas-fir in the Pacific Northwest.

This study identified the unique relationships between climate and soil productivity on Douglas-fir growth and fertilizer response in the Pacific Northwest. The wide range in climate and soil water and N availabilities strongly affected foliar properties. Forest floor C:N ratio was identified as the variable most associated with plant available N and regions with high forest floor C:N ratios were identified. Accordingly, the regions with the greatest forest floor C:N ratios and fertilizer response were identified as British Columbia glacial and Washington and Oregon igneous stands.

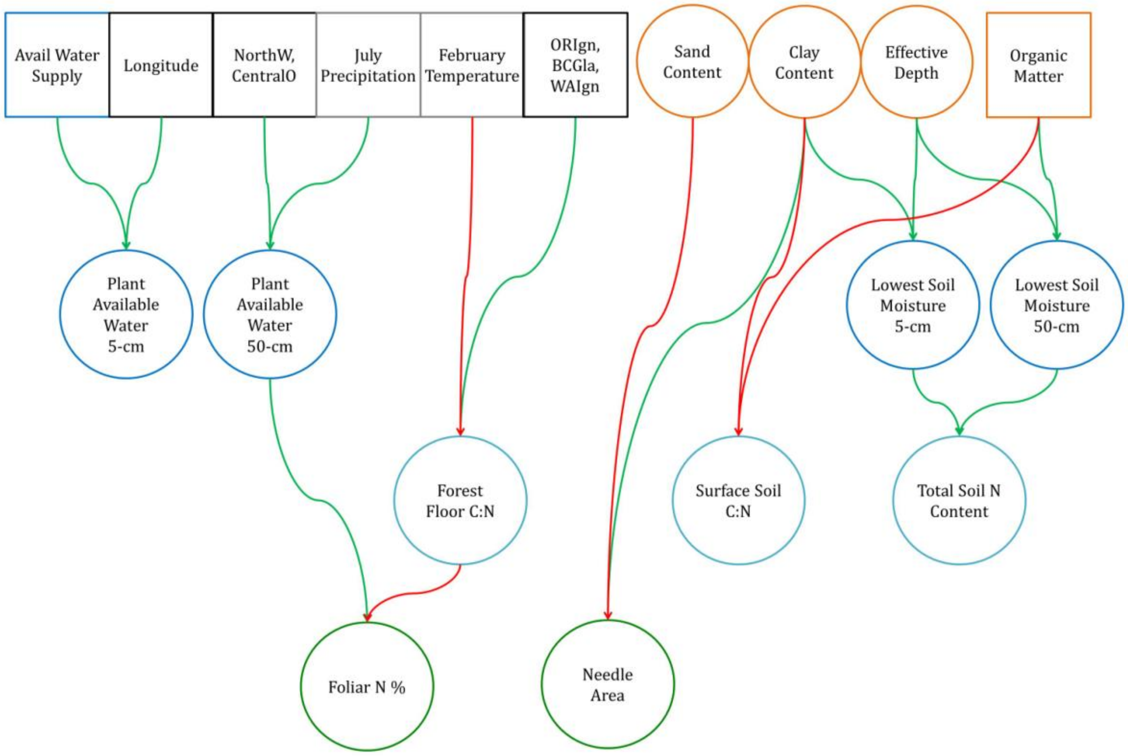


Figure 5.1 Summary of soil water, soil nitrogen, and foliar boosted regression tree models. Predictor and response variables of similar types are near each other and have the same colored circles (Tables 4.1 and 4.2). Predictor variables have arrows pointing to response variables. The link between the response variable and the two predictor variables with the greatest relative influence are shown for simplification (Tables 4.4 and 4.5). The effect of a high level of the predictor variable on the response variable is shown as positive (green) or negative (red).

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