Assessing the contribution of Red Alder (*Alnus rubra*) to forest stand nitrogen budgets

by

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Abstract

Red Alder (*Alnus rubra*) is a native coastal hardwood in British Columbia and has evolved a symbiotic relationship with the nitrogen-fixing actinomycete, *Frankia*. This research uses $\delta^{15}N$ signatures in soils, wood and litter to assess the contribution of nitrogen-fixing Red Alder to the components of stand nitrogen budgets. The stands used in this study are part of the B.C. Ministry of Forests' long-term Experimental Project 1121.01 which examines the interactions between conifers and Red Alder. Planted in 1994, the Holt Creek site contains stands of Douglas-fir and Red Alder in five proportions (Red Alder: Douglas-fir proportions: 100/0, 50/50, 25/75, 11/89, 0/100). Increment cores from 5 trees per species per plot were taken along with soil and litter samples and analyzed for essential mineral elements and $\delta^{15}N$. I hypothesized that Red Alder would enhance soil nitrogen stocks and elevate $\delta^{15}N$ signatures and that these changes would be observable in the $\delta^{15}N$ signature of the tree rings of both species. Forest floor soil under Red Alder in the 100/0 plot was enriched in total nitrogen, and $\delta^{15}N$ was elevated. This was due to the addition of nitrogen-rich litter, like followed by nitrogen discrimination in the forest floor during the process of nitrate leaching or denitrification. The litter of the two species did not differ in $\delta^{15}N$. The effect of forest floor nitrogen enrichment was visible in the tree rings of Douglas-fir in the 50/50 stand confirming that the effect of fixed-nitrogen can be observed in non-fixing species. Red Alder tree ring $\delta^{15}N$ exhibited an unexpected non-linear relationship with time that could be due to reduced nitrogen fixation associated with declining tree vigour or negative feedback from low soil pH. This research provides insight into nitrogen fixation by Red Alder over time and its influence on pure and mixed stand nitrogen budgets.

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Acknowledgments

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Dedication

To my father, Greg Nehring, for being my first science teacher. Love you Dad.

1. Introduction

1.1 Forest Soils

Many factors influence forest soil, including parent material, climate, topography, biota, and time (Jenny, 1941; Wagai et al., 2011). In the Pacific Northwest of North America, the soil parent material consists of glacial or marine deposits created during the last ice age (20,000 – 11,700 years ago) (Keser & St. Pierre, 1973). Temperate rainforests predominantly occupy coastal areas of this region today, with moderate temperatures in both summer and winter (MAT: 10–24°C) and high levels of rainfall (MAP: 300 cm per year or more) (Shanley et al., 2015).

Most forest soil nutrients absorbed by plants and soil microbes are in their ionic form (Robertson et al., 1999). An influence on nutrient availability is the soil cation exchange capacity (CEC) (Rhoades, 1983). CEC is the total amount of exchangeable cation that the soil can absorb or the capacity of the soil to hold cations (Jones, 1982, Sumner & Miller, 1996). Soil particles often carry a negative charge and are neutralized by the cations in the soil (Sumner & Miller, 1996). The cations on the soil particles are easily exchangeable with other soil cations and thus are plant available. The CEC of soil can be affected by several factors, including the number of clay particles, amount of organic particles, and pH (Ketterings et al., 2007). Organic matter can have 4-50 times higher CEC per weight than clay particles, and because the dissociation of organic acids depends on the soil pH, this is called pH-dependant CEC (Ketterings et al., 2007). In soils with high organic matter content and thus high pH-dependant CEC, the CEC will increase with an increase in pH.

1.2 Nitrogen Cycling

Nitrogen (N) is essential in plant growth and development (Kishorekumar et al., 2020). The natural cycling of nitrogen, including the important process of nitrogen mineralization, plays a fundamental role in the regulation of ecosystem structure and function (Moffat, 1998; Robinson, 2001). During nitrogen mineralization, organic nitrogen is obtained by decomposers and transformed into inorganic (or mineral) forms, including NH_3, NH_4^+ and NO_3^- (Girkin & Cooper, 2022). Mineralization occurs alongside nitrogen

immobilization, where soil organisms take up organic nitrogen, making it unavailable to plants (Hagemann et al., 2016). Soils with high carbon-to-nitrogen ratios can experience higher microbial nitrogen demand and thus have higher rates of nitrogen immobilization (Hagemann et al., 2016). On average, microbial nitrogen turnover can take up to 2 months in coniferous forests (Davidson et al., 1992). Mineralization rates are an important measure commonly used as indicators of critical ecosystem processes such as susceptibility of organic matter to degradation (Aber et al., 1989), nitrogen retention (Christ et al., 1995), and nitrogen loss through leaching (Verchot et al., 2001). Both net (time 0 – time X) and gross (total after time X) mineralization can be estimated in-situ by incubating a soil sample and measuring the value of or change in the extractable nitrogen pool (Verchot et al., 2001). Evidence suggests that gross extractable nitrogen is a more straightforward and precise method to determine soil nitrogen availability and immobilization effects on nitrogen availability (Kranabetter et al., 2007).

In many cool temperate and boreal forest ecosystems, nitrogen is a major limiting nutrient for plant growth, and there is high microbial and plant competition for organic nitrogen and NH_4^+, resulting in a 'closed' nitrogen cycle (Burnham et al., 2019; Högberg et al., 2017). These systems are 'closed' due to the high retention of nitrogen by plants, fungi, and bacteria and the low levels of nitrogen lost by nitrification (bacterial reduction of NH_4^+ to NO_2 and NO_3^-) (Kranabetter et al., 2020). Conversely, in areas where nitrogen is less limiting, ecosystems can exhibit more 'open' cycles (Kranabetter et al., 2020). These cycles have less competition for nitrogen and exhibit high rates of nitrogen mineralization and considerable nitrogen losses through nitrification (Högberg et al., 2017; Kranabetter et al., 2020).

1.3 Nitrogen Fixation

Biological nitrogen fixation is the process by which bacteria or some archaea convert molecular atmospheric nitrogen (N_2) into NH_3 that microbes and plants can use (Bluhum & Hibbs, 2006; Farrer & Pecoraro, 2003). In biological nitrogen fixation, a nitrogenase enzyme reduces N_2 to NH_3 (Farrer & Pecoraro, 2003). Some nitrogen-fixing organisms can form symbiotic relationships with plant species, often within nodules in the roots (Kuypers et al., 2018). These root nodule symbioses are classified into

leguminous and non-leguminous. The most well-researched biological nitrogen fixation process is leguminous, found within the Legume family and their bacteria *Rhizobia* (Zahran, 1999). The non-leguminous category includes the genus *Alnus*. Members of the *Alnus* genus have evolved a symbiotic relationship with the actinomycete bacteria *Frankia*, which fix atmospheric N_2 and can share the resulting NH_3 with the plant (Benson & Clawson, 2000).

Nitrogen fixation is an energetically expensive process as 20-30 ATP molecules are required to convert a single N_2 molecule to $2NH_3$ under normal conditions (Burris, 1991). Due to this, fixation rates are often highest during the growing season. The optimal temperature range for *Frankia* is around 30°C, but activity can still occur at temperatures as low as 10°C if the pH is favourable (Burggraaf & Shipton, 1982). Like other soil actinomycetes, *Frankia* appears to grow best between pH 6 and 8, but growth can still occur in the range of pH 4.6 to 8.6 (Johnstone, 1947; Waksman, 1922). Outside of this optimal range, or in the presence of a nitrogen-rich substrate, the levels of fixation decrease, and plant hosts may restrict or eliminate carbon supply to nitrogen-fixing nodulated roots to conserve energy (Chaia et al., 2007; Johnstone, 1947; Waksman, 1922). Actinomycetes are also generally absent in wet or waterlogged soils, and studies have shown that *Frankia* declines in growth and activity with increased or prolonged moisture (Chaia et al., 2007; Sayed et al., 1997; Shipton & Burggraaf, 1982).

1.4 Nitrogen Isotopes and $\delta^{15}N$

Nitrogen naturally occurs as two stable isotopes ^{14}N and ^{15}N (Denk et al., 2017). The relative abundance of these isotopes can vary in the soil, atmosphere or plant and animal tissue as the isotopes are selected for or against in a process known as isotopic fractionation or discrimination (Tiwari et al., 2015). Earth's atmosphere is 99.6% ^{14}N and 0.4% ^{15}N, and the change in the ^{15}N isotope can be measured (Stüeken et al., 2016). The selection for or against a specific isotope of nitrogen in a physiological or physical process changes the natural abundance in a tissue: the ratio of the trace isotope (^{15}N) to the more abundant isotope (^{14}N) (Dodds & While, 2020). As the natural abundance ratio of most systems is low, the isotopic

composition is expressed using the $\delta^{15}N$ notation, where atmospheric nitrogen is the reference standard (Eq. 1) (Coplen, 2011; Denk et al., 2017; Tiwari et al., 2015).

$$\text{Eq. 1} \quad \delta^{15}N = \left[\left(\frac{^{15}N_{sample}/^{14}N_{sample}}{^{15}N_{standard}/^{14}N_{standard}}\right) - 1\right] * 1000$$

units in ‰ (permil or parts per thousand)

As atmospheric nitrogen is the reference standard, the $\delta^{15}N$ is relatively constant at around 0‰ (Mariotti, 1983; Severinghaus et al., 1996). A value greater than atmospheric is considered enriched, and a lower value is considered depleted (Peterson & Fry, 1978). While some slight evidence that fractionation during nitrogen fixation does exist, it is widely accepted that biological nitrogen fixation by nitrogenase does not fractionate (Craine et al., 2015; Handley, 2002). For plants that reply exclusively on N_2 fixation, the $\delta^{15}N$ signatures of their tissues match that of the atmosphere ($\delta^{15}N$ ~0‰) (Handley, 2002). However, many nitrogen-fixing species show departures in $\delta^{15}N$ from 0‰ depending on their reliance on fixed nitrogen, but $\delta^{15}N$ signatures tend to fall within the range of -2.0‰ and 2.0‰ (Craine et al., 2009; Shearer & Kohl, 1986). The nodules that store the nitrogen-fixing bacteria are often highly enriched in ^{15}N ($\delta^{15}N$ 2.5-6.3‰) (Shearer & Kohl, 1986), but enrichment of the nodules has little effect on overall plant $\delta^{15}N$ values (Craine et al., 2015).

An advantage of studying nitrogen dynamics in natural systems using $\delta^{15}N$ is that these experiments do not require nitrogen additions through fertilizers. The nitrogen flux from fertilizers can negatively affect the surrounding ecosystem. When nitrogen fertilizer leaches into surrounding streamwater, it can cause large algal blooms that result in oxygen-depleted water (Robertson & Vitousek, 2009; Zhu et al., 2002). Nitrogen fertilizer can also inhibit nitrogen-fixation and disrupt soil nitrogen cycles (Fujikake et al., 2002, 2003; Ohyama et al., 2011).

1.5 Mycorrhiza and Nitrogen Uptake

Most mycorrhizal fungi fall into two major groups based on their morphology, anatomy, and physiology (Bunyard, 2020). While only forming ~2% of mycorrhizal associations, globally, many of the

recognizable mushroom-forming fungi in temperate and boreal forests form ectomycorrhizal (EM) associations where a dense hyphal sheath, or mantle, surrounds the root surface but does not penetrate the plant cell walls (Bunyard, 2020; Genre & Bonfante, 2012; Makarov, 2019). Arbuscular mycorrhizal (AM) associations comprise ~80% of associations. In AM associations, the fungus penetrates the plant host cell walls and forms tree-like, multi-branched arbuscules associated with the root cell plasma membrane (Genre & Bonfante, 2012; Makarov, 2019). Mycorrhizal fungi are essential in facilitating plant uptake of nitrogen, phosphorus, and other nutrients and EM can provide 80% or more of the nitrogen demand of plants (van der Heijden et al., 2015). Current estimates are that over 90% of plant species form a fungal symbiosis (Bonfante & Genre, 2010). The plant makes organic molecules, such as sugars, through photosynthesis and supplies them to the fungal symbiont in exchange for water and mineral nutrients from the soil (Smith & Read, 2010). The fungal hyphae occupy large volumes of soil, far beyond what plant roots can usually reach, increasing the absorptive surface area (Bunyard, 2020, Johnson & Gehring, 2007). Mycorrhizal fungi may also mobilize soil nutrients through the action of enzymes or acids (Bukovská et al., 2018; Frey, 2019; Toljander et al., 2007)

AM fungi are restricted to the uptake of mineralized nitrogen forms (NH_4^+ and NO_3^-) (Schweiger, 2016), while EM fungi can break down organic nitrogen with extracellular proteases and chitinase enzymes (Courty et al., 2010; Lindahl & Tunlid, 2015; Talbot & Treseder, 2010). EM fungi also can directly take up amino acids and small (2 – 6 amino acid residue) peptides (Alagramam et al., 1995; Chalot & Brun, 1998). After EM fungi take up mineral nitrogen (NH_4^+ or NO_3^-), the nitrogen is assimilated into amino acids (mainly arginine), transported through the hyphae, and then transferred to the plant in the form of NH_4^+ (Govindarajulu et al., 2005). The assimilation of NH_4^+ is more efficient and thus less costly than NO_3^- assimilation making NH_4^+ the preferred nitrogen form (Chalot & Passard, 2011; Govindarajulu et al., 2005; Ingraffia et al., 2020; Ngwene et al., 2013).

Patterns of nitrogen isotope fractionation are well documented in EM fungi but less so in AM (Hobbie & Colpaert, 2003, Schweiger, 2016). EM fungal sporocarps and sheaths are enriched in ^{15}N compared to

their host plant (Högberg et al., 1996; Taylor et al., 1997, 2003). The amino acid biosynthesis during EM fungal metabolism often creates amino acids that have lower $\delta^{15}N$ values than their precursors (Evans, 2001; Macko et al., 1986). The translocation of low $\delta^{15}N$ amino acids to the host plant and retention of high $\delta^{15}N$ amino acids by the fungi causes the fungi to become enriched, and the plant depleted when compared to the soil nitrogen source (Evans, 2001; Hobbie & Hobbie, 2008; Hobbie & Högberg, 2012). Greenhouse experiments have found mixed evidence for fractionation in AM fungi, from no effect (Courty et al., 2015; Michelsen et al., 1996), decreased $\delta^{15}N$ (Craine et al., 2009), to increased $\delta^{15}N$ (Aguilar et al., 1998; Handley et al., 1999). Schweiger (2016) reported fractionation by AM fungi during nitrogen assimilation and transformations, but only under nitrogen deficiency, suggesting that AM fractionation may depend on nitrogen availability.

1.6 Soil $\delta^{15}N$

Due to surface litter and fresh nitrogen inputs being more susceptible to leaching and absorption by fungi and plants than nitrogen in deeper soil horizons, mineral soil $\delta^{15}N$ values reflect longer-term records of nitrogen transformations and movement (Hobbie & Ouimette, 2009). $\delta^{15}N$ values increase with depth in forest and grassland (Högberg, 1997; Malo et al., 2005). At the surface, high rates of mineralization promote enriched $^{15}NH_4^+$ pools and high rates of $^{15}NO_3^-$ leaching in surface soils (Högberg, 1997; Piccolo et al., 1996). At the same time, the $^{15}NO_3^-$ is partially retained further down in the soil profile and can thus accumulate over time (Högberg, 1997; Piccolo et al., 1996).

Nitrogen mineralization introduces a large amount of variability into the $\delta^{15}N$ signatures of soil NH_4^+ due to fractionation during decomposition of larger molecules in the soil (Högberg, 1999). This inorganic N produced by mineralization and nitrification is consistently more depleted $\delta^{15}N$ values than bulk soil (Koba et al, 2010). Nitrification (NH_4^+ to NO_3^-) and denitrification (NO_3^- to N_2 gas) processes can fractionate against the ^{15}N isotope by to 20–30‰ (Högberg, 1997; Kritee et al., 2012; Mariotti et al., 1982). The level of fractionation is dependent on the concentration of NO_3^-. When NO_3^- concentrations are high, nitrate reductase is substrate saturated, and there is a high selection against the heavy isotope,

which decreases as NO_3^- concentrations decrease and there is less NO_3^- to bind to the enzyme (Kritee et al., 2012; Mariotti et al., 1982). Houlton et al. (2006) found that denitrification was driven to near completion in wet conditions, resulting in no net fractionation. In forests and grasslands, soil nitrogen processes appear to enrich mineral soil $\delta^{15}N$ with time through the breakdown of plant material and the remobilization of NH_4^+ (Boddey et al., 2000). The volatilization of NH_4^+ into the atmosphere has a high fractionation factor of 17.9‰ (Stern et al., 1999).

1.7 Foliar $\delta^{15}N$

The foliar $\delta^{15}N$ values of a plant are a result of the isotopic composition of the nitrogen taken up from the soil, as well as any fractionation that occurs during nitrogen uptake, assimilation, and reallocation within the plant (Kalcsits & Guy, 2013). Plant assimilation of nitrate or ammonium appears to exhibit enzymatic discrimination against the heavier ^{15}N isotope, causing plants to be depleted by about 2-3 ‰ compared to the source soil nitrogen (Evans, 2001). *In vitro* studies of two important enzymes in plant nitrogen processing, nitrate reductase (NR) and glutamine synthetase (GS), have found discrimination factors of 17-22‰ for NR (Cui et al. 2020; Ledgard et al. 1985; Liu et al. 2014; Needoba et al. 2004) and 16-29‰ for GS (Yoneyama et al. 1993; Yoneyama et al. 2001). It is important to note that these values are from *in vitro* studies. It is only very rarely that the $\delta^{15}N$ of leaves reflects the extent of this discrimination *in vivo* (Pritchard & Guy, 2005; Yoneyama et al., 2003).

Variation in $\delta^{15}N$ between plant parts shows fractionation within the plant itself. Studies have shown differences in root and shoot $\delta^{15}N$, with shoots being ^{15}N-enriched compared to roots (Kalcsits et al., 2015; Pritchard & Guy, 2005). This fractionation is due to the allocation of nitrogenous compounds to different parts of the plant (Evans, 2001). When nitrate is reduced in the roots by NR, the enzyme tends to discriminate against the molecules of $^{15}NO_3^-$, and these remaining enriched nitrate molecules tend to be translocated to the shoots (Comstock, 2001; Evans, 2001; Robinson et al., 1998).

Globally there is a strong positive correlation between foliar $\delta^{15}N$ and N concentrations (Craine et al., 2009). Plants almost always have lower foliar $\delta^{15}N$ values than soils, with ectomycorrhizal plants

averaging −4.0‰ (±0.2) and arbuscular plants −3.4‰ (±0.1) less than soil $\delta^{15}N$ values (Craine et al., 2015). There are three theories to explain this phenomenon, including increased discrimination during solubilization of dissolved organic nitrogen, higher discrimination by mycorrhizal fungi, or that current models using the $\delta^{15}N$ of dissolved organic matter are not a good indicator of the pool of plant available nitrogen (Craine et al., 2015). Plant $\delta^{15}N$ also appears to increase with nitrogen availability (Craine et al., 2015).

1.8 Tree-ring $\delta^{15}N$

While foliar $\delta^{15}N$ represents a single season, patterns in wood $\delta^{15}N$ can span decades to centuries. In regions with well-defined seasons, as a tree grows and deposits an annual growth ring, it includes nitrogen atoms within the wood that can be used to track changes in the nitrogen available to the plant over time (Balster et al., 2009). These compounds can provide critical information about soil nitrogen cycling for areas that lack long-term records (Burnham et al., 2016). The $\delta^{15}N$ signature in the wood of tree rings can be used as an indicator to study the dynamics of the soil nitrogen cycle over long periods (Burnham et al., 2016; Gerhart & McLauchlan, 2014). Using tree ring $\delta^{15}N$ has the benefit of covering extended periods, it is a signal directly reflecting plant uptake, and it can be associated with the geospatial information of the trees (Gerhart & McLauchlan, 2014). In contrast to foliar $\delta^{15}N$, there does not appear to be a consistent correlation between wood nitrogen concentration and the $\delta^{15}N$ value as positive correlations (Larry et al., 2010; Leonelli et al., 2012), negative correlations (Choi et al., 2007), and a lack of correlation (Doucet et al., 2012; Guerrieri et al., 2009) have been reported. Positive correlations appear to be consistent in the response of $\delta^{15}N$ to marine bird colonies (Mizota et al., 2011) and negative correlations are consistent under acid precipitation (Kwak et al., 2011).

Globally there is no consistent relationship between wood $\delta^{15}N$ and time (ring age). Instead, the relationship appears to be site-dependant (Gerheart & Mclauchlan, 2014). Even within a single species in two adjacent watersheds near Victoria on Vancouver Island, British Columbia (Canada), two sites had linear relationships of tree ring $\delta^{15}N$ with time, two had curvilinear relationships, and two had no

relationship (Kranabetter & Meeds, 2017). McLauchlan et al. (2017) found that the decline in wood $\delta^{15}N$ over time was most pronounced in cool, wet forests, and that wood $\delta^{15}N$ increased with time on the driest sites. Using ten year-segments, Hietz et al. (2010) found that younger wood had higher $\delta^{15}N$ values than older wood from the same decade. As noted by Kranabetter & Meeds (2017), many studies make no allowance for underlying soil fertility, which could be confounding as soils of low or modest fertility are more likely to be associated with stable or relatively low wood $\delta^{15}N$ values. Variation among species in wood $\delta^{15}N$ trends over time may also exist, and different methods of analysis can make comparison difficult.

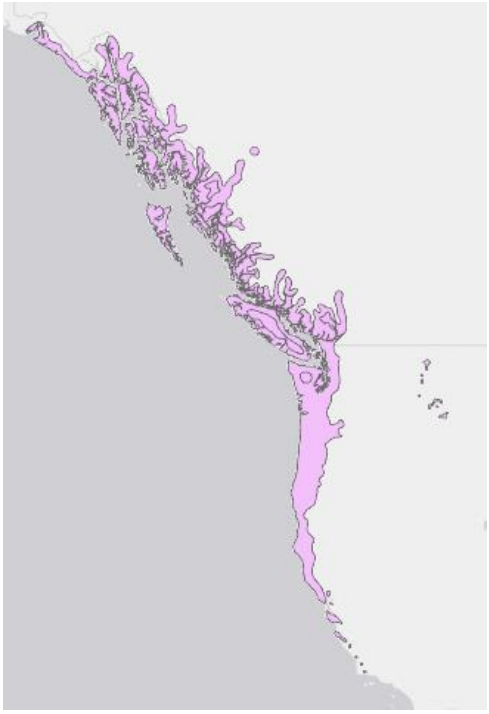

Figure 1. Natural range of Red Alder from southeast Alaska to southern California with isolated populations in Idaho. Source: Data Basin [Online]. Available at https://databasin.org/

1.9 Red Alder

Red Alder (*Alnus rubra* Bong.) is a member of the Betulaceae family and is the only *Alnus* species that reaches commercial size (Niemiec et al., 1995; Xie, 2008). The most commonly occurring coastal broadleaf tree in British Columbia, Red Alder grows at elevations below 200 m within 200 km of the coastline from southeast Alaska to southern California (Figure 1) (Burns & Honkala, 1990; Hamann, 2001; Harrington, 2006). Red Alder has a long legacy in the Pacific Northwest, with pollen data supporting Alder's appearance in the area soon after the last ice age (20,000 – 11,700 years ago) (Hebda et al., 2022; Mathewes & Pellatt, 2000).

Red Alder can be found on many soil types but is commonly found on Brunisols, Gleysols, Organics, Podzols, and Regosols in British Columbia (Harrington & Courtin, 1994; Harrington, 2006). Red Alder grows in pure- and mixed-species stands, but pure stands are often restricted to stream banks and slopes as they can tolerate poor drainage and some flooding (Harrington, 2006). Mixed-species stands have a

much wider distribution, with common associates being Douglas-fir, Western Hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Western Redcedar (*Thuja plicata* Donn ex D. Don), Grand Fir (*Abies grandis* (Douglas ex D. Don) Lindl.), Sitka Spruce (*Picea sitchensis* (Bong.) Carrière), Black Cottonwood (*Populus trichocarpa* Torr. & A. Gray ex Hook.), Bigleaf Maple (*Acer macrophyllum* Pursh), and Willow (*Salix* spp. L.) (Deal, 2006; Harrington, 2006). The most common undergrowth associations of Red Alder in British Columbia are Western Swordfern (*Polystichum munitum*) or Redwood Sorrel (*Oxalis oregana*) (Henderson et al. 1989).

Often referred to as a pioneer or disturbance species, Red Alder establishes quickly in openings with high light levels and exposed mineral soil created by logging, fire, and landslides (Haeussler et al., 1995, Harrington, 2006). Red Alder can colonize poor soils due to its symbiotic association with the nitrogen-fixing bacteria *Frankia* (Benson & Clawson, 2000). The nitrogen fixation rates of a Red Alder stand range between 10 to 150 kg N/ha per year, with rates as high as 320 kg N/ha per year being reported (Bormann et al., 1994; Van Miegroet et al., 1989). Trends in Red Alder nitrogen-fixation over time are not well reported, but observations by DeBell & Radwan (1984) show a slight decrease in foliar N% from 2.45% in young (9-year-old) Red Alder to 1.65% in mature Red Alder (45-years-old).

On sites with limited nitrogen, Red Alder can increase aboveground primary productivity by increasing total soil nitrogen, the availability of absorbable nitrogen, and the levels of exchangeable cations (Bormann & DeBell, 1981; Cole et al., 1991; Tarrant & Miller, 1963). On higher nitrogen sites, total nitrogen and nitrogen availability still increase, but primary productivity is less affected (Hart et al., 1996; Selmants et al., 2005). Higher nitrogen sites often show a decrease in pH and an increase in nitrate (NO_3^-) leaching when colonized by Red Alder (Hart et al., 1996). Soil acidification occurs when Red Alder's nitrogen fixation exceeds the ecosystem's capacity to accumulate nitrogen (Cole et al., 1991), but acidification may lead to an increase in weathered minerals (Teklehaimanot & Mmolotsi, 2007). Soil organic matter under Red Alder can be as much as 20% higher than in other areas (Binkley et al., 1992;

Bormann & DeBell, 1981). There is also evidence that Red Alder positively affects soil microbial communities with increased bacterial enzymatic activity in pure Red Alder stands (Selmants et al., 2005).

1.10 Red Alder Mycorrhizal Associations

In addition to its symbiotic association with *Frankia*, Red Alder forms symbiotic relationships with mycorrhizal fungal species that further contribute to the tree's rapid growth and positive influence on soil fertility and structure (Holmberg, 2006). Plants are generally thought only to form one type of mycorrhizal association, but there is increasing evidence that some genera can form both AM and EM (Bunyard, 2020). These "dual-mycorrhizal" plants offer insights into the biotic and abiotic factors that may affect mycorrhizal root colonization (Teste et al., 2020). *Alnus* is considered by many to be a dual-mycorrhizal genus (Hall et al., 1979; Hempel et al., 2013; Teste et al., 2020), with some evidence suggesting *Alnus* may commonly associate with EM, but form AM in areas with low EM inoculate (ex. dry areas) (Kilpelainen et al., 2017; Teste et al., 2020). Red Alder is highly species selective of its EM symbionts with a low number of potential associates (11–22 species) (Kennedy & Hill, 2010; McBurney et al., 2017).

1.11 Red Alder Mixed Plantings

Red Alder's rapid juvenile growth and contributions to the soil nitrogen pool have made it a popular species for land restoration and reclamation (Hamann, 2001). Red Alder is short-lived, reaching maturity at 60-70 years with a maximum lifespan of around 100 years (Harrington, 2006). In optimal conditions, the species can reach 30-40 m in height and 75 cm in diameter (Harrington. 2006). Red Alder's fast juvenile growth, and large overshadowing canopy lead some to consider it a weed species in conifer plantations (McBurney et al., 2017).

Red Alder often grows in association with Douglas-fir, one of the most economically important trees in British Columbia (Government of Canada, 2021). Douglas-fir is a common species throughout the

Cascade Range and a significant component of Pacific Northwest forests (Case & Peterson, 2005). The native range of Douglas-fir resembles an inverted "V," with the two arms being comprised of two subspecies (Figure 2). The Pacific Coast region is the range of Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) while the more inland region is the range of Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) (Hermann & Lavender, 1990). Pure stands can be found from their northern limit on Vancouver Island to as far south as the Santa Cruz Mountains (Herman & Lavender, 1990). Douglas-fir commonly reaches 500 years of age, with some exceeding 1000 years (Van Pelt, 2007). At maturity, the tree can exceed 100 meters in height and be 2.5 meters in diameter (Burns & Honkala, 1990). Red Alder is a strong competitor with young Douglas-fir due to Alder's rapid juvenile height growth (Fang et al., 2019). While Red Alder does compete early on, the tree is shade intolerant and highly susceptible to suppression from longer-lived conifers when they overtop alders (Deal et al., 2017; Newton & Cole, 1994). When overshadowed, the alders can die and, without a new disturbance, cannot re-establish (Deal et al., 2017; Smith, 1968). Red Alder was regularly removed from conifer plantations for many years to decrease competition (Kennedy et al., 2015).

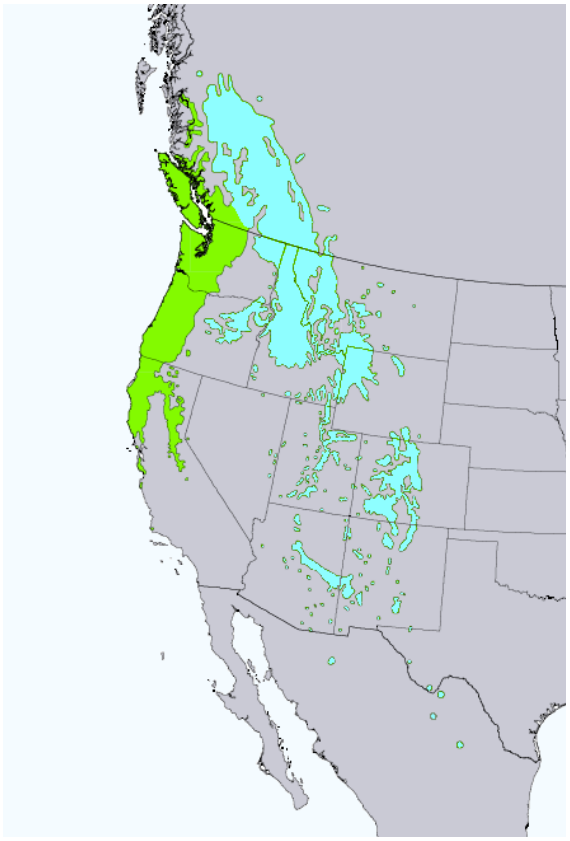

Figure 2. Range of Douglas-fir. Green: Coastal Douglas-fir. Blue: Rocky Mountain Douglas-fir. Source: USGS [Online]. Available at: https://www.feis-crs.org/feis/

In the 1950s, there was increased interest in Red Alder's soil-improving abilities and growth rate and the first evaluations of yield were completed (Bluhum & Hibbs, 2006). In the 1970s and 80s, Douglas-fir timber dropped in value, and Red Alder value increased (Bluhum, & Hibbs, 2006). This resulted in a

wave of studies on the positive benefits of planting Red Alder on soil dynamics and neighbouring tree species.

The introduction of Red Alder in a mixed stand increases the annual litterfall (Waring & Schlesinger, 1985) and, due to the higher nutrient concentration in the litter (Cole et al., 1978; Gessel & Turner, 1974), will accelerate nutrient cycling (Bormann et al., 1994). Red Alder tends not to re-absorb much of the nitrogen in the leaves during autumn, thus most of this nitrogen is deposited into the soil following leaf drop (Coté et al. 1989). Nitrogen concentration in Red Alder leaves averages around 2-2.5% (Perakis et al., 2012; Scott et al., 2008; Teklehaimanot & Mmolotsi, 2007). Soil organic matter also increases under alder (Bormann et al., 1994). This leads to improved soil aggregation, lower soil bulk density (Wild, 1988), and increased soil water-holding capacity (Crocker & Dickson, 1957). Mixed Red Alder forests can also support more wildlife species than pure stands, with higher numbers of frogs, salamanders, shrews, and newts (Aubry & Hall, 1991; Corn & Bury, 1991; McComb, 1994).

Mixed species trials have shown that Red Alder litter can promote growth of Douglas-fir and improve ecosystem productivity, especially on nitrogen-deficient sites (Binkley, 1983). Van Miegroet et al. (1988) reported that the inclusion of Red Alder in mixed species trials significantly increased the accumulation of nitrogen in above- and below-ground biomass. This process can increase the total biomass of an ecosystem around Red Alder (Binkley, 1983) but may have less impact if the area is already nitrogen-rich (Son et al., 2007). Growing Red Alder in mixed stands with conifers also enhances complexity (Deal, 2007), helps mitigate pests and pathogens of conifer species (Hibbs & DeBell, 1994; McComb, 1994), increases long-term productivity (Binkley, 1983), and increases adaption ability to climate change (Cortini et al., 2012).

The presence of Red Alder in mixed plantings increases the foliar nitrogen concentration of nearby conifers and the understory vegetation (Binkley, 1983; Rhoades et al., 2001). Some evidence suggests that this increased available nitrogen may cause other nutrients, such as phosphorus, to become limiting

(Binkley, 1983). However, others have found a significant increase in phosphorus soil levels under Red Alder (Rhoades et al., 2001)

1.12 Red Alder and $\delta^{15}N$

The soil under Red Alder is enriched in $\delta^{15}N$. This is thought to be due to increased levels of ammonia volatilization, denitrification during plant decomposition, plant uptake of NH_4^+ and NO_3^-, and NO_3^- leaching in relation to the increase of overall nitrogen availability due to Red Alder. In a pure Red Alder stand, Teklehaimanot & Mmolotsi (2007) reported a mean soil $\delta^{15}N$ of 5.95±0.22‰, which matches soil $\delta^{15}N$ values found under other nitrogen-fixing species, that range between 5.0 and 5.8‰ (Kreibich and Kern, 2000). In a study comparing pure conifer stands with mixed conifer/Red Alder stands, Binkley et al. (1985) found that soil $\delta^{15}N$ was significantly more ^{15}N enriched in mixed stands with soil $\delta^{15}N$ values ranging from -0.5–3.0‰ (Binkley et al., 1985), compared to -1.6‰ and -1.0‰ (Scott et al., 2008) under pure Douglas-fir.

1.13 Study Objectives and Hypotheses

Few studies exist of tree ring $\delta^{15}N$ changes over time and none have been conducted with nitrogen fixing trees. The Red Alder/Douglas-fir replacement series trial used in this study, is an ideal location to study tree ring $\delta^{15}N$ signatures over time with varying levels of natural nitrogen contribution as these plots contain different proportions of the two species on similar soils within the same climate zone. As a nitrogen fixing tree, Red Alder is known to directly affect soil nitrogen content, soil nitrogen cycling, and the isotopic composition of soil and plant cover. Based on previous research in nitrogen fixing plants, I hypothesize that: (1) Red Alder will enhance soil nitrogen stocks and elevate soil $\delta^{15}N$, (2) that Red Alder will have higher $\delta^{15}N$ values in both litter and tree rings than the non-fixing Douglas-fir, and (3) Douglas-fir planted with Red Alder will have elevated $\delta^{15}N$ values compared to the pure grown Douglas-fir.

2. Methods

2.1 Site Description

The study site is part of the ongoing B.C. Ministry of Forests' Broadleaf and Mixedwood Management experimental project 'Studies of interactions between coastal hardwoods and conifers (EP 1121.01)'. Of the five research sites planted for the experimental project, the Holt Creek site was used for this study. The Holt Creek site is located approximately thirty minutes drive west of Duncan, British Columbia [48°45'20.0"N 123°51'47.9"W] in the Cowichan River Watershed (Thomas et al., 2005). Holt Creek is within the very dry maritime Coastal Western Hemlock zone (CWHxm2) and has a mean annual precipitation of 1,618 mm and a mean annual temperature of 9°C (Wang et al., 2016).

The Holt Creek site contains an additive Red Alder/Douglas-fir mixedwood design and a replacement series planted in 1994. The replacement series plots were used for this study. Within a replacement series, a uniform planting density is maintained while the proportion of each species is changed. Holt Creek plots measure sixty by sixty meters with 742 trees/ha and a spacing of 3.67 meters between trees. Trees within a central 0.1 ha circle received a numbered tag for future Ministry of Forests surveys.

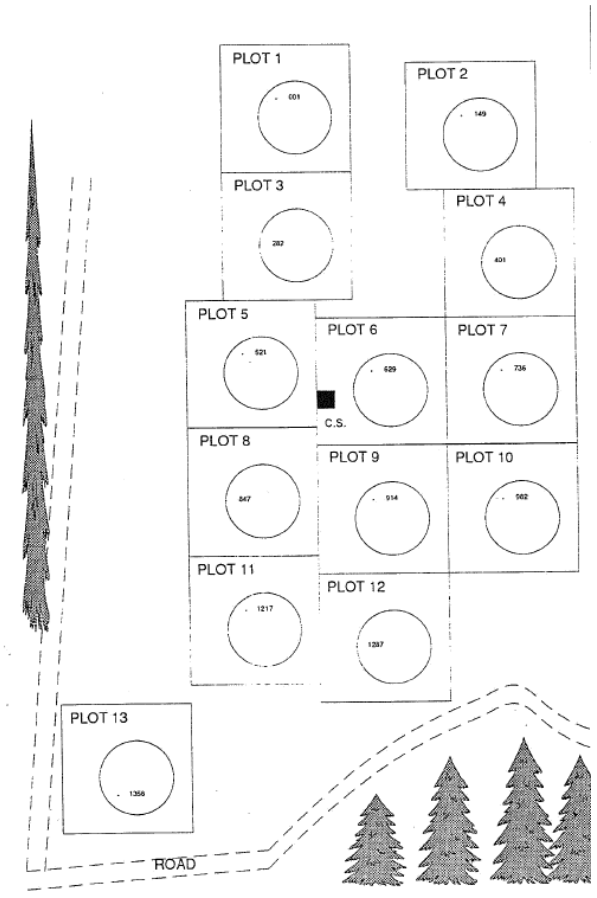

Figure 3. Holt Creek site map. Plots 1 – 7 form the additive series. Plots 8 – 12 form the replacement series. (Harper, 1995).

The trees species planted were Red Alder and Douglas-fir in five proportions: 100/0, 50/50, 25/75, 11/89, 0/100 (Figure 3). The Red Alder 100/0 plot understory is dominated by chest-

height Western Sword Fern (*Polystichum munitum*), Salmonberry (*Rubus spectabilis*), and Pacific Blackberry (*Rubus ursinus*). The Douglas-fir 0/100 plot has fewer and smaller understory plants, including Western Sword Fern, Salal (*Gaultheria shallon*), and Vanilla Leaf (*Achlys triphylla*). Mixed plots contain higher amounts of Salal and Vanilla Leaf, compared to the 0/100 plot, as well as Red Huckleberry (*Vaccinium parvifolium*) and Oregon Grape (*Mahonia aquifolium*).

A variety of microsites were noted within the 50/50 and 11/89 mixed plots. Approximately one-third of the 50/50 plot is covered in a swamp that contained standing water for most of the sampling period, resulting in some subplots being notably wet after precipitation. A dry creek bed leads out of the swamp and through the 11/89 plot, within a pronounced valley. Moving water was never observed in the creek bed, but evidence of water movement was seen after abnormally heavy rain in November 2021, suggesting the creek is ephemeral.

2.2 Subplots

Within each plot, five subplots were created. In the pure species plots, the five 0.01 ha (5.6 m radius) subplots were centered around a ‘core tree’, and all trees in the subplot were recorded. In mixed plots, five 'core' Red Alders were selected, and the closest Douglas-fir identified. The 0.01 ha subplots were centered between these tree pairs (Figure 4). Basal area (cross-sectional area of trees at 1.3m height) was determined for all trees within subplots and then summed for each species and multiplied by 100 to determine total basal area per hectare (TBA).

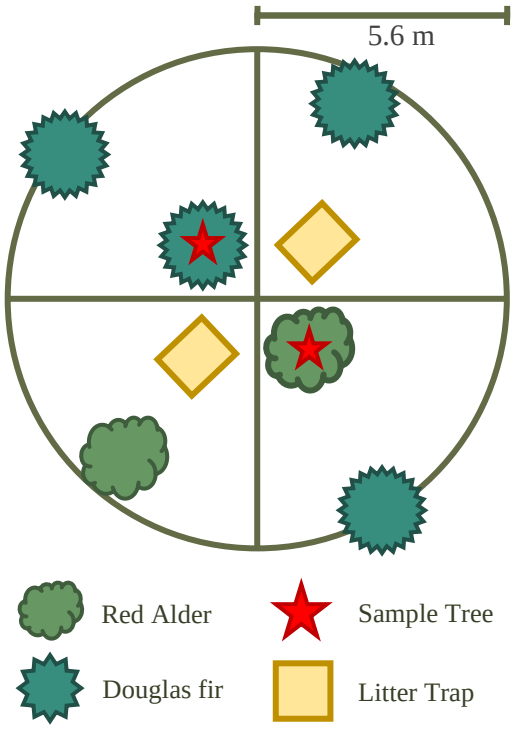

Figure 4. Mixed plot subplot layout

Subplots were located randomly in all plots. Within plots 25/75 and 11/89, high Red Alder mortality resulted in a low number of Red Alder to select. Subplots were located with a minimum spacing of 5 m between subplots.

2.3 In-Situ Buried Bags for Nitrogen Mineralization

Three in-situ buried bag setups were placed within each subplot to measure gross nitrogen (N) mineralization rates. First, a soil knife was used to cut a 10-cm diameter circle of the forest floor, which was placed into a polyethylene bag. A soil auger was then used to collect a 20-cm deep soil core below where the forest floor was removed. This mineral soil core was placed in its own bag, and then the bagged soils were placed back where they had been collected. Next, bags were covered with moss and leaves to prevent direct sunlight exposure and marked with a flag. In-situ buried bags were placed in the ground at the beginning of May 2021, left for an eight-week incubation, and collected at the end of June 2021. Samples were run through a 4.5 mm sieve, and a subsample of each was taken for moisture corrections.

2.4 Bulk Soil Sampling

Within each subplot, six forest floor (11-cm diameter) and 0-20 cm mineral soil samples were randomly collected in early spring and combined into three subsamples. Forest floor and mineral soil subsamples were dried in a greenhouse before being ground with a hammer mill and sieved (2 mm) to remove rocks and coarse root matter. The air and oven dry weights of subsamples were measured to determine the total forest floor weight (kg/ha) after oven drying correction.

2.5 Soil Chemical and Litter Mineral Nutrient Analysis

Concentrations of ammonium nitrogen (NH_4^+-N) and nitrate nitrogen (NO_3^--N) were determined using 2g and 5g dry-soil portions of mineral soil and forest floor, respectively (Carter & Gregorich, 2008). A 2 M KCl solution was added to the soils in a 1:10 w/v ratio, and samples were shaken for 1 hr at 20°C. Samples were clarified by centrifugation for 15 min at 850 g. The extract was pipetted from the clear

supernatant into an autoanalyzer cup for analysis. The NH_4^+-N and NO_3^--N in the extracts were measured colourimetrically using an Alpkem Flow System IV analyzer (OI Analytical, College Station, TX, USA).

Litter traps measured 0.13 m^2 and comprised a plastic web tray with plastic mesh (2 mm) over the bottom to catch foliage but allow water drainage. Each subplot received two litter traps placed horizontally and secured to the ground using two lawn staples each. In pure plots, litter trays were placed on opposite sides of the center tree, approximately 0.5 meters from the trunk. In mixed plots, one tray was placed between the two trees and the other on the opposite side of the Red Alder tree (Figure. 4).

Litter traps were emptied approximately every four weeks from June to September 2021. All litter collected over time was air dried and weighed to determine litter mass per unit area. All litter per subplot was composited into a single subsample. Subsamples of each bulk sample were weighed and dried at 60ºC for 24 hours to determine moisture corrections for each species. Samples were ground into a fine powder using a Wiley mill. After grinding, a subsample was used for oven-dry moisture correction of litter mass.

C, N, and S concentrations in soil and litter were measured using combustion elemental analysis with a Fisons/Carlo-Erba NA-1500 NCS analyzer (Thermo Fisher Scientific, Waltham, MA, USA) (Carter and Gregorich, 2008). The soil was ground to <0.15 mm (100 mesh sieve) before combustion analysis. The total organic and inorganic P of forest floor and mineral soils was determined by an ignition method using sulfuric acid and a UV/visible spectrophotometer (O'Halloran & Cade-Menum, 2007). Samples were analyzed by the B.C. Ministry of Environment Analytical Lab in Victoria, BC.

The abundance of ^{15}N for forest floor, mineral soil and litter was determined from a 5 mg sample of fine ground soil, 4 mg for Douglas-fir litter and 3 mg for Red Alder litter. Soil $\delta^{15}N$ was determined using a Flash 2000 elemental analyzer coupled to a ConFlo IV interface and DELTA Advantage isotope ratio mass spectrometer (all instruments Thermo Fisher Scientific, Waltham, MA, USA) at the Pacific Forestry Centre (Victoria, British Columbia). Instrument calibration was performed using certified reference

materials EMA-P2 ($\delta^{15}N_{air}$ −1.57‰), Sorghum Flour B 2159 ($\delta^{15}N_{air}$ −1.58‰) and USGS40 ($\delta^{15}N_{air}$ −4.52‰). Leaf litter $\delta^{15}N$ analysis was conducted by the Stable Isotope Facility, University of British Columbia (Vancouver, British Columbia).

2.6 Gravimetric Measures of Soil Moisture

Soil samples were collected from each plot once at the beginning of each month to span the moisture profile of the entire growing season. Three mineral soil cores (0-20 cm depth) were taken from random locations in each subplot (forest floor not included) and then bulked into one bag. Soils were returned to the lab and then sieved (4.5 mm) to remove rocks and root matter. A fresh sample of each subplot soil was weighed before being dried at 105ºC for 24 hours and then reweighed to obtain dry weight. Soil moisture was calculated as gram water/gram of dry soil.

2.7 Tree Cores

All subplot trees were cored using a 5-mm diameter increment corer (Haglöf Sweden, Torsång, Sweden) at the beginning of July 2021. Each tree was cored approximately 50 cm from the ground, and the cores were placed inside plastic straws for transport. Cores lacking pith or with visible damage were rejected and the tree re-cored.

Cores were air dried at room temperature for 24 hours before each core was measured, and the number and width of rings were recorded. Portions of wood were measured for length and then weighed before and after oven drying and a minimum length of 6.5mm was determined to meet the minimum requirement of 40 mg of wood material for $\delta^{15}N$ analysis. Cores were split into 2-year increment samples until the 2-year increment became <6.5mm, after which three or more rings were included in a sample. Samples were all dried at 60ºC for 24 hours before grinding. Each sample was ground into fine powder using a Wiley mill. $\delta^{15}N$ isotopic and N% analysis was conducted using a Carlo Erba NC2500 elemental analyzer (EA) interfaced with a Thermo Delta V+ isotope ratio mass spectrometer (IRMS) at the Central Appalachian Isotope Facility (University of Maryland, College Park, MD, USA).

2.8 Statistical Analysis

Soil nutrients and NO_3^-/NH_4^+ concentrations were determined for the three subsamples per subplot and then averaged by subplot. Leaf litter nutrient concentrations were determined from one sample per subplot. All measures were analyzed by one-way analysis of variance (ANOVA) (Table 1) with the plot (species proportion) as the independent variable to test for differences in plot averages. ANOVA is used to test if two (or more) population means are equal or statistically different using the *F*-ratio or *F*-distribution. The *F*-ratio has two degrees of freedom, the first corresponds one less than the number of samples or levels of the explanatory variable or treatment ($k - 1$), and the second to the remaining error of the total number of samples minus the levels of treatment ($n - k$). The sum of squares for treatment (SS_F) represents the squared distance between each data point and the sample mean and quantifies the variability among the populations of interest. The sum of squares of error (SS_E) is the squared distance between each data point and the population mean and quantifies the variability within the population of interest. The total sum of squares (SS_T) is the total variation in the observed data. The mean square (*MS*) is the average sum of squares for the treatment and the error. The *F*-ratio is the ratio of the between-sample or explained variance (MS_F) and the within-sample or unexplained variance (MS_E).

Table 1.
One-way ANOVA table. k: number of groups. n: number of samples

Source of Variation	Degree of Freedom (df)	Sum Square (SS)	Mean Square (MS)	*F*-ratio
Treatment	k-1	$SS_F = \sum_{j-1}^{k} n(\bar{X}_j - \bar{X})^2$	$MS_F = \frac{SS_F}{k-1}$	$F = \frac{MS_F}{MS_E}$
Error	n-k	$SS_E = \sum_{j-1}^{k}\sum_{i-1}^{n}(X - \bar{X}_j)^2$	$MS_E = \frac{SS_E}{n-k}$	
Total	n-1	$SS_T = SS_F + SS_E$		

Relationships between wood $\delta^{15}N$ and time and N% and time were tested as linear or curvilinear mixed effect models (Eq. 2), where β_0 is the intercept, β_i is the slope coefficient, and ϵ is the model's residual error.

$$\text{Eq. 2} \quad y = \beta_0 + \sum \beta_i x_i + \epsilon$$

The tree was included as a random effect to account for individual tree variations. Models were run with multiple random effect conditions and then run against each other using one-way ANOVAs. Both p-values and Akaike information criterion (AIC) were considered to determine best fit. This was done because a "non-significant p-value" may not mean there is no impact. AIC evaluates how well a model fits the data and estimates prediction error. Models with the lowest AIC were selected as they contain lower amounts of predicted error. See appendix 13 and 14 for complete model comparisons. Mixed models were analyzed for best fit in R package lme4 v 1.1-29. Outliers in the wood $\delta^{15}N$ and N% dataset were determined using the Z-score method using ±3 SD.

Statistical analysis was performed in R version 4.1.2 with packages lme4 v 1.1-29. Graphs were created using Microsoft 365 Excel.

3. Results

3.1 Tree Basal Area and Species Proportion

The proportions of Red Alder and Douglas-fir in the plots have changed over time from the original planting proportions (Figure 5). This shift is due to mortality of both species. Red Alder mortality was high in the 25/75, and 50/50 treatments (14 trees and 34 trees, respectively) and Douglas-fir mortality was high in the 11/89 treatment (23 trees). After almost three decades, the original Red Alder proportions of 50%, 25%, and 11% are now 26%, 8%, and 15% (Figure 5).

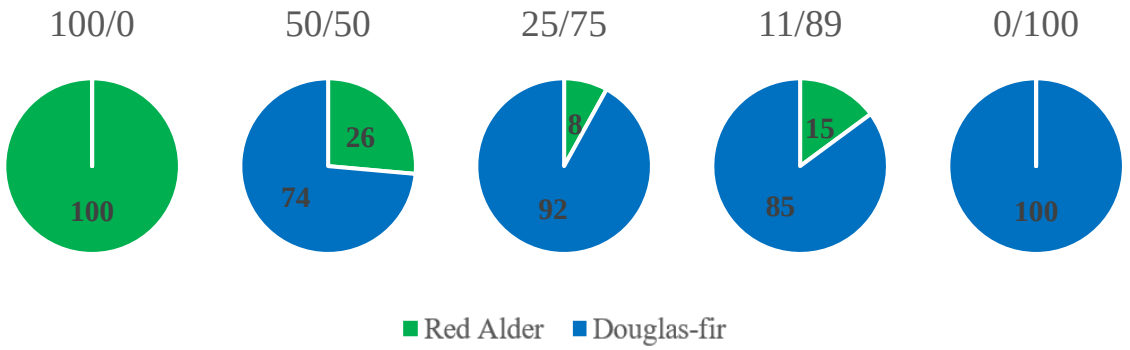

Figure 5. Percent of total basal area by species in five replacement series plots. Headings are the original planting proportions of Red Alder/Douglas-fir

Total basal area was calculated for each tree in each plot and then summed by species (Figure 6). Calculated values of basal area by species in the summer of 2021 differ little from B. C. Ministry of Forests surveys from Fall 2020 (Appendix 1).

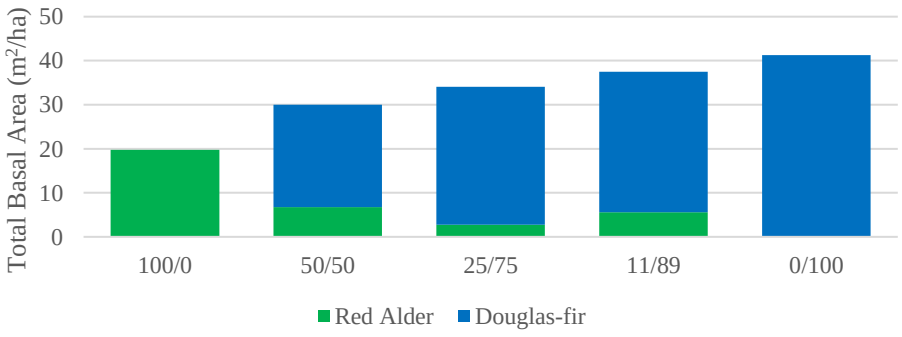

Figure 6. Tree total basal area (m^2/ha) by species in five replacement series plots

3.2 Tree Basal Area Over Time

The replacement series at Holt Creek has been remeasured 11 times since planting in 1994 (Years 1,2,3,4,6,9,11,12,17,22,27) (Fang et al, 2019) (Appendix 1). Trees were large enough to record basal area (m^2/ha) between 1997 and 1999 (Figure 7). Within the first four years, plots were fill-planted after tree mortality.

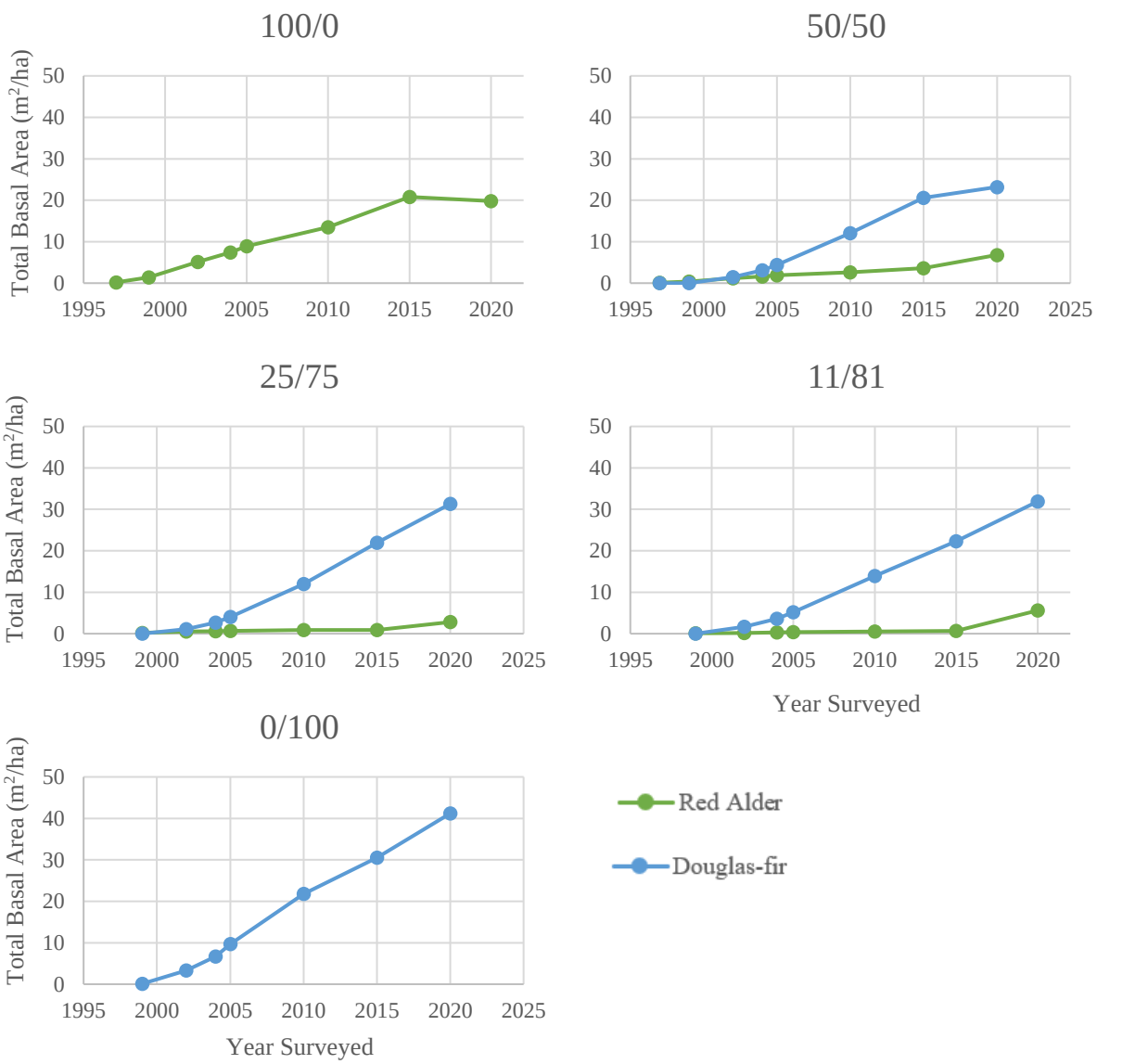

Figure 7. Trends in total basal area (TBA) by species per plot over time.

3.3 Soil Characteristics

Soil moisture varied across the four months measured, with June being the wettest and August the driest month, on average (Table 2). The 11/81 plot was, on average, the driest across all four months. Soil moisture did not significantly vary among the plots in May, June, and August (p=0.432, 0.107, 0.104) but did vary significantly in July (p=0.032) (Table 2).

The depth of the forest floor was significantly greater in the 100/0 plot than in all other plots (p=<0.001), being on average 2.2 cm deeper, thus, the total weight of forest floor soil per hectare also varied significantly by plot (p=0.012) (Table 3). The pH of the forest floor of the 100/0 Red Alder plot was significantly more acidic than all other plots (p=<0.001) (Table 3). Mineral soil pH was also significantly different among the plots (p=<0.001) (Table 3).

Table 2.
Gravimetric soil moisture measures in percent (%) across the growing season. N=15 per plot. Values are means ± SE. Means within rows followed by different letters are significantly different (p< 0.05)

Plot	**100/0**	**50/50**	**25/75**	**11/89**	**0/100**	**Average**
May	32 ± 7.4	26 ± 3.0	23 ± 3.0	35 ± 6.4	30 ± 2.3	29 ± 0.4
June	37 ± 2.8	36 ± 4.7	26 ± 2.3	28 ± 2.1	33 ± 4.6	32 ± 0.3
July	24 ± 2.2*a*	14 ± 3.3*ab*	13 ± 3.2*b*	19 ± 3.0*ab*	13 ± 0.7*b*	17 ± 0.3
August	13 ± 0.8	9 ± 0.9	9 ± 0.9	12 ± 2.0	10 ± 1.3	11 ± 0.1
Average	27 ± 3.1	21 ± 3.1	18 ± 2.2	23 ± 3.0	22 ± 2.9	

Table 3.
Soil characteristics of forest floor and mineral soil. N=15 per plot. Values are means ± SE. Means within rows followed by different letters are significantly different (p< 0.05)

		100/0	**50/50**	**25/75**	**11/89**	**0/100**
Mineral Soil	pH	4.6 ± 0.04*c*	4.9 ± 0.07*ab*	5.1 ± 0.06*a*	4.7 ± 0.06*bc*	4.9 ± 0.05*ab*
Forest Floor	pH	3.8 ± 0.07*c*	4.7 ± 0.06*a*	4.7 ± 0.04*a*	4.4 ± 0.07*b*	4.5 ± 0.05*ab*
	Depth (cm)	4.6 ± 1.1*a*	2.9 ± 0.8*b*	2.7 ± 0.6*b*	1.9 ± 0.7*b*	2.4 ± 0.5*b*
	Soil (kg/ha)	57101 ± 11287*a*	37080 ± 4631*ab*	34648 ± 4901*ab*	27291 ± 3363*b*	23200 ± 3680*b*

3.4 Soil Nitrogen Properties

The nitrogen concentration of the forest floor was not significantly different among plots (p=0.668) but did significantly differ among plots in the mineral soil (p=<0.001) (Table 4). The total amount of nitrogen in kg/ha differed significantly among plots in both the forest floor and mineral soil (p=0.007, 0.01, respectively) (Figure 8). Forest floor $\delta^{15}N$ was significantly affected by the Red Alder proportion, with the 100/0 and 50/50 treatments being significantly positive. In contrast, the remaining plots were negative in value (p=<0.001) (Table 4). Mineral soil $\delta^{15}N$ was not significantly different between plots (p=0.723) (Table 4).

Table 4.
Soil nitrogen concentration and $\delta^{15}N$ concentration of forest floor and mineral soil (0 – 20 cm). N=15 per plot. Values are means ± SE. Means within rows followed by different letters are significantly different (p< 0.05)

		100/0	**50/50**	**25/75**	**11/89**	**0/100**
N%	Forest Floor	2.1 ± 0.12	2.0 ± 0.12	1.6 ± 0.11	1.6 ± 0.13	1.8 ± 0.14
	Mineral Soil	0.16 ± 0.007*ab*	0.18 ± 0.007*a*	0.16 ± 0.016*ab*	0.12 ± 0.006*b*	0.18 ± 0.012*a*
$\delta^{15}N$	Forest Floor	1.32 ± 0.36*a*	1.00 ± 0.39*a*	-0.62 ± 0.24*b*	-0.65 ± 0.33*b*	-0.19 ± 0.35*b*
	Mineral Soil	3.08 ± 0.45	2.77 ± 0.52	2.62 ± 0.53	2.65 ± 0.67	3.09 ± 0.51

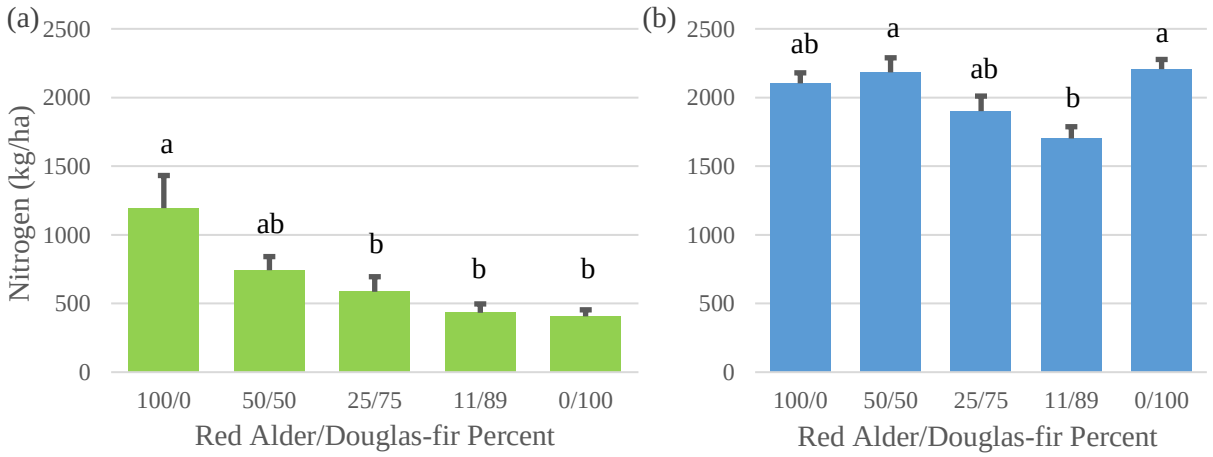

Figure 8. Mean (+SE) total soil nitrogen (kg/ha) in the forest floor (a) and mineral soil (b). Letters indicate significant differences (p<0.05)

The forest floor C:N ratio was significantly different among plots with the higher Red Alder proportion plots having lower C:N ratios (p=0.034) (Figure 9a). Mineral soil C:N ratio did not differ among plots (p=0.077) (Figure 9b.).

Plot mean content of NH_4^+ in the forest floor and mineral soil following an 8-week in-situ incubation did not differ significantly among plots (p=0.171, p=0.191, respectively) (Figure 10a, b). NO_3^- content was significantly different among plots in forest floor and mineral soil layers (p=<0.001, 0.014, respectively), with the 25/75 plot having the lowest NO_3^- content in both forest floor and mineral soils (Figure 10c, d). Soil NH_4^+ content was consistently lower than NO_3^- content. Gross nitrogen mineralization (NH_4^+ plus NO_3^-) after the 8-week in situ incubation of forest floor samples was significantly different among plots (p=0.002) but did not differ among plots in the mineral soil samples (p=0.112) (Figure 10e, f).

NH_4^+ content was not affected by changing Red Alder TBA in either soil layer (p=0.238 (forest floor), 0.895 (mineral soil)) (Figure 11a, b). Content of NO_3^- and gross mineralization increased significantly with increasing Red Alder TBA in both soil layers (forest floor p= 0.005, 0.010, mineral soil p=0.027, <0.001, respectively) (Figure 11c, d, e, f).

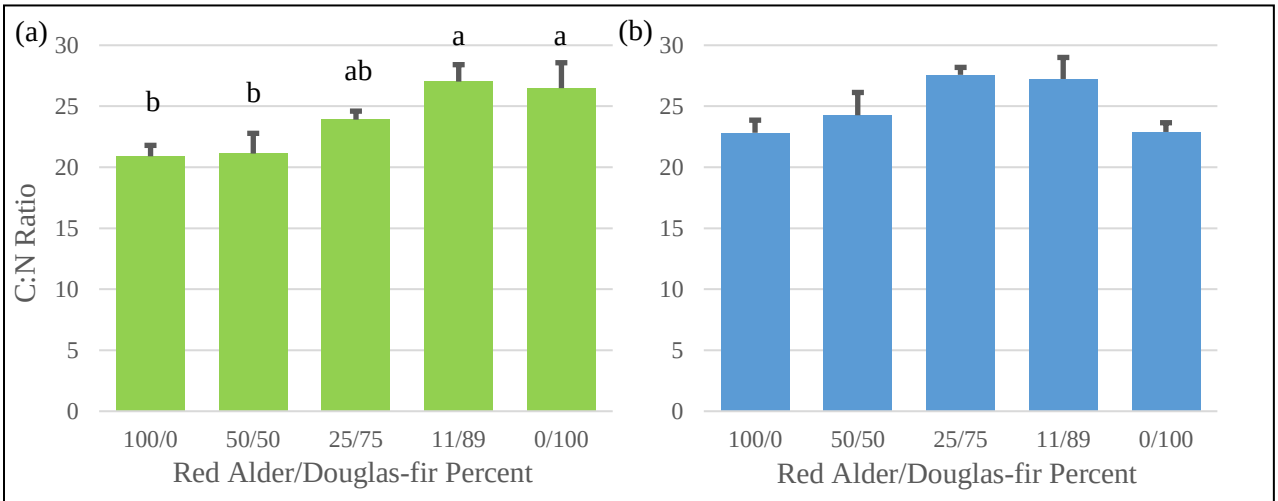

Figure 9. Average C:N ratio across treatment plots in forest floor (a) and mineral soil (b). Letters indicate significance (p<0.05) (n=5, SE as error bars)

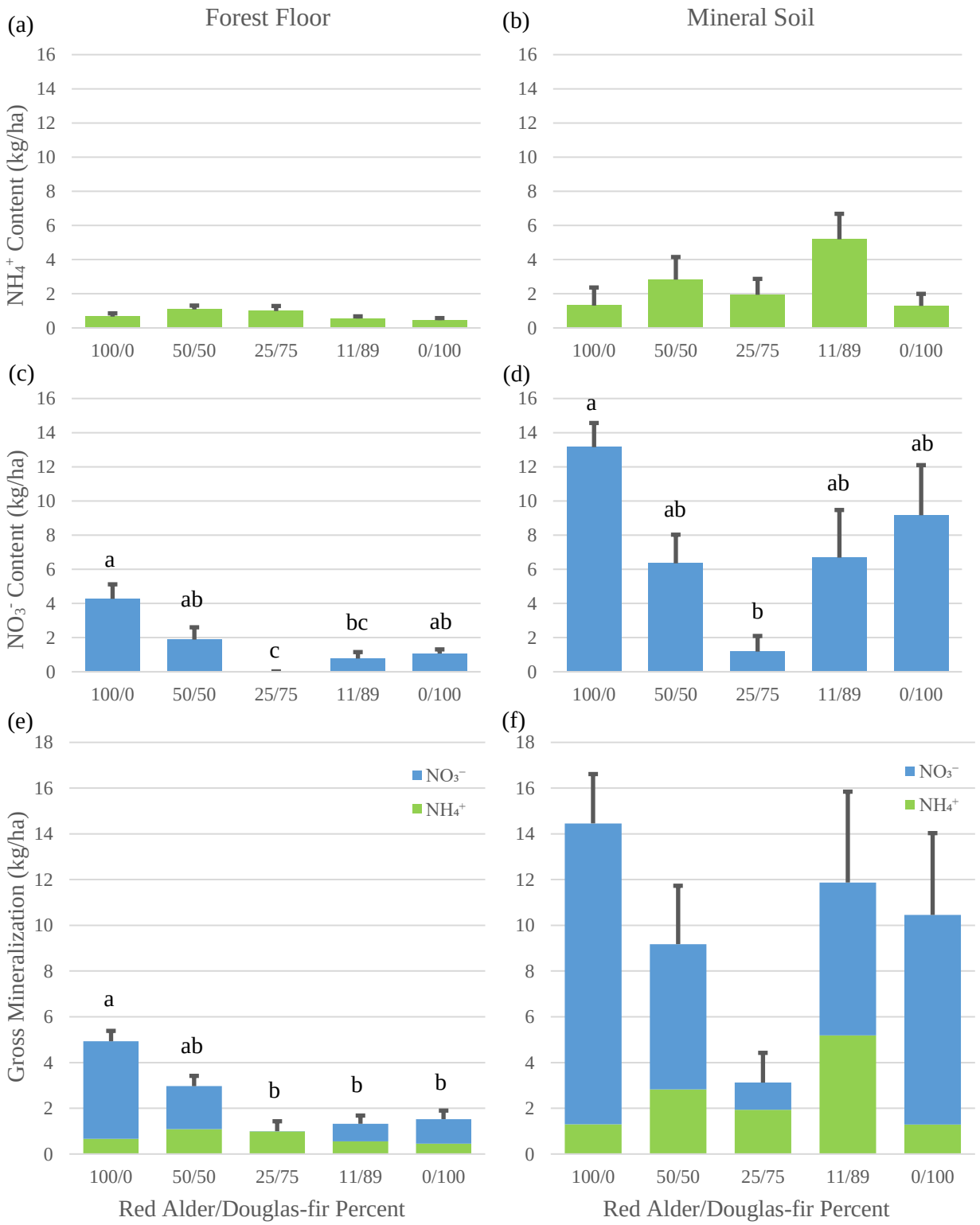

Figure 10. Averages of NH_4^+ (a, b) and NO_3^- (c, d) content and gross mineralization (e, f) (= total N) in forest floor (a, c, e) and mineral soil (b, d, f) layers after an 8-week in-situ incubation. Letters indicate significance ($p<0.05$) (SE as error bars)

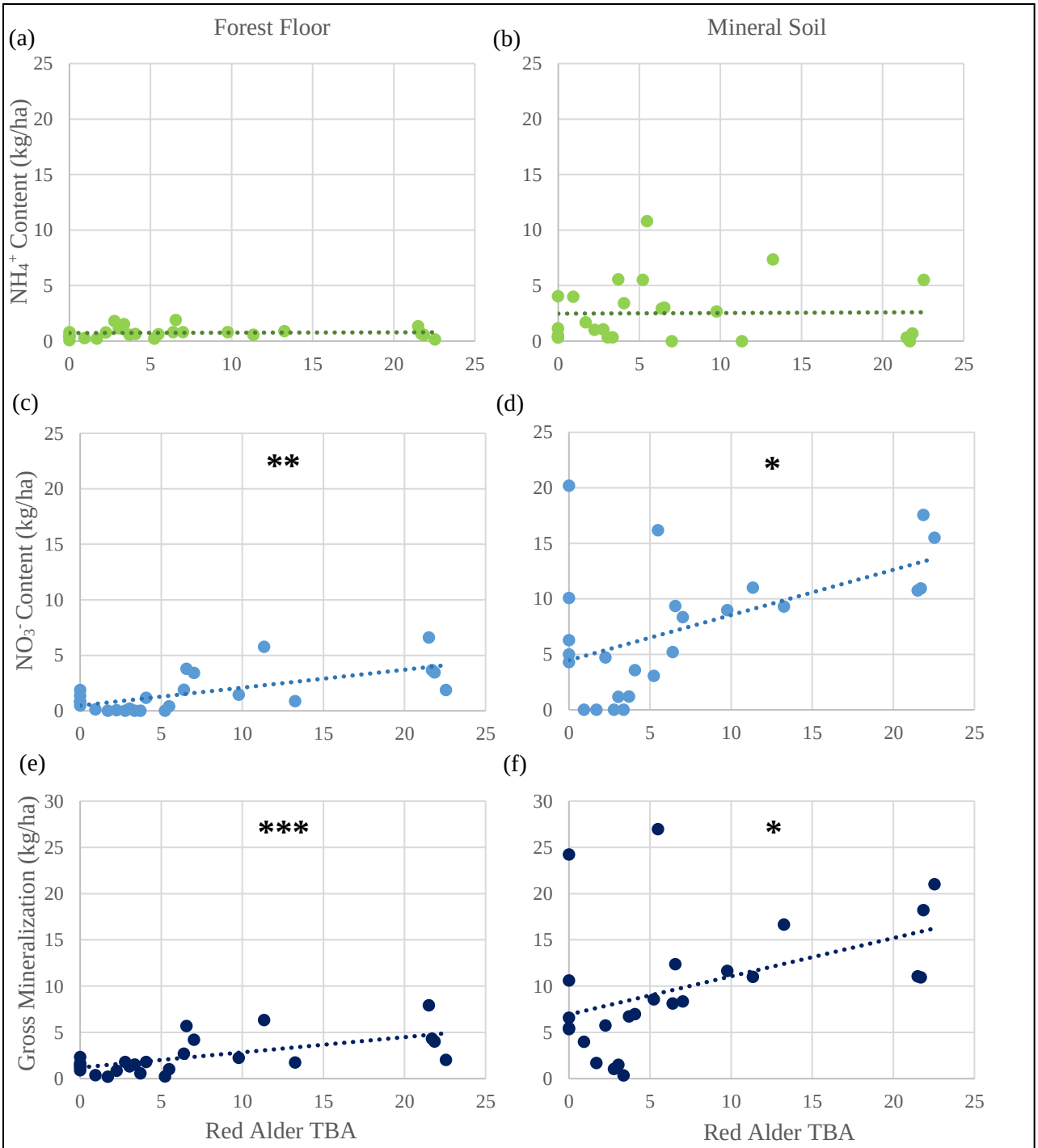

Figure 11. Content of NH_4^+ (a, b), NO_3^- (c, d), and gross mineralization (e, f) (=total N) in forest floor and mineral soil plotted against Red Alder total basal area (TBA; m^2/ha). Significant regression indicated by * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

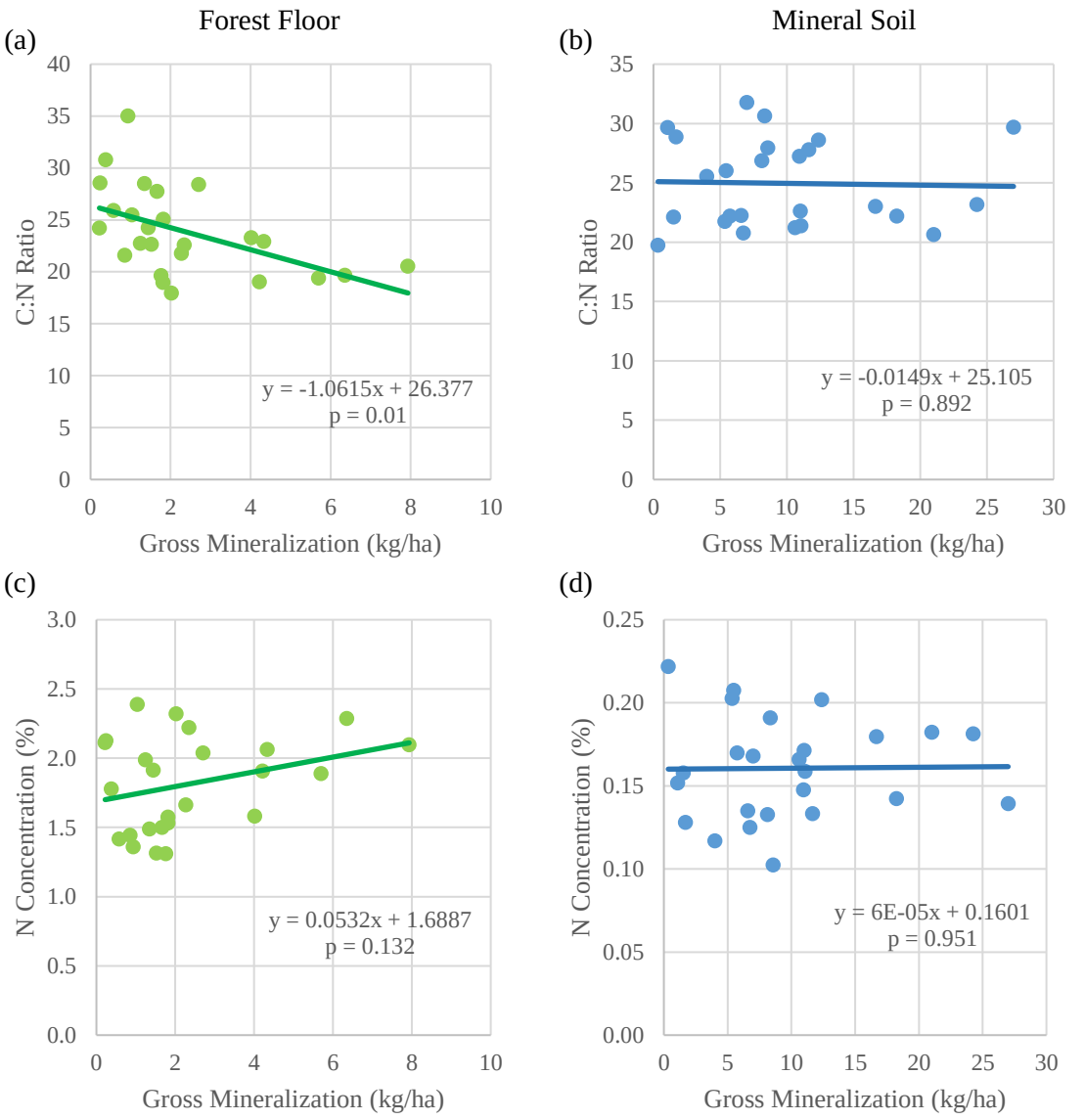

Figure 12. Trends in C:N ratio (a, b) and soil N concentration (c, d) of forest floor and mineral soil with gross mineralization of N (kg/ha).

Gross mineralization was significantly higher under pure Red Alder than pure Douglas-fir and generally increased with Red Alder proportion in the plots (Figure 9e) and with Red Alder TBA (Figure 10e, f). While both forest floor and mineral soil gross mineralization increased with Red Alder TBA, only forest floor mineralization significantly declined with an increased C:N ratio (p=0.01) (Figure 12). Gross mineralization was not affected by an increase N% in either soil layer (p=0.132 (forest floor), p=0.951 (mineral soil)) (Figure 12c, d).

3.5 Leaf Litter Nitrogen

Nitrogen concentration in Red Alder leaf litter did not differ significantly among plots (p=0.063). However, Douglas-fir litter nitrogen concentration did differ among plots (p=0.002) (Figure 13a). Total amount of leaf litter nitrogen in kg/ha was significantly greater in the 100% Red Alder plot compared to the 100% Douglas-fir plot (p=<0.001) (Figure 13b). Total Douglas-fir leaf litter collected did not differ among plots (p=0.394) (Appendix 7). Significantly more Red Alder leaf litter was collected in the 100/0 plot (p=<0.001) (Appendix 7). The mean concentrations of other leaf litter nutrients are presented in Appendix 9. Leaf litter $\delta^{15}N$ did not vary significantly among plots (p= 0.129, 0.233) or between species (p=0.129) (Figure. 14).

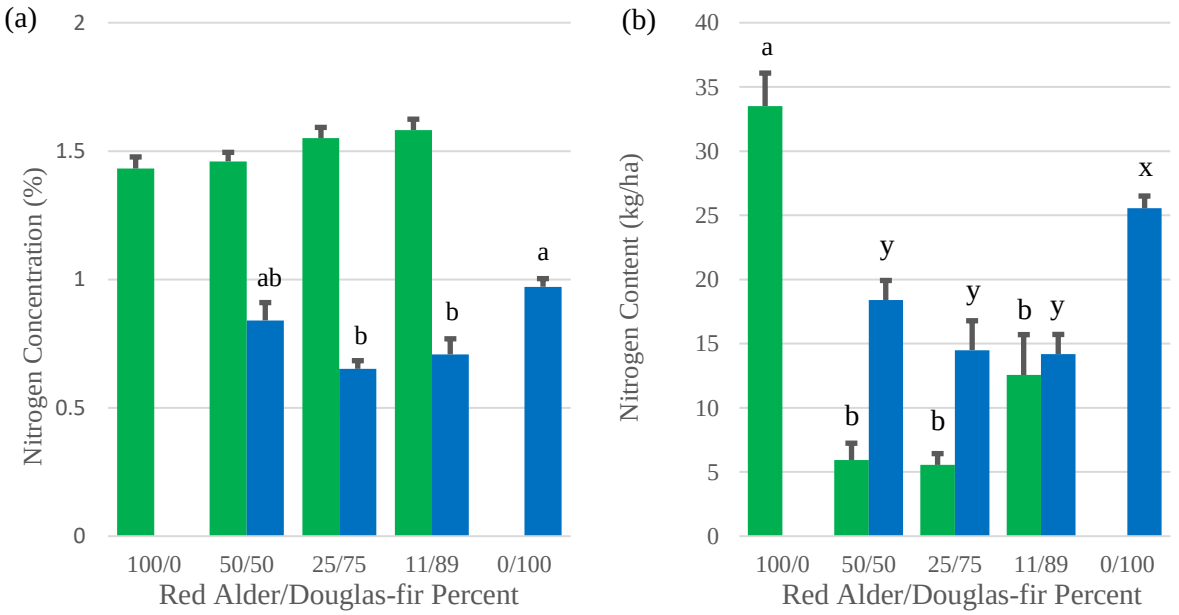

Figure 13. Average leaf litter N concentration by plot (a) and total nitrogen input from leaf litter by species per plot (b). (n=5, SE as error bars)

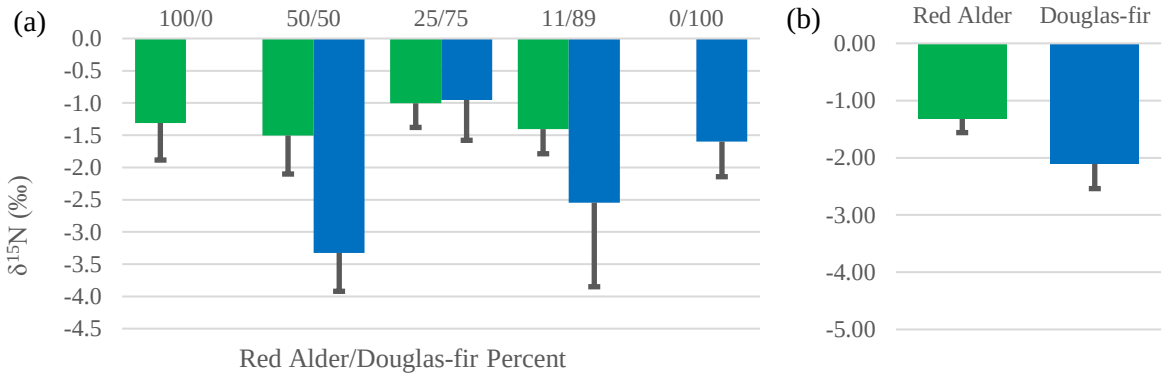

Figure 14. Mean leaf litter $\delta^{15}N$ values for Red Alder and Douglas-fir (a) and total average of each species (b). One Red Alder subsample from the 11/89 plot was omitted due to insufficient sample. (n=10, SE as error bars)

3.6 Tree-ring $\delta^{15}N$

The number of tree rings per core averaged 22 (SE = 0.14) for Red Alder and 25 (SE = 0.09) for Douglas-fir. Due to the lower DBH of Red Alder compared to Douglas-fir, Red Alder increment cores were divided into eight samples per core, on average, and Douglas-fir into 11 samples per core. In Red Alder, the mean plot $\delta^{15}N$ value was significantly more negative in the 11/89 plot than in the other three plots ($p=<0.001$) (Figure 15). For Douglas-fir, the mean plot $\delta^{15}N$ values were significantly higher in the 50/50 plot than in all other plots ($p=<0.001$) (Figure 15). The average wood $\delta^{15}N$ value was depleted in both Red Alder, -2.90‰ (SE 0.07), and Douglas-fir, -2.77‰ (SE 0.08) with no significant difference between the species, overall ($p=0.597$).

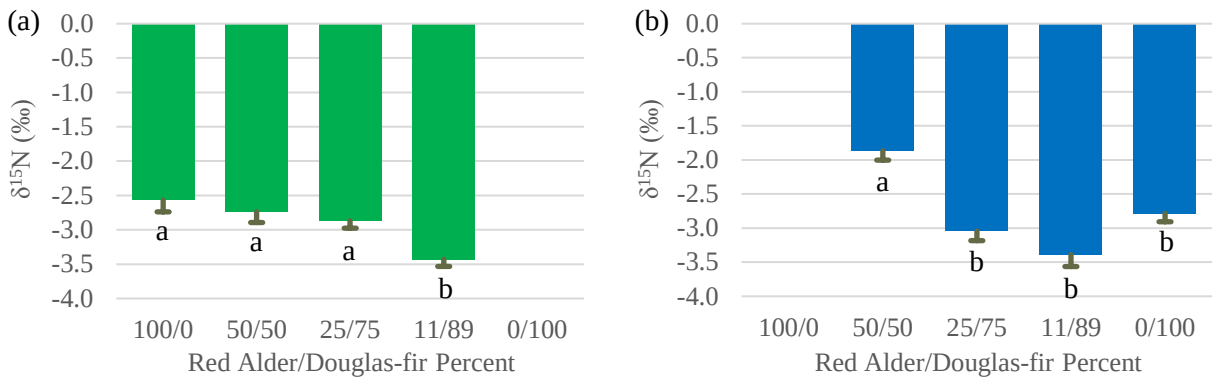

Figure 15. Average wood $\delta^{15}N$ (‰) value in (a) Red Alder and (b) Douglas-fir plots. Letters indicate significance differences among means ($p<0.05$) (n = 5, SE as error bars)

There was a significant linear decrease in Red Alder tree ring $\delta^{15}N$ values from youngest to oldest rings in the 25/75 and 11/89 mixed plots (p=0.026, 0.004, respectively) (Figure 16e, g). The 11/89 mixed plot was the only plot where Douglas-fir wood $\delta^{15}N$ values were significantly higher in younger rings (p=0.016) (Figure 16h). A non-linear mixed effect model of wood $\delta^{15}N$ over time had a significantly better fit when compared to a linear mixed model for the Red Alder 100/0 plot (p=0.005) (Appendix 13). For all other plots, there was no significant difference between a linear and non-linear mixed model. In all plots other than the 100/0 plot, linear-mixed effect models were selected based on lower AIC values (Appendix 13). When data from all plots were considered for each species, Red Alder tree ring $\delta^{15}N$ values had a nonlinear relationship with time (Figure 17). Douglas-fir tree ring $\delta^{15}N$ values had a linear relationship with time (Appendix 15, 16).

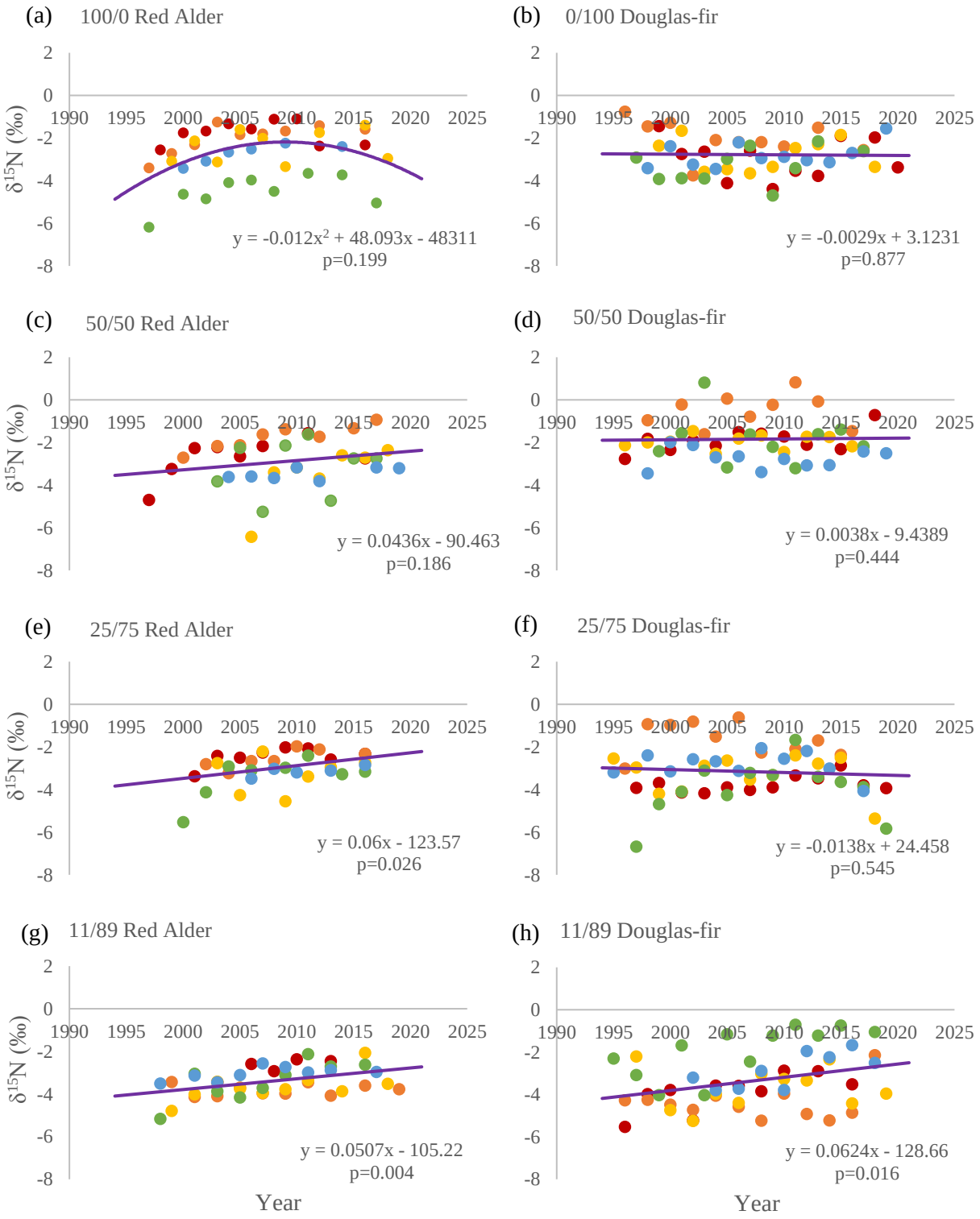

Figure 16. Trends in tree-ring $\delta^{15}N$ (‰) in 5 plots and 2 tree species (a-h) over the 27-year growth period. Each plot contained 5 cored trees shown in different colours. For each core segment, the representative point was plotted on the first year of the ring.

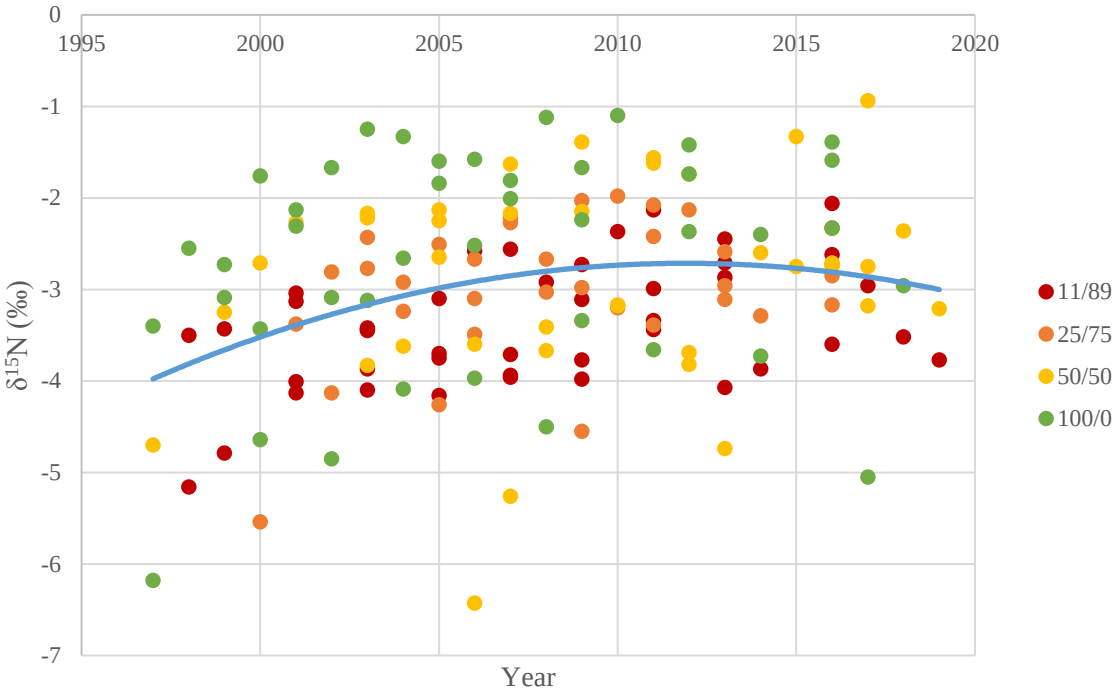

Figure 17. Red Alder tree-ring $\delta^{15}N$ (‰) in 5 plots over the 27-year growth period. Each plot contained 5 cored trees. For each core segment, the representative point was plotted on the first year of the ring.

For all Red Alder wood $\delta^{15}N$ values over time, a linear and non-linear model differed by <1 AIC (Appendix 15). The non-linear model was selected according to the method of AIC model determination outlined by Burnham & Anderson (2004) (Appendix 15). Douglas-fir had a linear relationship between tree ring $\delta^{15}N$ and time, but only relationship in the 11/89 plot was significant (Appendix 15, 16).

3.7 Tree-ring N%

The average N% wood value in Red Alder was 0.15% (SE = 0.002) and 0.05% (SE = 0.001) in Douglas-fir with a significant difference between the species (p=<0.001). Red Alder wood N% in the 100/0 plot was significantly lower compared to all other plots (p=<0.001, Figure 17). There was a significant difference among plots in Douglas-fir wood N% (p=<0.001, Appendix 16). Douglas-fir wood in the 50/50 plot had a significantly higher wood N% value compared to the pure grown Douglas-fir (p=0.01).

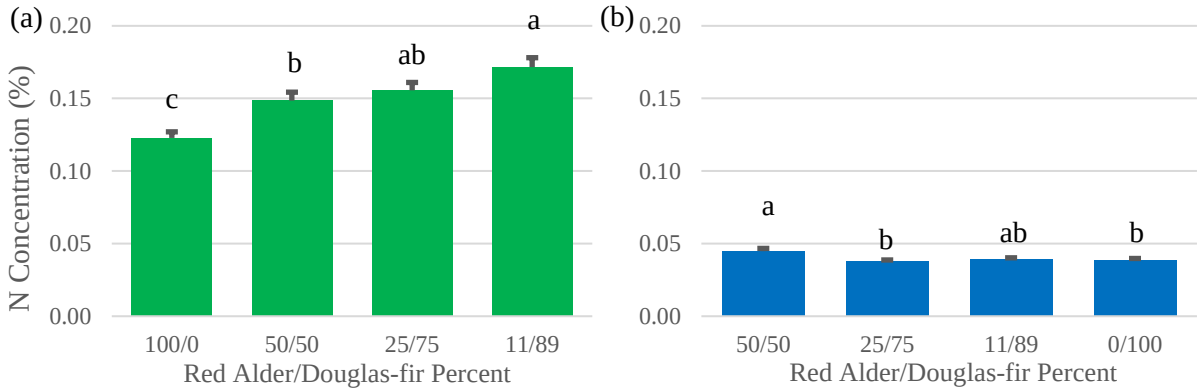

Figure 18. Average wood N% by plot in (a) Red Alder and (b) Douglas-fir (n=5). Error bars are SE. Letters indicate significance p<0.05.

When N% values over time were analyzed in mixed models, Red Alder and Douglas-fir wood N% followed a linear model according to the lowest AIC (Appendix 14). Douglas-fir wood in the 11/89 plot was the only plot with a significant relationship between wood N% and year (p=0.0119) (Appendix 12).

3.8 Trends in tree-ring N% and $\delta^{15}N$

Across all plots, Red Alder tree-ring $\delta^{15}N$ values decreased as tree-ring N% increased (p<0.001) (Figure 19). This trend was also significant in each individual Red Alder plot except the 11/89 plot (p=0.280) (Figure 20). No significant trends were seen for Douglas-fir tree-ring N% and $\delta^{15}N$ (Appendix 17, 18).

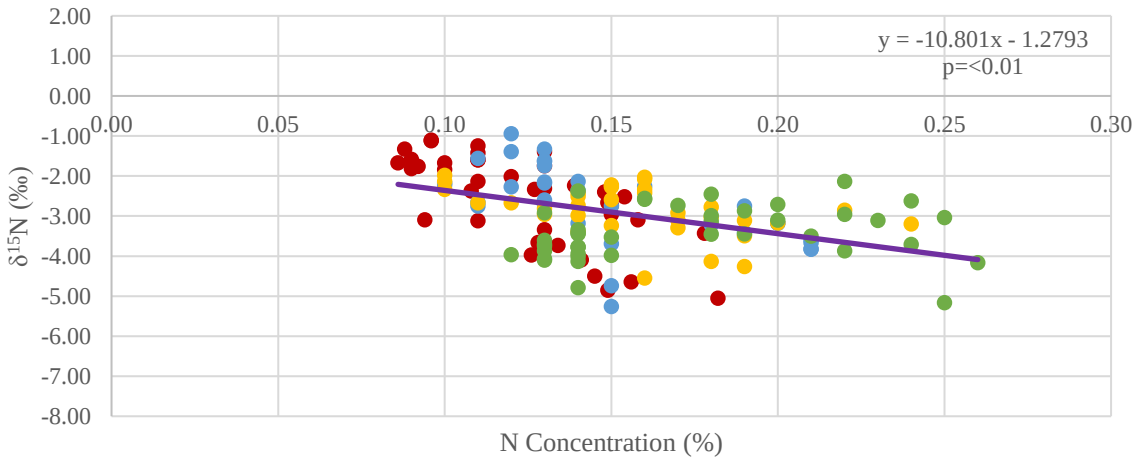

Figure 19. Tree-ring $\delta^{15}N$ versus N% for Red Alder, overall. Four plots indicated by different colours. Each plot contains five core trees

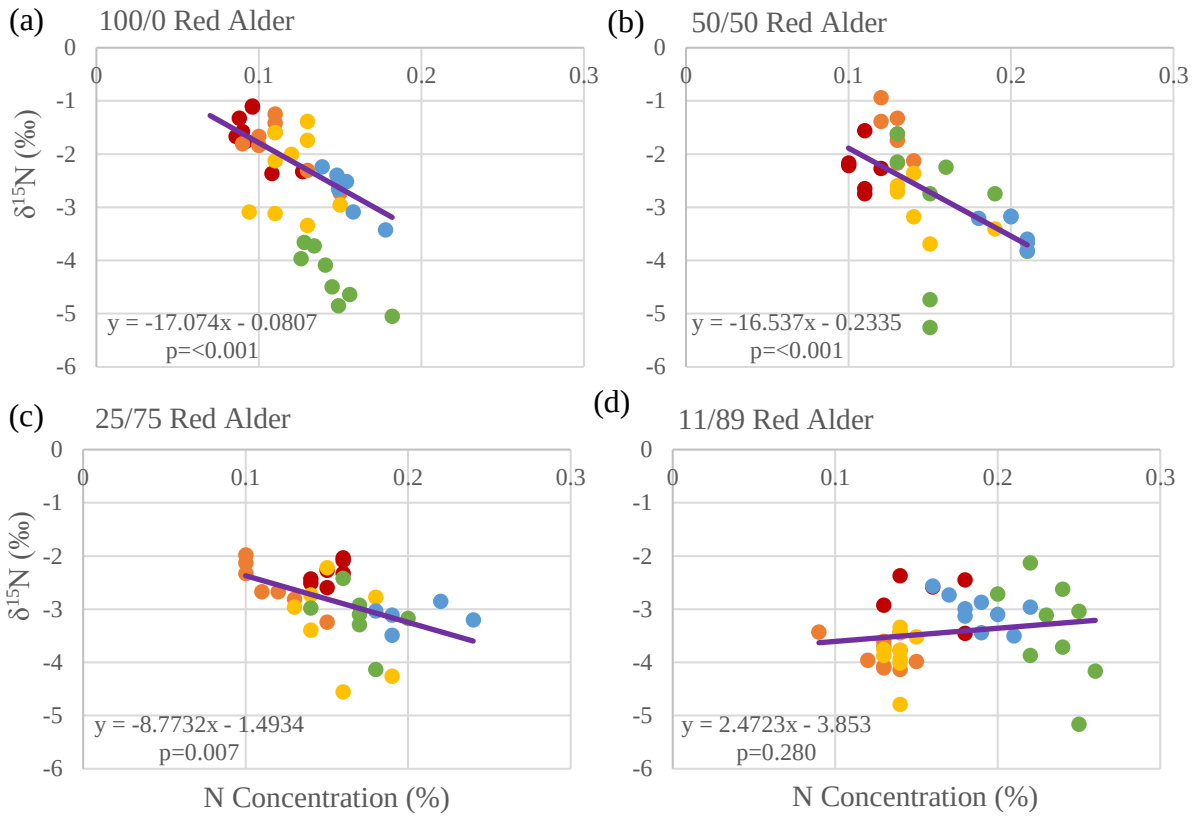

Figure 20. Tree-ring $\delta^{15}N$ and N% Comparisons for (a) 100/0 Red Alder, (b) 50/50 Red Alder, (c) 25/75 Red Alder, and (d) 11/89 Red Alder plots. Five individual core trees indicated by differing colours.

3.9 Soil Nutrients

There were significant differences among plots in forest floor organic, inorganic, and total P concentrations (p=0.007, 0.005, 0.011, respectively) (Table 5). There were also significant differences among plots in mineral soil inorganic and total P concentrations (p=0.003, 0.003) but not in organic P concentrations (p=0.121) (Table 6).

The 100/0 plot exhibited significant differences from other plots in the concentrations of some cations in the forest floor (Table 5). Both Al and Fe concentrations were significantly greater in the forest floor of the 100/0 plot (p=<0.001, <0.001, respectively), while Mg, Mn, and Ca concentrations were significantly lower in this plot compared to other plots (p= 0.011, <0.001, <0.001, respectively) (Table 5). Al was the

only cation that showed a significant difference among plots for concentrations in the mineral soil, being greatest in the 100/0 plot (p=<0.001) (Table 6).

Cation Exchange Capacity (CEC) of the forest floor differed significantly among plots (p=<0.001), and the CEC of the 100/0 plot was almost half that of the CEC of all other plots (Table 5).

Table 5.
Cation concentrations and CEC of the forest floor in five plots. N=5. Values are means ± SE. Means within rows followed by the same letter are not significantly different (p< 0.05)

(mg/kg)	**100/0**	**50/50**	**25/75**	**11/89**	**0/100**
Org. P	622 ± 25*b*	728 ± 24*ab*	688 ± 29*ab*	646 ± 59*b*	860 ± 62*a*
Inorg. P	87 ± 8*b*	103 ± 12*b*	213 ± 67*a*	203 ± 48*ab*	77 ± 8*b*
Ca	16 ± 1*b*	35 ± 3*a*	34 ± 3*a*	31 ± 3*a*	38 ± 2*a*
Mg	3.5 ± 0.4*b*	6.2 ± 0.3*a*	5.7 ± 0.8*a*	5.7 ± 0.4*a*	5.7 ± 0.5*a*
Al	3.7 ± 0.4*a*	0.9 ± 0.2*b*	1.2 ± 0.2*b*	2.0 ± 0.7*b*	1.0 ± 0.2*b*
Mn	0.5 ± 0.1*c*	2.0 ± 0.2*a*	1.0 ± 0.1*b*	1.2 ± 0.2*a*	1.4 ± 0.1*ab*
Fe	0.26 ± 0.03*a*	0.08 ± 0.01*b*	0.09 ± 0.005*b*	0.13 ± 0.03*b*	0.08 ± 0.003*b*
K	0.79 ± 0.07*b*	1.10 ± 0.1*a*	0.83 ± 0.07*ab*	0.80 ± 0.04*ab*	0.80 ± 0.06*b*
Na	0.15 ± 0.01*b*	0.19 ± 0.01*a*	0.19 ± 0.01*a*	0.18 ± 0.01*ab*	0.20 ± 0.01*a*
CEC	24 ± 2*b*	46 ± 3*a*	43 ± 4*a*	41 ± 3*a*	47 ± 3*a*

Table 6.
Cation concentrations and CEC of the mineral soil in five plots. N=5. Values are means ± SE. Means within rows followed by the same letter are not significantly different (p< 0.05)

(mg/kg)	**100/0**	**50/50**	**25/75**	**11/89**	**0/100**
Org. P	176 ± 8	174 ± 4	173 ± 18	136 ± 11	160 ± 10
Inorg. P	143 ± 37*b*	332 ± 131*b*	765 ± 166*a*	554 ± 125*ab*	212 ± 86*b*
Ca	1.0 ± 0.1	1.1 ± 0.2	1.4 ± 0.3	1.2 ± 0.2	1.5 ± 0.3
Mg	0.16 ± 0.02	0.22 ± 0.05	0.22 ± 0.1	0.29 ± 0.04	0.30 ± 0.1
Al	2.6 ± 0.3*a*	1.4 ± 0.2*c*	0.7 ± 0.1*bc*	2.0 ± 0.2*b*	1.5 ± 0.2*bc*
Mn	0.10 ± 0.02	0.11 ± 0.02	0.08 ± 0.02	0.10 ± 0.01	0.10 ± 0.02
CEC	4 ± 0.2	3 ± 0.3	3 ± 0.3	4 ± 0.4	4 ± 0.4

4. Discussion

As hypothesized, forest floor soils under Red Alder were enriched in nitrogen compared to pure Douglas-fir. The pure Red Alder plot contained almost triple the nitrogen content, and the 50/50 Red Alder nearly double the nitrogen content of the pure Douglas-fir plot. This agrees with other studies that have found a significant increase in soil nitrogen under Red Alder (Binkley et al., 1985; Rothe et al., 2002; Tarrant & Miller, 1963; Van Miegroet et al., 1992). The net gain of 1195 N kg/ha in 27 years (~45 kg N/year) is comparable to N accretion reported elsewhere in the Pacific Northwest (650 N kg/year in 28 years and 1095 N kg/ha in 17 years) (Berg & Doerksen, 1975; Bormann & DeBell, 1981). This increased total soil nitrogen is due to the high amount of forest floor found in the pure Red Alder plot, which was over double that of the pure Douglas-fir plot. As Red Alder loses all its leaves at the end of each season, while Douglas-fir can retain needles for up to eight seasons (Tarrant & Miller, 1963). There is increased nutrient turnover and carbon addition under Red Alder due to its litter being easily decomposable which results in the accumulation of forest floor. The 100/0 Alder plot had a total N content of ~1000kg N, averaging ~ 37kg N yr-1 over the 27 years. Previous research has found rates of fixation to range between 10 – 150 N kg N yr-1 (Bormann et al., 1994; Bluhum & Hibbs, 2006). My value of 37 kg N yr-1 is in the low range found in previous research but may result from my study plots being in a drier subzone than ideal for Red Alder (Harrington, 1994). As a result of the additional N, the pure Red Alder plot contains large (1.5-2 m) Sword Ferns that have formed large hummocks of decomposed fronds beneath them that could further contribute to the total forest floor mass.

Rhoades et al. (2001) found that Alder had mixed or no effect on forest floor NH_4^+ content but significantly increased NO_3^- content by three to 30 times. This matches the trend at Holt Creek as NH_4^+ was not significantly affected in either soil layer by plot, Red Alder TBA, or by increasing soil N%. In contrast, forest floor and mineral NO_3^- contents in the pure Red Alder plot were more than twice those in the pure Douglas-fir plot. Increasing Red Alder TBA had a significant positive relationship with NO_3^- content in both soil layers. Gross mineralization was significantly higher in the pure Alder plot compared

to the pure Douglas-fir plot and was significantly and positively affected by Red Alder TBA. Soil nitrogen mineralization is especially important in temperate forests for influencing the availability of nitrogen (Perakis & Sinkhorn, 2011). Previous studies have linked variation in mineralization to differences in tree species composition through differences in C:N ratios (Kranabetter et al., 2021; Pastor et al., 1984; Reich et al., 1997) or to increases in forest floor N% (Perakis & Sinkhorn, 2011).

Forest floor soil $\delta^{15}N$ values in the pure Red Alder plot were significantly more enriched than in the pure Douglas-fir plot, which is consistent with previous studies that also found $\delta^{15}N$ values to be enriched by 5.0 – 5.8‰ under pure Red Alder stands (Binkley et al., 1985; Kreibich & Kern, 2000, Teklehaimanot & Mmolotsi, 2007). The forest floor was also enriched in the heavy isotope in the 50/50 plot compared to the pure Douglas-fir plot. Previous studies have attributed this enrichment under Alder to ammonia volatilization, denitrification during plant decomposition, and increased plant uptake of NH_4^+ and NO_3^- as these processes all discriminate against the heavy isotope, causing the remaining soil nitrogen to become enriched with the heavier ^{15}N isotope (Hoberg, 1997; Piccolo et al., 1996; Teklehaimanot & Mmolotsi, 2007). Leaf litter $\delta^{15}N$ values did not show the same differences in enrichment of the heavy isotope among plots as observed in the forest floor soil, and litter was less enriched in the heavy isotope than soils, overall. This supports the suggestion that the plant uptake favours the lighter isotope, and that the nitrogen isotope discrimination in soil through processes such as leaching and denitrification has more influence on the forest floor $\delta^{15}N$ than the effect of the addition of relatively ^{15}N-depleted nitrogen litter. The enriching effect of Red Alder was only seen in the forest floor of the pure and 50/50 plots. Mineral soil N% and $\delta^{15}N$ did not show any Alder influence, which suggests the range in mineral soil N% and $\delta^{15}N$ may reflect site factors other than the Alder treatment.

Red Alder litter nitrogen concentrations were lower than those found in previous studies that ranged between 2 – 2.5% (Tarrant et al., 1969; Teklehaimanot & Mmolotsi, 2007; Perakis et al., 2012; Scott et al., 2008). Radwan et al. (1984) reported Red Alder litter to range between 1.7 – 2.3% N across 8 stands and for litter mass to average 4130 kg/ha/yr, resulting in an addition of approximately 80 kg N/yr. Litter

mass at Holt Creek averaged 2340 kg/ha/year, which contained approximately 34 kg N suggesting this site has a relatively low nitrogen input. This low nitrogen input could have been caused by adverse weather conditions as the Summer of 2021 contained an unprecedented heatwave between late June and mid-July, where temperatures were up to 15ºC higher than 2014-2020 summer averages.

Red Alder litter reflected the increase in nitrogen available to the plant from nitrogen-fixation and was significantly higher in nitrogen concentration than Douglas-fir. This was expected, in part, because Red Alder retranslocates little N from leaves before leaf drop (Coté et al. 1989). Douglas-fir litter nitrogen concentration did not consistently change across the plots. This could be due to a pattern of retranslocation of nitrogen in Douglas-fir, where the tree always takes as much nitrogen out of the needles as possible. The average Douglas-fir litter nitrogen concentration of 0.79% is on the higher end of values reported by Prescott et al. (2000), who found Douglas-fir litter to range between 0.3 – 0.8% N, and on the lower end of values reported by Perakis & Sinkhorn (2011) (0.83 – 1.43% N).

Litter $\delta^{15}N$ did not significantly vary among plots or between species, which was also reported by Binkley et al. (1985). Red Alder litter was at times more enriched in ^{15}N than Douglas-fir but variation among plots was also high with Douglas-fir exhibiting a much wider range of litter $\delta^{15}N$ values than Red Alder (1.16 to -6.94‰, 0.2 to -3.37‰, respectively). This agrees with Urli et al. (2020), who found a similar pattern of less variation in Alder litter $\delta^{15}N$ compared to Black Spruce and Jack Pine. A wide range in foliar $\delta^{15}N$ values has been observed across species globally (Burnham et al., 2016; McLauchlan & Craine, 2012). The variability could be caused by a higher degree of plant fractionation than predicted (Craine et al., 2015). The lack of difference in litter $\delta^{15}N$ could also be due to variation of $\delta^{15}N$ within the canopy. Domenach et al. (1989) found that the foliar $\delta^{15}N$ values in the upper canopy of Grey Alder (*A. incana*) were similar to fixed nitrogen values (2 to -2‰) while $\delta^{15}N$ in leaves from lower in the canopy were similar to foliar $\delta^{15}N$ values of non-fixing plants.

The average Red Alder litter $\delta^{15}N$ value of -1.3‰ falls into the range found by Scott et al. (2008) of -0.5‰ to -1.5‰ in Green Alder (*A. viridis*). Vogel & Curtis (1997) reported a similar litter $\delta^{15}N$ value

of -1.46‰ in the closely related Black Alder (*A. glutinosa*). A study on a wide range of other species with nitrogen-fixing symbioses reported $\delta^{15}N$ values of −1.41 to −1.90‰ (Tjepkema et al., 2000). This reflects the atmospheric source of the litter $\delta^{15}N$, as the $\delta^{15}N$ values of shoots of nitrogen fixing plants tend to fall between -2‰ and 2‰ (Shearer & Kohl, 1986). When comparing leaf $\delta^{15}N$, Urli et al. (2020) found Green Alder (*A. viridis*) was significantly closer to atmospheric $\delta^{15}N$, at -1.01±0.03‰, when compared to Black Spruce (-1.49±0.66‰) and Jack Pine (-2.05±0.67‰).

Some studies have found high degrees of unexplained variation in their foliar $\delta^{15}N$ values, which has led to some skepticism about interpreting these results (Burnham et al., 2016; McLauchlan & Craine, 2012). However, sampling intensity can partially explain the variability (Craine et al., 2015). The range of foliar $\delta^{15}N$ values at a site has been found to increase logarithmically with the number of plants sampled as individual plants can vary by up to 25‰ (Craine et al., 2012; Craine et al., 2015). Previous studies have reported a relationship between foliar $\delta^{15}N$ values and mean annual temperature or precipitation, but this relationship disappears when the number of plants sampled is included in the model (Craine et al., 2015). As this study did not vary in sampling intensity between species, it can be concluded that the variation in values observed is likely due to differences in individual plant fractionation, or the sources of nitrogen assimilated by the two species.

The effect of the increasing proportion of Red Alder was visible in the tree-ring $\delta^{15}N$ of Douglas-fir, as hypothesized. Douglas-fir in the 50/50 plot with the highest proportion of Red Alder had significantly more enriched wood $\delta^{15}N$ values compared to all other Douglas-fir plots. These trees contain more of the heavy ^{15}N isotope and have $\delta^{15}N$ values closer to 0‰. This enriched $\delta^{15}N$ value mirrors the enriched value in the forest floor soil of the 50/50 plot, suggesting that the 50/50 Douglas-fir are receiving more fixed nitrogen than trees in the 25/75 and 11/89 plots. The 50/50 plot was the only plot with positive tree-ring $\delta^{15}N$ values for Douglas-fir. The pure Douglas-fir plot wood $\delta^{15}N$ values match previous studies with values ranging between -1 and -5‰ (Balster et al., 2009; Kranabeter et al., 2013; Kranabetter & Meeds, 2017).

The wood $\delta^{15}N$ in the pure Douglas-fir plot showed no increase or decrease over time, indicating little to no fixed-nitrogen contribution in that plot. Previous wood $\delta^{15}N$ studies have found that areas with closed nitrogen cycles tend to lack trends with time (Kranabetter et al., 2013; Kranabetter et al., 2020). As the Holt Creek site is in the lower precipitation range for the CWH zone, there may be little nitrogen loss due to leaching which would result in little change in wood $\delta^{15}N$ over time. While the 50/50 Douglas-fir had a significantly more enriched wood $\delta^{15}N$ value overall, there was no significant relationship over time.

The average $\delta^{15}N$ of Red Alder wood was more depleted than values reported by Teklehaimanot & Mmolotsi (2007), who found an average wood value of 0.07‰. However, it should be considered that $\delta^{15}N$ is a measure of the ratio of the two isotopes in the sample, and Teklehaimanot & Mmolotsi (2007) used a bulk sample of the entire stem to achieve their value, making it hard to use their value for direct comparison. My average $\delta^{15}N$ value of Red Alder tree rings of -2.9‰ is closer to an observed value of -2.0‰ in woody debris of Green Alder (*A. viridis* ssp. *crispa*) (Rhoades et al., 2001). Overall average wood $\delta^{15}N$ values for the two species did not significantly differ, which contradicts previous research where nitrogen-fixing plants were more enriched than neighbouring non-fixing plants (Peeters et al., 2011; Roggy et al., 1999). This could be due to mycorrhizal association, as most nitrogen-fixation research is done in the AM legumes and Red Alder is an EM tree. Enrichment of the soil nitrogen was only seen in the forest floor and mineral soils had consistent $\delta^{15}N$ values across plots. As EM fungi are well documented in mineral soils (Ekblad et al., 2013; Lindahl et al., 2007; Roseling et al., 2003), both Red Alder and Douglas-fir likely receive similar amounts of $\delta^{15}N$ from the deeper soil layer. Within the Red Alder wood sampled, the 11/89 plot was significantly more depleted, suggesting trees in this plot were less reliant on fixed-nitrogen and more on fungi-absorbed nitrogen.

Previous studies have identified a $\delta^{15}N$ range of 2.0‰ to -2.0‰ for the tissues of nitrogen-fixing plants (Craine et al., 2009; Shearer & Kohl, 1986). As very few wood $\delta^{15}N$ values are available for nitrogen-fixing plant genera, the overall tissue range was used to interpreted wood $\delta^{15}N$ values. The average wood $\delta^{15}N$ of Red Alder of -2.9‰ is outside the 2.0‰ to -2.0‰ range. A difference in mycorrhizal association

type could explain this. Most studies on the tissue $\delta^{15}N$ of nitrogen-fixing plants have occurred within Legumes, of which most form AM fungal associations (Hayman, 1986; Oba et al., 2001; Shi et al., 2007). AM fungi are restricted to forms of nitrogen that have already been mineralized and uptake by these fungi appears to have little to no effect on $\delta^{15}N$ values (Hobbie & Colpaert, 2013; Michelsen et al., 1996; Schweiger, 2016). In contrast, significant fractionation is seen in EM fungi (Hobbie & Agerer, 2010; Makarov, 2019). Therefore, the lower wood $\delta^{15}N$ could result from the Red Alder at this site forming EM associations, rather than AM associations. This is supported by a study on Grey Alder by Schweiger (2016) that found that stem $\delta^{15}N$ was significantly more depleted in EM inoculated Grey Alder (-1.6‰) compared to AM inoculated Grey Alder (-0.9‰).

The pure Red Alder plot was the only plot that exhibited a curvilinear relationship between tree-ring $\delta^{15}N$ and time. The assumption, based on research in legumes, was that the wood of young Red Alder would initially be depleted in ^{15}N, but would become more enriched and increase linearly towards 0‰ as the amount of fixed nitrogen increased. Enrichment was seen in the early years of growth in the Alder plots, which would match this expectation. Red Alder may initially have had high fixation rates due to the disturbed soil and open canopy created by logging which provide optimal light conditions for growth and N fixation (Bukata & Kyser, 2007; Kreutzweiser et al., 2008; Smolander et al., 2019). The plateau in wood $\delta^{15}N$ values, followed by a decrease occurred approximately between 2007 and 2011 and could have been caused by several factors, independently or in combination. The decrease in soil pH in the pure Red Alder plot may have caused the curvilinear pattern found for Red Alder tree-ring $\delta^{15}N$. Low soil pH values are well documented under pure Red Alder and mixed Red Alder/conifer stands (Binkley & Sollins, 1990; Bollen et al., 1967; Bormann & DeBell, 1981; Hart et al., 1996; Perakis & Pett-Ridge, 2019). However, these low pH values can inhibit biological nitrogen fixation (Burgraaf & Shipton, 1982). The forest floor soil pH in the 100/0 plot averaged 3.8± 0.07, which is outside the optimum observed for both *Frankia* and the nitrogenase enzyme (Johnstone, 1947; Waksman, 1922). *Frankia* colonization and

activity can still occur at lower pH levels but appear to have a lower limit of pH 4.6 (Johnstone, 1947; Waksman, 1922), while nitrogenase activity slows at pH 4.7 to 5.4 (Schubert et al., 1990).

The decrease in wood $\delta^{15}N$ in the 100/0 also occurred when Red Alder was approximately 15 years old. Previous studies examining Red Alder nitrogen fixation over time have found that productivity appears to peak around age 15 (Hibbs & DeBell, 1994; Sharma & Ambasht, 1988) before declining by up to 30% by age 30 (Sharma et al., 2002). A decrease in fixation rates can result from the host plant relying less on nitrogen-fixing symbionts and more on mycorrhizal fungi for acquiring soil nitrogen. This will decrease the values of tree-ring $\delta^{15}N$ due to increased fungal fractionation. If the Red Alder had already raised the total soil nitrogen stocks sufficiently after 15 years, it would be plausible for the trees to decrease their investment in nitrogen-fixing nodules to conserve energy and increase efficiency.

The use of wood N% to assess the nitrogen cycle has mainly been discounted, with many studies no longer reporting wood N% data (Gerhart & McLauchlan, 2014). Many researchers have concluded that tree-ring N% reflects physiological patterns within the tree itself and cannot be used to infer ecosystem nitrogen supply or sources during growth (Bukata & Kyser, 2005; Doucet et al., 2011; Poulson et al., 1995). Positive (Larry et al., 2010; Leonelli et al., 2012), negative (Choi et al., 2005), and lack of correlation (Doucet et al., 2012; Guerrieri et al., 2009) between wood N% and $\delta^{15}N$ have been reported. However, all previous studies utilizing wood N% have been conducted in non-nitrogen fixing tree species or without considering the impact of nitrogen fixing species, thus the relationship of higher wood nitrogen content in nitrogen-fixing species and wood $\delta^{15}N$ values was unknown.

While no consistent trends were seen across all the Holt Creek plots, a significant negative trend between tree-ring N% and $\delta^{15}N$ was seen in the pure Red Alder plot and Red Alder overall. The apparent negative relationship between tree-ring N% and $\delta^{15}N$ might indicate that Red Alder is receiving a majority of its nitrogen from nitrogen-fixation, and this may be restricted to nitrogen-fixing trees as no relationship was seen in Douglas-fir. It is well document for legumes to receive over 90% of their nitrogen from nitrogen-

fixation (Androsoff et al., 1995; Szpak et al., 2014). However, as there are no other nitrogen-fixing tree N% and $\delta^{15}N$ datasets, more research is needed to investigate this theory.

Soil in the pure Red Alder plot had different concentrations of most cations compared to the pure Douglas-fir plot. This included increased amounts of Fe and Al and decreased organic P, Ca, Mg, Mn, and Na in the forest floor under Red Alder. Apart from nitrogen, the mineral nutrients most needed by plants are Ca, Mg, and P (Ketterings et al., 2007), and Ca and Mg were significantly depleted in the pure Alder plot. This is probably because the forest floor has a significantly lower CEC and pH. Decreased soil pH also decreases the soil CEC, with low CEC often being associated with deficiencies in P and Mg (Ketterings et al., 2007). A low soil pH has also been associated with increased Al mobilization and can lead to increased soil organic matter retention (Lawrence et al., 2020; Oulehle et al., 2017; Sabo et al., 2020; Sumner & Miller, 1996). The decreased soil and foliar Ca and Mg and increased soil Al and Fe under Red Alder match a pattern reported in other studies. Perakis et al. (2013) found that soils under Red Alder had less Ca and Mg and increased Al mobilization as nitrogen increased across a gradient.

As with other studies utilizing tree rings, it is common to bulk or group multiple years together to reach the minimum amount of wood for analysis. A downside of that approach is that there is a loss of temporal resolution. A method to decrease bulking in this study would have been to use a larger diameter increment bore or to take multiple cores from each tree and align them to increase the mass of wood available per ring. This would decrease the temporal variation due to bulking 3-6 years together in a sample.

While multiple cores would be possible in the Holt Creek site, this method may not be possible in other sites with difficult sampling conditions or in undisturbed old growth sites where less intense sampling is often required (Tsen et al., 2016). There are potential negative effects of coring a tree, such as wood discolouration (Nevalainen, 2006), canker formation due to pathogen invasion (Blanchette & Biggs, 1992; Hepting et al., 1949; Manion, 1991), and in extreme cases, death (Florens, 2013, 2014). Neo et al. (2017) found a survival rate of 97% when trees were cored twice, and that >70% of the trees had closed at least one borehole after a year. Overall, conifers appear to sustain less damage and decay from coring

than broadleaf taxa (Hepting et al., 1949; Lenz & Oswald, 1971). Within Douglas-fir, smaller and younger trees respond better to wounds than larger trees (Jones et al., 2019). This poses a problem as older Doulas-fir trees provide a longer-term record but would be more affected by coring. A trade-off accepted in other areas utilizing tree rings, especially dendroclimatology (using tree rings to determine past climate traits), is to make the best of imperfect data rather than resample and potentially cause damage (Hepting et al., 1949).

Holt Creek was planted in 1994 with 1+0 saplings and cored at a height of 50 cm to maximize the number of rings detected. Often trees are cored at breast height (~135 cm) which decreases the number of rings detectable due to the longer time needed for the tree to reach that height. It is also possible for a tree to not put down a visible ring, due to cold or drought stress damaging the vascular cambium (Cherubini et al., 2002). Missing rings are common in conifer species (Novak et al., 2016; Raventós et al., 2001) but less reported in deciduous species. The Red Alder rings in this study were identified and split with the naked eye, which could be improved using a microscope. This process allowed Smith (1978) to revise their estimated age of a Red Alder stump from 56 years to 75 years; however, they also found that the Red Alder was missing at least 21 rings when compared to the jointly planted Douglas-fir. Other assessments of Red Alder rings have also noted many missing rings, especially after 40 years of age (Hoyer et al., 1978; Smith, 1973).

Holt Creek has a sister replacement series established at East Wilson Creek near Gibson, B.C., on the Sunshine Coast. East Wilson Creek would provide an alternative location for the repetition of this study and would allow further investigation to determine if the trends seen in Red Alder are due to it being a nitrogen-fixing tree or are more dependent on site factors such as soil moisture, mean annual precipitation, and site elevation. Similar analysis on other pure stands of Red Alder would provide more data to support interpretation of my results.

The Pacific Northwest is one of a few areas globally that has more than one wood $\delta^{15}N$ study (Gerhart & McLauchlan, 2014). These studies give valuable long-term records of nitrogen cycling and allow

researchers to better understand ecosystems and how they will react to changes, including climate change. Douglas-fir is both an economically and ecologically important tree in the Pacific Northwest and better understanding its physiology and ecology will help to sustain growth and wood production in this species. Red Alder is an important component of Pacific Northwest forest stands following disturbance, and plays a role in soil formation and development. Understanding how Red Alder affects nitrogen cycling over time would provide important information to support sustainable forestry. As most nitrogen fixation studies are based on research in Legumes, the findings of this study add context with the addition of an ectomycorrhizal nitrogen fixing plant.

5. Conclusion

The Red Alder growing in a pure stand at Holt Creek significantly increased both the soil nitrogen stock and forest floor soil $\delta^{15}N$ due to its ability to fix atmospheric nitrogen. The nonlinear relationship between wood $\delta^{15}N$ and time in Red Alder from the 100/0 plot and overall was unexpected. It may have been caused by a negative feedback cycle between nitrogen-fixation and pH, decreasing Alder fitness after 15 years of age, a negative interaction between nitrogen-fixation and soil nitrogen content, or a combination of these factors. Litter and average wood $\delta^{15}N$ were not significantly different between Red Alder and Douglas-fir, possibly due to absorption of mineral soil nitrogen that is relatively uniform in $\delta^{15}N$ and/or discrimination by EM. The effect of enriched forest floor soil $\delta^{15}N$ under Red Alder was visible in the tree-rings of Douglas-fir grown in the 50/50 mixed plot, confirming it received more fixed nitrogen than pure grown Douglas-fir and that effects of nitrogen-fixation can be observed in the tree-rings of non-fixing trees.

The variation in the relationship between time and tree-ring $\delta^{15}N$ seen in Red Alder adds a complex element to interpreting tree-ring $\delta^{15}N$ values. More research is needed to determine if the nonlinear relationship between tree-ring $\delta^{15}N$ and time is a characteristic of nitrogen-fixing trees or a product of site-specific factors.

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Appendix 1. Growth and Yield Stand Summaries at Holt Creek

Growth and yield stand summaries for the five replacement series plots at Holt Creek. Total volume and basal area are the total for all trees of that species in the plot. Top height and mean DBH are averages across the species. Stems per Ha is the total number of merchantable trees per hectare. Dr = Red Alder. FD = Douglas-fir. XX = total (combined Dr and FD).

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Table 7.1.
Growth and yield stand summaries for MOF EP 1121.01 installation 5 plot 8 (11/89 Red Alder/Douglas-fir mix)

Total Age (years)	Species	Total Volume (m^3/ha)	Basal Area (m^2/ha)	Top Height (m)	Stems per Ha	Mean DBH (cm)
2	DR	0		0.4	60	`
2	FD	0		0.4	590	
2	XX	0		0.5	650	
3	DR	0		1	60	
3	FD	0		0.8	570	
3	XX	0		1	630	
4	DR	0		1.8	50	
4	FD	0		1.2	560	
4	XX	0		1.5	610	
5	DR	0		2.7	50	
5	FD	0		1.7	600	
5	XX	0		2.3	650	
7	DR	0.1	0.1	4	50	3.8
7	FD	0	2.9	680		
7	XX	0.1	0.1	3.5	730	1
10	DR	0.8	0.2	5.6	50	7.9
10	FD	4.1	1.7	6	670	5.6
10	XX	4.9	1.9	6.2	720	5.8
12	DR	1.2	0.3	6	50	9.3
12	FD	11	3.6	8	670	8.3
12	XX	12.2	4	8.2	720	8.4
13	DR	1.5	0.4	6.8	40	11.1
13	FD	17.4	5.2	9.1	660	10
13	XX	18.9	5.6	9.2	700	10.1
18	DR	2.8	0.5	9.2	30	14.7
18	FD	70.1	13.9	14	630	16.8
18	XX	72.9	14.4	14.1	660	16.7
24	DR	5	0.7	12	30	17.4
24	FD	151.3	22.3	19.5	540	22.9
24	XX	156.3	23	19.5	570	22.7

Table 7.2.
Growth and yield stand summaries for MOF EP 1121.01 installation 5 plot 9 (25/75 Red Alder/Douglas-fir mix)

Total Age (years)	Species	Total Volume (m^3/ha)	Basal Area (m^2/ha)	Top Height (m)	Stems per Ha	Mean DBH (cm)
2	DR	0		0.7	130	
2	FD	0		0.4	540	
2	XX	0		0.7	670	
3	DR	0		1.5	130	
3	FD	0		0.7	530	
3	XX	0		1.5	660	
4	DR	0		2.3	120	
4	FD	0		1.1	510	
4	XX	0		2.3	630	

5	DR	0	0	3.1	150	1.2
5	FD	0	1.5	530		
5	XX	0	0	3.1	680	0.6
7	DR	0.4	0.2	4.3	150	3.6
7	FD	0	3	540		
7	XX	0.4	0.2	4.3	690	1.7
10	DR	1.6	0.5	5.5	100	8.1
10	FD	2.7	1.1	5.8	520	5.3
10	XX	4.3	1.7	6.1	620	5.9
12	DR	1.9	0.6	5.9	80	9.8
12	FD	7.7	2.7	7.8	500	8.2
12	XX	9.7	3.3	7.4	580	8.5
13	DR	2.3	0.7	6	80	10.5
13	FD	13	4	8.7	510	10
13	XX	15.3	4.7	8.7	590	10
18	DR	3.7	0.9	8	70	12.6
18	FD	58.6	12	13.5	520	17.2
18	XX	62.3	12.9	13.5	590	16.7
24	DR	5.2	0.9	9.5	70	12.9
24	FD	144.5	21.9	19.2	520	23.1
24	XX	149.8	22.8	19.2	590	22.2

Table 7.3
Growth and yield stand summaries for MOF EP 1121.01 installation 5 plot 10 (100/0 Red Alder/Douglas-fir mix)

Total Age (years)	Species	Total Volume (m^3/ha)	Basal Area (m^2/ha)	Top Height (m)	Stems per Ha	Mean DBH (cm)
1	DR	0		0.9	580	
1	XX	0		0.9	580	
2	DR	0		2.1	580	
2	XX	0		2.1	580	
3	DR	0		3.3	550	
3	XX	0		3.3	550	
4	DR	0.5	0.2	4.6	650	1.9
4	XX	0.5	0.2	4.6	650	1.9
6	DR	4.1	1.4	6.1	750	4.9
6	XX	4.1	1.4	6.1	750	4.9
9	DR	18.9	5.1	8.7	720	9.5
9	XX	18.9	5.1	8.7	720	9.5
11	DR	30.1	7.4	10.1	720	11.4
11	XX	30.1	7.4	10.1	720	11.4
12	DR	38.5	8.9	10.6	720	12.6
12	XX	38.5	8.9	10.6	720	12.6
17	DR	74.4	13.5	13.2	720	15.5
17	XX	74.4	13.5	13.2	720	15.5
23	DR	133.1	20.8	15.3	1010	16.2
23	XX	133.1	20.8	15.3	1010	16.2

Table 7.4
Growth and yield stand summaries for MOF EP 1121.01 installation 5 plot 11 (50/50 Red Alder/Douglas-fir mix)

Total Age (years)	Species	Total Volume (m^3/ha)	Basal Area (m^2/ha)	Top Height (m)	Stems per Ha	Mean DBH (cm)
2	DR	0		0.7	290	
2	FD	0		0.4	350	
2	XX	0		0.7	640	
3	DR	0		1.9	280	
3	FD	0		0.7	330	
3	XX	0		1.9	610	

4	DR	0		2.8	280	
4	FD	0		1.1	340	
4	XX	0		2.8	620	
5	DR	0.2	0.1	4.1	290	1.9
5	FD	0	1.8	340		
5	XX	0.2	0.1	4.1	630	1.3
7	DR	1.1	0.4	5.3	340	3.8
7	FD	0	0	3.5	380	0.7
7	XX	1.1	0.4	5.3	720	2.7
10	DR	3.9	1.2	7	260	7.6
10	FD	4.2	1.5	6.7	340	7.6
10	XX	8.1	2.7	7.2	600	7.6
12	DR	5.4	1.6	7.6	240	9.1
12	FD	10.6	3.1	9	340	10.7
12	XX	16.1	4.6	8.8	580	10.1
13	DR	6.8	1.9	8.2	240	10
13	FD	16.4	4.4	9.9	340	12.8
13	XX	23.2	6.3	9.9	580	11.7
18	DR	12.3	2.6	11.1	230	12
18	FD	62.9	12.1	14.5	330	21.6
18	XX	75.2	14.7	14.5	560	18.3
24	DR	22.2	3.6	14.4	250	13.5
24	FD	139.1	20.6	18.5	330	28.2
24	XX	161.3	24.2	18.5	580	23

Table 7.5
Growth and yield stand summaries for MOF EP 1121.01 installation 5 plot 12 (0/100 Red Alder/Douglas-fir mix)

Total Age (years)	Species	Total Volume (m^3/ha)	Basal Area (m^2/ha)	Top Height (m)	Stems per Ha	Mean DBH (cm)
2	FD	0		0.5	670	
2	XX	0		0.5	670	
3	FD	0		0.9	630	
3	XX	0		0.9	630	
4	FD	0		1.4	630	
4	XX	0		1.4	630	
5	FD	0		2	620	
5	XX	0		2	620	
7	FD	0.3	0.1	3.9	770	1.5
7	XX	0.3	0.1	3.9	770	1.5
10	FD	9.5	3.3	7.3	720	7.6
10	XX	9.5	3.3	7.3	720	7.6
12	FD	24.2	6.7	9.3	700	11.1
12	XX	24.2	6.7	9.3	700	11.1
13	FD	38.1	9.7	10.8	710	13.2
13	XX	38.1	9.7	10.8	710	13.2
18	FD	120.9	21.8	15.9	660	20.5
18	XX	120.9	21.8	15.9	660	20.5
24	FD	226.9	30.5	21.5	600	25.4
24	XX					

Appendix 2. Holt Creek Subplot Tree Lists

Table 8.
Complete tree lists for Hold Creek Subplots. Cored trees are indicated in bold. Trees with tag numbers are those planted in the plot but outside of the 0.1ha Ministry resampling area. Tree with the tag number prefix "LN" are core trees outside of the 0.1ha area. Heights for ministry plots trees are from Fall 2020, other heights from Spring 2021. Subplot code is "plot number"- "subplot number within plot"- "subplot number out of total".
Dr = Red Alder. Fd = Douglas-fir.

Subplot Code	Species	Tag Number	DBH (cm)	Height (m)	Status
10-1-1	Dr	1208	11.1	10.9	
10-1-1	Dr		12.1		
10-1-1	Dr	1214	13.7	12	
10-1-1	Dr	1922	15.6	17.7	
10-1-1	Dr	91206	15.6	13.6	
10-1-1	Dr	1920	16.7	13	
10-1-1	Dr	1207	17.6	13	
10-1-1	Dr	**1919**	18	12.9	
10-1-1	Dr	1215	21	13.6	
10-1-1	Dr	1206	22	14.4	
10-2-2	Dr		4		
10-2-2	Dr	2833	8.1	10.9	
10-2-2	Dr	1080	15.7	14.7	
10-2-2	Dr	1078	18.2	13.6	
10-2-2	Dr	**1081**	28	14.9	
10-2-2	Dr	1070			dead
10-2-2	Dr	1082			dead
10-2-2	Dr	1093			dead
10-2-2	Dr	9008			dead
10-2-2	Dr	91080			dead
10-3-3	Dr	9999	9.2	11.6	dead
10-3-3	Dr	987	9.9	12.6	
10-3-3	Dr		11.3		
10-3-3	Dr	93830	13.3	13.2	
10-3-3	Dr	9006	13.5	13.9	
10-3-3	Dr	1923	17	15.5	
10-3-3	Dr		17.2		
10-3-3	Dr	3830	18.1	14.8	
10-3-3	Dr	2831	18.3	14	
10-3-3	Dr	2830	18.7	15.3	
10-3-3	Dr	**998**	21.7	14.2	
10-3-3	Dr	999			dead
10-4-4	Dr		11.9		
10-4-4	Dr		12.4		
10-4-4	Dr		12.6		
10-4-4	Dr		17.8		

10-4-4	Dr		18.5		
10-4-4	Dr		20.5		
10-4-4	Dr	**LN001**	23.0	12.9	
10-4-4	Dr		26.4		
10-5-5	Dr	9983	11.1	12.9	
10-5-5	Dr	982	16.2	13.4	
10-5-5	Dr		16.6		
10-5-5	Dr	984	17.6	13.8	
10-5-5	Dr	**983**	17.7	13.1	
10-5-5	Dr		18.0		
10-5-5	Dr	991	19.1	14.6	
10-5-5	Dr		20.7		
10-5-5	Dr	990	21.7	16.1	
9-1-6	Dr	**953**	20.7	18.2	
9-1-6	Fd	963	23	19.3	
9-1-6	Fd	962	23.6	20.4	
9-1-6	Fd	964	23.6	21.4	
9-1-6	Fd	946	25.2	22.4	
9-1-6	Fd	945	30.5	24.2	
9-1-6	Fd	**954**	34.5	23.2	
9-2-7	Dr	**951**	16.9	16.1	
9-2-7	Fd		11.5		
9-2-7	Fd	**950**	25.9	21	
9-2-7	Fd	948	26.6	22.6	
9-2-7	Fd	**932**	27.5	21	
9-2-7	Fd	949	27.5	23.5	
9-2-7	Fd	947	33.9	23.7	
9-2-7	Fd	933			dead
9-3-8	Dr	**LN002**	14.7	17.4	
9-3-8	Dr	933			dead
9-3-8	Fd		11.5		
9-3-8	Fd	931	20.3	20.8	
9-3-8	Fd	930	27.5	20.9	
9-3-8	Fd	**932**	27.5	21	
9-3-8	Fd	949	27.5	23.5	
9-3-8	Fd		28.6		
9-4-9	Dr	**LN003**	18.8	17.9	
9-4-9	Fd		18.3		
9-4-9	Fd		20.4		
9-4-9	Fd		22.3		
9-4-9	Fd		29.3		
9-4-9	Fd		29.6		
9-4-9	Fd	**LN005**	31.3	21.8	

9-5-10	Dr		18.8	17.9	dead
9-5-10	Dr	**LN004**	10.9	15.4	
9-5-10	Fd	**LN006**	27.4	28.1	
9-5-10	Fd		29.6	22.5	
9-5-10	Fd		31.2		
9-5-10	Fd		34.4		
8-1-11	Dr	**909**	10.9	15.4	
8-1-11	Fd		25.1		
8-1-11	Fd	**907**	28.1	22.5	
8-1-11	Fd	908	27.8	21.7	
8-1-11	Fd		29.9		
8-2-12	Dr	**LN007**	25.8	20.5	
8-2-12	Fd		13.7		
8-2-12	Fd		26.4		
8-2-12	Fd	**LN010**	28.5	23.9	
8-2-12	Fd	894	29.3	23.8	
8-3-13	Dr		22.9		
8-3-13	Dr	**862**	26.8	20.5	
8-3-13	Fd	860	19	20.5	
8-3-13	Fd		19.9		
8-3-13	Fd	861	25.8	23.7	
8-3-13	Fd	875	32.2	24.4	
8-3-13	Fd	**874**	32.6	22.5	
8-4-14	Dr		15.9		
8-4-14	Dr	**LN008**	21.1	19.5	
8-4-14	Fd		20.7		
8-4-14	Fd	852	22.8	21.3	
8-4-14	Fd		23.2		
8-4-14	Fd	851	24.9	22.5	
8-4-14	Fd		29.0		
8-4-14	Fd	**847**	31.1	24.7	
8-4-14	Fd		32.5		
8-5-15	Dr		19.4		
8-5-15	Dr	**LN009**	20.9	18.3	
8-5-15	Fd		23.4		
8-5-15	Fd		31.8		
8-5-15	Fd		32.8		
8-5-15	Fd	**LN011**	35.3	26.4	
8-5-15	Fd		33.4		
8-5-15	Fd		34.4		
11-1-16	Dr		7.3		
11-1-16	Dr	1234	12.7	16.7	
11-1-16	Dr	1235	17.8	13.4	

11-1-16	Dr	**91235**	19	14.9	
11-1-16	Fd		11.1		dead
11-1-16	Fd	**1236**	35.5	23	
11-1-16	Fd		36.0		
11-2-17	Dr		11.9		
11-2-17	Dr		14.3		
11-2-17	Dr		15.0		
11-2-17	Dr	**LN012**	16.2	18.2	
11-2-17	Fd	**1270**	23	19.8	
11-2-17	Fd	1271	25.5		dead
11-2-17	Fd	1269	37.3	23.9	
11-3-18	Dr	**1963 (9011)**	19.7	17.2	
11-3-18	Dr	1258			dead
11-3-18	Fd		9		
11-3-18	Fd	1274	31.3	24.1	
11-3-18	Fd	**1265**	35.1	23.5	
11-3-18	Fd	1249	36.1	24.2	
11-3-18	Fd	1259	36.2	22.9	
11-4-19	Dr	**1245**	17.7	15.5	
11-4-19	Dr	1244	36.1	22.7	
11-4-19	Dr	1262			dead
11-4-19	Dr	1962	8.4	11	
11-4-19	Fd	**1246**	34.8	23.4	
11-5-20	Dr		15.4		
11-5-20	Dr	**1222**	16.7	18.5	
11-5-20	Dr	1221			dead
11-5-20	Dr	91222			dead
11-5-20	Fd	1233	25.8	21.2	
11-5-20	Fd	**1223**	33.4	22.4	
11-5-20	Fd		33.7		
11-5-20	Fd		34.1		
12-1-21	Fd	1304	21.5	21.8	
12-1-21	Fd	1306	27.1	21.8	
12-1-21	Fd	1305	27.3	25.3	
12-1-21	Fd	1296	27.5	25.6	
12-1-21	Fd	1290	29.8	22.2	
12-1-21	Fd	**1297**	33.7	24.9	
12-2-22	Fd	1315	20.7	20	
12-2-22	Fd	1318	22.9	23.7	
12-2-22	Fd	**1317**	28.7	25.5	
12-2-22	Fd	1319	30.1	25	
12-2-22	Fd	1334	30.2	23.8	
12-2-22	Fd	1316	39.5	23.9	

12-3-23	Fd		19.1		
12-3-23	Fd		22.6		
12-3-23	Fd		25.3		
12-3-23	Fd	**1308**	26.4	22.4	
12-3-23	Fd	1326	26.5	23	
12-3-23	Fd	1973	31.7	26	
12-3-23	Fd		32.0		
12-4-24	Fd		26.7		
12-4-24	Fd		29.0		
12-4-24	Fd		29.6		
12-4-24	Fd		30.9		
12-4-24	Fd	1327	31.3	23.7	
12-4-24	Fd		31.5		
12-4-24	Fd	**LN013**	32.9	24.7	
12-4-24	Fd	1960/9008/1342			dead
12-5-25	Fd		21.0		
12-5-25	Fd		22.6		
12-5-25	Fd		23.9		dead
12-5-25	Fd		25.1		
12-5-25	Fd		27.4		
12-5-25	Fd	1351	31.3	24.9	
12-5-25	Fd	**1350**	33.3	26.6	

Appendix 3. Soil $\delta^{15}N$ values

Subplot code is: “plot number”- “subplot number within plot”- “subplot number out of total”.

Table 9.1
Forest Floor Soil $\delta^{15}N$ values. Average values were used for analysis.

Subplot	Rep 1	Rep 2	Rep 3	Average
10-1-1	1.70	0.04	2.10	1.28
10-2-2	1.65	0.22	0.81	0.89
10-3-3	2.27	2.49	0.59	1.78
10-4-4	0.75	1.28	1.33	1.12
10-5-5	2.44	1.72	0.42	1.53
9-1-6	-0.38	-0.08	-1.54	2.01
9-2-7	0.12	-1.20	0.01	1.00
9-3-8	-1.28	-0.81	-0.80	-0.04
9-4-9	-0.30	-0.47	-1.11	0.69
9-5-10	-1.06	-0.07	-0.31	1.36
8-1-11	-0.13	-2.29	-0.63	-0.67
8-2-12	-0.71	-0.35	-1.31	-0.36
8-3-13	-0.76	0.15	-0.25	-0.96
8-4-14	0.18	-0.14	-1.18	-0.63
8-5-15	0.04	-1.84	-0.56	-0.48
11-1-16	2.39	1.57	2.06	-1.01
11-2-17	0.16	1.72	1.13	-0.79
11-3-18	0.89	-0.51	-0.50	-0.29
11-4-19	0.39	1.13	0.54	-0.38
11-5-20	1.74	0.83	1.51	-0.79
12-1-21	-0.28	-1.08	-0.82	-0.72
12-2-22	-1.34	-0.09	-0.36	-0.60
12-3-23	0.29	1.19	-0.11	0.46
12-4-24	-1.51	0.19	0.88	-0.14
12-5-25	0.73	-0.60	0.01	0.05

Table 9.2
Mineral Soil $\delta^{15}N$ values. Average values were used for analysis.

Subplot	Rep 1	Rep 2	Rep 3	Average
10-1-1	2.57	3.07	2.52	2.72
10-2-2	1.46	2.33	2.56	2.12
10-3-3	3.80	3.76	3.35	3.64
10-4-4	5.50	3.44	1.81	3.59
10-5-5	4.05	3.31	2.60	3.32
9-1-6	3.08	2.49	1.50	3.72
9-2-7	2.16	3.72	2.77	2.98
9-3-8	2.04	1.95	4.88	2.26
9-4-9	2.40	1.11	0.84	1.64
9-5-10	4.20	1.97	4.27	3.23
8-1-11	2.11	3.08	5.90	2.36
8-2-12	1.40	4.32	4.40	2.88
8-3-13	2.07	1.53	2.08	2.95
8-4-14	1.55	2.03	2.44	1.45
8-5-15	-0.01	4.17	2.71	3.48
11-1-16	2.51	5.14	3.51	3.70
11-2-17	1.61	3.11	4.23	3.37
11-3-18	2.38	1.80	2.61	1.89
11-4-19	2.74	1.65	0.54	2.01
11-5-20	3.97	2.61	3.12	2.29
12-1-21	2.73	2.33	3.20	2.75
12-2-22	1.98	1.56	1.35	1.63
12-3-23	5.51	4.08	3.91	4.50
12-4-24	3.30	4.15	2.42	3.29
12-5-25	4.24	2.74	2.76	3.25

Appendix 4. Forest Floor NH_4^+ and NO_3^- Content

Subplot code is: “plot number”- “subplot number within plot”- “subplot number out of total”.

Table 10.1
Forest Floor NH_4^+ (mg/kg) content. Average values were used for analysis.

Subplot	Rep 1	Rep 2	Rep 3	Average
10-1-1	2.63	2.63	2.63	14.47
10-2-2	3.26	3.26	3.26	7.24
10-3-3	3.38	3.38	3.38	16.92
10-4-4	0.00	3.65	27.31	10.32
10-5-5	0.68	1.84	18.54	7.02
9-1-6	10.62	63.14	31.17	34.97
9-2-7	20.14	19.89	8.35	16.12
9-3-8	4.47	4.30	16.26	8.34
9-4-9	23.74	114.13	70.72	69.53
9-5-10	9.23	26.85	26.11	20.73
8-1-11	5.80	18.33	3.59	9.24
8-2-12	11.78	11.61	N/A	11.70
8-3-13	3.66	57.10	16.42	25.73
8-4-14	43.83	23.37	N/A	33.60
8-5-15	6.33	37.50	21.65	21.83
11-1-16	33.97	1.00	N/A	17.48
11-2-17	51.99	7.24	51.04	36.76
11-3-18	67.73	10.15	56.64	44.84
11-4-19	32.01	30.56	N/A	31.28
11-5-20	36.62	4.36	17.91	19.63
12-1-21	22.32	34.48	9.54	22.11
12-2-22	22.51	19.46	N/A	20.99
12-3-23	46.57	10.52	6.59	21.22
12-4-24	5.96	4.82	N/A	5.39
12-5-25	27.99	25.09	20.36	24.48

Table 10.2
Forest Floor NO_3^- (mg/kg) content. Averages were used for analysis.

Subplot	Rep 1	Rep 2	Rep 3	Average
10-1-1	98.1	65.0	102.4	88.52
10-2-2	69.0	63.3	82.8	71.71
10-3-3	117.6	54.7	78.2	83.52
10-4-4	34.9	58.1	79.3	57.40
10-5-5	62.8	74.7	103.4	80.30
9-1-6	0.00	0.00	0.00	0.00
9-2-7	0.00	3.42	0.00	1.14
9-3-8	0.00	0.00	0.00	0.00
9-4-9	0.00	0.00	0.00	0.00
9-5-10	0.00	0.00	0.00	0.00
8-1-11	0.00	11.66	0.00	3.89
8-2-12	0.00	0.00	N/A	0.00
8-3-13	63.57	10.05	63.59	45.73
8-4-14	17.37	24.85	N/A	21.11
8-5-15	0.00	135.10	20.34	51.81
11-1-16	74.50	73.65	N/A	74.08
11-2-17	67.66	145.38	4.52	72.52
11-3-18	0.00	17.71	4.44	7.38
11-4-19	57.73	2.81	N/A	30.27
11-5-20	43.53	35.91	27.21	35.55
12-1-21	28.75	15.58	24.21	22.85
12-2-22	10.71	31.85	N/A	21.28
12-3-23	90.61	96.46	55.00	80.69
12-4-24	90.16	79.53	N/A	84.84
12-5-25	41.59	40.99	51.43	44.67

Appendix 5. Mineral Soil NH_4^+ and NO_3^- Content

Subplot code is: “plot number”- “subplot number within plot”- “subplot number out of total”.

Table 11.1
Mineral Soil NH_4^+ (mg/kg) content. Average values were used for analysis.

Subplot	Rep 1	Rep 2	Rep 3	Average
10-1-1	1.19	0.00	0.00	0.40
10-2-2	0.00	0.00	0.00	0.00
10-3-3	0.00	0.00	0.57	0.19
10-4-4	0.00	0.00	0.00	0.00
10-5-5	1.50	2.18	6.59	3.42
9-1-6	0.00	0.78	0.00	0.26
9-2-7	0.00	0.00	2.12	0.71
9-3-8	1.05	0.91	1.12	1.03
9-4-9	0.56	0.90	0.72	0.72
9-5-10	8.07	0.61	1.13	3.27
8-1-11	5.59	0.92	0.77	2.43
8-2-12	1.55	5.83	1.76	3.05
8-3-13	2.37	0.99	1.09	1.48
8-4-14	17.36	0.00	1.32	6.23
8-5-15	4.91	0.00	0.85	1.92
11-1-16	0.00	0.00	0.00	0.00
11-2-17	4.65	0.64	0.81	2.04
11-3-18	0.00	0.70	0.00	0.23
11-4-19	1.48	3.77	10.93	5.39
11-5-20	3.26	1.61	1.28	2.05
12-1-21	0.00	0.00	0.97	0.32
12-2-22	1.36	0.51	0.72	0.86
12-3-23	0.54	0.00	0.00	0.18
12-4-24	1.27	1.29	5.39	2.65
12-5-25	0.00	0.00	0.74	0.25

Table 11.1
Mineral Soil NO_3^- (mg/kg) content. Averages were used for analysis.

Subplot	Rep 1	Rep 2	Rep 3	Average
10-1-1	23.70	8.16	5.78	12.55
10-2-2	4.19	19.55	2.24	8.66
10-3-3	5.15	12.56	6.13	7.95
10-4-4	6.10	5.06	15.15	8.77
10-5-5	13.22	13.85	9.02	12.03
9-1-6	0.00	0.00	0.00	0.00
9-2-7	0.00	0.00	12.29	4.10
9-3-8	0.00	0.00	0.00	0.00
9-4-9	0.00	0.00	0.00	0.00
9-5-10	0.67	0.00	1.95	0.87
8-1-11	0.00	0.00	0.00	0.00
8-2-12	1.37	3.65	1.30	2.11
8-3-13	5.82	0.00	12.86	6.23
8-4-14	0.00	9.55	25.40	11.65
8-5-15	1.40	2.41	8.99	4.27
11-1-16	13.59	2.23	3.63	6.48
11-2-17	5.87	0.96	16.86	7.90
11-3-18	0.00	0.00	2.99	1.00
11-4-19	7.10	11.27	7.21	8.53
11-5-20	1.51	4.48	2.02	2.67
12-1-21	6.24	13.51	2.99	7.58
12-2-22	2.74	7.96	1.19	3.96
12-3-23	6.88	1.45	4.81	4.38
12-4-24	23.12	4.35	22.10	16.52
12-5-25	3.44	1.59	7.48	4.17

Appendix 6. Soil characteristics for Forest Floor and Mineral Soil layers.

Subplot code is: “plot number”- “subplot number within plot”- “subplot number out of total”.

Table 12.1
Forest Floor soil characteristics

Subplot	pH	Organic P (mg/kg)	Inorganic P (mg/kg)	Al (cmol+/kg)	Ca (cmol+/kg)	Fe (cmol+/kg)	K (cmol+/kg)	Mg (cmol+/kg)	Mn (cmol+/kg)	Na (cmol+/kg)	CEC (cmol+/kg)
10-1-1	3.9	540	110	5.1	15	0.26	0.8	3.2	0.69	0.15	25
10-2-2	3.8	600	87	3	12	0.15	0.64	2.3	0.37	0.14	19
10-3-3	3.7	680	63	2.8	16	0.26	0.65	2.9	0.22	0.13	23
10-4-4	3.6	630	85	3.6	18	0.29	1	4.3	0.56	0.17	28
10-5-5	4.0	660	92	4.2	17	0.32	0.86	4.6	0.61	0.16	27
9-1-6	4.5	710	140	1.7	28	0.14	1	5.6	1.5	0.22	39
9-2-7	4.6	720	170	1	29	0.077	0.8	5.5	1.4	0.19	38
9-3-8	4.8	740	290	0.55	42	0.067	1.1	7.2	2.4	0.18	54
9-4-9	4.8	580	250	0.54	40	0.067	1.2	6.5	2.5	0.18	51
9-5-10	4.8	660	520	0.72	38	0.073	1.4	6	2	0.2	49
8-1-11	4.6	510	380	1.4	25	0.1	0.85	3.7	1.1	0.18	33
8-2-12	4.7	570	170	0.84	34	0.084	0.88	5.6	1.2	0.19	43
8-3-13	4.8	840	87	2	43	0.084	1	8.6	0.94	0.23	56
8-4-14	4.8	720	170	0.69	33	0.073	0.6	5.2	0.93	0.16	41
8-5-15	4.6	590	210	0.88	31	0.076	1	5.4	1.3	0.18	40
11-1-16	4.2	770	89	4.5	21	0.24	0.75	4.5	0.82	0.17	32
11-2-17	4.3	670	83	2.6	27	0.12	0.68	5.1	1.2	0.19	37
11-3-18	4.6	680	120	0.69	34	0.074	0.89	5.5	1.7	0.18	43
11-4-19	4.5	790	140	0.82	40	0.094	0.91	6.9	0.91	0.18	50
11-5-20	4.3	730	82	1.4	34	0.12	0.77	6.4	1.3	0.19	44
12-1-21	4.7	730	75	0.71	36	0.073	0.89	6.1	1.6	0.23	46
12-2-22	4.5	700	67	1.6	32	0.091	0.74	6	0.89	0.21	41
12-3-23	4.5	1,000	71	0.66	46	0.074	0.97	7	1.4	0.22	57
12-4-24	4.4	970	110	1	37	0.078	0.64	5.3	1.5	0.17	46
12-5-25	4.4	900	63	1.1	39	0.082	0.75	4.2	1.7	0.19	47

Table 12.2 Mineral soil characteristics. <DL is below detection limit											
Subplot	**pH**	**Organic P (mg/kg)**	**Inorganic P (mg/kg)**	**Al (cmol+/kg)**	**Ca (cmol+/kg)**	**Fe (cmol+/kg)**	**K (cmol+/kg)**	**Mg (cmol+/kg)**	**Mn (cmol+/kg)**	**Na (cmol+/kg)**	**CEC (cmol+/kg)**
10-1-1	3.9	4.7	180	160	2.2	0.77	<DL	0.12	0.11	0.089	<DL
10-2-2	3.8	4.5	200	91	3.3	0.98	<DL	0.12	0.14	0.079	<DL
10-3-3	3.7	4.6	170	74	2.8	1.1	<DL	0.13	0.22	0.089	<DL
10-4-4	3.6	4.5	150	280	2.8	0.78	<DL	0.095	0.12	0.16	<DL
10-5-5	4.0	4.7	180	110	1.8	1.4	<DL	0.11	0.22	0.072	<DL
9-1-6	4.5	4.7	230	400	2.1	0.84	0.16	0.098	0.19	0.047	<DL
9-2-7	4.6	4.7	180	470	1.6	0.52	0.075	<DL	0.13	0.14	<DL
9-3-8	4.8	5.0	120	990	0.87	0.95	<DL	<DL	0.13	0.1	<DL
9-4-9	4.8	5.0	160	1,200	1.5	1.8	0.1	0.12	0.39	0.12	<DL
9-5-10	4.8	5.0	150	1,100	0.9	1.4	<DL	0.12	0.24	0.12	<DL
8-1-11	4.6	5.0	170	930	0.91	1.4	<DL	0.082	0.15	0.078	<DL
8-2-12	4.7	5.2	120	500	0.61	1	<DL	0.089	0.15	0.058	<DL
8-3-13	4.8	5.0	150	250	0.89	0.88	<DL	<DL	0.15	0.043	<DL
8-4-14	4.8	5.3	110	350	0.55	2.5	<DL	0.094	0.42	0.13	<DL
8-5-15	4.6	5.0	130	740	0.91	1.3	<DL	0.11	0.24	0.16	<DL
11-1-16	4.2	4.6	170	89	2.8	1.1	0.11	0.094	0.32	0.07	<DL
11-2-17	4.3	4.7	160	100	1.9	0.92	<DL	<DL	0.19	0.083	<DL
11-3-18	4.6	4.9	180	640	1.5	1.4	<DL	0.13	0.33	0.14	<DL
11-4-19	4.5	4.6	180	660	2.1	1.8	0.088	0.095	0.38	0.092	<DL
11-5-20	4.3	4.8	180	170	1.7	0.81	<DL	0.093	0.21	0.09	<DL
12-1-21	4.7	4.9	200	130	1.6	1.3	<DL	<DL	0.34	0.087	<DL
12-2-22	4.5	5.0	150	180	1.2	2.6	<DL	0.1	0.72	0.16	<DL
12-3-23	4.5	4.9	150	99	1.3	0.77	<DL	0.081	0.14	0.093	<DL
12-4-24	4.4	4.9	150	550	1.2	1.8	<DL	<DL	0.16	0.07	<DL
12-5-25	4.4	4.7	150	100	2	0.9	<DL	<DL	0.16	0.073	<DL

Appendix 7. Total Oven-dry Leaf Litter

Table 13.1
Total leaf litter (kg/ha) collected per species and per plot. Subplot code is: "plot number"- "subplot number within plot"- "subplot number out of total".

Plot	Alder (kg/ha)	Douglas-fir (kg/ha)	Total (kg/ha)
10-1-1	2449.0	-	2449.0
10-2-2	1736.0	-	1736.0
10-3-3	2304.8	-	2304.8
10-4-4	2621.4	-	2621.4
10-5-5	2590.9	-	2590.9
11-1-16	472.8	2530.9	3003.8
11-2-17	276.9	2787.3	3064.2
11-3-18	486.4	2188.5	2674.9
11-4-19	338.4	1027.5	1365.9
11-5-20	211.6	2566.2	2777.8
9-1-6	164.1	2875.0	3039.0
9-2-7	1074.0	1881.3	2955.3
9-3-8	1273.2	1389.0	2662.2
9-4-9	908.8	2514.5	3423.2
9-5-10	531.7	1621.3	2153.0
8-1-11	675.1	2326.2	3001.4
8-2-12	515.3	1609.7	2124.9
8-3-13	228.5	1950.8	2179.3
8-4-14	216.4	2574.4	2790.7
8-5-15	387.2	2644.7	3031.9
12-1-21	-	2225.4	2225.4
12-2-22	-	2670.8	2670.8
12-3-23	-	2501.3	2501.3
12-4-24	-	3274.8	3274.8
12-5-25	-	2573.0	2573.0

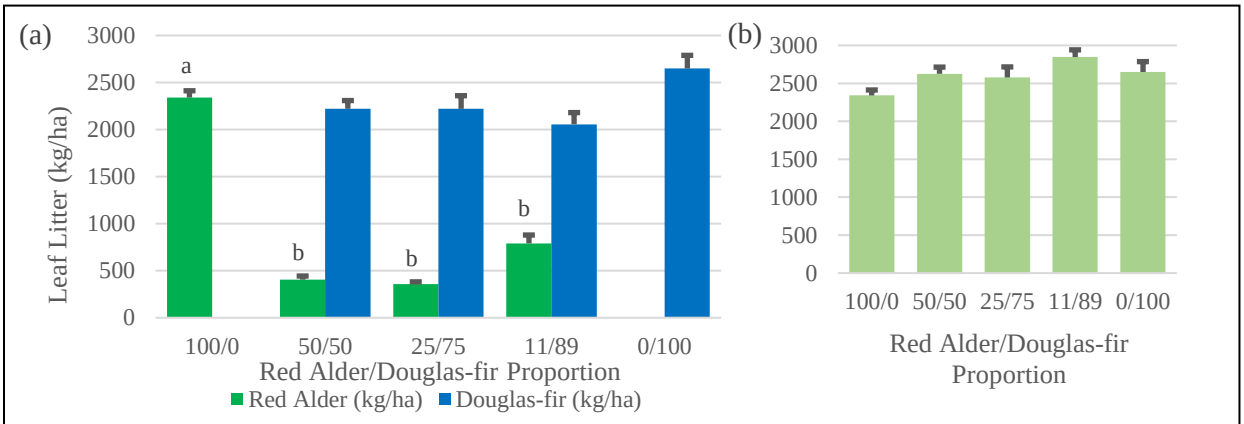

Figure 21. Average amount of leaf litter (kg/ha) collected by species (a) and total leaf litter (kg/ha) per plot (b). Letters indicate significance ($p<0.05$)

Appendix 8. Leaf Litter $\delta^{15}N$ values

Table 14.1
Leaf Litter $\delta^{15}N$ values for both species. Subplot code is: "plot number"- "subplot number within plot"- "subplot number out of total". Subplot 11-4-19 sample was excluded due to insufficient sample.

Subplots	Red Alder	Douglas-fir
10-1-1	-2.15	
10-2-2	0.16	
10-3-3	-0.54	
10-4-4	-0.97	
10-5-5	-3.05	
11-1-16	0.00	-0.88
11-2-17	-0.63	-0.51
11-3-18	-1.62	-2.80
11-4-19	N/A	-1.58
11-5-20	-1.77	1.01
9-1-6	-0.54	1.16
9-2-7	-0.67	-1.83
9-3-8	-1.21	-2.06
9-4-9	-2.34	-3.06
9-5-10	-2.26	-6.94
8-1-11	-1.76	-5.05
8-2-12	0.20	-3.23
8-3-13	-0.74	-1.31
8-4-14	-1.85	-3.59
8-5-15	-3.37	-3.44
12-1-21		-1.18
12-2-22		-1.87
12-3-23		-1.93
12-4-24		-3.18
12-5-25		0.16

Appendix 9. Leaf Litter Nutrients

Table 15
Leaf Litter nutrients. Subplot code is: "plot number"- "subplot number within plot"- "subplot number out of total". Dr = Red Alder. Fd = Douglas-fir. <DL is 'under detection limit'.

Subplot	Species	Al (mg/kg)	B (mg/kg)	Ca (mg/kg)	Cu (mg/kg)	Fe (mg/kg)	K (mg/kg)	Mg (mg/kg)	Mn (mg/kg)	Na (mg/kg)	P (mg/kg)	S (mg/kg)	Zn (mg/kg)	N (%)	C (%)	S (%)
10-1-1	Dr	62	<DL	8600	6	78	2100	1100	380	57	650	1100	30	1.36	50	0.093
10-2-2	Dr	71	<DL	8700	5.7	80	2800	1200	310	56	410	1100	26	1.43	50	0.100
10-3-3	Dr	89	<DL	9800	5.9	110	2700	1200	400	66	420	1100	29	1.47	50	0.100
10-4-4	Dr	83	<DL	8700	5.7	89	2600	1300	470	75	740	1100	28	1.32	50	0.091
10-5-5	Dr	60	11	9600	6	91	1800	1100	520	62	450	1200	35	1.58	50	0.100
9-1-6	Dr	69	<DL	8500	6.6	99	2600	1800	300	93	920	1200	25	1.59	49	0.108
9-2-7	Dr	73	12	12000	7.6	110	3100	2000	380	97	990	1300	33	1.66	49	0.119
9-3-8	Dr	110	10	12000	6.7	140	2900	1900	400	66	940	1100	24	1.58	49	0.100
9-4-9	Dr	84	<DL	12000	6.2	110	2100	2100	420	96	620	1100	18	1.41	49	0.092
9-5-10	Dr	72	<DL	10000	6.8	98	5600	1600	400	60	980	1100	26	1.51	48	0.098
8-1-11	Dr	110	15	13000	10	140	2800	2000	480	87	920	1200	35	1.55	48	0.110
8-2-12	Dr	58	11	10000	6.6	85	4300	1400	180	47	630	1200	16	1.55	49	0.105
8-3-13	Dr	81	12	12000	6.9	110	2500	1600	160	54	460	1200	21	1.54	49	0.080
8-4-14	Dr	110	12	14000	7	160	2900	2000	160	67	680	1300	20	1.75	48	0.118
8-5-15	Dr	84	14	13000	7.4	150	5900	2400	270	83	820	1300	26	1.52	47	0.109
11-1-16	Dr	71	11	11000	7	90	1600	1600	450	72	540	1100	29	1.49	49	0.100
11-2-17	Dr	72	11	11000	7.1	210	1900	1400	380	66	460	1200	37	1.49	50	0.103
11-3-18	Dr	120	14	13000	8.3	170	2300	1500	300	82	760	1100	28	1.56	49	0.103
11-4-19	Dr	99	15	16000	5.1	160	2700	2200	350	78	1300	1300	26	1.38	48	0.110
11-5-20	Dr	97	10	8900	5.2	140	3100	1700	320	70	550	1100	23	1.38	50	0.096
9-1-6	Fd	220	<DL	11000	1.6	71	3000	1500	520	81	850	900	15	0.65	51	0.073
9-2-7	Fd	160	<DL	12000	1.8	59	1100	1300	450	37	630	840	14	0.75	52	0.067
9-3-8	Fd	270	<DL	11000	1.7	160	1900	1200	550	43	820	820	14	0.65	52	0.068
9-4-9	Fd	250	<DL	9400	1.7	77	4300	1200	690	75	1400	970	20	0.66	52	0.077
9-5-10	Fd	230	11	19000	1.2	58	1200	1300	780	40	780	800	17	0.55	51	0.061
8-1-11	Fd	180	<DL	14000	1.2	63	1200	890	730	33	800	790	19	0.59	52	0.064
8-2-12	Fd	150	<DL	12000	1.7	60	1800	1000	330	47	590	850	10	0.68	52	0.067
8-3-13	Fd	150	<DL	9900	2.1	71	1900	1000	240	59	490	970	12	0.93	52	0.083
8-4-14	Fd	130	<DL	14000	1.7	73	1100	1200	210	50	480	810	9.3	0.73	52	0.063
8-5-15	Fd	180	<DL	12000	1.7	89	1700	1000	360	71	630	840	12	0.61	52	0.049
11-1-16	Fd	150	<DL	10000	1.9	54	1700	1300	830	92	470	930	12	0.89	52	0.076
11-2-17	Fd	150	<DL	10000	1.9	69	1500	1100	580	45	610	1100	12	1.07	52	0.082
11-3-18	Fd	220	<DL	10000	1.8	88	3000	1200	400	120	980	910	16	0.69	51	0.063
11-4-19	Fd	180	<DL	14000	1.8	86	1500	1000	380	45	660	810	13	0.70	51	0.060
11-5-20	Fd	160	<DL	12000	1.6	73	1600	1200	410	52	490	900	9.5	0.85	52	0.067
12-1-21	Fd	170	<DL	9800	2.1	91	2500	1200	400	86	490	1100	13	1.06	51	0.095
12-2-22	Fd	160	<DL	11000	1.9	84	2400	1300	270	57	530	1100	13	0.97	51	0.094
12-3-23	Fd	220	<DL	10000	2	110	2000	1300	350	47	540	1000	14	1.02	51	0.097
12-4-24	Fd	210	<DL	9800	2	120	1700	1100	260	53	580	940	13	0.88	52	0.075
12-5-25	Fd	180	<DL	14000	1.7	77	1400	950	510	49	450	1000	13	0.93	51	0.074

Appendix 10. Complete tree-ring $\delta^{15}N$ datasets

$\delta^{15}N$ values were assigned to the earliest ring in the sample. Samples were assigned in 2-year increments until measuring >6.5 mm, where then additional rings were adding until the length measured >6.5mm.

Table 16.1
100/0 Red Alder $\delta^{15}N$ values by tree-ring

Year	10-1-1	10-2-2	10-3-3	10-4-4	10-5-5
1994					
1995					
1996					
1997		-3.40		-6.18	
1998	-2.55				
1999		-2.73	-3.09		
2000	-1.76			-4.64	-3.43
2001		-2.31	-2.13		
2002	-1.67			-4.85	-3.09
2003		-1.25	-3.12		
2004	-1.33			-4.09	-2.66
2005		-1.84	-1.60		
2006	-1.58			-3.97	-2.52
2007		-1.81	-2.01		
2008	-1.12			-4.50	
2009		-1.67	-3.34		-2.24
2010	-1.10				
2011				-3.66	
2012	-2.37	-1.42	-1.74		
2013					
2014				-3.73	-2.40
2015					
2016	-2.33	-1.59	-1.39		
2017				-5.05	
2018			-2.96		
2019					
2020					
2021					

Table 16.2
50/50 Red Alder $\delta^{15}N$ values by tree-ring

Year	11-1-16	11-2-17	11-3-18	11-4-19	11-5-20
1994					
1995					
1996					
1997	-4.70				
1998					
1999	-3.25				
2000		-2.71			
2001	-2.27				
2002					
2003	-2.22	-2.17		-3.83	
2004					-3.62
2005	-2.65	-2.13		-2.25	
2006			-6.43		-3.60
2007	-2.17	-1.63		-5.26	
2008			-3.41		-3.67
2009		-1.39		-2.15	
2010			-3.18		-3.17
2011	-1.56			-1.62	
2012		-1.74	-3.69		-3.82
2013				-4.74	
2014			-2.60		
2015		-1.33		-2.75	
2016	-2.75		-2.71		
2017		-0.94		-2.75	-3.18
2018			-2.36		
2019					-3.21
2020					
2021					

Table 16.3 25/75 Red Alder $\delta^{15}N$ values by tree-ring					
Year	**9-1-6**	**9-2-7**	**9-3-8**	**9-4-9**	**9-5-10**
1994					
1995					
1996					
1997					
1998					
1999					
2000				-5.54	
2001	-3.38				
2002		-2.81		-4.13	
2003	-2.43		-2.77		
2004		-3.24		-2.92	
2005	-2.51		-4.26		
2006		-2.67		-3.10	-3.49
2007	-2.27		-2.22		
2008		-2.67			-3.03
2009	-2.03		-4.55	-2.98	
2010		-1.98			-3.20
2011	-2.08		-3.39	-2.42	
2012		-2.13			
2013	-2.59		-2.96		-3.11
2014				-3.29	
2015					
2016	-2.33	-2.33	-2.73	-3.17	-2.85
2017					
2018					
2019					
2020					
2021					

Table 16.4 11/89 Red Alder $\delta^{15}N$ values by tree-ring					
Year	**8-1-11**	**8-2-12**	**8-3-13**	**8-4-14**	**8-5-15**
1994					
1995					
1996					
1997					
1998				-5.16	-3.50
1999		-3.43	-4.79		
2000					
2001		-4.13	-4.01	-3.04	-3.13
2002					
2003	-3.45	-4.10	-3.42	-3.87	-3.44
2004					
2005		-3.70	-3.75	-4.16	-3.10
2006	-2.58				
2007		-3.96	-3.94	-3.71	-2.56
2008	-2.92				
2009		-3.98	-3.77	-3.11	-2.73
2010	-2.37				
2011		-3.44	-3.34	-2.13	-2.99
2012					
2013	-2.45	-4.07		-2.71	-2.87
2014			-3.87		
2015					
2016		-3.60	-2.06	-2.62	
2017					-2.96
2018			-3.52		
2019		-3.77			
2020					
2021					

Table 16.5 50/50 Douglas-fir $\delta^{15}N$ values by tree-ring					
Year	**11-1-16**	**11-2-17**	**11-3-18**	**11-4-19**	**11-5-20**
1994					
1995					
1996	-2.78		-2.13		
1997					
1998	-1.83	-0.96	-2.00		-3.45
1999				-2.41	
2000	-2.35		-1.97		-1.99
2001		-0.22		-1.56	
2002	-1.91		-1.47		-2.12
2003		-1.61		0.80	
2004	-2.16		-2.53		-2.7
2005		0.06		-3.17	
2006	-1.52		-1.82		-2.65
2007		-0.79		-1.62	
2008	-1.59		-1.67		-3.39
2009		-0.24		-2.21	
2010	-1.72		-2.45		-2.78
2011		0.82		-3.21	
2012	-2.11		-1.74		-3.08
2013		-0.08		-1.61	
2014			-1.75		-3.06
2015	-2.31			-1.40	
2016		-1.47	-2.18		
2017				-2.18	-2.42
2018	-0.72				
2019					-2.51
2020					
2021					

Table 16.6 25/75 Douglas-fir $\delta^{15}N$ values by tree-ring					
Year	**9-1-6**	**9-2-7**	**9-3-8**	**9-4-9**	**9-5-10**
1994					
1995			-2.55		-3.20
1996		-3.02			
1997	-3.93		-2.97	-6.69	
1998		-0.94			-2.40
1999	-3.70		-4.20	-4.69	
2000		-0.98			-3.15
2001	-4.15		-4.10	-4.11	
2002		-0.82			-2.58
2003	-4.18		-2.89	-3.12	
2004		-1.52			-2.68
2005	-3.90		-2.65	-4.26	
2006		-0.63			-3.13
2007	-4.02		-3.54	-3.22	
2008		-2.27			-2.06
2009	-3.90		-3.33	-3.32	
2010					-2.56
2011	-3.35	-2.10	-2.40	-1.68	
2012					-2.20
2013	-3.48	-1.70	-2.79	-3.41	
2014					-3.02
2015	-2.87	-2.38	-2.51	-3.65	
2016					
2017	-3.81			-3.89	-4.07
2018			-5.37		
2019	-3.94			-5.84	
2020					
2021					

Table 16.7 11/89 Douglas-fir $\delta^{15}N$ values by tree-ring					
Year	**8-1-11**	**8-2-12**	**8-3-13**	**8-4-14**	**8-5-15**
1994					
1995				-2.30	
1996	-5.52	-4.27			
1997			-2.20	-3.08	
1998	-3.98	-4.25			
1999				-4.03	
2000	-3.78	-4.48	-4.73		
2001				-1.68	
2002	-5.22	-4.72	-5.24		-3.20
2003				-4.03	
2004	-3.58	-4.05	-3.96		-3.80
2005				-1.16	
2006	-3.59	-4.57	-4.39		-3.72
2007				-2.44	
2008	-3.85	-5.23	-3.02		-2.88
2009				-1.22	
2010	-2.87	-3.95	-3.26		-3.78
2011				-0.70	
2012		-4.92	-3.33		-1.95
2013	-2.90			-1.22	
2014		-5.22	-2.34		-2.24
2015				-0.74	
2016	-3.51	-4.85	-4.41		-1.67
2017					
2018		-2.14		-1.04	-2.50
2019			-3.95		
2020					
2021					

Table 16.8 0/100 Douglas-fir $\delta^{15}N$ values by tree-ring					
Year	**12-1-21**	**12-2-22**	**12-3-23**	**12-4-24**	**12-5-25**
1994					
1995					
1996		-0.76			
1997				-2.92	
1998		-1.45			-3.42
1999	-1.44		-2.36	-3.92	
2000		-1.28			-2.39
2001	-2.75		-1.66	-3.89	
2002		-3.75			-3.24
2003	-2.64		-3.58	-3.90	
2004		-2.1			-3.45
2005	-4.11		-3.46	-2.98	
2006		-2.19			-2.21
2007	-2.59		-3.66	-2.36	
2008		-2.19			-2.94
2009	-4.39		-3.35	-4.70	
2010		-2.40			-2.88
2011	-3.54		-2.47	-3.42	
2012					-3.04
2013	-3.78	-1.52	-2.29	-2.16	
2014					-3.14
2015	-1.90		-1.85		
2016					-2.70
2017		-2.57		-2.61	
2018	-1.98		-3.35		
2019					-1.55
2020	-3.38				
2021					

Appendix 11. Complete tree-ring N% datasets

N% values were assigned to the earliest ring in the sample. Samples were assigned in 2-year increments until measuring >6.5 mm, where then additional rings were adding until the length measured >6.5mm.

Table 17.1
100/0 Red Alder N% values by tree-ring

Year	10-1-1	10-2-2	10-3-3	10-4-4	10-5-5
1994					
1995					
1996					
1997		0.07		0.22	
1998	0.14				
1999		0.15	0.09		
2000	0.09			0.16	0.18
2001		0.13	0.11		
2002	0.09			0.15	0.16
2003		0.11	0.11		
2004	0.09			0.14	0.15
2005		0.10	0.11		
2006	0.09			0.13	0.15
2007		0.09	0.12		
2008	0.10			0.15	
2009		0.10	0.13		0.14
2010	0.10				
2011				0.13	
2012	0.11	0.11	0.13		
2013					
2014				0.13	0.15
2015					
2016	0.13	0.11	0.13		
2017				0.18	
2018			0.15		
2019					
2020					
2021					

Table 17.2
50/50 Red Alder N% values by tree-ring

Year	11-1-16	11-2-17	11-3-18	11-4-19	11-5-20
1994					
1995					
1996					
1997	0.13				
1998					
1999	0.16				
2000		0.08			
2001	0.12				
2002					
2003	0.10	0.13		0.21	
2004					0.09
2005	0.11	0.14		0.16	
2006			0.25		0.21
2007	0.10	0.13		0.15	
2008			0.19		0.21
2009		0.12		0.13	
2010			0.14		0.20
2011	0.11			0.13	
2012		0.13	0.15		0.21
2013				0.15	
2014			0.13		
2015		0.13		0.15	
2016	0.11		0.13		
2017		0.12		0.19	0.20
2018			0.14		
2019					0.18
2020					
2021					

Table 17.3 25/75 Red Alder N% values by tree-ring					
Year	**9-1-6**	**9-2-7**	**9-3-8**	**9-4-9**	**9-5-10**
1994					
1995					
1996					
1997					
1998					
1999					
2000				0.24	
2001	0.16				
2002		0.13		0.18	
2003	0.14		0.18		
2004		0.15		0.17	
2005	0.14		0.19		
2006		0.12		0.17	0.19
2007	0.15		0.15		
2008		0.11			0.18
2009	0.16		0.16	0.14	
2010		0.10			0.24
2011	0.16		0.14	0.16	
2012		0.10			
2013	0.15		0.13		0.19
2014				0.17	
2015					
2016	0.16	0.10	0.14	0.20	0.22
2017					
2018					
2019					
2020					
2021					

Table 17.4 11/89 Red Alder N% values by tree-ring					
Year	**8-1-11**	**8-2-12**	**8-3-13**	**8-4-14**	**8-5-15**
1994					
1995					
1996					
1997					
1998				0.25	0.21
1999		0.09	0.14		
2000					
2001		0.14	0.14	0.25	0.18
2002					
2003	0.18	0.13	0.14	0.22	0.19
2004					
2005		0.13	0.13	0.26	0.20
2006	0.16				
2007		0.12	0.14	0.24	0.16
2008	0.13				
2009		0.15	0.14	0.23	0.17
2010	0.14				
2011		0.14	0.14	0.22	0.18
2012					
2013	0.18	0.13		0.20	0.19
2014			0.13		
2015					
2016		0.13	0.11	0.24	
2017					0.22
2018			0.15		
2019		0.14			
2020					
2021					

Table 17.5 50/50 Douglas-fir N% values by tree-ring. Outliers (+/- 3 SD) in parentheses					
Year	**11-1-16**	**11-2-17**	**11-3-18**	**11-4-19**	**11-5-20**
1994					
1995					
1996	0.13		0.04		
1997					
1998	0.06	0.15	0.04		(0.24)
1999				0.04	
2000	0.06		0.04		0.06
2001		0.04		0.03	
2002	0.04		0.04		0.05
2003		0.03		0.04	
2004	0.05		0.04		0.04
2005		0.03		0.04	
2006	0.04		0.04		0.04
2007		0.03		0.05	
2008	0.04		0.04		0.04
2009		0.03		0.05	
2010	0.04		0.05		0.05
2011		0.04		0.05	
2012	0.04		0.04		0.05
2013		0.03		0.04	
2014			0.05		0.06
2015	0.11			0.04	
2016		0.04	0.05		
2017				0.05	0.07
2018	0.04		(0.21)		
2019				(0.37)	0.07
2020					
2021					

Table 17.6 25/75 Douglas-fir N% values by tree-ring. Outliers (+/- 3 SD) in parentheses					
Year	**9-1-6**	**9-2-7**	**9-3-8**	**9-4-9**	**9-5-10**
1994					
1995			0.04		0.05
1996		0.12			
1997	0.04		0.03	0.04	
1998		0.03			0.07
1999	0.03		0.03	0.03	
2000		0.03			0.04
2001	0.03		0.03	0.03	
2002		0.03			0.04
2003	0.04		0.03	0.03	
2004		0.03			0.04
2005	0.04		0.03	0.03	
2006		0.04			0.05
2007	0.03		0.03	0.03	
2008		0.04			0.05
2009	0.03		0.03	0.04	
2010					0.04
2011	0.04	0.04	0.03	0.03	
2012					0.05
2013	0.03	0.03	0.03	0.04	
2014					0.04
2015	(0.23)	0.04	0.04	0.04	
2016					
2017	0.04			0.05	(0.12)
2018			(0.11)		
2019	0.06			(0.16)	
2020					
2021					

Table 17.7
11/89 Douglas-fir N% values by tree-ring. Outliers (+/- 3 SD) in parentheses

Year	8-1-11	8-2-12	8-3-13	8-4-14	8-5-15
1994					
1995				0.05	
1996	0.04	(0.15)			
1997			0.05	0.03	
1998	0.04	0.04			
1999				0.03	
2000	0.04	0.03	0.04		
2001				0.03	
2002	0.03	0.03	0.04		0.06
2003				0.03	
2004	0.04	0.03	0.04		0.04
2005				0.03	
2006	0.04	0.03	0.03		0.05
2007				0.04	
2008	0.04	0.03	0.04		0.05
2009				0.04	
2010	0.03	0.03	0.05		0.05
2011				0.04	
2012		0.04	0.05		0.05
2013	0.04			0.04	
2014		0.04	0.04		0.05
2015				0.04	
2016	0.04	0.04	0.04		0.06
2017					
2018		0.03		(0.10)	0.06
2019			0.11		
2020					
2021					

Table 17.8
0/100 Douglas-fir N% values by tree-ring. Outliers (+/- 3 SD) in parentheses

Year	12-1-21	12-2-22	12-3-23	12-4-24	12-5-25
1994					
1995					
1996		0.07			
1997				0.05	
1998		0.03			0.05
1999	(0.07)		0.05	0.04	
2000		0.03			0.05
2001	0.03		0.04	0.04	
2002		0.03			0.04
2003	0.03		0.04	0.04	
2004		0.03			0.05
2005	0.03		0.04	0.04	
2006		0.03			0.04
2007	0.03		0.04	0.04	
2008		0.03			0.05
2009	0.03		0.05	0.04	
2010		0.03			0.05
2011	0.03		0.04	0.05	
2012					0.05
2013	0.03	0.03	0.04	0.04	
2014					0.06
2015	0.04		0.05		
2016					(0.12)
2017		0.04		0.12	
2018	0.03		0.10		
2019					0.05
2020	0.03				
2021					

Appendix 12. Trends in tree-ring N%

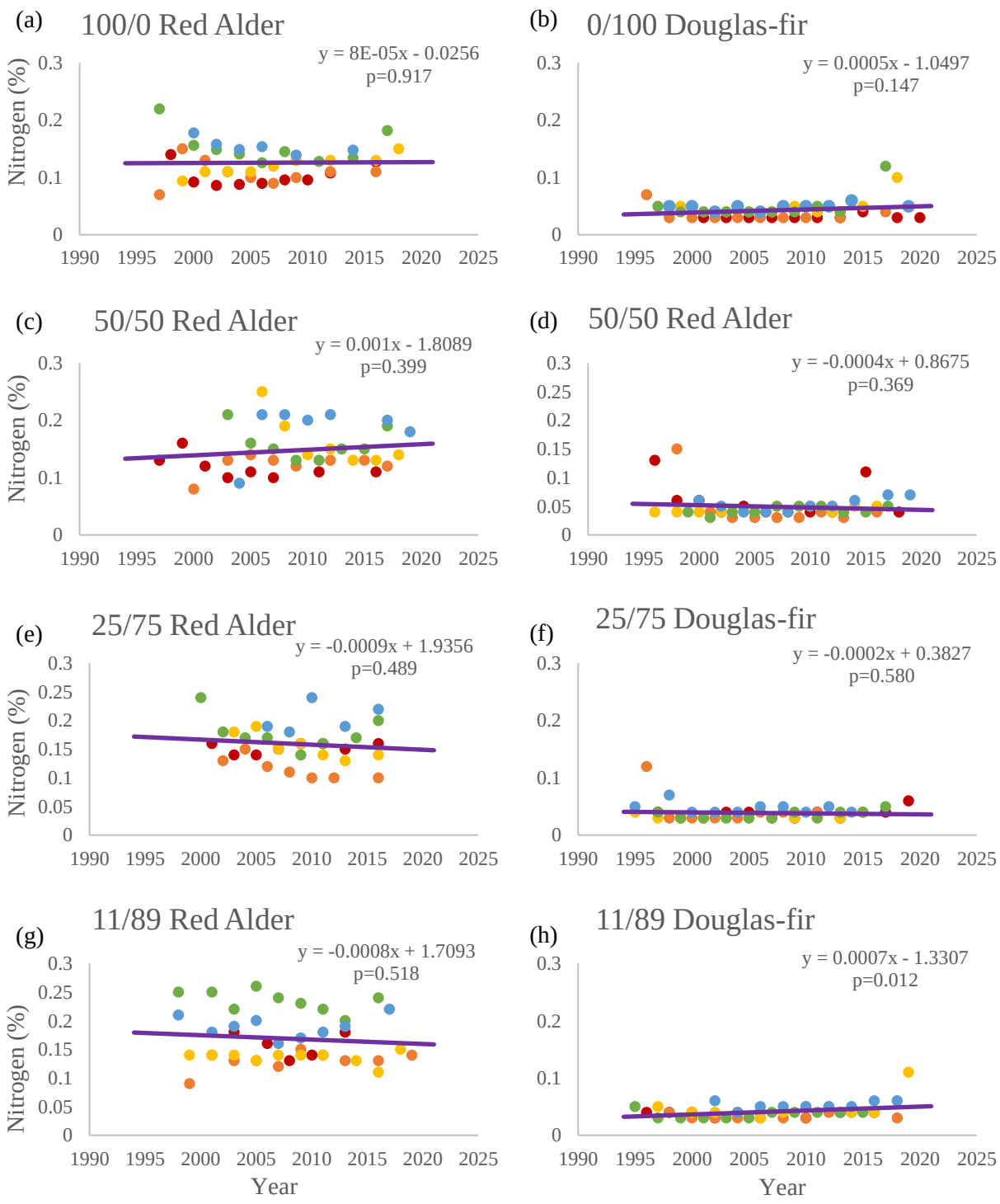

Figure 22. Trends in tree-ring N (‰) in 5 plots and 2 tree species (a-h) over the 27-year growth. Each plot contained 5 cored trees shown in different colours. For each core segment, the representative point was plotted on the first year of the ring.

Appendix 13. AIC Model Comparisons for tree-ring $\delta^{15}N$

Table 18.1
AIC Comparison Table for 100/0 plot Red Alder tree-ring $\delta^{15}N$ values over time

Models
lmer.10ra.lin: $\delta^{15}N \sim year.cr + (1|tree)$
lmer.10ra.par: $\delta^{15}N \sim year.cr + year.cr^2 (1|tree)$

Model	AIC	BIC	P-value
lmer.10ra.lin	107.05	114.00	
lmer.10ra.par	101.14	109.83	0.00491**

Table 18.2
AIC Comparison Table for 50/50 plot Red Alder tree-ring $\delta^{15}N$ values over time

Models
lmer.11.lin: $\delta^{15}N \sim year.cr + (1|tree)$
lmer.11.par: $\delta^{15}N \sim year.cr + year.cr^2 (1|tree)$

Model	AIC	BIC	P-value
lmer.11ra.lin	119.58	126.13	1
lmer.11ra.par	129.66	137.85	

Table 18.3
AIC Comparison Table for 25/75 plot Red Alder tree-ring $\delta^{15}N$ values over time

Models
lmer.9ra.lin: $\delta^{15}N \sim year.cr + (1|tree)$
lmer.9ra.par: $\delta^{15}N \sim year.cr + year.cr^2 (1|tree)$

Model	AIC	BIC	P-value
lmer.9ra.lin	83.69	89.92	1
lmer.9ra.par	89.20	96.98	

Table 18.4
AIC Comparison Table for 25/75 plot Red Alder tree-ring $\delta^{15}N$ values over time

Models
lmer.8ra.lin: $\delta^{15}N \sim year.cr + (1|tree)$
lmer.8ra.par: $\delta^{15}N \sim year.cr + year.cr^2 (1|tree)$

Model	AIC	BIC	P-value
lmer.8ra.lin	85.83	92.87	1
lmer.8ra.par	95.83	104.64	

Table 18.5
AIC Comparison Table for 50/50 plot Douglas-fir tree-ring $\delta^{15}N$ values over time

Models
lmer.11df.lin: $\delta^{15}N \sim year.cr + (1|tree)$
lmer.11df.par: $\delta^{15}N \sim year.cr + year.cr^2 (1|tree)$

Model	**AIC**	**BIC**	**P-value**
lmer.11df.lin	194.74	202.62	1
lmer.11df.par	200.49	210.34	

Table 18.6
AIC Comparison Table for 25/75 plot Douglas-fir tree-ring $\delta^{15}N$ values over time

Models
lmer.9df.lin: $\delta^{15}N \sim year.cr + (1|tree)$
lmer.9df.par: $\delta^{15}N \sim year.cr + year.cr^2 (1|tree)$

Model	**AIC**	**BIC**	**P-value**
lmer.9df.lin	170.26	178.43	1
lmer.9df.par	172.59	182.81	

Table 18.7
AIC Comparison Table for 11/89 plot Douglas-fir tree-ring $\delta^{15}N$ values over time

Models
lmer.8df.lin: $\delta^{15}N \sim year.cr + (1|tree)$
lmer.8df.par: $\delta^{15}N \sim year.cr + year.cr^2 (1|tree)$

Model	**AIC**	**BIC**	**P-value**
lmer.8df.lin	161.83	169.78	1
lmer.8df.par	173.47	183.41	

Table 18.8
AIC Comparison Table for 0/100 plot Douglas-fir tree-ring $\delta^{15}N$ values over time

Models
lmer.12df.lin: $\delta^{15}N \sim year.cr + (1|tree)$
lmer.12df.par: $\delta^{15}N \sim year.cr + year.cr^2 (1|tree)$

Model	**AIC**	**BIC**	**P-value**
lmer.12df.lin	144.79	152.60	1
lmer.12df.par	150.21	159.97	

Appendix 14. AIC Model Comparisons for tree-ring N%

Table 19.1
AIC Comparison Table for 100/0 plot Red Alder tree-ring N% values over time

Models
lmer.10ra.lin: N% ~ year.cr + (1 | tree)
lmer.10ra.par: N% ~ year.cr + year.cr^2 + (1 | tree)

Model	AIC	BIC	P-value
lmer.10ra.lin	-163.60	-156.65	1
lmer.10ra.par	-155.29	-146.60	

Table 19.2
AIC Comparison Table for 50/50 plot Red Alder tree-ring N% values over time

Models
lmer.11.lin: N% ~ year.cr + (1 | tree)
lmer.11.par: N% ~ year.cr + year.cr^2 + (1 | tree)

Model	AIC	BIC	P-value
lmer.11ra.lin	-119.22	-112.67	1
lmer.11ra.par	-101.58	-93.39	

Table 19.3
AIC Comparison Table for 25/75 plot Red Alder tree-ring N% values over time

Models
lmer.9ra.lin: N% ~ year.cr + (1 | tree)
lmer.9ra.par: N% ~ year.cr + year.cr^2 + (1 | tree)

Model	AIC	BIC	P-value
lmer.9ra.lin	-131.52	-125.30	1
lmer.9ra.par	-120.53	-112.75	

Table 19.4
AIC Comparison Table for 25/75 plot Red Alder tree-ring N% values over time

Models
lmer.8ra.lin: N% ~ year.cr + (1 | tree)
lmer.8ra.par: N% ~ year.cr + year.cr^2 + (1 | tree)

Model	AIC	BIC	P-value
lmer.8ra.lin	-181.09	-174.04	1
lmer.8ra.par	-164.30	-155.50	

Table 19.5
AIC Comparison Table for 50/50 plot Douglas-fir tree-ring N% values over time

Models
lmer.11df.lin: N% ~ year.cr + (1 | tree)
lmer.11df.par: N% ~ year.cr + year.cr^2 + (1 | tree)

Model	**AIC**	**BIC**	**P-value**
lmer.11df.lin	-211.71	-203.98	1
lmer.11df.par	-203.56	-193.90	

Table 19.6
AIC Comparison Table for 25/75 plot Douglas-fir tree-ring N% values over time

Models
lmer.9df.lin: N% ~ year.cr + (1 | tree)
lmer.9df.par: N% ~ year.cr + year.cr^2 + (1 | tree)

Model	**AIC**	**BIC**	**P-value**
lmer.9df.lin	-269.28	-261.40	1
lmer.9df.par	-260.59	-250.74	

Table 19.7
AIC Comparison Table for 11/89 plot Douglas-fir tree-ring N% values over time

Models
lmer.8df.lin: N% ~ year.cr + (1 | tree)
lmer.8df.par: N% ~ year.cr + year.cr^2 + (1 | tree)

Model	**AIC**	**BIC**	**P-value**
lmer.8df.lin	-286.06	-278.26	1
lmer.8df.par	-278.37	-268.62	

Table 19.8
AIC Comparison Table for 0/100 plot Douglas-fir tree-ring N% values over time

Models
lmer.12df.lin: N% ~ year.cr + (1 | tree)
lmer.12df.par: N% ~ year.cr + year.cr^2 + (1 | tree)

Model	**AIC**	**BIC**	**P-value**
lmer.12df.lin	-243.27	-235.62	
lmer.12df.par	-232.78	-223.22	0.6435

Appendix 15. AIC Model Comparisons for tree-ring $\delta^{15}N$ by Species

Table 20.1 **AIC Comparison Table for all Red Alder tree-ring $\delta^{15}N$ values over time**		
Models lmer.ra.lin: $\delta^{15}N \sim$ year.cr + (1|tree) lmer.ra.par: $\delta^{15}N \sim$ year.cr + year.cr^2 (1|tree)		
Model	**AIC**	**P-value**
lmer.ra.lin	377.25	
lmer.ra.par	377.66	1

Table 20.2 **AIC Comparison Table for all Douglas-fir tree-ring $\delta^{15}N$ values over time**		
Models lmer.df.lin: $\delta^{15}N \sim$ year.cr + (1 | tree) lmer.df.par: $\delta^{15}N \sim$ year.cr + year.cr^2 + (1 | tree)		
Model	**AIC**	**P-value**
lmer.df.lin	624.71	
lmer.df.par	636.74	1

Burnham & Anderson (2004) outline a method of model determination for when model AICs differ by small amount (Eq. 2). In this method, AIC_i represents the model of interest and AIC_{min} represents the model with the lowest AIC. Burnham & Anderson (2004) state that models having $\Delta_i \leq 2$ have substantial support, those in which $4 \leq \Delta_i \leq 7$ have moderate support, and models having $\Delta_i > 10$ have almost no support.

$$Eq\ 2.\ \Delta_i = AIC_i - AIC_{min}$$

Appendix 16. Tree-ring $\delta^{15}N$ over time for Douglas-fir

Figure 23. Douglas-fir tree-ring $\delta^{15}N$ (‰) in 5 plots over the 27-year growth period. Each plot contained 5 cored trees. For each core segment, the representative point was plotted on the first year of the ring.

Appendix 17. Tree-ring $\delta^{15}N$ and N% Comparisons by Plot

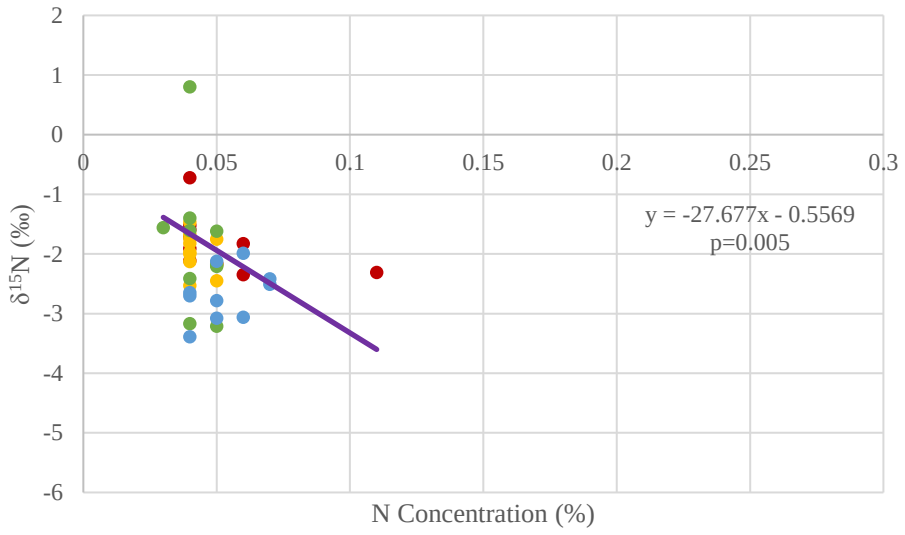

Figure 24. Tree-ring $\delta^{15}N$ and N% Comparisons for Plot 50/50 Douglas-fir. Five individual core trees indicated by differing colours

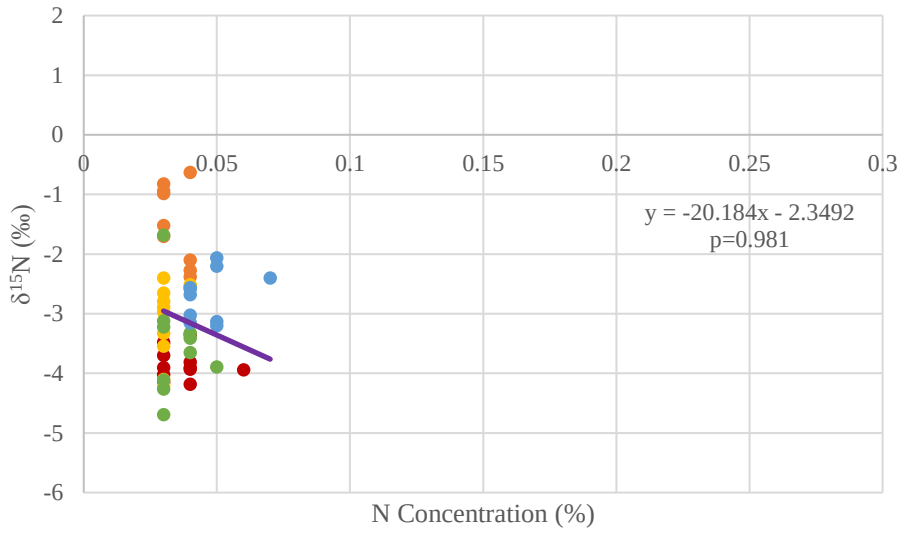

Figure 25. Tree-ring $\delta^{15}N$ and N% Comparisons for Plot 25/75 Douglas-fir. Five individual core trees indicated by differing colours

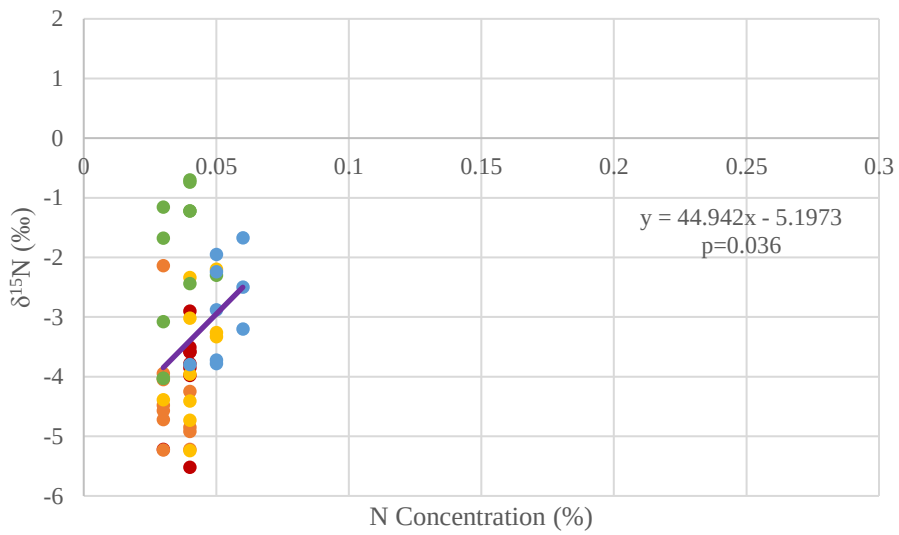

Figure 26. Tree-ring $\delta^{15}N$ and N% Comparisons for Plot 11/89 Douglas-fir. Five individual core trees indicated by differing colours

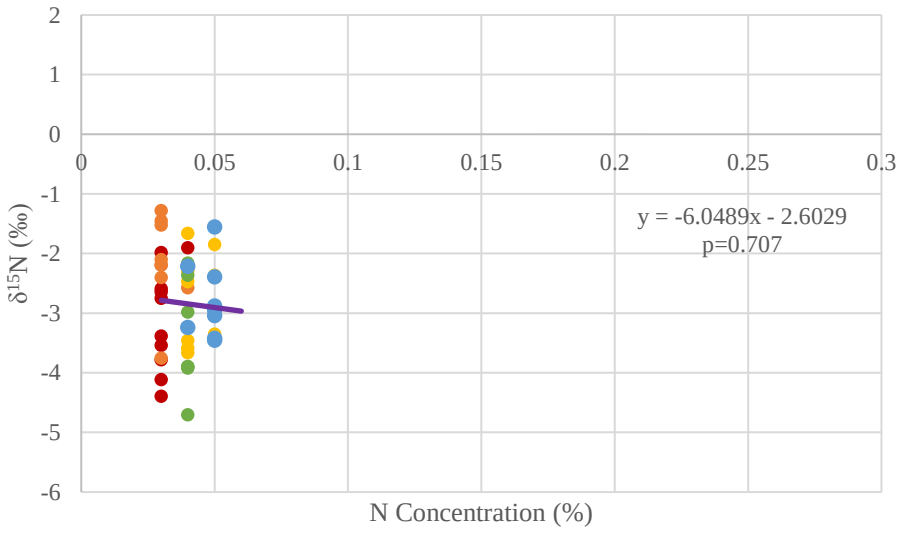

Figure 27. Tree-ring $\delta^{15}N$ and N% Comparisons for Plot 0/100 Douglas-fir. Five individual core trees indicated by differing colours

Appendix 18. Douglas-fir Tree-ring $\delta^{15}N$ and N% Comparisons

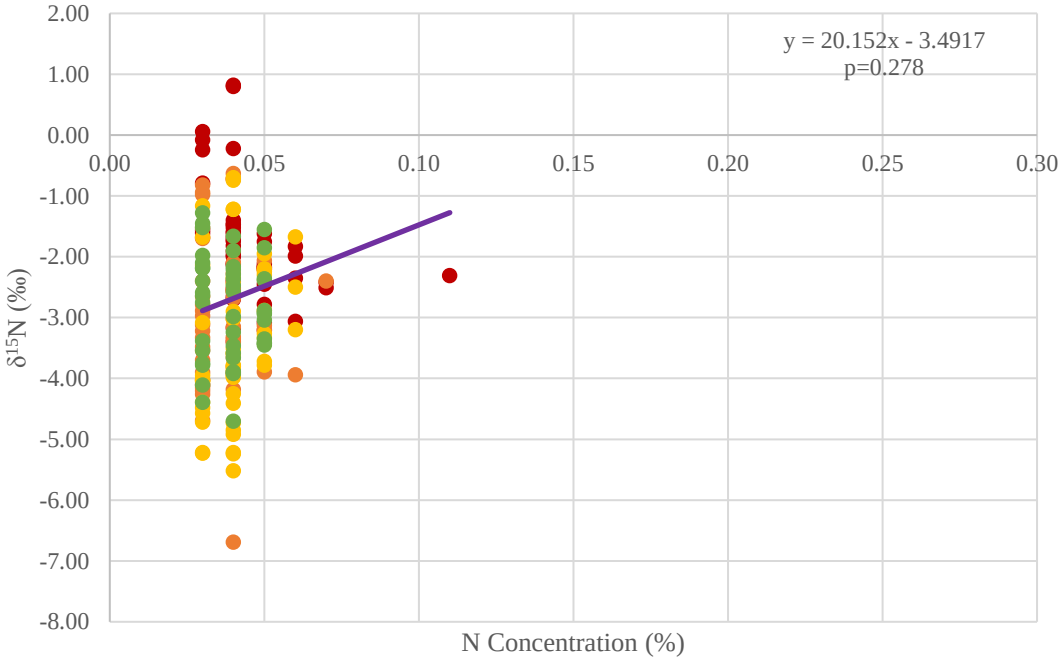

Figure 28. Tree-ring $\delta^{15}N$ versus N% for Douglas-fir overall. Four plots indicated by different colours. Each plot contains five core trees.

Appendix 19. Leaf Litter $\delta^{15}N$ and N% Comparisons by Species

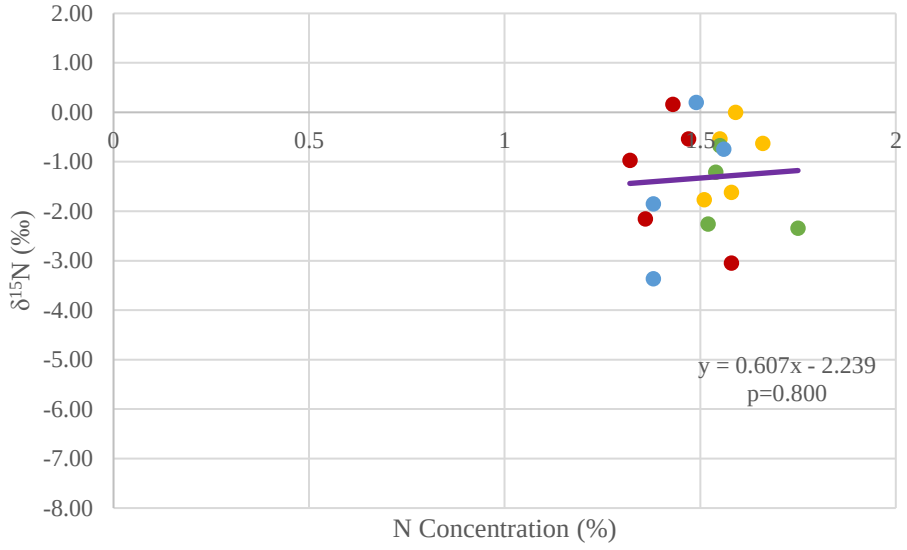

Figure 29. Leaf Litter $\delta^{15}N$ and N% Comparisons for Red Alder overall. Four plots indicated by different colours.

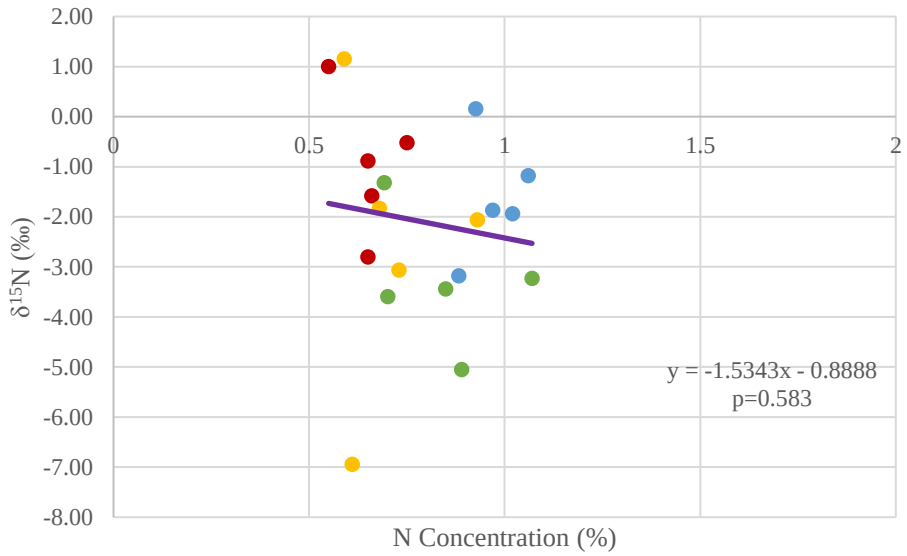

Figure 30. Leaf Litter $\delta^{15}N$ and N% Comparisons for Douglas-fir overall. Four plots indicated by different colours.