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Basal area growth, carbon isotope discrimination, and intrinsic water use efficiency after fertilization of Douglas-fir in the Oregon Coast Range

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ABSTRACT

Many hectares of intensively managed Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) stands in western North America are fertilized with nitrogen (N) to increase growth rates, but only about ⅔ of all stands respond. Understanding the mechanisms of response facilitates prioritization of stands for treatment. The primary objective of this study was to test the hypothesis that the short-term basal area growth response to a single application of 224 kg N ha^{-1} as urea was associated with reduced stable carbon isotope discrimination ($\Delta^{13}C$) and increased intrinsic water use efficiency (*i*WUE) in a 20-yr-old plantation of Douglas-fir in the Oregon Coast Range, USA. Increment cores were measured to estimate earlywood, latewood, and total basal area increment over a time series from 1997 to 2015. Stable carbon isotope discrimination and *i*WUE were estimated using earlywood and latewood stable carbon isotope concentrations in tree-ring holocellulose starting seven years before fertilization in early 2009 and ending seven years after treatment. A highly significant ($p < 0.01$) interaction effect between fertilization treatment and year was found for total basal area growth and earlywood basal area increment. Specifically, fertilized trees showed significant responses ($p < 0.05$) in total basal area growth and earlywood basal area increment in the first (2009) and second (2010) growing seasons after fertilization in 2009. A marginally significant ($p < 0.10$) fertilization effect was found for latewood basal area increment only in the first growing season after treatment. A significant treatment × year interaction was also found for $\Delta^{13}C$ and *i*WUE in earlywood and latewood. Fertilization significantly reduced earlywood $\Delta^{13}C$ and increased earlywood *i*WUE in the first and second growing seasons after fertilization. Only a marginally significant fertilization effect was detected for latewood $\Delta^{13}C$ and *i*WUE in the second growing season after treatment. Previous studies of N fertilization of Douglas-fir forests have reported consistently increased growth and *i*WUE on low productivity sites treated with relatively high fertilization rates. This study suggested that these responses can also be observed on highly productive sites despite their lower frequency and apparently shorter duration. Other key mechanisms driving growth responses appear less important than *i*WUE, including an increase in LAI and shift from belowground to aboveground carbon allocation.

1. Introduction

Nitrogen (N) is the most important limiting nutrient in terrestrial ecosystems in most of the world (Field and Mooney, 1986; LeBauer and Treseder, 2008), including Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) ecosystems of the U.S. Pacific Northwest (PNW) and southwestern British Columbia (Miller et al., 1986; Gessel et al., 1990; Brix, 1991; Chappell et al., 1991; Hanley et al., 2006; Perakis and Sinkhorn, 2011). Nitrogen can limit plant growth on a given site for several reasons: (1) small N pools; (2) large N pools but low availability; (3) rapid leaching of available N below the root zone (particularly nitrate, NO_3^-); and (4) conversion of nitrate to gas by denitrifying bacteria (Field and Mooney, 1986; Binkley and Fisher, 2013). The importance of N to optimal

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physiological functioning of plants is directly related to its role as a fundamental component of amino acids, proteins, nucleic acids, and enzymes (including Rubisco), with particularly high concentrations in foliage as part of the photosynthetic apparatus (Field and Mooney, 1986; Binkley and Fisher, 2013).

Due to this key role of N, a positive relationship between photosynthetic rate and leaf N content has been reported for a wide variety of plant species including Douglas-fir (Brix, 1981; Field and Mooney, 1986; Mitchell and Hinckley, 1993; Ripullone et al., 2003; Manter et al., 2005; Duursma and Marshall, 2006). This relationship, however, requires sufficiently high intensity of incident photosynthetically active radiation (PAR; Brix, 1971; Tarvainen et al., 2016). The limitation that N availability places on forest productivity has been demonstrated repeatedly by N fertilization experiments. In one Douglas-fir field trial at Shawnigan Lake, British Columbia, leaf N concentrations of 1.74% shortly after fertilization increased photosynthetic rates by approximately 30% over that measured at leaf N concentrations of 1.0% in unfertilized plots (Brix, 1981). Although foliage N concentrations returned to pre-fertilization levels within 3–5 years after fertilization, a concurrent but slower increase in total leaf area (and total canopy N) contributed to longer-term growth responses relative to unfertilized control plots (Brix, 1981). Concurrent shifts in carbon allocation from belowground to aboveground tree components have also been required to explain the full magnitude of stem growth responses to fertilization (Gower et al., 1994; Lim et al., 2015). The aggregate response to N fertilization is therefore commonly conceived of as an initial increase in photosynthetic rate and growth efficiency (biomass or stem volume growth per unit of initial foliage), grading into shifts in carbon allocation and a longer term phase of elevated leaf area index (Brix, 1983; Lim et al., 2015).

Experimental research on operational N fertilization of Douglas-fir in the PNW began in the early 1950s in mid-rotation natural stands, generally with additions of ammonium nitrate, urea, or ammonium sulfate, and sometimes in combination with other elements such as P, K, and Ca in the form of lime (Gessel and Walker, 1956; Gessel and Shareeff, 1957). Observed growth responses to N fertilization at Shawnigan Lake and on larger plot networks in the Douglas-fir region have led to widespread operational N applications in Douglas-fir (Peterson and Hazard, 1990), amounting to 50,000–55,000 ha treated annually in the late 1980s through the 1990s (Chappell et al., 1991).

Despite this widespread N application and favorable average growth response in the PNW, it has long been recognized that approximately one third of fertilized Douglas-fir stands do not respond to N fertilization. In the current operational environment, it has become essential to optimize the economic and environmental performance of forest fertilization by applying N to only those stands or sites that can uptake the added N (preventing leaching and degradation of surface water) and accelerate growth (generating positive economic returns).

The Giustina fertilization trials in Douglas-fir were initiated to validate and refine the current conceptual model of mechanisms driving growth responses to N fertilization, with the ultimate goal of developing a site evaluation system derived from these mechanisms to provide improved predictions of site-specific growth responses, particularly on higher quality sites where responses are more erratic. Detailed physiological studies have long been needed, but are difficult to implement on a regional basis. However, analysis of carbon isotope ratios in annual growth rings before and after fertilization offer considerable promise for inferring physiological mechanisms driving growth responses to silvicultural treatments at a scale directly transferrable to operational prescriptions (Brooks and Coulombe, 2009; Brooks and Mitchell, 2011; Wei et al., 2014).

Stable isotopes of elements can serve as integrators or tracers of many key physical and biological processes (Sulzman, 2007; Dawson et al., 2002). Carbon fixation during the process of photosynthesis, for example, discriminates against the heavier stable isotope of carbon (^{13}C) in favor of the lighter isotope (^{12}C), but the intensity of this discrimination depends on environmental conditions such as vapor pressure deficit and soil-water availability, as they affect physiological responses like stomatal conductance. Therefore, the carbon stable isotopic composition of C_3 plant tissues is often expressed as carbon isotope discrimination ($\Delta^{13}C$), a parameter that has often been used to track how environmental conditions affect leaf gas exchange (Farquhar et al., 1982; Farquhar et al., 1989; Dawson et al., 2002; Marshall et al., 2007; Voelker et al., 2016). Carbon isotope discrimination is typically employed as a proxy for a plant's intrinsic water-use efficiency (*i*WUE), or ratio of net assimilation (A) to stomatal conductance (g_s).

Tree-rings are composed of annual increments of xylem tissue, so increment cores can be used to retrospectively estimate past diameter or basal area growth (Phipps and Whiton, 1988; Biondi and Qeadan, 2008; Voelker et al., 2008; Heres et al., 2012; Voelker et al., 2014). Furthermore, carbon stable isotopes in the tree rings record a canopy-integrated signal of annual leaf gas-exchange (Francey and Farquhar, 1982; Brooks and Coulombe, 2009; Gessler et al., 2014; Voelker et al., 2014). To the extent that growth responses to N fertilization are influenced by A/g_s, differences in carbon isotope discrimination should lend insight into the mechanisms of fertilization response. For example, Brooks and Coulombe (2009) measured tree-ring growth and both carbon and oxygen stable isotopes in response to three levels of N fertilization (157, 314, 417 kg ha^{-1}) in an 85 year-old Douglas-fir plantation located at Wind River Experimental Forest in Washington. The annual basal area increment (BAI) of these trees peaked in the third growing season after fertilization (1966), after which the values decreased slowly back to control-levels over the next 20 years. In response to N fertilization, $\Delta^{13}C$ was reduced and *i*WUE was increased in both earlywood and latewood components, but only for three years before returning to pretreatment levels. This short-term $\Delta^{13}C$ response was attributed to an increase in leaf N concentration and photosynthetic rate per unit leaf area, while longer-term growth responses were attributed to the increase in total leaf area observed in many other studies (Brix, 1983; Vose and Allen, 1988). Brooks and Mitchell (2011) found similar responses to N fertilization (448 kg N ha^{-1} as urea) in a 41 year-old Douglas-fir plantation located at Shawnigan Lake, Vancouver Island, BC. The direct effect of N on tree growth lasted six years after application, but $\Delta^{13}C$ was only reduced for the first few years, again related to an increase in leaf N and photosynthetic rate, prior to a subsequent increase in leaf area, which sustained the longer-term increase in growth. In contrast, Balster et al. (2009) did not find decreased $\Delta^{13}C$ in fertilized Douglas-fir plantations in the U. S. northern Rocky Mountains, despite a significant growth response to treatment. They speculated that their relatively coarse 3-yr growth period may have prevented detection of shorter-term response of $\Delta^{13}C$, and that increases in leaf area were largely responsible for the increases in growth, as demonstrated by previous analyses (Balster and Marshall, 2000).

Earlier studies of growth, $\Delta^{13}C$, and *i*WUE responses to N fertilization in Douglas-fir forests from the PNW region were conducted on lower productivity sites with treatments that exceeded standard industry practice for plantation management (Brooks and Coulombe, 2009; Brooks and Mitchell, 2011). The goal of the Giustina Fertilization Trials was to test the generality of apparent mechanisms of Douglas-fir response to N fertilization. Of particular interest was the degree of consistency in mechanisms at sites with much higher site index than either Shawnigan Lake or Wind River,