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The importance of seasonal temperature and moisture patterns on growth of Douglas-fir in western Oregon, USA

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ABSTRACT

Douglas-fir growth in the Pacific Northwest is thought to be water limited. However, discerning the relative influence of air temperature and plant available soil water (W) on growth is difficult because they interact with each other, with other climate factors and with the inherent seasonal timing of cambial activity. Douglas-fir growth response to air temperature and W patterns during the growing season was examined using time series regression analysis of dendrometer data collected at approximately four-week intervals from 1998 through 2009. Five study sites were located in mature forest stands along an elevation gradient from the Pacific coast to the west slope of the Cascade Mountains (~1200 m) in Oregon, USA. Maximum daily air temperature (T) and W were similar in relative importance to tree growth at four of the five sites. W was substantially more important at one site. Growth rate increased with T to an optimum (T_{opt}) and decreased with higher T. At the two drier sites T and W affected growth interactively in that T_{opt} decreased with decreasing W. We conclude that both T and W affect growth and that T consistently limits growth at three of the five sites and at all sites in years with above average summer temperature. Should climate change result in hotter summers in the region as predicted by climate models, we suggest that Douglas-fir will experience progressive temperature limitation.

1. Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is an ecologically and economically important tree species in forests of the North American Pacific Northwest (PNW) (Waring and Franklin, 1979). The species is adapted to a wide range of climatic conditions from moderate winter temperatures and ample precipitation near the coast to cold winters and dry summers at higher elevations inland (Zhang and Hebda, 2004). It is the major timber species in the region constituting approximately 77% of the saw timber stumpage volume and 87% of sales in the states of Washington and Oregon in 2005 (Howard, 2007). Over 50% of the carbon in aboveground biomass in the state of Oregon is stored in Douglas-fir (Donnegan et al., 2008) making it a key species for the practice of carbon offset forestry (Ryan et al., 2010).

Annual summer drought, which typically lasts from July to October, plays a major role in the functioning of PNW forests (Waring and Franklin, 1979). Shoot elongation and most wood formation occur before the onset of summer drought and the depletion of soil moisture (Emmingham, 1977; Grotta et al., 2005; Li and Adams, 1994). Global climate change (GCC) could alter the onset, magnitude and duration of the summer drought. Climate model simulations suggest that by mid-century the PNW will experience hotter, drier summers and warmer, wetter winters with substantial decreases in snowpack (Mote and Salathé, 2010). Such climate changes will affect growth and reproduction of Douglas-fir in the region both positively and negatively depending on elevation and site conditions (Littell et al., 2010). Changes in the timing and magnitude of summer drought will alter patterns of temperature and moisture within the growing season. Understanding the relative importance of temperature and soil moisture in the context of seasonal timing of Douglas-fir growth will improve assessments of GCC effects on forest productivity and carbon sequestration.

Soil moisture during summer is a primary factor limiting Douglas-fir growth in the PNW (Brubaker, 1980; Zhang and Hebda, 2004). Radial growth in Douglas-fir can be limited by low temperature at the highest, snowiest elevations, but growth is often limited by moisture in places that develop modest snowpack (Case and Peterson, 2005; Littell et al., 2008). At elevations below the seasonal snowpack, growth is negatively related to summer and annual temperature (Case and Peterson, 2005). The negative temperature effect is thought to result from increasing water deficit in trees as soil moisture is depleted during summer drought (Littell et al., 2008).

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The effects of soil moisture and temperature on tree growth are complex and interdependent. Tree water deficits develop when water uptake by roots is exceeded by transpirational loss from leaves, which is affected primarily by atmospheric Vapor Pressure Deficit (VPD) (Kramer, 1983). Water deficits reduce stomatal conductance, net CO_2 assimilation, cell division and cell enlargement (Hsiao and Acevedo, 1974) and develop under high or low soil moisture conditions (Lassoie, 1982). Temperature directly affects VPD as well as biochemical and enzymatic processes involved in cambial growth (Rossi et al., 2006; Savidge and Förster, 1998; Uggla et al., 1998). Further, the effects of temperature and soil moisture on annual growth can change during the growing season (Lee et al., 2009).

Tree rings effectively represent annual growth over long time periods, but the interactive effects of seasonal environmental factors on growth are difficult to discern. Periodic measurement of changes in stem radius or circumference using dendrometers allows the timing of growth to be dated and, hence, associated with seasonal climate factors (Bormann and Kozlowski, 1962). However, growth measured with dendrometers can be complicated by the shrink and swell caused by changes in tissue water content (Deslauriers et al., 2003b; Gall et al., 2002; Herzog et al., 1995; Lassoie, 1979; Zweifel and Häsler, 2001) and xylem water potential (Abe et al., 2003; Irvine and Grace, 1997). Despite issues of shrink–swell, dendrometer data taken at weekly to monthly intervals accurately represent both the timing and rate of growth (Deslauriers et al., 2007; Rossi et al., 2006; Tardif et al., 2001).

The objective of this study is to determine the relative importance of temperature and water to Douglas-fir growth. Dendrometer measurements were taken year-round at approximately four-week intervals from five Douglas-fir stands located along a gradient from the Pacific coast to ~1200 m elevation in the Cascade Mountains of western Oregon, USA. Dendrometer derived basal area increment data were compared with site specific meteorological and soil moisture data for the years 1998 through 2009. We hypothesized that the importance of those factors would vary across the region depending on elevation and site characteristics.

2. Materials and methods

2.1. Research sites

Five mature, closed-canopy forest stands dominated by Douglas-fir were located in western Oregon, USA (Fig. 1). The Coast site is in the Cascade Head Experimental Forest (US Forest Service) on the west slope of the Oregon Coast Range 8.5 km from the Pacific Ocean. The other four stands, collectively referred to as the Mountain sites, are located in the Willamette National Forest (US Forest Service) on the west slope of the Cascade Mountains. Two sites, Falls Creek and Moose Mt., were at mid-elevation and two sites, Toad Creek and Soapgrass were at high elevation (Table 1).

Paired meteorological stations at each site were located in the forest stand and in an adjacent open area (Beedlow et al., 2007a). Aboveground meteorological data from the open site were used to represent conditions at the top of the tree canopy. Data collected from duplicate sensors located in the top of each forest canopy throughout 2010 indicated that during the growing season, air temperature at the open sites was within a degree of the canopies. At the Mountain sites the open areas were recent clear cuts (~16 ha) within 500 m of the forest sites with similar elevation, slope and aspect. At the Coast site the open meteorological station was placed at an established weather monitoring station near the town of Otis, Oregon (~1 km from the Coast forest site, ~2 ha open area).

Data were collected automatically at 5-min intervals and averaged hourly year-round throughout the study with Campbell Scientific data loggers (Campbell Scientific, Logan, Utah). Sensors were placed at a height of 3 m at each site. Air temperature and relative humidity (RH) were measured using Campbell Scientific HMP45 temperature–humidity sensors. Vapor pressure deficit (VPD, MPa) was calculated from temperature and RH data. Photosynthetically Active Radiation (PAR) data were collected using LI-COR, LI-190SL sensors (Lincoln, NE, USA). Precipitation was measured hourly using Texas Electronics TES25I (Dallas, TX, USA) tipping bucket rain gages. Quality-assurance calibrations for the air temperature and RH sensors were completed by the manufacturer annually and every four years for dataloggers.

Volumetric soil moisture (Campbell Scientific CS-615 reflectometers) and soil temperature (Campbell Scientific 107 Thermistors) at 0.2 m increments to a depth of 0.6 m were automatically collected at each forest meteorological station at 5-min intervals and averaged hourly year-round throughout the study. Plant available soil water (W, mm) was calculated for the top 0.6 m of soil from moisture release curves developed for each site. Detailed soil characteristics and soil moisture calculations are provided in Lee et al. (2007) and Beedlow et al. (2007a).

Swiss Needle Cast (SNC) (*Phaeocryptopus gaeumannii*), a fungal disease of Douglas-fir needles common in near-coastal forests, was found at the Coast site. SNC affects both stomatal conductance and needle longevity with consequent reduction in tree growth while the inter-annual infection severity is affected by temperature and precipitation (Manter et al., 2005). Annual surveys of the areal extent of infection in coastal areas of the PNW conducted by the Swiss Needle Cast Cooperative at Oregon State University (Shaw and Woolley, 2009) were used as a proxy for infection severity at the Coast site.

2.2. Growing season

We defined the growing season as May 1 through October 31 at the Coast and mid-elevation sites, and June 1 through October 31 at the high elevation sites. Our cambial activity data supported this definition as did previous studies of Douglas-fir in western Oregon (Emmingham, 1977; Grotta et al., 2005; Lassoie, 1982). A soil temperature growth threshold of ~5 °C has been shown for Douglas-fir (Bailey and Harrington, 2006; Emmingham, 1977) and other northern hemisphere conifer species (Deslauriers et al., 2003b; Rossi et al., 2007; Shönenberger and Frey, 1988). Growth was assumed not to occur when the average soil temperature was <5 °C. Soil temperature typically reached 5 °C at the mid-elevation sites in May and at the high elevation sites in June. During years with cold springs, soil temperatures reached 5 °C later, which delayed the onset of growth. Soil temperature at the Coast site was consistently >5 °C throughout the year. While the cessation of wood production in the fall was more difficult to determine and can occur at higher temperatures than necessary for growth initiation (Denne, 1971), the growing season was considered to end when soil temperature dropped to 5 °C, or by 31 October at all sites.

2.3. Growth measurements

Stem growth is defined as increase in size over time (Vaganov et al., 2006) and is commonly determined by measuring positive changes in stem Basal Area (BA) (Avery, 1975). Increases in BA result from wood and bark formation or increased water content of the elastic tissues, or both, while decreases result from shrinkage of elastic tissues associated with water deficit (Zweifel et al., 2005). During shrinkage, growth is slowed or stopped as wood formation tends to cease when trees are under water stress for several days or more (Abe et al., 2003). In Douglas-fir, cambial growth abruptly ceases when pre-dawn xylem pressure potential falls below about