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# EFFECTS OF BIOTIC INTERACTIONS ON CLIMATE-GROWTH RELATIONSHIPS OF DOUGLAS-FIR AND PONDEROSA PINE

By

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Plant processes depend on the interplay between intrinsic characteristics (e.g., photosynthetic capacity) and external variables, such as light, temperature and water availability. However, these factors are often tightly interconnected and vary significantly among species with different life history strategies and within a species across environmental gradients. Moreover, plant-plant interactions may directly affect both intrinsic variables and local environment through direct effects on resource availability and habitat structure. Yet, despite general scientific agreement that the relative effects of abiotic stress and competition are directly linked, relatively little is known about the effects of competitive interactions on climate-growth relationships of trees. This is largely because previous research addressing the issue has relied almost exclusively on short-term studies using short-lived, herbaceous species. However, unlike most short-lived plants, trees can substantially modify their ability to tolerate stress or acquire resources as a consequence of plastic responses to external environmental conditions experienced in their lifetimes, resulting in individualistic responses to environmental change. A clearer understanding of the relationship between competition and climate-growth relationships of mature trees is critically needed in order to accurately predict forest ecosystem responses to climate change and understand how local management actions could be used to influence these responses — arguably the most important research and management challenges of our time.

To address these issues, I quantify the relative influence of competition and environmental conditions on the climate-growth relationships of two dominant conifer species, *Pinus ponderosa and Psuedotsuga menziesii*, across their full range of growing conditions within the Colville National Forest of eastern Washington. Specifically, I analyze tree ring records using time series analysis and mixed effects models to, (1) investigate the effect of competition on climate-growth relationships; (2) assess how these relationships change between species and across environmental gradients; and, (3) explore linkages between environmental factors and drought responses across multiple spatial scales. Findings will help improve predictions about vegetation responses to climate change, address conflicting hypotheses about the dynamic role of competition along environmental gradients and help managers better understand how manipulating stand density and structure will modify tree responses to climate change.

# Table of Contents

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This work is dedicated to my beautiful daughter, Grace. I love you.

## Introduction

The relationship between climate and vegetation has always been central to ecological theory (Merriam 1898). Recently, this area of investigation has received renewed interest because of evidence linking climate change and drought to forest dieback (Breshears et al. 2005) and dramatic shifts in forest productivity, phenology, and demographic patterns (Parmesan and Yohe 2003, Boisvenue and Running 2006, van Mantgem et al. 2009). Still, there has been little effort to integrate knowledge about the effects of climate change into management and restoration planning at local scales – largely due to two fundamental gaps in knowledge: inadequate information about the degree of risk that climate change poses to particular ecosystem components and habitats; and uncertainty about how stand-level management actions will affect responses to climate change. For example, although silvicultural treatments that mechanically manipulate competitive stand dynamics and growing conditions (e.g., by altering stand density, structure and species composition) are a primary tool for forest restoration and management activities, little is known about how inter-tree competition, or potential interactions between climate and competition, influence tree responses to climate change. Yet, it is well-established that biotic interactions can profoundly influence how plants respond to changing environmental conditions (Tylianakis et al. 2008), and there is a growing consensus that competition will play a key in moderating species distribution patterns and responses to climate change (Brooker 2006). Given the fact that “thinning forests to increase tolerance to drought” is a central component of forest management (e.g., the U.S. Forest Service Strategic Framework for Responding to Climate Change [USFS 2008]), there is a pressing need to understand if and when competition influences climate-growth relationships of mature trees.

Previous research on climate-growth-competition relationships has often centered around two opposing theories. One suggests that competition is primarily important in productive environments with high resource availability (Grime 1977). The other argues that competition is universally important but in productive environments plants will compete strongly for light while in “harsh” environments, plants will compete just as strongly but for below-ground resources (Tilman 1982). Currently, the effect of climate variability on the strength and direction of biotic interactions is not well understood (Goldberg et al. 1999), and the potentially important role of competition remains generally overlooked in climate-change research. For example, current strategies for predicting responses of individual species to climate change often rely on estimating geographic shifts in a species-specific “climate-envelope” and do not consider the effects of direct or indirect species interactions (Thomas et al. 2004, Rehfeldt et al. 2006). Significant changes in plant-plant interactions, brought on by changing environmental conditions, limit inference from previous vulnerability assessments (Davis and Shaw 2001, Walther et al. 2002, Pearson et al. 2006) and can potentially lead to inappropriate forest management practices.

To address these issues, this research explores the dynamic relationship between climate, competition and growth among mature trees in unmanaged forests. Specifically, I assessed the relative influence of competition and environmental conditions on the climate-growth relationships of two dominant conifer species, *Pinus ponderosa and Psuedotsuga menziesii*, across their full range of growing conditions within the Colville National Forest of eastern Washington. To do so, I analyzed tree ring records using time series analysis and mixed effects models to, (1) investigate the effect of competition on climate-growth relationships; (2) assess how these relationships change between species and across environmental gradients; and, (3) explore linkages between environmentally-mediated expressions of phenotypic plasticity and climate sensitivity. This information will be critical to accurately predict tree responses to climate change (Araujo and Guisan 2006) and to understand how management actions, such as altering stand density and structure, influence the resilience and adaptive capacity of forest ecosystems (Choi 2007).

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# Chapter 1:

# Competition Modulates Climate Sensitivity of Douglas-fir

## Abstract

Despite strong experimental and observational evidence suggesting that competition affects vegetation responses to climate, current research has largely ignored the role of competition in modulating climate-growth relationships of mature trees. In this study, I assessed the combined influences of competition and climate variability on radial growth of Douglas-fir (*Pseudotsuga menziesii*) by analyzing over 200 tree-ring series from 10 biophysically similar yet well-distributed sites in northeastern Washington. I found that competition significantly modified the impact of climate on growth, but its effect varied significantly with climatic conditions. During dry years (i.e. when soil moisture was below the long-term average), competition was somewhat negatively associated with responsiveness to climate variability. However, in wet years, competition had a much more pronounced and opposite effect: growth of high-competition was tightly coupled to climate variability but low-competition trees exhibited no response. Notably, I found no relationship between competition and tree responses to extreme drought conditions – all trees exhibited a nearly 30% reduction in radial growth during drought years regardless of their competitive status. The proportion of sapwood area in latewood – a morphological trait associated with greater drought resistance – was significantly higher for high-competition trees 0.35 (SE = 0.013) relative to low-competition trees 0.28 (SE = 0.011). Although often overlooked, these results suggest that long-term, plastic responses to competitive stress may significantly modify the effect of climate on growth for long-lived species. Findings have important implications for individual-tree and stand-level growth models and may help

managers better understand how manipulating stand density and structure will modify tree responses to climate change.

**Keywords:** *climate change, climate-growth relationship, competition, dendroecology, Douglas-fir, facilitation, importance, intensity, latewood, Pseudotsuga menziesii*

## Introduction

Climate variability can exert a powerful – and often unexpected – influence on the outcome of biotic interactions (e.g. Dunnett and Grime 1999; Greenlee and Callaway 1996; Kikvidze et al. 2006). Although dendrochronologists have been studying the effects of climate on tree growth for nearly a century (Douglass 1914b), previous investigations have generally tried to minimize the variability in climate-growth relationships among sampled trees, usually by sampling only the most dominant trees at a site and analyzing mean, site-level time series (Cook et al. 1990). Consequently, despite a growing consensus that competition will play a key role in moderating species' distribution patterns and responses to climate change (Brooker 2006; Tylianakis et al. 2008), relatively little is known about the relationship between competition and climate responses of mature trees. However, given extensive empirical evidence demonstrating greater climate sensitivity – i.e. a tighter coupling of stemwood production to climate – in trees that die from abiotic stress compared to those that survive (McDowell et al. 2010; Ogle et al. 2000; Pedersen 1998; Suarez et al. 2004), there is a pressing need to understand if and when biotic interactions influence climate-growth relationships of trees to accurately predict responses to climate change (Araujo and Guisan 2006) and design stand-level management actions to enhance ecosystem resilience.

In this study, I assess the relationship between tree growth, climate variability and competition. Following Begon et al. (1996), competition is defined here as the interaction that arises between neighboring plants due to the shared use of limiting resources, which leads to a reduction in survival or growth. Thus, I focus on competition in terms of the negative effect of neighbors on an organism's ability to capture resources (the mechanism of competition), recognizing that this "is only part of the mechanism whereby a plant may suppress the fitness of a neighbor by modifying its environment" (Grime 2002).

The dominant conceptual models regarding the relative importance of competition in structuring plant communities across environmental gradients – including the C-S-R plant-strategy theory (Grime 2002) and the stress-gradient hypothesis (Bertness and Callaway 1994) – recognize that the importance of competitive interactions is tightly connected to climate. The arguments underlying these theories suggest that under favorable climatic conditions (i.e. where or when environmental conditions permit the rapid acquisition of resources), competitive interactions strongly influence plant performance because the successful, pre-emptive acquisition of limiting resources is a critical factor regulating plant performance (Grime 2002; Tilman 1988). However, in harsh conditions (e.g., drought years), the overall effect of competition should be less pronounced: as abiotic stress increases, competitive ability becomes less important relative to the ability to tolerate or avoid physiological stress (Callaway 2007). While there is substantial empirical evidence supporting this general relationship (Greenlee and Callaway 1996; Kikvidze et al. 2006), numerous studies have also shown the opposite pattern (Tielborger and Kadmon 2000) and the underlying relationship between competition and abiotic stress remains a topic of debate (Brooker et al. 2008; Lortie and Callaway 2006; Maestre et al. 2005).

Previous research addressing this issue has relied almost exclusively on short-term experiments using short-lived, herbaceous species (but see Kunstler et al. 2011). However, unlike most short-lived species, trees are able to significantly modify their ability to tolerate stress or acquire resources as a consequence of phenotypic responses to external environmental conditions experienced during their lifetimes (Awad et al. 2010; Via et al. 1995). This is critical to the survival of many long-lived tree species because, even within a stand, environmental conditions – including temperature, light, and water availability – can vary dramatically (Aussenac 2000). Consequently, some individuals may spend decades, even centuries, growing slowly in the forest understory (where resources can be strongly limiting), while others of this same species must grow rapidly to compete with neighbors for access to resources. As a result of such high plasticity, trees of the same species and age within a stand can exhibit life-history traits (e.g. growth rates, seed production, etc.) associated with both "competitor" and "stress-tolerator" plant strategies (sensu Grime 2002; e.g. Antos et al. 2005). Therefore, assessing the relationship between competition and climate sensitivity for mature trees requires considering not just the proximate effects of neighbors on resource availability, but also understanding how expressions of phenotypic plasticity and long-term adaptations to competitive stress may influence the ability to cope with environmental variability (Barnard et al. 2011; Woods 2008).

One way that trees can adapt to local growing conditions is by modifying water relations through the coordinated adjustments of xylem biophysical properties. However, structural traits that increase xylem safety and improve a tree's ability to tolerate water stress often result in reduced transport capacity and lower growth efficiency (Zimmermann 1983). Consistent with this tradeoff, reduced hydraulic conductivity has been associated with increased resistance to cavitation in Norway spruce (Rosner et al. 2008), ponderosa pine (Domec and Gartner 2003), and Douglas-fir (Domec et al. 2006; Domec et al. 2008). For Douglas-fir, this tradeoff appears to be directly related to structural differences between earlywood and latewood: although the conductivity of earlywood is 10 times greater than that of latewood, latewood is more than twice as dense, significantly less vulnerable to cavitation at extremely low water potentials, and capable of storing substantially more water than can be stored by earlywood tracheids (Domec and Gartner 2002). Individual Douglas-fir trees with a higher ratio of latewood to earlywood have been shown to be more resilient (less needle loss; De Kort 1993) and more likely to survive a severe drought (Martinez-Meier et al. 2008) than those with a lower proportion of latewood.

Because stemwood production effectively integrates the effects of abiotic and biotic factors (Schweingruber 1983; Vaganov 2006b) and generally occurs as a low-allocation priority (Waring and Running 1998), tree rings represent an extremely useful biological record for documenting the combined effects of competition and climate variability over time (see review by Dobbertin 2005). In this study, I analyzed patterns of tree-ring variability to investigate climate-growth relationships within the context of competitive interactions and life history traits that strongly regulate growth and species distributions in western forests. First, we compared climate responses among Douglas-fir trees growing on biophysically similar sites, but experiencing a wide range of crowding from neighbors. Based the principles of dendrochronology (Cook and Kairiukstis 1990; Fritts 1976), I predicted that competition would dampen the direct effects of climate on growth and, therefore, trees experiencing high levels of competition would be less climate sensitive (i.e. the growth of trees with more neighbors would be less coupled to climate variability). Based on previous observations that competitive interactions are less important under stressful abiotic conditions (Callaway 2007; Grime 2002), I also predicted that competition-related differences in climate responses would be less pronounced in dry years relative to wet years. In addition, I investigated whether variability in climate responses is related to plasticity in sapwood characteristics associated with an adaptive tradeoff between xylem safety and efficiency. Here, I predicted that trees experiencing high levels of competitive stress would maintain sapwood with a greater proportion of latewood relative to earlywood.

## Methods

**Study area and site selection —** This study was conducted on the Colville National Forest (CNF) in northeastern Washington (USA) between 48ºN and 49ºN latitude and 117ºW and 119ºW longitude. The climate and vegetation of this area is more similar to the Northern Rocky Mountains than the Cascade Mountains. With a range of 30 to 135 cm of precipitation per year, the west side of the CNF is strongly influenced by a rain shadow formed by the Northern Cascades, while the north eastern region has a near maritime climate, due to a westerly airflow forced over the Selkirk and Kettle River mountain ranges. This gradient in temperature and moisture is reflected in vegetation patterns: Douglas-fir and ponderosa pine (*Pinus ponderosa*) forests dominate to the west and mixed-conifer forests to the east.

Because I was interested in both biotic and abiotic influences on climate sensitivity, I used a combination of physical and ecological parameters to identify suitable sampling locations. First, all stands were located in the Douglas-fir/ninebark plant association (*Pseudotsuga menziesii/Physocarpus malcaeus* [PSME/PHMA]). Plant associations separate distinct biophysical environments by aggregating geographic areas based on shared floristics, environment and productivity (Williams et al. 1995). Soils in this association are gravelly to cobbly silts and loams, generally unconsolidated, and well to excessively-well drained. Douglas-fir is the most common tree species, but stands are usually mixed with ponderosa pine. Ninebark and oceanspray (*Holodiscus discolour*) are the most prevalent shrubs; serviceberry (*Amelanchier arborea*) and Orgeon grape (*Mahonia aquifolium*) are also common.

Within the PSME/PHMA plant association, I selected sites with similar elevation, aspect and slope (factors known to influence the climate-growth relationship) that were broadly distributed across the region. To do so, I used a GIS to identify areas with the following criteria: 1) southwest-southeast aspect; 2) mid-slope position on an approximately 40% slope; 3) approximately 1,000 m in elevation; 3) no significant disturbance (such as logging or fire) in the last 60 years; and 4) no current evidence of pathogenic outbreaks, substantial mistletoe or windthrow. Prior to sampling, all potential sites were visited to verify that these conditions were met. Through this process, 10 suitable sites were identified; each located approximately 25 km apart and well distributed across the study region (Fig. 1; Table1).

**Field sampling and competition index —** Sampling was conducted in 2008 and 2009. In order to insure that I sampled from a wide range of competitive environments, within each stand I sampled 10-15 dominant and 10-15 intermediate trees. Trees receiving full light from above and partly from the sides were considered dominant, while trees in definitively subordinate positions, receiving little direct light from above (through small holes in the canopy) and no light from the sides, were classified as intermediate. Within each stand, individual subject trees were carefully selected based on the following criteria: 1) no obvious defects such as cankers, scars, rot, substantial lean or mistletoe infestation; 2) >50 years old at breast height (1.3 m); 3) >50 m from the edge of the stand and other sampled trees of the same canopy class; 4) >10 cm diameter at breast height (DBH); and 5) >10 m from the nearest dead tree. For each sampled tree, two cores to the pith were taken at breast height from opposite sides of the stem and perpendicular to the slope.

Competitor trees around each subject tree were identified using a fixed angle gauge (Basal Area Factor = 10) (Biging and Dobbertin 1992). Based on its performance in other studies of competition in Douglas-fir, I used a distance- and size-dependent competition index (CI) to quantify crowding around subject trees (Hegyi 1974):

$$CI_i = \sum_{j=1}^{N} \left(DBH_j / DBH_i\right) / L_{ij} \qquad [1]$$

where $CI_i$ is the competition index value for subject tree *i*, $DBH_i$ is the *i*th subject diameter, $DBH_j$ the diameter of the *j*th competitor, and $L_{ij}$ the distance from the subject to the competitor. Trees with a CI value in the lower (≤ 1.2), middle (>1.2 and < 3.8), and upper (≥ 3.8) quartiles for the observed range of CI values were grouped into “low” (n = 58; mean CI = 0.60), “medium” (n = 115; mean CI = 2.26) and “high” (n = 58; mean CI = 5.46) competition classes, respectively.

I focused on the time period from 1990 to 2007 in order to be sure that measurements from 2008 and 2009 accurately characterized the competitive stress of subject trees across all years of analysis.

**Dendrochronological methods —** Sample cores were transported to the lab in protective straws and the full length of each core was visually crossdated using standard techniques (Fritts 1976; Stokes 1968). Based on ring counts, age at breast height was recorded for each core. When the pith was absent from increment cores, a pith locator was used to estimate the number of missing rings (Applequist 1958).

Total ring-widths as well as earlywood and latewood widths were measured to the nearest 0.01 mm using CooRecorder (Larsson 2003b). Measured samples were then checked for missing rings and other crossdating errors with the programs COFECHA (Holmes et al. 1986) and CDendro 7.1 (Larsson 2003a). To minimize potential dating errors, cores suspected of missing rings during the primary time-period of analysis (1990-2007) were excluded from further analysis. Ring-width measurements and age estimates from cores of the same tree were averaged to produce one tree-ring series for each tree, resulting in a total of 228 tree-ring series for analysis.

To assess the effects of competition, ring-width measurements were converted into basal area increments (BAI). BAI is generally a better representation of whole-tree growth than is raw ring width (LeBlanc 1990). Also, because BAI approaches an asymptotic level in mature trees, it accounts for age and size-related growth trends but does not filter out variability due to climate like other de-trending techniques (Biondi and Qeadan 2008). BAI was calculated by assuming a circular cross section and subtracting ring-width area from the inside-bark diameter and then each subsequent ring according to the following formula:

$$BAI = \pi(r_n^2 - r_{n-1}^2) \qquad [2]$$

where $r$ is the inside-bark radius of the tree and $n$ is the year of tree-ring formation. Inside-bark tree diameter was calculated according to the formula developed for interior Douglas-fir by Monserud and Forest (1979).

To standardize differences in absolute growth rates among sampled trees and emphasize the year-to-year variation in BAI associated with climate variability, each tree ring series was individually standardized to a unit-less relative growth rate (ring-width index; RWI). RWI was calculated by dividing BAI from the year of ring formation by the mean BAI from 1990-2007.

This resulted in a relative growth index for each tree with a mean value of one. Stand-level chronologies were then developed by averaging these standardized series for trees of each competition class (n = 3) within each stand (n = 10) using a robust estimation of the mean (Cook et al. 1990).

**Climate data —** In order to select the best source of the available climate data, I compared correlations between standardized chronologies and climate data from two sources: 1) regional measures of palmer drought severity index (PDSI) – an estimate of overall, regional departures from average soil moisture conditions (Alley, 1984);  and 2) gridded estimates of water deficit calculated using PRISM precipitation and temperature data (Daly et al. 2008) along with the USGS Thornthwaite monthly water balance model (McCabe and Markstrom 2007). For water balance calculations, I used assumed a field capacity of 100 mm (Stephenson 1988, Webb et al. 2000), and a latitude of 49 degrees north for all stands.  I found that measures of PDSI during the primary growing season provided the best linear predictor of the standardized chronologies. Therefore, I used July PDSI as a metric of growing season water availability in all analyses. Climate data was obtained from the National Climate Data Center for Climate Division 9 of Washington State (northeastern Washington; available at http://www.ncdc.noaa.gov).

**Statistical analysis —** I examined the effect of competition on climate responses in three ways. First, I calculated climate sensitivity as Pearson's correlation coefficient (r) between PDSI and the stand level chronologies for each competition class. I tested for differences in climate sensitivity (r) among competition classes using analysis of variance (ANOVA; n = 30), with site as a fixed effect.  Because I was interested in comparing the relative influence of competition under “stressful” and “non-stressful” abiotic conditions separately, I performed this analysis across all 18 years (hereafter “all years”) as well as for the subset of nine years in which PDSI was below the long-term average (PDSI < 0; hereafter “dry years”) and for the nine years in which it was above the long-term average (PDSI > 0; hereafter “wet years”).

Next, to most accurately quantify the relative effects of PDSI and competition on tree growth, I developed a comprehensive linear mixed-effects (LME) model for RWI ($n$ =4104; 228 subject trees with 18 observations each), using the nlme package in R (Team 2010). Unlike traditional methods of estimating environmental effects on growth, such as ordinary least squares, LME models distinguish between distinct sources of variation: population-averaged (main effects) and group-specific (random effects) (Pinheiro and Bates 2009) thus allowing for more accurate inference about the fixed effects of interest: climate (PDSI), competition (CI) and their interaction.. I designated stand and year as random effects to account for non-independence of data from the same stand or within the same year. A first-order autocorrelation structure was used to account for temporal correlation in model residuals. To assess differences in the effects of competition in wet versus dry years, I tested for significant interactions between the main effects (CI and PDSI) and a dummy variable representing relative water stress (“Wet” if PDSI > 0 and “Dry” if PDSI < 0). Significance of parameter estimates, random effect terms and error autocorrelation were evaluated using AIC and likelihood ratio tests at a significance level of 0.05 (Pinherio and Bates, 2000). Effects of tree age were originally tested in all LME models by including cambial age as a random factor. However, age effects were either insignificant or had a negligible influence on fixed effect estimates and, therefore, I did not include age in any of the final models.

Finally, to examine how competition influences sensitivity to extreme environmental conditions, I computed an index of each tree's drought response (DRY) as well as its response to extremely wet conditions (WET) in the following way:

$$\mathrm{DRY} = \frac{RWI_{dry} - RWI_{avg}}{RWI_{avg}}; \quad \mathrm{WET} = \frac{RWI_{wet} - RWI_{avg}}{RWI_{avg}} \qquad [3,4]$$

where *dry*, *wet*, and *avg* are the average RWI during the two driest years (2001 and 2004; PDSI = -3.55 and -2.45 respectively), the two wettest years (1997 and 1990; PDSI = 3.97 and 3.31 respectively), and the two years when environmental conditions were closest to the long-term average (2006 and 1999; PDSI = -0.02 and -0.08 respectively). I calculated the averages of DRY and WET responses among trees within each competition class within each stand, and tested for among-competition-class differences using ANOVA (*n* = 30), with site as a fixed effect and separate models for each sensitivity index (DRY and WET).

To test the hypothesis that trees growing under high levels of completion have greater allocation to latewood than do trees growing under less competitive stress, I calculated the average proportion latewood (PLW) for each tree and developed stand-level means (n = 10) for each competition class (n = 3). I assessed differences in PLW among competition classes using ANOVA (n = 30) and Tukey HSD post-hoc comparisons. Here again, I performed separate analyses for all years, dry years and wet years.

## Results

From 1990 to 2007, PDSI ranged from -3.6 (extremely dry) to 4.0 (extremely wet), with an average of 0.1 (Fig. 2A). During this time, there were nine "dry" years (PDSI < 0) and nine "wet" years (PDSI > 0). The average BAI for low-, medium-, and high-competition trees was 2,157 $\mathrm{mm}^2$ (SE = 33.3), 1,292 $\mathrm{mm}^2$ (SE = 21.7), and 316 $\mathrm{mm}^2$ (SE = 7.3), respectively (Fig. 2B).

There was a strong positive correlation between the mean standardized chronologies of high-competition and low-competition trees ($r = 0.86$; $p < 0.001$; Fig. 2C), indicating a shared climatic signal among all trees. Tree height and DBH were closely associated with competition ($R^2 = 0.36$; $p = <0.0001$ and $R^2 = 0.56$; $p = <0.0001$ for height and DBH respectively). However, there was only a weak relationship between tree age and competition ($R^2 = 0.06$; $p = <0.0002$). Table 2 shows stand-level means (± SE; N = 10) for tree age, height, and DBH.

There were significant among-competition-class differences in the correlation (*r*) between PDSI and growth (i.e. climate sensitivity) across all years ($F_{(2,18)} = 15.4$; $p = 0.0001$; Fig. 3A), with significantly higher correlation coefficients for high-competition ($r = 0.61$) than for low-competition ($r = 0.39$) trees. The trend for the subset of years in which PDSI > 0 (wet years) was similar to that of all years: significant differences among competition classes ($F_{(2,18)} = 13.4$; $p = 0.0003$; Fig.3B), with stronger correlations between climate and growth for high-competition ($r = 0.36$) than low-competition trees ($r = 0.07$). However, the opposite trend occurred in dry years: although there were significant among-competition-class differences in dry years ($F_{(2,18)} = 7.3$; $p = 0.005$; Fig. 3B), mean *r* values for high-competition trees were significantly lower than those for low-competition trees (mean = 0.28 and 0.43, respectively). For low-competition trees, mean correlation between PDSI and growth was lower in wet years than in dry years ($r = 0.07$ and 0.44, respectively), but for high-competition trees the pattern was reversed ($r = 0.36$ and 0.28, respectively).

The LME model results showed that competition significantly modified the effect of climate on growth, but this relationship was significantly different in wet years compared to dry years (PDSI*CI*Wet/Dry; $t = 5.21$; $p < 0.0001$). Plotting the magnitude of the PDSI effect (i.e. the slope of PDSI) against CI (Fig. 4 showed that PDSI had a highly significant effect on RWI in dry years, regardless of competition. However, during wet years, competition strongly moderated the effect of climate on growth; trees with low CI values were largely unaffected by PDSI, while those with high CI values were even more responsive to climate variability in wet years than they were in dry years.

Sensitivity to extreme drought did not vary by competition class ($p > 0.5$). DRY values ranged from -0.27 to -0.29 (for low- and high-competition classes, respectively) – a consistent reduction in growth of nearly 30% in drought years relative to average climatic conditions across all trees (Fig. 4). In contrast, there were significant among-competition-class differences in sensitivity to extremely wet conditions ($F_{(2,18)} = 22.97$; $p < 0.0001$; Fig. 5. For low-competition trees, values of the sensitivity index for wet years (WET) were near zero (mean = -0.02; SE = 0.04), indicating that their growth in wet years was no different than growth in years with average climatic conditions. However, for high-competition trees, WET values averaged 0.36 (SE = 0.09), indicating that growth of high-competition trees was almost 40% greater in wet years relative to average years.

Across all years, mean values of PLW ranged from 0.28 (SE = 0.011), 0.31 (SE = 0.005), and 0.35 (SE = 0.013) for low-, medium-, and high competition trees, respectively (Figure 6A), and the effect of competition was significant ($F_{(2,18)} = 13.14$, $p = 0.0003$). Mean values of PLW did not differ significantly between wet and dry years for any competition class ($p > 0.13$), and there was no significant difference in the effect of competition on PLW in all years compared to its effect in wet years or dry years ($p = 0.39$; Figure 6B).

## Discussion

I found that competition significantly modifies the impact of climate on growth of Douglas-fir, but that this effect is dramatically different between wet years and dry years.

Consistent with my hypothesis, competition decreased growth sensitivity to climate during dry years. However, during wet years, competition greatly increased climate sensitivity. I also found that trees experiencing high levels of competitive stress maintain sapwood with a greater proportion of latewood relative to low-competition trees; these results indicate that the relationship between competition and climate sensitivity may be associated with plasticity in xylem characteristics reflecting long-term, adaptive responses to competitive stress.

When water availability was above the long-term average, low-competition trees showed no response to fluctuations in PDSI, suggesting that water availability was no longer a limiting factor. In contrast, high-competition trees were even more responsive to PDSI in wet years relative to dry years. In other words, although low-competition trees generally occupied dominant canopy positions – and consequently had a higher capacity to access and capture light relative to high-competition trees – they did not respond to wet conditions by increasing relative growth rates. This was surprising given that light is presumably an important limiting resource when soil moisture is well above average and that previous observations have shown that competitive ability (the ability to capture limiting resources) is a primary factor influencing differences in relative growth rates under favorable environmental conditions (Grime 2002; Tilman 1988).

One possible explanation for this seemingly unintuitive pattern is related to what Connell (1980) referred to as the "ghost of competition past." In other words, the climate-growth relationships of mature trees may be overwhelmingly driven by phenotypic adaptations to the historic effects of competition on the average degree of water stress that trees experience in their *lifetimes* rather than by the direct, immediate effects of neighbors on resource availability in recent years (1990 to 2007). Over the long-term, conifers experiencing significant competitive pressure often exhibit a significantly lower ratio of leaf area to sapwood area (McDowell et al. 2007) as well as reduced rooting depths (McMinn 1963) and a higher shoot-to-root ratio (Newton and Cole 1991) relative to individuals of the same species growing on the same site but with less competition from neighbors. These structural differences likely reflect a reduction in allocation to roots in trees experiencing a high degree of competition, which results in less water available to support transpiring leaves as well as an increased need to maintain large amounts of sapwood for water storage. By limiting their ability to acquire and transport water and nutrients, these traits would be expected to severely restrict growth rates of high-competition trees relative to low-competition trees, particularly under favorable environmental conditions. However, these adaptations could also buffer the negative effects of stressful years and decrease drought sensitivity. This idea of a tradeoff between water-use efficiency and stress tolerance – mediated by phenotypic adaptations to low resource availability associated with high competitive stress – is also supported by studies on the relationship between stand density and Douglas-fir growth: trees with more neighbors had significantly lower ratios of leaf area to sapwood area and experienced less stomatal limitation on carbon gain (Renninger et al. 2007).

In my analysis of latewood allocation patterns, I found that high-competition trees contained a significantly greater percent of latewood (~7% higher) compared to low-competition trees. I also found that only low-competition trees produced a greater proportion of latewood in wet years relative to dry years. The consistently higher levels of latewood in high-competition trees relative to low-competition trees may be related to their shallower roots and the earlier onset of critically low levels of late-season soil moisture (Beedlow et al. 2007). However, the fact that latewood production for high-competition trees was not affected by year-to-year variability in soil moisture suggests that latewood production might not be strictly controlled by late-season water availability and may reflect an adaptive response of high-competition trees to better cope with chronic water stress. Thus, although more research is needed, my results seem to support a growing body of evidence suggesting that for Douglas-fir, the ratio of latewood to earlywood in the sapwood may also play a key role in regulating stress tolerance (De Kort 1993; Martinez-Meier et al. 2008), presumably by decreasing vulnerability to cavitation at extremely low-water potentials and significantly increasing internal water storage capacity (Domec and Gartner 2002). If true, plasticity in allocation to latewood may be an important, yet often overlooked, mechanism by which individual trees can adjust water relations in response to variability in environmental conditions.

These differences in hydraulic architecture – stemming from plastic responses to the competitive environment under which individual trees developed – can have a profound effect on water relations. As a result, growth-limiting factors may diverge among competition classes in a manner consistent with my observations: when soil water moisture reaches levels well above average, high-competition trees continue to be water-limited because of morphological constraints on their ability to capture and transport water, while low-competition trees – which have presumably optimized their hydraulic architecture to maximize growth under the most common environmental conditions experienced in their lifetimes – would become limited by something else, perhaps nutrient availability or photosynthetic capacity.

I found strong evidence that the importance of competition shifts over environmental gradients.  Competition had a relatively small effect on relative growth rates in years that were drier than average and had no significant effect on tree responses to extreme drought conditions. To understand these results within a broader ecological context, it is helpful to first clearly define the importance of competition and distinguish it from intensity the other component of competitive interactions (Kikvidze et al. 2011). Whereas the intensity of competition refers to the absolute effect that competition alone has on plant fitness (however measured), importance denotes the proportional impact of competition, relative to the full suite of environmental factors influencing plant performance (Welden and Slauson 1986). The overall importance of competition is not necessarily related to its intensity and can vary depending on tolerances to low resource availability (Gaucherand et al. 2006; Maestre et al. 2009). In this study, I am primarily concerned with the relative effect of competition on growth across a gradient of resource availability. Therefore, I am primarily addressing the issue of competition importance.

Although previous research on the shifting importance of competition over environmental gradients has been primarily focused on herbaceous species, my results are consistent with recent investigations in mature trees. For example, in a study of *Abies pinsapo*, Linares et al. (2009) found that the strength of the relationship between growth and competition was significantly weaker in dry years. Most recently, in an extensive analysis of more than 15 common tree species in the French Alps, Kunstler et al. (2011) concluded that the importance of competition significantly decreased with increasing abiotic stress. Thus, this study provides additional support for what appears to be a general pattern among plant communities: the importance of competition decreases with increasing abiotic stress (Callaway 2007; Grime 2002).

As others authors have noted (e.g. Callaway et al. 2003; Werner and Peacor 2003), there are several methodological limitations that arise when an individual or species modifies its phenotype in response to environmental conditions. In this case, phenotypic plasticity prevents the simultaneous expression of a “low-competition hydraulic strategy” in a high-competition environment and vise-versa. In addition, because plastic responses to competitive stress in the past can significantly modify the outcome of future biotic interactions (i.e. a trait-mediated interaction [Werner and Peacor 2003 ]), it is impossible to separate the confounding effects of the process that induced the phenotypic response from the consequences of that response. Here, that means one cannot formally distinguish between the effects of competition (the interaction that arises due to shared requirements for a limiting resource) and the effects of differences in morphology. Ultimately, these interacting factors can only be disentangled using an experimental framework. Unfortunately, such an approach is not feasible for organisms that weigh several tons, grow to be greater than 50 meters tall and live for hundreds of years. For this reason, investigators interested in the effects of the abiotic environment on the outcome of biotic interactions rely upon controlled removal experiments using short-lived herbaceous species and primarily focus on differences across spatial environmental gradients. Nevertheless, given that most forest biomass and stored carbon is found in mature trees, future research should increasingly focus on long-lived species and the effects of in-situ (temporal) environmental variability on the outcome of biotic interactions. Although careful analysis of tree-rings and radial growth patterns will certainly continue to be a fundamental component of future research, this effort will also require an enhanced understanding of (and techniques for measuring) carbon allocation to all parts of the tree as well as an emphasis on other components of plant performance and fitness, including reproduction and establishment.

### ***Conclusions and implications for management–***

My results show that tree responses to climate are sensitive to their competitive environment and provide additional evidence that the influence of competitive interactions on plant performance becomes less important in more stressful abiotic conditions. Although numerous studies have found greater climate sensitivity in trees that die from environmental stress compared to those that survive (McDowell et al. 2010; Ogle et al. 2000; Pedersen 1998; Suarez et al. 2004), my results indicate that the general relationship between competition, climate sensitivity and vulnerability to climate change is likely highly context-dependent and may vary across environmental gradients and with life-history traits. For example, I found that drought responses cannot be accurately predicted by a tree's competitive status, measures of its average climate sensitivity (e.g. the slope of a regression between PDSI and growth; McDowell et al. 2010; Pedersen 1998), or by comparing growth responses in wet relative to dry years (e.g. Fekedulegn et al. 2003; Knutson and Pyke 2008; McDowell et al. 2010). This finding is potentially important as it may indicate that commonly used indicators of climate sensitivity may not be accurate predictors of drought responses.

Although additional research is needed, my results suggest that changes in water relations and biomass-allocation patterns related to the effects of long-term competitive stress (and the associated exposure to chronic water stress) may be a critical, though generally overlooked, factor influencing responses of long-lived species to climate change. Several experimental studies have shown that conifers that are preconditioned by exposure to mild or moderate water stress have higher survival rates and improved water relations during subsequent drought events (Cregg 1994; Zwiazek and Blake 1989). The ability to alter water relations by shifting biomass allocation from leaves to woody parts has been noted as an adaptive response of trees living in areas that have experienced significantly increased warming and drying due to climate change (Parmesan 2006). If, in a similar way, trees growing amid the harsher abiotic conditions associated with intense competition from neighbors are better adapted to water stress than are trees that are under less water stress, then current forest management activities across the western US that focus on removing trees under competitive stress to increase overall stand resilience to drought may need to be reconsidered. In fact, the individuals that are often targeted in such treatments (generally small-diameter trees growing beneath the forest canopy) may actually be the most drought-tolerant individuals (i.e. the least susceptible to mortality in an extreme drought event). Recent finding that stands with fewer trees do not necessarily experience lower tree mortality in extreme drought events (e.g. van Mantgem et al. 2009, Floyd et al 2009, and Ganey and Vojita 2011) lend support to this idea. Furthermore, in a recent tree-ring study of 1,433 *Pinus sylvestris* trees from 393 plots, Martínez-Vilalta et al. (2012) also concluded that growth of larger trees was significantly more affected by extreme drought than that of smaller trees (i.e. large trees were more drought sensitive). Our study reinforces the idea that retaining diversity – in this case, diversity in stand structure – is a sound approach to maximizing the adaptive capacity of forest ecosystems.

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Table 1. **For each sampled stand, geographic location (latitude and longitude), aspect, slope, elevation, number of trees sampled, mean tree age, mean competition index (CI), mean diameter at breast height (DBH), and mean correlation (*r*) of all RWI series with the master chronology from all trees for the time period from 1990-2007. Numbers in parentheses are standard errors.**

| Stand ID | Latitude , Longitude (º) | Aspect (º) | Slope (%) | Elevation (m) | # Trees | Tree Age (Yrs) | CI | DBH (cm) | *r* |
|---|---|---|---|---|---|---|---|---|---|
| A | 48.8396, -117.2462 | 201 | 50 | 1097 | 20 | 143 (7) | 2.5 (.44) | 44 (4) | 0.63 (.03) |
| B | 48.7931, -117.6152 | 196 | 40 | 1158 | 27 | 93 (7) | 3.0 (.47) | 39 (4) | 0.70 (.03) |
| C | 48.2404, -117.5628 | 180 | 34 | 1128 | 26 | 68 (5) | 2.8 (.37) | 37 (3) | 0.65 (.02) |
| D | 48.9082, -118.1531 | 171 | 34 | 914 | 23 | 110 (5) | 2.1 (.30) | 38 (3) | 0.77 (.02) |
| E | 48.6070, -118.3071 | 160 | 24 | 1250 | 25 | 80 (4) | 2.8 (.38) | 41 (3) | 0.78 (.02) |
| F | 48.3504, -117.1752 | 181 | 54 | 1250 | 19 | 82 (3) | 2.4 (.43) | 38 (3) | 0.58 (.03) |
| G | 48.8407, -118.2823 | 182 | 41 | 1311 | 23 | 112 (9) | 2.1 (.32) | 46 (3) | 0.79 (.02) |
| H | 48.8123, -118.5376 | 207 | 29 | 1128 | 19 | 118 (7) | 2.2 (.43) | 46 (4) | 0.74 (.03) |
| I | 48.6419, -117.2876 | 181 | 32 | 975 | 23 | 75 (9) | 3.1 (.50) | 33 (3) | 0.66 (.03) |
| J | 48.9752, -117.3284 | 197 | 39 | 884 | 23 | 86 (2) | 2.8 (.37) | 33 (3) | 0.66 (.03) |

**Table 2. Age, height and diameter at breast height (DBH) for each competition class (stand-level means [± SE]; N = 10)**

| Competition class | Age (Years) | Height (m) | DBH (cm) |
|---|---|---|---|
| Low | 116 (8) | 28.3 (0.9) | 55.5 (1.5) |
| Medium | 105 (7) | 25.4 (1.1) | 40.1 (1.6) |
| High | 96 (8) | 17.8 (0.5) | 20.4 (0.7) |

## Figure Captions

**Figure 1.** Location of study sites (letters A-J) on the Colville National Forest (darker shaded area) in northeastern Washington State (inset). The lightly shaded area shows NCDC Climate Division 9.

**Figure 2.** Time series for primary period of analysis (1990-2007) showing PDSI (A), and stand-level means (+/- 1 SE; n = 10) of basal area increment (BAI) (B) ,standardized growth index values (ring width index; RWI) (C), and the proportion of latewood (PLW) (D) for low- (squares; solid lines), medium- (circles; short-dashed lines) and high- (triangles; long-dashed lines) competition trees. All growth indices have a mean value of 1 (horizontal dashed line).

**Figure 3.** Mean correlation coefficient (+/- 1 SE; $n = 10$) between PDSI and the standardized growth chronologies for low- (squares), medium- (circles) and high- (triangles) competition trees. Correlations were calculated for all years (1990-2007) (A) as well as the nine years with PDSI < 0 (dry years; dashed lines) and the nine years PDSI > 0 (wet years; solid lines) (B). Different letters indicate significant differences ($p < 0.05$) among competition classes.

**Figure 4.** Results from a linear mixed effects model (n = 4104; 228 subject trees with 18 observations each) showing change in the effect of PDSI (+/- 1 SE) on growth (RWI) in dry years (dashed line; PDSI < 0) and wet years (solid line; PDSI > 0) as a function of competition.

**Figure 5.** Mean growth responses (+/- 1 S.E; n = 10; see Methods) to extreme drought (DRY; dashed lines) and extreme wet conditions (WET; solid lines) for low- (squares), medium-

(circles) and high- (triangles) competition trees. Different letters indicate significant differences ($p < 0.05$) among competition classes in DRY (uppercase letters) or WET (lowercase letters).

**Fig. 6.** Mean (+/- 1 S.E.; n = 10) proportion of latewood (PLW) across (A) all years (1990-2007) as well as (B) for dry years (PDSI < 0) and wet years (PDSI > 0) separately. Different letters indicate significant differences among competition classes.

**Figure 1**

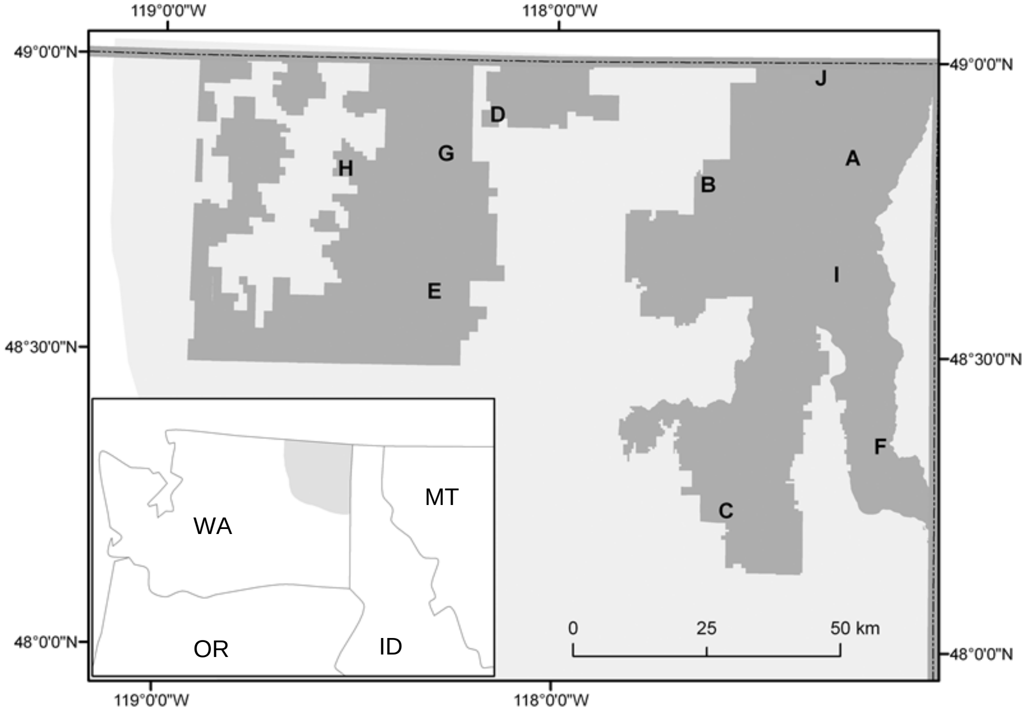

119°0'0"W
118°0'0"W
49°0'0"N
48°30'0"N
48°0'0"N
J
D
G
H
A
B
E
I
F
C
WA
MT
OR
ID
0
25
50 km

**Figure 2**

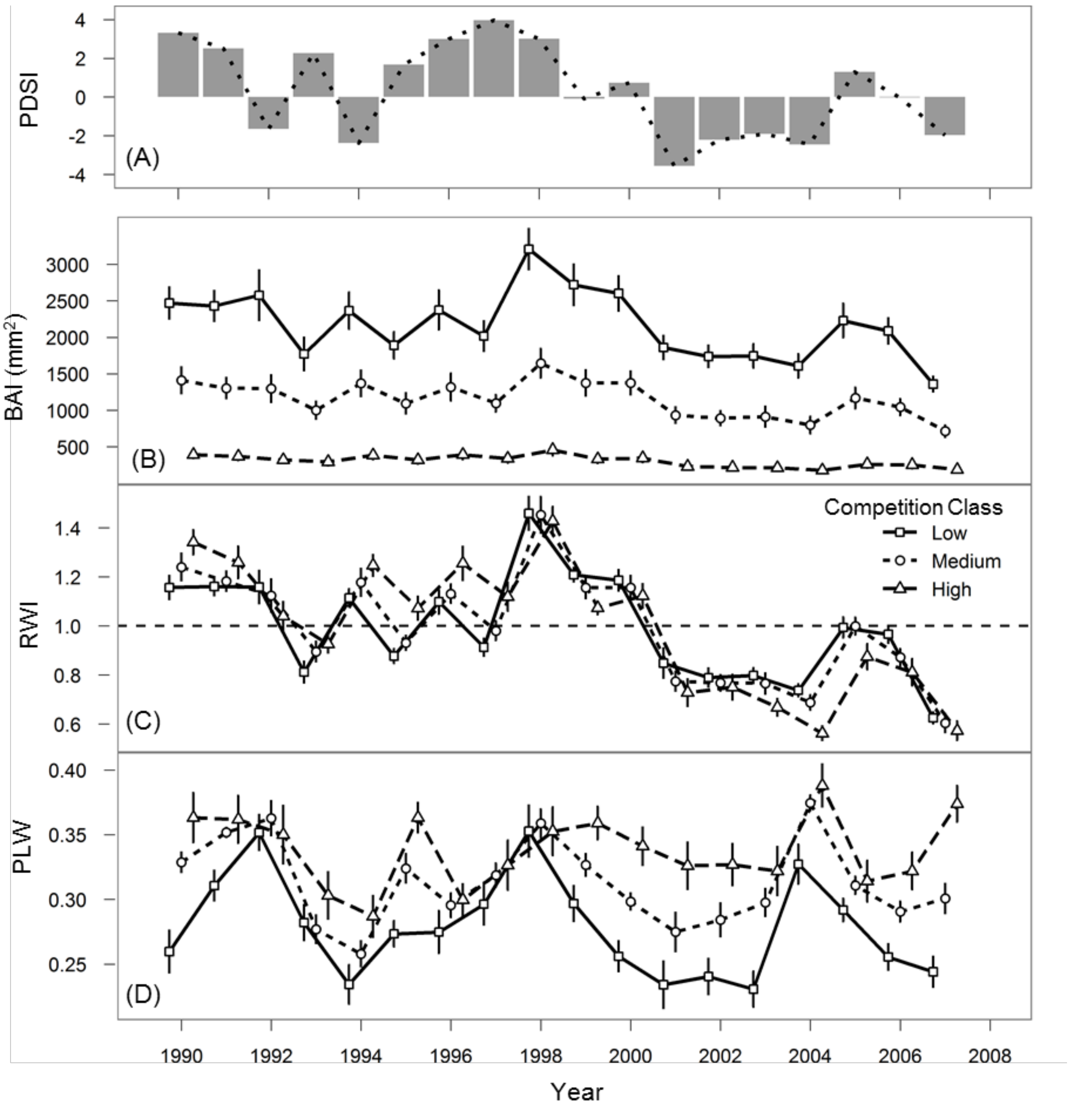

PDSI
4
2
0
-2
-4
(A)
BAI ($mm^2$)
3000
2500
2000
1500
1000
500
(B)
RWI
1.4
1.2
1.0
0.8
0.6
(C)
Competition Class
Low
Medium
High
PLW
0.40
0.35
0.30
0.25
(D)
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
Year

**Figure 3**

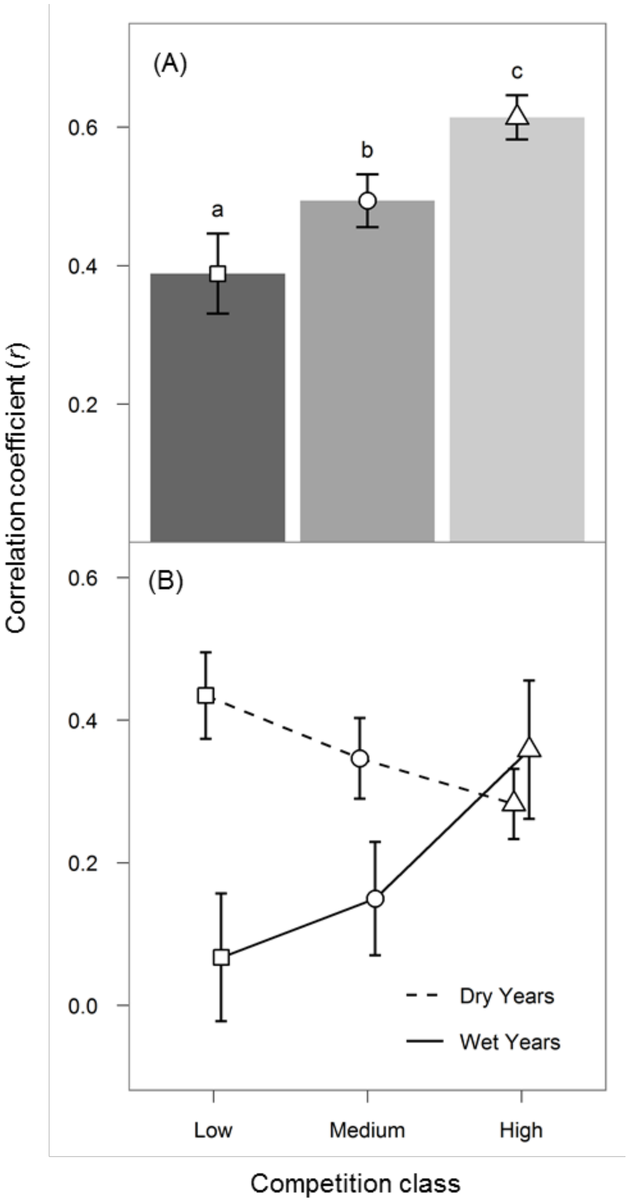
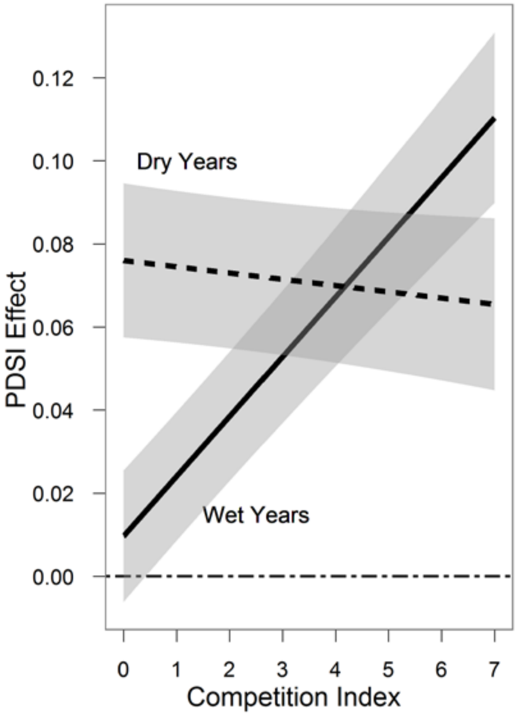

(A)
a
b
c
0.6
0.4
0.2
Correlation coefficient (*r*)
(B)
0.6
0.4
0.2
0.0
Dry Years
Wet Years
Low
Medium
High
Competition class

**Figure 4**



0.12
0.10
0.08
0.06
0.04
0.02
0.00
PDSI Effect
Dry Years
Wet Years
0
1
2
3
4
5
6
7
Competition Index

**Figure 5**

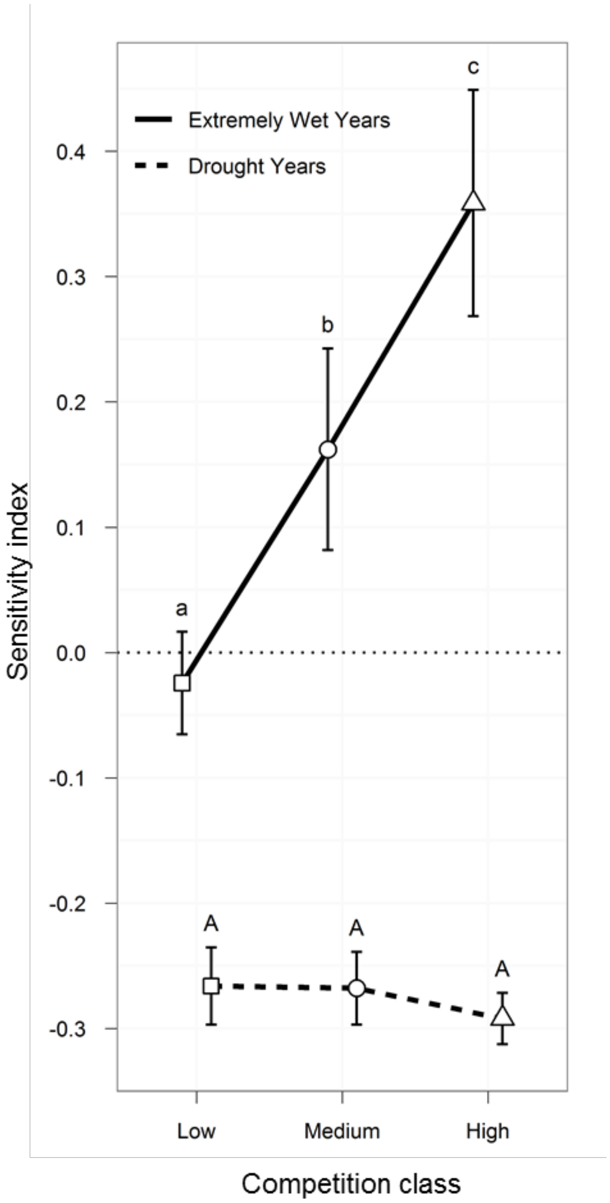
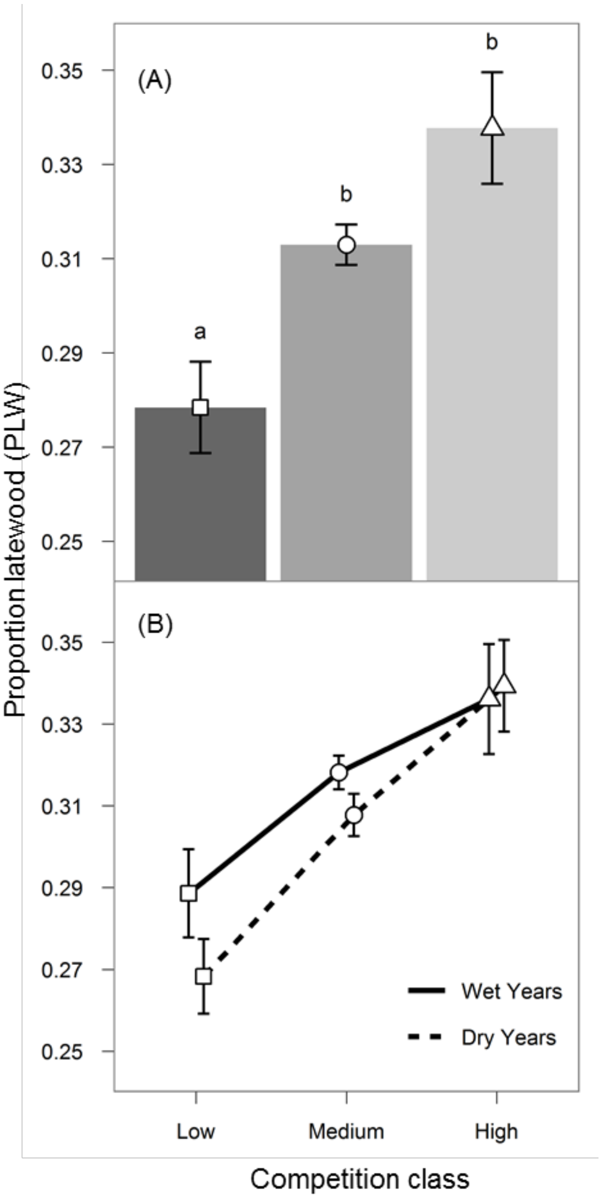

c
Extremely Wet Years
Drought Years
0.4
0.3
b
0.2
0.1
a
0.0
-0.1
-0.2
A
A
A
-0.3
Sensitivity index
Low
Medium
High
Competition class

**Figure 6**


(A)
a
b
b
0.35
0.33
0.31
0.29
0.27
0.25
(B)
0.35
0.33
0.31
0.29
0.27
0.25
Wet Years
Dry Years
Proportion latewood (PLW)
Low
Medium
High
Competition class

# Chapter 2:

# Effect of crown class on climate-growth relationships of ponderosa pine and Douglas-fir over an environmental gradient

## Abstract

There is increasing interest in actively managing forests to increase their resilience to climate-related changes. Although forest managers rely heavily on the use of silvicultural treatments that manipulate stand structure and stand dynamics to modify responses to climate change, few studies have directly assessed the effects of stand structure or canopy position on climate-growth relationships – or examined how this relationship may vary among species or across environmental gradients. In this study, I analyzed variability in tree-ring series from 15 low-elevation stands in northeastern Washington (USA) using time series analysis and linear mixed effects models. My objective was to assess the relative influences of species (*Pinus ponderosa* vs. *Pseudotsuga menziesii*), crown class (dominant vs. intermediate), and habitat type (Xeric vs. Dry-Mesic) on the climate responses of mature trees in unmanaged forests. I found that climate-growth relationships varied significantly between canopy classes and across habitat types but that these effects were highly species-specific. For *Pseudotsuga menziesii*, growth responses to temperature and precipitation did not vary between canopy classes. For *Pinus ponderosa*, however, regression coefficients for the relationship between temperature and radial growth were nearly twice as large for dominant trees compared to intermediate trees, and 84% of dominant trees were significantly influenced by precipitation, compared to only 62% of intermediate trees. In contrast, habitat-type did not significantly affect the climate responses of *Pinus ponderosa*, but did affect responses of *Pseudotsuga menziesii.* For example, for *Pseudotsuga menziesii* only

51% of trees in Dry-Mesic sites, were significantly affected by drought (PDSI), compared to 93% in Xeric sites. A better understanding of the relationship between climate sensitivity, species-specific hydraulic strategies, and stand dynamics is crucial for accurately predicting tree responses to climate change and designing forest treatments that will effectively reduce the climatic vulnerability of key forest species and habitats. Results may assist managers with understanding how altering stand dynamics will differentially affect climate-responses of individual species.

## 1. Introduction

Vegetation responses to climate change will reflect both physiological limitations and the outcome of biotic interactions(Tylianakis *et al.*, 2008). Although dendrochronologists have used tree rings to study the effect of climate on tree growth for nearly a century (Douglass, 1914), surprisingly little is known about the effects of competition and stand dynamics on the climate-growth relationships of mature trees. This is largely because tree-ring-based studies of climate-growth relationships traditionally have assumed that endogenous factors – such as stand dynamics and competition – modify the direct effects of climate on tree processes, thereby reducing climate sensitivity (the degree of growth response to climate variability) and obscuring the true climate-growth relationship (Fritts, 1976; Cook and Briffa, 1990). For this reason, previous research has primarily been conducted on populations growing at their climatically controlled distribution limits and analyses are generally based on mean site chronologies – time series of detrended growth indices averaged across all trees at a single site (Cook *et al.*, 1990). This approach assumes a common, shared growth response to climate among sampled trees on a site and uses averaging to reduce random variability among trees within years. Although this method effectively emphasizes the shared climate signal from a particular site, it also discards tree-to-tree variability in climate response.

There is reason, however, to suspect that climate-growth relationships could vary substantially among individuals within a site. At a local scale, stand density and structure are known to significantly influence microclimatic conditions and create sharp gradients in the environmental factors that regulate tree growth, including light, water and temperature (Aussenac, 2000; Zhu *et al.*, 2000). Environmental conditions vary vertically within the forest canopy and at different soil depths; thus, trees growing in sub-dominant canopy positions are consistently exposed to different environmental conditions than dominant trees. This, in turn, may lead to significantly different morphological and physiological characteristics in suppressed trees relative to dominant trees, including a lower ratio of leaf-area to sapwood-area (McDowell *et al.*, 2006; Renninger *et al.*, 2007) and reduced rooting depths (McMinn, 1963). Differences in environmental conditions and morphological traits are likely to cause significant differences in resource requirements and growth-limiting factors and, therefore, significant differences in climate-growth relationships between dominant and sub-dominant trees within a site.

Previous research supports the idea that climate-growth relationships may vary significantly among trees of the same species within a stand, but results have been highly species-specific and even contradictory. For example, greater growth reductions during drought were found for dominant overstory trees relative to suppressed understory trees in studies of *Pinus nigra* (Martín-Benito *et al.*, 2008) and *Picea sitchensis* Bong. (Wichmann, 2001). However, dominant trees were found to be less drought-sensitive than understory trees in studies of *Abies pinsapo* Boiss. (Linares *et al.*, 2010), *Pinus sylvestris* (Pichler and Oberhuber, 2007), *Pinus strobus* L.(Vose and Swank, 1994), and *Picea Abies* L. (Van Den Brakel and Visser, 1996). In other studies of *Picea Abies* L., Pichler and Oberhuber (2007) found that the effect of canopy class differed significantly between north- and south-facing sites (i.e. a significant site by canopy class interaction), but Meyer and Braker (2001) did not find significant differences in climate-growth relationships of dominant and suppressed trees at two sites with very different elevations. Although highly inconsistent and often based on small sample sizes, these studies demonstrate that stand structure can significantly alter tree growth responses to climatic variability, suggesting that targeted management actions that alter stand structure could also significantly modify tree growth responses to climatic variability and change.

The sensitivity of conifers to climate is also known to vary significantly among species (Hurteau *et al.*, 2007) and over numerous environmental gradients such as latitude (Peterson and Peterson, 2001; Littell *et al.*, 2008), elevation (Kienast *et al.*, 1987; Peterson and Peterson, 2001; Kusnierczyk and Ettl, 2002), aspect (Villalba *et al.*, 1994; Fekedulegn *et al.*, 2003), and soil nutritional status (Ogle *et al.*, 2000; Pinto *et al.*, 2007). In general, environmental factors related to water supply, such as precipitation, are the most powerful controls on cambial activity in arid ecosystems, while energy (e.g., temperature and growing season duration) is most important in areas with adequate water supply, such as areas of high elevation and latitude (Gholz, 1982; Stephenson, 1990; Waring and Running, 1998). While some researchers have found that inter-specific differences in climate-growth relationships are more significant than site-to-site differences (Graumlich, 1993; Peterson and Peterson, 1994), others have reached the opposite conclusion (Villalba *et al.*, 1994), underscoring the fact that tree growth responses to climate are highly context-dependent. This high degree of variability makes it difficult to apply results from one species to another or to draw general conclusions about variation in climate-growth relationships from site to site across heterogeneous landscapes. As such, it is becoming increasingly clear that well-replicated information at sub-regional or local scales is needed to successfully disentangle the numerous (and likely interacting) environmental factors that influence climate-growth relationships in heterogeneous landscapes (Rehfeldt *et al.*, 1999).

In this study, I used time series analysis and mixed-effects models to analyze nearly 700 tree-ring growth index series and assess how canopy position and forest type affect the climate-growth relationships of *Pinus ponderosa* (ponderosa pine) and *Pseudotsuga menziesii* (Douglas-fir) in northeastern Washington, USA. In light of strong evidence that competitive interactions can profoundly influence vegetation responses to climate change (Brooker, 2006; Tylianakis *et al.*, 2008), this information will be critical to accurately predict ecosystem responses to climate change (Araujo and Guisan, 2006). Moreover, silvicultural treatments such as thinning that change competition intensity and stand structure are a primary tool for forest restoration; therefore, a clear understanding of the relationship between competition, climate and growth is important for sustainable forest management.

## 2. Methods

### 2.1. Study area and site selection

This study was conducted on the Colville National Forest (CNF) in northeastern Washington between 48ºN and 49ºN latitude and 117ºW and 119ºW longitude (Fig. 1). With a range of 30 to 135 cm of precipitation per year, the west side of the CNF is strongly influenced by a rain shadow formed by the Northern Cascades, while the northeastern region has a near-maritime climate due to a westerly airflow forced over the Selkirk and Kettle River mountain ranges. These temperature and moisture gradients are reflected in vegetation patterns: Douglas-fir and ponderosa pine forests dominate to the west, while mixed-conifer forests dominate to the east.

Because I was interested in analyzing climate-growth relationships in contrasting environments, sampling was stratified by the Forested Plant Association Group (PAG) (Williams *et al.*, 1995). Similar to the Habitat Type concept (Daubenmire and Daubenmire, 1968), PAGs aggregate geographical areas based on shared floristics, environment and productivity. I used PAGs for sample stratification because they effectively separate distinct biophysical environments and because they form the basic unit for vegetation modeling on the CNF. Stands were selected for sampling in the ponderosa pine-Douglas-fir/bluebunch wheatgrass plant association (*Pinus ponderosa-Pseudotsuga menziesii/Agropyron spicatum* [PIPO-PSME/AGSP]) and the Douglas-fir/ninebark plant association (*Pseudotsuga menziesii/Physocarpus malcaeus* [PSME/PHMA]). PIPO-PSME/AGSP is the hottest and driest plant association in the CNF and generally occurs at lower elevations on well-drained and course-textured soils. The vegetation is characterized by open stands of ponderosa pine and Douglas-fir with a bunch-grass-dominated understory and few shrubs. By contrast, PSME/PHMA is cooler and wetter than PIPO-PSME/AGSP and is the most common plant association group (hereafter, "habitat type") in this region. It is found across a wider range of elevations and aspects, generally in gravelly to cobbly silts and loams. Douglas-fir is the most common tree species but stands are usually mixed with ponderosa pine. Ninebark and oceanspray (*Holodiscus discolour***)** are the most prevalent shrubs; serviceberry (*Amelanchier arborea*) and Orgeon grape (*Mahonia aquifolium*) are also quite common.

To reduce stand-level variability and thereby minimize the influence of extraneous factors on the climate-growth relationship, I carefully selected sites within each habitat type that were as similar as possible. To do so, I used a geographic information system to identify stands with the following criteria: 1) southwest-southeast aspect; 2) mid-slope position on an approximately 40% slope; and 3) no significant disturbance (such as logging or fire) in the last 60 years. Prior to sampling, I visited all potential sites to see that these conditions were met and to verify that there was no evidence of pathonogenic outbreaks, substantial mistletoe or windthrow.

I identified a total of 15 suitable sites broadly distributed across the study area: five in the PIPO-PSME/AGSP habitat type (hereafter "Xeric") and 10 in the PSME-PHMA type (hereafter "Dry-Mesic"; Fig. 1). Xeric sites received, on average, 20% less total precipitation in the months of May, June, and July than dry-mesic sites during the period 1950-2007. Average maximum temperatures during this period were 1.5° C hotter on Xeric sites then on Dry-Mesic sites, in part because the Xeric sites were at lower elevations (Table1).

### 2.2. Dendrochronological methods

From each stand, I sampled 10-15 dominant/co-dominant trees (trees receiving full light from above and partly from the sides; hereafter "dominant") and 10-15 intermediate trees (trees in definitively subordinate positions, receiving little direct light from above and no light from the sides; hereafter, "intermediate") of each species. Trees selected for sampling met the following criteria: 1) no obvious defects such as cankers, scars, rot, substantial lean or mistletoe infestation; 2) >50 years old at breast height (1.3 m); 3) >50 m from the edge of the stand and other sampled trees of the same canopy class; 4) >10 cm diameter at breast height (DBH); and 5) >10 m from any dead or dying trees. For each sampled tree, I extracted two cores with an increment borer at breast height from opposite sides of the stem and perpendicular to the fall line of the slope.

I transported tree cores to the lab in protective straws and mounted and sanded them using standard techniques (Stokes, 1968; Fritts, 1976). I visually crossdated all cores and recorded their age at breast height. When the pith was absent from increment cores, I used a pith locator to estimate age (Applequist, 1958). I scanned increment cores using an optical scanner at 1200 dpi resolution and measured ring-widths using the CooRecorder software (Larsson, 2003b). I then checked for missing rings and other crossdating errors with the software programs COFECHA (Holmes *et al.*, 1986) and CDendro 7.1 (Larsson, 2003a). Finally, I averaged tree-ring measurements from the same tree by year to produce one mean ring-width time series for each sampled tree.

To remove age-related growth trends from each ring-width time series, I fit a 30-year cubic spline function with a 50% frequency response cut off (Cook and Peters, 1981). I then calculated ring-width indices (RWI) by computing the ratio between observed ring-widths and the corresponding expected values produced by the spline function. I chose this method because it is a simple technique that could be applied to all trees and resulted in high correlations between the standardized ring-width indices and climate variables.

For each site, I calculated a stand-level chronology for each canopy class-species combination by averaging the standardized tree-ring series using a bi-weighted robust mean (Cook *et al.*, 1990). I generated descriptive statistics for each stand-level chronology, including mean sensitivity and mean intra-series correlation (Briffa and Jones, 1990). Mean sensitivity is a unit-less measure of year-to-year variation in growth that is independent of ring size and is calculated as the absolute difference between adjacent indices divided by the mean of the two values. Higher mean sensitivity values generally indicate more climatically sensitive chronologies (Fritts, 1976). Intra-series correlation represents the average of all pairwise correlations between individual tree ring series and is used as a measure of similarity of inter-annual growth variability among groups of trees. Stand-level chronology statistics are available in Supplementary File 1 and summarized in Table 2. Detrending and statistical calculations were accomplished in R (Team, 2010) using the package dplR (Bunn, 2008).

### 2.3. Climate data

To identify the most important climate variables for analysis, I first developed mean growth chronologies for the study area that represented the shared, high frequency variation of each population (species-habitat combination) by averaging the stand-level chronologies for each species-habitat type combination (Cook *et al.*, 1990). I then calculated product moment correlations between these mean growth chronologies and monthly climate variables for the study area using a 15-month climate window in which tree growth in year *t* was compared to monthly climate variables for a period extending from June of year *t*-1 to September of year *t*. I estimated the mean climate response using correlation functions from the R package bootRes (Zang, 2009), based on DENDROCLIM2002 (Biondi and Waikul, 2004).

I used temperature, precipitation and estimated soil water availability as climate predictors. To select the best source of available temperature and precipitation data, I compared correlations between the mean growth chronologies for each species and monthly climate data from two sources: 1) the regional total precipitation and average daily temperature data from NCDC Climate Division 9 of Washington State (available from the National Climate Data Center; http://www.ncdc.noaa.gov); and 2) gridded total precipitation and average daily maximum temperature data obtained from PRISM (Parameter-elevation Regressions on Independent Slopes Model), a 4-km gridded model that accounts for topographic and elevation differences (Daly *et al.*, 2008). Precipitation and temperature data in the months of May, June and July (hereafter “the growing season”) from PRISM were the most consistent and significant predictors of growth as represented by the mean growth chronologies; I therefore used these data in analyses. Specifically, I used PRISM estimates of the total precipitation during the growing season (hereafter "precipitation") and the mean maximum daily temperature from the warmest month in each year (hereafter "temperature") as predictor variables.

To analyze the combined effects of precipitation and temperature on radial growth, I again compared climate-growth correlations from two sources: 1) the Palmer drought severity index (PDSI) – an estimate of overall, regional departures from average soil moisture conditions (Alley, 1984) – obtained from NCDC Climate Division 9; and 2) gridded estimates of actual evapotranspiration, soil moisture storage and water deficit calculated using PRISM data along with the USGS Thornthwaite monthly water balance model (McCabe and Markstrom, 2007). For water balance calculations, I assumed a field capacity of 100 mm (Stephenson 1988, Webb et al. 2000) and a latitude of 49° north for all stands. I found that, overall, divisional PDSI was the best linear predictor of the standardized chronologies. Here again, climate-growth correlation values for the months of the growing season in the year of ring formation were similar and all highly significant. As such, I used the average of the divisional PDSI throughout the growing season (May-July) as a metric of water availability during the entire growing season. PDSI data was obtained from the National Climate Data Center for Climate Division 9 of Washington State (northeastern Washington, available at http://www.ncdc.noaa.gov). To insure that climate data was highly accurate and consistent across the study area, I limited my analysis of climate-growth relationships to the time period of 1950 to 2007.

### 2.4. Statistical analysis

I assessed tree growth responses to climate in three steps. First, I equalized the variance among trees by subtracting the mean RWI and dividing by the standard deviation for each series. Next, I estimated each tree's growth response to single climate variables by developing first-order autoregressive models for each tree and each climate variable (693 trees x 3 climate variables [PDSI, precipitation, and temperature] = 2,079 models). For all models, temporal autocorrelation of the error term was accounted for using a lag 1 correlation structure, but the coefficients were allowed to vary in the optimization of each model correlation. Finally, I analyzed the variability in the estimated coefficients using linear mixed-effects (LME) models to assess the statistical significance and relative influence of the three fixed effects of interest: species (ponderosa pine vs. Douglas-fir), canopy class (dominant vs. intermediate), and habitat type (Xeric vs. Dry-Mesic). I designated tree age as a covariate and site as a random effect (to account for the statistical effects [non-independence] of analyzing trees from the same stand).

To evaluate which fixed effects were the most important for explaining tree growth responses to each climate variable, I followed the mixed-model selection protocol outlined by Zuur et al. (2009). To do this, I began with a “beyond optimal” model containing all fixed effects and their possible interactions and then compared a series of reduced models that differed only by the term being tested (the least significant term in the model). I used maximum likelihood parameter estimations and compared nested models using likelihood-ratio tests and then refit the final model using restricted maximum likelihood estimation. I plotted residuals against fitted values to verify normality and homogeneity of variance.

Climate variables were standardized by subtracting the mean and dividing by the standard deviation to allow for direct comparison of climate coefficients among different predictor variables. Model fitting was done in R using the nlme package (Pinheiro *et al.*, 2010). To test for statistically significant differences among groups in the number of trees exhibiting significant ($p < 0.05$) climate-growth relationships, I used a function for analyzing LME models with binomial data distribution within the R-package MASS (Venables and Ripley, 2002). Post-hoc comparisons between groups were carried out using Tukey contrasts with the package multcomp(Hothorn *et al.*, 2008).

## 3. Results

I found that climate-growth relationships varied significantly between canopy classes and across habitat types and that effects were highly species-specific. However, for both species, canopy class effects were consistent across habitat types (i.e. I found no significant interactions between habitat type and canopy class). Tree age did not emerge as an important variable in any of the LME models.

### *3.1 Species-specific effects of canopy class on climate sensitivity*

Results of LME models showed a significant interaction between canopy position and species for all three climate variables ($t = 4.15$ and $p = < 0.001$ for PDSI; $t = 3.08$ and $p = 0.002$ for precipitation; and $t = -5.07$ and p = < 0.001 for temperature; Table 3). For ponderosa pine, dominant trees were significantly more sensitive to PDSI than were intermediate trees ($p < 0.001$; Fig. 3) and a substantially greater percentage of the dominant trees exhibited a significant relationship to PDSI compared to intermediates (70% vs. 53%, respectively; $p = 0.003$; Fig. 4). For Douglas-fir, however, dominant trees were significantly *less* sensitive to PDSI than were intermediate trees ($p < 0.001$), and fewer dominant Douglas-fir trees than intermediate trees exhibited significant growth responses to PDSI (60% versus 71%, respectively; $p = 0.018$; Fig. 4). Dominant ponderosa pine trees were also significantly more sensitive to precipitation ($p = 0.016$) and temperature ($p < 0.001$) than were intermediate ponderosa pine (Fig. 3), but there were no between-canopy-class differences in sensitivity to precipitation or temperature for Douglas-fir (Fig. 3).

With respect to *between-species* differences in canopy-class effects, intermediate Douglas-fir were more sensitive to PDSI and precipitation relative to intermediate ponderosa pine ($p < 0.001$ for both variables) and, accordingly, a greater proportion of intermediate Douglas-fir were significantly sensitive to PDSI and precipitation compared to intermediate ponderosa pine (for PDSI, 71% vs. 53% respectively, and $p < 0.001$; and for precipitation 75% vs. 62%, respectively, and $p < 0.001$; Fig. 4). There were no significant between-species differences in the response of intermediate trees to temperature (Fig. 3). Conversely, dominant trees did not have significant species-related differences in sensitivity to PDSI or precipitation, but dominant ponderosa pine were approximately twice as temperature-sensitive as dominant Douglas-fir ($p < 0.001$, coefficient estimates = -0.21 [SE = 0.01] and -0.11 [SE = 0.01], respectively; Fig. 3). Approximately 27% of dominant ponderosa pine exhibited a significant relationship to temperature compared to only 5% of dominant Douglas-fir (Fig. 4).

### *3.2 Species-specific effects of habitat type on sensitivity to climate*

I found a significant interaction between species and habitat type for both PDSI and precipitation ($t = -4.39$ and $p < 0.001$ for PDSI; and $t = -2.56$ and $p = 0.01$ for precipitation; Table 3), but the effect of temperature did not vary for either species between habitat types. While both species trended toward greater sensitivity to PDSI and precipitation in Xeric relative to Dry-Mesic sites, this difference was only significant for Douglas-fir ($p < 0.001$ for both variables; Fig. 3). Approximately 93% of Douglas-fir trees in Xeric sites were significantly influenced by

PDSI compared to 51% in Dry-Mesic sites ($p < 0.001$; Fig. 4). The relative proportion of trees with a significant sensitivity to precipitation followed a similar pattern as PDSI (Fig. 4).

With respect to between-species differences in the effect of habitat type on climate sensitivity, I found that for Xeric sites, Douglas-fir was significantly more sensitive to PDSI and precipitation relative to ponderosa pine ($p < 0.001$ for both variables; Fig. 3), but for Dry-Mesic sites, there were no significant between-species differences in response to these variables. In both Xeric and Dry-Mesic habitat types, ponderosa pine was significantly more sensitive to temperature than was Douglas-fir ($p < 0.001$ for both variables; Fig. 3). Only approximately 5% of Douglas-fir exhibited a significant relationship to temperature in each habitat type, compared to approximately 16% of ponderosa pine in the Xeric habitat type and 21% in the Dry-Mesic habitat (Fig. 4).

## 4. Discussion

Predicting climate change threats to dry coniferous forests and designing stand-level treatments that will increase forest resiliency to climate change requires assessing the sensitivity of mature trees to climatic variability and identifying the key environmental factors that influence climate responses across complex landscapes. To address these issues, I quantified the relative influences of species (*Pinus ponderosa* vs. *Pseudotsuga menziesii*), crown class (dominant vs. intermediate), and habitat type (Xeric vs. Dry-Mesic) on the climate responses of mature trees in typical, unmanaged forests in northeastern Washington (USA).

The high percentage of trees exhibiting significant correlations with PDSI and precipitation suggests that growth of each species is primarily limited by water availability during the growing season. This finding is consistent with findings from other investigations of climate-growth relationships for ponderosa pine and Douglas-fir in dry forests of the Interior Northwest (e.g. Kusnierczyk and Ettl, 2002; Littell *et al.*, 2008). In general, environmental factors related to water supply, such as precipitation, are the most powerful controls on cambial activity in arid ecosystems, while energy (e.g. temperature and growing season duration) are most important in areas with adequate water supply, such as areas of high elevation and latitude (Gholz, 1982; Stephenson, 1990; Waring and Running, 1998).

### ***4.1 Species-specific effects of canopy class on climate sensitivity***

I found strong evidence that canopy position affects climate-growth relationships of ponderosa pine but not Douglas-fir: dominant ponderosa pines are significantly more responsive to precipitation and substantially more sensitive to high temperatures than are intermediate ponderosa pines. Perhaps the most striking example of this key finding can be seen in the dramatically different responses to temperature. Whereas the temperature sensitivity of Douglas-fir did not vary across canopy classes, temperature had a substantially impact greater (approximately double) on dominant ponderosa pine relative to intermediate ponderosa pine. The contrasting effects of canopy position on temperature responses of these two species likely reflect fundamental differences in their physiology, morphology and hydraulic strategies. For example, relative to Douglas-fir, ponderosa pine are able to substantially modify stomatal conductance in response to changing environmental conditions (Stout and Sala, 2003; Domec *et al.*, 2004) – better stomatal control greatly reduces the chance of hydraulic failure (McDowell *et al.*, 2008). Because the leaves of dominant trees are exposed to full sunlight and significantly higher temperatures than those of intermediate trees, growth of dominant ponderosa pine is much more tightly coupled to temperature compared to intermediate ponderosa pines that are buffered from the direct effects of temperature by shading. This idea is consistent with numerous studies showing that shading is a primary mechanism by which neighboring plants modify external environmental conditions, in this case ameliorating the negative impact of high temperatures and low water-availability on growth (Callaway, 2007; Brooker *et al.*, 2008). Relative to ponderosas pine, however, there are important differences in basic life history traits of Douglas-fir, including significantly greater shade tolerance (Niinemets and Valladares, 2006). As such, it is not surprising that canopy positioning is not an important factor influencing climate sensitivity for this species.

Based on previous observations showing greater climate sensitivity – i.e. a tighter coupling of stemwood production to climate – in trees that die from abiotic stress compared to those that survive (Pedersen, 1998; Ogle *et al.*, 2000; Suarez *et al.*, 2004; McDowell *et al.*, 2010), my results suggest that dominant ponderosa pine may be more vulnerable to climate change than intermediate ponderosa pine. This conclusion seems consistent with several recent investigations showing a positive relationship between tree size and drought sensitivity among *Pinus* species. For example, Ganey and Vojta (2011) found that mortality in *Pinus ponderosa* forests was significantly lower than expected in smaller-diameter size classes but larger than expected in the largest size classes. Also, in a tree-ring study of *Pinus sylvestris,* Martínez-Vilalta et al. (2012) analyzed 1,433 trees from 393 plots and concluded that large trees were significantly more drought sensitive than smaller ones. If these observed differences in tree sizes and mortality rates are related to stand dynamics, such as competition and social status, thinning treatments in dry ponderosa pine forests may not effectively create stands that are more resilient to climate change (USFS, 2008). Although reducing stand density and leaf area could reduce water stress for residual trees (Stone *et al.*, 1999; Wallin *et al.*, 2004), thinning small-diameter trees growing beneath the dominant canopy actually may remove the individuals that are the least vulnerable to the negative effects of increasing temperatures and extreme drought events associated with climate change.

### *4.2 Species-specific effects of habitat type on sensitivity to climate*

I found that Douglas-fir, but not ponderosa pine, was significantly more sensitive to water availability in Xeric sites relative to Dry-Mesic ones. This observation is consistent with previous work showing that relatively small differences in elevation can significantly influence climate-growth relationships of Douglas-fir but are generally less important to ponderosa pine (Kienast *et al.*, 1987; Kusnierczyk and Ettl, 2002; Case and Peterson, 2005). Here again, species-specific differences in climate responses most likely reflect the contrasting hydraulic strategies and life history traits of ponderosa pine and Douglas-fir. Despite the fact that ponderosa pine is a more drought-tolerant species (Niinemets and Valladares, 2006), Douglas-fir is actually more resistant to cavitation under high pressure gradients (Pinol and Sala, 2000; Domec and Gartner, 2002; Stout and Sala, 2003). This ability to withstand (but not avoid) significant water stress allows Douglas-fir to persist in dry habitats, but it also means that fluctuations in soil water and physiological processes become more tightly coupled in increasingly xeric sites. Ponderosa pine, on the other hand, has developed structural adaptations that allow it to avoid dangerously low water potentials. For example, Barnard (2011) found that ponderosa pine had almost twice the sapwood area supplying water to a given leaf area as Douglas-fir, leading to a 50% decrease in the pressure gradient required to conduct a given amount of water. Moreover, ponderosa pine, but not Douglas-fir, is able to significantly modify the ratio of biomass in leaf area relative to sapwood area ($A_L$:$A_S$) across environmental gradients in response to increasing aridity (Delucia *et al.*, 2000). Thus, through a combination of better stomatal control, lower $A_L$:$A_S$, and better regulation of $A_L$:$A_S$ across contrasting sites, ponderosa pine is less affected by an overall decrease in mean water availability in increasingly xeric sites. Consequently, greater sensitivity to water availability of Douglas-fir, but not ponderosa pine, in xeric sites most likely reflects known differences in hydraulic architecture and life history strategies of these two species and is consistent with the idea of an adaptive tradeoff between xylem efficiency and hydraulic safety (e.g. Pinol and Sala, 2000; Barnard *et al.*, 2011).

I also found that ponderosa pine was significantly more sensitive to temperature than Douglas-fir, regardless of habitat type. Unlike soil water deficits, the effects of air temperature on tree growth processes are significantly more direct and immediate. As such, sensitivity to maximum temperatures reflects a tree's capacity to respond quickly to discrete events (e.g. heat waves during the growing season), and a short-term tradeoff between carbon assimilation and loss of water to transpiration. The consistent high temperature-sensitivity of ponderosa pine (i.e. greater reductions in radial growth in response to high temperatures) is again consistent with this species' "stress-avoidance" strategy and higher stomatal sensitivity. These results suggest that differences in climate sensitivity among species reflect fundamental differences in physiology and life history traits and, as such, are not necessarily correlated to vulnerability to drought-induced mortality.

## 5. Conclusions

I found that climate sensitivity of tree growth is significantly modulated by tree social status (canopy class) and habitat conditions, but these effects are highly species-specific. Most notably, I found that canopy position substantially modified tree growth responses to high temperatures and precipitation for ponderosa pine, but not Douglas-fir. These findings may have important implications for understanding the effects of stand structure on climate sensitivity and the differential effects of altering stand structure on climate-growth relationships of common forest trees, both of which may help managers promote forests that are resilient to future climatic conditions. I also found that differences in climate sensitivity were closely related to species-specific strategies for coping with water stress. This means that for certain species, high climate sensitivity may indicate a close coupling between environmental conditions and physiological stress, while for others a high degree of climate sensitivity may reflect an adaptive trait for avoiding dangerously low water potentials. Therefore, in contrast to numerous tree-ring studies demonstrating a positive correlation between climate sensitivity and drought-induced mortality within-species (e.g. Pedersen, 1998; Ogle *et al.*, 2000; Suarez *et al.*, 2004; McDowell *et al.*, 2010), differences in climate sensitivity among-species does not necessarily reflect differences in vulnerability to climate change. Future research should investigate the issue of climate sensitivity within a framework of species-specific life history traits and adaptive hydraulic strategies to more clearly establish the relationship between climate sensitivity and vulnerability to climate change.

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**Table 1.** Attributes of the 15 study sites (see Fig. 1), including habitat type, elevation and mean growing season (May-July) climate (precipitation and temperature) from 1950-2007.

| Site ID | Habitat type | Elev. (m) | Total precip. (mm) | Max temp. (°C) |
|---|---|---|---|---|
| A | Xeric | 945 | 110 | 26.2 |
| B | Xeric | 640 | 140 | 27.4 |
| C | Xeric | 975 | 153 | 27.2 |
| D | Xeric | 930 | 130 | 26.3 |
| E | Xeric | 1066 | 158 | 28.3 |
| F | Dry-Mesic | 1097 | 199 | 23.3 |
| G | Dry-Mesic | 1158 | 180 | 27.9 |
| H | Dry-Mesic | 1128 | 157 | 26.0 |
| I | Dry-Mesic | 914 | 153 | 27.2 |
| J | Dry-Mesic | 1250 | 188 | 24.8 |
| K | Dry-Mesic | 1250 | 176 | 25.7 |
| L | Dry-Mesic | 1311 | 166 | 23.3 |
| M | Dry-Mesic | 1128 | 131 | 25.2 |
| N | Dry-Mesic | 975 | 162 | 26.1 |
| O | Dry-Mesic | 884 | 162 | 26.7 |

**Table 2.** Tree characteristics, including number of sampled trees (n), mean tree age (Age), diameter at breast height (DBH), and height, and chronology statistics, including mean sensitivity (MS) and mean intra-site correlation (Rbar), for dominant (DO) and intermediate (IN) *Pinus ponderosa* and *Pseudotsuga menziesii*.

| | | Tree characteristics | | | | Chronology statistics | |
|---|---|---|---|---|---|---|---|
| Species | Canopy Class | n | Age | DBH (cm) | Height (m) | MS* | Rbar* |
| *Pseudotsuga* | DO | 220 | 110 (37) | 48 (12) | 27 (5) | 0.24 | 0.57 |
| *menziesii* | IN | 187 | 90 (28) | 23 (6) | 17 (4) | 0.26 | 0.47 |
| *Pinus* | DO | 161 | 143 (61) | 53 (14) | 28 (5) | 0.23 | 0.46 |
| *ponderosa* | IN | 125 | 96 (36) | 26 (7) | 18 (4) | 0.26 | 0.36 |

* See Methods

**Table 3.** Results of the linear mixed-effects model including effect of species (*Pinus ponderosa* vs. *Pseudotsuga menziesii*), canopy class (dominant vs. intermediate), and habitat type (Xeric vs. Dry-Mesic) on tree responses to monthly measures of average PDSI, total precipitation and average maximum temperature during the growing season (May-July). Results for insignificant covariates are not shown.

| | Coefficient value | Standard error | t-value | p-value |
|---|---|---|---|---|
| PDSI | | | | |
| Intercept | 0.324 | 0.037 | 8.676 | <0.001 |
| Habitat Type | -0.083 | 0.046 | -1.818 | 0.092 |
| Species | 0.093 | 0.020 | 4.590 | <0.001 |
| Canopy Class | -0.047 | 0.017 | -2.741 | 0.006 |
| Species*Canopy Class | 0.091 | 0.022 | 4.154 | <0.001 |
| Species *Habitat Type | -0.102 | 0.023 | -4.387 | <0.001 |
| Precipitation | | | | |
| Intercept | 0.434 | 0.031 | 14.169 | <0.001 |
| Habitat Type | -0.073 | 0.037 | -1.956 | 0.072 |
| Species | 0.054 | 0.022 | 2.472 | 0.014 |
| Canopy Class | -0.089 | 0.018 | -4.878 | <0.001 |
| Species*Canopy Class | 0.073 | 0.024 | 3.076 | 0.002 |
| Species*Habitat Type | -0.064 | 0.025 | -2.577 | 0.010 |
| Temperature | | | | |
| Intercept | -0.214 | 0.014 | -15.826 | <0.001 |
| Species | 0.108 | 0.013 | 8.121 | <0.001 |
| Canopy Class | 0.099 | 0.015 | 6.605 | <0.001 |
| Species*Canopy Class | -0.098 | 0.019 | -5.066 | <0.001 |

## Figure Captions

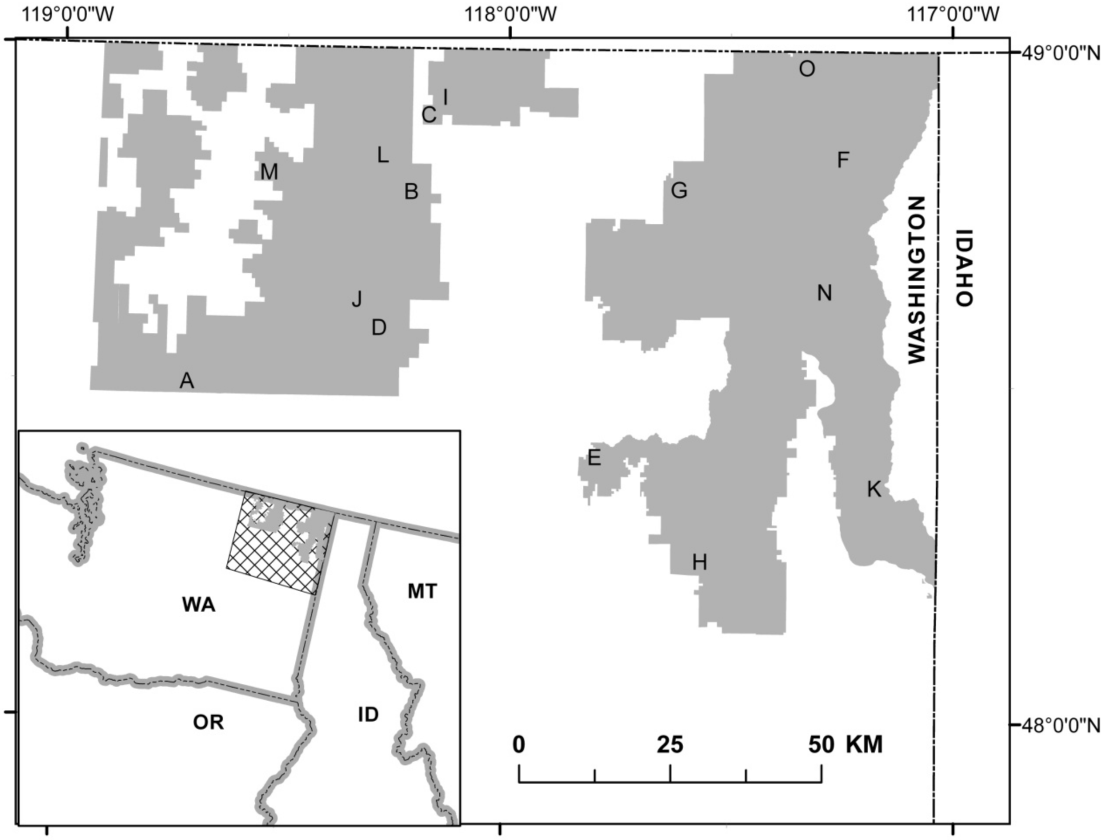
Figure 1. Location of the study sites in the Xeric (letters A-E) and the Dry-Mesic (letters F-O) Habitat Types on the Colville National Forest (darker shaded area) in northeastern Washington State (inset). The lightly shaded area shows NCDC Climate Division 9.

Figure 2. Time series from primary period of analysis (1950-2007) showing variation for dominant (solid traces) and intermediate (dashed traces) canopy classes of *Pinus ponderosa* (left column) and *Pseudotsuga menziesii* (right column) in (A) mean raw ring widths and (B) mean ring width indices (RWI) in Xeric and Dry-Mesic habitat types. Dotted line indicates average ring-width (RWI = 1).

Figure 3. Mean climate response (+/- SE) of *Pinus ponderosa* (PIPO; squares) and *Pseudotsuga menziesii* (PSME; triangles) between canopy classes (left column) and habitat types (right column). Letters indicate significant mean contrasts between groups; symbols with the same letter are not significantly different from each other. Dotted lines indicate significant within-species differences. Greater deviation from 0 (either positive or negative) indicates greater sensitivity.

Figure 4. Percent of *Pinus ponderosa* and *Pseudotsuga menziesii* trees exhibiting significant relationships with PDSI (top panel), precipitation (middle panel), and temperature (bottom panel). Data are grouped by canopy classes (left column) and habitat types (right column). Letters indicate significant mean contrasts among groups; bars with the same letter are not significantly different from each other.

**Figure 1**



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118°0'0"W
117°0'0"W
49°0'0"N
48°0'0"N
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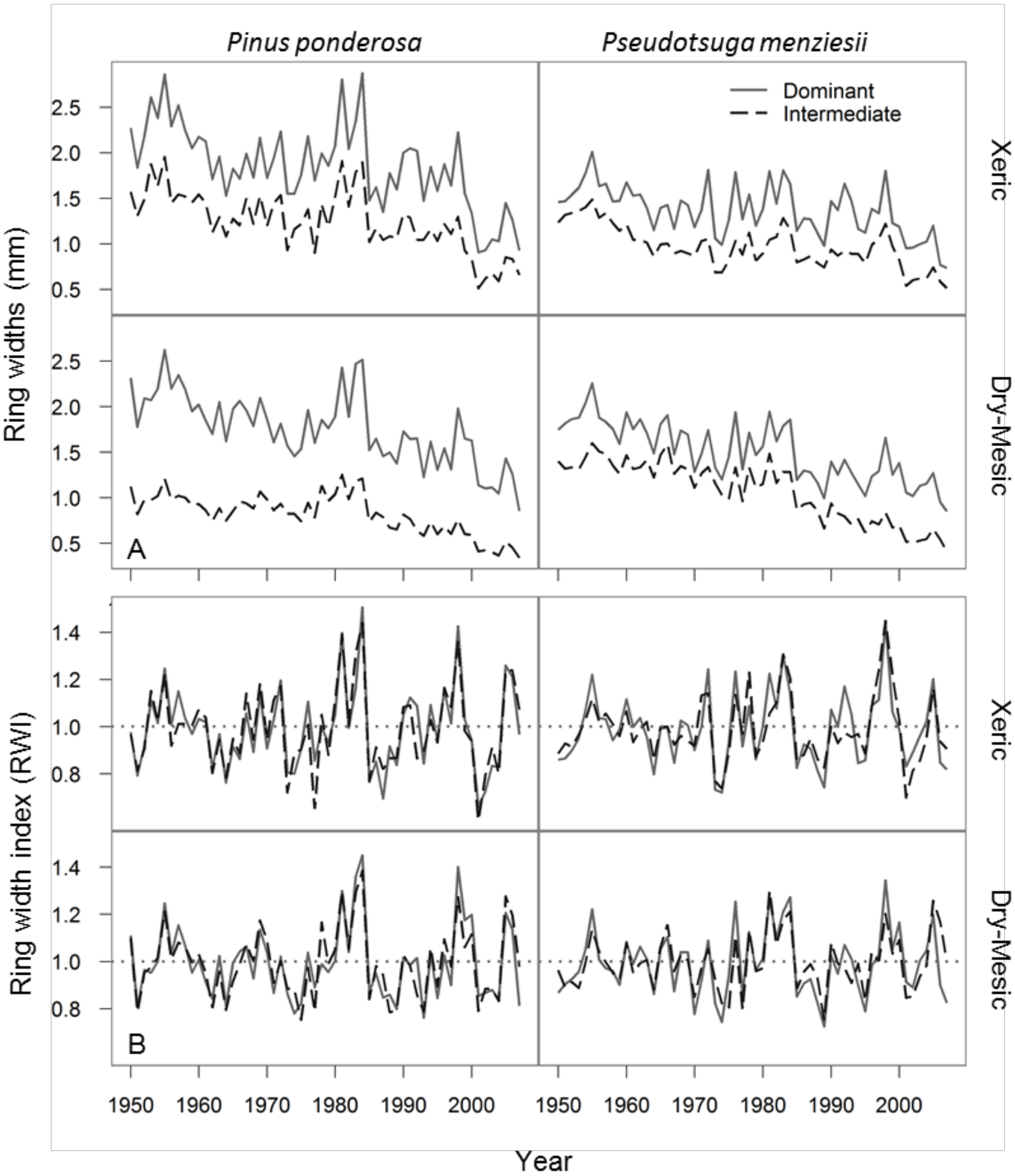
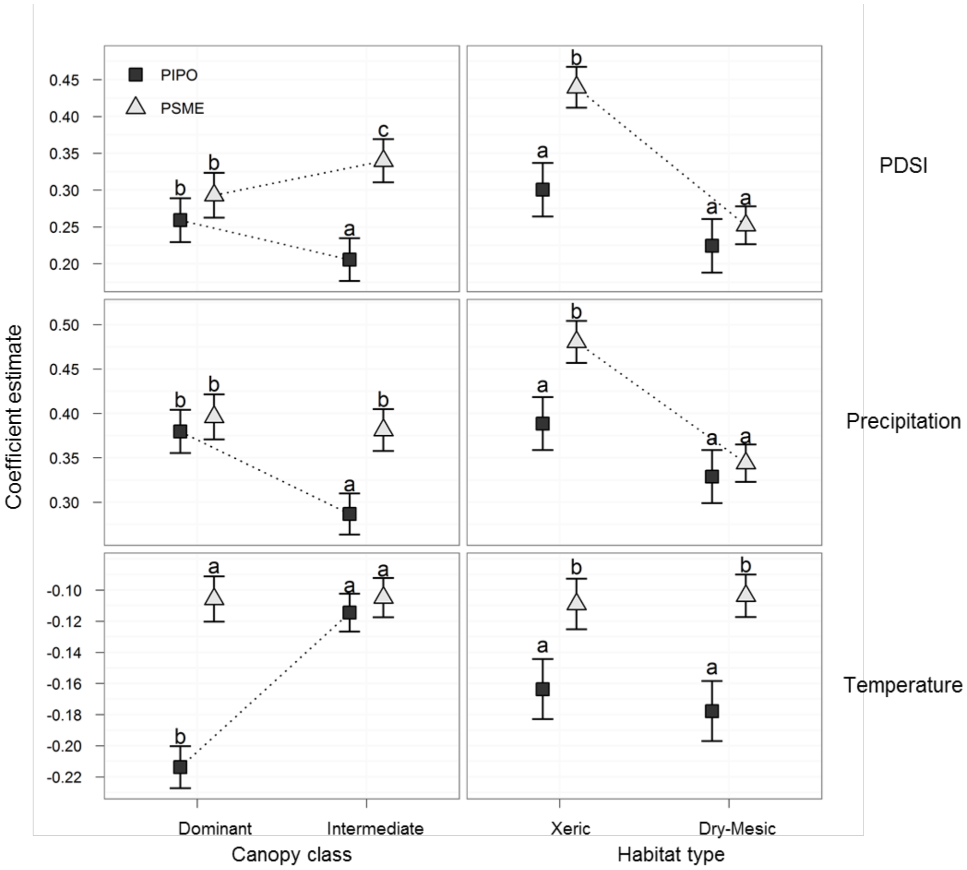
25
50 KM

**Figure 2**

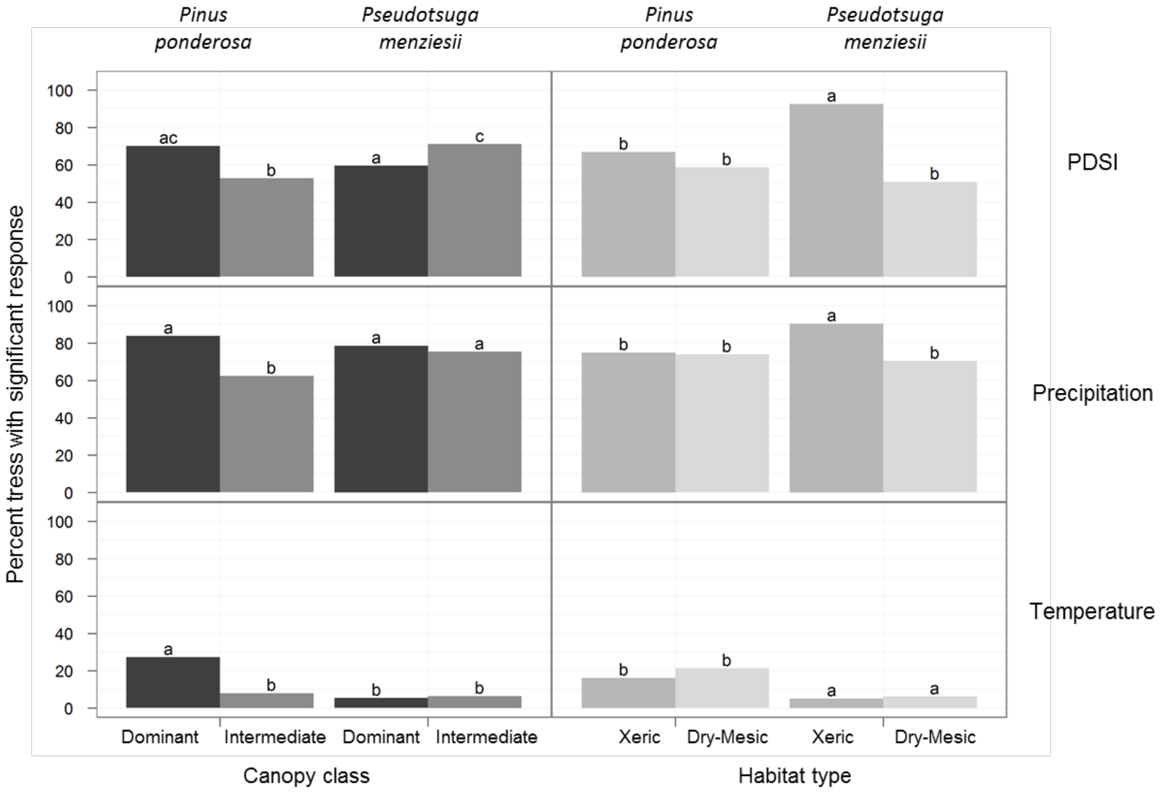


Pinus ponderosa
Pseudotsuga menziesii
Dominant
Intermediate
Xeric
Dry-Mesic
Xeric
Dry-Mesic
Ring widths (mm)
0.5
1.0
1.5
2.0
2.5
A
Ring width index (RWI)
0.8
1.0
1.2
1.4
B
1950
1960
1970
1980
1990
2000
Year

## Figure 3


PIPO
PSME
PDSI
Precipitation
Temperature
Coefficient estimate
0.45
0.40
0.35
0.30
0.25
0.20
0.50
0.45
0.40
0.35
0.30
-0.10
-0.12
-0.14
-0.16
-0.18
-0.20
-0.22
a
b
c
Dominant
Intermediate
Xeric
Dry-Mesic
Canopy class
Habitat type

## Figure 4


Pinus ponderosa
Pseudotsuga menziesii
Pinus ponderosa
Pseudotsuga menziesii
PDSI
Precipitation
Temperature
Percent tress with significant response
0
20
40
60
80
100
ac
b
a
c
b
b
a
b
a
b
a
a
b
b
a
b
a
b
b
b
b
b
a
a
Dominant
Intermediate
Dominant
Intermediate
Xeric
Dry-Mesic
Xeric
Dry-Mesic
Canopy class
Habitat type

**Supplementary File 1.** For each site (A-0), number of sampled trees (n), mean tree age (Age), mean sensitivity (MS), and mean intra-site correlation (Rbar) for dominant (DO) and intermediate (IN) chronologies. Dashes indicate no data.

| | | *Pseudotsuga menziesii* | | | | *Pinus ponderosa* | | | |
|---|---|---|---|---|---|---|---|---|---|
| Site | Canopy Class | n | Age | MS* | Rbar* | n | Age | MS* | Rbar* |
| A | DO | 12 | 123 | 0.26 | 0.61 | 10 | 221 | 0.24 | 0.42 |
| | IN | 17 | 75 | 0.28 | 0.65 | 17 | 86 | 0.27 | 0.34 |
| B | DO | 12 | 101 | 0.22 | 0.50 | 12 | 142 | 0.22 | 0.48 |
| | IN | 18 | 73 | 0.25 | 0.53 | 17 | 98 | 0.22 | 0.47 |
| C | DO | 14 | 111 | 0.29 | 0.60 | 16 | 131 | 0.25 | 0.66 |
| | IN | 10 | 68 | 0.29 | 0.50 | 11 | 108 | 0.31 | 0.39 |
| D | DO | 15 | 95 | 0.26 | 0.54 | 14 | 141 | 0.25 | 0.40 |
| | IN | 10 | 77 | 0.26 | 0.48 | 14 | 119 | 0.26 | 0.34 |
| E | DO | 15 | 86 | 0.25 | 0.62 | 14 | 104 | 0.24 | 0.53 |
| | IN | 13 | 83 | 0.24 | 0.51 | 11 | 86 | 0.26 | 0.41 |
| F | DO | 13 | 160 | 0.24 | 0.67 | - | - | - | - |
| | IN | 15 | 135 | 0.26 | 0.45 | - | - | - | - |
| G | DO | 14 | 118 | 0.21 | 0.55 | 13 | 119 | 0.24 | 0.45 |
| | IN | 15 | 76 | 0.25 | 0.34 | 8 | 99 | 0.27 | 0.20 |
| H | DO | 19 | 80 | 0.23 | 0.52 | 17 | 106 | 0.24 | 0.51 |
| | IN | 10 | 65 | 0.23 | 0.52 | 9 | 74 | 0.25 | 0.41 |
| I | DO | 15 | 117 | 0.28 | 0.54 | 20 | 193 | 0.24 | 0.5 |
| | IN | 12 | 109 | 0.31 | 0.53 | 5 | 114 | 0.28 | 0.4 |
| J | DO | 17 | 86 | 0.23 | 0.64 | 16 | 140 | 0.23 | 0.49 |
| | IN | 11 | 76 | 0.28 | 0.39 | 5 | 74 | 0.28 | 0.4 |
| K | DO | 15 | 82 | 0.19 | 0.50 | - | - | - | - |
| | IN | 12 | 90 | 0.25 | 0.30 | - | - | - | - |
| L | DO | 16 | 127 | 0.26 | 0.54 | - | - | - | - |
| | IN | 10 | 95 | 0.27 | 0.50 | - | - | - | - |
| M | DO | 15 | 130 | 0.27 | 0.67 | - | - | - | - |
| | IN | 8 | 111 | 0.33 | 0.54 | - | - | - | - |
| N | DO | 13 | 86 | 0.22 | 0.44 | 16 | 120 | 0.21 | 0.31 |
| | IN | 12 | 66 | 0.21 | 0.34 | 13 | 56 | 0.23 | 0.38 |
| O | DO | 15 | 96 | 0.23 | 0.63 | 13 | 120 | 0.20 | 0.33 |
| | IN | 14 | 87 | 0.25 | 0.43 | 15 | 93 | 0.22 | 0.20 |

* See Methods

## Chapter 3:

# Effects of Biotic and Abiotic Factors on Resistance versus Resilience of Douglas-fir to Drought

### Abstract

Significant increases in tree mortality due to drought-induced physiological stress have been documented worldwide. This trend is likely to continue with increased frequency and severity of extreme drought events in the future. Therefore, understanding the factors that influence variability in drought responses among trees will be critical to predicting ecosystem responses to climate change and developing effective management actions. In this study, I used hierarchical mixed-effects models to analyze drought responses of *Pseudotsuga menziesii* in 20 unmanaged forests stands across a broad range of environmental conditions in northeastern Washington, USA. I aimed to, 1) identify the specific biotic and abiotic attributes most closely associated with individual-tree drought responses and 2) quantify the variability in drought responses at different spatial scales. I found that growth rates and competition for resources significantly affected resistance to a severe drought event in 2001: slow-growing trees and trees growing in subordinate canopy positions and/or with more neighbors suffered greater declines in radial growth in 2001. In contrast, the ability of a tree to return to normal growth when climatic conditions improved (resilience) was unaffected by competition or relative growth rates. Drought responses were significantly influenced by tree age: older trees were more resistant but less resilient than younger trees. Finally, I found that a significant proportion (approximately 50%) of the variability in drought resistance across the study area was at broad spatial scales, most likely due to differences in the total amount of precipitation received at different elevations. However, variation in resilience was overwhelmingly (82%) at the level of individual trees. My results

suggest that for *Pseudotsuga menziesii* resistance and resilience – the key components of stability – are driven by different factors and vary at different spatial scales.

## Introduction

During the last 40 years, there have been significant global increases in the intensity and duration of droughts; current climate models predict this trend will continue with increased frequency in the future (IPCC 2007). Although vegetation responses to periodic water stress is an important structuring force across multiple biological scales (Kramer 1983), recent research has underscored the potential for these more extreme events to push ecosystems beyond stability thresholds (Scheffer et al. 2001). Numerous studies across a range of forest types have already reported regional, drought-induced mortality of overstory trees (Allen et al. 2010; Breshears et al. 2005; van Mantgem et al. 2009) with cascading effects ranging from changes in phenology of understory vegetation (Rich et al. 2008) to food web disruption (Carnicer et al. 2011) and even to major shifts in ecosystem carbon cycling (Ma et al. 2012; Van der Molen et al. 2011). However, the effects of extreme events on tree mortality likely is not uniform but rather varies significantly both at large (e.g., within a region) and small (among individuals of the same species in the same population) spatial scales (Gitlin et al. 2006). Therefore, understanding the key factors influencing variability in drought responses within species and across sites will be critical for accurately predicting vegetation responses to climate change and developing effective management actions that enhance ecosystem stability.

Drought-stress occurs when soil water content is so low that trees can no longer maintain normal life processes. Physiological responses to drought vary as a function of the relative decrease in water availability (drought intensity) and the length of the event (drought duration) (reviewed by McDowell et al. 2008). In the short term, trees can minimize water lost through transpiration by closing stomata. However, if a drought is sufficiently intense, high evaporative demand coupled with low soil water availability leads to extreme tension in the xylem and, potentially, to hydraulic failure and desiccation of living tissues. During periods of prolonged water stress, trees may begin to shed leaves and shift allocation of resources from leaves to roots and sapwood. Although these physiological responses buffer xylem tensions and minimize risk of cavitation, they may also have longer-term consequences, including reduced carbon assimilation and growth. Consequently, trees often exhibit the effects of extreme climatic events for several years after they occur (Dobbertin 2005), and drought-induced mortality can lag anywhere from years to decades following extreme droughts (Bigler et al. 2007).

The physiological consequences of water stress also vary with stand- and tree-level factors. For instance, within a species, drought-induced mortality of overstory trees can vary substantially among stands of different forest types (Ganey and Vojta 2011) as well as among trees within a stand (Floyd et al. 2009; Mueller et al. 2005). At the tree level, numerous studies have shown that the effect of water stress on tree growth varies with tree size and age (Carrer and Urbinati 2004; Szeicz and MacDonald 1994). This may be related to shifts in carbon allocation associated with ageing (Ryan et al. 1997) or to increasingly negative water potentials associated with longer path lengths as trees reach their maximum size (McDowell et al. 2008).

In addition, long-term stressors such as competition may also “weaken” a tree and reduce its resistance to short-term inciting factors, including extreme drought events (Franklin et al. 1987; Manion 1981).  Linares et al. (2010), for example, found that *Abies pinsapo* with high levels of competition suffered greater growth declines during dry periods and suggested that the interacting effects of competition and drought contribute to drought-induced mortality. However, suppressed trees are also exposed to substantially different environmental conditions compared to dominant trees, including lower wind velocity, temperature and vapor pressure deficit (Aussenac 2000). These factors have direct and immediate impacts on transpiration rates and have been shown to ameliorate the negative effects of particularly intense or prolonged drought events (Brooker 2006).

It is well established that trees growing on xeric sites are more sensitive to annual fluctuations in water availability than are those growing in cool, moist forests or in sheltered conditions (Fritts 1976). There is also ample evidence that stand-level differences in aspect (Fekedulegn et al. 2003; Oberhuber and Kofler 2000; Villalba et al. 1994), elevation (Case and Peterson 2005; Holman and Peterson 2006; Zhang and Wilmking 2010), and latitude (Littell et al. 2008; Peterson and Peterson 2001) can significantly affect mean climate responses of mature trees. There is reason to believe that these general climate-growth relationships may not hold under extreme conditions (Allen et al. 2010; Phipps 1982). However, the relative impact of extreme climatic conditions on trees growing on contrasting sites is not well understood. Previous studies of the effects of physical site conditions on drought responses have produced variable, even contradictory, results. For example, radial growth of *Thuja occidentalis* was more affected by drought when growing in xeric sites than when growing in mesic sites (Tardif and Bergeron 1997), but Orwig and Abrams (1997) found the opposite results for *Pinus virgniana*. Similarly, in separate studies of drought-induced mortality of *Pinus edulis* in northern Arizona, Ogle et al. (2000) found significant soil-related differences following a severe drought in 1996, but Koepke et al. (2010) reached the opposite conclusion following a drought in the same region in 2002, suggesting a possible interaction between site conditions and drought duration and/or the timing of drought events. Stand-level variability in abiotic factors (soils, elevation, slope, aspect) may also interact with biotic factors, like stand structure and composition (e.g. Battles et al. 2008; Ganey and Vojta 2011) or site–specific differences in disturbance history (e.g. Lloret et al. 2011), leading to patchiness and spatial complexity in drought responses at the stand or forest level.

Ecological stability – the tendency of an ecosystem, population or individual to return to equilibrium following environmental disturbance or stress – has been described as a function of two related characteristics: *resistance* (the degree of response to a perturbation) and *resilience* (the ability of a system to return to its former state; i.e. engineering resilience sensu Holling (1973) (Pimm 1984). It is becoming increasingly clear that factors influencing the resistance and resilience of trees to extreme drought events are complex, operate at multiple scales, and interact in ways difficult to predict (McDowell et al. 2011). Resistance and resilience of ecological systems are generally estimated by comparing performance of organisms responding to stress from disturbance to that of a control population or a standardized baseline (MacGillivray and Grime 1995; Orwin and Wardle 2004). Using tree-rings, tree growth during stressful years and the years following the disturbance can be accurately measured, compared to growth under baseline conditions, and then simultaneously analyzed across space and time to reveal and disentangle the key environmental factors that regulate drought responses and influence susceptibility to drought-induced mortality. In the present study, I analyzed tree-ring series of *Pseudotsuga menziesii* from 20 stands across a broad range of environmental conditions and assessed variation in responses of individual trees to a severe drought event in 2001. My primary objectives were to 1) identify the specific biotic and abiotic attributes that were most closely associated with ecological stability (i.e. resistance and resilience as defined above); and 2) assess the variability in drought responses at different spatial scales. A better understanding of these dynamics is crucial to accurately predicting tree and stand-level responses to climate change.

## Methods

### Study area and site selection

This study was conducted on the Colville National Forest (CNF) in northeastern Washington between 48ºN and 49ºN latitude and 117ºW and 119ºW longitude (Fig. 1). With a range of 30 to 135 cm precipitation per year, the west side of the CNF is strongly influenced by a rain shadow formed by the northern Cascades, while the northeastern region has a near-maritime climate due to a westerly airflow forced over the Selkirk and Kettle River mountain ranges. To capture the variation in drought responses of Douglas fir at different spatial scales, I used a multi-level sampling design in which individual trees (the sampling unit) were nested within stands, which were then further nested within distinct forest types. At the broadest scale, sampling was stratified by the Forested Plant Association Group (PAG) (Williams et al. 1995). PAGs separate distinct biophysical environments based on shared floristics, environment and productivity and are a central component of commonly used vegetation models, including recent efforts attempting to link effects of climate change with project-level planning (e.g. FVS-CLIM Crookston et al. 2010).

Three PAGs (hereafter "Forest Type") were selected for sampling: 1) *Pinus ponderosa-Pseudotsuga menziesii/Agropyron spicatum* (hereafter "PIPO"); 2) *Pseudotsuga menziesii/Physocarpus malcaeus* (hereafter "PSME"); 3) *Abies lasiocarpa/Vaccinium membranaceum* (hereafter "ABLA"). PIPO is the hottest and driest Forest Type in the CNF and generally occurs below 1,000 m; vegetation is characterized by open stands of ponderosa pine and Douglas-fir, with a bunch-grass-dominated understory and few shrubs. PSME is the most common Forest Type in this region. It is generally cooler and wetter than PIPO and occurs at a broad range in elevation (approximately 500 - 1,500 m). *Physocarpus malcaeus* and *Holodiscus* *discolour* are the most prevalent shrubs, but *Amelanchier arborea* and *Mahonia aquifolium* are also quite common. Douglas-fir is the most common tree species and ponderosa pine is a major seral species. The ABLA Forest Type, which is well distributed across the study area at elevations above 1,500 m, includes upland forest stands with either *Abies lasiocarpa* or *Picea engelmannii* as the climax species

Within each Forest Type, I used a GIS to identify stands with the following criteria: 1) minimum size of 8 ha; 2) southwest-southeast aspect; 3) mid-slope position on an approximately 40% slope; and 4) no significant disturbance (such as logging or fire) in the last 60 years. Prior to sampling, all potential sites were visited to see that these conditions were met and to verify that there was no evidence of pathonogenic outbreaks, substantial mistletoe or windthrow. Through this process, I identified a total of 20 suitable sites broadly distributed across the study area (Table1, Fig. 1).  PIPO sites were an average of approximately 200 m lower in elevation than PSME sites and 600 lower than ABLA sites. From 1950-2007, the average annual precipitation ranged from 47 mm in PIPO stands to 60 mm and 121 mm in PSME and ABLA sites, while average annual temperatures were 6.6° C, 5.9° C and 3.9° C  respectively.

From each stand, I sampled 10-15 dominant/co-dominant trees (trees receiving full light from above and partial from the sides; hereafter "dominant") and 10-15 intermediate trees (trees in definitively subordinate positions, receiving little direct light from above and no light from the sides; hereafter "intermediate"). Fewer intermediate trees were sampled in ABLA stands because Douglas-fir generally occurs as seral remnants and individuals in sub-dominant canopy positions were relatively scarce in this plant association. Trees selected for sampling met the following criteria: 1) no obvious defects such as cankers, scars, rot, substantial lean or mistletoe infestation; 2) >50 years old at breast height (1.3 m); 3) >50 m from the edge of the stand and other sampled trees of the same canopy class; 4) >10 cm diameter at breast height (DBH); and 5) >10 m from any dead or dying trees.

For each subject tree, tree height was measured using a laser hypsometer, and canopy width was estimated as the average length from the stem to the tip of the longest branch at each of the four cardinal directions. Competition from understory vegetation was estimated within the drip line using four wedge-shaped subplots. In each subplot, abundance was estimated separately for herbs and shrubs using broad percent-cover categories (0%, 1-25%, 26-50%, 51-75%, 76-100%). The zone of influence around each subject tree was identified using a fixed-angle gauge (Basal Area Factor [BAF] = 10 for PIPO sites and 20 for PSME and ABLA sites respectively) (Biging and Dobbertin 1992). To estimate the basal area (BA) of competitor trees, I multiplied the total number of trees identified in this zone by the BAF.

Site index (SI) was used a measure of site quality and productivity. SI is strongly correlated with temperature and growing season length and can be strongly affected by climate conditions (Crookston et al. 2010). Site index was estimated using all dominant and co-dominant trees from each site according to the method described by Monserud (1984) for inland Douglas-fir.

### Dendrochronological methods

For each sampled tree, I extracted two cores with an increment borer at breast height from opposite sides of the stem and perpendicular to the fall line of the slope. Cores were transported to the lab in protective straws, mounted in wooden mounts, and sanded with progressively finer sandpaper using standard techniques (Fritts 1976; Stokes 1968). I visually cross-dated all cores and calculated tree age by counting annual rings. When the pith was absent from increment cores, I used a concentric ring pith locator to estimate age (Applequist 1958).

Increment cores were scanned using an optical scanner at 1200 dpi resolution and all rings of each core were measured to the nearest 0.001 mm using the CooRecorder software (Larsson 2003b). Occasionally, the image resolution was inadequate to confidently measure the smallest rings. In these cases, cores were measured using a microscope and a Velmex sliding stage micrometer interfaced with a computer. I checked for cross-dating errors with the software programs COFECHA (Holmes et al. 1986) and CDendro 7.1 (Larsson 2003a). Only cores that could be confidently cross-dated were statistically analysed. Finally, I averaged tree-ring measurements from the same tree by year to produce one mean ring-width time series for each sampled tree.

Basal area (BA) of each subject tree was calculated by assuming a circular cross section and using inside-bark radius ($BA = \pi r^2$). Bark thickness was calculated according to the formula developed for interior Douglas-f1ir by Monserud and Forest (1979). A relative growth rate (RGR) was calculated for each tree as the ratio of total radial growth ($cm^2$) from 1998 to 2007 ($BAI_{10}$) to tree size in 1998 (RGR = $BAI_{10}/BA - BAI_{10}$ ).

## Climate data

The Parameter-elevation Relationships on Independent Slopes Model (PRISM) dataset (Daly et al. 2008) was used to obtain fine-scale (800m) gridded monthly precipitation and temperature climate data for each sampled stand. PRISM weighs individual climate station data and estimates values across a landscape accounting for differences in elevation, aspect, and topographic exposure.

Regional water stress was estimated using Palmer drought severity index (PDSI) (Alley, 1984) data obtained from the National Climate Data Center for Climate Division 9 of

Washington state (northeastern Washington, available at http://www.ncdc.noaa.gov). The PDSI scale is centered on zero with negative numbers indicating drier than average conditions; values less than negative 3 are classified as “severe” drought, while negative 4 is considered “extreme” drought.

### Quantifying drought responses

I focused on tree responses to a severe drought that occurred in 2001. According to data obtained from the National Climate Data Center for Climate Division 9, the total precipitation received in the study area during the growing season (May – August) was 9.5 cm; approximately 64% of the long–term (1950-2000) average. Based on PDSI, 2001 was the most extreme drought year over a 30 year period in this region (average annual PDSI = -3.8). 2001 was also a year of abnormally low growth across the entire study area (Fig. 2b), suggesting that this disturbance event was driven by regional climate patterns – specifically high temperatures coupled with low precipitation - and not local drivers such as insect outbreaks.

I assessed resistance by comparing tree performance in the year of drought to performance without the effects of drought disturbance (*sensu* Pimm 1984). To estimate expected tree growth in the absence of drought disturbance (i.e. the baseline), I fit a regression curve to each tree-ring series. This commonly used method, known as “detrending”, accounts for low-frequency biological growth trends (related to changes in tree age and size). To do this, I used cubic splines with a 50% frequency-response cut-off at 30-year periods (Cook and Peters 1981). To quantify the degree of departure from average growth (i.e. resistance and resilience), I computed the ratio between measured ring-widths and the corresponding fitted values. This resulted in a dimensionless ring-width index (RWI) that has numerous advantages over using raw data including removing differences in ring widths related to variability in tree size or age, and rescaling each series to a mean of one and near constant variance (Fritts 1976). RWI values > 1 indicate above average growth while RWI < 1 denotes below average growth. To assess variability in resistance (i.e. the degree of change in radial growth caused by the disturbance event), I used RWI values in 2001, the severe drought year, as the primary response variable.

To assess resilience – defined here as a tree's ability to return to average growth following a disturbance (*sensu* Pimm 1984) – I analyzed RWI values in 2005, the first year PDSI returned to near 0, indicating that soil moisture had returned to average. In addition, in order to characterize the full curve of recovery, I also analyzed growth responses (RWI) each year from 2002 to 2004 (hereafter "recovery"). These three years were significantly drier than the long-term average (average annual PDSI = -2.5, -1.9 and -2.4 for 2002, 2003, and 2004 respectively). As such, the recovery period is characterized by consistently moderate, though not severe, soil water deficits.

### Statistical analysis

To characterize the factors that were most important in determining the drought responses of individual trees, I used multi-level linear mixed effects (LME) models. By explicitly distinguishing between distinct sources of variation – population-averaged (main effects) and group-specific (random effects) – LME models allow for uneven sample sizes and for the covariance of error within groups associated with a nested data structure (Pinheiro and Bates 2009). As such, mixed-effects models specifically account for the spatial autocorrelation between trees at the same scale, which allows for a more accurate inference of the fixed effects of interest. Using separate models for each year, I modeled drought resistance (RWI in 2001), recovery (RWI in years 2002-2004) and resilience (RWI in 2005) of tree $i$, in Forest Type $j$ and stand $k$ as:

$$RWI_{ijk} = \beta_0 + \beta_1 \ldots . \beta_p + b_j + \gamma_{j(k)} + \varepsilon_{ijk} \qquad [1]$$

where $\beta_0$ represents the intercept; $\beta_{1 \ldots}\beta_p$ are the coefficients for tree- and stand-level attributes modeled as fixed effects (see Table 2 for a full list of fixed effects); $b_j$ and $\gamma_{j(k)}$ are the random effects of Forest Type and stand respectively; and $\varepsilon_{ijk}$ is the random error. The significance of fixed-effect coefficients were estimated using maximum-likelihood (ML) along with the Markov Chain Monte Carlo (MCMC) method. Insignificant variables (at $P > 0.05$) in any model year were removed from the final model. However, if a variable was significant in at least one year, it was retained in the final model and fit to all years to facilitate informal comparison of coefficient estimates between years. An estimate of the total variance explained ($R^2$) in each model was calculated using likelihood ratio statistics (Magee 1990). Diagnostic plots were used to validate assumptions about residuals and random effects (Pinheiro and Bates 2009); no deviations from assumptions were detected. Predictor variables were log transformed to improve normality when needed (see Table 2). Multicollinearity of predictor variables was assessed via the variance inflation factor (VIF); VIF values were low (< 3), indicating low collinearity.

I used the random effect components of Equation 1 to assess the proportion of the variability in drought responses at each scale of the sampling (Pinheiro and Bates 2009) [i.e. the same model structure as in Equation 1 but without fixed effects $\beta_{1 \ldots}\beta_p$]. The proportion of the total variance associated with $b_j$ (Forest Type), $\gamma_{j(k)}$ (stand) and $\varepsilon_{ijk}$ (individual trees) was calculated and converted to a percentage. I fit the models for each year using restricted maximum-likelihood and then tested the significance of random effects using likelihood ratio tests.

All calculations and analyses were accomplished with the statistical software R (v 2.14, R Foundation for Statistical Modeling) along with the packages *dplR* for detrending tree-ring series and *nlme* for LME modeling.

### Results

In 2000, the year before the drought, average RWI across all three Forest Types was 1.06, indicating that mean growth rates were slightly above average in the study area. In 2001, mean RWI decreased approximately 30% to 0.77. Trees in the driest Forest Type, PIPO, had lower mean RWI than trees in ABLA, the highest and wettest Forest Type (0.63 and 0.86 respectively; Fig. 2b).

Drought resistance (measured as RWI in 2001) was significantly influenced by five biotic factors and one abiotic factor (Table 3). Growth in the prior year (RWI_Lag1) had a significant positive influence on growth ($t = 9.45$; $P < 0.001$), while basal area of neighboring trees (competition) had a significant negative effect ($t = -5.02$; $P < 0.001$). Trees in subordinate canopy positions had greater growth reductions relative to dominant or co-dominant individuals ($t = -2.38$; $P = 0.018$; Table 3). Older trees and individuals with high relative growth rates were also significantly more drought resistant ($t = 2.56$; $P = 0.011$ and $t = 2.71$; $P = 0.007$ for Age and RGR respectively; Table 3). The only abiotic variable assessed that significantly affected resistance was total precipitation received that year ($t = 3.44$; $P = 0.004$; Table 3).

In the three years following the 2001 drought (drought recovery), the relative effects of both biotic and abiotic variables fluctuated substantially. RWI in the previous year had a significant effect in all years, but its influence was the least pronounced by 2004 ($t = 3.44$; $P =$

0.001). The effect of RWI two years prior (RWI_Lag2) was most important in 2002 ($t = 5.09$; $P < 0.001$, but was also highly significant in 2003 ($t = 3.59$; $P < 0.001$), two years after the drought event. Tree height had a significant positive effect in 2003 ($t = 2.94$; $P = 0.003$) and no significant effect any other year. Similarly, there were no significant differences between canopy classes in 2002 or 2004, but in 2003 the effect of a subordinate canopy position was significantly positive ($t = 2.51$; $P = 0.012$). With regard to abiotic variables, site index was a significant factor in 2002 ($t = -2.95$; $P = 0.01$). In contrast to the year of the severe drought (2001) variability in precipitation among stands did not have a significant effect on variability in RWI during the moderately dry, post-drought period from 2002-2004. By 2003, abiotic factors were no longer significant.

Drought resilience (measured as RWI in 2005, when soil moisture returned to normal) was significantly affected by three biotic factors. RWI_Lag1 had a significant positive influence ($t = 8.12$; $P < 0.001$), and RWI_Lag2 (i.e. growth in 2003) had a significant negative influence ($t = -4.53$; $P < 0.001$) on drought resilience. The only other biotic variable that was significant in 2005 was age ($t = -2.51$; $P < 0.012$). No abiotic factors significantly affected resilience.

The total amount of variation explained by the model was fairly high in 2001 ($R^2 = 0.61$) but progressively declined as the dry conditions persisted in the following years ($R^2 = 0.47$, 0.30, 0.17 in 2002, 2003 and 2004 respectively; Table 3). When soil moisture recovered in 2005, $R^2$ increased to 0.34 (Table 3).

Thirty-two percent of the overall variance in drought resistance was related to differences among Forest Types ─ the broadest spatial scale ($L= 6.11$; $df = 1$; $P = 0.014$). In 2002, the first drought recovery year, variability at the Forest Type level increased slightly to 36% ($L=11.35$; $df = 1$, $P = < 0.0001$; Fig. 3). For the remaining recovery and resilience period, however, variability associated with Forest Type, , was not significant. In contrast, variability at the stand-level accounted for a significant amount of variation in RWI each year. The strongest effect was in 2005 (30% variance; L=128.69; *df* = 1, $P < 0.0001$), but results were also significant in 2001 through 2004 ($34.13<L<111.07$, df = 1, $P < 0.0001$). The percent of total variance in RWI was generally highest at the smallest spatial scale, the tree-level. Although it was significant every year, variation associated with among-tree differences changed substantially over time: it was lowest in 2001 (45%), increased to 54% in 2002 and then to 85%, 87% and 70% in 2003, 2004 and 2005 respectively (Fig. 3).

## Discussion

This study reinforces the idea that ecosystem stability must be considered in terms of at least two distinct components – resistance and resilience – and suggests that these components are likely controlled by different mechanisms that vary at different spatial scales within a landscape. The primary findings were that 1) competition and relative growth rates affected resistance but not resilience; 2) older trees were more resistant but less resilient than younger trees; and 3) there was a high degree of variability in drought resistance at the broadest spatial scale (Forest Type) and relatively low variability at the smallest scale (tree-level), while the opposite trend was observed for resilience.

Both the basal area of neighboring trees and the effect of growing in a subordinate canopy position had significantly negative parameter estimates, suggesting that trees growing with a high degree of competition suffered the greatest growth reductions during drought. Previous studies investigating the effects of competition on drought responses of conifers have found similar results for *Abies pinsapo* (Linares et al. 2009), *Pinus strobus* (Vose and Swank 1994), *Picea abies* (Van Den Brakel and Visser 1996) and *Pinus sylvestris* (Pichler and

Oberhuber 2007). Relative to dominants, competitively subordinate Douglas-fir trees are known to exhibit significantly reduced rooting depths and a greater shoot-to-root ratio (Eis 1974). In the face of sudden severe droughts, these structural limitations lead to lower drought resistance by significantly limiting their ability to acquire scarce resources, including access to deep soil water. This finding is consistent with ecological theory suggesting that when a single resource is limiting, competitive dominance will strongly regulate differences in plant performance (Tilman 1982).

Four years post-drought, when climatic conditions returned to normal after a prolonged dry period, growth responses no longer varied as a function of competition or relative growth rates. In addition, the influence of tree age from positive to negative, suggesting that older trees were significantly more drought resistant but less resilient. Previous studies of drought responses in conifers have also found that the primary factors influencing resistance and resilience can differ in both magnitude and direction, but results have been highly variable and difficult to generalize. For example, Lloret et al. (2011) found that fast-growing and younger *pinus ponderosa* were generally more drought resistant, but older trees recovered better from recent drought events. In a recent study of *pinus sylvestris*, Martínez-Vilalta (2012) also found that older trees were less able to recover (less resilient), but, regardless of age, fast growing trees were more severely affected (less resistant). The finding that fast growing trees were more drought resistant but younger trees were more resilient suggests different mechanisms underlying these two attributes of stability and points toward tree-level changes associated with increasing age or size.

Understanding the key mechanisms and possible tradeoffs between resistance and resilience in long-lived species such as trees is a critical but underdeveloped research area in ecology and climate change science. In an investigation of the relationship between ecosystem stability and biodiversity in conifer forests of the Sierra Nevada, DeClerck et al. (2006) found that community resilience, but not resistance, was positively associated with species richness. They suggested that whereas resistance was primarily driven by competition for a limiting resource, resilience is driven by the ability of a community to partition resources in the absence of a single limiting resource. In this study, I also found significant differences in the factors driving resistance and resilience and, consistent with this theory, that trees with a greater ability to acquire resources (i.e. individuals with high relative growth rates and fewer neighbors) were significantly more drought resistant but not necessarily more resilient. This also seems generally consistent with previous research demonstrating greater growth reductions during drought in high-density stands (e.g. Klos et al. 2009; Moreno-Gutiérrez et al. 2011) but no relationship between stand density and drought-induced mortality – perhaps the ultimate measure of resilience (Floyd et al. 2009; Ganey and Vojta 2011). It is possible, then, that when water becomes more abundant, a tree's competitive ability becomes less crucial relative to the partitioning of other resources, such as the relative availability of soil nutrients. Other studies have suggested that tradeoffs between resistance and resilience of conifers may be associated with the production of secondary compounds (Martín-Benito et al. 2008) or the use of stored carbohydrate reserves (Galiano et al. 2011); however, the numerous interactions between drought stress and other pathogens as well as high variability in drought responses among species and sites (McDowell et al. 2011) makes it difficult to generalize about the mechanisms or tradeoffs.

Although the relationship between competition and resistance was significant, the proportion of the variance in RWI at the individual tree-level was lowest in 2001, while variance at the broader spatial scales, particularly the Forest Type level, was quite high (accounting for more than half the variance in drought resistance). These results counter those of Martínez-Vilalta et al. (2012), who found that drought responses of *Pinus sylvestris* were mostly determined by tree-level factors, but that large-scale climatic differences (measured across 393 plots with an 800 m elevation gradient) were relatively unimportant. Here, I found that site-to-site variability in the total amount of precipitation received was a highly significant factor influencing resistance, but not resilience. This suggests that the importance of different Forest Types during the drought is most likely due to broad-scale gradients in precipitation and water availability. This finding is consistent with the results of Adams and Kolb (2005), who showed that the sensitivity of eight tree species to a regional drought event in northern Arizona was significantly related to differences in elevation and consistently greater at the dry end of each species' regional distribution. The relatively low proportion of variance at the tree-level during the drought suggests that all trees were strongly affected by the severe drought, regardless of their size or individual growing conditions. Thus, although competition among trees for water was clearly intense in 2001, at the ecosystem-scale it was not very important relative to broad differences in precipitation and water availability: trees growing in cooler, moister forest types suffered the least regardless of competitive status.

Ultimately, a rigorous understanding of tree responses to drought will require careful consideration of several factors not addressed in this study including the role of genetic variability – both within populations and along environmental gradients (White 1987) – as well as a whole tree approach that integrates simultaneous measurements of water and carbon fluxes to make accurate inferences about physiological stress and plant carbon balance (Ryan 2011). However, such studies are extremely costly and time intensive; as such, investigations of drought responses at landscape or ecosystem scales will continue to rely on more simplistic analyses of radial growth, particularly tree-ring series. To date, numerous tree-ring based studies, such as those cited above, have made important contributions in this field. However, a meaningful synthesis of results is lacking and problematic, largely because of highly inconsistent tree-ring-based metrics for quantifying drought responses. This barrier stems in part from a lack of agreement on how to define a drought event (particularly the duration of the event), but also reflects a failure to appreciate and explicitly account for how variability in the timing of wet and dry years (both prior to the event and during the recovery stages) could modify drought responses. Here, I used a transparent and straightforward method of quantifying drought responses that avoids the need to designate an arbitrary point in time as *the* dividing point separating resistance from resilience. This approach allowed us to characterize the curve of recovery following a drought event and reveal trends that might have been lost in an analysis of growth responses averaged over multiple years. Better and more consistent tree-ring-based metrics for measuring drought resistance and resilience would increase our ability to synthesize results to increase predictive power and better inform future forest management decisions.

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**Table 1** For each sampled stand, Forest Type, geographic location (degrees latitude and longitude), elevation, basal area, site index, average annual precipitation and temperature, number of trees sampled (# Trees), and mean tree age.

| Stand ID | Forest type | Latitude | Longitude | Elevation (m) | BA (m$^2$/ha) | Site index | Precip. (mm) | Temp. (°C) | # Trees | Mean age |
|---|---|---|---|---|---|---|---|---|---|---|
| AV01 | ABLA | 48.80 | -117.254 | 1748 | 51.2 | 41 | 111 | 4.0 | 14 | 156 |
| AV02 | ABLA | 48.99 | -117.058 | 1653 | 49.4 | 48 | 150 | 2.1 | 19 | 187 |
| AV03 | ABLA | 48.77 | -117.322 | 1613 | 45.0 | 48 | 101 | 5.5 | 15 | 111 |
| AV04 | ABLA | 48.69 | -117.279 | 1592 | 31.7 | 50 | 142 | 3.1 | 20 | 67 |
| AV05 | ABLA | 48.83 | -117.477 | 1561 | 45.9 | 50 | 101 | 4.7 | 17 | 72 |
| PA01 | PIPO | 48.50 | -118.713 | 957 | 31.4 | 41 | 33 | 5.5 | 29 | 95 |
| PA02 | PIPO | 48.82 | -118.211 | 651 | 27.1 | 57 | 43 | 7.3 | 30 | 88 |
| PA03 | PIPO | 48.90 | -118.181 | 976 | 13.1 | 37 | 51 | 7.5 | 24 | 97 |
| PA04 | PIPO | 48.58 | -118.285 | 933 | 23.4 | 68 | 45 | 5.5 | 24 | 88 |
| PA05 | PSME | 48.39 | -117.799 | 1069 | 25.0 | 51 | 61 | 7.2 | 27 | 90 |
| PP01 | PSME | 48.84 | -117.245 | 1097 | 33.7 | 42 | 77 | 4.4 | 28 | 153 |
| PP02 | PSME | 48.79 | -117.615 | 1158 | 38.3 | 56 | 67 | 7.1 | 26 | 102 |
| PP03 | PSME | 48.24 | -117.563 | 1128 | 41.3 | 65 | 60 | 6.1 | 29 | 78 |
| PP04 | PSME | 48.91 | -118.153 | 914 | 34.4 | 51 | 51 | 7.5 | 25 | 119 |
| PP05 | PSME | 48.61 | -118.307 | 1250 | 45.9 | 74 | 59 | 4.9 | 27 | 88 |
| PP06 | PSME | 48.35 | -117.175 | 1250 | 40.9 | 60 | 80 | 6.2 | 26 | 90 |
| PP07 | PSME | 48.84 | -118.282 | 1311 | 34.0 | 55 | 52 | 5.1 | 26 | 120 |
| PP08 | PSME | 48.81 | -118.538 | 1128 | 40.9 | 59 | 39 | 5.2 | 22 | 127 |
| PP09 | PSME | 48.64 | -117.288 | 975 | 35.4 | 64 | 62 | 6.1 | 25 | 83 |
| PP10 | PSME | 48.98 | -117.329 | 884 | 34.9 | 52 | 55 | 6.7 | 28 | 95 |

**Table 2** Variables included in mixed effects models.

| | Variable Name | Description | Units |
|---|---|---|---|
| **Biotic Factors** | | (All tree-level variables measured in 2008 and 2009) | |
| | DBH | Diameter at breast height | cm |
| | Height | Tree height; measured with a laser hypsomter | m |
| | LCR | Live crown ratio, the ratio of the vertical distance from the tip of the leader to the base of the crown (the lowest live whorl) to tree height | - |
| | Age | Tree age, estimated from annual rings | years |
| | Canopy | Canopy class, a classification of the position of an individual tree's crown relative to the rest of the forest canopy; levels = dominant (DO) or intermediate (IN) | |
| | Competition | Basal area of competitor trees, estimated from variable radius plots centered on each subject tree | $m^2$ $ha^{-1}$ |
| | RWI_Lag1 | Ring width index in previous year | - |
| | RWI_Lag2 | Ring width index two years prior | - |
| | Shrubs | Index of shrub cover under dripline of subject tree; levels = 1-5 | - |
| | Herbs | Index of herbaceous plant cover under dripline of subject tree; levels = 1-5 | - |
| | CW | Crown width, average span of tree crown | m |
| **Abiotic Factors** | | | |
| | SI | Site index, index of potential productivity of a site based on the height of dominant trees at 50 years | - |
| | ELEV | Elevation | m |
| | TEMP | Average annual temperature in current year, estimated using PRISM climate data | °C |
| | PRCP | Total precipitation in current year, estimated using PRISM climate data | mm |

**Table 3** Results of linear mixed-effects models of ring width index (RWI) in 2001 (severe drought year; resistance), 2002 – 2004 (moderately dry years; recovery), and 2005 (return to average soil moisture; resilience). Results for insignificant covariates are not shown. See Table 2 for a description of variables. (n = 481 trees from 20 stands)

| | | ***Resistance*** | | | | ***Recovery*** | | | | | | | | | | | | ***Resilience*** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 2001; $R^2$ = 0.61 | | | | 2002; $R^2$ = 0.47 | | | | 2003; $R^2$ = 0.30 | | | | 2004; $R^2$ = 0.17 | | | | 2005; $R^2$ = 0.34 | | | |
| *Fixed effect* | *df* | Value | SE | *t* value | *P* value | Value | SE | *t* value | *P* value | Value | SE | *t* value | *P* value | Value | SE | *t* value | *P* value | Value | SE | *t* value | *P* value |
| ***Biotic*** | | | | | | | | | | | | | | | | | | | | | |
| Intercept | 455 | **0.570** | **0.184** | **3.101** | **0.002** | **0.568** | **0.165** | **3.436** | **0.001** | **0.434** | **0.197** | **2.200** | **0.028** | **0.562** | **0.198** | **2.846** | **0.005** | **1.734** | **0.256** | **6.768** | **<0.001** |
| RWI_Lag1 | 455 | **0.295** | **0.031** | **9.452** | **<0.001** | **0.320** | **0.038** | **8.382** | **<0.001** | **0.337** | **0.040** | **8.419** | **<0.001** | **0.140** | **0.041** | **3.444** | **0.001** | **0.310** | **0.038** | **8.129** | **<0.001** |
| RWI_Lag2 | 455 | -0.023 | 0.031 | -0.727 | 0.468 | **0.156** | **0.031** | **5.091** | **<0.001** | **0.149** | **0.041** | **3.593** | **<0.001** | 0.052 | 0.039 | 1.329 | 0.184 | **-0.178** | **0.040** | **-4.495** | **<0.001** |
| Competition | 455 | **-0.054** | **0.011** | **-5.024** | **<0.001** | 0.020 | 0.012 | 1.708 | 0.088 | -0.005 | 0.012 | -0.402 | 0.688 | -0.008 | 0.013 | -0.646 | 0.519 | -0.008 | 0.014 | -0.586 | 0.558 |
| Canopy = IN | 455 | **-0.042** | **0.018** | **-2.379** | **0.018** | -0.003 | 0.019 | -0.138 | 0.890 | **0.050** | **0.020** | **2.512** | **0.012** | -0.035 | 0.022 | -1.596 | 0.111 | 0.027 | 0.024 | 1.145 | 0.253 |
| Height | 455 | -0.001 | 0.002 | -0.714 | 0.476 | -0.001 | 0.002 | -0.346 | 0.730 | **0.005** | **0.002** | **2.936** | **0.003** | 0.001 | 0.002 | 0.327 | 0.744 | 0.002 | 0.002 | 0.874 | 0.383 |
| Age | 455 | **0.069** | **0.027** | **2.562** | **0.011** | -0.011 | 0.028 | -0.394 | 0.694 | -0.055 | 0.030 | -1.815 | 0.070 | 0.032 | 0.032 | 0.977 | 0.329 | **-0.089** | **0.035** | **-2.512** | **0.012** |
| RGR | 455 | **0.213** | **0.079** | **2.710** | **0.007** | -0.008 | 0.086 | -0.096 | 0.923 | -0.029 | 0.089 | -0.332 | 0.740 | **0.416** | **0.098** | **4.247** | **<0.001** | -0.160 | 0.106 | -1.514 | 0.131 |
| ***Abiotic*** | | | | | | | | | | | | | | | | | | | | | |
| Precipitation | 15 | **0.197** | **0.057** | **3.444** | **0.004** | 0.048 | 0.031 | 1.530 | 0.147 | -0.039 | 0.050 | -0.780 | 0.448 | 0.024 | 0.035 | 0.702 | 0.494 | -0.027 | 0.087 | -0.316 | 0.756 |
| Site Index | 15 | -0.003 | 0.002 | -1.501 | 0.154 | **-0.003** | **0.001** | **-2.952** | **0.010** | 0.003 | 0.002 | 1.939 | 0.071 | -0.001 | 0.002 | -0.904 | 0.380 | -0.004 | 0.003 | -1.203 | 0.248 |

## Figure Captions

**Fig. 1** Location of study sites in on the Colville National Forest (darker shaded area) in northeastern Washington State (inset). Capital letters indicate the Forest Type [PIPO = *Pinus ponderosa-Pseudotsuga menziesii/Agropyron spicatum*; PSME = *Pseudotsuga menziesii/Physocarpus malcaeus*, ABLA = *Abies lasiocarpa/Vaccinium membranaceum*]

**Fig. 2** Time series from 1998 to 2005 showing a) annual average Palmer drought severity index (PDSI) for Climate Division 9, Washington, and b) standardized growth index values (RWI; stand-level mean ± SE) of *Pseudotsuga Menziesii* by Forest Type [PIPO = *Pinus ponderosa-Pseudotsuga menziesii/Agropyron spicatum* (circles; n = 5), PSME = *Pseudotsuga menziesii/Physocarpus malcaeus* (squares; n = 10) , ABLA = *Abies lasiocarpa/Vaccinium membranaceum* (triangles; n = 5). Dashed line indicates average growth (RWI = 1)

**Fig. 3** Time series showing change in the proportion of the total variance explained in random effects models for each of three nested spatial scales: Forest Type (squares), stand (circles), and individual trees (triangles)

**Figure 1**

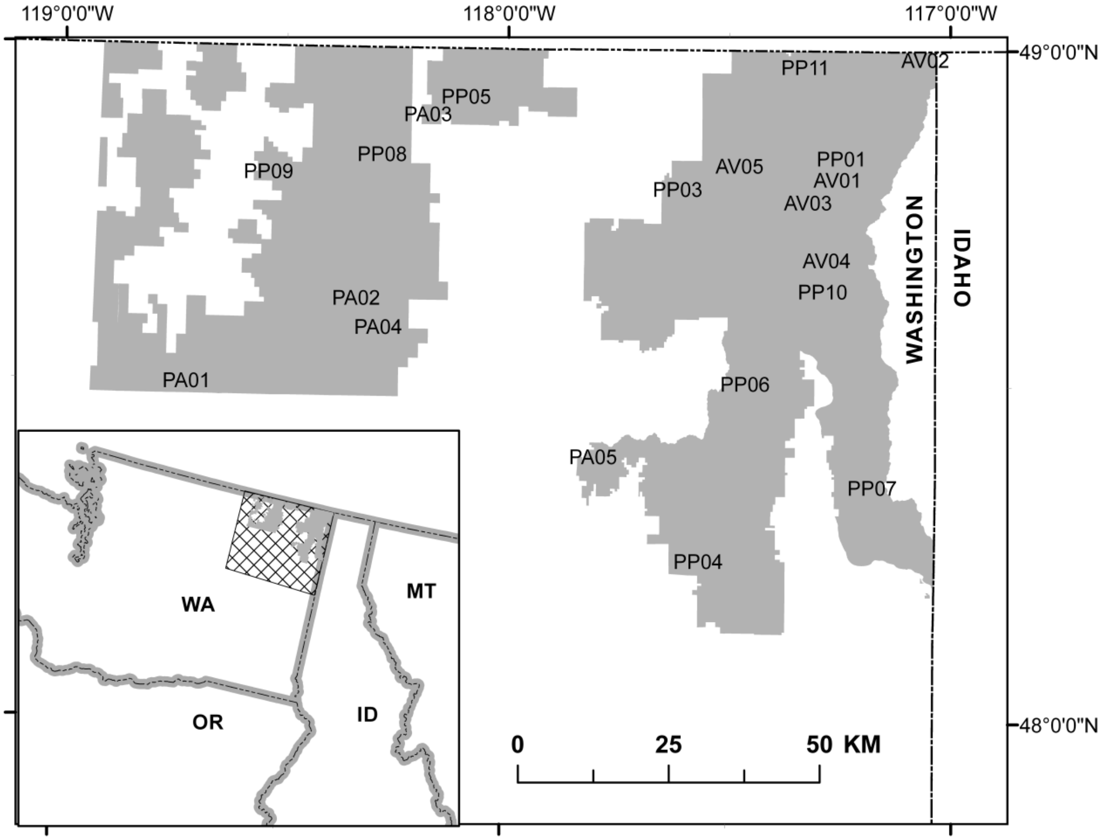

119°0'0"W
118°0'0"W
117°0'0"W
49°0'0"N
48°0'0"N
PP11
AV02
PP05
PA03
PP08
PP09
AV05
PP01
AV01
PP03
AV03
AV04
PP10
PA02
PA04
PA01
PP06
PA05
PP07
PP04
WASHINGTON
IDAHO
WA
MT
OR
ID
0
25
50 KM

**Figure 2**

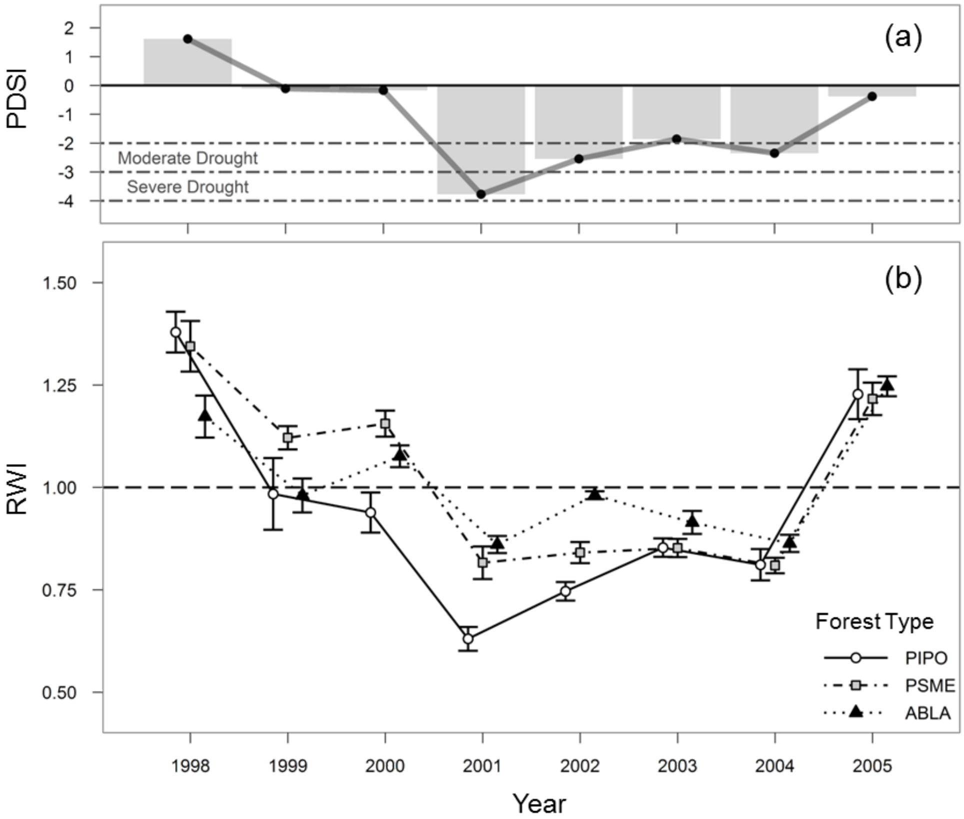
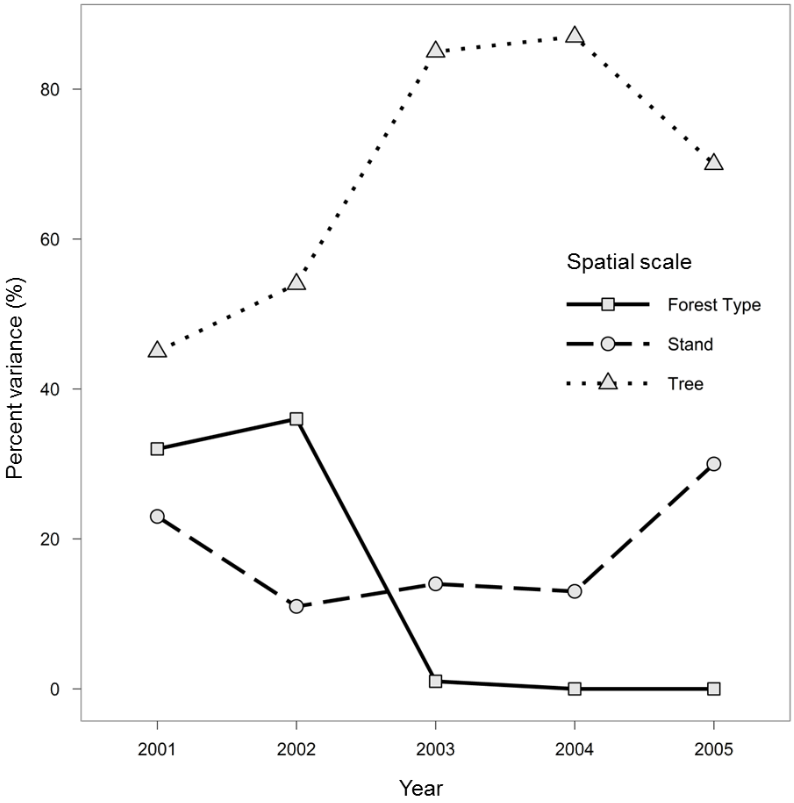

(a)
PDSI
2
1
0
-1
-2
-3
-4
Moderate Drought
Severe Drought
(b)
RWI
1.50
1.25
1.00
0.75
0.50
Forest Type
PIPO
PSME
ABLA
1998
1999
2000
2001
2002
2003
2004
2005
Year

**Figure 3**


Percent variance (%)
0
20
40
60
80
2001
2002
2003
2004
2005
Year
Spatial scale
Forest Type
Stand
Tree