Effects of climate on competitive dynamics in mixed conifer forests of the Sierra Nevada

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A B S T R A C T

Trees in more competitive environments appear to respond to climate differently than trees in less competitive environments. In turn, climate patterns may affect inter- or intra-specific competition, favoring certain individuals over others. Using dendrochronological methods, we sampled cores from dominant pine trees and their nearby competitors in 40 stands in the northern Sierra Nevada. Our dendroclimatic analyses showed complex responses to climate for the dominant pine and their competitors. Pinus lambertiana Doug. and Pinus ponderosa Doug. Ex P. & C. Laws benefited from cooler temperatures in the past May; all species benefited from warmer winter temperatures; Calocedrus decurrens (Torr.) Florin benefited from cooler temperatures in the past summer, while Abies concolor (Gord. & Glend.) Lindl. and the two pine species benefited from cooler temperatures in the present summer. All species showed consistently positive effects from increased precipitation and increased moisture availability. A competition ratio calculated as the ratio between the dominant tree’s radial increments to the competitor’s indicated that climate could influence competition through one of two mechanisms. One, negative responses to climate conditions that were negative for one species but neutral for another tended to drive the competition ratios. Two, conditions that were negative for both competing trees tended to hurt competitors more than dominant trees, while conditions that were generally positive tended to help competitors more than dominant trees. These results suggest that the dominant pine trees may be more resilient to climate stress than competitors. Reducing competition via management such as thinning may increase climatic resilience for all species and possibly have positive competitive results for competitors. Increasing temperatures will tend to harm Sierra Nevada conifers in the summer and spring, but may show some benefit over the winter as long as precipitation is not reduced.

1. Introduction

It has been well established that competition from other nearby trees can have a limiting effect on tree growth (e.g. Gómez-Aparicio et al., 2011; Das, 2012; Ruiz-Benito et al., 2013). Although competition is often not the primary factor in the mortality of old-growth trees, old-growth trees in more competitive environments are at a higher risk of mortality (Das et al., 2011). Reduction of competition via thinning have shown to have a number of positive effects on survival. In a ponderosa pine forest of northern California, old-growth trees have significantly higher mortality in un-thinned stands versus thinned stands (Ritchie et al., 2008). Thinning treatments in addition to decreasing the risk of high-intensity fire promote the growth of the residual trees (Magruder et al., 2013; van Mantgem and Das, 2014; Pukkala et al., 2015). Thinning has also been shown to reduce mortality from Dendrocopus bark beetles without harming stand productivity (Zhang et al., 2013). Thinning treatments to reduce competition may also increase a stand’s resiliency to climate stresses (Misson et al., 2003; Linares et al., 2010; Magruder et al., 2013; Guillemot et al., 2015). Just as competition may increase a tree’s sensitivity to climate, climatic conditions may also affect competition with other trees. Temperature and precipitation have been shown to shift the competitive advantages of different species in an area (Gómez-Aparicio et al., 2011; Cavin et al., 2013). Interactions between climate and competition can be complex, and effects may vary by species, region, tree age, and tree size.

Dendrochronological analysis is the technique of measuring radial tree growth and relating this to available climate records.
for the same time periods. Using these techniques, the response of radial growth to climatic conditions can be inferred over many years (e.g. Chhin et al., 2008a). One can form a picture of how whole forest stands have changed over time, and how they have responded to disturbances, yearly variations in climate, and changes in competition. Studies have reported some interesting and complex relationships of tree response to climate and competition. For example, Gedalof and Smith (2001) found that for mountain hemlock (Tsuga mertensiana (Bong.) Carriere), warmer summer temperatures were associated with positive growth in the present year, but negative growth in the following year. They attributed this to warm summers being favorable for initiating large crops of cones, which then matured in the following year at a significant energetic cost to the tree. Other studies have found that site conditions as a surrogate for climate had dendroclimatic responses. For example, trees that are located near bodies of water showed less response to drought stress in dry years, but were more susceptible to harm from flooding in wet years (Potito and MacDonald, 2008; Chhin et al., 2013). Responses also vary by species. Hurteau et al. (2007) found that for Sierra Nevada conifers under high-density conditions, such as white fir (Abies concolor (Gord. & Glend.) Lindl.), showed the strongest and most consistent response to climate, with most species showing stronger responses under more open conditions.

Larger trees may show different responses to climate and competition than smaller trees (Castagneri et al., 2012; Rozas, 2014), because larger trees have greater non-structural carbon pools to draw on (Niinemets, 2010) and greater access to sunlight (Thomas and Winner, 2002), but are also slower growing in general. Differences in drought response between saplings and mature trees may also depend on species. In a deciduous forest, He et al. (2005) found that some species showed little difference in drought response between old trees and young ones, while other species showed greater drought-related growth reductions in older trees. Individual trees may also show different responses to climate than the population does as a whole, due to differences in microclimate, competition, and tree age and size (Rozas and Olano, 2013). To control for age and size effects, some dendrochronology studies have chosen to study even-age plantations (de Luis et al., 2009), to separate trees out into different size classes before analysis (Chhin et al., 2008b), or to focus on a particular age group such as seedlings of 0.5–2 m in height (Chhin and Wang, 2008).

While most studies in dendrochronology focus on either establishment dates or responses to climate (Chhin and Wang, 2002), there is less research on interactions between climate and competition. Studies show that competition cannot be neglected in studying tree growth over time. For example, fires that reduce competition can have a benefit to the growth of surviving trees, especially smaller trees, in spite of the cost of fire damage (Valor et al., 2013). Additionally, while trees with low competition may show strong climatic signals in their yearly growth, trees that are more suppressed due to competition do not have such sensitivity to climate (Piatti and Cescatti, 1997; Gaa-Izquierdo et al., 2009; Rozas, 2014). Instead, their growth is more dependent on the previous year’s growth (Rozas and Olano, 2013). Competition can be a more important factor in tree growth than climate, although climate can influence a tree's sensitivity to competition and can affect which species are the dominant competitors (Gómez-Aparicio et al., 2011).

Some studies have also attempted to determine which Sierra Nevada conifers give the most reliable records of climate: Hurteau et al. (2007) found that of Sierra Nevada mixed-conifer species growing in high-density conditions, white fir growth showed the closest correspondence with the Palmer drought severity index (PDSI). Incorporating lagged climate effects generally did not improve the chronology alignment with PDSI, except for Jeffrey pine (Pinus jeffreyi Grev. & Balf.). Potito and MacDonald (2008), on the other hand, found that Jeffrey pine growth corresponded more strongly with winter (October-February) PDSI than western juniper (Juniperus occidentalis Hook.) or lodgepole pine (Pinus contorta Loud.).

While many studies exist on dendrochronology in the Sierra Nevada as well as the impacts of weather patterns on growth, or the impacts of competition on growth, studies that cover interactions between these two factors are lacking. This is in spite of the fact that factors such as temperature and precipitation may influence which species are most competitive. Greater competition, in turn, may decrease sensitivity to climate but increase tree mortality in old-growth forests (Smith et al., 2005). Dendrochronology provides a method by which to study decades of growth responses, and to examine how climate and competition influences growth. In this study, dendrochronology was used to study effects of monthly and seasonal climate on growth of four common Sierra Nevada mixed-conifer species: white fir, ponderosa pine (Pinus ponderosa Dougl. ex. P. & C. Laws), sugar pine (Pinus lambertiana Dougl.), and incense cedar (Calocedrus decurrens (Torr.) Florin). We used ring width data to examine whether monthly and seasonal climate influences trees differently based on their dominance in the stand. This study has important implications towards managing and safeguarding the productivity and health of old-growth pine species. This will help ensure the resilience of old-growth pines towards the impact of climate change and the effects of competition from the encroachment of shade tolerant conifers such as white fir and incense cedar.

2. Methods

2.1. Study site

Study sites were located in Lassen National Forest at an elevation of approximately 1525 m (Fig. 1). In approximate order of abundance, the most common tree species are white fir (ABCO), sugar pine (PILA), ponderosa pine (PIPO), and incense cedar (CADE). Ponderosa pine is the least shade tolerant, followed by sugar pine; incense cedar is somewhat shade tolerant; and white fir is by far the most shade tolerant. Older trees also tend to be less shade-tolerant than young trees (Kinloch and Scheuener, 1990).

The climate is Mediterranean, with cool wet winters and hot dry summers (Grantham et al., 2010). The Sierra Nevada is a unique ecosystem in that it has very large trees and high productivity despite growth that is limited by extremely dry conditions in the summer and cold conditions in the winter. Based on data from the PRISM climate group (Daly et al., 2008), average daily temperature for December-February was 1.4 °C for 1980–2010. Average precipitation for June-August was only 1.25 cm per month. The main growing season begins in the spring but continues throughout the summer, with growth continuing to occur to a lesser extent in the fall and winter. Kelly and Goulden (2016) measured gross ecosystem productivity and found that 32% occurs in the spring, 32% in the summer, 21% in the fall, and 15% even in the winter.

The season for radial growth begins in mid-April for sugar pine, ponderosa pine, and incense cedar, and in early May for white fir. Radial growth lasts until August or September (Powells, 1941). Shoot growth tends to begin after radial growth, in June, and needle growth begins even later in late June or early July (Royce and Barbour, 2001). Shoot growth may also begin at the same time as radial growth, but may proceed very slowly until June when rapid growth begins. Radial growth may be based on water availability, beginning with snow-melt and ending when water potentials drop with summer drought. Shoot growth instead may be based on photoperiod and temperature (Royce and Barbour, 2001).
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