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Facilitative and competitive effects of a N-fixing shrub on white fir saplings

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Abstract

In Sierra Nevada forests, shrubs are considered strong soil moisture competitors with regenerating trees, reducing seedling establishment, and slowing growth. Recent studies, however, suggest that in some circumstances shrubs can facilitate tree establishment and growth by modifying harsh microclimate conditions; increasing acquisition of water, carbon, and/or nutrients via shared mycorrhizal connections; or enhancing soil fertility, particularly under nitrogen-fixing shrubs such as *Ceanothus* spp. We examined the establishment dates and growth rates and patterns of white fir saplings growing in greenleaf manzanita, whitethorn ceanothus, and bare patches to examine whether establishment was correlated with past wet years, whether saplings growing in ceanothus had nitrogen-enriched foliage or faster growth rates than in the other two patches, and whether saplings in shrub patches experienced competition for light.

Sapling establishment was not correlated with high precipitation or heavy snowpack years, suggesting shade-tolerant saplings do not need wet years to become established. Soils under ceanothus were nitrogen enriched, but white fir sapling foliage did not have higher nitrogen concentrations and saplings did not grow faster in ceanothus than in the other two patches. Because growth rates of saplings were comparable in all patch types examined despite significantly different edaphic and abiotic conditions, we inferred that the various competitive and facilitative interactions affecting tree growth are in net balance across the patch types examined. However, competition for light is important—a significant percentage of growth release events occurred after saplings emerged above their host shrubs. Where shrubs are present, shade-tolerant species (i.e., white fir) are favored over drought-tolerant (pine) species. Our results may help interpret changes in understory conditions that are contributing to mixed conifer's compositional shift toward more shade-tolerant species after a century of fire-suppression.

Keywords: Forest regeneration; Mixed conifer; Shade tolerance; Soil fertility; Plant competition; Fire suppression; Nitrogen fixation

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1. Introduction

In seasonally dry forests, shrubs are often considered strong competitors with regenerating trees, inhibiting seedling establishment, and significantly slowing sapling growth (Conard and Radosevich, 1982; Vilá and Sardans, 1999; Royce and Barbour, 2001). Recent studies in Mediterranean-type forests, however, suggest that in some environments, shrubs may facilitate tree establishment and growth by modifying microclimate conditions (Callaway et al., 1996; Gomez-Aparicio et al., 2004), providing an established mycorrhizal network for saplings (Horton et al., 1999), and increasing organic soil enrichments (Walker et al., 2001). In California's Sierra Nevada, fire suppression has significantly increased shrub cover, due to both the absence of frequent understory fires (Parsons and DeBenedetti, 1979) and the development of shrub fields following high-intensity wildfires (Wilken, 1967). Shrubs have historically been an integral influence on seral development in the Sierra Nevada (Nagel and Taylor, 2005), but given significant changes in fire frequency and intensity, may play an increasingly important role in forest regeneration via competitive or facilitative effects on the establishment and growth of tree seedlings.

In the Sierra Nevada, soil moisture has been shown to be a key factor limiting coniferous tree growth. Shrubs can significantly deplete near-surface soil moisture content (Tappeiner and Helms, 1971; Conard and Radosevich, 1981) making them a difficult environment for establishment (Gray et al., 2005). Tree seedlings, however, can become established

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in shrub patches during heavy precipitation years which significantly reduce moisture stress and have been shown to produce pulses of tree establishment in mixed-conifer forests (North et al., 2005a). Within a shrub patch, buffered microclimate conditions (Callaway and Walker, 1997; Gomez-Aparicio et al., 2004) can enhance sapling growth by reducing temperatures and transpiration rates or slow growth by limiting light and soil moisture (Conard and Radosevich, 1982).

When growing within or near shrubs which can fix nitrogen (N), saplings may benefit from faster soil formation and enhanced soil fertility associated with N-fixing plants (Johnson, 1995), both of which have been shown to increase tree growth (Zavitkowski and Newton, 1968; Cole and Rapp, 1980) and to facilitate post-disturbance succession (Crocker and Major, 1955; Ugolini, 1968; Bormann and Sidle, 1990). Some of the most common shrubs in the Sierra Nevada are N-fixing species belonging to the genus *Ceanothus*, which have been shown to significantly enrich soils with available forms of N (Binkley and Husted, 1983; Oakley et al., 2003), the most limiting nutrient in many temperate forests. If tree saplings, however, are predominantly limited by moisture or light, N availability should have little or no effect on their growth. While the positive and negative effects of shrubs on tree saplings are likely variable through time, field experiments are needed which can synthesize the net effect on growth rates and compare sapling growth response in different shrub types and non-shrub patch types.

In this study we compared white fir saplings growing within patches of the N-fixing shrub whitethorn ceanothus (*Ceanothus cordulatus*) to those growing within two other common patch types—greenleaf manzanita (*Arctostaphylos patula*) and areas without shrub cover (bare) to examine a series of hypotheses about the potential competitive or facilitative effects of shrubs on tree saplings. We addressed four specific questions: (1) is sapling establishment correlated with wet climate years? (2) Once established, does foliar nitrogen content differ between saplings growing in the three patch types? (3) Do saplings in ceanothus patches grow significantly faster than in the other two patch conditions? (4) Are saplings released from competition for light once their leaders emerge above the shrub canopy? This study took place at the Teakettle Experimental Forest where higher levels of total and plant-available N in ceanothus patches relative to other common patch types has been documented (Oakley et al., 2003). Despite the widely held assumption among forest managers that shrubs hinder tree establishment and/or growth, few studies have examined seedling establishment or sapling growth patterns in nitrogen and non-nitrogen-fixing shrubs, and explicitly considered the relative importance of soil moisture, light, and soil N in their long-term effects on tree establishment and growth.

2. Methods

2.1. Study area

This study took place within the mixed-conifer portions of the Teakettle Experimental Forest in the southern Sierra Nevada of California. Teakettle is located on the High Sierra Ranger District of the Sierra National Forest, approximately 80 km east of Fresno above the north fork of the Kings river. The Experimental Forest is 1300 ha and ranges in elevation from 1880 to 2485 m, consisting of old-growth, mixed-conifer and red fir forests typical of mid-elevations on the Sierra Nevada western slopes.

Teakettle has hot, dry summers and mild, wet winters. More than 80% of the annual precipitation falls as snow between November and May, and accumulations of snow generally persist until late May or early June (North et al., 2002). Mean annual precipitation from 1958 to 1969 and 1977 to 1983 was 125 cm/year (Kattelmann, 1982).

Trees in this study were growing on one of three main soil types—Dystric Xeropsamments, Lithic Xeropsamments, and Typic Xerumbrepts (Giger and Schmitt, 1993). Soils have A horizons from 18 to 38 cm deep, B horizons up to 90 cm deep, and are well-drained and coarse textured (Giger and Schmitt, 1993). These poorly developed soils also have very low clay content, usually less than 5%.

2.2. Sampling design

Based on extensive previous surveys of Teakettle's ca. 500 ha of mixed conifer, we were able to locate as many replicates as possible of trees growing within three different patch types, manzanita, ceanothus, and bare areas. We focused on white fir because it is the dominant regenerating sapling at Teakettle (85% of stems; Gray et al., 2005), and because saplings of other mixed-conifer species were rare in shrub patches. To guard against the possibility that a particular sapling had not been associated with its current patch type throughout its lifetime, we only sampled saplings that met several criteria. First, a rough limit on age was established in the field by only sampling saplings less than 5 m tall. Second, saplings closer than 1 m to the edge of a shrub patch were not sampled to avoid saplings which may have only recently been influenced by shrubs. Finally, to ensure that tree saplings were experiencing similar light environments, only shrub patches that were growing under an open overstory tree canopy (<40% canopy cover as measured with a moosehorn device (Garrison, 1949)) were sampled. Sampling was also restricted to saplings that had at least five annual growth whorls above the shrub canopy.

To avoid the problem of pseudoreplication (Hurlbert, 1984), each shrub patch was considered a sampling unit. For cases in which there were multiple trees growing within a single shrub patch, we randomly selected a sample tree within the patch. Within each shrub patch, we measured several parameters: slope, aspect, overstory canopy cover, litter depth at shrub center, litter depth at shrub edge, and shrub height. For each tree sapling we measured total height, height above shrub canopy, sapling canopy height, canopy diameter measured at two cardinal directions, distance from shrub edge, and stem diameter at the base and at breast height. Canopy shapes approximated an ellipsoid and so canopy volumes were calculated using the formula $V = 3/4\pi \times ((x + y)/4)^2 \times z$,