

# 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.

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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  $V = 3/4\pi \times ((x + y)/4)^2 \times z$ ,

where  $x$  and  $y$  represent the diameters at crown base and  $z$  represents crown height. Tree growth within each of the patch types was compared using three estimates of growth rates: age-diameter, age-height, and age-canopy volume relationships. Linear regression lines with  $Y$  intercepts set to zero were constructed for each patch type and the slope of each line compared for each growth parameter using analysis of covariance (Zar, 1984) and a significance threshold of  $p < 0.05$ .

Foliage samples from the previous year's growth were collected from three locations at ca. 120 degree intervals around each tree at breast height, pooled, and analyzed for CHN content in a Perkin-Elmer Autoanalyzer (model 2400) in the College of Forest Resources' Analytical Laboratory at the University of Washington. Cross-sections from the base of each sapling and where the sapling emerged from the shrub canopy were collected in the field, and aged and crossdated in the lab. Samples were taken as close to the ground as possible (generally within 5 cm of the soil surface). Based upon cross-sections taken in another demography study at Teakettle (North et al., 2005a), we assumed ages calculated from cross-sections would underestimate true establishment age by no more than 2 years.

To investigate possible influences of climate on tree establishment by patch type, we used two approaches. We estimated past climate for each year in our tree ring record using the North American Drought Variability PDSI Reconstructions (PDSI) data for the gridpoint nearest to Teakettle ( $-119.5^\circ$  longitude,  $37^\circ$  latitude; only 25 km away). PDSI is a relative measure of moisture stress calculated from a network of 425 tree ring datasets (Cook et al., 1999). The mean PDSI is zero and most values range between plus 6 (very wet) and minus 6 (very dry). We averaged the PDSI values for a 2-year period for each sapling; the estimated year of establishment and the year before. We compared tree establishment between patches using the average of the PDSI value calculated for all trees in each patch type. We also examined establishment patterns against a 60-year record of maximum snow depth from a weather station 30 km south of Teakettle at the same elevation (Grant Grove, Kings Canyon National Park, California Department of Water Resources, <http://cdec.water.ca.gov>). Almost all moisture used by trees during the growing season comes from melting snow. In the Sierra, snow pack depth has been shown to be a good measure of plant available water because it represents both moisture abundance and the duration of release (Major, 1988).

### 2.3. Tree ring analysis

Annual growth rings were counted from sanded cross-sections and ring widths were measured on a sliding bench micrometer. Initial crossdating was performed with the COFECHA program (University of Arizona Tree Ring Laboratory's Dendrochronology Program Library) and by visual inspection (Holmes et al., 1986). Outliers (annual ring measurements varying from the mean ring width for a given year in a particular patch type by  $>3$  standard deviations) were flagged in COFECHA and re-measured although crossdating

was complicated by relatively steady growth exhibited by virtually all of the samples collected.

Annual basal area increment was calculated for each tree using the formula  $BAI = \pi r_t^2 - \pi r_{(t-1)}^2$ , where  $\pi r_t^2$  is the sum of basal area through year  $t$  and  $\pi r_{(t-1)}^2$  is the sum of basal area through year  $t - 1$  (Stokes and Smiley, 1968). To determine if tree saplings growing within shrub patches exhibited rapid growth patterns characteristic of a release from suppression, a release index was calculated for each tree. We defined a release as a doubling of growth over a 5 year average relative to the previous 5 year average (Fastie, 1995; Parish et al., 1999). Because the definition of a release event is somewhat subjective, we also considered growth increases of 50%, with both 3 and 5 years averages on both basal area increment and raw ring width data. All of these variations gave similar results.

### 3. Results

Edaphic conditions significantly varied between patch types. Although soils were poorly developed in all patch types, litter depth significantly differed with manzanita patches (3.2 cm)  $>$  ceanothus patches (2.2 cm)  $>$  bare patches (1.8 cm) (Table 1). Soil moisture in May was significantly higher in both shrub patches relative to bare patches, while in October, soil moisture was significantly lower in the shrub patches (Table 1). Ceanothus patches were significantly enriched in total and mineral N in the litter layer and the upper 10 cm (roughly correspondent to the A horizon) of mineral soil (Table 1). Overstory canopy cover was not significantly different among the three patch types (mean = 27%). Almost all trees were growing on level slopes (NSD mean for all patch types = 18%).

The average age of trees sampled within the manzanita, bare, and ceanothus patch types was 44, 47, and 43 years, respectively, and was not significantly different. The oldest tree was estimated to have established in 1885, but 1962 represented the mode of establishment dates for trees in all three patch types. Mean PDSI values for sapling establishment in each of the three patches was not significantly different from zero (one tailed  $t$ -test,  $p > 0.1$ ), indicating there was not a significant association with wet or dry years. This was consistent with the comparison of sapling establishment by patch type and the 1930–1992 Grant Grove snow depth (Fig. 1). Total number of saplings and number of saplings by patch type was not correlated with April 1st snow depth (Spearman's correlation test,  $p > 0.2$ ).

Nitrogen concentrations were significantly higher and the C:N ratio significantly lower in ceanothus leaves than in manzanita leaves (Fig. 2). However, foliar N concentrations for saplings growing within *Ceanothus* patches were not significantly different than values for saplings growing within the other two patch types ( $p = 0.25$ ) (Fig. 2). C:N ratios of sapling foliage were also not significantly different ( $p = 0.17$ ) among the three different patch types.

For two of the three growth measures, saplings within ceanothus patches were not significantly different than saplings in manzanita or bare patches. Both dbh-age

Table 1

Patch conditions and characteristics of white fir saplings in each of three sampled patches, manzanita, ceanothus, and bare ground

	Manzanita (n = 35)	Ceanothus (n = 36)	Bare ground (n = 35)
<b>Patch conditions</b>			
Litter depth (cm)	3.2 <sup>a</sup>	2.2 <sup>b</sup>	1.8 <sup>c</sup>
May soil moisture (%) <sup>a</sup>	16.3 <sup>a</sup>	16.2 <sup>a</sup>	13.1 <sup>b</sup>
October soil moisture (%) <sup>a</sup>	7.8 <sup>a</sup>	8.2 <sup>a</sup>	9.9 <sup>b</sup>
Overstory canopy cover (%)	26	22	34
Total PPFD <sup>a</sup> (μmol s <sup>-1</sup> m <sup>-2</sup> )	17.4 <sup>a</sup>	16.5 <sup>a</sup>	22.3 <sup>b</sup>
<b>Total N (kg ha<sup>-1</sup>)<sup>b</sup></b>			
Litter layer	644 <sup>b</sup>	931 <sup>a</sup>	85 <sup>b</sup>
0–10 cm	1507	1600	1368
15–25 cm	767	911	958
<b>Mineral N (NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, NO<sub>2</sub><sup>-</sup>; μg g<sup>-1</sup>)<sup>b</sup></b>			
Litter layer	6.1 <sup>b</sup>	32.0 <sup>a</sup>	8.5 <sup>b</sup>
0–10 cm	2.7	4.7	2.3
15–25 cm	2.3	2.8	1.9
<b>C:N ratio<sup>b</sup></b>			
Litter layer	35.9 <sup>b</sup>	27.4 <sup>a</sup>	40.9 <sup>b</sup>
0–10 cm	30.0	26.8	25.7
15–25 cm	23.4	24.5	20.3
Slope (%)	20	16	18
Shrub height (cm)	118	72	n/a
<b>Sapling characteristics</b>			
Mean sapling age (min, max)	44 (14, 74)	42 (11, 100)	47 (15, 116)
Mean sapling height (m)	2.4	2.4	2.5
Mean PDSI	-0.574	-0.032	-0.103

Mean values within the same row with different superscripts are significantly different (ANOVA with Tukey's post hoc analysis, *p* < 0.05).

<sup>a</sup> From North et al. (2005b).

<sup>b</sup> From Oakley et al. (2003).

(Fig. 3a) and height-age (Fig. 3b) regression lines for trees in ceanothus patches were slightly steeper than for saplings growing in the other two patch types but the differences were not significant. For saplings of a given age, canopy volume

was slightly higher within ceanothus patches than the other two patch types (Fig. 3c), but, differences between ceanothus and bare patches were not significant. Canopy volume of saplings growing in manzanita patches was significantly

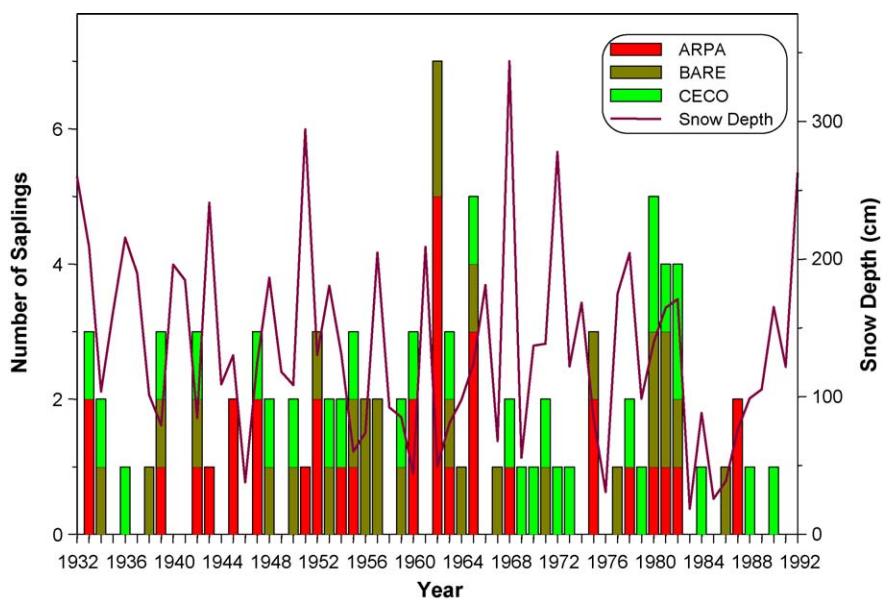


Fig. 1. Establishment dates for Teakettle white fir saplings by patch types relative to April 1st snow depth at Grant Grove, Kings Canyon N.P. from 1932 to 1992 (earliest establishment date, 1885, for one sapling in a manzanita patch is not shown). Number of saplings for each patch type (ARPA: manzanita patches, BARE: areas with no shrub cover, CECO: ceanothus patches) is shown on the primary y-axis and snow depth in centimeters is shown on the secondary y-axis.

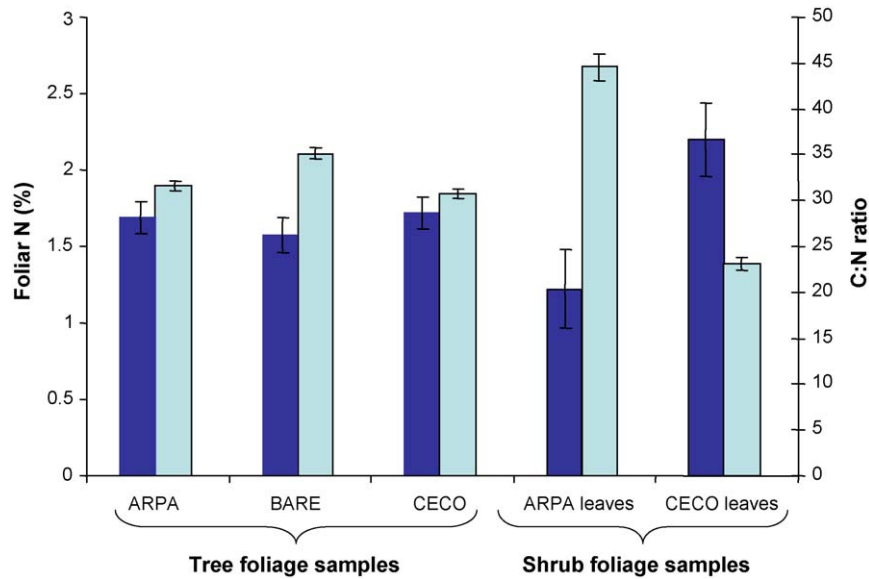


Fig. 2. Foliar N content (%) and C:N ratios for white fir saplings growing within each patch type and for foliage of manzanita and ceanothus shrubs. N content is represented by the bar on the left for each pair and C:N ratio by the bar on the right. For each sample, foliage was taken from three locations on the plant and pooled for analysis. (ARPA: manzanita patches, BARE: areas with no shrub cover, CECO: ceanothus patches)

lower than that of saplings in the two other patch types (Fig. 3c).

Using the definition of a release event as a 5 years average ring width  $2\times$  greater than the previous 5 years average, we identified 345 release events for the 59 saplings sampled in the two types of shrub patches. For saplings in manzanita and ceanothus patches, 68% and 76% of the release events, respectively, followed sapling emergence from the shrub canopy (Fig. 4). Both release percentages were significantly greater than 50% (one-tailed  $t$ -test,  $p < 0.05$ ), but did not significantly differ from each other (two-tailed  $t$ -test,  $p > 0.3$ ).

#### 4. Discussion

Taken as a whole, our results do not support a facilitative effect of enhanced soil N availability associated with ceanothus on tree establishment or growth, but do suggest that competition for light between tree saplings and shrubs limits tree growth rates. By one measure (canopy volume), saplings in ceanothus patches were more vigorous than those in manzanita, however, canopy volume for saplings in ceanothus and bare patches were not significantly different. It is possible that N additions to the soil by ceanothus compensate for light competition and lead to a net growth rate equivalent to bare patches, however, more specific data are required to adequately test this hypothesis.

Facilitative effects have been shown to increase with increasing abiotic stress (Greenlee and Callaway, 1996; Pugnaire and Luque, 2001), however, by most measures there were no significant differences among trees by patch type. In all patch types, tree growth appeared severely limited by one or more factors. Saplings measured in this study are significantly smaller than those in adjacent tree groups where average white fir diameter at 50 years is 37 cm (North unpublished data). Site

index for Teakettle's forest is 18 m (average height of an open grown tree at 50 years) (Giger and Schmitt, 1993)) while average height of our white fir saplings with a mean age of 46 years was 2.5, 2.4, and 2.5 m in manzanita, bare, and ceanothus patches, respectively.

The most significant growth trend was the higher number of growth releases for saplings once they emerged above the shrub canopy, regardless of shrub type. We did not sample other species of saplings because mixed conifer's other principal species, incense cedar, sugar, and Jeffrey pine, were rare or absent in shrub patches within the 500 ha area we surveyed. This suggests shrubs do not exclude tree regeneration, but they may act as a filter where only the most shade-tolerant tree saplings become established and can survive with slow growth rates until they emerge above the shrub canopy. Competition for light between shrubs and saplings may be an important influence on tree regeneration based on the scarcity of shade-intolerant tree species within shrub patches, the predominance of the shade-tolerant white fir, and significant increases in white fir growth after the estimated year of emergence above shrub canopies.

Nitrogen levels in shrub foliage and the upper soil horizons suggests ceanothus provides a nitrogen-enriched environment, but tree saplings growing in these patches did not have higher foliar nitrogen levels or faster growth than trees in the other patch types measured. Although Teakettle's soils are generally nutrient poor (North et al., 2002; Erickson et al., 2005), nitrogen enrichment in ceanothus patches did not produce higher sapling growth rates. Many studies have shown improved soil nutrient status in the presence of nitrogen-fixing plants (Crocker and Major, 1955; Youngberg et al., 1979; Binkley et al., 1982; Binkley and Husted, 1983; Johnson, 1995; Oakley et al., 2003) and positive plant growth response (Lathja and Schlesinger, 1986). Plants on N-poor sites can be expected to show a greater

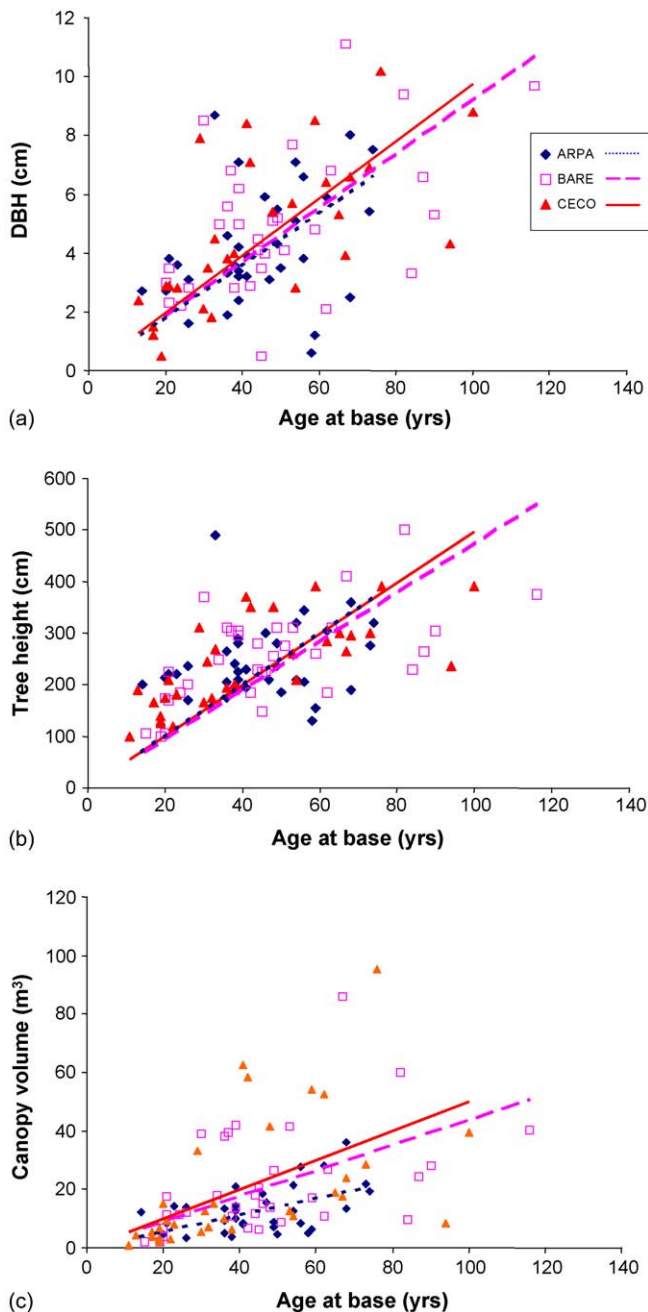


Fig. 3. Age-diameter (a), age-height (b), and age-canopy volume (c) relationships for white fir saplings growing within each patch type. Trend lines represent simple linear regressions, with  $Y$  intercepts set to zero. For (a) and (b), slopes of regression lines are not significantly different ( $p > 0.25$ ). For (c), slope of regression line for trees in manzanita patches is significantly ( $p < 0.025$ ) different from lines for the bare and ceanothus patches which are not significantly different from one another ( $p > 0.25$ ). (ARPA: manzanita patches, BARE: areas with no shrub cover, CECO: ceanothus patches)

response than those on N-rich sites, but long-term data from interplanting of red alder and Douglas-fir show that contributions of N-fixation to coniferous tree growth may not manifest themselves for many decades (Binkley, 2003).

Models of plant growth and resource use that suggest growth is constrained by whichever resource is most limiting were originally formulated by Von Liebig (1840) and Sprengel (van

der Ploeg et al., 1999) and more recently modified and formalized (e.g., Tilman, 1988). Arrigo (2005) has further refined this theory to suggest that even if the limitation of one resource is removed, others may still limit growth. This idea of multiple resource limitation may be important in our study system. Nutrients, moisture, and light availability likely limit tree sapling growth within the patch types we studied, but their dynamics and relative importance probably differ between patches and change seasonally and over the life of the sapling. Clearly, competitive and facilitative interactions among species do not represent a simple dichotomy, but must be considered within a matrix of biological and physical interactions that are dynamic through time.

For example, with nearly equal sapling growth rates in shrubs and bare patches, we hypothesize that shrub shade could reduce evaporative demand and partially compensate for drier soil conditions. Soil moisture is significantly higher in bare patches in July through October when sapling shoots are elongating (Gray et al., 2005), however during this same period maximum daily surface soil temperatures are almost  $5^{\circ}\text{C}$  higher than under shrub canopies (North et al., 2002, Siyan Ma, unpublished data).

We were surprised that sapling establishment was not correlated with past wet years. Previous studies have suggested that soil moisture availability strongly affects tree establishment (Gray et al., 2005; North et al., 2005a) and growth in the Sierra Nevada (Tappeiner and Helms, 1971; Conard and Radosevich, 1981, 1982). These studies have also shown shrub patches have less available soil moisture than other adjacent substrates and that shrubs can effectively mine more water than trees (Royce and Barbour, 2001). Although ceanothus and manzanita patches have higher soil moisture than bare patches in May, possibly due to slower snow melt, they become substantially drier than bare patches (Table 1) or adjacent tree groups (North et al., 2005b) by October. The absence of shade-intolerant saplings in shrub patches suggests low-light conditions may limit establishment more than soil moisture. For example, although shade-intolerant Jeffrey pine is the most drought tolerant of mixed-conifer species and often occurs on porous, thin soils (Gray et al., 2005), we rarely found Jeffrey pine saplings in shrub patches.

We caution that our interpretation of these results is restricted by the limitations of our approach. Our dating estimates probably contain some error, but because the likelihood of encountering missing or false rings was minimized by young age (only one tree was older than 100 years) and the consistency of growth, we believe those errors to be small. We did not employ greenhouse experiments that could better have isolated individual mechanisms of competition but that might miss how the combined effect of shade, water, and nitrogen affect sapling growth in complex field conditions. In this study, we used sapling establishment dates and growth rates as integrated bioassays of growing conditions over the life of the sapling. Using a series of hypotheses we can infer how shrubs ultimately affect sapling growth, but a better understanding of individual mechanisms and the duration and effect of their influence requires a more controlled experimental approach.

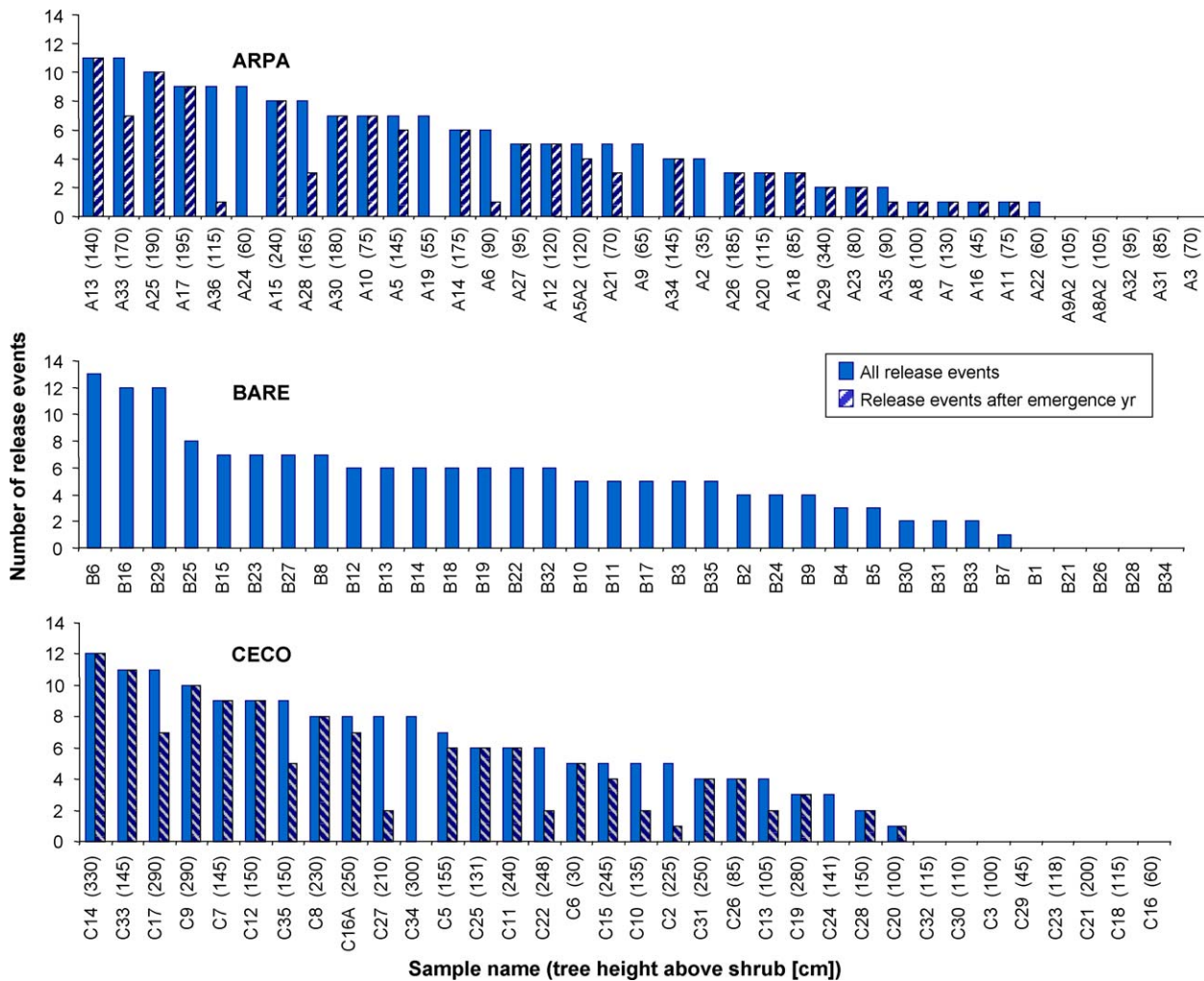


Fig. 4. Number of release events (5 years average ring width  $\geq$  twice previous 5 years average) for all trees within each patch type (ARPA: manzanita, BARE: areas with no shrub cover, CECO: ceanothus). For saplings within manzanita and ceanothus patches, the bar on the left is the total number of releases and the bar on the right is the number of releases after sapling emergence above the shrub canopy. Sample numbers are shown along the X-axis, followed by the height (cm) of each sapling above the shrub canopy.

Traditionally, forest managers in the Sierra Nevada have viewed shrubs as inhibiting tree regeneration and growth. Our research does not contradict that impression for most mixed-conifer species, but it does suggest that shrubs may provide regeneration and slow growth sites for shade-tolerant white fir. A restoration goal for fire-suppressed Sierra Nevada forests is to increase the number of pines and reduce the percentage of shade-tolerant firs (SNFPA, 2004). With an increase in shrub cover from fire suppression, it may become more difficult to meet this compositional objective unless shrub cover is reduced. This suggests prescribed fire may benefit pine regeneration not only by providing more mineral seedbed for establishment (Fowells and Stark, 1965) but also in reducing shrub cover under which only shade-tolerant saplings can survive low-light conditions.

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