

CONIFER SEEDLING SURVIVAL UNDER CLOSED-CANOPY AND
MANZANITA PATCHES IN THE SIERRA NEVADA

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ABSTRACT

After a century of fire suppression, prescribed fire and mechanical thinning are widely used to restore mixed-conifer forests in California's Sierra Nevada, yet after these treatments, trees sometimes fail to regenerate on many sites, for several possible reasons. Notably, competition between shrubs and tree seedlings for scarce water during prolonged summer dry seasons is suspected to influence seedling survival, yet this hypothesis has been tested in few manipulated field experiments. We investigated the effects of vegetation patch types, root competition, putative mycorrhizal connections, soil moisture, and microclimate on the establishment of sugar pine (*Pinus lambertiana*) and white fir (*Abies concolor*) seedlings in an old-growth, mixed-conifer forest in the southern Sierra Nevada. Seedling survival rates were significantly higher under closed tree canopies than in patches dominated by manzanita (*Arctostaphylos patula*) shrubs. Treatments that allowed seedlings to connect with existing ectomycorrhizal networks did not enhance their survival. Isotope signatures suggest that mature conifer trees rely on water from deep soil layers (>50 cm), while shrubs and tree saplings (1–3 m in height) rely on water from shallower layers (0–50 cm) at the beginning of the season, but as soils become drier the shrub's and the sapling's primary zone of uptake shifts downward in the soil profile. These findings imply that shrubs may inhibit the survival of establishing tree seedlings until the seedlings have a deep enough root system to extract soil moisture from soil below 50 cm. Our study suggests that tree seedling survival may depend on a seedling's ability to compete with shrubs for scarce soil moisture in the near-surface soil layers.

Key Words: *Abies concolor*, *Arctostaphylos patula*, mycorrhizae, *Pinus lambertiana*, root competition, stable isotopes, water uptake depth.

Seedling establishment is a critical stage in the life history of most plant species, and in forests can have a significant influence on a stand's species composition and development for centuries. In the forests of the Californian Sierra Nevada, managers often have problems regenerating trees on sites after they are treated for fuels reduction (McDonald 1976; Helms and Tappeiner 1996). Currently there is little information on the effects of important site factors on tree regeneration in mixed (shrub/tree) vegetation and under closed canopy conditions (Tappeiner and McDonald 1996). A century of fire suppression has significantly increased fuel loads, increasing stem densities and canopy cover in many western forests, reducing understory light and soil moisture conditions for establishing seedlings (Minnich et al. 1995; Gray et al. 2005). Mixed-conifer, the dominant forest type on the Sierran Nevada's western slopes, has been characterized as having a mixture of closed canopy,

shrub and gap patch conditions, each with significantly different microclimates (North et al. 2002; Gray et al. 2005). Sierran forests have a prolonged summer drought, typical of a Mediterranean climate (Parker 1994; Stephenson 1998), and shrub competition for scarce soil water is believed to influence seedling survival and growth rates. For example, a study of tree demography in the Sierran Nevada forest found that many Jeffrey pines (*Pinus jeffreyi*; nomenclature follows Hickman 1993) and sugar pines (*Pinus lambertiana*), which often become established on drier microsites favored by shrubs, had become established in wet El Niño years (North et al. 2005). However, research suggests that shrubs may facilitate tree seedling establishment by ameliorating microclimate extremes (Gómez-Aparicio et al. 2004) or by providing an ectomycorrhizal network that establishing tree seedlings can tap into (Horton et al. 1999). Thus, further research into the influence of shrubs on conifer regeneration and microclimate conditions is needed to improve the management of Sierran forests.

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One factor that strongly influences the establishment of tree seedlings in Sierran forests is likely to be the availability of below-ground resources, which may make a significant contribution to the patch conditions and gaps that characterize mixed-conifer forests. Royce and Barbour (2001) found that shrubs generally depleted soil moisture more rapidly and ultimately extracted a greater proportion of the available soil water than conifers. Shrubs, however, also provide shade, thereby reducing surface temperatures and the evaporative demand for establishing seedlings. Recent research in drought-stressed chaparral also suggests that conifer seedlings may benefit from shrub mycorrhizae. Horton et al. (1999) studying *Pseudotsuga* seedling survival in sites dominated by *Arctostaphylos* spp. suggested that the ectomycorrhizal fungi associated with *Arctostaphylos* spp. contributed to the establishment of *Pseudotsuga menziesii* seedlings. It has been postulated that the sharing of ectomycorrhizal fungi between conifers and *Arbutus* or *Arctostaphylos* spp. may play a major role in plant community development (Molina and Trappe 1982; Perry et al. 1989). However, there have been no studies, to date, in which the possible transfer of water has been rigorously excluded from the mechanisms whereby shrubs facilitate seedling establishment in dry chaparral ecosystems, or in Sierran forests where prolonged drought occurs during most of the growing season.

In this study, we examined the microclimate, water use, and conifer seedling survival rates in manzanita shrub (*Arctostaphylos patula*) and mature forest patches in Sierran mixed-conifer forests. The objective was to determine whether (and if so how) seedling dynamics vary between two dominant patch types; areas dominated by shrubs with shallow roots, and closed canopy forest with deep rooting systems. Our hypotheses were (i) survival rates of tree seedlings would be higher for seedlings where mycorrhizal connections were not blocked; (ii) shrubs and overstory trees extract soil water from different depths (as measured by $^{18}\text{O}/^{16}\text{O}$ and $^2\text{H}/^1\text{H}$ ratios of xylem water) and (iii) seedling survival rates would be higher in forest than in manzanita patches. To elucidate mechanisms potentially influencing these responses we also examined microclimatic (air temperature and soil moisture) differences between patch types, and the effects of and irrigation treatment on seedling transpiration rates. Water availability was also manipulated in the irrigation study to examine tree seedlings survival.

MATERIALS AND METHODS

Field Site

The study was conducted in Teakettle Experimental Forest, 80 km east of Fresno, California,

in the north drainage catchment of the Kings River (36°44'N, 117°30'W). The experimental forest consists of 1300 ha of old-growth mixed-conifer. Elevation ranges from 1980 m along the eastern boundary to 2590 m at the top of Patterson Mountain on the western boundary. Annual precipitation averages 125 cm at 2100 m and falls mostly as snow between November and April. Mean, maximum, and minimum July temperatures are 17°C, 30°C, and 3°C, respectively (North et al. 2002). In Teakettle Forest there is a gradation in the vegetation from a mixture of white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), incense-cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), and red fir (*Abies magnifica*) at the lower elevations to red fir, lodgepole pine (*Pinus contorta*), and western white pine (*Pinus monticola*) at higher elevations. Soils are Dystric and Lithic Xeropsamments of loamy sand to sandy loam textures (Anonymous 1993), derived from granitic rock, with exposed weathered and un-weathered rock common throughout the study area.

Treatments

Three manzanita (*Arctostaphylos patula*) patches and three closed-canopy patches (Fig. 1) were selected subjectively in the autumn of 2000 for a study of the survival of sugar pine (*Pinus lambertiana*) and white fir (*Abies concolor*) seedlings. Patches were selected which were large enough ($\geq 70 \text{ m}^2$) for the field experiment, distinct (separated by gaps), and yet close enough to be on the same mapped soil type. Manzanita and closed-canopy patches were separated by at least 80 m to ensure that there were no below-ground connections between patch types. White fir seedlings were transplanted from the surrounding area in October 2000 into three different types of cylinders (Fig. 1), which were inserted into the ground in both the manzanita and closed-canopy patches. The above-ground height of the transplanted white fir seedlings averaged ~ 10 cm and root length averaged ~ 15 cm, a size associated with 1–4 yr old seedlings. There were not enough sugar pine seedlings at Teakettle to transplant, so five seeds were sown within each cylinder at the end of October 2000 and covered with a steel mesh to exclude predation of the seeds. In the spring of 2001, 90 cylinders each contained three established white fir seedlings, while another 90 cylinders contained three to five sugar pine seedlings which had germinated from the sown seed. Each cylinder was 35 cm long, 15.5 cm in diameter, and 65% of its area was open to the surrounding soil (control treatment), covered with a 50 μm mesh, or covered with a 5 μm mesh (Fig. 1). The 50 μm mesh was sized to prevent root penetration but provide openings

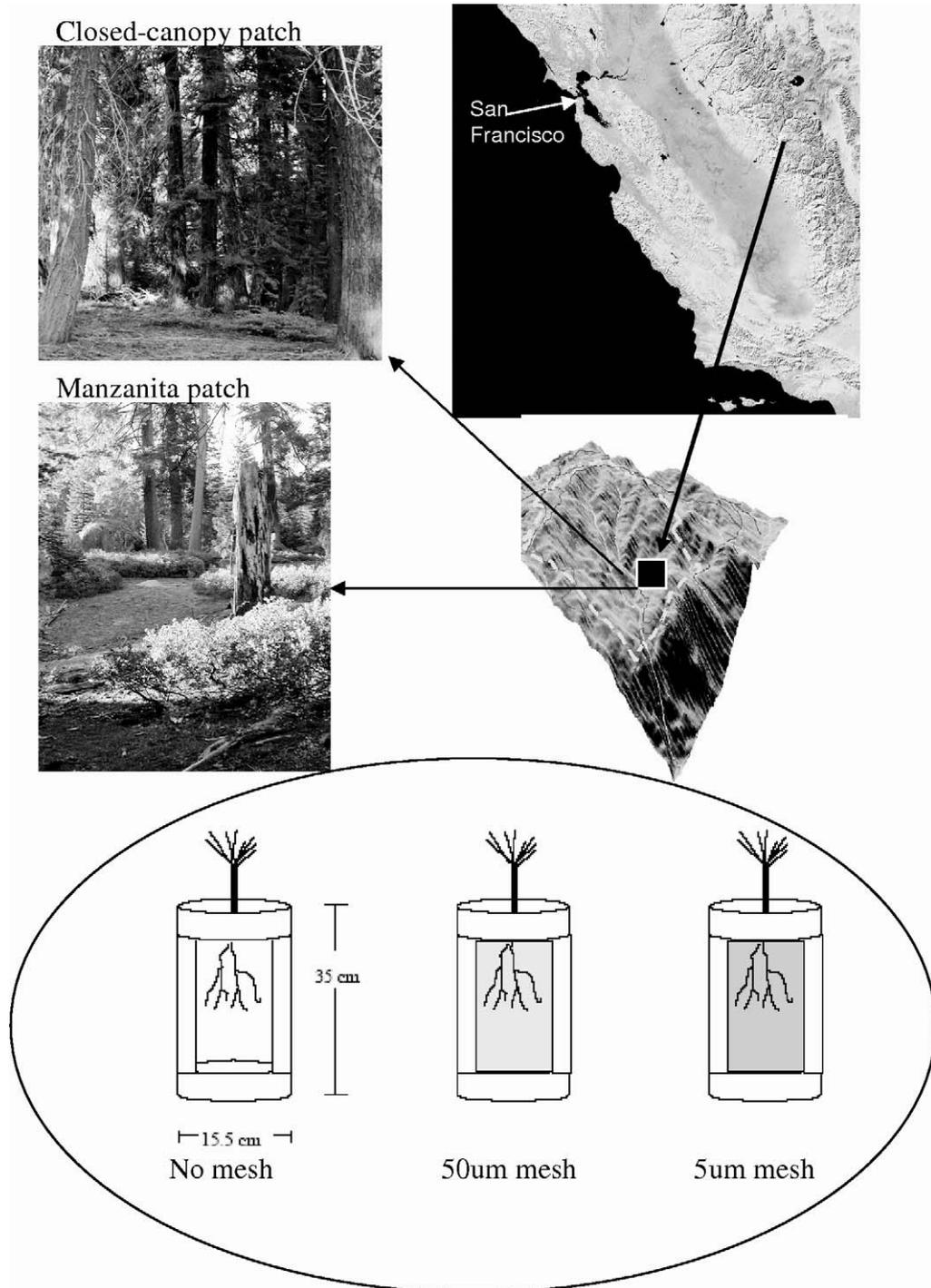


FIG. 1. Map of California showing the location of the Teakettle Experimental Forest, the manzanita and closed-canopy patches, and the design of the three different cylinder treatments; control, 50 μm pore-size mesh, and 5 μm pore-size mesh.

large enough to allow mycorrhizae to establish across it. The 5 μm mesh was designed to prevent penetration of both roots and mycorrhizae. In total, 180 cylinders (2 plant species \times 3 enclosure treatments \times 5 replicates \times 6 sites) were installed. The seedlings were allowed to establish until 2002 in order to allow adequate time for external hyphal colonization in the chambers open to the surrounding soil (control treatment) and the chambers covered with a 50 μm mesh (root enclosure treatment). We stress that the cylinder treatments allow hyphal connections to occur, but we did not sample roots to determine whether actual connections were established.

We applied an irrigation treatment to assess how seedlings in closed-canopy and shrub patches assimilate water. August was chosen because it is the driest, warmest month with dry upper soil layers that will affect the transpiration of the seedlings. During August 2002, nine cylinders from each treatment (36 cylinders in total) were selected at random and irrigated twice a week for three weeks. Eighteen cylinders received 250 ml dl of water at each irrigation, and 18 cylinders received 500 ml at each irrigation. Transpiration rates in seedlings were measured to assess relative water-use efficiency in the different patch and root enclosure treatments.

Field Sampling

To infer the depth at which plants were taking up water, $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of water extracted from mature conifers, conifer saplings (1–3 m in height) and manzanitas was compared to $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of water extracted from soil taken at different depths. From May to September 2001 soil samples were collected from every 10 cm layer down to ~ 70 cm depth and water was extracted from each sample and analyzed. One soil pit from each of the manzanita and the closed-canopy patches was sampled on May 19, June 26, August 9, September 5, and September 29. At the same time, wood cores were extracted from mature conifers, conifer saplings and manzanita shrubs for xylem water extractions. More than 10 plant samples were collected in the vicinity of each soil pit on every sampling occasion. The soil and wood samples were kept in airtight plastic bottles that were stored in plastic bags and refrigerated ($\sim 5^\circ\text{C}$) until cryogenic distillation (Ehleringer et al. 2000).

The temperature, relative humidity, and absolute humidity were recorded with eight HOBO data loggers (Onset Computer Corporation, MA), calculating averages over 30 min during 2001 and 2002 in the manzanita and closed-canopy patches at 20 cm and 150 cm above the ground. In 2002, the relative humidity and absolute humidity were used to calculate the vapor pressure deficit (VPD) using the formula:

$$VPD = \left(\frac{ab.humidity}{rel.humidity} \right) - ab.humidity. \quad (1)$$

Volumetric soil water content was estimated using time-domain reflectometers (TDR, model No. 1502C, Tektronix Inc., Beaverton, OR) in two soil pits; one in a manzanita shrub area and one in closed-canopy forest. Only two soil pits were excavated because while soil depth differs between the two patch types, within each patch the soils are fairly homogenous (Erickson et al. 2005). The computed volumetric water content was based on the “low-C” calibration described in Gray and Spies (1995). This method averages water content over the length of steel probes left in the soil. The stainless probes were 30 cm long and installed horizontally at depths of 5 cm, 10 cm, 20 cm, 30 cm, 40 cm, 50 cm and 60 cm, while at 70 cm the probes were installed vertically (giving an average for the 70–100 cm profile).

Depth to bedrock for each study area was measured by Gasch & Associates (G&A, Sacramento, CA), using a seismic refraction (SR) method, which measures the velocity at which a seismic wave is propagated through a soil or rock medium. Higher seismic primary-wave velocities indicate material of higher density, typically indicating the strength or composition of the material, and wave velocity is used as an index of depth to bedrock.

The seedling survival was checked during four occasions, starting mid-June, during 2002. The seedlings were considered dead if all needles were brown.

To determine how irrigated seedlings in closed-canopy and shrub patches assimilated irrigation water, leaf conductance rates ($\text{mmol m}^{-2} \text{s}^{-1}$) of 36 seedlings representing each of the irrigation treatments were measured at the beginning of September using a LI-1600 null-balance steady state porometer (LI-COR, Inc., Lincoln, NE). Eighteen non-irrigated seedlings were also measured to allow for comparison between irrigated and non-irrigated seedlings. Porometer measurements were taken from 9:00 to 12:00 a.m.

Preparation and Analysis

Soil and wood cores were stored for one to four weeks before soil and xylem water was extracted from the soil and seedling samples, respectively, by cryogenic distillation. The extracted water was used for isotope analyses. The $^2\text{H}/^1\text{H}$ ratios of the water from the different soil depths were determined using an isotope mass spectrometer (IRMS; a Finnigan-MAT Delta Plus XL, coupled to a H/Device at the UC Berkeley Center for Stable Isotope Biogeochemistry). Results are expressed in standard notation ($\delta^2\text{H}$) in parts per thousand (‰) relative to V-SMOW, where $\delta^2\text{H} = [(R_{\text{sample}}/R_{\text{V-SMOW}}) - 1] \times$

1000‰ and R is the molar ratio of heavy to light isotopes (D/H) with a sample precision of $\pm 1\%$.

The $^{18}O/^{16}O$ ratios of xylem sap and soil water were determined using the same IRMS, but coupled to a Gas Bench II; a universal on-line interface which allowed automated isotope ratio determinations of small gas samples after 50 to 200 μ l of water had equilibrated with CO_2 after a set time (following Dugan et al. 1985). Results were expressed in standard notation ($\delta^{18}O$) in parts per thousand (‰) relative to V-SMOW, with a sample precision of $\pm 0.05\%$.

The proportions of deep water and surface water used by the shrubs and the conifers were calculated using the following equations:

$$V_{\text{surface}} + V_{\text{deep}} = V_{\text{plant}} \quad (2)$$

where V_{plant} is the total water taken up by the plant, V_{surface} is the fraction of water from upper soil layers (0–50 cm) and V_{deep} is the fraction of water from deeper soil layers (>50 cm).

$$C_{\text{surface}}^{t1} V_{\text{surface}} + C_{\text{deep}}^{t1} V_{\text{deep}} = C_{\text{plant}}^{t1} V_{\text{plant}} \quad (3)$$

$$C_{\text{surface}}^{t2} V_{\text{surface}} + C_{\text{deep}}^{t2} V_{\text{deep}} = C_{\text{plant}}^{t2} V_{\text{plant}} \quad (4)$$

where C^{t1} and C^{t2} are the concentrations of the δ^2H and $\delta^{18}O$ tracers, respectively, and the subscripts surface, deep and plant refer to water from the upper soil layers, deeper soil layers and xylem sap of the plant, respectively. With one hydrological tracer for the source of xylem sap water, two mass balance equations can be written (Eqs. 2, 3), making it possible to determine the proportion of uptake from two sources. This study had two hydrological tracers, which could allow uptake from three sources to be determined, but because of the covariance between ^{18}O and 2H due to kinetic effects (Dansgaard 1964) it was only possible to determine the proportion of uptake from two sources. For this reason, we divided the soil profile into just two layers, 0–50 cm and >50 cm deep.

Analysis of variance was used to compare differences between closed-canopy and manzanita shrub areas and between treatments using the GLM ANOVA procedure of the SPSS statistical package (version 10, 1999, SPSS Inc., Chicago, IL), and differences were assumed to be statistically significant if $P < 0.1$.

RESULTS

Diurnal temperature differences during the growing season (June–August) were larger in the shrub-dominated areas than in the closed-canopy patches ($F_{df1} = 8110$, $P < 0.001$; Fig. 2) and greater near the ground, at a 20 cm height, than 150 cm above the ground ($F_{df1} = 1625.4$, $P < 0.001$; Fig. 2). The soil profile was significantly

drier in the shrub than in the closed-canopy patches during the 2001 growing season ($F_{df1} = 6.728$, $P = 0.016$). The increase in soil moisture at the end of 2001 was caused by an unusual rain storm in the early fall. During the 2002 growing season there was no significant difference in soil moisture between shrub and closed-canopy patches ($F_{df1} = 2.502$, $P = 0.145$; Fig. 3). For all sites, the soil profile was drier during the 2001 growing season than in 2002 ($F_{df2} = 88.4$, $P < 0.001$). The seismic data indicate that the active soil profile is deeper in the closed-canopy areas (2.8 ± 0.5 m) than in manzanita areas (1.6 ± 0.28 m), but the depth to the solid bedrock was ~ 3.3 m in both the closed-canopy and shrub areas.

In the beginning of the growing season, the soil profile had $\delta^{18}O$ and δ^2H values of -13% and 95% , respectively, because of the water from the snow melt. As the upper layers in the soil profile gets drier and the $\delta^{18}O$ values in the soil become less negative and the δ^2H values increase. Dwell water had $\delta^{18}O$ and δ^2H values of -13 and 93% , respectively, during the whole growing season. Plant isotope values differed between shrubs, trees, and saplings. The overstory sugar pines and white firs had consistent $\delta^{18}O$ values over the whole growing season. Throughout the June–September sampling period, they extracted water with $\delta^{18}O$ values of -12 to -13% similar to soil profiles >70 cm. Both shrub and conifer sapling water composition changed during the sample period. The shrubs having $\delta^{18}O$ of -12% in early growing season (May–July 1st) after which the $\delta^{18}O$ values became less negative in September.

Unfortunately, we discovered that the 50 μ m mesh did not prevent fine manzanita roots growing through the mesh as we had intended, though it did exclude tree roots from cylinders in the closed canopy-patch. Due to this compromise in our design, our seedlings in the manzanita patches had only two treatments; mycorrhizae enclosure and no enclosure. The closed-canopy patches, however, still had three treatments. Transpiration from seedlings in all three cylinder treatments under the closed-canopy increased with irrigation volume ($F_{df8} = 2.869$, $P = 0.035$; Fig. 4). In closed-canopy conditions, there was also a significant difference between species, with sugar pine seedlings having greater transpiration rates ($1.66 \text{ mmol m}^{-2} \text{ s}^{-1}$) than white fir seedlings ($1.4 \text{ mmol m}^{-2} \text{ s}^{-1}$; $F_{df1} = 3.925$, $P = 0.065$). The seedlings in the 50 μ m pore-size mesh and 5 μ m pore-size meshes that were not irrigated had similar transpiration rates in both the manzanita and closed-canopy patches, while the transpiration rates from the seedlings in the control treatment were greater in the closed-canopy than in the manzanita patches ($F_{df1} = 6.36$, $P = 0.086$; Fig. 4). The vapor pressure deficit (VPD) was greater in the manzanita areas

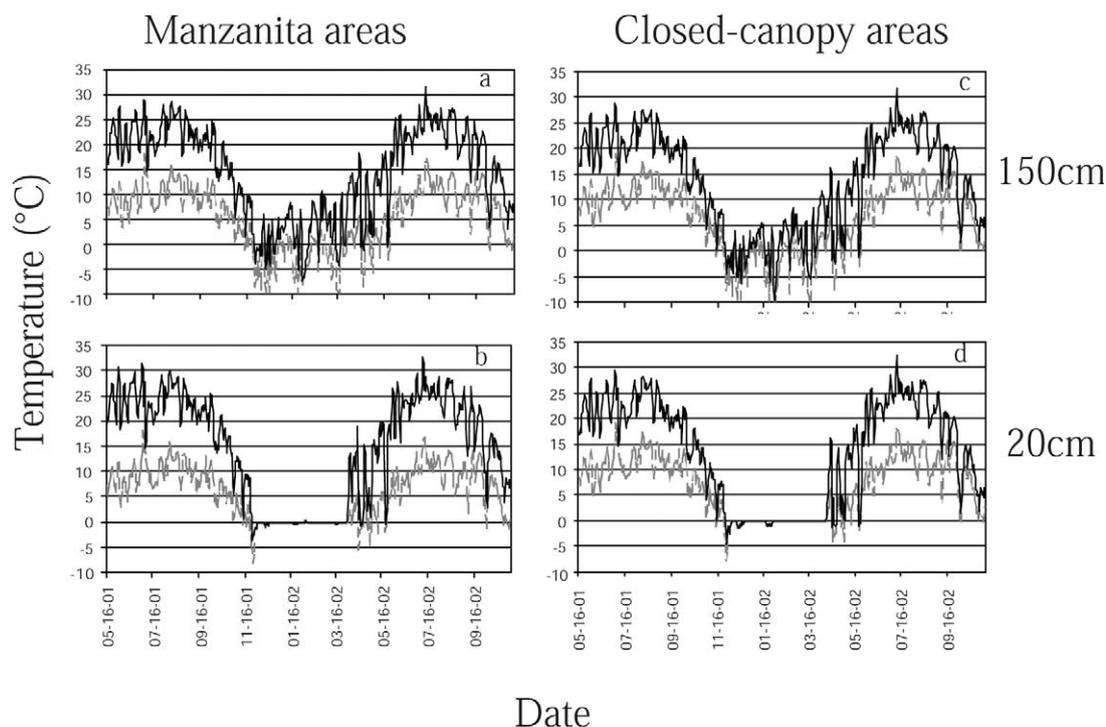


FIG. 2. Mean daytime (solid line) and night time (dotted gray line) temperatures from two different heights above the ground, 150 cm (a, c) and 20 cm (b, d). Figures a and b show temperatures from the manzanita patches, while c and d show temperatures from the closed-canopy patches.

than in the closed-canopy areas during the growing season ($F_{df1} = 7.823$, $P = 0.031$; Table 1), but it did not differ between the areas in June to August.

Survival rates of both sugar pine and white fir seedlings at the end of 2002 were greater in the closed-canopy than in the manzanita patches ($F_{df1} = 9.359$, $P = 0.03$). In the closed-canopy patches, the survival rates for both species did not differ between the different mesh treatments. However, in the manzanita patches, both white fir and sugar pine seedlings in the 5 μm pore-size mesh treatment had greater survival rates than seedlings in cylinders which did not exclude manzanita roots ($F_{df1} = 9.365$, $P = 0.092$; Fig. 5).

DISCUSSION

Our study suggests that tree seedlings may be water stressed in shrub patches until they develop a root structure that can access relatively deep soil water. We found no evidence suggesting that seedlings that could establish mycorrhizal connections were any less water stressed than seedlings growing in soil where tree roots were excluded. Low survival rates of tree seedlings and the strong positive response in transpiration rates when irrigation was provided suggest that dry summers and shrub competition for water

resources may be strong influences on seedling survivorship. To facilitate seedling establishment and survival, managers may need to make greater use of prescribed fire because it is more effective at reducing moisture competing shrubs than thinning in mixed-conifer forests (Wayman and North 2007).

The seismic information on active soil profile suggests that in our study area closed-canopy forest was on deeper soils with a higher water holding capacity than in the manzanita areas (Meyer et al. 2007). Because of the dry summers associated with the Mediterranean climate of the study site, during the growing season, plants depend on available water that has accumulated in the soil from snow melt in May. However, in a study based in an area with similar soils in southern California, Hubbert et al. (2001) found that calculations of plant-available water may need to include the weathered bedrock profile, from which roots of Jeffrey pine extracted a significant portion of late summer moisture. At Teakettle Forest, the depth to the solid bedrock in both the closed-canopy and shrub areas was ~ 3.3 m. We do not know, however, whether overstory white fir and sugar pine were extracting water from this weathered bedrock layer.

Isotope signatures suggest that overstory trees rely on deep water during the whole growing

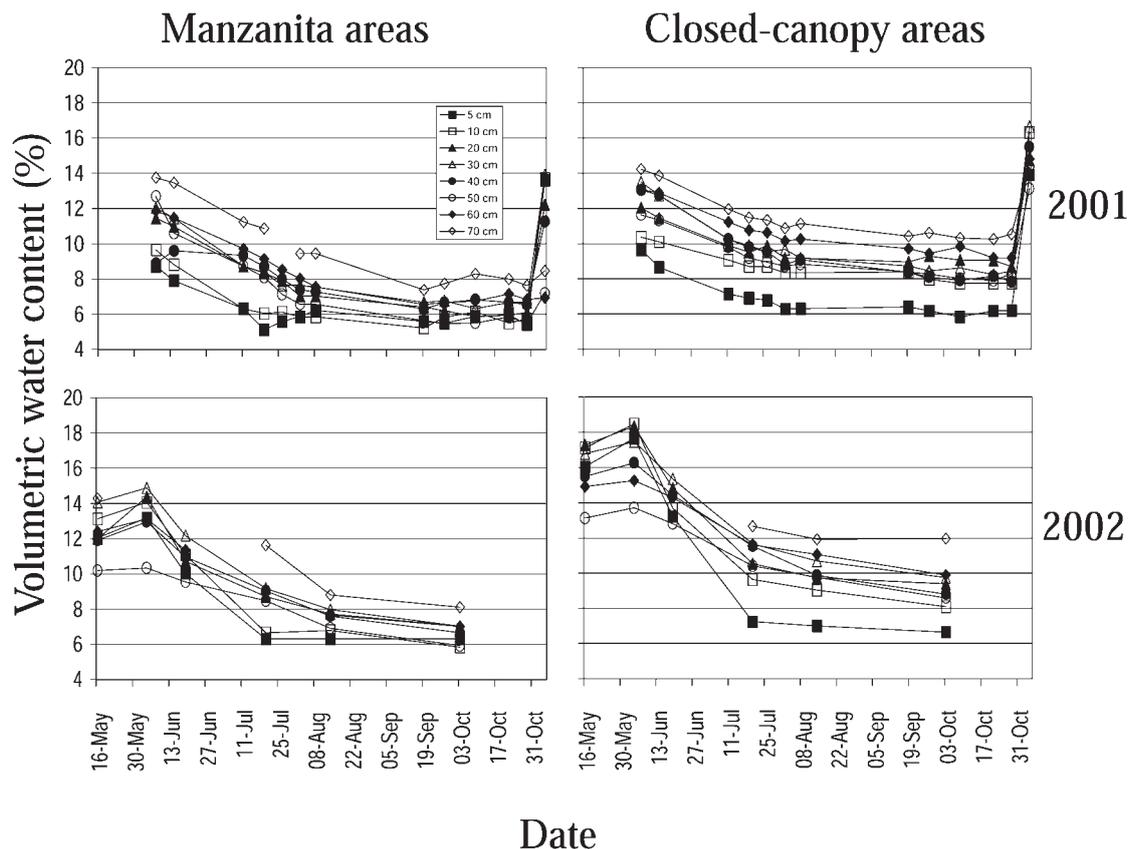


FIG. 3. Volumetric water contents (%) in a manzanita and a closed-canopy patch at eight different soil depths during the 2001 and 2002 vegetation seasons.

season, while shrubs rely on water from shallower horizons at the beginning of the growing season and as the soils become drier the primary zone of water uptake shifts to deeper horizons (Fig. 6). Tree saplings show a similar shift in their primary zone of water uptake to the shrubs; utilizing shallow horizons early in the season, then deeper layers as the soil becomes drier. This utilization pattern would put shrubs and tree saplings in

direct competition for water early in the growing season (May and June). Furthermore, tree seedlings, which are known to be shallow-rooted, with roots down to $\sim 20\text{--}30$ cm, would be competing with shrubs and tree saplings for water during the whole growing season. Rose et al. (2003) found similar differences in patterns of water between Jeffrey pine and manzanita shrubs. Their results suggest that 25–30 yr old

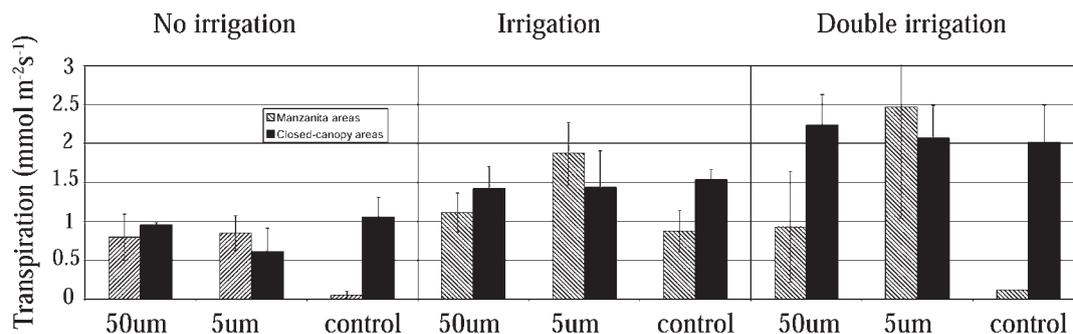


FIG. 4. Transpiration in September 2002 from seedlings in the cylinder treatments in manzanita and closed-canopy areas that had been exposed to different irrigation treatments for three weeks. Bars show ± 1 SE ($n = 3$).

TABLE 1. MONTHLY MEAN VALUES FOR THE VAPOUR PRESSURE DEFICIT IN THE MANZANITA AND THE CLOSED-CANOPY AREAS DURING THE VEGETATION SEASON OF 2002.

Month	Manzanita	Forest
	Vapour pressure deficit (mbar) ± std	Vapour pressure deficit (mbar) ± std
May	6.8 ± 1.0	5.7 ± 1.7
June	11.3 ± 1.6	11.3 ± 2.9
July	16.7 ± 1.9	16.6 ± 3.2
August	14.9 ± 0.7	14.8 ± 2.7
September	15.8 ± 0.9	13.2 ± 1.1
October	9.9 ± 0.9	7.1 ± 0.1

Jeffrey pine use more bedrock water and have a functional rooting depth that is slightly deeper than the manzanita, which rely on shallow soil water. Anderson and Helms (1994) showed that manzanita shrubs were able to extract more water from moisture-depleted soil profiles than pines, perhaps by achieving greater reductions in total water potentials. Osmotic adjustments and the consequent ability to use soil water held at relatively low water potentials are traits common to both Jeffrey pine and manzanita (Anderson and Helms 1994). Similar studies have not been

conducted with white fir, although it is generally considered to be much less drought tolerant than Jeffrey pine (Minore 1979; Royce and Barbour 2001). Unlike pine, however, manzanita also has low cell elasticity (Anderson and Helms 1994). Consequently, small reductions in relative water content lead to relatively large reductions in turgor pressure in manzanita shrubs, allowing them to use water held at lower water potential than pine trees.

Several investigators have reported that associated mycorrhizae increases drought tolerance and recovery from water stress in various woody species (Parke et al. 1983; Boyle and Hellenbrand 1991; Smith and Read 1997). Fungal hyphae and rhizomorphs extend the root system, entering soil pores too small to be penetrated by roots, and often have longer lifespans than fine roots (Parke et al. 1983). Several laboratory-based labeling experiments have also found indications that carbon is transported between plants connected via ectomycorrhizal and vesicular arbuscular networks (Read et al. 1985; Finlay and Read 1986; Watkins et al. 1996; Simard et al. 1997; Fitter et al. 1998). Furthermore, Querejeta et al. (2003) found that water may be transferred from oaks to their mycorrhizal symbionts during severe soil drying. In a laboratory-based experi-

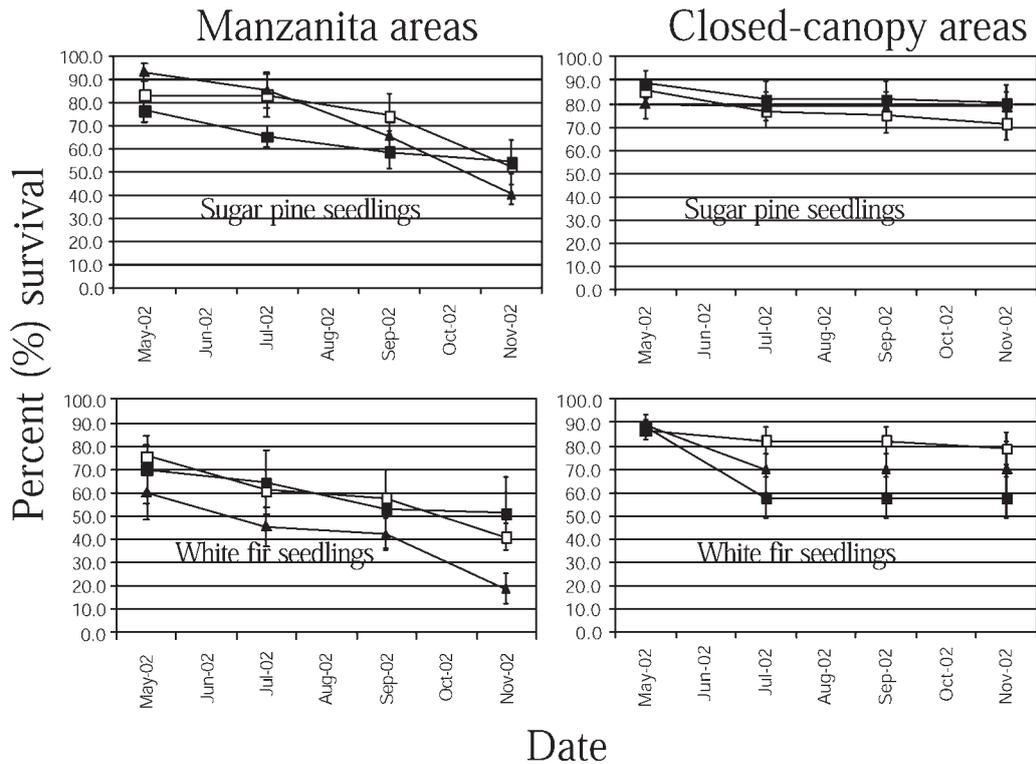


FIG. 5. Percentage survival of seedlings in the different treatments in manzanita areas and closed-canopy areas during 2002. Triangles represent the control treatment, filled squares the 50 µm pore-size mesh treatment and open squares the 5 µm pore-size mesh treatment. Bars show ±1 SE (n = 27–45).

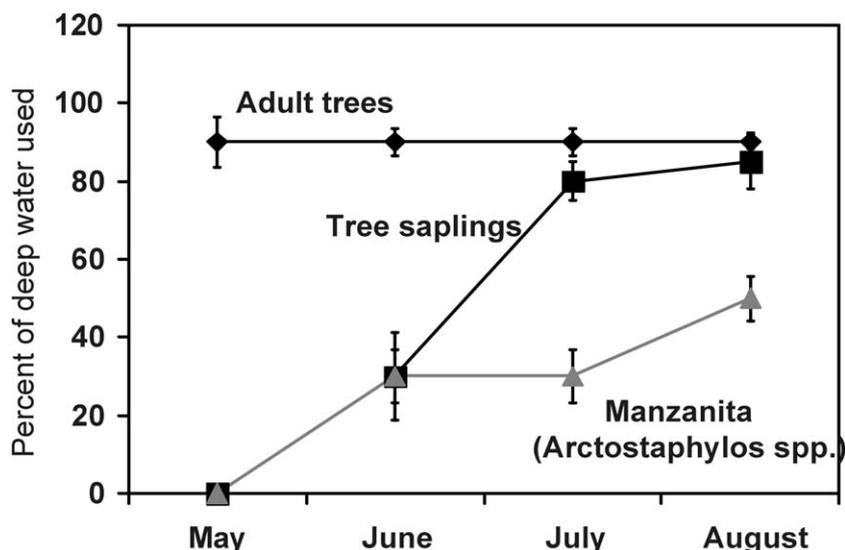


FIG. 6. Uptake depths of water for shrubs, overstory trees (>40 m tall) and tree saplings (1–3 m tall) during May to August 2001. Water from below 50 cm of depth in the soil profile is considered to be deep water. Bars show ± 1 SE ($n = 3$ –8).

ment, using tripartite mesocosms containing manzanita and young seedlings of sugar pine and Douglas-fir (*Pseudotsuga menziesii*), Plamboeck et al. (2007) showed that water can be transported via mycorrhizal hyphae to conifer seedlings. If the transport of resources from shrubs or mature trees to seedlings was important for the survival of the seedlings in our system, the seedling survival rates in the control and the 50 μ m pore-size mesh treatment would have been higher than in the 5 μ m pore-size mesh treatment. However, seedling survival rates in the 5 μ m pore-size mesh treatment were not significantly less than survival rates in the two treatments that allowed associations with an established mycelial network (Fig. 5). Survival rates were actually greater for tree seedlings planted in the manzanita patches when they were enclosed in the 5 μ m pore-size mesh, possibly because this treatment successfully excluded manzanita roots.

Our results show that conifer seedling survival rates were greater in the closed tree canopy than in patches dominated by manzanita shrubs. Isotope signatures suggest that in closed-canopy patches there may be soil-water partitioning between mature canopy trees (deep) and establishing seedlings (shallow) that reduces competition for critical water resources. In manzanita patches, however, we found that water competition between tree seedlings and shrubs negatively affected seedling establishment. Treatments that allowed the establishing seedlings to tap into an already existing ectomycorrhizal network did not enhance their survival. Shrubs may help modify microclimate conditions compared to open gaps, but diurnal temperature fluctuations were still

much greater than in closed-canopy forest. When roots were not excluded (the control treatment), seedling transpiration was very low and survival rates were significantly lower in manzanita patches than in closed-canopy forest. These results suggest that shrubs may inhibit the survival of tree seedlings until they establish roots deep enough to extract moisture from soil profiles below the depths at which the shrubs root.

With fire suppression, shrub cover has significantly increased in mixed-conifer forests (Parson and DeBenedetti 1979; Minnich et al. 1995). Our study suggests that forest managers may need to reduce shrub cover with treatments such as prescribed fire to enhance survival of conifer seedlings and facilitate restoration of the historic forest composition.

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LITERATURE CITED

- ANDERSON, P. D. AND J. A. HELMS. 1994. Tissue water relations of *Pinus ponderosa* and *Arctostaphylos patula* exposed to various levels of soil moisture depletion. *Canadian Journal of Forest Research* 24:1495–1505.

- ANONYMOUS. 1993. Soil survey of Sierran National Forest areas, California. USDA Forest Service Pacific Southwest Region, Clovis, CA.
- BOYLE, C. D. AND K. E. HELLENBRAND. 1991. Assessment of the effect of mycorrhizal fungi on drought tolerance of conifer seedlings. *Canadian Journal of Botany* 69:1764–1771.
- DANSGAARD, W. 1964. Stable isotopes in precipitation. *Tellus* 16:436–468.
- DUGAN, J. P., J. BORTHWICK, R. S. HARMON, M. A. GAGNIER, J. E. GLAHN, E. P. KINSEL, S. MACLEOD, J. A. VIGLINO, AND J. W. HESS. 1985. Guanidine hydrochloride method for determination of water oxygen isotope ratios and the oxygen-18 fractionation between carbon dioxide and water at 25°C. *Analytical Chemistry* 57:1734–1736.
- EHLERINGER, J. R., J. RODEN, AND T. E. DAWSON. 2000. Assessing ecosystem-level water relations through stable isotope ratio analyses. Pp. 181–198 in O. Sala, R. Jackson, and H. A. Mooney (eds.), *Methods in ecosystem science*. Academic Press, San Diego, CA.
- ERICKSON, H. E., P. SOTO, D. W. JOHNSON, B. ROATH, AND C. HUNSAKER. 2005. Effects of vegetation patches on soil nutrient pools and fluxes within a mixed-conifer forest. *Forest Science* 51:211–220.
- FINLAY, R. D. AND D. J. READ. 1986. The structure and function of the vegetative mycelium of ectomycorrhizal plants: I. translocation of ¹⁴C-labeled carbon between plants interconnected by a common mycelium. *New Phytologist* 103:143–156.
- FITTER, A. H., J. D. GRAVES, N. K. WATKINS, D. ROBINSON, AND C. SCRIMGEOUR. 1998. Carbon transfer between plants and its control in network of arbuscular mycorrhizas. *Functional Ecology* 12:406–412.
- GÓMEZ-APARICIO, L., R. ZAMORA, J. M. GÓMEZ, J. A. HÓDAR, J. CASTRO, AND E. BARZA. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14:1128–1138.
- GRAY, A. N. AND T. A. SPIES. 1995. Water content measurement in forest soils and decayed wood using time domain reflectometry. *Canadian Journal of Forest Research* 25:376–385.
- GRAY, A., H. ZALD, R. KERN, AND M. NORTH. 2005. Stand conditions associated with tree regeneration in Sierran mixed-conifer forests. *Forest Science* 51:198–210.
- HELMS, J. A. AND J. C. TAPPEINER. 1996. Silviculture in the Sierras. Pp. 439–476 in *Sierra Nevada Ecosystem Project: final report to Congress, Vol. II, assessments and scientific basis for management options*. Center for Water and Wildland Resources, University of California, Davis, CA.
- HICKMAN, J. C. (ed). 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley, CA.
- HORTON, T. R., T. D. BRUNS, AND V. T. PARKER. 1999. Ectomycorrhizal fungi associated with *Arctostaphylos* contribute to *Pseudotsuga menziesii* establishment. *Canadian Journal of Botany* 77:93–103.
- HUBBERT, K. R., J. L. BEYERS, AND R. C. GRAHAM. 2001. Roles of weathered bedrock and soil in seasonal water relations of *Pinus jeffreyi* and *Arctostaphylos patula*. *Canadian Journal of Forest Research* 31:1947–1957.
- MCDONALD, P. M. 1976. Forest regeneration and seedling growth from five major cutting methods in north-central California. Research Paper PSW-115. USDA Forest Service, Pacific Southwest Forest and Range Experimental Station, Berkeley, CA.
- MEYER, M., M. NORTH, A. GRAY, AND H. ZALD. 2007. Influence of soil thickness on stand characteristics in a Sierra Nevada mixed-conifer forest. *Plant and Soil* 294:113–123.
- MINNICH, R. A., M. G. BARBOUR, J. H. BURK, AND R. F. FERNAU. 1995. Sixty years of change in Californian conifer forest of the San Bernardino Mountains. *Conservation Biology* 9:902–914.
- MINORE, D. 1979. Comparative autecological characteristics of Northwestern tree species: a literature review. General Technical Report GTR-PNW-87. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- MOLINA, R. AND J. M. TRAPPE. 1982. Lack of mycorrhizal specificity by the ericaceous host *Arbutus menziesii* and *Arctostaphylos uva-ursi*. *New Phytologist* 90:495–509.
- NORTH, M., B. OAKLEY, J. CHEN, H. ERICKSON, A. GRAY, A. IZZO, D. JOHNSON, S. MA, J. MARRA, M. MEYER, K. PURCELL, T. RAMBO, B. ROATH, D. RIZZO, AND T. SCHOWALTER. 2002. Vegetation and ecological characteristics of mixed-conifer and red fir forests at the Teakettle Experimental Forest. USDA Forest Service General Technical Report PSW-186. United States Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.
- , M. HURTEAU, R. FIEGENER, AND M. BARBOUR. 2005. Influence of fire and El Niño on tree recruitment varies by species in Sierran mixed conifer. *Forest Science* 51:187–197.
- PARKE, J. L., R. G. LINDERMAN, AND C. H. BLACK. 1983. The role of ectomycorrhizae in drought tolerance of Douglas-fir seedlings. *New Phytologist* 95:300–304.
- PARKER, A. J. 1994. Latitudinal gradients of coniferous tree species, vegetation, and climate in the Sierran-Cascade axis of northern California. *Vegetatio* 115:145–155.
- PARSONS, D. J. AND S. H. DEBENEDETTI. 1979. Impact of fire suppression on mixed-conifer forest. *Forest Ecology and Management* 2:21–33.
- PERRY, D. A., M. P. AMARANTHUS, J. G. BORCHERS, S. L. BORCHERS, AND R. E. BRAINERD. 1989. Bootstrapping in ecosystems. *BioScience* 39:230–237.
- PLAMBOECK, A. H., T. E. DAWSON, L. M. EGERTON-WARBURTON, M. NORTH, T. D. BRUNS, AND J. I. QUEREJETA. 2007. Water transfer via ectomycorrhizal fungal hyphae to conifer seedlings. *Mycorrhiza* 17:439–447.
- QUEREJETA, J. I., L. M. EGERTON-WARBURTON, AND M. F. ALLEN. 2003. Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. *Oecologia* 134:55–64.
- READ, D. J., R. FRANCIS, AND R. D. FINLAY. 1985. Mycorrhizal mycelia and nutrient cycling in plant communities. Pp. 193–217 in A. H. Fitter (ed.), *Ecological interaction in soil*. Blackwell Scientific Publications, Oxford, United Kingdom.

- ROSE, K. L., R. C. GRAHAM, AND D. R. PARKER. 2003. Water source utilization by *Pinus jeffreyi* and *Arctostaphylos patula* on thin soils over bedrock. *Oecologia* 134:46–54.
- ROYCE, E. B. AND M. G. BARBOUR. 2001. Mediterranean climate effects: I. conifer water use across a Sierra Nevada ecotone. *American Journal of Botany* 88:911–918.
- SIMARD, S. W., M. D. JONES, D. M. DURALL, D. A. PERRY, D. D. MYROLD, AND R. MOLINA. 1997. Reciprocal transfer of carbon isotopes between ectomycorrhizal *Betula papyrifera* and *Pseudotsuga menziesii*. *New Phytologist* 137:529–542.
- SMITH, S. E. AND D. J. READ. 1997. Mycorrhizal symbiosis. 2nd ed. Academic Press, London, United Kingdom.
- STEPHENSON, N. L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *Journal of Biogeography* 25:855–870.
- TAPPEINER, J. C. AND P. M. McDONALD. 1996. Regeneration of Sierra Nevada forests. Ch. 12 in *Sierra Nevada Ecosystem Project: final report to Congress, Vol. III, assessments, commissioned reports, and background information*. Centers for Water and Wildland Resources, University of California, Davis, CA.
- WATKINS, N. K., A. H. FITTER, J. D. GRAVES, AND D. ROBINSON. 1996. Carbon transfer between C₃ and C₄ plants linked by a common mycorrhizal network, quantified using stable carbon isotopes. *Soil Biology and Biochemistry* 28:471–477.
- WAYMAN, R. AND M. NORTH. 2007. Initial response of a mixed-conifer understory community to burning and thinning restoration treatments. *Forest Ecology and Management* 239:32–44.