

GROWTH AND WATER RELATIONS OF *PINUS PONDEROSA* SEEDLINGS IN COMPETITIVE REGIMES WITH *ARCTOSTAPHYLOS PATULA* SEEDLINGS

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SUMMARY

(1) Ponderosa pine (*Pinus ponderosa* Dougl. ex P&C Lawson) seedlings were planted into hand-thinned plots of manzanita (*Arctostaphylos patula* Greene) seedlings in a modified replacement series with five tree-to-shrub proportions approximating 0:100, 25:75, 50:50, 75:25 and 100:0. Competitive performance in mixture and monoculture was assessed from relative growth rates and relative yields that were calculated from estimates of canopy volume.

(2) Soil-moisture depletion and photosynthetically active radiation were measured monthly in each treatment plot. Leaf water potential and leaf conductance to water vapour of both species were assessed monthly.

(3) Soil moisture was more depleted in mixed stands than in pine monocultures, but no change in the light environment was observed. Leaf water potential of trees was less negative and leaf conductance was significantly greater in monoculture than in mixed stands.

(4) Leaf conductance of manzanita seedlings was consistently higher than that of pine seedlings. Ponderosa pine seedlings were less competitive and had lower relative yields and lower relative growth rates in mixed stands than in monoculture.

(5) Results suggest that competition with greenleaf manzanita for soil moisture can reduce ponderosa pine productivity significantly during early site development.

INTRODUCTION

After disturbance by fire or logging, mixed coniferous forest sites of the Sierra Nevada Range are recolonized rapidly by early seral shrub species of the genera *Arctostaphylos* and *Ceanothus* (Fowells & Schubert 1951; Ahlgren & Ahlgren 1960). Conifer seedlings present during this shrub-dominated successional phase grow slowly and may remain suppressed for decades (Conard & Radosevich 1982a), but growth of naturally seeded and planted conifers may increase dramatically after shrub removal (Bentley, Carpenter & Blakeman 1971; Powers & Jackson 1978; Conard & Radosevich 1982b; Oliver 1984; Lanini & Radosevich 1985). Removal of the shrub canopy often results in increased availability of limiting site resources, particularly soil moisture and solar radiation (Conard & Radosevich 1982b; Lanini & Radosevich 1985). Studies in which soil moisture and radiation have been varied experimentally demonstrate that reduction in either of these resources may result in declining photosynthesis (Brix 1962; Cleary 1970; Helms 1976; Beadle & Jarvis 1977; Havranek & Benecke 1978; Conard & Radosevich 1981) and eventual reduction in growth (Jarvis & Jarvis 1963; Lotan & Zahner 1963; Kaufmann 1968).

Most studies of shrub-conifer interactions have assessed tree growth in response to manipulation of shrub populations with mechanical or chemical tools (Stewart 1981).

Such studies are instructive and may meet the immediate needs of forest managers, but they neither quantify adequately the relationship between conifer growth and shrub density nor elucidate underlying mechanisms of shrub-conifer competition. Shrub density in such studies is rarely varied systematically and the use of systematic designs that are diagnostic of competitive relationships may quantify shrub-conifer interactions more definitively.

In this study, the shrub population was manipulated systematically by hand thinning to establish specific densities so that the relationship of tree growth to shrub abundance could be examined within replicated shrub populations. Interactions between seedlings of greenleaf manzanita (*Arctostaphylos patula* Greene) and ponderosa pine (*Pinus ponderosa* Dougl. ex P&C Lawson), both with C₃ metabolism, were investigated in a modified replacement series (de Wit 1960; Harper 1977). The data represent the initial phase of a long-term experiment designed to explore the interactions between the two plant species. The objectives here were (i) to assess the competitive capacity of the two species during the initial stage of succession, (ii) to determine the effects of competitive regimes on photosynthetically active radiation and soil moisture, (iii) to compare physiological responses of each species in a given competitive regime, and (iv) to relate physiological responses of each species to competitive capacity and growth.

MATERIALS AND METHODS

The study site was located at 1350 m elevation on a southwest facing slope at the University of California Blodgett Research Forest near Georgetown, California (UTM Zone 10S, 690000E, 4310000N). The site was logged and cleared of all shrub crowns and roots in 1978. At the beginning of the experiment in September 1981, a stand of 3-year-old greenleaf manzanita seedlings occupied the site.

In establishing the treatment and design, the manzanita stand was divided into 340 m² plots and hand-thinned to densities of zero, four, eight, twelve and sixteen plants per square metre in September 1981. Manzanita densities were chosen after a census of the manzanita population before manipulation. The mean population density, sixteen shrubs per square metre, was used as the maximum shrub density in the replacement series. Treatments were established by thinning to approximately 75, 50, 25 and 0% of maximum density. Actual shrub densities, determined after thinning by quadrat sampling, were found to be within one standard deviation of the desired percentages (Table 1). For simplicity, treatments will be referred to here by the theoretical proportions.

TABLE 1. Experimental design for the ponderosa pine-greenleaf manzanita modified replacement series

Manzanita density (stems m ⁻²)		Pine density (stems m ⁻²)	Relative tree : shrub proportion*	
Theoretical	Actual	Planted	Theoretical	Actual
16	14.0	0.00	0:100	0:100
12	12.1	0.10	25:75	25:77
8	7	0.21	50:50	50:48
4	4.2	0.32	75:25	75:27
0	0	0.43	100:0	100:0

* Relative proportion = $(P/P_m) \times 100 : (S/S_m) \times 100$ where P is the pine density in mixture, P_m is the pine density in monoculture, S is the shrub density in mixture and S_m is the shrub density in monoculture.

Nursery-grown ponderosa pine seedlings (1 year old, bare root) were planted into the plots on 1 May 1982. The seedlings had been grown at the U.S. Forest Service Nursery at Placerville, California from seed collected at the Blodgett Experimental Forest. Seedling density varied from 0 to 0.43 trees per square metre (Table 1). The experimental design consisted of five proportions of tree to shrubs arranged in randomized complete-block design with three replicates (Table 1). Tree density for the 50:50 mixture approximated current management practices for planting ponderosa pine. The series was established such that $(P_i/P_m) + (M_i/M_m) = 1$, where P_i and M_i are pine and manzanita densities, respectively in treatment i , and P_m and M_m are pine and manzanita monoculture densities. Actual densities of both species resulted in a weighting of the manzanita densities such that $M_m = P_m \times 37$. This weighting produces a modified replacement series in which total density and proportion change simultaneously. Because of planting failure and soil heterogeneity in the third replicate, the data are from two replicates only.

Tree and shrub measurements

At the beginning of the experiment, ten randomly chosen pines in each plot were numbered for monthly measurements of height and crown width. Tree canopy volume was calculated from these measurements (Wakimoto 1977). Total canopy volume for each plot was determined at the end of the second growing season by calculating volume from the height and crown width of thirty individual trees and multiplying the mean by the number of surviving trees. Total canopy volume of manzanita in each plot was calculated from the height and crown width of each shrub in 2.25 m² quadrats surrounding each of the ten sample trees (Wakimoto 1977). Tree and shrub volumes calculated in this manner are highly correlated with tree and shrub dry weight (Lanini & Radosevich 1985).

Relative yields of each species were calculated from canopy volumes measured at the end of the second growing season (September 1983). Relative yield of a given species in a given mixture was determined by dividing the total canopy volume on a mixed plot by the total attained by the species in monoculture.

Relative canopy growth rate (RCGR) was calculated by regression of the natural logarithm of monthly estimates of canopy volume against time (Evans 1972; Hunt 1978). Slopes of the functions represent mean RCGR during the period of growth.

Volumetric soil moisture content was measured monthly with a neutron probe (Hydroprobe Model 503, Campbell Pacific Nuclear, Pacheco, CA) at 30, 60, 90 and 120 cm in the soil profile. One carbon steel access tube was installed in each plot. The depletion of soil moisture over the course of the growing season was calculated by summing changes at all depths from May to September.

Photosynthetically active radiation (PAR) on coniferous foliage was measured with a quantum sensor (Type 1905, Li-cor Inc., Lincoln, NE) simultaneously with leaf conductance measurements. Measurements were made at tree height on three individuals of each species in each plot.

Leaf water potential (LWP) of ponderosa pine and greenleaf manzanita was measured monthly with a pressure chamber (Model 3005, Soilmoisture Co., Santa Barbara, CA) (Scholander *et al.* 1965) over 2-hour periods beginning at 04.00, 10.00 and 14.00 Pacific Standard Time. The fully expanded pine fascicles and manzanita leaves obtained in May, June and July were from the previous year and those obtained in August and September from the current year. One sample was taken from three individuals per species in each plot at each sampling time (six individuals per treatment). The same

individuals were sampled throughout a given day, but different individuals were sampled each month to minimize foliage loss from any one plant. Measurements were made on 7 June, 8 July, 1 August, 30 August and 27 September 1983.

Leaf conductance to water vapour of each species was measured monthly with a Licor 1600 null-balance porometer during 2-hour periods beginning at 10.00 and 14.00 Pacific Standard Time. The most fully expanded needles and leaves were sampled from three individuals of each species in each treatment plot, the same individuals in morning and afternoon periods, but different individuals each month. Both sides of the leaf were measured for each species. At the morning measurement, pine needles were marked with zinc oxide at the point of chamber attachment. When the same needles were sampled in the afternoon, they were excised at the mark, bagged and transported to the laboratory on dry ice, where they were stored at 0 °C until leaf area measurements were made. Surface area was calculated from measurements of fascicle length and radius made with an ocular micrometer (Paley & Radosevich 1984). A constant leaf area of 4 cm² was measured on the manzanita in the porometer chamber.

Statistical analysis

Two-way analyses of variance for a randomized complete-block design (Steel & Torrie 1980) were performed to test for significant differences among treatments and species with respect to relative yield and soil-moisture depletion. Analyses of variance for a split-plot design (Steel & Torrie 1980) were performed to test for significant differences in physiological responses due to species and treatment at a given sampling date, or due to treatment and sampling date for a given species. Treatment represented the main plot, species and time the subplots. The most robust least significant difference was calculated from pooled error parameters (Steel & Torrie 1980) with *t*-values for alpha at 0.05. RCGR was determined with simple regression analysis and the significance of differences between the regression coefficients with a test for the homogeneity of variances.

RESULTS AND DISCUSSION

Competitive performance

The replacement diagram (Fig. 1) indicates that greenleaf manzanita was the superior competitor at the end of the second growing season. The observed relative yields of manzanita in mixture with ponderosa pine consistently exceeded yield predicted from monoculture. Conventional interpretation (Harper 1977) is that these results imply that the manzanita seedlings used more site resources and the pine seedlings less than would be predicted from their performances in monoculture. The resources may include soil moisture, nutrients and PAR.

The relative importance of interspecific and intraspecific interactions in determining the biomass of each species could be inferred because of the weighted manzanita densities. Most manzanita seedlings had as nearest neighbours other manzanita seedlings, while all pine seedlings had manzanita as nearest neighbours. Therefore, interspecific interactions appear more influential than intraspecific effects in determining yield of ponderosa pine seedlings. The reverse was true for manzanita, although Jolliffe, Minjas & Runeckle (1984) point out that competitive effects cannot be partitioned into discrete intraspecific and interspecific components unless the relationship between yield and density is first determined for each species in monoculture. Extrapolation of data from Oliver (1979) suggests that tree densities at the stage of site development selected for this experiment

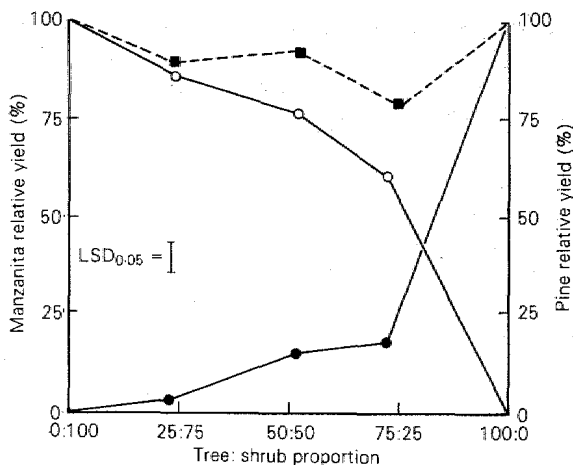


FIG. 1. Replacement series diagram for relative yields of ponderosa pine seedlings (●) and greenleaf manzanita seedlings (○), and their relative yield totals (■), after two growing seasons (1982–83). Relative yield of a given species was calculated by dividing its total canopy volume in mixture by its total canopy volume in monoculture. Relative yield totals are the sums of relative yields of both species in a given mixture.

are not sufficiently high to allow intraspecific interactions between pine seedlings. Studies in which tree densities are sufficiently high to register intraspecific competition indicate that interactions with competing brush influence tree growth more than intraspecific interactions (Powers & Jackson 1978; Oliver 1984).

RCGR of the ponderosa pine seedlings (Table 2) was significantly affected by manzanita ($P < 0.01$). The pine monocultures had maximum RCGR, but as the proportion of manzanita seedlings increased, pine RCGR decreased.

RCGR of manzanita seedlings did not differ with the various tree:shrub proportions (Fig. 2). It was significantly less than the rate calculated for the pine monoculture but was not significantly different from that determined for pine seedlings in mixed stands ($P < 0.01$). These data suggest that these species differ in the sensitivity of their growth rates to competitive regimes.

TABLE 2. Relative canopy growth rates (RCGR) for ponderosa pine and greenleaf manzanita seedlings in a modified replacement series

Tree:shrub proportion	Pine		Manzanita	
	RCGR* (cm ³ day ⁻¹)	R ² †	RCGR (cm ³ day ⁻¹)	R ²
0:100	—	—	5.8 a	0.86
25:75	2.2 aa‡	0.80	5.6 ab	0.91
50:50	7.6 ba	0.97	6.6 aa	0.91
75:25	9.0 ca	0.96	7.8 aa	0.93
100:0	15.0 d	0.96	—	—

* RCGR was calculated as the slope of the line for the log of individual canopy volume plot over time from April to September.

† All R² are significant at the $P < 0.01$ level.

‡ The first letter following RCGR values indicates within-species comparisons, the second letter between-species comparisons. Values with different letters are significantly different at the $P < 0.01$ level.

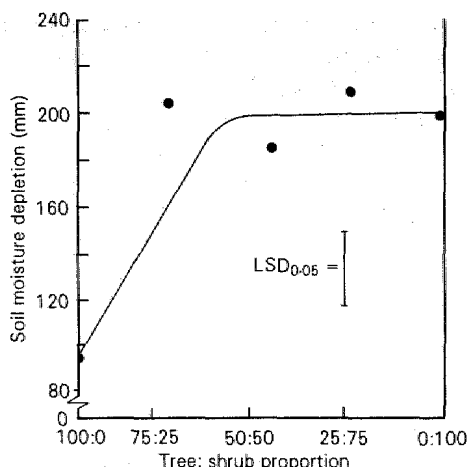


FIG. 2. Soil moisture depletion from May to September 1983 summed for 30, 60, 90 and 120 cm depths in the ponderosa pine-greenleaf manzanita replacement series. Each point represents the mean for two replicates.

PAR and soil moisture

Treatment did not significantly affect the amount of PAR reaching tree foliage. The manzanita seedlings had little height advantage over the trees during this phase of the study and, because of the vertical orientation of manzanita leaves, significant shading probably occurred only early in the morning or late in the afternoon. However, if the growth rate of the pine in mixtures with manzanita continues to lag behind that of the manzanita, and if a height differential develops between trees and shrubs, light may become a limiting factor, influencing pine productivity, as has been suggested by data from Lanini & Radosevich (1985) and Conard & Radosevich (1982b).

Seasonal soil moisture depletion, summed over all sampled depths, was examined as a function of the proportion of trees to shrubs (Fig. 2). Depletion of soil moisture for the entire season was significantly lower in pine monocultures than in mixed culture ($P < 0.05$), but no significant differences appeared among treatments with manzanita. These data, along with the reductions in RCGR (Table 2) and the suppressed yield of the tree seedlings in mixture (Fig. 1) suggest that productivity of ponderosa pine seedlings in mixed stands with manzanita may have been limited by water stress.

Physiological response

Increasing the proportion of manzanita in mixture resulted in depressed predawn leaf water potential of pine seedlings, and the effects intensified as the season progressed (Fig. 3). Morning and afternoon LWP followed trends similar to those at predawn in response to treatment, although values were typically lower during the day. No significant differences in LWP were observed among manzanita seedlings in the various treatments. Predawn LWP fluctuated greatly throughout the season and, during morning and midday, declined as the season progressed.

Few significant differences in LWP appeared between species. In late August and September values for the shrubs during all sampling times tended to be higher than those for the pine seedlings in mixed stands, although most differences were significant

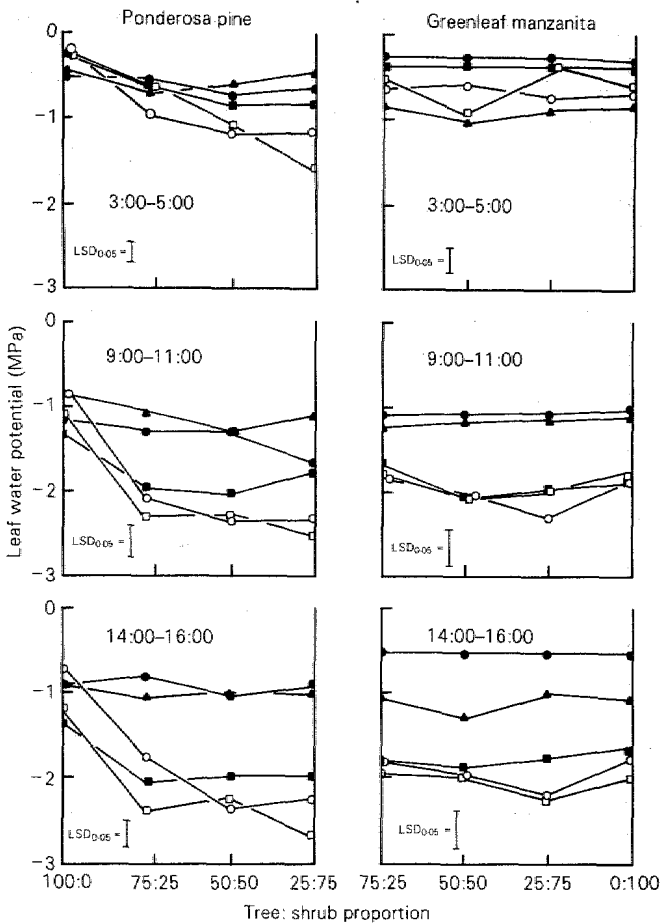


FIG 3. Leaf water potential of ponderosa pine and greenleaf manzanita seedlings in response to competitive regimes. Sampling dates in 1983: ●, 4 June; ▲, 7 July; ■, 1 August; ○, 30 August; □, 28 September. Each point represents the mean for six individuals.

only at the 0.1 level. During this period, pines in monoculture had significantly higher morning and midday LWP than did manzanita in monoculture ($P < 0.05$).

The depression of LWP of pine seedlings in mixed culture indicates that soil moisture was again limiting for those trees relative to trees grown in monoculture. The seasonal decline in LWP of both species was associated with the depletion in soil moisture as the season progressed. Maintenance of higher LWP by the shrubs, relative to the pine in mixtures, suggests that the manzanita had greater access to soil moisture late in the growing season than did the pine. The maintenance of higher LWP by the pine seedlings in monoculture reflects the more favourable soil moisture environment in the absence of transpiring shrub canopies.

As the growing season progressed, the effect of manzanita seedlings upon leaf conductance of trees grown in mixture was increasingly significant (Fig. 4). Leaf conductance in mixtures declined throughout the growing season, while values for the trees

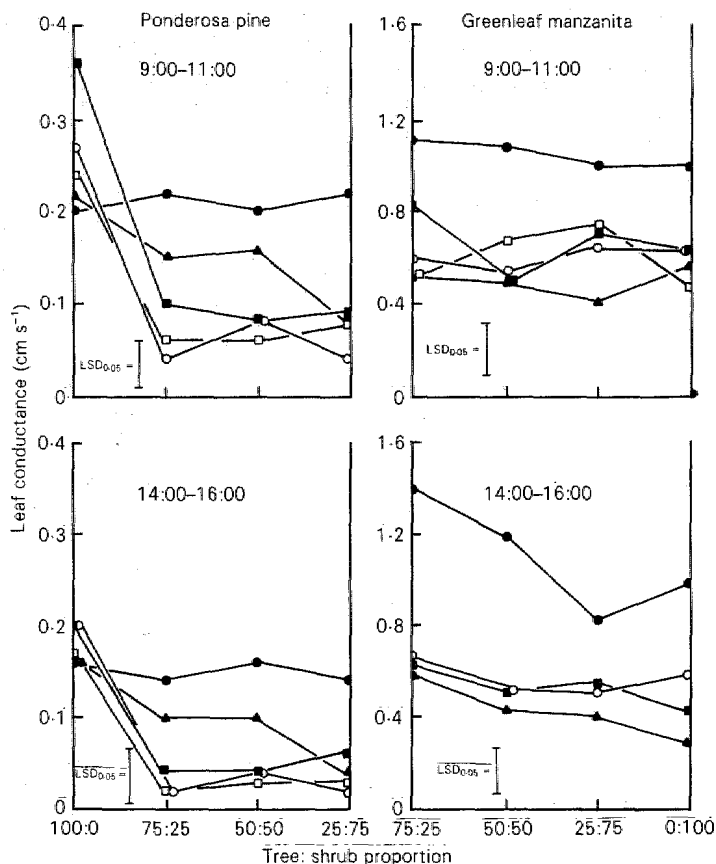
Ponderosa pine in competitive regimes

FIG. 4. Leaf conductance to water vapour of ponderosa pine and greenleaf manzanita seedlings in response to competitive regimes. Note difference in scale. Sampling dates in 1983: ●, 3 June; ▲, 6 July; ■, 2 August; □, 30 August; ○, 27 September. Each point represents the mean for six individuals.

in monoculture remained consistently high. Values for manzanita seedlings were relatively constant and significantly greater ($P < 0.05$) than that for the pines throughout the season, regardless of treatment (Fig. 4). No significant treatment differences were detected among manzanita seedlings.

Photosynthetic rates of ponderosa pine and manzanita have been correlated to leaf conductance (Helms 1976; Conard & Radosevich 1981). The results from the present study indicate that gas exchange by pine seedlings grown with manzanita was severely restricted in both magnitude and duration. A decline in LWP and concomitant stomatal conductance of the pine seedlings in the mixed stands was associated with the depletion of soil moisture by transpiring manzanita seedlings. Pine seedlings in monoculture were able to maintain higher rates of gas exchange later in the season than the trees in mixed culture (Fig. 4). The observed increase in RCGR and relative yields of the trees in monoculture are associated with the more favourable water relations conducive to carbon uptake.

The competitive performance of greenleaf manzanita and ponderosa pine may be

attributed to several factors. Early resource capture has been cited as a key determinant in competitive success (Grime 1979; Harper 1977). Manzanita colonization 2 to 3 years before the conifers were planted allowed pre-emptive root growth and development through the soil profile by the shrubs. Under these and natural densities, the shrubs have a numerical advantage as well, such that the pine in all mixtures have manzanita seedlings as nearest neighbours.

The pre-emption of soil moisture by the shrubs and the reduction of moisture available to the trees probably contributed greatly to the competitive success of the manzanita. The classic interpretation of the de Wit diagram, indicating that manzanita seedlings use disproportionately more of the limiting resources (Fig. 1), is in accord with results of Lanini & Radosevich (1985) and Conard & Radosevich (1982b) that demonstrate that the soil moisture environment is significantly modified by a transpiring shrub canopy.

Competitive success may also be determined by the capacity of a species to maintain productivity in a competitive environment (Grime 1979). In the less competitive environment of the tree monoculture, RCGR of pine seedlings was greater than that for the manzanita seedlings in all treatments. However, RCGR of the pine seedlings declined in response to a competitive environment, while that of manzanita remained constant. Although these rates are for aboveground biomass only, and changes in biomass allocation in response to competitive regimes cannot be assessed, the aboveground growth rate of manzanita shrubs demonstrated marked insensitivity to competitive regimes, evidence of their capacity to tolerate stress associated with depleted resources.

Maintenance of key physiological functions while under potentially stressful conditions permits the shrub seedlings to maintain productivity. Depletion of soil moisture in plots with manzanita was associated with a decline in LWP of both species. While the decline was associated with a reduction in leaf conductance for the pine seedlings in mixture, the manzanita sustained high conductance throughout the summer, despite a similar decline in water potential. Both rate and duration of gas exchange of manzanita seedlings were superior to those of pine seedlings, even as soil moisture declined. Modification of the soil moisture environment by manzanita significantly affected the physiological functioning of the pine seedlings, reducing their RCGR and biomass. A reduction in LWP not only lowers conductance to water vapour and carbon dioxide, but also arrests leaf expansion (Boyer 1968). A reduction in both the rate of carbon uptake and the surface area of exchange combine to limit productivity of trees grown with manzanita seedlings.

The competitive superiority shown by manzanita seedlings at the initial stage of site development in the Sierra Nevada Range may not indicate a long-term competitive advantage, as the dynamics and nature of interactions between the two species may change. At this stage of development, light is not limiting tree growth, and the primary limitation is soil moisture, but the significance of nutrient competition remains untested. If the shrubs overtop the trees, light limitation may change the nature of the competitive responses. Over time, the trees may overtop the manzanita. Continuous monitoring of this system will elucidate the population shifts and physiological responses underlying the evolving competitive relationship.

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