EFFECT OF SHRUB COMPETITION ON PLANTATION GROWTH

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ABSTRACT

An evaluation was made of the effect of four levels of shrub release, in the first year after treatment, on annual growth and physiological functioning of 4-yr-old ponderosa pine saplings. The study was done at Latour Demonstration State Forest, California, which is about 50 miles east of Redding at an elevation of approx. 5,400 feet. At the start of the study, the plantation had 100 percent predominantly manzanita shrub cover. In 1986, twelve 20-tree plots were established to provide three replications of four completely randomized levels of shrub cover. These treatments consisted of leaving 0, 15, 30, and 100 percent shrub cover by removing the appropriate proportion of leaf area. Measurements taken included total height growth, stem diameter, needle length, soil water depletion, fine root production, leaf water potential, and stomatal conductance.

At the end of the summer, soil water content was 36.5% in plots with no shrub cover and 25.6% where shrub cover was 100%. Pines growing with no shrub competition had, relative to trees growing with 100% shrub cover: 3-cm greater needle length, seven-times greater average daily stomatal aperture, six-times higher average daily transpiration; and half the average daily water stress. Over the summer, water relations of the pines steadily deteriorated from the 0% to the 15, 30, and 100% shrub cover areas. At the end of the summer manzanita had twice the leaf conductance and transpiration of the pines, in all levels of shrub cover, despite having consistently higher water stress.

It is well known that release from shrub competition often results in enhanced growth of pine plantations. This study shows that this release is associated with improved soil water content and less plant water stress.

JUSTIFICATION

The reduction in growth of conifer plantations by shrub competition is probably the single most important silvicultural issue in California. In previous decades, this problem has been met by the use of herbicides. Currently, curtailment of herbicide applications, potential environmental concerns regarding the use of mechanical methods, and doubts regarding the efficacy and logistical possibility of using manual methods, combine to make the control of shrub competition a prime managerial issue.

The reduction in plantation growth is critically important to private landowners. The State encourages reforestation through its CFIP program, but the benefits to both the landowner and the State are in jeopardy if growth is substantially reduced by inability to control competition. The U.S. Forest Service recognizes the importance of competition effects and estimates that plantations will sustain a 20 to 70 percent reduction in growth if shrub competition is not controlled (USDA Draft EIS, 1983). What is needed, by both land managers and policy makers, is more detailed knowledge on both the magnitude of growth loss on a variety of sites in California, and an understanding of the mechanism by which competition develops.

Some research is underway by both the USDA Forest Service PSW Station, and by the University of California, evaluating both growth reductions and mechanisms. However, the task is large due to the number of important species and sites. Studies need to be made on more sites and on more species if answers to this problem are to have Statewide application.

PAST STUDIES

Due to its importance to the California timber industry, much of the previous research on brush release has been directed towards ponderosa pine. In general, these studies have demonstrated reductions in height, diameter, and volume when ponderosa pine is grown in the presence of brush. The reduction in growth becomes apparent within 3 to 4 years and continues to increase throughout the sapling stage of stand development (Fiske, 1981). Bentley et al (1971) examined the relationship between brush crown volume and 5th-year seedling heights. It was found that total height decreased almost linearly as brush volume increased from 10,000 to 40,000 ft^3 (280 to 1130 m^3). The mean height of all seedlings was not influenced by brush volumes less than 10,000 ft^3.

If left untreated, most planted conifers will eventually grow free of competing brush due to their greater long-term dominance potential (Newton 1973, Fiske 1981). However, the time required for plantations to grow beyond the competition is a critical issue. Oliver (1979) estimated that reduction in ponderosa pine diameter after 12 years was equivalent to 1.1 year's growth with 30 percent brush cover and 2.6 year's growth with 120 percent brush cover. Given the relatively low rates of return on most forestry investments, even a few year's loss in growth may make a great difference in the economic feasibility of plantation establishment.

Barrett (1973) demonstrated some interesting interactions among time since release and plantation spacing in the effect on growth of ponderosa pine with and without brush competition. Mean tree height and stand volume four years after release were greater in non-released plots than in released plots for densities of 250 tpa (620 trees/ha) or greater. However, twelve years following release, mean tree height and stand volume were greater on released plots for all but the greatest density of 1,000 tpa (2470 trees/ha). Diameter development was generally greater in the absence of brush regardless of density. In this case, prior to the onset of inter-tree competition, brush may moderate microclimate to favor plantation establishment. As the conifers develop, demands on site resources increase to a level where utilization by brush constrains conifer development.

The influence of soil type on the response of 9-year-old ponderosa pine to release from whiteleaf manzanita (Arctostaphylos viscida) was studied by Powers and Jackson (1978). Released and non-released plots were established in plantations growing in close proximity on both a relatively low quality Mariposa soil (Dunning site 11, 111) and a relatively high quality Cohasset soil (Dunning site 1A, 1). Measurements one year following release indicated 40 and 60 percent increases in needle weight for trees on the Cohasset and Mariposa soils respectively. In addition, needle length increased by 47 percent in seedlings on the Mariposa soil. Thus sapling crown development on plots without brush was becoming more favorable for tree growth and the effect of brush removal was greater on the low quality Mariposa soil.

This research illustrates considerable variability in ponderosa pine growth in response to brush competition. This variability is due to differences in brush species and density, plantation spacing and age, and to site quality. It is evident that knowledge is lacking on the competitive effects of manzanita on ownerships where ponderosa pine is growing on Windy soil series. In addition, there are no data on the effect of manzanita cover of different densities on the rate of soil water depletion or whether observed reductions in growth are due to less leaf area or closure of stomates in response to water stress.

STUDY OBJECTIVES

1. To evaluate the effect of four levels of shrub release, in the first year after treatment, on annual growth and physiological functioning, of ponderosa pine saplings planted in 1982. Measurements will be made on both ponderosa pine and competing manzanita of:
   1) annual height and diameter growth.
   2) diurnal patterns of leaf and xylem water status in spring, summer, and fall.
   3) seasonal patterns of fine root development.
   4) seasonal patterns of soil water depletion.
   5) water use efficiency.

METHODS

Study Site: The research was done at the Latour Demonstration State Forest located approximately 50 miles (80 km) east of Redding in Shasta County. The forest is situated between 4800 and 6800 ft (1460 and 2070 m) in the Cascade Mountains. The general climate is characterized by an average annual temperature of 44 to 48 ^{O}F (6.6 to 8.8 ^{O}C), approximately 55 inches (1400 mm) of annual precipitation, and a frost-free growing season of 90 to 100 days.

The plantation studied is situated at 5400 ft (1640 m) elevation (Figure 1). The native forest vegetation consisted of stands of mixed conifer species with a high proportion of white fir (Abies concolor). The soils on the site belong to the Windy series and are derived from igneous extrusive basalt. The site is classified as U.S. Forest Service Site Class 111. The plantation was established in 1982 with 1-0 ponderosa pine bare-root stock at a nominal spacing of 6 x 6 ft (1.8 x 1.8 m). At the initiation of the study, the plantation had 100 percent brush cover of predominantly manzanita (Arctostaphylos patula var. platyphylla) mixed with chinquapin (Castanopsis chrysophyllum).

Twelve 20-tree plots (6 study trees with a row of surrounding buffer trees) were established in the summer of 1986 (Figure 2). This provided for four completely randomized treatments and three replications.

Treatments consisted of leaving 0, 15, 30, and 100 percent shrub cover by uniformly cutting shrub stems throughout each plot to remove the appropriate proportion of leaf area.

Measurements

The extent of shrub competition in each plot was determined in terms of percent cover using transect methods.

Growth of conifers was measured in terms of stem caliper, total height, and length of 1987 terminal shoot. Average needle lengths were measured for the 1986 and 1987 cohorts.

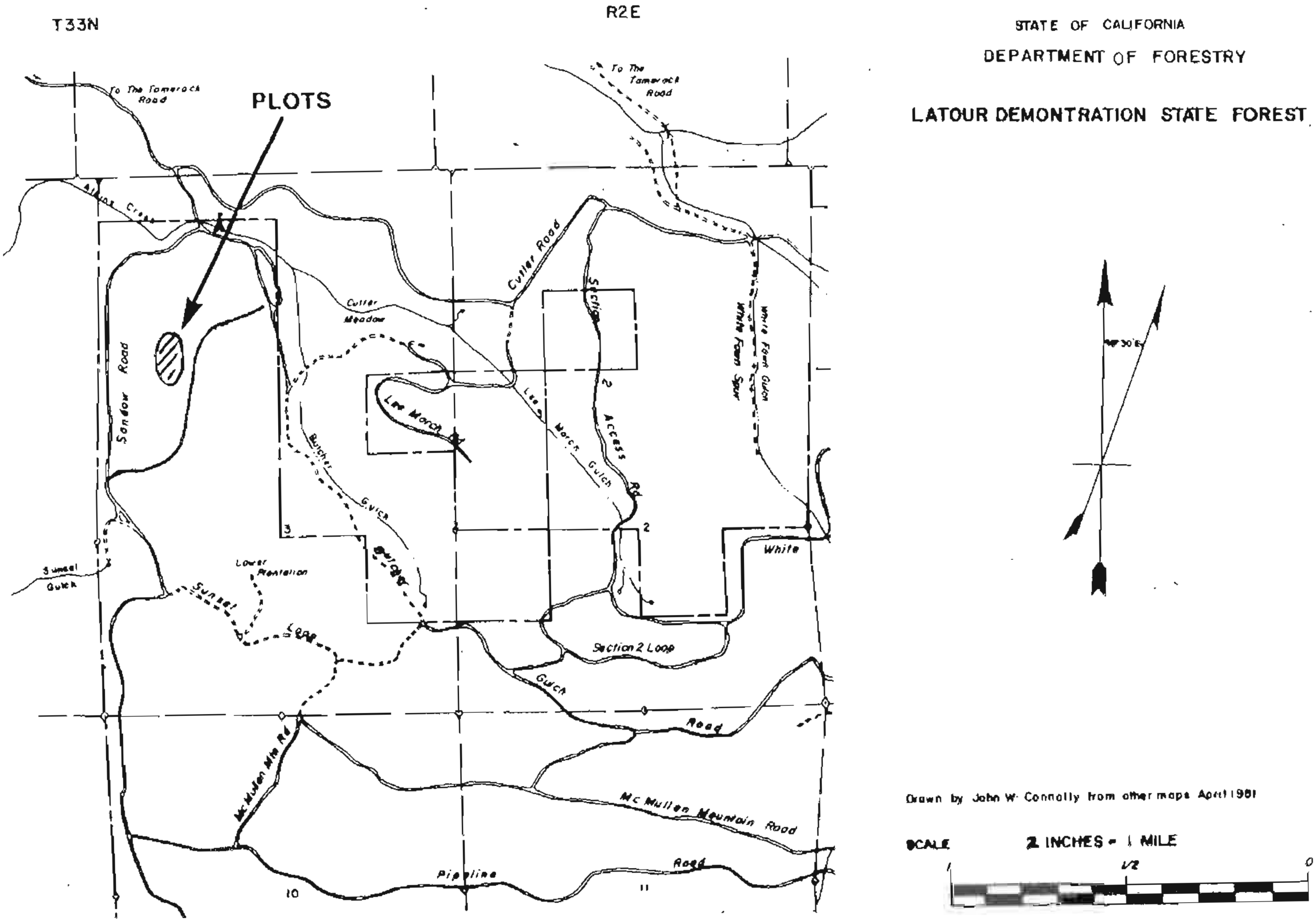

Figure 1. Map of Latour State Demonstration Forest showing location of study site.

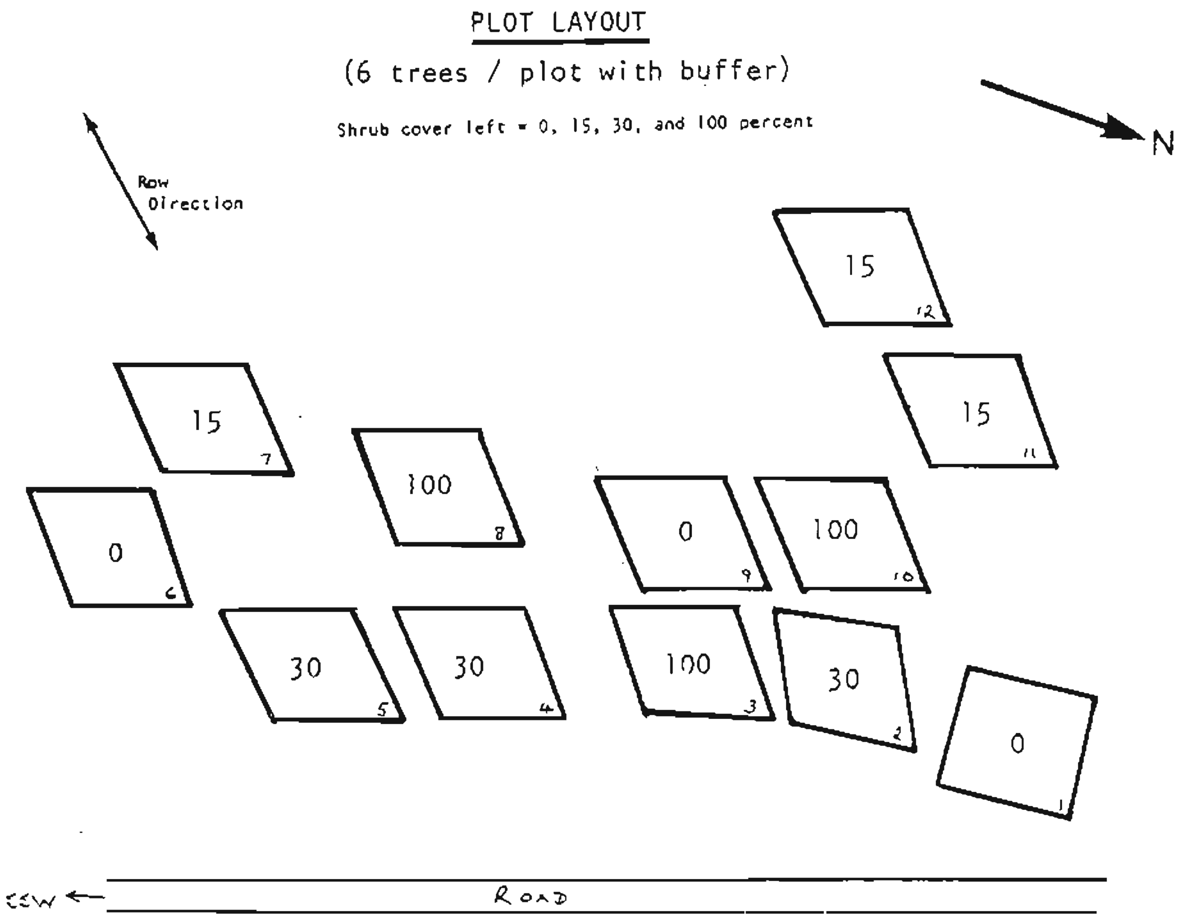

Figure 2. Layout of study plots. Three replications of 0, 15, 30, and 100 percent shrub cover.

Three times during 1987 (June 15, July 20, and September 13) the following data were obtained:

a) Soil water depletion was measured at 3 depths (25, 50, and 75 cm) by neutron probe at three access sites per plot.

b) Fine root production was sampled at 3 depths (25, 50 and 75 cm) at 3 random locations per plot using soil augers. The rock content of the soil often hindered penetration by the auger, consequently it was sometimes not possible to obtain samples at the 50 and 75 cm depths. Root biomass was determined by separating roots from soil, sorting by three diameter classes (F_1 <0.5mm, F_2 0.5-2.0 mm, and F_3 2.0-5.0 mm), and by species. Identification of dead roots was facilitated by using triphenyl-2H-tetrazolium chloride dye.

c) Tree and shrub water relations were monitored by obtaining diurnal response data for stomatal conductance using LICOR 1600 leaf diffusion porometers. Each diurnal consisted of 5 sample times from 0730 - 1800 hr. Two age classes of foliage were monitored on the conifers and one age class on the shrubs. Leaf water potential was measured using Scholander-type pressure chambers.

Analysis

Analysis of variance was used to determine whether main factor effects were significant. Student Newman-Kuels multiple range test was used to test whether treatment means were significantly different.

RESULTS

1. **COMPOSITION AND COVER OF SHRUBS**

Species composition was recorded along seven transects totalling 1 km in length.

TABLE 1: Proportion of area covered by various species (%)

Manzanita	Chinquapin	Bare Ground	Snowbrush	Ponderosa Pine
54.5	24.6	1.4	5.2	4.3

Shrub cover within the plantation was therefore predominantly manzanita with half as much cover in chinquapin. Height of the shrubs was commonly 0.5 - 1.0 m tall. Consequently, although the plantation was fully stocked with pine saplings almost 2 m tall, the site and the demand for available soil water were obviously dominated by shrubs.

2. **SOIL WATER DEPLETION**

The following three tables present results of statistical analyses. Main effects were very highly significant ($P < 0.001$). None of the interactions was significant ($P < 0.05$).

TABLE 2: Soil water content (percent by volume) pooled in each treatment over the growing season. Dissimilar subscripts indicate very highly significant differences ($P < 0.001$).

	Treatment (Shrub Cover %)			
	0 (n=24)	15 (n=18)	30 (n=26)	100 (n=25)
% Soil Water	36.5_a	27.6_b	30.4_b	25.6_b

These are important because they show that the complete removal of shrubs had a real effect in making more water available to the site. Table 2 also shows that the available water in the soil was the same regardless of whether the plots had 15 or 100 percent shrubs present. These data support the commonly held belief that shrub cover should be below 20-30 percent in order to keep competition at an acceptable level. In fact, the data suggest that once shrub cover exceeds 15 percent the amount of water removed in transpiration is similar to that removed in plots with 30 or 100 percent shrub present.

TABLE 3: Soil water content at each depth (percent by volume) pooled over the growing season. Dissimilar subscripts indicate very highly significant differences ($P < 0.001$).

	Soil Depth (cm)		
	25 (n=32)	50 (n=32)	75 (n=29)
% Soil Water	25.9_a	31.0_b	34.0_c

TABLE 4: Soil water content at each measurement period (percent by volume) pooled over the growing season. Dissimilar subscripts indicate very highly significant differences (P <0.001).

	Measurement Date		
	June 15 (n=33)	July 20 (n=31)	Sept 13 (n=31)
% Soil Water	33.5_a	30.2_b	26.3_c

3. **GROWTH OF PONDEROSA PINE**

a) Stem Caliper

Although there were some statistically significant differences among stem mean diameter and diameter growth in the various shrub cover treatments (Table 5), these differences are probably associated with initial differences in tree size.

TABLE 5: Stem diameter, and diameter growth (cm) of ponderosa pine during 1987 growing season. Dissimilar subscripts indicate significant differences (P <0.001, N = 36).

	Treatment (Shrub Cover %)			
	0	15	30	100
Diameter	5.30_a	5.70_{ab}	4.80_a	6.41_b
Diam. Growth	0.80_a	0.62_a	0.18_b	0.51_a

Table 5 shows that the stem diameter in plots less than 30 percent shrub cover were essentially the same. Trees in the plots with 100 percent shrub cover had significantly larger stem diameters, however as shown in Table 6, these trees were also significantly taller. Diameter growth in all treatment areas was not really different (Table 5), however there seems to be a trend for stem growth to be highest in plots with no shrub competition. The apparently low mean stem growth in the 30% plots is probably associated with the fact that trees in those plots had smaller diameters.

b) Total Height

Differences in total height at the two dates of measurement, June and September, and the interaction between measurement date and treatment, were not significantly different. Trees in the plots with highest shrub density (100%) had significantly taller trees than those in the other treatments (Table 6). This was no doubt associated with the fact that trees in the 100% cover plots had trees that were initially significantly taller than trees in the remaining plots (Table 7).

TABLE 6: Total height of ponderosa pine (m) after the 1987 growing season. Dissimilar subscripts indicate highly significant differences (P <0.001, N = 36).

Treatment (Shrub Cover %)			
0	15	30	100
1.54_a	1.59_a	1.56_a	1.82_b

TABLE 7: Total heights (m) and stem diameter (cm) of trees, with standard errors, at the June and September measurement dates.

	Shrub Density (% cover)							
	0		15		30		100	
	June	Sept	June	Sept	June	Sept	June	Sept
Tot. Ht	152.4	156.9	157.0	162.1	154.6	158.2	180.3	184.7
Std Err.	11.0	11.4	12.0	12.9	6.2	6.5	11.6	11.2
Diameter	4.9	5.7	5.4	6.0	4.8	4.8	6.2	6.6
Std Err.	0.5	0.7	0.4	0.6	0.3	0.4	0.4	0.5

c) Terminal Shoot Growth

TABLE 8: Growth of terminal shoot (cm) in ponderosa pine during 1987 (N = 18). Dissimilar subscripts indicate highly significant differences.

Treatment (Shrub Cover %)			
0	15	30	100
25.4_a	29.3_{ab}	25.0_a	32.3_b

Care needs to be taken in interpreting Table 8 because trees in the 100 percent shrub treatment were shown to be taller at the beginning of the study. However, using beginning of season heights as a covariate in the ANOVA determinations did not change the analysis. It resulted in much higher model sum of squares and a much lower error sum of squares, consequently a much higher level of significance compared with standard ANOVA analyses. Thus, despite the fact that trees in the 100 percent shrub plots were initially taller, shoot growth in these plots was in fact greater than in the plots that had complete or partial shrub removal.

d) Needle Length

TABLE 9: End-of-growing-season length of current (1987) and previous year (1986) ponderosa pine needles (cm) (N = 18). For each year separately, dissimilar subscripts indicate highly significant differences (P <0.001).

Year	Treatment (Shrub Cover %) 0	15	30	100
1986	11.8_a	12.2_a	12.5_a	12.8_a
1987	15.4_x	12.5_y	12.5_y	12.2_y

These data are interesting in that they show that needle length prior to shrub treatments was essentially the same in all plots. However, in the year after treatment, needle length of trees in plots with zero shrub cover was significantly greater (3 cm) than needles of trees in plots with either partial or complete shrub cover. This result is important because needle length is well recognized as an indicator of environmental conditions.

4. **PHYSIOLOGICAL EVALUATION**

a) Xylem Water Potential

TABLE 10: Summary statistics for water potential:

Species	Treatment (% cover)	N	Mean (MPa) June	July	September
Pine	0	42	-1.68±0.06	-1.11±0.04	-1.99±0.06
Manz.	0	--	-----	-----	-----
Pine	15	34	-1.93±0.06	-1.08±0.05	-2.21±0.04
Manz.	15	30	-2.06±0.06	-1.04±0.05	-2.31±0.10
Pine	30	39	-1.71±0.04	-1.18±0.05	-2.38±0.06
Manz.	30	30	-1.60 0.04	-0.97 0.07	-2.63±0.08
Pine	100	36	-1.71±0.04	-1.16±0.05	-2.54±0.06
Manz.	100	30	-1.86±0.06	-0.97±0.06	-2.96±0.08

Figure 3 presents these data graphically.

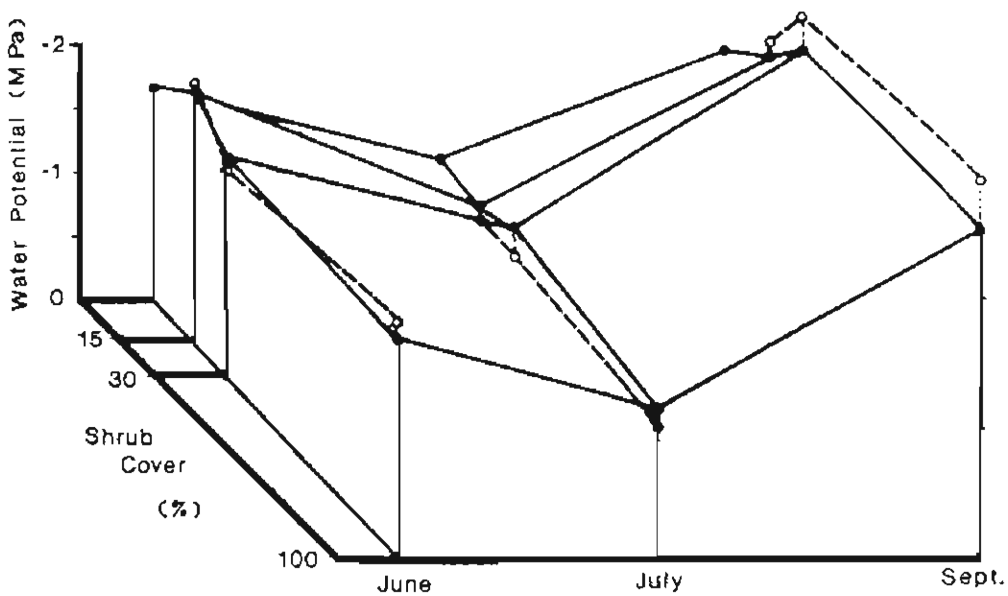

Figure 3. Mean daily xylem water potential of pine (●) and manzanita (O) in June, July, and September, at 0, 15, 30, and 100% shrub covers.

TABLE 11: Comparison of water potentials of ponderosa pine and manzanita by treatment (data for June and September pooled).

Species	Treatment (% Cover)	N	Mean Water Potential (MPa)
Pine	0	102	-1.82 ± 0.04
Manz.	0	--	----
Pine	15	94	-2.11 ± 0.04
Manz.	15	60	-2.18 ± 0.06
Pine	30	99	-2.11 ± 0.05
Manz.	30	60	-2.11 ± 0.08
Pine	100	96	-2.13 ± 0.06
Manz.	100	60	-2.41 ± 0.09

Table 11 shows that ponderosa pine developed least stress where shrubs were absent. In the 15 and 30% shrub cover, pine and manzanita had very similar stress levels. In the 100% shrub cover treatment, manzanita had substantially higher stress than the pine. All levels of shrub cover, from 15 to 100%, produced the same average stress levels in the pines.

Results of the ANOVA show that all main effects (date, treatment, and species) and the interaction of date x treatment were very highly significantly different ($P < 0.001$, Table 12).

TABLE 12: Mean xylem water potential (MPa) for (a) date, (b) treatment, and (c) species.

a)

Date	Mean (MPa)	N
June 14	-1.78_a	241
Sept 12	-2.37_b	336

b)

Treatment (% Cover)	Mean (MPa)	N
0	-1.86_a	102
15	-2.14_b	159
30	-2.11_b	159
100	-2.30_c	106

c)

Species	Mean (MPa)	N
Pond. Pine	-2.07_a	180
Manzanita	-2.24_b	391

These results show that when species were combined, there was a highly significant difference between the water potential measured in June and in September. It was also shown (Table 12_b) that, among the treatments, significantly less stress was developed in the plots with zero shrub cover, stress levels in the 15 and 30 percent treatments were indistinguishable, and the highest stress levels were developed in the plots with 100 percent shrub cover. When dates were combined (Table 12_c), manzanita was shown to have higher levels of average stress than the pine.

The ANOVA also showed that the interaction between date and treatment, date and species, and between treatment and species were all significant (P <0.001, <0.01, <0.05 respectively).

c) Transpiration

At each sampling date, measurements were obtained of leaf temperature, relative humidity, light intensity, leaf conductance and transpiration. Table 13 presents transpiration data for all three dates. It should be recognized that data obtained during July were atypical due to unseasonal snow and cold temperatures.

TABLE 13: Average daily transpiration rates of ponderosa pine and manzanita in June, July, and September in each treatment area.

Species	Treatment (% Cover)	N	Transpiration Rate ($\mu g\ cm^{-1}\ s^{-1}$) June	July	September
Pine	0	45	3.27±0.18	1.69±0.23	4.29±0.24
Manz.	0	--	----	----	----
Pine	15	60	3.34±0.21	1.69±0.28	1.97±0.16
Manz.	15	30	3.53±0.40	0.65±0.09	2.93±0.39
Pine	30	55	3.03±0.16	1.56±0.24	1.03±0.08
Manz.	30	30	2.85±0.32	0.91±0.16	1.74±0.17
Pine	100	55	3.26±0.21	1.85±0.33	0.72±0.08
Manz.	100	30	3.17±0.23	0.82±0.15	1.61±0.18

Data in Table 13 and Figure 4 show the unusually low rates of transpiration in July due to unseasonally cold weather and snow (Table 14). These data also show the relatively high rates of transpiration in all treatment areas in June when soil moisture conditions were high. Rates of transpiration in September were low due to low soil water availability. Of particular interest are the substantially higher rates of transpiration of manzanita than pine in

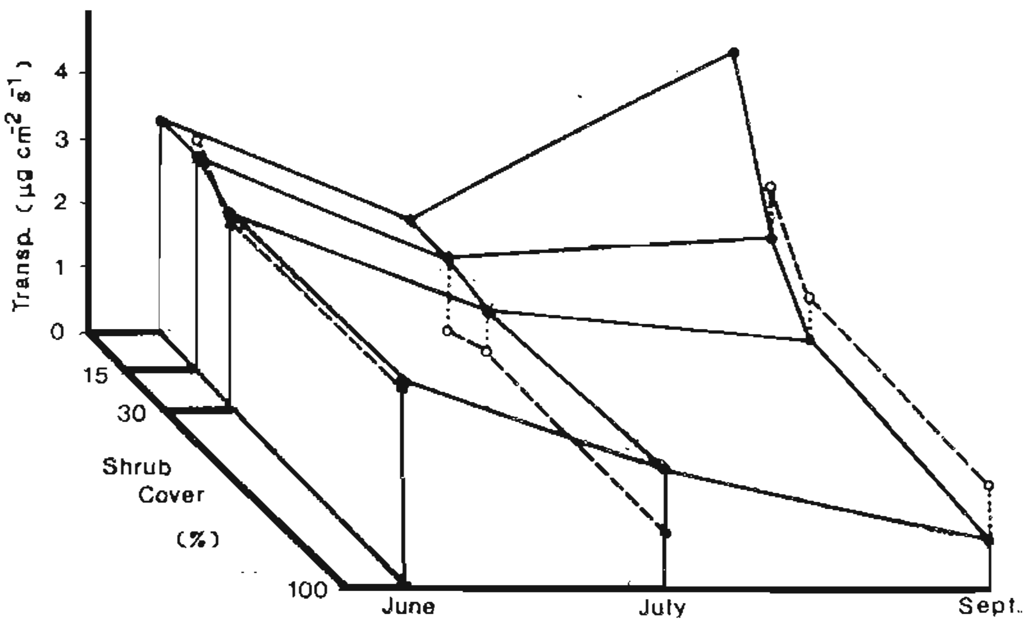

Figure 4. Mean daily transpiration of pine (●) and manzanita (O) in June, July, and September, at 0, 15, 30, and 100% shrub covers.

September in those plots (15, 30, and 100 percent shrub cover) where shrubs were competing with the pines, causing the pines to close stomates due to stress.

TABLE 14: Comparison of mean daily leaf temperatures, relative humidity, and light intensity at each measurement date.

Date	Leaf Temp. (°C)	Rel. Hum. (%)	Light ($\mu E\ cm^{-2}\ s^{-1}$)
June 14	20.9	47.2	755
July 21	10.3	76.9	320
Sept. 12	21.4	33.3	745

Table 14 clearly shows lower leaf temperature, higher relative humidity, and lower light levels associated with the unseasonal cold period in July.

TABLE 15: Transpiration rates of ponderosa pine and manzanita on each treatment area combining June and September measurement dates.

Species	Treatment (% Cover)	N	Mean Transp. ($\mu g\ cm^{-2}\ s^{-1}$)
Pine	0	105	3.85 ± 0.16
Manz.	0	---	----
Pine	15	120	2.66 ± 0.14
Manz.	15	59	3.24 ± 0.26
Pine	30	115	1.98 ± 0.13
Manz.	30	60	2.30 ± 0.20
Pine	100	115	1.94 ± 0.16
Manz.	100	59	2.40 ± 0.18

In Table 15, data for July were excluded because of the atypically cold and snowy conditions. This Table shows that transpiration rate of ponderosa pine was greatest in areas with no shrub competition. Also, throughout the growing season, transpiration of manzanita consistently exceeded that of ponderosa pine in each treatment area.

Use of Student Newman-Kuels multiple range test showed which mean values of conductance and transpiration were significantly different (Tables 16, 17, 18).

d) Conductance

Measurements of leaf conductance provide a direct measure of stomatal aperture.

TABLE 16: Average daily leaf conductance of ponderosa pine and manzanita in June, July, and September in each treatment area.

Species	Treatment (% Cover)	N	Leaf Conductance ($cm\ s^{-1}$) June	July	September
Pine	0	45	0.35±0.02	1.53±0.38	0.36±0.01
Manz.	0	--	----	----	----
Pine	15	60	0.34±0.02	1.69 0.45	0.16±0.01
Manz.	15	30	0.38±0.03	0.30±0.04	0.26±0.03
Pine	30	55	0.33±0.02	2.85±1.36	0.09±0.01
Manz.	30	30	0.32±0.04	0.64±0.18	0.15±0.01
Pine	100	55	0.34±0.02	2.53±0.93	0.05±0.01
Manz.	100	30	0.35±0.02	0.42±0.14	0.12±0.01

Table 16 and Figure 5 show that, in the beginning of the growing season in June, stomata of both pine and manzanita were uniformly partially open in all treatment areas. The unseasonally cool and rainy conditions in July resulted in the pines having wide open stomata all day, and the manzanita stomatal apertures being similar to conditions in early summer. In September when soil water availability was lowest, pine stomata were almost closed whereas manzanita stomata were still partially open.

TABLE 17: Leaf Conductance and transpiration of combined species within each treatment area. Dissimilar subscripts within each row indicate very highly significant differences ($P < 0.001$, $N = 175$).

	Treatment (Shrub Cover %) 0	15	30	100
Cond. ($cm\ s^{-1}$)	0.35_a	0.27_b	0.21_c	0.21_c
Transp. ($\mu g\ cm^{-2}\ s^{-1}$)	3.85_x	2.85_y	2.09_z	2.10_z

Table 17 shows that leaf conductance and transpiration were significantly higher in the plots with zero shrub cover, and that rates of conductance and transpiration were the same in plots with 30% and 100% shrub cover.

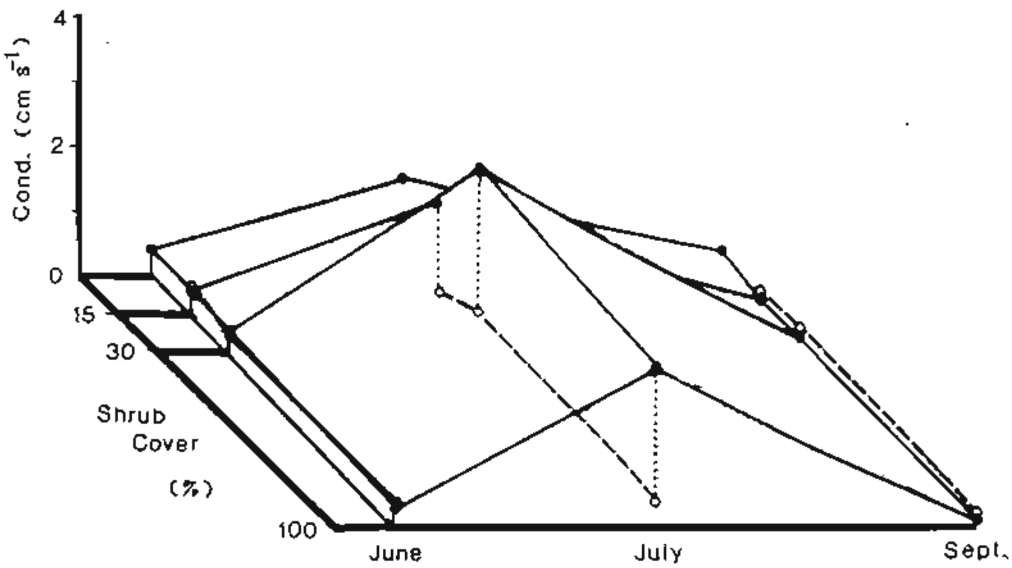

Figure 5. Mean daily leaf conductance of pine (●) and manzanita (○) in June, July, and September, at 0, 15, 30, and 100% shrub cover.

TABLE 18: Leaf conductance of species, data for June and September combined. Similar subscripts within each parameter indicate that the means are not significantly different ($P < 0.001$).

Species	N	Mean Conductance (cm s^{-1})	Transpiration (μg cm^{-2} s^{-1})
Pine	455	0.25_a	2.58_x
Manz.	178	0.26_a	2.64_x

Table 18 shows that there was no significant difference in leaf conductance or transpiration among ponderosa pine and manzanita when data for June and September were combined.

TABLE 19: Leaf conductance and transpiration of ponderosa pine and manzanita combined for June and September. Dissimilar subscripts within each parameter indicate that the means are significantly different ($P < 0.001$).

Date	N	Leaf Conductance (cm s^{-1})	Transpiration (μg cm^{-2} s^{-1})
June 14	305	0.34_a	3.21_x
Sept. 12	328	0.17_b	2.02_y

Table 19 shows that stomates of both species tended to be closed in September, probably associated with depletion of soil moisture. This resulted in transpiration rates being significantly lower for the combined species in September.

5. **ROOT ANALYSIS**

In June, July, and September, soil samples were obtained from three locations in each plot from three depths (rock content permitting). Roots were extracted from these soil samples and divided into three size classes (F_1 <0.5 mm, F_2 0.5-2.0 mm, and F_3 2.0-5.0 mm) by species. The dry weight of each of these classes was determined. Determinations of analysis of variance showed very highly significant differences ($P < 0.001$) among the means for species and depth, and highly significant differences ($P < 0.01$) for the interaction between species and depth (Table 20). Differences among the means for date of sampling, and for plots of different shrub cover, were not significantly different.

TABLE 20: Mean root dry weight (g/kg soil) for a) date, b) species, c) treatment, and d) depth. Dissimilar subscripts indicate means that are significantly different (P <0.001).

a)

Date	Mean Dry Weight (g)	N
June 14	0.106_a	880
July 21	0.107_a	744
Sept 12	0.099_a	728

b)

Species	Mean Dry Weight (g)	N
Pine	0.021_a	882
Manz.	0.248_b	882
Other	0.012_a	588

c)

Percent Cover	Mean Dry Weight (g)	N
0	0.100_a	656
15	0.106_a	408
30	0.094_a	672
100	0.118_a	616

d)

Depth (cm)	Mean Dry Weight (g)	N
25	0.142_a	832
50	0.091_b	808
75	0.075_b	712

Table 20 shows: a) there were no significant differences in root dry weight among dates; b) that dry weight of manzanita roots was significantly greater than that of pine (and other unidentified roots); c) there were no significant differences in dry weight among treatment areas; and d) that the biomass of roots in the upper 25 cm was significantly greater than that in the 50 and 75 cm depths.

6. DISCUSSION

The study plan prescribed three measurement dates, June 15, July 20, and September 13. Just prior to the July date, the study site had several days of unseasonal cold temperature accompanied by snow. Cold rain fell during the taking of measurements on July 20. Because of these unseasonal conditions (Table 14), measurements of leaf conductance, transpiration, and water stress taken on the July date were not included in the analysis. Seasonal trends in stress development were restricted to a comparison of early season (June) and late season (September) data.

The removal of shrubs was clearly shown to enhance soil water content (Table 7). The effect was only evident in the 0% shrub treatment. All other plots with 15, 30, and 100 % shrub cover had the essentially the same soil water content. This supports the view that essentially all shrubs must be removed in order to enhance soil water availability. Soil water content was shown to increase with depth (Table 8) and to diminish to 26.3% by volume by the end of the season (Table 9).

This study has shown that shrub cover had no measurable effect on stem diameter growth (Table 2) but the 100% shrub cover may have resulted in trees with longer terminal shoot growth (Table 5). This result should be interpreted with caution because trees within the 100% shrub cover plots were initially taller at the beginning of the growing season. However, using initial height as a covariate in ANOVA determinations did not change the finding that trees within the 100% shrub cover plots had significantly longer terminal shoots in the first year after treatment.

The needle length data are important in that it was clearly shown that prior to the treatments, needle length of trees in all plots was the same (Table 6). At the end of the first growing season, needle length of trees in plots with 0% shrub cover was 3 cm (15 vs 12 cm) longer than needles of trees in all other plots -- regardless of whether shrub cover was 15, 30, or 100 %. This result clearly shows the effect of shrub removal on enhancing photosynthetic area of pine saplings.

Xylem water potential data showed that, at the beginning of summer, mean stress levels in both pine and manzanita, regardless of level of shrub cover, were -1.6 to -1.8 MPa (-16 to -18 bars) (Table 10). This indicates uniform and moderate stress. At the end of the summer, average stress level in plots with 0% shrub cover had only risen from -1.6 to -2.0 MPa (-16 to -20 bars), whereas the pines in the 15, 30, and 100% shrub cover all increased average stress from approx. -1.8 to -2.4 MPa (-18 to -24 bars). Manzanita commonly had higher stress levels than the pine (from -2.3 to -3.0 MPa) at the end of the summer (Table 10). Despite this higher level of stress, it was shown (Table 17) that manzanita had open stomates and higher rates of transpiration than the pines at the end of the summer.

Analysis of water stress data clearly showed (Table 12_b) that increasing levels of shrub cover significantly increased plant water stress.

At the beginning of the summer in June, transpiration of pine and manzanita was essentially the same (Table 13). In September, transpiration of pine growing without shrub competition remained high, and was 2 to 3 times greater than that of both pine and manzanita growing at 15, 30, and 100% shrub cover. These results are associated with the substantially greater growth of needles on pines growing with 0% shrubs. Table 13 also clearly shows, in September, the rapidly declining rates of transpiration of pines with increasing shrub cover. Over the season as a whole, transpiration of manzanita was consistently greater than that of ponderosa pine, and was highest in the 0% and 15% treatments (Table 15). Transpiration rates in the 30 and 100% shrub cover plots were not different (Table 17).

Analysis of fine root dynamics showed that manzanita produced 10 times the quantity of roots than pine, that most roots were at the 25 cm depth, but that shrub cover had no effect on root biomass (Table 20). This last result is not surprising since the different shrub cover treatments were obtained from manipulating the leaf area on a site which initially had 100% shrub cover. Root biomass was not manipulated and undoubtedly remained unaffected by the shrub cover treatments.

7. CONCLUSIONS

Manipulating the extent of shrub competition in a 6-year-old, 2-m-tall pine plantation produced the following major results in the first year after treatment:

1) At the end of the summer, soil water content was 36.5% in the plots with no shrub cover and 25.6% in plots with 100% shrub cover.

2) Effect of shrub competition on diameter and height growth was inconclusive due to high between-tree variability.

3) At the end of the summer, pines growing with no shrub competition had, relative to pines growing in 100% shrub cover:
   a) 3-cm greater needle length.
   b) seven-times greater average daily leaf conductance (stomatal aperture).
   c) six-times higher average daily transpiration.
   d) half the average daily water stress.

4) Over the growing season, physiological functioning of the pines steadily deteriorated from the 0% treatment to the 15, 30 and 100% shrub cover areas.

5) At the end of the summer, manzanita had twice the leaf conductance and transpiration of the pines, in all levels of shrub cover, despite having consistently higher water stress.

6) The enhanced physiological condition of the pines at the end of the first year will probably be reflected in greater above-ground biomass production in subsequent years. To test this, the plot treatments should be maintained over a five-year period and a follow-up study of relative physiology and biomass should be carried out at that time.

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