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Abies concolor Growth Responses to Vegetation Changes Following Shrub Removal, Northern Sierra Nevada, California

Susan G. Conard **Steven R. Sparks**

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Conifer productivity in western North America is often severely inhibited by competing vegetation. *Abies concolor* [Gord. and Glendl.] Lindl. (white fir) is an important species over much of this area, yet little information is available on response of *A. concolor* to vegetation management treatments. We revisited two sites in the northern Sierra Nevada to assess the responses of naturally regenerated *A. concolor* saplings to vegetation recovery 8-9 years after release treatments. Treatments caused major and persistent shifts in vegetation structure and composition on both sites. Differences in individual tree growth within treatments were strongly correlated with structure and composition of neighboring vegetation, even where no treatment effects were observed. At Rice Canyon, height growth of trees was still 270 to 380 percent of controls after 8 years. At Sattley, positive growth responses had disappeared after 6 years. We attribute different site responses to better site quality at Rice Canyon and poorer success of treatments at controlling competitors at Sattley. Great variability in response between sites illustrates the strong effect of site characteristics on response to release treatments and the importance to managers of anticipating such differences before making treatment decisions.

Retrieval Terms: Abies concolor, white fir, conifer release, vegetation management, competition, Sierra Nevada

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Cover: Clockwise from top: Released *Abies concolor* saplings at the Sattley study site; *Arctostaphylos patula* (greenleaf manzanita) in flower; *Ceanothus velutinus* (snowbrush ceanothus) in flower (photos by Susan G. Conard); *Abies concolor* saplings in montane chaparral dominated by *Ceanothus velutinus* and snowbrush ceanothus at the Sattley site (photo by Susan C. Barro)

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In Brief . . .

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Conifer productivity in western North America is often severely inhibited by competing vegetation. White fir (*Abies concolor* [Gord. and Glendl.] Lindl.) is an important species over much of this area, yet little information is available on response of *A. concolor* to vegetation management treatments. We revisited two sites in the northern Sierra Nevada to assess the responses of naturally regenerated *A. concolor* saplings to vegetation recovery 8-9 years after a series of release treatments. Shrub removal treatments continued to enhance white fir sapling growth 8 years after treatment at Rice Canyon, but not at Sattley. We hypothesize that this difference in response is due to a combination of better site quality at Rice Canyon and poorer control of competing vegetation at Sattley. Based on responses to shade treatments, moisture is apparently the most important limiting resource for white fir growth on these study sites. Benefits of shading on growth did not persist after shade was removed, nor was there evidence that shading had inhibited growth.

Individual trees grew most in a treatment where shrubs were completely removed. In this treatment we also observed the greatest tree mortality. Where stocking is high enough that tree mortality is not a concern, complete shrub removal may produce the greatest long-term growth benefits for surviving trees. Where stocking is low or marginal, however, the optimum response will probably result from a treatment that effectively controls brush without removing dead shade.

Cover of and distance to important shrub species were correlated with tree growth at both sites, providing evidence that the local competition environment strongly influences white fir sapling growth. We observed large differences between sites and among treatments in variables useful for modeling tree growth responses. These differences illustrate the difficulty in developing generalizable models for predicting and evaluating competitive interactions, and reinforce the need for caution in applying such models to situations different from those in which they were developed.

Treatments also caused rapid and dramatic changes in species dominance, especially at Sattley, where the rhizomatous *Chrysolepis sempervirens* rapidly invaded after removal of other shrubs. This change reinforces the need to evaluate carefully the potential impact of vegetation management treatments on reproduction or expansion of minor species once site resources are made available to them through suppression of competitors.

Introduction

Development of mature conifer stands in California and the Pacific Northwest after logging or fires is often delayed for several decades by the presence of woody and herbaceous competitors (Walstad and others 1987). These competitors, by their ability to colonize quickly after disturbance and usurp resources, can inhibit conifer seedling establishment and suppress growth of planted or natural saplings. Suppressed saplings may be relegated to the understory for many decades before finally overtopping shrubby competitors (Bolsinger 1980, Conard and Radosevich 1982b, Gratkowski and others 1973, Skau and others 1970, Walstad and others 1987). Even after conifers overtop them, shrubs may continue to suppress conifer growth until closure of the conifer canopy shades them out.

Various chemical and mechanical treatments are used to suppress competitors and enhance growth of conifers, and research has frequently demonstrated short-term benefits from these treatments (Conard and Radosevich 1982a; Hughes and others 1990; Lanini and Radosevich 1986; Newton 1982; Petersen and Newton 1982, 1985; Stewart and others 1984; Walstad and others 1987; Zavitkovski and others 1969). Yet only a few studies report growth responses for western conifers beyond the first few years after competitor removal (Douglas-fir: Gratkowski 1979, Radosevich and others 1976; ponderosa pine: Barrett 1981, 1983, McDonald and Oliver 1984). Much remains to be learned about how density and cover of competing shrubs affect conifer growth; how responses vary with differing species composition of competing shrubs, for different conifer species, or with site characteristics; and appropriate ways of quantifying these interactions on an operational basis.

In most instances, increased conifer growth after shrub removal likely is due to increased availability of light or water, although other factors such as allelopathy (Conard 1985, Tinnin and Kirkpatrick 1985) or soil nutrient limitations may play a role. Light is doubtless a limiting resource for conifer growth on some sites (Brand 1986), particularly for understory trees in the often cloudy coastal Pacific Northwest (Walstad and others 1987). But, with increasing duration and severity of summer drought as one moves from the Pacific Northwest south into California, water availability appears to limit growth on a wide range of sites (Lanini and Radosevich 1986, Petersen and Maxwell 1987, Petersen and others 1988, Show 1924).

Mixed conifer forests dominated by white fir *(Abies concolor)* are common at middle elevations throughout southern Oregon, California, and east to the Rocky Mountains. After fire or logging in these forests, extensive montane chaparral brushfields, often characterized by species of *Ceanothus*, typically develop. These shrubs may suppress white fir growth for many years on untreated sites (Conard and Radosevich 1982b) with the result that large areas of potential commercial forest are essentially unproductive. Little research has been done on the dynamics of this vegetation in response to suppression of competing shrubs.

In 1975, a study was established in the northern Sierra Nevada of California to evaluate the effects of shrub competition for light and soil moisture on height and volume growth of naturally regenerated white fir saplings. After four growing seasons, conifer growth in the most favorable shrub removal treatments was 140 to 200 percent of that in untreated controls (Conard and Radosevich 1982a). Water stress apparently was the major factor in suppressing conifer growth, while the presence of dead shade enhanced growth. Considerable differences were noted between growth responses on two study sites (Conard and Radosevich 1982a).

We reexamined conifer growth on the same plots in 1982 and 1983, 8 or 9 growing seasons after treatments were established. By this time, structure and composition of recovering vegetation differed widely among treatments, and within and among plots. This follow-up study had three objectives: (1) to evaluate the continuing influence of the 1975 shrub removal treatments on white fir growth and on recovery of competing vegetation, and to document any changes in the relative effectiveness of the various treatments; (2) to investigate the effect of the local competition environment on the growth of the conifer saplings; and (3) to describe continuing differences in responses between study sites.

Study Areas and Methods

Experiments had been established on two sites in Sierra County, California, in spring 1975, to evaluate the effects of release from shrub competition on white fir growth. Both sites are on north-facing 20° to 30° slopes which had supported white fir-dominated mixed conifer forests before severe fires destroyed most of the mature conifers. Fires occurred in 1918 and 1939 at Rice Canyon and in 1925 at Sattley. By 1975, both sites supported montane chaparral with white fir saplings up to 1.5 m tall in the understory.

The Rice Canyon site was dominated by snowbrush ceanothus (*Ceanothus velutinus* Dougl. ex Hook), with greenleaf manzanita (*Arctostaphylos patula* Greene) as a common associate (plant nomenclature follows Munz and Keck 1973). The soil was a Trojan sandy loam of volcanic origin (Sketchley 1975) underlain by decomposed granite at a depth of 1.5 to 2 m.

The Sattley site supported a mixed shrub cover of greenleaf manzanita, snowbrush ceanothus, and bush chinquapin (*Chrysolepis sempervirens* [Kell.] Hjelmquist). Soils are granitic-based loamy coarse sands of the Haypress series (Sketchley 1975).

The Rice Canyon site is more mesic than the Sattley site, probably due to a combination of higher rainfall and finer soil texture (higher water holding capacity) at Rice Canyon. During the summers of 1976 and 1977 control plots at Rice Canyon had minimum soil water potentials 0.4 to 1.0 MPa higher than those at Sattley (Conard and Radosevich 1982a). Results of soil nutrient analysis conducted by University of California, Davis, Cooperative Extension Service on surface soils (top 15 cm) from the two sites are presented in *table 1*. Nitrogen, carbon, and potassium levels were substantially higher in the samples from Rice Canyon than in those from Sattley, as was cation exchange capacity. All these factors suggest higher site quality at Rice Canyon.

Additional site information is reported in Conard and Radosevich (1982a).

Table 1—*Chemical characteristics of surface soils (0 to 15 cm) at Sattley and Rice Canyon study sites, northern Sierra Nevada, California*[1]

Site	CEC[2]	N	P	K	Carbon	OM[3]
	meq/100g	*pct*	*ppm*	*ppm*	*pct*	*pct*
Rice Canyon	26.0	0.21	65.0	520	7.6	13.4
Sattley	12.0	0.11	70.5	210	4.6	6.6

[1]Data are means from two samples per site.
[2]Cation exchange capacity (CEC) is in milliequivalents per 100 g soil (meq/100 g).
[3]OM = Soil organic matter.

Initial Experimental Design

Five treatments had been established at each site in 1975 to investigate the effects of interference by shrubs on growth of naturally established white fir saplings. At each site, treatments were replicated three times in a randomized complete block design, where blocks represented slope position. Treatment plots were 18 by 18 m with 2-m buffer strips. Treatments are described briefly below. See Conard and Radosevich (1982a) for additional detail.

Treatment A (Control)—Montane chaparral with white fir saplings in the understory was undisturbed.

Treatment B—All shrub stems were cut and removed from plot. Plants were allowed to sprout.

Treatment C—Shrub canopies were removed manually as in treatment B, and herbicides applied to inhibit sprouting. White fir saplings were shaded with cut shrub branches to approximate the shade levels under undisturbed canopies. Shade decreased gradually as foliage dried and fell off. All remaining shade material was removed after the 1978 growing season.

Treatment D—Treatment was identical to C, except that saplings were not shaded.

Treatment E—Plots were treated with glyphosate (n-[phosphonomethyl]glycine) at 6.7 kg/ha (active ingredient) to simulate a potential operational release treatment.[1] At Sattley, the treatment was repeated in October 1976 because the initial treatment was ineffective.

Tree Growth Measurements

Tree growth had been evaluated initially in fall 1978 by measuring internode lengths on the main stem for the 1971 to 1978 growing seasons (Conard and Radosevich 1982a). Stem diameters (at 30 cm) had also been measured at that time, but were not reported. A total of 130 trees had been measured at Rice Canyon and 126 at Sattley. We revisited Rice Canyon in 1982 (8 years after treatment) and Sattley in 1983 (9 years after treatment), to remeasure height and annual height growth (internode lengths) since 1977 on all the original sample trees that could be located (102 trees at each site). Seven trees at Rice Canyon with dead terminal buds at the time of remeasurement were eliminated from the analysis. These trees were randomly distributed among treatments, showing no evidence that bud damage was a treatment effect. Stem diameters at 30 cm were remeasured. Diameters were used to calculate stem volume growth since 1978 using the formula for volume of a cone: $V=(\text{area} \times \text{height})/3$.

Measurements of Potential Competing Vegetation

In 1978, overall cover was estimated for shrub and herbaceous canopies in the various treatment plots. In 1982-83 potential competing vegetation was measured in much greater detail to evaluate the effects of treatments on vegetation structure and the impacts of individual species and varying levels of competition on continued growth of the white fir trees.

A circular plot (1.5-m radius) was established around each white fir sample tree. The plot was divided into quadrants (N,S,E,W) for vegetation measurements. Because no systematic differences were detected among quadrants, data are reported on a whole-plot basis. For each species of shrub, percent canopy cover was estimated in the quadrant, and distances from the sample tree to the nearest and farthest edges (maximum 1.5 m) of the shrub canopy were measured, to quantify spatial distribution of shrub canopies within the plots. Canopy height was estimated to the nearest decimeter. Nearest and farthest distances, stem height, and cover were also measured for conifers in the plot. Nearest and farthest distances were averaged over the four quadrants in each plot. Herbaceous cover for each quadrant was estimated to the nearest 5 percent. A similar approach was recommended by Wagner (1982).

Statistical Analyses

Differences in white fir growth among the original treatments were evaluated by analysis of variance of treatment plot means, using a mixed effects model with treatment and slope position as fixed effects and plot as a random effect. The mean square associated with the interaction between treatment and slope position was used to estimate the variance of the random factor associated with plot (since the interaction itself was

[1]This publication neither recommends the herbicide uses reported nor implies that they have been registered by the appropriate governmental agencies.

assumed to be zero). This interaction mean square was also used to test the hypothesis of no treatment effect. Treatments were compared within sites using linear contrasts.

Differences in canopy cover of major shrub and tree species among the treatments were also evaluated using a mixed effects analysis of variance model, again using treatment plot means, followed by within-site comparisons of individual treatments using linear contrasts.

Tree mortality occurred in nearly all treatments at both sites, but was especially severe in treatment D at Rice Canyon. At Rice Canyon, only 10 trees remained in treatment D by 1982, while the remaining treatments each had 16-24 trees. At Sattley, the number of trees in treatment D (initially only 18) was reduced to 14 by 1983, while the remaining treatments each had 25-30 trees. Since treatment plot means and residuals for treatment D were much more variable than for other treatments, treatment D was dropped from the statistical analyses.

For all analyses of tree height and height growth, only trees that survived through the last year of data collection (1982 at Rice Canyon or 1983 at Sattley) were included.

Height and height growth data from both sites tended to be non-normal, with the standard deviation strongly and positively correlated with the mean. Log-transformed data were used where appropriate to correct these problems.

Tree growth parameters used in analyses of effects of neighboring vegetation were height growth in 1982 (Rice Canyon) or 1983 (Sattley), mean height growth over the most recent 2-year period, mean height growth since 1978, and volume growth since 1978. Relationships between these parameters and characteristics of neighboring vegetation in circular plots were explored through correlation coefficients and through simple, multiple, and stepwise multiple regression procedures using data from individual tree-centered plots within each treatment. As block differences in ANOVA analyses were not significant, blocking was ignored. During this process, an initial field of 23 variables was narrowed down considerably. Initial variables included nearest distances; mean of nearest and farthest distances; shrub and conifer volume (area covered times height); and shrub, conifer, and herb cover. Variables were computed for individual species as well as for life form groups (e.g., shrubs, herbs, and conifers). Based on inspection of scatter plots, relationships among variables were assumed to be linear.

We considered several factors in deciding which regression models to present. Because the number of trees in each treatment was relatively small, we limited the number of independent variables to no more than two in each model. For a variable to be added to a model, it had to increase the coefficient of determination by at least 0.05 without decreasing the overall significance of the model. The probability level for significance of adding that variable had to be at least 0.2, and the significance level for the overall model had to be at least 0.02 (most were much higher). Where R^2 (or r^2) and significance of models were similar, we selected those with more general variables (e.g., distance to any shrub rather than to a particular species). All models were also inspected graphically for the presence of overly influential outliers before being accepted.

Tree height in 1982 was compared between sites with analysis of variance. In these analyses blocking was not considered, since the site-slope position interaction was nonsignificant for this variable.

All analyses were carried out using SAS (Statistical Analysis System) (SAS Institute 1985).

Results and Discussion

Vegetation Structure and Composition

Changes in plant cover, vegetation structure, and species composition resulting from initial treatments were still evident 8 or 9 years later. The magnitude and persistence of these effects were much greater at Rice Canyon than at Sattley.

In the Rice Canyon control plots, shrub cover was still strongly dominated by *Ceanothus velutinus* in 1982 *(fig. 1a)*. *Abies concolor* contributed substantial cover to these plots as well (7.5-14.0 pct). In treatments B, C, and D, *C. velutinus* cover remained greatly reduced even eight growing seasons after treatment. Grasses and forbs increased in importance relative to controls, particularly in some plots in treatments C and D, where sprouting shrubs had been almost completely eliminated. In general, herbicide-sprayed plots (treatment E) closely resembled the control plots *(fig. 1)*. However, *C. velutinus* cover in sprayed plots (42 pct) was significantly ($p<0.0001$) less than in controls (57 pct).

At Sattley, plant cover on the control plots was dominated by three shrub species: *C. velutinus*, *Arctostaphylos patula*, and *Chrysolepis sempervirens (fig. 1b)*. Shrub cover manipulation in treatments B, C, and D greatly reduced *A. patula*, and little recovery had occurred even by 1983. *C. velutinus* cover in these treatments in 1983 did not differ from the control, although its canopy height of 0.50 m was still lower than in the controls (0.75 m, $p<0.0001$). At Sattley, the rhizomatous *C. sempervirens* quickly colonized areas vacated by other species (Conard and Radosevich 1982a). Nine years after treatment, it was clearly becoming the dominant species in many of the treatment plots, including those sprayed with herbicide.

Average shrub cover over the five treatments ranged from 5 to 60 percent at Rice Canyon and from 35 to 60 percent at Sattley. The greater range at Rice Canyon was largely due to greater and more persistent reductions in shrub cover after treatments at Rice Canyon, and to rapid colonization by *C. sempervirens* at Sattley. Ranges of total plant cover (38-64 pct at Sattley; 22-62 pct at Rice Canyon) differed less between the two sites because of large increases in herbaceous species for some plots in treatments C and D at Rice Canyon.

Changes in species composition and vegetation structure were clearly influenced by the type of treatment, as well as by initial differences in vegetation composition between the two

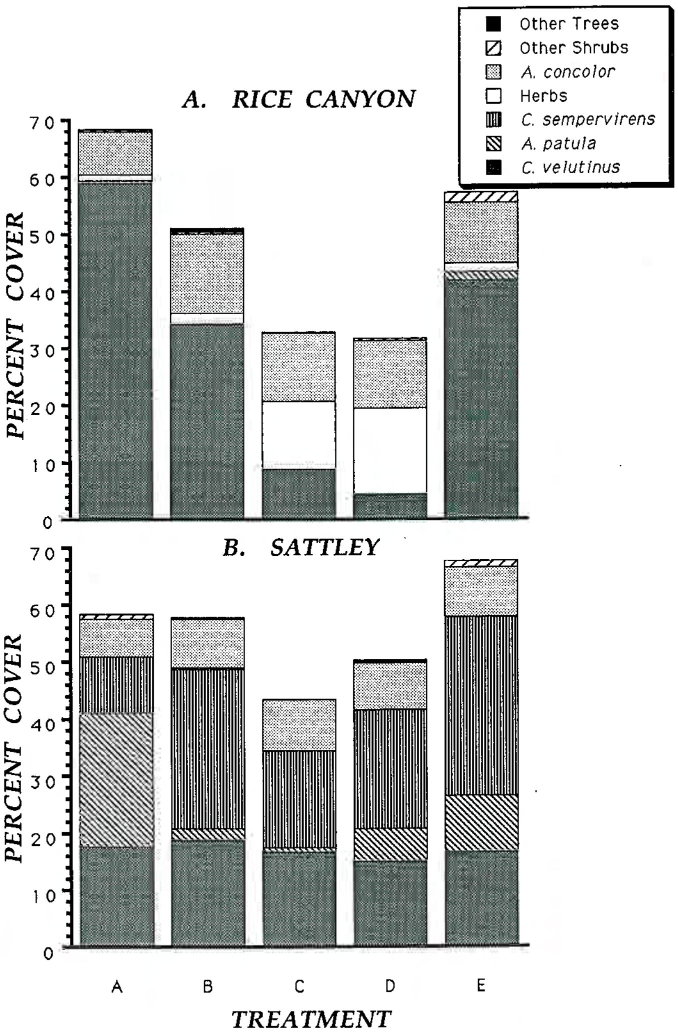

Figure 1—Vegetation composition by treatment, based on averages of data from tree-centered vegetation plots at Rice Canyon (A) and Sattley (B). (Treatments: A—control; B—canopy removed; C—shade present, roots killed; D—canopy removed, roots killed; and E—herbicide applied.)

sites. Reproductive strategies of minor species in the vegetation (such as *C. sempervirens* at Sattley) need to be carefully considered in predicting response of montane chaparral to manipulation. The rhizomatous habit of this species allowed it to colonize rapidly where other species were suppressed, and essentially negated the effect of release treatments in a short time.

Competition from neighboring shrubs and trees strongly influenced height and volume growth of *Abies concolor* saplings. Two kinds of evidence demonstrate the importance of competition: (1) the response of sapling height growth to the shrub removal treatments at Rice Canyon; and (2) relationships between sapling growth and the structure and composition of neighboring vegetation at both sites.

White Fir Growth

Height Growth in Response to Shrub Removal

Height growth provided a more sensitive index of conifer growth response than did absolute tree height for two reasons: initial height of saplings varied, and accurate repeated measurements of height on steep sites with heterogeneous surface materials are difficult. Therefore, only height growth is reported here.

Rice Canyon—Annual height growth at Rice Canyon remained unchanged and virtually identical for both the control (treatment A) and the herbicide-sprayed plots of treatment E, providing continuing evidence that the herbicide application was ineffective at releasing the trees *(fig. 2a)*. In treatments B and C, annual height increments began to increase in 1978 (four growing seasons after treatment) and they remained high through 1982 despite year-to-year variation. Log-transformed height growth for 1982 differed significantly among treatments ($p<0.046$), as did log-transformed 4-year mean height growth (mean height growth, 1978-82; $p<0.037$) and log-transformed volume growth (1978-82; $p<0.011$). For all three dependent variables, growth was greater in treatments B and C than in A and E. Differences for these pooled contrasts were significant at $p<0.002$ to $p<0.009$. Differences between treatments B and C or A and E were not significant.

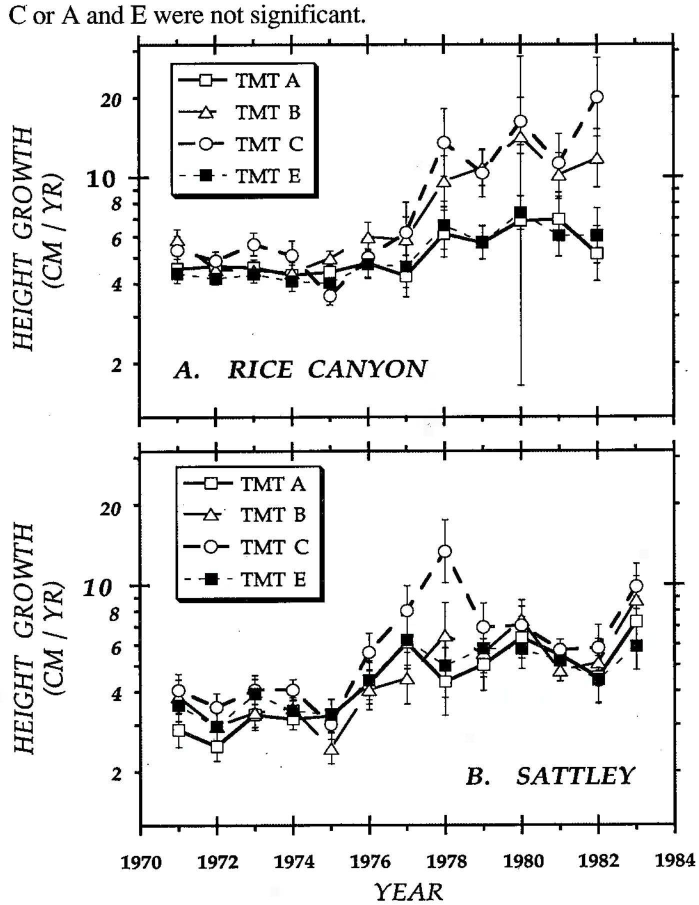

Figure 2—Mean annual height growth (± 1 s.e.) of *Abies concolor* saplings from the 1971 growing season through 1982 at Rice Canyon (A) and through 1983 at Sattley (B). Treatments A-E are as described in *figure 1*. Treatment D was dropped from the analysis.

Although treatment D was not included in these analyses, height growth of surviving trees also increased dramatically relative to trees in treatments A and E. In fact, 3 of the remaining 10 trees in treatment D had the greatest annual height increments of any trees at the Rice Canyon site.

The delayed response to shrub removal until 1978 may be because 1978 (1977-78 hydrologic year) was the first wet year after a major drought, or it simply may have taken that long for the saplings to recover from the initial shock of shrub removal. Delays of 1-5 years in the growth response of trees to competitor removal have been reported in Douglas-fir, ponderosa pine, sugar pine, and white spruce (Brand 1986, Gratkowski 1979, Lanini and Radosevich 1986, Oliver 1984, Yang 1989).

The continuing strong growth responses to treatments between 1978 and 1982 resulted in greater cumulative height growth and total height in trees in treatments B and C compared with treatments A and E *(fig. 3a)*. A similar response occurred in treatment D, although it is based on only a few trees. The trajectory of increasing growth rates in these treatments since 1977 suggests that growth differences are likely to be sustained in the future. This continuing growth response to competitor removal supports other evidence that a single shrub removal treatment may produce long-term benefits in conifer growth at some sites. After an initial lag, the growth response may intensify a few years after treatment (Barrett 1981, Gratkowski 1979).

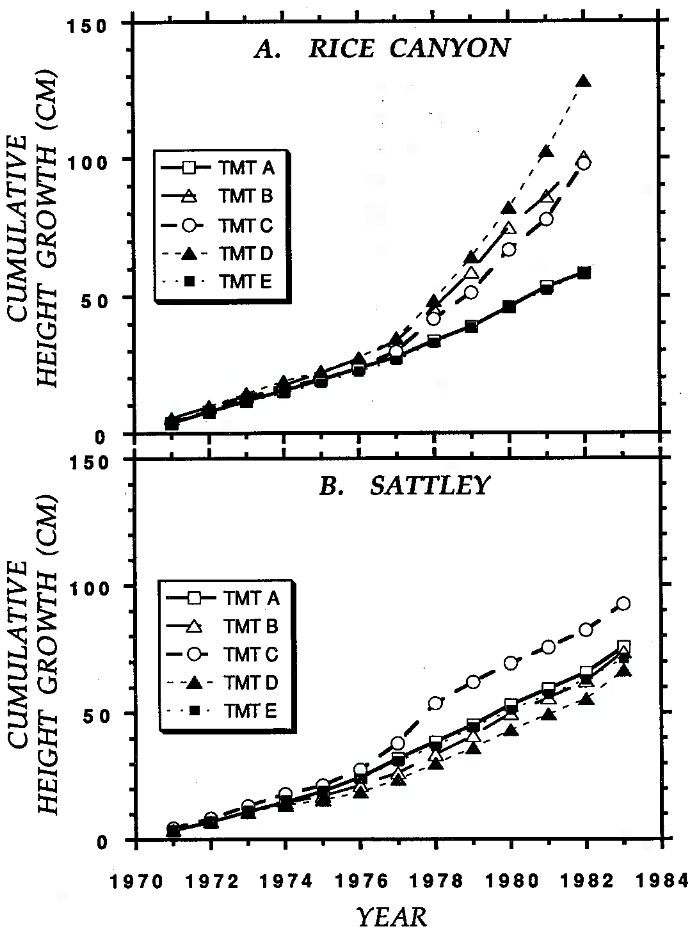

Figure 3—Cumulative height growth at Rice Canyon (A) and Sattley (B), based on means for treatments A-E as described in *figure 1*.

Sattley—Annual height growth did not differ significantly among the treatments at Sattley, except in 1978 when annual height increment in treatment C was greater than that in treatments A ($p<0.009$), B ($p<0.017$), and E ($p<0.008$) *(fig. 2b)*. Although treatment D was excluded from the statistical analysis, annual height increment appeared not to differ from that in treatments A, B, and E. By 1979 height growth no longer differed among treatments.

In treatment C the 1977-78 increase in height growth did result in greater cumulative height growth for all the years following this brief growth surge *(fig. 3b)*. This slight growth advantage may continue into the future. Nonetheless, the response to the 1975 shrub removal treatments was minor and short-lived compared with the larger and more persistent response shown by trees at Rice Canyon.

Relationships with Neighboring Vegetation

Correlations between independent variables characterizing the competition environment and dependent variables describing sapling height and volume growth demonstrate that the structure and composition of neighboring vegetation exerted a great influence on the height and volume growth of individual trees. We attempted to derive general models of tree growth responses to competition variables, but correlation coefficients for relationships across treatments were, in general, extremely low. These coefficients reflect the variation in species dominance, vegetation structure, and growth dynamics of white fir among treatments, as well as variation due to parameters not measured in this study. Correlations based on responses within treatments were far superior. Therefore, separate models were constructed to reflect competitive interactions for each treatment.

In the following discussion, competition is suggested by two situations: positive correlations between the dependent variables and distance; and negative correlations between dependent variables and shrub cover and volume.

Rice Canyon—Average distance to the nearest *C. velutinus* shrub was strongly correlated with all three measures of tree growth in treatments A and B at Rice Canyon ($r=0.59$ to 0.88; $p=0.002$ to 0.0001). *C. velutinus* cover was also negatively correlated with 2-year height growth in treatment C ($r=-0.50$; $p=0.046$). A moderate correlation between 2-year height growth and heights of neighboring *A. concolor* saplings ($r=-0.66$, $p=0.0517$) in treatment C probably reflects the low shrub cover (average of 8.9 pct) on these plots and suggests an increasing importance of intraspecific competition as cover of other competitors decreases. Shrub cover in treatment D was greatly reduced by 1982 (mean cover less than 5 pct). The variability in shrub cover on these plots was also low, making it difficult to detect any influences of shrub competition. Although positive correlations were found between herbaceous cover and all three measures of tree growth in treatment D ($r=0.89$ to 0.95; $p=0.0006$ to 0.0001), these correlations were based on a very small number of rapidly growing trees and may be spurious. High herbaceous cover may simply reflect low cover of shrubby competitors. Also, once trees are established, grasses may not provide substantial competition, due to their relatively shallow root systems. Herbaceous cover was not used to construct growth models for treatment D.

No significant correlations were found for treatment E except with initial tree height (r=0.45 to 0.65; p=0.03 to 0.0003). This is probably a result of minor herbicide injury to the conifers in these plots (Conard and Radosevich 1982a). Since injury might be expected to affect exposed trees more than those directly under shrub canopies, effects of local competitive interactions on conifer growth may have been masked.

After initial exploration with stepwise multiple regression, independent variables were chosen subjectively and evaluated by standard multiple regression techniques for use in models of tree height and volume growth. Distance to the nearest *C. velutinus* (combined with initial tree height) produced the best overall models on this site. Although these overall models were highly significant, coefficients of determination were much higher in general for models based on individual treatments, reflecting the vast differences in vegetation structure and dynamics among treatments. Models for tree growth incorporating these variables in treatments A and B explained from 43.2 to 77.4 percent of the total variation in white fir sapling height and volume growth *(table 2)*. For treatment C, however, where overall shrub cover was low, the height of neighboring white fir, when combined with initial tree height, proved to be a better predictor. In treatment E, only initial tree height showed any relationship to tree growth, as might have been expected based on correlation coefficients.

Sattley—The greater diversity at Sattley resulted in more species with significant correlations with the dependent variables than at Rice Canyon, but coefficients of determination were seldom as large. In addition, initial tree height in 1975 was more often an important covariate at Sattley than at Rice Canyon *(table 2)*, perhaps due to the greater range in tree height at Sattley.

In the control plots, the only species significantly correlated with the three dependent variables was *A. patula* (for cover: r=-0.39 to -0.47; p=0.05 to 0.02). The great decline in importance of *A. patula* in the other treatments resulted in other species becoming influential on sapling growth, particularly *C. sempervirens*. In treatments B, C, and E, correlations of all three dependent variables with one or more of the variables indicating *C. sempervirens* importance (cover, volume, and height) were significant. Correlation coefficients ranged from -0.40 to -0.54 and p-values from 0.05 to 0.004. Clearly, effects of the treatments on species dominance determined which species were the best predictors of growth for individual treatments.

As with Rice Canyon, a significant positive correlation was found at Sattley (here in treatment B) between 2-year height growth and herbaceous cover (r=0.41 to 0.49; p=0.034 to 0.009). This correlation is difficult to explain, as herbaceous cover was never more than a few percent *(fig. 1b)*. We hypothesize that herb cover at Sattley serves as an indicator of low shrub cover or of some other environmental factor, such as moisture availability, that was not measured.

Curiously, 2-year height growth in treatment D was positively correlated with *C. sempervirens* cover and volume (r=0.54, 0.58; p=0.045, 0.03). This positive association may simply be the result of the small number of trees in treatment D at Sattley (N=14), or it may indicate that shrub abundance and tree survival and growth were highest at the best microsites. We found no other positive correlations between any measure of tree growth and any index of shrub abundance (cover, height, or volume) at either site.

Cover of *A. patula* (23 pct) was best correlated with sapling growth in the treatment A (control) plots, despite nearly equal cover of *C. velutinus* (18 pct). This is perhaps due to the somewhat more even distribution (and lower variance in cover) of *C. velutinus*, such that *A. patula* better represents differences in levels of shrub competition between plots.

With the suppression of *A. patula* and *C. velutinus*, the colonizing *C. sempervirens* became the major influence on sapling growth in all treatments. For consistency, we have used average distance to the nearest shrub (AVNR) as an independent variable wherever models were similar in significance and coefficients of determination to models that used individual species characteristics *(table 2)*. For treatments B, C, and E, however, the best models incorporated *C. sempervirens* volume or height as independent variables. The best models for treatment A incorporated *A. patula* characteristics. Again, models for individual treatments were frequently better than overall models including data from all treatments. This difference illustrates the difficulty of generalizing over a range of vegetation structures and dominance patterns. The relationships between tree growth parameters (especially VOLG) and initial tree height (HT75) were often strong, illustrating the importance of initial tree size and vigor in predicting growth.

The sensitivity of individual conifers at Sattley to variations in neighboring vegetation indicates that they were responsive to variations in competition, even where shrub control was not sufficient to elicit an overall treatment response.

Factors Affecting Growth Responses

Tree height in 1982 in the control plots did not differ significantly between Rice Canyon (91.3 cm±7.96 SE) and Sattley (107.0 cm±8.02 SE), even though the Sattley site had burned 14 years earlier than Rice Canyon. These data suggest a lower long-term average annual growth rate at Sattley. Soil nutrient levels and seasonal trends in soil water potentials also suggest lower site quality at Sattley, where response to shrub removal was weaker than at Rice Canyon.

Initially, shaded trees (treatment C) had the strongest height growth response of all treatments *(fig. 2)*. Conard and Radosevich (1982a) attributed this response primarily to improved water balance of shaded trees. The similar large growth responses of treatments B and C at Rice Canyon by 1982 suggest that, while dead shade may ease the transition to full sun during the first few years after shrub removal, the initial advantage is attenuated in subsequent years. The lack of increased growth follow-

Table 2—***Regression models for height and volume growth in each of the shrub removal treatments at Rice Canyon and Sattley, northern Sierra Nevada, California. Overall models for each site are included for comparison purposes. Coefficients of determination (r^2) or coefficients of multiple determination (R^2) and significance level are shown for each model. No significant models were derived for treatment D.***[1]

Model	Fit
Rice Canyon[2]	
Overall Models	
4YRHG = 0.101*CVNR + 0.091*HT75 + 1.449	R^2 = 0.244 p<0.0001
2YRHG = 0.123*CVNR + 0.088*HT75 + 0.412	R^2 = 0.311 p<0.0001
VOLG = 949.0*CVNR + 1365.3*HT75 - 49822.0	R^2 = 0.251 p<0.0001
Treatment A	
4YRHG = 0.188*CVNR + 0.058*HT75 - 0.633	R^2 = 0.432 p<0.0035
2YRHG = 0.289*CVNR + 0.178	r^2 = 0.434 p<0.0005
VOLG = 967.7*CVNR + 623.5*HT75 - 29968.5	R^2 = 0.500 p<0.0003
Treatment B	
4YRHG = 0.548*CVNR - 3.474	r^2 = 0.774 p<0.0001
2YRHG = 0.471*CVNR - 2.293	r^2 = 0.579 p<0.0001
Treatment C	
VOLG = -247.3*ACHT + 1403.9*HT75 + 31565.0	R^2 = 0.625 p<0.0198
Treatment E	
4YRHG = 0.120*HT75 + 0.835	r^2 = 0.493 p<0.0003
2YRHG = 0.146*HT75 - 0.639	r^2 = 0.508 p<0.0002
VOLG = 1450.7*HT75 - 37758.1	r^2 = 0.710 p<0.0001
Sattley[3]	
Overall Models	
5YRHG = 0.122*AVNR + 4.209	r^2 = 0.195 p<0.0001
2YRHG = 0.131*AVNR + 4.701	r^2 = 0.130 p<0.0001
VOLG = 1870.0*HT75 - 56621.1	r^2 = 0.469 P<0.0001
Treatment A	
5YRHG = 0.168*AVNR + 0.066*HT75 - 0.155	R^2 = 0.486 p<0.0025
2YRHG = 0.148*AVNR + 0.094*HT75 - 0.575	R^2 = 0.336 p<0.0110
VOLG = 1773.6*HT75 - 65244.8	r^2 = 0.489 p<0.0001
Treatment B	
5YRHG = 0.146*AVNR + 4.055	r^2 = 0.380 p<0.0010
2YRHG = 3.403*HBCOV - 8.709*CSHT + 10.973	R^2 = 0.330 p<0.0081
VOLG = 1719.1*AVNR + 927.2*HT75 - 54576.3	R^2 = 0.537 p<0.0003
Treatment C	
5YRHG = 0.135*AVNR + 3.629	r^2 = 0.224 p<0.0127
2YRHG = 0.179*AVNR + 3.06	r^2 = 0.266 p<0.0059
VOLG = 1966.6*HT75 - 41342.4	r^2 = 0.295 p<0.0028
Treatment E	
5YRHG = -1.361*CSVOL + 0.033*HT75 + 6.857	R^2 = 0.379 p<0.0033
2YRHG = -9.022*CSHT + 0.045*HT75 + 9.423	R^2 = 0.383 p<0.0030
VOLG = 2056.9*HT75 - 76660.8	r^2 = 0.567 p<0.0001

[1]2YRHG, 4YRHG, 5YRHG = 2-, 4-, and 5-year average height growth (cm), VOLG = stem volume growth (cm^3), HT75 = initial tree height (cm).

[2]CVNR = distance to nearest *Ceanothus velutinus* (cm), ACHT = average height of *Abies concolor* (cm).

[3]AVNR = distance to nearest shrub (cm), HBCOV = percent cover of herbaceous species, CSHT, CSVOL = average height (cm), shrub volume (cm^3) of *Chrysolepis sempervirens*.

ing removal of shade from treatment C plots in 1978 provides further evidence that water, and not light, is the primary limiting resource for white fir growth on these sites.

Although treatment D was dropped from the statistical analyses, 3 of the surviving 10 trees in this treatment responded with the greatest height growth of any tree at either site. The severity of this shrub removal treatment (shade removed, roots killed) may be why tree mortality was so high at Rice Canyon. The adjustment from shade to sun probably requires the replacement of shade leaves by new sun leaves (Nobel 1991). Trees in treatment D at Rice Canyon had neither dead shade nor neighboring sprouting shrubs to decrease evapotranspirational demand during this adjustment period, resulting in high mortality. Trees that survived this adjustment period were growing in an environment where resource availability was greatly increased, and could potentially show a strong release response.

Although the trees in treatment C (shade) at Sattley showed a significant increase in height growth relative to the other treatments in 1978, by 1980 growth of these trees was indistinguishable from that in the other release treatments *(fig. 2)*. As at Rice Canyon, dead shade may have initially enhanced height growth at Sattley by reducing evapotranspirational demand, thereby allowing the trees to respond to the increased water availability brought about by shrub removal and increased precipitation. Shrub removal at Sattley was not as successful as at Rice Canyon, however, and vigorous recolonization by *C. sempervirens* rapidly negated any treatment benefit.

At Rice Canyon, release was observed even on treatment B, where mean canopy cover of competing shrubs was 27 percent in 1982. The lowest mean shrub canopy cover at Sattley was 35 percent (treatment C), which was not sufficient to sustain release. This observation supports the earlier hypothesis that shrub canopy cover on these types of sites must be reduced to around 30 percent before detectable increases in growth will occur (Conard and Radosevich 1982a). We found no evidence on either site that herb cover had a negative effect on conifer growth. Therefore, herbaceous competition, while of potential importance in the establishment phase, may have little effect on growth of established *Abies concolor* saplings.

Conclusions

We hypothesize that where conifer saplings are under the shrub canopy, complete shrub removal may be more detrimental to overall development of a well-stocked conifer stand than more standard chemical treatments, which leave some dead shade. This shade may reduce the likelihood of mortality in exposed saplings and suppress other colonizing competitors. On the other hand, in overstocked stands where mortality is not a concern, complete removal of competing shrubs may provide the greatest growth benefits to surviving trees, and total canopy removal may thin out some of the less vigorous trees and lead to increased average long-term growth rates. We expect these relationships to vary among sites and among conifer species.

Our results illustrate the difficulty of developing general models for assessing response of young plantations and natural stands to competition or to release treatments when interstand dynamics may vary greatly among different sites or treatments depending on site history or physical factors. Ideally, broad-based, multifactorial models could be developed that would incorporate physical site factors (soils, nutrient status, climatic parameters) and biotic influences into physically based models of resource availability and stress. In the interim, models developed under a limited number of site conditions and treatment regimes should be used with caution.

Recommendations

1. Shrub removal treatments continued to enhance white fir sapling growth 8 years after treatment at Rice Canyon, but not at Sattley. We hypothesize that this difference in response is due to a combination of better site quality at Rice Canyon and poorer control of competing vegetation at Sattley. How these factors may interact is unclear.

2. Moisture is apparently the most important limiting resource for white fir growth on our study sites. Benefits of shading on growth did not persist after shade was removed, nor did shading appear to inhibit growth.

3. Where tree mortality is not a concern, complete shrub removal may produce the greatest long-term growth benefits for surviving trees. Where stocking is low or marginal, however, the optimum response will probably result from a treatment that effectively controls brush without removing dead shade.

4. Cover of important shrub species and their distance from white fir trees were correlated with tree growth at both sites, providing evidence that the local competition environment strongly influences white fir sapling growth.

5. The large differences between sites and among treatments in variables useful for modeling tree growth responses illustrate the difficulty in developing generalizable models for predicting and evaluating competitive interactions and reinforce the need for caution in trying to apply such models to situations different from those in which they were developed.

6. The rapid changes in dominance induced by our treatments illustrate the need to evaluate carefully the potential impact of vegetation management treatments on reproduction or expansion of minor species in the vegetation once site resources are made available to them through suppression of potential competitors.

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