Valley Oak Seedling Growth Associated with Selected Grass Species[1]

Karen C. Danielsen William L. Halvorson[2]

Abstract: Valley oak (*Quercus lobata* Née) has exhibited inadequate regeneration since the last century. Seedlings become established, but few develop into saplings. We hypothesized that the invasion of alien annual grasses into native perennial grasslands has increased oak seedling mortality by decreasing soil moisture availability. We conducted greenhouse experiments to test if the alien annual grass *Avena fatua* L. and the native perennial grass *Stipa pulchra* Hitchc. differentially effect soil moisture and valley oak seedling growth. Results showed that valley oak seedlings in the *A. fatua* treatments grew significantly smaller than seedlings in the *S. pulchra* treatments. In addition, valley oak seedling growth showed a positive correlation with soil moisture during the growing season. The results suggest that the introduction of alien annual grasses has reduced valley oak seedling growth and survivorship by limiting soil moisture availability.

It appears that, since the early 1900's, valley oaks have shown limited regeneration because of high seedling mortality (Griffin 1976, Bartolome and others 1987). Just prior to this time period, settlers introduced alien annual plants both accidently and purposely. These alien plants replaced much of the native plant species composition which, according to some researchers (Clements 1934, Beetle 1947, Barry 1981), consisted primarily of perennial bunchgrasses. Presently, alien annual grasses dominate valley oak habitat (Swirsky and Halvorson 1984, Swirsky 1986). Some researchers have suggested that this replacement of native grasses by alien grasses may be linked to the observed high seedling mortality (Welker and Menke 1987, McCreary 1989).

Field surveys revealed that soil moisture generally measured lower in alien grasslands than in native grasslands during the growing season (White 1967, Hull and Muller 1977). Jackson and Roy (1986) demonstrated that annual grasses grow and utilize soil moisture faster than perennial grasses. This faster rate of decline in soil moisture associated with alien annual grasses may be a significant factor effecting valley oak seedlings.

Phytophysiological studies demonstrated that when soil moisture declines slowly oak seedlings avoid water stress by accumulating solutes in their cells which promotes the influx of water. The accumulation of solutes lowers cell water potential without significantly reducing cell water content. If soil moisture declines too rapidly, however, water content decreases before cellular solutes can accumulate and water stress ensues (Osonubi and Davies 1981, Flower and Ludlow 1986, Welker and Menke 1987, Gordon and others 1989). Water stress limits plant growth (Kramer 1969, Matthews and Boyer 1984) and eventually results in the collapse of cell walls and senescence of the plant (Flower and Ludlow 1986). Consequently, competition for water by alien annual grasses may induce severe water stress in valley oak seedlings that results in slowed growth and ultimately death.

This paper reports on a greenhouse experiment designed to determine if valley oak seedlings established with alien grasses experience reduced growth as compared to those established with native grasses. We conducted a second greenhouse experiment to compare the soil moisture associated with alien and native grasses.

METHODS

Seeds of valley oak; the native perennial grass, *Stipa pulchra;* and the alien annual grass, *Avena fatua,* were collected from the Santa Monica Mountains of the Transverse Ranges north of Los Angeles, CA. The experiments were conducted in the greenhouse of California State University, Los Angeles.

In the first experiment, we measured valley oak seedling growth using waxed cardboard tubes lined with polyethylene bags as planting containers.

During the first week of December 1987, we planted *A. fatua* seeds into each of 50 containers (density = 2000/m^2), and we transplanted one-year-old *S. pulchra* plants into each of another 50 containers (basal cover = 11 percent). Density and basal cover approximated field conditions (Heady 1958, White 1967, Gordon and others 1989). Last, we left 50 containers devoid of grasses for controls. During the last week in December, after the grasses had become established, we planted one germinated acorn per container.

Throughout the experiment, we watered 75 of the containers to simulate dry years (25 for each grass treatment) and 75 to simulate wet years. Dry year treatments received 5 times less water than wet year treatments. Precipitation data from the Santa Monica Mountains (U.S. Weather Bureau) served as a basis to determine this watering regime.

[1]Presented at the Symposium on California's Hardwood Rangeland Management, October 31-November 2, 1990, Davis, California.

[2]Botanist, Vandenberg AFB, California; Research Biologist, Channel Islands National Park, Ventura, California.

In February 1988, as valley oak seedling shoots emerged, we initiated the biweekly recording of the growth measurements: height, number of leaves, and length of the largest leaf. In September 1988, we removed the valley oak seedlings and recorded final root and shoot lengths and dry weights.

In the second experiment, we measured soil moisture between December 1988 and May 1989. We used an experimental design similar to that used in the growth experiment. However, we did not use controls, and we reduced the sample size of each grass treatment to 10 containers. Each month we extracted two soil samples from different levels from each container. We measured the soil moisture (water potential) of the samples using a thermocouple psychrometer (Decagon SC-10). For further details on methodology and data analysis refer to Danielsen (1990).

RESULTS

Growth Experiment

In all treatments, valley oak seedling shoots emerged during February and March (*fig. 1*). Though all acorns were viable and developed roots, some never developed shoots; particularly in the *Avena fatua* treatments.

Seedling Growth Experiment

Simultaneous analysis of seedling height, number of leaves, and length of largest leaf for the sampling dates combined (*fig. 2* and *3*) showed that seedlings in the controls grew significantly larger than seedlings in the grass treatments for both the dry and wet year regimes (canonical variates test, sample size = number of emerged shoots, probability <.05). Between grass treatments, seedlings in the *S. pulchra* treatments grew significantly larger than seedlings in the *A. fatua* treatments.

A comparison of the maximum averages for each growth variable (*table 1*) further illustrates that seedlings grew largest in the controls and smallest in the *A. fatua* treatments. Data for each growth variable and sampling date were analyzed separately (Kruskal-Wallace test). For all three growth variables in both the dry and wet year regimes, significant differences between the controls and the grass treatments and between the differing grass treatments occurred during March and April.

From May through August, significant differences continued to occur for all three growth variables between the control and grass treatments. Between the grass treatments, significant differences continued to occur for the height and length of largest leaf variables.

Seedling Root and Shoot Measurements

Seedling roots and shoots in the controls were significantly longer and heavier than those in the grass treatments in both the dry and wet year regimes (*tables 2* and *3*). Between the grass treatments, in the dry year regime, seedling shoots in the *S. pulchra* treatments were significantly longer and heavier than those in the *A. fatua* treatments.

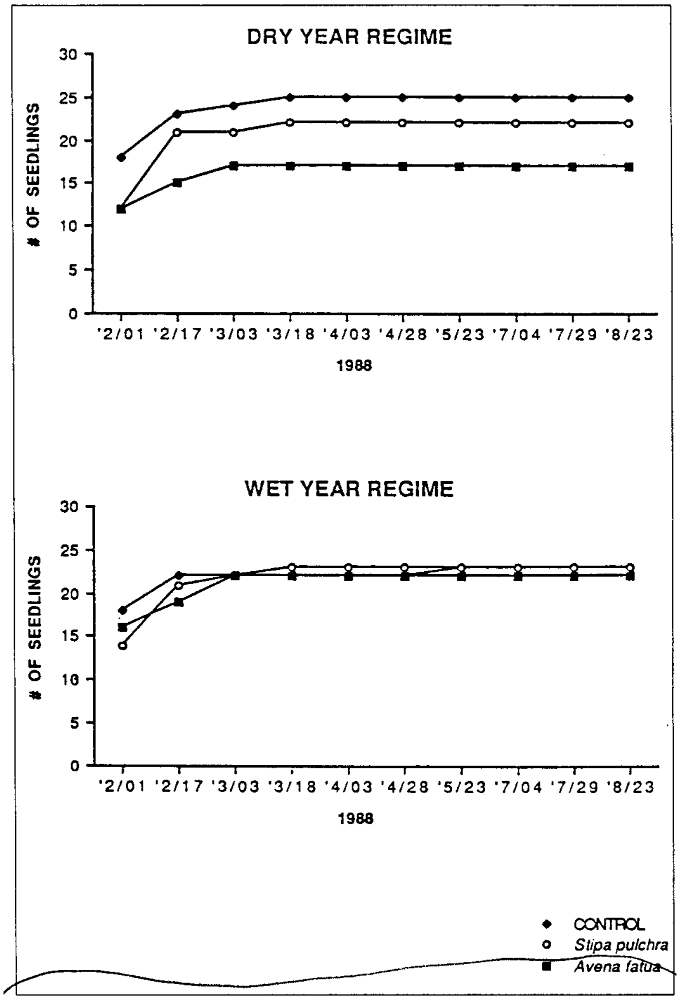

Figure 1—Number of valley oak seedlings with emerged shoots for each sampling date.

Root/shoot ratios were calculated to determine allocation of biomass. Valley oak seedlings in the *A. fatua* treatments showed greater root/shoot ratios than seedlings in the controls or *S. pulchra* treatments. Dry weight root/shoot ratios, in the dry year regime, averaged 10.0 in the *A. fatua* treatments, 3.7 in the *S. pulchra* treatments, and 5.9 in the controls. In the wet year regime, dry weight root/shoot ratios averaged 6.0 in the *A. fatua* treatments, 2.6 in the *S. pulchra* treatments, and 4.0 in the control treatments. Length root/shoot ratios, in the dry year regime, averaged 8.3 in the *A. fatua* treatments, 3.9 in the *S. pulchra* treatments, and 2.8 in the controls. In the wet year regime, length root/shoot ratios averaged 5.1 in the *A. fatua* treatments, 3.4 in the *S. pulchra* treatments, and 2.2 in the controls.

Soil Moisture Experiment

Soil water potentials remained high in both grass treatments from December through February. The maximum mean soil

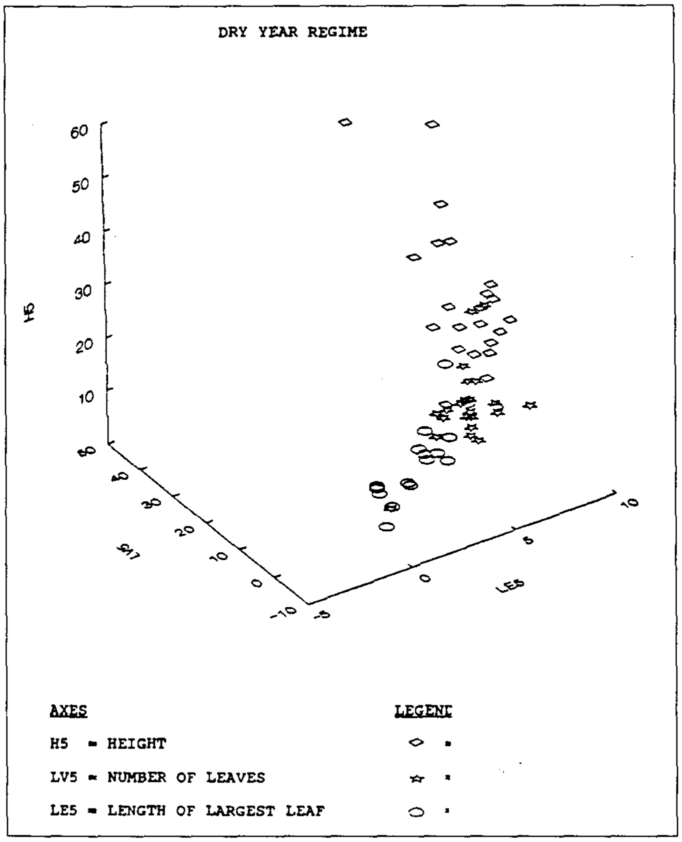

Figure 2—Overall growth in dry year regime: height, number of leaves, and length of largest leaf were plotted for each valley oak seedling with respect to grass treatment for sampling date, 3 April 1988. Simultaneous analysis of these growth variables for the sampling dates combined showed significant differences between the control and grass treatments and between the differing grass treatments (canonical variates test, N=# of seedlings with emerged shoots, p<.05).

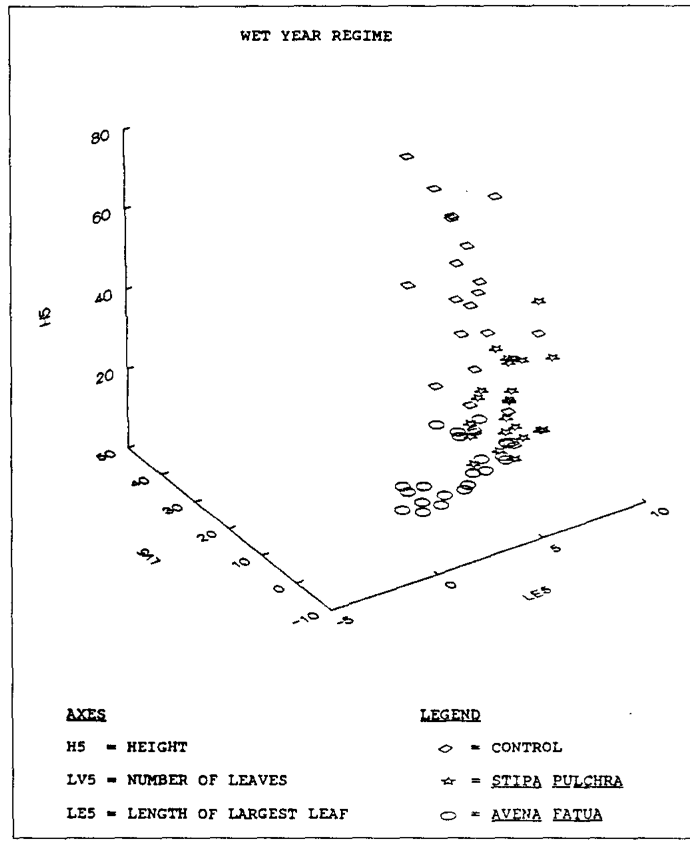

Figure 3—Overall growth in wet year regime: height, number of leaves, and length of largest leaf were plotted for each valley oak seedling with respect to grass treatment for sampling date, 3 April 1988. Simultaneous analysis of these growth variables for the sampling dates combined showed significant differences between the control and grass treatments and between the differing grass treatments (canonical variates test, N=# of seedlings with emerged shoots, p<.05).

water potential during December measured -425.6 (38.08 SE) J/kg.

During March, potentials decreased; particularly in the *A. fatua* treatments. In the dry year regime, upper level mean potentials measured only 3 percent of the maximum measured in December in the *A. fatua* treatments and 6 percent in the *S. pulchra* treatments. Lower level mean potentials measured 6 percent of the maximum measured in December in the *A. fatua* treatments and 8 percent in the *S. pulchra* treatments. In the wet year regime, upper level mean potentials measured 9 percent of the maximum in the *A. fatua* treatments and as much as 58 percent in the *S. pulchra* treatments. Lower level mean potentials measured 9 percent of the maximum in the *A. fatua* treatments and 70 percent in the *S. pulchra* treatments. Analysis of the soil water potential data in March showed significant differences between the grass treatments at both levels in the wet year regime (Mann-Whitney U-test, sample size = 5, p<.05).

During April, in the wet year regime, mean potentials remained lower in the *A. fatua* treatments than those in the *S. pulchra* treatments (2 percent and 5 percent of the maximum, respectively, at the upper level; and 7 percent and 12 percent of the maximum at the lower level). In the dry year regime, mean potentials in the *A. fatua* treatments actually increased at the lower level. The senescence of the *A. fatua* resulted in potentials equal to or higher than those in the *S. pulchra* treatments (upper level: 1 percent of the maximum in both treatments; and lower level: 12 percent of the maximum in the *A. fatua* treatments and 7 percent in the *S. pulchra* treatments). Analysis of the soil water potential data in April showed no significant differences between the grass treatments.

DISCUSSION

Indications of water stress in valley oak seedlings were most prevalent in the *Avena fatua* treatments, followed by the *Stipa pulchra* treatments, and finally the controls. Oak seedlings allocate water and, subsequently, biomass in order of roots, stems, and leaves. Consequently, during the growing season, oak seedlings initially respond to water stress with reduced leaf growth (Kramer 1969). Seedling leaves measured significantly smaller in the *A. fatua* treatments than in the *S. pulchra* treatments or the controls. Furthermore, seedlings in the *A. fatua*

Table 1—***Maximum averages of valley oak seedling height (measured in centimeters), number of leaves, and length of largest leaf with respect to grass treatment. Standard error in parentheses. For all three growth variables in both the dry and wet year regimes, significant differences occurred between the control and grass treatments and between the differing grass treatments (Kruskal-Wallace test, N=# of seedling emerged, $p<05$).***

	HEIGHT (CM)	# OF LEAVES	LENGTH (CM)
PRY YEAR REGIME			
Control	28.7 (2.41)	20.8 (l.75)	7.5 (0.22)
S. pulchra	12.3 (l.34)	8.8 (0.71)	6.0 (0.17)
A. fatua	6.7(l.16)	6.2 (0.55)	4.0 (0.47)
WET YEAR REGIME			
Control	38.1 (4.56)	29.0 (2.89)	7.3 (0.28)
S. pulchra	17.2(l.72)	9.7 (0.67)	6.6 (0.32)
A. fatua	10.8 (1.31)	6.8 (0.57)	4.0 (0.26)

Table 2—***Valley oak seedling average root and shoot lengths (cm); final measurements. RL=root length and SL-shoot length. Standard error in parentheses.***

	RL	SL	RS/SL
DRY YEAR REGIME			
Control	92.8 (3.89)	33.7 (3.55)	2.8
S. pulchra	69.7 (3.79)	17.9 (2.04)	3.9
A. fatua	65.5(l.97)	7.9(l.47)	8.3
WET YEAR REGIME			
Control	89.5 (4.23)	39.9 (4.96)	2.2
S. pulchra	74.3 (3.64)	21.7 (2.22)	3.4
A. fatua	72.2 (3.01)	14.1 (1.55)	5.1

Table 3—***Valley oak seedling average root and shoot dry weights (gm); final measurements. RW=root dry weight and SW-shoot dry weight. Standard error In parentheses.***

	RW	SW	RW/SW
DRY YEAR REGIME			
Control	13.0 (0.88)	2.2 (0.22)	5.9
S. pulchra	1.1 (0.07)	0.3 (0.03)	3.7
A. fatua	1.0 (0.07)	0.1 (0.02)	10.0
WET YEAR REGIME			
Control	13.3(l.55)	3.3 (0.45)	4.0
S. pulchra	1.3 (0.19)	0.5 (0.08)	2.6
A. fatua	1.2 (0.12)	0.2 (0.03)	6.0

treatments produced the fewest number of leaves.

A high root-to-shoot ratio also indicates water stress (Gordon and others 1989). The valley oak seedling root/shoot ratio for the length measurement averaged highest in the *A. fatua* treatments and lowest in the controls. The root/shoot ratio for the dry weight measurement averaged highest in the *A. fatua* treatments and, interestingly, lowest in the *S. pulchra* treatments; not in the controls. Roots of seedlings in the controls, unlike in the grass treatments, developed woody tissue. Therefore, in the controls, secondary growth, not necessarily water stress, produced higher weight root/shoot ratios. Nevertheless, the resulting root/shoot ratios demonstrate that seedlings in the *A. fatua* treatments experienced the greatest water stress.

As previously mentioned, oak seedlings exposed to a rapid decline of soil moisture experience water stress and display reduced growth during the growing season. Oak seedlings exposed to a slower decline of soil moisture are subjected to less water stress, through physiological adjustments, and continue growth. *A. fatua* grew rapidly in February and March, and reduced available soil moisture. *S. pulchra* grew more slowly and utilized less soil moisture. The valley oak seedlings grew largest in the controls, next largest in the *S. pulchra* treatments and smallest in the *A. fatua* treatments.

In April, *A. fatua* became senescent and soil water absorption decreased. *S. pulchra* growth accelerated with an accompanying increase in soil water absorption. In the dry year regime, soil water potentials were higher in the *A. fatua* treatments than in the *S. pulchra* treatments. In the wet year regime, available soil moisture in the *A. fatua* treatments allowed the development of new leaves on four valley oak seedlings. However, seedlings remained significantly larger in the *S. pulchra* treatments than in the *A. fatua* treatments.

In this experiment, valley oak seedlings grew most rapidly in February and March. During this growing season, soil water potentials corresponded with valley oak seedling growth. After the growing season, soil water potentials failed to significantly alter established seedling growth patterns. Consequently, the phenology of the different grass species, and the resulting soil moisture availability during the growing season, determined the ultimate size of the valley oak seedlings.

Other studies have obtained similar results. Adams and others (1987) observed reduced seedling survival of valley oak and blue oak (*Quercus douglasii* H.& A.) in the presence of alien annuals. Gordon and others (1989) documented a significant positive correlation between soil moisture availability associated with alien annuals and blue oak seedling growth. Welker and Menke (1987) noted that soil moisture loss caused by decreased amounts of mulch resulting from cattle grazing also limits blue oak seedling growth.

CONCLUSION

In this research, associated grasses inhibited the growth of valley oak seedlings. The particular species of grass, however, determined the degree of inhibition. Seedlings in the *Stipa pulchra* (a native grass species) treatments grew significantly larger than seedlings in the *Avena fatua* (an alien grass species) treatments. Furthermore, soil moisture measured lower in the grass treatments, particularly in the *A. fatua* treatments, and thus correlated with seedling growth. Therefore, these results suggest that the replacement of native perennial grasses by alien annual grasses has reduced valley oak seedling growth and survivorship by limiting soil moisture availability.

ACKNOWLEDGMENTS

We thank Richard Vogl, David Soltz, Carlos Robles, Sherri Gust, Robert Descharnais, James Griffin, and Doria Gordon for offering a copious amount of advice. The following people helped with the experimental setup and data collection: Paul Edelman, Monica Finn, Liv Johannson, Eva Morgan, Dale Thomas, and Maria Vela. This research was funded by the National Park Service, the *Quercus* Fund, and the California Native Plant Society.

REFERENCES

Adams, Jr., T.E., P.B. Sands, W.H. Weitkamp, N.K. McDougald, and J. Bartolome. 1987. Enemies of white oak regeneration in California. In: Proc. Symposium on the Multiple-use Management of California's Hardwood Resources; 1986 Nov. 12-14; San Luis Obispo, CA. Gen. Tech. Report PSW-100. Berkeley, CA. Pacific Soutwest Forest and Range Exp. Stn., Forest Service, USDA; 459-462.

Barry, J.W. 1981. Native grasses then and now. Fremontia 9(1):18.

Bartolome, J.W., P.C. Muick, and M.P. McClaren. 1987. Natural regeneration of Californian Hardwoods. In: Proc. Symposium on the Multiple-use Management of California's Hardwood Resources; 1986 Nov. 12-14; San Luis Obispo, CA. Gen. Tech. Report PSW-100. Berkeley, CA. Pacific Soutwest Forest and Range Exp. Stn., Forest Service, USDA; 26-3 1.

Beetle, A.A. 1947. Distribution of the native grasses of California. Hilgardia 17: 309-357.

Clements, F.E. 1934. The relict method in dynamic ecology. J. Ecol. 22: 39-68.

Danielsen, K.C. 1990. Seedling growth rates of *Quercus lobata* Née. (valley oak) and the competitive effects of selected grass species. Los Angeles: California State Univ.; 74 p. M.S. Thesis.

Flower, D.J. and M.M. Ludlow. 1986. Contribution of osmotic adjustment to the dehydration tolerance of water-stressed pigeonpea (*Cajunus cajan* (L.) Millsp.) leaves. Plant Cell Environ. 9: 33-40.

Gordon, D.R., J.M. Welker, J.M. Menke, and K.J. Rice. 1989. Neighborhood competition between annual plants and blue oak (*Quercus douglasii*) seedlings. Oecol. 79: 533-541.

Griffin, J.R. 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. Amer. Midl. Natur. 95(2): 422-435.

Heady H.F. 1958. Vegetational changes in the California annual type. Ecology 39: 402-416.

Hull, J.C. and C.H. Muller. 1977. The potential for dominance by *Stipa pulchra* in a California grassland. Amer. Midl. Natur. 97(1): 147-175.

Jackson, L.E. and J. Roy. 1986. Growth patterns of meditterrean annual and perennial grasses under simulated rainfall regime of Southern France and California. Oecol. Plant 7(21): 191-212.

White, K.L. 1967. Native bunchgrass (*Stipa pulchra*) on Hastings Reservation, California. Ecol. 48(6): 949-955.

Kramer, P.J. 1969. Plant and Soil Water Relations - A Modern Synthesis. USA: McGraw-Hill, Inc.; 482 p.

Matthews M.A. and J.S. Boyer. 1984. Acclimation of photosynthesis to low leaf water potentials. Plant Physiol. 74: 161-166.

McCreary, D.D. 1989. Regenerating native oaks in California. Calif. Agric. 43(1): 4-6.

Osonubi, O. and W.J. Davies. 1981. Root growth and water relations of oak and birch seedlings. Oecol. 51: 343-350.

Swirsky, K.L. 1986. Valley oak savanna: an ecological approach to habitat restoration. Los Angeles: California State Univ. 73 p. M.S. Thesis

Swirsky, K.L. and W.L. Halvorson. 1984. Valley oak restoration (California). Restoration and Management Notes II(2): 75.

Welker, J.M. and J.W. Menke. 1987. *Quercus douglasii* seedling water relations in mesic and grazing-induced xeric environments. Proc. International Conference on Measurements of Soil and Plant Water Status, Volume 2; Logan, Utah; 229-234.