Soil Water Effects on Blue Oak Seedling Establishment[1]

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Abstract: A field experiment was conducted to examine the effects of soil water availability on blue oak (*Quercus douglasii*) seedling establishment. Acorns were planted either into cleared plots of 0, 10, 20, or 40 cm diameter. The cleared plots were located in two grazed and one ungrazed site. Half of the plots received drip irrigation in a split plot design. Soil water and plot size, depending on the site, and initial acorn weight and parent tree all influenced oak seedling growth. Survival and height in subsequent growing seasons was dependent on early growth. Soil water availability in the first growing season, therefore, influences both oak seedling establishment and growth in subsequent years.

Earlier work (Gordon and others 1989, Gordon and Rice 1990, Rice and others these proceedings) indicates that blue oak (*Quercus douglasii* Hook. & Am.) seedling establishment, water relations, and growth depend on the rate of soil water depletion. Further, this rate has been demonstrated to depend on the composition of the herbaceous neighborhood in which a blue oak seedling is planted. In addition to the effects of the competitive environment, seedling growth varies with tree of acorn origin and initial acorn weight (Rice and others these proceedings). Thus, maternal or genetic differences in source material interact with the competitive characteristics of the environment to influence the probability of oak seedling establishment and survival.

The above experiments were all conducted in containers. This paper describes a field experiment in which soil water availability and proximity of herbaceous competitors were varied around establishing blue oak seedlings to examine the questions: 1) Are seedling emergence and growth in the field reduced under rapidly drying soil water conditions? 2) Do parent tree and initial acorn weight interact to influence seedling response to environmental conditions? 3) Does seedling growth in the first growing season influence survival and growth in subsequent years?

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METHODS

The experiment was conducted at the University of California Sierra Foothill Range Field Station (SFRFS) in Yuba Co., California. A 1 ha area encompassing grazed land and adjacent land which had not been grazed since 1972 was fenced to exclude both livestock and deer. Soils are derived from metamorphic parent materials and consist of reddish Alfisols and brownish Ochrepts. Annual precipitation averages 740 mm; temperature extremes range from -2 to 40°C.

This experiment examined the growth, water status, and survival of oak seedlings in cleared circular plots of 1, 10, 20, and 40 cm diameter, with or without irrigation in the spring. The watering treatment was established as the main plot in a split-plot design, with plot size as a subplot treatment. Ten blocks were established in each of three sites: grazed with oak canopy removed, grazed open, and ungrazed low canopy sites. The canopy-removed site was established so that the effects of canopy-influenced soil could be examined without a confounding reduction in light availability.

The surface 1-2 cm of soil and litter were removed from the plots in fall, 1986. Plots were weeded as necessary during the first 2 years of the experiment. Blue oak acorns, collected from four trees at the SFRFS, were planted in the center of each subplot in winter, 1987. All acorns showed healthy radicle development of up to 10 mm when planted. Parent tree and initial acorn weight in 0.5 g classes were recorded for use as covariates in the analysis. Tree and weight were randomly distributed among the subplots. To reduce herbivory on seedlings, each subplot was caged with aluminum screening.

Soil water content was increased for 2 months with drip irrigation tubing in one main plot of each block. Each watered plot received about 7 liters of water weekly starting April 23. Soil water potential at 40 cm depth was measured biweekly with calibrated screen-cage thermocouple psychrometers (J.D. Merrill Specialty Equip.) placed in 2 replicates each of the 0, 20, and 40 cm unwatered plots and in the 20 cm watered plots.

Shoot emergence, stem height, leaf number, and estimated leaf area of oak seedlings were measured weekly. Mid-day leaf conductance and transpiration rates (Licor null-balance porometer) were also taken weekly. Initial and final seedling height in 1988, and final height in 1989 and 1990 were also recorded to determine the relationship between initial seedling growth and subsequent survival.

BMDP logistic regression (Dixon 1985) was used to examine the effects of watering treatment and plot size on oak seedling emergence in 1987 and 1988. Chi-square analysis examined the influence of parent tree and acorn weight class on emergence. The general SAS linear model analysis of split plot designs (Freund and others 1985) was used to compare oak growth responses to treatments. Acorn weight and parent tree identity were included as covariates in these analyses. Parameters measured over time were tested in ANCOVA models through an orthogonal polynomial decomposition of the time effect. Main and interactive effects and Tukey tests were thus tested against specified nested Type I error terms (Gordon and Rice 1990). Correlations of seedling growth within and among seasons were also examined. Continuous variables were log-transformed while count variables were square root-transformed to increase consistency with linear model assumptions.

RESULTS

The watering treatment maintained the water potential above -1.5 MPa at the 40 cm depth in cleared plots during most of June (fig. 1). Plot size did not affect the rate of soil water decrease through the season at any of the sites (fig. 1). Average water potential tended to increase with plot diameter, but significant differences were not detected.

By early April, 23, 4, and 0 percent of the acorns had produced shoots in the grazed canopy-removed, ungrazed, and grazed open sites, respectively. In mid-May, 48, 33, and 36 percent had emerged in the three sites. However, between the second and third weeks of May, 94 percent of the new shoots emerging were in irrigated plots. Actual numbers of plots with acorns were lower than the percentages indicate, however, because of shoot mortality and disappearance from several plots. Gopher activity (focussed on irrigated plots) appeared to be the major cause of this loss. Overall, only about 40 percent of the acorns planted produced shoots in the plots.

Logistic regression of block, plot size, and water treatment effects on seedling emergence within each of the three sites revealed significant effects of watering in the grazed open (F=3.88, p=.05) and the grazed canopy-removed (F=4.3 1, p<.05) sites. These effects were most dramatic in the grazed open site, where 30 percent of the unwatered and 59 percent of the watered acorns showed shoot growth (fig. 2). Conversely, the main and interactive effects of block and plot size significantly influenced emergence in the ungrazed site (F=6.48, p<.0001); emergence was significantly lower than expected in the 10 cm (p<.005) and higher than expected in the 20 cm (p<.004) diameter plots.

Interactions between planting site and acorn weight (F=2.97, p=.05) and site and parent tree (F=3.81, p<.0005) influenced the probability of oak shoot emergence. Smaller acorns from three of the four parent trees emerged later than did larger acorns; the opposite relationship between size and emergence date existed for the remaining tree (fig. 3). When sites were evaluated separately, emergence was positively dependent on acorn size

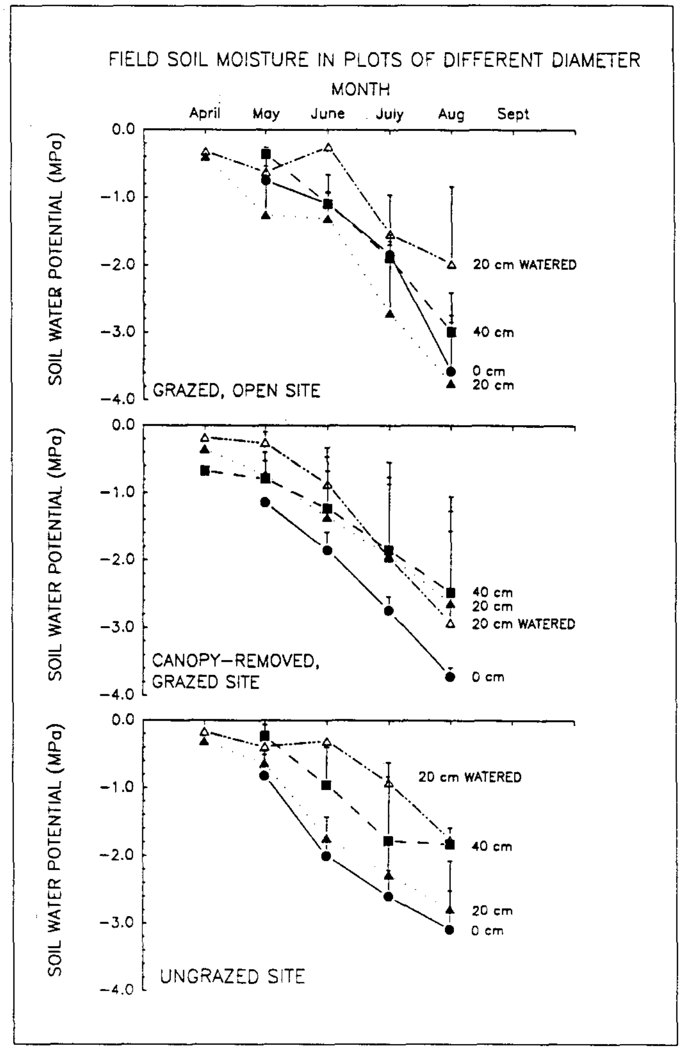

Figure 1—Soil water potential (mean and 1 s.e.) at 40 cm depth in cleared plots by site, plot size, and irrigation treatment.

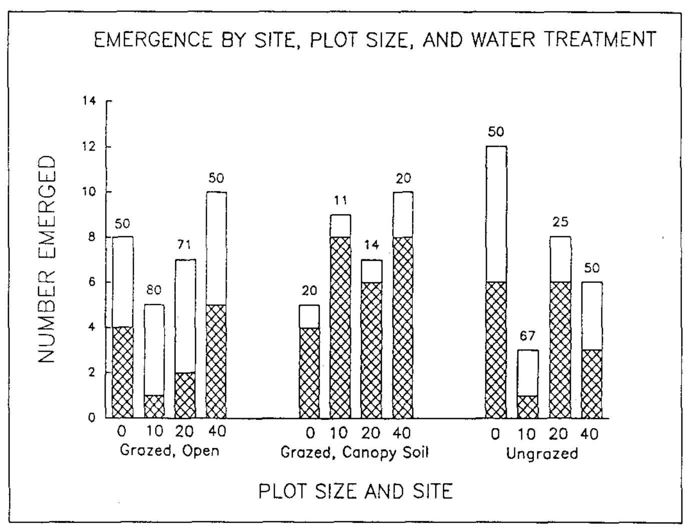

Figure 2—Number of shoots which emerged from acorns planted in plots of different size in each of three sites. Open bars are total number emerged; hatched bars show the number which emerged prior to irrigation. The numbers above the bars are the percent emergence following irrigation.

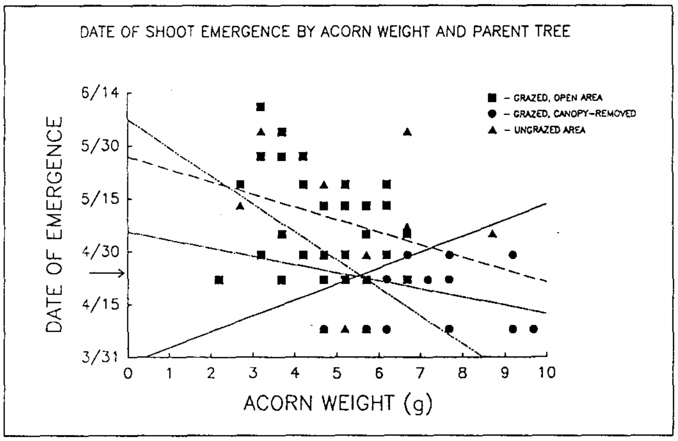

Figure 3—Emergence dates of seedlings from acorns of different weights by parent tree. Planting sites are designated by symbol. The arrow on the y- axis indicates the date on which irrigation started.

only in the ungrazed site: 73 percent of the seedlings emerged from acorns larger than the mean sowing weight. Parent tree identity significantly (X^2=9.49, p<.025) influenced the probability of shoot growth only in the open grazed site. Following emergence, however, neither acorn weight nor parent tree had further effects on height or leaf growth.

All seedling growth and gas exchange responses measured were significantly dependent on soil water potential over time (table 1). Seedlings in irrigated plots were larger than were those in non-irrigated plots. Plot size had significant but inconsistent effects on seedling growth (table 1). Leaf number, for example, was higher (p<.05) in 0 and 20 cm irrigated plots than in 0 or 10 cm non-irrigated plots. Seedlings in irrigated 40 cm plots had more leaves than did those in 0, 10 or 20 cm non- irrigated, or 10 cm irrigated plots. Final height was correlated with the number of leaves (r=.90, p<.0001).

About 60 percent of the 1987 seedlings showed further growth in 1988, with the probability of regrowth being dependent only on emergence in 1987 (F=46.18, p<.0001) across all sites and treatments. An additional 7 percent of the acorns in the grazed open site, and 2 percent in the ungrazed site which had not grown in 1987 showed shoot growth in 1988. These delayed emergences were independent of plot size or watering treatment.

Excavation of those plots from which no shoots emerged in either 1987 or 1988 revealed that acorns in 56 percent of the plots had either been eaten or attacked by fungi and showed no evidence of root growth. Acorns were missing from 27 percent of the plots. Only 8 percent of the plots had acorns present which showed root development prior to death. More acorns were missing from the ungrazed site relative to the 2 grazed sites.

Seedling height and leaf number were significantly correlated in both 1987 and 1988 (r=.90, p<.0001 and r=.96, p<.0001, respectively). Final height in 1988 was correlated with that in 1987 (i-.56, p..0001), although neither the length of the 1987 growing season nor the experimental treatment influenced 1988 growth. Height in 1989 was also correlated with that in 1988 (r=.86, p<.0001). Only those seedlings which emerged in 1987 were included in these analyses.

Table 1—***Summary of ANCOVA results of the dependence of blue oak seedling growth and stomatal conductance on soil water potential over time. Seedlings were grown in cleared plots of various size (plot), in the Sierra Nevada foothills.***

	Stem Height (cm)	Number of Leaves	Leaf Area (cm^2)	Stomatal Conductance (mmol $m^{-2}s^{-1}$)
Overall model F	9.07	14.34	12.21	9.09
p	.0001	.0001	.0001	.0001
Block*	0.58	0.39	0.59	1.35
	.80	.92	.78	.33
Soil Water	62.51	48.55	70.56	4.83
Potential*	.0001	.0001	.0001	.06
Tree*	0.01	0.14	3.62	3.34
	.94	.73	.09	.10
Acorn Weight*	0.46	0.55	0.14	0.53
	.52	.48	.72	.48
Plot(block)	2.73	5.41	3.21	6.37
	.005	.0001	.001	.0001
Date	0.29	1.25	1.54	17.94
	.59	.26	.23	.0001
Water Potential	5.04	6.39	4.90	1.66
x Date	.02	.01	.03	.20

*tested against the Type I error term Plot(block)

Seedlings senesced their leaves earlier in the grazed canopy-removed and the ungrazed sites than in the grazed open site in 1988. Close to 50 percent of the seedlings in the two former sites had no remaining green tissue in early October, 1988, while 75 percent of the seedlings from the grazed open site retained green leaves.

Chi-square analysis revealed that the probability of surviving through 4 growing seasons was independent of height at the end of the first growing season across all sites. However, individuals greater than 8 cm in height by the end of 1987 tended to survive through 1990 at greater than expected frequency than did those below that height (fig. 4). Small sample sizes preclude confident evaluation of these data. Seedlings which were taller than 7.5 cm after their first growing season had a significantly higher probability of surviving through 3 growing seasons in another field experiment (Gordon unpub. data).

DISCUSSION

Results from this experiment support the hypothesis that water availability significantly affects blue oak seedling recruitment in the field. Shoot emergence of the pre-germinated acorns

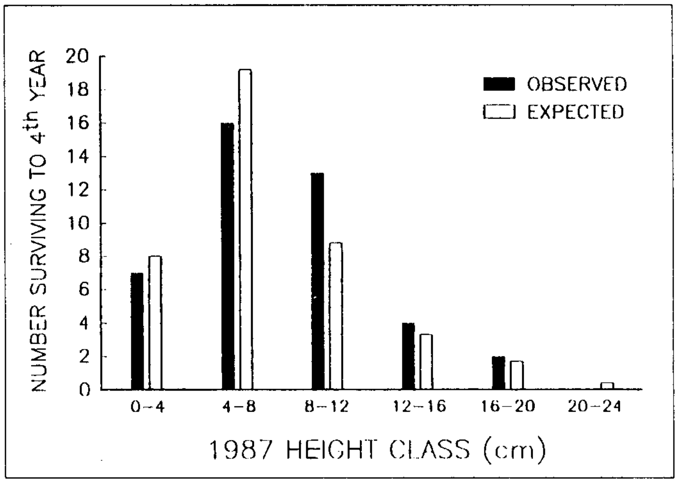

Figure 4—Expected and observed number of seedlings surviving through the 1990 growing season by height class at the end of the first growing season (1987).

was significantly enhanced by late season water availability in grazed areas. The reduced response of seedlings in cleared plots in the ungrazed area may be partially explained by gopher depredation of watered plots in that site.

Plot size effects, though significant, were secondary to those of irrigation. These results are explained by the insignificant effect of plot size, or proximity of competitors for soil water, on the resource. Plot size appeared to have the greatest influence in the ungrazed site, where plant densities were already the lowest (unpub. data) and where soil water tended to be highest. Root encroachment into the plots may have reduced plot size treatment effects.

Following emergence, water potentials continue to determine the extent of growth and stomatal conductance in oak seedlings. These results are consistent with others for both blue oak (Borchert and others 1989, Gordon and others 1989, Gordon and Rice unpublished draft, Welker and Menke 1990) and for valley oak (*Q. lobata*) (Danielsen 1990) in California. Further, influences of soil water potential on growth in the first growing season continue to influence seedling growth in subsequent seasons. Griffin (1971) also reported enhanced blue oak survivorship when competing grasses were experimentally removed.

The results from the blue oak experiments discussed here and elsewhere (Gordon and Rice 1990, Rice and others these proceedings) also suggest that blue oak sensitivity to competition for soil water has a genetic component. Acorns were collected from trees ranging in elevation and aspect at the SFRFS. Both the distribution of acorn weights and the responses of acorns to the environment varied among these parent trees: acorn weight and parent tree interacted with site conditions to influence seedling emergence and growth. Significant variation in acorn size distributions and influence of acorn weight and parent tree on seedling establishment have been documented for *Q. petraea* (Jarvis 1963), *Q. kelloggii* and *Q. agrifolia* (Hunter and van Doren 1982), and *Q. rubra* (Kolb and Steiner 1989). Thus, potential genetic influence on such characters as leaf number holds implications both for survival and growth over several growing seasons, and for regrowth following browsing because axillary buds for lateral branches are formed at the base of the petiole.

These data indicate that the interaction between maternal characters and the water environment surrounding establishing blue oaks may influence the success of establishment. A more gradual decline of soil water when the oak understory was dominated by perennial rather than annual grasses (White 1967, Welker and Menke 1990) would allow higher oak growth rates for longer into the summer drought. The larger seedlings developed would be better able both to exploit soil resources not available to the herbaceous understory and to survive into subsequent growing seasons. This scenario may partially explain why reduced recruitment in oak populations coincides with the conversion of the oak woodland understory to annual grassland.

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