Factors Limiting the Establishment of a Chaparral Oak, *Quercus durata* Jeps., in Grassland[1]

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Abstract: We studied factors that restrict colonization of grassland by *Quercus durata* Jeps., an oak commonly found in chaparral on serpentine soils. The study site contained a chaparral/grassland border that had been stable for at least 50 years. Monitoring of acorns planted in the chaparral understory and grassland revealed that, although initial seedling emergence was similar in the different sites, seedling survival was much higher in the chaparral. No seedling in the open grassland survived beyond the third year of the study, while 25 percent in the chaparral understory were still alive at the end of 6 years. The differences in survival could not be explained by differences in animal activity and herbivory. Rather, the high solar radiation load on seedlings in the grassland appeared to play a major role in mortality. Experimental shading of seedlings in the grassland with light shade cloth increased seedling survival.

Little successful oak seedling establishment has been observed in California grasslands and savannas in recent decades (Griffin 1977, White 1966). Over historical time, oak cover has been reduced and oak woodland has been converted to grassland in many areas (Holmes 1990). Because of this, concern has focused on the ability of oaks to establish in grasslands. Studies addressing this problem have identified several bottlenecks to seedling establishment. Acorns suffer high levels of predation by a wide variety of mammals, rodents and birds (Griffin 1980, Borchert and others 1989, McCreary 1989). In addition, germination of acorns may be reduced by heating and drying, conditions often encountered at the soil surface after acorn drop (Griffin 1971, Keeley 1987, McCreary 1989). Despite these pre-germination obstacles, seedlings often emerge (Griffin 1971). Seedlings rarely survive, however, and browsing of seedlings (above- and belowground) has been identified as a major factor preventing oak establishment (Griffin 1976).

In addition to animal damage, physical characteristics of the grassland environment may be hostile to oak seedling survival. In the mediterranean-type climate of California, high radiation loads, high soil surface temperatures and drought coincide in grasslands during the summer. While the grassland annuals escape these conditions by dying, the oak seedlings must survive them. There are some indications that mesic sites, such as those provided by tree cover and north-facing aspects, are more conducive to oak seedling survival in some areas of California (Griffin 1971, Muick and Bartolome 1987). This study was implemented to determine whether simple shading could increase oak seedling survival in a grassland setting.

We studied the survival of seedlings of *Quercus durata* Jeps. at Stanford University's Jasper Ridge Biological Preserve, San Mateo County, California. *Quercus durata is* a shrubby oak, commonly occurring in stands of chaparral on serpentine soil. Our site had serpentine soil with a stand of chaparral adjacent to an area of grassland. Aerial photographs revealed that the chaparral/grassland boundary had not moved in at least 50 years (Davis and Mooney 1985). Cattle grazing, which may have prevented invasion of the grassland by oak, was removed from the site in 1960. Acorns reach the grassland and germinate, as evidenced by small scattered *Quercus durata* seedlings found several meters from the edge of the chaparral during the course of this study. The stability of the chaparral/grassland boundary suggests, however, that survival of these seedlings is nil. We planted acorns across this boundary and compared the survival of seedlings in the chaparral understory, in the bare zone adjacent to the chaparral, in the grassland, and in the grassland with artificial shading.

METHODS

Acorns were collected from *Quercus durata* shrubs at our site in October of 1984, during the time of natural seed dispersal, and planted in plots along four transects: one through the chaparral understory, one along the bare zone and two parallel to the bare zone in the grassland. Acorns were planted approximately 2-3 cm deep and at least 25 cm apart (234-240 acorns per transect). During the summer months, 40-percent shade cloth was erected over half of each grassland transect.

Planting locations (located with a grid) were examined every 2-4 weeks. Initial emergence of a shoot from the soil surface was noted and the presence or absence of a live shoot was subsequently monitored. Condition of the shoot (browning leaves, herbivory) was also noted. A live shoot was defined as one having some green leaf area. After the first summer, it became obvious that oak seedlings did not resprout during the summer drought. Therefore, only plants with previously live shoots were monitored during the summer. Seedlings were monitored for six years (1985-1990). Because the seedlings often resprouted following shoot loss, a seedling was only

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

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considered dead if it did not resprout the following year. Differences among treatments and sites in the fraction of acorns producing aboveground shoots (percent emergence) and in the fraction of seedlings surviving six years were compared using G-tests.

Because of the patchiness of shade within the chaparral understory, planting locations were scored for degree of shadiness. At four times during one sunny day in July of 1986, planting locations were visually scored to estimate their daily interception of direct sunlight. A score of 1 to 4 was assigned depending on whether direct sunlight impinged on >95, 50-95, 5-50, or <5 percent of the soil surface. Summation of these scores over the day yielded an arbitrary ranking of shadiness for the locations in which acorns were planted. The association of plant survival with shade was examined by using a Mann-Whitney two sample test to compare the shade score distribu-tions of sites in which seedlings emerged and sites in which they survived.

To compare the degree of shading imposed by the shade cloth with that produced by other, natural sources of shade, daily courses of photosynthetically active radiation (PAR) were measured (1) in full sun, (2) under shade cloth, (3) under the edge of the chaparral canopy, and (4) under small, isolated shrubs in the grassland at Jasper Ridge. Measurements were collected on a clear midsummer day (4 July 1990) using gallium-arsenide sensors (PH 201 A, NEC, Tokyo, Japan) monitored by Campbell 21x data loggers (Campbell Scientific, Logan, UT).

RESULTS

Plant emergence (the percent of acorns producing aboveground shoots) ranged from 65 percent in the unshaded grassland to 76 percent in the bare zone. While emergence was statistically higher in the shaded grassland and bare zone than in the unshaded grassland, high numbers of seedlings emerged in all sites.

Site	Percent emergence[1]
Grassland	65[a]
Shaded grassland	73 [b]
Bare zone	76[b]
Chaparral	69 [ab]

[1] Values superscripted by the same letter are not significantly different, G-test, $p<0.05$.

Experimental shading increased the survival of oak seedlings in the grassland (fig. 1). In the natural, unshaded grassland, no seedling survived past the third year. Six percent of the seedlings in both the bare zone and shaded grassland were alive at the end of six years. Seedlings in the chaparral understory had the highest survival at the end of six years (25 percent). Survival in the chaparral understory was significantly higher than that in any other treatment (G-test, $p<0.01$). Survival in shaded grassland was significantly higher than that in natural, unshaded grassland (G-test, $p<0.01$).

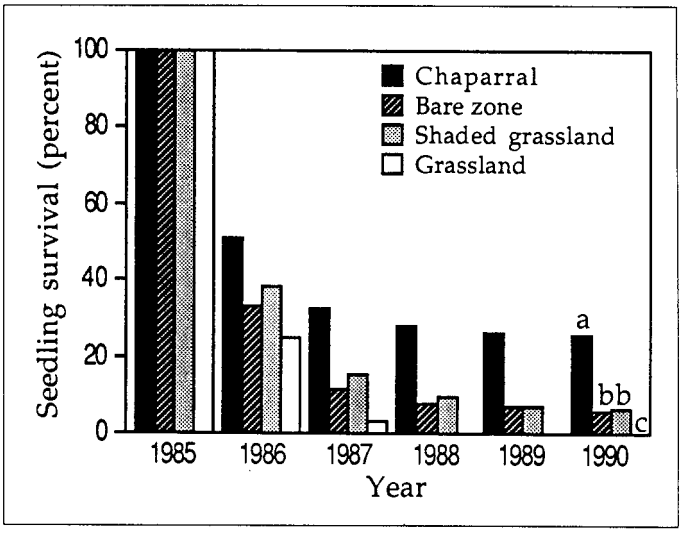

Figure 1—Seedlings alive each year in different treatments and sites. Numbers are percentages of those seedlings alive the first year: 133 in the open grassland, 158 in the shaded grassland, 161 in the bare zone and 143 in the chaparral understory. (Because some seedlings were destructively harvested the first year, these numbers are lower than the number of seedlings that emerged.) Letters indicate statistical differences among treatments and sites for final (1990) survival. Values superscripted by the same letter are not significantly different, G-test, $p<0.05$.

The shade provided by the shade cloth in the grassland was much less than that cast by either the chaparral canopy or small isolated shrubs in the grassland. The shade cloth transmitted approximately 55 percent of the photosynthetically active radiation (fig. 2). The scatter in the data was due to the small sensors detecting shadows cast by the weave of the shade cloth. Light levels under a small, 40 cm tall poison oak in the grassland (fig. 2) were only 5-6 percent of full sunlight during much of the day. The light regime in the chaparral understory was extremely

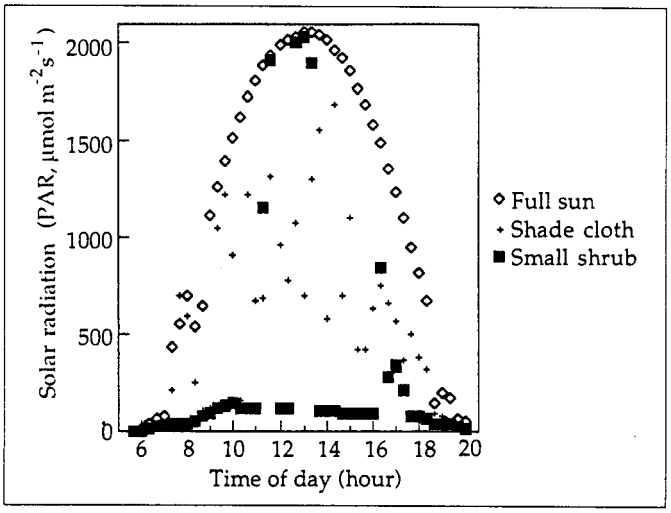

Figure 2—Photosynthetically active radiation (µmol $m^{-2}s^{-1}$) in full sun, under the shade cloth and under a small shrub in the grassland.

variable. Light levels in full shade (no direct sunlight) were also approximately 6 percent of full sun (data not shown).

Within the chaparral understory, seedling survival was higher in the shadier microsites (fig. 3). Comparing the distribution of shade among sites in which seedlings emerged and sites in which they survived revealed that survival was higher in the shadier sites (Mann-Whitney two sample test, $p<0.01$).

The higher seedling survival in the chaparral did not appear to be related to a lower incidence of animal damage. On the contrary, levels of animal damage appeared higher in the chaparral than in other sites and treatments. A greater proportion of the plants that died in the chaparral died with evidence of severe animal damage (severe browsing or evidence of gopher damage), compared to plants that died in any other site (G-test, $p<0.01$) (fig. 4). Root damage to seedlings was difficult to assess, but gopher disturbance was observed in all sites (grassland, bare zone and chaparral understory).

DISCUSSION

Artificial shading of seedlings in the grassland increased survival, but final survival (at the end of six years) was still low. It is uncertain how many of these seedlings will ultimately survive to adulthood. At the end of six years, the tallest seedling in any site was only 15 cm tall. The fact that seedling mortality was very low for the past three years, however, suggests that the remaining seedlings may be well established and have a high probability of continued survival.

The association of high seedling survival with shady microsites within the chaparral understory is consistent with the hypothesis that shade increases seedling survivorship, but is not conclusive. The canopies of the adult shrubs may coincide with some feature of the underlying rock and soil that actually controls shrub distribution. However, such possible associations were not factors in the grassland shading experiment, and shading increased seedling survivorship in both grassland transects.

The mechanism by which shading increased seedling survival is not clear. Shading may reduce leaf temperatures of the seedlings or improve their water status by reducing the transpiration rate of both the oak seedlings and the competing grassland annuals. Additionally, some interaction of high light, high temperature and water stress, all of which may be reduced by shading, may have a negative impact on seedling metabolism. Some evidence exists that water stress in some California grasslands contributes to poor performance of oak seedlings. Gordon and others (1989) showed that competition from grassland annuals for soil moisture reduced emergence and growth rates of blue oak seedlings (*Quercus douglasii* Hook. & Arn.). Griffin (1971, 1980) found that clearing competing grassland vegetation decreased rates of mortality in seedlings of several oak species, but a study on *Quercus lobata* Née (Griffin 1976) showed little effect of grass interference on seedling survival. Snow (1973) observed that, while seedlings of *Quercus agrifolia* Née experienced lower water potentials when competing with herbaceous vegetation, visible injury (browning of leaves) was associated with whether or not the seedling was shaded rather than its degree of water stress. Thus, while alleviation of water stress may improve oak seedling performance, other factors associated with shading may interact with seedling water status to affect survival.

The difference in seedling survival between the bare zone and the grassland in this study may have resulted partly from improved soil water status in the bare zone and partly from shading by the adjacent chaparral. The soil moisture regimes in the grassland, bare zone and chaparral at our study site are quite different. Davis and Mooney (1985) showed that, below approximately 60 cm, soil was driest in the chaparral during the summer. At shallower depths soil dried most rapidly in the grassland, presumably due to water depletion by the grassland

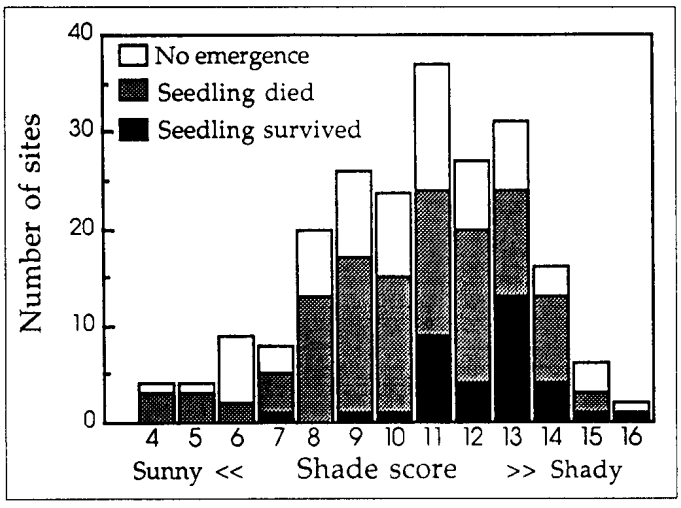

Figure 3—Distribution of shade among planting sites in the chaparral understory. Graph indicates sites in which seedling emergence occurred and sites in which seedlings survived six years.

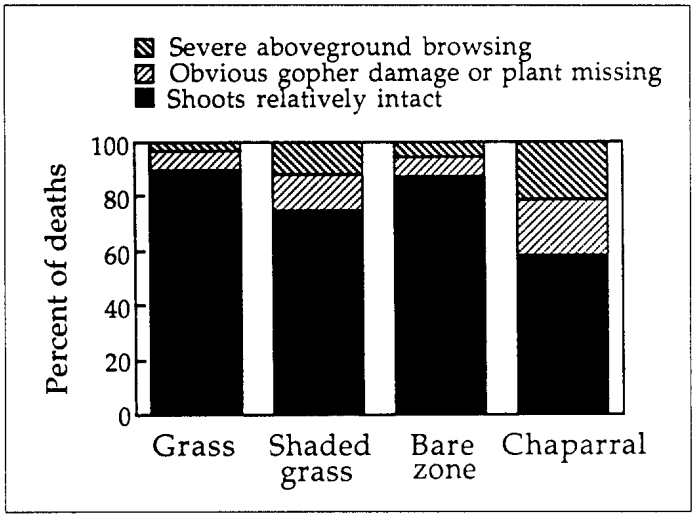

Figure 4—Final symptoms or fates of plants that died in the different sites and treatments.

annuals. Soil water potential in the bare zone was higher than that in the grassland during a large part of the summer drought. The higher soil water potentials in the bare zone, as well as partial afternoon shading of some seedlings by adjacent chaparral, may have increased seedling survival in the bare zone over that in the grassland.

Our main conclusion is that high summer radiation loads in the grassland contribute to the lack of oak seedling survival there. The shade provided by the mature chaparral canopy increases seedling survival in the chaparral. Other factors may vary between the chaparral and grassland, contributing to the difference in seedling survival between habitats. These factors, however, are not obvious. The soil in the grassland was similar to that in the chaparral (Davis and Mooney 1985) and evidence of animal damage to seedlings (this study) actually indicated a higher incidence of animal damage in the chaparral. Despite the possible existence of other factors restricting the establishment of oak seedlings in the grassland, artificial shading in the grassland did increase seedling survival. Furthermore, the artificial shading imposed was unnaturally light. The numbers of seedlings surviving under the shade cloth may have increased with a heavier shade treatment that more realistically imitated the shade cast by the chaparral canopy or by isolated shrubs in the grassland.

The results of this study are consistent with the observations of other investigators, noting increased seedling survival in shade for various California oak species (Griffin 1980, Griggs 1987, Muick and Bartolome 1987, Snow 1973). Increased survival of oak seedlings has been associated with shade, not only in California, but also in the central Rocky Mountain region, where seedlings of *Quercus gambelii* Nutt. were shown to survive much better under canopy protection (Neilson and Wullstein 1983). Observations such as this, combined with the results of this study, suggest that, in and open habitats, shading can improve oak seedling survival. Although artificial shading may be unrealistic as a large-scale management practice, the use of nurse plants to provide shade in grassland settings for fostering oak seedling establishment may prove profitable.

ACKNOWLEDGMENTS

We thank H.A. Mooney, Stanford University, for encouragement and support, and the Jasper Ridge administration for their cooperation. This work was supported in part with funds from the Mellon Foundation, the McKnight Foundation, and a post-doctoral fellowship from the Swedish Natural Sciences Research Council to PSK.

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