Morphological and Physiological Responses of Three California Oak Species to Shade

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MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSES OF THREE CALIFORNIA OAK SPECIES TO SHADE

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Interspecific differences in morphological and physiological responses to shade commonly correspond to ecological roles in mesic woodlands but rarely have been studied in semiarid woodlands and savannas. I compared shoot mass, root mass, root:shoot ratio, taproot elongation rate, whole-seedling leaf area, whole-seedling specific leaf area, leaf area ratio, and photosynthetic capacity among three species of California oaks in three experimental shade treatments: full sunlight (I_{full}), 50% of full sunlight ($I_{50\%}$), and 10% of full sunlight ($I_{10\%}$). Although there were no intraspecific differences in the percentage of seedling biomass allocated to leaves, stems, and roots in different shade treatments, interspecific differences in biomass allocation, shade-induced changes in leaf morphology, whole-seedling photosynthetic capacities, and taproot elongation rates may explain, in part, shade tolerance of *Quercus agrifolia* and shade intolerance of *Q. lobata* seedlings reported in the literature. However, morphological and physiological responses of *Q. douglasii*, which recruits in shade, were similar to those of *Q. lobata* and do not adequately explain the high recruitment of *Q. douglasii* seedlings in shade reported in the literature. At $I_{10\%}$, root weights of *Q. lobata* and *Q. douglasii* seedlings decreased by 46% and 60%, respectively, and showed similar decreases in total seedling biomass and root:shoot ratios. Shade did not affect whole-seedling biomass, root weight, or root:shoot ratio of *Q. agrifolia* seedlings. Total seedling leaf area of *Q. lobata* and *Q. douglasii* did not increase in shade, whereas at $I_{10\%}$ *Q. agrifolia* seedlings doubled in leaf area. Specific leaf area and leaf area ratio of *Q. agrifolia* seedlings also increased substantially more than the other two species. For seedlings grown at $I_{10\%}$, photosynthetic capacity per leaf area did not differ among species, but whole-seedling photosynthetic capacity at 150 μE m^{-2} s^{-1} was 111.3 μmol g^{-1} s^{-1} of oxygen evolved for *Q. agrifolia* grown at $I_{10\%}$ compared with 34.7 and 51.3 μmol g^{-1} s^{-1} for *Q. lobata* and *Q. douglasii*, respectively. At $I_{10\%}$, the taproot elongation rate of *Q. agrifolia* was 63% of the rate at I_{full}, while *Q. douglasii* and *Q. lobata* elongation rates dropped to 54% and 26% of rates at I_{full}, respectively. This variation in shade acclimation may partially explain interspecific differences in ecological functions, including interactions with other species, patterns of recruitment, and successional roles.

Introduction

Shade tolerance or intolerance generally is attributed to plant species on the basis of leaf-level responses to low irradiance; however, leaf-level responses to shade do not always correlate with whole-plant carbon uptake and growth in shade (Küppers et al. 1988). Actual shade tolerance is demonstrated by the survival and maturation of plants in shady habitats and appears to be the product of complex combinations of whole-seedling responses, including biomass allocation, morphological changes, leaf orientation, and leaf-level photosynthetic changes (Givnish 1988). Complex effects of shade on seedlings of many tree species is well documented in mesic temperate forests, where interspecific variation in morphological and physiological responses to shade is associated with patterns of regeneration, spatial distribution within communities, and successional roles in forests in eastern North America (Kramer and Decker 1944; Kozlowski 1949; Ferrell 1953; Loach 1967, 1970; Christensen and Peet 1981; Hicks and Chabot 1985; Kolb et al. 1990; Lei and Lechowicz 1990), Britain (Watt 1919; Ovington and MacRae 1960; Jarvis 1964),

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Mexico (Gonzalez-Espinosa et al. 1991), and Asia (Endo and Oikawa 1985; Rao 1988). However, there have been few comparative studies of shade responses of trees with different ecological roles in semiarid woodlands and savannas in western North America.

Recruitment patterns, interspecific associations, and field experiments indicate that three widely distributed California oak species, *Quercus douglasii* H. & A. (blue oak), *Q. lobata* Nee (valley oak), and *Q. agrifolia* Nee (coast live oak), vary in shade tolerance. *Quercus douglasii* and *Q. lobata* are winter-deciduous trees and are in leaf between late March and November. Acorns of these species germinate in the fall and seedlings usually retain leaves for at least the first year. Both species are endemic to California and are widespread on the interior slopes of the Coast Ranges and the foothills of the Sierra Nevada (Griffin and Critchfield 1972), but many extant populations do not appear to be regenerating at rates capable of maintaining current distributions and densities (White 1966; Griffin 1971, 1976; Muick and Bartolome 1987; Bolsinger 1988). *Quercus douglasii* appears to be relatively shade tolerant as shrubs act as nurse plants for seedlings that recruit heavily in shaded habitats and survive longer in shaded habitats and in shaded field manipulations than in the open (Muick and Bartolome 1987; Muick 1991; Callaway, in press). *Quercus lobata* seedlings, however, appear to be

relatively shade intolerant, as seedlings do not survive in shade under shrubs or in shaded field manipulations (Callaway, in press). These differences appear to result in part from the ability of Q. douglasii seedlings to maintain higher rates of taproot elongation and leaf-level photosynthetic capacities in shade than Q. lobata (Callaway, in press). Quercus agrifolia, an evergreen oak tree common on the western side of the Coast Ranges, overlaps substantially in distribution with Q. douglasii and Q. lobata. Quercus agrifolia appears to be shade tolerant, as recruitment is higher in shrublands and shaded habitats than in open habitats (Muick and Bartolome 1987; Callaway and Davis, unpublished data) and seedling survival is enhanced by artificial shade (Muick 1991). Seedlings of this species are also often spatially associated with shrubs, and survival of seedlings in field experiments is enhanced by the shelter of shrub canopies (Callaway and D'Antonio 1991).

To investigate mechanisms that may determine these apparent interspecific differences in shade tolerance, I have compared whole-seedling response to artificial shade among Q. lobata, Q. douglasii, and Q. agrifolia seedlings and related these differences to patterns of regeneration, distribution, and succession in semiarid woodlands and shrublands of California.

Material and methods

I compared shoot and root biomass, leaf areas, taproot elongation rates, and photosynthetic rates of Quercus lobata, Q. douglasii, and Q. agrifolia seedlings grown outdoors in the spring, in Santa Barbara, California, in three irradiance treatments: full sunlight (I_{full}) and approximately 50% ($I_{50\%}$) and 10% of full sunlight ($I_{10\%}$). Irradiance was controlled with green shadecloth. Based on measurements taken between 12:00 and 1:00 PM, on one cloudless day in each month of the experiment, the average maximum irradiance for each treatment was 1,890, 1,050, and 240 μE m^{-2} s^{-1}, respectively.

Seedlings used in these treatments were grown in specially designed root observation tubes that were constructed by attaching halves (cut lengthwise) of PVC pipe to glass sheets with silicone. Each individual chamber was 3.5 cm in radius and 120 cm deep and was filled with 60 grit sand. These tubes were kept on an outdoor rack, and all parts of the tubes that contained soil were shaded with canvas sheets to prevent soil in the unshaded treatment from disproportionate heating.

One hundred acorns were collected in the Santa Ynez Valley in Santa Barbara County, California (34°30'N, 119°45'W) from each of 10 parent trees for each species between November 1 and November 7, 1988. For each species, test acorns were chosen randomly from all 1,000 acorns within the following mass categories: Q. agrifolia, 3.0–3.5 g; Q. douglasii, 3.5–4.0 g; and Q. lobata, 5.0–5.5 g. These masses were chosen because they represented the approximate intraspecific means of the acorns that were collected, and to reduce intraspecific variation from acorn size. One pregerminated acorn was planted in each chamber, and chambers were tilted so roots would grow along the glass. For each light level, I planted 10 pregerminated acorns of each species, but because of mortality during the experiment the final number of seedlings for each species-treatment combination was 8–10. Taproot elongation was measured by marking the location of the taproot tip on the glass every 7 d for 140 d, at which time taproots began to reach the bottom of the tubes. Shade treatment and species effects were tested with two-way repeated measures ANOVA. Between measurements the glass surface was covered with black plastic, and seedlings were watered every 10 d with 1/20 strength Hoagland's solution.

After 20 wk, one mature leaf was chosen randomly from each of five individuals of each species in each treatment for photosynthetic measurements. Five to 10 leaves per day were removed from the stems over a 7-d period and net rates of photosynthetic O_2 exchange were measured at 25 C and 5% hydrated CO_2 with a leaf-disk oxygen electrode system (model LD-2, Hansatech, Kings Lynn, Norfolk, U.K.; Björkman and Demmig 1987). Irradiances used for the photosynthetic capacity measurements were as follows: for seedlings grown at I_{full}, 2,000 μE m^{-2} s^{-1}; for seedlings grown at $I_{50\%}$, 850 μE m^{-2} s^{-1}; and for seedlings grown at $I_{10\%}$, 150 μE m^{-2} s^{-1}. Measurement of oxygen evolution in CO_2-saturated conditions permits comparisons of photosynthetic potential of leaves, but it does not permit comparisons of diffusion limited rates of gas exchange, such as stomatal control.

Photosynthetic capacity per seedling mass (PS_{mass}) was calculated by multiplying the average photosynthetic capacity of the five sample leaves (for each species-treatment combination) at irradiances close to that in which they had been grown, by total leaf area to obtain total seedling photosynthetic capacity, and dividing the product by the total seedling mass. These measurements thus represent photosynthetic capacities of seedlings at respective growth irradiances, not maximum photosynthetic capacity.

Seedlings were harvested after 140 d in the tubes and separated into leaves, stems, and roots. Leaf areas of each entire seedling were measured with a Decagon Model Digital Analysis System (Decagon Devices, U.S.A.) using photocopied reproductions of the leaves. All plant material was dried at 60 C to constant mass. Seedling mass and leaf area were used to calculate total seedling

Table 1

PHOTOSYNTHETIC CAPACITIES AS A FUNCTION OF LEAF AREA AND TOTAL
SEEDLING MASS FOR QUERCUS LOBATA, Q. DOUGLASII, AND Q.
AGRIFOLIA SEEDLINGS GROWN IN THREE SHADE TREATMENTS

Photosynthetic capacity and growth irradiance	Q. lobata	Q. douglasii	Q. agrifolia
Per leaf area (μmol m^{-2} s^{-1}):			
I_{full}	17.30 ± 2.32[a]	14.90 ± 2.72[ab]	12.44 ± 2.74[b]
$I_{50\%}$	7.62 ± 1.74[b]	11.75 ± 2.30[a]	7.30 ± 1.50[b]
$I_{10\%}$	1.49 ± .57[a]	2.06 ± .67[a]	2.38 ± .44[a]
Per seedling mass (μmol g^{-1} s^{-1}):			
I_{full}	228.7 ± 14.1[a]	237.9 ± 26.1[a]	310.0 ± 37.7[b]
$I_{50\%}$	168.1 ± 17.7[a]	251.1 ± 21.2[b]	265.5 ± 17.7[b]
$I_{10\%}$	34.7 ± 4.1[a]	51.3 ± 6.6[b]	113.5 ± 10.9[c]

Note. Photosynthetic capacities were measured at 150 μE m^{-2} s^{-1} for seedlings grown at $I_{10\%}$, 850 μE m^{-2} s^{-1} for seedlings grown at $I_{50\%}$, and 2,000 μE m^{-2} s^{-1} for seedlings grown at I_{full}; thus, statistical comparisons were made only within an irradiance treatment. Data are means ± 2 SE, and shared letters within an irradiance treatment designate no significant difference as determined by post-ANOVA Tukey HSD tests ($P < .05$).

leaf area, total specific leaf area (total leaf area per seedling/total leaf mass per seedling), and leaf area ratio (LAR = total seedling leaf area/total seedling mass). Differences among species and treatments were tested with two-way ANOVA and post-ANOVA Tukey HSD tests.

Results

Seedling biomass allocation, leaf morphology, and photosynthetic capacities differed among species at I_{full}. Even though initial acorn weights were less, *Quercus agrifolia* shoot mass was approximately 1.6 times greater than that of *Q. douglasii* or *Q. lobata* (fig. 1), and *Q. agrifolia* seedlings allocated proportionally more biomass to leaves than the other two species (ANOVA, $F_{species} = 11.97$, df = 2, 23, $P < .001$; fig. 2). However, root mass of *Q. lobata* at I_{full} was 1.4 and 2.9 times higher than *Q. douglasii* and *Q. agrifolia*, respectively (fig. 3), resulting in much higher root : shoot ratios of *Q. lobata* seedlings compared with the other species. At I_{full} the percentage of *Q. agrifolia* seedling biomass allocated to roots was 50% and 60% lower than for *Q. douglasii* and *Q. lobata*, respectively (fig. 2). When grown in full sunlight, leaf area did not differ significantly among species (fig. 4). *Quercus lobata* and *Q. douglasii* seedlings grown at I_{full} had higher specific leaf areas but lower LAR than *Q. agrifolia* (figs. 5, 6), primarily because of the large differences in root weights among these species. Light-saturated photosynthetic capacity, on a leaf area basis, of *Q. agrifolia* was 12.44 ± 2.74 (2 SE) μmol m^{-2} s^{-1} compared with 17.30 ± 2.32 and 14.90 ± 2.72 μmol m^{-2} s^{-1} for *Q. lobata* and *Q.*

douglasii seedlings grown at I_{full}, respectively, but only the rates of *Q. agrifolia* and *Q. lobata* were significantly different (table 1). PS$_{mass}$, however, was approximately 1.3 times higher for *Q. agrifolia* than for the other two species (table 1). In contrast to substantial interspecific differences in seedling morphology and physiology, seedling taproot elongation rates at I_{full} were very similar among all three species (table 2).

Allocation of biomass to leaves, stems, and roots did not vary within species in the different shade treatments (fig. 2), but I found highly significant interspecific shade effects for every variable measured except leaf-level photosynthetic

Table 2

ROOT ELONGATION RATES OF QUERCUS LOBATA, Q. DOUGLASII, AND Q. AGRIFOLIA SEEDLINGS GROWN IN FULL SUNLIGHT AND 50% AND 10% OF FULL SUNLIGHT

Growth irradiance	Root elongation (mm/d)		
	Q. lobata	Q. douglasii	Q. agrifolia
I_{full}	8.38 ± .66[a]	8.81 ± .64[a]	9.00 ± .28[a]
$I_{50\%}$	5.09 ± .45[b]	6.60 ± .97[c]	7.35 ± 1.00[c]
$I_{10\%}$	2.23 ± .66[d]	4.75 ± .80[b]	5.68 ± .67[bc]

Note. Elongation rates presented were for the last 42 d of the experiment, when acorn reserves were assumed to contribute less to seedling growth than leaf photosynthate. Data are means ± 2 SE, and shared letters within and among irradiance treatments designate no significant difference as determined by post-ANOVA Tukey HSD tests ($P < .01$). Two-way ANOVA, irradiance × species, $F_{treatment} = 107.0$, df = 2, $P < .001$; $F_{species} = 24.0$, df = 2, $P < .001$; $F_{treatment \times species} = 3.7$, df = 4, $P = .008$.

Fig. 1 Shoot mass of *Quercus lobata*, *Q. douglasii*, and *Q. agrifolia* seedlings grown in full sunlight and 50% and 10% of full sunlight. Error bars represent 2 SE. Shared letters designate no significant difference within and among species as determined by two-way ANOVA and post-ANOVA Tukey HSD tests; $P < .01$.
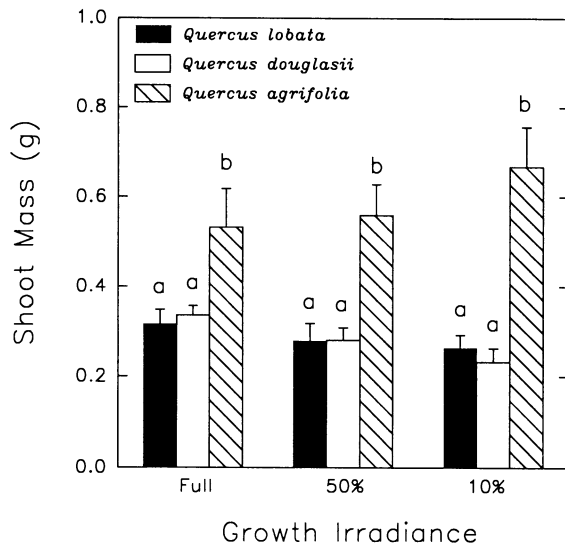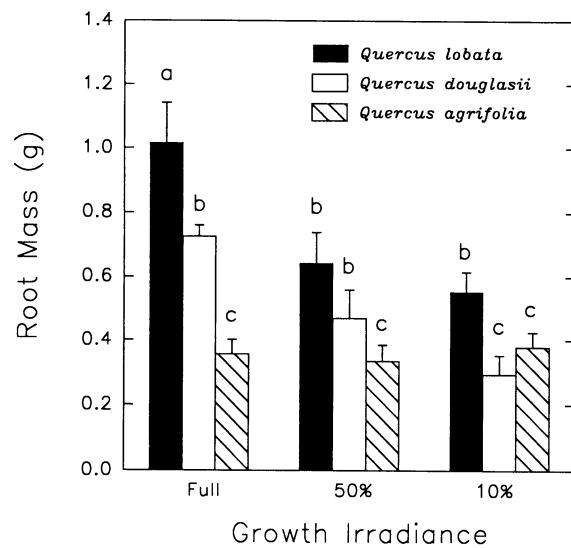

Fig. 3 Root mass of *Quercus lobata*, *Q. douglasii*, and *Q. agrifolia* seedlings grown in full sunlight and 50% and 10% of full sunlight. Error bars represent 2 SE. Shared letters designate no significant difference within and among species as determined by two-way ANOVA and post-ANOVA Tukey HSD tests; $P < .01$.

capacity and shoot mass. At $I_{10\%}$, root mass of *Q. lobata* and *Q. douglasii* decreased by 46% and 60% of I_{full}, respectively, but root mass of *Q. agrifolia* did not change (fig. 3). Interspecific changes in root : shoot ratios were similar to those found for root mass. Total leaf area of *Q. lobata* and *Q. douglasii* seedlings did not increase in the shade treatments. In comparison, total leaf area of *Q.*
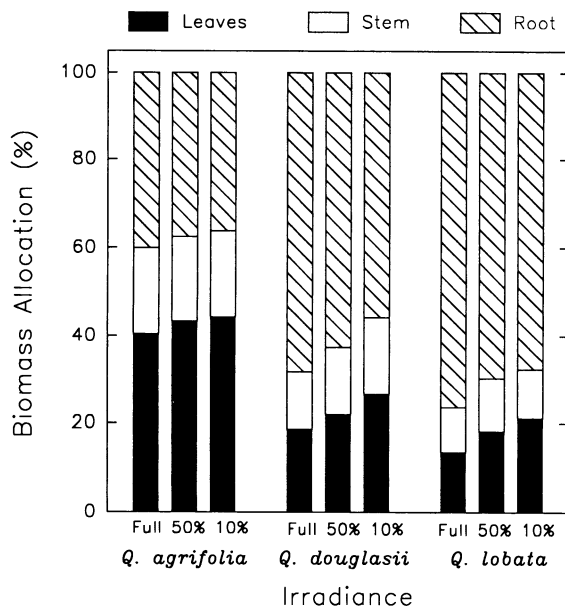

Fig. 2 Percent biomass allocated to leaves, stems, and roots by *Quercus lobata*, *Q. douglasii*, and *Q. agrifolia* seedlings grown in full sunlight and 50% and 10% of full sunlight. Intraspecific biomass allocation did not differ among shade treatments (two-way ANOVA, $P_{shade\ treatment}$ for leaves, stems, and roots > .05).

agrifolia seedlings increased 200% at $I_{10\%}$ (fig. 4). Leaf area increase of *Q. agrifolia* seedlings in shade resulted from expansion of individual leaves rather than an increase in leaf number. Areas of individual leaves of *Q. agrifolia* seedlings increased from an average of 2.27 ± 0.21 (1 SE) cm^2 at I_{full} to 6.99 ± 0.47 cm^2 at $I_{10\%}$ (ANOVA, $F_{shade\ treatment} = 30.6$, df = 1, 16, $P < .001$). Specific leaf area of *Q. lobata* and *Q. douglasii* did not increase significantly in shade; however, it increased by over 40% for *Q. agrifolia* seedlings (fig. 5). LAR of all species increased in shade, but proportionally more for *Q. agrifolia* seedlings (fig. 6).

At $I_{10\%}$, PS_{mass} was 113.5 μmol g^{-1} s^{-1} for *Q. agrifolia* compared with 34.7 and 51.3 μmol g^{-1} s^{-1} for *Q. lobata* and *Q. douglasii*, respectively (table 1). At $I_{50\%}$, PS_{mass} of *Q. lobata* was 35% lower than that of the other two species, which did not differ significantly from each other. High photosynthetic capacities of *Q. agrifolia* seedlings at $I_{10\%}$ were primarily the result of greater leaf areas per seedling (fig. 4), as photosynthetic capacities per leaf area at $I_{10\%}$ did not differ significantly (table 1). At $I_{50\%}$, however, PS_{leaf} of *Q. agrifolia* and *Q. lobata* were significantly lower than that of *Q. douglasii*. During the last 42 d of the experiment, taproot elongation rates of *Q. lobata* seedlings at $I_{50\%}$ were 61% of the rates at I_{full}, and at $I_{10\%}$ decreased to 26 % of the full sunlight rates (table 2). During the last week of the experiment *Q. lobata* taproot elongation rates at $I_{10\%}$ were 4% of rates at I_{full}. At $I_{10\%}$, *Q. agrifolia* and *Q. douglasii* maintained taproot elongation rates of 63% and 54% of I_{full} rates, respectively.
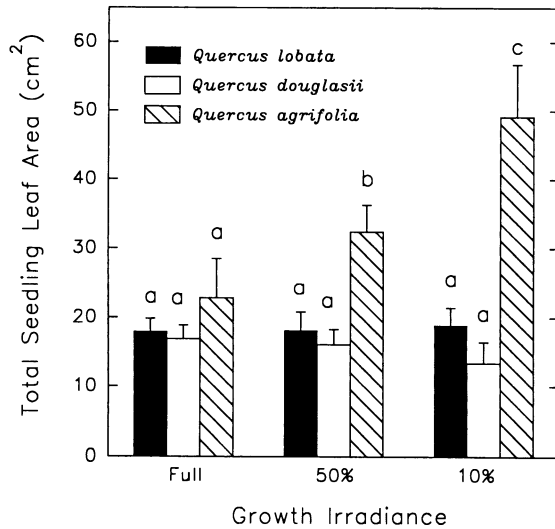
Fig. 4 Total leaf area of *Quercus lobata, Q. douglasii,* and *Q. agrifolia* seedlings grown in full sunlight and 50% and 10% of full sunlight. Error bars represent 2 SE. Shared letters designate no significant difference within and among species as determined by two-way ANOVA and post-ANOVA Tukey HSD tests; $P < .01$.

Fig. 5 Specific leaf area of *Quercus lobata, Q. douglasii,* and *Q. agrifolia* seedlings grown in full sunlight and 50% and 10% of full sunlight. Error bars represent 2 SE. Shared letters designate no significant difference within and among species as determined by two-way ANOVA and post-ANOVA Tukey HSD tests; $P < .01$.

Discussion

Differences in initial acorn mass obscured interspecific differences in total seedling biomass within irradiance treatments; however, interspecific differences in biomass allocation that occurred under full sunlight may have important ecological implications. Root : shoot ratios of shade-tolerant or drought-intolerant species are generally lower than those of shade-intolerant or drought-tolerant species. *Quercus agrifolia,* which had much lower root mass and root : shoot ratio than *Q. lobata* and *Q. douglasii,* and allocated more biomass to leaves, commonly recruits in shaded habitats and appears to occur in relatively mesic habitats and where water tables are shallow (Cannon 1914; Griffin 1973). *Quercus lobata* and *Q. douglasii,* which allocated larger amounts of biomass to roots in full sunlight than *Q. agrifolia,* appear to be able to tap deep water tables and are common on comparatively xeric alluvial plains or slopes (Lewis and Burghy 1964; Griffin 1971; Matsuda and McBride 1986; Callaway et al. 1991). High root biomass and root : shoot ratios that were observed for *Q. lobata* and *Q. douglasii* seedlings are commonly associated with plants adapted to drought stress and have been reported for other oaks (Loach 1970; Rao 1988; Kolb et al. 1990). I found that interspecific differences in the proportion of roots and shoots of seedlings grown in full sunlight correspond well with those that have been reported for the same species in other experiments (Matsuda and McBride 1986; Callaway 1990), even though different soil media were used. This indicates that species-specific allocation of biomass may be
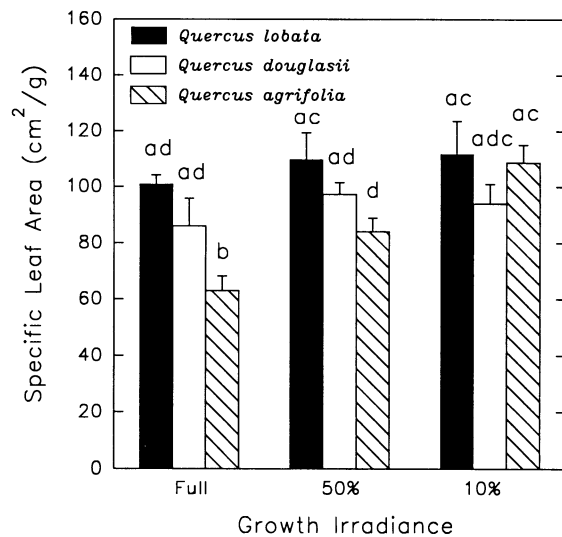
consistent over a range of edaphic conditions, a characteristic shared by *Q. rubra,* a species common in mesic forests (Kolb et al. 1990).

Although the root biomass of *Q. agrifolia* was less than that of the other species in full sunlight, root elongation rates were the same, indicating that in some soils roots of *Q. agrifolia* seedlings may penetrate to depths comparable to those reached by *Q. lobata* and *Q. douglasii* seedlings
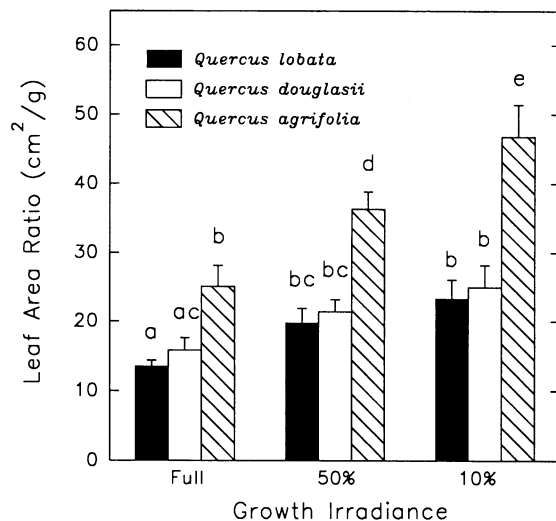

Fig. 6 Leaf area ratio of *Quercus lobata, Q. douglasii,* and *Q. agrifolia* seedlings grown in full sunlight and 50% and 10% of full sunlight. Error bars represent 2 SE. Shared letters designate no significant difference within and among species as determined by two-way ANOVA and post-ANOVA Tukey HSD tests; $P < .01$.

but with less biomass allocated to the root system. This suggests that *Q. agrifolia* seedlings have thinner taproots (supported by measurements of oven-dried roots; Callaway [personal observation]), although root biomass per length also may have been affected by shade-associated differences in wood density (Lei and Lechowicz 1990). Although acorns of *Q. lobata* and *Q. douglasii* are larger than those of *Q. agrifolia,* in this experiment shoots of *Q. agrifolia* seedlings emerged earlier. Early contribution of photosynthate may account for the ability of *Q. agrifolia* to maintain high taproot elongation rates. My results for taproot elongation and the timing of shoot emergence differ from those reported by Matsuda and McBride (1986), who found that *Q. lobata* taproot elongation rates exceeded those of *Q. agrifolia* in greenhouse conditions, and that final taproot length of *Q. douglasii* and *Q. lobata* exceeded that of *Q. agrifolia* in the field under adult *Q. agrifolia* canopies. Their results may have differed from mine because of their use of longer acorn storage periods before planting, soils with higher organic matter, different acorn sources and initial acorn weights, and a later planting date, different growth environments, or species-specific interference from adult trees.

Even though *Q. agrifolia* and *Q. douglasii* seedlings appear to be equally shade tolerant in natural conditions (Callaway and D'Antonio 1991; Muick 1991; Callaway, in press), morphological and physiological responses to shade were not similar. Whole-seedling biomass of *Q. agrifolia* seedings at $I_{10\%}$ was not significantly different than at I_{full}, and shoot mass, root mass, root : shoot ratios, and taproot elongation rate were minimally affected by shade. Shade tolerance was also indicated by increases in whole-seedling leaf area, specific leaf area, and LAR (Jarvis 1964; Loach 1967; Givnish 1988). In comparison, *Q. douglasii* whole-seedling biomass was 50% lower at $I_{10\%}$ than at I_{full}, and seedlings underwent large decreases in root mass, root : shoot ratios, and taproot elongation rates in shade. Shade intolerance was also indicated by insignificant shade effects on total seedling leaf area, specific leaf area, and comparatively low PS_{mass} at low light. Comparatively high leaf-level photosynthetic capacity for *Q. douglasii* at $I_{50\%}$, however, indicates that moderate shade intensities may favor *Q. douglasii*. These differences in shade responses may reflect adaptations to survival in the shade of the canopies of conspecific adults, which is diffuse and seasonally variable under the winter-deciduous *Q. douglasii* but dense in all seasons under *Q. agrifolia*. Recruitment in conspecific woodlands and under the canopies of mature conspecifics, however, is very low for *Q. douglasii* (White 1966; Harvey 1989; Callaway, in press) and geographically inconsistent for *Q. agrifolia* (Muick and

Bartolome 1987; Callaway and Davis, unpublished data).

Response of *Q. lobata* seedlings to shade was characteristic of shade-intolerant plants and corresponded with poor survival in natural and experimental shade reported by Callaway (in press). Shade intolerance may explain low recruitment under shrubs but is inadequate to explain widely reported low recruitment in conspecific woodlands and savannas in which deep shade is uncommon (White 1966; Griffin 1971, 1976; Bolsinger 1988). *Quercus lobata* seedlings underwent large decreases in root mass, root : shoot ratios, and taproot elongation rates in shade. Shade intolerance was also indicated by insignificant shade effects on total seedling leaf area and specific leaf area, small increases in LAR, and comparatively low PS_{mass} in low light when grown in low light.

Most morphological and physiological shade responses were similar for *Q. lobata* and *Q. douglasii*. However, recruitment of these species in shade is strikingly different in the field and has been attributed to differences in leaf-level photosynthesis and root elongation (Callaway, in press). Recruitment in shade may be due to complex responses to shade, soil moisture, and soil nutrients (e.g., see Osmond 1983 and Küppers et al. 1988). Tolerance to low soil moisture may contribute to the survival of *Q. douglasii* seedlings in shade (see Abrams and Kubiske 1990). Reduced taproot elongation rates, reduced allocation to root mass, and low root : shoot ratios of *Q. lobata* and *Q. douglasii* seedlings growing in shade probably impair their capability to root below dry surface soils during typically rainless summers and thus expose them to severe drought (Mahall and Schlesinger 1982). However, *Q. douglasii* seedlings may be better adapted to survive exposure to xeric conditions than is *Q. lobata*. Based on comparisons of spatial distributions and water relations, mature *Q. douglasii* appear to be more tolerant of low soil moisture than *Q. lobata* (Cooper 1926; Griffin 1973; Rundel 1980; Hollinger 1984; Callaway et al. 1991), and Griffin (1971) reported that *Q. douglasii* seedlings were more drought tolerant than *Q. lobata* seedlings. Field shade tolerance of *Q. douglasii* seedlings, in comparison with *Q. lobata* seedlings, also may result from higher photosynthetic capacities and taproot elongation rates in shade (Callaway, in press).

Quercus douglasii and *Q. lobata* seedlings grown in shade did not substantially increase leaf area, as did *Q. agrifolia*. Shade-induced increases in leaf area may enhance energy acquisition and maintain high root mass and taproot elongation and is clearly favorable when soil water is abundant. In dry habitats, where *Q. lobata* and *Q. douglasii* are common, large increases in leaf area in shade and consequent transpiration losses may

be a greater overall disadvantage than low-light harvesting capabilities (Schlesinger and Gill 1980; Mahall and Schlesinger 1982). Shade tolerance of *Q. lobata* may vary substantially among ecotypes on a moisture gradient. In northern and more mesic parts of the range of *Q. lobata,* seedlings appear to be more common in shady riparian habitats (Knudson 1984) and appear to grow well in artificial shade treatments (Tyson Holmes, unpublished data). The Santa Ynez Valley, where the acorns used in this study were collected, is in the southern and more xeric portion of the range of *Q. lobata,* and all acorns were collected from trees in upland savannas and woodlands that are more xeric than riparian zones.

The striking differences in interspecific seedling responses to shade may explain in part the interspecific differences in the intensity of facilitative interactions between seedlings and shrubs. In some habitats *Q. agrifolia* and *Q. douglasii* seedlings are naturally associated with shrubs, and seedling survival in field experiments is enhanced by shrub cover. In contrast, *Q. lobata* seedling survival is not facilitated by shrubs (Callaway and D'Antonio 1991; Callaway, in press). The shade responses of *Q. agrifolia* and its propensity to recruit beneath and potentially replace the shrubs (McBride 1974; Short and Short 1987; Callaway

and Davis, unpublished data) in semiarid shrublands and woodlands of California appear to parallel patterns of regeneration and succession of other oak species in many different environments (Kozlowski 1949; Bordeau 1954; Loach 1970; Geis et al. 1971; Christensen and Peet 1981; Hicks and Chabot 1985). However, little is known about successional roles of oaks in California. In some locations, chaparral dominated by *Adenostoma fasciculatum* appears to be invaded and replaced by *Q. douglasii* (Holland 1986), and *Q. agrifolia* has been reported to invade and replace coastal sage scrub and coastal chaparral on some substrates in the absence of fire (McBride 1974; Short and Short 1987; Callaway and Davis, unpublished data). These dynamic processes may be facilitated by the ecophysiological shade responses reported here.

Acknowledgments

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