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Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings

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Summary. We examined the competitive effects of two annual species on soil water potential and blue oak (*Quercus douglasii* Hook & Arn.) seedling growth and water relations. Two densities of the annual grass *Bromus diandrus* (Roth.) (100/dm^2, 3.6/dm^2) and one density of the annual forb *Erodium botrys* (Cav.) (3.6/dm^2) comprised plant neighborhoods around the oak seedlings grown in 1 m deep boxes. Rates of soil water depletion differed among neighborhoods. Soil in the *Erodium* neighborhoods dried significantly more slowly than did soil in the *Bromus* neighborhoods at either density. Differences in the rates of soil water depletion were correlated both with the 30% lower root biomass developed by *Erodium*, and the lower water extraction rates of *Erodium* relative to *Bromus* roots at constant root biomass. These results suggest that the annual species are not equivalent competitors for water: fibrous grass roots had greater competitive effect than did forb tap-roots. In a control container without an annual neighborhood, soil water potentials remained high for the duration of the experiment. Oak seedling emergence and growth responses were significantly affected by annual plant density. High density of annual plants suppressed oak root growth and shoot emergence. Only 20% of the acorns planted in high density *Bromus* neighborhoods showed aboveground shoot growth; 56% of those planted in low density *Bromus* or *Erodium* emerged. Ninety percent emerged in the control box. Relative growth rates of oak seedling roots and shoots were directly dependent on soil water potentials. Soil water was also closely correlated with oak seedling predawn water potentials and gas conductance measurements. Higher soil water potentials, greater dry weights, and longer growing seasons were found for oak seedlings in the *Erodium* neighborhood and the container with no annuals than in *Bromus* neighborhoods of either density. These results suggest that competition for soil water with introduced annual species contributes to the increased rate of blue oak seedling mortality currently observed in California woodland systems.

Key words: Neighborhood competition – *Quercus douglasii* – Root morphology – Soil water potential – Plant water relations

The competitive equivalence of different plant species with similar phenological characteristics has been assumed or demonstrated in several studies (Goldberg and Werner 1983; Fowler 1986; Goldberg 1987; Miller and Werner 1987). The spatial arrangement and size of adjacent plants, rather than species identities, has partially explained the variability in the growth and seed production of individual target plants in experimental and model systems (Mack and Harper 1977; Weiner 1982; Heywood and Levin 1986; Firbank and Watkinson 1987). However, if morphological attributes of a species influence the acquisition of limiting resources, species identity within a neighborhood may affect the intensity of interspecific competition. Partitioning of soil resources through differential rooting patterns has been hypothesized to permit species coexistence in semi-arid and arid environments (Yeaton et al. 1977; Caldwell and Richards 1986; Hunt and Nobel 1987). Different water potentials of adjacent species has suggested the utilization of different soil water pools (Gulmon et al. 1983; Robberecht et al. 1983; Davis and Mooney 1986).

Where spatial and temporal resource use overlap, differences in the rates and absolute levels of depletion of a resource like water will influence both the intensity of competition experienced by individual plants and their potential responses to the strain induced. Although some species have physiological and structural mechanisms which maintain leaf turgor as soil water potentials decline (Roberts and Knorr 1977; Davis and Mooney 1986), rapid decreases in plant water potentials can inhibit operation of these mechanisms (Flower and Ludlow 1985). The plant water potential at which turgor loss occurs varies positively with the rate at which soil water potentials decline (Osonubi and Davies 1981; Matthews and Boyer 1984; Flower and Ludlow 1986; Wraith et al. 1987). Thus, changes in neighborhood species composition or density which modify the timing or degree of water use may alter the extent of physiological adjustment and compensation.

Changes in the species composition of California's grassland systems may demonstrate the impacts of temporal shifts in water availability on species establishment. Nonnative annuals that now represent 50 to over 90% of the cover in many grasslands (Biswell 1956), potentially have altered the seasonal availability of soil moisture. Annual species and grazing animals were introduced to California by European settlers in the 1800's (Burcham 1957). Interactions between grazers, fire suppression, and introduced annuals resulted in the replacement of native perennial bunchgrass and annual species by introduced annual species (Schultz and Biswell 1952; Griffin 1971; Bartolome et al.

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1986; Saenz and Sawyer 1986). A shift in soil water availability may have accompanied this replacement because perennial grasses gradually deplete the soil water from about February through July, while annual plants cause the same depletion within the shorter period of February to May (White 1967; Jackson and Roy 1986).

An increase in the seedling mortality of several native oak species which compose the overstory in woodland areas has coincided with the conversion from native annual and perennial to introduced annual grassland species (White 1966; Griffin 1971; Griffin 1976). Current populations of oaks, including those of the deciduous blue oak (*Quercus douglasii* Hook & Arn.), exhibit bimodal age structures, biased towards individuals under 5 or over 60 years old (Bolsinger 1986; McClaren 1986; Muick and Bartolome 1986). Dendrochronological analyses suggest no evidence of historically episodic regeneration (McClaren 1986). This gap in sapling age classes threatens blue oak stand regeneration in over three million hectares in the Coast Range and Sierra foothills surrounding California's Central Valley.

Although the suppression of woody species establishment by herbaceous vegetation has been documented (Schultz et al. 1955; Da Silva and Bartolome 1984; Williams et al. 1987), both the mechanisms which regulate the interaction and the developmental stage on which suppression operates are less clear. Studies which couple neighborhood composition and resource utilization in a controlled setting are necessary if the mechanisms regulating species interactions are to be identified.

This study examines competition for soil moisture between blue oak seedlings and two commonly sympatric annual grassland species: *Bromus diandrus* (Roth.), an introduced annual grass with an extensive fibrous root system, and *Erodium botrys* (Cav.), an introduced tap-rooted rosette-forming forb. The species were selected because of their similar phenologies, both completing their life cycles before the onset of summer drought, but different root morphologies. Interplanting of acorns in high and low density *Bromus* neighborhoods and in low density of *Erodium* allowed us to examine whether: 1) identity of annual species with significantly different root morphologies or 2) density within the annual neighborhood influences the competition for soil water.

We hypothesized that the fibrous-rooted grass would deplete soil moisture throughout the depth of root penetration more rapidly than would the forb, and that this depletion rate would be density-dependent. Rapid drought development would shorten the period during which blue oak seedlings maintain positive turgor potentials, reducing the effective growing season and root and shoot biomass. Thus, differences in competitive effects of annual species should be reflected in both oak seedling establishment and the amount of perennating oak biomass developed in the different neighborhoods.

Methods

Neighborhood effects on soil water and oak seedling growth were examined in four treatments: high or low density *Bromus diandrus*, low density *Erodium botrys*, and no annual plants (control). The high grass density was 1 seed/cm^2 (10000/m^2). The low grass and *Erodium* densities were 0.036 seed/cm^2 (360/m^2). These densities are within the natural range in the California annual grassland (Heady 1958). Eighteen blue oak acorns were planted within each neighborhood in three rows of six each. Acorns in the low density neighborhoods were equally close to three annual plants. Each acorn was planted in the center of a square with 8 cm sides. Two replicates of all treatments except that with no annuals were established. The experiment was conducted from the time of annual neighborhood planting in December, 1986 until leaves of the control oaks senesced in August, 1987.

We conducted this experiment in seven boxes, each having one slanted glass side for root growth observations. The boxes were 1 m in height, 48 × 24 cm at the top and 48 × 12 cm at the base. They were filled with sifted soil (Mollic Haploxeralf) from an oak woodland area in the north-western foothills of the Sierra Nevada (Yuba Co., California). Field soil layers of 0–10, 10–30, and 30+ cm were separately collected and placed in the boxes. The upper layer (without surface litter) was autoclaved to remove interference from resident seeds. Soil in the boxes was saturated with water during the filling process to increase compaction.

Boxes were kept outside on the University of California, Davis campus in Yolo Co., California. The treatments were allocated randomly to boxes arranged in a double row along a north-south axis. Each glass surface was covered to prevent light penetration and a white plywood frame from the ground to soil surface level shielded all boxes from solar heating. Collars of welded wire caging with 56% shade cloth were attached around the tops of the boxes to reduce wind impacts around the plants and to simulate the lateral shading of a continuous canopy. After two months of annual neighborhood canopy development, the soil surface in the control box was covered with 1 cm of sterilized grass litter to maintain similarity in soil evaporation and reflectivity across all treatments.

Soil moisture

Soil in the the boxes was saturated at the time of planting. Boxes were subsequently watered to simulate precipitation conditions in Davis for an average year (U.S. NOAA 1978). Three calibrated screen cage thermocouple soil psychrometers (Merrill 74-3V) were placed along a vertical transect through the center of each box at 15, 40, and 75 cm depths. Soil moisture and temperature measurements were made biweekly with a Campbell CR-7 data logger.

Annual plants

We sowed the annual neighborhoods with pregerminated seed in December, 1986. Growth of ten marked plants per box was measured monthly. Shoot height or rosette diameter, number of leaves, number of grass tillers, and flower number were measured. The number of annual plant roots intersecting horizontal transects of the glass surface was recorded for 11 depths in the boxes as long as roots were visible. Both root length and density are closely correlated with these counts of intersections (Pearson 1974). *Erodium* viable seed production was assessed at the end of April. Seed number in *Erodium* is correlated with plant size and biomass (Rice, unpublished data). Entire *Bromus* individuals were removed for simultaneous measurements of total biomass and seed production.

When the treatments with annuals were too dry for ac-

curate measurement of soil moisture, the glass panels were removed and soil from 30–50, 50–70, and 70–100 cm depths was washed through aluminum screening (2.75 squares/cm). Roots were retained for dry biomass determination.

Oak seedlings

Blue oak acorns were collected near the site of soil collection in September, 1986. Acorns were dried to 60% of their original weight and were then refrigerated (3° C) in sealed plastic bags filled with moist vermiculite. Captan was added to minimize fungal damage. Oak radicles emerged after 5–6 weeks of refrigeration. Pregerminated acorns with up to 10-mm radicle development were planted at 1-cm depth in early February. Germinated wet weights of the acorns ranged from 3.9 to 10.2 g; equal numbers of acorns with wet weights above and below 5 g from each of 2 trees were selected for planting. Parent tree identity and acorn weight at planting were recorded at each sowing position for later use as covariates.

Oak seedling shoot height, leaf number, and leaf area were measured weekly. Length and growth rate of the six blue oak seedling roots along the glass fronts were recorded every 4–5 days through the season. Relative growth rates (RGR) were calculated as the difference in natural logs of root length, leaf area, or maximum height over the time interval in days.

Midday oak stomatal conductance and transpiration rates were measured weekly with a null balance porometer (Licor 1600) on all seedlings with green leaf tissue.

Predawn xylem water potential of entire oak seedlings was measured with a pressure chamber (Soil Moisture, Inc.) after 10 weeks of growth. Only one oak seedling from each block of the two grass neighborhoods was used, since all shoots were desiccating. Two seedlings from each of the *Erodium* boxes and the control box were measured. Subsequent determinations of predawn water potential were made monthly on seedlings with green leaves.

Seedlings in the box without annuals were permitted to grow until they senesced in August. Dry weights of shoot, acorn, and root tissue were determined for the six oak seedlings grown along the glass in each box.

Data analysis

Treatment effects on soil water potential and oak growth parameters were analyzed using the SAS general linear model for nested analysis of variance (Freund et al. 1986). Relationships between soil and seedling water potentials, oak water relations variables, and annual root biomass and soil water potential were analyzed with SAS linear and nonlinear regression and correlation techniques. Responses of individual oak seedlings were nested within replicate or replicates were nested within treatment for the analyses of growth and water relations, or whole box measurements, respectively. All ANOVA, regression, and correlation analyses were conducted on individual measurements at each time point rather than on means over time or over samples at each date. The lack of replication of the control treatment meant that its within-box variance was not independently estimated, and that the pooled within-box variance used in the GLM analyses may have been biased. Large between-box sums of squares values relative to values between treatments or between the nested measure of individual oaks

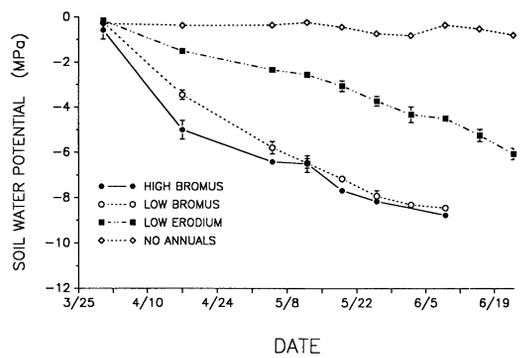

Fig. 1. Soil water potential at 40 cm depth in the four neighborhoods. Error bars represent 1 standard error (n = 2) where data were available and where bars were larger than symbols

within a box would indicate this potential problem. In no case was bias evident: the between box values were one to three orders of magnitude below those of the other variance components. We therefore included all treatments in the analyses.

Annual plant and oak growth parameter differences between replicate boxes were examined using Mann-Whitney U tests, and between neighborhoods using Tukey tests on nested analysis of variance models. Growth, biomass, water potential, and gas exchange parameters were natural log transformed, and count data were square root transformed for the analyses; residuals were examined for consistency with model assumptions.

Results

Soil moisture

Two way analysis of variance showed that the rate of soil water depletion at all depths was treatment and time dependent, with a significant interaction ($P < 0.0001$, $F = 38.99$; overall model $P < 0.0001$, $F = 86.96$). All boxes started at field capacity and experienced similar soil temperatures throughout the experiment. The consistency in soil water potentials in all neighborhoods for over three months from the planting of annuals (Fig. 1) indicates that the surface litter did not enhance moisture retention in the control box over that in the others. Soil water depletion occurred most rapidly in the high density *Bromus* neighborhoods, though the low density treatment *Bromus* reached similar water potentials soon afterwards. *Erodium* boxes were significantly more moist throughout the drought period, and no change in soil water potential was observed when oaks were planted alone. Oak transpiration alone was not high enough to deplete soil moisture in the control treatment. Soil water potentials at the three depths were highly correlated with each other throughout the experiment (15 and 40 cm: $P < 0.0001$, $r = 0.73$, 40 and 75 cm: $P < 0.0001$, $r = 0.85$).

Soil water and temperature in the boxes was also compared to field measurements taken at 40 cm depth over the same period (Gordon, unpublished data). Water potentials decreased more rapidly in the boxes than in the field, probably due to the restricted soil volume, lower soil compaction, and greater penetration of the annual roots (see below) in the containers. Average mid-morning soil temperatures were not significantly different either between boxes

Table 1. Annual plant growth responses within the neighborhoods. Average values per individual plant ± one standard error ($n=10$). Root weights are replicate box totals divided by plant numbers to get values for individuals ($n=2$)

Neighborhood	Rep.	Maximum leaf height or rosette diameter	Max. No. tillers	Max. No. leaves (per tiller in grass)	Number of flowers	Number of seeds	No. seeds/ flower	Seed weight (mg)	Shoot weight (g)	Root weight (g)	Root/ shoot ratio
High density *Bromus*	1	33.2[a] ±1.5	1.0[a] ±0	3.8[a] ±0.2	3.6[a] ±0.6	6.5[a] ±1.2	1.67[a] ±0.22	5.2[a] 0.3	0.185[a] ±0.03	0.035[a] –	0.189[a] –
	2	35.6[a] ±1.6	1.0[a] ±0	3.1[a,b] ±0.2	3.7[a] ±0.7	7.0[a] ±2.3	1.84[a] ±0.36	4.9[a] 0.4	0.180[a] ±0.03	0.030[a] –	0.167[a] –
Low density *Bromus*	1	38.9[a] ±1.7	10.0[b] ±0.5	6.0[a,c] ±0.2	44.2[b] ±4.2	63.4[b] ±6.4	1.48[a] ±0.15	5.3[b] 0.2	2.700[b] ±0.20	0.847[b] –	0.314[b] –
	2	43.9[a] ±1.7	6.6[c] ±0.5	4.9[a,d] ±0.2	42.6[b] ±2.8	74.8[b] ±4.6	1.81[a] ±0.15	5.8[c] 0.2	2.386[b] ±0.10	0.661[b] –	0.277[b] –
Low density *Erodium*	1	32.7[e] ±1.6	–	23.6[e] ±2.4	26.8[e] ±4.7	65.5[e] ±12.2	2.37[e] ±0.67	–	–	0.317 –	–
	2	36.5[e] ±0.8	–	21.7[e] ±2.2	16.8[e] ±2.3	37.1[e] ±6.5	1.97[e] ±0.34	–	–	0.265 –	–

[a] Numbers designated with the same letter were not significantly different ($P>0.05$) as indicated between replicates by Mann-Whitney U and between *Bromus* neighborhoods by Tukey tests. The nested error term replicate within neighborhood was specified for Tukey tests ($n=4$). Interspecific comparisons were not made

Table 2. Annual plant aboveground growth in the neighborhoods. Means ± 1 standard error ($n=2$). Box totals calculated from averages per individual multiplied by the number of plants per box

Neighborhood	Total No. leaves	Total No. flowers	Total No. seeds	Total shoot weight (g)
High density *Bromus*	3912[a] ±397	4134[a] ± 51	7104[a] ±267	207[a] ±3
Low density *Bromus*	1942[a] ±570	1822[b] ± 35	2902[b] ±238	107[b] ±7
Low density *Erodium*	951 ± 40	916 ±210	2156 ±596	–

[a] Numbers designated with the same letter were not significantly different ($P>0.05$) as indicated by Bonferroni tests ($n=2$) with a specified error term of replicate box nested within treatment. Interspecific comparisons were not made

or between the boxes and the field measurements. Values for the boxes ranged from 14.98 to 24.12° C, and those from the field, from 18.72 to 27.27° C.

Annual plant response

Annuals were sown in the boxes prior to the oaks, such that annual cover was 100% in the high density *Bromus* treatment and less than 50% in both low density treatments when acorns were planted. Cover was 100% in all annual plant neighborhoods prior to oak shoot emergence.

Grass growth responses differed between the high and low density treatments (Table 1). *Bromus* individuals did not produce multiple tillers at high density, but averaged over eight tillers per plant at the low density. Leaf number and height also tended to be greater in the low density neighborhoods. Final biomass in the boxes reflected this higher productivity under low densities, since total aboveground biomass was 50% of that in the high density treatments despite the two order of magnitude difference in plant number (Table 2).

Differences in *Bromus* shoot productivity also were reflected in seed production (Table 1). The number of seeds per flower was not different between boxes or treatments, but plants grown at low densities produced both more and heavier seeds per plant than did those grown at high density. The greater seed numbers resulted from greater tiller densities and more florets per tiller.

At low density, *Erodium* rosettes were up to 40 cm in diameter, and averaged 22 leaves per plant. No significant differences in shoot, flower, or seed development existed between the two replicate neighborhoods (Table 1). Shoot weight was not determined for the *Erodium* because its leaves senesce during flowering and seed maturation.

Rooting patterns of the annuals revealed species-specific differences over time. *Erodium* roots were initially deeper than were those of the *Bromus* (Fig. 2). Unlike in the field, where grass roots are sparse below 30 cm (Jackson et al. 1988), roots in all treatments had penetrated to the bottom of the boxes after two months. Root/shoot ratios of the grass were within the range of 0.6 to 1.9 reported for California annual grasslands (Savelle 1977), however. Root length and density, extrapolated from point intersections along the glass fronts (Pearson 1974), were greater in both *Bromus* than in the *Erodium* neighborhoods. Little difference in total root density existed between the two *Bromus* treatments (Fig. 3). Individual belowground standing crop, like that aboveground, was substantially greater under low plant density (Table 1). The grass developed on average 30% more root biomass than did the forb at every depth class except that of 30–50 cm (Fig. 3). Analysis of variance of average root biomass over all depths by treatment showed significant differences between species ($P<0.02$, $F=21.85$), but not between the *Bromus* densities. Figure 3 indicates a more even distribution of *Erodium* roots with

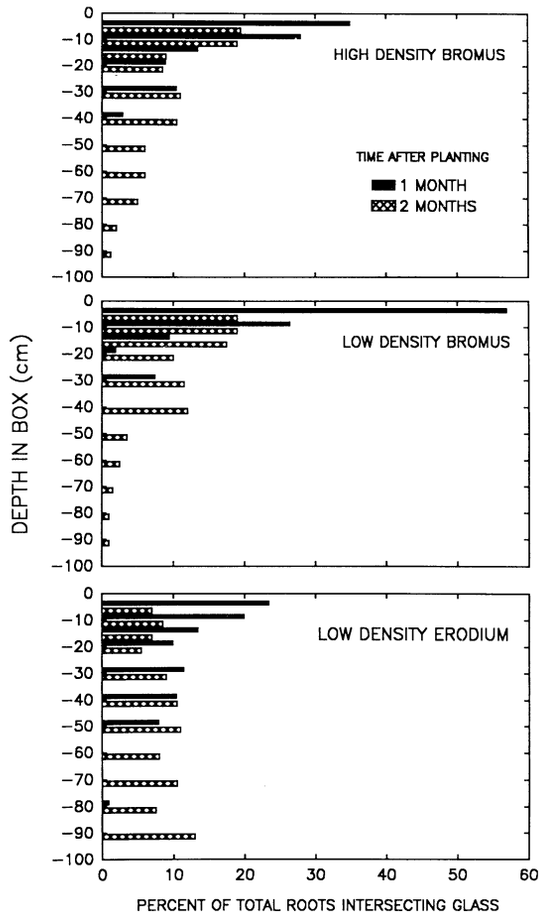

Fig. 2. Average annual plant root distribution (%) as a function of neighborhood and depth. After two months shallow roots were no longer visible because the soil receded from the glass as it dried

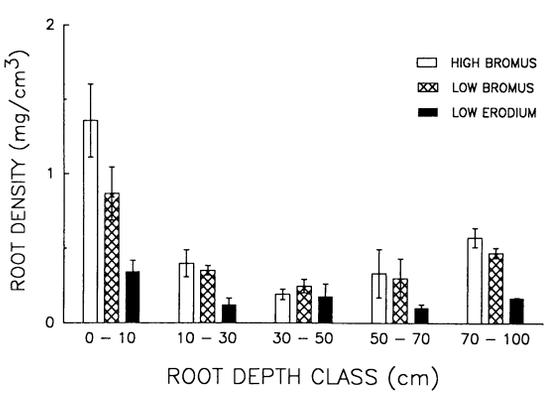

Fig. 3. Annual plant root density after plant senescence and soil drying (25 June). Values are averages ± 1 standard error for two boxes over the specified soil depth class

depth relative to *Bromus*, which concentrated its roots in the upper 10 cm. Small sample sizes precluded statistical evaluation of these trends.

The final soil water potential induced by the annual root biomass in each treatment ($n=3$) showed significant neighborhood dependence as revealed by analysis of variance ($P<0.0001$, $F=15.44$). Comparison of the water potentials resulting from a given density of fibrous *Bromus*

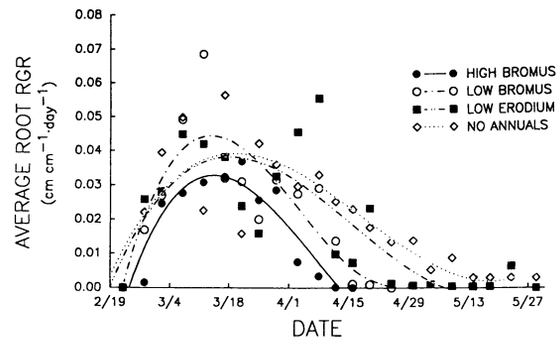

Fig. 4. Relative root growth rate of blue oak seedlings over time. Lines are quadratic regressions (high density *Bromus* $r^2=0.86$; low density *Bromus* $r^2=0.82$; low density *Erodium* $r^2=0.52$; no annuals $r^2=0.59$)

roots with that resulting from the same density of *Erodium* roots reveals differences between species in their water use ($P=0.05$, $F=3.17$). For example, 0.2 mg/cm^3 of *Bromus* roots at either density resulted in an average final water potential of −6.7 MPa (9 June); 0.2 mg/cm^3 of *Erodium* roots resulted in a potential of −3.6 MPa. Thus, rooting morphology coupled with biomass may explain the influence of the annual neighborhoods on soil water availability.

Oak seedling response

Competition from annual plants was also expected to be directly reflected in oak seedling growth and development. Analyses of relative growth rates were of individual seedlings over time by treatment using individual within replicate box as a specified error term for testing the analysis of variance models.

Oak root relative growth rates were dependent on treatment and sampling date with a weak interaction ($P=0.06$, $F=1.59$; overall model $P=0.055$, $F=2.66$). Acorn wet weight was included as a covariate but had no significant effect ($P=0.2$). Analysis of all seedlings over time showed that root growth rate was correlated with soil water potential ($P=0.002$, $r=0.25$). Comparison of the dates at which growth decreased in Fig. 4 with the corresponding soil water potentials in Fig. 1 reveals that growth slowed at potentials lower than −1.0 MPa and ceased at −3.0 to −4.0 MPa. As a result, root growth directly reflected the differences in the neighborhood-induced soil drying rates (Fig. 4). Final root lengths were least in the high density grass boxes (Table 3), where growth ceased the earliest (9 April). Oak root growth continued in the *Erodium* neighborhood (until 19 May) for a month longer than in the same density of grass (19 April) but, because of high variance, no significant differences in maximum root length or in dry weight were detected. Roots of oak seedlings growing without annual plant competition reached the greatest depths; control seedlings had roots that were twice as long as were those growing in the high density *Bromus* treatment (Table 3).

Oak seedling shoot emergence followed the same pattern of treatment dependence as root length using analysis of variance of transformed counts from each box ($P<0.006$, $F=42.06$). Shoots were visible in the neighborhood without annuals a week earlier than in any other neighborhood (22 March). Emergence in all boxes was complete by the end

Table 3. Blue oak seedling growth responses within the neighborhoods. Average values per individual ± one standard error (n is variable and based on six seedlings/box measured over time for the root variables, and on the number of shoots emerged/box measured over time for stem and leaf variables). Seedlings without shoots are not represented in stem and leaf averages, but are included in the root/shoot ratios

Growth responses	Neighborhood			
	High density *Bromus*	Low density *Bromus*	Low density *Erodium*	No annuals
Root				
Ave. RGR ($cm\ cm^{-1} day^{-1}$)	0.012[a] ±0.016	0.017[b] ±0.002	0.017[a,b] ±0.002	0.013[a] ±0.003
Maximum length (cm)	45.56[a] ±4.64	66.71[a] ±2.67	74.43[a] ±3.30	101.60[a] ±0.40
Dry weight (g)	0.359[a] ±0.072	0.611[a,b] ±0.049	0.768[b] ±0.111	1.845[b] ±0.511
Stem				
Number emerged	3.5[a] ±0.5	10.0[b] ±1.0	10.0[b] ±0.0	16[c] –
Ave. RGR ($cm\ cm^{-1} day^{-1}$)	0.006[a] ±0.003	0.020[a] ±0.005	0.018[a] ±0.007	0.052[a] ±0.008
Maximum height (cm)	4.94[a] ±0.86	8.36[a] ±0.67	7.02[a] ±0.81	11.32[b] ±1.97
Dry weight (g)	0.026[a] ±0.003	0.069[b] ±0.012	0.056[b] ±0.009	0.354[c] ±0.167
Leaf				
Ave. RGR ($cm\ cm^{-1} day^{-1}$)	0.004[a] ±0.006	0.014[a] ±0.008	0.005[a] ±0.018	0.013[a] ±0.030
Maximum No. leaves	2.4[a] ±0.5	4.5[a] ±0.5	4.4[a] ±0.6	19.9[b] ±2.5
Maximum area (cm^2)	1.46[a] ±0.41	6.86[a] ±1.61	7.90[a,b] ±1.72	79.03[b] ±16.73
Root/shoot dry weight	18.46[a] ±2.35	13.56[a,b] ±3.54	15.12[a] ±2.29	6.33[b] ±1.02

[a] Numbers designated with the same letter were not significantly different ($P > 0.05$) as indicated between replicates by Mann-Whitney U and between neighborhoods by Tukey tests. Where effects of replicate were not small ($F > 1$), the nested error term replicate within neighborhood was specified for Tukey tests ($n = 7$)

of April. High densities of *Bromus* suppressed shoot development in all but 20% (3.5/18) of the planted acorns despite the observed root growth of all acorns along the glass. Intermediate densities of annuals, independent of species involved, allowed 56% of the oak shoots to emerge in both treatments; in the absence of annual competition, 89% of the planted acorns developed shoots (Table 3).

Oak shoot relative growth rates showed the same neighborhood and time dependence as did root growth (interaction $P = 0.03$, $F = 1.73$; overall model $P < 0.0001$, $F = 15.19$). Both the relative rate and the maximum amount of stem growth were dependent on relative root growth rates ($P < 0.0001$, $F = 3.16$). Initial acorn weight covaried significantly ($P < 0.0001$) with final shoot height but not with shoot relative growth rates in the above analyses.

Analysis of variance also revealed the dependence of relative leaf area growth rates on treatment ($P < 0.0001$, $F = 18.01$) but not on root and shoot growth rates or acorn weight. Average leaf number and area were weakly treatment dependent (Table 3). Leaf senescence occurred first in the high and low density grass treatments (27 April), followed a month later when soil water potential was about −4.0 MPa in the forb treatment, and three months after that in the control.

Xylem water potential in the oak seedlings identified the probable mechanism of the treatment-dependent emergence, growth, and senescence timing observed (Fig. 5a). Predawn potential of the oaks grown alone was −0.7 MPa, whereas those grown with *Erodium* and *Bromus* at either density were at −2.6 MPa and at less than −7.5 MPa, respectively.

Oak leaf stomatal conductance and transpiration rates corroborated water potential data. Analysis of all seedling water data taken throughout the experiment demonstrated that both gas exchange variables were correlated with oak predawn water potential (conductance: $P = 0.0004$, $r = 0.83$; transpiration: $P = 0.001$, $r = 0.80$). Gas exchange ceased at soil water potentials below −4.0 MPa (Fig. 5b), corresponding to the observed potential at which seedling growth ceased. These parameters substantiate evidence of neighborhood influence on oak carbon gain indicated by shoot and root biomass and growth data.

Seedling biomass was consistently greatest in seedlings grown without competition (Table 3). Root/shoot ratios were highest in the high density *Bromus* neighborhoods and lowest when oaks were grown alone, reflecting differences among treatments in the length of the growing season for shoots. Only seedlings that produced aboveground shoot tissue were included in this calculation.

Discussion

This experiment has demonstrated that annual plant neighborhoods can influence the local availability of soil water for oak seedlings. The rate of drought onset induced by the neighborhood determined the intensity of competition (*sensu* Weldon and Slauson 1986) as reflected by oak growth responses and physiological strain.

The impact of neighborhood composition may be separated into species density and species identity components that have specific effects on the oak seedlings. The direct relationship between annual plant density and soil moisture depletion is consistent with the well documented density-dependence of resource removal (Harper 1977; Caldwell and Richards 1986). Soil water potential decreased most rapidly in the high density *Bromus* treatment, although the higher individual productivity in the lower density grass treatment caused the curves to converge after about two weeks (Fig. 1). The brief period during which soil water potentials in the two grass treatments were significantly different translated into a longer period of oak root growth with a higher probability of shoot emergence. Deeper root penetration and greater oak above- and belowground biomass resulted. Seedling emergence and growth differences in the zero density control treatment follow the same pattern. However, the rapid convergence in the level of water stress in the two grass treatments apparently accelerated leaf senescence in the oaks.

The annual species also differed in their ability to complete for soil water on a biomass basis. Differences in both the rate and extent of soil drying in the low density grass

and forb neighborhoods may result from the different root morphologies of the species. *Erodium* developed fewer, larger roots which initially penetrated deeper in the boxes than did the *Bromus* roots. Eventually, the grass developed a higher biomass and number of roots at all depths, which were more efficient at removing water on a per weight basis. Greater competitive effects of grasses relative to forbs have been demonstrated in other studies (McCown and Williams 1968; Berendse 1981; Gerakis et al. 1985; Elliott and White 1987; Goldberg and Fleetwood 1987). Water uptake and competitive success are linked with root density and surface area in both model (Gardner 1960; Novak 1987) and experimental systems (Caldwell 1987).

Surprisingly, the higher availability of water experienced by oak seedlings in the forb neighborhood resulted in neither significantly greater root prodution nor greater shoot emergence than in the corresponding grass neighborhood. Oak seedlings growing with *Erodium*, however, maintained higher leaf water potentials, greater rates of stomatal conductance, and experienced a longer growing season than did those under more rapidly drying soil conditions. No apparent increase in carbon gain resulted from this reduced stress in the *Erodium* neighborhoods, although the seedlings grown without competitors accumulated more biomass in all tissues (Table 3). The resulting lower oak root/shoot ratio in the control is consistent with other observations that the ratio varies inversely with water stress in plants (Pearson 1974).

Although competition for moisture appears to explain the differences in oak seedling development between the treatments, competition may have been for other resources. Light is often important for seed germination and development responses (Bliss and Smith 1985). However, the planting of pregerminated acorns and the complete cover of annuals prior to oak shoot emergence reduced differences in the light environment in all treatments with annual plant neighborhoods. The distribution of natural blue oak seedlings in the California foothills is limited to areas under mature oak canopies (Muick and Bartolome 1986), where incident light is reduced by 50–60%. Although factors other than light probably cause this distribution, seedling presence under oak canopy suggests shade tolerance. Investigation of the photosynthetic response of blue oak seedlings has demonstrated that carbon gain is 50% of the maximum when light intensity is only 25% of full sunlight (Welker, unpublished data). These data reduce the probability that light limited seedling development in this experiment.

Competition for nutrients, especially those which are water soluble, was not addressed in this experiment but may have influenced oak seedling development. Comparisons of nutrients in *Bromus mollis* and *Erodium botrys* tissue reveal different uptake rates which interact with plant density and soil water (McCown and Williams 1968; Gerakis et al. 1985). Although neighborhood-induced differences in soil nutrient levels may have contributed to oak seedling growth, the correlation between final shoot height and initial acorn wet weight indicates that seed supplied nutrients may overwhelm those from the soil in early development.

The consistent density-dependence of oak seedling shoot emergence, regardless of neighborhood species, suggests that oak seedlings may require a period of high soil water potentials after radicle growth is initiated if shoot elongation is to proceed. If this hypothesis is true, the brief gap during which the slopes of the soil water depletion curves

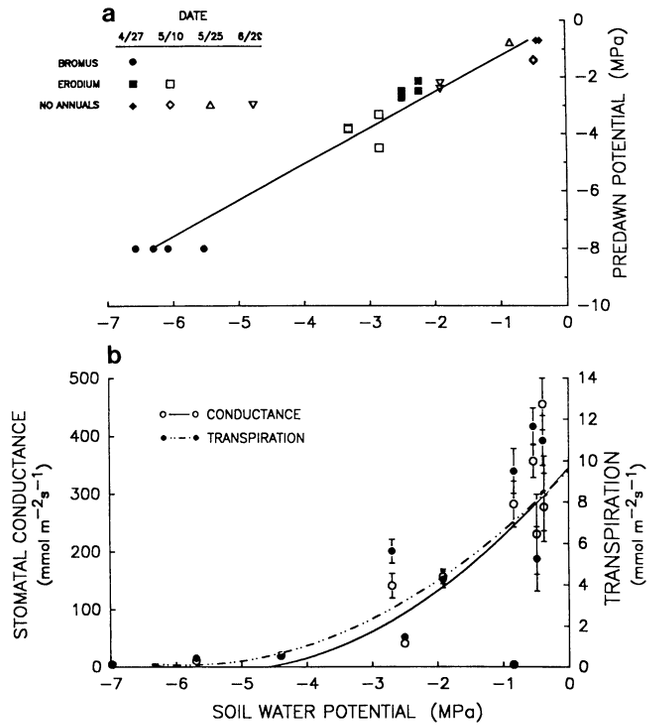

Fig. 5. a Blue oak seedling predawn xylem water potential as a function of soil water potential at 40 cm depth ($r^2 = 0.92$). Potentials of two seedlings per box were measured at each date except for the *Bromus*, where only one seedling was sampled per box since all were senescing. **b** Blue oak seedling midday leaf stomatal conductance and transpiration as a function of soil water potential at 40 cm depth. Plots are quadratic regressions on means ± 1 standard error for all individuals within a box (conductance $r^2 = 0.61$; transpiration $r^2 = 0.56$)

differed between the high and low grass densities (Fig. 1) was enough to suppress shoot development in about 35% of the acorns. Both a threshold potential or rate of soil water depletion and a tight correspondence between soil and plant water potentials are assumed in this hypothesis.

Aside from the observed cessation of root growth at soil water potentials below -4.0 MPa, little evidence is available from which to evaluate the existence of a threshold water potential which permits or suppresses blue oak shoot development. Ontogenetically, root and shoot development are simultaneously initiated (Bonner and Vozzo 1987). Radicle elongation precedes that of the epicotyl. In several of the acorns which showed below- but not aboveground growth, some shoot extension was evident. Since oaks undergo hypogeal germination, suppression may act on epicotyl elongation.

More evidence supports a tight correspondence between oak seedling water status and soil water potential. Predawn analysis demonstrated the direct dependence of seedling xylem potential on soil water both here (Fig. 5a) and in the Sierra foothills (unpublished data). Leaf gas exchange was also correlated with soil moisture in this experiment (Fig. 5b), and with predawn xylem potential of natural blue oak seedlings in the field (Welker and Menke 1987).

The rate of soil water depletion also affected oak seedling growth responses. Root and shoot growth and the timing of leaf senescence were treatment dependent. *Quercus robur*, a deciduous oak species in Great Britain, maintains

leaf turgor potential in drought conditions through osmotic adjustment. This adjustment is not possible if soil water potentials drop too rapidly (Osonubi and Davies 1981). Blue oaks are similarly capable of concentrating vacuolar solutes if soil water potentials decrease gradually (Momen 1988). Seedlings which can adjust to changing water potentials experience a longer growth season, resulting in increased final biomass both in this controlled and in a field setting (Welker and Menke 1987).

Although the rate of soil water depletion was more rapid in this experiment than in the field, the above field data demonstrate similar relationships between seedling and soil water status. Thus, results from this experiment may be cautiously extrapolated to a mechanistic explanation of seedling mortality in the field. If the replacement of the native vegetation in California by an introduced annual flora has resulted in a more rapid pattern of soil water utilization (Jackson and Roy 1986), several mechanisms of blue oak seedling suppression may be operating. Shoot suppression in drought years and in neighborhoods of dense fibrous-rooted species would compound the impacts of a shorter growing season for emerged seedlings. The resulting reduction in growth and photosynthesis would reduce allocation to aboveground perennating biomass and delay growth into sapling size classes. Final mortality may result from insufficient carbon reserves necessary to root-sprout in successive years, compounded by the hazards of remaining in a size class particularly vulnerable to herbivory.

Blue oaks are hypothesized to be more tolerant of drought than other California oak species (Griffin 1973; Baker et al. 1981; Matsuda and McBride 1986). These results indicate, however, that the species may be more sensitive to moisture availability than has previously been thought. Tolerance may extend across only a relatively narrow range of soil water and interacting competitive and herbivore conditions. The historical distribution of blue oaks demonstrates that this range once extended over a broad area in California (Bolsinger 1986). Understanding of the factors which influence seedling success may facilitate the restoration of conditions necessary for blue oak regeneration.

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