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Vegetational and Environmental Changes beneath Isolated Live Oak Trees (*Quercus agrifolia*) in a California Annual Grassland

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ABSTRACT: The composition and structure of the annual vegetation beneath isolated live oak (*Quercus agrifolia*) canopies differed considerably from the surrounding annual grasslands. The grasslands were strongly dominated by *Avena fatua*. Beneath the live oaks, the dominants were the forb, *Pholistoma auritum*, and an important grassland species, *Bromus diandrus*. The environment beneath the live oak canopies was characterized by reduced light, increased levels of essential mineral nutrients and soil moisture, and moderation of temperature extremes compared to the grassland. A reciprocal transplant study, manipulating the dominant annual species and soil types, indicated that light levels and soil nutrients were significant factors in the differential distribution of the annuals. Competition for nutrients between the two grasses did not account for their differential distribution. While most factors contributed to the distributional changes in annual species, decreases in light levels caused by the live oak canopy had the greatest effect.

INTRODUCTION

The ground vegetation beneath trees is often different from that of surrounding areas (Ovington, 1955). Such vegetational changes are especially apparent beneath isolated trees in savannas (Bray, 1955 cited in Curtis, 1959; Holland, 1973; Parker, 1977). Various aspects of the environment are modified by the trees relative to adjacent open areas, especially light intensity, temperature, soil moisture and soil nutrients. These factors all contribute to the patterns of the ground vegetation but, in some circumstances, one factor may be of particular importance. Changes in understory of Wisconsin oak savanna were found by Bray (1955) to be correlated with the amount of shade cast by the canopies. His data indicated three patterns of response, species peaking in frequency in either shade, intermediate or full sunlight conditions. Holland (1973) found differences in composition and relative density between the annual species beneath the deciduous canopies of solitary *Quercus douglasii* H. & A. and the surrounding central California grasslands. He concluded that the most important impact of the oak tree on the annual species was through the alteration of soil properties. Live oak trees *Quercus agrifolia* Née also occur in savannas in southern California annual grasslands. Parker (1977) found 44 species in the adjacent grasslands but only 17 beneath the oak canopies. Eight of these species were common to both habitats. This study characterizes those vegetational changes associated with live oaks and examines the contribution of different environmental factors to the distribution pattern.

METHODS

Vegetation analysis.—The study site was located in the E-W-trending Santa Ynez valley in southern Santa Barbara Co., Calif. An assortment of vegetation types are located here, their distribution being based upon slope, aspect and sometimes substrate differences. Annual grasslands are limited primarily to gentle slopes on fine soils in this area and often contain scattered and usually isolated oak trees. The percent cover method was used to determine relative dominance of herbaceous species in open grassland and under live oak canopy habitats of the study area at peak cover during the

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1974-1975 and 1975-1976 growing seasons (30 April-2 May 1975 and 5-7 May 1976, respectively). A point-frame with 10 pins spaced 1 dm apart (Tinney *et al.*, 1973; Brown, 1952) was used to determine plant cover. Four 30-m transects were randomly established in the grassland and the point-frame placed alternately every 3 m to the left or right of the transect line. Except in ravines, live oaks occurred as isolated individuals within the grasslands. Beneath those oaks ($N = 59$) whose canopies did not overlap and which were surrounded by grassland the ground surface was divided into four quadrants, each centered on the cardinal compass headings. Three randomly chosen point-frame samples were located in each quadrant (12 readings per tree, $N = 708$). Percent frequency was calculated from presence or absence per point-frame sample.

Environmental factor analysis.—Anderson (1964 a,b,c) has summarized the difficulties involved in accurately measuring light, especially under tree canopies. For this investigation, two methods were used to characterize the oak canopy and grassland habitats. The quantity of photosynthetically active radiation was determined under a number of canopies ($N = 7$) and open grassland areas ($N = 10$) with a Lambda quantum light meter (Li-Cor Model LI-185) and repeated on several days during the growing season between October 1976 and March 1977. Measurements were taken between 1000-1400 hr with a horizontal sensor 25 cm above the ground. In addition, a Weston ft-c meter (Model 756) was used to show fluctuations in the light intensity levels throughout the day for a single tree canopy. Readings were taken at 2-hr intervals 1 m from the trunk, at the canopy edge, and 2 m outside of the canopy along N-S and E-W transects.

Temperature was monitored at 2 cm above the ground and at depths of 2 cm and 5 cm in the soil. Data were collected weekly from a combination of hygrothermographs and max-min thermometers ($N = 8$ per habitat). Thermometers were placed 1 m N of the tree trunk and randomly in the grassland to determine the maximum differences between the two habitats. Vapor pressure deficit was calculated using data from recording hygrothermographs. Rainfall was measured weekly using rain gauges ($N = 2$) and soil moisture was measured biweekly in the 1-5 cm and 10-15 cm level by the gravimetric method ($N = 20$).

Five soil samples from the 1-5 cm and 10-15 cm levels in each habitat were randomly collected for textural, organic matter, pH and permanent wilting point analyses. The method of Bouyoucos (1936) was used for the textural analysis, weight loss on ignition (Baer, 1964) for organic matter and pH using the method of Black *et al.* (1965). Permanent wilting point of the soil was determined with a 15 bar soil-pressure plate (Soil Moisture, Inc., Santa Barbara, Calif.).

Soils were sampled for nitrogen at approximately monthly intervals throughout the 1975-1976 and 1976-1977 growing seasons. Each habitat was randomly sampled ($N = 5$) at the 1-5 cm and 10-15 cm depth. Available soil ammonium was extracted using 2N KCl by the method described by Bremner (1965). Analysis of the extraction for $\text{NH}_4\text{-N}$ was by the microdiffusion method of Tetlow and Wilson (1964) during 1975-1976 and by an Orion ammonia electrode (Orion Ammonia Electrode Handbook 1975) during 1976-1977. These techniques were calibrated against each other using standards and soil extracts. Soil nitrate was extracted by the method described by Bremner (1965) and analyzed for $\text{NO}_3\text{-N}$ using the phenol disulphonic acid method (Bremner, 1965) during 1975-1976 and by the Orion Nitrate Electrode method (Orion Nitrate Electrode Handbook 1976) during 1976-1977. These techniques were also calibrated against each other using standards and soils extracts.

In addition to monitoring the levels of soil nitrogen, throughfall was collected at six sites in both habitats, using the method of Hart and Parent (1974), and analyzed for ammonium and nitrate using the procedures outlined above for soil.

Field experiment.—A field experiment was designed to test for differential responses to soil and light of three dominant annuals. Two 100 m² areas were fenced, one in open grassland and one beneath several interlaced oak canopies. Seeds of three annuals were

individually planted in 4-inch pots filled with 500 g of sifted field soil from either the grassland or oak canopy area. Replicates of all six pot combinations (three species x two soils) were placed randomly in each site, level with the soil surface. The plants were germinated by the first winter rains, and after 2 weeks each pot was thinned to one plant. Because seeds of *Pholistoma auritum* would not germinate, individuals were transplanted into the pots from field collections of seedlings at the cotyledon stage. In 1975-1976, 16 pots per treatment (species x soil x habitat) were used; in 1976-1977, 12 pots per treatment.

For both seasons, the pots were collected after 12 weeks of growth and brought into the laboratory. Leaf punches (30 per treatment) were taken for leaf area:dry wt analysis. Plants were then harvested at ground level and dried for 48 hr at 75 C. Leaf area was calculated by weighing dried samples of known area to determine the area:dry weight relationship for each species in each treatment. The data for dry weight were analyzed by a factorial design analysis of variance (Snedecor and Cochran, 1973).

Light experiment. — Because temperature also varies concurrently with light between habitats, a growth experiment was performed in environmental chambers using different light levels with the same temperature regime. Three light levels were created with fiberglass screen: (1) 4-10 $\mu\text{E m}^{-2} \text{sec}^{-1}$ corresponding to light levels within growing annual plant cover beneath oak canopies; (2) 30-40 $\mu\text{E m}^{-2} \text{sec}^{-1}$ corresponding to light levels without sunflecks just above the annual plant cover, and (3) 450-600 $\mu\text{E m}^{-2} \text{sec}^{-1}$ corresponding to about $\frac{1}{4}$ full sunlight. An air temperature regime of 18 C day and 8 C night approximated average field temperature beneath the tree canopies for the 1st 4 weeks of the growth period for 1976. Ten 4-inch plastic pots per treatment were filled with 500 g of sifted oak habitat soil, were planted with six plants and thinned to four after 1 week. The pots were rotated within treatments every 4-5 days and the response of the three species was measured as increase in average aboveground dry weight per individual with increases in light.

Competition experiment. — A replacement series experiment (de Wit, 1960) was performed to test whether changes in field nutrient levels influenced the potential of *Bromus* and *Avena* to dominate. The grassland soils are lower in nitrogen than the oak habitat soils. A low nitrogen condition used 500 g of field-collected soil from the open grassland in 4-inch pots, and a high nitrogen condition used field collected soil from beneath *Quercus agrifolia*. Twice during the experiment, each treatment received modified Hoagland's nutrient solution. The low nitrogen condition received a solution adjusted to add 10 $\mu\text{g N}$ per g soil (10 ppm) [as $\text{Ca}(\text{NO}_3)_2$ and KNO_3], the field average at the beginning of the growing season, and the high nitrogen condition with Hoagland's adjusted to add 115 $\mu\text{g N}$ per g soil, the oak habitat average at the growing season start. This design used eight plants per pot: *Avena* in pure culture, three different mixtures of *Avena* and *Bromus* (6:2, 4:4, 2:6), and *Bromus* in pure culture. Each treatment had five replicate pots and the entire experiment was replicated twice. The pots were set up in five randomized blocks on a rotating table under greenhouse conditions with supplemental "Gro-lite" and U.V. lights. After 5 weeks, the aboveground portions were harvested, dried for 48 hr at 75 C and weighed.

RESULTS

Vegetation analysis. — There was a marked difference in the structure and composition of the annual vegetation between the two habitats. While a large number of species (44) were present, the grasslands were dominated by relatively few species (Table 1). *Avena fatua* with over 63% cover and *Bromus diandrus* with 20% cover were most abundant. *Bromus mollis* (12% cover) was less important than reported for other grasslands (Holland, 1973; Heady, 1977) and occurred mainly in drier or disturbed areas (*e.g.*, gopher mounds, animal trails). All other species combined amounted to less than 5% cover in undisturbed, ungrazed grasslands. Beneath the oak canopies, *Avena fatua* dropped to less than 6% cover while *Bromus diandrus* increased to 34% cover. Three

new annual species usually found in shaded areas became important (*Pholistoma auritum*, *Bowlesia incana* and *Galium aparine*). *Pholistoma auritum*, at over 37% cover, was codominant with *Bromus diandrus* beneath the oak canopies. The mean frequency of most species was high (Table 1), suggesting that the mixture of species found beneath any tree was generally the same. Even *Bowlesia incana*, with less than 4% cover, was found beneath 61% of the trees. *Avena fatua*, with more cover than *Bowlesia incana*, was found far less frequently beneath the canopies.

Environmental factor analysis.—Several environmental factors were significantly different between the habitats. The quantum flux of light beneath the live oak canopy averaged about 2% of that outside the canopy on a sunny day (Table 2). Each tree canopy is variable in the pattern, size and number of sunflecks. The sunfleck values ranged naturally from just above full canopy shade to full sunlight and averaged about 30% of full sun. The median value was 10% of full sunlight, reflecting the large numbers of sunflecks with low light values. In addition to sunflecks, location of the canopy shadow varied throughout the day, differentially raising light levels, especially on the S side. This pattern was accentuated by the low angle path of the sun in the winter growing season. Except for the N side, the canopy edges received close to full sunlight for extended periods while interior areas generally did not exceed 10% of full sunlight, although some locations received as much as 60% full sunlight for at least a portion of the day.

The interception of solar radiation and reduction of reradiation combined to moderate diurnal temperature fluctuations beneath the canopies compared to the open grassland (Fig. 1). During both growing seasons in which temperature was monitored, the grassland maximum at 2 cm above the soil averaged about 5 C higher and the grassland minimum about 6 C lower than the canopy areas. Soil temperatures fluctuated even more in the grassland habitat; at the 2 cm depth the grasslands experienced a 20 C greater diurnal range on occasions. Temperature ranges in both habitats were small, however, at the 5 cm depth, although the grasslands did in general experience a greater seasonal and daily range of temperature than the oak canopy areas. Following heavy rains there was little difference in soil temperature between the two habitats.

The soils of the two habitats were similar clay loams. Soil pH did not differ between

TABLE 1.—Percent cover and frequency of species in open grassland and beneath *Quercus agrifolia*

Species	Grassland habitat		<i>Q. agrifolia</i> habitat		
	% cover	% freq	% cover	% freq	% freq/tree
<i>Avena fatua</i>	64	100	5	19	47
<i>Bromus diandrus</i>	20	87	34	77	100
<i>Bromus mollis</i>	12	60	0	0	0
<i>Bromus rubens</i>	2	3	0	0	0
<i>Pholistoma auritum</i>	0	0	38	73	93
<i>Galium aparine</i>	0	0	12	62	93
<i>Bowlesia incana</i>	0	0	4	15	61
all others	4	27	5	12	69

TABLE 2.—Mean quantum flux \pm 95% confidence intervals in $\mu\text{Einsteins m}^{-2} \text{sec}^{-1}$ on a clear day between 1000 and 1400 hr on 8 October 1976 (N = 20 except for sunflecks where N = 35)

Open grassland	2024.75 \pm 18.92
Oak canopy shade	33.70 \pm 7.90
\bar{x} Sunfleck	628.73 \pm 286.31
Shade under annual vegetation beneath oak canopy	6.46 \pm 3.23

habitats in the upper layers ($pH = 6.6$), but the grassland soils were slightly more acidic ($P < 0.05$) at the lower depths (10-15 cm). The structures of the upper soil strata were, however, greatly different. Organic matter is important in the development of aggregate structure in a soil and the oak canopy soils had about twice the amount of organic matter at the 1-5 cm level (11.1% vs. 6.0%, $p < 0.01$). Even more organic matter was concentrated near or at the soil surface of the oak canopy areas. Differences in soil organic matter disappeared gradually at depths of 12 cm and below. The oak canopy soils had higher permanent wilting points at the 1-5 cm level ($p < 0.02$), but these differences also disappeared with depth. Except during extended droughts, soil moisture was significantly higher ($p < 0.05$) beneath the live oaks at both the 1-5 cm and 10-15 cm levels during the growing seasons. Vapor pressure deficits were significantly lower ($p < 0.05$) beneath the oaks due to higher humidity and lower maximum temperatures.

Ammonium was measured throughout the growing season only during 1976-1977. Both habitats were low in ammonium, typically less than 2 ppm, and there were usually no significant differences between them. This was especially true of periods following the autumn rains after which germination typically occurs.

Nitrate patterns were, however, very different between the two habitats. Levels of nitrate were always significantly greater and more variable in the oak habitat soils (Table 3). Amounts of NO_3-N in the 1-5 cm depth beneath the oaks averaged more than the lower depths and ranged in samples from 10 ppm to over 200 ppm. Within the oak habitat there were also significant differences between years; the 1975-1976 growing season, for example, averaged less than the seasons before or after. The grasslands averaged less than 5 ppm at the beginning of annual growth, falling to only trace amounts as the season progressed.

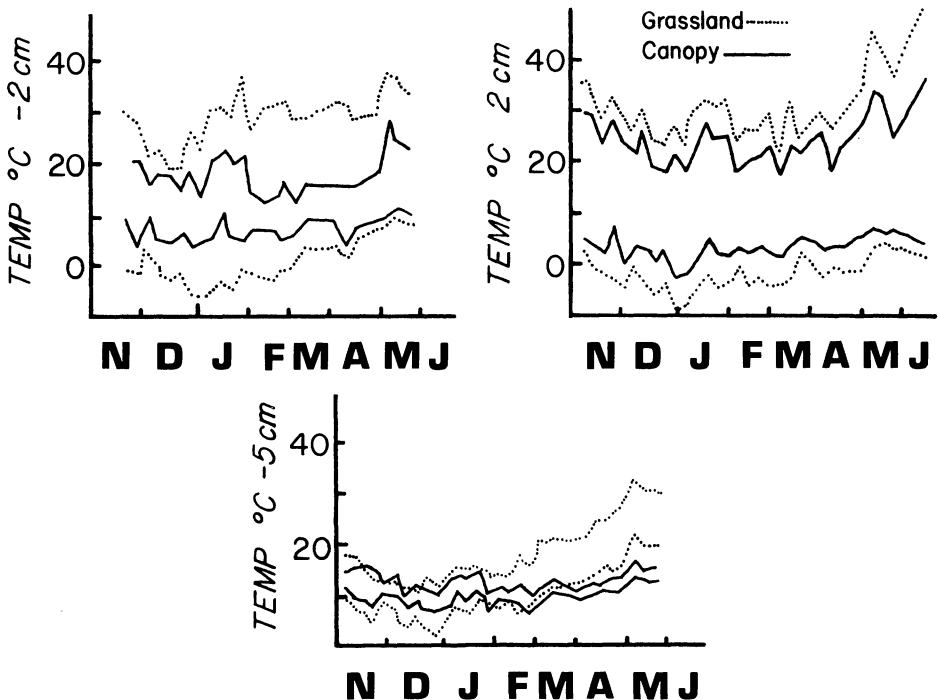


Fig. 1. — Maximum and minimum temperatures for the 1975-1976 growing season in both oak canopy and grassland habitats at 2 cm above the soil and at depths of 2 cm and 5 cm

Considerable nitrogen entered the oak canopy soils from throughfall, ranging from 65 to over 260 mg m² nitrogen for storms with more than 15 mm rain (smallest rain measurable by our technique) (Table 4). Levels of nitrogen in rainwater falling on grasslands were always below the sensitivity of the technique (1 ppm).

Field experiment.—Conditions differed following the initiating rains of the two seasons the field experiment was run. The first season's temperatures were low for the early stages of growth and subsequent rainfalls were frequent. An unusual tropical storm initiated the second season's germination and for the duration of this replication drought and warm temperatures prevailed. *Pholistoma* data are not available for this second season (1976-1977) because of a fatal fungal disease which started among the naturally occurring, drought-stressed *Pholistoma* plants spreading to the experimental plants (Table 5). Treatment of the data by ANOVA indicated highly significant results ($p < 0.0001$) for the responses of each species to light differences, soil differences and a light-soil interaction. Several trends are apparent in these data. Regardless of soil treatment, *Avena fatua* was always the most productive in full sun and increased in production proportionately more than the other two species in full sun. Although all sources of variance were highly significant, in the case of *Avena*, light accounted for a higher percentage (35%) of the variability. On the other hand, *Avena* was, in all cases but one, the least productive in the shade, especially in oak soil. Under the same conditions of shade and oak soil, *Pholistoma* was over twice as productive as either grass. Comparing just the two grasses, *Bromus* was more productive than *Avena* in shade with one exception.

Pholistoma responded most to soil changes, and the soil factor accounted for most of its variability (47%) in the ANOVA. Relative increases in production were highest in

TABLE 3.—Mean ppm soil NO₃-N ± 95% confidence intervals for the 1975-1976 and 1976-1977 growing seasons

	Grassland soil		Oak canopy soil	
	1-5 cm	10-15 cm	1-5 cm	10-15 cm
31 October 1975	trace ^c	trace ^a	15.33 ± 3.87	1.83 ± 1.84
5 December 1975	4.57 ± 0.50 ^c	2.12 ± 0.62 ^b	50.80 ± 22.99	6.77 ± 2.92
16 January 1976	3.30 ± 2.08 ^c	1.94 ± 0.76 ^c	11.89 ± 3.78	5.92 ± 1.55
13 February 1976	2.30 ± 2.16 ^a	2.34 ± 1.49 ^a	25.10 ± 16.7	9.90 ± 6.77
12 March 1976	2.97 ± 1.98 ^c	trace ^c	14.62 ± 2.70	8.54 ± 2.41
19 May 1976	trace ^b	trace ^a	19.93 ± 4.89	9.56 ± 1.41
24 September 1976	4.37 ± 1.83 ^b	3.09 ± 0.76 ^a	133.11 ± 26.16	55.60 ± 26.6
22 October 1976	trace ^b	trace ^b	34.60 ± 15.9	19.26 ± 7.75
30 November 1976	trace ^b	trace ^b	70.87 ± 32.9	25.81 ± 10.8
24 January 1977	trace ^b	trace ^b	48.89 ± 31.3	21.78 ± 7.91
2 March 1977	trace ^b	trace ^b	61.19 ± 29.8	31.71 ± 19.9

^aSignificant difference exists between the grassland and oak canopy soils at the same depth at $p < 0.05$

^b $p < 0.01$

^c $p < 0.001$

TABLE 4.—Inorganic nitrogen in throughfall as mg NO₃-N or mg NH₄-N/m² ± 95% confidence intervals. All rainfalls over 15 mm in the 1976-1977 season are shown

	mg NO ₃ -N/m ²	mg NH ₄ -N/m ²
1976-1977		
11 November 1976	144.3 ± 41.9	75.1 ± 11.2
5 January 1977	264.2 ± 29.5	161.5 ± 32.9
12 January 1977	23.9 ± 3.9	41.4 ± 6.7
17 March 1977	151.1 ± 24.76	177.4 ± 3.6

Pholistoma comparing grassland to oak soils, particularly in the shade. *Bromus* was more responsive than *Avena* to the soil variable and was proportionally more productive than *Avena* in oak soil.

The dominant species in the oak canopy areas (*Pholistoma* and *Bromus*) responded most to the increased nutrient levels of the oak soil under shaded conditions. In all treatments but one, *Pholistoma* produced the greatest leaf area per individual, and in all cases *Bromus* produced more than *Avena* (Table 6). *Pholistoma* produced its largest leaf areas in the shaded treatments, whereas both grasses did so in full sun. *Bromus* produced proportionately more leaf area than *Avena* in shaded treatments, especially in the more fertile oak soil. Allocation of photosynthate between leaves and stem differed among the species. A smaller percentage of aboveground dry weight was allocated to leaf production in *Avena* than in the other two species. In shade in oak soil, for example, *Avena* allocated 52% of aboveground dry weight to leaves, *Bromus* 61% and *Pholistoma* 63%.

Light experiment. — Because the growth chambers were limited to $\frac{1}{4}$ full sunlight and as this approximated mean sunlight and gap light beneath the canopies, responses in the growth chamber light experiment were considered responses of plants in the shaded habitat (Table 7). Two lower light levels were used corresponding to constant heavy oak shade and to the low levels within the ground vegetation in oak shade. At these low light levels, *Pholistoma auritum* increased most in dry weight. While *Bromus diandrus* had a slightly higher average aboveground production than *Avena fatua* at the highest light level ($p < 0.05$), the difference was smaller than the differences between the grasses and *Pholistoma*. The proportional differences are similar to the oak shade-oak soil results produced in the field (Table 5).

Although growth was slow, counts of the numbers of leaves during the experiment indicated that even the lowest light levels were above the compensation point for *Pholistoma auritum*. The grasses grew even more slowly and the dry weights at this lowest light level were probably a reflection of seed weight, since, similar to seed weight differences, *Avena* seedlings were approximately 70% larger. With increases of light from this lowest level, *Pholistoma* production increased the most, 379% at the intermediate light treatment, and 5254% at the highest light treatment value. *Bromus diandrus* increased in the highest light intensity to 3540% of its size in low light and *Avena* increased only 1941%.

In all these experiments, light was clearly an important differentiating factor among these three species. As discussed earlier, light levels are highest on southern sides of canopies and diminish towards the N side. To test the responses of the dominant annuals to intracanalopy variation in light, a cross-classification ANOVA (Snedecor and Cochran, 1973) was performed on the cover data relative to species distribution in four quadrants, each centered about the cardinal compass directions.

TABLE 5. — Field growth experiment mean dry weight values \pm 95% confidence intervals in mg per individual. ANOVA results $p < 0.0001$ with each species for light, soil and light-soil interaction. Values with shared letters within rows are significantly different at $p < 0.05$ or smaller

Species	Treatment			
	Grassland soil (Low N)		Oak soil (High N)	
	Oak shade	Full sun	Oak shade	Full sun
1975-1976				
<i>Avena fatua</i>	154.9 \pm 58.8 ^a	398.3 \pm 149.3 ^a	213.2 \pm 58.1 ^a	1779.3 \pm 412.6 ^a
<i>Bromus diandrus</i>	137.4 \pm 30.9 ^{ab}	247.3 \pm 36.9 ^a	250.5 \pm 31.5 ^b	1136.2 \pm 168.2 ^{ab}
<i>Pholistoma auritum</i>	154.9 \pm 40.6 ^a	280.9 \pm 51.9 ^a	513.3 \pm 102.6 ^a	1188.1 \pm 219.8 ^a
1976-1977				
<i>Avena fatua</i>	88.1 \pm 37.0 ^{ab}	162.2 \pm 56.2 ^a	167.9 \pm 61.8 ^b	496.4 \pm 238.2 ^{ab}
<i>Bromus diandrus</i>	121.9 \pm 40.8 ^a	112.0 \pm 66.0 ^b	278.3 \pm 81.8 ^{ab}	471.1 \pm 102.6 ^{ab}

For all species tested, except *Galium aparine*, there was significant variation in cover among the quadrants ($p < 0.0001$ for *Avena fatua*, *Bromus diandrus* and *Pholistoma auritum*; $p < 0.01$ for *Bowlesia incana*). The distributions of the two grasses (*B. diandrus* and *A. fatua*) within the four quadrants showed a similar trend (Table 8). Both species had their greatest percent cover in the southern quadrants and the least in the northern. Forty-two percent of the total cover of *A. fatua* was in the southern quadrant, whereas *B. diandrus* had 32% of its total cover in the southern quadrant. The intracanopy distribution for the three woodland annuals differed from that of the grasses (Table 8). Both *Pholistoma auritum* and *Bowlesia incana* differed significantly in their cover between their northern and southern quadrants. For *Galium aparine* the trend is the same but the differences were not statistically significant.

Competition experiment. — *Bromus* becomes dominant over *Avena* beneath the live oak canopies. This dominance shift is present with or without *Pholistoma auritum*. A competition experiment using a replacement series design (de Wit, 1960) was performed between the grasses at two field nutrient levels: low and high nitrogen. At low-nitrogen levels in pure culture, *Avena* was nearly 30% larger than *Bromus* (Fig. 2A). In mixture, *Avena* increased in size per individual ($p < 0.01$) and consequently pot totals increased while in the same treatments *Bromus* was apparently unaffected by *Avena*. In the high nitrogen treatments *Bromus* increased in size relative to *Avena* (only 5% smaller) (Fig.

TABLE 6. — Field growth experiment mean leaf area values \pm 95% confidence intervals for 1975-1976 in dm^2 per individual. Values with shared letters within rows are significantly different at $p < 0.05$ or less

Species	Treatment			
	Grassland soil		Oak soil	
	Oak shade	Full sun	Oak shade	Full sun
<i>Avena fatua</i>	0.1379 \pm 0.0524 ^a	0.1820 \pm 0.0609 ^b	0.1945 \pm 0.0520 ^c	0.7169 \pm 0.1421 ^{abc}
<i>Bromus diandrus</i>	0.1970 \pm 0.0398 ^a	0.1963 \pm 0.0277 ^b	0.3488 \pm 0.0496 ^{ab}	0.9760 \pm 0.1419 ^{ab}
<i>Pholistoma auritum</i>	0.5125 \pm 0.1370 ^a	0.4654 \pm 0.0792 ^b	1.0281 \pm 0.2224 ^{abc}	0.3744 \pm 0.0653 ^c

TABLE 7. — Growth chamber light experiment results as mean dry weight \pm 95% confidence intervals in mg per individual. Percentages of the values relative to the low light treatment are given below the numbers

Species	Light treatment		
	4-10 $\mu\text{Em}^{-2} \text{sec}^{-1}$	30-40 $\mu\text{Em}^{-2} \text{sec}^{-1}$	400-600 $\mu\text{Em}^{-2} \text{sec}^{-1}$
<i>Avena fatua</i>	11.8 \pm 2.2	19.0 \pm 4.4	229.1 \pm 9.9
	100%	161%	1941%
<i>Bromus diandrus</i>	7.3 \pm 1.0	15.3 \pm 1.2	258.4 \pm 33.1
	100%	210%	3540%
<i>Pholistoma auritum</i>	8.1 \pm 1.0	30.7 \pm 2.6	425.6 \pm 32.9
	100%	379%	5254%

TABLE 8. — Distribution of annual species beneath the live oak canopies expressed as % of each species average total cover \pm 95% confidence intervals. Values with shared letters within rows are significantly different at $p < 0.05$ or smaller

Species	Quadrant			
	North	East	West	South
<i>Avena fatua</i>	16.3 \pm 6.7 ^a	20.5 \pm 7.9 ^b	19.3 \pm 6.7 ^c	43.9 \pm 12.9 ^{abc}
<i>Bromus diandrus</i>	18.7 \pm 3.1 ^{ab}	22.9 \pm 2.9 ^a	26.07 \pm 3.37 ^b	32.23 \pm 3.37 ^{ab}
<i>Pholistoma auritum</i>	30.4 \pm 3.4 ^a	27.0 \pm 3.4 ^b	24.9 \pm 3.4 ^a	17.8 \pm 3.0 ^{ab}
<i>Bowlesia incana</i>	33.1 \pm 12.0 ^a	23.3 \pm 10.5	30.8 \pm 12.0 ^b	12.78 \pm 6.0 ^{ab}
<i>Galium aparine</i>	25.7 \pm 4.3	26.9 \pm 3.9	24.5 \pm 3.6	22.8 \pm 3.9

2B). *Avena* increased again in mixture ($p < 0.05$ for pure culture vs. 50% mixture, $p < 0.0001$ for others) while *Bromus* was unaffected. Neither plant exerted a negative influence on the other at either low- or high-nitrogen conditions. *Avena* in fact apparently grew significantly better when in mixture with *Bromus*.

DISCUSSION

Remarkable vegetational changes were associated with the live oak trees. The greatest differences existed between tree canopy area and grassland composition and structure (Table 1); however, distinct patterns also occurred within the canopy area (Table 8). This led to the testing of several hypotheses about canopy effects current in the literature (e.g., Moir, 1966; Anderson *et al.*, 1969; Holland, 1973; Veblen *et al.*, 1979). While these investigators emphasized the impact of one or a few factors, each implicitly recognized the complexity of these situations. The relative influence of some factors will differ by a great degree from year to year. Our emphasis was on differential responses of the dominant annuals to changes in several predominant factors.

Light or soil differences are commonly suggested as controlling influences. The reciprocal transplant field experiment, in particular, and other tests confirmed the long-term importance of these factors. For example, according to Munz (1974) and Searcy (1970), *Pholistoma auritum* is restricted to partially shaded habitats. Its field distribution in this study confirmed this. Additionally, individuals of *P. auritum* in the field experiment were morphologically greatly modified in size and shape in the full sun treatments compared to individuals from shaded habitats. Total leaf area of *Pholistoma* individuals was also much greater in shaded treatments (Table 6) relative to corresponding full sun treatments (in contrast to the grasses), both characteristics of shade-tolerant plants (Björkman and Holmgren, 1963). *Pholistoma* was, furthermore, the most productive of the three annuals under shaded conditions. It was twice as pro-

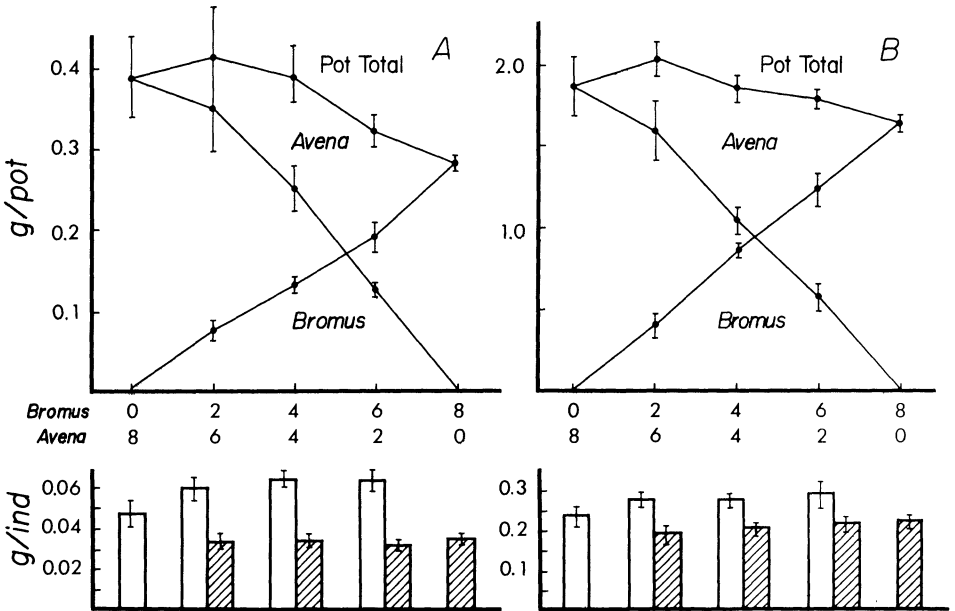


Fig. 2. — Competition experiment results as mean total g per species and per pot \pm 95% confidence intervals. Results as mean g per individual \pm 95% confidence intervals are presented below, clear bars for *Avena fatua*, cross-hatched bars for *Bromus diandrus*. The low nitrogen condition is shown in "A," the high nitrogen condition in "B"

ductive as the grasses in both the field experiment (Table 5) and the growth chamber experiment (Table 7).

Avena was the most productive of the annuals under full sunlight and, in proportion, especially so when soil nutrients were low as is typical for grassland areas (Table 5). *Bromus* had the larger leaf area and was the more productive of the two in shade, especially with the higher soil nutrient levels typical of the oak canopy habitat (Tables 5, 6, 7). The relative differences between *Bromus* and *Avena* were similar both in the field and under controlled conditions (compare Table 5, oak soil and shade, with Table 7, column on right). These responses correspond to the distribution patterns of these two grasses, *Bromus* being more abundant beneath the live oaks, *Avena* more abundant in open grasslands. A more detailed comparison between these two grasses was later completed by Mahall *et al.* (1981) and supports the above findings. In their study of plants grown under low light conditions, *Bromus diandrus* had more than twice the relative growth rate of *Avena fatua*. Because the net photosynthetic rates per unit area were not significantly different at low light levels, growth rate differences were accounted for in part by greater leaf areas in *Bromus* and in its unit leaf-area growth rate exceeding that of *Avena* by 60%. On the other hand, *Avena fatua* was interpreted as relatively more sun-adapted in respect to light-saturated photosynthetic rates (30% higher) and levels of soluble protein (over two times greater).

Holland (1973, 1980) reported that both *Avena fatua* and *Bromus diandrus* increased in density and productivity beneath isolated *Quercus douglasii*, a deciduous oak, relative to surrounding open grasslands. Holland believed soil differences were primarily responsible for productivity differences. These canopies, however, are without leaves for the first half of the annual plant growing season and consequently do not produce a shaded environment during the critical seedling establishment stage. Similar to Holland's findings, *B. diandrus* and *A. fatua* were also observed to dominate the annual vegetation beneath the deciduous *Quercus lobata* Née, which occasionally occurs with *Q. agrifolia* in the grasslands under study here. Like *Q. douglasii* in Holland's study, *Q. lobata* lacks leaves during the first half of the annual plant growing season. The reversal of the importance of *A. fatua* beneath the evergreen *Q. agrifolia* as compared with the deciduous oaks suggests that *Avena* is very sensitive to shade. *Bromus diandrus* increased in importance both in Holland's study and in this study beneath an evergreen oak, the latter suggesting a relative tolerance of the grass to shade as found by Mahall *et al.* (1981). On the other hand, shade-tolerant herbs like *Pholistoma auritum* and *Galium aparine* were rarely, if ever, found beneath the deciduous *Q. lobata*, re-emphasizing their dependence upon the low irradiance beneath live oak canopies.

While the distributional differences and relative growth responses among the annuals correlated well with changes in light, changes in soil characteristics were also important. Nitrogen was the limiting soil mineral nutrient for all three species in both habitats (Hull and Muller, 1976; Parker, 1977). Between the two habitats, however, there is a substantial difference in the levels of available nitrogen (Tables 3, 4). The sources of these differences were not specifically determined; however, it must be in part a result of the breakdown of oak litter in an area much smaller than the range of the rooting system and in part a result of the large canopies acting as effective collectors of dry fallout. In any case, throughfall added significant amounts of nitrogen (Table 4). Tukey (1970) has shown the removal of these ions by leaching and Schlesinger and Hasey (1980) have also shown high inputs of nitrogen as dry fallout in an area less than 30 km from this study. The grassland would receive little nitrogen through rainfall since less than 0.20 ppm NO₃-N and 0.02 ppm NH₄-N are reported for rainfall in this area (Schlesinger and Hasey, 1980).

Under full sunlight, all of the annuals responded significantly to the higher soil nitrogen levels, especially *Avena fatua* (Table 5). In shaded treatments, *Pholistoma* and *Bromus*, however, grew better than *Avena* in the oak soil. Under shade and oak soil conditions, *Pholistoma* increased 3-6 times as much as *Bromus* and *Avena*, respectively,

which may reflect more a shade limitation for the grasses than a differential stimulation for *Pholistoma*.

Fertilization experiments in California grasslands have shown that brome species tend to dominate areas in which the major nutrient deficiencies are removed (Jones, 1963; Walker and Williams, 1963). Jones and Winans (1967) found that *Bromus diandrus* usually dominated heavily fertilized areas. Hull and Muller (1976) observed increases in size, yield and density of *B. diandrus* with fertilization, whereas *Avena fatua* decreased in yield and density in the same treatments. The substantial mineral nutrient differences between the oak canopy and open grassland habitats (Tables 3, 4; Parker, 1977) may thus also play an important role in the changes in annual vegetation, especially with regard to *B. diandrus*. As a result of the increased levels of nutrients beneath the oak canopies, *B. diandrus* might compete more vigorously and thereby tend to exclude *A. fatua* from the canopy areas. The competition experiment, however, showed that under both low and high nutrient levels, the biomass of *Avena* was greater in mixture than in pure culture and *Bromus* showed no biomass changes among treatments (Fig. 2). In the high nitrogen treatment, however, *Bromus* did show a substantial proportional size increase relative to *Avena*. McCown and Williams (1968) found in competition studies between *B. mollis* and *Erodium botrys* that *Erodium* always removed the largest share of nutrients and, therefore, at low levels significantly reduced the growth of *B. mollis*. At the higher nutrient levels, however, *B. mollis* was able to depress the growth of *Erodium* by overtopping the shorter plant, and at high densities limited the levels of light received by *Erodium*. While *B. diandrus* did not depress the growth of *Avena fatua* by nutrient-related competition in this study, it is possible that the relatively more robust *B. diandrus* plants may be able to reduce growth of *Avena* in the dense seedling stands in the canopy shade simply by shading the more shade-intolerant and slower-growing *Avena* seedlings. The lower productivity and smaller leaf area of *Avena* plants compared to *Bromus* combine to suggest that in the shaded habitat created by oak canopies any further decrease in light may result in the exclusion of *Avena* from the canopy habitat.

While light and soil changes are important, other factors contribute to the observed vegetation patterns. In shifting from a shaded habitat to an open one, temperature and drought stress also vary concurrently with light and probably contribute significantly to those distribution patterns in some years. For example, whereas much less than average rainfall fell both years, the second season could be considered more stressful for the experimental plants due to the pattern of rainfall. In the second season, no rain fell after the 2nd week following germination and the temperatures were warm instead of the usual colder temperatures of winter. The experimental plants were dependent upon once weekly supplemental watering. The differential impact of this drought stress on the growth of the three dominant annual plants can be seen in Table 5. For both grasses, growth in the open, more stressful habitat decreased in the drought season (1976-1977) over 50% compared to the preceding year. Growth of the grasses in the shade was not as affected by the drought and warmer temperatures, and all shade treatments increased in the 1976-1977 season in proportion to the full sun treatments compared with the previous year. Whereas *Avena* produced less in all treatments compared with 1975-1976, growth of *Bromus diandrus* increased in the shaded treatments with oak tree soil and about the same in grassland soil. During this drought, a fatal fungus epidemic spread throughout the *Pholistoma* populations. While this may have been coincidental, it is also possible that the drought contributed to the susceptibility of *Pholistoma* to the fungus.

Other types of biotic influences also play a role in the vegetation patterning. Seed caches of several types indicated no differential impact of grazing by either insects or larger animals among the species or between the habitats (Parker, 1977). Within each habitat, however, there was considerable variation in seed cache predation which indicates that particular locations experience animal impacts to very different degrees.

Vegetation changes beneath trees are often the result of allelopathic interactions between the tree and the ground flora (del Moral and Muller, 1969, 1970; DeBell, 1971; Jameson, 1971; del Moral *et al.*, 1978). Laboratory and field germination tests revealed no such influence in this case (Parker, 1977). Among the annuals, however, Parker and Muller (1979) found *Pholistoma auritum* strongly dominated the grasses allelopathically.

The presence of these live oaks scattered in the annual grasslands is essentially a transitional overlap between two vegetation types. The responses of the component annual species in this circumstance illustrate that the process of spatial vegetation change results from the influence of many environmental factors. Some of these factors are long-term and continuous in their impact, *e.g.*, light and soil changes, and their relative influence on the same time scale may be more significant. Other physical environmental and biotic factors, however, which may not be continuous in time or space, *e.g.*, drought or allelopathy, also contribute their influence to the structure and composition of the associated annual vegetation.

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