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FACILITATION AND INTERFERENCE OF *QUERCUS DOUGLASII* ON UNDERSTORY PRODUCTIVITY IN CENTRAL CALIFORNIA¹

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Abstract. Controversy over the effect of *Quercus douglasii* on the productivity of California grassland has been fueled by conflicting reports. In some studies, understory grassland productivity was <25% of open grassland productivity, whereas in other studies understory productivity exceeded 200% of that of surrounding grassland. We examined light, temperature, soil nutrients, soil moisture, and fine tree root distributions under selected *Q. douglasii* trees (12 that appeared to have suppressive effects on understory productivity, and 12 that appeared to enhance understory productivity) in order to determine how variations in these factors were associated with the differences in understory grassland productivities. We found that grassland productivity is likely to be facilitated by nutrient inputs via litterfall and throughfall under all trees, but that trees with low understory grassland productivities had substantially higher amounts of fine roots in the upper 50 cm of soil and much lower predawn xylem pressure potentials than trees with high understory productivities and presumably deeper root systems. Root exclosures reduced the negative effects of these trees on the dominant understory grass species, and further experiments indicated that the negative effects of the tree roots may partially result from allelopathic oak root exudates. Thus, shallow fine tree roots may inhibit understory productivity, and variations in *Q. douglasii* root morphology may explain the intertree variations in facilitating/interfering effects on understory species.

Key words: allelopathy; California; canopy effect; competition; facilitation; grassland; interactions; interference; oak woodland; Quercus; roots; savanna; soil nutrients.

INTRODUCTION

Most of the interactions between plant species that have been reported in the literature fall into one of two categories: facilitation, the positive effect of one species on another species, or interference, the negative effect of one species on another. We use the term "interference" as inclusive of competition and allelopathy, sensu Harper (1961). Interspecific interactions do not occur in isolation from each other, and the overall effect of one species on another may be dependent on physical factors and the combination of competition for different resources, allelopathic chemicals released into the environment, and facilitative factors such as shade and protection from herbivory.

Previous research indicates that these different mechanisms by which plants interact may have a cumulative effect. Allelopathy has been reported to act in concert with resource competition as a factor influencing the overall interactive effect of a species (Chambers and Holm 1965, Bucholtz 1971, Bell and Knoppe 1972, McPherson and Thompson 1972). Additionally, Muller (1953) and Muller and Muller (1956) reported

that several species of desert shrubs, which had facilitative effects on the distribution and growth of annual species, also produced toxins that suppressed the growth of the same annuals under greenhouse and laboratory conditions. This suggests that the overall facilitative effects of shade provided by these shrubs on the annuals may have masked the allelopathic potentials of the shrubs. Interactive effects of canopy facilitation and belowground interference have been suggested by Ellison and Houston (1958) who reported that the growth of some species under aspen was stunted unless aspen roots under them were killed by trenching, and that the growth of these species after trenching exceeded that in the surrounding open areas. Walker and Chapin (1986) reported that stands of *Alnus tenuifolia* facilitated the seedling growth of other species through the addition of soil nitrogen, but that this effect was outweighed by competitive inhibition of the seedlings by root competition and shading. Franco and Nobel (1989) reported that facilitative effects of nurse plants in the Sonoran Desert improved seedling survival even though shading and competition for water reduced seedling growth.

In reviews of competition Connell (1983) and Schoener (1983) reported 12 different examples of plant com-

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petition that varied temporally or spatially in intensity, indicating that the effect of one species on another changes in response to variability in the physical and biological environment. Although the intensity of interspecific interactions may vary, to our knowledge there is no example in the literature of a plant species whose cumulative effect on other species may be either facilitative or interfering depending on variations in the intensities of the mechanisms of these interactions.

We chose to investigate facilitative and interfering effects of *Quercus douglasii* H. & A. (blue oak) on the productivity of understory grasses and forbs because both negative (e.g., Murphy and Crampton 1956, Kay and Leonard 1980, Kay 1987) and positive (e.g., Holland 1980, Holland and Morton 1980) effects have been reported. We have also observed a continuum in variation between these two extreme effects of *Q. douglasii* on understory growth at our study site in the central Coast Ranges of California. Here we have found apparent facilitating ("positive") and interfering ("negative") trees growing within several metres of each other. In this paper we investigate several mechanisms by which *Q. douglasii* and understory species may interact simultaneously, and whose independent variations in intensity may determine whether an individual *Q. douglasii* facilitates or interferes with its understory.

STUDY AREA AND SPECIES

We conducted this study at the University of California Hastings Natural History Reservation in the Santa Lucia Mountains of central California. The climate is Mediterranean, with 90% of the annual precipitation of 540 mm occurring between November and April. Monthly mean minimum temperatures range from 1.4°C in January to 9.7°C in August, and monthly mean maximum temperatures range from 8.5°C in January to 20.1°C in July.

Q. douglasii is a California endemic, but it is widespread within the state (Griffin and Critchfield 1976). Even though the climate in which it occurs is characterized by winter rain and summer drought, it is winter-deciduous, and leafs out in mid-March and drops its leaves between November and December. The morphology of *Q. douglasii* is variable. At reproductive maturity, height ranges from 5 to 25 m, diameter at breast height (dbh) from 15 to 150 cm, leaf length from 1.5 to 6.0 cm, and acorn mass from 2 to 12 g (R. M. Callaway, *personal observation*). Morphological variability appears to be partially correlated with topographical and other environmental conditions (R. M. Callaway, *personal observation*); although hybridization with other oaks in the subgenus *Lepidobalanus* including *Q. lobata* Nee (valley oak) and *Q. turbinella* Greene subspecies *californica* Tucker (desert oak) does occur in the general area of our study sites.

Three species of grass were dominant in the open grassland and in the oak understories: *Avena fatua* L., *Bromus mollis* L., and *Bromus diandrus* Roth., all of

which are European annual grasses that have become naturalized in grasslands throughout much of California. The grassland at Hastings has not been grazed by livestock for over 60 yr.

Measurements were taken in two different sites dominated by *Q. douglasii*. The first site was a south-facing savanna, with scattered individual trees and small groups of trees and a total tree density of 100 per hectare. Slope angles in the savanna site ranged from 5 to 10%, and the site was underlain by Vaqueros sandstone. The second site was a north-facing woodland, with the canopies of most trees touching other tree canopies and scattered pockets of open grassland among the trees. Tree density was 690 per hectare, slope angles ranged from 5 to 20%, and the site was underlain by Santa Lucia granite.

METHODS

Open grassland and oak understory productivity

Biomass under individual *Q. douglasii* canopies appeared to vary continuously from understories with much higher biomass than nearby open grassland to understories with much lower biomass than open grassland. Because our sampling design was not intended to measure the range and scale of the effects of *Q. douglasii* on understory plants, we nonrandomly chose trees with understories with clearly lower biomass or higher biomass than the surrounding open grassland to represent the extremes in the continuum. We sampled 12 trees in each site (south-facing savanna or north-facing woodland), 6 trees with understory biomass that was exceptionally high ("positive trees"), and 6 trees with understory biomass that was exceptionally low ("negative trees"). To reduce the effect of microsite factors not caused by oaks we sampled trees as close to each other as possible and on similar slope angles, aspects, and positions.

Grassland biomass was sampled between 20 and 24 April 1987 in random locations in the open savanna and in openings in the woodland. In each site, above-ground vegetation was collected from 40 $\frac{1}{8}$ -m² plots, separated by species and sorted for the current year's growth, which was dried at 60°C for 3 d and weighed. At the same time, understory biomass was sampled using five $\frac{1}{8}$ -m² plots under each tree canopy. Because the biomass sampled represented one year's growth (over 95% of the herbaceous biomass was composed of annual species) the data are presented as annual productivity. We refer to the sampling areas of positive trees, negative trees, and open grassland as "habitats" within a site.

Aboveground biomasses of individual plants of the three dominant understory species, *A. fatua*, *B. diandrus*, and *B. mollis*, were compared among habitats by clipping 10 randomly chosen plants of each species under 3 positive and 3 negative trees and 40 randomly chosen plants from the open in both sites in April,

1988. The clipped plants were dried at 60°C for 3 d before weighing. Annual productivity (sampled as above) of understory and open grassland was also compared on transects that were aligned at due north and that began at tree trunks and ended 8 m outside of the edges of the canopies. Seven 1/8-m² quadrats were located at 1/4, and 1/2 the distance between the trunk and the canopy edge, 50 cm inside the canopy edge, 50 cm outside the canopy edge, and 2, 4, and 8 m outside the canopy edge on each quadrat. Transect samples were taken at four positive trees and four negative trees in the savanna.

Light and temperature

Light interception by *Q. douglasii* canopies was measured in the savanna under four negative and four positive trees, one day per month, throughout the growing season of the understory plants. Stacks of 40 squares (2 × 2 cm) of light-sensitive blueprint paper were enclosed in opaque containers and exposed through 0.5-cm holes in the tops of the containers. Collectors were placed at each cardinal compass point, midway between the canopy edge and the trunk of each of the eight trees, and at three random locations in the open grassland, and were left out throughout the entire day. After sunset, the sheets were developed in ammonia vapors, and comparisons of the number of exposed sheets provided measurement of relative light intensity in each habitat.

We measured subcanopy and open grassland air and soil temperatures for all 24 sample trees with an Omega 2176A digital thermocouple thermometer. Samples were taken in April 1987, which was during the time of maximum canopy leaf area, near the end of the growing season of the understory, and February 1988 when the trees were leafless and phenologically representative of most of the understory growing season. Temperatures were measured between 0800 and 0900, 1200 and 1300, and 1600 and 1700. For each tree, five understory and five nearby open measurements were taken within 10 min, and the difference between the averages was recorded. Soil and air temperatures were recorded simultaneously with two thermocouples.

Soil bulk density and nutrients

Five randomly located soil cores for bulk density were collected under each of the 24 sample trees and at 12 random locations in the open grassland in each site. Cores were 8 cm in diameter, 50 cm deep, and were divided into 10-cm sections by depth for analysis. Soil bulk density was calculated as the dry mass (in grams) of a soil sample of a known volume divided by the volume (in cubic centimetres).

Soil nutrients were measured using soil cores 10 cm deep and 2 cm in diameter that were collected in January 1987 at each of the 200 plots where understory and open grassland productivity was sampled. Soil

samples were dried at 60°C for 3 d and analyzed for total Kjeldahl nitrogen and phosphorus, and exchangeable potassium, calcium, and magnesium. In November 1987, January 1988, and March 1988 cores for available soil nitrogen (ammonium and nitrate) analyses were collected in each habitat at three random points under each of four positive and four negative trees and at 12 random locations in the open grassland in each site. All nutrient analyses followed Setaro and Jones (1989). Subsamples of soil cores were placed in a block digester and subsequently analyzed for total nitrogen with a modified indophenol method and for total phosphorus with a modified molybdenum blue assay. Exchangeable cations were extracted in ammonium acetate, and absorbances were recorded with a Perkin-Elmer Atomic Absorption Spectrophotometer (AAS). Soil nitrate was measured using a copperized cadmium reduction method (Page et al. 1982). Available ammonium was extracted with potassium chloride and measured with a modified indophenol method.

Canopy nutrient inputs

Litterfall was collected monthly under three positive trees and three negative trees in the woodland from June 1987 to May 1988. Litter was collected at five stations per tree using 25 cm diameter plastic buckets attached to steel bar tripods 1.5 m tall. Litter was dried at 60°C for 3 d and weighed before it was analyzed for total nitrogen, phosphorus, potassium, calcium, and magnesium. Litter samples from each tree class in each month were combined, and subsamples from the combined litter were placed in a digester. Total nitrogen and phosphorus were measured following the procedures for the soil analyses. Absorbances for cations in the digest mixture were read on a Perkin-Elmer AAS.

Throughfall and precipitation were collected monthly between October and June 1987–1988. Collectors consisted of 10 cm diameter funnels attached by 0.5 m of Tygon tubing to 1-L Nalgene bottles. Collectors were fastened to steel stakes, and the Tygon tubing was looped to slow evaporative water loss. Four collectors were placed under each of the trees sampled for litterfall, and four collectors were placed in the open. One millilitre of formaldehyde was added each month to prevent bacterial and algal growth. Collected water was frozen for up to 6 mo before analysis for total nitrogen, phosphorus, potassium, calcium, and magnesium. Each sample was individually digested and analyzed with the procedures used for soil and litter. The average annual throughfall nutrient input for each tree was added to the average input via litterfall, and these total annual inputs were compared among the habitats.

Soil moisture

Soil moisture was measured once per month between December 1987 and October 1988 using a Campbell-Pacific Model 503 neutron moisture probe placed 30

cm below the soil surface. One measurement was recorded under each tree per month at randomly chosen, fixed locations in the northern quarter of the canopy areas and at 12 random locations in the open grassland at each site. Soil cores were collected at these locations and gravimetric soil moisture measurements of the initial soil cores were used to calibrate neutron probe readings.

Fine root biomass and predawn xylem pressure potentials of Quercus douglasii

At each location where understory productivity was sampled ($n = 5$ per tree), *Q. douglasii* roots were sampled in soil cores 8 cm in diameter and 50 cm deep. The cores were divided into 10-cm sections by depth, and oak roots were separated by sifting the soils and floating them in water. After roots were separated, they were rinsed with 3% hydrogen peroxide to remove clay particles (Bohm 1979). Roots <2 mm diameter were dried at 60°C for 3 d and weighed. If there was doubt about the species of the root it was excluded from the analysis. Some of the finest oak roots may have been missed because they were similar in appearance to grass roots, but this was not a problem for the majority of samples collected.

Predawn xylem pressure potentials (PDXPP) were measured with a Scholander Pressure Bomb (Waring and Cleary 1967), and were taken monthly for each of the 24 sample trees from April to November 1987 and from April to November 1988. During the 1st yr, three twigs were sampled per tree, and during the 2nd yr, two twigs were sampled per tree.

Experimental analyses of soil, litterfall, and throughfall effects

Bioassays for the effects of soils from under positive trees and negative trees and from the open grassland were conducted in the greenhouse with the same soils that were collected for the nutrient analyses. One *B. diandrus* seed was planted in 13 g of dry soil in a polyethylene test tube with 1-mm holes drilled in the bottom for drainage and aeration, and watered every 3 d. Each of the six combinations of site and habitat was replicated 30 times, and replicates were arranged in a completely randomized design. *B. diandrus* was used because it was the dominant understory species. Germination was $\approx 95\%$. The grass plants were grown for 43 d, harvested, dried at 60°C, and weighed.

A second bioassay experiment was designed to test for the effects of natural litterfall and throughfall on the growth of *B. diandrus* plants. From both positive and negative trees, litterfall was collected and air-dried, and throughfall was collected and frozen. *B. diandrus* plants were grown either in 13 g of soil from the open grassland, and watered with rainwater, or in 13 g of open grassland soil plus 0.25 g of positive or negative oak leaf litter, and watered with positive or negative oak throughfall. These plants were grown for 45 d. Soils

used in this experiment were from the savanna site only, and each treatment was replicated 30 times.

Oak root enclosures

To determine the effects of oak roots on grass growth in the field, water-porous clay root enclosures were made with a Yokota Hand Tube Extruder. Hollow tubes, 8 cm diameter, were extruded from soft clay (40% Fire Clay, 40% Ball Clay, and 20% sand), then cut into 30-cm sections. Bottom pieces, which had 2-mm holes drilled in them for drainage, were attached to the tubes. These enclosures were air-dried for 5 d and then fired at 1800°C, a temperature that was low enough to maintain the porosity of the clay to water. After firing, the enclosures were 25 cm deep and 7 cm in diameter. Enclosures were inserted into holes cored under the trees, and refilled with the soil that had been removed from the holes and sifted free of oak roots to prevent any effects of the decaying oak roots. A control was established for each enclosure by removing the soil core, sifting roots from it, and replacing the soil into the hole without a root enclosure. Five *B. diandrus* seeds were planted in each enclosure or control. Over 95% of the seeds germinated, providing a grass density approximately equal to that under the positive trees. Three replicates of these root enclosures and controls were located under each of four positive and four negative trees in the savanna site midway between the trunks and the canopy edges. The seeds were planted in December 1987, and aboveground biomass was harvested, dried at 60°C for 3 d, and weighed in April 1988 at the inception of senescence.

Subcanopy soil transplants in oak root enclosures

To separate soil effects from tree effects, a second root enclosure experiment was conducted at the same time as the first, and under the same four positive trees and four negative trees in the savanna site. Soil cores, sifted free of oak roots, were reciprocally exchanged between holes under positive and negative trees. Under each tree, treatments consisted of positive tree soil with and without oak root enclosures, and negative tree soil with and without oak root enclosures. Root enclosures in this experiment were PVC tubes, 30 cm long, 8 cm in diameter, with open ends. Each treatment was replicated three times under each tree. Five *B. diandrus* seeds were planted in each container in December 1987, and the aboveground biomass was harvested, dried at 60°C for 3 d, and weighed in April 1987.

Oak root leachate

The effect of *Q. douglasii* root leachate on the growth of *B. diandrus* was tested using methods similar to those of Stevens and Tang (1985). *Q. douglasii* seedlings were planted in "donor pots" made from 3.8-L brown glass solvent bottles with the bottoms removed. *B. diandrus* seeds were planted in 50 mL polyethylene "acceptor" test tubes. Donor pots contained silica sand

(average particle diameter of 0.30 mm) as a rooting medium, with a layer of Perlite under the sand. A perforated Teflon disk and a thin layer of glass wool were placed under the perlite. The acceptor tubes contained only silica sand on top of a layer of glass wool. Two-year-old *Q. douglasii* seedlings were planted in six donor pots; three were drained through an empty glass tube, and three were drained through a glass column containing 5 g Amberlite (Sigma, Saint Louis, Missouri) XAD-4 polymeric adsorbent resin with a high adsorbent capacity for hydrophobic compounds. Many allelopathic compounds are hydrophobic (Whitaker and Feeny 1971). Three other pots did not contain oaks and were drained through empty glass tubes (controls). Each of the nine donor pots was used to feed six acceptor tubes ($n = 3$ donor pots per treatment and six *B. diandrus* per donor pot). Once per week the donor pots were watered with $\frac{1}{4}$ strength Hoagland's solution that was collected after it had passed through the roots of the oaks, and then was used to water the acceptor *B. diandrus* plants. The acceptor tubes were drained back into the donor pots, and the cycle was repeated twice during each watering. After 60 d the *B. diandrus* plants were harvested, dried at 60°C for 3d, and weighed.

Statistics

Savanna and woodland sites were always analyzed separately. When more than one sample per tree was collected, samples for each tree were averaged. One- or two-way parametric ANOVAs were used as appropriate, and repeated-measures ANOVAs when samples were collected over time. When three or more treatments were compared with ANOVAs, Tukey honestly significant difference (hsd) means comparisons were used. The specific factors tested are noted in the *Results*.

RESULTS

Sample tree characteristics

The locations of positive and negative trees were intermixed at the woodland site, but less so at the savanna site, where most of the positive trees were located lower on the slope (Callaway 1990a). Positive trees were much larger than negative trees in both sites (Table 1). Annual ring counts and general impressions indicated that positive trees were also older (sample trees ranged from ≈ 60 to > 150 yr old) than negative trees (sample trees ranged from ≈ 50 to 90 yr old), but annual rings were often difficult to distinguish and tree centers were often rotten, thus accurate ages for sample trees were not obtained. Slope angle and soil texture within sites (i.e., woodland and savanna) were not significantly different between habitats (i.e., positive trees and negative trees) (t test, for each variable $P > .10$).

Understory and open grassland productivity

Our initial evaluations of biomass patterns were confirmed as positive tree understories were twice as pro-

TABLE 1. Sizes (diameters at breast height [dbh] and canopy area) of positive and negative trees* at the savanna and woodland sites (means ± 1 SE).†

| | dbh (cm) | Canopy area (m ²) |
|----------------|----------------|-------------------------------|
| Woodland | | |
| Positive trees | 42.3 \pm 5.5 | 70.0 \pm 8.7 |
| Negative trees | 19.3 \pm 1.5 | 17.2 \pm 2.6 |
| Savanna | | |
| Positive trees | 69.0 \pm 8.7 | 114.8 \pm 20.1 |
| Negative trees | 24.5 \pm 1.9 | 26.2 \pm 2.6 |

* Trees that had exceptionally high (positive trees) or exceptionally low (negative trees) understory biomass.

† dbh and canopy area for positive trees were larger than negative trees in each site (t test, $df = 5$, $P < .01$ for all comparisons).

ductive as open grassland, and open grassland was twice as productive as negative tree understories (Table 2). In the open grassland the most common species was *A. fatua*, whereas in the oak understories it was *B. diandrus*. In general, the biomass of individual plants of these three species tended to be the highest under positive trees, intermediate in the open grassland, and lowest under the negative trees (Fig. 1); however, differences between open grassland and negative tree understories were never significant. Although variation in grassland productivity (Table 2) was associated with the abundance of different species, biomass of individual species in each habitat was in the order, positive trees $>$ open grassland $>$ negative trees, suggesting that variation in habitat productivity was not likely to be caused only by different species compositions. The differences in productivity among habitats were also confirmed on the tree trunk to open grassland transects (Fig. 2). At the northern edges of positive tree canopies, understory productivity dropped precipitously to the levels equivalent to those in the open grassland. Outside of the canopy edges of negative trees the increase in productivity was more gradual, and within 4 m productivity equaled that of the surrounding open grassland.

Light and temperature

Subcanopy irradiance ranged from $\approx 90\%$ of that in the open during the winter when the trees were leafless and the understories were active, to $\approx 45\%$ of open irradiance in the late spring when the trees were in full leaf and herbs were at the end of their life cycles (Fig. 3). Positive and negative trees did not differ in irradiance. To avoid variation due to different sampling days, soil and air temperatures in the three different habitats were not directly compared (see *Methods: Light and temperature*). Instead, the average temperature differences between subcanopy and open grassland were compared between positive and negative tree habitats. In April, under fully leafed-out oak canopies, air temperatures were 3°–4°C lower than in the open grassland at both sites, but there were no differences between

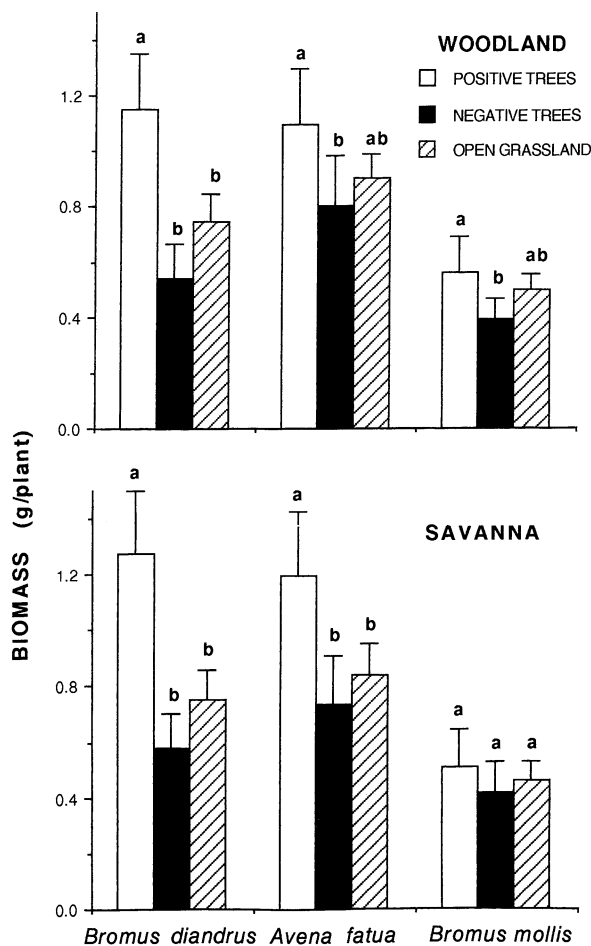


FIG. 1. Biomass of individual plants of *Bromus diandrus*, *Avena fatua*, and *Bromus mollis* under positive and negative *Quercus douglasii* (trees with, respectively, exceptionally high or low understory productivity) and in the open grassland at the end of the growing season. Error bars show two standard errors, for habitat, $n = 3$ for trees, with 10 plants averaged per tree, $n = 40$ for open grassland. In both sites, *B. diandrus* $F_{\text{habitat}} > 7.45$, $df = 2,3$, $P < .001$ and *A. fatua* $F_{\text{habitat}} > 3.40$, $df = 2,3$, $P < .01$. For *B. mollis* at the woodland site, $F_{\text{habitat}} = 3.16$, $df = 2,3$, $P < .05$; in savanna, $F_{\text{habitat}} = 0.74$, $df = 2,3$, $P > .50$. Shared letters within a species and site designate means that were not significantly different (Tukey $P < .05$).

positive and negative trees in either site (habitat, i.e., positive and negative tree habitats and habitat \times tree effects in two-way ANOVA, $P > .50$ at each site). In February 1988, when the trees were leafless, understory air temperatures were never more than 0.2°C higher than the open grassland, and positive trees and negative trees were not different (habitat and habitat \times tree effects in two-way ANOVA, $P > .50$ at each site). In April and February, positive and negative tree soil temperatures did not differ (habitat and habitat \times tree effects in two-way ANOVA, $P > .50$ at each site).

Soil bulk density and nutrients

Surface soils under *Q. douglasii* were less dense than in the open grassland (Fig. 4), which was probably due

to the effects of accumulated litterfall. Deep soils were not different, suggesting that surface differences were not due to microsite differences. Shallow positive tree soils tended to be less dense than negative tree soils, but these trends were not significant (Tukey, $P > .10$).

Total nitrogen, total phosphorus, and exchangeable potassium, calcium, and magnesium in shallow soils (0–10 cm) were usually higher under *Q. douglasii* canopies than in the open grassland (Fig. 5). In 6 of 10 comparisons soil under positive trees was significantly higher (Tukey, $P < .05$) in nutrients than under negative trees, and in 8 of 10 comparisons both positive and negative tree soil nutrient concentrations significantly exceeded those of the open grassland (Tukey, $P < .01$).

In November, before any substantial understory or grassland growth began, soil levels of ammonium and nitrate were significantly higher under *Q. douglasii* canopies than in the open grassland (Fig. 6). In March, soil ammonium under positive trees and in the open grassland had decreased significantly in comparison to under negative trees. In contrast, nitrate under negative trees decreased significantly between November and March relative to the other habitats. This suggests that uptake of ammonium or nitrate differed between habitats and/or nitrification may have occurred more slowly under negative trees than in other habitats.

Canopy nutrient inputs

Canopy input of nutrients via litterfall and throughfall was 5–10 times as high under either positive or negative trees as via dry deposition and precipitation in the open grassland (Fig. 7). There were no differences

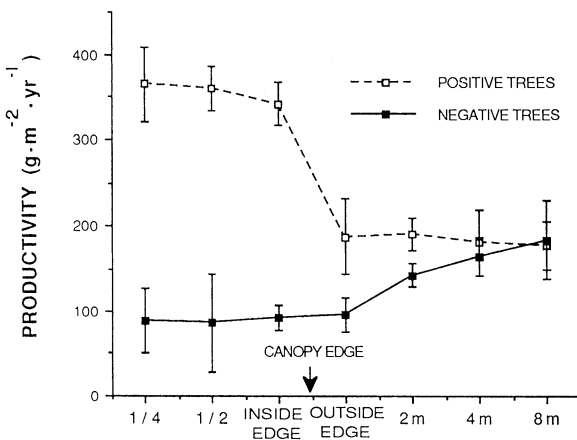


FIG. 2. Annual productivities in the savanna site of *Quercus douglasii* understories and open grassland sampled on transects that were aligned at due north from the trunks. Understory measurements were taken at 1/4 and 1/2 the distance between the trunks and canopy edges, 50 cm inside and outside of the canopy edges, and 2, 4, and 8 m outside the canopy edge. Positive and negative trees as in Fig. 1. Error bars show two standard errors on either side of the means based on four replicates per value.

TABLE 2. Productivity of understory and open grassland plants in the savanna and the woodland sites.

| Species | Productivity* ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) | | | | | |
|--------------------------|---|-------------------------------|--------------------------------|-------------------------------|-------------------------------|--------------------------------|
| | Woodland | | | Savanna | | |
| | Positive trees ($n = 6$) | Negative trees ($n = 6$) | Open grassland ($n = 40$) | Positive trees ($n = 6$) | Negative trees ($n = 6$) | Open grassland ($n = 40$) |
| <i>Avena fatua</i> | 36.6 | 14.1 | 142.1 | 35.4 | 12.4 | 144.2 |
| <i>Bromus diandrus</i> | 231.0 | 53.3 | 1.2 | 289.1 | 71.8 | 0.5 |
| <i>Bromus mollis</i> | 50.2 | 7.4 | 4.1 | 10.2 | 3.0 | 16.1 |
| <i>Hordeum leporinum</i> | 4.8 | 0.2 | 2.7 | 14.0 | 0.0 | 0.0 |
| <i>Stipa pulchra</i> | 0.3 | 0.1 | 1.5 | 0.2 | 3.7 | 4.4 |
| <i>Erodium botrys</i> | 0.5 | 0.2 | 1.5 | 0.1 | 0.2 | 6.0 |
| Others | 3.0 | 3.3 | 1.5 | 2.4 | 2.8 | 5.4 |
| Total | 326.4 ^a | 78.7 ^b | 152.4 ^c | 351.4 ^a | 93.9 ^b | 176.6 ^c |

* Total productivity differs significantly among positive tree, negative tree, and open grassland habitats (one-way ANOVAs, woodland $df = 2$, $F = 47.66$, $P < .001$, all Tukey comparisons for total $P < .001$; savanna $df = 2$, $F = 109.07$, $P < .001$, all Tukey comparisons for total $P < .001$). Significant differences in total productivity within a habitat are designated by different letters.

between positive and negative trees for any nutrient measured (Tukey, $P > .10$).

Soil moisture

Soil moisture, as measured with a neutron probe 30 cm deep, did not differ significantly among positive trees, negative trees, and the open grassland in either site during the understory growing season (Fig. 8). When the entire year was analyzed, habitats did not differ in soil moisture (Fig. 8); however, after senescence of the understory plants and leafing out of the oak trees (April–October), soil moisture under negative trees was lower than that under positive trees and that in the open grassland (one-way repeated-measures ANOVA, April–October, woodland $df = 2, 21$, $F_{\text{habitat}} = 4.18$, $P < .05$; savanna $df = 2, 21$, $F_{\text{habitat}} = 8.77$, $P < .01$).

Quercus douglasii fine root biomass and PDXPP

Oak fine (<2 mm) root biomass was significantly higher under negative trees than under positive trees in both the woodland and the savanna at all depths with no interaction between depth and habitat (Fig. 9). Within a habitat, individual trees did not differ (two-way ANOVA, habitat \times tree, $F_{\text{tree}} < 0.50$, $df = 5, 50$, $P > .50$; $F_{\text{depth} \times \text{tree}} < 0.45$, $df = 5, 50$, $P > .50$) so individual trees were used as replicates. In the upper 20 cm of soil, where understory plant roots were concentrated, density of fine oak roots under negative trees was 3.8 and 4.9 times as high as under positive trees in the woodland and the savanna, respectively.

Negative tree predawn xylem pressure potentials (PDXPPs) decreased rapidly during the rainless summers, suggesting that they were dependent on their dense lateral root systems for water in shallow soil (Fig. 10). On the other hand, positive tree PDXPPs were consistently higher (1–2 MPa in the late summer and fall) than negative tree PDXPPs. These data, and the comparatively low amounts of shallow fine roots ($2.5 \times$ lower in the upper 50 cm of soil), indicate that positive trees tap a relatively permanent source of deep water,

probably the water table. Additionally, PDXPPs were more highly correlated with soil moisture at 30 cm for negative trees (woodland $r = 0.77$, savanna $r = 0.67$) than for positive trees (woodland $r = 0.56$, savanna $r = 0.26$). Although trends were similar in both years, in the woodland in 1988, positive tree PDXPPs decreased more rapidly and in the late summer were more similar to the PDXPPs of the negative trees. The summer of 1988, however, was one of the driest on record at Hastings Reservation and the third consecutive drought year. The flow of wells and springs that are dependent on deep ground water was very low (J. R. Griffin, *personal communication*), which suggests that the low PDXPPs of positive trees in 1988 may have been due to unusually low levels of water in the water table.

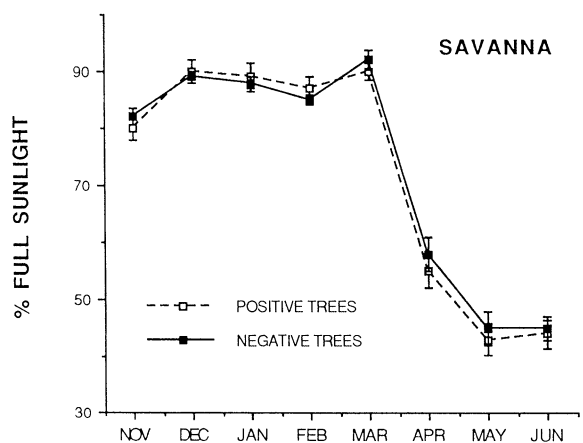


FIG. 3. Irradiances under positive and negative *Quercus douglasii* (defined as in Fig. 1) in the savanna site as percentages of irradiance in open grassland. Error bars show two standard errors on either side of the means. Repeated-measures ANOVA, $F_{\text{habitat}} = 0.31$, $df = 1, 7$, $P > .50$. For the habitat variable, $n = 4$ trees (four samples averaged per tree), $n = 3$ for open grassland.

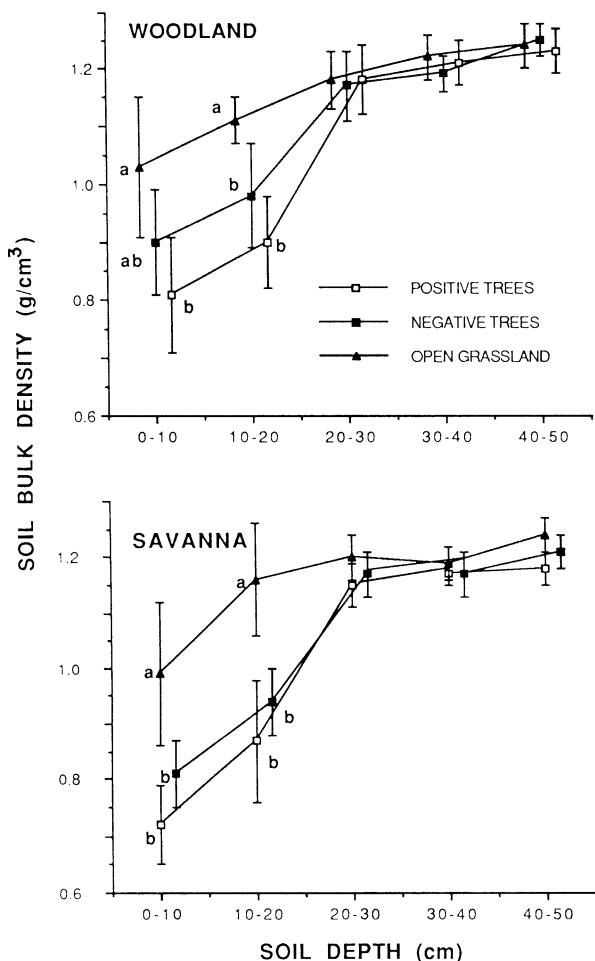


FIG. 4. Soil bulk density in the woodland and the savanna sites under positive and negative *Quercus douglasii* (defined as in Fig. 1) and in the open grassland. Error bars show two standard errors on either side of the means. For the habitat variable, $n = 6$ for trees, $n = 12$ for open grassland. For both sites, two-way ANOVA, $F_{\text{depth}} > 17.00$, $df = 4, 105$, $P < .001$; $F_{\text{habitat}} > 9.80$, $df = 2, 105$, $P < .001$; $F_{\text{depth} \times \text{habitat}} > 4.35$, $df = 8, 105$, $P < .001$. Shared letters within sites and depths designate means that were not significantly different as determined by Tukey means comparisons ($P < .05$).

Greenhouse experimental analyses of soil, litterfall, and throughfall effects

Soils that had been collected under both positive trees and negative trees produced larger *B. diandrus* plants in greenhouse experiments than did soils collected from open grassland, with the exception that dry masses of *B. diandrus* grown in soils from under negative trees in the savanna site did not differ significantly from those of *B. diandrus* grown in soils either from under positive trees or from the open grassland (Fig. 11a).

Litter that had fallen naturally from canopies and field-collected throughfall from both positive and negative *Q. douglasii* were found to have positive effects on the growth of *B. diandrus* using open grassland soil

from both sites (Fig. 11b), but positive and negative trees did not differ.

Field effects of oak roots and soil type (exclosures and subcanopy soil transplants)

B. diandrus plants were significantly larger in clay oak root exclosures than in controls under negative trees, but were not different under positive trees (Fig. 12). With or without the root exclosures, *B. diandrus* plants were significantly larger under positive trees than under negative trees (Tukey, $P < .05$) paralleling the results for growth of naturally occurring plants (Fig. 1).

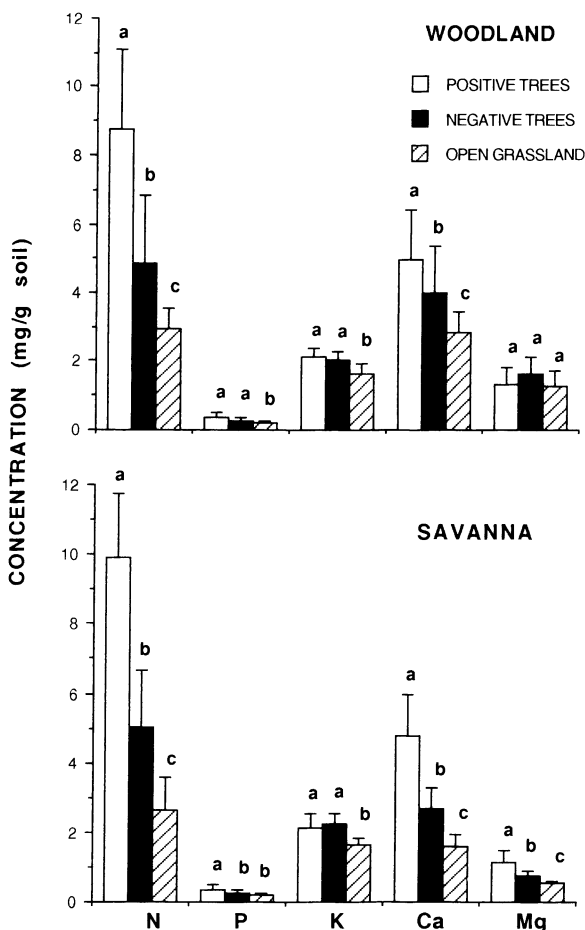


FIG. 5. Total nitrogen and phosphorus, and exchangeable potassium, calcium and magnesium, in the woodland and savanna sites, in soils (0-10 cm deep) under positive and negative *Quercus douglasii* (defined as in Fig. 1) and in the open grassland. Error bars show two standard errors above the means. For the habitat variable, $n = 6$ trees (five samples averaged per tree), $n = 40$ for open grassland. For both sites, one-way ANOVA, nitrogen $F_{\text{habitat}} > 65.0$, $P < .001$; phosphorus $F_{\text{habitat}} > 16.5$, $P < .001$; potassium $F_{\text{habitat}} > 21.4$, $P < .001$; calcium $F_{\text{habitat}} > 20.5$, $P < .001$; magnesium $F_{\text{habitat}} > 3.30$, $P < .05$; all $df = 2, 5$. Shared letters within sites and nutrients designate means that were not significantly different (Tukey means comparisons, $P < .05$). Data for phosphorus, potassium, and magnesium were log transformed before ANOVA.

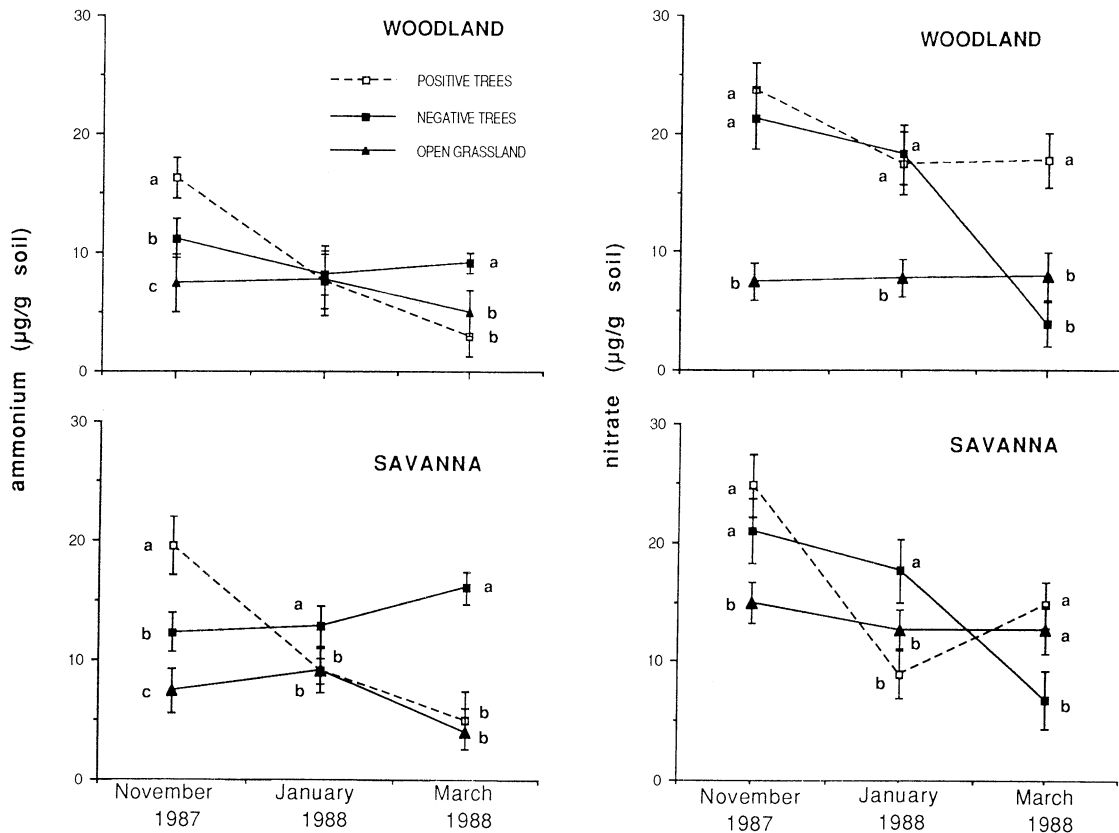


FIG. 6. Ammonium and nitrate in soils in the woodland and the savanna sites under positive and negative *Quercus douglasii* (defined as in Fig. 1) and in the open grasslands. Error bars show two standard errors on either side of the means. For the habitat variable, $n = 4$ trees (three samples averaged per tree), $n = 12$ for grassland. For soil ammonium at both sites, one-way repeated-measures ANOVA, $F_{\text{habitat}} > 8.45$, $df = 2,17$, $P < .01$; $F_{\text{date}} > 27.25$, $df = 2,34$, $P < .001$; $F_{\text{habitat} \times \text{date}} > 11.00$, $df = 4,34$, $P < .001$. For soil nitrate at both sites $F_{\text{habitat}} > 6.90$, $df = 2,17$, $P < .01$; $F_{\text{date}} > 6.90$, $df = 2,17$, $P < .01$; $F_{\text{habitat} \times \text{date}} > 23.00$, $df = 4,34$, $P < .001$. Significant differences within a date are designated by different letters (Tukey, $P < .01$).

Under negative trees, the dry masses of mature *B. diandrus* plants grown in soils from under either positive or negative trees were significantly lower (Tukey, $P < .01$ for each comparison) without PVC root enclosures than they were with root enclosures (Fig. 13). Under positive trees, there were no differences between enclosure-soil treatments (Tukey, $P > .10$). Unlike results for the clay root enclosures, *B. diandrus* grown in enclosures under negative trees and enclosures under positive trees were not significantly different (Tukey, $P > .10$).

The results of these experiments indicate that the large amounts of fine roots under negative trees (relative to positive trees) suppress understory productivity. Although there was little phenological overlap between oak leaf out and understory growth, we observed new oak roots (whitish in color and without cork layers) in the winter before the emergence of oak leaves.

Oak root leachate

The dry mass of *B. diandrus* plants was significantly lower (Tukey, $P < .01$) when watered with Hoagland's

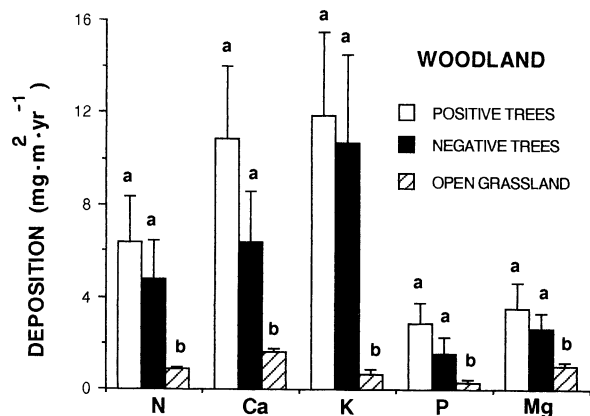


FIG. 7. Total nutrients deposited via litterfall, throughfall, dry deposition, and precipitation in the woodland site under positive and negative *Quercus douglasii* (defined as in Fig. 1) and in open grassland between June 1987 and May 1988. Error bars show two standard errors. For each nutrient in each habitat, $n = 6$ for trees (five samples averaged per tree), $n = 4$ for open grassland. Significant differences (one-way ANOVAs for each nutrient in each site, all $df = 2,2$, $F_{\text{habitat}} > 10.0$, $P < .001$; Tukey $P < .01$) are designated by different letters.

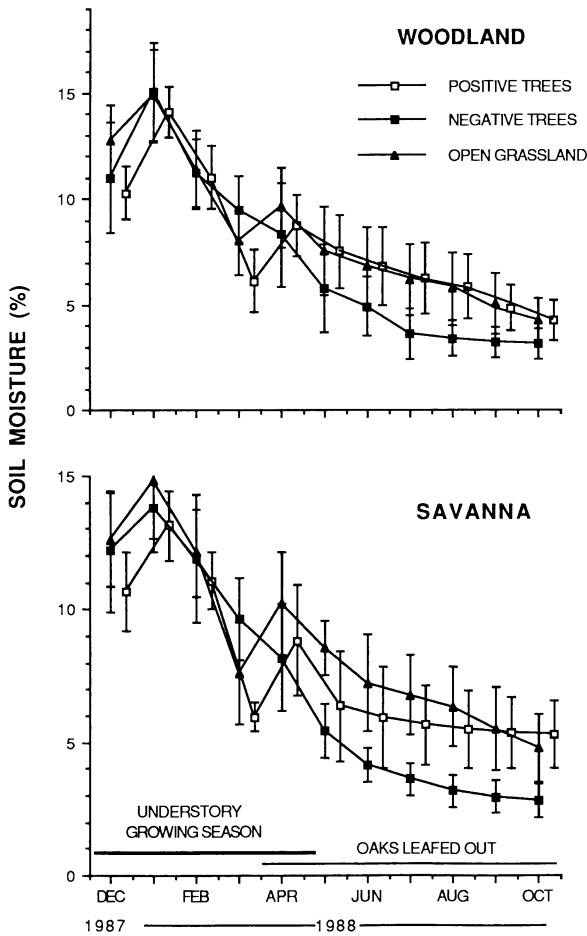


FIG. 8. Soil moisture in the woodland and savanna sites under positive and negative *Quercus douglasii* (defined as in Fig. 1) and in the open grassland. Measurements in all habitats were taken on the same day each month; points are separated on graph for clarity. Error bars show two standard errors on either side of the means. For the habitat variable, $n = 6$ for trees, $n = 12$ for open grassland. There were no significant differences among habitats at either site (one-way repeated-measures ANOVA; for the woodland, $F_{\text{habitat}} = 2.39$, $df = 2,21$, $P > .10$; $F_{\text{date}} = 103.94$, $df = 10,210$, $P < .001$; $F_{\text{habitat} \times \text{date}} = 2.87$, $df = 20,220$; for the savanna $F_{\text{habitat}} = 2.68$, $df = 2,21$, $P > .05$; $F_{\text{date}} = 145.75$, $df = 10,210$, $P < .001$; $F_{\text{habitat} \times \text{date}} = 4.84$, $df = 20,210$, $P < .01$).

solution that had been flushed through pots containing living *Q. douglasii* roots ($\bar{X} \pm 1 \text{ SE} = 0.125 \pm 0.016 \text{ g}$) than it was in the controls with no oak in the donor pot ($0.182 \pm 0.017 \text{ g}$). When *B. diandrus* was watered with oak root leachate that had been filtered through the XAD-4 gel column the final biomass was intermediate to the nonfiltered and the control treatments ($0.152 \pm 0.018 \text{ g}$) and not significantly different from either.

DISCUSSION

Q. douglasii canopy-mediated differences in light or temperature are unlikely to have either facilitative or

interfering effects on understory productivity for several reasons. First, there were minimal differences in light and temperature between tree understories and the open grassland during the time of year when the understory plants were growing rapidly. Yet, tree effects on understory growth were clearly evident throughout the winter and spring (R. M. Callaway, *personal observation*), and negative effects have been quantified elsewhere as early as November (Bartolome 1986). Second, there were no differences in light or temperature between positive trees and negative trees at any time of year. Third, our tree trunk to open grassland transect productivity measurements showed that there was no displacement of the understory patterns to the north of the canopy edges (Fig. 2). If *Q. douglasii* effects were mediated by shade, herbaceous productivity would have been affected at least 9 m north of the canopy (calculated for the latitude of our

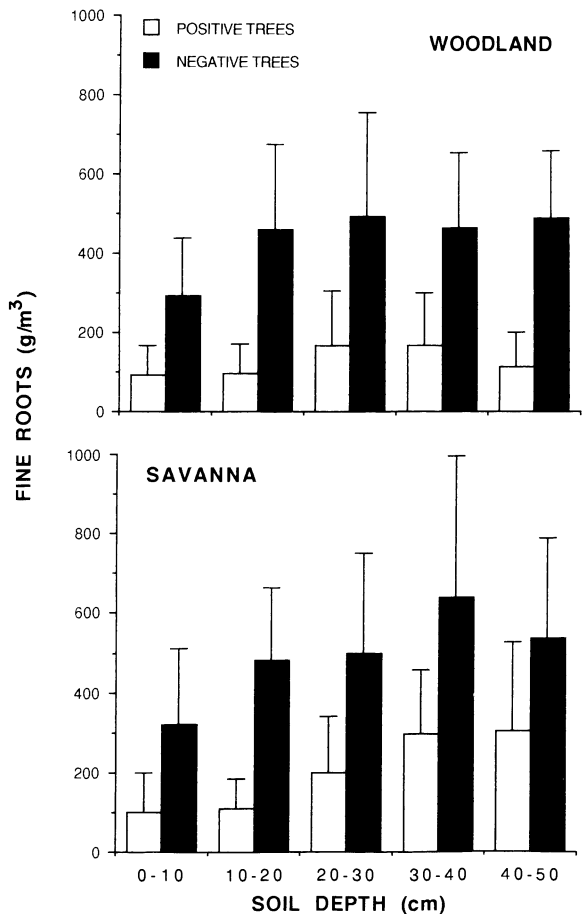


FIG. 9. Fine (< 2 mm diameter) *Quercus douglasii* root biomass in the upper 50 cm of soil under positive and negative oaks (defined as in Fig. 1) in the woodland and savanna sites. Error bars show two standard errors above the means. For the habitat variable, $n = 6$ trees (five samples averaged per tree) in each site. For each site, two-way ANOVA, $F_{\text{depth}} > 8.25$, $df = 4,50$, $P < .001$; $F_{\text{habitat}} > 89.00$, $df = 1,50$, $P < .001$; $F_{\text{depth} \times \text{habitat}} < 1.00$, $df = 4,50$, $P > .04$.

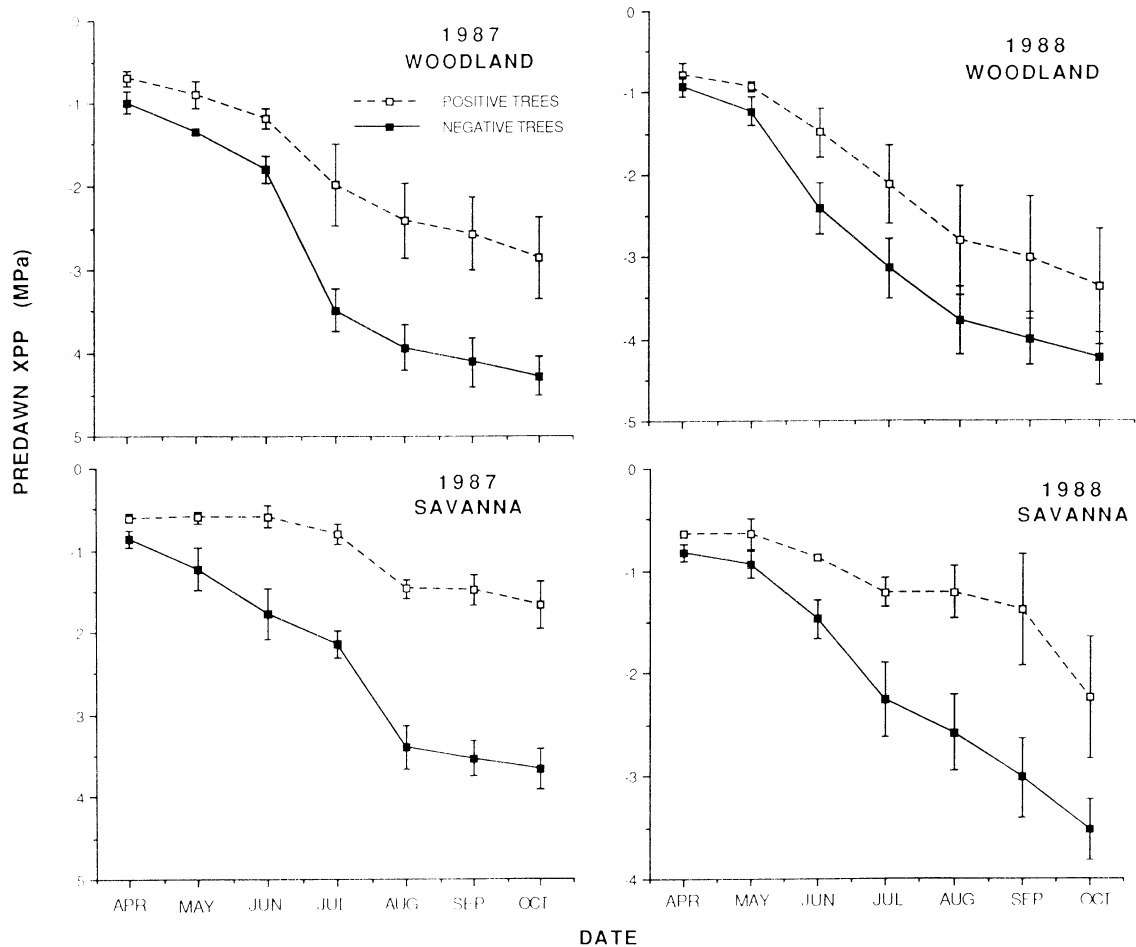


FIG. 10. Predawn xylem pressure potentials for positive and negative *Quercus douglasii* (defined as in Fig. 1) in the woodland and savanna sites in 1987 and 1988. Error bars show two standard errors on either side of the means, $n = 6$ trees. For both sites in 1987, repeated-measures one-way ANOVA, $F_{\text{habitat}} > 40.25$, $df = 1,10$, $P < .001$; $F_{\text{date}} > 160.00$, $df = 6,60$, $P < .001$; $F_{\text{habitat} \times \text{date}} > 16.00$, $df = 6,60$, $P < .001$. For both sites in 1988, $F_{\text{habitat}} > 9.35$, $df = 1,10$, $P < .05$; $F_{\text{date}} > 76.50$, $df = 6,60$, $P < .001$; $F_{\text{habitat} \times \text{date}} > 4.05$, $df = 6,60$, $P < .01$.

study site). Our transect data (aligned north of the trees) showed that facilitative and negative effects ended at or near the canopy edge.

Because habitats did not differ in soil moisture in the rooting zone of the annual understory plants during the time of year when these plants were phenologically active (Fig. 8), competition for water between *Q. douglasii* and understory plants probably did not cause the differences between positive tree and negative tree understory productivities. The lowest soil moisture means during the winter and early spring were under positive trees (not significant), where understory biomass was the highest, suggesting that understory transpiration may have had a greater effect on soil water potentials in shallow soils during the winter than the oaks, which were leafless. After leaves emerged on the trees, soil moisture tended to decrease under negative trees. During this time, however, understory plants were dead. Because of the coarse scale of our measurements, and

because we did not measure rates of water use, we have not eliminated competition for water as a factor determining productivity differences. Soil moisture measurements and the lack of phenological overlap between trees and herbs, however, suggest that other factors may be more important.

Although soil bulk density differed between tree understories and the open grassland, the fact that positive trees and negative trees were not different from each other demonstrates that this factor probably did not cause the differences between their understory productivities (Fig. 4). Soil bulk density was lower under both positive trees and negative trees than in the open grassland, and thus is a potential factor for the facilitation of understory growth when not combined with high levels of shallow fine roots. Soil compaction under *Q. douglasii* trees may have been reduced by the accumulation of litter and/or tree root activity in the surface soils. Kay (1987) also found that soil under *Q. douglasii*

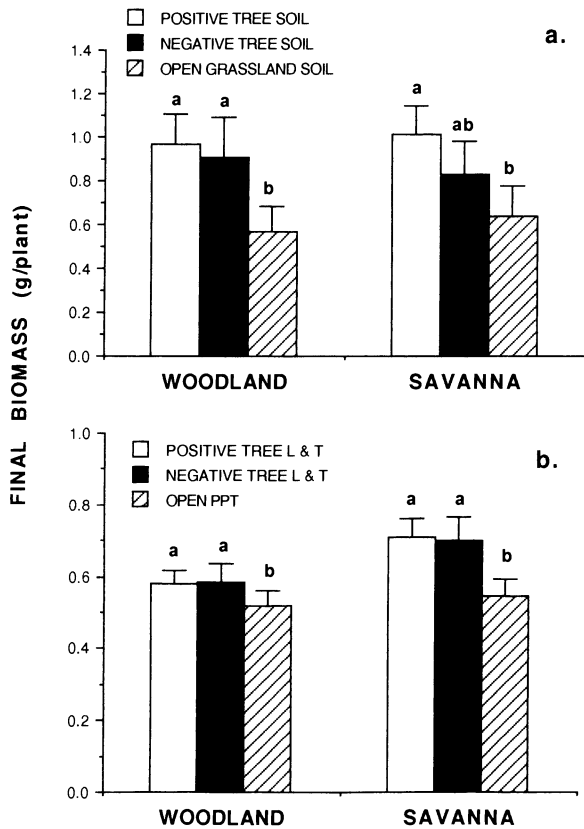


FIG. 11. Biomass of individual *Bromus diandrus* plants grown in soil from under positive and negative *Quercus douglasii* (defined as in Fig. 1) and from the open grassland in the woodland and savanna sites (a), and grown in the greenhouse in soil from open grassland and watered with precipitation collected in the open (open PPT), with 0.25 g of negative *Quercus douglasii* leaf litter and watered with negative *Q. douglasii* throughfall (negative L & T), or 0.25 g of positive *Q. douglasii* leaf litter and watered with positive *Q. douglasii* throughfall (b). Error bars show two standard errors above the means. In one-way ANOVA, all soil bioassay treatments $n = 27-30$, $F_{\text{habitat}} > 26.4$, $df = 2,83$, $P < .001$. For all litter and throughfall or PPT additions $n = 28-30$, $F_{\text{habitat}} > 4.95$, $df = 2,84$, $P < .05$. Shared letters within a site designate means that were not significantly different (Tukey $P < .05$). Data for both experiments were log transformed before ANOVA.

trees was less dense than open grassland soil, and that when trees were removed soil bulk density increased.

It is also unlikely that the differences between positive and negative tree understory productivities are caused by differences in soil nutrients. In both the woodland and the savanna sites, both positive and negative trees generally had higher soil nutrient concentrations than did soils in the open grassland (Figs. 5 and 6), and *B. diandrus* plants grew larger in soils that had been removed from under both positive trees and negative trees than in soils from the open grassland (Fig. 11a). Additionally, nutrient deposition via litterfall and throughfall did not differ between positive trees and negative trees (Fig. 7), and in greenhouse experiments the biomass of *B. diandrus* increased when litter

and throughfall from either positive or negative trees was added to soil from the open grassland (Fig. 11b). These results indicate that a canopy-mediated increase in soil nutrients was the most likely mechanism of the facilitative effect of *Q. douglasii* on the growth of understory grasses and forbs, but that this phenomenon also occurs under negative trees and is eliminated in the presence of large quantities of fine oak roots. *Q. douglasii* has much deeper roots than understory annuals and may act as a “nutrient pump” (sensu Richards and Caldwell 1987), absorbing nutrients in soils below the rooting zone of the understory plants, and eventually depositing these nutrients at the surface via litterfall and throughfall.

The decrease in soil nitrate under negative trees relative to the other habitats (Fig. 6) may be due to high uptake of nitrate by oak roots before leaves emerge on the tree (see *Results: Field effects of oak roots and soil type*). The effects of negative trees, however, are evident in November through January (Bartolome 1986, R. M. Callaway, *personal observation*), when soil nitrate under these trees is much higher than the that of the open grassland.

The association of facilitative effects of *Q. douglasii* and canopy nutrient input has also been reported by Holland (1980) and Holland and Morton (1980), who found that subcanopy biomass and soil nutrients correlated with each other along transects under individual trees, with both decreasing sharply at the canopy edges. They also reported that the facilitative *Q. doug-*

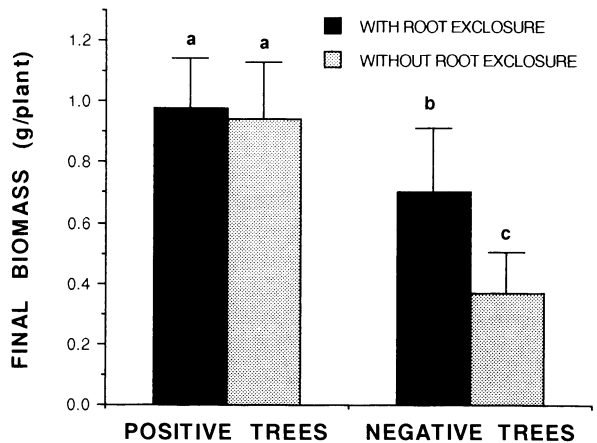


FIG. 12. Biomass of individual *Bromus diandrus* plants grown in clay root exclusions and in controls without root exclusions under positive and negative *Quercus douglasii* (defined as in Fig. 1) in the savanna site. Error bars show two standard errors above the means. In two-way ANOVA, $F_{\text{habitat}} = 177.78$, $df = 1,151$, $P < .001$, $F_{\text{exclusion}} = 22.14$, $df = 1,151$, $P < .001$; $F_{\text{habitat} \times \text{exclusion}} = 33.22$, $df = 1,151$, $P < .001$. Shared letters designate means that were not significantly different (Tukey $P < .01$). Initial $n = 60$ for all treatment-habitat combinations; after germination and animal damage $n = 32$ (positive tree, exclusion), $n = 46$ (negative tree, exclusion), $n = 29$ (positive tree, control), $n = 48$ (negative tree, control). Data were log transformed before ANOVA.

lasii canopy effect persisted in intensity and pattern for over a decade after the death of overstory oaks.

Others have reported that grassland productivity under *Q. douglasii* canopies was much lower than that in the surrounding open grassland (Murphy and Crampton 1964, Kay and Leonard 1980). In these same studies, it was found that the removal of the *Q. douglasii* trees resulted in an increase in the productivity of the former understory area up to twice that of the surrounding open grassland. The fact that growth increased substantially beyond that of open grassland not affected by the presence of oaks suggests that the understory soils possessed latent facilitative effects that were suppressed by the trees, and that soil resources had not been depleted by tree uptake although pre-removal growth may have been reduced by short-term depletion of individual nutrients and postremoval growth may have been enhanced by nutrients released by decaying oak roots. This apparent latent facilitative effect was shown to decrease over time by Kay (1987), who found that 20 yr after cutting the trees, the productivity of former *Q. douglasii* understory areas had decreased to that of the open grassland. This indicates that the effect was caused by the oaks, and was not related to microsite differences. Kay and Leonard (1980) reported that the percent of nitrogen, phosphorus, and sulfate in plants under living *Q. douglasii* (with suppressed understories) was higher than in plants in the open grassland, and after tree removal the percentage of these nutrients in plant tissues decreased in plants in the former understory area to levels equal to plants in the open grassland. These data, considered together with the soil nutrient and bioassay data presented in this paper, suggest that under negative trees, understory growth is not limited by low levels of these nutrients.

Litter from other oak species has been found to improve the growth of understory plants. Monk and Gabrielson (1985) found that the addition of litter from the floors of oak-dominated forests generally improved the overall productivity of understory plots, although the effects of litter on individual understory species ranged from suppression to facilitation. McPherson and Thompson (1972) found that leachate from dead leaves of *Q. marilandica* and *Q. stellata* stimulated the growth of *Bromus japonicus*, a common understory species. Callaway (1990a) found that fresh leaves of *Q. douglasii* significantly suppressed the growth of *B. diandrus*, whereas in experiments reported here litter collected under the trees (primarily senescent leaves) stimulated the growth of *B. diandrus*. Facilitative effects of *Q. douglasii* trees appear to be mediated by nutrients added to the soil by litterfall and throughfall, but the annual inputs did not differ between positive and negative trees, thus they do not account for the differences in productivity.

The most striking difference between positive trees and negative trees was the low biomass of shallow, fine oak roots under the former, and the high biomass of

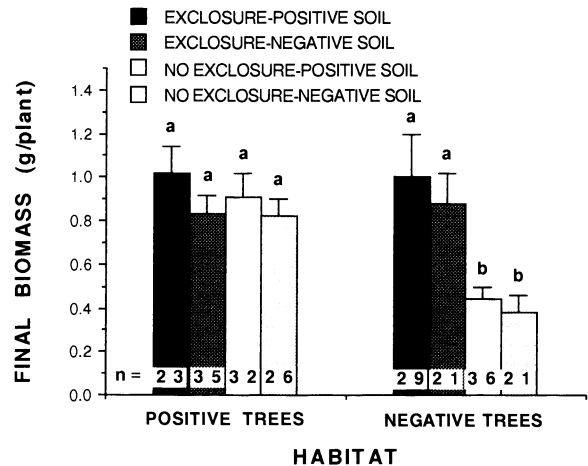


FIG. 13. Biomass of individual *Bromus diandrus* plants grown in soils reciprocally transplanted between positive and negative trees (defined as in Fig. 1), and in PVC root exclosures and controls without exclosures under positive and negative *Quercus douglasii*. Error bars show two standard errors above the means. In two-way ANOVA, $F_{\text{habitat}} = 11.89$, $df = 1, 197$, $P < .001$; $F_{\text{exclosure-soil combination}} = 22.47$, $df = 7, 197$, $P < .001$; $F_{\text{habitat} \times \text{exclosure-soil}} = 6.25$, $df = 7, 197$, $P < .01$. Shared letters designate means that were not significantly different using combinations of positive trees, negative trees, soil sources, and exclosure-control treatments as categories (Tukey $P < .01$). Data were log transformed before ANOVA.

shallow, fine oak roots under the latter (Fig. 9). Oak root exclosures under negative trees (with high oak fine root biomasses) significantly improved the growth of *B. diandrus* (Figs. 12 and 13), suggesting that lateral roots of *Q. douglasii* mediate the interfering effect on understory productivity, thereby counteracting the potential facilitative effects of nutrient accumulation. This assertion is supported by the fact that oak root exclosures had no measurable effect on the growth of *B. diandrus* plants under positive trees, where shallow, fine oak roots were less abundant. Thus, natural distributions of understory productivities and shallow oak fine roots and experimental manipulations suggest a causal relationship between shallow oak fine roots and inhibition of understory productivity.

We found little direct evidence for resource competition. Soil water and soil nutrient (with the exception of nitrate in March) patterns do not explain grassland productivity patterns. This supposition is supported by the lack of phenological overlap between grass growth and oak leaf out. The results of the oak root leachate experiment suggest that interference of understory plant growth by *Q. douglasii* in the field could be due, at least in part, to allelopathic root exudates, although there are alternative interpretations. The oak roots may have removed large percentages of nutrients from the solution as it passed over them, thereby limiting nutrients available for *B. diandrus* growth. However, the fact that we used large quantities of a concentrated nutrient solution makes this unlikely.

Additionally, when the leachate was passed through XAD-4 gel columns, which would have had no effect on nutrient content but would have removed potentially toxic oak root leachates, the inhibition of the leachate was reduced, but not significantly. Differences in osmotic potential or pH between treatments may also explain our results. Root leachates of other oaks, *Q. marilandica* and *Q. stellata*, have also been reported to have toxic effects on the growth of understory species (McPherson and Thompson 1972).

Wilson and Rice (1968) reported that root exudates of many plants inhibited growth of nitrifying bacteria, and Lodhi (1977) found that soils under *Q. alba* and *Q. rubra* contained lower populations of nitrifying microorganisms than soils from under other species. The decline in nitrate and increase in ammonium in soil under negative trees relative to the other habitats may be due to inhibition of nitrification by *Q. douglasii* roots.

The fundamental cause of the differences in rooting depth between positive and negative trees is not known, but several possibilities exist. The differences may be due to genetic variation, tree age, a non-uniform deep substrate, or taproot injury or death. *Q. douglasii* hybridizes with both *Q. lobata* (valley oak) and *Q. turbinella* (desert oak) in the vicinity of our study site (J. R. Griffin, *personal communication*). These latter two species are very different in aboveground morphology and may also differ in belowground morphology. Analysis of the leaf and acorn cup characteristics of our 24 sample trees, however, indicates that hybridization is unlikely to explain the difference between positive and negative trees (R. M. Callaway, *unpublished data*). An analysis conducted by the Pacific Southwest West Experiment Station at Berkeley of selected isozymes of our 24 sample trees also showed that differences between positive and negative trees due to hybridization were unlikely (Callaway 1990a).

It is possible that the lack of fine lateral root development may occur when deep soil water, at relatively high water potentials, is reached and when surface soil water, at relatively low water potentials, is unnecessary for survival. In contrast, the development of a large shallow root system may occur when deep, permanent water sources are not encountered. The development of larger lateral root systems in response to desiccation of taproot tips (Callaway 1990b) suggests that damage to root tips by animals, dry soils, or abrasion could stimulate changes in root morphology. Sampled positive trees were significantly larger than negative trees (Table 1), suggesting that older trees may eventually develop a root system with deep roots reaching the water table and fewer shallow fine roots. The differences in size, however, may also be due to greater water availability as is indicated by the differences in PDXPPs. Deep substrates (e.g., hardpans or rock layers) with variable penetrability to oak roots may vary spatially, permitting deep roots in some microhabitats and not

in others. We did not encounter hardpans when soil cores were removed to a depth of 1 m, but they are common in our study area and vary in depth (J. R. Griffin, *personal communication*). Slope position and topography may also affect water table access. Positive oaks appear to be more common in valleys and on lower slopes, whereas negative oaks appear to be more common on upper slopes and ridges where the probability of water table access may be reduced (R. M. Callaway, *personal observation*). Most of our positive and negative sample trees, however, were intermixed along gradients of elevation and slope position in each site.

Our evidence that *Q. douglasii* varies in its root system morphology and its dependence on the water table and shallow soil water is supported by the contradictory findings of others. Griffin (1973), Rundel (1980), and Baker et al. (1981) reported very low PDXPPs (from -4.0 to -5.0 MPa) for *Q. douglasii* at several different sites, which suggests that these oaks did not root in the water table. On the other hand, Lewis and Burghy (1964) reported that *Q. douglasii* in the Sierra Nevada foothills were able to take up tritiated water that was placed in the water table over 20 m below the soil surface.

Interspecific variation in root morphology has often been interpreted as structural niche partitioning (sensu Cody 1986), and has been cited as a factor that contributes to plant distributions, dispersion patterns, associations, or community diversity in deserts (Yeaton and Cody 1976, Yeaton et al. 1977, Cody 1986), tropical forests (Jenik 1978), prairies (Weaver 1958), and old fields (Parrish and Bazzaz 1976). Evidence for the effects of structural root niche partitioning on community structure in the field, however, is largely indirect, and comparisons of species within communities that have different degrees of niche overlap are few. Our study provides an intraspecific comparison of individual trees with and without a high degree of overlap of rooting zones with herbaceous plants. When the niche overlap was high (negative trees), the productivity of understory species was reduced, and when niche overlap was low (positive trees), the productivity of understory species was enhanced.

The cumulative effect of a *Q. douglasii* tree on the productivity of its understory appears to result from positive (facilitation) effects elicited by litterfall and throughfall combined with negative (interference) effects of shallow roots. Both facilitation and interference may vary in intensity among trees. Root morphology appears to determine the relative importance of these effects and where the cumulative effect of a *Q. douglasii* tree on its understory falls on the continuum between facilitation and interference. Thus, the variation in intensity (e.g., Connell 1983, Schoener 1983) of interactions between plant species may be greater than previously recognized, and a single species may have individuals that interfere with neighbors and others

that facilitate them. Because interactions between other species also vary in intensity (Connell 1983, Schoener 1983) future evaluation of the intensity and importance of species interactions (e.g., Weldon and Slauson 1986) may require research approaches that presume multiple, interacting causes, including facilitation, resource competition, allelopathy, and abiotic factors.

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