

WATER AND TREE–UNDERSTORY INTERACTIONS: A NATURAL EXPERIMENT IN A SAVANNA WITH OAK WILT

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Abstract. Savanna trees influence water, light, and nutrient availability under their canopies, but the relative importance of these resources to understory plants is not well understood. In a three-year study in a Texas savanna, trees infected with the disease oak wilt were used in a natural experiment to isolate the effects of light and soil resources, particularly water, in oak–understory interactions. Herbaceous biomass and survival of transplanted *Prosopis glandulosa* (mesquite) seedlings were monitored in plots under healthy and symptomatic *Quercus fusiformis* (live oak) trees, and in open sites. Shade cloth maintained similar midday light levels in plots under symptomatic and healthy trees. Plant physiological attributes, soil parameters, and woody plant densities were also compared across habitats. Water availability was significantly lower near healthy trees than near symptomatic trees or in the open. Shade-cloth plots under symptomatic trees had over twice the herbaceous biomass of ambient-light plots under healthy trees. As shade–symptomatic plots had similar light and lower nutrient levels than ambient–healthy plots, greater water availability under symptomatic trees was probably a major factor increasing herbaceous productivity. Shade also affected herb growth, and its importance varied seasonally and annually with water availability. Woody seedling densities and 1996 mesquite transplant survival were significantly higher under trees than in the open, indicating facilitation of young woody plants by oaks. However, lower water potentials in larger shrubs near healthy trees and similar shrub densities across habitats (in contrast to seedling densities) suggested that oaks may compete with other woody species as the latter plants age. Our data indicate that both facilitation and competition have important roles in this savanna community, and competition for water may be a key mechanism in oak–understory interactions.

Key words: *Bothriochloa ischaemum*; *Ceratocystis fagacearum*; *competition*; *Diospyros texana*; *facilitation*; *Juniperus ashei*; *oak wilt*; *Prosopis glandulosa*; *Quercus fusiformis*; *savanna*; *Texas (USA)*; *water availability*.

INTRODUCTION

Woody plants in savannas strongly influence the environments under their canopies, changing soil moisture, soil nutrients, microbial activity, light availability, and temperature in these sites (Belsky and Canham 1994, Scholes and Archer 1997, Casper and Jackson 1997). Through these environmental effects, woody plants can influence the productivity and distributions of other savanna species. However, while many studies have explored how trees alter conditions under their crowns, the relative importance of water, light, and nutrients as factors influencing understory plant performance is not well understood. For example, if plant

performance is limited beneath tree canopies, are plants suppressed by shade or by competition for water? Only a few studies have distinguished among these factors in the field (Callaway et al. 1991, Belsky 1994, Holzapfel and Mahall 1999). Our work explored mechanisms underlying interactions between trees and understory plants in a savanna in Central Texas, USA, with the goal of separating the influences of light from soil resources, particularly water availability.

Water has long been recognized as a key resource affecting plant distributions and performance in savannas (Scholes and Archer 1997). However, it has proved difficult to predict the effects of savanna trees on soil moisture. Some studies have found higher soil moisture in undercanopy sites than in the open grassland (e.g., Joffre and Rambal 1988, 1993, Ko and Reich 1993). This could be due to reduced evaporation in shaded sites, lower transpiration by understory plants (Scholes and Archer 1997), or hydraulic lift (e.g., Richards and Caldwell 1987). Alternatively, savanna trees can reduce moisture under their canopies through tree transpiration and rainfall interception (Thurow et al. 1987, Vetaas 1992). Other workers have found the effect of trees on moisture to vary seasonally (e.g., Bel-

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sky et al. 1989) or have concluded that moisture differences between undercanopy and open grassland sites are small and have little influence on understory productivity (Mordelet et al. 1993).

Competitive and facilitative interactions between woody and herbaceous plants and among woody species in savannas are also variable. In some cases, woody plants suppress herbaceous productivity (Ko and Reich 1993, Belsky 1994, Mordelet and Menaut 1995), or are themselves suppressed by the herb layer (Knoop and Walker 1985), suggesting that competitive interactions dominate. There are also many examples of savanna trees facilitating herbs and other woody species (Belsky et al. 1989, reviewed in Callaway 1995), implying that positive interactions dominate. Factors that determine the balance of positive and negative interactions among species are not well understood. Life stage, plant density, species-specific physiological responses, indirect interactions with other species, and abiotic stress may all have significant effects (Callaway and Walker 1997). Recognizing the importance of water in savanna plant interactions, several workers have explained the variability in tree-understory relationships based on precipitation. Belsky et al. (1993) and Belsky (1994) suggested that competition is more important in mesic savannas, while facilitation dominates in arid savannas. In contrast, Mordelet and Menaut (1995) found little relationship between precipitation and the ratios of herbaceous productivity under trees to grassland sites for several savanna habitats. If we can determine the importance of water in positive-negative interactions between trees and understory plants, we may understand why one interaction dominates in a particular savanna. Such data may also contribute to current discussions on the roles of competition and facilitation in structuring plant communities (e.g., Callaway and Walker 1997, Brooker and Callaghan 1998).

Savannas with oak wilt provide an excellent experimental opportunity to explore trees' effects on understory soil moisture and the importance of water availability as a mechanism in interactions between oaks and understory plants. Oak wilt is a fungal vascular disease that blocks xylem tissue, leading to extensive leaf loss (MacDonald and Hindal 1981). Presumably, water use and rainfall interception by the tree are dramatically reduced while understory light levels increase. Plants under adjacent healthy and symptomatic trees can be compared to determine the effects of these resource changes. Similar light levels can be maintained under healthy and symptomatic oaks with artificial shading, and changes in plant performance can then be related to differences in other resources. By measuring water and nutrient levels under healthy and symptomatic oaks, we can determine how oaks affect soil resources and relate plant performance to changes in these factors.

This study addressed the following questions: (1) what are the predominant effects of oaks on understory

herbaceous and woody plants in this savanna (e.g., do oaks compete with or facilitate understory plants), (2) how do oaks influence understory water resources compared to open sites, and (3) is water important in oak-understory interactions? Our approach was to compare plants and environmental variables under healthy and symptomatic trees and in open sites in a savanna with oak wilt, using the disease as a natural oak removal treatment as described above. Permanent plots were monitored for herbaceous productivity and woody transplant survival over two years; shade cloth maintained similar midday light levels in plots under symptomatic and healthy trees (Fig. 1). These observations were coupled with measurements of soil moisture, nutrients, and plant physiological attributes in shrubs and grasses to assess the effects of trees on understory resources. Standing herbaceous biomass and woody vegetation density in untreated plots were also measured to describe the natural community structure and relate these patterns to our experimental results.

METHODS

Site description

The study site was a 2.5-ha savanna at Camp Creek Resource Area, 80 km NW of Austin, Texas, USA. The dominant tree was *Quercus fusiformis* (Small) Sarg. (live oak), a large evergreen species with a dense, spreading canopy. The site had 86 mature oaks 10–15 m tall with a mean canopy radius of 3.75 m, interspersed with shrubs 0.5–3 m tall. About 20% of the site area was under oak canopies. The most common shrubs were *Diospyros texana* Scheele (Texas persimmon), *Prosopis glandulosa* Torr. (honey mesquite), and *Juniperus ashei* Buchholz (Ashe juniper). Mesquite and persimmon are deciduous, juniper is evergreen, and seeds of all three are dispersed by animals (Vines 1984). The dominant grasses were *Bothriochloa ischaemum* (L.) Keng. var. *songarica* (Rupr.) Celerier and Harlan (King Ranch bluestem) and *Nassella leucotricha* (Texas wintergrass, formerly *Stipa leucotricha*). King Ranch bluestem is a warm-season C₄ perennial introduced from Europe and Asia, while Texas wintergrass is a native cool-season C₃ perennial (Gould 1978). Before 1993, the site was grazed by cattle and burned regularly to control juniper.

Soils at Camp Creek are stony, shallow clays classified as thermic, Lithic Calcicustolls. Depth to limestone bedrock is 20–50 cm (Dittemore and Allison 1979). Mean annual precipitation at the nearest weather station (12 km SE of the study site) is 734 mm, with bimodal peaks in spring and fall (mean for 1971–1990, NOAA, National Weather Service, Austin-San Antonio). Rainfall varied dramatically during our study period (1995–1998); a severe drought occurred in the spring and summer of 1996 when precipitation was 47% below normal for the period of December 1995 through July 1996 (observed precipitation = 242 mm,

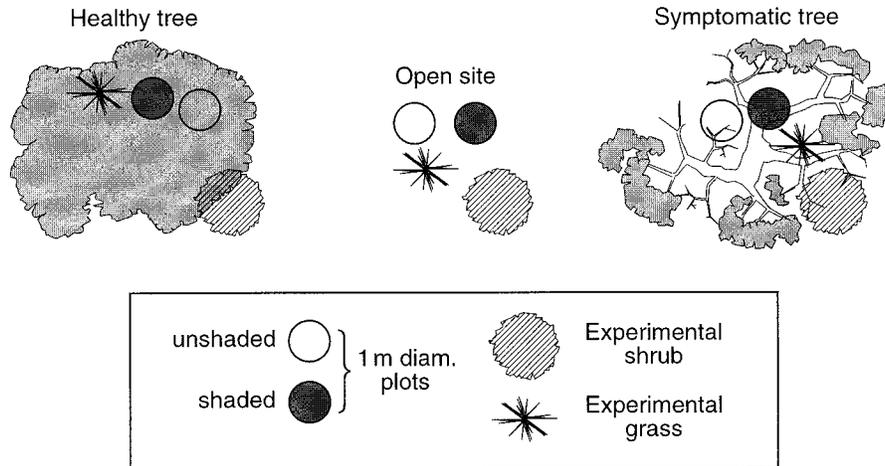


FIG. 1. A conceptual diagram of the experimental design in an aerial view (not to scale). For clarity, objects such as different shrub species, experimental shrubs under trees, woody plant density plots, and TDR probes are not shown. In the field, experimental shrubs were located under different trees than the 1 m diameter plots.

normal = 460 mm). In contrast, the spring and early summer of 1997 were very wet, with precipitation from November 1996 through June 1997 at 83% above normal (observed precipitation = 853 mm, normal = 466 mm, NOAA, National Weather Service, Austin-San Antonio). The mean summer (June–August) and winter (December–February) air temperatures in the region are 28.6°C and 10.6°C, respectively (means for 1961–1990, NOAA, National Weather Service, Austin-San Antonio). The mean frost-free period is 234 d (Dittemore and Allison 1979).

Oak wilt biology and identification of symptomatic trees

Oak wilt is caused by *Ceratocystis fagacearum* (Bretz) Hunt, a fungus that colonizes xylem. The host tree responds by forming tyloses and secreting gums and resins that block vascular elements, leading to leaf wilt (Beckman et al. 1953). In live oak, typical symptoms include veinal necrosis in leaves and gradual canopy thinning; the most common mode of transmission is via root grafts (MacDonald and Hindal 1981). Live oaks usually die within a year after symptoms appear, but may live several years, or, in rare cases, recover (Appel 1994).

Oaks at our study site were surveyed visually for leaves with veinal necrosis each spring from 1995 to 1997. In May 1995 there were 16 symptomatic, 54 healthy, and 11 dead trees. By May 1997 10 additional trees were infected. Trees with symptomatic leaves also showed canopy thinning. The degree of thinning varied substantially: some trees had almost total canopy loss with <10 branches carrying leaves, while others had losses in only small sections of the canopy. The Texas A&M Plant Pathology Department confirmed the presence of oak wilt on the site by isolating *C. fagacearum* from branch samples we provided.

Oak influences on herbaceous productivity and woody seedling survival

A field experiment in a two × three factorial design (two shade treatments, three location treatments) was established to explore how oaks affect understory plants and identify the importance of soil resources in these interactions. Pairs of circular 1 m diameter plots (plot area = 0.785 m²) situated ~1 m apart were placed under healthy trees, under symptomatic trees, and in open sites (seven trees or open sites per treatment, Fig. 1). Under trees, plots were on the north side 1 m from the bole. As symptomatic trees varied in canopy loss, we chose living trees with the greatest losses (>75%, estimated visually) to minimize light variability in the symptomatic treatment. Open plot pairs were located randomly, with restrictions that plots be >10 m from any tree bole and >1 m from any shrub.

Vegetation in the plots was cleared to ground level in April 1996. A covered, circular enclosure of 2.6 × 5.1 cm wire mesh 1 m in diameter and 0.5 m high was placed over each plot to exclude large mammals. A 1.0 × 1.2 m piece of 63% shade cloth was wired to the cage top of one random plot in each pair. There were seven plots in each of six treatments: shaded under healthy tree (shade–healthy), ambient light under healthy tree (ambient–healthy), shaded under symptomatic tree (shade–symptomatic), ambient light under symptomatic tree (ambient–symptomatic), shaded in the open (shade–open), and ambient light in the open (ambient–open).

Mesquite were grown in the greenhouse from seed collected in Bexar County, Texas. Seeds were germinated in a 1:1 mix of Scotts Metro Mix 700 potting medium and vermiculite, and were planted in 21 cm deep pots of site soil at 3 wk old. Seedlings were transplanted to the field 20 April 1996 at 6–8 wk old. Plots

within treatments randomly received either two or three seedlings, planted 50 cm apart (18 seedlings per treatment, 108 total). Shrubs outside the plots >30 cm tall and within 1 m of seedlings were cut off at the base. Seedlings were hand watered (0.5 L each) just after planting and twice per week for 1 mo to minimize transplant shock. No water was applied if it had rained in the previous 24 h. Survival was monitored monthly.

Other vegetation in the plots was hand-clipped to ground level in May, July, and September 1996. Starting in July, clippings were saved to measure regrowth biomass and sorted into grasses, forbs, live oaks, and other woody plants. Oak seedlings and oak root sprouts were not distinguished. Transplanted mesquite shoots were harvested 10 October 1996. Seedlings and clippings were oven dried to constant mass.

The experiment was repeated in the same plots in 1997, with minor changes. Mesquite were grown from seed collected in Kimble County, Texas in pots 7 cm deep in a 2:1 mixture of field soil and perlite, and were transplanted to the site 8 April at 3 wk old. Each plot had three seedlings, giving 21 plants per treatment (126 total). Seedlings were watered only four times in the month after transplanting due to heavy rains. Seedlings were harvested 21 October 1997.

Oak influences on understory resources

Environmental variables were compared under healthy oaks, under symptomatic oaks, and in the open to determine how oaks influence understory resources, particularly water availability. Soil volumetric water content (θ_v) was measured using time domain reflectometry (TDR). A 20-cm TDR probe was installed vertically near each pair of plots. Probes under trees were 1 m from the bole on the south side. Data were taken monthly from March 1997 to March 1998 using a Moisture Point 917 TDR (Environmental Sensors, San Diego, California). Instrument values of θ_v were corrected with a site-specific calibration developed with field soil cores (Jackson et al. 2000). Predawn leaf water potentials in shrubs and grass plants were also used as a measure of water availability in different habitats (see *Methods: Oak influences on . . . understory plants*).

Soil cores 10 cm deep and 2.5 cm diameter were collected near each experimental plot pair for nutrient analyses in March 1997 and January 1998. In the open, two cores were taken at random points within 1 m of the plots and pooled. Under trees, two cores were taken 1 m from the bole on the north and south sides and pooled. Soils were air-dried, and 1997 samples were analyzed commercially at the Texas A&M Soil, Water, and Forage Testing Laboratory for NO_3^- , P, K, Ca, Mg, and pH. NO_3^- was extracted with 0.10 mol/L KCl and extracts were analyzed colorimetrically using a TRAACS 800 autoanalyzer (Bran+Luebbe, Buffalo Grove, Illinois, USA). P, K, Mg, and Ca were extracted with a solution containing 1.43 mol/L ammonium acetate, 1 mol/L HCl, and 0.25 mol/L EDTA (ethylene-

diamine-tetra-acetic acid). Extracts were analyzed using a Spectro ICP spectrophotometer (Model FTP08, Spectro Analytical, Pittsburgh, Massachusetts, USA). The 1998 samples were analyzed at the University of Wisconsin Soils and Physical Geography Laboratory for total N, C, NO_3^- , and NH_4^+ . NO_3^- and NH_4^+ were extracted with 2 mol/L KCl and ion concentrations were measured with Orion specific-ion probes (Orion Research, Boston, Massachusetts, USA). Total N and C were measured with a Carlo-Erba CHN analyzer (CE Elantech, Lakewood, New Jersey, USA).

Light levels in plots were measured with a LI-COR (Lincoln, Nebraska, USA) quantum sensor at 1100–1400 (midday) in July 1996. Measurements were taken at seedling height at three random points in each plot and averaged. In August 1997, surface soil temperatures were measured at midday within 10 cm of each transplanted mesquite (two to three points per plot) with a Barnant 100 J-type thermocouple thermometer (Barnant, Barrington, Illinois, USA). Temperatures were averaged by plot. Temperatures were also measured at the surface and 10-cm depth in undisturbed vegetation next to the TDR probe at 15 of 21 plot pairs.

Oak influences on growth and physiology of understory plants

Oak effects on shrub physiology and growth were studied in mesquite and persimmon, the most common shrubs at the site. Persimmon 0.5–1.5 m tall were chosen in five locations: under healthy and symptomatic trees (<3 m from the bole on the south side), at canopy edges of these same trees (<1 m from the dripline on the south side and not fully shaded), and in the open (>10 m from any tree bole). Symptomatic oaks in these treatments varied in canopy loss (20–75%, estimated visually). There were five persimmon per treatment in 1995, and seven in 1996. For mesquite, shrubs 0.75–1.75 m tall were chosen in three locations: at canopy edges on the south sides of healthy and symptomatic trees, and in the open. Very few mesquite >50 cm tall were found under trees. There were five mesquite per treatment in 1995, and eight in 1996.

Leaf water potentials (Ψ_l) were taken at predawn and midday (1030–1500) for mesquite and persimmon using a pressure chamber (PMS Instrument, Corvallis, Oregon, USA). Persimmon were measured from July 1995 to August 1996 (five predawn, four midday dates). Mesquite were measured from July 1995 to August 1997 (six predawn, four midday dates). Ψ_l was assessed in one to three leaves per shrub and multiple leaves were averaged. For persimmon, stomatal conductance (g ; in millimoles of water per square meter per second) was measured in June and July 1995 with a LI-COR 1600 steady state porometer. Persimmon photosynthesis (A , in micromoles of CO_2 per square meter per second) and g were measured in May 1996 with a LI-COR 6200 infrared gas analysis system. Shrub gas exchange rates were means of two to four leaves. Data

were taken at midday at light levels of $>1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for unshaded shrubs. For shrubs under trees, leaves with the most light exposure were measured.

For persimmon in 1996, leaf length (excluding petiole) was measured with calipers on four marked leaves per plant on 23 March and 13 April. In 1997, terminal shoot length (from base to apical meristem) was measured for four marked shoots per plant on 10 April and 8 May. For mesquite, leaf length (from base of first leaflet to tip of last leaflet) was measured for two to four marked leaves per plant on the same dates in 1997.

Physiological traits were also measured in King Ranch bluestem. Mature, flowering grasses were chosen under healthy and symptomatic oaks <1 m from the canopy dripline and in the open (seven plants per treatment), within 2 m of each pair of plots. Predawn and midday Ψ_1 and g (using the porometer) were measured for each plant in August 1997. Midday Ψ_1 and g were taken between 1100 and 1400 on one to two fully expanded leaves per plant and multiple leaves were averaged.

Oak influences on natural vegetation distributions

To assess long-term effects of oaks on savanna community structure, natural vegetation distributions were surveyed under healthy oaks, under symptomatic oaks, and in open sites. To determine densities of woody seedlings in different habitats, 1×1 m plots were surveyed for plants <30 cm tall in the fall of 1996. A total of 13 healthy oaks, 13 symptomatic oaks, and 30 open sites were randomly chosen. Under each tree, a 1×1 m frame was placed along a random compass direction from the bole and its opposite direction, giving two undercanopy survey sites per tree. For each direction a plot was also placed at the canopy edge, extending 1 m out from the dripline. The same directions were used for a random pair of healthy and symptomatic trees so that similar orientations were surveyed across treatments. All mesquite, persimmon, and juniper <30 cm tall in each plot were counted, and the two plots in each treatment were averaged. Surveys were repeated in June and July 1997 for 14 sites in each of five treatments (70 sites total). To measure standing biomass in 1997, a random 0.5×0.5 m area bordering each plot was clipped, avoiding large shrubs. Biomass was oven dried, sorted into grasses, forbs, oaks, and other woody plants, and weighed.

To estimate densities of larger shrubs, the diameter of each oak canopy was measured in a north-south and east-west direction. The mean of the two diameters was used to estimate a canopy radius, and the ground area covered by each canopy was calculated. Mesquite, persimmon, and juniper >50 cm tall were counted under the same trees where seedling densities were sampled in 1997. In the same open sites, shrubs were counted in circular plots 3.75 m in radius (the mean for living tree canopies at the site).

Statistics

Data were analyzed with SPSS for UNIX and Windows (SPSS, Chicago, Illinois, USA). All continuous variables measured more than once on the same experimental unit (e.g., TDR, Ψ_1) were analyzed using repeated-measures analysis of variance (RM ANOVA), with location relative to oaks as the between subjects factor and measurement date as the within subjects factor. In most cases, different years were analyzed separately as sample size variation resulted in unbalanced designs. If a significant location effect was found in a RM ANOVA, multiple pairwise comparisons were done among locations across measurement dates using the estimated marginal means option in SPSS 8.0 for Windows. Significance levels for these comparisons were adjusted using the Bonferroni method (Milliken and Johnson 1992). Multiple comparisons within measurement dates were done using Tukey's Honestly Significant Difference (hsd test).

For herbaceous biomass from experimental plots, multivariate analysis of variance (MANOVA) was used to assess treatment effects (location relative to oaks, shade) on different plant types (grass, forb, and woody) within the repeated-measures design (measurement date was the within-subjects factor, different years were analyzed separately). An a priori contrast was used to compare shade-symptomatic plots to ambient-healthy plots. As MANOVA showed significant effects of plant type, a RM ANOVA was done for each plant type separately to explore treatment effects on grasses, forbs, and woody plants in greater detail. The same a priori contrast was used in these analyses as in the overall analysis. Significance levels for individual analyses were adjusted using the Bonferroni method.

All other continuous variables were analyzed using analysis of variance (ANOVA) or Kruskal-Wallis tests if the data did not meet ANOVA assumptions. Ammonia concentrations, mesquite midday Ψ_1 , King Ranch bluestem midday Ψ_1 , predawn Ψ_1 , and g , persimmon g , and leaf growth data were log-transformed before ANOVA due to variance heterogeneity. Multiple pairwise comparisons were done using Tukey's hsd test or nonparametric tests described in Zar (1996). A priori independent contrasts were used to compare predawn and midday Ψ_1 under healthy and symptomatic trees in King Ranch bluestem. Biomass totals from 0.5×0.5 m plots were analyzed with a Kruskal-Wallis test followed by nonparametric multiple comparisons tests. Additional Kruskal-Wallis tests were done on these same data for each plant type separately using adjusted significance levels. A Pearson's correlation was done for persimmon A , g , and Ψ_1 to determine if linear relationships existed among these variables. Mesquite transplant survival data were analyzed using logistic regression for each year separately. Survival in shade-symptomatic plots was compared to that in ambient-

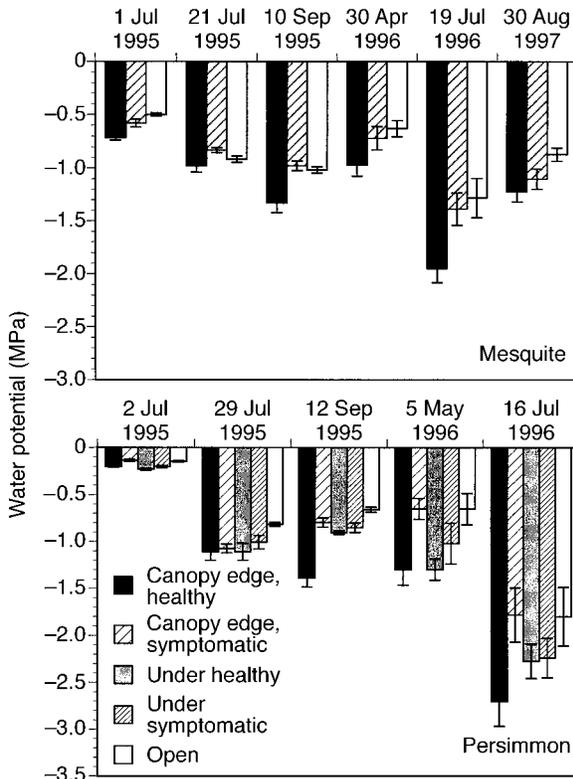


FIG. 2. Predawn Ψ_1 for mesquite and persimmon shrubs in different locations relative to oaks from 1995 through 1997 (mean \pm 1 SE). N for each bar = 4–10 shrubs. Ψ_1 was consistently lowest in plants near healthy trees, with the largest differences among treatments during the 1996 drought. For clarity, significant differences are not indicated on the graphs: see Table 1 for P values.

healthy plots using the special contrast option for logistic regression in SPSS.

RESULTS

Oak influences on understory resources

Healthy oaks reduced water availability under and at the edges of their canopies as measured by Ψ_1 and TDR. In 1996–1997, mesquite growing at the canopy edge of healthy oaks had significantly lower predawn Ψ_1 s than plants near symptomatic trees or in the open (RM ANOVA, $P = 0.004$, Fig. 2, Table 1), with the largest differences among locations in July 1996 (RM ANOVA, location \times date interaction $P = 0.018$). Multiple comparisons tests within dates showed significant differences between mesquite near healthy oaks and those in other sites in April and July 1996, and significant differences between mesquite near healthy oaks and those in the open in August 1997 (Fig. 2). A similar pattern was seen for mesquite in 1995 ($P = 0.057$, Fig. 2, Table 1).

Persimmon at the canopy edge of healthy oaks also had significantly lower Ψ_1 s than plants at the canopy edge of symptomatic oaks and in the open in 1996 (RM ANOVA, location $P = 0.046$, Fig. 2, Table 1). Multiple comparisons within measurement dates showed these same significant differences in May and July (Fig. 2). Persimmon directly under healthy vs. symptomatic oaks did not differ significantly in predawn Ψ_1 , although plants under healthy oaks always had slightly lower values (Fig. 2, Table 1). In 1995, persimmon did not differ significantly among locations when data from all dates were combined, but plants at the canopy edge of healthy oaks had much lower Ψ_1 s than those in other sites in September 1995 (RM ANOVA, location \times date $P = 0.009$).

Midday Ψ_1 was significantly lower for mesquite at the canopy edge of healthy oaks than mesquite at the canopy edge of symptomatic oaks or in the open in

TABLE 1. Results from repeated-measures ANOVAs of predawn water potentials for mesquite and persimmon in a Texas savanna with oak wilt (see Fig. 2).

Data set	Location effect (P)	Date effect (P)	Location \times Date (P)	Significant location differences	
				Difference	(P)
Mesquite results					
1995	0.057	<0.001	0.304	NA	
1996–1997	0.004	<0.001	0.018	CH < CS	0.044
				CH < O	0.004
Persimmon results					
1995	0.093	<0.001	0.009	NA	
1996	0.046	<0.001	0.390	CH < CS	0.009
				CH < O	0.010

Notes: CH = Canopy edge, healthy oak; CS = canopy edge, symptomatic oak; O = open location, away from oaks. Note that water potentials are expressed as negative numbers, such that values for CH shrubs are significantly *less* than those for CS or O shrubs. The multiple-comparisons tests reported examine different levels of the location factor across all measurement dates. P values were adjusted using the Bonferroni method. Details of location comparisons within measurement dates are reported in *Methods: Statistics*, but analyses are not shown. NA = no multiple comparisons tests done among locations as the overall location effect was not significant.

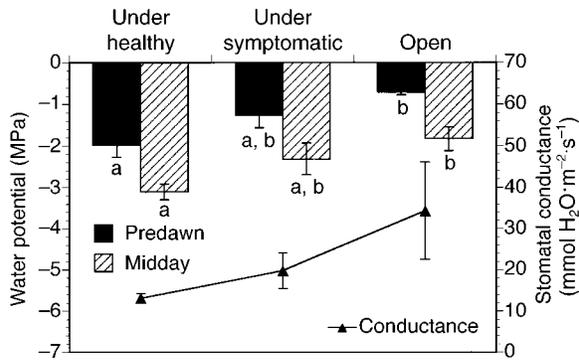


FIG. 3. Predawn and midday Ψ_1 and g for King Ranch bluestem in sites under healthy trees, under symptomatic trees, and in the open (mean \pm 1 SE). N for each bar or point = 6–7 plants. Each plant was located within 2 m of the experimental 1 m diameter plots but was not in the plots, and therefore not subject to clipping or shading treatments. Measurements were done on 28 August 1997. Values of Ψ_1 were significantly lower in plants under healthy trees compared to those in the open (predawn $P = 0.002$, midday $P = 0.023$), while plants under symptomatic trees were intermediate (predawn $P = 0.065$, midday $P = 0.062$ [ANOVA with independent contrasts for plants under healthy and symptomatic trees, followed by Tukey's hsd test for multiple comparisons]). Bars that do not share letters show means that are significantly different among locations; predawn Ψ_1 was not statistically significant compared to midday Ψ_1 . There were no significant differences in g among locations ($P = 0.281$).

1995 ($P = 0.011$), and showed the same pattern in 1996 and 1997, although differences were not significant ($P = 0.094$ and 0.241 in 1996 and 1997, respectively; data not shown). Persimmon at the canopy edge of healthy trees also had slightly lower midday Ψ_s than plants in other locations, but differences were not significant ($P = 0.522$ in 1995, $P = 0.526$ in 1996; data not shown).

Predawn Ψ_s in King Ranch bluestem under healthy trees were almost three times lower than in grasses in the open ($P = 0.002$, Fig. 3), and 1.6 times lower than grasses under symptomatic trees, although this difference was not statistically significant ($P = 0.065$). Grass midday Ψ_1 showed the same pattern ($P = 0.023$, Fig. 3). Grass g tended to be lower under healthy trees, but differences were not significant ($P = 0.281$, Fig. 3).

TDR measurements reinforced the Ψ_1 data, showing a clear pattern of lower soil moisture under healthy trees compared to sites under symptomatic trees or in the open, although the overall location effect was not statistically significant (RM ANOVA, location $P = 0.077$, Fig. 4). This lack of an overall location significance is likely due to dramatic variation in soil moisture among dates: differences among locations were small in the wet spring of 1997 but increased late in the year into 1998 (RM ANOVA, location \times date interaction $P = 0.011$, date $P < 0.001$).

Soil temperatures were significantly cooler under healthy trees than in the open, in both shaded and unshaded experimental plots and in undisturbed vegetation (Table 2, $P < 0.05$). Sites under symptomatic trees

had intermediate soil temperatures, except for surface soils in undisturbed vegetation, where sites under symptomatic trees were slightly warmer than open sites and significantly warmer than sites under healthy trees (Table 2, $P < 0.05$). Other than this case, soil temperatures under symptomatic trees did not differ significantly from temperatures in other sites.

Soil NO_3^- concentrations were significantly higher under healthy trees than under symptomatic trees or in the open in 1997 (Table 3, $P < 0.05$), but NO_3^- was similar among locations in 1998. NH_4^+ concentrations were significantly higher under healthy trees than under symptomatic trees or in the open in 1998, and healthy tree soils had significantly higher K concentrations than open soils in 1997 ($P < 0.05$). There were no other significant differences in nutrients and other soil variables across locations. These limestone soils contained large amounts of CaCO_3 , resulting in high values for calcium and percent carbon.

Midday light levels in ambient–healthy plots were similar to those in shade–symptomatic plots (557 and 582 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively), allowing these treatments to be compared without large differences in midday light quantity (Fig. 5). Light levels ranged from 2118 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for ambient–open plots to 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for shade–healthy plots.

Oak influences on herbaceous productivity and woody seedling survival

Location relative to oaks and shading both significantly influenced herbaceous productivity in experimental plots (Figs. 6 and 7, Table 4). Overall, biomass was lowest under healthy trees, intermediate under symptomatic trees, and highest in the open (location effect: $P < 0.001$ for 1996 and 1997). Shade–symptomatic plots had significantly greater biomass than ambient–healthy plots in 1996 (a priori contrast: $P =$

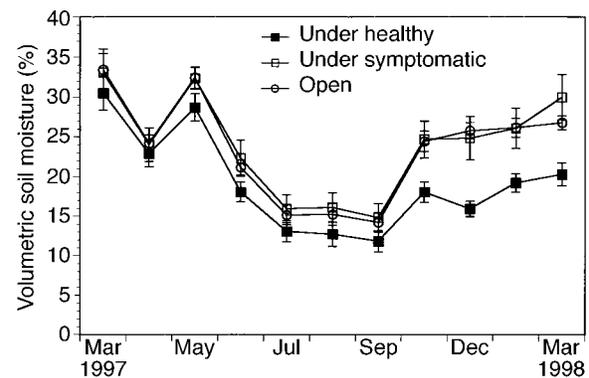


FIG. 4. Volumetric soil moisture (percentage bulk soil volume) in the top 20 cm in different locations relative to trees from March 1997 through March 1998 (mean \pm 1 SE). N for each point = 7 different sites. Soil moisture was always lowest under healthy trees, with the greatest differences in late 1997 and 1998 (RM ANOVA: location $P = 0.077$, date $P < 0.001$, Location \times Date $P = 0.011$).

TABLE 2. Soil temperatures ($^{\circ}\text{C}$; means \pm 1 SE) in three locations relative to trees for experimental plots ($N = 7$) and sites in undisturbed adjacent vegetation ($N = 5$).

Measurement location	Under healthy oaks		Under symptomatic oaks		Open	
	Ambient	Shaded	Ambient	Shaded	Ambient	Shaded
In experimental plots						
Surface soil	39.7 ^{a,b} \pm 1.3	37.0 ^a \pm 0.7	50.1 ^{b,c} \pm 2.4	43.5 ^{a,b} \pm 1.3	59.4 ^c \pm 0.5	47.3 ^{b,c} \pm 0.6
Outside experimental plots						
Undisturbed vegetation, surface soil	37.3 ^a \pm 0.2		47.2 ^b \pm 1.9		46.3 ^b \pm 1.3	
Undisturbed vegetation, 10-cm depth	31.0 ^a \pm 1.1		33.2 ^{a,b} \pm 0.9		35.8 ^b \pm 0.6	

Notes: A Kruskal-Wallis test compared means among the six location/shade treatment combinations for the experimental plots. ANOVAs compared means across the three locations for the measurements in undisturbed vegetation. Surface soil and 10 cm depth temperatures were not statistically compared. Tukey's hsd tests or nonparametric multiple comparisons tests were used to compare specific pairs of means. Values that do not share superscript letters are significantly different ($P < 0.05$).

0.015) and 1997 (a priori contrast: $P = 0.046$), despite similar light levels. Shade treatments also affected herb growth: shade-cloth plots had less biomass overall than plots with ambient light (shade effect: $P = 0.046$ in 1996, $P = 0.002$ in 1997), although the strength of the shade effect varied with harvest date (shade \times date interaction: $P = 0.004$ in 1996, $P = 0.027$ in 1997). For example, differences in biomass in ambient compared to shaded plots ranged from 9 to 117% under healthy trees, 5 to 64% under symptomatic trees, and 13 to 67% in the open across dates (Table 5). Absolute amounts of biomass in different treatments also varied across dates, ranging from a mean of 91.1 g/m² for ambient–open plots in September 1996 to 1.18 g/m² for shade–healthy plots in September 1997 (MANOVA: location \times date interaction $P < 0.001$ in 1997). Lower biomass in 1997 may reflect repeated clipping of vegetation.

Location, shade, and date effects on biomass differed among plant types, as shown by significant interactions between these factors and plant type in 1996 and 1997 (Table 4). Individual analyses for grasses (78% of total biomass on average) showed strong effects of location, shade, and date on biomass, similar to the patterns described above for total biomass in the overall MANOVA, but effects were not always significant for $\alpha = 0.013$ (Bonferroni adjustment; see *Methods, analyses not shown*). In 1997, forb biomass (19% of total biomass) varied significantly among locations and harvest dates, and was a large component of increased herbaceous growth in plots under symptomatic trees and in the open compared to plots under healthy trees ($P < 0.013$, analyses not shown). Location and shade effects were usually not significant for oaks and other woody plants, as their biomass was small and variable among plots (<3% of total biomass, analyses not shown).

TABLE 3. Soil nutrient content in three locations relative to trees ($N = 7$ experimental sites, mean \pm 1 SE).

Soil variable	Under healthy oaks	Under symptomatic oaks	Open
1997 soil collection			
NO ₃ ⁻	1.3 ^a \pm 1.0	<0.05 ^b	< 0.05 ^b
P	14.4 ^a \pm 2.6	10.1 ^a \pm 3.0	20.6 ^a \pm 9.3
K	359 ^a \pm 28	334 ^{a,b} \pm 23	267 ^b \pm 25
Ca	28 277 ^a \pm 1897	29 121 ^a \pm 3118	27 986 ^a \pm 3007
Mg	495 ^a \pm 56	356 ^a \pm 24	462 ^a \pm 92
pH	7.80 ^a \pm 0.02	7.81 ^a \pm 0.05	7.91 ^a \pm 0.04
1998 soil collection			
NO ₃ ⁻	1016 ^a \pm 36	1021 ^a \pm 22	993 ^a \pm 31
NH ₄ ⁺	3.8 ^a \pm 0.3	2.2 ^b \pm 0.1	2.5 ^b \pm 0.2
Percentage dry mass N	0.34 ^a \pm 0.03	0.26 ^a \pm 0.02	0.25 ^a \pm 0.03
Percentage dry mass C	5.7 ^a \pm 0.6	4.4 ^a \pm 0.3	4.6 ^a \pm 0.9
C/N ratio	17.5 ^a \pm 1.3	17.6 ^a \pm 1.6	17.8 ^a \pm 1.8

Notes: Units are mg/kg, except where otherwise specified. Soil samples were collected on 23 March 1997 and 30 January 1998 near each pair of experimental plots. Note that different variables were measured for the 1997 and 1998 samples. NO₃⁻ concentration was measured for both the 1997 and 1998 samples and was below detection limits for soils under symptomatic trees and in the open in 1997. ANOVA or Kruskal-Wallis tests were applied for each nutrient to compare means across the three locations. Tukey's tests or nonparametric multiple comparisons tests were used for pairwise comparisons. Values that do not share superscript letters are significantly different ($P < 0.05$).

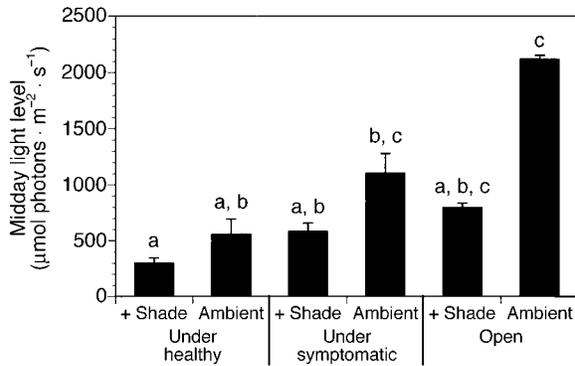


FIG. 5. Midday light levels in experimental plots with different location and shade treatments (mean \pm 1 SE). *N* for each bar = 7 experimental plots. Measurements were done on 23 July 1996. There were significant differences among treatments, but light levels were similar in ambient–healthy plots and shade–symptomatic plots (Kruskal-Wallis, $P < 0.001$, followed by nonparametric multiple comparisons; bars that do not share letters indicate means that are significantly different).

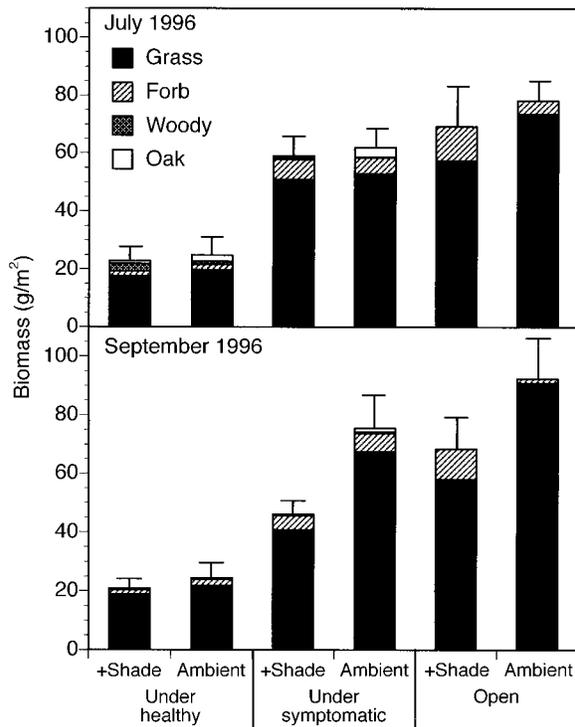


FIG. 6. Regrowth biomass in experimental plots in 1996 (mean \pm 1 SE). *N* for each bar = 5–7 experimental plots. “Woody” in the figure key refers to biomass of woody species other than live oak. “Oak” refers to live oak biomass. Clipping for each month took place over several days, but clipping of plots in different treatments was distributed evenly across days. See Table 3 for analysis details and *P* values.

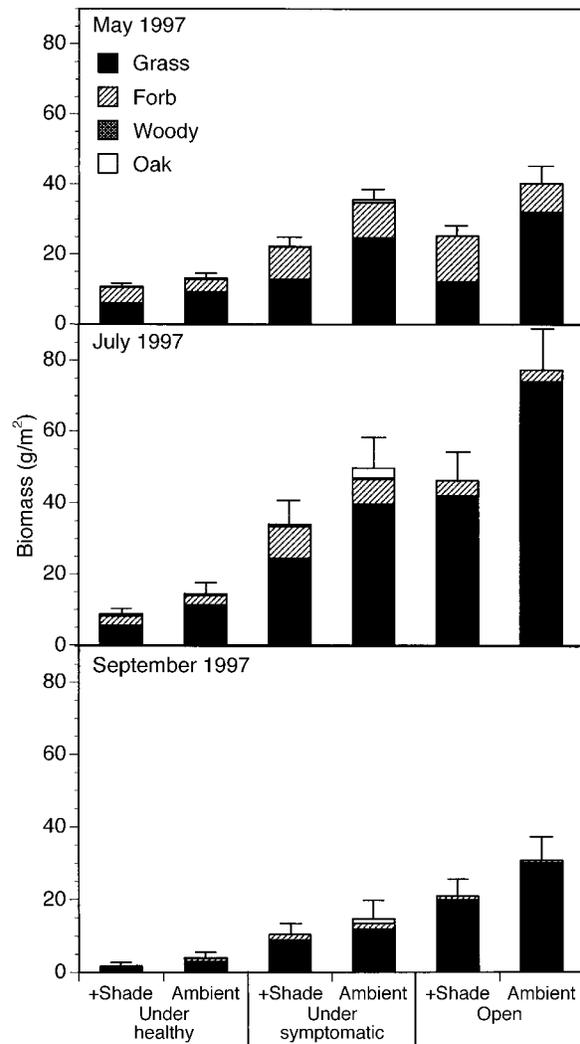


FIG. 7. Regrowth biomass in experimental plots in 1997 (mean \pm 1 SE). *N* for each bar = 7 experimental plots. See Fig. 6 legend and Table 3 for details.

The distribution of plant biomass in undisturbed sites in different locations relative to oaks matched that of the regrowth biomass in experimental plots: sites at the canopy edge of healthy trees had the least biomass and open sites had the most ($P = 0.023$), while sites under and at the canopy edge of symptomatic trees were intermediate (Fig. 8). Biomass was similar in under-tree and canopy edge sites, despite different light levels. Analyses of individual plant types showed less forb biomass under healthy trees than at the canopy edge or in the open ($P = 0.005$). Sites under healthy and symptomatic trees tended to have more woody and oak biomass than other sites, but differences were not significant for $\alpha = 0.013$ ($P = 0.045$ and 0.177 for woody plants and oaks, respectively). Grass biomass tended to be lower near healthy trees and higher in the open, but differences across locations were not significant ($P = 0.123$).

TABLE 4. *P* values for multivariate ANOVAs of biomass harvests from experimental plots.

Variable	Drought year (1996)	Wet year (1997)
Main effects		
Location	0.001***	0.001***
Shade	0.046*	0.002**
Location × Shade	0.590	0.186
A priori contrast within main effects		
Under healthy trees without shade cloth vs. under symptomatic trees with shade cloth	0.015*	0.046*
Within subjects factors		
Date	0.295	0.001***
Plant type	0.001***	0.001***
Plant type × Date	0.394	0.001***
Plant type × Location	0.001***	0.001***
Plant type × Shade	0.142	0.008**
Date × Shade	0.004**	0.027*
Date × Location	0.189	0.001***
Plant type × Date × Location	0.356	0.001***
Plant type × Date × Shade	0.022*	0.086
Date × Location × Shade	0.258	0.517
Plant type × Location × Shade	0.541	0.236
Plant type × Date × Location × Shade	0.388	0.719

Note: *P* values for variables involving plant type in 1996 and plant type and date in 1997 are from the multivariate test Pillai's trace.

* *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

Location relative to oaks was a significant predictor of survival of transplanted mesquite seedlings in experimental plots in 1996 (logistic regression, $P = 0.005$, Fig. 9), with the overall pattern suggesting that oaks facilitated survival. For example, in ambient light plots survival was 50% under healthy and symptomatic trees, and only 11% in the open. Survival tended to be higher in shade-symptomatic than in ambient-healthy plots (the treatments with similar light levels), but this difference was not significant. Overall, shade effects were not significant, but shade tended to improve survival under symptomatic trees and in the open, and tended to reduce survival under healthy trees, suggesting a Location × Shade interaction ($P = 0.094$). There were no significant treatment effects on survival in 1997 (Fig. 9). High mortality resulted in small, variable sample sizes for transplant aboveground biomass, such that differences among treatments were not significant in either year (range 0.19–0.90 g in 1996 and 0.12–0.25 g in 1997; data not shown).

TABLE 5. Percentage increases in biomass in ambient light plots (no shade cloth) compared to plots with shade cloth for different harvest dates.

Harvest date	Under healthy oaks	Under symptomatic oaks	Open
July 1996	9	5	13
September 1996	18	64	35
May 1997	23	60	60
July 1997	66	46	67
September 1997	117	39	46

Oak influences on natural vegetation distributions

Naturally growing woody seedlings were far more abundant under healthy and symptomatic oaks than in open sites. Densities of mesquite <30 cm tall were 13 times greater under healthy trees than in the open in 1996 (Fig. 10, $P = 0.028$), and showed the same trend in 1997 (data not shown). No persimmon or juniper

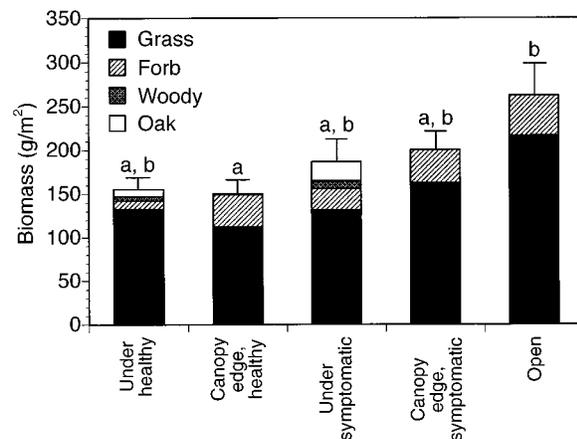


FIG. 8. Biomass in 0.5 × 0.5-m plots for undisturbed vegetation in different locations relative to trees (mean ± 1 SE). See Fig. 6 legend for comments on the key. Biomass was collected over several days from late June to mid-July 1997. Clipping of plots in different treatments was distributed evenly across days. Plots at the canopy edge of healthy trees had significantly less biomass than plots in the open (Kruskal-Wallis, $P = 0.023$, followed by nonparametric multiple comparisons; bars that do not share letters indicate means that are significantly different). See *Methods: Statistics* for analyses of different plant types.

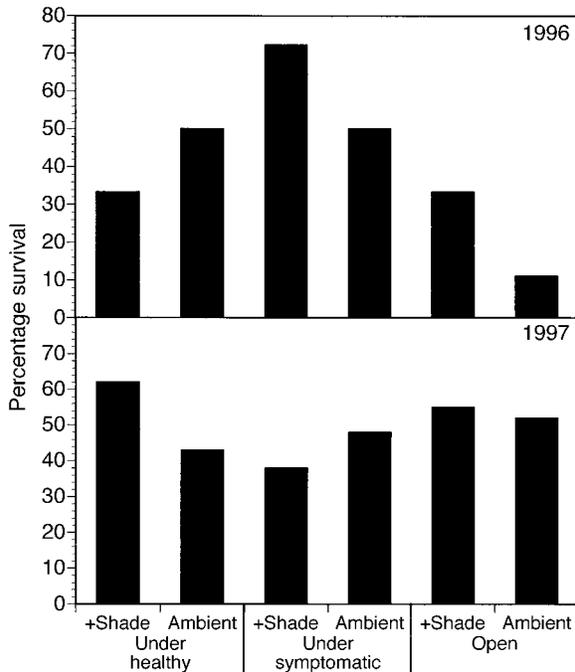


FIG. 9. Percentage survival for transplanted mesquite seedlings in experimental plots for 1996 and 1997. Location relative to trees was a significant predictor of survival in 1996 (logistic regression, $P = 0.005$). Location and shade treatments were not significant predictors of survival in 1997.

seedlings were found in open sites in 1996 (Fig. 10), and in 1997 densities of these species were five to twelve times higher under trees than in the open ($P < 0.05$; data not shown). Densities under healthy and symptomatic trees were not significantly different for any species. Densities at canopy edges of healthy and symptomatic trees were low and similar to open sites for persimmon and juniper, and differed significantly from densities under healthy trees for persimmon in 1997 ($P < 0.05$, data not shown). Canopy edge densities were low and did not differ significantly from other locations for mesquite in either year (data not shown).

In contrast to seedlings, mesquite and persimmon >50 cm tall were evenly distributed across habitats. Both species had somewhat higher densities in under-tree sites, but differences were not significant (Fig. 10, mesquite: $P = 0.853$, persimmon: $P = 0.117$). However, the distribution of juniper >50 cm matched that of the seedlings, with higher densities under trees than in the open ($P < 0.001$). Juniper densities under healthy and symptomatic trees were not significantly different.

Oak influences on growth and physiology of understory shrubs

Larger shrubs near healthy oaks tended to have slower leaf growth and lower gas exchange rates than shrubs near symptomatic trees or in the open, but patterns were variable. Leaf growth for mesquite and persimmon in

1996 tended to be lower for plants near healthy trees, but differences were not significant (Table 6). In 1997, persimmon shoot growth patterns were the opposite of 1996 leaf growth patterns; shoots grew significantly faster in plants under healthy trees than in plants at the canopy edge of symptomatic trees ($P < 0.05$, Table 6). In May 1996, photosynthetic rates (A) were almost three times lower in persimmon under healthy trees than in plants at the canopy edge of symptomatic trees ($P = 0.017$, Table 6). A and stomatal conductance (g) were also positively correlated with predawn Ψ_1 , suggesting that reduced water availability in the understory may be one factor limiting gas exchange (for A and Ψ_1 , Pearson's $r = 0.64$, $P < 0.01$; for g and Ψ_1 , $r = 0.62$, $P < 0.01$). In 1995, persimmon near healthy trees tend-

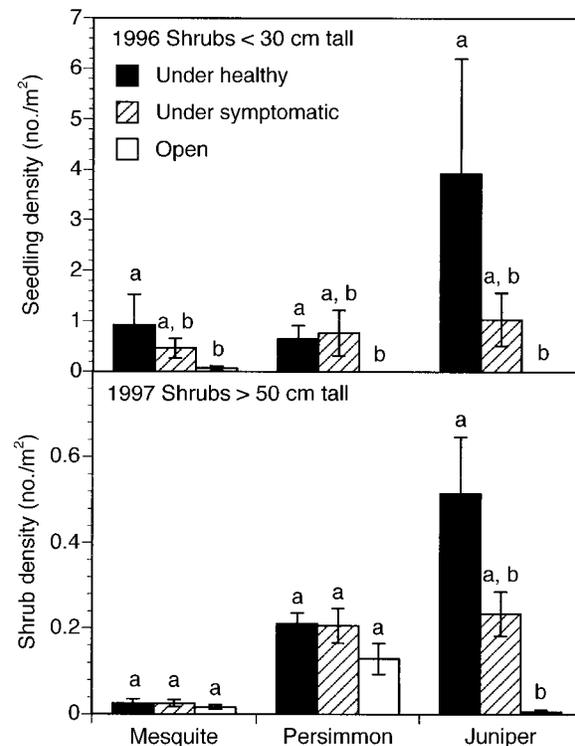


FIG. 10. Densities of mesquite, persimmon, and juniper shrubs <30 cm tall (1996 survey) and >50 cm tall (1997 survey) in different locations relative to trees (mean \pm 1 SE). Note the different scales on the y-axis of each panel. N for each bar = 13–30 survey sites. Bars that do not share letters indicate means that are significantly different. Statistical comparisons are among locations within species, not among species. Seedling densities under trees were significantly higher than densities in the open (Kruskal-Wallis: juniper $P < 0.0001$, persimmon $P = 0.0002$, mesquite $P = 0.028$). Seedling densities under healthy and symptomatic trees were not significantly different for any species. The 1997 seedling data had the same patterns and are not shown (Kruskal-Wallis: juniper $P = 0.018$ in 1997, persimmon $P = 0.010$, mesquite $P = 0.095$). Densities of larger shrubs were not significantly different among habitats for mesquite ($P = 0.853$) and persimmon ($P = 0.117$), but juniper densities were greater under trees than in the open (Kruskal-Wallis: $P < 0.001$).

TABLE 6. Growth and physiology of understory shrubs in different locations relative to oak trees (mean \pm 1 SE).

Variable	Under healthy oak		Under symptomatic oak		Canopy edge healthy oak	
	Mean \pm 1 SE	<i>N</i>	Mean \pm 1 SE	<i>N</i>	Mean \pm 1 SE	<i>N</i>
Percentage change in leaf length						
Mesquite (1997)		32.5 ^a \pm 5.5	5
Persimmon (1996)	79.0 ^a \pm 13.6	4	130.0 ^a \pm 13.0	5	85.0 ^a \pm 10.7	5
Percentage change in shoot length						
Persimmon (1997)	122.1 ^a \pm 36.9	7	43.5 ^{ab} \pm 15.5	7	41.8 ^{ab} \pm 10.2	7
Persimmon gas exchange (1996)						
<i>A</i> ($\mu\text{mol CO}_2\text{-m}^{-2}\text{-s}^{-1}$)	3.7 ^a \pm 0.5	5	7.0 ^{ab} \pm 1.1	4	7.2 ^{ab} \pm 1.8	5
<i>g</i> ($\text{mmol H}_2\text{O}\text{-m}^{-2}\text{-s}^{-1}$)	104 ^a \pm 13	5	165 ^{ab} \pm 24	4	170 ^{ab} \pm 33	5

Notes: Numbers in parentheses are numbers of shrubs upon which leaves were measured. There were no significant differences in mean percentage length changes (growth) across locations for mesquite. There was a tendency for persimmon near symptomatic trees to grow faster than those near healthy trees for leaves in 1996 (ANOVA, $P = 0.078$). There was significantly faster growth in persimmon shoots in 1997 under healthy trees than at the canopy edge of symptomatic trees (Kruskal-Wallis, $P = 0.036$). Photosynthesis (*A*) and conductance (*g*) rates were significantly lower in persimmon under healthy trees than at the canopy edge of symptomatic trees (ANOVA, $P = 0.017$ for *A*, $P = 0.006$ for *g*). Values that do not share superscript letters are significantly different. Statistical comparisons are among locations, not species.

ed to have lower *g* than plants near symptomatic trees or in the open, but differences were not significant (data not shown).

DISCUSSION

Oak influences on herbaceous productivity and understory resources

Our goals in this study were to (1) describe the effects of oaks on understory herbaceous and woody plants, (2) determine how oaks influence understory water resources, and (3) determine if water is an important factor in oak-understory interactions. Herbaceous regrowth biomass was significantly lower under healthy oaks than under symptomatic oaks or in open sites (Figs. 6 and 7), and standing biomass in undisturbed sites showed the same general pattern (Fig. 8). Healthy oaks also strongly influenced water resources under and at the edges of their canopies. Ψ_1 s in three different species were consistently lowest at the canopy edge or under healthy oaks, intermediate near symptomatic oaks, and highest in the open (Figs. 2 and 3). Soil water content was also lowest under healthy oaks (Fig. 4). Therefore, we suggest that greater water availability was an important contributor to higher herbaceous regrowth under symptomatic oaks and in open sites compared to regrowth under healthy oaks. As plots under symptomatic and healthy trees had similar light levels (Fig. 5), greater biomass under symptomatic oaks could be attributed largely to competitive release in response to improved soil resources (Figs. 6 and 7). Differences in nutrient levels under healthy and symptomatic trees were not correlated with herbaceous productivity (see further discussion of nutrients below). Our data point to water as a key resource in our system. These findings are consistent with the decreases in water use and rainfall interception expected with canopy loss in symptomatic trees. Our work is also consistent with other studies that have found reduced water availability (e.g., Thurow et al. 1987, Owens et al. 1995)

and lower herbaceous biomass (e.g., Callaway et al. 1991, Ko and Reich 1993, Haworth and McPherson 1994) under woody plants in savannas.

Differences in Ψ_1 and TDR among locations were not statistically significant for every species and every measurement date. Clearly, reductions in understory water availability by oaks are not as great during wet periods. In addition, Ψ_1 measurements are influenced by plant gas exchange patterns as well as soil moisture, such that light and water availability work in combination to influence plant water stress, and hence Ψ_1 . The water effects documented here are variable and do not necessarily exclude effects of other factors on oak-understory relationships. However, several independent data sets pointed consistently to reduced soil moisture under healthy trees compared to symptomatic trees and open sites. Therefore, we argue that competition for water is important in oak-understory interactions.

Our data cannot determine whether rainfall interception by the oak canopy or oak water use is the major factor reducing soil moisture under trees compared to open sites. Both are likely to be important. Shrubs at the canopy edges of healthy trees had significantly lower predawn Ψ_1 s than those at the canopy edges of symptomatic trees or in the open (Fig. 2, Table 1), and were not fully shielded by the canopy. This suggests oaks were reducing water in these areas through root uptake, rather than rainfall interception. However, live oak canopies can decrease precipitation in the understory by 46% (Thurow et al. 1987), so this influence cannot be disregarded.

Other work in savannas has shown that woody plants significantly enhance soil nutrient levels under their canopies compared to open sites, and has linked improved plant productivity under trees to higher nutrient availability (reviewed in Vetaas 1992, Callaway 1995, Scholes and Archer 1997). We found significantly higher NO_3^- , NH_4^+ , and K concentrations in soils under healthy trees compared to symptomatic trees and open

TABLE 6. Extended.

Canopy edge symptomatic oak		Open	
Mean \pm 1 SE	N	Mean \pm 1 SE	N
38.5 ^a \pm 9.0	10	61.1 ^a \pm 17.1	8
91.0 ^a \pm 12.6	4	94.5 ^a \pm 7.0	6
20.0 ^b \pm 5.8	7	25.6 ^{ab} \pm 7.9	8
10.6 ^b \pm 1.5	4	8.4 ^{ab} \pm 1.0	5
310 ^b \pm 54	4	228 ^{ab} \pm 35	5

sites (Table 3), consistent with earlier studies. However, herbaceous productivity was not positively associated with soil nutrient availability in our system. It is not known how oak wilt influences soil nutrients under tree canopies. Root mortality in diseased trees may lead to enhanced nutrient availability in deeper soils that we did not sample. However, this does not explain high herbaceous productivity in open sites. Greater soil moisture under symptomatic trees and in the open could increase soil nutrient mobility, leading to improved nutrient uptake and enhanced growth. There is some suggestion that woody plants in our system may respond positively to nutrients under healthy trees in wet periods. In summary, there may be important effects of nutrients that our methods did not detect, but our soil nutrient data do not explain patterns of herbaceous productivity in this system.

Shade had a significant influence on herbaceous growth (e.g., Mordelet and Menaut 1995), but the importance of shade varied with harvest date (Figs. 6 and 7, Table 4). These changes in the influence of shade may be related to annual or seasonal changes in water availability. Shade had stronger suppressive effects during wet periods, as shown by larger differences in biomass between shaded and unshaded plots within a location during times of high rainfall (shade \times date interaction, Table 4). In July 1996 (the drought year), ambient plots had 5–13% more biomass than shaded plots within locations, while in July 1997 (the wet year) biomass differences between ambient and shaded plots ranged from 46–67% (Table 5, Figs. 6 and 7). Similarly, differences between ambient and shaded plots increased from 5–13% in July 1996 to 18–64% in September 1996 (Table 5, Figs. 6, and 7), after the site received a heavy rainfall in August 1996. Thus, it seems light had stronger effects on plant growth when belowground resources were more abundant. Precipitation variation cannot explain all differences observed between ambient and shaded plots. For example, differences between September 1996 and September 1997 are not clearly related to precipitation, and increasing differences between ambient and shaded plots under healthy trees over time suggest a cumulative suppressive effect of shade in the understory (Table 5). However, interactions between light and water may be one

important influence on patterns of herbaceous productivity in this and other savannas.

Earlier research has identified differences in species composition between microsites under woody plants and those in the open (e.g., Belsky et al. 1989; reviewed in Vetaas 1992, Scholes and Archer 1997). Species differences among habitats could influence the productivity patterns we observed. While species composition across locations was not quantified, field observations suggested that the two dominant grasses, King Ranch bluestem (C_4) and Texas wintergrass (C_3), were both commonly found both under trees and in the open. These dominants made up the majority of collected biomass, and were temporally rather than spatially segregated, with Texas wintergrass active in the spring and King Ranch bluestem active in the summer and fall (L. J. Anderson, *personal observation*). Forbs, the second largest biomass component, were more diverse. Although no strong changes in composition were noted across locations, forbs in 1997 were a significantly larger fraction of biomass under symptomatic trees and in open sites compared to biomass under healthy trees (Figs. 7 and 8). There may be species influences contributing to these patterns that were not obvious without quantification. Forbs were particularly abundant in the spring of 1997. This was probably a seasonal effect: forbs were present in spring when water was available while C_4 grasses became dominant in the drier summer.

Differences in herbaceous biomass under healthy and symptomatic trees were smaller in our survey of standing, undisturbed vegetation compared to differences seen for herbaceous biomass between healthy and symptomatic trees in our clipped experimental plots (Fig. 8). Because of disturbance involved in constructing the experimental plots, vegetation surveys and shrub physiology measurements were done under different oaks than those with plots. Symptomatic oaks in this group were more variable in their degree of canopy loss. Some had developed oak wilt symptoms only recently, and therefore may have still been suppressing understory plants in a manner similar to healthy trees. This may also explain the small differences between predawn Ψ_s s for persimmon under healthy trees and those under symptomatic trees (Fig. 2).

Our data contrast with several savanna studies that found increased herbaceous production under tree canopies compared to open sites (e.g., Belsky et al. 1989, 1993). Clearly, relationships between herbaceous and woody plants in savannas are variable, and no general model yet predicts the strength and direction of these relationships consistently (Scholes and Archer 1997). One factor that is important at our site and may explain discrepancies among studies is soil depth. For example, the two-layer hypothesis regarding woody–herbaceous resource partitioning in savannas assumes a deep soil profile (Walter 1971). In this model, herbs and woody plants compete for water in upper soil layers, and grass-

es are superior competitors in this case. In contrast, shrubs and trees often rely on water in subsoils that shallowly rooted herbs cannot access. This model successfully explains herbaceous–woody interactions in some savannas (e.g., Soriano and Sala 1983, Knoop and Walker 1985, Sala et al. 1989, Brown and Archer 1990). However, bedrock lies only 20–50 cm deep at our site, intensifying competitive interactions among roots of plants constrained to the upper soil layers. Even though trees and shrubs can penetrate cracks in bedrock (Noy-Meir 1973, Jackson et al. 1999), the majority of root biomass is concentrated near the surface in this and other deep-rooted ecosystems (Jackson et al. 1996, 1997). Marshall and Gilman (1997) found that field grown *Q. virginiana* nursery trees have >50% of their root cross-sectional area in the top 25 cm of the soil profile. Several other savanna studies have also shown that woody plants and herbs occupy similar soil profiles and draw from surface resources (e.g., Ansley et al. 1990, Belsky 1994, Le Roux et al. 1995, Le Roux and Bariac 1998), which could intensify competition between growth forms. For example, in a California grassland, Callaway et al. (1991) showed that understory productivity was reduced under those *Q. douglasii* trees with high concentrations of roots in the upper 50 cm of soil. It could be valuable to review savanna studies showing a range of herbaceous–woody interactions and determine if soil depth is a useful predictor of the direction of these interactions.

Variations in tree–herb interactions among savanna studies may also be due to differences in tree canopy morphology across sites. Large trees such as live oak may have stronger negative (or positive) effects on the understory than do small trees (e.g., Mordelet and Menaut 1995; but see Belsky et al. 1989). In addition, evergreens may be more likely than deciduous trees to have negative effects because they can grow, use resources, and cast shade all year (Owens and Schreiber 1992), and may have lower nutrient requirements and better nutrient retention than herbs (Scholes and Archer 1997). In a grassland with a mix of deciduous and evergreen oaks, the deciduous oak enhanced herbaceous production relative to the open grassland while the evergreen oak suppressed it, despite greater soil nutrients under both species (Frost and Edinger 1991).

Oak influences on woody seedling survival and distributions

Despite lower soil water and light availability under oaks, the greatest densities of mesquite, persimmon, and juniper <30 cm tall occurred in understory sites, and transplanted mesquite seedlings had higher survival under trees than in the open in 1996. Therefore the influence of oaks on woody species was facilitative, at least for small plants. This is consistent with other observations of woody plant distributions in savannas (Fowler 1986, Callaway 1995, Archer et al. 1988), but in contrast to the oak–herb interactions we observed.

One testable, physiological explanation for the positive effects of oaks on woody seedlings is that reductions in thermal stress and evaporative demand under trees (Table 2, Fig. 5) are more important for small woody plants than reductions in soil moisture (e.g., Holmgren et al. 1997). With a lower evaporative gradient, seedlings under trees may maintain higher midday Ψ_i , despite drier soil. This is one explanation for why trees and shade cloth facilitated mesquite transplant survival in the 1996 drought, but did not have beneficial effects in 1997 (Fig. 9). In this wet year, there may have been enough water to compensate for high evaporative demands in the open. Hoffmann (1996) also found that woody cover enhanced woody seedling establishment to a greater extent during dry periods.

Mesquite survival in shade–healthy plots also improved in 1997 compared to 1996, while survival in shade–symptomatic plots decreased (Fig. 9). Because planting techniques varied slightly between years, differences must be interpreted cautiously. However, greater water availability in 1997 may have allowed seedlings under healthy trees to take advantage of nutrient resources in these sites (Table 3), while seedlings under symptomatic trees may have been more affected by herbaceous competition than in 1996. For woody seedlings, there may be trade-offs between competition with oaks and herbs that change with environmental conditions. In 1996, shade–symptomatic plots may have been optimal for mesquite survival because competition with the oak was reduced (due to oak wilt) and herbaceous biomass was lower than in open sites. In 1997, negative effects of oaks could have been ameliorated with greater water availability, while herbaceous competition, possibly for nutrients, increased. Further work with nutrient and water relations in woody plants under different precipitation regimes is needed to test these hypotheses.

Other savanna work has shown strong negative effects of herbs on woody seedlings (Walker and Noy-Meir 1982, Bush and Van Auken 1990, Skarpe 1992). Van Auken and Bush (1997) found that mesquite biomass was significantly higher in seedlings grown without grass roots relative to those grown with grass roots. Shade did not affect biomass. These data are consistent with the high natural densities of mesquite we found in shaded sites with low herbaceous productivity. In contrast, Brown and Archer (1989, 1999) found that the physiology and survival of mesquite seedlings were not strongly influenced by herb defoliation, suggesting that herbs have little effect on mesquite recruitment. They also documented deep seedling taproots that could allow partitioning of soil resources between mesquite and grasses (Brown and Archer 1990). The soils in their studies were much deeper than those at Camp Creek, which may intensify belowground competition, as noted above. Oak facilitation of woody seedlings may also be related to animal dispersal patterns that concentrate seeds under oaks (Belsky and Canham

1994). In addition, differences in germination may influence woody seedling distributions among microsites, as found in other systems (e.g., Anderson and Winter-ton 1996; reviewed in Fenner 1985).

Oak influences on distributions, growth, and physiology of larger woody plants

Interactions between species may change from facilitative to competitive or neutral depending on the life history stages of the plants involved (Callaway 1995, Barnes and Archer 1996, Callaway and Walker 1997). Our shrub distribution data suggest oaks switch from a positive to a negative effect on persimmon and mesquite as these latter species mature. While there were greater densities of mesquite and persimmon <30 cm tall under trees than in the open, these species were more evenly distributed among habitats when >50 cm tall (Fig. 10). This suggests poor survival in under-canopy sites for woody plants in the 30–50 cm range. This could be due to intensifying competition with the oak or conspecifics as seedlings age (e.g., Martens et al. 1997).

Some physiological evidence suggested larger shrubs were negatively affected by oaks. Mesquite at the canopy edge of healthy oaks had the lowest Ψ_1 (Fig. 2), and tended to have lower leaf growth rates than shrubs in other sites (Table 6). For persimmon, patterns were more complex and variable. Persimmon at the canopy edge of healthy trees always had the lowest Ψ_1 , but Ψ_s for persimmon under healthy trees were often only slightly more negative than Ψ_s under symptomatic trees or in open sites (Fig. 2). This could be due to shade suppressing leaf gas exchange for understory persimmon (Table 6), leading to slower water use compared to plants in open sites. Therefore, despite reduced soil moisture under oaks, shade may contribute positively to leaf water status in persimmon. Shrubs under and at the canopy edge of healthy oaks tended to have slower leaf expansion rates than shrubs in other sites during 1996, but the opposite pattern occurred for persimmon shoot growth in 1997 (Table 6). The majority of data for both species suggest that oaks suppress larger shrubs by limiting water and light availability, making it less likely that these species will replace the oaks under which they establish. However, more data on survival, growth, and fecundity in shrubs are needed to describe the full extent and importance of this competitive effect, and to explain the rapid growth of persimmon shoots under healthy trees in the wet year (Table 6). Differences between leaf and shoot growth patterns among years may be due to changes in precipitation allowing shrubs to take advantage of understory nutrient resources, or morphological differences in carbon allocation to leaves relative to shoots.

Community implications

Relative to other savannas, our site is mesic (annual precipitation = 734 mm), using the definition of Belsky

(1994). Our data support the assertion of Belsky (1994) and Le Roux et al. (1995) that competition is important in wetter savannas. However, our data also emphasize that efforts to develop broad theories about the roles of competition and facilitation in shaping community structure along productivity, stress, or disturbance gradients (e.g., Brooker and Callaghan 1998) will be complicated by the effects of species and life stages in plant–plant interactions. Oaks in our system facilitated small woody plants but suppressed herbs, and possibly larger shrubs. Oaks had no influence on mesquite trans-plant survival in 1997. Therefore, discussions of competition and facilitation must take into account the species and maturity of the plants in question, as well as annual environmental variation (Callaway and Walker 1997).

Oak wilt adds to the complexity of species interactions in our savanna. The oak wilt fungus *Ceratocystis fagacearum* clearly has an indirect interaction with understory species through its direct effects on live oak. An indirect interaction is a situation in which one species modifies the interactions between two or more other species (Connell 1990). The differences we observed in herbaceous biomass, seedling survival, and shrub water relations between sites under healthy and symptomatic oaks demonstrate that this disease is changing community dynamics in our savanna, as has been documented for oak wilt in woodlands (Menges and Loucks 1984, McCune and Cottam 1985, McCune et al. 1988), and other pathogens in other habitats (Castello et al. 1995). Oak wilt is widespread in the central and eastern U.S. (e.g., Mielke et al. 1983), and thousands of hectares of oaks have been lost in Central Texas (Appel and Maggio 1984, Appel et al. 1989). Our data suggest oak mortality may lead to increased herbaceous biomass and decreased woody seedling establishment. Woody plants already growing under oaks may experience competitive release when trees die. However, to understand long-term vegetation changes in sites with oak wilt, we need data on herbaceous biomass, species replacement, and seedling recruitment patterns in oak wilt centers of different ages. The effects of oak wilt must also be weighed against other factors affecting savanna community structure, such as grazing, drought, fire, and land-use change (e.g., Skarpe 1992, Hoffmann and Jackson 2000). Further research on the ecological consequences of oak wilt could make important contributions to our understanding of savanna ecosystems and management of oak wilt sites.

Conclusions

Live oaks suppress herbaceous plants, facilitate woody seedlings, and may compete with larger shrubs in our savanna. Live oaks also reduce soil moisture under and at the edges of their canopies compared to open sites, suggesting that negative effects of oaks on some plants are related to low water availability in the understory. This idea is strengthened by the fact that

plant productivity was higher in shade-symptomatic plots than ambient-healthy plots, despite similar light levels in these treatments. Thus, when oak leaf area was reduced, water increases in the understory led to improved herbaceous productivity. Soil nutrients, while known to be important in tree-understory interactions in other savannas, did not appear to play as strong a role as water in our system. However, water influences varied seasonally and annually, and differed among species and growth forms. Other factors, such as light and nutrients, may become increasingly important in plant interactions when water is more abundant, and water and light may interact to influence individual plant water status and productivity patterns among habitats. Finally, oak wilt has the potential to strongly affect community and ecosystem processes in savannas, and pathogens in general should be recognized as significant agents for ecological change.

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LITERATURE CITED

- Anderson, L. J., and A. J. Winterton. 1996. Germination as a determinant of seedling distributions among natural substrates in *Picea engelmannii* (Pinaceae) and *Abies lasiocarpa* (Pinaceae). *American Journal of Botany* **83**:112–117.
- Ansley, R. J., P. W. Jacoby, and G. J. Cuomo. 1990. Water relations of honey mesquite following severing of lateral roots: influence of location and amount of subsurface water. *Journal of Range Management* **43**:436–442.
- Appel, D. N. 1994. Identification and control of oak wilt in Texas urban forests. *Journal of Arboriculture* **20**:250–258.
- Appel, D. N., and R. C. Maggio. 1984. Aerial survey for oak wilt incidence at three locations in central Texas. *Plant Disease* **68**:661–664.
- Appel, D. N., R. C. Maggio, E. L. Nelson, and M. J. Jaeger. 1989. Measurement of expanding oak wilt centers in live oak. *Phytopathology* **79**:1318–1322.
- Archer, S., C. Scifres, C. R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* **58**:111–127.
- Barnes, P. W., and S. Archer. 1996. Influence of an overstory tree (*Prosopis glandulosa*) on associated shrubs in a subtropical savanna parkland: implications for patch dynamics. *Oecologia* **105**:493–500.
- Beckman, C. H., J. E. Kuntz, A. J. River, and J. G. Berbee. 1953. Host responses associated with the development of oak wilt. *Phytopathology* **4**:448–454.
- Belsky, A. J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* **75**:922–932.
- Belsky, A. J., R. G. Amundson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwonga. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology* **26**:1005–1024.
- Belsky, A. J., and C. D. Canham. 1994. Forest gaps and isolated savanna trees. *BioScience* **44**:77–84.
- Belsky, A. J., S. M. Mwonga, R. G. Amundson, J. M. Duxbury, and A. R. Ali. 1993. Comparative effects of isolated trees and their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology* **30**:143–155.
- Brooker, R. W., and T. V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* **81**:196–207.
- Brown, J. R., and S. Archer. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* **80**:19–26.
- Brown, J. R., and S. Archer. 1990. Water relations of a perennial grass and seedling vs. adult woody plants in a subtropical savanna, Texas. *Oikos* **57**:366–374.
- Brown, J. R., and S. Archer. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* **80**:2385–2396.
- Bush, J. K., and O. W. Van Aiken. 1990. Growth and survival of *Prosopis glandulosa* seedlings associated with shade and herbaceous competition. *Botanical Gazette* **151**:234–239.
- Callaway, R. M. 1995. Positive interactions among plants. *Botanical Review* **61**:306–349.
- Callaway, R. M., N. M. Nadkarni, and B. E. Mahall. 1991. Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology* **72**:1484–1499.
- Callaway, R. M., and L. R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**:1958–1965.
- Casper, B. B., and R. B. Jackson. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* **28**:545–570.
- Castello, J. D., D. J. Leopold, and P. J. Smallidge. 1995. Pathogens, patterns, and processes in forest ecosystems. *BioScience* **45**:16–24.
- Connell, J. H. 1990. Apparent vs. “real” competition in plants. Pages 9–26 in J. B. Grace and D. Tilman, editors. *Perspectives on plant competition*. Academic Press, New York, New York, USA.
- Dittmore, W. H., Jr., and J. E. Allison. 1979. Soil survey of Blanco and Burnet Counties, Texas. United States Department of Agriculture, Soil Conservation Service, in cooperation with the Texas Agricultural Experiment Station.
- Fenner, M. 1985. *Seed ecology*. Chapman and Hall, New York, New York, USA.
- Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics* **17**:89–110.
- Frost, W. E., and S. B. Edinger. 1991. Effects of tree canopies on soil characteristics of annual rangeland. *Journal of Range Management* **44**:286–288.
- Gould, F. W. 1978. *Common Texas grasses: an illustrated guide*. Texas A&M University Press, College Station, Texas, USA.
- Haworth, K., and G. R. McPherson. 1994. Effects of *Quercus emoryi* on herbaceous vegetation in a semi-arid savanna. *Vegetatio* **112**:153–159.

- Hoffmann, W. A. 1996. The effects of fire and cover on seedling establishment in a neotropical savanna. *Journal of Ecology* **84**:383–393.
- Hoffmann, W. A., and R. B. Jackson. 2000. Vegetation-climate feedbacks in the conversion of tropical savanna to grassland. *Journal of Climate* **13**:1593–1602.
- Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. *Ecology* **78**:1966–1975.
- Holzappel, C., and B. E. Mahall. 1999. Bi-directional facilitation and interference between shrubs and annuals in the Mojave desert. *Ecology* **80**:1747–1761.
- Jackson, R. B., L. J. Anderson, and W. T. Pockman. 2000. Measuring water availability and uptake in ecosystem studies. Pages 199–214 in O. E. Sala, R. B. Jackson, H. A. Mooney, and R. W. Howarth, editors. *Methods in Ecosystem Studies*. Springer-Verlag, New York, New York, USA.
- Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**:389–411.
- Jackson, R. B., H. A. Mooney, and E.-D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences, USA* **94**:7362–7366.
- Jackson, R. B., L. A. Moore, W. A. Hoffmann, W. T. Pockman, and C. R. Linder. 1999. Ecosystem rooting depth determined with caves and DNA. *Proceedings of the National Academy of Sciences, USA* **96**:11387–11392.
- Joffre, R., and S. Rambal. 1988. Soil water improvement by trees in the rangelands of southern Spain. *Oecologia Plantarum* **9**:405–422.
- Joffre, R., and S. Rambal. 1993. How tree cover influences the water balance of Mediterranean rangelands. *Ecology* **74**:570–582.
- Knoop, W. T., and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* **73**:235–253.
- Ko, L. J., and P. B. Reich. 1993. Oak tree effects on soil and herbaceous vegetation in savannas and pastures in Wisconsin. *American Midland Naturalist* **130**:31–42.
- Le Roux, X., and T. Bariac. 1998. Seasonal variations in soil, grass and shrub water status in a West African humid savanna. *Oecologia* **113**:456–466.
- Le Roux, X., T. Bariac, and A. Mariotti. 1995. Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. *Oecologia* **104**:147–155.
- MacDonald, W. L., and D. F. Hindal. 1981. Life cycle and epidemiology of *Ceratocystis*. Pages 113–144 in M. E. Mace, A. A. Bell, and C. H. Beckman, editors. *Fungal wilt diseases of plants*. Academic Press, New York, New York, USA.
- Marshall, M. D., and E. F. Gilman. 1997. Production method and irrigation affect root morphology of live oak. *Journal of Environmental Horticulture* **15**:84–87.
- Martens, S. N., D. D. Breshers, C. W. Meyer, and F. J. Barnes. 1997. Scales of above-ground and below-ground competition in a semi-arid woodland detected from spatial pattern. *Journal of Vegetation Science* **8**:655–664.
- McCune, B., C. L. Cloonan, and T. V. Armentano. 1988. Tree mortality and vegetation dynamics in Hemmer Woods, Indiana, USA. *American Midland Naturalist* **120**:416–431.
- McCune, B., and G. Cottam. 1985. The successional status of a southern Wisconsin oak woods. *Ecology* **66**:1270–1278.
- Menges, E. S., and O. L. Loucks. 1984. Modeling a disease-caused patch disturbance: oak wilt in the midwestern United States. *Ecology* **65**:487–498.
- Mielke, M. E., C. Haynes, and C. O. Rexrode. 1983. Local spread of oak wilt in northeastern West Virginia, USA during 1970–1982. *Plant Disease* **67**:1222–1223.
- Milliken, G. A., and D. E. Johnson. 1992. *Analysis of messy data*. Chapman and Hall, New York, New York, USA.
- Mordelet, P., L. Abbadie, and J.-C. Menaut. 1993. Effects of tree clumps on soil characteristics in a humid savanna of West Africa (Lamto, Cote d'Ivoire). *Plant and Soil* **153**:103–111.
- Mordelet, P., and J.-C. Menaut. 1995. Influence of trees on above-ground production dynamics of grasses in a humid savanna. *Journal of Vegetation Science* **6**:223–228.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**:25–51.
- Owens, M. K., and M. C. Schreiber. 1992. Seasonal gas exchange characteristics of two evergreen trees in a semi-arid environment. *Photosynthetica* **26**:389–398.
- Owens, M. K., R. B. Wallace, and S. R. Archer. 1995. Landscape and microsite influences on shrub recruitment in a disturbed semi-arid *Quercus-Juniperus* woodland. *Oikos* **74**:493–502.
- Richards, J. H., and M. M. Caldwell. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* **73**:486–489.
- Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* **81**:501–505.
- Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**:517–544.
- Skarpe, C. 1992. Dynamics of savanna ecosystems. *Journal of Vegetation Science* **3**:293–300.
- Soriano, A., and O. Sala. 1983. Ecological strategies in a Patagonian arid steppe. *Vegetatio* **56**:9–15.
- Thurrow, T. L., W. H. Blackburn, S. D. Warren, and C. A. Taylor, Jr. 1987. Rainfall interception by midgrass, shortgrass, and live oak mottes. *Journal of Range Management* **40**:455–460.
- Van Auken, O. W., and J. K. Bush. 1997. Growth of *Prosopis glandulosa* in response to changes in aboveground and belowground interference. *Ecology* **78**:1222–1229.
- Vetaas, O. R. 1992. Micro-site effects of trees and shrubs in dry savannas. *Journal of Vegetation Science* **3**:337–344.
- Vines, R. A. 1984. *Trees of Central Texas*. University of Texas Press, Austin, Texas, USA.
- Walker, B. H., and I. Noy-Meir. 1982. Aspects of stability and resilience of savanna ecosystems. Pages 556–590 in B. J. Huntley and B. H. Walker, editors. *Ecology of tropical savannas*. Springer-Verlag, New York, New York, USA.
- Walter, H. 1971. *Ecology of tropical and subtropical vegetation*. Oliver and Boyd, Edinburgh, UK.
- Zar, J. H. 1996. *Biostatistical analysis*, Third edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.