

Spatial relations between shrubs and *Prosopis glandulosa* canopies

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Abstract. *Prosopis glandulosa*, an arborescent legume, may act as a nurse plant that facilitates the establishment of other woody species. We hypothesized that attenuation of radiant energy and increased soil nutrients beneath *P. glandulosa* canopies facilitate establishment of subordinate shrubs and shrub cluster development. We determined the spatial distribution pattern of shrubs under *P. glandulosa* at three locations in southern Texas. Density of *Celtis pallida*, *Zanthoxylum fagara*, and total woody plants were comparable among the four cardinal directions at each location, which countered the prediction that shrub density would be greater on the north side of *P. glandulosa* canopies if attenuation of solar energy was a factor in cluster development. Total woody plant density increased with increasing *P. glandulosa* basal diameter, canopy radius, and height only at one location. Total woody plant density decreased with increasing total N in the upper 15 cm of soil at two of the three locations. Late in shrub cluster development, extraction of N from the soil and incorporation of N into plant tissue in dense shrub clusters may operate to inhibit further increases in subordinate shrub density.

Keywords: *Celtis pallida*; Facilitation; Nurse plant; Soil nitrogen; Soil nutrient; *Zanthoxylum fagara*.

Nomenclature: Hatch et al. (1990).

Introduction

The nurse plant phenomenon has been described in arid and semiarid regions throughout the world. Examples include seedling establishment of *Euclea divinorum* in southern Africa, which is restricted to areas beneath the canopy of *Acacia nilotica* individuals (Smith & Goodman 1987). *Acacia schaffneri* apparently facilitates establishment of *Opuntia streptacantha* in the southern Chihuahuan Desert in Mexico (Yeaton & Manzanares 1986). Seedlings of the saguaro cactus (*Carnegiea gigantea*) in the Sonoran Desert depend upon nurse plants for survival (Turner et al. 1966; Franco & Nobel 1989).

Despite its ubiquitous nature, the mechanisms that underlie the facilitation process have not been well quantified (Valiente-Banuet et al. 1991). Franco & Nobel (1988, 1989) found that nurse plants facilitate seedling establishment of *Agave deserti* and *Carnegiea gigantea*

by reducing high temperatures near the soil surface and by providing a microhabitat with greater soil nitrogen (N). Valiente-Banuet & Ezcurra (1991) concluded that shading reduced temperatures and evaporation resulting in greater seed germination and survival of the cactus *Neobuxbaumia tetetzo* under canopies of the nurse plant *Mimosa luisana* than in open spaces, and suggested that differences in soil fertility are of secondary importance.

Prosopis glandulosa, a widespread arborescent legume in the southwestern United States and northern Mexico, may act as a nurse plant that facilitates the establishment of other woody species in grassland, resulting in formation of shrub clusters (Gilbert in press; Archer et al. 1988). Archer (1989) documented distinct chronosequences of shrub cluster development under *P. glandulosa* canopies. Archer et al. (1988) speculated that cluster development is an intermediate successional stage between grassland and woodland which is followed by cluster expansion and ultimate coalescence to form thorn woodland.

Prosopis glandulosa canopies reduce incoming solar radiation (Bush & Van Auken 1990) and moderate soil temperatures (Fulbright 1991) beneath them. Soil nutrients may increase under *P. glandulosa* canopies following establishment (Tiedemann & Klemmedson 1973; Johnson & Mayeux 1990). Our hypothesis was that increased soil nutrients and attenuation of solar radiation beneath *P. glandulosa* canopies facilitate establishment of subordinate shrubs and shrub cluster development. We predicted that if shading is a factor in the nurse plant effect, (1) shrub density should be greatest on the northern side of *P. glandulosa* canopies, since direct solar radiation comes predominantly from the south in southern Texas, and (2) density of shrubs beneath *P. glandulosa* canopies will be greater with increased *P. glandulosa* size (height, canopy radius, and stem diameter). A third prediction was that if soil nutrients are an important factor in the nurse plant effect, density of subordinate shrubs in clusters beneath *P. glandulosa* would increase with increasing soil nutrients. We tested these predictions focusing on *Celtis pallida* and *Zanthoxylum fagara* because they were the most abundant shrubs beneath *P. glandulosa* individuals.

Methods

Study areas

The study was conducted at three locations in southern Texas. The climate in southern Texas is subtropical and humid, with hot summers and relatively mild winters. The 92-ha Texas A&M University-Kingsville Range and Wildlife Research Area (Site I) is in Kleberg County, 15 km south of Kingsville, Texas (27° 36' N, 97° 57' W). Mean maximum summer temperature is 35 °C and minima range between 24 and 27 °C (Norwine et al. 1977). The mean annual rainfall of the area is 770 mm and the growing season averages 314 days. Vegetation is dominated by *P. glandulosa* that forms an overstory with a dense understory of shrub species (Ham 1979). Herbaceous vegetation includes an upper layer of tall forbs and grasses such as *Chloris pluriflora* and a lower layer dominated by forbs and grasses including species of *Aristida*, *Bouteloua*, *Chloris* and *Eragrostis* (McClendon 1991). The area was heavily grazed by cattle before 1970 (Drawe 1977) and was not grazed after 1985. Soils of the study area were Delfina fine sandy loam (hyperthermic Aquic Paleustalf); Hidalgo sandy clay loam (hyperthermic Typic Calciustoll); and Willacy fine sandy loam (hyperthermic Udic Argiustoll) (Anon. 1977).

Site II, the Texas A&M University La Copita Research Area, is a 2726-ha station in western Jim Wells County, 24 km south and west of Alice, Texas (27° 40' N, 98° 12' W). Mean annual temperature is 22 °C and the mean growing season 280 days. Average annual precipitation is 680 mm with maxima in May and September. Vegetation is dominated by *P. glandulosa* with variable combinations of shrubs and clearings between shrubs are dominated by species of *Paspalum*, *Setaria*, *Bouteloua* and *Chloris* (Archer et al. 1988). The 10-ha area sampled was excluded from livestock grazing since 1985, and has never been subjected to mechanical or chemical brush control. Soils of the sampled area consisted of Miguel fine sandy loam and Papalote loamy fine sands (hyperthermic Aquic Paleustalfs) with gentle 1-3 % slopes (Scifres & Koerth 1987; Archer et al. 1988).

Site III, the 4856-ha Rio Paisano Ranch, is in the southwest corner of Kleberg County, 20 km west of Riviera, Texas (27° 21' N, 98° 00' W). Mean annual temperature is 23 °C and the growing season averages 314 days (Norwine et al. 1977). Average annual precipitation is 640 mm with maxima in May and September. Vegetation is dominated by a *P. glandulosa*-mixed shrub community with clearings dominated by herbs characteristic of the *Schizachyrium scoparium* var. *littoralis*-*Elyonurus tripsacoides* association (McClendon 1991). The area was grazed by 63 steers/km² for 90 days in 1988, was not grazed in 1989, and was grazed by 100

steers/km² for 45 days during 1990 (A. Adams, ranch manager, pers. comm. 1992). Soils of the area are fine sandy loams and loamy fine sands of the Delfina (hyperthermic Aquic Paleustalfs), Nueces (hyperthermic Aquic Arenic Paleustalfs), and Edroy (hyperthermic Vertic Haplaquolls) series (Anon. 1977).

Spatial distribution of shrubs

To determine the spatial patterns of woody plant distribution, transects were placed radiating out in the four cardinal directions from trunks of 30 randomly selected *P. glandulosa* individuals (> 6 cm basal diameter) at each of the three locations. The transects extended to the center of clearings between *P. glandulosa* individuals and mean transect length in each cardinal direction ranged from 4.5 ± 2.0 m (± SD) at site II to 7.5 ± 3.0 m at site III. The length of each transect beneath *P. glandulosa* canopies in each direction averaged from 2.2 ± 0.9 m at site II to 4.1 ± 1.4 m at site III. Density of woody plants and height, canopy radius in each cardinal direction, and basal stem diameter of each *P. glandulosa* individual were recorded in adjacent 0.5 m × 0.5 m plots placed along each transect. Vegetation was sampled during November-December 1989 at site I, May 1990 at site II, and June 1990 at site III.

Mean density of *C. pallida*, *Z. fagara* and total woody plant density among the four cardinal directions under the canopy of *P. glandulosa* ($n = 30$) was compared by ANOVA. Regression analysis was used to determine relationships between density of *C. pallida*, *Z. fagara*, and total woody plant density (beneath *P. glandulosa* canopies) and *P. glandulosa* height, stem diameter, and mean canopy radius (the average of N, S, E, and W) (Snedecor & Cochran 1967). Data from each location were analyzed separately.

Edaphic characteristics

Soil samples were collected at each of the three locations during August-September 1990 from 0-15 cm and 15-30 cm depth. Soil samples ($n = 10$) were obtained in each cardinal direction at a distance of 0.5-1.0 m from the trunk of each of 10 *P. glandulosa* individuals; these were thoroughly mixed. Samples were also taken from the center of the widest clearing adjacent to the *P. glandulosa* individual sampled. Four samples were removed at each depth and mixed. Soil samples were dried in thin layers to a constant mass (for 48 hours) at 40 °C, screened through a 2-mm mesh, and analyzed for particle size distribution (Bouyoucos 1962), total N (determined colorimetrically following Kjeldahl digestion) (Horneck et al. 1989), NO₃-N (Keeney & Nelson 1982), and available P (Olsen & Dean 1965).

Characteristics of soil from under *P. glandulosa* canopies and from the adjacent clearings were compared with paired *t*-tests ($P \pm 0.05$). Relationships among total N, NO_3N , and available P under *P. glandulosa* canopies and density of *C. pallida*, *Z. fagara*, and total woody species were examined with regression analyses. The three locations and two depths were analyzed separately. For all analyses $n = 10$, except for total N ($n = 6$).

Results

At all locations, density of *C. pallida*, *Z. fagara* and total woody species declined with increasing distance from the trunk (Figs. 1-3). There was a slight increase in density at the edge of the *P. glandulosa* canopy at each location. At site II, density of *C. pallida* was lower at 0-0.5 m from the trunk than at 0.5-1.0 m from the *P. glandulosa* trunk, whereas at site I it was greatest at 0-0.5 m from the trunk. At site III, *C. pallida* density was similar within 0-2 m from the *P. glandulosa* trunk.

Total woody plant density was greatest within 0.5 m of the *P. glandulosa* trunk at sites I and II (Fig. 3). At site III, total woody plant density was greatest 0.5-1 m from the *P. glandulosa* trunk.

Celtis pallida, *Z. fagara* and total woody plant density did not differ ($P > 0.05$) among the four cardinal directions at each location (Table 1). At sites I and III, there was no significant ($P > 0.05$) relationship between the mean basal diameter of *P. glandulosa* and density of *C. pallida*. At site II, *C. pallida* density increased with both *P. glandulosa* diameter ($Y = -0.4 + 0.04X$) and height ($Y = -1.0 + 0.3X$) (Table 2). *Z. fagara* density also increased with increasing *P. glandulosa* basal diameter ($Y = 0.4 + 1.2X$) at site II.

Total woody plant density increased with increasing *P. glandulosa* basal diameter ($Y = 0.7 + 0.2X$), canopy

radius ($Y = 1.9 + 1.5X$), and height ($Y = 0.4 + 1.2X$) at site II (Table 2). In contrast, total woody plant density was negatively related to *P. glandulosa* canopy radius ($Y = 2.9 - 0.3X$) and height ($Y = 3.6 - 0.4X$) at site III.

Soils from under the canopy of *P. glandulosa* and from the adjoining grass-dominated clearings of sites I and II were predominantly sandy loams. Loamy sands were predominant at site III. 15 % of the samples from site I were sandy clay loams (depth 15-30 cm), and 20 % of the samples from site III were sand (at both depths). In comparison to soils from herbaceous clearings, nutrient concentrations were generally greatest in soils from underneath the canopy of *P. glandulosa* at both depths (Table 3).

There were no significant ($P > 0.05$) relationships between available P or $\text{NO}_3\text{-N}$ and density of *C. pallida*, *Z. fagara*, or total woody plants (data not shown). Total woody plant density increased with decreasing total N in the upper 15 cm of soil at site I ($R^2 = 0.80$, $P = 0.02$; $Y = 4.5 - 3.3X$, $n = 6$) and at site III ($R^2 = 0.80$, $P = 0.02$; $Y = 4.6 - 3.6X$, $n = 6$).

Discussion

Our results were counter to the prediction that shrub density would be greater on the north side of *P. glandulosa* canopies. In contrast to our results, Valiente-Banuet & Ezcurra (1991) found that five of six succulent species showed a significant pattern of greater establishment on the northern side of nurse shrubs in the Vizcaino and Altar deserts of Mexico. In central Mexico, Valiente-Banuet et al. (1991) found that four of five cacti species were randomly distributed beneath nurse plants. They speculated that the latitude of central Mexico was too far south for the microclimate on the northern side of nurse plants to differ sufficiently from the southern side for a

Table 1. Density of *Celtis pallida*, *Zanthoxylum fagara*, and total woody plants in relation to cardinal direction from the *Prosopis glandulosa* trunk at three locations in southern Texas ($n = 30$).

Location	Cardinal direction from <i>Prosopis</i> trunk								P
	East		North		South		West		
	<i>x</i>	SD	<i>x</i>	SD	<i>x</i>	SD	<i>x</i>	SD	
	plants/m ²								
Site I (Texas A&M-Kingsville)									
<i>C. pallida</i>	0.9	1.5	0.7	0.8	0.7	1.0	0.7	0.9	0.72
<i>Z. fagara</i>	0.7	1.0	1.0	1.4	0.9	1.5	0.8	1.1	0.57
Total woody	1.8	2.1	2.0	1.9	1.8	1.9	1.6	1.4	0.82
Site II (La Copita)									
<i>C. pallida</i>	0.3	0.7	0.3	0.8	0.3	0.9	0.4	0.7	0.74
<i>Z. fagara</i>	2.3	2.1	2.3	1.9	1.7	1.9	2.2	2.5	0.63
Total woody	5.9	3.9	5.9	3.5	4.8	3.4	5.1	4.4	0.55
Site III (Rio Paisano)									
<i>C. pallida</i>	0.5	0.6	0.5	0.6	0.6	0.5	0.4	0.6	0.60
Total woody	1.3	1.2	1.4	1.3	2.0	1.4	1.3	1.3	0.06

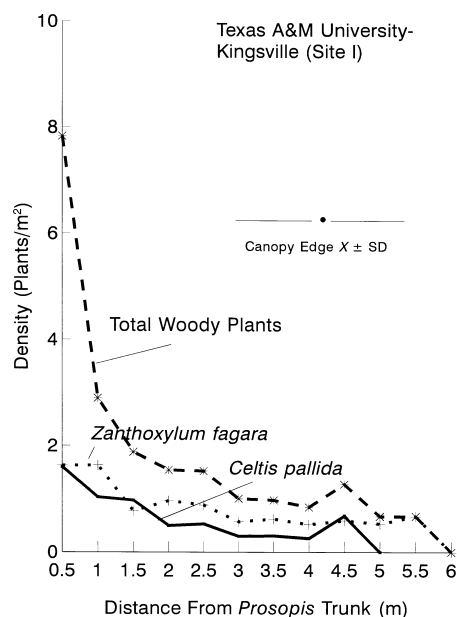


Fig. 1. Density (plants/m²) of *Celtis pallida*, *Zanthoxylum fagara*, and total woody plants in relation to distance from the trunk of *P. glandulosa*, averaged across the four cardinal directions, at Site I at Kingsville, southern Texas ($n = 30$).

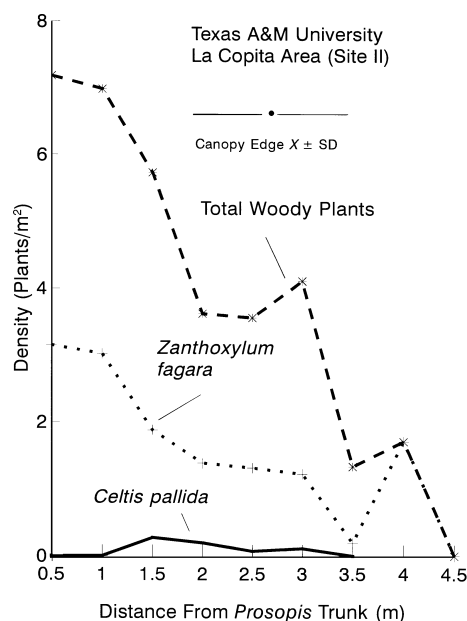


Fig. 2. Density (plants/m²) of *Celtis pallida*, *Zanthoxylum fagara*, and total woody plants in relation to distance from the trunk of *P. glandulosa*, averaged across the four cardinal directions, at Site II near Alice, southern Texas ($n = 30$).

non-random pattern of cacti distribution to exist. The latitude of our study areas was similar to the Vizcaino desert. Thus, the random pattern of shrub distribution in our study area can probably not be attributed to location with respect to latitude.

Relationships between *P. glandulosa* size parameters and *C. pallida*, *Z. fagara*, and total woody plant density did not support the prediction that shrub density would be greater with increased *P. glandulosa* size, except at site II. *Prosopis glandulosa* individuals at sites I and III were considerably larger than those at site II (Table 4). Based on basal diameter as an index of age (Archer et al. 1988), *P. glandulosa* individuals at sites I and III may have been older than those at site II. *Prosopis glandulosa* may have colonized site II more recently

than the other sites and shrub clusters at site II were possibly in earlier stages of development. Attenuation of solar radiation by *P. glandulosa* may be more important in early stages of cluster development when *P. glandulosa* individuals are smaller. The negative relationship between *P. glandulosa* canopy radius and height and total woody plant density at site III, and the lack of a relationship between *P. glandulosa* size parameters and total woody plant density at site I, may have resulted because shrub cluster development is more advanced at those sites.

Franco-Pizaña (1993) reported that seedling growth of *C. pallida* was greater in soils high in N from beneath *P. glandulosa* canopies than in low-N soils from interspaces. If subordinate shrubs require high levels of

Table 2. Coefficients of determination (R^2) and P -values between density (plants/m²) of *Celtis pallida*, *Zanthoxylum fagara*, and total woody plants and basal diameter (cm), height (m), and canopy radius (m) of *Prosopis glandulosa* at three locations in southern Texas ($n = 30$).

Location	<i>Prosopis glandulosa</i>	<i>Celtis pallida</i>		<i>Zanthoxylum fagara</i>		Total density	
		R^2	P -value	R^2	P -value	R^2	P -value
Site I (Texas A&M-Kingsville)	Basal diameter	0.05	0.238	0.01	0.585	0.05	0.245
	Canopy radius	0.05	0.215	0.11	0.074	< 0.01	0.759
	Height	0.02	0.519	0.01	0.677	0.05	0.237
Site II (La Copita)	Basal diameter	0.32	0.001	0.30	0.002	0.45	< 0.001
	Canopy radius	0.07	0.153	0.08	0.142	0.14	0.043
	Height	0.47	< 0.001	0.04	0.274	0.22	0.009
Site III (Rio Paisano)	Basal diameter	0.06	0.199	0.10	0.086		
	Canopy radius	0.01	0.593	0.16	0.027		
	Height	< 0.01	0.915	0.30	0.002		

Table 3. Soil chemical characteristics beneath *Prosopis glandulosa* canopies and in grass-dominated interspaces at the locations in southern Texas ($n = 10$, except for total N: $n = 6$).

Soil characteristic	Canopy		Interspace		<i>P</i>
	<i>x</i>	SD	<i>x</i>	SD	
Site I (Texas A&M- Kingsville)					
0-15 cm					
Total N (g/kg)	0.64	0.29	0.36	0.03	0.074
NO ₃ -N (mg/kg)	6.9	8.2	1.3	0.8	0.065
Phosphorus (mg/kg)	10.4	9.6	4.0	0.7	0.060
15-30 cm					
Total N (g/kg)	0.55	0.11	0.34	0.15	0.015
NO ₃ -N (mg/kg)	4.4	3.5	3.9	3.3	0.808
Phosphorus (mg/kg)	4.4	1.1	3.3	0.7	0.007
Site II (La Copita)					
0-15 cm					
Total N (g/kg)	0.73	0.20	0.40	0.06	0.020
NO ₃ -N (mg/kg)	4.9	4.6	0.9	0.5	0.024
Phosphorus (mg/kg)	7.3	4.2	4.5	1.0	0.056
15-30 cm					
Total N (g/kg)	0.48	0.10	0.44	0.08	0.546
NO ₃ -N (mg/kg)	3.3	2.9	1.7	0.9	0.039
Phosphorus (mg/kg)	4.9	2.0	3.7	0.6	0.140
Site III (Rio Paisano)					
0-15 cm					
Total N (g/kg)	0.85	0.13	0.39	0.05	< 0.001
NO ₃ -N (mg/kg)	16.5	5.6	2.8	1.0	< 0.001
Phosphorus (mg/kg)	9.8	2.9	4.1	0.8	< 0.001
15-30 cm					
Total N (g/kg)	0.36	0.06	0.27	0.03	0.012
NO ₃ -N (mg/kg)	6.5	3.5	7.1	1.9	0.541
Phosphorus (mg/kg)	5.6	0.8	3.8	0.4	0.022

N for initial seedling growth and establishment, decreased total N with increased subordinate shrub density, as occurred at sites I and III, may be a factor in the stabilization of shrub clusters. Extraction of N from the soil and incorporation of N into plant tissue in dense clusters may reduce seedling establishment of subordinate shrubs, inhibiting further increases in subordinate shrub density in later stages of cluster development. In contrast to our prediction, available P was apparently not related to subordinate shrub density.

The greater nutrient content of soils from beneath canopies was consistent with previous studies (Tiedemann & Klemmedson 1973, Virginia & Jarrel 1983, Johnson & Mayeux 1990, Frost & Edinger 1991). Phosphorus was higher under the canopy of *P. glandulosa* than in grass-dominated clearings at the Rio Paisano Ranch, but not at the other locations. Tiedemann & Klemmedson (1973) also reported no difference in P

Table 4. Height, basal diameter, and canopy radius of *Prosopis glandulosa* at the research sites in southern Texas ($n = 30$).

Parameter	Site I		Site II		Site III	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Height (m)	5	1	4	1	6	1
Basal diameter (cm)	31	12	18	7	37	16
Canopy radius (m)	4	1	3	1	4	1

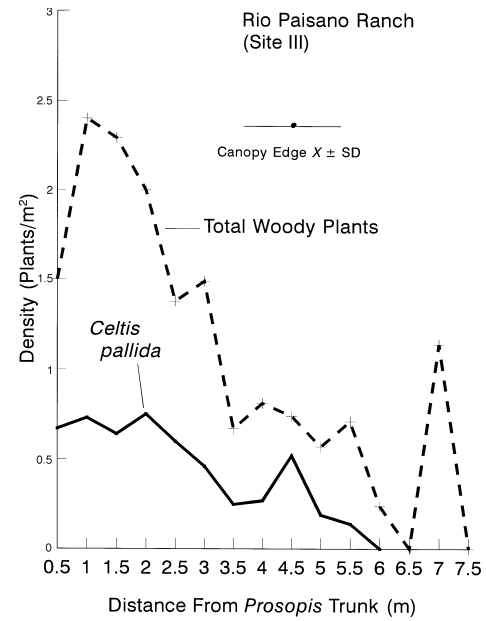


Fig. 3. Density (plants/m²) of *Celtis pallida* and total woody plants in relation to distance from the trunk of *P. glandulosa*, averaged across the four cardinal directions, at Site III, Rio Paisano Ranch, in southern Texas ($n = 30$).

content in soil from *Prosopis* canopies and adjacent open areas in Arizona.

Smith & Goodman (1986) reported spatial patterns of seedling distribution of five woody species beneath *A. tortilis* canopies similar to the spatial patterns of woody plants that we observed beneath *P. glandulosa*, except densities did not increase at the canopy edge. The decline of woody plant density with distance from the canopy edge may reflect a decrease in soil nutrients along these transects. Carbon, N, and P decreased with increasing distance from the trunk in all studies in which nutrient distribution under shrubs has been examined (Vetaas 1992). The increase in *C. pallida* density at the edge of the canopy possibly resulted from seed dispersal by birds that feed on *C. pallida* fruits and perch on the outer side of the crown of *P. glandulosa* trees (Archer et al. 1988). In contrast to our results, Smith & Goodman (1986, 1987) reported that density of woody species such as *Ehretia rigida*, *Euclea divinorum* and *Ziziphus mucronata* was greatest about halfway between the trunk and the edge of *Acacia* canopies.

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