Influence of an overstorey tree (*Prosopis glandulosa*) on associated shrubs in a savanna parkland: implications for patch dynamics

**Abstract** The arborescent legume, honey mesquite (*Prosopis glandulosa*), appears to play a central role in patch dynamics of southern Texas savannas by modifying soils and microclimate and by facilitating the ingress, establishment and/or growth of shrubs in its understorey. As an indirect test for the occurrence and persistence of facilitation in mature shrub clusters (patches), we examined the gas exchange, water relations and production of associated shrubs growing in patches where a *Prosopis* overstorey was present and in patches where *Prosopis* had succumbed to natural mortality. Surface (0–10 cm) soils associated with shrub patches were enriched in total [N] and [C] compared to soils of neighboring herbaceous zones. However, there were no detectable differences in soil [N] or [C] in patches with and without *Prosopis*. Foliar [N] and biomass of various shrub species were also statistically comparable for patches with and without *Prosopis*. These results are in accordance with other studies that indicate the nutrient legacy associated with *Prosopis* occupation of a patch may persist for decades after its demise. In comparison to plants growing in the absence of *Prosopis*, leaf water potentials (predawn and midday), and net photosynthesis and water vapor conductance (morning and midday) of outer-canopy sunlit leaves over an annual growth cycle were comparable for two common evergreen shrubs, *Zanthoxylum fagara* and *Berberis trifoliolata*, growing in patches with a live *Prosopis*. These findings indicate that the presence of *Prosopis* was not enhancing the growth or activity of mature understorey shrubs; facilitation may, therefore, be important only during early stages of cluster development. In addition, we found no indication that the loss of *Prosopis* has initiated a downward phase in a cyclic succession of patch initiation, growth and death. Rather, the understorey shrubs appear to be able to maintain growth and productivity in the absence of a *Prosopis* overstorey, and may, therefore, represent persistent components of woody patches on these savanna landscapes.

**Keywords** Facilitation · Nurse plant · Photosynthesis · Primary production · Water relations

**Introduction**

Savanna ecosystems are characterized by a continuous layer of graminoids interrupted by sparsely-spaced trees or shrubs. These discontinuities represent patches where both the microclimate and the availability of resources have been altered in concentric zones surrounding the woody vegetation (Kellman 1979; Belsky et al. 1989; Vetaas 1992). Isolated trees can influence the growth and productivity of the understorey herbaceous layer (Belsky 1994) and are thought to serve as nuclei (i.e., nurse plants) for subsequent vegetation development in tropical, sub-tropical and temperate savanna ecosystems (Tupas and Sajise 1977; Hacker 1984; Rykriel and Cook 1986; Smith and Goodman 1987; Archer et al. 1988; Fowler 1988; McPherson et al. 1988). Through their role as nurse plants, savanna trees can thereby significantly influence long-term patterns of community structure and function, landscape heterogeneity and ecosystem processes (Archer 1995).

While the characteristics of woody patches in savannas have been widely studied, little is known of their dynamics and how patch properties change as trees establish, develop and die (Belsky and Canham 1994). In an ongoing case study in southern Texas, United States, succession from grassland to woodland has been
shown to begin when honey mesquite (Prosopis glan-
dulosa) invades and establishes in grassland sites and
then facilitates the ingress, establishment and/or
growth of various subordinate shrub species in its
understorey (Archer et al. 1988). Over time, distinct
shrub clusters (patches) thereby develop within a matrix
of herbaceous grassland vegetation (Whittaker et al.
1979). Under certain conditions, shrub clusters orga-
nized around the Prosopis nucleus expand and coalesce
to form a continuous, closed-canopy woodland (Archer
1989). For some clusters, however, the central Prosopis
eventually dies leaving isolated patches of understorey
shrubs (Archer et al. 1988).

Understanding the nature and persistence of the
facilitative effects of Prosopis is necessary for predict-
ing patch dynamics and future landscape states in these
subtropical savannas and woodlands. If facilitation is
operationally significant at latter stages of cluster devel-
opment, we might expect that loss of Prosopis would
be reflected in reduced physiological activity and/or
growth of understorey shrubs. These responses should
precede shifts in species composition and could, there-
fore, be indicative of the first stages in the downward
phase in a cyclic pattern of patch initiation, growth and
death (e.g., Watt 1947; Yeaton 1978; Soriano et al.
1994). On the other hand, facilitation may be critical
only at the seedling stage. Following establishment,
resource limitations may increase progressively as
seedlings develop into adults and competitive effects
might eventually outweigh the beneficial effects of habi-
tat modification by the nurse plant (e.g., McAuliffe
1984; Franco and Nobel 1990; Aguiar et al. 1992;
Aguiar and Sala 1994). In this scenario, we would
expect understorey shrubs to maintain or increase their
physiological activity and growth following the loss of
Prosopis, and we would infer that shrub patches may
be relatively stable and persistent components of the
landscape.

To test for the continued dependence of understorey
shrubs on Prosopis and the possibility of cyclic suc-
cession in these woody patches, we compared the phys-
iological activity and biomass production of associated
shrubs growing in mature clusters containing a living
Prosopis to those of plants growing where Prosopis had
succumbed to natural mortality. Two of these shrub
species differ in their time of arrival in cluster devel-
opment [Zanthoxylum fagara = 10-15 years after
Prosopis establishment; Berberis trifoliolata = 30-40
years later (Archer et al. 1988; Archer 1989)]. Thus, we
further hypothesized that these species would be differen-
tially affected by the loss of Prosopis.

Materials and methods

Studies were conducted at the Texas Agricultural Experi-
ment Station La Copita Research Area located in Jim Wells county
in the eastern Rio Grande Plains of southern Texas (27° 40' N; 98°
12' W; elevation above sea level = 75-90 m). Contemporary vege-
tation in this region has been classified as subtropical thorn wood-
land (McLendon 1991). Vegetation at the study site, which has been
grazed by domestic livestock since the late 1800s, consists of savanna
parklands in the uplands and closed-canopy woodlands in lowland
drainages and playas (Archer 1995). Uplands exhibit a mosaic of
herbaceous vegetation (dominated by C4 grasses) and discrete clus-
ters of woody plants that vary in successional age-size states (Archer
et al. 1988). The overstory in upland and lowland habitats is dom-
inated exclusively by the winter-deciduous honey mesquite [Prosopis
glandulosa var. glandulosa Torr.; nomenclature follows Correll and
Johnston (1979)] while the understorey woody vegetation consists of
a diverse mixture of evergreen [e.g., Zanthoxylum fagara (L.)
Sarg., Berberis (= Mahonia) trifoliolata Moric.], semi-evergreen
(e.g., Condalia hookeri M.C. Johnst., Diospyros texana Scheele,
Celtis pallida Torr.) and summer (drought)-deciduous [e.g.,

The climate of the region is subtropical with warm winters,
hot summers (mean annual temperature = 22.4 °C) and bimodally
distributed rainfall (mean annual precipitation = 680 mm; maxima
in May/June and September). Soils on the landscapes used in our
study were sandy loams underlain by a distinctive argillic (clay-rich)
horizon (Loomis 1989).

Studies were conducted in several upland, savanna landscapes
on discrete shrub clusters which either possessed or lacked a live
Prosopis overstorey. We restricted our sampling to “mature” clus-
ters (approximate age = 30-60 years), in terms of successional sta-
tus (Archer et al. 1988). When present, the overstorey consisted of a
single, central Prosopis. In the clusters which lacked a live Prosopis,
there was often, but not always, remnants of a dead Prosopis near
the cluster’s center. The factors responsible for this mortality are,
at present, unknown.

Surface soil samples (0-10 cm) collected from near the center of
shrub patches with and without Prosopis and adjacent herbaceous
zones were analyzed for total carbon and nitrogen by an automated
(Carlo Erba NA-1500 elemental analyzer. Fisons Instruments,
Saddle Brook, N.J., USA) Dumas combustion procedure (Pella and
Colombo 1973). Coarse roots were removed from samples prior to
grinding to a fine powder.

Samples for foliar nitrogen concentration [N] and canopy bio-
mass were obtained by harvesting all leaf tissue from within duplic-
ate 0.3 x 0.3 x 0.3 m cubes positioned in the top- (i.e., upper canopy)
and bottom-most (i.e., lower canopy) regions of both Prosopis and
shrub canopies. Samples were typically collected from 12 woody
patches (6 each from clusters with and without Prosopis) periodi-
cally over the course of 1-2 years. Kjehldahl digestion (Nelson and
Somers 1980) and autoanalysis (Lachat System 4 autoanalyzer) was
used to determine total organic [N] on a subsample of harvested
tissue. In addition, [N] was also determined for leaves of Berberis
and Zanthoxylum used for gas exchange analysis. Because shrub
species differed in their occurrence within the harvest cubes, the
number of replicates per species for foliar [N] from these harvest
data varied with species, canopy position and time of harvest.

Canopy biomass determinations were made from harvested foliar
tissue that was oven-dried (60 °C) and weighed, and these data are
reported here as foliar biomass density (g/m²). Canopy height and
two perpendicular diameters were measured to test for differences
in shrub cluster sizes when Prosopis was present or absent. Studies
in other ecosystems have demonstrated strong relationships between
whole-shrub production and estimates derived from canopy dimen-
sions and small quadrant samples of the canopy (e.g., Sala et al.
1989; Fernández et al. 1991). These sampled shrub clusters were
also inventoried with respect to species composition and relative
abundance (based on visual estimates of contribution to total
canopy cover).

Measurements of net CO₂ uptake and H₂O loss were made on
fully-expanded, outer-canopy, sunlit leaves from plants of Berberis
and Zanthoxylum using a closed-path, portable photosynthesis
system (LI-6200, LiCor, Inc., Lincoln, Neb., USA) with a 0.25-l
cuvette. For most gas exchange measurements, one or several leaves
were enclosed in the cuvette for 15-45 s in their natural orienta-