



Annual rainfall, topographic heterogeneity and growth of an arid land tree (*Prosopis glandulosa*)

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Basal area growth rates for *Prosopis glandulosa* were quantified for contrasting landscape elements in a subtropical savanna. We hypothesized that growth rates of *P. glandulosa* plants (1) are a function of seasonal or annual rainfall; and (2) vary with patch type and in the rank order observed for large trees. *Prosopis glandulosa* growth was responsive to changes in rainfall ($-0.974 \text{ cm}^2 \text{ year}^{-1}$ in a dry year; 9.108 in a wet year), but correlations with rainfall were low. Growth of trees in contrasting patches was not consistently different, suggesting that contrasts in tree sizes across the landscape reflect differences in establishment dates rather than differences in growth rates.

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Introduction

Proliferation of woody vegetation in grasslands and savannas in recent history has been reported worldwide (Archer, 2000). The resulting displacement of herbaceous vegetation by woody plants has the potential to threaten the sustainability of commercial and pastoral livestock production systems (Scifres, 1980; Noble, 1997) and alter wildlife habitat (e.g. Scifres *et al.*, 1988; Ben-Shaher, 1992), biodiversity, biogeochemistry (Hibbard *et al.*, in press; Archer *et al.*, in press) and land surface-atmosphere interactions (Guenther *et al.*, 1999; Hoffman and Jackson, 2000). In south-western U.S.A. and northern Mexico, *Prosopis glandulosa* (mesquite) is an arborescent legume that has increased in abundance in grasslands and savannas since Anglo-European settlement (Buffington & Herbel, 1965; Hennessy *et al.*, 1983; Archer *et al.*, 1988). While its expansion in grasslands has long been of concern to land managers (Fisher, 1950), little is known of the rates and dynamics of stand development and how tree growth rates might vary across topographically diverse landscapes. Such information is fundamental to developing effective grassland conservation and brush management plans (Scifres *et al.*, 1985) and for reconstructing and predicting the ecosystem consequences of changes in life-form composition (e.g. Schlesinger *et al.*, 1990; Archer *et al.*, in press).

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Woody plant encroachment has been the focus of a series of studies at the La Copita savanna parkland site in southern Texas, U.S.A. Stable isotopes of soil organic carbon indicate *P. glandulosa* and associated shrubs have displaced C₄ grasses in both uplands and lowlands (Boutton *et al.*, 1998) but provide no clear time-line of the rates and dynamics of this change. Analysis of historical aerial photos indicates that woody plants were abundant in 1941, and that their canopy cover increased 3–4 fold by 1983 (Archer *et al.*, 1988). Models based on transition probabilities (Scanlan & Archer, 1991) and canopy expansion rates (Archer, 1989) suggest most woody plants have established since 1900. However, these transition and canopy expansion reconstructions were based on aerial photos from only three points in time (1941, 1960 and 1983) and do not explicitly account for topoedaphic or annual variation in plant growth across the landscape. While woody cover has increased on average across the entire landscape, some topoedaphic elements have lagged substantially behind others (Stroh, 1995). In uplands, for example, *P. glandulosa* trees occur in small discrete clusters and in large groves (Archer, 1995). The discrete clumping pattern of woody plants in uplands is not evident in intermittent drainages, where woody plant cover is nearly continuous. Field observations suggest the rank order of mature *P. glandulosa* sizes (basal area, height, canopy area) is lowland woodlands \geq upland groves \gg upland discrete clusters (Archer 1995). It is not clear whether the size differences of mature *P. glandulosa* plants in these different landscape elements represent different establishment dates or different growth rates.

Here, we test the hypothesis that the growth rate of *P. glandulosa* plants (1) is a function of seasonal or annual rainfall; and (2) varies significantly with patch type and in the rank order observed for mature tree sizes: lowland woodlands \geq upland groves \gg upland discrete clusters. To test these hypotheses, we used dendrometer bands to quantify bole growth of mature *P. glandulosa* plants over a 6-year period.

Site description

The study was conducted on the Texas Agricultural Experiment Station La Copita Research Area in Jim Wells County near Alice, Texas, U.S.A. (27°40N;98°12W). This site, located in the eastern Rio Grande Plains of the Tamaulipan Biotic Province, is characterized by a savanna parkland/woodland vegetation complex. Uplands are sandy loams, characterized by discrete clusters and groves of woody vegetation embedded within a matrix of C₄ grasses and C₃ forbs. Discrete clusters occur where the Bt horizon is well-developed in uplands, while groves of large *P. glandulosa* plants occur where the Bt is poorly expressed (see Archer, 1995 for details). These grade (1–3% slopes) into clay loam intermittent drainages with closed-canopy woodlands. *Prosopis glandulosa* dominates the overstory of discrete clusters, groves and woodlands. The understory of each of these landscape elements is characterized by a dense and diverse mixture of shrubs.

The site has a history of heavy, continuous livestock grazing dating back to the late 1800s. The climate is subtropical with warm winters and hot summers. The growing season is 289 days, with a mean annual temperature of 22.4°C. Mean annual rainfall (680 mm) is bimodal (peaks in May and September) and highly variable (coefficient of variation = 0.35; Le Houerou & Norwine, 1988).

Methods and materials

The study was designed as a randomized complete block consisting of two blocks (= landscapes) and three treatments (= patch types) with repeated measurements on the experimental units over a 4–6-year period of time. Experimental units were selected

in the following manner. On one landscape (Block 1), adult (basal diameter $> 15 \text{ cm}^2$) *P. glandulosa* plants were selected randomly from discrete clusters on upland sandy loam sites with an argillic horizon (Treatment 1; $n = 17$), from groves on upland sandy loam soil inclusions lacking an argillic horizon (Treatment 2; $n = 25$), and from woodlands in clay loam intermittent drainages (Treatment 3; $n = 20$). Boles of these plants were fitted with dendrometer bands (Palmer & Ogden, 1983) in March 1988. On a second landscape (Block 2), additional trees were randomly selected and instrumented in September 1989 ($n = 22$ in discrete cluster and woodland patch types; and $n = 26$ in grove patch types). Basal growth was recorded periodically over 6 years on Landscape 1 and over 4 years on Landscape 2. Annual readings are presented as growth from July 1 to June 30.

All statistical analyses were conducted using SAS (1990). Given the large range of initial tree sizes ($15\text{--}1700 \text{ cm}^2$), initial basal area was included as a covariate in all statistical analyses of annual basal area growth. Differences in annual growth of *P. glandulosa* in contrasting patch types were evaluated with a mixed model repeated measures analysis for years 1990–1993. Initial basal area was included as a covariate in the model and an AR(1) covariance structure was used to model the repeated measurements across the 4 years. The 1988 and 1989 data from Landscape 1 was excluded since *P. glandulosa* plants on Landscape 2 were not measured until 1990. Within each year, multiple comparisons of patch differences in basal area growth were tested using the Tukey-Kramer procedure. The relationship between annual growth and precipitation (1 July–30 June) and late winter/spring precipitation (1 January–30 June) was examined using correlation analysis. To examine the relationships between annual growth rate in a given year to the amount of precipitation in the previous year, an assortment of precipitation variables were constructed. The dependent variable consisted of the 12 individual monthly precipitation amounts plus various combinations of monthly precipitation amounts, e.g. Jan.; Jan. + Feb.; Jan. + Feb. + Mar.; etc. Stepwise regression analysis was then used to search for precipitation variables influencing annual basal area growth.

In addition to analysis of annual growth for pooled data, (all trees, regardless of initial size), a separate analysis of 4-year (1990–1993; two landscapes) and 6-year (1988–1993) accumulated basal area growth was conducted for trees separated into four size classes. Based on a qualitative inspection of the graphical relationship between initial basal area and growth rate, we placed plants into one of four 145-cm^2 size categories, (30–175, 175–320, 320–455, > 455). Comparison of bole growth could not be made among all patch types for all size classes since some size classes were not adequately represented in all patch types. In addition, the smallest trees in the discrete clusters were eliminated to prevent errors associated with highly unbalanced sample sizes. Because the number of plants per size class varied markedly among patch types, tests for differences in accumulated basal area growth were conducted using a one-way analysis of variance and a Bonferroni analysis of the least-squares means.

Results

Growth rate data were obtained for a wide range of adult (i.e. non-sapling) tree initial basal areas (Table 1). Initial mean basal area of *P. glandulosa* trees, measured in woodlands and groves, were comparable ($p = 0.480$) and greater than that of trees in discrete clusters ($p < 0.001$). It was not our intent to sample trees in sufficient numbers to represent the population size-class distribution. Tree sizes in our study were skewed toward larger trees than have been encountered in more intensive samplings (Boutton *et al.*, 1998). Hence, the data in Table 1 should not be interpreted in a demographic sense.

Table 1. Size (mean + S.E.; min and max, n) of mature *P. glandulosa* plants instrumented with dendrometer bands in discrete cluster, grove and woodland patches.

	Sandy loam uplands		Clay loam drainages
	Discrete cluster	Grove	Woodland
Argillic horizon	Present	Absent	Present
Sample size (<i>n</i>)	39	46	42
Basal area (cm ²)			
Mean (S.E.)	105 (14)	442 (39)	402 (55)
Max	315	1719	1581
Min	16	32	64

Differences between replicated landscapes were not significant, so pooled values are presented.

Basal area growth of *P. glandulosa* was comparable on both landscapes sampled ($p = 0.639$). Bole growth varied significantly ($p < 0.001$) between patch types and among years ($p < 0.001$) (Fig. 1). Growth in driest year (1989) was negligible and comparable ($p = 0.786$) among patch types. In years of normal to above-normal annual rainfall, basal area growth increased, but its magnitude and rank order of patch types varied across years. As a result, there was a significant interaction ($p < 0.001$) between patch type and year. Growth rates were comparable among patch types in some years (1989, 1991 and 1993). In other years (1990), bole growth was greater for *P. glandulosa* in lowlands (woodlands) than uplands (discrete clusters and groves). Only in the highest rainfall year (1992) did grove and drainage trees have greater bole growth than discrete clusters. Mean (\pm S.E.) maximum basal area growth rates, were 13.7 ± 1.3 , 11.8 ± 0.83 , and 2.5 ± 0.32 cm² year⁻¹ for woodland, grove and cluster trees, respectively. Maximum bole growth rates for grove woodland trees occurred in the year with the highest annual rainfall (1992), whereas maximum growth rates in clusters occurred in the second of consecutive 'normal' annual rainfall years (1991).

Over the duration of the 4–6 year monitoring period, lowland (woodland) trees consistently accumulated basal area at rates comparable to or greater than of trees in upland clusters and groves (Table 2). The differences were most pronounced in the small size class (30–175 cm²), where tree growth in lowland woodlands was ca. three times that of trees in upland clusters.

Annual (1 July – 30 June) rainfall varied considerably during the monitoring period, ranging from well below to well above the long-term average (Fig. 1). The frequency and size of rainfall events also varied considerably between years (Table 3). The greatest 12 month total rainfall occurred during the last 2 years of the study. During these years, the maximum number of consecutive days without rain was < 47 ; this contrasts with the dry 1988/89 period, when there was an 84-day period without rain. In addition, the two high annual rainfall years were characterized by more rainfall events and a higher frequency of large (> 25 mm) rainfall events. The correlation between annual precipitation and basal area growth was significant for cluster, grove and woodland trees ($p < 0.001$ in each case). However, annual rainfall accounted for only 12, 19 and 29% of the variance in *P. glandulosa* growth for clusters, groves and woodlands, respectively. Correlations between spring rainfall and annual growth were similar. Multiple regression incorporating various combinations of cumulative monthly rainfall from previous years were not significant.

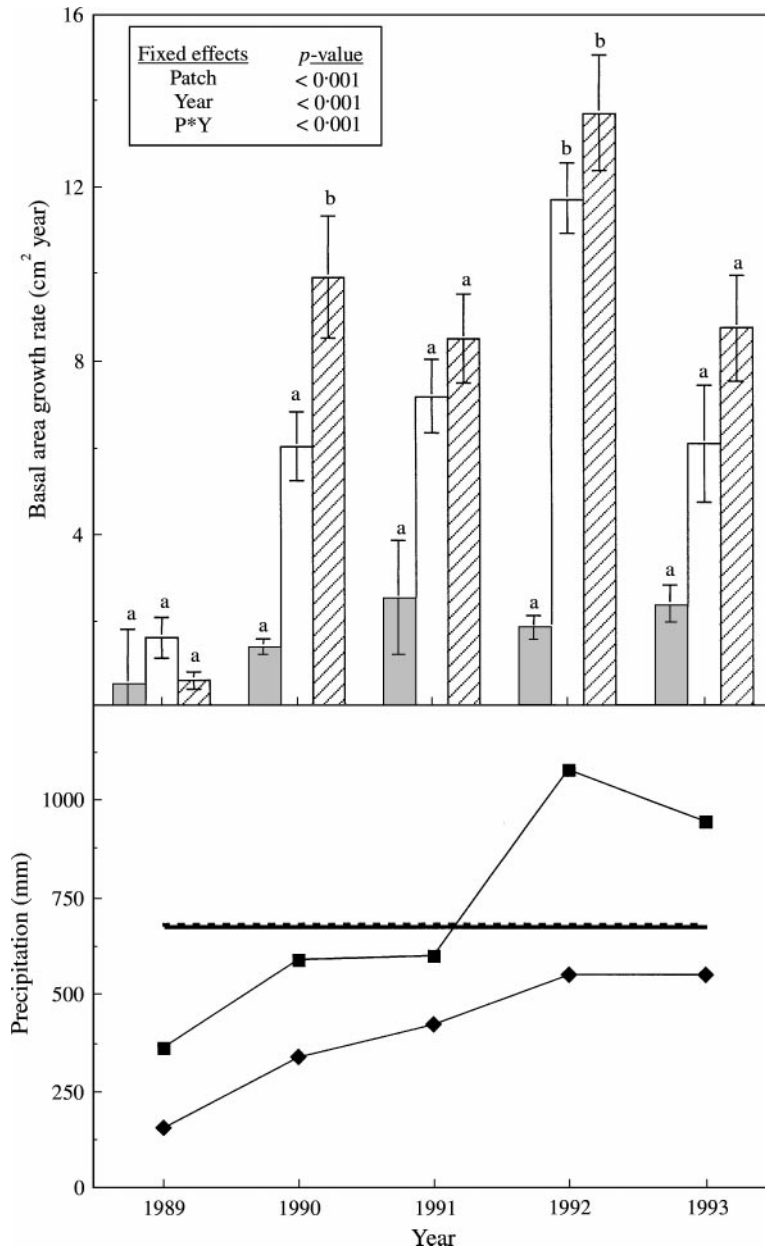


Figure 1. (a) Mean (\pm S.E.) basal area growth ($\text{cm}^2 \text{ year}^{-1}$) of *Prosopis glandulosa* trees over an annual cycle (1 July – 30 June) in contrasting topoeconomic settings [sandy loam uplands with (clusters, ■) and without (groves, □) an argillic horizon; clay loam intermittent drainages (woodlands, ▨)]. Means within a year followed by different letters differed at $p < 0.05$. Result of repeated measures analysis of variance. (b) Annual (1 July – 30 June —■—) and spring (1 January – 30 June —◆—) rainfall (—) and the long-term mean annual rainfall (—) for the site. Annual rainfall 1988, the year preceding our first growth measurements, was also well below the long-term mean (377 mm). Statistical analyses and mean separations were run on data adjusted to incorporate the effect of initial basal area on growth; unadjusted means and standard errors are presented here.

Table 2. Accumulated basal area growth (cm^2) of mature *P. glandulosa* plants in discrete cluster, grove and woodland patches by size class over a 6-year (1988–1993; one landscape) and 4-year (1990–1993; two landscapes) period

Size class (initial basal area, cm^2)	Patch type	<i>n</i>	6 years	<i>n</i>	4 years
30–175	Cluster	7	5.56a	17	7.58a
	Woodland	9	19.32b	12	20.37b
175–320	Cluster	5	14.30a	10	14.67a
	Grove	4	17.28a	12	17.17a
	Woodland	5	25.11a	10	30.15b
320–465	Grove	11	42.08a	13	35.58a
	Woodland	4	35.19a	5	32.09a
> 465	Grove	8	n/a	15	43.13a
	Woodland	1	n/a	14	68.68b

Growth differences ($p < 0.05$) within a size class are indicated with different letters.

Table 3. Characteristics of precipitation (ppt) during the years *P. glandulosa* bole growth was quantified at the La Copita Research Area, Texas

Variable	1988–9	1989–90	1990–1	1991–2	1992–3
Total rainfall (1 July – 30 June)	388	548	654	962	910
Max. no. consecutive days with < 5 mm ppt	84	38	94	43	47
No. times there were ≥ 15 consec. days with < 5 mm ppt	16	11	13	8	6
No. rainfall events > 25 mm	2	9	4	11	7
No. rainfall events > 50 mm	1	1	1	4	2
Days with > 1 mm rainfall	48	36	55	77	86
No. months with ≥ 1 event ≥ 25 mm	2	6	4	8	6
No. months with ≥ 1 event ≥ 50 mm	1	1	1	4	2
Three largest rainfall events (mm)	51 32 23	69 48 44	50 41 33	128 73 54	159 72 37

Discussion

Knowledge of plant growth in relation to topoedaphic and climatic factors is useful for reconstructing, predicting and modeling changes in vegetation structure and ecosystem processes associated with *P. glandulosa* stand development (cf. Archer *et al.*, in press; Hibbard *et al.*, in press). Growth of *P. glandulosa* in cluster, grove and woodland patch types differed and was influenced by annual rainfall. The first year of observation (1988/89) was very dry and growth rates were uniformly low. Annual rainfall in

subsequent years was 'normal' to 'above-normal', and tree annual basal area growth increased three- to eight-fold. However, the rank order and magnitude of the difference in tree growth on the contrasting patch types were inconsistent. Although R^2 values for the relationship between annual rainfall and tree basal area growth rates were low, greatest basal area growth of trees in upland groves and drainage woodland patches occurred during the year with the highest annual rainfall. In contrast, trees in upland cluster patches were markedly de-coupled from annual rainfall. These trees exhibited some 'lag' behavior in that their highest mean basal area growth occurred in the second of two consecutive years of average annual rainfall.

Low quantitative correlations between *P. glandulosa* growth and seasonal/annual rainfall may be a reflection of the fact that plants on this site are deeply rooted (Watts, 1993) and are capable of utilizing deep stores of soil water (Brown & Archer, 1990; Midwood *et al.*, 1998). For example, pre-dawn leaf water potentials, measured monthly in 1991–1992 on upland *P. glandulosa* trees never dropped below -1.5 MPa, despite marked variation in monthly (e.g. 14 mm in August 1991 *vs.* 143 mm in September 1991) and annual (July–June) rainfall (e.g. 654 mm in 1990–1991 *vs.* 962 mm in 1991–1992); by contrast, pre-dawn leaf water potentials of shallow-rooted understory shrubs were as low as -6.5 MPa during this same period (Archer, 1995). These data suggest that *P. glandulosa* growth may be relatively independent of soil moisture fluctuations in the upper soil profile. Also, given the extreme variation in the frequency, distribution and size of rainfall events within and between years (Table 3), our growth measurements may not have been made with sufficient frequency to capture a dynamic relationship that might exist between *P. glandulosa* growth and rainfall.

Differences in the magnitude of *P. glandulosa* growth on contrasting patch types and inconsistencies with respect to statistical differences may reflect offsetting interactions between topography (runon/runoff) and soil physical properties (presence/absence of a restrictive argillic horizon). For example, growth rates of *P. glandulosa* in upland clusters peaked in 1991, the second of two consecutive years of nearly 'average' annual rainfall, but failed to respond in years with the highest annual rainfall (1992 and 1993) and several large rainfall events (Table 3). Why was growth non-responsive in years with highest rainfall? We suggest that because these upland cluster patch types occur on soils with well-developed argillic horizons that impede water percolation, large (> 100 mm) rainfall events generate surface (as shown by Weltz & Blackburn 1995 at this site) and subsurface runoff, such that only a fraction of the water from large rainfall events may be available to promote *P. glandulosa* growth in cluster patches. By way of contrast, we hypothesize that in upland groves, where the soil profile is coarse-textured throughout and where percolation rates are higher than in grove patches (Loomis, 1989), runoff would be minimal. As a result, peak growth rate of *P. glandulosa* in upland groves occurred in the year with the highest rainfall. For trees growing in lowland landscape positions, runoff from upland sites underlain by an argillic horizon would have augmented precipitation, thus producing the high growth rates observed in this landscape element in 1992. These topography-soil texture-storm size interactions likely complicate the elucidation of *P. glandulosa* growth-rainfall relationships.

Competition between overstory *P. glandulosa* and various understory species may have also interacted with rainfall and topographic modulators to variously influence *P. glandulosa* growth rates in the different patch types. Species diversity, size and density of understory shrubs is a function of *P. glandulosa* size/age at the La Copita (Archer, 1995). Further more, the dominant understory shrubs are shallow-rooted (Watts, 1993; Midwood *et al.*, 1998), and their presence markedly influences *P. glandulosa* growth (see Barnes & Archer, 1998 in Table 4), survival and utilization of annual rainfall (Barnes & Archer, 1998). The extent to which this competition might vary on the different soil types is unknown.

Table 4. Comparison of reported *P. glandulosa* basal diameter (b.d.) growth increments (cm year⁻¹). Studies vary with respect to tree ages, soils, competitive influences and methods used for estimating growth increments

Study	Basal growth rate (GR; cm year ⁻¹)	Treatment or setting	Technique/notes
Archer 1989	0.16–0.38	Mature trees; native rangeland	Aerial photos*
Cornejo-Oviedo <i>et al.</i> (1992)	0.61 0.26	Mature trees; agroforestry [†] mature trees; controls [‡]	Dendrometer bands; mean initial b.d. = 15.7–17.9 cm
Duff <i>et al.</i> 1994	1.69	Saplings; agroforestry	Seedlings < 1 cm b.d.
Patch & Felker 1997a	0.27–0.61 0.12	Mature trees; agroforestry mature trees; controls	Seedlings < 1 cm b.d. initial b.d. = 5.7–40.7 cm
Patch & Felker 1997b	1.21 0.54	Saplings; agroforestry saplings; controls	Dendrometer bands; mean initial b.d. = 3.3–3.7 cm
Barnes & Archer 1998	Cluster = 0.09 Cluster = 0.34	Full competition, native rangeland Understory removed, native rangeland	Dendrometer bands; 1989–1993 average; La Copita site; initial b.d. = 5–20 cm
Archer, (unpublished data)	Cluster = 0.31 ± 0.01 Grove = 0.40 ± 0.02 Drainage = 0.39 ± 0.01	Native rangeland	GR = basal diam/no. annual rings; La Copita site; b.d. = 3–44 cm
This study	Cluster = 0.11 ± 0.01 Grove = 0.20 ± 0.02 Woodland = 0.26 ± 0.02	Native rangeland	Dendrometer bands; 1989–1993 average; La Copita site; initial b.d. = 5–45 cm

*Plant model parameterized using tree canopy expansion measurements from historical aerial photographs and tree canopy-bole size relationships.

†Agroforestry: indicates planted trees, thinning, fertilizing, reduced interspecific competition, etc.

‡Controls: trees in agroforestry settings with minimal inputs.

When interpreted in the context of rainfall variability, our data on growth rates of adult plants suggest that differences in the size of the largest *P. glandulosa* trees in contrasting patch types are likely to be more indicative of different establishment dates than of different growth rates. This is consistent with tree ring records from the site (compiled since this study was conducted). Median and maximum ages recorded for *P. glandulosa* trees at the La Copita site were lowest in upland clusters (20 and 44 yrs, respectively) and highest in grove (45 and 109 years) and woodland (44 and 87 years) patches (Boutton *et al.*, 1998).

Comparisons with other studies, other techniques

Our 6-year dendrometer band study generated annual increments comparable to those reported for *P. glandulosa* on other sites using various measurement techniques (Table 4). Archer (1989) estimated bole growth of upland *P. glandulosa* trees from a plant growth model parameterized using canopy expansion measurements obtained from historical aerial photographs (1941, 1960 and 1983) and canopy-bole allometric relationships. This approach bracketed the growth rates measured in this study (Table 4), suggesting that indirect, coarse-resolution approaches can be used with some confidence to assess plant growth and dynamics when other approaches are not possible.

Tree ring analysis of *P. glandulosa* plants at our site, undertaken since completion of this dendrometer study, indicate growth rates integrated over the life of trees (bole diameter divided by number of annual rings, across a wide range of bole diameters) were higher than the averages derived from our 6-year study (Archer, unpublished data in Table 4). However, the rank-order was comparable, suggesting that short-term dendrometer band measurements can effectively represent relative differences in bole growth. *Prosopis glandulosa* wood is extremely dense and not amenable to coring; and staining techniques which highlight annual rings require stem cross-sections (Flinn *et al.*, 1994) and hence destructive sampling. Dendrometer bands may therefore credibly, but conservatively estimate *P. glandulosa* bole growth when tree ring records are not available or obtainable.

Finally, this study suggests that tree ring studies of *P. glandulosa* plants in this region would have merit. Our dendrometer data indicates that *P. glandulosa* trunk growth is responsive to changes in rainfall (Fig. 1), albeit in a complicated fashion. Long-term patterns or trends in the *P. glandulosa* annual rings record may help resolve or explain some of the variability observed within and between patch types in our 6-year study.

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