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# Leaf demography and growth responses to altered resource availability in woody plants of contrasting leaf habit in a subtropical savanna

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## Abstract

Leaf demography and growth of six common, co-occurring woody plant species that varied in stature (tree vs. shrub) and leaf texture (sclerophyllous, coriaceous, malacophyllous) were examined in a subtropical savanna parkland in southern Texas, USA. We tested the hypotheses that, (a) leaves of plants with evergreen canopies would have longer life spans than those of deciduous species; (b) supplementation of soil moisture would decrease leaf life span in both evergreen and deciduous species; (c) species responses to increased soil moisture availability would be inversely related to leaf longevity; and (d) deciduous growth forms would exhibit a greater growth response to increased soil moisture availability than their evergreen counterparts.

A variety of seasonal leaf habits (evergreen, winter-deciduous and summer-deciduous canopies) and leaf life spans (median = 66 to 283 days) were represented by the targeted species, but there was no clear relationship between seasonal leaf habit and leaf longevity. Among species with evergreen canopies, median leaf longevity ranged from short (*Zanthoxylum fagara* = 116 days; *Condalia hookeri* = 158 days) to long (*Berberis trifoliolata* = 283 days) but did not exceed 1 yr. In fact, leaf longevity in evergreen shrubs was often comparable to, or shorter than, that of species with deciduous canopies (*Ziziphus obtusifolia* = 66 days; *Diospyros texana* = 119 days; *Prosopis glandulosa* = 207 days). Augmentation of surface soil moisture had no detectable effect on median leaf life span in any species and there was no clear relationship between leaf longevity and species growth responses to irrigation. Contrary to expectations, species with evergreen canopies responded to irrigation by producing more leaf biomass, longer shoots and more leaf cohorts/year than did deciduous species.

Species differences in the annual cycle of leaf initiation, leaf longevity and canopy development, combined with contrasts in root distributions and a highly variable climate, may allow for spatial and temporal partitioning of resources and hence, woody species coexistence and diversity in this system. However, the lack of expected relationships between leaf longevity, leaf habit and plant responses to resource enhancement suggests that structure-function relationships and functional groupings developed in strongly seasonal environments cannot be applied with confidence to these subtropical savannas and thorn woodlands.

## Introduction

Leaf life span and leaf habit (i.e., evergreen, deciduous, etc.) are important plant life history traits that have been linked to a number of plant and ecosystem-level processes, including photosynthetic capacity, growth rate, primary productivity and nutrient cycling (e.g., Shaver 1981; Coley 1988; Reich et al. 1992; Gower et al. 1993). Thus, these traits are widely regarded as important attributes in the classification of plant functional types (Chabot & Hicks 1982; Mooney & Gulmon 1982; Box 1995; Chapin et al. 1996; Reich et al. 1997).

Several hypotheses have been proposed to explain the adaptive significance of leaf longevity. One widely-held hypothesis argues that leaf life span is an evolutionary 'strategy' to maximize leaf and plant carbon gain under the constraints of the habitat (Johnson & Tieszen 1976; Chabot & Hicks 1982; Kikuzawa 1991, 1995; Kikuzawa & Kudo 1995; Diemer & Körner 1996). This 'carbon balance' hypothesis has been used to explain latitudinal gradients in leaf longevity and the long leaf life span of species of nutrient-poor habitats (Kikuzawa 1991, 1995). An alternate hypothesis suggests that older leaves function as sources of nutrients used in the production of new tissue (Reader 1980; Shaver 1981; Chabot & Hicks 1982; Lajtha & Whitford 1989) and variation in leaf life span reflects evolutionary responses to nutrient availability.

Leaf life span shows some degree of plasticity within a species and has been found to vary along environmental gradients (Ewers & Schmid 1981) and to be influenced by resource availability. For example, leaf life span has been shown to decrease in response to increased availability of soil nutrients (Shaver 1981; Lajtha & Whitford 1989) and light (Bazzaz & Harper 1977; Nilsen 1986; Williams et al. 1989; Lowman 1992; Ackerly & Bazzaz 1995). Fewer studies have examined the effect of water availability on leaf life span and these show conflicting results. While irrigation increased leaf life span in two tropical understory species of *Psychotria* (Mulkey et al. 1993), it had no effect on leaf longevity in the warm desert evergreen shrub *Larrea tridentata* (Lajtha & Whitford 1989). In moisture-limited environments, increases in soil moisture availability could potentially increase leaf carbon gain by reducing stomatal limitations to $CO_2$ uptake and/or by increasing nitrogen availability which might then increase leaf [N] and photosynthetic capacity (Field & Mooney 1983; Reich et al. 1992; Ackerly & Bazzaz 1995). Consequently, if leaf life span is influenced by its carbon balance over ecological time, one might predict that increased moisture availability would shorten leaf life span due to a faster payback of leaf construction costs.

In highly seasonal environments, such as occurs in temperate and high-latitude regions (well-defined winters) and many dry tropical savannas and woodlands (distinct wet/dry seasons), leaf life span and leaf habit in plants often show predictable patterns, with evergreens typically displaying longer leaf life spans than co-occurring deciduous species (Reich et al. 1992; Kikuzawa 1995; Eamus 1999). Evergreens in these habitats often exhibit low relative growth rates and respond slowly to pulses in resource availability (Aerts et al. 1990; Chapin 1993). It has also been suggested that evergreens with long-lived foliage should respond 'physiologically' to increased resource availability, whereas deciduous species with short-lived foliage should respond 'morphologically' to resource pulses (Grime & Campbell 1991). However these structure-function generalizations may not necessarily apply to plants inhabiting non-seasonal environments (Kikuzawa 1995). For example, certain evergreen tree species in wet tropical regions have leaf longevities less than one year (Shukla & Ramakrishnan 1984; Coley 1988; Reich et al. 1991, 1992; Lowman 1992) and possess leaf physiological and structural traits similar to those of deciduous plants in temperate ecosystems (Reich et al. 1992; Walters & Reich 1999).

The Rio Grande Plains of the Tamaulipan Biotic Province in southern Texas and northern Mexico support a rich and diverse assemblage of woody plants that vary in stature (i.e., trees = arborescent; shrubs = fruticose; sub-shrubs = suffrutescent) and leaf texture (i.e., sclerophyllous = hard; coriaceous = thick and leathery; malacophyllous = thin and pliable) (Blair 1950; Reid et al. 1990). Field observations and litter-fall studies (Angerer 1991; Hibbard et al. 2000) suggest woody plants of this thornscrub floristic province also exhibit considerable variation in leaf life span and leaf habit, but these patterns have not been quantified. Within a given landscape, the relative abundance of these woody plants varies along successional (early successional, open savanna parklands to late-successional, closed-canopy woodlands) and topo-edaphic sequences (upland, coarse-textured duplex soils to lowland, fine-textured soils) that differ in light, nutrient and moisture availability (Archer et al. 1988, 2000; Archer 1995). At present, our understanding of factors influencing community organization and vegetation change in this system is constrained by our limited knowledge of the autecology of these woody plants and how they might respond to changes in resource availability that occur along these environmental and successional gradients (Tilman 1985).

In this study, we characterize leaf habit and life span of common, co-occurring woody species in these subtropical savannas, and evaluate whether these traits can be used as indicators of plant functional type to predict woody plant responses to resource (soil moisture) availability in mixed-species assemblages. Specifically, we test the hypotheses that (a) leaves of plants with evergreen canopies will have longer life spans than those of deciduous species; (b) supplementation of soil moisture will decrease leaf life span in both evergreen and deciduous species; (c) species responses to increased soil moisture availability will be inversely related to leaf longevity; and (d) deciduous growth forms will show greater growth responses to increased soil moisture availability than their evergreen counterparts.

## Methods

### *Study site*

Experiments were conducted at the Texas Agricultural Experiment Station La Copita Research Area (elevation above sea level = 75–90 m) located 80 km west of Corpus Christi in Jim Wells County in the eastern Rio Grande Plains of southern Texas, USA (27°40′ N, 98°12′ W). The La Copita is habitat for 39 tree and shrub species and 10 suffrutescent species (Coffey 1986). Contemporary vegetation is savanna parkland in sandy loam uplands and thorn woodland in clay loam intermittent drainages (McLendon 1991; Archer 1995). Our experiment was conducted on woody species in upland discrete clusters occurring on soils with a well-developed argillic (clay-rich) horizon. Upland shrub clusters at this site vary in successional age, size and shrub composition (1 to 15 woody species) and typically possess an overstory of honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) (Archer et al. 1988; Barnes & Archer 1996). The experimental plants selected for this study occurred in mature clusters (estimated age = 30–60 years; Archer 1990) that had a sparsely-developed *P. glandulosa* canopy (i.e., overstory shading of shrubs was minimal). Plant nomenclature follows Correll & Johnston (1979).

The climate of the study site is subtropical with mild winters and hot summers (mean annual temperature = 22.4 °C; Scifres & Koerth 1987). During our study (March 1994–July 1995), the monthly mean air temperature deviated only slightly from the long-term (30 year) average for the region; however, mean monthly temperatures during late-autumn and winter (October–February) were 1–2 °C above average. Average annual rainfall at the site (1984–1995) was 645 mm, and precipitation during 1994 and 1995 was 641 and 655 mm, respectively. During the first year of the study (1994), monthly precipitation was above-average in March (139% above normal), June (+26%), August (+99%) and October (+140%) 1994, but was below average in May (−67%) and September (−29%) 1994. The second year of the study (1995) was characterized by severe drought from January-July (precipitation = 45% below average).

### *Irrigation experiment*

In January 1994, mature plants growing in mixed-species, upland woody clusters were selected for experimental study from within a 5 ha livestock grazing exclosure established in 1984. Woody clusters containing unirrigated 'control' plants received only natural rainfall; separate clusters containing 'irrigated' plants received surface irrigation that augmented natural precipitation. Irrigation was supplied by an aboveground sprinkler system using nearby well water. Sprinkler heads were situated 15–30 cm aboveground to minimize interception of water by shrub canopies and were spaced at ca. 1 m intervals within, and 0.5–1 m beyond, each cluster. Irrigated clusters received approximately 30 cm of supplemental rainfall over a two-hour period every two to four weeks. Uniformity of irrigation was verified with a grid of rain gauges. Irrigation treatments were initiated on 24 May 1994 and continued through 21 August 1995. Technical problems prevented irrigation in November and December 1994. Volumetric soil moisture content ($q_v$) was measured (15–30, 30–60, 60–90, 90–120 cm depths) from two access tubes within each woody cluster before and after irrigation using a neutron probe (Troxler, Model 3322) calibrated against gravimetric soil moisture samples collected at the time of tube installation (April 1994).

### *Leaf demography and growth measurements*

Six common woody species representing a range of potential 'functional groups' were selected for study (Table 1). Leaf demography was quantified on two terminal shoots per plant on a total of 6 to 8 plants per treatment (except irrigated *Diospyros texana*, where $N = 4$ plants). Outer canopy shoots were selected and tagged in January (winter) 1994. Leaves on new shoots were identified upon emergence (= 'birth') by placing a small mark on the abaxial base of the petiole with a permanent marker. A leaf was considered 'born' when visible on the shoot. Detailed drawings depicting each shoot and corresponding leaves were also constructed. The total number of leaves/shoot censused ranged from 7 in *P. glandulosa* to 50 in *Condalia hookeri*. Leaves were censused every 30 to 60 days

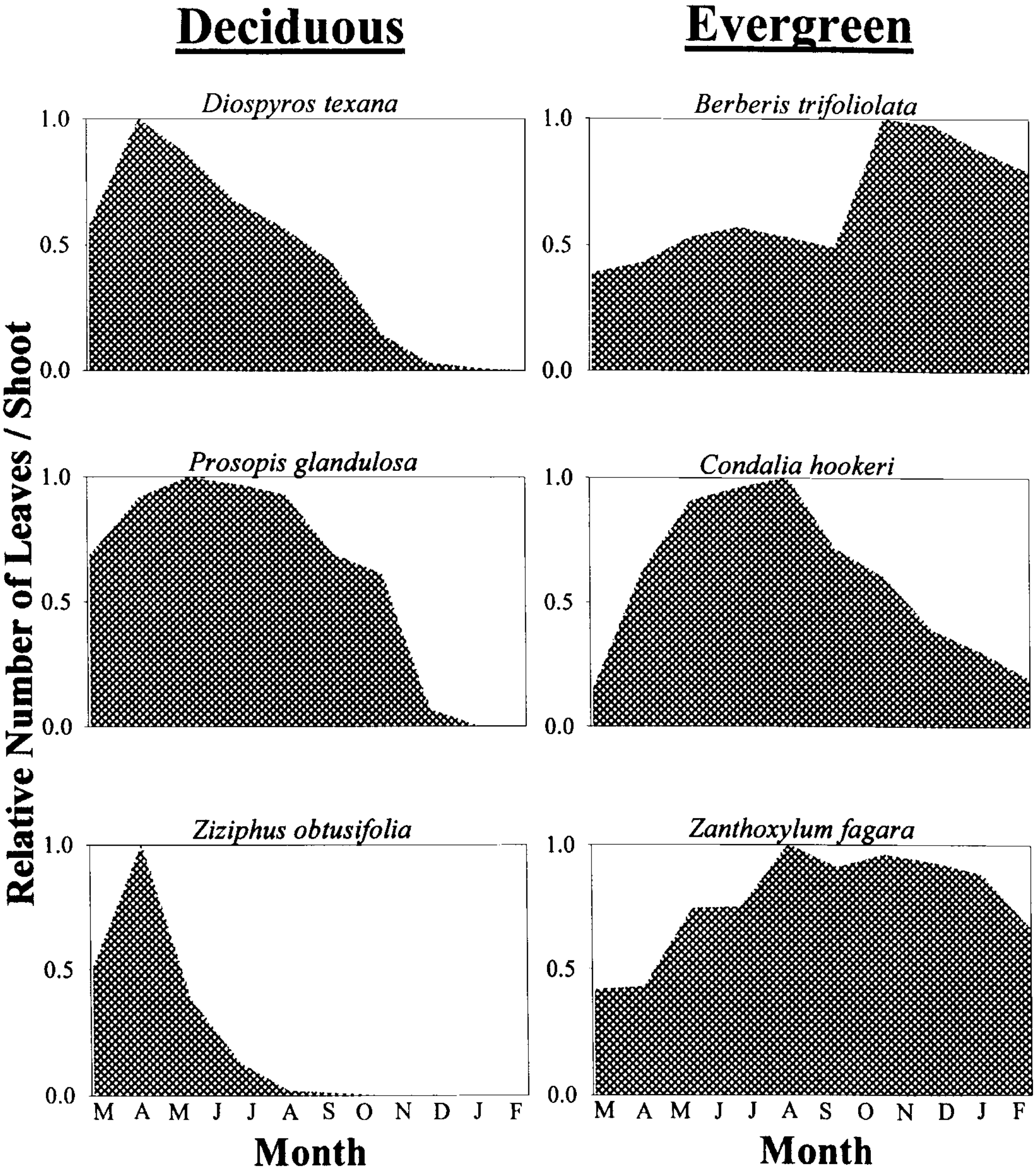

*Figure 1.* Phenogram depicting temporal changes in the relative number of leaves for co-occurring woody species in a subtropical savanna parkland from March 1994 through February 1995. Shaded area designates the number of leaves relative to the yearly maximum number of leaves for each species. Species maintaining leaves in their canopies year-round were classified as evergreen, while those whose canopies were bare for at least part of the year were classified as deciduous.

until death. A leaf was considered dead when it was missing or when more than half of its area was yellow or brown in color. Leaves that showed evidence of herbivory were noted. New leaves encountered at each subsequent census were mapped, marked and treated as different-aged cohorts.

In October 1994, after an 8-month growing period (5 month exposure to irrigation), five terminal shoots, one each from the canopy crown and the four cardinal directions, were collected from 4 to 6 plants per species in each treatment and current season shoot length and leaf biomass (dry weight after drying 48 h at 80 °C) was determined. Current season shoot growth was identified by locating the terminal bud scale scars persistent from bud break and harvesting the shoot from that point outward. Bud scale

*Table 1.* Characteristics of the woody plant species examined in this study. *Prosopis glandulosa* is an overstory arborescent whereas other species are understory shrubs. Unless otherwise noted, information is for co-occurring species growing on sandy loam uplands underlain by a well-developed argillic (clay-rich) horizon. Data are means ± SE.

| Species[a] | Family | Leaf texture | Specific leaf area ($cm^2$ $g^{-1}$)[b] | Leaf [N] (%)[b] | Leaf habit[c] | Rooting depth (m)[d] | Stature |
|---|---|---|---|---|---|---|---|
| *Berberis trifoliolata* Moric. | Berberidaceae | sclerophyllous | 61 ± 17 | 1.3 ± 0.3 | evergreen | 1.6 | shrub |
| *Condalia hookeri* M.C. Johnst. | Rhamnaceae | malacophyllous | 145 ± 54 | 2.4 ± 0.5 | evergreen | 0.8 | shrub |
| *Diospyros texana* Scheele | Ebenaceae | coriaceous | 135 ± 41 | 2.1 ± 0.2 | winter deciduous | 'shallow' | tree-shrub |
| *Prosopis glandulosa* Torr. | Fabaceae | coriaceous | 106 ± 34 | 2.8 ± 0.3 | winter deciduous | 1.2 | tree |
| *Zanthoxylum fagara* (L.) Sarg. | Rutaceae | coriaceous-malacophyllous | 130 ± 34 | 2.3 ± 0.4 | evergreen | 0.4 | shrub |
| *Ziziphus obtusifolia* (Torr. & Gray) Gray | Rhamnaceae | malacophyllous | 70 ± 2 | no data | summer deciduous | 0.4 | shrub |

[a] Nomenclature follows Correll and Johnston (1979).

[b] Data from bulk leaf samples (S. Zitzer, S. Archer & P. Barnes, unpubl. data) except for *Z. obtusifolia* data which are from single leaf samples (McMurtry 1997).

[c] This study.

[d] Depth containing >80% of total root biomass from Watts (1993); no rooting depth data are available for *D. texana* but this species is thought to be functionally shallow rooted based on seasonal predawn shoot water potential data from McMurtry (1997) and $\delta^2$H from Boutton *et al.* (1999). Data are all from plants growing on sites with an agrillic soil horizon except *B. trifoliolata*.

scars were easily discernable in all species except *C. hookeri*, which produced new shoot growth through sympodial lateral branching, and consequently, lacked distinct terminal bud scale scars. For this species, we located and harvested segments of outer canopy twigs that appeared to represent new growth, based on distinct changes in stem color and degree of periderm development. This technique was standardized across irrigated and control plants. Though not necessarily precise, we felt confident this technique accurately quantified relative differences in *C. hookeri* shoot production between treatments.

Leaf biomass, shoot growth and leaf life span data were analyzed using analysis of variance (SAS GLM; SAS Institute 1985) for a completely randomized design. Median rather than mean leaf life spans were calculated for each marked shoot, because the median appeared to better represent the rate at which individual leaves died between sampling periods (i.e., 30-day intervals). Also, mean leaf life spans could not be determined for *Berberis trifoliolata*, which had some leaves that lived longer than the study period. For all species, excluding *B. trifoliolata*, leaf life spans determined using medians or means were generally comparable (data not shown). For statistical analyses, the individual shrubs were considered to be the experimental units (i.e., replicates) and shoots on each shrub were treated as subsamples within the replicate. Mean comparisons were made using Tukey's Studentized Range (HSD) Tests and Least Squares Means with differences reported as significant when $P < 0.05$.

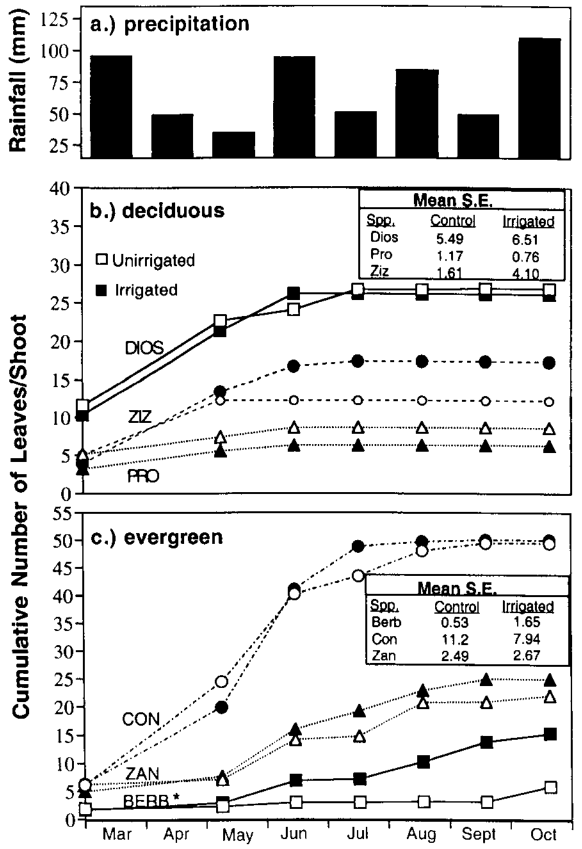

*Figure 2.* Mean ($N = 4$–$8$ plants) cumulative leaf production per shoot for deciduous species (b) and evergreen (c) species over an eight month growing period (March–October 1994) in unirrigated (open symbols) and irrigated (closed symbols) plants in upland shrub clusters (DIOS = *Diospyros texana*; ZIZ = *Ziziphus obtusifolia:* PRO = *Prosopis glandulosa*; CON = *Condalia hookeri*; ZAN = *Zanthoxylum fagara*; BERB = *Berberis trifoliolata*). Differences between unirrigated and irrigated plants were significant (* = $P < 0.05$) only for *B. trifoliolata*. Insets in panels b and c show mean standard errors for irrigated and control plants of each species. Panel a shows monthly precipitation recorded on-site.

## Results

### *Seasonal leaf habit and leaf longevity*

All species initiated leaf production in early- to mid-March and plants had a full complement of leaves by early June. *Diospyros texana*, *Prosopis glandulosa*, and *Ziziphus obtusifolia* were leafless for at least one month prior to this spring-time initiation of leaves and were therefore classified as deciduous. However, *D. texana* and *P. glandulosa* were winter-deciduous (full leaf drop by February), while *Z. obtusifolia* was distinctly summer-deciduous, having dropped all its leaves by late July (Figure 1). The three deciduous species produced leaves throughout the spring and early summer (March–June), but produced no new leaves during the summer and autumn months (July–October) (Figure 2b). By comparison, *Berberis trifoliolata*, *Condalia hookeri*, and *Zanthoxylum fagara* retained significant amounts of foliage year-round and were therefore classified as evergreens (Figure 1). New leaves in these evergreen species were also produced in a distinct spring flush, but additional leaf production occurred throughout the growing season (March–October). Generally, summer/autumn leaf flushes in these species occurred soon after small precipitation events (>15 mm of rainfall for *C. hookeri* and *Z. fagara*; >100 mm of rainfall for *B. trifoliolata*) or in response to irrigation (Figure 2c).

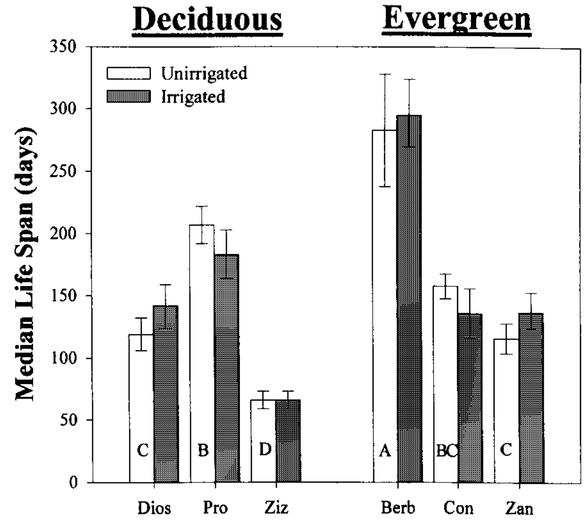

*Figure 3.* Average (±1 S.E.; $N = 4$–$8$ plants) median leaf life span for the March cohort in *Diospyros texana* (Dios), *Prosopis glandulosa* (Pro), *Ziziphus obtusifolia* (Ziz), *Berberis trifoliolata* (Berb), *Condalia hookeri* (Con) and *Zanthoxylum fagara* (Zan) in unirrigated and irrigated plants growing in upland shrub clusters. Letters within bars denote significant ($P < 0.05$) differences between species in unirrigated control plants. Within species, no significant ($P > 0.05$) effects of irrigation were detected.

The number and longevity of leaf cohorts varied significantly ($P < 0.05$) among species. Three distinct cohorts of leaves (March, May, and June) were recognized for the deciduous species, whereas a total of six leaf cohorts (March, May, June, July, August, and September) were evident among the evergreen species. The earliest (March) leaf cohorts in unirrigated shrubs showed a wide range of life spans among the species. The sclerophyllous evergreen *B. trifoliolata* displayed the longest median (283 days) and maximum (>500 days) leaf life span; the summer-deciduous *Z. obtusifolia* had the shortest leaf life span (median and maximum = 66 and 150 days, respectively) (Figure 3). The evergreens, *C. hookeri* and *Z. fagara*, and the winter-deciduous *D. texana* had statistically comparable median leaf life spans. The winter-deciduous *P. glandulosa* had a significantly ($F = 25.87$, df = 5, $P < 0.05$) longer median leaf life span than all species except *B. trifoliolata* and *C. hookeri* (Figure 3). Leaf survivorship curves (Figure 4) were Type I (Deevey 1947) for all species.

When averaged across species, median leaf life span varied significantly among the different-aged cohorts in both the deciduous ($F = 17.35$, df = 2) and evergreen ($F = 7.06$, df = 5) species ($P = 0.0001$ for both groups; Figure 4); however the species differed considerably in their individual responses. In the winter-deciduous *P. glandulosa* and the summer-deciduous *Z. obtusifolia*, the March leaf cohorts had significantly longer median leaf life spans than those produced in May ($P = 0.0001$ and $P = 0.02$, respectively) and June ($P = 0.001$ for *P. glandulosa*; *Z. obtusifolia* did not produce an unirrigated June cohort of leaves) (Figure 4). This general pattern of decreased longevity for the later-produced leaves was not observed in two (*B. trifoliolata* and *Z. fagara*) of the three evergreens. Rather, leaf longevity in these two species appeared to be influenced more by the prevailing environmental conditions than the time of their initiation. For example, the May cohort of leaves in unirrigated *B. trifoliolata* and *Z. fagara* plants, produced during a relatively dry period, had a shorter median leaf life span than leaves produced during wetter conditions in June ($P = 0.06$ and 0.003 for *B. trifoliolata* and *Z. fagara*). The August cohort had shorter median life spans than the March cohort in *Z. fagara* ($P = 0.06$) and the March ($P = 0.03$) and June ($P = 0.04$) cohorts in *B. trifoliolata.* Median leaf life spans in *C. hookeri* and *D. texana* leaf cohorts were comparable ($P > 0.13$ and $P > 0.35$).

### *Response to supplemental moisture*

Irrigation increased soil moisture content relative to that in unirrigated control clusters, but the magnitude of the treatment difference declined with time after irrigation and soil depth (Figure 5). Immediately following irrigation events, volumetric soil moisture contents ($q_v$; cm$^3$ m$^{-3}$) averaged over the entire study period were 7.3 vs. 14.7 (15–30 cm depth), 11.6 vs. 14.7 (30–60 cm depth), and 10.3 vs. 12.3 (90–120 cm depth) in control and irrigated clusters, respectively. Field capacities for sandy loam soils associated with woody clusters at this site range from 12 to 16 cm$^3$ m$^{-3}$ (Loomis 1989). Consequently, irrigation increased soil moisture levels to near field capacity immediately following application. Despite the high frequency and amount of water application, irrigation did not provide continually high soil moisture conditions. Time-course measurements of $q_v$ made over several precipitation-free periods, indicated rapid 'dry down', with soil moisture levels approaching that of unirrigated clusters by the time of the next irrigation event ca. 2 weeks later (Figure 5).

When averaged over species, there was no significant ($P = 0.87$) overall effect of irrigation on median leaf life span for the first (March) leaf cohort. There was also no indication that irrigation differentially affected median leaf life span in deciduous vs. evergreen species ($P = 0.98$ for the treatment × leaf habit interaction). Pooled median leaf life spans for deciduous and evergreen growth forms in control and irrigated plants were 130 vs. 136 days ($P = 0.75$) and 183 vs. 188 days ($P = 0.83$), respectively. Likewise, irrigation had no differential effect on median leaf life span in the various leaf cohorts (treatment × cohort interaction not significant) in deciduous ($P = 0.14$) or evergreen ($P = 0.93$) species. Survivorship curves for control and irrigated plants for each species were also generally similar (data not shown).

Despite the minimal effect on leaf life span, irrigation significantly influenced shoot elongation and biomass production. When averaged over irrigation and control treatments, the greatest number of leaves/shoot were produced by *C. hookeri* (mean = 50; $n = 7$); the fewest leaves/shoot were produced by *P. glandulosa* (mean = 7; $n = 6$) (Figure 2b–c). Irrigation elicited a 3-fold increase ($P = 0.01$) in the number of leaves/shoot in *B. trifoliolata* (Figure 2c).

Leaf dry biomass after 5 months of irrigation ranged from 20.6 g/shoot in *C. hookeri* to 1.4 g/shoot in *D. texana*. When averaged over species, leaf biomass/shoot was greater ($P = 0.001$) in irrigated than unirrigated plants (Figure 6a). However, the species responded differently to irrigation ($F = 3.19$, df = 5, $P = 0.01$ for species x treatment interaction). The deciduous species (*D. texana*, $P = 0.94$; *P. glandulosa*, $P = 0.78$; *Z. obtusifolia*, $P = 0.19$) showed no detectable increases in leaf biomass in response to irrigation, whereas a significant ($P < 0.004$), and more than two-fold increase in leaf biomass/shoot, was seen in the evergreen species (*B. trifoliolata*, *C. hookeri* and *Z. fagara)* (Figure 6a).

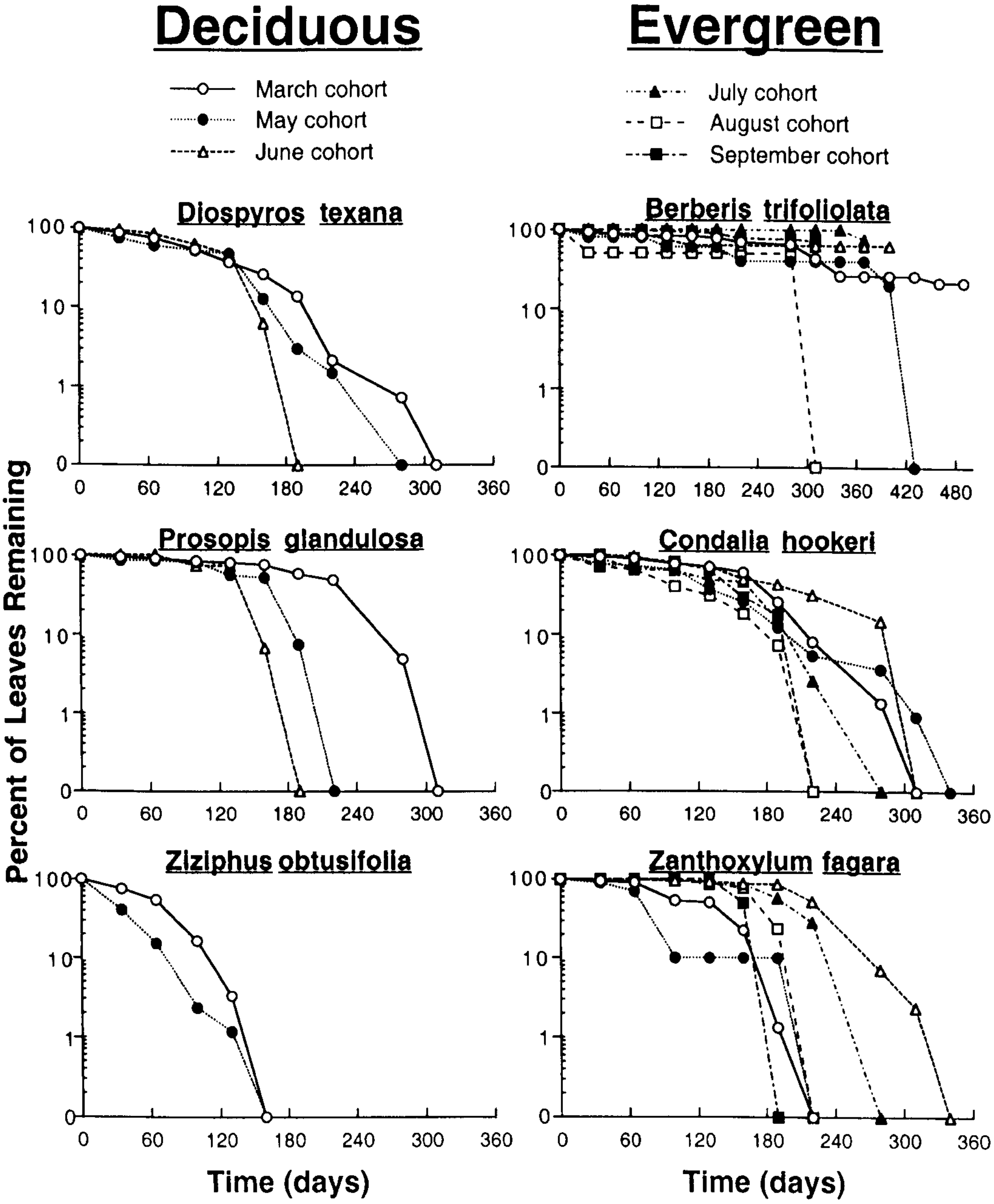

*Figure 4.* Leaf cohort survivorship curves for unirrigated (control) deciduous (*Diospyros texana*, *Prosopis glandulosa* and *Ziziphus obtusifolia*) and evergreen (*Berberis trifoliolata*, *Condalia hookeri* and *Zanthoxylum fagara*) species. Irrigation had no significant ($P > 0.05$) effect on leaf survivorship (see text). Note differences in x-axis scale for *B. trifoliolata*. *Z. obtusifolia* did not produce a June cohort of leaves and the July and September cohorts in *B. trifoliolata* were from irrigated plants.

Shoot elongation from May to October varied five-fold (maximum = *C. hookeri* [46.2 cm]; minimum = *D. texana* [7.9 cm]) and when averaged over all species, increased significantly ($P = 0.0001$) with irrigation (Figure 6b). As with foliar biomass, individual species varied in their response ($F = 5.45$, df = 5, $P = 0.0001$ for species × treatment interaction). *Prosopis glandulosa* and *Z. obtusifolia* (both deciduous) showed no increase in shoot elongation in response to irrigation ($P = 0.29$ and $P = 0.69$,

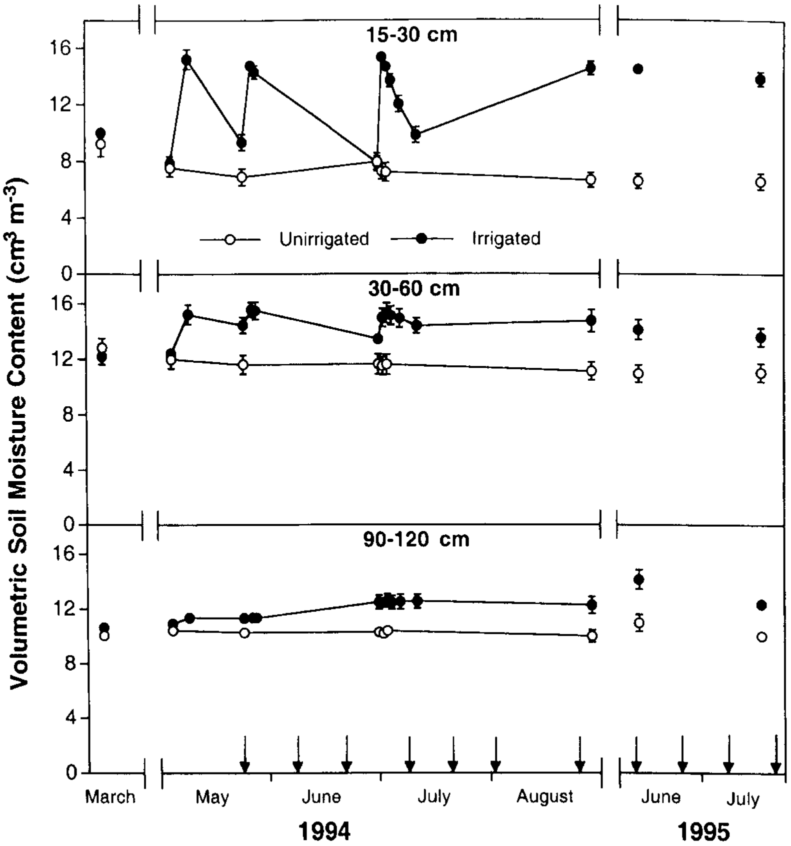

*Figure 5.* Mean (± 1 S.E.) volumetric soil moisture content at three depths (15–30, 30–60 and 90–120 cm) in unirrigated and irrigated upland shrub clusters. Arrows indicate timing of irrigation events.

respectively). Among those species that did respond, shoot elongation was generally greater in the evergreens (*B. trifoliolata* = 153%; *C. hookeri* = 35%; and *Z. fagara* = 165%) than in the deciduous *D. texana* (36%) ($P < 0.02$ for all species; Figure 6b).

## Discussion

### *Leaf habit-leaf longevity patterns*

Our results demonstrate the variety of seasonal leaf habits (summer deciduous, winter deciduous and evergreen) among the trees and shrubs in these subtropical savanna parklands. However, contrary to expectations, we found no clear relationship between leaf habit and leaf longevity among these species. The evergreen shrubs at our subtropical savanna site had median leaf life spans considerably less than one year and, in several instances, had shorter leaf life spans than those of their deciduous neighbors. Further, there was substantial variation within leaf habit groups. For example, *Berberis trifoliolata* and *Zanthoxylum fagara* could both be classified as evergreens, yet they achieved this leaf habit in strikingly different ways. Whereas *B. trifoliolata* possessed sclerophyllous leaves with a median longevity of 283 days, *Z. fagara* initiated a number of cohorts of short-lived (median leaf life span = 116 days), coriaceous leaves whose birth and death appeared to be closely coupled with short-term fluctuations in moisture and temperature. In other species, the classification of leaf habit may be very dependent on environmental conditions. For example, under winter temperature regimes that are colder than those experienced during our study, and which are known to occur in this region (Lonard & Judd 1985), there may be near complete leaf drop in *Condalia hookeri*, which behaved as an evergreen during this study. On the other hand, *Diospyros texana*, classified as deciduous in the present study, may retain significant numbers of leaves in some winters (Angerer 1991). Thus, *C. hookeri* and *D. texana* might be more

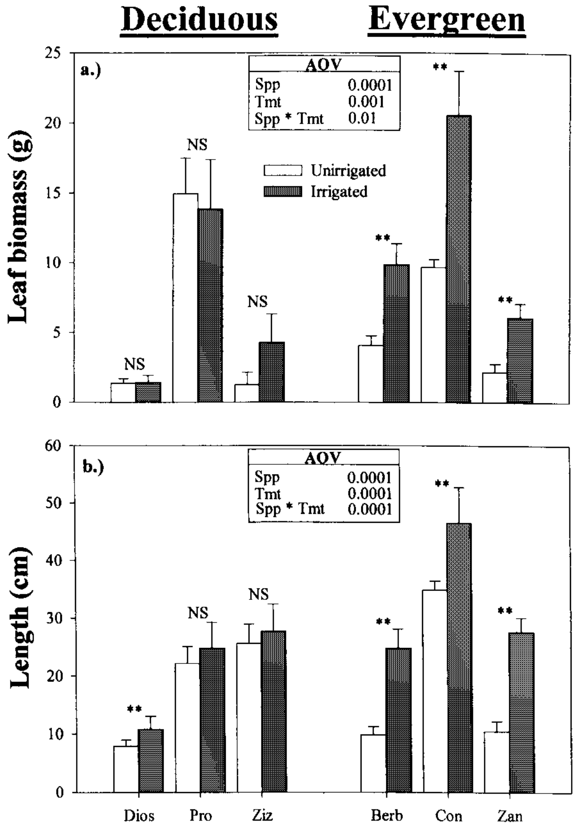

*Figure 6.* Standing leaf biomass (a) and current years' shoot length (b) in unirrigated and irrigated plants of *Diospyros texana* (Dios), *Prosopis glandulosa* (Pro), *Ziziphus obtusifolia* (Ziz), *Berberis trifoliolata* (Berb), *Condalia hookeri* (Con) and *Zanthoxylum fagara* (Zan) in October 1994. Data are means (± 1 S.E.) after an eight month growing period and five months of irrigation ($N = 4$–$6$ plants). Asterisks (**) denote significant ($P < 0.001$) differences between irrigated and non-irrigated plants; NS = not significant ($P > 0.05$). Insets show P values for analysis of variance (AOV) main effects (species = Spp; irrigation treatment = Tmt) and species × treatment interaction.

aptly classified as facultatively evergreen. Overall, our data indicate that the woody plants in this subtropical ecosystem do not adhere to the broad generalizations of leaf habit-leaf longevity relationships developed in highly seasonal temperate, high-latitude or tropical locations; but rather, more closely resemble patterns observed in non-seasonal, tropical environments (Kikuzawa 1995).

The evergreen leaf habit is often considered advantageous in climatic regions where precipitation and temperature allow for year-round photosynthesis, with the deciduous habit increasing in prevalence as the unfavorable season (e.g., cold winter or summer drought) increases in length and/or severity (Chabot & Hicks 1982; Kikuzawa 1995). In southern Texas, the frequency, duration and severity of unfavorable growth periods is highly variable and unpredictable. For example, weather records from Alice, Texas (28 km from the La Copita Research Area) indicate that freezing temperatures have not occurred in 28 of the last 86 years. Likewise, annual precipitation is highly variable (C.V. = 35%; Le Houerou & Norwine 1988). Thus, in some years, growth and photosynthesis may be possible year-round, whereas in others, drought or cold winter temperatures may curtail photosynthesis and cause significant leaf mortality. In this subtropical savanna system, characterized by a high degree of variability and uncertainty in climatic conditions, there appears to be a continuum of viable survival 'strategies' between the obligate evergreen and the obligate deciduous extremes, with none of the growth forms able to consistently outperform and hence exclude the others. The temporal variation in leaf initiation, leaf longevity and canopy development observed in this study, together with temporal separation in photosynthetic activity (Barnes & Archer 1996; McMurtry 1997) and a pronounced vertical stratification of root distributions (Watts 1993) may be factors that allow for the continued coexistence and relatively high woody plant diversity in this system. Gradient analyses suggest precipitation patterns and low temperatures similarly influence the abundance and distribution of plant functional types in dry tropical savannas (Skarpe 1996). However, unlike seasonally dry tropical savannas and woodlands (Eamus 1999), we find no close relationship between leaf habit and rooting depths in these subtropical woody plant assemblages (i.e., evergreens are not necessarily deeper rooting than co-occurring deciduous species; Table 1) (Watts 1993; Midwood et al. 1998; Boutton et al. 1999).

### *Leaf longevity and resource availability*

We initially hypothesized that, if leaf longevity in these woody species was influenced by leaf carbon balance over an ecological time-frame, increased moisture availability would result in increased leaf carbon gain and this would then translate into a decrease in leaf life span. The irrigation treatment in the present study increased surface soil moisture content approximately two-fold relative to unirrigated clusters, and moisture levels in irrigated clusters were near field capacity during much of the study. Irrigation substantially decreased plant water stress (measured as plant water potential) and significantly increased daily net photosynthesis in all species, especially during drought periods (McMurtry 1997). Despite these effects, we detected no differences in median leaf life span between control and irrigated plants. It is possible that the effects of irrigation on leaf life span may only be manifested over longer time frames. With nutrient augmentation, changes in leaf life span in other woody plants may occur only after two or more years (Shaver 1981; Lajtha & Whitford 1989). In the present study, the 1994 cohorts were censused until complete leaf abscission occurred (ca. 340 days in the deciduous species; ca. 450 days in the evergreen species, except in *B. trifoliolata* which was well over 500 days), but new leaf cohorts produced in March of 1995 were not followed. It is also possible that irrigation reduced leaf longevity in a manner consistent with the carbon balance hypothesis, but that simultaneous drought stress in control plants caused premature leaf drop in some, or all species (e.g., Mulkey et al. 1993; Wendler & Millard 1996). Thus, relative to the controls, reductions in leaf life span in the irrigated plants would not have been apparent. Indeed, within the unirrigated controls, the different-aged cohorts of leaves in *B. trifoliolata*, *Z. fagara*, *P. glandulosa* and *Z. obtusifolia* had significantly different median life spans, and these differences appeared to be closely related to precipitation patterns. Both senescence and drought have been implicated in the leaf shedding in trees of dry tropical forests (Martin et al. 1994), and these processes may also influence leaf life span in some of the woody plants in these semi-arid, subtropical savannas.

### *Woody plant functional groups*

We hypothesized that, within this assemblage of woody plants, species responses to increased soil moisture would be inversely related to leaf longevity and that deciduous growth forms would be more responsive in their growth to increased resource (soil moisture) availability than plants with evergreen canopies. Neither hypothesis was supported. Although the species we studied exhibited a wide range of leaf life spans, we found no indication that leaf longevity, *per se*, was correlated with a species' growth response to alterations in moisture availability. Also, counter to expectations, deciduous species were found to be more deterministic and constrained in their growth responses to increased moisture availability than evergreens. Specifically, the deciduous species appeared limited in their abilities to produce new leaves in response to resource pulses, whereas the evergreens were more flexible and thus, more opportunistic, producing more leaf cohorts/year and exhibiting greater leaf growth and shoot elongation. Because the plants we measured were growing together in mixed-species shrub clusters, it is possible that interspecific competition may have constrained some species' responses to irrigation more than that of others. Our assessment therefore represents 'realized' rather than 'potential' responses to resource enrichment.

Across diverse ecosystems and plant growth forms, leaf life span has been shown to be correlated with other leaf-level attributes (i.e., photosynthetic capacity, stomatal conductance, leaf nitrogen concentration, and specific leaf area; Diemer et al. 1992; Gower et al. 1993; Reich et al. 1992, 1997), whole-plant performance (i.e., leaf area index, relative growth rate; Coley 1988; Reich et al. 1992) and fundamental ecosystem processes (e.g., productivity, decomposition and nutrient cycling; Shaver 1981; Chabot & Hicks 1982; Gower & Richards 1990; Reich et al. 1992). Thus, leaf life span has been promoted as a potentially important avenue for scaling from leaf to landscape, continental or global scales in models of vegetation-atmosphere interactions and the global carbon cycle (Reich et al. 1997). Our results, however, indicate that, within the diverse group of woody species found in the subtropical savannas and thorn woodlands of southern Texas, leaf life span could not reliably predict relative growth responses to increased resource availability. In addition, we have found no correlation between leaf life span and photosynthetic capacity (McMurtry 1997) or leaf nitrogen concentration (Table 1; P. Barnes & S. Archer ms. in prep.) among these species. In this system, plant attributes that appear to best predict physiological and growth responses to resource availability seem to be rooting depth (McMurtry 1997) and leaf habit (i.e., evergreen vs. deciduous; this study). However, the latter behaved contrary to generalizations derived from temperate and high latitude regions in that the evergreen species were more dynamic and more responsive to increased resource availability than deciduous species. Our results suggest caution must be exercised when inferring structure-function relationships in these subtropical savannas and woodlands.

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