



Arroyo water storage and soil nutrients and their effects on gas-exchange of shrub species in the northern Chihuahuan Desert

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A variable fraction of the rain falling on desert landscapes runs off and accumulates in ephemeral channels (arroyos), where some of the water is transported downslope. Relatively large amounts of water are stored in arroyo sediments. This water may support high rates of gas-exchange in some riparian species. We examined differences in the timing of flow events, soil water storage, and soil nutrients on gas-exchange rates of shrubs growing on arroyo margins and in adjacent piedmont areas in the Chihuahuan Desert of southern New Mexico, USA. The semi-riparian shrub, *Fallugia paradoxa* (Apache plume), had very different photosynthetic rates between two arroyos, but transpiration rates did not differ. This may result from nutrient limitation differences between arroyos. At one site, the semi-riparian shrub, *Prosopis glandulosa* (mesquite), on arroyo margins had access to more water and showed higher rates of gas-exchange compared with non-arroyo mesquite located on nearby piedmont areas. The obligate riparian shrub, *Chilopsis linearis* (desert willow), had intermediate gas-exchange rates when compared with Apache plume and mesquite, and neither soil water nor nutrient concentrations appeared to affect photosynthesis during the growing season. Variation between and within arroyos was high; however, our data suggest that stored water enabled mesquite of arroyo margins to maintain relatively high rates of gas-exchange. When water was relatively abundant, nutrient availability appeared to limit photosynthetic rates of Apache plume.

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Introduction

High-intensity, short-duration, localized, convective thunderstorms are common in the Chihuahuan Desert. Because of the sparse vegetation and compacted soils a large proportion of the rain runs off into ephemeral drainage channels (arroyos) and ephemeral lakes (playas). Much of the water entering an arroyo may be 'lost' through transmission losses. On an annual basis transmission losses may be as high as 90% of the runoff that reaches an arroyo channel (Burkham, 1970). This water may be stored (Ludwig & Whitford, 1981), evapotranspired (Hillel & Tadmor, 1962), or used for recharge (Constantz *et al.*, 1994). In the Chihuahuan Desert, arroyos and playas had the greatest amount of stored water (Ludwig & Whitford, 1981). However, water content in shallow soils beneath mesquite growing on arroyo margins only slightly exceeded that of soils beneath mesquite in grassland and dune areas (Virginia *et al.*, 1992).

While the role of arroyos as conduits for water is relatively well known (e.g., Renard & Keppel, 1966), less is known about their capacity to act as storage areas for water and nutrients. Although the distribution of moisture at various positions along arroyos may be variable, plants are able to exploit the richer resources of arroyos. Differences between arroyo and non-arroyo areas are often striking in species composition (Krausman *et al.*, 1985) and in the greater size of arroyo plants (Balding & Cunningham, 1974; Ehleringer & Cooper, 1988). Evidence supporting the hypothesis that arroyos store water has come from studies showing that plants growing on arroyo margins have higher transpiration rates and stomatal conductances than species in adjacent non-arroyo areas (Schmitt *et al.*, 1993; Smith *et al.*, 1995). Shallow soils under mesquite along arroyo margins have also been shown to have slightly higher levels of organic carbon, total nitrogen, and total phosphorus than soils beneath mesquite in dune and grassland areas (Virginia *et al.*, 1992). Nitrogen mineralization rates were somewhat lower in soils of arroyo margin areas.

In the northern Chihuahuan Desert of southern New Mexico, USA, the species composition of vegetation along arroyo margins is very variable, but usually dominated by perennial shrubs. Shrub species occurring along arroyo margins can be categorized based on life-form and the degree to which they are restricted to riparian habitats (Dick-Peddie, 1993). However, little is known about the factors that determine the relative abilities of shrub species to establish and grow along arroyos.

It is hypothesized that access to stored water and nutrients enable arroyo shrubs to have higher gas-exchange rates than shrubs of adjacent piedmont areas. This study was designed to investigate differences in soil water storage and soil nutrients on gas-exchange characteristics of species inhabiting arroyo and non-arroyo areas.

Materials and methods

Study sites and plants

The study sites were located on the Chihuahuan Desert Rangeland Research Center in the Jornada del Muerto Basin of the northern Chihuahuan Desert. The center is approximately 40 km NNE of Las Cruces, Doña Ana County, New Mexico, USA. The sites (designated A1 and A2) were located on east-facing alluvial piedmonts of the Doña Ana Mountains. Mean annual rainfall for this area is 233 mm, of which 64% occurs during the summer (Conley *et al.*, 1992). Mean maximum summer (July–October) temperature is 31°C while mean minimum winter (November–March) temperature is –5°C. The arroyos studied were two medium sized, unconnected channels located approximately 0.5 km apart, at approximately the same elevation. The sites were located in the mid-section of the arroyos. Arroyo margins

(banks) were approximately 0.5 m in height on each side of the channel at both sites. Each site was approximately 100 × 100 m (including non-arroyo mesquite of the adjacent piedmont). Maximum width of the channels was 20 m. The channel at A1 is braided. Braided channels divide into two or more separate channels, often consisting of bars and islands and poorly defined margins (Gordon *et al.*, 1992). A2 has a relatively straight, single channel. At the upslope and downslope ends of the study area we placed a 0.1 m wide line of lime (CaCO₃) across the width of the channel. The lime was minimally affected by precipitation, but was washed away by water flowing through the channel. This enabled us to determine when a flow event had occurred.

At each site we randomly selected two adult shrubs of *Fallugia paradoxa* (D. Don) Endl. (Apache plume), *Chilopsis linearis* (Cav.) Sweet (desert willow), and *Prosopis glandulosa* Torrey (arroyo mesquite) growing on the margins of the arroyos. All plants selected were at least 5 m apart to ensure that they were functionally distinct individuals. We also selected four mesquite plants on the adjacent piedmont at each site at a distance of 32–67 m from the nearest arroyo channel (non-arroyo mesquite). We selected mesquite at these distances to ensure that lateral roots would not likely reach the channel (Gile *et al.*, 1997). Apache plume and mesquite are classified as semi-riparian (facultative) species and desert willow is designated as an obligate riparian species (Dick-Peddie, 1993). Both mesquite and desert willow have been reported to be phreatophytic in the Sonoran Desert (Nilsen *et al.*, 1984). Mesquite occurs in both riparian and non-riparian areas; however, desert willow only occurs along the margins of larger arroyo channels. Apache plume is not usually phreatophytic but is obligate to arroyos in the area of this study.

Soil water storage

Aluminum neutron probe access tubes were installed under the canopy of each shrub. Soil volumetric water contents were measured using a neutron probe (Rundel & Jarrell, 1991) with a 503DR Hydroprobe Moisture Depth Gauge (CPN Corp., Pacheco, CA). Five probe tubes were also installed at 20 m intervals in the center of the main channel at each site. Measurements were taken at 0.3, 0.6 and 0.9 m depths at monthly intervals, and additionally on the same days that gas-exchange measurements were taken. Soil water contents were estimated from calibration equations derived for the hydroprobe from soil samples excavated along a transect close to the sites of this study (see Wierenga *et al.*, 1987 for a description of the transect). Soil water storage (S) was calculated by integrating (trapezoidal method) the soil water content values for the three depths (see Haverkamp *et al.*, 1984; Chen *et al.*, 1995).

Soil organic matter and total nitrogen

Soil samples were collected at 0.1, 0.5 and 1.0 m depths during neutron probe tube installation and analysed for percent organic matter (OM) and total nitrogen (TN). For OM, soil samples were sieved (2 mm Tyler sieve) and heated to 105°C to remove moisture. A 50 g sub-sample was heated at 400°C for 12 h in a muffle furnace and re-weighed to calculate OM based on change in sample weight (Nelson & Sommers, 1982). No corrections for CaCO₃ were used (Davies, 1974). TN samples were further ground to pass through a 0.15 mm sieve. TN was determined on a 0.5 g soil sample using the Kjeldahl method with an automated continuous flow analyser (Orion Scientific Instruments Corp., Pleasantville, NY, USA) (Crooke & Simpson, 1971; Nelson & Sommers, 1980).

Gas-exchange

On each shrub we selected two leaves (mesquite) or stem apical segments with several leaves (Apache plume and desert willow) and loosely tagged these with colored yarn. We measured net photosynthesis and transpiration rate using a LI 6200 Portable Photosynthesis Measurement System (LI-Cor, Inc., Lincoln, NE, USA). The tags enabled us to identify leaves or stem segments for repeated measurements during the day. Data collected under unsaturated light conditions or unusually high ambient CO₂ concentrations (indicating contamination with exhaled air) were excluded from analyses. Leaves used for gas-exchange measurements were harvested at the end of each day and leaf areas were measured using a LI 3000 Portable Area Meter (LI-Cor, Inc., Lincoln, NE, USA). Gas-exchange was measured one to three times during the day, weather permitting. We calculated an integrated (trapezoidal method) value for photosynthetic rate (P_{int}) and transpiration rate (E_{int}) based on two sequential measurements of gas-exchange over a period of 4 h between 9 am and 1 pm.

Statistical analysis

The design of the study was unbalanced; therefore, least-square means (LSMEANS) of the GLM procedure (SAS, 1989) were used to evaluate differences among species and between sites for the OM, TN and gas-exchange data. S was analysed using Contrasts following a repeated measures analysis of variance (ANOVA) of the GLM procedure (SAS, 1989) to detect differences among species and channels and between sites (Potvin *et al.*, 1990).

Results

Climate

Data from the Jornada Long-Term Ecological Research (Jornada LTER) site weather station located approximately 1.0 km north of A2 indicate that maximum temperatures in the summer of 1994 were above average and total rainfall was slightly below average (Fig. 1; Conley *et al.*, 1992). Daily maximum air temperatures peaked in June, and maximums were over 30°C from late April through September. Water flowed along the arroyo channels on several occasions during the growing season (Table 1). Flows resulted from large rainfall events occurring in late May, late July through early August, early September, and mid-October.

Soil organic matter and total nitrogen

Mean soil OM and TN declined with increasing depth (Table 2). We found significant differences between sites for mean OM and TN only in soils under Apache plume at the 0.5 and 1.0 depths (A1 > A2). Within sites, mean OM was significantly different only in soils at A2 at the 0.5 m depth. At A2, arroyo mesquite and non-arroyo mesquite soils had significantly greater concentrations of OM than soils beneath Apache plume. There are within site differences for mean TN at A1 at 0.1 and 1.0 m. Soils beneath desert willow had significantly greater concentrations than non-arroyo mesquite soils at 0.1 m. At 1.0 m, soils under Apache plume had the greatest mean TN. At A2, arroyo mesquite had significantly greater mean TN than all other soils at 0.5 m.

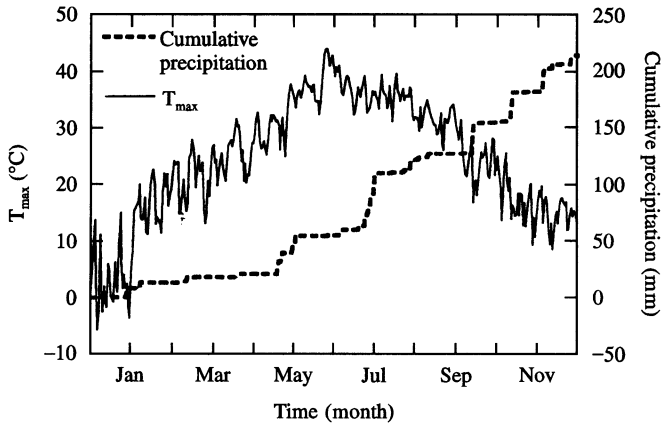


Figure 1. Maximum air temperature and cumulative rainfall measured near the study sites during 1994.

Soil water storage and gas-exchange

The patterns of soil water storage (S) were very different at A1 and A2 (Fig. 2(a) & 2(d)). At A1, S was highest in soils under Apache plume and lowest in soils beneath desert willow except during July/August 1994 when S under desert willow increased and was higher than arroyo and non-arroyo mesquite following flow events (Table 1). However, these changes were transient and did not change the ranking of seasonal means for S at A1 (Apache plume > non-arroyo mesquite > arroyo mesquite > desert willow) or A2 (arroyo mesquite > non-arroyo mesquite > desert willow > Apache plume) (Table 3). There were no significant differences in mean S between soils under arroyo mesquite and non-arroyo mesquite at A1. At A2, mean S under arroyo mesquite was significantly higher than mean S under non-arroyo mesquite during winter–spring and summer. Unlike A1, S at A2 remained relatively unchanged in soils under all species throughout the year (Fig. 2(d)). Mean S was significantly higher under Apache plume at A1 than at A2 in all seasons, and the same was true for non-arroyo mesquite in summer only (Table 3). The arroyo channel at A1 when compared to the channel at A2 had significantly higher mean S during winter–spring and summer, but A2 had significantly higher S in fall–winter, coinciding with September and October flow events that only occurred at A2 (Table 1). Mean S at A1 in arroyo channels was higher than in soils beneath desert willow, arroyo mesquite, and non-arroyo mesquite in

Table 1. Dates of arroyo channel flow events recorded at the two study sites during 1994

Date	Study site	
	A1	A2
May 21	Flow	No Flow
July 21	No Flow	Flow
July 29	Flow	No Flow
August 2	Flow	Flow
August 7	Flow	No Flow
September 5	No Flow	Flow
October 14	No Flow	Flow

Table 2. *Distribution of mean organic matter (OM; %) and total nitrogen (TN; µg/g) at three soil depths under the shrub species at the two study sites*

Species	Nutrient	Depth (m)	A1		A2	
			<i>n</i>	Mean	<i>n</i>	Mean
Apache plume	OM	0.1	2	1.28 Aa	3	1.16 Aa
Desert willow			2	1.51 Aa	2	2.30 A
Mesquite (arroyo)			2	1.57 Aa	2	2.20 Aa
Mesquite (non-arroyo)			4	1.21 Aa	4	1.43 Aa
Apache plume		0.5	2	1.22 Aa	3	0.46 Ba
Desert willow			2	0.70 Aa	2	0.61 Aac
Mesquite (arroyo)			2	1.36 Aa	2	1.30 Ab
Mesquite (non-arroyo)			4	1.21 Aa	4	0.93 Ac
Apache plume		1.0	2	1.17 Aa	3	0.47 Ba
Desert willow			2	0.59 Aa	2	0.94 Aa
Mesquite (arroyo)			2	0.89 Aa	2	0.72 Aa
Mesquite (non-arroyo)			4	0.86 Aa	4	0.75 Aa
Apache plume	TN	0.1	2	983 Aab	3	890 Aa
Desert willow			2	1625 Aa	2	1480 Aa
Mesquite (arroyo)			2	872 Aab	2	1584 Aa
Mesquite (non-arroyo)			4	718 Ab	4	1014 Aa
Apache plume		0.5	2	852 Aa	3	309 Ba
Desert willow			2	578 Aa	2	412 Aac
Mesquite (arroyo)			2	759 Aa	2	1107 Ab
Mesquite (non-arroyo)			4	679 Aa	4	649 Ac
Apache plume		1.0	2	790 Aa	3	314 Ba
Desert willow			2	376 Ab	2	813 Aa
Mesquite (arroyo)			2	476 Ab	2	588 Aa
Mesquite (non-arroyo)			4	441 Ab	4	475 Aa

Same upper-case letter indicates no statistically significant differences between the same species at the same depth at different sites, and same lower-case letter indicates no statistically significant differences at the same depth within sites among species (LSMEANS, $p < 0.05$).

all seasons, but mean S of channels was higher than in soils beneath Apache plume in summer only (Table 3). At A2, mean S in the channel was higher than in soils beneath Apache plume, desert willow, and non-arroyo mesquite in all seasons, but mean S in the channel was higher than in soils under arroyo mesquite in winter–spring and fall–winter only.

Photosynthesis and transpiration were measured on 4 days at A1 (May 25, June 15, July 30, and October 8) and A2 (May 28, June 25, July 24 and October 10). At A1, early season (May 25) P_{int} of non-arroyo mesquite was significantly higher than in desert willow, but by June 15 P_{int} of Apache plume and arroyo mesquite was higher than in desert willow and non-arroyo mesquite (Fig. 2(b)). By July 30 there were no significant differences in P_{int} and this pattern continued through to October 8. Early season differences for P_{int} at A1 were not paralleled by corresponding differences in E_{int} (Fig. 2(c)). However, by June 15 Apache plume and arroyo mesquite had

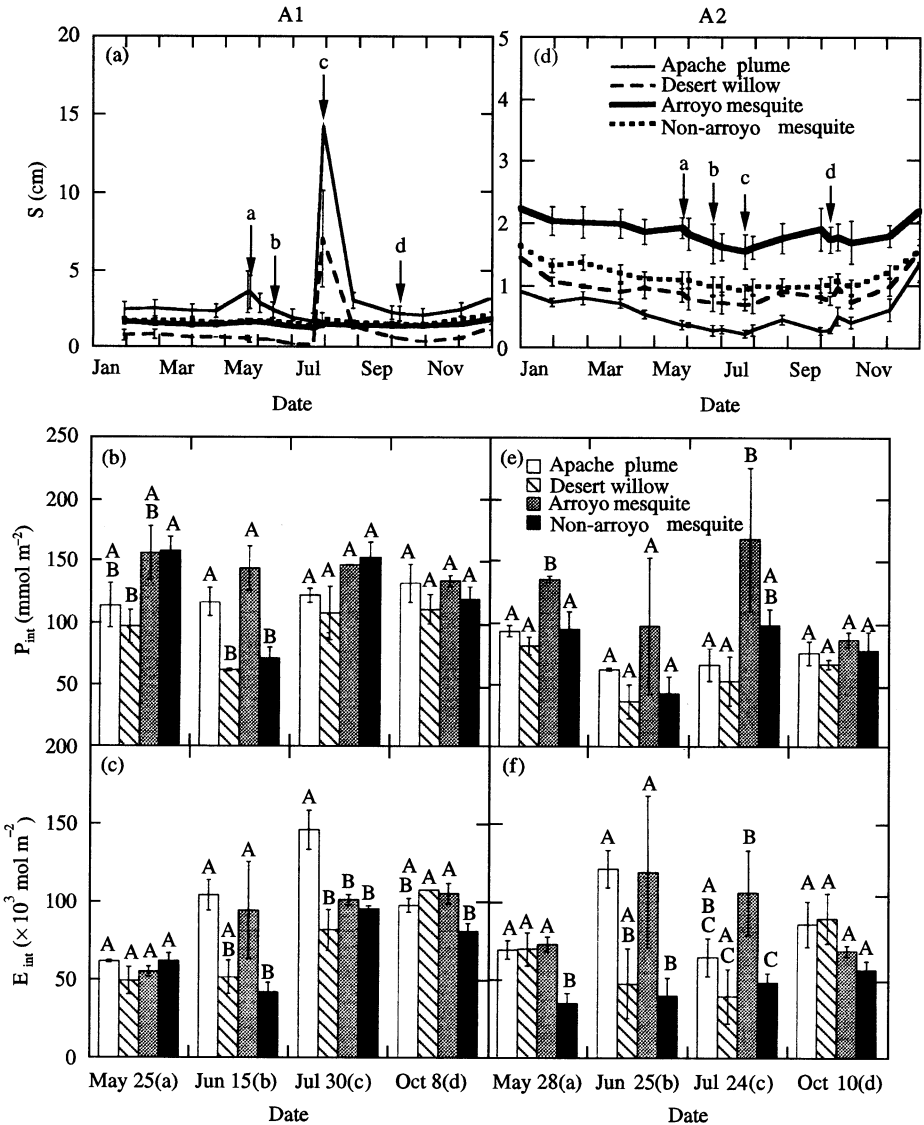


Figure 2. Pattern of soil water storage (S) under the study species at sites A1 (a) and A2 (d). Error bars indicate standard error. Arrow with letter indicates dates when gas-exchange was measured and shown as: (b) (A1) and (e) (A2) integrated photosynthesis rate (P_{int}) and (c) (A1) and (f) (A2) integrated transpiration rate (E_{int}). Within each day, different capital letters indicate statistically significant differences among species (LSMEANS, $p < 0.05$).

significantly higher E_{int} than non-arroyo mesquite. By July 30 the E_{int} of Apache plume was higher than that of any other species. However, by October 8 the E_{int} of Apache plume was not significantly different from that of the other species; but, E_{int} of desert willow and arroyo mesquite was higher than E_{int} of non-arroyo mesquite.

At A2, early season P_{int} was significantly higher in arroyo mesquite than in all other species (Fig. 2(e)). On June 25 all shrubs had similar P_{int} rates, but by July 24 arroyo mesquite again had higher P_{int} rates than Apache plume and desert willow. By the latter

Table 3. Seasonal mean soil water storage (S ; cm) under plant species and channels at the two study sites

Species or Channel	Site			
	n	A1	n	A2
	*Winter-Spring 1994			
Channel	20	3.58 Aa	20	2.89 Ba
Apache plume	8	2.48 Aac	12	0.70 Bb
Desert willow	8	0.79 Abd	8	0.99 Abd
Mesquite (arroyo)	8	1.60 Acd	8	1.99 Ac
Mesquite (non-arroyo)	16	1.74 Acd	16	1.26 Ad
	†Summer 1994			
Channel	40	5.78 Aa	35	1.94 Ba
Apache plume	16	4.21 Ab	21	0.34 Bb
Desert willow	16	1.42 Ac	14	0.79 Abc
Mesquite (arroyo)	16	1.57 Ac	14	1.72 Aa
Mesquite (non-arroyo)	31	1.72 Ac	28	1.02 Bc
	‡Fall-Winter 1994			
Channel	25	3.26 Aa	30	4.45 Ba
Apache plume	10	2.52 Aac	18	0.58 Bb
Desert willow	10	0.79 Ab	12	0.97 Abc
Mesquite (arroyo)	10	1.60 Abc	12	1.86 Ac
Mesquite (non-arroyo)	20	1.77 Ac	24	1.15 Abc

*January 1994–April 1994.

†May 1994–August 1994.

‡September 1994 – December 1994.

Same upper-case letter indicates no statistically significant differences between sites of the same species or channel within a season, and same lower-case letter indicates no statistically significant differences within seasons (Contrasts following repeated measures ANOVA, $p < 0.05$).

part of the growing season (October 10) all species again had similar rates of P_{int} . On May 28 non-arroyo mesquite had the lowest E_{int} (Fig. 2(f)). The E_{int} of non-arroyo mesquite was also lower than the E_{int} of Apache plume and arroyo mesquite on June 25. By July 24 E_{int} was significantly higher in arroyo mesquite than in desert willow and non-arroyo mesquite, but by October 10 all shrubs had similar E_{int} .

Gas-exchange of shrubs at A1 could not be compared with measurements from A2 because the measurements were taken on different days. Therefore, we calculated season-long means for measurements taken on the four days for each site reported above (Table 4). P_{int} rates were significantly higher at A1 than at A2 for Apache plume, desert willow, and non-arroyo mesquite. E_{int} rates were significantly higher at A1 than at A2 for non-arroyo mesquite only.

Discussion

Our results document that arroyos within a desert landscape, even those spatially close to each other, had different frequencies and timing of channel flow events. Patterns of water storage also were very different. Additionally, shrub species growing along the margins of an arroyo were subjected to different conditions, and therefore had

Table 4. Season-long mean P_{int} and E_{int} based on four measurements between May 25 and October 10, 1994

Site	Species	<i>n</i>	Mean P_{int} (mmol m ⁻²)	Mean E_{int} (× 10 ³ mol m ⁻²)
A1	Apache plume	8	121.42 a	102.69 a
A2	Apache plume	12	76.10 b	85.63 a
A1	Desert willow	8	94.55 a	72.81 a
A2	Desert willow	8	61.20 b	61.88 a
A1	Arroyo mesquite	8	145.29 a	89.37 a
A2	Arroyo mesquite	8	122.96 a	92.10 a
A1	Non-arroyo mesquite	16	125.38 a	70.32 a
A2	Non-arroyo mesquite	15	78.97 b	45.97 b

Same lower-case letter indicates there were no significant differences between a species at A1 and A2 (LSMEANS, $p < 0.05$).

different physiological responses to the same species growing in adjacent non-arroyo areas. Primary production in desert ecosystems is limited by both water and nutrients (for reviews see Hadley & Szarek, 1981; Ludwig, 1987). Arroyos, along with playas, are areas in arid and semi-arid ecosystems that have relatively high moisture levels (Ludwig & Whitford, 1981) where water may be more available and thus, less limiting than in most desert areas.

The organic matter content of Chihuahuan Desert soils is positively related to concentrations of other nutrients (Whitford *et al.*, 1987). The sandy soils of arroyos are usually nutrient-poor. Therefore, we believe arroyo plants probably rely on three major sources of nutrients for their annual growth: (1) resorption of nutrients from deciduous leaves before abscission; (2) recycling of nutrients from organic litter accumulating under plant canopies; and (3) nutrients (including organic litter) transported from upstream areas by arroyo channel flow events. While resorption of nutrients may enable plants to get a head-start on growth the following season, a true long-term increase in biomass may be achieved only if additional nutrients can be absorbed by the plant. Channel flow events that transport nutrients to a plant from upstream may also remove organic litter and nutrients from under the plant and transport them downstream and away from the plant.

Plant and soil characteristics associated with Apache plume were different at A1 compared with A2. Soils beneath Apache plume had more organic matter and total nitrogen at A1 (Table 2). The presence of greater quantities of organic matter at A1 may be due to topographic characteristics of the arroyo. A1 is a narrow, braided, channel segment, while A2 is a relatively wide, straight segment of arroyo. Osborn *et al.* (1977) noted that a straight channel was three times more efficient in sediment transport than a meandering channel. We also found that A2, on average, produced twice as much particulate matter from runoff events than a bifurcated channel (data not presented). If A1 retains more organic materials than A2, why is Apache plume the only species able to exploit this potential source of nutrients? The answer may lie in the architecture of the species. Apache plume is a shrub with slender branches that often extend to the base of the plant (Benson & Darrow, 1981). Instead of a single, main trunk, as is usual for riparian desert willow and mesquite, Apache plume has an architecture similar to that of multi-stemmed tamarisk or saltcedar species (e.g., *Tamarix ramosissima*). Tamarisk is known to increase roughness and reduce velocity of flow in arroyos (Hadley, 1961). There was also more soil water storage beneath Apache plume at A1 (Table 3). However, while season-long mean integrated photosynthetic rates of Apache plume

were higher at A1 than at A2, season-long mean integrated transpiration rates were similar at the two sites (Table 4). If the higher photosynthetic rates of Apache plume at A1 were due to the greater availability of water, transpiration rates also should have been higher. Since transpiration rates of Apache plume were not higher at A1, the higher photosynthetic rates of Apache plume at A1 may be attributable to greater nutrient availability.

Non-arroyo mesquite and desert willow also had higher season-long mean photosynthetic rates at A1 than at A2 (Table 4). However, unlike Apache plume, non-arroyo mesquite also had significantly higher mean E_{int} at A1. This suggests that gas-exchange in non-arroyo mesquite was principally water limited. The higher mean P_{int} of desert willow at A1 cannot be explained by either soil water storage or nutrient concentrations because there were no statistical differences in these resources between the two sites (Tables 2 and 3). Desert willow can maintain near normal water potentials and gas-exchange rates during periods of low water availability (Odening *et al.*, 1974; de Sozya *et al.*, in review). This obligate riparian species appears to be highly adapted to minimizing its physiological responses to the often extreme environmental changes common to arroyo habitats.

A major consideration when comparing soil moisture differences between arroyo and non-arroyo shrubs is the role of the arroyo channel. Of the shrubs studied at the landscape position of A1 and A2, only mesquite grows along arroyo channels and in the surrounding non-arroyo areas. Mesquite is known to be capable of fixing large quantities of nitrogen (Lajtha & Schlesinger, 1986; Jenkins *et al.*, 1988). Thus, water may be more limiting for mesquite growth in desert habitats. The relationship between soil water storage and gas-exchange rates was evident from our results. In winter-spring and summer at A2, higher soil water storage under arroyo mesquite (Table 3) enabled higher gas-exchange rates (particularly transpiration) than in non-arroyo mesquite (Fig. 2). At A1, soil water storage at the depths we studied was the same beneath arroyo mesquite and non-arroyo mesquite, but gas-exchange rates were sometimes higher in arroyo mesquite (e.g., June 15). Arroyo mesquite are able to extend their lateral roots into nearby arroyo channels (Ludwig, 1977), but non-arroyo mesquite is probably too distant to efficiently access arroyo water resources. In our study, the minimum distance of non-arroyo mesquite to channels was 32 m. The longest lateral roots of mesquite in the literature we could find was 22 m (Gile *et al.*, 1997). Therefore, at A1, the higher gas-exchange rates without higher soil water storage found beneath arroyo mesquite may be due to the ability of these shrubs to access the relatively moist soil of the arroyo channel. Arroyo mesquite appeared able to maintain relatively high gas-exchange rates, but non-arroyo mesquite often had low gas-exchange rates (Fig. 2). Large rainfall events in July and August increased gas-exchange rates of non-arroyo mesquite.

While there are often striking differences between the vegetation along arroyos and the surrounding non-arroyo desert areas, the factors that cause these differences are not well known. In some instances the differences among arroyos may be greater than the differences between arroyo and non-arroyo areas. In desert landscapes arroyos have the greatest temporal variability in primary production (Ludwig, 1987). While the two arroyo sites we studied were spatially close (0.5 km), they had substantially different biotic and abiotic characteristics. These variations highlight the importance of considering multiple arroyos and sites within arroyos when attempting to understand arroyo function. Even though variation between and within arroyos is high, our data suggest that some of the water from arroyo channel flow events is stored in the arroyo and is used by riparian shrubs. When water is not limiting, nutrient availability may limit photosynthesis.

Of the three species studied, mesquite is an example of a historically riparian species that has rapidly spread into a dominant position throughout large areas of desert grasslands in response to changes in its environment (Buffington & Herbel, 1965; Gibbens & Beck, 1988). Given changed environmental conditions, other arroyo species

may have this potential to expand from arroyo habitats into non-arroyo areas (see Stidham *et al.*, 1982). Therefore, understanding the physical and biological characteristics of arroyos and the plants associated with them is essential to understanding the structure and functioning of desert ecosystems as they continue to evolve with changes in the environment.

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