

Response of dominant grass and shrub species to water manipulation: an ecophysiological basis for shrub invasion in a Chihuahuan Desert Grassland

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Abstract Increases in woody vegetation and declines in grasses in arid and semi-arid ecosystems have occurred globally since the 1800s, but the mechanisms driving this major land-cover change remain uncertain and controversial. Working in a shrub-encroached grassland in the northern Chihuahuan Desert where grasses and shrubs typically differ in leaf-level nitrogen allocation, photosynthetic pathway, and root distribution, we asked if differences in leaf-level ecophysiology could help explain shrub proliferation. We predicted that the relative performance of grasses and shrubs would vary with soil moisture due to the different morphological and physiological characteristics of the two life-forms. In a 2-year experiment with ambient, reduced, and enhanced precipitation during the monsoon season, respectively, the encroaching C₃ shrub (honey mesquite *Prosopis glandulosa*) consistently and substantially outperformed the historically dominant C₄ grass (black grama *Bouteloua eriopoda*) in terms of photosynthetic rates while also maintaining a more favorable leaf water status. These differences persisted across a wide range of soil moisture conditions, across which mesquite photosynthesis was

decoupled from leaf water status and moisture in the upper 50 cm of the soil profile. Mesquite's ability to maintain physiologically active leaves for a greater fraction of the growing season than black grama potentially amplifies and extends the importance of physiological differences. These physiological and phenological differences may help account for grass displacement by shrubs in drylands. Furthermore, the greater sensitivity of the grass to low soil moisture suggests that grasslands may be increasingly susceptible to shrub encroachment in the face of the predicted increases in drought intensity and frequency in the desert of the southwestern USA.

Keywords Drought · Photosynthesis · Precipitation manipulation · Water potential · Woody encroachment

Introduction

Grasslands, shrublands, and savannas cover approximately 50% of the Earth's land surface. Although characterized by low and highly variable rainfall, drylands represent 30–35% of the terrestrial net primary production (NPP; Field et al. 1998) and are home to >30% of the global human population and the majority of the global livestock (Safriel and Adeel 2005). As such, these ecosystems play an important role in global change via their influence on the carbon (C), water, and nitrogen (N) cycles and human health (Campbell and Stafford Smith 2000). A directional shift from herbaceous to woody plant dominance is one of the most striking land-cover changes over the past 150 years (Archer 2010). In drylands, increases in shrubs at the expense of grasses are often accompanied by accelerated wind and water erosion (Breshears et al. 2009; Wainwright et al. 2000). Furthermore, this vegetation change may affect

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primary production, nutrient cycling and soil organic matter accumulation, hydrology, livestock production, and biodiversity (Archer 2010; Barger et al. 2011; Eldridge et al. 2011). Despite the diverse implications of this global phenomenon, little is known about the ecophysiological basis of woody encroachment and how this might influence vegetation dynamics in the face of predicted climate changes.

The causes of this global land-cover change are a topic of active debate. Traditional explanations center around the intensification of livestock grazing, changes in fire regimes, non-native woody species introductions, and declines in browser abundance (Archer 1994; Naito and Cairns 2011). Changes in climate, N deposition, and atmospheric CO₂ have also been suggested as potential drivers (Archer et al. 1995), and the occurrence of woody plant proliferation in drylands worldwide over the past 150 years hints that large-scale forcings may be at work. It is probable that many of these drivers interact to varying degrees in various locales, making it unlikely that any individual driver holds primacy.

To what extent are the outcomes of interactions between shrubs and grasses dictated by differences in life-form ecophysiology? Shrubs typically have higher leaf N than grasses (Yuan and Chen 2009), which could result in a physiological advantage for shrubs over grasses. Leaf N is generally positively correlated with photosynthesis (Reich et al. 1995) and is also associated with compounds such as proline that enhance the avoidance of water stress (Delauney and Verma 1993). In addition, many dryland shrubs are from families in which symbiotic N₂-fixation occurs (e.g., Fabaceae, Rhamnaceae), thus giving them a further potential advantage over grasses in drylands where N is often co-limiting with water (Yahdjian et al. 2011). In addition to affecting the N economy, contrasting root architectures of grasses and shrubs may affect water uptake (Jackson et al. 1996). Walter (1971) suggested that while grasses and shrubs compete for water and nutrients in the upper soil layers, shrubs have greater access to deep resources. This hypothesis has been generally supported in geographically disparate drylands (e.g., Brown and Archer 1990; Knoop and Walker 1985; Sala et al. 1989). Thus, shrubs may be favored on sites where deep moisture is typically available, whereas grasses would be favored where shallower soil moisture occurs (Sala et al. 1997). Changes in the depth of water distribution that accompany changes in climate may therefore affect the competitive balance between grasses and shrubs with their contrasting rooting patterns.

In low- to mid-latitude regions, grasses typically possess the C₄ photosynthetic pathway, whereas shrubs typically possess the C₃ pathway. Thus, C₄ grasses should have a physiological advantage by virtue of their higher maximum potential photosynthetic rates and greater water-use and N-use efficiencies (Sage and Monson 1999). However, while much is known about the physiological costs and

benefits of different photosynthetic pathways, there have been few direct ecophysiological comparisons in drylands between C₄ grasses and encroaching C₃ shrubs, particularly in the context of variation in soil moisture availability. McCarron and Knapp (2001) found that the dominant C₄ grass in a mesic grassland typically had higher photosynthetic rates and instantaneous water-use efficiency (WUE) than did three encroaching C₃ shrubs. Similarly, in a high-elevation Chihuahuan Desert grassland, Patrick et al. (2009) found that photosynthetic rates for a C₄ grass were typically greater per unit leaf area than those for a deep-rooted, woody C₃ monocot. In contrast, the photosynthesis of C₃ mesquite (*Prosopis glandulosa*) shrubs was found to be generally comparable to or higher than that of C₄ grasses in the south-central Great Plains (Ansley et al. 2002) and higher than that for the dominant perennial C₄ grass in the southern Great Plains (Brown and Archer 1990). Some of these inconsistencies may reflect other characteristics of C₃ shrubs (e.g., leaf N content and rooting depth) that could compensate for the disadvantages typically associated with the C₃ photosynthetic pathway. However, future global environmental conditions [e.g., predicted decreases in precipitation–evaporation ratios in southwestern drylands (Seager et al. 2007), coupled with elevated atmospheric CO₂] may alter the relative advantages of these morphological and physiological characteristics (Morgan et al. 2011).

The Chihuahuan Desert in the southwestern USA is a model ecosystem of woody plant proliferation as it has undergone a dramatic, well-documented transformation (Gibbens et al. 2005). This region is characterized by a C₄ grass flora and a climate where the majority (62%) of the total annual precipitation (PPT) falls during June–September when temperatures are conducive to rapid plant growth (Wainwright 2006). Hypotheses related to grazing and climate change have been proposed to explain this transformation, but none of these account for all existing evidence. For example, reductions in livestock grazing in the mid-20th century did not curtail shrub invasion (Fredrickson et al. 1998), and there is little evidence to suggest the change was climate-driven (Conley et al. 1992). Although there have been studies on the ecophysiology of C₃ and C₄ plants in the Chihuahuan Desert, there have been very few direct comparisons between C₄ grasses and C₃ shrubs, and none within the context of their relative response to broad changes in water availability. Projections for future increases in drought and PPT variability in this region (Seager et al. 2007; Solomon et al. 2007) make understanding comparative ecophysiological responses to PPT extremes a potentially critical component of predicting future encroachment dynamics.

In the study reported here, we sought to address one of the determinants for shifts from grass to shrub dominance from a first-principle basis by quantifying the ecophysio-

logical performance of grass and shrub life-forms in the context of a PPT manipulation. We used as model plants black grama grass (*Bouteloua eriopoda*), the historic dominant grass of Chihuahuan Desert grasslands, and honey mesquite (*P. glandulosa*), a prominent woody invader. Our first objective was to characterize the leaf-level photosynthetic response of black grama and mesquite across a broad range of soil moisture conditions during the monsoon season, when both life-forms have photosynthetically active tissue. We hypothesized that the C_4 grass would maintain higher photosynthetic rates than the C_3 shrub under drier conditions. In contrast, we hypothesized that the shrub, with its N_2 -fixing capacity, would outperform the grass under wetter conditions. A second objective was to determine if leaf water potential, leaf N concentration, stomatal conductance, transpiration, and/or WUE differentially influence grass and shrub photosynthetic performance across a broad range of soil moisture conditions. A combination of rainout shelters and irrigation treatments was used to test these hypotheses. Precipitation manipulations, which ranged from an 80% reduction to an 80% supplementation of ambient, were designed to encompass the full range of variation recorded at the site during the last 90 years (Fig. 1). Through this direct comparison of C_3 shrub and C_4 grass performance under a PPT manipulation, we aimed to determine if leaf-level physiological differences may help explain the recent displacement of grasses by shrubs in this ecosystem.

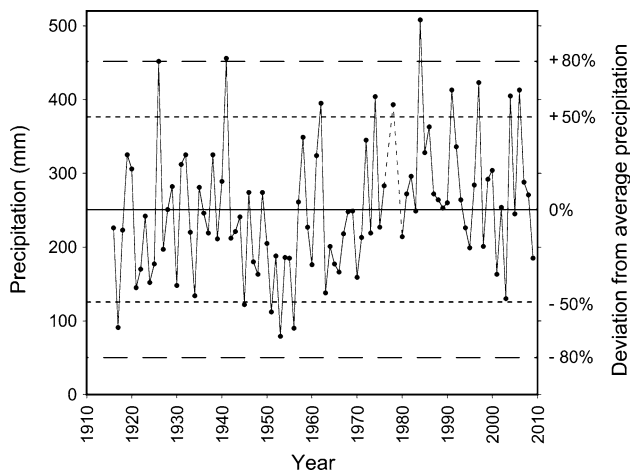


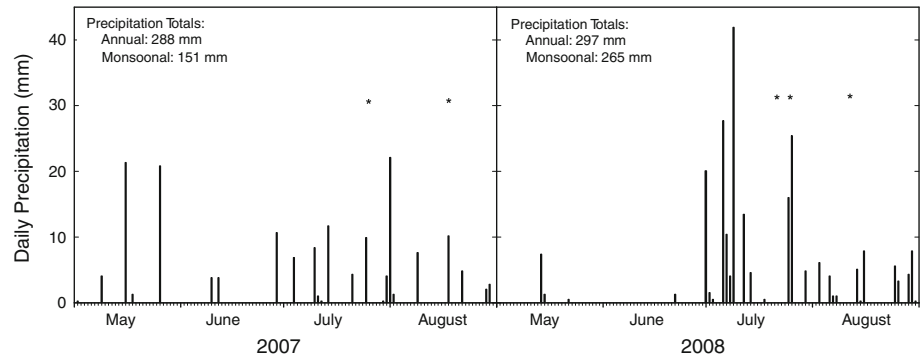
Fig. 1 Time-series of yearly precipitation at the Jornada Basin LTER (Long Term Ecological Research) study site from 1916 to 2009 (points connected by solid lines), showing the site average over this period (horizontal solid line) and 50 and 80% departures from the site average (horizontal dashed and dotted lines, respectively). Dashed lines denote missing data for 1977 and 1979. Data were obtained from EcoTrends (Ecotrends resource: 1311.1; <http://www.ecotrends.info>), and these data are from the Jornada Basin (<http://jornada-www.nmsu.edu>), Climate and Hydrology Database Projects (CLIMDB/HYD-RODB; <http://www.fsl.orst.edu/climdb/>)

Materials and methods

The study took place at the Jornada Basin LTER (Long Term Ecological Research) study site (32.5°N, 106.8°W; 1,188 m a.s.l.) in the northern Chihuahuan Desert, approximately 40 km north–northeast of Las Cruces, New Mexico. Mean annual precipitation (1928–2008) is 240 mm, with most (>60%) occurring as monsoonal thunderstorms between 1 June and 1 October. Average temperature is 15°C, with a mean monthly minimum of 4°C (January) and a mean monthly maximum of 36°C (June). Experiments were conducted in a livestock enclosure that had been subjected to light to moderate grazing before enclosure construction in 1998 (Drewa 2003). The site is situated on a level upland with deep fine-loamy, thermic Typic Haplargid soils. The dominant species are *Bouteloua eriopoda*, a C_4 grass with dense, fine roots concentrated within 30 cm of the soil surface, and *Prosopis glandulosa*, a C_3 shrub with shallow, lateral roots and a tap root system that may extend many meters into the soil (Gibbens and Lenz 2001). Cover at the beginning of the study was roughly 50% bare soil, 20% black grama, 10% mesquite, and 20% other species (L.G. Reichmann, unpublished data). See Drewa et al. (2006) for additional details on vegetation and soils at the site.

Manipulations during the 2007–2008 growing seasons consisted of five levels of PPT relative to ambient: –80, –50%, control, +50, +80%, with 12 replicates per treatment. Time constraints to perform ecophysiological measurements on both species simultaneously led us to measure these variables in four replicate plots for each of the five PPT treatments. Plots were 2.5 × 2.5 m, and each was centered around a single mature mesquite shrub that was similar in size to other mesquite on this ecological site (mean height 0.5 m, canopy diameter 1.1 m; Drewa 2003). Shrubs were surrounded by black grama (mean basal area 11.48 cm²; Drewa et al. 2006); black grama individuals selected for measurements were >0.75 m from plot edges. Reductions in PPT were achieved via passive rainout shelters; supplementation was achieved via a sprinkler irrigation system. Desired levels of rainfall reduction (–80 and –50%) relative to ambient were achieved by modifying the number of transparent V-shaped acrylic strips per shelter [Acrylite FF; CYRO Industries, Parsippany, NJ; see Yahdjian and Sala (2002) for a detailed description of shelter design and their minimal effect on the microenvironment]. A PVC-pipe irrigation system was used at the enhanced PPT plots, which were irrigated the day after PPT events >2 mm, with an amount of water equal to 50 or 80% of the event. Supplementation occurred during the spring and fall of 2007 and 2008 using PPT that was captured nearby and stored. Control plots received ambient PPT and had neither shelters nor irrigation systems.

Fig. 2 Distribution of daily precipitation during the summer growing seasons of 2007 and 2008. Monsoonal rain is defined as precipitation between 1 June and 1 October. *Asterisks* Dates of ecophysiological measurement campaigns (see Table 1)



Soil volumetric water content (VWC) was quantified simultaneously with ecophysiological measurements. VWC was measured in six plots per treatment at depths of 0–5 and 30–50 cm using EC-5 and EC-20 soil moisture sensors (Decagon Devices, Pullman, WA), respectively. Probes were calibrated for soils at the site following the protocol developed by the manufacturer (r^2 of 0.98 and 0.96 for EC-5 and EC-20 probes, respectively).

Leaf ecophysiology was quantified during the 2007 and 2008 growing seasons on dates with contrasting PPT patterns in the days preceding the sampling date (Fig. 2). Pre-dawn xylem water potential (ψ_{pd}), photosynthetic rate under saturating light conditions (A_{max}), and leaf N content were measured. One mesquite and one black grama leaf from each plot ($n = 20$ plots; 5 PPT treatments \times 4 replicate plots/treatment) were measured on two dates in 2007 (25 July and 18 August) and three dates in 2008 (21 July, 25 July, 13 August). Predawn xylem water potential was quantified with pressure chambers (black grama: model 1000, with 100 bar capacity; PMS Instrument Co, Corvallis, OR; mesquite: model 2005, Soil Moisture Equipment Corp, Santa Barbara, CA). Leaves were excised from plants and immediately measured for ψ_{pd} . Measurements were completed at least 0.5 h before dawn. A_{max} was quantified with a portable gas exchange system (model 6400; LiCor, Lincoln, NE) under standardized conditions [photosynthetically active radiation (PAR) 2,000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$; relative humidity 50–80%; CO_2 sample 370 ppm; leaf temperature 28–32°C]. Stomatal conductance of water vapor (g_s) and transpiration (E) were recorded concurrently with A_{max} . Instantaneous WUE was calculated as A_{max}/E . Ecophysiological data were recorded when photosynthetic rates became visually stable, usually within 5 min of inserting a leaf in the cuvette. Measurements began approximately 2 h after dawn and were completed by noon. Treatments were blocked by time to reduce the influence of diurnal patterns. The portions of leaves within the 6-cm² cuvette were excised and kept on ice for transport to the lab where they were immediately scanned (model 8800F flatbed scanner; Canon, Tokyo, Japan). Leaf area was determined

with ImageJ 1.38 \times software (National Institutes of Health, Bethesda, MD) and was used to express gas exchange on a one-sided leaf area basis. Leaves used for ψ_{pd} and A_{max} area determination within a plot on a given date were pooled, dried at 60°C, ground in a ball mill, and analyzed on an elemental analyzer (model ECS 4010; Costech Analytical, Valencia, CA) for N content (percentage N by mass; N_{leaf}).

Ecophysiological responses were analyzed in two different ways. First, responses (ψ_{pd} , g_s , A_{max} , E) to the PPT manipulation were quantified separately for each species for the wettest and driest sampling dates (Table 1) using one-way analysis of variance (ANOVA). Second, to explore overall patterns of plant response to soil moisture conditions, which were a function of both PPT treatment and natural PPT patterns, data for each species were pooled for all PPT treatments and sampling dates. Relationships between environmental and response variables (VWC, ψ_{pd} , A_{max} , N_{leaf} , g_s , E , and WUE; non-transformed and transformed variables) were then analyzed using simple and stepwise linear regression. Analyses were carried out with JMP ver. 7 software (SAS Institute, Cary, NC). Given the co-occurrence of the two species in plots, physiological responses to PPT treatments include responses to interspecific interactions.

Results

Precipitation manipulations dramatically enhanced natural variability and generated a range of rainfall scenarios that could have been studied only after a multi-decade effort using natural conditions (Fig. 1). Annual PPT in control plots was comparable each year of the study, but monsoonal PPT (01 June to 1 October) was greater and more temporally concentrated in 2008 than in 2007 (Fig. 2). Soil moisture varied broadly among treatments, reflecting the PPT manipulations (Table 1). We obtained the desired objective, with soils in irrigated plots typically having higher VWCs than in those in non-irrigated plots. Responses were highly asymmetric, with PPT additions

Table 1 Mean volumetric soil water content at two depths from five sampling dates

Year	Sampling date	Depth (cm)	Precipitation treatment				
			−80%	−50%	Control	+50%	+80%
2007	25 July	0–5	7.5 ± 0.47	9.1 ± 1.12	8.9 ± 1.17	9.7 ± 1.07	10.7 ± 1.63
		30–50	13.1 ± 0.70	13.4 ± 1.32	12.1 ± 0.58	14.1 ± 2.10	15.1 ± 2.42
	18 August (D)	0–5	5.7 ± 0.56	5.9 ± 0.34	6.3 ± 0.62	7.9 ± 0.99	7.3 ± 0.72
		30–50	11.6 ± 0.72	10.8 ± 1.13	10.8 ± 0.57	12.8 ± 1.40	13.5 ± 1.27
2008	21 July	0–5	9.6 ± 0.72	8.8 ± 0.72	7.8 ± 0.40	11.6 ± 1.39	10.9 ± 0.57
		30–50	15.3 ± 0.97	15.6 ± 0.94	14.2 ± 0.42	16.8 ± 0.82	16.9 ± 0.68
	25 July (W)	0–5	11.7 ± 0.41	12.1 ± 0.64	12.9 ± 0.46	13.7 ± 1.42	14.3 ± 1.09
		30–50	14.8 ± 1.06	15.6 ± 0.81	14.6 ± 0.42	17.4 ± 0.70	18.1 ± 0.74
	13 August	0–5	7.1 ± 0.48	7.4 ± 0.65	7.8 ± 0.54	9.2 ± 1.33	9.0 ± 0.62
		30–50	13.5 ± 0.85	13.8 ± 0.67	12.8 ± 0.39	15.9 ± 0.98	16.2 ± 0.90

Data are presented as the mean ± standard error (SE)

Precipitation treatments consist of manipulations of rainfall relative to ambient. The driest and wettest sampling dates are indicated by (D) and (W), respectively. Data from these days were used for comparing ecophysiological responses to the precipitation manipulations (see Fig. 3)

generally influencing VWC to a greater extent than PPT reductions. Desert soils are usually close to their minimum water content (Sala et al. 1992) and thus when soils were dry, the effects of reducing PPT were relatively minor compared to the effects of adding PPT. Volumetric soil water content was, on average, lower and more variable at the shallower (0–5 cm) depth (mean $9.3 \pm 0.14\%$; range 5.7–14.3%) than at the deeper (30–50 cm) depth (mean $14.4 \pm 0.12\%$; range 10.8–18.1%; Table 1).

On the wettest sampling date, black grama and mesquite ψ_{pd} 's were high [mean ± standard error (SE) across all treatments: -0.4 ± 0.04 MPa black grama and -0.4 ± 0.03 MPa mesquite], comparable, and unresponsive to PPT manipulations (Fig. 3a). On the driest sampling date, mesquite ψ_{pd} was depressed slightly (-1.6 ± 0.07 MPa) and exhibited a slight, but significant response to PPT manipulations ($P < 0.05$), with a decrease in ψ_{pd} from irrigated to PPT reduction plots. In contrast, black grama ψ_{pd} was much lower than mesquite ψ_{pd} on the driest date and was highly responsive to PPT, decreasing from -2.4 MPa in the +80% treatment to -5.2 MPa in the −50 and −80% treatments ($P < 0.001$; Fig. 3a). The effects of PPT manipulation on ψ_{pd} were also reflected in patterns of morning g_s , A_{max} , and E , with black grama having lower values for these variables on both the dry and wet dates, regardless of the PPT treatments (Fig. 3b–d).

Pooled across all PPT treatments and dates, the mean ψ_{pd} of mesquite shrubs (-1.2 ± 0.07 MPa) was higher than that of black grama grass (-2.6 ± 0.26 MPa). ψ_{pd} declined exponentially with decreases in VWC at both depths and for both plant life forms ($P < 0.001$ for all; Fig. 4). The slope of the VWC– ψ_{pd} relationship was steeper for black grama than for mesquite, indicating that the grass was more

sensitive to changes in water availability than the shrub at both soil depths (Fig. 4). There was a significant positive relationship between ψ_{pd} and g_s for black grama grasses, but no relationship between ψ_{pd} and g_s for mesquite shrubs (Fig. 5).

Mean leaf N concentrations (N_{leaf}) were consistently higher in mesquite shrubs ($3.7 \pm 0.06\%$; range 2.42–4.80%) than in black grama grasses ($1.9 \pm 0.09\%$; range 0.66–3.25%). Accordingly, mean (\pm SE) morning photosynthesis across all treatments and dates under saturating light conditions (A_{max}) was more than twofold higher in mesquite ($24.8 \pm 1.02 \mu\text{mol C m}^{-2} \text{s}^{-1}$) than in black grama ($11.6 \pm 0.99 \mu\text{mol C m}^{-2} \text{s}^{-1}$). A positive relationship between ψ_{pd} and A_{max} was evident for black grama, but not mesquite (Fig. 6a). Similarly, A_{max} was positively related to N_{leaf} for black grama but not mesquite (Fig. 6b). Stepwise linear regression indicated that the prediction of A_{max} was slightly enhanced for black grama by including both ψ_{pd} and N_{leaf} in the model ($A_{max} = 10.13 + 1.64*\psi_{pd} + 3.19*N_{leaf}$; $r^2 = 0.35$, $P < 0.001$). Including both terms for mesquite did not improve predictive capability over N_{leaf} alone. There was a positive relationship between g_s and A_{max} for both species (Fig. 6c). WUE was generally higher for black grama (mean $7.6 \pm 1.00 \mu\text{mol CO}_2$ per mmol H_2O , range 0.5–26.7) than for mesquite (mean $4.4 \pm 0.19 \mu\text{mol CO}_2$ per mmol H_2O , range 1.6–10.1). WUE in black grama increased under decreasing soil moisture conditions at both depths (0–5 cm depth: $\text{WUE} = 19.96 - 1.28*\text{VWC}$, $r^2 = 0.19$, $P < 0.01$; 30–50 cm depth: $\text{WUE} = 23.47 - 1.10*\text{VWC}$, $r^2 = 0.10$, $P < 0.05$), but WUE in mesquite did not respond to changes in VWC (0–5 cm depth: $\text{WUE} = 5.75 - 0.15*\text{VWC}$, $r^2 = 0.04$, $P > 0.05$; 30–50 cm depth: $\text{WUE} = 6.35 - 0.14*\text{VWC}$, $r^2 = 0.03$, $P > 0.05$).

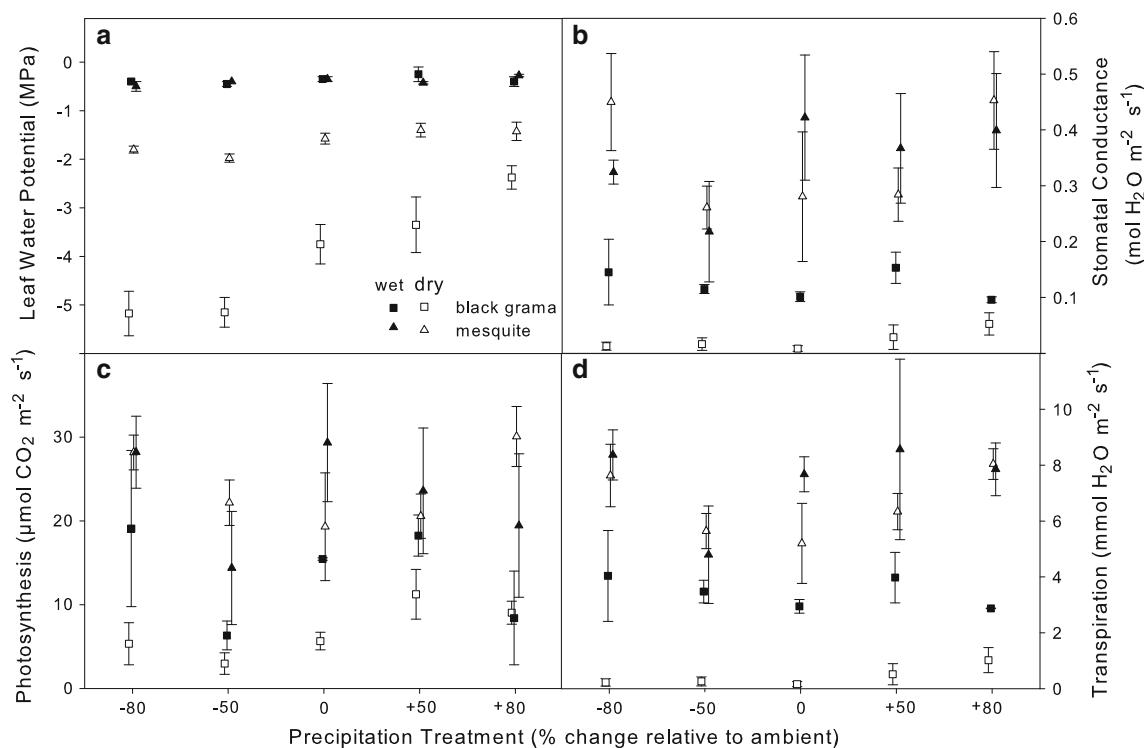


Fig. 3 Response of black grama grasses and mesquite shrubs to precipitation manipulation treatments on the driest and wettest sampling dates (see Table 1). Mean [\pm standard error (SE)] ecophysiological responses of pre-dawn leaf water potential (a), mid-morning stomatal

conductance (b), photosynthesis (c), and transpiration (d) are illustrated. The x-coordinate values are slightly offset to facilitate visual interpretation of the data

Discussion

Explanations for shrub proliferation in grasslands typically revolve around changes in climate, atmospheric CO_2 , and disturbance regimes. With the exception of broad generalizations regarding photosynthetic pathways, there has been little consideration of the suite of physiological characteristics that affects the performance and growth of these contrasting life-forms. Furthermore, there have been few direct comparisons of the physiological performance of C_3 shrubs and C_4 grasses under field conditions, particularly in the context of woody encroachment. Our results reveal that with respect to photosynthesis and water relations, the C_3 shrub encroaching into the Chihuahuan Desert consistently and substantially outperforms the historically dominant C_4 grass. Our a priori hypothesis that the C_4 grass would maintain higher photosynthetic rates than the C_3 shrub under drier soil moisture conditions was not supported, as C_3 mesquite shrubs consistently exhibited higher ψ_{leaf} , N_{leaf} , and A_{max} than the C_4 grass across the full gamut of experimental PPT regimes ranging from extreme drought (−80% PPT) to extremely wet conditions (+80% PPT). Thus, while C_4 plants theoretically have the leaf-level biochemical potential for greater C assimilation than C_3 plants in warm, dry, sunny environments, this advantage is not being realized in this bioclimatic region during the hot monsoon season.

Differences in N metabolism and allocation may be an important driver of ecophysiological differences between the two life-forms studied. Black grama exhibited a significant positive relationship between N_{leaf} and A_{max} , whereas mesquite did not. Goedhart et al. (2010) obtained similar results, suggesting fundamental differences in grass versus shrub N relations. Moreover, the range of variation in mesquite N_{leaf} was narrower than that in black grama, and the highest levels of grass N_{leaf} approximated the lowest levels of mesquite N_{leaf} . The positive relationship between N_{leaf} and A_{max} for the grass suggests that photosynthetic rates are limited, at least in part, by carboxylating enzymes. The lack of an $N_{\text{leaf}}-A_{\text{max}}$ relationship in mesquite suggests that photosynthetic rates were not limited by N-rich carboxylating enzymes within the N_{leaf} range encountered. These combined observations suggest that a significant fraction of mesquite N_{leaf} may be allocated to osmotically active compounds that help avert water stress (e.g., proline) and/or reduce the probability of herbivory, rather than to the carboxylating enzyme. Mesquite in this study was at the high end of N_{leaf} reported globally (Reich and Oleksyn 2004), presumably reflecting its ability to obtain a considerable portion of its leaf N via fixation (Lajtha and Schlesinger 1986; Zitzer et al. 1996). This high N_{leaf} may be a factor in mesquite's greater photosynthetic capacity not only in comparison to black grama, but also in comparison to other

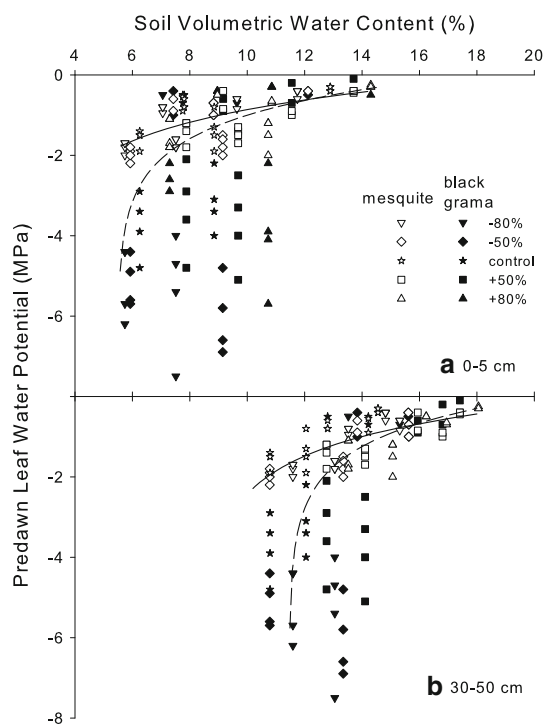


Fig. 4 Relationship between soil volumetric water content and predawn xylem water potential (ψ_{pd}) for black grama grasses and mesquite shrubs in: **a** shallow soils [depth 0–5 cm; mesquite: $\psi_{pd} = \ln(-0.149 + 0.057 \cdot \text{VWC})$, $r^2 = 0.44$; black grama: $\psi_{pd} = \ln(-0.444 + 0.081 \cdot \text{VWC})$, $r^2 = 0.38$]; **b** deeper soils [depth 30–50 cm; mesquite: $\psi_{pd} = \ln(-0.613 + 0.070 \cdot \text{VWC})$, $r^2 = 0.51$; black grama: $\psi_{pd} = \ln(-1.295 + 0.113)$, $r^2 = 0.55$ for black grama]. Points Individual plants in precipitation (PPT) manipulation treatments and include all five sampling dates in 2007 and 2008, symbols PPT treatment and species, lines fitted responses of mesquite (solid line through open symbols) and black grama (dashed line through closed symbols). ψ_{pd} Predawn xylem water potential, VWC volumetric water content

native Chihuahuan Desert shrubs (de Soyza et al. 2004). In contrast, black grama appears to have lower photosynthetic rates, stomatal conductances, and leaf water potentials than other co-occurring C_4 grasses in the Chihuahuan Desert (Senock et al. 1994), despite its historical dominance. While N_{leaf} alone cannot ensure high photosynthetic rates in the presence of co-limitation by water or other resources, the costs associated with high N_{leaf} in mesquite may be offset if constraints to water acquisition are mitigated by deep or extensive root systems.

Increased efficiency of the C_4 pathway has long been posited as an important driver of vegetation patterns. In particular, greater WUE afforded by the C_4 pathway should allow greater relative photosynthetic rates in water-limited conditions. Accordingly, the dominant C_4 grass in a mesic tallgrass prairie maintained greater WUE and photosynthetic rates than did three encroaching C_3 shrubs (McCarroll and Knapp 2001). However, despite the fact that WUE in our study was typically higher for the C_4 grass than the C_3 shrub, the shrub photosynthetically out-performed the

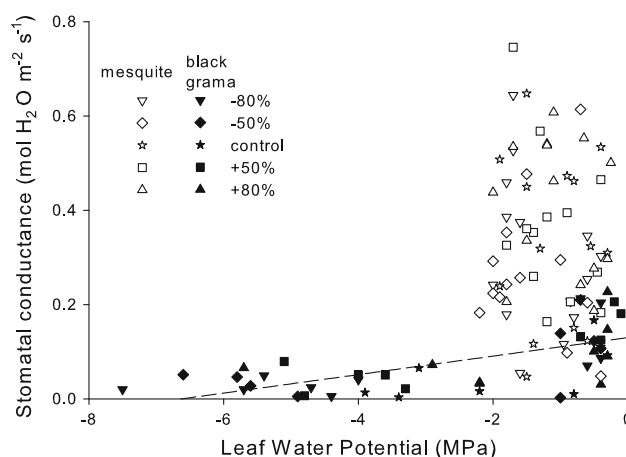


Fig. 5 Relationship between predawn xylem water potential (ψ_{pd}) in leaves and mid-morning stomatal conductance (g_s) for black grama and mesquite. Points Individual plants in PPT manipulation treatments, including all five sampling dates in 2007 and 2008, symbols PPT treatment and species. There was a significant linear relationship for black grama (dashed line through filled symbols; $g_s = 0.130 + 0.020 \cdot \psi_{pd}$, $r^2 = 0.40$, $P < 0.001$); there was no relationship for mesquite ($g_s = 0.306 + 0.026 \cdot \psi_{pd}$, $r^2 < 0.01$, $P > 0.05$)

grass throughout the growing season, regardless of PPT manipulations. This suggests WUE is not the basis for observed photosynthetic rate differences. However, longer term integrative assessments of WUE (e.g., $\delta^{13}C$) may provide better perspectives on WUE than our instantaneous cuvette measurements, as leaf morphology and canopy architecture can influence leaf-to-air vapor pressure deficits and subsequent calculated WUE (Marshall et al. 2007).

Relative to black grama, the minimal response of mesquite to variation in soil moisture in the upper 50 cm of the profile suggests that water acquisition trumps WUE as a basis for ecophysiological differences. Mesquite’s dimorphic root system (extensive lateral roots combined with deep tap roots; Gibbens and Lenz 2001) may give access to ephemeral moisture in upper soil horizons and to more stable moisture resources lower in the soil profile (Ansley et al. 1990). This would explain why mesquite water status in this study (e.g., ψ_{pd} ; Figs. 3a, 4) was largely decoupled from soil moisture conditions at the measured depths. The greater rooting extent of the shrub also likely limited the influence of PPT manipulations on the shrub relative to the grass, as shrub roots almost certainly penetrated to depths below those monitored for VWC and laterally beyond the plots and into areas not impacted by our PPT manipulations. In contrast, black grama, with nearly all of its roots concentrated in the upper 40 cm of the soil profile (Gibbens and Lenz 2001), was more tightly coupled to soil moisture availability in the upper 50 cm of the soil profile (Fig. 4). Similar patterns were demonstrated in the southern Great Plains, where photosynthetic rates of grasses varied with soil moisture in the 0–30 cm portions of the soil, whereas

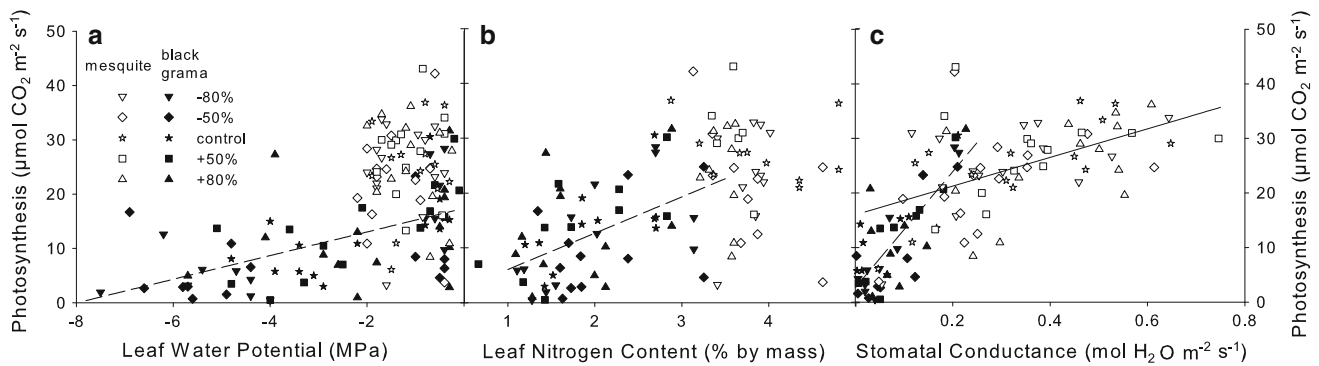


Fig. 6 Response of photosynthesis under saturating light conditions (A_{\max}) in black grama grasses and mesquite shrubs to: **a** xylem water potential (ψ_{pd} ; black grama: $A_{\max} = 17.41 + 2.18 \cdot \psi_{pd}$, $r^2 = 0.32$, $P < 0.001$; mesquite: $A_{\max} = 25.87 + 0.73 \cdot \psi_{pd}$, $r^2 = 0.002$, $P > 0.05$); **b** leaf nitrogen content (N_{leaf} ; black grama: $A_{\max} = -0.57 + 6.62 \cdot N_{\text{leaf}}$, $r^2 = 0.24$, $P < 0.001$; mesquite: $A_{\max} = 36.94 - 3.47 \cdot N_{\text{leaf}}$, $r^2 = 0.03$, $P > 0.05$); **c** stomatal conductance (g_s) (black grama: $A_{\max} = 2.59 +$

$106.38 \cdot g_s$, $r^2 = 0.64$, $P < 0.001$; mesquite: $A_{\max} = 16.01 + 26.26 \cdot g_s$, $r^2 = 0.26$, $P < 0.001$). *Points* Individual plants in PPT manipulation treatments and include all five sampling dates in 2007 and 2008. *Symbols* PPT treatment and species. Linear responses are indicated for significant ($P < 0.05$) relationships for mesquite (solid line through open points) and black grama (dashed line through solid points)

photosynthesis in adult mesquite tracked soil moisture at depths >90 cm (Brown and Archer 1990). The ability of shrubs to acquire deep water, while potentially still maintaining uptake in shallower layers as well, may result in stability of the available soil moisture for shrubs relative to grasses in this ecosystem (Eggemeyer et al. 2009). Thus, the relatively lower WUE of mesquite compared to black grama may be of relatively little consequence if it is able to access more dependable sources of water than black grama. Furthermore, greater access to soil moisture would allow mesquite to realize the higher photosynthetic rates afforded by high N_{leaf} .

The inherent advantages of mesquite leaf-level physiology, when coupled with phenological differences in leaf initiation and longevity, magnify mesquite's C accumulation advantage over black grama within an annual cycle. Mesquite leaves are typically initiated earlier and persist longer than those of black grama (Kemp 1983), thus enabling the shrub to fix C during a larger fraction of the year. Some of this difference in phenology is ostensibly related to differences in photosynthetic pathway temperature optima. However, it may also be related to percolation of winter rains into deep soil layers combined with hydraulic redistribution that transfers dormant season PPT downward by mesquite roots (Scott et al. 2008). Perennial grasses in the Chihuahuan Desert, in contrast, are almost exclusively dependent on the summer monsoons for green-up and photosynthesis (Huenneke et al. 2002). This was evident in our study, to the point that we were unable to conduct physiological measurements in 2009 because black grama produced little green biomass until late August (approx. 2 months later than an 'average' monsoon year), and then entered dormancy in September. In contrast, mesquite plants initiated leaves in March 2009 and maintained green leaves through

to the end of October. Although hydraulic redistribution can occur in mesquite (Hultine et al. 2004; Zou et al. 2005), we saw no evidence that this might have been benefiting grasses during the dry portion of the 2009 monsoon season.

Based on available phenological data, mesquite would have photosynthetically active tissue for approximately 210 days in an average PPT year, compared to approximately 90 days for black grama (Table 2). A coupling of these phenological perspectives with our photosynthesis data suggests annual C gain per unit leaf area would be on the order of fivefold higher in mesquite than black grama on average and dry years, and threefold higher in wet years (Table 2). We predict that differences in C uptake would be even greater on a per plant basis, given that shrubs typically project greater leaf areas with less self-shading than grasses (Knapp et al. 2008).

Projected climate changes would be expected to broaden the performance gap between mesquite and black grama, potentially making remaining grasslands increasingly susceptible to shrub encroachment. The Intergovernmental Panel on Climate Change (IPCC) A1B scenario suggests a 5–10% decrease in PPT for the southwestern USA and a concomitant increase in interannual variability (Solomon et al. 2007); most general circulation models agree on increasing aridity (Seager et al. 2007). Higher temperatures would further decrease water availability by increasing evapotranspiration, and the non-linear relationship between VWC and ψ_{pd} (Fig. 4) suggests reductions in soil water availability would impact black grama more adversely than mesquite. Furthermore, dynamic vegetation models predict that the performance gap between C_3 woody plants and C_4 grasses will widen in favor of shrubs under higher atmospheric CO_2 concentrations (Scheiter and Higgins 2009).

Table 2 Estimated per unit leaf area carbon gain for black grama and mesquite plants in the northern Chihuahuan desert taking phenological status in a wet, average and dry year, respectively, into account

Species	Average photosynthetic rate ($\mu\text{mol C m}^{-2} \text{s}^{-1}$)	Wet year			Average PPT year			Dry year		
		Months with green aerial tissue	Number of days	Carbon gain per unit of leaf area ($\text{g C cm}^{-2} \text{year}^{-1}$)	Months with green aerial tissue	Number of days	Carbon gain per unit of leaf area ($\text{g C cm}^{-2} \text{year}^{-1}$)	Months with green aerial tissue	Number of days	C gain per unit of leaf area ($\text{g C cm}^{-2} \text{year}^{-1}$)
Black grama	11.6	Late April through to mid-November	195	0.046	Mid-July through to mid-October	90	0.021	Mid August through to late October	75	0.018
Mesquite	24.8	Early April through to late November	240	0.120	Mid-April through to mid-November	210	0.105	Late April through to late October	180	0.090

PPT, precipitation; C, carbon

Photosynthetic rates (the mean of all measurements for each species) were multiplied by the total number of hours of photosynthetic activity based on leaf phenology in years with differing PPT. Leaf phenology was defined according to Kemp (1983). For simplicity, we assumed 4 h of photosynthetic activity per day for both species

The results from our manipulative field study suggest that the greater N_{leaf} of the shrub, coupled with its minimal reliance on ephemeral near-surface soil moisture, more than offsets the WUE advantages of the C_4 grass, thus offering a possible mechanistic basis for the propensity of shrubs to displace grasses in this hot desert ecosystem. In the absence of disturbances, such as fire, which would prevent shrubs from realizing their superior performance potential, their continued proliferation in desert grasslands should be expected. The continued encroachment of shrubs will affect a variety of regional ecosystem services, resulting in reduced cattle production, altered wildlife habitat, increased wind and water erosion, and changes in C dynamics and non-methane hydrocarbon emissions (Archer 2010).

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