

Variation in monsoon precipitation drives spatial and temporal patterns of *Larrea tridentata* growth in the Sonoran Desert

Ryan A. Sponseller^{*1}, Sharon J. Hall², David P. Huber³, Nancy B. Grimm², Jason P. Kaye⁴, Christopher M. Clark⁵ and Scott L. Collins⁶

¹Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden; ²School of Life Sciences, Arizona State University, Tempe, AZ, USA; ³Department of Biological Sciences, Idaho State University, Pocatello, ID, USA; ⁴Department of Crop and Soil Sciences, College of Agricultural Sciences, The Pennsylvania State University, University Park, PA, USA; ⁵U.S. Environmental Protection Agency, Global Change Research Program, Washington, DC, USA; and ⁶Department of Biology, University of New Mexico, Albuquerque, NM, USA

Summary

1. Broad-scale patterns of above-ground net primary production (ANPP) are closely coupled to climate features, particularly the distribution and magnitude of rainfall. In arid and semi-arid regions, however, the precipitation regime, together with local geomorphology and plant life history traits, combine to regulate soil water availability and patterns of growth, complicating simple correlations with climatic variables.

2. To better understand the drivers of plant growth in desert ecosystems, we characterized the rates and spatial heterogeneity of stem elongation by the dominant perennial shrub, creosote bush (*Larrea tridentata*) in the northern Sonoran Desert of Arizona (USA). Estimates of stem growth were made over a 5-year period (2006–2010) from 60 plots at 15 sites spanning *c.* 120 km across the Central Arizona–Phoenix (CAP) Long-term Ecological Research (LTER) area.

3. We observed both the highest and lowest rates of stem growth during summer, and these patterns were related to the amount of monsoon rainfall and local rates of water infiltration. The relationship between growth and precipitation in the summer was nonlinear, with rates increasing more than eightfold at plots receiving more than 100 mm of seasonal rainfall. Conversely, growth during the winter/spring was intermediate in magnitude, similar among years and poorly correlated with seasonal precipitation.

4. The spatial heterogeneity of stem growth also differed markedly between seasons and was greater both within and among sites during summer compared to winter/spring growing periods. At broad scales, spatial heterogeneity of shrub growth was correlated with seasonal changes in the spatial variability of rainfall across the study area. At small spatial scales, greater heterogeneity during the summer appears linked to local soil properties that influence infiltration and water availability following monsoon storms.

5. Overall, the strong, nonlinear growth response by *L. tridentata* to monsoon rainfall suggests that the recurrence interval of wet summer seasons is an important driver of ANPP for this long-lived shrub. More generally, our results illustrate how regional climate variability and local soil properties can interact to influence the rates and heterogeneity of desert plant growth at multiple scales.

Key-words: Heterogeneity, *Larrea tridentata*, monsoon, shrub growth, Sonoran Desert

*Correspondence author: ryan.sponseller@slu.se

Introduction

One of the foundational patterns in ecosystem ecology is the broad-scale correlation between annual rainfall and ANPP (Sala *et al.* 1988; Knapp & Smith 2001; Huxman *et al.* 2004; Beer *et al.* 2010). This relationship reflects the coupling of water loss and carbon gain at the leaf scale (Farquar & Sharkey 1982) and represents a major link between global water and carbon (C) cycles. The importance of water as a resource is particularly notable in arid and semi-arid ecosystems (Noy-Meir 1973), and desert plant communities are thought to be highly responsive to rainfall patterns at multiple spatial and temporal scales (Schwinning & Sala 2004). Despite this recognition, predicting temporal patterns of plant growth in arid and semi-arid settings is still a challenge (e.g. Reynolds *et al.* 2004), and understanding how dominant plant functional groups respond to variation in rainfall regimes and local soil properties continues to be a research priority for water-limited regions.

Current models of desert ecosystems are based on the assumption that the rainfall regime is a primary driver of biological activity (Noy-Meir 1973). These models consider the different thresholds in soil moisture required to induce activity by plant and microbial functional groups, the time-lags associated with biological responses to precipitation pulses and geomorphic factors that constrain water availability and redistribution across landscapes (e.g. Reynolds *et al.* 2004; Loik *et al.* 2004; Welter *et al.* 2005; Collins *et al.* 2008). Overall, this conceptual development provides a general framework for understanding how deserts respond to climate variability, especially spatial and temporal rainfall patterns within and among seasons. These perspectives integrate the biophysical drivers of soil water dynamics, life history traits of dominant plant species and seasonal phenological cues (e.g. light and temperature), which together constrain rates of productivity at any given time (e.g. Ogle & Reynolds 2004).

Despite intensive work on the relationships between climate and ANPP in arid ecosystems, a clear understanding of the relative importance of seasonal rainfall characteristics remains elusive. In deserts of the south-western United States and northern Mexico, annual precipitation is partitioned between winter/spring and summer monsoon seasons, which differ in terms of the amount, intensity and predictability of rainfall (e.g. Scott *et al.* 2000; Notaro *et al.* 2010). The prevailing hypothesis is that lower-intensity and longer-duration winter/spring precipitation more effectively recharges soils and thus represents the more important resource for C_3 shrubs and annual plants. In contrast, brief and intense summer monsoon storms promote run-off and occur when water is subject to rapid evaporation, thus restricting its availability for vegetation (e.g. Etheredge, Gutzler & Pazzaglia 2004; Reynolds *et al.* 2004; Shen *et al.* 2005). However, to the extent that temperature influences rates of biological processes (Brown *et al.* 2004; Allen *et al.* 2008), periods of water availability during hot, summer months may assume greater importance, despite being restricted in time by low soil water infiltration and rapid drying (e.g. Sharifi *et al.* 1988; Barker

et al. 2006; Jenerette, Scott & Huete 2010). In addition, inter-annual variability in winter/spring rainfall and deep soil moisture recharge may require that shrubs also use shallow, ephemeral soil water during the monsoon season (Scott *et al.* 2000; Pockman & Small 2010). Finally, seasonal temperature effects on plant phenology may constrain activity during periods of ample water availability, thereby creating time-lags in the statistical relationship between ANPP and rainfall (e.g. Muldavin *et al.* 2008).

Given the uncertainty in the strength of these diverse and potentially interactive drivers, we use a long-term, spatially extensive design to determine how rainfall patterns and local soil properties together influence seasonal growth of the dominant perennial shrub, *Larrea tridentata*, in the northern Sonoran Desert of central Arizona (USA). *L. tridentata* grows ubiquitously across the Chihuahuan, Sonoran and Mojave Deserts of the south-western United States and Mexico (Chew & Chew 1965; Barbour 1969), contributing as much 70% to ecosystem ANPP (Shen *et al.* 2005). We compare the magnitude and spatial heterogeneity of stem elongation, a proxy for ANPP, between winter/spring and summer growing seasons from 60 plots at 15 sites over a 5-year period. These measurements are used to test predictions of the prevailing hypotheses describing seasonal growth patterns of *L. tridentata*. Specifically, we expected (i) that stem elongation would increase with seasonal precipitation during both winter/spring and summer growing periods; (ii) that winter/spring rainfall would represent the more important overall determinant of annual growth; and (iii) that spatial heterogeneity in growth would be linked to the patchy distribution of rainfall. In addition, we use estimates of soil texture and infiltration to ask whether the effects of seasonal rainfall on plant growth are constrained or facilitated by local soil properties.

Materials and methods

SITE SELECTION AND DESCRIPTION

We measured plant and soil features at 15 native and remnant Sonoran Desert sites distributed across the Phoenix metropolitan area, Arizona, USA (Table 1). Sites were located primarily within the 6400-km² area defined by the boundaries of the Central Arizona–Phoenix Long-term Ecological Research (CAP LTER; Hall *et al.* 2011) project. Our design included five sites each located in outlying lands east and west of the Phoenix metropolitan area, and an additional five desert-remnant sites located within the boundaries of the urban core. Mean daily maximum and minimum temperatures in this region are 30 and 15 °C, respectively. Mean annual rainfall in Phoenix is 191 mm, distributed bimodally, with *c.* 35% as convective monsoon storms from June to September and *c.* 63% from Pacific cyclonic storms between October and April (for 1933–2010; Western Regional Climate Center, <http://www.wrcc.dri.edu>). Annual average rainfall varies considerably among our sites; however, precipitation generally increases along a west-to-east gradient from 130 mm at Sonoran Desert National Monument (SNW) to 281 mm at the McDowell Mountain Regional Park (MCN) (Table 1; FCDMC 2010).

Table 1. Characteristics of the 15 Sonoran Desert sites used in this study, organized according to increasing mean annual rainfall (MAP)

Site name	Abbreviation	LSP*	Elevation (m)	MAP (mm)†	Sand (%)‡	Silt (%)	Clay (%)	Soil classification§
Sonoran Monument West	SNW	West	375	130	70.0	23.5	6.5	Typic Camborthids
Sonoran Monument East	SNE	West	492	143	75.1	18.4	6.5	Typic Camborthids
Estrella Mountain West	EMW	West	382	164	75.3	16.3	8.4	Typic Haplargids
Salt River Recreation Area	SRR	East	434	167	69.0	19.8	11.2	Typic Calcicargid
Desert Botanical Gardens	DBG	Core	396	172	51.4	34.9	13.6	Typic Paleorthids
Piestawa Peak	PWP	Core	456	177	53.1	37.2	9.7	Typic Haplargids
South Mountain West	SMW	Core	458	180	64.1	25.9	10.1	Typic Durorthids
Estrella Mountain East	EME	West	331	186	72.7	19.0	8.3	Typic Haplargids
Mountain View Park	MVP	Core	397	190	58.2	29.8	12.0	Typic Haplargids
South Mountain East	SME	Core	372	194	68.3	21.6	10.1	Typic Haplargids
White Tank Mountain	WTM	West	454	195	58.2	31.9	10.0	Typic Haplargids
Lost Dutchman Park	LDP	East	620	203	64.1	24.9	11.0	Typic Haplargids
Usery Mountain Park	UMP	East	592	205	73.7	18.0	8.3	Typic Haplargids
McDowell Mountain South	MCS	East	539	241	59.4	26.6	14.0	Typic Haplargids
McDowell Mountain North	MCN	East	476	281	66.0	23.3	10.7	Typic Calcicargids

*landscape position (LSP) described here relative to the urban core (Core).

†Mean annual precipitation (MAP) values based on 3–18 years of data (excluded first and last year in series); FCDMC (2010).

‡Particle size analysis (0–20 cm) for inter-plant spaces only.

§Classification from NRCS (2009) except for SRR. Soil from SRR classified according to field and laboratory methods described in USDA (1993, 1998).

All study sites were located on valley bottoms or alluvial fans with gentle slopes and sandy loam soils (Table 1). At each site, we established four 20 m × 20 m plots that contained at least five individuals of *L. tridentata* in addition to several other common shrubs (e.g. bursage; *Ambrosia* spp.) and cacti, such as saguaro (*Carnegiea gigantea*) and cholla (*Cylindropuntia* spp.). In December 2005, we initiated a field experiment in which inorganic nitrogen (N) and phosphorus (P) were added to plots at each site in a factorial design. Fertilizer was broadcast as solids at 60 kg N ha⁻¹ year⁻¹ as NH₄NO₃; P as triple superphosphate at 120 kg P ha⁻¹ year⁻¹, and both N and P in combination. Results following the first 5 years of this experiment showed no significant effects of nutrient addition on *L. tridentata* stem growth or leaf density (Hall *et al.* 2011). Given this lack of treatment effect, in this paper we assess spatial and temporal patterns of *L. tridentata* growth using elongation data from all 60 plots across all nutrient treatments.

ESTIMATES OF STEM ELONGATION

Seasonal growth of *L. tridentata* was estimated by measuring elongation of stems between the months of October and April–May (winter/spring) and April–May and October (summer). Stem elongation captures one important aspect of shrub growth but is not a complete measure of ANPP. Surveys conducted at these sites in 2006, however, do indicate that *L. tridentata* stem length is closely related to total stem biomass ($r^2 = 0.86$, $P < 0.001$, $n = 149$) and leaf number ($r^2 = 0.87$, $P < 0.001$). Moreover, leaf density does not vary systematically among the sites considered here (Hall *et al.* 2011). Finally, *L. tridentata* has a root-to-shoot ratio that typically varies from 0.2 to 0.5 (Chew & Chew 1965; Allen *et al.* 2008), and estimates of the relative contribution by different plant structures to overall growth suggest that leaves and 'leaved stems' represent 60–70% of cumulative above-ground production in mature plants (Chew & Chew 1965).

We calculated stem elongation for five individual *L. tridentata* at each plot (300 plants in total), selected to encompass the range of sizes found at a given site. Average plant height across all plots was 147 cm

(± 3.0 cm SE, $n = 297$) and ranged from 32 to 315 cm. Differences in plant size did not appear to strongly influence patterns of stem elongation: from 2006 through 2007, correlations between elongation and height (for each plant) were not significant; in summer 2009, plant height was negatively correlated with elongation ($r = -0.21$, $P < 0.001$, $n = 300$), and for the remaining seasons, this relationship was positive but with low correlation coefficients (r range, 0.15–0.24; P range, < 0.001–0.01; n range, 274–300). Elongation was measured from four apical branches selected from each of four cardinal directions on each of the five individuals per plot. Branches were marked with tape several centimetres from the tip, and all distal stems (main and branching) were measured at the beginning and end of each growth period. Elongation (mm) was calculated as the change in the summed stem length during each measurement interval. With the exception of spring 2006, stems were re-taped at the beginning of each growing season. Data were not included in the analysis in cases where tape was not found or stems were otherwise lost. Average stem growth for each plot was calculated as the mean value across the entire season for the five individual plants. Because we recognize that the 'seasonal' time interval used (several months) does not necessarily capture the actual weeks or even days during which stem elongation may have occurred, we therefore simply report seasonal growth.

SOIL PROPERTIES AND INFILTRATION

To characterize soil properties that may influence the growth of deep-rooted perennial plants, we measured a suite of subsurface soil characteristics during Spring 2008 from nearby patches between tagged plants ('inter-plant space') within a subset of plots at each site. Soils were collected in 10-cm depth intervals in control (not fertilized) plots (one per site; $n = 15$) using a bucket auger to a depth of 60 cm or until the auger reached bedrock or impenetrable caliche, and samples from each 10-cm increment were analysed for the clay fraction using the hydrometer method (Elliott *et al.* 1999) following removal of carbonates (modified from Gee & Bauder 1986). The sand fraction was

determined gravimetrically by sieving to 53 μm , and the silt fraction was calculated by difference.

We estimated infiltration rate as the field-saturated hydraulic conductivity, K_{fs} (cm min^{-1}), using a modified single-ring infiltrometer method at two locations in each site (Reynolds & Elrick 1990). A brass ring $c. 7.5 \text{ cm}$ (diameter) $\times 16 \text{ cm}$ (height) was inserted into the soil to a depth of 5 cm, and a 5-cm ponding depth was maintained using a Mariotte reservoir. Infiltration was allowed to proceed until a steady rate of vertical hydrological transport was achieved. Once a steady rate of flow was reached, the time and water height in the Mariotte reservoir were recorded for 10 min to determine the infiltration rate (cm min^{-1}). The ponding depth was then set at 10 cm and the process repeated. K_{fs} was calculated using both a single- and dual-head approach (Reynolds & Elrick 1990). At two sites (MVP and EMW), there were problems reaching equilibrium, and only single-head K_{fs} values were calculated. Because single- and dual-head approaches generated estimates that were highly correlated (Spearman $r = 0.88$, $P < 0.001$), single-head K_{fs} values were used for statistical analyses because values were available for all sites.

DATA ANALYSIS

Spearman rank correlations were used to evaluate relationships between average elongation for each plot and seasonal rainfall using (i) all data from all seasons ($n = 600$), (ii) data from winter/spring and summer seasons separately ($n = 300$), and (iii) each individual season separately ($n = 60$). We use this nonparametric correlation because it provides a comparable metric describing the strength of seasonal correlations of rainfall and shrub growth across different temporal windows without making assumptions about the form of specific relationships. In addition, the relationship between summer stem elongation and rainfall was clearly nonlinear, with an apparent threshold in rainfall past which seasonal growth increased markedly. This relationship appeared best approximated by a sigmoidal function, which also is ecologically reasonable, and so we tested this model using nonlinear regression with data from all summer seasons ($n = 300$). Finally, to complement these bivariate tests, we used all-subsets multiple regression analysis with data from the smaller subset of control plots ($n = 15$) where soil features were also quantified. Here, we evaluated the predictors of plant growth from the following noncorrelated independent variables: seasonal rainfall, soil texture (% silt + clay, 0–20 cm) and infiltration rate. For multiple regression analyses, negative elongation values were set to zero, and dependent variables were ln-transformed to meet regression assumptions. We used R^2 values, Mallows' C_p and Akaike Information Criterion scores to help guide final model selection. Correlations and nonlinear regression were carried out in SIGMA PLOT 11.0 (Systat Software, Inc., Chicago, IL); all-subsets multiple regression analyses were performed in SYSTAT 13 (Systat Software, Inc., Chicago, IL).

The coefficient of variation (% CV), described at two spatial scales, was used to assess the heterogeneity of stem elongation and to evaluate how the spatial structure of plant growth differs between winter/spring and summer growing seasons. At the broadest scale, we used the % CV of elongation among sites ($n = 15$) to characterize heterogeneity at the extent of the entire study area; for this analysis, site values were determined as the average among the four plots. Next, to assess small-scale heterogeneity of stem growth, we calculated the % CV of elongation among all individual plants within each site ($n = 18\text{--}20$ plants per site). For each season, we calculated the small-scale heterogeneity in growth as the within-site CV averaged across all 15 sites; as above, negative growth was assigned a value of zero for calculating % CV. We used t -tests to compare the average % CV

between winter/spring and summer seasons at both broad and small spatial scales. Finally, to ask whether the broad-scale heterogeneity of plant growth is correlated with the 'patchiness' of precipitation, we calculated the % CV of rainfall on each date where at least one site had an event of at least 5 mm, which is a suggested threshold amount for shrub responses in arid and semi-arid ecosystems (e.g. Ogle & Reynolds 2004). For each season ($n = 10$), we estimated the heterogeneity of rainfall at each site as the average of all individual events and used linear regression to evaluate the correlation between spatial variation in precipitation and stem growth.

Results

Rainfall during this study varied among sites and seasons. Consistent with longer-term annual trends (Table 1), seasonal rainfall was typically greater to the east and north-east of Phoenix (UMP, MCS, MCN) and lowest to the west of the urban core (SNW, SNE, EMW). Considering all sites, average winter/spring rainfall ranged from 55 mm in 2005–06 (range, 42–77 mm) to 144 mm in 2007–08 (range, 78–267 mm). Average summer rainfall was lowest in 2007 at 26 mm (range, 8–41 mm) and greatest in 2008 at 119 mm (range, 66–156 mm). Average daily air temperature from three stations located within (SMW), west (EME) and north-east (UMP) of Phoenix was 17.7–18.3 °C during the winter/spring season (here: 1 Nov–Apr 29) and 31.5–33.0 °C during the summer (1 May–30 Sept). There was no evident directional change in summer temperature among years at any station; however, at both SMW and UMP, winter/spring temperatures differed by nearly 2.0 °C between 2006 and 2010 (18.6–16.8 at SMW, and 18.3–16.4 at UMP).

Larrea tridentata stem elongation varied considerably among the 10 sampling intervals (Fig. 1), was both greatest and lowest for the summer growing seasons and was intermediate during the winter/spring. For example, average stem growth during wet summers (248 mm, averaged between 2006 and 2008) was 4.3 times greater than the overall average winter/spring growth (58 mm). On the other hand, elongation during the driest summers (15 mm, averaged between 2007 and 2009) was almost four times lower than the winter/spring average. In addition, compared to the wide range of values observed among summer seasons (range, 9 mm in 2009 to 256 mm in 2008; average % CV among seasons, 96%), there was far less inter-annual variability in elongation among winter/spring growing periods (range, 40 mm in 2009 to 78 mm in 2006; average % CV among seasons, 25%).

The relationship between stem elongation and rainfall differed depending on which seasons and what time-windows were considered. For example, using all plots and years, we found a significant, positive correlation between seasonal rainfall and stem growth (Spearman $r = +0.52$, $P < 0.001$, $n = 600$); however, this relationship was much stronger when using data only from the summer seasons ($r = +0.79$, $P < 0.001$, $n = 300$). Further, the relationship between summer elongation and rainfall was fit with a sigmoidal function that suggested a rainfall amount of $c. 100 \text{ mm}$ at which rates of stem growth increased most sharply with precipitation ($r^2 = 0.49$, $P < 0.001$, $n = 300$; Fig. 2). Conversely, there

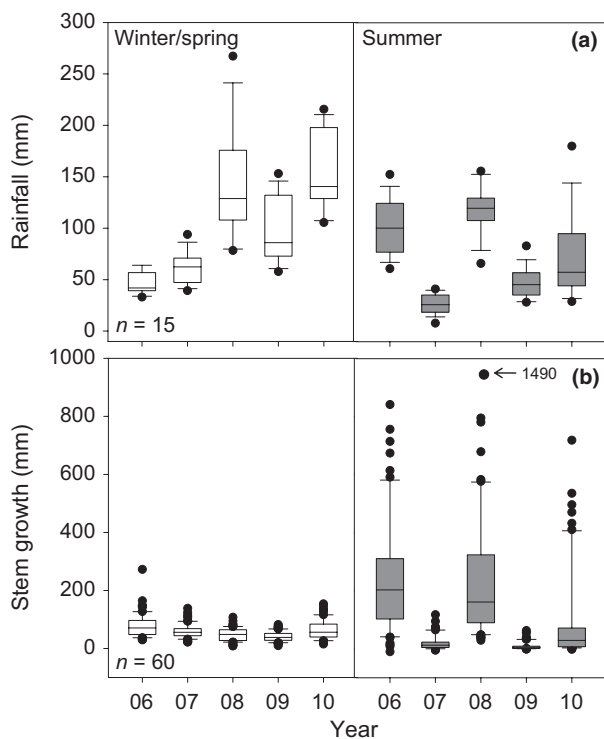


Fig. 1. (a) Seasonal rainfall (mm) and (b) stem growth (mm) of *L. tridentata* shrubs at 15 Sonoran Desert sites across the Phoenix metropolitan area from 2006 to 2010. Rainfall data include seasonal estimates for each study site based on nearby climate stations (FCDMC 2010, $n = 15$). Stem growth data include the average values for all plots and sites ($n = 60$) for each season. Whiskers represent the 90th and 10th percentiles, and all additional outlying observations are shown as points.

was no statistically significant correlation between rainfall and stem elongation when considering the five winter/spring seasons together ($r = +0.02$, $P = 0.79$, $n = 300$), despite the broad range in precipitation observed among years. However, assessing these rainfall–stem growth relationships for individual seasons resulted in significant ($P < 0.05$) positive correlations for each summer (Spearman r range, $+0.26$ to $+0.72$; $n = 60$), as well as significant, positive correlations for three of five winter/spring seasons (2008, 2009 and 2010; $r = +0.50$, $+0.73$, $+0.48$ respectively, $n = 60$).

In addition to seasonal rainfall, multiple regression analysis indicated that stem growth in the summer also increased with rates of soil water infiltration. Infiltration rate varied markedly among sites from $0.007 \text{ cm min}^{-1}$ (MVP) to 0.15 cm min^{-1} (SME) and was included in the regression model with seasonal rainfall as a predictor of summer stem growth in control plots across all years (2006–2010; $r^2 = 0.62$, $P < 0.001$, $n = 75$). In this case, however, seasonal rainfall alone produced a model that explained nearly 60% of the variation in elongation. Considering all winter/spring seasons, multiple regression analysis suggested that stem growth increased with soil % silt + clay, but this model explained only 10% of the variability in elongation ($r^2 = 0.10$, $P = 0.005$, $n = 75$). The regression model describing winter/spring growth was markedly improved,

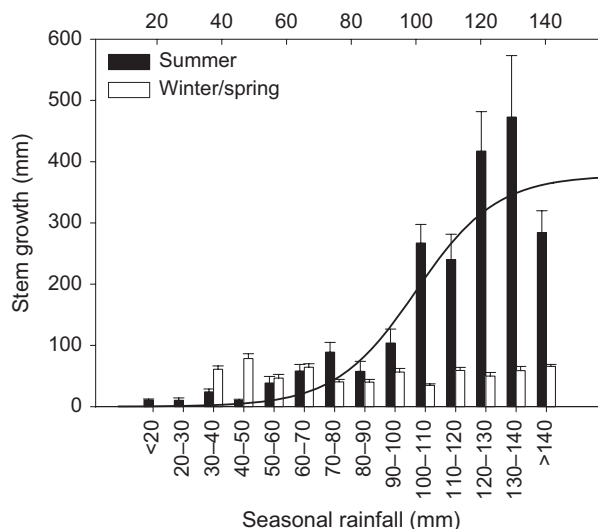


Fig. 2. Stem growth (mm) for winter/spring and summer growing seasons binned according to rainfall (mm). Bars represent the mean (\pm SE) stem growth based on a variable number (4–64) plots, with an average of 24 and 21 plots per bar in the winter/spring and summer growing seasons, respectively. The curve represents the nonlinear regression line describing the relationship between summer rainfall (top x-axis) and stem growth based on all plots and seasons. This relationship was best described by a sigmoidal function where $y = 377.6 / (1 + \exp(-(x - 100.0) / 12.4))$, $r^2 = 0.49$, $P < 0.001$, $n = 300$.

however, if data from the dry winters of 2006 and 2007 were removed from the analysis. In this case, stem elongation from 2008 to 2010 increased among sites with rainfall and % silt + clay, with a comparatively stronger fit ($r^2 = 0.47$, $P < 0.001$, $n = 45$).

In addition to variation in the magnitude of stem elongation, there were significant differences in the spatial heterogeneity of growth between winter/spring and summer seasons (Table 2). First, considering spatial heterogeneity at the broadest scale (i.e. among sites), the % CV of elongation was significantly higher during the summer (average CV = 117%), than during the winter/spring (average CV = 42%; $n = 5$; $t = 3.9$; $P = 0.02$). Seasonal differences in the spatial variability of elongation at this broad scale were correlated with the spatial heterogeneity of rainfall events $> 5 \text{ mm}$ ($r^2 = 0.69$, $P = 0.003$, $n = 10$; Fig. 3), which also was significantly greater in the summer (average CV = 173%) compared to winter/spring (CV = 72%) (Fig. 3a,b; Mann–Whitney $U = 5624$, $P < 0.001$). Finally, the within-site heterogeneity of plant growth was comparable in magnitude to that observed among sites and was also significantly greater for the summer (average CV = 101%) compared to winter/spring seasons (average CV = 48%; $n = 5$, $t = 5.7$, $P = 0.002$; Table 2).

Discussion

Patterns of *Larrea tridentata* stem elongation observed within and among sites, as well as between seasons

Table 2. Spatial variation in stem elongation quantified as the coefficient of variation (% CV) for each season. Overall seasonal differences are described as the average of CVs from each year (\pm SE) taken across the 5 years of study

Season/year	% CV among sites	% CV within sites
Spring		
2006	48.8	45.3 (2.3)
2007	32.8	45.1 (3.1)
2008	45.8	46.7 (4.0)
2009	37.8	43.1 (2.4)
2010	44.0	59.4 (5.7)
Summer		
2006	74.0	74.7 (5.0)
2007	115.4	116.6 (19.5)
2008	79.2	85.9 (3.9)
2009	144.3	109.0 (19.7)
2010	174.1	118.9 (14.8)
Overall average		
Spring	41.8 (2.9)	47.6 (3.0)
Summer	117.4 (19.1)	101.2 (8.9)

% CV among sites = standard deviation/mean of average seasonal growth from 15 sites within each year. % CV within sites = standard deviation/mean of seasonal growth from 18 to 20 plants within a site in each year (\pm SE of 15 within-site CVs).

and among years, illustrate the high degree of spatial and temporal heterogeneity that is characteristic of arid ecosystems (Noy-Meir 1973; Ludwig 1987).

Contrary to our expectations, stem elongation did not increase with rainfall in every season (prediction 1), nor did the winter/spring season appear to be the more important growing period for *L. tridentata* in northern Sonoran Desert (prediction 2). Instead, over a 5-year study across a large number of sites and plots, both the highest and lowest rates of stem elongation were associated with the summer monsoon. In contrast, growth during winter/spring was intermediate in magnitude and far less variable among years, despite large differences in rainfall among these seasons. Others have reported similar seasonal growth patterns for *L. tridentata* (e.g. Reynolds *et al.* 1999; Muldavin *et al.* 2008), and the high ratio of summer to winter elongation observed in 2006 and 2008 (summer/winter elongation, 3.1 and 5.5 in 2006 and 2008, respectively) is similar to that seen elsewhere in the Sonoran Desert (e.g. Sharifi *et al.* 1988). Despite these prior observations, current models for the northern Sonoran Desert suggest that ANPP is linked primarily to winter rainfall (e.g. Shen *et al.* 2005). Our results challenge the generality of this perspective and suggest that the major driver of variation in stem growth for this dominant shrub is the amount of monsoon rainfall and subsequent responses to these pulsed events.

DRIVERS OF SEASONAL STEM GROWTH

The observed relationships between stem growth and monsoon rainfall are generally consistent with studies showing that high rates of shrub production are triggered by water pulses during warm periods (e.g. Reynolds *et al.* 1999; Barker *et al.* 2006). More novel, however, is that the nonlinear rela-

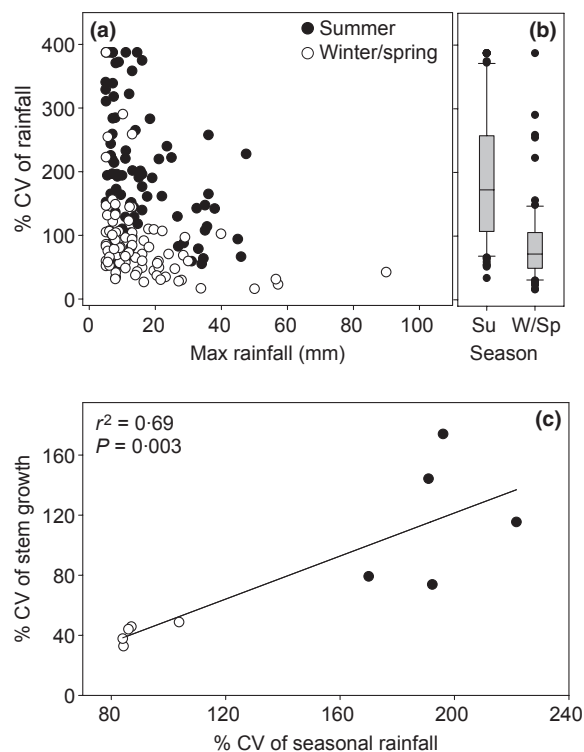


Fig. 3. Spatial heterogeneity in stem growth by *L. tridentata* is related to the spatial variation in seasonal rainfall. (a) The relationship between the spatial coefficient of variation (% CV) of rainfall across all 15 sites plotted against the maximum precipitation amount (mm) observed for any site on each given day; observations include only days where at least 5 mm of rainfall was reported at one of the 15 sites. (b) The distribution of spatial CV of precipitation for all dates where any site had ≥ 5 mm of rainfall, organized into winter and summer seasons; whiskers as described in Fig. 1. (c) The statistical relationship between the average patchiness of seasonal rainfall and the broad-scale % CV of stem elongation (i.e. among sites) for each season ($n = 10$ seasons; note x -axis does not start at zero; symbols as in Panel a).

tionship between summer rainfall and growth indicated a threshold of *c.* 100 mm precipitation, past which rates of stem growth increased more than eightfold (average of 40 and 320 mm stem elongation for rainfall < 100 and > 100 mm, respectively). Similarly, the efficiency of stem growth (i.e. elongation per unit rainfall) increased by more than threefold (0.7 vs. 2.5) across this same threshold. While the specific mechanism(s) behind such a threshold is unclear, the pattern itself was robust (Fig. 2) and observed repeatedly in the high-rainfall summers of 2006, 2008 and 2010. In contrast, summers of 2007 and 2009 were dry (27 and 47 mm of rainfall, respectively), and stem elongation was extremely low across the entire study area and essentially zero at several sites.

These rainfall–growth relationships during the monsoon point to the importance of large storm events which wet comparatively deep soil layers, and thus more of the plant root volume (Pockman & Small 2010; Cavanaugh, Kurc & Scott 2011), allowing for greater water uptake and extended periods of biotic activity (e.g. Heisler-White, Knapp & Kelly 2008, Kurc & Benton 2010). Furthermore, regression analysis

suggested that these dynamics may be facilitated or constrained locally by water infiltration rates, although this statistical effect was minor compared to seasonal rainfall amount. Which aspect(s) of the summer rainfall regime is most important to these plant responses remains unclear. For example, the number of large rain events (> 10 mm), the mean and maximum size of events and total seasonal rainfall amount were all autocorrelated (pairwise correlations range from 0.75 to 0.90). Nevertheless, sites that crossed the 100-mm threshold of total seasonal rainfall had at least one event > 18 mm. In fact, the average maximum size of monsoon rainfall events for sites beyond this apparent threshold was 32 mm, compared to only 15 mm for sites receiving < 100 mm of precipitation.

In contrast to inter-annual differences in summer growth, we were able to explain much less of the variance in stem elongation among winter/spring seasons. Poor predictive relationships between precipitation and production have been observed previously for *L. tridentata* (Reynolds *et al.* 2004), and our results suggest that stem growth during the winter/spring is fairly constrained across a wide range of seasonal climatic conditions. The analysis of rainfall–growth relationships based on all winter/spring seasons was influenced by the fact that stem growth in 2006 and 2007 was comparatively high, despite dry conditions across the region (Fig. 1). If we consider only the last 3 years of the study (2008–10), which had greater winter/spring precipitation, then differences in rainfall among sites, together with local soil texture, explained more of the variance in stem growth. One potential explanation is that elevated growth during 2006 and 2007 was linked to warmer air temperatures observed during those seasons. The importance of temperature as a cue for *L. tridentata* production has been previously noted (Chew & Chew 1965), and these results suggest that inter-annual differences in temperature may influence patterns of winter/spring stem growth. Even if this is the case, these effects appear modest as the total amount of variability in stem growth among these seasons was far lower than that observed among summers.

Antecedent precipitation is thought to be another important modulator of plant growth in desert ecosystems – both in the short term, as biological processes take time to ‘turn on’ after water becomes available (e.g. BassiriRad *et al.* 1999), and in the long term, as deeper water reserves stimulate activity when temperatures become favourable (e.g. Muldavin *et al.* 2008). Despite the potential for these relationships to affect plant growth, we did not observe any clear effects of prior-season rainfall on elongation during this period of study. Rates of summer stem growth increased with total monsoon precipitation, regardless of whether the prior winter/spring season was wet (e.g. 2008) or dry (e.g. 2006), and overall, there was no correlation between summer growth and antecedent rainfall (Spearman $r = 0.02$, $P = 0.75$, $n = 300$). One potential exception to the lack of antecedent effects was observed at one site (WTM) in one season, which received an unusually large amount of rain in January 2010 (127 mm). During this time, *L. tridentata* at this site grew considerably more than would be expected (average,

152 mm) based on the low amount of rainfall that site received during the subsequent monsoon (53 mm). Although anecdotal, this case illustrates the potential for extreme rainfall events to create time-lags in the growth of desert shrubs. Given that such events are predicted to occur more frequently in the future (Diffenbaugh *et al.* 2005), understanding their significance to patterns of desert plant growth, particularly the time-scales over which extreme rainfall pulses and growth are coupled, is necessary to predict how ANPP might change under future climatic conditions (Heisler-White, Knapp & Kelly 2008; Thomey *et al.* 2011).

SPATIAL HETEROGENEITY OF STEM GROWTH

In addition to observed variation in the magnitude of stem elongation, the spatial heterogeneity of stem elongation differed fundamentally between growing seasons. Heterogeneity was more than twice as high in summer compared to winter/spring periods and at broad spatial scales was correlated with the spatial variability of larger (> 5 mm) rainfall events, which was also greater for monsoon compared to winter rainfall seasons (see also: Goodrich *et al.* 2008; Jenerette, Scott & Huete 2010). Together with the nonlinear response by shrubs to summer pulses of water, the patchy distribution of monsoon rainfall creates pronounced heterogeneity in stem growth across our study sites, supporting prediction 3. This broad-scale heterogeneity also differed in magnitude by more than a factor of two among the five summers of record (range of spatial CVs in summer rainfall, 74–174%), illustrating the high sensitivity of this spatial pattern to the idiosyncratic nature of the North American monsoon (e.g. Englehart & Douglas 2006; Liebmann *et al.* 2008). In contrast, stem growth during winter/spring was comparatively homogenous among sites, and the magnitude of spatial variance much more constrained among years (range, 33–49%). Together, these observations suggest that the broad-scale spatial pattern of growth in the winter/spring is governed by factors that operate more similarly across the study area and consistently on an inter-annual basis. This pattern is potentially linked to the large size and relative homogeneity of Pacific fronts that deliver winter rainfall to the region; however, the weak relationships observed between precipitation and stem growth suggest that other drivers of plant growth (e.g. temperature, humidity) may also influence broad-scale spatial heterogeneity during the winter.

Consistent with hierarchical perspectives on ecosystem functioning (O'Neill *et al.* 1986; Wu & Loucks 1995; Schwinning & Sala 2004), we observed considerable small-scale heterogeneity in stem growth nested within the broader-scale patterns imposed by regional climate. In fact, variation in growth among individual plants within sites was often similar in magnitude to that observed among sites. At this smaller scale, spatial patterns are unlikely to be linked to the broader distribution of rainfall, as most plots within sites are arranged in close proximity and likely experience similar climatic conditions. Instead, differences in growth among plants are more likely linked to variation in soil structure and local

topography, which together govern small-scale patterns of water availability to plants following rainfall events (e.g. McAuliffe 1994; Hamerlynck *et al.* 2004; Pockman & Small 2010). In our study, variation in infiltration rate and texture, indices of local soil structure, contributed significantly to regression models describing summer and winter stem growth, respectively. These variables did not add much explanatory power to regression models, however, likely because estimates of soil structure were based on a small number of locations within our plots and thus did not capture small-scale variation in deep soil properties. Indeed, the estimates of within-site heterogeneity in stem growth indicate that, at least during the monsoon season, local differences in soil structure are potentially more important to stem growth than the regression models would suggest.

THE LONG-TERM RELEVANCE OF MONSOON RAINFALL

Given the magnitude of stem elongation observed during summers with high rainfall (i.e. > 100 mm), coupled with the low inter-annual variability in winter/spring growth, the recurrence interval of 'wet monsoon' seasons appears to be an important and heretofore underappreciated driver of the long-term growth of *L. tridentata*. As an example, for sites near the centre of our study area, long-term precipitation records show that summers with more than 100 mm of rain occur about every 4–5 years (Western Regional Climate Center, 2010). Based on this rainfall regime, and given that the average elongation during wet summers was 4–5 times greater than that observed during the winter/spring seasons, shrub responses to monsoon precipitation could account for c. 50% of the long-term stem growth. For study sites west of Phoenix that receive less annual rainfall, however, this recurrence interval is longer (c. 6–8 years), and thus the potential importance of the monsoon response to long-term growth is reduced (c. 25%). Further, for sites east/north-east of Phoenix, wet monsoons occur every 2–3 years, and in this case summer growth likely contributes more to the long-term production than does the winter/spring period (c. 65% during the summer). Although these are coarse estimates, they nonetheless serve to illustrate how inter-annual variation in the rainfall regime during the summer growing season might influence the long-term seasonal growth patterns of this dominant species.

More broadly, *L. tridentata* is distributed throughout the south-western United States and Mexico, an extensive range that includes major transitions in the amount and seasonality of precipitation (Reynolds *et al.* 2004). Within this range, the relative contribution of the summer monsoon to annual rainfall decreases along an east-to-west gradient linking the Chihuahuan and Mojave Deserts. Thus, while studies have documented responses by this species to summer precipitation in each of the south-western US deserts (e.g. Sonoran: Sharifi *et al.* 1988; Chihuahuan: Reynolds *et al.* 1999; Mojave: Barker *et al.* 2006), the relative importance of the monsoon season for long-term shrub growth is undoubtedly influenced by

broad-scale gradients in the seasonality of rainfall. Nevertheless, results here suggest that future changes to the seasonal distribution of precipitation across this geographical range would have important consequences for both the magnitude and spatial heterogeneity of *L. tridentata* growth. While current climate models predict an increased frequency of drought for the western United States (Seager *et al.* 2007), models predict no net change in monsoon precipitation but increased inter-annual variability and extreme events (Gutzler & Robbins 2011). Given the non-linear nature of the summer rainfall response and the potential significance of *L. tridentata* growth to overall ecosystem productivity (Shen *et al.* 2005), our data suggest that even small changes in the distribution of monsoon rainfall, or increases in the frequency of large summer storm events, could have important consequences for patterns of ANPP in the northern Sonoran Desert. In addition, our results raise the possibility that, for locations subjected to frequent and strong monsoon seasons, shrub responses to summer rainfall could potentially provide a buffer to consistent but lower growth rates that may occur in response to reduced winter/spring rainfall as a consequence of anthropogenic climate change.

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