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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Seasonal stomatal behavior of a common desert shrub and the influence of plant neighbors

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Abstract Stomata simultaneously regulate plant carbon gain and water loss, and patterns of stomatal conductance (g_s) provide insight into water use strategies. In arid systems, g_s varies seasonally based on factors such as water availability and temperature. Moreover, the presence and species identity of neighboring plants likely affects g_s of the focal plant by altering available soil water and microclimate conditions. We investigated stomatal behavior in *Larrea tridentata*, a drought-tolerant, evergreen shrub occurring throughout the arid southwestern United States. We measured g_s in *Larrea* over multiple seasons in the presence of neighbors representing different woody species. The data were analyzed in the context of a commonly used phenomenological model that relates g_s to vapor pressure deficit (D) to understand spatial and temporal differences in stomatal behavior. We found that g_s in *Larrea* was affected by neighborhood association, and these effects varied seasonally. The greatest effect of neighborhood association on g_s occurred during the winter period, where *Larrea* growing alone (without neighbors) had higher g_s compared to *Larrea* growing with neighbors. *Larrea*'s stomatal sensitivity to D and reference conductance (i.e., g_s at $D = 1$ kPa) also differed significantly among different neighbor associations. Random effects indicated reference g_s varied over short time scales (daily), while stomatal sensitivity showed little daily or seasonal variation, but was notably affected by neighbor associations such that neighboring species, especially trees, reduced *Larrea*'s sensitivity to D. Overall, seasonal dynamics and neighborhood conditions appear critical to understanding temporal and spatial variation in *Larrea*'s physiological behavior.

Keywords Bayesian modeling · Deserts · *Larrea tridentata* · Plant water use · Neighborhood interactions

Introduction

Stomata play a key role in regulating the trade-off between photosynthesis (A) and transpiration (E) (Farquhar and Sharkey 1982). Plants in arid environments typically have low stomatal conductance (g_s) compared to plants in mesic systems, and slight variations in g_s often result in large differences in A and E (Hetherington and Woodward 2003). Thus, variations in g_s provide insight into E dynamics and water-use strategies because g_s both responds to and is influenced by plant photosynthetic status, plant water potential, and available soil water (Buckley 2005; Medlyn et al. 2011; Héroult et al. 2013).

In arid systems, E and g_s are influenced by seasonal patterns in water availability and temperature (Noy-Meir 1973; Fischer and Turner 1978; Schwinning and Sala 2004). Studies of g_s in arid systems indicate that maximum daily g_s, diel trends, and stomatal responses to vapor pressure deficit (D) differ between wet and dry seasons (Nilsen et al. 1983; Ogle and Reynolds 2002; Barker et al. 2006; Tinoco-Ojanguren 2008). Variation in g_s across seasons can arise in part from plant traits such as root distributions and hydraulic conductance and from differences in environmental conditions (Comstock 2000; Xu and Baldocchi 2003). The duration of dry periods can influence g_s due to prolonged soil water stress, whereas rainy seasons result in increased g_s due to high water availability and less

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extreme D (Reynolds et al. 1999). In most deserts, extreme high temperatures that often occur in late spring and summer, coupled with low humidity, result in high D, leading to rapid water loss through stomatal opening (Noy-Meir 1973; Jones 1998). Studies of seasonal patterns of g_s in warm deserts, however, are often limited in their temporal scope, focusing on a couple of seasons or a small number of days within a season (Smith et al. 1995; Ogle and Reynolds 2002; Ignace and Huxman 2009).

Stomatal behavior can vary among individuals of a species for a variety of reasons, representing the effects of, for example, climatic gradients or soil texture (Oren et al. 1999; Hamerlynck et al. 2000; Comstock 2000). However, the effect of neighboring plants on g_s dynamics has not been evaluated in arid environments, but neighborhood associations can affect g_s by altering soil water availability and microclimate conditions (Callaway and Walker 1997; Schwinning and Weiner 1998). For example, neighboring plants can potentially modify water availability through competition or facilitation (Casper and Jackson 1997; Chesson et al. 2004; Gebauer et al. 2010). Plants that share similar soil water sources likely compete for water, such that neighbors can reduce the amount of water available for E (Fowler 1986; Briones et al. 1996; Novoplansky and Goldberg 2001). Facilitative interactions can increase water availability through mechanisms such as shading and hydraulic redistribution (Armas and Pugnaire 2005; Prieto et al. 2012; Holmgren et al. 2013). When there is little overlap in water sources, then neighboring species would likely have little impact on a plant's water use (Ehleringer et al. 1991; Silvertown 2004). An understanding of how plant interactions affect g_s dynamics can help explain variation within a species and lead to improved estimates of E.

Larrea tridentata (creosote bush) provides an excellent model system to explore g_s behavior of an arid-adapted species and to evaluate the potential effects of neighborhood associations on seasonal g_s dynamics. *Larrea* is a drought-tolerant, evergreen shrub found throughout the arid southwestern United States (Barbour 1969; Reynolds et al. 1999). *Larrea* is capable of withstanding very low leaf water potentials and can remain photosynthetically active in periods of high water stress (Odening et al. 1974; Meinzer et al. 1986). *Larrea* commonly co-occurs with other desert woody species, such as species of *Ambrosia* (bursage) and *Prosopis* (mesquite) (Shreve 1942; Phillips and Macmahon 1978), thus, there is the potential for neighbors to affect *Larrea*'s physiological behavior. In this regard, this study addresses the question: how does *Larrea*'s stomatal behavior vary across seasons and among shrubs characterized by different neighborhood associations? This study evaluates 2 years of field-based measurements of g_s in the context of a phenomenological model that relates g_s to D (Oren et al. 1999). In doing so, this study examines the understudied influence of plant neighborhood associations on stomatal behavior and in arid systems. Improved estimates of g_s are important for better constraining models of E and for improving predictive models of the hydrological cycle under climate change (Neilson 1995; Reynolds et al. 2000).

Materials and methods

Study site and focal species

This study was conducted in the Sonoran Desert outside of Phoenix, Arizona at the McDowell Mountain Regional Park (33.7261, −111.6987, 476 m a.s.l.). Mean daily temperature ranged from 12.2 °C (December) to 33 °C (July) from 1979–2013 [Western Regional Climate Center (WRCC) 2013], and mean annual precipitation over an 18-year period (1992–2010) was 281 mm (Hall et al. 2011). The soil is classified as an Aridisol and has a sandy loam texture (Hall et al. 2011). The perennial plant community is dominated by *Larrea*, *Olenya tesota* (ironwood), *Prosopis velutina* (velvet mesquite), and *Ambrosia deltoidea* (triangle leaf bursage). *A. deltoidea* is a small, drought deciduous shrub with periods of high activity during the wet winter and wet summer months (McAuliffe and Hamerlynck 2010). *P. velutina* and *O. tesota* are N-fixing trees that can access deep soil water (Suzan et al. 1997; Huxman et al. 2005), and *P. velutina* is known for hydraulically redistributing water from deep soil layers to shallower depths (Hultine et al. 2004).

We focused on quantifying the stomatal behavior of *Larrea* across different seasons and neighborhood associations. An association with another species was considered to occur when an individual of that species was growing in close proximity to the target *Larrea* shrub (i.e., when the two plant canopies overlapped). We also included "lone" *Larrea* shrubs (shrub canopy >1.5 m away from plant canopies of other species). We focused on four different neighborhood associations (i.e., lone *Larrea* shrubs, and *Larrea* shrubs growing in close proximity to *O. tesota*, *P. velutina*, or *A. deltoidea* plants); a total of 24 study shrubs were selected with six replicates per neighborhood type. However, most sampling occasions focused on a subset of 12 "intensively studied" shrubs, with a minimum of three replicates per neighborhood type due to the time-intensive nature of sample collection. Seasons were classified based on monthly temperature and precipitation averages (WRCC 2013) and included winter (cool and rainy; December–March), spring (dry and warm; April–May), summer (hot with episodic rain; June–September), and fall (cool and dry; October–November).

g_s measurements

g_s was measured with a portable photosynthesis system (Li-Cor 6400XT; Li-Cor, Lincoln, NE) on 30 days from December 2011 to November 2013. The Li-Cor chamber conditions were set to external ambient conditions. Measurements typically began around 0800 hours and ended around 1500–1600 hours in the winter and began around 0600 hours and ended around 1300 hours in the summer, when g_s was very low; g_s was measured approximately every 2 h for each study shrub. During each measurement period, a cluster of leaves (e.g., 8–30 leaves) were placed in the Li-Cor chamber, and once the g_s values stabilized and the total coefficient of variation was <0.03, then five values of g_s were logged during a ~1-min period. Due to the high frequency of measurements, non-destructive methods were used to estimate leaf area in the cuvette chamber. The average leaf area per leaf was determined for each study shrub based on at least 30 leaves collected throughout the canopy of the shrub. Following each Li-Cor measurement, the number of leaves in the cuvette were counted and the data were corrected based on the estimated total leaf area in the chamber (i.e., shrub-specific estimate of leaf area per leaf × number of leaves in chamber). A, atmospheric [CO$_2$] (C_a), and leaf-to-air D were simultaneously recorded with each g_s measurement.

g_s model

Although several g_s models have been described (e.g., Leuning 1995; Buckley et al. 2003; Tuzet et al. 2003; Damour et al. 2010), we focus on a model that relates g_s to D (Oren et al. 1999), which we refer to as the "Oren model." According to Oren et al. (1999), this phenomenological model of g_s agrees very well with a theoretical analyses of stomatal regulation of transpiration E in response to E and leaf water potential. Moreover, the Oren model has been successfully applied to understand variation in g_s across and within species in multiple biomes, including multiple desert species (Ogle et al. 2012), and, in particular, *Larrea* (see also, Ogle and Reynolds 2002; Oren et al. 1999).

The Oren model considers g_s to decrease linearly in response to the natural log scaled D (Oren et al. 1999; Ogle et al. 2012):

$$g_s = g_{\text{ref}} - m \cdot \ln\left(\frac{D}{D_0}\right) \tag{1}$$

D_0 is a reference D, which we set to 1 kPa; g_{ref} is the reference g_s when $D = 1$ kPa, and m represents the responsiveness of g_s to changes in D. A unitless index of stomatal sensitivity to D is given by (Ogle et al. 2012):

$$S = \frac{m}{g_{\text{ref}}} \tag{2}$$

where $S < 0.6$ or $S > 0.6$ indicate the potential for anisohydric or isohydric behavior (Ogle et al. 2012; Oren et al. 1999), respectively, where isohydric plants regulate g_s to maintain constant leaf water potential, whereas anisohydric plants exhibit greater diurnal variation in leaf water potentials. Importantly, S is devoid of the scale-dependence issues associated with m. For example, plants with higher g_{ref} are also expected to be more sensitive to changes in D (higher m) (Kaufmann 1982). Thus, we reparameterized Eq. 1 in terms of g_{ref} and S, which we use in subsequent analyses:

$$g_s = g_{\text{ref}}\left(1 - S \cdot \ln\left(\frac{D}{D_0}\right)\right) \tag{3}$$

Statistical model

For each individually logged observation i ($i = 1, 2, \ldots, 6{,}879$), the vectors of observed g_s and D were assumed to follow a multivariate normal distribution with a (vector) such that:

$$\begin{pmatrix} g_{s_i} \\ D_i \end{pmatrix} \sim Normal\left(\begin{pmatrix} \bar{g}_{s_n} \\ \bar{D}_n \end{pmatrix}, \sum\right) \tag{4}$$

The means ($\bar{g}_s$ and $\bar{D}$) correspond to the latent (unobserved) average g_s and D values associated with each unique measurement period, n ($n = 1, 2, \ldots, 1371$), representing a particular cluster of leaves on an individual shrub at a given time point (recall, there were ~five replicate logged observations per measurement period). Σ is a 2 × 2 covariance matrix that quantifies potentially correlated measurement errors resulting from the simultaneous measurement of g_s and D. Common analysis approaches ignore replicate-level measurement uncertainty and potentially correlated g_s and D measurement errors. Here, however, Eq. 4 can be interpreted as a measurement error model such that we explicitly account for replicate-level measurement uncertainty.

The latent measurement period g_s value ($\bar{g}_s$), the response of interest, was also assumed to follow a normal distribution, with a variance component that was estimated separately for each sampling day j ($j = 1, 2, \ldots, 30$):

$$\bar{g}_{s_n} \sim Normal(\tilde{g}_{s_n}, \sigma_j) \tag{5}$$

The mean or predicted value ($\tilde{g}_s$) is modeled according to the Oren model via Eq. 3, but D in Eq. 3 is replaced with the corresponding latent measurement period value, $\bar{D}_n$ (Eq. 4).

We implemented the above model in a Bayesian framework (Ogle and Barber 2008; Ogle et al. 2012; Gelman et al. 2013), which facilitated simultaneous implementation of the bivariate measurement error model in Eq. 4, the univariate latent g_s model in Eq. 5, and the non-linear mean model defined by Eq. 3. Within the Bayesian model, we specified

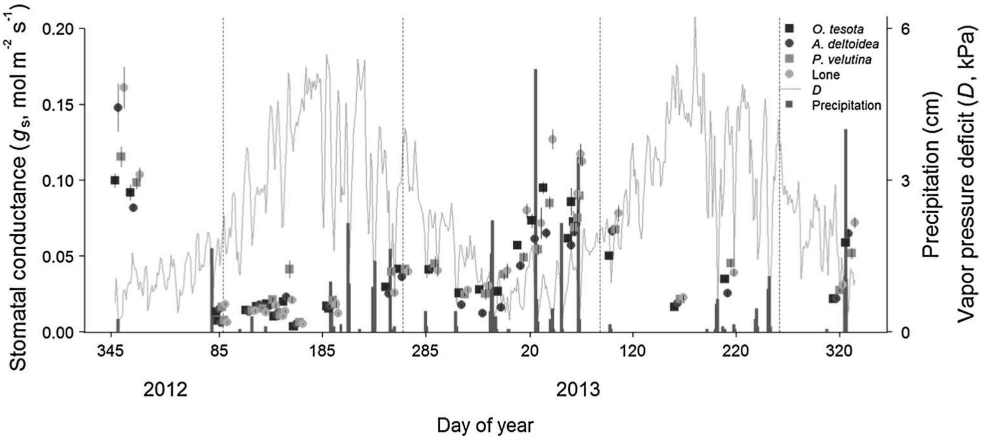

Fig. 1 Mean (±1 SE) daily stomatal conductance (g_s) of *Larrea tridentata* under four different neighborhood associations (i.e., growing in close proximity to *Olenya tesota*, *Prosopis velutina*, or *Ambrosia deltoidea*, or growing alone). *Vertical bars* associated with each measurement day indicate the total daily amount of precipitation (cm). Daily mean vapor pressure deficit (D; kPa) is indicated by the *gray line*. *Dashed vertical lines* indicate the end of winter and summer seasons

hierarchical parameter models for g_{ref} and S that are motivated by the sampling design. That is, g_{ref} and S in the model for $\tilde{g}_{\text{s}}$ were allowed to vary at the level of sampling day j and shrub k [$k = 1, 2, \ldots, 24$ for $j = 1, 2, \ldots, 9$, and $k = 1, 2, \ldots, 12$ (subset of shrubs) for $j = 10, 11, \ldots, 30$] associated with each measurement period. The hierarchical models for each shrub- by day-level parameter treated shrubs as being nested in neighborhood type p ($p = 1, 2, 3, 4$):

$$g_{\text{ref}_{k,j}} \sim Normal(\bar{g}_{\text{ref}_{p,j}}, \sigma_{\text{ref}}) \tag{6}$$

$$S_{k,j} \sim Normal\left(\bar{S}_{p,j}, \sigma_{\text{S}}\right) \tag{7}$$

That is, note that the means ($\bar{g}_{\text{ref}}$ and $\bar{S}$) vary by p and j, and the SDs (σ_{ref} and σ_{S}) describe the variability in these parameters among shrubs within each neighborhood type and day combination. The mean terms were decomposed into a base-line value for each neighborhood type (g_{base} and S_{base}) plus a day random effect (ε_{ref} and ε_{S}):

$$\bar{g}_{\text{ref}_{p,j}} = g_{\text{base}_p} + \varepsilon_{\text{ref}_j} \tag{8}$$

$$\bar{S}_{p,j} = S_{\text{base}_p} + \varepsilon_{\text{S}_j} \tag{9}$$

To complete the Bayesian model, we assigned relatively non-informative priors to all remaining parameters. The priors for g_{base} and S_{base} were given vague normally distributed priors; ε_{ref} and ε_{S} were each assigned normal distributions with means of zero and their own associated SDs. The measurement period-specific SDs (σ_n; Eq. 5) were modeled hierarchically such that each is treated as coming from an overall, population-level distribution described by a folded Cauchy distribution, centered at zero with a scaling parameter (e.g., $\tau_{p,s}$) for each neighborhood type ($p = 1, 2, 3, 4$) and season s ($s = 1, 2, \ldots, 4$) (Gelman et al. 2013). Each $\tau_{p,s}$ and all other SD terms were assigned relatively non-informative uniform priors, and the covariance matrix (Σ; Eq. 4) was assigned a relatively non-informative inverse-Wishart prior (Gelman et al. 2013).

The statistical model described above (Eqs. 1–9) represents the final model structure that we arrived at after having explored several other model variants; this model generally fits the data the best while minimizing model complexity.

Model implementation and evaluation

The above model was implemented in OpenBugs (Spiegelhalter et al. 2003; Lunn et al. 2009) to obtain posterior distributions of the model parameters using Markov chain Monte Carlo (MCMC). Three parallel MCMC chains were run for a total of 472,006 iterations. The built-in BGR tool was used to evaluate convergence of the MCMC chains, and a burn-in of 140,000 samples was discarded (prior to convergence). The chains were thinned by every 200 samples to reduce autocorrelation and reduce storage requirements. Thus, a final posterior sample size of 5,034 was obtained. Parameter estimates are reported as posterior means and 95 % credible intervals (CIs), which are defined by the 2.5th and 97.5th percentiles.

Results

Seasonal patterns of g_s and the influence of neighbors

Mean observed daily g_s in *Larrea* exhibited distinct seasonal patterns, with the highest values occurring in winter for all neighborhood associations (Fig. 1). *Larrea* growing alone generally had the highest g_s (Fig. 2; mean = 0.089 mol m^{-2} s^{-1}) on most winter days compared to all other neighborhood associations (means ranged from 0.061 to 0.069 mol m^{-2} s^{-1} for *Larrea* growing next to *A. deltoidea* and *P. velutina*, respectively). The winter to spring transition was characterized by an increase in D (Fig. 1), which was paralleled by a sharp decline in g_s and a shift to similar mean g_s among the neighborhood

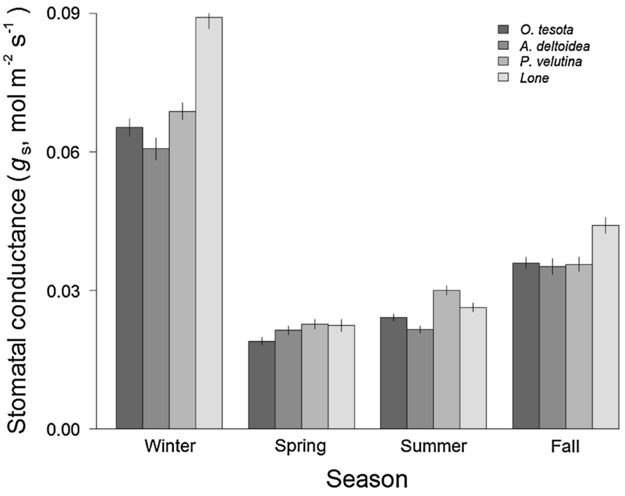

Fig. 2 Mean (±1 SE) seasonal g_s for *L. tridentata* under four different neighborhood associations (see Fig. 1 for description)

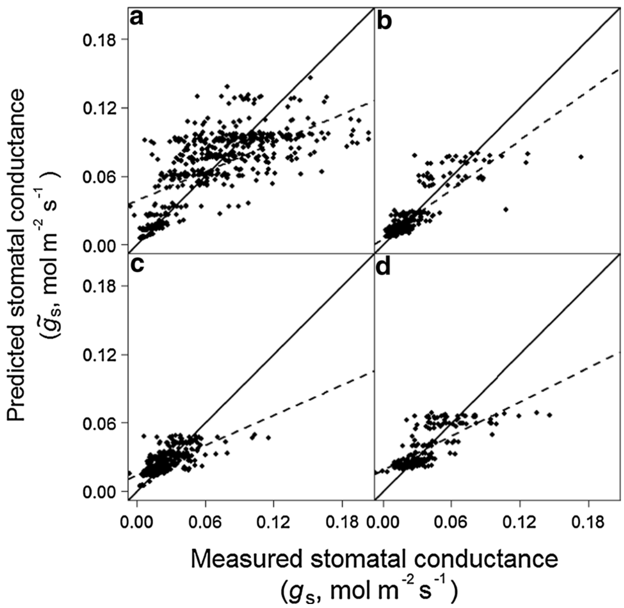

Fig. 3 The model fits of predicted versus observed g_s for each season: **a** winter ($R^2 = 0.45$), **b** spring ($R^2 = 0.73$), **c** summer ($R^2 = 0.46$), and **d** fall ($R^2 = 0.53$). The *solid black line* is a 1:1 line, and the *dashed line* indicates the best-fit regression line. Four points are not shown because they exceeded the axis limits, and their inclusion renders the plot more difficult to visualize

types. *Larrea* growing next to *O. tesota* had the lowest g_s (mean = 0.019 mol m^{-2} s^{-1}), and *Larrea* next to *P. velutina* had the highest g_s (mean = 0.024 mol m^{-2} s^{-1}). *Larrea* growing next to *P. velutina* also had slightly higher g_s during the summer (mean = 0.03 mol m^{-2} s^{-1}) compared to other neighborhood associations (mean ranged from 0.021 to 0.026 mol m^{-2} s^{-1} for *Larrea* growing next to *A. deltoidea* and alone, respectively). For all neighborhood associations, a slight increase in g_s occurred in the late summer and early fall, following the monsoon rainy season, but g_s subsequently declined by late fall. *Larrea* growing alone had the highest g_s (mean = 0.044 mol m^{-2} s^{-1}) relative to all other neighbor associations, which had very similar g_s (means varied from 0.035 to 0.036 mol m^{-2} s^{-1}).

Model fit and comparison

The model (Eqs. 1–9) fit the data reasonably well ($R^2 = 0.62$ for observed vs. predicted g_s). The model had the highest fit during the spring (Fig. 3b; $R^2 = 0.71$), the lowest during the winter (Fig. 3a; $R^2 = 0.45$) and summer (Fig. 3d; $R^2 = 0.46$), and an intermediate fit in the fall (Fig. 3d; $R^2 = 0.53$). In general, the model often underpredicted high values of g_s (Fig. 3), which often occurred at low D. The results from the multivariate measurement model (e.g., Eq. 5) indicate the within-measurement period measurement errors in g_s and D were not significantly correlated [$r = -0.01$ (−0.04, 0.01), posterior mean and 95 % CI].

Components underlying variation in g_s

The Bayesian application of the Oren model provides insight into g_s components that underlie the variation in *Larrea*'s stomatal behavior. The baseline reference g_s (g_{base}; Eq. 8) indicates the effects of neighbors; g_{base} was significantly lower for *Larrea* growing next to *O. tesota* or *P. velutina* compared to *Larrea* growing alone or next to *A. deltoidea* (Table 1). The day random effects ($\varepsilon_{\mathrm{ref}}$) capture the temporal variability in g_{ref}, and the daily $\varepsilon_{\mathrm{ref}}$s were generally significantly greater than zero (i.e., higher than expected g_{ref} given the predicted g_{base}) in the winter and negative (i.e., lower than expected g_{ref}) in the spring, summer, and fall (Fig. 4). Moreover, notable daily variation in g_{ref} occurred within each season (Figs. 4, 5); for example, g_{ref} was often significantly lower in early winter compared to late winter. An increase in g_{ref} corresponded with the summer monsoon season, and g_{ref} was typically lower during the dry, hot late spring and early summer. Moreover, g_{ref} generally declined from late summer to early winter, corresponding to increasing dryness during the fall after monsoon rains and before the onset of the winter rainy season. These temporal trends are reflected in the season-level average g_{ref}. For example, posterior results indicate that g_{ref} was lowest in the spring and hightest in the winter (Table 1). Overall, season effects accounted for the majority of the variation on g_{ref} relative to neighborhood effects (Table 1).

All daily and seasonal stomatal sensitivity to D (S) estimates were consistently less than 0.6 (i.e., both 95 % CI limits ≤0.6, Fig. 6; Table 1), but S differed significantly

Table 1 Posterior estimates [mean and 95 % credible interval (CI)] of the reference conductance (g_{ref}; mol m^{-2} s^{-1}) at vapor pressure deficit (D) = 1 kPa and stomatal sensitivity (S)

Season	Neighbor	g_{ref} Mean	g_{ref} 2.5th	g_{ref} 97.5th	S Mean	S 2.5th	S 97.5th
Winter	*Olenya tesota*	0.072	0.066	0.079	0.132	0.003	0.254
	Ambrosia deltoidea	0.081	0.073	0.091	0.298	0.198	0.391
	Prosopis velutina	0.072	0.065	0.079	0.145	−0.012	0.275
	Lone	0.082	0.073	0.092	0.294	0.190	0.386
Spring	*O. tesota*	0.035	0.028	0.042	0.166	0.035	0.270
	A. deltoidea	0.044	0.034	0.055	0.333	0.247	0.398
	P. velutina	0.034	0.027	0.042	0.179	0.030	0.290
	Lone	0.045	0.035	0.055	0.329	0.244	0.395
Summer	*O. tesota*	0.032	0.025	0.040	0.111	−0.027	0.220
	A. deltoidea	0.041	0.032	0.052	0.277	0.187	0.347
	P. velutina	0.032	0.024	0.040	0.124	−0.033	0.241
	Lone	0.042	0.033	0.052	0.273	0.182	0.341
Fall	*O. tesota*	0.037	0.033	0.042	0.141	−0.012	0.272
	A. deltoidea	0.047	0.040	0.054	0.307	0.173	0.420
	P. velutina	0.037	0.033	0.042	0.154	−0.010	0.293
	Lone	0.048	0.041	0.055	0.303	0.164	0.416
Base	*O. tesota*	0.048	0.043	0.053	0.136	0.011	0.243
	A. deltoidea	0.058	0.050	0.067	0.303	0.215	0.375
	P. velutina	0.048	0.042	0.053	0.149	0.001	0.263
	Lone	0.058	0.050	0.067	0.299	0.210	0.371

The 95 % CI is given by the 2.5th and 97.5th percentiles. The season × neighbor estimates are obtained by averaging $\bar{g}_{ref}$ (Eq. 8) across all days within each season × neighborhood type. The overall season estimates are obtained by averaging $\bar{g}_{ref}$ across all neighbor types and days within each season. The overall neighborhood type estimates represent the g_{base} (Eq. 8) estimates

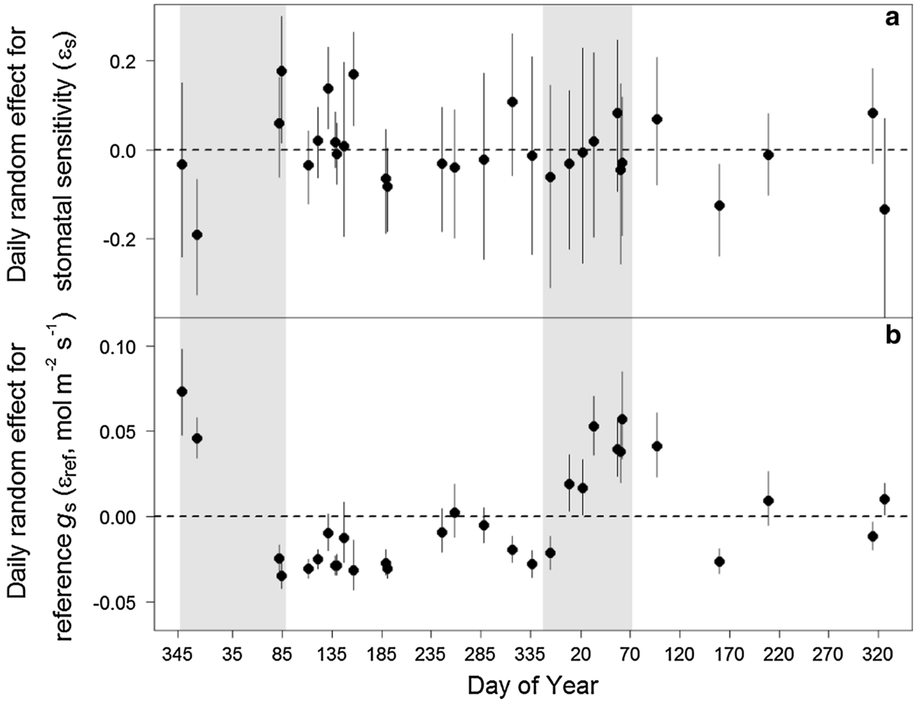

Fig. 4 Posterior estimates [mean and 95 % credible interval (CI)] for the daily random effects associated with: **a** stomatal sensitivity (S) to D and **b** the reference stomatal conductance (g_{ref}). The *gray regions* indicate winter periods

between neighborhood associations (Table 1). Baseline S (S_{base}) was significantly higher for *Larrea* growing alone or next to *A. deltoidea* compared to *Larrea* growing next to *O. tesota* or *P. velutina* (Table 1). For example, g_s is expected to be significantly more sensitive to changes in D when *Larrea* is growing alone or in association with *A. deltoidea* (posterior means for season-level S range from 0.27 to 0.33, Table 1). Conversely, when *Larrea* is growing in association with the trees (*P. velutina* and *O. tesota*), g_s is predicted to be insensitive (95 % CIs for overall and season-level

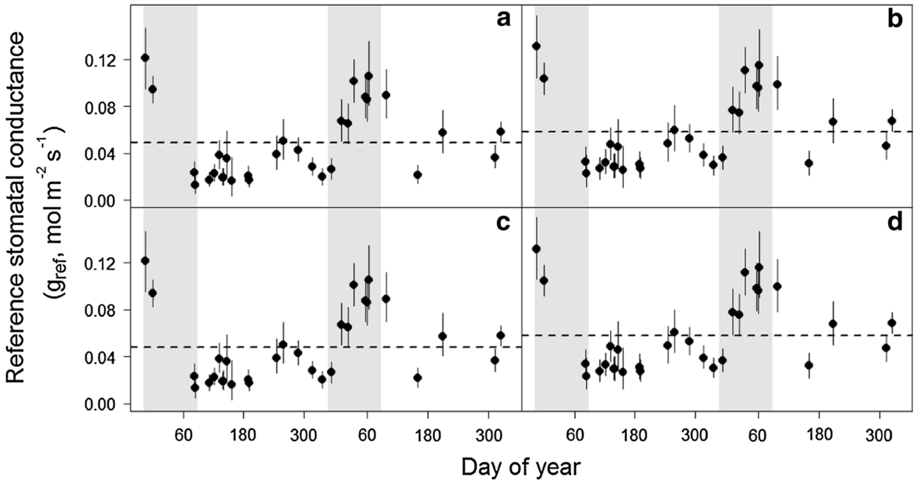

Fig. 5 Posterior estimates (mean and 95 % CI) from for g_{ref} for each day for *Larrea* growing **a** next to *O. tesota*, **b** next to *A. deltoidea*, **c** next to *P. velutina*, and **d** alone. *Dashed lines* indicate the baseline (g_{base}) posterior means for each neighborhood association. The *gray regions* indicate winter periods

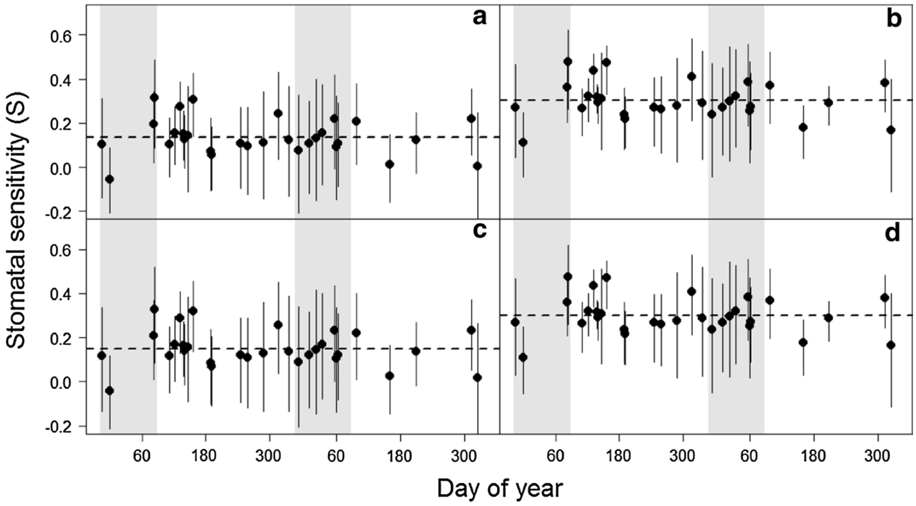

Fig. 6 Posterior estimates (mean and 95 % CI) for S to D for each day for *Larrea* growing **a** next to *O. tesota*, **b** next to *A. deltoidea*, **c** next to *P. velutina*, and **d** alone. *Dashed lines* indicate the baseline (S_{base}) posterior means for each neighborhood association. The *gray regions* indicate winter periods. For other abbreviations, see Figs. 1 and 4

neighbor-specific S values contain zero) to changes in D (*P. velutina*, all seasons except spring; *O. tesota*, summer and fall) or only weakly sensitive to D (posterior mean for $S < 0.18$) (Table 1). Based on the daily random effects (ε_S; Eq. 9), S showed little temporal variability, and 40 % of the daily level S estimates were indistinguishable from zero (i.e., their 95 % CIs contained zero), with the exception of a few days, mostly in the spring (Fig. 6). When averaged across days within each season, S showed little seasonal variation; in contrast to g_{ref}, most of the variation in S can be attributed to neighbhorhood effects (Table 1).

Discussion

Seasonal patterns of g_s and the influence of neighbors

As expected in a water-limited system (Rodriguez-Iturbe et al. 2001), this study shows that g_s in a common desert shrub (*Larrea tridentata*) varies seasonally in accordance with precipitation patterns. For example, the g_s patterns are consistent with previous studies of *Larrea*'s water relations that observed decreased water stress and peaks in g_s during wet seasons (Monson and Smith 1982; Meinzer et al. 1988; Hamerlynck et al. 2000). The highest g_s values occur during the winter in association with a period of low D and increased soil water from winter rains (Fig. 1) (Reynolds et al. 2004). A slight increase in g_s was observed at the height of the monsoon season (August and early September), and g_s declined again in the late fall to early winter, coinciding with a dry period before the onset of the winter rains (Fig. 1).

Seasonal variation in g_s, however, was also related to neighborhood characteristics. Past studies demonstrate the importance of plant neighbor interactions for *Larrea's* rooting distribution, phenology, and biomass (Fowler 1986; Brisson and Reynolds 1994; Briones et al. 1996), but offer little insight into the effects of plant neighbors on *Larrea*'s physiological responses. This study indicates the importance of plant neighbors on *Larrea*'s stomatal behavior, whereby the greatest differences in g_s between neighborhood associations occurred during the winter, summer, and fall (Fig. 2). Differences between the neighborhood associations were greatest in the winter, an important period of productivity in the Sonoran Desert that is associated with the highest level of plant greenness and low water stress for *Larrea* (Monson and Smith 1982; Notaro et al. 2010). *Larrea* and the neighbor species considered here exhibit high growth and physiological activity in the winter, resulting in a period of high water use (Nilsen et al. 1983; Tewksbury and Lloyd 2001; Reynolds et al. 2004; McAuliffe and Hamerlynck 2010). In the winter, *Larrea* growing alone has the highest g_s, indicating that growing in isolation may be beneficial during periods of potential heightened competition. Overall, the effect of neighbors on *Larrea*'s g_s dynamics likely results from altered water availability due to competition or facilitation (Novoplansky and Goldberg 2001) and/or the alteration of the microclimate by the canopies of neighboring plants (Montana et al. 1995; Callaway and Walker 1997).

Larrea neighboring the shallow-rooted *A. deltoidea* has the lowest g_s in the winter, which may be a result of intense competition for soil water since these two species are likely to have overlapping root distributions (Brisson and Reynolds 1994). The similar g_s for *Larrea* growing alone or in association with *A. deltoidea* was expected during the spring and early summer since *A. deltoidea* is dormant during these periods (Szarek and Woodhouse 1977). During the summer, *Larrea* growing next to *A. deltoidea* has the lowest average g_s, suggesting that competition for soil water may also be important during *A. deltoidea*'s monsoon period of physiological activity (Szarek and Woodhouse 1977). Despite the end of *A. deltoidea*'s activity in September, the g_s of *Larrea* growing next to *A. deltoidea* remains significantly lower than g_s of *Larrea* growing alone, indicating that the effects of competition for water or heightened soil water depletion persist as the dry period continues.

The relatively high mean summertime g_s of *Larrea* growing near *P. velutina* suggests that facilitation may influence g_s periodically throughout the year. For example, *Larrea* growing next to *P. velutina* has higher g_s during summer, which may be a result of improved water relations since *P. velutina* is expected to enhance soil moisture (via hydraulic redistribution) and nitrogen (via N fixation) under its canopy compared to bare ground (Schade et al. 2003). Despite *O. tesota*'s reported facilitative benefits via shading (Suzan et al. 1996; Tewksbury and Lloyd 2001), little effect of *O. tesota* neighbors on *Larrea*'s g_s was observed during the dry spring and hot summer periods. However, *Larrea* growing next to *O. tesota* had higher mean g_s than *Larrea* growing near *A. deltoidea* during the winter and summer, suggesting that interactions between *O. tesota* may offer a degree of improved water relations. Differences between *P. velutina* and *O. tesota* may be partly explained by its canopy architecture, as *O. tesota*'s canopy likely provides less shading compared to *P. velutina*. For example, qualitative differences between *O. tesota* and *P. velutina* canopies are obvious at our site, with *P. velutina* having a lower, more branched canopy compared to *O. tesota*, which agrees with a study comparing canopies of *O. tesota* and *Prosopis glandulosa* (closely related species to *P. velutina* in the arid southwestern USA) (Suzán-Azpiri and Sosa 2006).

Components underlying variation in g_s

Daily and/or seasonal controls had the greatest influence on g_{ref} (i.e., g_s at $D = 1$ kPa), suggesting that short-term (i.e., over days to a weeks) stomatal acclimatization (e.g., Smith and Dukes 2013) to prevailing environmental conditions is important for g_s. For example, Ogle and Reynolds (2002) found that growth temperature (i.e., average temperature over the past week) regulated *Larrea*'s maximum g_s and associated g_{ref}. In our study, lower g_{ref} occurred during the early winter, late spring, and beginning of summer, which may be associated with changing temperature and/or moisture regimes that are characteristic of these periods. Declines in g_{ref} throughout the late spring, early summer, and fall may also be associated with decreases in soil moisture. Drying soils lower plant hydraulic conductivity, which is known to be correlated with g_s and g_{ref} (Meinzer et al. 1988; Ward et al. 2008; Domec et al. 2009). Soil drying can also lead to increases in abscisic acid (ABA), ultimately decreasing maximum g_s (Thomas and Eamus 1999).

While the effect of plant neighbors was not as pronounced as seasonal variation, g_{ref} was significantly lower for *Larrea* growing next to the tree species compared to growing next to *A. deltoidea* or alone (Fig. 5; Table 1). Differences in *Larrea*'s g_{ref} based on plant neighbor associations likely reflect long-term adjustments to the altered microclimate or water availability created by neighbors. Prolonged exposure to more xeric conditions—likely analogous to *Larrea* growing alone or near *A. deltoidea*—can result in changes in hydraulic architecture, such as tree height and sapwood area to leaf area, and these changes can lead to increases in g_{ref} (Addington et al. 2006). Alternatively, *Larrea*'s biomass is known to decrease with proximity to plant neighbors, and differences in g_{ref} may partly be a result of shrub size (Fowler 1986; Briones et al. 1996). Franco et al. (1994) found that large *Larrea* had greater g_{ref} when xylem water potential is low compared to small *Larrea*, and thus the higher g_{ref} of *Larrea* growing alone could also reflect differences in *Larrea* size among the different neighborhood association, although we do not have direct estimates of plant size to evaluate this hypothesis.

In contrast to g_{ref}, variation in *Larrea*'s stomatal sensitivity to D (i.e., S) was predominately driven by neighbor effects (Fig. 6; Table 1). The effect of neighbors indicates that *Larrea*'s S may be controlled by long-term acclimatization or microclimate effects. Studies indicate that higher soil moisture occurs below *O. tesota* and *P. velutina* canopy as a result of shading and/or hydraulic redistribution (Suzan et al. 1996; Schade et al. 2003; Hultine et al. 2004). A study of an anisohydric vine, *Vitis vinifera*, found stomatal sensitivity to D was only increased under drought conditions and it was essentially insensitive to D in moist to moderately dry soils (Rogiers et al. 2012). *Larrea* growing alone or next to *A. deltoidea* may experience increased exposure to drought conditions with greater, more frequent soil drying, resulting in increased sensitivity to D compared to *Larrea* growing under trees. The influence of neighbors on *Larrea*'s root distributions could affect access to soil water, which in turn is expected to affect g_s. Spatial variation in *Larrea*'s rooting depth and root area could allow *Larrea* growing near trees greater access to more stable, deeper soil water, whereas *Larrea* growing alone or next to *A. deltoidea* may rely on more unstable, shallower soil water or experience longer durations of low soil water availability (Fowler 1986; Montana et al. 1995; Briones et al. 1998; Schade et al. 2003; Reynolds et al. 2004; Armas and Pugnaire 2005). As for g_{ref}, altered hydraulic architecture resulting from higher exposure to soil drying could also influence the magnitude of S (Addington et al. 2004). Lastly, lower S in *Larrea* growing next to tree species could be explained by lower boundary layer conductance (g_c) resulting from protection by the tree canopies. An increased boundary layer (lower g_c) would weaken the coupling of *Larrea*'s leaves to the atmospheric conditions, thus making g_s less responsive to changes in D (lower S) compared to more exposed *Larrea* growing alone or next to *A. deltoidea* (Monteith 1995; Damour et al. 2010).

Given *Larrea* exhibits anisohydric behavior, the weak coupling of g_s to D, especially when it grows next to trees, agrees with prior studies of anisohydric plants (Tardieu and Simonneau 1998; Oren et al. 1999; Ogle et al. 2012). In anisohydric plants, Tardieu and Simonneau (1998) found little stomatal sensitivity to changes in D or leaf water potential, and stomatal aperture was primarily governed by xylem ABA. Our results support this finding such that S exhibited little daily/seasonal variation in S, whereas g_{ref} varied notability across seasons. Variables such as leaf and tree hydraulic conductance, ABA, and plant water potential—which have been shown to be important in mesic and/or isohydric trees—may also be important for the overall magnitude of *Larrea*'s g_{ref}, but appear to have little influence on S (Tardieu and Davies 1983; Thomas and Eamus 1999; Addington et al. 2004; Domec et al. 2009; Ocheltree et al. 2014). In general, our evaluation of *Larrea*'s stomatal response components demonstrates the importance of understanding the influence of drivers over varying time scales, such as intra-annual or seasonal responses that may reflect short-term acclimatization or interannual or decadal adjustments that may be partly governed by plant neighbor interactions.

Conclusions and implications for modeling g_s

Identifying the specific drivers and mechanisms underlying the short- and long-term g_s responses presents a fruitful avenue for future research. While our model explains 61 % of the variation in *Larrea*'s g_s, higher g_s values are often underpredicted, especially at low D. The daily random effects indicate that g_{ref} is governed by unexplained temporal variation, and such variation could arise from environmental effects (i.e., temperature, soil moisture, plant water status), physiological factors (whole-plant hydraulic resistance, photosynthetic feedbacks), or interactions among these (e.g., short-term acclimatization) (Domec et al. 2009; Damour et al. 2010) that were not explicitly included in our model. For example, plant water status (e.g., water potentials or plant hydraulic resistance) is known to feed back to affect g_s (Meinzer et al. 1988; Jones 1998; Ogle and Reynolds 2002), but the data necessary (e.g., frequent plant water potentials) for such modifications would require destructive sampling that can be prohibitive when studying the same shrubs frequently over multiple years. Additionally, finer resolution and more frequent observations of g_s, soil water, microclimate, and plant water status would allow for improved estimates of how seasonality and neighborhood interactions influence g_s, especially during transitions between seasons. Such data would also allow for further exploration of the influence of environmental covariates on different components of the g_s response, such as g_{ref} and S (Ogle and Reynolds 2002; Tuzet et al. 2003).

This study indicates the importance of accounting for spatial variability that can arise from plant neighborhood interactions. Studies of plant water use often do not explicitly consider the neighborhood surrounding study shrubs or may select more isolated plants for study (Pataki et al. 2000; Ogle and Reynolds 2002; Ogle et al. 2012). The assumption that plants will exhibit similar stomatal behavior, and thus water use and loss dynamics, across space may not be appropriate, and estimates of plant water fluxes should explicitly include temporal (e.g., season) and spatial (e.g., neighborhood characteristics) effects. Moreover, current semi-mechanistic approaches to modeling g_s, and hence plant water loss, require improvements if such temporal and spatial effects are to be accurately represented in plants from desert systems.

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