The Effect of Plant Neighbors on a Common Desert Shrub's Physiology and Evapotranspiration

by

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ABSTRACT

Hydrological models in arid and semi-arid ecosystems can be subject to high uncertainties. Spatial variability in soil moisture and evapotranspiration, key components of the water cycle, can contribute to model uncertainty. In particular, an understudied source of spatial variation is the effect of plant-plant interactions on water fluxes. At patch scales (plant and associated soil), plant neighbors can either negatively or positively affect soil water availability via competition or hydraulic redistribution, respectively. The aboveground microclimate can also be altered via canopy shading effects by neighbors. Across longer timescales (years), plants may adjust their physiological (water-use) traits in response to the neighbor-altered microclimate, which subsequently affects transpiration rates. The influence of physiological adjustments and neighbor-altered microclimate on water fluxes was assessed around *Larrea tridentata* in the Sonoran Desert. Field measurements of *Larrea*'s stomatal behavior and vertical root distributions were used to examine the effects of neighbors on *Larrea*'s physiological controls on transpiration. A modeling based approach was implemented to explore the sensitivity of evapotranspiration and soil moisture to neighbor effects. Neighbors significantly altered both above- and belowground physiological controls on evapotranspiration. Compared to *Larrea* growing alone, neighbors increased *Larrea*'s annual transpiration by up to 75% and 30% at the patch and stand scales, respectively. Estimates of annual transpiration were highly sensitive to the presence/absence of competition for water, and on seasonal timescales, physiological adjustments significantly influenced transpiration estimates. Plant-plant interactions can be a significant source of spatial variation in ecohydrological models, and both physiological adjustments to neighbors and neighbor effects on microclimate affect small scale (patch to ecosystem) water fluxes.

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1. INTRODUCTION

Arid and semi-arid ecosystems cover roughly 40% of Earth’s land area and are predicted to increase in coverage under climate change (D’Odorico and Porporato 2006, Seager and Vecchi 2010). Furthermore, climate change is expected to increase the aridity of dryland ecosystems, altering ecosystem water cycles (Ravi et al. 2010, Maestre et al. 2012). However, predictions of future dryland water cycles can be subject to bias and a high degree of uncertainty (Gerten et al. 2004), and improvements in model estimates are necessary for better predictive capability (Weltzin et al. 2003, Trenberth 2011). One source of model uncertainty in dryland ecosystems is the high spatial and temporal variability of components of the water cycle, such as evapotranspiration and soil moisture (Vivoni 2012, Long 2014). Quantifying the drivers of spatial and temporal variability of such processes can help to reduce uncertainty in model estimates (Rastetter et al. 2003, Shields and Tague 2012).

In dryland ecosystems, spatial variation in water fluxes can arise from heterogeneity in abiotic drivers, vegetation cover, and vegetation interactions. Abiotic factors such as soil texture, terrain slope, and precipitation can vary across meter to kilometer scales, and this variation can affect soil moisture and water fluxes such as run-off, infiltration, and evapotranspiration (Wainwright 2006, Vivoni et al. 2010). The composition of plant species in an ecosystem also influences the magnitude and temporal trends of transpiration depending on the vegetative life-forms and functional traits (Roberts 2000, Sperry and Hacke 2002). In addition to transpiration, vegetative cover also decreases runoff and the importance of evaporation versus transpiration (Raz-Yaseef et al. 2010). The effect of vegetation on spatial variation in water fluxes depends on the amount of bare soil, and the abundance and aggregation of plants (Ludwig et al. 2005).

Plant-plant interactions are an understudied potential source of variability in water fluxes in dryland ecosystems with aggregated plant spatial distributions. Plant neighbors can alter the microclimate around a particular plant and the soil that surrounds it (patch scale), ultimately leading to differences in soil moisture and evapotranspiration (Synodinos et al. 2015). The belowground microclimate can be affected by altered soil water availability arising from the negative effects of competition for water between neighboring plants with overlapping roots or the potential positive effects of plant-mediated hydraulic redistribution of water (Callaway and Walker 1997). The aboveground microclimate around a plant may also be affected by canopy shading effects from neighboring plants (Barbier et al. 2008). Canopy shading reduces temperature and evaporative demand, which can affect soil evaporation and the stomatal conductance of the neighboring plants (Breshears et al. 1998). The direct alteration of the microclimate around plants can influence transpiration and evaporation through effects on soil moisture, and the evaporative demand that can be temporally variable (Breshears et al. 1997, Zavala and Bravo De La Parra 2005).

The impact of plant neighbor interactions on transpiration also depends on the physiology and functional traits that control plant water use (e.g., stomatal conductance, root distribution), and these water-use traits can affect the nature of the neighbor interaction (i.e., competitive, facilitative, or neutral) (Sperry and Hacke 2002, Aschehoug and Callaway 2014). Over longer timescales (annual to multiple years), adjustments in plant water-use traits may occur in response to neighbor-altered environments (Brisson and Reynolds 1994, Callaway et al. 2003). However, few studies have quantified variation in water-use traits arising from plant interactions, or have evaluated the implications of water-use trait adjustments for ecological or ecohydrological processes (Callaway et al. 2003).

The effects of plant-plant interactions on water fluxes through both microclimate alterations and adjustments in water-use traits are not well quantified in arid and semi-arid ecosystems. Ecohydrological models can include competitive and facilitative plant-plant interactions, but adjustments in plant water-use traits in response to neighbor environments have yet to be evaluated in the context of ecohydrological models and are often rarely measured (Breshears et al. 1998, Callaway et al. 2003, Arnold et al. 2009, Tietjen et al. 2010). Thus, in my dissertation research, I examined the influence plant-plant interactions on plant water-use traits and water fluxes by addressing four main questions: 1.) How do plant neighbors influence the aboveground controls of transpiration through stomatal conductance (Chapter 1)? 2.) How do the belowground controls on transpiration associated with rooting profiles and water sources vary in the presence of neighbors (Chapter 2)? 3.) How sensitive are patch- and stand-scale evapotranspiration estimates to the effects of plant neighbors (Chapter 3)? 4.) What is our current state of knowledge about the importance of plant neighbors for predicting water fluxes and multiple temporal and spatial scales, and how can we improve upon this knowledge (Chapter 4)?

The first three questions were addressed using data collected on a common desert shrub, *Larrea tridentata*, growing under different neighbor associations defined by the presence/absence of overlapping canopies: *Larrea* growing with *Ambrosia deltoidea*, *Olneya tesota*, or *Prosopis velutina*, or *Larrea* growing alone. A variety of measurement approaches were employed to quantify *Larrea*'s stomatal behavior (porometry and gas exchange analysis) and vertical root distributions (stable isotopes, molecular techniques, root biomass). These data were analyzed via hierarchical Bayesian statistical techniques and process-based models to examine the effects of neighbors on *Larrea*'s physiological controls on transpiration. A forward-modeling, simulation-based approach that was informed by my field data was employed to explore the sensitivity of evapotranspiration and soil moisture to neighbor effects, and to identify the most important mechanisms underlying the neighbor effects. This paired field and modeling approach incorporates both the indirect influence of neighbors on water-use traits and the direct effects of plant neighbors on microclimate to explore the understudied effects of plant-plant interactions on patch and ecosystem scale water fluxes. Finally, I addressed the fourth questions by conducting a literature review to compliment my site-based, individual-species focused work to explore the broader implications of neighbor effects for patch and ecosystem water fluxes, and to make recommendations for improving upon future empirical and modeling work.

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2. SEASONAL STOMATAL BEHAVIOR OF A COMMON DESERT SHRUB AND THE INFLUENCE OF PLANT NEIGHBORS

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 occuring 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 phenomomlogical 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 = 1KPa) 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 sensivity 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, stomatal conductance

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 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 transpiration (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 (creosotebush) provides an excellent model system to explore g_s behavior of an arid-adpated 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 two 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).

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 asl). Mean daily temperature ranged from 12.2°C (December) to 33°C (July) from 1979-2013 (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 >1.5m 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. testota*, *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).

Stomatal Conductance Measurements

Stomatal conductance (g_s) was measured with a portable photosynthesis system (Li-Cor 6400XT, 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 08:00h and ended around 15:00-16:00h in the winter and began around 06:00h and ended around 13:00h in the summer, when g_s was very low; g_s was measured approximately every two hours 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 was 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). Photosynthesis (A), atmospheric [CO_2] (C_a), and leaf-to-air D were simultaneously recorded with each g_s measurement.

Stomatal Conductance 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 linearly relates g_s to (natural) log-scale D (Oren et al. 1999; Ogle et al. 2012):

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

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):

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

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 contant 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 Eqn (1) in terms of g_{ref} and S, which we use in subsequent analyses:

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

Statistical Model

For each individually logged observation i (i = 1,2,..,6879), the vector of observed g_{s} and D were assumed to follow a multivariate normal distribution with a (vector) such that:

$$\begin{pmatrix} g_{\mathrm{s}_i} \\ D_i \end{pmatrix} \sim Normal\left(\begin{pmatrix} \bar{g}_{\mathrm{s}_n} \\ \bar{D}_n \end{pmatrix}, \Sigma\right) \tag{4}$$

The means ($\bar{g}_{\mathrm{s}}$ and $\bar{D}$) correspond to the latent (unobserved) average g_{s} and D values associated with each unique measurement period, n (n = 1,2,…,1371), representing a particular cluster of leaves on an individual shrub at a given time point (recall, there were ~5 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, Eqn (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 ($\bar{g}_{\mathrm{s}}$), 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, …, 30):

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

The mean or predicted value ($\tilde{g}_\mathrm{s}$) is modeled according to the Oren model via Eqn (3), but D in Eqn (3) is replaced with the corresponding latent measurement period value, $\bar{D}_n$ (Eqn (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 Eqn (4), the univariate latent g_s model in Eqn (5), and the non-linear mean model defined by Eqn (3). Within the Bayesian model, we specified 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 $\tilde{g}_\mathrm{s}$ were allowed to vary at the level of sampling day j and shrub k (k = 1, 2, …, 24 for j = 1, 2, …, 9, and k = 1, 2, …, 12 [subset of shrubs] for j = 10, 11, …, 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):

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

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

That is, note that the means ($\bar{g}_\mathrm{ref}$ and $\bar{S}$) vary by p and j, and the standard deviations (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):

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

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

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; $\varepsilon_{\mathrm{ref}}$ and ε_{S} were each assigned normal distributions with means of zero and their own associated standard deviations. The measurement period specific standard deviations (σ_n, Eqn 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, …, 4) (Gelman et al, 2004). Each $\tau_{p,s}$ and all other standard deviation terms were assigned relatively non-informative uniform priors, and the covariance matrix (Σ, Eqn 4) was assigned a relatively non-informative inverse-Wishart prior (Gelman et al. 2013).

The statistical model described above (Eqns 1-9) represents the final model structure that we arrived at after having explored several other model variants; this model generally fit 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 Stomatal Conductance 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. 1.1 . *Larrea* growing alone generally had the highest g_s (Fig. 1.2; 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. 1.1), which was paralleled by a sharp decline in g_s and a shift to similar mean g_s among the neighborhood 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 (Eqns 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. 1.3B, $R^2 = 0.71$), the lowest during the winter (Fig. 1.3A, $R^2 = 0.45$) and summer (Fig. 1.3D, $R^2 = 0.46$), and an intermediate fit in the fall (Fig. 1.3D, $R^2 = 0.53$). In general, the model often underpredicted high values of g_s (Fig. 1.3), which often occurred at low D. The results from the multivariate measurement model (e.g., Eqn 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 Stomatal Conductance

The Bayesian application of the Oren model provides insight into g_s components that underlay the variation in *Larrea*'s stomatal behavior. The baseline reference g_s (g_{base}, Eqn 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 1.1). The day random effects (ε_{ref}) capture the temporal variability in g_{ref}, and the daily ε_{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. 1.4). Moreover, notable daily variation in g_{ref} occurred within each season (Figs. 1.4 and 1.5); 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 highest in the winter (Table 1.1) . Overall, season effects accounted for the majority of the variation on g_{ref} relative to neighborhood effects (Table 1.1).

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. 1.6, Table 1.1), but S differed significantly between neighborhood associations (Table 1.1). Baseline S (S_{base}) was significantly higher for *Larrea* growing alone or next to *A. deltoidea* compared to *Larrea* growing next to *O. testota* or *P. velutina* (Table 1.1). 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 1.1). 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 neighbord-specific S values contain zero) to changes in D (*P. velutina*, all seasons except spring; *O. tesota*, summer and fall) or only weakly sensivite to D (posterior mean for $S <$ 0.18) (Table 1.1). Based on the daily random effects (ε_S, Eqn 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. 1.6). 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 1.1).

Discussion

Seasonal Patterns of Stomatal Conductance and the Influence of Neighbors

As expected in a water-limited system (Rodriguez-Iturbe et al. 2001), this study shows that stomatal conductance (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. 1.1) (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. 1.1).

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. 1.2). 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 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 1977). Despite the end of *A. deltoidea*'s activity in September, the g_s of *Larrea* growing next to *A. deltoidea* remains siginificantly 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 banched 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 U.S.) (Suzán-Azpiri and Sosa 2006).

Components Underlying Variation in Stomatal Conductance

Daily and/or seasonal controls had the greatest influence on reference g_s (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 et al (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 abscic 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. 1.5, Table 1.1). 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 sensitivtivity to D (i.e., S) was predominately driven by neighbor effects (Fig. 1.6, Table 1.1). The effect of neighbors indicates that *Larrea*'s S may be controlled by long-term acclimitaztion 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 expecred to g_{s}. Spatial variation in *Larrea*'s rooting depth and root area could allow *Larrea* growing near trees greater access 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 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 (lowr 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 growing next to trees, agrees with prior studes 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 aperature 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 magnitdude of *Larrea*'s g_{ref}, but appear 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 of over varying time scales, such as intra-annual or seasonal responses that may reflect short-term acclimatization or inter-annual or decadal adjustments that may be partly governed by plant neighbor interactions.

Conclusions and Implications for Modeling Stomatal Conductance

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 under-predicted, especially at low D. The daily random effects indicate that reference g_s (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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Tables

Table 1.1 Posterior estimates (mean and 95% credible interval) of the reference conductance (g_{ref}, mol m^{-2} s^{-1}) at D = 1 kPa and stomatal sensitivity (S)*.

		g_{ref}			S		
Season	Neighbor	Mean	2.5th	97.5th	Mean	2.5th	97.5th
Winter	*O. tesota*	0.072	0.066	0.079	0.132	0.003	0.254
	A. deltoidea	0.081	0.073	0.091	0.298	0.198	0.391
	P. 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 season × neighbor estimates are obtained by averaging across all days within each season × neighborhood type. The overall season estimates are obtained by averaging across all neighbor types within each season.

Figures

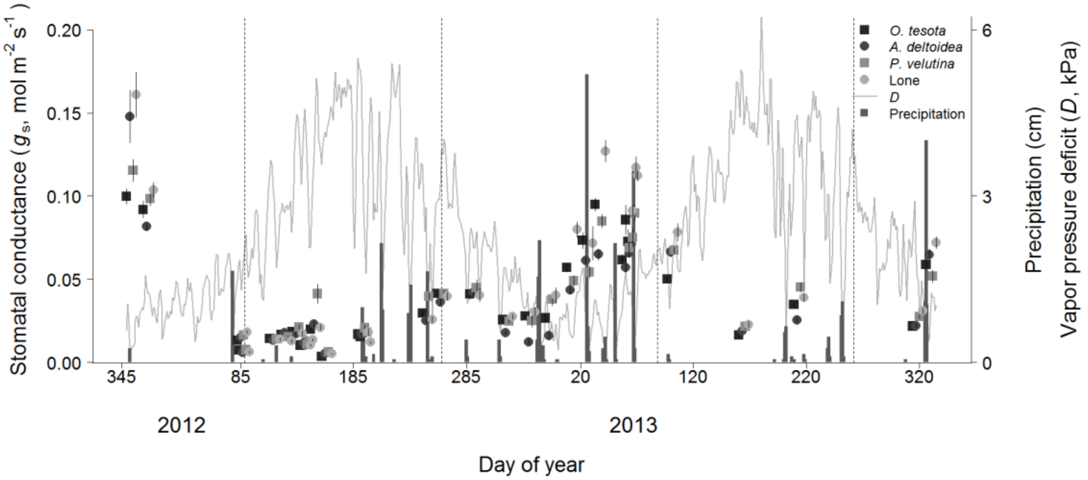

Figure 1.1. Mean (± 1 s.e.) daily stomatal conductance (g_s) of *Larrea tridentata* under four different neighborhood associations (i.e., growing in close proximity to *Olenya tesota*, *Prosopis velutina*, or *Ambrosia deltoidea*, or growing alone). Vertical bars associated with each measurement day indicate the total daily amount of precipation (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.

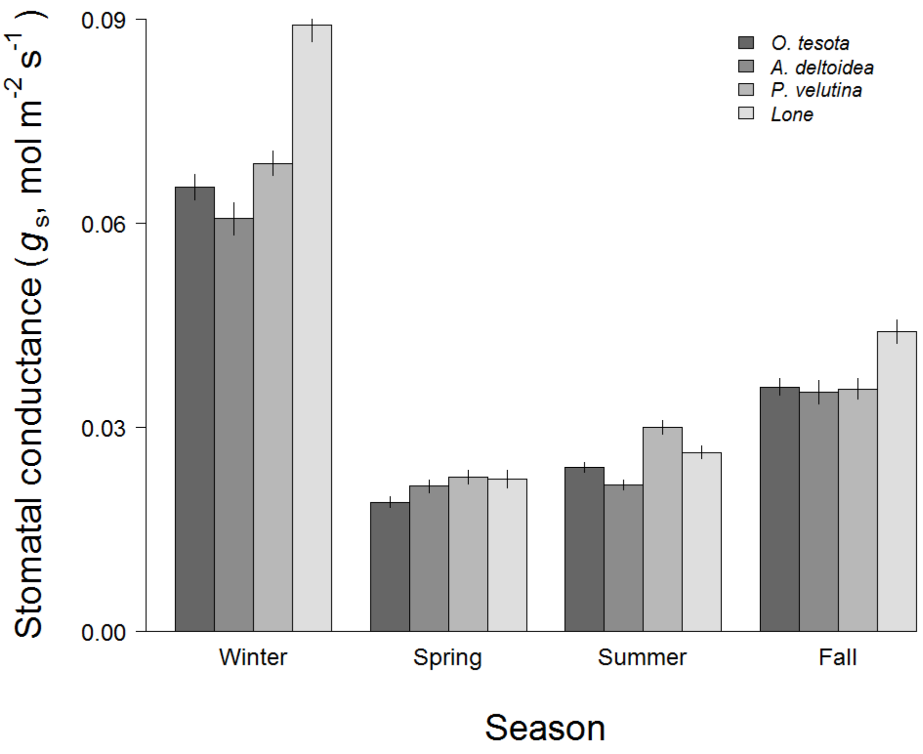

Figure 1.2. Mean (± 1 s.e.) seasonal stomatal conductance (g_s) for *Larrea tridentata* under four different neighborhood associations (see Fig. 1 for description).

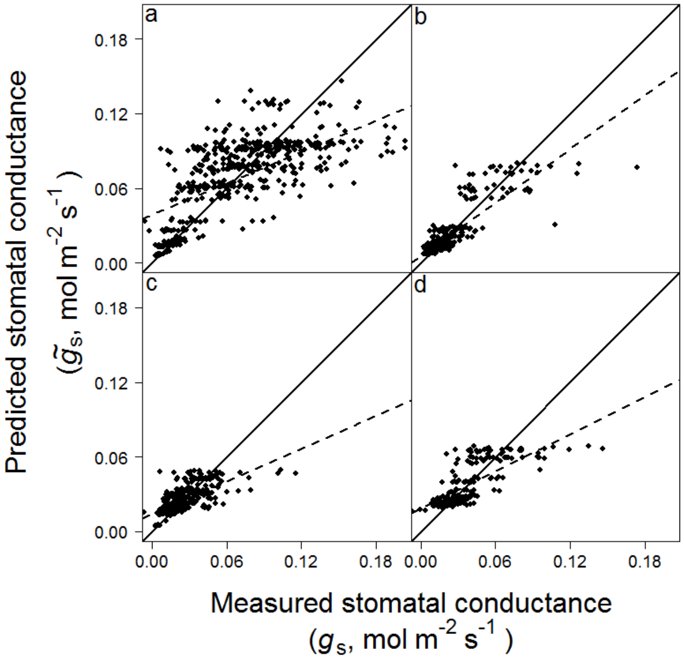

Figure 1.3. The model fits of predicted versus observed stomatal conductance for each season: A) winter (R^2 = 0.45), B) spring (R^2 = 0.73), C) summer (R^2 =0.46), and D) fall (R^2 = 0.53). The solid black line is a 1:1 line, and the dashed line indicates the best fit regression line. Four points are not shown because they exceeded the axis limits, and their inclusuion renders the plot more difficult to visualize.

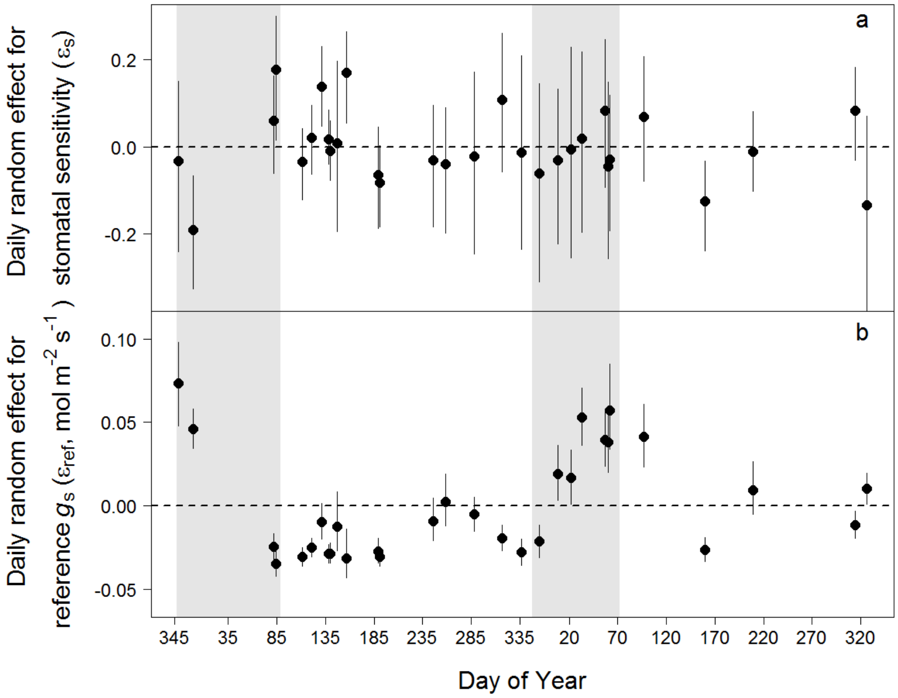

Figure 1.4. Posterior estimates (mean and 95% credible interval) for the daily random effects associated with: A) stomatal sensitivity (*S*) to vapor pressure deficit (*D*) and B) the reference stomatal conductance (g_{ref}). The gray regions indicate winter periods.

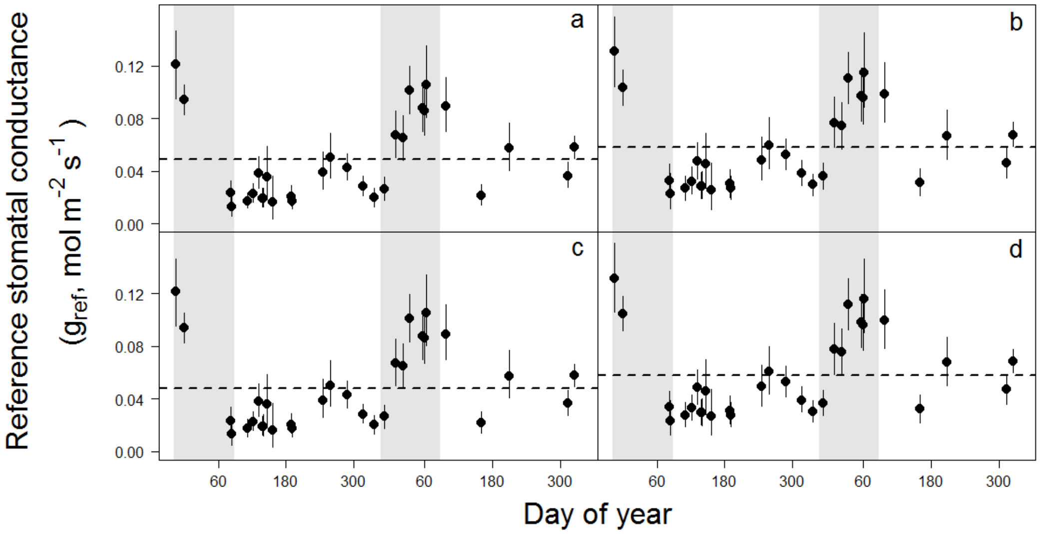

Figure 1.5. Posterior estimates (mean and 95% credible interval) from for the reference stomatal conductance (g_{ref}) for each day for *Larrea* growing A) next to *O. tesota*, B) next to *A.deltoidea*, C) next to *P. velutina*, and D) alone. Dashed lines indicate the baseline (g_{base}) posterior means for each neighborhood association. The gray regions indicate winter periods.

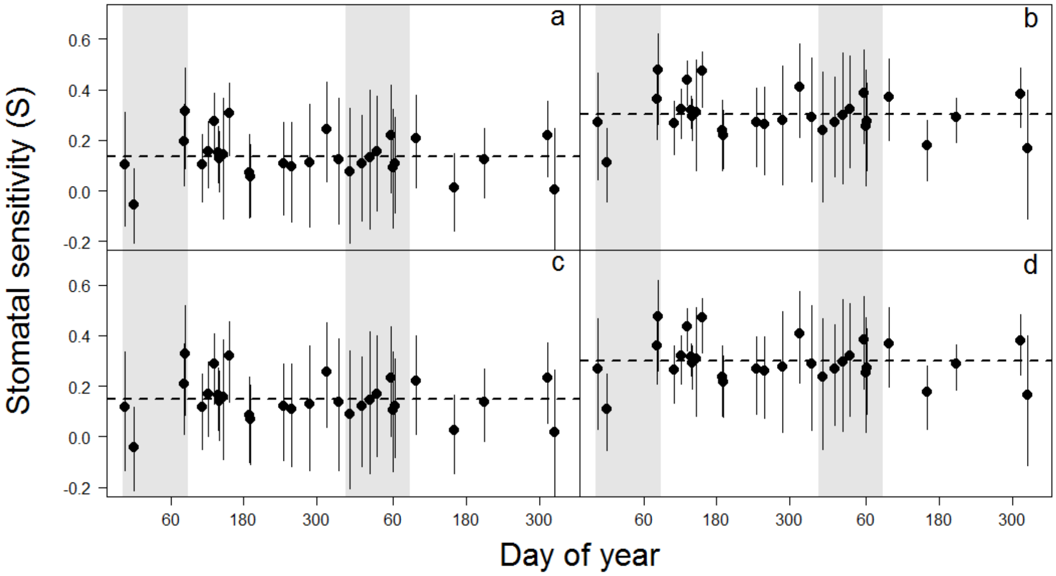

Figure 1.6. Posterior estimates (mean and 95% credible interval) for stomatal sensitivity (*S*) to vapor pressure deficit (*D*) for each day for *Larrea* growing A) next to *O. tesota*, B) next to *A. deltoidea*, C) next to *P. velutina*, and D) alone. Dashed lines indicate the baseline (S_{base}) posterior means for each neighborhood association. The gray regions indicate winter periods.

3. A FRAMEWORK FOR PARTITIONING PLANT ROOTING PROFILES FROM NEIGHBORS USING MULTIPLE DATA TYPES

Abstract

1. Vertical root distributions (“profiles”) influence plant water use and productivity, and the differentiation of root profiles between neighboring species can indicate the degree of plant interactions and niche partitioning. However, quantifying multiple species’ root distributions in the field can be labor intensive and highly destructive to the soil and plants. We describe a method for partitioning multiple species roots using minimally destructive methods to determine if neighbor interactions alter the root profile of a common desert shrub, *Larrea tridentata* (creosote bush).

2. We obtained root and soil samples from soil cores collected around *Larrea* growing alone and next to three different neighboring species. Bulk root mass was measured for each soil sample, and *Larrea* and neighboring species root presence was determined with molecular identification methods. Water extracted from the soil and paired stem samples was analyzed for its stable isotope composition (D and ^{18}O). Species-specific (i.e., *Larrea* and neighboring species) root biomass and fractional active root area were estimated through a hierarchical statistical modeling approach that combined all three datasets and accounted for detection errors.

3. The combined data-model successfully partitioned *Larrea*’s root biomass from neighboring plants and provided biologically relevant estimates of rooting profiles with greater certainty than individual analyses of each data source. The data-model results indicate that plant neighbors alter *Larrea*’s root profile; *Larrea* growing under tree

species had significantly higher root biomass in shallow soil layers than *Larre*a growing alone.

4. We provide a framework for estimating a target species root profile in the presence of multiple species. A major advantage of our framework is that it requires minimally destructive sampling methods, and it accounts for sampling errors associated with different methods. We demonstrate the utility of our approach with a common desert shrub species, which illustrated that our approach is useful in problematic study systems fraught with sample collection issues or supporting species with inhibitory compounds that prohibit the use of more sophisticated molecular methods to identify the presence of other species' roots.

Introduction

Vertical root distributions ("profiles") play an integral role in plant survival and productivity, influencing the ability of plants to acquire water and nutrients from the soil (Schwinning & Ehleringer 2001; Ogle & Reynolds 2004). The degree of overlap of roots between neighboring plants can be an important factor determining competition for belowground resources (Casper & Jackson 1997; Schenk 2006). Studies of species' coexistence and competition in plant communities are often interested in the influence of vertical differentiation of root distributions on competition for soil water or nutrient pools (Ogle & Reynolds 2004; Mommer *et al.* 2008). However, studies of vertical root differentiation require the quantification of root profiles for multiple species, an often difficult undertaking (Jackson *et al.* 1996; Mommer *et al.* 2011).

Root distribution studies are typically limited in scope as a result of methodological challenges that involve trade-offs between the spatial extent of the root system studied, time investment, and level of destruction to the plant and soil. Excavation techniques are commonly used (Bohm 1979; Brisson & Reynolds 1994; Jackson *et al.* 1996) because they offer a detailed assessment of vertical and horizontal rooting patterns. However, excavations are time consuming, highly destructive, and prohibit simultaneous aboveground studies on the plants (Polomski & Kuhn 2002; Danjon & Reubens 2007).

Molecular genetic techniques (e.g., polymerase chain reaction [PCR]) offer an alternative approach to identify species in mixtures of root samples collected from minimally destructive soil cores (Mommer *et al.* 2011), and have been applied in diverse ecosystems, from temperate to alpine systems (Bobowski *et al.* 1999; Mommer *et al.* 2010; Brunner *et al.* 2001). However, high concentrations of PCR inhibitors in roots

(Mommer *et al.* 2011) combined with the small cross-sectional area of a typical soil core may under-estimate root presence, and previous studies have not addressed these sources of uncertainty in subsequent data analysis (Bobowski *et al.* 1999; Brunner *et al.* 2001; Mommer *et al.* 2008).

Another minimally destructive technique for quantifying root profiles involves the evaluation of stable isotopes in plant and soil water samples, which offer insight into the depths that roots actively acquire water (Ehleringer & Dawson 1992; Dawson *et al.* 2002). Stable isotope data are typically analyzed with simple linear mixing (SLM) models (Phillips & Gregg 2003) that do not provide direct estimates of rooting profiles. However, linking SLM models with a model of root water uptake can provide estimates of the root area profile (Ogle *et al.* 2004, 2013).

This study applies a novel modeling approach that partitions root biomass between neighboring species through the combination of three distinct datasets—molecular identification of roots, bulk root biomass, and stable isotopes—while accounting for method-based detection and measurement errors in a hierarchical Bayesian framework. Individual datasets are limited in scope, offering incomplete information on the root profile of a species. For example, molecular identification indicates species' presence throughout the soil profile, but does not provide information on the overall magnitude of root biomass. Likewise, stable isotope data indicate the relative distribution of a species' active roots, but is not a direct measure of biomass. Finally, bulk root biomass data consists of a mixture of multiple species' roots that must be partitioned to examine the root biomass of singular species. However, the combined datasets offer information on the root profiles of a target species and its surrounding neighbors, allowing for the quantification of a species' fractional distribution of active roots and root biomass throughout the soil profile.

We describe and illustrate our framework by applying it to data collected for a common desert shrub (Barbour 1969), *Larrea tridentata* (Sessé & Moc. ex DC.) Coville (creosote bush). *Larrea*'s root distribution can be impacted by competition with neighboring shrubs (Brisson & Reynolds 1994). We quantified *Larrea*'s vertical root distribution under different neighborhood associations that could represent different competition environments (Yeaton *et al.* 1977): *Ambrosia deltoidea* (Torr.) W.W. Payne (triangle-leaf bursage), *Olneya tesota* A. Gray (desert ironwood), and *Prosopis velutina* Wooton (velvet mesquite). *Ambrosia* is a drought deciduous small shrub (Szarek 1977), and *Olneya* and *Prosopis* are deeply rooted tree species (Suzan *et al.* 1996; Schade *et al.* 2003). We apply our analysis framework to quantify *Larrea*'s root profile to address two questions: 1) Does *Larrea*'s root profile vary depending on plant neighbor identity? 2) To what degree do *Larrea*'s roots overlap (vertically) with roots of neighboring species? We assess rooting profiles through indices of both root biomass and active root area for water uptake.

Methods

Site Description and Root Collection

Root samples were collected in the Sonoran Desert near Phoenix, Arizona, at the McDowell Mountain Regional Park (33.7261N, -111.6987W, 476 m asl). The site is dominated by *Larrea tridentata*, *Ambrosia deltoidea*, *Prosopis velutina,* and *Olneya* *tesota*, with many shrubs growing in close proximity with overlapping canopies. Mean annual precipitation (1981-2010) was 29.6 cm and mean daily temperature ranged from 11.5°C (December) to 33°C (July) (WRCC, 2013).

Plants with overlapping canopies were considered to be neighbors, and *Larrea* growing with a canopy separated by at least 1 m from another plant's canopy was considered to be growing alone. Four neighborhood associations were studied: *Larrea* growing near *Ambrosia, Olneya,* or *Prosopis,* and *Larrea* growing alone. Soil cores for both root identification and stable isotope analysis were collected on August 20 and 21, 2012 in five soil layers (0-10, 10-20, 20-30, 30-40, and 40-60 cm), and a full description of the field sample collection is included in Appendix A.

Molecular Identification

Genomic DNA was extracted using a method developed for roots with high concentrations of PCR inhibitors, such as polysaccharides and polyphenolics (Brunner *et al.* 2001). We highlight the methods here and provide a full description in Appendix A. Despite the targeted DNA extraction protocol to remove inhibitors, viscous brown materials sometimes persisted in samples after extraction, indicating the presence of potential PCR inhibitors (Lodhi *et al.* 1994; Paterson *et al.* 1993). High concentrations of phenolics and tannins, known PCR inhibitors, have been observed in *Larrea* roots (Hyder *et al.* 2002). Thus, additional purification steps were adapted from Paterson *et al.* (1993). The nuclear rDNA Internal Transcribed Spacer region (ITS1-5.8S gene-ITS2; Baldwin *et al.* 1995) was amplified with primers ITS4 and ITS5 (White *et al.* 1990), and PCR was initially conducted on DNA extracts that were diluted with deionized water at ratios of

1:10 and 1:20. However, if PCR did not result in the amplification of fragments of the expected sizes (Table 2.1), additional dilutions (1:30 and 1:40) were attempted to reduce interference with PCR inhibitors (Picard *et al.* 1992). All PCR products were digested with restriction endonuclease RsaI and samples from the *Prosopis* pair were also digested with BssHII; the distinct fragment lengths from digestions with RsaI and BssHII (Thermo Scientific) are shown in Table 2.1 for each species. Extensive testing of the methods (described in Appendix A) was conducted since the PCR methods described above have not previously been applied to roots of the desert species in this study.

Stable Isotope Analysis

Water from the stem and soil samples (Appendix A) was extracted using cryogenic distillation (West *et al.* 2006) at the University of Wyoming Stable Isotope Facility. Soil water extracts were analyzed for natural abundance of D and ^{18}O using a Liquid Water Isotope Analyzer (Los Gatos, Mountain View California) at Arizona State University. Stem water extracts were analyzed at the Cornell University Stable Isotope Laboratory for natural abundance of D and ^{18}O using an Thermo Delta V Isotope Ratio Mass Spectrometer interfaced to a Temperature Conversion Elemental Analyzer (Thermo Scientific, Waltham, Massachusetts) to avoid possible issues with organic contaminants that may arise with the Liquid Water Isotope Analyzer (Schultz *et al.* 2011).

Overview of Modeling Approach

Root profiles were quantified with a latent variable, the fraction of active root area (f), a relative measure of the vertical distribution of functional roots. We estimated f

based on three linked sub-models: (1) a biophysical model of root water uptake informed by stable isotope data, (2) root presence informed by molecular identification, and (3) an empirical root biomass model that pairs bulk biomass data with presence data (Fig. 2.1a-c). Ogle *et al* (2004, 2013) consider f to be a mixture of normalized gamma distributions (eqn 1) that allows for a continuous, flexible root profile that can be either unimodal or bimodal. Relevant to all three datasets, for neighbor association j (j = 1, 2, 3, 4) and soil depth z (z = 1, 2, …, 60 cm), *Larrea*'s active root profile is modeled as:

$$f_{j,z} = w_j Gamma(z \mid a_1, m_{1_j}) + (1 - w_j) Gamma(z \mid a_2, m_{2_j}) \qquad \text{(eqn 1)}$$

The mixture weight, w, represents the relative importance of roots in the shallow layers, and the mean depths of the shallow and deep roots (m_1 and m_2, respectively; *i.e.*, means of the associated gamma distributions) vary among neighbor associations. Conversely, for simplicity, a_1 and a_2, which influence the shape of the gamma distributions, are assumed to be the same across neighbor associations.

Water Uptake Model and Stable Isotopes

Following Ogle et al. (2004), a biophysical model of root water uptake (Schwinning & Ehleringer 2001; Ogle *et al.* 2013) was paired with stable isotope data using a process-based isotope mixing model that informs f. The predicted stem isotope values ($\delta^{pred}_{stem,m,j}$) for each neighbor association j (j=1,…4), for both deuterium (δD, m=1) and δ^{18}O (m=2) were considered to be a mixture of the observed soil water isotope values

($\delta^{obs}_{soil,m,j,i}$) based on the proportion of water (p) obtained from each soil layer i (i = 1 [0-10 cm], 2 [10-20 cm], …, 5 [40-60 cm]):

$$\delta^{pred}_{stem,m,j} = \sum_{i=1}^{5} p_{j,i}\delta^{obs}_{soil,m,j,i} \qquad \text{(eqn 2)}$$

The observed soil isotope values were averaged across soil cores within each depth increment and neighbor association, and the observed stem isotope values were assumed to be normally distributed around the predicted value in eqn 2.

We model the layer-specific p for each neighborhood association as *Larrea*'s predicted water uptake from each layer (q), normalized by the total water uptake from all layers such that:

$$p_{j,i} = \frac{q_{j,i}}{\sum_{i=1}^{5} q_{j,i}} \qquad \text{(eqn 3)}$$

The predicted water uptake is based on a biophysical model of root water uptake:

$$q_{j,i} = f_{j,i}\frac{K_{soil,j,i}K_{root,j}}{K_{soil,j,i}+K_{root,j}}(\Psi_{soil,j,i} - \Psi_{tloss}) \qquad \text{(eqn 4)}$$

With the exception of the latent quantity f, quantities in eqn 4 were obtained from field data where Ψ_{soil} is the soil water potential, Ψ_{tloss} is the root water potential at the turgor loss point, and K_{soil} and K_{root} are the hydraulic conductance of the soil and roots, respectively. A full description of how the soil and root hydraulic properties were determined is provided in Appendix A. Note that $f_{j,i}$ above is the fraction of roots in layer i, which is obtained by summing $f_{j,z}$ (eqn 1) over all z within layer i, for each neighbor association j.

Root Presence Model

A model of *Larrea*'s root presence from molecular identification was motivated by occupancy models that explicitly incorporate detection probabilities associated with imperfect sampling (Mackenzie *et al.* 2002). False negatives could be generated by two different processes, and the first source was associated with soil core sampling. Roots in desert systems tend to be sparsely distributed across space (Wilcox *et al.* 2004), and thus the soil auger may under-sample roots within its small cross-sectional area. The second source of false negatives results from the imperfect nature of PCR as a result of high concentrations of inhibitors and/or low concentrations of DNA. Problems with inhibitors often required multiple PCR attempts with higher dilutions on a single sample, and inhibitors potentially contributed to false negatives.

The likelihood of observing a species' roots ($r = 1$, root is present; $r = 0$, root is not present) in each soil core sample is assumed to depend on the probability that a species' has roots in a given layer in the soil, ϕ, and the probability of detecting the presence of roots, p_d, given the soil sampling and PCR methods. Thus, the likelihood of observed $r = 1$ or $r = 0$ in each soil sample n ($n = 1, 2, \ldots, 95$) is:

$$\begin{aligned} P(r=1 \mid \phi, p_d) &= p_d\phi \\ P(r=0 \mid \phi, p_d) &= \phi(1-p_d)+(1-\phi) \end{aligned} \qquad \text{(eqn 5)}$$

p_d can be defined as the product of two probability terms: β, the probability of collecting roots in a sample, and γ, the probability of PCR successfully detecting the presence of a species' roots given the sample contains roots:

$$p_d = \beta\gamma \qquad \text{(eqn 6)}$$

Since multiple PCR attempts were conducted at various dilutions until PCR successfully detected root presence, the probability that PCR successfully amplifies genetic material, γ, is informed by the number of observed failures (f) prior to a successful result. Assuming the number of failure (F) until a success follows a geometric distribution, then:

$$P(F = \mathrm{f}) = (1-\gamma)^{\mathrm{f}}\,\gamma \qquad \text{(eqn 7)}$$

Detection issues associated with soil auger sampling were accounted for by considering the successful collection of roots in a soil sample (S) to be a Bernoulli random variable where the presence of roots occurs with probability $P(S = 1) = \beta$. Soil core samples that do not contain roots are assumed to be the result of the soil auger missing roots, which occurs with probability $P(S = 0) = 1- \beta$. We assumed that p_d was the same for each species (eqns 6-7), with the exception of *Prosopis*. *Prosopis* roots could only be detected under *Prosopis*-*Larrea* neighbors, where roots were analyzed individually (see Appendix A for details), and thus the detection probability was set to zero for *Prosopis* for all other neighbor types.

Finally, the probability that *Larrea* has roots in a given layer i, ϕ, describes the presence of roots within the soil profile, with values near one indicating a high likelihood of *Larrea* root presence. Thus, we expect ϕ to be directly related to the fraction of *Larrea*'s active roots, f, such that:

$$\phi_{j,i} = \phi^{*}\left(1-e^{-a\,f_{j,i}}\right) \qquad \text{(eqn 8)}$$

Here, ϕ^{*} is the probability that would occur as f goes to infinity, but since $0 \le f_{j,i} \le 1$, the maximum probability that *Larrea* has roots in any layer i is $\phi^{*}(1-e^{-a})$.

We used a simpler model with coarser, soil layer resolution for the probability of non-*Larrea* species (v = 1 [*Prosopis*], 2 [*Olneya*], 3 [*Ambrosi*a], or 4 [other unidentified species]) rooting in a soil layer, ϕ, since there was no additional data help inform their root distributions (i.e., no stable isotopes). We assumed that ϕ declines with distance (d) to the closest shrub of that species (d is relative to the target *Larrea* shrub, l) for shallow soil layers (g = 1, 0-20 cm) and deep layers (g = 2, 20-60 cm):

$$\operatorname{logit}\left(\phi_{v,g,l}\right) = b_v - \alpha_{v,g} \times d_l \qquad \text{(eqn 9)}$$

The parameters, b and α, varied with each species v since vertical and lateral root distributions are expected to vary by species (Schenk & Jackson 2002; Ogle & Reynolds 2004). Additionally, the lateral extent of shallow versus deep roots is expected to differ (Jackson *et al* 1996), and thus α varied by g.

Bulk Root Biomass Model

The observed bulk root biomass (R) collected from each soil sample n (n = 1, 2, …, 95) was assumed to be normally distributed:

$$R_n \sim Normal(\mu_{R_{i,l}}, \sigma_R) \qquad \text{(eqn 10)}$$

Where the mean root biomass (μ_R) varies by soil layer i and *Larrea* shrub l (l = 1…13) associated with each sample; μ_R was modeled as a mixture of roots from *Larrea* and its neighbors:

$$\mu_{R_{i,l}} = \left(p_{larrea_l} f_{j,i} + \left(1 - p_{larrea_l}\right) f_{o_i} \right) R_{tot_l} \qquad \text{(eqn 11)}$$

Again, *f* (eqn 1) is the fractional active root profile of *Larrea*, and f_o is the root profile of "other" neighboring species, which is based on summing the f_o's in eqn 13 over depths *z* corresponding to each layer *i*. R_{tot} is the observed total root biomass in the soil profile below each *Larrea* shrub, and p_{larrea} is the relative proportion of *Larrea* roots compared to all other species. Soil samples without roots or at depths that could not be sampled were treated as missing data and are estimated from eqn 10, and these estimates were subsequently used to compute R_{tot}.

The proportion of *Larrea*'s roots under each shrub is based on the probability of *Larrea* and the neighboring species having roots in a soil layer, ϕ, for each neighbor association *j* associated with shrub *l*:

$$p_{larrea,l} = \frac{\sum_i \phi_{i,j}}{\sum_i \phi_{i,j} + \sum_g \sum_v \lambda_{v,g,l}} \qquad \text{(eqn 12)}$$

Since soil samples were collected around *Larrea* canopies, the contribution of root biomass from neighboring plants is expected to consist mainly of lateral roots that occur more frequently in surface layers (Schenk & Jackson 2002), and thus the fractional rooting area of neighboring plants (f_o) was expected to decline exponentially with depth *z* ($z = 1, 2, \ldots, 60$ cm) with rate parameter (ρ) that varies by neighbor association *j*.

$$f_{o,j,z} = \rho_j e^{-\rho_j z} \qquad \text{(eqn 13)}$$

Data-Model Performance

We compared the degree of uncertainty and model fit in the analysis of each individual dataset (*e.g.*, stable isotope, molecular identification, and bulk root biomass) to the combined model to evaluate the improvement in estimates and inference with the multiple datasets approach.

The process-based isotope mixing model was compared to a simpler mixing model that did not include a biophysical water uptake model. We avoided over-parameterization by grouping the soil into three layers and the proportion, *p*, of water acquired from each layer was assumed to be proportional to soil water content, s*wc*, times an index of the proportion of water taken-up from each layer, *u*. Thus, for neighborhood association *j*, isotope type *m*, and layer *i* (*i* = 1 [0-10 cm], 2 [10-40 cm], 3 [40-60 cm]):

$$\delta_{stem,m,j}^{pred} = \sum_{i=1}^{3} p_{j,i}\delta_{soil,m,j,i} \qquad \text{(eqn 14)}$$

$$p_{j,i} = \frac{swc_{j,i} \times u_{j,i}}{\sum_{i=1}^{3} swc_{j,i} \times u_{j,i}} \qquad \text{(eqn 15)}$$

Similar to a Bayesian implementation of a simple linear mixing (SLM), the vector $\boldsymbol{u}_j$ (length 3) was given a non-informative dirchlet prior (Moore & Semmens 2008). Model fit was evaluated by computing the coefficient of determination (R^2) from a regression of the observed versus predicted stem isotope data, for both the simple model (isotope only data) and the combined, process-based model (all three datasets).

The simplified analysis of the molecular data was conducted using an occupancy model applied only to the molecular data, with a uniform, U(0,1), prior for ϕ (see eqn 8). For both the simple and combined model, model fit was assessed by computing the prediction accuracy (percent of the model predicted samples with *Larrea* roots present compared to the observed samples with *Larrea* roots present).

The simplified analysis of root biomass data involved comparing the bulk root biomass estimates to a more traditional model of root mass profiles where the bulk fractional root biomass declines non-linearly with depth (Gale & Grigal 1987; Jackson *et al.* 1996). The mean model of bulk root biomass (eqn 10) was modified such that R_{tot} was only scaled by f in eqn 16, where f was defined as:

$$f_{j,z} = 1 - \kappa_j^{\ z} \qquad \text{(eqn 16)}$$

and is summed over all z within layer i for application to eqn 11. κ describes the decline of bulk root biomass with depth. For both the simple (biomass data only) and combined models, model fit was assessed by calculating the R^2 from a regression of the observed and predicted root biomass.

Implementation

The above models were implemented in OpenBUGS (Spiegelhalter *et al.* 2003), and posterior estimates are presented as posterior means with 95% credible intervals (2.5th and 97.5th percentiles). A full description of the prior distributions, model implementation, and model code is included in the Appendix A.

Results

Model Evaluation

The model that analyzed all datasets simultaneously was able to partition root biomass between *Larrea* and neighboring plants, and generally yielded more precise estimates of parameters associated with *Larrea*'s root profile in comparison to analyses of individual datasets (Table 2.3). Moreover, the predicted ^{18}O composition of stem water obtained from the combined model had a slightly higher R^2 (Table 2.3) than the isotopes-only data model. However, the isotopes-only data model predictions of the δD composition of stem water had a higher R^2 than the combined data model, but the former produced unrealistic estimates of water uptake, allowing water to be taken up from layers in the soil that had water potentials below *Larrea*'s estimated turgor loss point (Fig S2.1, Appendix B).

Importantly, the full model that combined all three datasets provided estimates with narrower credible intervals for the probability of *Larrea* root presence (ϕ) compared to analyzing each data set independently with relatively non-informative priors (Fig S2.2, Appendix B). On average, the combined data model predicted the presence of *Larrea* in 79% of the observed samples containing *Larrea*. The analysis using only the occupancy model with the molecular data with relatively non-informative priors predicted *Larrea*'s presence in 67% of the actual observed samples containing *Larrea* (Table 2.3). The root biomass model of the combined dataset explained more variation compared to the traditional, nonlinear model (eqn 16), which had a lower fit compared to the gamma mixture model (eqn 1) (Table 2.3).

Model Application: Effect of Neighbors on Larrea's Root Profile

Larrea's active root area (*f*, Fig. 2.2) and root biomass (μ_R, Fig. 2.3) profiles varied based on neighborhood association. *Larrea* growing next to the tree species

(*Prosopis* and *Olneya*) had higher *f* and root biomass in shallower depths (Fig. 2.2a, c) compared to *Larrea* growing alone (Fig. 2.2d) or next to *Ambrosia* (Fig. 2.2b). Moreover, *f* of *Larrea* growing next to *Prosopis* peaked between 30-40 cm depths (Fig. 2.2c), and *Larrea*'s predicted root biomass was significantly higher when growing near *Prosopis* (Fig. 2.3a) compared to *Larrea* in other neighborhood associations (Fig. 2.3b-d). *Larrea*'s root biomass growing alone and next to *Ambrosia* (Figs. 2.3a and 2.3c, respectively) was generally low between 0-40 cm, with comparatively high biomass between 40-60 cm. Summing over depths, *Larrea*'s total root biomass was significantly greater when growing next to *Olneya* or *Prosopis* than when growing next to *Ambrosia* or alone. *Larrea's* root biomass when growing alone or next to *Ambrosia* was minimal at 0-10 cm (Fig. 2.3b and 2.3d), and the root biomass of neighboring species' was greatest in the upper 10 cm of the soil (Fig 2.3f and 2.3h), indicating minimal overlap between *Larrea* roots and neighboring species. However, *Larrea* growing next to tree species had vertical root distributions that had greater overlap with neighboring species root biomass compared to *Larrea* growing next to *Ambrosia* (Fig. 2.3a, 2.3c, 2.3e, and 2.3g).

Discussion

Model Performance and Applications

Plant root distributions are difficult to quantify directly, and methods involving direct observation are subject to limitations (Lynch 1995; Jackson *et al.* 1996). Soil core sampling is minimally destructive, but can under-sample roots or provide limited information on bulk root biomass (Danjon & Reubens 2007; Polomski & Kuhn 2002).

However, we demonstrate that the combination of multiple data types can offer a more detailed quantification of root systems. Stable isotopes are commonly used to estimate depths of active water uptake, and the prevalence of stable isotope laboratories and technologies allows for straightforward sample preparation and analysis (Dawson *et al.* 2002; Ogle *et al.* 2004; West *et al.* 2006). Our multi-dataset approach that linked *Larrea*'s active rooting area to stable isotope data produced biologically realistic and more precise estimates of proportional soil water uptake with finer depth resolution (Fig S2.1) compared to a simpler mixing model approach that was only informed by isotope data and soil water content. While the simpler mixing model had a higher R^2 (Table 2.2) for predicted stem δD, the smaller R^2 for predicted stem δ^{18}O and the biologically unrealistic estimates of proportional water uptake from dry soil layers suggest the simpler, isotope-only approach does not adequately capture root water uptake dynamics, and it does not provide direct estimates of rooting distributions.

The combined model approach allowed for the partitioning of *Larrea*'s root biomass from other species and improved estimates of the presence of species' roots relative to the molecular-only data analysis. (Table 2.3, Fig. S2.2). Mommer *et al* (2008) presented a method to partition the proportion of biomass belonging to each species using real time PCR (qPCR). However, in systems such as our study system, where plant roots contain high amounts of inhibitory compounds, method development for qPCR requires additional costs and time commitment, and samples may be subject to higher failure rates (Mommer *et al.* 2011). Our approach of pairing simpler PCR methods with a stable isotope analysis for studying belowground rooting distributions provides an alternative to more labor intensive approaches such as qPCR. We also demonstrate the importance of accounting for detection issues associated with PCR, and our PCR success rate of 0.54 [0.48, 0.60] indicates that false negatives are common and must be explicitly considered. We present a detection modeling framework that can be adapted to other systems with modifications to the model structure. Previous studies have not specified a statistical framework for accounting for false negatives, and our occupancy-inspired model framework may be useful in other PCR-based studies (Bobowski *et al.* 1999; Brunner *et al.* 2001).

We also demonstrate the usefulness of incorporating uncertainty and process information in estimating latent (unobservable) species-specific active root area or root biomass (see also, Cressie *et al.* 2009). Our model predicts species-specific root biomass in each soil layer, and accounts for limitations in sampling and the contributions of neighboring species' root biomass. The inclusion of multiple datasets combined with the fractional root area model predicted bulk root biomass better than a more classical, simple model fit to bulk root biomass (Table 2.3). Models of root biomass typically assume an exponential or nonlinear decline with depth, but woody plant roots may not necessarily be concentrated at the surface (Gale & Grigal 1987; Lynch 1995; Ogle *et al.* 2004). In arid or semi-arid systems, deep roots may be more important for physiological activity during dry periods than shallow roots (Schwinning *et al.* 2002; Ogle & Reynolds 2004).

Ecological application: Larrea tridentata*'s root profile*

Our statistical framework for partitioning the root profiles of *Larrea tridentata* and select neighboring species demonstrates that plant neighbors alter *Larrea*'s vertical root distribution (Fig. 2.2 and Fig. 2.3). *Larrea* had greater root biomass and more active roots at shallow depths (<40 cm) when growing next to tree species neighbors. *Olneya* and *Prosopis* are known to have facilitative effects on understory shrubs via canopy shading, and *Larrea*'s roots may be more active in shallow layers as a result of increased water availability (Suzan *et al.* 1996; Schade *et al.* 2003).

Under stressful drought conditions, arid shrubs can shift water uptake and root activity to deeper soil layers (Schwinning *et al.* 2002; Ogle & Reynolds 2004). *Larrea* growing alone or next to *Ambrosia* had very little biomass or root area in shallow soil layers, and these neighbor associations may experience greater limitations in surface soil water as a result of increased evaporation due to decreased canopy shading (Suzan *et al.* 1996). *Larrea* and *Ambrosia* roots have been shown to avoid overlap (Yeaton *et al.* 1977; Brisson & Reynolds 1994), and little vertical overlap in root biomass was also observed in this study (Fig 2.3). The variation in *Larrea*'s root profile arising from plant neighbor associations highlights a source of variation in *Larrea* root profiles, in addition to previously reported variation across deserts (Ogle & Reynolds 2004).

Conclusions

Ecological data are complex, often affected by multiple sources of uncertainty and methodological limitations, and models that combine diverse datasets and mechanistic constraints can help to evaluate such data, lending insight into latent quantities or processes of interest (Cressie *et al.* 2009). Previous studies demonstrate the merits of combining diverse datasets, and a similar multi-data modeling approach has been applied to ecosystem processes that are difficult to measure, such as belowground autotrophic respiration or the effect of permafrost thaw on plant transpiration (Cable *et al.* 2014; Tucker *et al.* 2014). Our approach to partition root biomass between *Larrea* and other species provided additional information on *Larrea*'s rooting patterns and improved model fits compared to more simplistic, independent analyses of each dataset. Our combined multi-model, multi-data approach provides a framework for analyzing root distributions using minimally destructive sampling and is particularly useful in ecological systems suffering from methodological difficulties, such as arid regions (Jackson *et al.* 1996; Mommer *et al.* 2011).

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Tables

Table 2.1. Species information for genetic analysis to identify presence in root samples based on the presence of unique fragment base pair (bp) lengths.

Species	Accession Number	Length of Amplified Fragment (bp)	Identifying Fragment length RsaI (bp)	Identifying Fragment length BssHII (bp)
Larrea tridentata	JF267309.1*	660	600†	660
Olneya tesota	KR020829	730	325, 170†	730
Prosopis velutina	AY145703.1* AY145702.1 *	750	750	100, 250, 350
Ambrosia deltoidea	KR020830	800	470, 250†	800

*Fragment patterns that were verified against pre-existing sequence data in Genbank.

†Fragments below 100 bp are expected to be present. However, fragment lengths below 100 bp were not readily detected in our gel electrophoresis approach, and thus we do not include fragments below 100 bp as unique, identifying fragments for a given species.

Table 2.2. Description of parameters and variables in each sub-model of the combined, process model.

Symbol	Description	Source/type
Fractional rooting area		
f	fractional area of active roots	eqn 1
w	proportion of surface roots	parameter
a_1,a_2	describes shape of vertical root distributions	parameter
m_1,m_2	average rooting depths for deep and shallow roots	parameter
Water uptake		
p	proportional water uptake	eqn 3
δ_{soil}^{obs}	soil water isotope abundance	data
δ_{stem}^{pred}	stem water isotope abundance	parameter
K_s	soil hydraulic conductance	computed from data*
K_r	root hydraulic conductance	computed from data*
Ψ_{tloss}	turgor loss water potential	computed from data*
Ψ_s	soil water potential	computed from data*
Root presence		
β	probability of sampling roots in the soil core	parameter
γ	probability of PCR success	parameter
ϕ	probability of root presence	parameter
ϕ_*	maximum probability of root presence	parameter
a	slope of probability of root presence as fractional active root area increases	parameter
r	presence of root in sample	data
d	distance of closest shrub	data
b	intercept for logit ϕ (non-*Larrea* species)	parameter
α	slope for logit ϕ (non-*Larrea* species)	parameter
Root biomass		
μ_R	mean root biomass in each soil layer	eqn 11
R_{tot}	total root biomass under each shrub	data
p_{larrea}	proportion of *Larrea* roots in root mixtures	eqn 12
f_o	fractional root of non-*Larrea* species	eqn 13
ρ	decay of root area with depth of non-*Larrea* species	parameter
Simple linear mixing model		
p_{slm}	fractional water uptake from each layer	eqn 15
s	soil water scaled proportional water uptake	parameter
Simple root biomass model		
κ	shape parameter describing root decline with depth	parameter

* Additional information about data collection and parameterization is included in the Appendix A.

Table 2.3. Evaluation of model performance between the combined, process model approach and simpler, individual analyses of datasets.

Dataset	Model	Model Fit	Measure of Fit
Stable isotope (stem ^{18}O)	Isotopes-only	0.18	R^2
	Combined datasets	0.21	R^2
Stable isotope (stem D)	Isotopes-only	0.49	R^2
	Combined datasets	0.15	R^2
Molecular	Molecular-only	67%	Prediction accuracy
	Combined datasets	79%	Prediction accuracy
Root biomass	Biomass-only	0.06	R^2
	Combined datasets	0.26	R^2

Figures.

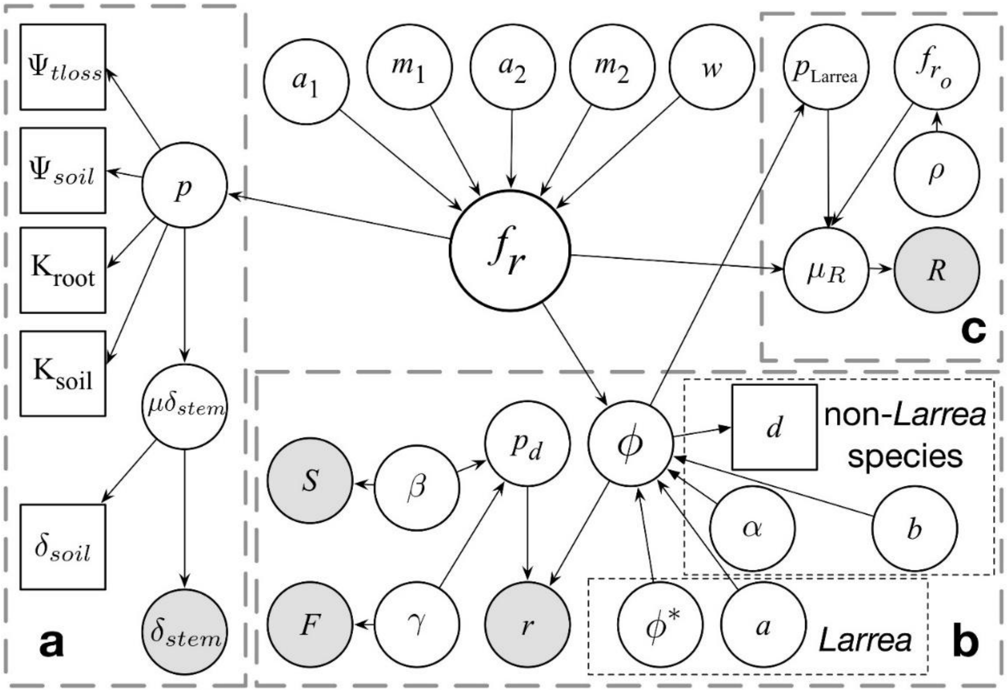

Figure 2.1. A directed acyclic graph (DAG) that represents the combined dataset model, with sub-models (panels a-c) in relation to *Larrea tridentata*'s fraction of active root area (*f*). Each sub-model depicts the analysis of a dataset in relation to *f*, such as in a biophysical model of active root water uptake (panel a, eqns 2-4) using stable isotope data (δ_{stem} and δ_{soil}). A sub model (panel b) of the presence of *Larrea* and non-*Larrea* species roots in the soil profile accounts for detection issues (eqn 5-9) and uses molecular identification data (*r*). The third sub-model (panel c) accounts for the contribution of both *Larrea* and neighboring species roots (eqn 10-12) to the bulk root biomass (*R*) non-*Larrea* species (f_o, eqn 13) as well as *Larrea*'s root profile (*f*, eqn 1). Arrows indicate conditional dependency; circles indicate stochastic nodes, with shaded circles representing stochastic data nodes and open circles representing unknown quantities; squares indicate deterministic data nodes.

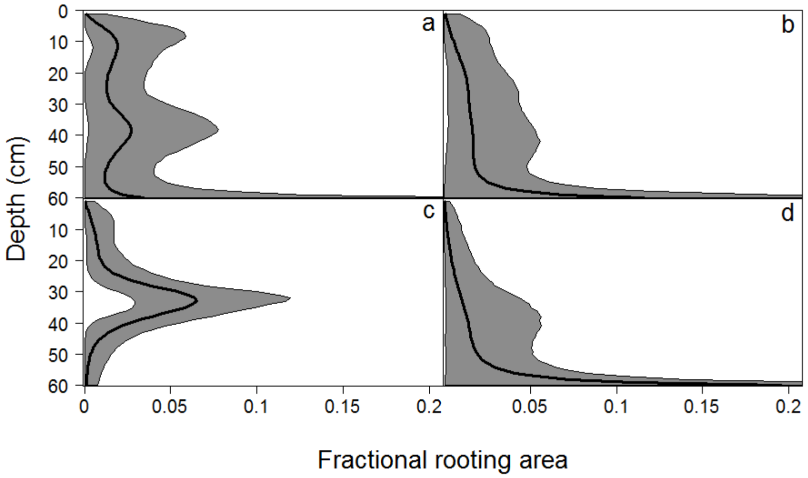

Figure 2.2. The fractional active root area (*f*) of *Larrea tridentata* under four different neighborhood associations, with *Larrea* growing next to: (a) *Olneya tesota*, (b) *Ambrosia deltoidea*, or (c) *Prosopis velutina*, or (d) growing alone. The solid black line indicates the posterior mean and shaded grey regions show the 95% credible regions.

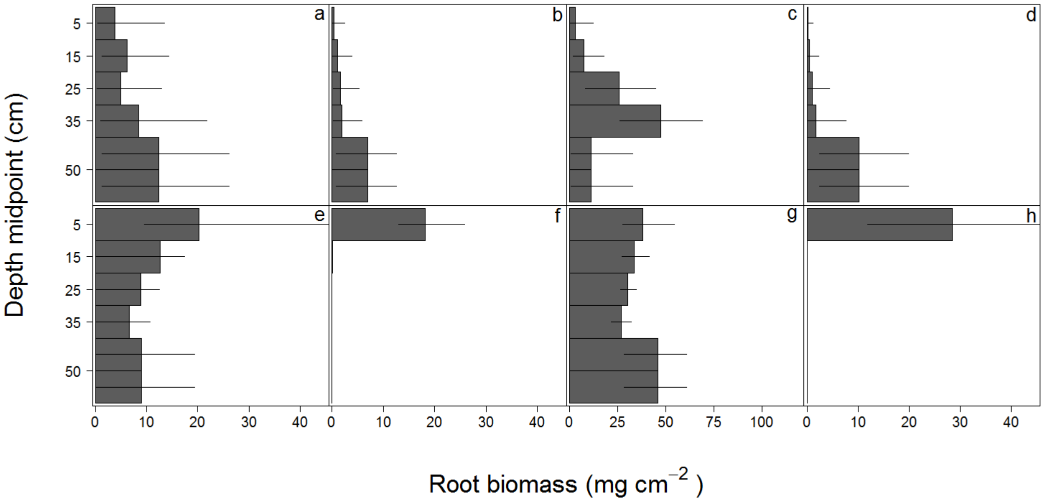

Figure 2.3. Posterior estimates (mean and 95% credible interval) of root biomass (μ_R) partitioned into each soil layer, for *Larrea tridentata* (a-d) and all other neighboring species combined (e-h), for four neighborhood associations, with *Larrea* growing next to *Olneya tesota* (a, e), *Ambrosia deltoidea* (b, f), or *Prosopis velutina* (c, g), and growing alone (d, h).

4. THE SENSITIVITY OF EVAPOTRANSPIRATION TO PLANT NEIGHBOR INTERACTIONS: IMPLICATIONS FOR PATCH- and STAND- SCALE MODELS

Abstract

Evapotranspiration is a key water loss in ecosystem water cycles, and quantifying the spatial and temporal variation of evapotranspiration is key for improving hydrological models in arid ecosystems. Plant neighbor interactions may be a source of spatial and temporal variation in evapotranspiration due to their effect on the above- and belowground microclimate around a plant. Over longer timescales (year to multiple years), adjustments in plant physiological traits may occur in response to neighbor environments, potentially affecting transpiration dynamics. The sensitivity of evapotranspiration and soil moisture to plant neighbors around *Larrea tridentata* was assessed using field measurements paired with a dynamic soil water model. We assessed the sensitivity of model estimates to neighbor effects on soil moisture via competition for water, aboveground microclimate effects via canopy shading, and physiological adjustments of *Larrea* to neighbor environments under two different precipitation years. Neighbors impacted transpiration of *Larrea* by as much as 75% at the patch scale (plant and surrounding soil) and 30% at the stand scale. Patch and stand scale evaporation estimates were also affected by neighbors, and evaporation was reduced by roughly 50% at the patch-scale and 25% at the stand-scale. Annual transpiration model estimates were highly sensitive to the impact of neighbors on soil moisture via competition for water, and the inclusion of physiological adjustments to neighbor environments significantly impacted seasonal transpiration. Neighbors also impacted the seasonal dynamics of the transpiration of *Larrea* under the two different precipitation years. Plant neighbor interactions can be a significant influence on evapotranspiration and soil moisture and

can help explain spatial and temporal variation in models of water fluxes in arid ecosystems. Furthermore, physiological adjustments to neighbor environments may be an important source of variation in ecohydrological models over seasonal timescales or in studies focused on plant responses to precipitation under climate change.

Introduction

Evapotranspiration (ET) is a key component of ecosystem water cycling and is linked to plant productivity and net ecosystem carbon exchange (Fischer and Turner 1978, Reynolds et al. 2004). Altered temperature and precipitation patterns associated with global climate change are expected to shift seasonal trends in ET and affect annual ET across a diversity of ecosystems through impacts on atmospheric demand and changes in plant physiology (Reynolds et al. 2000, Wetherald 2002, Huntington 2006). Models seeking to predict the impacts of climate change on ET require a mechanistic understanding of water movement across the soil-plant-atmosphere continuum (Asbjornsen et al. 2011, Wang et al. 2012, Hawkins et al. 2015). Terrestrial plants are an important determinant of ET, controlling transpiration (T) rates and altering evaporation (E) through canopy shading effects on soil temperature, canopy interception and throughfall (Rodriguez-Iturbe et al. 2001). However, plant controls of ecosystem- level ET vary spatially and temporally (Vivoni 2012), and an understanding of the mechanisms that drive variation in ET can improve models and predictions under future climate change scenarios (Asbjornsen et al. 2011, Jenerette et al. 2012, Hawkins et al. 2015).

In arid and semi-arid ecosystems, ET is typically tightly coupled to soil water availability, and slight variations in climate, vegetation, and plant-soil moisture feedbacks can significantly impact soil water content (SWC) and ET (Rodriguez-Iturbe et al. 2001, Hultine and Bush 2011). In ecosystems with aggregated plant spatial distributions, variation in ET and SWC at the patch scale (plant and surrounding soil) may arise as a result of the effect of neighboring plants on the patch environment (Mahall and Callaway 1996, Callaway and Walker 1997, Schade et al. 2003). For example, plants growing under a tree canopy may experience reduced rainfall infiltration due to the effects of interception by the tree canopy (Mcnaughton and Jarvis 1983). Moreover, overlapping root systems can impact the soil water available for transpiration through competition (Callaway and Walker 1997, Schenk 2006). Facilitative interactions also affect ET via canopy shading effects that decrease temperature or through the hydraulic redistribution of deep soil water by neighboring roots (Suzan et al. 1996, Caldwell et al. 1998).

Such facilitative and competitive interactions are not necessarily static over time, and interactions can vary seasonally, in response to precipitation and soil water dynamics (Briones et al. 1996, Zou et al. 2005). For example, the degree that plants compete for similar water sources can depend on precipitation frequency and magnitude, leaf area, and root distributions (Manning and Barbour 1988, Chesson et al. 2004). The prolonged modification of the patch microclimate by neighbors can eventually result in plant physiological adjustments to the altered environment, such as changes in root distribution, stomatal behavior, and canopy leaf area (Briones et al. 1996, Albert et al. 2011, Kropp and Ogle 2015). However, the relative impact of the neighbor-adjusted physiology on annual and seasonal ET and SWC at the patch scale is not well understood, and studies typically assume that species physiology and functional morphology are similar across all plant neighbor associations (Callaway and Walker 1997, Schwinning et al. 2003).

We evaluate the sensitivity of ET to plant neighbors and the mechanisms that underlie the neighbor effects at the patch and stand scales using a simulation analysis paired with data collected in the field. We focus on a drought-tolerant, evergreen shrub, *Larrea tridentata* (Sesse & Moc. ex DC.; creosotebush), that is dominant throughout the hot deserts of the southwestern United States and northwestern Mexico (Barbour 1969, Meinzer et al. 1986). The effect of neighbors on the ET and SWC associated with *Larrea* patches was assessed for neighboring plants of differing functional types including a small sub-shrub *Ambrosia deltoidea* (Torr; W.W. Paynel; triangle leaf bursage), and two tree species *Olneya tesota* (A. Gray; desert ironwood) and *Prosopis velutina* (Wooten; velvet mesquite). *Ambrosia* is a shallow rooted, drought deciduous shrub known to have belowground competitive interactions with *Larrea* (Brisson and Reynolds 1994). *Prosopis* and *Olneya* are deeply rooted trees, with large canopies that can have facilitative effects on understory plants as a result of canopy shading and hydraulic redistribution (Suzan et al. 1996, Tewksbury and Lloyd 2001). We address three questions: (1.) Do plant neighbors of different functional types differentially affect seasonal and annual estimates of ET in *Larrea* patches? (2.) How sensitive are transpiration estimates for *Larrea* to the different mechanisms underlying the plant neighbor effects? (3.) What are the implications of plant neighbor interactions for predicting ET around *Larrea* at the stand scale? We evaluate these questions using a simulation analysis that utilizes a coupled soil moisture and transpiration model that is calibrated with data collected from *Larrea* patches associated with the aforementioned neighbor associations.

Methods

Simulation Experiments

We implemented an incomplete factorial approach to assess the relative impact of plant interactions on evapotranspiration (ET) and soil water content (SWC) in *Larrea* patches via three underlying mechanisms: (1) direct competition for soil water, (2) neighboring tree canopy effects on the patch microclimate, and (3) adjustments of physiological behavior to neighbor environments (see Table 3.1 for a summary of the simulation scenarios and the notation used for each). The overall effect of plant neighbors was assessed by comparing ET and SWC for *Larrea* growing alone (L) versus growing next to each neighboring species (N) under the assumption that all three aforementioned neighbor effects occur. We refer to this as the base-line scenario that reflects real, observed interactions. The effect of competition for soil water on the T of *Larrea* was evaluated through two scenarios that assumed: (1) complete root overlap (RO) with no vertical root differentiation between species, and (2) neighbor root profiles do not overlap with the *Larrea* rooting zone such that *Larrea* does not compete (NC) with its neighbors for soil water. A comparison between RO and N scenarios provides insight into the degree that *Larrea* and neighboring species compete for similar soil water sources, and the T of *Larrea* is expected to be lower in the RO scenarios compared to the N scenarios if vertical root differentiation occurs between *Larrea* and the neighboring species in N scenarios. The overall effect of competition for water on *Larrea* T was assessed by comparing the N and NC scenarios, and *Larrea* T is expected to be higher if competition limits water availability for *Larrea* in the N scenarios.

Tree canopies alter the microclimate around *Larrea* via shading impacts on air temperature and vapor pressure deficit (D), altering both stomatal conductance and the evaporative demand for ET. Tree (*Olneya* and *Prosopis*) canopies also intercept precipitation, thus decreasing precipitation inputs into the soil in *Larrea*-tree patches (Suzan et al. 1996, Tewksbury and Lloyd 2001). The sensitivity of T estimates of *Larrea* to tree canopy effects on patch microclimate was evaluated by removing the microclimate (NM) effects such that neighboring tree canopies do not intercept precipitation, and do not alter temperature and D (no shading) in *Larrea*-tree neighbor associations. If *Olneya* or *Prosopis* are facilitative through canopy shading, *Larrea*'s T is expected to be higher under the NM scenarios compared to N scenarios.

Larrea's physiological adjustments to neighbor-altered environments were incorporated through shifts in the root distributions, stomatal behavior, and leaf area index (LAI) specific to each neighbor association. We examined how *Larrea*'s neighbor adjusted physiology impacts T estimates for *Larrea* and ET by assuming *Larrea*'s physiology was the same in the presence of neighbors as *Larrea* growing alone (LN). Decreases in T under the LN scenarios (compared to N) indicates that *Larrea's* physiological adjustments are important for understanding the impacts of neighbor altered environments. Higher T under the LN compared to the N scenarios would indicate that prolonged exposure to neighbor environments negatively impacts *Larrea*'s physiological controls on T. We also assessed the impact of *Larrea*'s neighbor-adjusted physiology in the absence of neighbors (NN) in comparison to *Larrea* growing alone (L) to examine how neighbor adjusted physiology affects T without the direct effects of neighbors on SWC or patch microclimate.

Each scenario was evaluated across two years with similar annual precipitation (27.15 cm in 2014 and 27.52 cm in 2004), that was approximately 2 cm less than the thirty year average (29.6 cm) near the study site. The precipitation periods differed with respect to the seasonality and the frequency of precipitation events (Fig. 1a and b). For example, 2014 was characterized by high summer precipitation (68% of annual) and low winter precipitation (28%), whereas 2004 had low summer (12%) and high winter precipitation (59%). The two years were compared to examine how sensitive neighbor effects are to differing seasonality in precipitation under years with similar annual precipitation.

Dynamic Soil Water Model

All simulation experiments were implemented using a dynamic soil water model, HYDRUS1D V4.16.0090 (Šimůnek et al. 2008, 2013) which provides numerical solutions to the Richards equations (Richards 1931) to simulate soil water flow and root water uptake in a one dimensional soil profile. Soil water content (SWC) and root water uptake were simulated in layers of 1cm increments down to a depth of 60 cm, based on available root profile data (described below). Studies of *Larrea* indicate that 70-80% of root water uptake occurs in the upper 40 cm of the soil, and thus 60 cm likely captures the majority of water uptake by *Larrea* (Reynolds et al. 2000, Ogle et al. 2004). The lower boundary condition of the soil profile was set to free drainage since the vadose zone extends beyond our focal 60 cm (Seyfried et al. 2005). The van Genutchen model (1980) was used to describe soil hydraulic properties, and the model parameters were estimated from soil moisture retention and texture data (described in full in Appendix C). Root stress limitations on potential transpiration were included using the S-shaped root stress function, α (van Genuchten 1987):

$$\alpha_z = \frac{1}{1+\left(\frac{h_z}{h_{50}}\right)^p} \qquad (18)$$

where h represents the hydraulic head of a given soil layer, h_{50}, the 50% reduction in water uptake, which has a hydraulic head of -25,000 cm and, p, is a dimensionless exponent that affects the sensitivity of water stress to hydraulic head, and was set to 3 based empirical studies (Pockman and Sperry 2000, Gutierrez-Jurado et al. 2006, Šimůnek et al. 2013).

The HYDRUS1D model simulated water fluxes at the soil surface through the input of daily precipitation, potential evaporation (PE), and potential transpiration (PT) in each scenario (Table 3.1). We considered PT to be primarily dependent on the atmospheric evaporative gradient (vapor pressure deficit, D, and the daily atmospheric pressure, P) and plant related controls including stomatal conductance (g_s) and leaf area index (LAI):

$$PT = g_s \frac{D}{P} LAI \tag{19}$$

Daily precipitation data were averaged from nearby precipitation gauges (Hesperus Dam, Hesperus Wash, and Asher Hills) for both 2004 and 2014 (FCDMC, 2015). PE was estimated using the Hargreave's equation (Hargreaves et al. 2003), which is based on daily minimum and maximum temperature.

Initial values of SWC in all soil layers were set to field capacity and a 31 day period was used before the start of each year to allow for model spin up in all simulations. The simulations were divided into seasons to account for seasonal variation in root distributions. Winter and summer season definitions were based on 30 year records (WRCC), with a colder, rainy winter period (December-March; 11.5-16.4°C) and a hot summer characterized by an early-summer drought followed by monsoonal storms

(June-September; 29.5-32.7°C). A full description of the seasonal implementation of HYDRUS1D is included in Appendix C.

The daily actual T, actual E, and SWC were obtained from the model output. When *Larrea* was paired with a neighboring species, the PT in the scenario accounted for both *Larrea* and the neighboring species, and thus the modeled T (T_{all}) was the actual T for both *Larrea* and the neighboring species. T was partitioned between *Larrea* and neighboring species based on the proportional contribution of *Larrea* (p_{lt}) to the PT of both neighboring species and the root stress (α) and fractional rooting distribution (f_{r}) of *Larrea*:

$$T = p_{lt} T_{all} \int_{1}^{60} \alpha(z) f_r(z) dz \tag{20}$$

The integral was estimated using a trapezoidal numerical integration (Šimůnek et al. 2013). The parameterization of the PT function and root distributions are described below (see Data Inputs).

Stand scale T was calculated from patch level T using a weighted average from the proportion of each neighbor association occurring in the study site. Neighbor associations were determined using a map of the shrubs at the study site (see Figure S3.1, Appendix D). Each *Larrea* patch was classified into the four, aforementioned neighbor associations dependent on the distance to neighbors. *Larrea* was considered to be associated with *Olneya* or *Prosopis* if it was within 3.5 m of the tree, otherwise *Larrea* was considered to be associated with *Ambrosia* within 1 m of *Ambrosia*, and *Larrea* was considered to grow alone if it did not fall into the above associations. We recognize that this represents an over-simplification of the ecosystem since it ignores other types of neighboring species and intra-specific interactions, but our stand level predictions are meant to explore the sensitivity of stand scale T predictions to the inclusion of neighbor effects rather than provide an exact estimate of stand level T at the site.

Data Inputs

Simulations were parameterized from data collected on *Larrea tridentata* in the Sonoran Desert near Phoenix, Arizona, at the McDowell Mountain Regional Park (33.7261,-111.6987, 476 m asl). The site is dominated by *Larrea*, *Ambrosia deltoidea*, *Prosopis velutina*, and *Olneya tesota* with many shrubs growing in close proximity, with overlapping canopies. Plants with overlapping canopies were considered to be neighbors, and *Larrea* growing with a canopy separated by at least 1 m from a small shrub canopy and 3.5 m from a tree canopy was considered to be growing alone. Average daily temperature ranged from 12.2°C (December) to 33°C (July) over the period 1981-2010 (WRCC, 2013). The soil is predominately sandy loam consisting of 82% (standard error [se], .06%) sand, 13% (se .06%) loam, and 5% (se .03%) clay and is classified as an Aridisol (Hall et al. 2011). Simulations used micrometeorological data to parameterize PT calculations, and a full description of micrometeorological data sources (Temperature, *D*, SWC) are provided in Appendix C.

PT was treated as a maximal transpiration rate when soil water is not limiting, and thus we consider g_s in Eqn. 2 to be the maximum stomatal conductance (g_s) under the given meteorological conditions. We parameterized a potential g_s model using stomatal conductance measurements made under “low moisture stress” by only using data collected within one week of $\geq$0.5 cm rain event, the minimum size considered to be biologically relevant (Reynolds et al. 2004, Ogle and Reynolds 2004). The g_s and leaf-to-air D data for *Larrea* were collected with a portable photosynthesis system (Li-Cor 6400XT; Li-Cor, Lincoln, NE) on 10 days during the winter and summer periods from December 2011 to September 2014. Additional details on data collection are given in Kropp and Ogle (2015).

For potential g_s, of *Larrea*, we adapted a model from Ogle and Reynolds (2002) that successfully described stomatal behavior of *Larrea* in the Chihuahuan Desert in response to D and growth temperature (T_{gro}, average 24-hour air temperature over the previous week):

$$g_s = g_{ref} + m \log\left(\frac{D}{D_o}\right)\left(\frac{4\left(T_{\max} - T_{gro}\right)\left(T_{gro} - T_{\min}\right)}{\left(T_{\max} - T_{\min}\right)^2}\right) \qquad (21)$$

Where D_o is a reference D of 1kPa, g_{ref} is the reference g_s at D=1 kPa, and m describes stomatal sensitivity to D. The first term on the left-hand side of Eqn **Error! Reference source not found.** quantifies g_s under optimal T_{gro}, and the second term accounts for the effect of variation in T_{gro}, such that g_s decreases under sub-optimal temperatures and $g_s = 0$ if $T_{gro} < T_{min}$ (minimum T_{gro}) or $T_{gro} > T_{max}$ (maximum T_{gro}). The values for T_{max} and T_{min} were obtained from Ogle and Reynolds (2002) where T_{max}=37°C and T_{min}=5°C. Eqn **Error! Reference source not found.** was fit to the g_s data in a Bayesian framework following the approach described by Kropp and Ogle (2015).

The potential g_s of neighboring species (*Prosopis*, *Olneya*, and *Ambrosia*) was estimated with a simpler model based purely on the g_s response to D (Oren et al. 1999), which has successfully described the stomatal behavior of a wide range of species in arid ecosystems (Oren et al. 1999). The model is essentially the same as Eqn

Error! Reference source not found., but the term on the right-hand side describing the effects of T_{gro} was not included given lack of data on the effect of T_{gro}. This simplified model was fit to g_s measurements made during periods of low water stress in the winter. Given the limited observations and simplicity of the neighboring species' potential g_s model, neighbor stomatal conductance parameters were estimated via a least squares regression.

Potential g_s in PT (Eqn 2) was subsequently calculated for *Larrea* (Fig. 1D) and its neighboring species by evaluating Eqn 4 (Larrea) and the simplified version (neighbor) at the observed temperatures and *D* values for each study period, using the point estimates that were obtained for the parameters (g_{ref}, m) for each season and parameter values are provided in the Appendix C (Table S3.1).

The LAI of *Larrea* was measured using a PAR ceptometer (Accu-PAR LP-80, Decagon, Pullman, WA) in August of 2014 and February 2015 for *Larrea* shrubs in each neighbor association for (n=6 per neighbor, Table S3.1). LAI was measured on neighboring species (n=6 per species) in April 2015, and the LAI of *Olneya* and *Prosopis* was assumed to be constant across all seasons. *Ambrosia* typically undergoes a period of senescence in May through the beginning of the monsoon season in July, and thus its LAI was set to zero during that period (Szarek 1977).

Vertical Root Distributions

The vertical root distributions of *Larrea* were parameterized as fractional root distributions (f_r), representing the relative amount of roots in each 1 cm layer over the 0-60 cm profile. The f_r values are based on chapter 2, and were determined from an combined analysis of stable isotope data in soil and plant water (collected in the summer), molecular identification of roots, and root biomass data to separate the root distributions of *Larrea* from its neighbors (Fig. 3.2A-D). Neighboring species' fractional root distributions were estimated from molecular presence and root biomass data in the same analysis (chapter 2). We assumed that neighboring root distributions declined exponentially with depth (Fig. 3.2E) because the contribution of neighboring root biomass below *Larrea* canopies was expected to consist of lateral roots, which tend to be more shallowly distributed (Schenk and Jackson 2002). Molecular identification and isotope data were not collected in the winter, but a similar model was fit to the winter root biomass data, and a description of the model is included in Appendix C.

Results

Effect of Neighbors on Patch and Stand Scale Evapotranspiration

For a majority of the year, the daily transpiration (T) of *Larrea* was lower when growing next to plant neighbors of all functional types compared to *Larrea* growing alone (Fig. 3.3A and B). *Larrea* growing alone had the highest annual T (Table 3.2) and *Larrea* growing next to *Prosopis* and *Ambrosia* had the lowest annual T, with annual T being 71% and 54% lower than *Larrea* growing alone, respectively. Annual evaporation (E) was also the greatest in patches defined by *Larrea* growing alone, and annual E generally did not differ among the different *Larrea*-neighbor patches (Table 3.1, Fig. 3.3C and B). The T/ET ratio around *Larrea* was the lowest in patches where *Larrea* was growing with *Ambrosia* and *Prosopis*, due to *Larrea*'s low T in these patches. A description of our simulation validation is provided in the Appendix D.

Sensitivity of Patch-level Transpiration to Mechanisms Underlying Plant Interactions

Competition for soil water had the greatest effect on *Larrea*'s transpiration rates, and the scenario that assumed neighbors root water uptake did not overlap with *Larrea*'s root profile (NC) led to the largest increases in both seasonal and annual T for *Larrea* compared to the base-line N scenarios, for all neighbor associations (Fig. 3.4). *Larrea* growing next to *Prosopis* had the lowest annual T compared to all other *Larrea* patches (Table 3.2 and Fig. 3.4D and H) and had the largest increase in annual T (256% in 2014) in the absence of competition for water with *Prosopis* (NC-P) compared to the base-line scenario that included competition (N-P). The scenarios that assumed complete overlap of *Larrea* and its neighbor's root distributions (RO) did not significantly decrease T estimates for *Larrea* compared to the base-line (N) scenarios (Fig. 3.4), with the exception of a 25% decline in annual T for *Larrea* growing next to Ambrosia (RO-A) compared to the N-A scenario. *Larrea* growing next to neighbors (N) had lower soil moisture that coincided with markedly faster soil drying following precipitation events compared to *Larrea* growing alone (L, Fig. 3.3E and F), confirming that competition for soil water likely results in decreased water availability for *Larrea* in *Larrea*-neighbor patches (i.e. *Larrea* growing next to *Olneya*, *Ambrosia*, or *Prosopis*).

Despite the reduction of temperature and D (Fig 3.1A and B), tree canopies (*Prosopis* and *Olneya*) had little impact on estimates of T for *Larrea*, and scenarios that assumed that microclimate around *Larrea* was not affected by neighboring canopies (NM) had similar or higher seasonal and annual T in comparison to the base-line N scenario (Fig. 3.4). For the base-line scenarios, with included neighbor effects on microclimate, D was lower beneath tree canopies during the summer months (Fig. 3.1C) and *Larrea* had higher potential g_s when growing next to tree neighbors (N-P and N-O) compared to the scenarios without tree canopy microclimate effects (NM, Fig. 3.1D). However, the increased potential g_s did not result in greater T, and summer T did not differ between NM-O and N-O (Fig. 3.4B and F). The scenario that assumed that *Prosopis* did not alter the microclimate (NM-P) resulted in mixed effects, and in the summer when the effects of shading are the greatest, *Larrea* had 22% higher T in 2014 and 30% lower T in 2004 compared to the base-line scenario (N-P, Fig. 3.4D and H).

Estimates of annual T for *Larrea* were moderately affected by variation in *Larrea*'s physiology. The assumption that *Larrea*'s physiology in the presence of neighbors was the same as *Larrea* growing alone (LN) tended to affect estimates of annual T for *Larrea* on the order of 10-20% compared to the base-line N scenarios with neighbor-specific physiological adjustments (Fig. 3.4). In the absence of neighbor competition and canopy microclimate effects (NN-O, NN-P, NC-A), variation in *Larrea*'s physiology also resulted in differences in the annual T for *Larrea* between 10-20% compared to *Larrea* growing alone (L, Fig 3.4). For example, *Larrea*'s physiological behavior when growing with *Olneya* (NN-O) resulted in higher annual T (20% higher in 2014) compared to *Larrea* growing alone (L) (Fig. 3.4A and B). When *Larrea*'s physiology in *Larrea-Olneya* patches was assumed to be the same as *Larrea* growing alone (LN-O), annual T of *Larrea* decreased by 15% in 2014 compared to the base-line scenario (N-O). The effect of physiological adjustment on annual T for *Larrea* in *Larrea-Prosopis* patches tended to minor both with neighbors (LN-P vs. N-P) and without neighbors (NN-P vs. L). The effect of an *Ambrosia* neighbor on *Larrea*'s physiology (NC-A) resulted in 12% (2014) and 17% (2004) lower annual T compared to *Larrea* growing alone (L). When *Larrea*'s physiology in *Larrea-Ambrosia* patches was assumed to be the same as *Larrea* growing alone (LN-A), annual T of *Larrea* decreased by 14% in 2014 and increased by 12% in 2004 compared to the base-line scenario (N-A) (Fig. 3.4C and G).

Estimates of seasonal T for *Larrea* were sensitive to physiological adjustments, and the replacement of *Larrea*'s neighbor-adjusted physiology with lone *Larrea*'s physiology (LN) resulted in different seasonal T (Fig 3.4) compared to the base-line scenario with neighbor adjusted physiology (N). For instance, if *Larrea*'s physiology was set equal to a lone *Larrea* when growing next to *Ambrosia* (LN-A) or *Prosopis* (LN-P), winter T increased by 59% in 2014 and 93% in 2004 for LN-A (Fig. 3.4c and 3.4g) and by 20% in 2004 compared to the base-line scenarios (N-A and N-P, respectively). Conversely, when *Larrea* was assigned the lone physiology when growing next to *Olneya* (LN-O), Summer T for *Larrea* decreased by 61% in 2014 and 42% in 2004 compared to the base-line scenario (N-O, Fig 3.4b). Likewise, when *Larrea* growing next to *Prosopis* was considered to have the same physiology as *Larrea* growing alone (LN-P), summer T of *Larrea* decreased by as much as 42% in 2014 compared to the base-line scenario (N-P). The scenario that assumed *Larrea* growing next to *Ambrosia* had the same physiology as *Larrea* growing alone, summer T of *Larrea* decreased by 51% (2014) and 56% (2004) compared to the N-A scenario.

Implications for Predictions of Evapotranspiration

Accounting for plant neighbors (N scenarios) impacted annual ET estimates for Larrea at the stand-level and reduced stand estimates of annual T by as much as 3 cm (30%) in a year (Table 3.2) compared to estimates based on the lack of neighbor effects (*Larrea*-lone conditions). The inclusion of neighbor influences on the T and ET dynamics in *Larrea* patches also resulted in decreased stand scale E by ~2 cm (25%). The ratio T/ET was slightly reduced in the presence of neighbors compared to the assumption of no neighbor effects, which likely resulted from decreases in T of *Larrea* in *Larrea*-neighbor patches (Table 3.2). Stand scale predictions of the T/ET that included neighbor effects decreased by 13% under the 2004 (Table 3.2).

Annual evaporation (E) and transpiration (T) for *Larrea* patches were slightly different between the two years (Table 3.2 and Fig. 3.4), and estimates of annual T for *Larrea* in 2004 was generally 10-12% lower than in 2014, with the exception of a decrease by 28% in *Larrea-Ambrosia* patches. The seasonal T of *Larrea* had the greatest variation between years and varied by neighboring species identity (Fig. 3.1 and Fig. 3.4). For instance, precipitation events in the late winter and early spring in 2004 (Fig. 3.1B) resulted in higher spring T for all *Larrea*-neighbor associations (N) compared to 2014. *Larrea* growing next to *Prosopis* and *Ambrosia* had the greatest differences in T by 355% and 209%, respectively for 2004 as compared to 2014. *Larrea* growing alone (L) had spring T in 2004 that was 173% greater than in 2014 (Fig. 3.4B, F, D, and H). Summer T in 2004 was lower than 2014 for all neighbor associations. For example, *Larrea* growing next to *Prosopis* had 85% less T in the summer of 2004 compared to 2014 (Fig. 3.4D and H), and supported the lowest summer T of all *Larrea*-neighbor patches, with 75% lower T than *Larrea* growing alone. *Larrea* growing next to *Ambrosia* had the smallest difference in summer T, with 55% lower T in 2004 than 2014 (Fig 3.4C and G). *Larrea* growing next to *Ambrosia* also had the highest summer T in 2004 of all *Larrea* neighbor associations, and was 33% greater than *Larrea* growing alone.

Discussion

Effects of Neighbors on Evapotranspiration in Larrea *Patches*

The simulation results indicate that plant neighbors influence transpiration (T) of *Larrea*, soil water content (SWC), and evaporation (E) in *Larrea* patches (Fig 3.3). Estimates of annual T for *Larrea* were lower in all *Larrea*-neighbor patches (i.e. growing next to *Olneya*, *Ambrosia*, or *Prosopis*) compared to *Larrea* growing alone (Table 3.2). T of *Larrea* was largely affected by competition for water from neighbors compared to the other mechanisms of neighbor interactions for all *Larrea*-neighbor patches (Fig. 3.4). On seasonal timescales, neighbor-associated adjustments in *Larrea*'s physiology significantly influenced T, even mitigating the effects of competition between *Larrea* and *Ambrosia* during periods in the summer with a higher T than *Larrea* growing alone (Fig. 3.3A and B and Fig. 3.4C and G).

The reduction in E was similar across all *Larrea*-neighbor patches compared to *Larrea* growing alone (Table 3.2). Although E is tightly coupled to SWC, vapor pressure gradients (D), and radiation (Breshears et al. 1997, Raz-Yaseef et al. 2010a), little difference was observed between *Larrea* patches affected by tree canopy microclimate alterations of D (N-P, N-O) and without microclimate effects (NM-P, NM-O), indicating that SWC limitations and competition may be more important than changes in D. The reduction of E in *Larrea*-neighbor patches is likely driven by limitations in available soil water that arise from higher overall T due to soil water uptake from both *Larrea* and the neighboring species compared to *Larrea* growing alone (Reynolds et al. 2004, Raz-Yaseef et al. 2010a).

Sensitivity to Mechanisms Underlying Neighbor Effects on Transpiration

The removal of neighboring plant water uptake from *Larrea*'s root profile (NC) resulted in the greatest increases in annual T for *Larrea* growing next to neighbors (WN, Fig. 3.4). A variety of studies also demonstrate that *Larrea* competes for water with a number of species of varying functional types such as grasses, succulents, and shrubs (Phillips and Macmahon 1981, Briones et al. 1996, Schenk et al. 2003). With the exception of *Larrea*-*Ambrosia* patches, T estimates for *Larrea* marginally decreased under the assumption of complete root overlap (RO) compared to scenarios with neighboring species intrinsic profiles (N, Fig 3.4), suggesting that little vertical partitioning of water occurs between *Larrea* and the tree species. *Larrea* and neighboring grasses and shrubs were previously found to take up water from similar depths, likely because water rarely infiltrated deep soil layers (>40 cm) due to high E and T (Kemp and Reynolds 1997, Reynolds et al. 2000). Some degree of root water partitioning likely occurs between *Larrea* and *Ambrosia*, as indicated by a 25% reduction of T estimates for *Larrea* under the assumption of complete root overlap (RO-A) compared to different root distributions (N-A). *Ambrosia*'s shallow root distribution may allow *Larrea* and *Ambrosia* to utilize soil water in different depths since a majority of *Ambrosia*'s roots occur in in the upper 5 cm (Fig. 2E). *Larrea* and *Ambrosia* roots have been shown to avoid overlap when growing in close proximity (Brisson and Reynolds 1994, Mahall and

Callaway 1996), which may explain the lack of deeper *Ambrosia* roots under *Larrea* canopies. Our study only considers vertical root distributions, and lateral partitioning of roots may also contribute to reduced competitive interactions (Brisson and Reynolds 1994, Yoder and Nowak 1999).

Olneya and *Prosopis* are often considered to have facilitative effects on neighboring plants due to the more favorable microclimate created by their canopy shading that reduces understory temperature and D (Suzan et al. 1996, Tewksbury and Lloyd 2001). However, T of *Larrea* was not greatly impacted by canopy microclimate. T of *Larrea* increased in *Prosopis* neighbor patches under the removal of canopy microclimate effects, likely a result of increased water inputs to the soil due to the removal of canopy interception of rainfall (Mcnaughton and Jarvis 1983). A similar arid tree species, *Prosopis glandulosa*, was previously found to provide little facilitative effect on understory vegetation's water use, and competition for water outweighed the benefits of canopy shading (Barnes and Archer 1996, 1999). However, our study does not consider increases in soil water from hydraulic redistribution that may be performed by *Olenya* and *Prosopis* during dry periods (Hultine et al. 2004, Prieto et al. 2012); however, the facilitative effects of this process may be negligible since *P. glandulosa*'s hydraulic redistribution was found to have limited impacts on understory T (Zou et al. 2005).

Over long timescales, annual T estimates for *Larrea* were less sensitive to assumptions about *Larrea*'s physiology compared to competition for water with neighbors. One hypothesis for *Larrea*'s physiological adjustments to neighbor environments is that its physiology adjusts to optimize water use by varying water sources and root overlap to reduce competition (Chesson et al. 2004, Ogle and Reynolds

2004). However, the presence of neighbors did not greatly affect the difference in annual T estimates for *Larrea* between *Larrea*'s neighbor-adjusted physiology and the physiology of *Larrea* growing alone (Fig 3.4). *Larrea*'s root distribution and leaf area is known to rapidly adjust to changes in seasonal precipitation and soil moisture dynamics (Reynolds et al. 1999), and physiological adjustments may result from the varied patterns of SWC in neighbor patches. However, the extent that physiological adjustment can ameliorate competitive effects may be limited, and the evaluation of coexistence through physiological differences is often under-evaluated in studies (Chesson et al. 2004).

Conversely, over short time scales, seasonal patterns in the T of *Larrea* were highly sensitive to physiological adjustment (Fig 3.4). When the physiology of *Larrea* growing alone was applied to *Larrea* growing next to neighbors (LN), *Larrea* in *Larrea*-neighbor patches tended to have greater winter T and decreased summer T compared to scenarios accounting for *Larrea*'s neighbor-adjusted physiology (N). *Larrea*'s physiology (e.g., root growth, gas exchange) can quickly shift in response to water availability (Reynolds et al. 1999), and thus variation observed in *Larrea*'s physiology (Fig 3.1D and Fig 3.2) is likely a response to prolonged differences in above- and below-ground microclimate created by neighbor environments. In summary, the variation in *Larrea*'s physiology arising from plant neighbors was important for T on short time scales (daily to seasonal), particularly around summer precipitation pulses (Fig 3.3).

Implications for Predictions of Evapotranspiration

Plant neighbors significantly reduced ET of *Larrea* patches, and we demonstrate that accounting for neighbors at the patch scale affects predictions of *Larrea*'s stand-level estimates of ET by as much as 28% (Table 3.2). As expected in an arid ecosystem, E was a considerable portion of ET (Reynolds et al. 2000, Lauenroth and Bradford 2006), and neighbors further decreased the T/ET ratio in *Larrea* patches, especially under the 2004 precipitation regime (Table 3.2). The ratio of T/ET can vary based on aridity, site location, and plant species (Kemp and Reynolds 1997, Huxman et al. 2005), and plant neighbors further contribute to variation in the ratio of T/ET at the patch and stand scale, altering the water balance around *Larrea* (Table 3.2).

Climate change is predicted to alter precipitation regimes, affecting both the seasonality of rainfall and the magnitude and frequency of rain pulses (Easterling 2000), and studies focused on ET under altered precipitation regimes typically do not consider the influence of plant neighbor interactions (Gao and Reynolds 2003, Knapp et al. 2008, Raz-Yaseef et al. 2010b). The degree that neighbors compete for soil water may influence the degree that seasonal T is affected by different precipitation regimes. For example, *Larrea* growing next to *Prosopis* and *Ambrosia* experienced the greatest competition for water from neighbors, and increased late winter/spring rainfall resulted in the largest increases in spring T across the neighbor associations. Predicted decreases in late winter rainfall under climate change (Seager and Vecchi 2010) may heighten water limitations in competitive environments in the Sonoran Desert. Neighbor-adjusted physiology can also be an important aspect of estimates of seasonal T for *Larrea* under different precipitation regimes. The effects of competition between Larrea-Ambrosia in the stressful, low rainfall summer of 2004 may have been ameliorated as a result of *Larrea*'s slightly greater fractional root area at shallow soil layers. In comparison, *Larrea* growing next *Prosopis* was the most affected by differences in summer precipitation and had the lowest T of all *Larrea* patches, which may be a result of higher root area at deeper depths that had decreased access to smaller rainfall events. Variation in physiology arising from plant neighbors may be important to capturing the influences of plant neighbors on ET under altered precipitation regimes, but it remains largely understudied due to simplifying assumptions about plant physiology (Reynolds et al. 2004a, Schwinning and Kelly 2013).

The influence of plant neighbors on estimates of ET was dependent on the temporal scale. Studies focusing on annual or longer time scales may adequately incorporate plant interactions solely through the inclusion of competition; whereas, studies focused on daily or seasonal timescales need to incorporate both competition and adjustments in physiology to neighbor environments to accurately reflect variation in ET. Regardless of the temporal scale, the impacts of competition and neighbor-adjusted physiology on patch scale SWC and ET provides a mechanistic understanding of the drivers behind plant community composition (Callaway and Walker 1997, Chesson et al. 2004). Further study is needed to understand how both competition and neighbor-induced physiological variation interact to affect water fluxes under future climate conditions, particularly in regards to a finer temporal resolution of root distributions and stomatal behavior of both neighboring plants (Chesson et al. 2004, Albert et al. 2011). Scaling ET from the patch to stand or ecosystem scales is sensitive to the scaling assumptions, and subject to bias in estimates or over-simplification of spatial heterogeneity (Roberts 2000, Rastetter et al. 2003), and we demonstrate that plant neighbors represent an important source of spatial variation that can result in the biased estimates of ET at the patch and stand scales.

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Tables

Table 3.1. Description of simulation scenarios for evaluating the effect of plant neighbors on *Larrea tridentata*'s evapotranspiration. The presence of neighbor influences are indicated by X and absence is indicated by dashes (-).

Competition for water	Canopy micro-climate effects	Adjustments in *Larrea*'s physiology	Main scenario	Specific scenario **	Brief description
-	-	-	L	L	Lone *Larrea*, no neighbor effects.
X	X	X	N	N-A N-P N-O	Neighbor affects *Larrea*'s microclimate, physiology, and competes for water.
X*	X	X	RO	RO-A RO-P RO-O	Neighbor roots completely overlap with *Larrea* roots, and neighbor affects *Larrea*'s microclimate and physiology.
-	X	X	NC	NC-A NC-P NC-O	No competition for water, but neighbor affects *Larrea*'s microclimate and physiology.
X	-	X	NM	NM-P NM-O	Neighbor does not affect microclimate, but neighbor affects *Larrea*'s physiology and competes for water.
X	X	X[†]	LN	LN-A LN-P LN-0	Neighbor competes for water and effects microclimate, but neighbor does not affect *Larrea*'s physiology.
-	-	X	NN	NN-A NN-P NN-0	No competition for water, and neighbor does not affect microclimate, but neighbor affects *Larrea*'s physiology.

*****Neighbor vertical root distributions are altered to completely overlap with *Larrea*'s root distribution (i.e., the root distributions of the neighboring plants are the same as *Larrea*'s root distribution).

[†] Lone *Larrea*'s stomatal conductance and root distributions are used to represent *Larrea*'s behavior in the presence of neighbors.

**Scenarios followed by -A, -P, and -O indicate the species identity of the neighbor (*Ambrosia*, *Prosopis*, and *Olneya*, respectively).

Table 3.2. The effect of neighbors on annual transpiration (T), soil evaporation (E) and evapotranspiration (ET) for *Larrea tridentata* patches across two years (2004 and 2014) with differing precipitation years.

Scale	Neighbor association	T (cm/year)		E (cm/year)		T/ET	
Patch		2014	2004	2014	2004	2014	2004
	Lone	10.42	9.39	10.12	10.43	0.51	0.47
	Olneya tesota	7.10	6.26	5.82	7.09	0.55	0.47
	Ambrosia deltoidea	4.82	3.47	5.61	6.62	0.46	0.34
	Prosopis velutina	3.06	2.69	5.34	6.5	0.36	0.29
Stand							
	Lone assumption	10.42	9.39	10.12	10.43	0.51	0.47
	Neighbor weighted	7.24	6.25	7.62	8.36	0.49	0.43

Figures

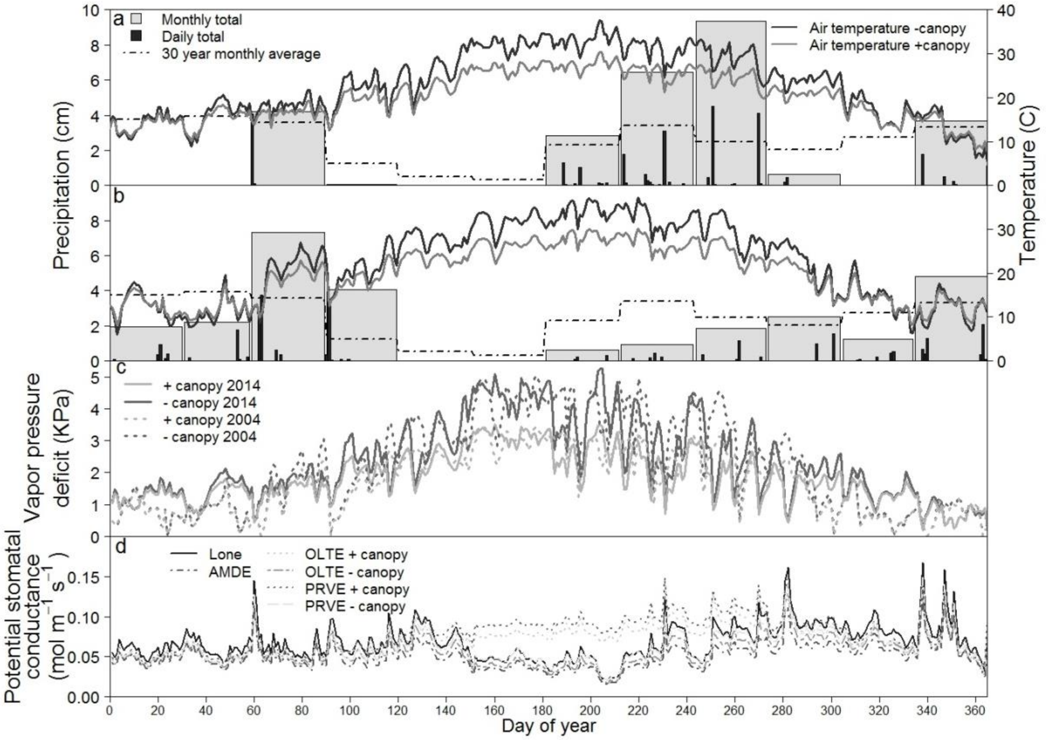

Figure 3.1. The simulation inputs for two precipitation periods for *Larrea tridentata* patches including: daily precipitation and average air temperature data for 2014 (a) and 2004 (b), (c) average daily vapor pressure deficit and (d) *Larrea*'s daily potential stomatal conductance (g_s) for each neighbor association scenario for 2014 for Larrea growing next to *Ambrosia deltoidea* (AMDE), *Olneya testota* (OLTE), and *Prosopis velutina* (PRVE). The labels "+ canopy" and "-canopy" indicate inclusion or exclusion of canopy microclimate effect.

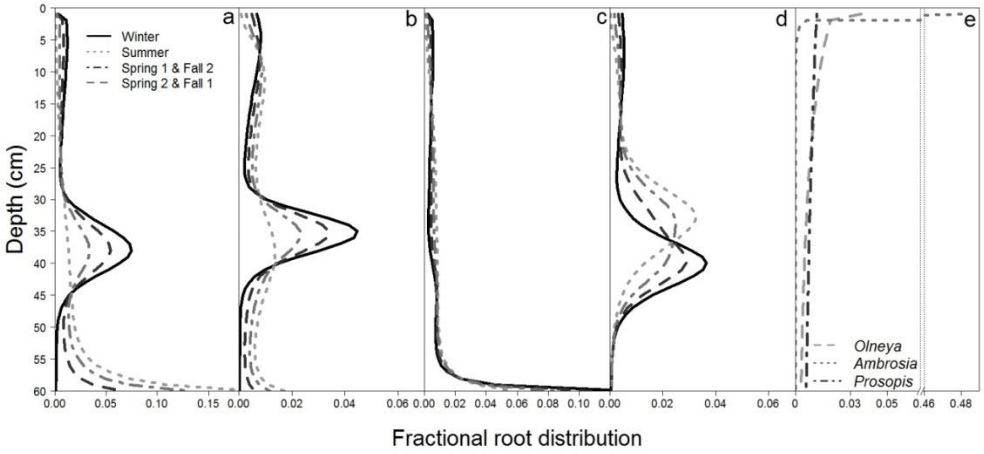

Figure 3.2. *Larrea tridentata*'s fractional rooting distribution (f_r) during different seasonal periods, under four neighbor associations including *Larrea* growing a) alone or next to b) *Olneya tesota*, c) *Ambrosia deltoidea*, or d) *Prosopis velutina*. Neighboring species' fractional rooting distribution: e) below *Larrea*'s canopy in *Larrea*-neighbor patches.

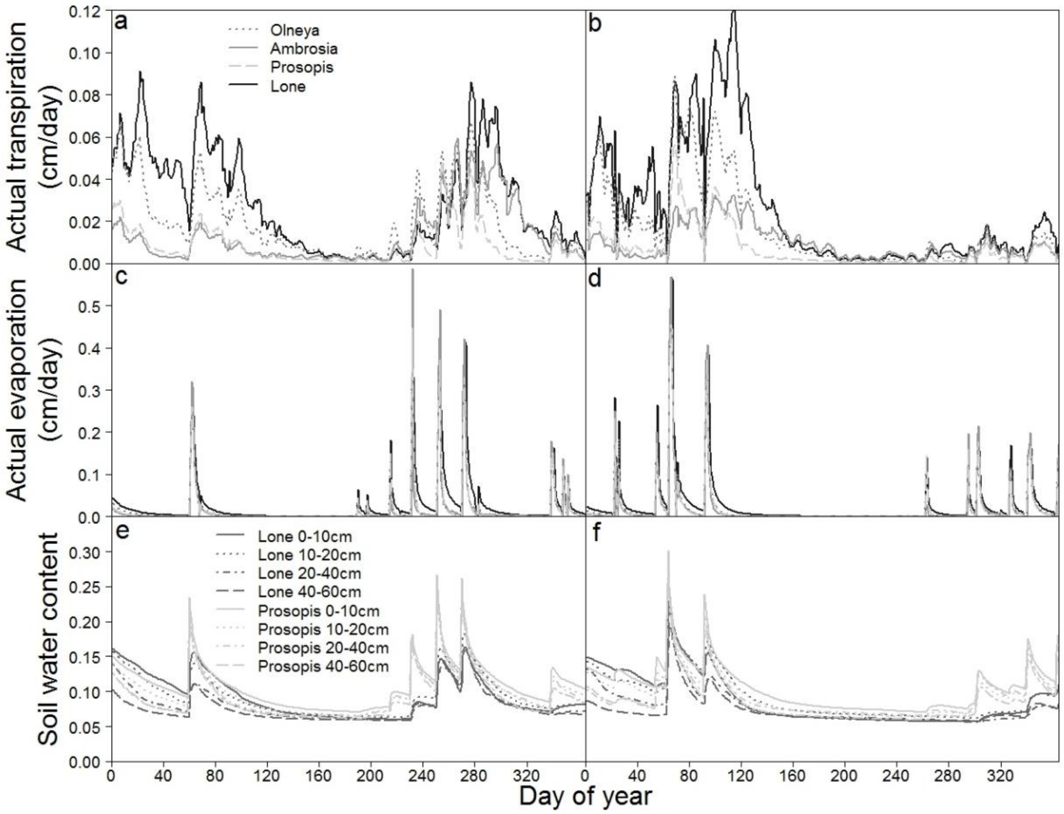

Figure 3.3. The effect of plant neighbor association on *Larrea tridentata's* daily transpiration (T) (panels a and b), soil evaporation (E) (c and d), and volumetric soil water content (SWC) (e and f) across two differing precipitation regimes occurring during 2014 (a, c, and e) and 2004 (b, d, and f).

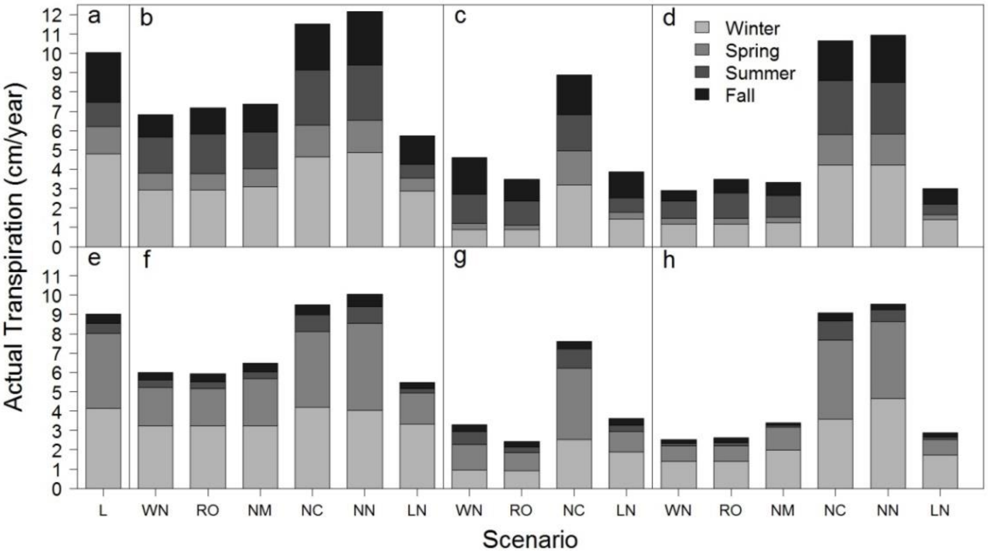

Figure 3.4. *Larrea tridentata*'s annual and seasonal transpiration (T) under differing competitive, physiological, and canopy microclimate scenarios for the 2014 (a-d) and 2004 (e-h) precipitation years. Scenarios were run under *Larrea*'s four neighbor associations: *Larrea* growing alone (a, e) and next to *Olneya tesota* (b, f), *Ambrosia deltoidea* (c, g), and *Prosopis velutina* (d, h). The simulation scenarios are described in Table 1.

5. AN ECOHYDROLOGICAL PERSPECTIVE ON PLANT-PLANT INTERACTIONS IN ARID AND SEMI-ARID ECOSYSTEMS

Abstract

Model estimates of evapotranspiration and soil moisture can be subject to high uncertainty in arid ecosystems. Model uncertainty may in part arise from the heterogeneous nature of abiotic and biotic drivers of evapotranspiration across space and time. Plant-plant interactions (PPI) may be a potential source of spatial variation for patch scale (plant and surrounding soil) water fluxes, which is largely under-evaluated in ecohydrological models. The alteration of plant environments arising from neighbor effects on microclimate can directly affect patch scale water fluxes, and across longer timescales can indirectly affect water fluxes by resulting in physiological adjustments in plant water-use traits (*e.g.*, stomatal conductance, root distribution) . We assessed the current state of the literature relating to the direct and indirect effects of plant neighbors and evaluate the implications of the effects of PPI on water flux components across different spatial and temporal scales. Our literature survey found a lack of plant physiological and water-use data related to the direct and indirect effects of PPI. A literature survey of ecohydrological models found that only 26% of models explicitly included PPI, and both small (patch) and large (landscape) spatial scales were highly under-represented in models that include PPI. We recommend additional studies that include both empirical data and ecohydrological models to directly address the variation in water fluxes that arises from PPI across varied temporal and spatial scales.

Introduction

Arid and semi-arid ecosystems cover roughly 40% of the Earth's land area and are a common focus in many ecohydrological studies (D'Odorico and Porporato 2006, Newman et al. 2006). For example, approximately 26% of original research articles in the journal *Ecohydrology* (n=337, 2011- Sept 2015) included research in arid or semi-arid ecosystems. Evapotranspiration is a primary water loss flux in ecosystem water cycles and a key component in ecohydrological models (Guswa et al. 2002, Scanlon et al. 2005). However, evapotranspiration model estimates in dryland ecosystems can be associated with high uncertainty (Shields and Tague 2012, Long 2014). Model uncertainty may in part arise from the degree of spatial variability in abiotic and biotic drivers of hydrological fluxes across a range of scales from the plant to landscape level (Newman et al. 2006, Vivoni 2012).

Spatial variability in evapotranspiration fluxes in dryland ecosystems can be driven by heterogeneity in precipitation and abiotic factors such as terrain aspect and soil texture that affect runoff and soil moisture (Vivoni 2012, Chen et al. 2014). Water fluxes and soil moisture also vary among areas covered by plant canopies versus open, bare soil (Ludwig et al. 2005, Turnbull et al. 2012). Plants can influence the amount of water that infiltrates into the soil through canopy interception of precipitation and areas below plant canopies can act as sinks for runoff (Mcnaughton and Jarvis 1983, Ludwig et al. 2005). Soil moisture around plant canopies is affected by losses due to water uptake for transpiration and by modulation of such losses via canopy shading effects on temperature and evaporative demand (Breshears et al. 1998, Raz-Yaseef et al. 2010). The degree of spatial variation in water fluxes arising from vegetation depends on the amount of bare soil, and the abundance and aggregation of plants at different spatial scales (Ludwig et al. 2005).

In ecosystems with aggregated plant spatial distributions, neighboring plant-plant interactions (PPI) contribute additional variability in water fluxes resulting from the effect of neighbors on the plant microclimate. PPI can directly affect patch scale (plant and surrounding soil) water fluxes by altering the soil microclimate through decreases in soil water availability arising from competition for water between overlapping roots (Fowler 1986, Casper and Jackson 1997). However, these negative effects can potentially be counteracted by facilitative effects. The direct effects of facilitative interactions can arise from plant canopy shading effects on the aboveground microclimate, especially during hot, dry seasons (Callaway 1995). Facilitative effects may also occur belowground through the hydraulic redistribution of water from neighboring roots, which can result in increased water availability to more shallowly rooted plants (Dawson 1993). The direct effects of PPI on water fluxes can vary over short timescales (daily-seasonal) depending on neighbor influences on microclimate and soil moisture (Zou et al. 2005).

Across longer timescales (annual to multiple years), the prolonged exposure to an altered microclimate arising from the direct effects of PPI can lead to indirect effects on water fluxes through physiological adjustments of functional traits affecting water use strategies in response to neighbor environments (Fig. 4.1). Adjustments in functional traits related to plant water use such as root distribution, maximal stomatal opening, and leaf area (henceforth referred to as water-use traits) can alter transpiration dynamics. Many species in arid ecosystems show variation in above- and belowground water-use traits in response to different soil moisture regimes that can arise under variable precipitation regimes, soil texture, or aspect (Nobel and Linton 1997, Hamerlynck et al. 2000, Ogle and Reynolds 2004). However, variation in water-use traits arising from neighbor influences is less commonly studied (Callaway et al. 2003). Root distributions can vary based on neighboring plants, and many plants adjust their rooting distributions to reduce overlap with neighbors (Mahall and Callaway 1996, Callaway et al. 2003). Adjustments in aboveground water-use traits in response to neighbors can occur in plants in mesic ecosystems through changes in canopy morphology and photosynthetic physiology (Callaway et al. 2003), but the impact of neighbors on aboveground controls on transpiration are not well studied, particularly in arid plants. Variation in both above- and belowground water-use traits may be key to understanding PPI effects on water fluxes, but few studies have addressed this source of variation in arid plants and associated implications for ecohydrological models.

Through both direct and indirect effects, the contribution of PPI to temporal and spatial variation in water cycles is largely under-evaluated, despite indications that PPI can affect soil moisture and water fluxes (Asbjornsen et al. 2011, Tietjen 2015). Many ecohydrological models do not account for PPI, and data associated with PPI impacts on water fluxes and the physiological controls over transpiration are under-represented. Instead, a majority of PPI studies focus on the implications for plant community demographics and infer the effects of neighbors on water availability from spatial distributions or plant size without directly measuring the impacts on plant-scale water fluxes (Fig. 4.2). Pattern based approaches provide insight into the longer term implications of PPI on plant community composition, but do not offer a mechanistic explanation of plant neighbor impacts on plant or ecosystem water fluxes (Callaway and

Walker 1997). The objective of this review is to explore the effects of PPI on water fluxes and their implications for ecohydrological models across a range of spatial and temporal scales. We highlight two understudied aspects of PPI and their implications for ecohydrological models: 1.) the role of direct and indirect effects of PPI for understanding ecohydrological processes, and 2.) the influence of plant neighbor interactions on transpiration and water cycling across varied temporal and spatial scales. We examine the current state of understanding by conducting a literature review. By doing so, we identify gaps in our understanding, and we make suggestions for improvement in methodological approaches that could advance the understanding of PPI for both ecohydrologists and ecologists.

Direct Effects of Plant-Plant Interactions on Water Fluxes

Belowground Direct Effects

The direct effects of plant-plant interactions (PPI) on evapotranspiration are the effects that a neighbor has on soil moisture, and these effects can vary over short timescales from days to seasons (Holmgren et al. 1997). The degree that neighboring species' roots overlap (Fowler 1986, Brisson and Reynolds 1994) and the magnitude of each species' root water uptake both influence the soil moisture limitations on transpiration (Fig. 4.1). Soil water availability throughout the rooting profiles is also key to understanding the degree to which overlapping root distributions compete for water. For example, three warm desert species with overlapping roots experienced heightened competition for water around precipitation events but experienced little competition for water sources under dry conditions (Briones et al. 1998).

Facilitative interactions can also arise between neighboring plants depending on the canopy cover and rooting depth of neighbors (Fig. 4.1). Hydraulic redistribution occurs in plants with roots in both deep and shallow soil layers, and neighboring plants with shallow root distributions may experience increased water availability if soil water is redistributed by the deeply root neighbor to shallow soil layers (Dawson 1993). Understory species growing under *Prosopis glandulosa* (honey mesquite), a deeply rooted semi-arid tree, experienced increased soil water availability from hydraulic distribution during periods of the year that were characterized by a dry upper soil layer (Zou et al. 2005). However, the effects of hydraulic redistribution of soil water can also be outweighed by competition for soil water between neighboring plants, ultimately resulting in decreased water availability (Ludwig et al. 2004).

Neighboring canopy cover can also impact soil moisture through shading effects on soil temperature and evaporative demand (Fig. 4.1), which can lead to decreased soil water evaporation and higher soil water availability in shallow layers (Breshears et al. 1998, Raz-Yaseef et al. 2010). The belowground effects of PPI on soil moisture can be highly variable, and can also depend on aboveground drivers such as air temperature, precipitation, and canopy controls of transpiration.

Aboveground Direct Effects and Controls

The direct effects of PPI on the aboveground microclimate depend largely on the neighbor canopy size (Fig. 4.1). Canopies of neighboring plants intercept precipitation and ultimately decrease soil water inputs below neighboring plants (Mcnaughton and Jarvis 1983). Canopy shading can also impact the transpiration rates through effects on the evaporative demand (i.e., vapor pressure deficit, VPD), resulting in a decreased VPD and potentially higher stomatal conductance (i.e., reduced stomatal closure) (Kropp and Ogle 2015).

Aboveground controls on transpiration are also important for understanding the direct effects of PPI on transpiration since they influence the degree to which roots acquire water, affecting the degree of competition for water. Stomatal behavior and hydraulic conductance control transpiration losses from leaves and regulate the magnitude of transpiration losses in response to soil water availability and climatic conditions (Ogle and Reynolds 2004). Leaf area and phenology also affect competition for water, and some plants may lose leaves during drought periods, reducing belowground competition during stressful periods, but potentially heightening competition during wet seasons (Smith et al. 1995). Plants with greater leaf area may also benefit by using more water following precipitation events, but they may be more susceptible to drought conditions (Angert et al. 2009). Aboveground plant water-use traits and belowground (*e.g.*, root distributions) traits are a key aspect in accurately describing transpiration, and accounting for physiological controls over transpiration that are a necessary in quantifying the direct effects of neighbors on patch scale water fluxes.

Understanding Direct Effects

Despite the role of plant water-use traits in understanding the direct effects of PPI, plant water-use traits remain a largely understudied component in competition and facilitation studies. In 104 studies that we found that focused on competition, facilitation, and water use in arid systems, the majority of studies did not directly include data on plant water-use traits (Fig. 4.2). The majority of data types used to assess PPI were related to patterns in plant communities (Fig. 4.2). Data related to community demographics (*e.g.*, abundance, survival, fecundity) were utilized in 58% of studies, 44% used measures of plant size or biomass, and 28% included spatial data to infer the nature of the PPI (Fig. 4.2). Studies that rely on spatial patterns and demographics provide insight into the potential influences of competition and facilitation on plant communities, but offer little mechanistic explanation and may not accurately reflect the effects on water fluxes. For example, the arid shrubs, *Ericameria cooperi* (goldenbush) and *Chrysothamnus teretifolius* (rabbitbrush), have overlapping root distributions and experience decreased water availability from competition, but spatial patterns associated with these shrubs did not reflect the degree of competition observed from physiological data (Manning and Barbour 1988).

In the PPI studies that we surveyed, measurements of water-use traits were far less common than pattern based data (Fig. 4.2). Root biomass or length was measured in 14% of studies (Fig. 4.2). Aboveground controls such as stomatal behavior and/or transpiration were included in 6% of studies, and leaf area indices only in 4% (Fig. 4.2). Direct measures of the overlap of soil water sources between neighbors were the rarest data type, found in only 4% of studies. Plant water potential, a measure of plant water status, had the highest representation and was included in 19% of the studies (Fig. 4.2). However, plant water potential is an integrated measure of plant water status, and alone provides limited mechanistic insight into the source of variation in plant water status or water fluxes (Sperry et al. 2002). Our analysis suggests that there is a limited mechanistic understanding of the direct effects of PPI on water fluxes, and future studies would benefit from measuring direct effects on water fluxes and the physiological controls that influence the degree that PPI directly affect transpiration and evaporation.

Indirect Effects of Plant-Plant Interactions on Water Fluxes

Adjustments in water-use traits in response to neighbor altered environments are a potential indirect effect of PPI. However, many studies of arid plant water-use traits do not report proximity to the nearest neighbor, the distribution of study shrubs, or address the intra-specific variation that can arise from PPI (Violle et al. 2009). Variation in water-use traits arising from neighbor associations can ameliorate the effects of competition (Novoplansky 2009), potentially altering the effects of competition on soil moisture and transpiration. In dryland ecosystems, implications for the adjustment of plant water-use traits and their impact on water fluxes remains largely unevaluated.

Belowground Indirect Effects

A number of studies in arid ecosystems have demonstrated that root distributions can be affected by neighboring roots (Mahall and Callaway 1996, Kroon et al. 2003). For example the lateral distribution of roots of a drought tolerant, warm desert shrub, *Larrea tridentata* (creosotebush), changed in the presence of a small, drought deciduous shrub, *Ambrosia dumosa* (white bursage), such that its rooting distribution adjusted to avoid neighboring roots (Brisson and Reynolds 1994). Differences in root distributions can alter the magnitude of belowground interactions by differentiating the depths that neighbors acquire soil water. For example, deeply rooted phenotypes of a semi-arid tree, *Quercus douglasii*, were facilitative to neighboring grasses; however, shallowly rooted phenotypes of *Quercus* competed with grasses for water (Aschehoug and Callaway 2014). Changes in root distributions in response to neighbors can also change access to different soil water sources. Neighbors reduced root growth in a semi-arid perennial grass, *Nassella pulchra* (purple needlegrass), resulting in an inability to access deep soil water sources (Dyer and Rice 1999). PPI may be an important source of variation in root distributions, and a better understanding of the degree that variation in root distributions affects PPI and the direct effects of PPI on transpiration is necessary.

Aboveground Indirect Effects

Aboveground water-use traits can be indirectly affected by a neighbor via its effects soil water availability and, if the neighbor has a large canopy via its canopy shading effects on air temperature and evaporative gradients (*i.e.*, VPD). Adjustments in aboveground water-use traits can change the rate of transpiration under different soil moisture and climatic regimes. For example, an arid grass, *Hilaria rigida* (big galleta), was affected by intraspecific competition with other *Hilaria* neighbors. Neighbors reduced stomatal conductance and increased rolling of leaf blades (Robberecht et al. 1983), which can result in decreased transpiration. The stomatal behavior of a warm desert shrub, *Larrea tridentata*, was also affected by neighbors, such that facilitative tree neighbors significantly decreased stomatal sensitivity to vapor pressure gradients compared to *Larrea* growing alone or with a competitive shrub, *Ambrosia deltoidea* (triangleleaf bursage) (Kropp and Ogle 2015). These changes in stomatal behavior resulted in significantly higher summer stomatal conductance in *Larrea* growing under a tree species (*Olneya tesota* and *Prosopis velutina* [ironwood and velvet mesquite, respectively]) compared to *Larrea* growing alone, and such changes can lead to seasonal differences in transpiration rates among *Larrea* growing under different PPI conditions. However the degree to which adjustments in aboveground water-use traits occur in response to PPI, and their subsequent impacts on water fluxes are not well quantified within and across dryland ecosystems.

Furthermore, PPI can also indirectly affect ET by influencing allometric traits (Bell and Galloway 2007). Allometric relationships are integral to scaling plant and leaf water fluxes to broader spatial scales, and changes in leaf area relative to root area or sapwood area can affect estimates of whole plant transpiration rates (West et al. 1999). Altered root distributions or leaf area can also lead to a difference in the ratio of aboveground to belowground biomass, and competition between semi-arid grasses was found to alter aboveground to belowground biomass ratios depending on the identity of the neighboring grass (Novoplansky and Goldberg 2001). Additionally, variation in water availability arising from the effects of PPI could result in adjustments in leaf area to sapwood area, which would alter transpiration rates and affect plant stress under different soil moisture dynamics. Although studies have not evaluated the effect of neighbors on the ratio of leaf area to sapwood area, this ratio is known to vary in response to differences in water availability (Hultine et al. 2005). In summary, changes in plant allometries as a result of PPI could largely affect the scaling of leaf- and plant- level transpiration, and not accounting for such variation may be a potential source of scaling error or model bias.

Implications of Indirect Effects for Model Estimates

The inclusion of physiological adjustments in models may be necessary for accurately accounting for the impacts of plant neighbors and estimating transpiration. Patch scale transpiration predictions for a warm desert shrub, *Larrea tridentata*, were sensitive to the adjustments in stomatal behavior and root distributions arising from neighboring species (Kropp and Ogle 2015; chapter 2).For example, differences in physiology among different neighbor associations resulted in different seasonal transpiration estimates depending on physiological assumptions, and for example, not including the neighbor-specific physiological adjustments would have resulted in an under-prediction of summer transpiration by as much as 56% (chapter 3). However, our survey did not find any other ecohydrological modeling studies that accounted for physiological adjustments due to neighbor effects in vegetative parameters. The empirical, ecological studies that describe physiological adjustments of water-use traits do not address the timescales over which these adjustments occur and their impact on water fluxes or ecosystem processes (Brisson and Reynolds 1994, Callaway et al. 2003). To incorporate the indirect effects of neighbors on water fluxes, more data is needed about the temporal scales of the adjustments and the degree to which various species lead to adjustments of water-use traits. Such data should be paired with ecohydrological models to better understand and account for the importance of indirect effects on transpiration and soil moisture across a range of temporal and spatial scales.

Plant-Plant Interactions across Different Spatial Scales

Plant-plant interactions (PPI) are a largely understudied component in ecohydrological studies, and the impact of plant interactions on ecosystem water fluxes is not well quantified, particularly in regards to the significance of neighbor interactions across spatial scales. We evaluated 50 ecohydrological studies that included a model of transpiration and soil moisture, and we assessed the approach to parameterizing vegetative controls on transpiration (e.g. root distributions, leaf area, stomatal conductance). Only 10% of studies parameterized PPI to include both competition for water and facilitative effects or allowed the PPI effects to vary temporally ("detailed interaction", Fig 4.3). A simpler parameterization for PPI that included interactions only through competition for water between plant roots was found in 18% of studies ("competition only", Fig 4.3), but 72% of the studies did not explicitly consider any interactions between plant neighbors (Fig. 4.3). The most common parameterization used traits of a species or functional type that was dominant to patches within the study spatial scale, but did not explicitly allow interactions between patches ("species/functional type", Fig. 4.3). Many studies (33%) treated vegetation as homogenous and considered all vegetative parameters to be the same across all patches within the study spatial scale ("single parameter", Fig. 4.3). To approach PPI from a water cycle oriented perspective, the direct and indirect effects of PPI should be studied across multiple scales (Bielenberg 2011).

PPI Effects at Small Spatial Scales: from Patches to Ecosystems

The effect of plant neighbors on water fluxes is likely the greatest at the patch scale (plant and surrounding soil), since the direct effects of plant neighbors on the soil and above-ground microclimate predominately act at the patch scale. Transpiration at the patch scale has been found to be reduced by as much as 75% as a result of plant neighbor interactions (chapter 3). However, few of the ecohydrological studies we surveyed focused on patch-scale water fluxes, and no patch scale studies in our survey included detailed plant interactions (Fig. 4.3). A number of patch-scale models involving PPI include transpiration, competition, and facilitation, but focus on tracing plant mortality and carbon dynamics rather than quantifying the effects of PPI on transpiration or soil moisture (van Wijk and Rodriguez-Iturbe 2002, Synodinos et al. 2015). Accurately describing patch-scale water fluxes can be an important aspect in scaling plant-level transpiration to larger scales.

The effect of PPI on community or ecosystem scale water fluxes is largely driven by the abundance and spatial distribution of plant neighbors, and the magnitude of the direct effects of PPI (Ludwig et al. 2005). For example, a model of soil moisture in a savannah ecosystem found variation in soil moisture was dependent on the percent cover of woody and herbaceous plants within the community (Breshears and Barnes 1999). Accounting for the effect of different neighbor associations on transpiration across a stand of an arid shrub, *Larrea tridentata*, affected stand level predictions at the ecosystem scale by 30% (chapter 3). However, less than 10% of the community and ecosystem scale studies we surveyed to into account PPI (competition only or detailed, Fig. 4.3). Further study is needed to assess the contribution of PPI to variation in water fluxes across the ecosystem level. For example, PPI may have variable importance in different ecosystems depending on both abiotic drivers and the spatial distribution of plants in the ecosystem. However, few studies have explored the importance of PPI for spatial variation at ecosystem scales and the relative importance of PPI compared to other sources of spatial variability.

PPI Effects at Large Spatial Scales: from Catchments to Landscapes

At larger spatial scales such as a catchment or landscape, the contribution of variability attributed to PPI versus spatial heterogeneity in other biotic and abiotic drivers remains unclear. Several catchment scale models indicate that model estimates can be improved by including vegetative parameters that account for competition or allow for temporal variation in vegetative parameters (Sivandran and Bras 2013). Franz et al (2002) applied a model focused on variation in seasonal plant water use found that the transpiration can vary between landscapes characterized by highly aggregated plants versus more dispersed plant distributions depending on the gradient of hillslope of a watershed (Franz et al. 2012). However, across larger scales, other studies have suggested that variation in vegetation may not be as important for water fluxes compared to other abiotic factors such as soil depth and anthropogenic influences such as grazing or urbanization (Popp et al. 2009, Shields and Tague 2012). We suggest that more large scale studies are needed that specifically focus on the spatial variation that arises from PPI and its relative importance for water fluxes compared to other drivers of spatial variation.

Implications for Scaling

Further study is needed to specifically understand how PPI affect estimates of water fluxes across different spatial scales, and the sensitivity of scaling models to PPI (Rastetter et al. 2003, Asbjornsen et al. 2011). Furthermore, neighbor influences are often considered as two neighbors whose canopies clearly overlap, but neighbor configurations can vary in the number of neighbors, distance between plants, and neighbor size. Future studies should address the implications of PPI using more complex, realistic measures of interactions that treat plant neighbor associations as continuous measures and account for temporal variation in water availability and plant characteristics.

Plant-Plant Interactions across Varied Temporal Scales

Plants occurring with a neighbor may experience a mixture of competition, facilitation, or neutral effects across time as a result of differential soil water availability, for example, from precipitation and temperature (Holmgren et al. 1997, Tielbörger and Kadmon 2000). Plant water use traits can also vary seasonally, impacting the degree that neighbor effects influence transpiration (Holmgren et al. 1997). Incorporating temporal variation in vegetative parameters that may vary between wet and dry seasons is important for capturing the effects of PPI across seasonal and annual timescales (Manning and Barbour 1988, Briones et al. 1998). However, the impact of temporal variation in PPI effects and the impact of temporally variable water-use traits on PPI for predictions of transpiration across long timescales (decadal-century) is not well understood since many modeling studies that focus on century timescales treat vegetative parameters as temporally fixed (Reynolds et al. 2000, van Wijk and Rodriguez-Iturbe 2002). Temporal variability from PPI can help explain transpiration and soil moisture dynamics, and seasonal variability arising from PPI is rarely evaluated across longer timescales.

Conclusions and Future Studies

Models of water fluxes are commonly used in ecohydrological studies and can improve our fundamental understanding of ecohydrological processes (King and Caylor 2011, Vivoni 2012). Plant-plant interactions (PPI) are largely under incorporated in ecohydrological models, and the spatial nature of PPI requires integrative methodological approaches that pair multiple data types with process-based models to understand the effects of PPI on water fluxes (Newman et al. 2006, Vivoni 2012). However, the paucity of data related to the direct and indirect effects of PPI on water fluxes requires additional data collection on plant water-use traits (across space and time) coupled with observations of evapotranspiration and soil moisture. The lack of PPI data related to water fluxes may stem from a general lack of empirical data, and a meta-analysis of 267 ecohydrological studies found only 31% of ecohydrological models used empirical data to parameterize models (King and Caylor 2011). Additionally, the meta-analysis found that modeling studies under-utilized experimental approaches of more traditional disciplines and only 3% of the modeling studies included data from experimental manipulations. Traditional ecological experimental approaches (i.e. plant neighbor manipulation experiments) used to study PPI can be paired with hydrological data to inform underlying mechanisms of PPI on water fluxes (Aarssen and Epp 1990, King and

Caylor 2011). An improved understanding of PPI influences on water fluxes is necessary for developing mechanistic models that include spatial variation in evapotranspiration that arises from biotic drivers.

Climate change is expected to affect plant community dynamics and hydrological fluxes on both global and smaller scales (Scanlon et al. 2005, Huntington 2006, Grant et al. 2014), and well informed, mechanistic models are necessary for realistic predictions of future water fluxes and vegetation dynamics (Rastetter et al. 2003). Arid ecosystems tend be associated with high uncertainty in evapotranspiration estimates (Long 2014), and accounting for biotic processes such as PPI is likely to reduce such uncertainty (Asbjornsen et al. 2011, Shields and Tague 2012). However, the importance of PPI across different spatial and temporal scales, and identifying the underlying mechanisms, requires further research and data to help inform mechanistic models that can be linked to other hydrological models or paired with models of plant carbon dynamics. Furthermore, PPI can also affect water fluxes in more mesic ecosystems (Breda et al. 1995, Loranty et al. 2010), and incorporating PPI into dryland models can provide a reference point for the influence of PPI on water fluxes under extreme water limitations in other ecosystems. A better understanding of the effects of PPI on water fluxes is important for accurately estimating water fluxes and providing a mechanistic understanding of PPI as a source of spatial variability in ecohydrological models.

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Figures

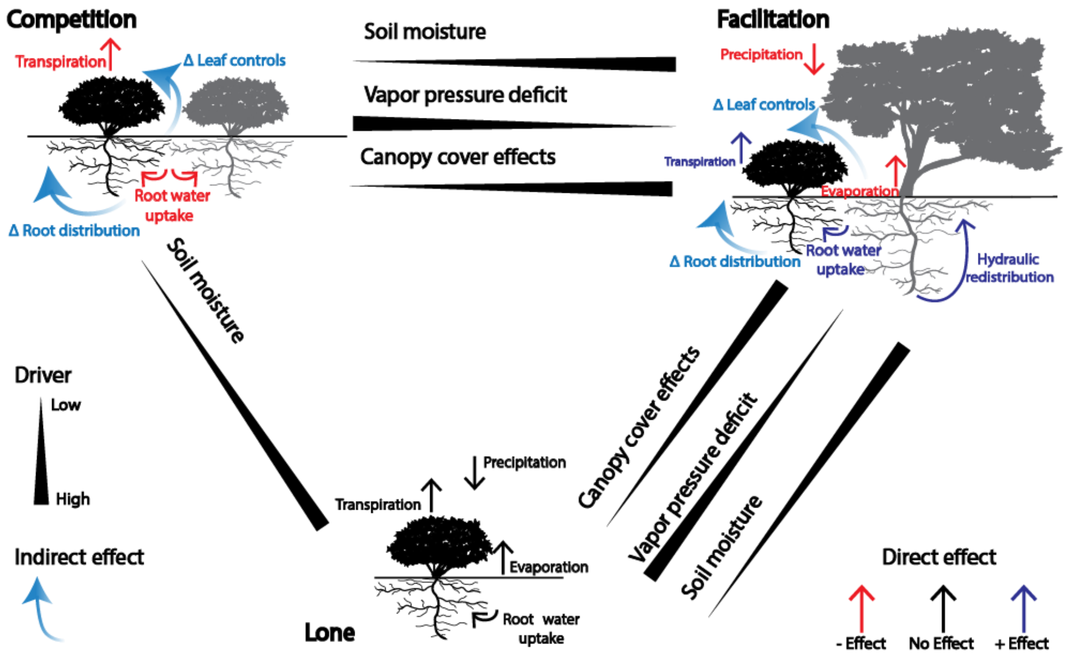

Figure 4.1. A conceptual diagram of the direct and indirect effects of plant-plant interactions (PPI) on patch scale water fluxes. We illustrate the potential effects in scenarios where only competition, facilitation, or complete isolation (lone) occur, and these scenarios represent extreme ends of a spectrum of neighbor interactions. The effects of PPI likely lie within this spectrum, experiencing mixed effects of positive, negative, or neutral interactions with neighbors. Direct effects on water fluxes are indicated with straight arrows: a decrease in the water flux (negative effect) is indicated in red, and an increase in a water flux is indicated in dark blue (positive effect). Indirect effects arising from adjustments of water-use traits in response to altered environments created by neighbors are indicated with light blue arrows. The drivers of water fluxes that are altered by neighbor environments are indicated with black wedges between the three scenarios where the thickness of the bar indicates the magnitude of the driver.

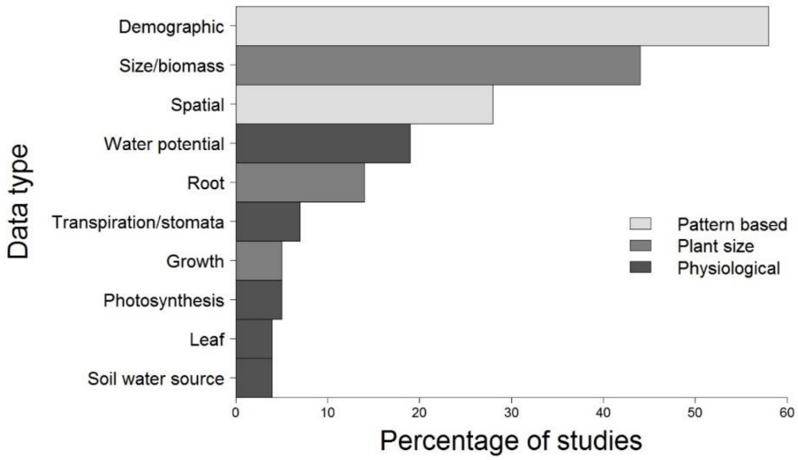

Figure 4.2. Percentage of data types utilized in 104 arid or semi-arid plant-plant interaction (PPI) studies to draw inferences about competition and facilitation. Bar colors indicate the general categories of data types including 1) observations of patterns in plant communities (pattern based), 2) measures of plant size, 3) data related to physiological traits and behavior. A full citation list of studies and search parameters is included in Appendix E.

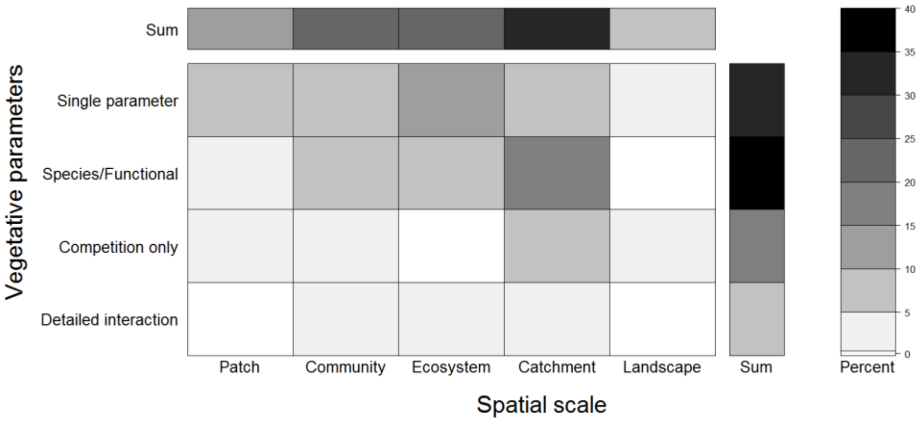

Figure 4.3. The distribution of the spatial scale and parameterization approach of vegetative characteristics (e.g. root distribution, stomatal conductance, leaf area) in 50 ecohydrological modeling studies that include models of transpiration and soil moisture. The parameterization of vegetation in models was categorized based on whether or not the study included parameters that: 1.) had a single parameter that assumed all vegetation is homogeneous throughout the study spatial scale and all vegetative parameters are given a single value that does not account for PPI, 2.) reflect the dominant species or functional type within the study scale and do not explicitly account for the neighbor interactions between patches, 3.) parameters represent competition for water between overlapping roots for soil water, 4.) parameters account for detailed plant interactions that include both competition, facilitation and/or temporal variation in vegetative parameters. Spatial scales range from patch (m^2) to landscape (>100 km^2). A full list of studies and search criteria is included in Appendix E.

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APPENDIX A

SOIL PROPERTIES AND ROOT IDENTIFICATION: ADDITIONAL DESCRIPTIONS OF FIELD AND LABORATORY METHODS

Soil Core and Field Sample Collection

For the *Larrea* shrubs with a neighbor, one soil core was taken beneath the overlapping canopies and a second core was taken beneath *Larrea*'s canopy opposite from the neighbor. One core was collected below the canopy for *Larrea* growing alone. Cores were taken as deep as possible, and rocks prevented cores from going deeper than 60 cm. A total of 13 *Larrea* shrubs were sampled; three *Larrea* shrubs in each neighborhood association were sampled, and an additional fourth shrub was sampled for *Larrea* growing next to *Ambrosia* since rocky soils prevented deep coring below one of the initial three shrubs.

Soil samples were kept on ice in the field, and after sampling, roots were immediately sorted, rinsed in deionized water, dried, and stored at -80°C. A subset of the soil samples and two stem samples were collected in the early morning from each shrub, and were also kept on ice in the field and stored at -20°C in the lab for stable isotope analysis. Pre-dawn twig water potential was measured on study shrubs using a 1505D pressure chamber instrument (PMS Instrument Company, Albany OR), which was assumed to be equal to the root water potential.

Soil and Root Hydraulic Properties for the Biophysical Model of Water Uptake

The soil and root hydraulic properties (Table 2) were obtained from data and largely reliant on the relationship between soil water content and soil water potential (Ψ). Soil moisture holding curves were conducted by sequentially measuring Ψ and gravimetric soil water content on drying soils using a WP4 potentiometer (Decagon, Pullman, WA). The gravimetric soil water content was converted to volumetric water content (θ) via soil bulk density, which was calculated from soil texture under each shrub *l* (*l*=1, 2, …, 13) and of each depth layer *i* (*i*= 1 [0-10 cm], 2 [10-20 cm]…5 [40-60 cm]) using the soil water characteristics program (v6.02.74, Saxton & Rawls 1986, 2006). Then, the Campbell & Norman (1998) model was used to establish a relationship between θ and Ψ from the WP4 measurements such that for soil sample *n* (*n* = 1, 2, …, 531) the predicted Ψ is give by:

$$\psi_n = \psi_e \left(\frac{\theta_n}{\theta_{s,l,i}} \right)^{2b_{l,i}+3} \qquad \text{(eqn S1)}$$

The air entry water potential (Ψe), saturated water content (θ_{sat}), and the dimensionless exponent (*b*) were allowed to vary by shrub *l* and soil layer *i* associated with sample *n*. θ_{sat} was calculated based on a relationship established by Saxton et al (1986) using the percent sand and clay associated with each sample. Soil texture and particle size distribution (% sand, silt, clay) were determined via the hydrometer method (Gee & Bauder, 1986).

The model (eqn S1) was fit in a Bayesian framework in OpenBUGS (v3.2.1, Spiegelhalter et al 2003; Lunn et al 2009) by assuming that the log-scale observed Ψ, log(-Ψ), was normally distributed around the log-scale predicted value, log($-\Psi^{pred}$), in eqn S1. Semi-informative priors were assigned to Ψe and *b* by assuming uniform distributions based on the range of “nominal” values for all soil types (Campbell & Norman 1998), resulting in priors of log(Ψe) ~ U(-6, 2) and b ~ U(1.5, 7.8). OpenBUGS uses Markov chain Monte Carlo (MCMC) methods to sample from the posterior distribution of the parameters; three MCMC chains were run, and a burn-in of 3,000 samples was discarded.

The MCMC chains were run for an additional 2,000 samples each after burn in, resulting in a final posterior sample size of 6,000.

The posterior means for parameters Ψ*e* and *b* were used for additional data calculations. For example, soil water potential (Ψ_{soil}) associated with each shrub at the time of sample collection was calculated using eqn S1, given the field observation of θ for each soil sample and the posterior means for Ψ*e* and *b*. The Ψ_{soil} was averaged across each neighbor association, j, in eqn 4. Soil hydraulic conductance (K_{soil}) was calculated using the following relationship from Campbell & Norman (1998):

$$K_{s,l,i} = K_{sat,l,i}\left(\frac{\theta_{l,i}}{\theta_{s,l,i}}\right)^{2b_{l,i}+3} \qquad \text{(eqn S2)}$$

Saturated hydraulic conductivity (K_{sat}) was obtained from Campbell & Norman (1998) based on observed values for the soil texture associated with each sample. The Ksoil was averaged across each neighbor association for eqn 4.

The root water potential (Ψ_r) was assumed to be equal to the pre-dawn stem water potential measured on each shrub. The hydraulic conductance between the root and the soil (K_{root}) for each shrub *l* and soil layer *i* was calculated using the Campbell & Norman (1998) equation:

$$K_{root,l,i} = K_{sat,l,i}\left(\frac{\Psi e_{l,i}}{\Psi_{root,l}}\right)^{2+3/b_{l,i}} \qquad \text{(eqn S3)}$$

The turgor loss water potential (Ψ_{tloss}) was determined using leaf pressure volume curves conducted with a WP4 potentiometer (Decagon, Pullman, WA). Measurements of relative water content (RWC) and leaf water potential (Ψ_{leaf}) were taken simultaneously on leaves from five shrubs. In the lab, measurements were taken 5-8 times as leaves dried, and a total of 40 measurements (s= 1…40) were obtained across all shrubs. A least squares linear regression was fit to $1/\Psi_{leaf,s}$ versus RWC in R v 3.1.2 (R core team, 2014), for observations associated with data that had $RWC_s < 0.95$ (i.e., the linear portion of the $1/\Psi_{leaf,s}$ versus RWC_s curve). The RWC at turgor loss (RWC_{tloss}) was estimated from the predicted regression at $1/\Psi_{leaf}=0$.

The linear relationship between $1/\Psi_{leaf,s}$ and RWC_s described above is used to define RWC_{tloss}, but a non-linear model that describes the relationship between RWC_s and $\Psi_{leaf,s}$ is necessary to predict the Ψ_{leaf} that is associated with RWC_{tloss}. A nonlinear regression was established between RWC_s and $\Psi_{leaf,s}$ across the entire range of RWC_s values (0.1-1.0):

$$\left|\Psi_{leaf,s}\right| = \Psi_{\max} e^{-\omega RWC_s} \qquad \text{(eqn S4)}$$

The parameters Ψ_{max} and ω were fit via a non-linear least squares regression in R (R core team, 2014), and the predicted Ψ_{leaf} at the turgor loss RWC_{tloss} was used in eqn S4 to obtain Ψ_{tloss}.

Genomic DNA Extraction

Frozen root samples were ground with a mortar and pestle in the presence of liquid nitrogen. Approximately 30 mg of root powder was added to a buffer containing 100 mM Tris-HCl (pH 8.0), 25 mM Ethylenediaminetetraacetic acid (EDTA, pH 8.0), 2 M NaCl, 2% (w/v) hexadecyltrimethylammonium bromide (CTAB), 500 mg/L

Spermidine, 2% (w/v) Polyvinylpyrrolidone K30, 5% (w/v) Polyvinylpolypyrrolidone, and 2% (v/v) β-mercaptoethanol. The mixture was incubated at 65°C for 30 min and periodically mixed. An equal volume of a chloroform/isoamyl alcohol (24:1) was added to the aqueous layer, samples were mixed for two min, and centrifuged at 10,000 xg for 10 min, and repeated a second time. DNA was precipitated out of the aqueous solution by adding 1.5 volume of isopropanol and stored overnight in a -20°C freezer. DNA was recovered by centrifugation for 30 min at 20,000 xg. The DNA pellet was washed twice with 70% ethanol, dried, and dissolved in 150 µL of 10 mM Tris-HCl (pH 8.4) and 1 mM EDTA. If brown, viscous mixtures were produced from the dissolution of the DNA pellet, additional purification steps were taken based on methods outlined by Paterson et al (1993). An additional 100 µL of 10 mM Tris-HCl (pH 8.4) and 1 mM EDTA was added, and the DNA was heated in a 65°C water bath for 20 min. The impurities were pelleted out by centrifuging the sample at 10,000 xg for 5 min. The supernatant was removed, and DNA was precipitated with cold 100% ethanol at -20°C overnight. Washing procedures were conducted again and the pellet was dissolved in 150 µL of 10 mM Tris-HCl (pH 8.4) and 1 mM EDTA.

PCR and Restriction Digests

PCR was conducted using Phire Hot Start II DNA Polymerase (Thermo Scientific) on reactions (20 µL total volume) included 1X Phire reaction buffer, 200 µM dNTPs, and 1 µL of each primer, 7 µL of DNA, and 0.4 µL of polymerase. Amplification was done on a Bio-Rad DNA Engine thermocycler with an initial denaturation of 98°C for 30s, followed by 35 cycles of denaturation at 98C for 5s, an annealing step at 52°C for 5s, and an extension of 72°C for 15s and a final extension of 1min at 72°C. Digestions were conducted with 10 μL of PCR product, 1 μl of enzyme, 2 μL of buffer Tango, and 18 μl of water for a minimum of 2 hours at 37°C. Digestion mixtures were analyzed using gel electrophoresis on a 2% agarose gel in Tris-borate-EDTA buffer at 40V.

Methodological Testing

Leaf DNA from each plant was used to establish positive controls, and roots were excavated around the base of the stem from each species to verify that the methods matched the leaf DNA results and are not prone to contamination. Additionally, PCR was conducted on known root extracts created from equal ratios of all four species and in pairwise combinations (e.g., *Larrea* and *Ambrosia*) to test for any limitations in visualizing root fragment patterns in mixtures. *Prosopis* was not detected in the presence of other species, and thus all large roots (≥ 2 mm) collected below *Prosopis* neighbor associations were analyzed individually to detect the presence of *Prosopis* (individual analysis of fine roots was logistically impossible). Detection issues associated with *Prosopis* were accounted for in the model formulation, and no other species exhibited issues with false negatives (inability to detect species despite presence). The sequences of surrounding non-focal species (*Cylindropuntia acanthocarpa*, *Encelia farinosa, Lycium fremontii, Celtis pallida*) were obtained from GenBank, and determined not to have any expected cleavage sites for the restriction endonucleases RsaI and BssHII, and thus the presence of a non-cleaved fragment was scored as the presence of “other” species.

Priors and Model Implementation

The parameters in the gamma mixture model (eqn 1) for the fraction of active roots (*f*) were assigned semi-informative based on Ogle et al. (2004). Priors were assigned on the log or logit scale such $\log(m_1)$, $\log(m_2)$, and $\text{logit}(w)$ were assumed to follow a multivariate normal distribution with a semi-informative covariance matrix as given in Ogle et al. (2004). The priors for $\log(a_1)$ and $\log(a_2)$ were slightly altered from Ogle et al. (2004), and assigned univariate normal distributions with semi-informative variances. Uniform, U(0,1), priors were assigned to probability parameters β, γ, and φ^* (eqn 6-8). Priors for b, α, ρ, and κ (eqn 13 and 17) were constrained to be positive by assigning diffuse normal distributions truncated at zero such that only positive values were allowed. The proportion of water uptake in the simple, isotope-only mixing model (u; eqn 16) was given a non-informative Dirichlet distribution following Moore & Semmens (2008).

The posterior distributions of the model parameters associated with the combined data model described in the main text were obtained in OpenBUGS (Spiegelhalter *et al.* 2003; Lunn *et al.* 2009) by running three parallel MCMC chains. The first 182,500 samples were discarded as burn in, and the model was run for 180,000 after burn in. Chains were thinned every 30 iterations to minimize autocorrelation and reduce storage requirements, and a final posterior sample size of 6,000 was obtained.

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APPENDIX B

ROOT PRESENCE AND WATER UPTAKE FIGURES

Figures

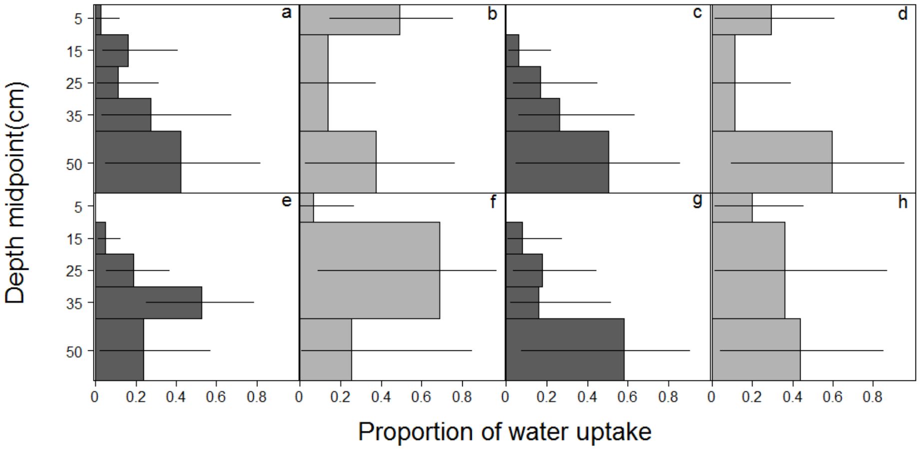

Figure S2.1. Posterior estimates (mean and 95% credible interval) of *Larrea tridentata*'s proportional water uptake (*p*, eqn 3 in main text) based on stable isotope data coupled with a biophysical model of water uptake (dark grey shading; a,c,e,g) or with a simpler, isotope-only mixing model that assumed water uptake was proportional to soil water content (light grey shading; b,d,f,h). Four neighborhood associations are represented: *Larrea* growing next to *Olneya tesota* (a, b), *Ambrosia deltoidea* (c, d), or *Prosopis velutina* (e, f), and growing alone (g, h).

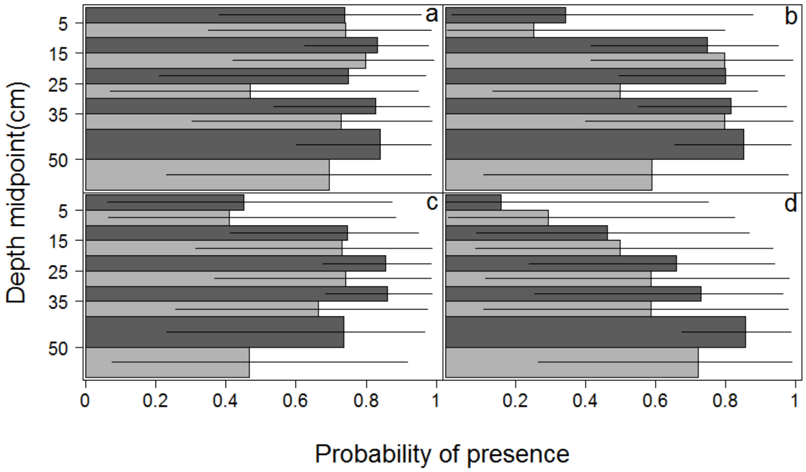

Figure S2.2. Posterior estimates (mean and 95% credible interval) of the probability of root presence for *Larrea tridentata* under four different neighborhood associations, for *Larrea* growing next to: (a) *Olneya tesota*, (b) *Ambrosia deltoidea*, or (c) *Prosopis velutina*, or (d) growing alone. Dark grey bars represent results from the occupancy model that uses combined datasets and light grey bars show the estimates using only molecular identification data and non-informative priors.

APPENDIX C

DESCRIPTION OF DYNAMIC SOIL WATER MODEL IMPLEMENTATION AND DATA INPUTS

HYDRUS Seasonal Implementation

Data associated with *Larrea*'s root distribution and above-ground controls on transpiration were primarily collected in winter and summer periods; therefore, spring and fall parameters were linearly interpolated between winter and summer. Linear interpolations prevented abrupt transitions in parameters between seasons that do not realistically reflect the timeframe for seasonal adjustments in plant physiology. Simulations were implemented in seven periods (winter 1= Jan-Mar; spring month 1= April; spring month 2= May; summer= June-Sept; fall month 1= Oct; fall month 2= Nov; winter= Dec). The seasonal simulations were run sequentially, and SWC from the last day of a season for each profile node was used for the initial SWC values for the start of the next season's simulation. The sequential Hydrus runs were conducted using an automated script (Python v2.7, CITE) (github repository link).

Meteorological Data Sources

Simulations used D (Fig 1c) calculated from hourly relative humidity and air temperature data (Fig 1A and B; CS215, Campbell Scientific, Logan, UT) collected at the site in 2014 using a CR1000 and CR10X dataloggers (Campbell Scientific, Logan, UT). Missing data was gap-filled based on a linear relationship established between observations at the site and a nearby weather station (Fountain Hills; FCDMC, 2015). Atmospheric pressure (P) was also obtained from the FCDMC weather station. Since the field site was established in 2011, all measurements of temperature and relative humidity for the 2004 climate year were taken from the FCDMC weather station and corrected based on the linear relationship established for 2014. A linear relationship between temperature data reported in literature outside and beneath *Olneya* and *Prosopis* canopies (Tewksbury et al. 1999, Suzán-Azpiri and Sosa 2006, Suzán et al. 2014).was used to account for the effect of tree canopies on air temperature and subsequently, D (Fig. 1A, B, and C).Volumetric SWC (CS615, Campbell Scientific) was collected simultaneously in the late summer and in December of 2014 to validate the Hydrus model output.

Winter Vertical Root Distributions

Winter soil cores (December, 2011 and March, 2012) did not have detailed molecular identification and isotope data to partition *Larrea* and neighbor root profiles. However, neighbor fractional root distributions were assumed to stay the same, *Larrea's* fractional root distribution was considered to be the remainder of the fractional bulk root biomass ($f_{r,b}$) after neighbor root profiles were accounted for:

$$f_{r,l} = f_{r,b} - \left(f_{r,b} \times (1 - p_{larrea}) \times f_{o,m} \right) \tag{26}$$

where f_r is *Larrea*'s fractional root profile, p_{larrea} is the proportion of Larrea roots in the bulk mixture (cite chapter 2), and f_o is the fractional root profile of neighboring species. The fractional bulk root distributions were fit in a Bayesian framework, using the mixture of gamma distributions to describing the shape of the root distribution across depth (Ogle et al. 2004, 2013). The model was implemented in OpenBugs (Spiegelhalter et al. 2003) for three chains for a burn in of 50,000 and run for 70,000, thinned by 100 iterations for autocorrelation, and a total sample size of 6,000 was obtained. Priors for root distribution were based on Ogle et al 2004 and 2013.

Soil texture model

Soil water curves were fit for soil samples from 17 shrubs for each soil depth layer (n=6, total measurements n=65. Soil hydraulic parameters were determined using water holding curves constructed by sequentially measuring the water potential(ψ) and gravimetric water content for drying soils using a WP4 potentiometer (Decagon, Pullman, WA).

$$\theta(\psi) = \theta_r + \frac{\theta_s - \theta_r}{\left[1 + |a\psi|^n\right]^{1-\frac{1}{n}}}$$

(27)

The saturated soil water content (θ_s) was determined graphically, with data at low water potentials close to zero at a soil water content of 0.40. The residual soil water content θ_r, air entry potential, α, and n, an unitless parameter related to texture were fit in a Bayesian framework in Openbugs (Spiegelhalter et al. 2003, Lunn et al. 2009). Soil hydraulic parameters were did not significantly vary for each shrub and shrub x soil layer, so posterior mean across all shrubs and soil layers. Soil texture data (n=158) supports our assumptions of similar soil hydraulic properties, with the soils predominately consisting of 82% (standard error [se], .06%) sand, 13% (se .06%) loam, and 5% (se .03%) clay. The saturated hydraulic conductivity was parameterized based on predictions from soil texture data in Hydrus' neural network prediction application, Rosetta (Šimůnek et al. 2008).

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APPENDIX D

DATA PARAMETERS, SITE MAP, AND SOIL MOISTURE VALIDATION DATASET RESULTS

Results

Simulation Validation

The model slightly under-predicted the average observed volumetric SWC for L and N scenarios from 0-30 cm (Fig. S2, ESI) across each neighbor association, and goodness of fit R^2 ranged from 0.71 (for N-A) to 0.81 (for N-O).

Tables

Table S3.1. Parameters describing potential stomatal conductance (g_s) and leaf area index (LAI) for *Larrea tridentata* and neighboring species.

Parameter	Equation	Season	Species parameter value			
			Larrea tridentata			
			Lone	*Olneya*-association	*Ambrosia*-association	*Prosopis*-association
$g_{\mathrm{ref}*}$	Eqn 4	winter	0.098	0.078	0.077	0.084
		spring 1/fall 2	0.117	0.094	0.086	0.1
		spring 2/ fall 1	0.137	0.11	0.095	0.117
		summer	0.156	0.127	0.104	0.134
m_*	Eqn 4	winter	-0.055	-0.042	-0.045	-0.051
		spring 1/fall 2	-0.049	-0.038	-0.037	-0.042
		spring 2/ fall 1	-0.044	-0.033	-0.029	-0.033
		summer	-0.038	-0.029	-0.021	-0.024
LAI†	Eqn 2	summer	0.148	0.115	0.106	0.149
		winter	1	1.17	0.9	0.97
		spring 1/fall 2	0.88	0.99	0.82	0.83
		spring 2/ fall 1	0.76	0.82	0.74	0.7
		summer	0.64	0.64	0.66	0.56
			Neighboring Species			
			Olneya tesota	*Ambrosia deltoidea*	*Prosopis velutina*	
$g_{\mathrm{ref}*}$	Eqn 6	annual	0.04	0.145	0.088	
m_*	Eqn 6	annual	-0.003	-0.075	-0.018	
LAI†	Eqn 2	annual	0.88	1.2	1.58	

†indicates units of m^2 leaf m^{-2} ground

*indicates units of mol m^{-2} s^{-1}

Figures

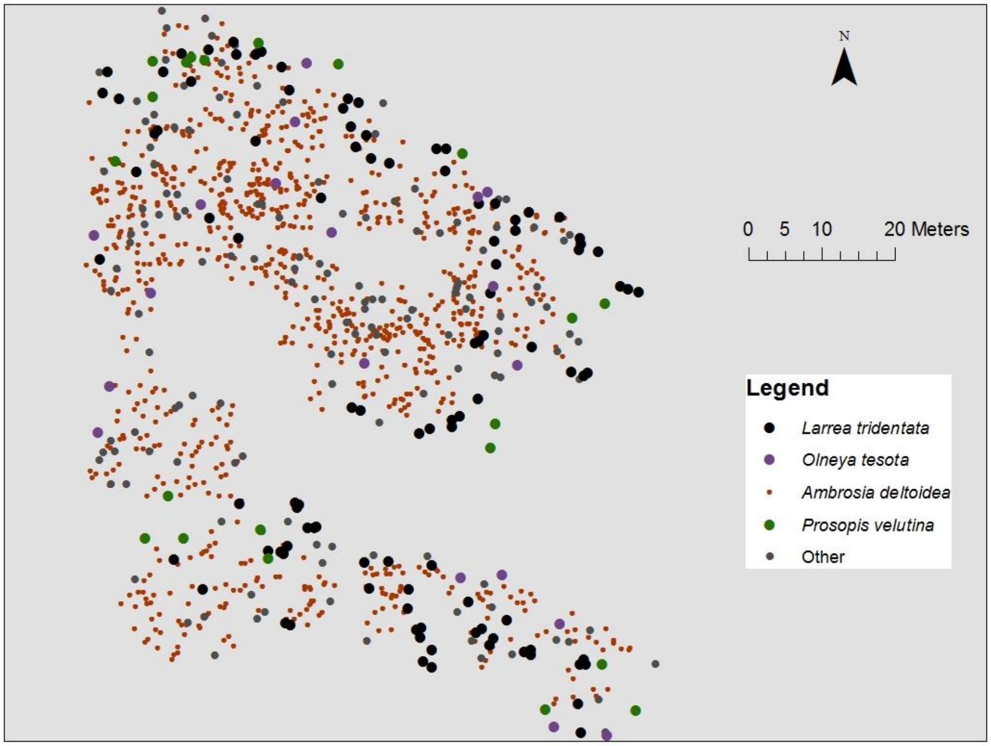

Figure S3.1. Map of study site used to classify *Larrea*-neighbor patches for stand level calculations. Non-focal species (n=9, e.g. *Cylindropuntia acanthocarpa*, *Lycium fremontii*, *Carnegiea gigantean*) are designated as other.

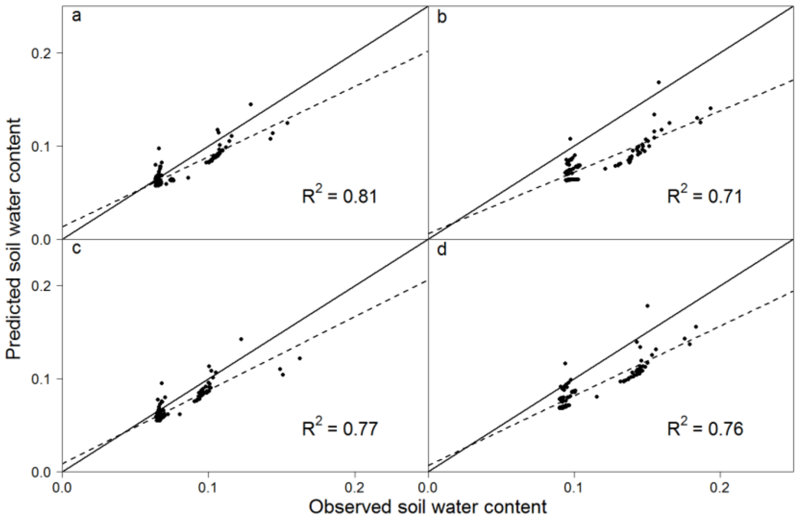

Figure S3.2. Volumetric soil water content model goodness of fit for the Hydrus simulations of *Larrea tridentata* growing next to: a) *Olneya tesota*, b) *Ambrosia deltoidea*, c) *Prosopis velutina*, d) alone. The solid black line indicates the 1:1 line and the dashed line indicates the best fit regression line.

APPENDIX E

SEARCH PARAMETERS AND STUDIES INCLUDED IN META-ANALYSES

Meta-analysis of Plant-Plant Interaction Data Types

A search for plant-plant interaction studies was conducted on August, 4th and 5th 2015. The following terms were searched in Web of Science: arid, desert, plant interaction, competition, facilitation, plant competition, water, plant facilitation. Search terms in Google Scholar included: arid, plant facilitation, water, arid plant-plant interaction. All studies focused on plant-plant interactions with empirical data from semi-arid and arid ecosystems were included.

Meta-analysis of Ecohydrological Model Parametrization

A search for ecohydrological models was conducted on August, 5th and 6th, 2015. Web of Science search terms included: transpiration, soil moisture, model, arid. An additional search was conducted in Google Scholar using the terms: Ecohydrology, model, arid, transpiration. Evapotranspiration and soil moisture in arid and semi-arid ecosystems had to be explicitly modeled, and models that included only empirical data without a model for evapotranspiration were excluded.

List of Studies Included in Data Type Meta-analysis

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