Antecedent soil water content and vapor pressure deficit interactively control water potential in Larrea tridentata

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Summary

- Plant water potential $\Psi$ is regulated by stomatal responses to atmospheric moisture demand $D$ and soil water availability $W$, but the timescales of influence and interactions between these drivers of plant $\Psi$ are poorly understood.
- Here, we quantify the effects of antecedent $D$ and $W$ on plant $\Psi$ in the desert shrub Larrea tridentata. Repeated measurements of plant baseline water potential $\Psi_B$ and diurnal water potential $\Psi_D$ were analyzed in a Bayesian framework to evaluate the influence of antecedent $D$ and $W$ at daily and subdaily timescales.
- Both $\Psi_B$ and $\Psi_D$ exhibited negative, 2- to 4-d lagged responses to daily-scale $D$; conversely, plant $\Psi$ responded almost instantaneously to subdaily $D$, though the direction of this response depended on antecedent moisture conditions. Plant $\Psi_B$ and $\Psi_D$ responded positively and immediately (no lag) to shallow $W$, which contrasts the negative, lagged $(6-7\text{ d})$ response to deep $W$.
- The changing sensitivity of $\Psi_D$ to subdaily $D$ highlights shifting modes of plant $\Psi$ regulation: $D$ effects on $\Psi_D$ range from negative to neutral to positive depending on past conditions and time of day. Explicit consideration of antecedent conditions across multiple timescales can reveal important complexities in plant responses.

Introduction

Water potential $\Psi$ of a plant leaf or stem is an integrated measure of plant water status that interacts with critical functions such as stomatal conductance (Tardieu & Davies, 1992), hydraulic conductivity (Pockman & Sperry, 2000), sugar transport (Hölttä et al., 2009), and whole-plant transpiration (Sperry et al., 2002). Plant $\Psi$ must be regulated above a critical threshold to prevent hydraulic failure (Sperry et al., 2002), wherein xylem conduits are fully embolized and the plant can no longer supply its leaves with water (Brodribb & Cochard, 2009; Urli et al., 2013). To maintain tissue hydration, plant $\Psi$ is exogenously influenced by soil water content $W$ and vapor pressure deficit $D$ (Cowan, 1965; Jarvis, 1976) and endogenously regulated by stomatal responses to $W$ and $D$ (Jones & Sutherland, 1991; Cochard et al., 1996). Regulation of plant $\Psi$ can be interpreted in terms of iso-/anisohydric stomatal behavior (sensu Tardieu & Simonneau, 1998; and see Hochberg et al., 2018 for a broader set of definitions): isohydric species maintain fairly constant plant $\Psi$ due to strict stomatal control, whereas anisohydric species exhibit wider ranges of plant $\Psi$ due to loose stomata regulation (Jones, 1998; Tardieu & Simonneau, 1998). However, plant responses and regulation may lag behind environmental stimuli, partly due to delays associated with plants sensing the stimuli and subsequently transporting the associated signal (Chaves et al., 2009).

Though quantitative studies of plant hydraulic function often assume that physiological variables respond to environmental conditions in near real time (e.g. Jones & Sutherland, 1991; Oren et al., 1999), physiological processes often depend on antecedent (past) conditions (Ogle et al., 2015). For example, stomatal conductance can remain suppressed days to weeks after a watering event that breaks soil drought (Gallé & Feller, 2007; Flexas et al., 2009; Xu et al., 2009), possibly because the rate of water infiltration (Castillo et al., 2003; Rigby & Porporato, 2006) and recovery of hydraulic conductance (Lo Gullo et al., 1998; Blackman et al., 2009) depend on antecedent $W$. More directly, stomatal sensitivity to $D$ can depend on past $D$ conditions (Barbour & Buckley, 2007), resulting in delayed shifts in rates of transpiration and carbon uptake (Goldstein et al., 2000; Pfautsch & Adams, 2013). Stomatal and plant $\Psi$ responsiveness to soil and atmospheric moisture are therefore not always immediate (BassiriRad et al., 1999; Yan et al., 2000; Resco et al., 2008) and can occur on longer temporal scales than previously thought (Ogle et al., 2015; Kropp et al., 2017). Because cumulative effects of lagged plant responses have the potential to impact ecosystem-scale carbon and water fluxes (e.g. Anderegg et al., 2015; Ryan et al., 2015; Shen et al., 2016; Kropp et al., 2017; Schwalme et al., 2017), it is important to quantify and understand the temporal lags in plant ecophysiological responses.
The evergreen desert shrub Larrea tridentata (creosote bush, referred to hereafter as Larrea) is the most abundant perennial plant of the North American warm deserts (Smith et al., 1997). Larrea is remarkably drought tolerant and actively photosynthesizes despite high temperatures (Mooney et al., 1978) and low Ψ (Franco et al., 1994). Year-round maintenance of a hydrated canopy (Runyon, 1936) and positive carbon uptake (Oechel et al., 2007; Fisher et al., 2010), subdaily changes in diurnal Ψ due to nocturnal transpiration rates (Sellin, 1999; Barbour & Buckley, 2005), which can be up to 25% of daytime transpiration in Larrea (Ogle et al., 2012). Therefore, predawn Ψ could depend not only on soil Ψ but also on antecedent atmospheric conditions (e.g. D) that affect nocturnal transpiration rates (Sellin, 1999; Barbour & Buckley, 2007; Fisher et al., 2007; Ogle et al., 2012). Diurnal variation in Ψ is generally more negative than predawn Ψ, given higher day-time transpiration rates (Caird et al., 2007; Forster, 2014). Since stomata typically respond to D on the order of minutes to hours (Damour et al., 2010), subdaily changes in diurnal Ψ are likely closely linked to subdaily variation in D, but the sensitivity of diurnal Ψ to subdaily D and the timescales over which D affects diurnal Ψ are not clearly known.

Temporal patterns of plant responses may be particularly important in arid regions, as prolonged dry periods unsuitable for plant function are unpredictably interrupted by episodic precipitation (Noy-Meir, 1973; Loik et al., 2004). Anticipated future conditions in the southwestern USA – higher temperatures, greater aridity, and lower soil moisture (Seager et al., 2007; Garfin et al., 2013; Prein et al., 2016) – are expected to amplify plant water stress via extreme or prolonged episodes of low Ψ and high D (Williams et al., 2013). Consequently, more negative plant Ψ may lead to increased hydraulic dysfunction (Sperry et al., 2002) and drought-induced mortality (McDowell et al., 2013; Sperry & Love, 2015). Hence, clarifying the environmental conditions and associated timescales of influence that determine plant Ψ are important for predicting plant hydraulic responses under a changing climate. To address this challenge, we quantified the effects and timescales of influence (e.g. temporal lags) of antecedent W and D on plant ΨB and ΨD in Larrea by addressing the following questions: (Q1) How do soil and atmospheric moisture conditions control plant Ψ? (Q2) Over what timescales do these environmental drivers influence plant Ψ? (Q3) How might antecedent conditions impact regulation of plant Ψ in response to subdaily variation in atmospheric conditions (D)? We address these questions by analyzing repeated (within a day and across the growing season) observations of plant ΨB and ΨD in the context of the stochastic antecedent modeling (SAM) framework (Ogle et al., 2015). This study is novel because we explicitly quantify the temporal lags in plant Ψ responses to soil and atmospheric moisture (W and D) by exploiting the variable moisture conditions of an arid system and drawing upon the SAM analysis approach.

Materials and Methods

Site description and data collection

From June 1998 to July 1999, 16 mature individuals of L. tridentata [DC] Cov. were selected for study at the Jornada Long-Term Ecological Research site in New Mexico, USA (described in Ogle & Reynolds, 2002). All shrubs occurred in a fenced enclosure and were within 20 m of a micrometeorological station and a centralized data collection and sensor operation system. Eight control shrubs were randomly selected to receive only ambient rainfall, whereas the other eight treatment shrubs were watered twice in summer 1998 (30 and 40 mm) and once in early spring 1999 (45 mm) in addition to receiving ambient rainfall. Irrigation was supplied by a gravity-fed hose and watering tank and confined to a circular area that extended about 0.25 m beyond the canopy drip line of each shrub. In the context of this study, irrigated and control groups are simply used to create greater variation in soil moisture conditions.

During the study period, small terminal twigs were repeatedly excised from each shrub between 05:00 h and 20:30 h local time on each sampling day. Plants were sampled on 11 d during the summer of 1998 and 6 d during the spring and summer of 1999, spanning a range of D and W conditions (Supporting Information Fig. S1). Plant Ψ was measured on excised stems with a

Scholander-type pressure chamber (Scholander et al., 1965) between two and 10 times per sampling day (total \( n = 1036 \)), spanning a range of plant water stress (Fig. 1). Four control and four treatment shrubs were intensely sampled (\( n \geq 109 \) measurements per shrub); the remaining shrubs were infrequently sampled (\( n \leq 20 \) per shrub). For logistical reasons, only nine measurements were made before sunrise (‘predawn’), so we deemed plant \( \Psi \) measured before or within 1 h of sunrise as \( \Psi_B \) (\( n = 151 \)). The remaining measurements represent \( \Psi_D \) time-series (\( n = 885 \)) and were completed before sunset (Fig. 1).

The plant \( \Psi \) measurements were paired with shrub-level soil water content \( W \) and site-level atmospheric vapor pressure deficit \( D \) (Notes S1). Time-domain reflectometry probes were placed under eight of the 16 shrubs to measure 30 min \( W \) at two depth intervals (0–30 and 30–60 cm). Larrea has a small fraction of active roots in the top 2 cm, and the bulk of its active root area is found between 20 and 45 cm (Ogle et al., 2004). Mean daily volumetric \( W \) was determined by daily averages of the half-hourly values, yielding shallow (\( W_{30,0} \), 0–30 cm) and deep (\( W_{60,3} \), 30–60 cm) estimates of water availability. Noninstrumented shrubs were paired with treatment-level (control or watered) \( W_{30} \) and \( W_{60} \) daily means. The micrometeorological station provided half-hourly averages of air temperature and relative humidity, which were used to compute \( D \) (Monteith & Unsworth, 1990); maximum daily \( D \) (\( \text{max} \) \( D \)) was calculated as the daily maximum of the half-hourly values.

Model description

The relationship between plant \( \Psi \) and antecedent moisture conditions (Table 1) was analyzed in a hierarchical Bayesian framework (Clark, 2005; Gelman et al., 2014) to evaluate temporal relationships (e.g. lags) between plant \( \Psi \) and environmental conditions. Plant \( \Psi_B \) and \( \Psi_D \) were modeled separately to independently estimate the effects and temporal lags of the shared antecedent covariates (Notes S2, S3). To define the likelihood of these data, observed \( \Psi \) values were assumed to be normally distributed, such that for observation \( i \):

\[
\Psi_{B,i} \sim \text{Normal}(\mu_{B,i}, \sigma_B^2) \\
\Psi_{D,i} \sim \text{Normal}(\mu_{D,i}, \sigma_D^2)
\]

Eqn 1

where \( \mu \) is the predicted plant \( \Psi \) and \( \sigma^2 \) describes the observation variance, both of which differ among \( \Psi_B \) and \( \Psi_D \) data, as indicated by the B and D subscripts. Next, we model \( \mu_B \) and \( \mu_D \) as linear combinations of antecedent covariates (denoted as \( X_{ij} \)).
Table 1 Notation used to denote antecedent covariates, their antecedent importance weights, the time-steps used to compute antecedent variables (Eqn 3), and the mean (nominal) values used to center the covariates in the baseline (Ψ_b) and diurnal (Ψ_D) water potential regressions (Eqn 2)

<table>
<thead>
<tr>
<th>Symbolic variable*</th>
<th>Vectors of importance weights</th>
<th>Covariate</th>
<th>Definition</th>
<th>Units</th>
<th>Time step size, ( T_{\text{lag}} )</th>
<th>Mean value</th>
</tr>
</thead>
<tbody>
<tr>
<td>( X_{\text{shrub}}^{\text{ant}} )</td>
<td>( \omega_1 )</td>
<td>( \max D^{\text{ant}} )</td>
<td>Daily maximum vapor pressure deficit</td>
<td>kPa</td>
<td>Daily</td>
<td>7</td>
</tr>
<tr>
<td>( X_{\text{shrub}}^{\text{ant}} )</td>
<td>( \omega_2 )</td>
<td>( W_{30}^{\text{ant}} )</td>
<td>Volumetric soil water content from 0 to 30 cm</td>
<td>m(^3) m(^{-3})</td>
<td>Daily</td>
<td>7</td>
</tr>
<tr>
<td>( X_{\text{shrub}}^{\text{ant}} )</td>
<td>( \omega_3 )</td>
<td>( W_{60}^{\text{ant}} )</td>
<td>Volumetric soil water content from 30 to 60 cm</td>
<td>m(^3) m(^{-3})</td>
<td>Daily</td>
<td>7</td>
</tr>
<tr>
<td>( X_{\text{shrub}}^{\text{ant}} )</td>
<td>( \omega_4 )</td>
<td>( D^{\text{ant}} )</td>
<td>Vapor pressure deficit ( D )</td>
<td>kPa</td>
<td>Half-hourly</td>
<td>7</td>
</tr>
<tr>
<td>( X_{\text{shrub}}^{\text{ant}} )</td>
<td>( \omega_5 )</td>
<td>( \Delta D^{\text{ant}} )</td>
<td>Change in ( D ) relative to previous value</td>
<td>kPa</td>
<td>Half-hourly</td>
<td>7</td>
</tr>
</tbody>
</table>

Weight vectors \( \omega_1, \omega_2 \) and \( \omega_3 \) were estimated separately for the \( \Psi_b \) and \( \Psi_D \) models, and weight vectors \( \omega_4 \) and \( \omega_5 \) only apply to the \( \Psi_D \) model. *Superscript ‘ant’ denotes the antecedent version of the covariate.

covariate \( j \), including antecedent daily maximum \( D \) (max \( D \)), daily \( W_{30} \) and daily \( W_{60} \) (\( \mu_b \) and \( \mu_D \)), and antecedent half-hourly \( D \) and change in \( D \) (\( \Delta D \), \( \mu_D \) only), and all two-way interactions (see Table 1 for a list of covariates):

\[
\begin{align*}
\Psi_{B,ij} &= \beta_{0,i} + \sum_{j=0}^{3} \beta_{j,i} \cdot X_{ij}^{\text{ant}} + \sum_{k=1}^{5} \beta_{kj,i} \cdot X_{ij}^{\text{ant}} \cdot X_{kj}^{\text{ant}} \\
\Psi_{D,ij} &= \alpha_{0,i} + \sum_{j=0}^{3} \alpha_{j,i} \cdot X_{ij}^{\text{ant}} + \sum_{k=1}^{5} \alpha_{kj,i} \cdot X_{ij}^{\text{ant}} \cdot X_{kj}^{\text{ant}}
\end{align*}
\]

Eqn 2

The \( \beta \) and \( \alpha \) parameters were allowed to vary by shrub, akin to a random coefficients model, where \( s(i) \) indicates shrub \( i \) associated with observation \( i \). The antecedent covariates are continuous in time, and \( t \) indicates the specific time associated with observation \( i \). The shrub-level main effects of covariate \( j \) on \( \Psi_B \) and \( \Psi_D \) are denoted by \( \beta_j \) and \( \alpha_j \), respectively, and \( \beta_{jk} \) and \( \alpha_{jk} \) indicate the interaction effects for covariates \( j \) and \( k \). Antecedent covariates were centered near their mean values so that the intercepts (\( \beta_0 \) and \( \alpha_0 \)) are interpreted as the predicted shrub-level \( \Psi_B \) and \( \Psi_D \), respectively at ‘nominal’ environmental conditions (see Table 1 for the nominal values).

While we expect plant \( \Psi \) to respond to antecedent conditions, the relative importance of environmental drivers at different times into the past is not known a priori. Thus, to complete the specification of the mean model (Eqn 2), we employed the SAM approach (Ogle et al., 2015) to simultaneously estimate the magnitude of the covariate effects and the timescale over which each variable influences plant \( \Psi_b \) and \( \Psi_D \). Antecedent variables were constructed using continuous time-series of each covariate \( X_j \) such that:

\[
X_{ij}^{\text{ant}} = \sum_{p=1}^{T_{\text{lag}}} \omega_{j,p} \cdot X_{i,t-p}
\]

Eqn 3

where \( j \) indicates the identity of the covariate (Table 1), \( t \) indicates the time period, \( T_{\text{lag}} \) indicates the total number of past time periods to sum over, \( \omega_{j,p} \) represents the weight or relative importance of the \( p \)-th time step into the past, and \( X_{i,t-p} \) is the observed value of variable \( j \) at \( p \) time steps ago. Antecedent variable \( X_{ij}^{\text{ant}} \) is thus a weighted average of past \( X_j \) values, where the weights \( \omega_{j,p} \) are determined stochastically by the data. Variation in \( \omega_{j,p} \) with respect to past time period \( p \) reveals the temporal pattern of the relationship between plant \( \Psi \) and variable \( X_j \). Because \( \Psi_b \) measurements were made within 1 h of sunrise, we used the previous day’s daily-scale variables (\( p = 1 \)) to represent ‘current’ conditions for both the \( \Psi_B \) and \( \Psi_D \) models.

To complete the Bayesian model, we specified priors for the unknown parameters, including hierarchical priors for the shrub-level main effects and interaction terms (see Eqn 2):

\[
\begin{align*}
\beta_j &\sim \text{Normal}(\mu_{\beta,j}, \sigma_{\beta,j}^2), j = 0, \ldots, 3 \\
\alpha_{jk} &\sim \text{Normal}(\mu_{\alpha,j,k}, \sigma_{\alpha,j,k}^2), j = 1, \ldots, 3, k = j + 1, \ldots, 5
\end{align*}
\]

Eqn 4a

\[
\begin{align*}
\beta_{0,j} &\sim \text{Normal}(\mu_{\beta,0,j}, \sigma_{\beta,0,j}^2), j = 0, \ldots, 5 \\
\alpha_{0,k} &\sim \text{Normal}(\mu_{\alpha,0,k}, \sigma_{\alpha,0,k}^2), j = 1, \ldots, 5, k = j + 1, \ldots, 5
\end{align*}
\]

Eqn 4b

We assigned relatively noninformative, standard priors to all remaining parameters, including the population-level means (\( \mu_\alpha \) and \( \mu_\beta \) terms), all variance-related terms (e.g. \( \sigma_{\alpha,j} \), \( \sigma_{\beta,j} \) and \( \sigma_{\alpha,j,k} \)), and the antecedent importance weights (\( \omega_j \) vectors). Only the population-level intercept for the \( \Psi_D \) model (\( \mu_{\Psi_0,D} \)) was given a semi-informative prior, Uniform(–16, 0), because plant \( \Psi \) at mean environmental conditions is unlikely to exceed these bounds (Maherali et al., 2004; Chot et al., 2012; Larter et al., 2015). See Methods S1 for a complete description of the priors.

Model interpretation and implementation

Eqns (1)–(4b) were combined to produce posterior distributions for all parameters of interest (e.g. covariate effects and antecedent importance weights), which are summarized by their posterior means and 95% central credible intervals (CIs) defined by the 2.5 and 97.5 percentiles of the posterior. In addition to the shrub- and population-level regression coefficients (covariate effects), we also computed treatment-level effects by averaging shrub-level parameters across shrubs within each treatment group (control vs watered), producing a posterior distribution for these...
quantities. An effect is deemed significant if its 95% CI does not overlap zero, indicating that the associated environmental variable or interaction term was important for determining plant $\Psi$.

We also quantified the sensitivity of $\Psi_D$ to subdaily $D$ ($S_{\Psi,D} = d\Psi_D/dD^{ant}$), which describes the degree to which $\Psi_D$ changes for a unit change in $D$. We computed $S_{\Psi,D}$ for different combinations of $max D^{ant}$ and $W^{ant}_{90}$, at three levels of $\Delta D^{ant}$ representing, roughly, morning ($\Delta D^{ant} > 0$), midday ($\Delta D^{ant} = 0$), and afternoon ($\Delta D^{ant} < 0$). Negative values of $S_{\Psi,D}$ indicate a drop in $\Psi_D$ with increasing $D$, implying weak stomatal regulation. Values of $S_{\Psi,D}$ not significantly different from zero indicate no change in $\Psi_D$ in response to changing $D$, implying strong stomatal regulation. Finally, positive values of $S_{\Psi,D}$ indicate increasing $\Psi_D$ with increasing $D$, implying excessive stomatal closure.

If a covariate effect was significant, then the associated antecedent importance weights $\omega_j$ reveal the temporal response pattern to the environmental variable. A significant time lag exists between plant $\Psi$ and $X_j$ if, first, the 95% CI of a particular $\omega_j$ does not overlap the prior mean (a flat prior gives a prior mean of 0), or if, second, the 95% CI of one or more $\omega_j$ does not contain the posterior mean of an $\omega_j$ for another past time period. For $\omega_j$ values with narrow CIs, the posterior means indicate the relative contribution of that variable at the corresponding time step to the overall antecedent variable; wide CIs signify potential difficulty in resolving the timescales of influence.

The Bayesian models (Eqns (1)–(4b) and corresponding priors) were implemented in JAGS 4.2.0 (Plummer, 2003) via R (R Core Team, 2016), using the packages ‘rjags’ (Plummer, 2013) and ‘CODA’ (Plummer et al., 2006). Three parallel Markov chain Monte Carlo (MCMC) sequences were assigned widely dispersed starting values, and initial iterations were run until convergence was achieved as measured by the Gelman statistic (Gelman & Rubin, 1992). Raftery and Lewis’s diagnostic (Raftery & Lewis, 1992) was performed on initial chains to determine required Monte Carlo (MCMC) sequences were assigned widely dispersed starting values, and initial iterations were run until convergence was achieved as measured by the Gelman statistic (Gelman & Rubin, 1992). Raftery and Lewis’s diagnostic (Raftery & Lewis, 1992) was performed on initial chains to determine required MCMC sample size. These diagnostics led us to run 200 000 (400 000) iterations for the $\Psi_B$ ($\Psi_D$) model, and to thin the sequences by 40 (80) to obtain a posterior sample size of 5000 for each parameter. Thinning was implemented to reduce both within-chain autocorrelation and storage requirements.

Results

Model fit

A regression of predicted vs observed plant $\Psi$ yielded $R^2 = 0.84$ for $\Psi_B$ and 0.65 for $\Psi_D$ (Table 2; Fig. S2), which represented improved model fit by ~0.1 from models without antecedent covariates (Methods S2, $R^2 = 0.74$ and 0.56 respectively). Both models showed some bias (slopes of predicted vs observed of 0.80 and 0.61 respectively), with underestimation at high (less negative) $\Psi$ and overestimation at low (more negative) $\Psi$, particularly for $\Psi_D$ (Fig. S2b). Such bias is typical of hierarchical models that allow for borrowing of strength (e.g. among shrub-level parameters; Greenland, 2000), but greater borrowing of strength reduces the effective numbers of parameters (here, $\Psi_B = 44.1$ and $\Psi_D = 105.3$; Spiegelhalter et al., 2002). When predicted and observed plant $\Psi$ were averaged across individual shrubs (for each round of measurements) to yield estimates of mean plant $\Psi$ for all shrubs, model fit ($R^2 = 0.94$ for $\Psi_B$ and 0.76 for $\Psi_D$) and bias (slope: 0.89 for $\Psi_B$ and 0.68 for $\Psi_D$) improved for both models (Fig. S3).

Covariate effects

Variation in $\Psi_B$ was primarily explained by the main effects of the daily-scale antecedent variables: maximum vapor pressure deficit $max D^{ant}$, shallow soil water $W_{90}^{ant}$ and deep soil water $W_{60}^{ant}$; none of their interaction terms were significant (see Table 3 for coefficient estimates, Fig. 2a). Both max $D^{ant}$ and $W_{60}^{ant}$ exerted negative effects on $\Psi_B$, whereas $W_{30}^{ant}$ exerted a positive influence. The covariate effects (posterior means and 95% CIs) associated with the $\Psi_B$ model were fairly similar across shrubs and treatments, although three and seven out of 16 shrubs did not experience the negative effects of max $D^{ant}$ and $W_{60}^{ant}$ respectively. Population-level $\Psi_B$ at nominal environmental conditions (intercept, $\mu_{B0}$) was estimated at $-3.4$ MPa (posterior mean), with minimal variation among shrubs or treatments and relatively narrow CIs (Fig. S4).

Variation in $\Psi_D$ was associated with the same significant main effects as for $\Psi_B$: the effects of $max D^{ant}$, $W_{90}^{ant}$ and $W_{60}^{ant}$ had the same direction and similar magnitudes across both models (Table 3; Fig. 2b). However, the covariate effects associated with the $\Psi_D$ model exhibited greater variability among shrubs and treatments than the $\Psi_B$ model did. Although shrubs in both treatment groups experienced a similar positive effect of $W_{90}^{ant}$ on $\Psi_D$, control and watered shrubs were differentially affected by $max D^{ant}$ and $W_{90}^{ant}$. $\Psi_D$ of control shrubs was negatively affected by $max D^{ant}$ and not by $W_{60}^{ant}$, whereas $\Psi_D$ of watered shrubs was negatively affected by $W_{90}^{ant}$ and not by $max D^{ant}$. Moreover, unlike the $\Psi_B$ model, several interaction terms were significant in the $\Psi_D$ model, at both the population and treatment levels (Table 3; Fig. 2b,c). The max $D^{ant} \times W_{90}^{ant}$ and max $D^{ant} \times W_{60}^{ant}$ terms were significantly negative, indicating that high (low) soil moisture at either depth enhances (reduces) the negative effect of max $D^{ant}$ on $\Psi_D$ (Fig. S5a, b). The population-level $\Psi_D$ at nominal environmental conditions $\mu_{B0}$ was estimated to be $-3.8$ MPa (Fig. S4), and shrub-level means did not differ significantly among treatment groups. However, control shrubs had greater between-shrub variation in posterior means and wider CIs than watered shrubs.

Since $\Psi_D$ varies on a subdaily timescale, we also evaluated responses to antecedent half-hourly $D$ variables ($D^{ant}$ and $\Delta D^{ant}$), which were not considered in the daily-scale $\Psi_B$ model. Surprisingly, the main effects of $D^{ant}$ and $\Delta D^{ant}$ were not significant (Fig. 2c); however, these variables often interacted significantly with daily-scale antecedent covariates to affect $\Psi_B$. For example, the effect of $W_{90}^{ant}$ was modified by half-hourly $D$ variables such that high $D^{ant}$ reduced the positive effect of $W_{90}^{ant}$ on $\Psi_D$ (Fig. S5c). Moreover, the significant $W_{90}^{ant} \times \Delta D^{ant}$ interaction indicates a hysteretic pattern, wherein the positive effect of $W_{90}^{ant}$ on $\Psi_D$ is stronger when $D$ is increasing ($\Delta D^{ant} > 0$) than when $D$ is decreasing (Fig. S5d, $\Delta D^{ant} < 0$). The positive max $D^{ant} \times \Delta D^{ant}$ interaction indicates that $\Psi_D$ is negatively correlated with $D^{ant}$ only when max $D^{ant}$ is low (Fig. S5e). Finally, the $D^{ant} \times \Delta D^{ant}$ interaction
Shrubs 1–8 belong to the control group; shrubs 9–16 received supplemental irrigation (watered). Shrubs are ordered by descending $R^2$ for the $\Psi_B$ model. Population refers to the overall population of 16 shrubs.

### Table 3 Population-level regression coefficients for the baseline water potential $\Psi_B$ and diurnal water potential $\Psi_D$ models, their associated covariate, posterior mean (mean), and 95% central credible interval (95% Cl)

<table>
<thead>
<tr>
<th>Coef.</th>
<th>Associated covariate</th>
<th>Mean</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\mu_{\Psi_B}$</td>
<td>Intercept</td>
<td>$-3.398$</td>
<td>$(-3.631, -3.191)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_B}$</td>
<td>$\text{max } D^\text{ant}$</td>
<td>$-0.334$</td>
<td>$(-0.489, -0.185)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_B}$</td>
<td>$W^\text{ant}$</td>
<td>$0.186$</td>
<td>$(0.137, 0.232)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_B}$</td>
<td>$W^\text{ant}_{60}$</td>
<td>$0.222$</td>
<td>$(0.139, 0.308)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_B}$</td>
<td>$\text{max } W^\text{ant} \times W^\text{ant}_{60}$</td>
<td>$-0.005$</td>
<td>$(-0.042, 0.028)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_B}$</td>
<td>$\text{max } D^\text{ant} \times W^\text{ant}_{60}$</td>
<td>$0.044$</td>
<td>$(0.157, 0.062)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_B}$</td>
<td>$\text{max } D^\text{ant} \times D^\text{ant}_{60}$</td>
<td>$0.007$</td>
<td>$(-0.018, 0.028)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_D}$</td>
<td>Intercept</td>
<td>$-3.811$</td>
<td>$(-4.169, -3.423)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_D}$</td>
<td>$\text{max } D^\text{ant}$</td>
<td>$-0.262$</td>
<td>$(-0.508, -0.068)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_D}$</td>
<td>$W^\text{ant}$</td>
<td>$0.171$</td>
<td>$(0.104, 0.220)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_D}$</td>
<td>$W^\text{ant}_{60}$</td>
<td>$-0.329$</td>
<td>$(-0.531, -0.150)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_D}$</td>
<td>$D^\text{ant}$</td>
<td>$-0.023$</td>
<td>$(-0.101, 0.047)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_D}$</td>
<td>$\Delta D^\text{ant}$</td>
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<td>$(-0.559, 0.222)$</td>
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<tr>
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<td>$\text{max } D^\text{ant} \times W^\text{ant}_{60}$</td>
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<td>$(-0.081, 0.007)$</td>
</tr>
<tr>
<td>$\mu_{\Psi_D}$</td>
<td>$\text{max } D^\text{ant} \times D^\text{ant}_{60}$</td>
<td>$-0.125$</td>
<td>$(-0.231, -0.023)$</td>
</tr>
<tr>
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<td>$\text{max } D^\text{ant} \times \Delta D^\text{ant}$</td>
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<td>$(0.008, 0.053)$</td>
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<tr>
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<td>$\text{max } D^\text{ant}$</td>
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<td>$(-0.279, 0.450)$</td>
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<td>$W^\text{ant}_{60}$</td>
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<td>$(-0.017, 0.042)$</td>
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<td>$\mu_{\Psi_D}$</td>
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<td>$0.163$</td>
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<td>$(-0.256, 0.201)$</td>
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<td>$W^\text{ant}_{60} \times \Delta D^\text{ant}$</td>
<td>$-0.411$</td>
<td>$(-0.680, -0.112)$</td>
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Interaction was significantly negative, leading to another case of hysteretic: $\Psi_D$ decreases with $D$ when $D$ is increasing ($\Delta D^\text{ant} > 0$), yet $\Psi_D$ increases with $D$ when $D$ is decreasing ($\Delta D^\text{ant} < 0$) (Fig. S5f).

Though the main effect of $D^\text{ant}$ was not significant, some combinations of antecedent daily soil and atmospheric moisture conditions yield significantly positive or negative sensitivities ($S_{\Psi_D} = d\Psi_D/d D^\text{ant}$), depending on the sign of $\Delta D^\text{ant}$. Negative $S_{\Psi_D}$ (increasing $D^\text{ant}$ leads to more negative $\Psi_D$, and vice versa) dominates when $\Delta D^\text{ant}$ is positive (morning), and the magnitude increases under more favorable (wetter) antecedent moisture conditions (Fig. 3a). By contrast, positive $S_{\Psi_D}$ (increasing $D^\text{ant}$ leads to less negative $\Psi_D$, and vice versa) occurs when $\Delta D^\text{ant}$ is negative (afternoon), with increasing magnitude under less favorable (drier) antecedent moisture conditions (Fig. 3c). Neutral values of $S_{\Psi_D}$ (not responsive to $D^\text{ant}$) can occur across a range of antecedent moisture conditions, but primarily when antecedent conditions are dry and $\Delta D^\text{ant}$ is positive (Fig. 3a) or when antecedent conditions are wet and $\Delta D^\text{ant}$ is negative (Fig. 3c). When $\Delta D^\text{ant} \approx 0$ (midday), $S_{\Psi_D}$ spans negative, neutral, or positive values, depending on antecedent moisture conditions (Fig. 3b).

**Antecedent weights**

While the covariate effects were modeled hierarchically, antecedent weights $\omega$ were only modeled at the population level. For $\Psi_B$, $\omega$ for $\text{max } D^\text{ant}$ peaked 4 d before the $\Psi_B$ measurement (Fig. 4a). The $\omega$ for $W^\text{ant}_{60}$ and $W^\text{ant}_{60}$ were associated with different timescales of influence: the highest $\omega$ for $W^\text{ant}_{60}$ occurred on the day leading up to the $\Psi_B$ measurement (Fig. 4b), indicating
that current shallow moisture has the strongest influence on $\Psi_B$, with no lag period. By contrast, the highest $\omega$ for $W_{ant}$ occurred 6–7 d before the $\Psi_B$ measurement (Fig. 4c), reflecting a week-long time lag and a much longer timescale of influence.

With respect to the $\Psi_D$ response, which included the effects of daily and subdaily scale covariates, the $\omega$ for max $D_{ant}$ was highest 2 d before the $\Psi_D$ measurement (Fig. 4d). Interestingly, the $\omega$ for $W_{30 ant}$ was similarly high for 1 and 7 d prior (Fig. 4e), a bimodal pattern that indicates an effect of $W_{30 ant}$ on multiple timescales. For $W_{60 ant}$, $\omega$ was extremely low for 1 to 5 d into the past, moderate for 6 d ago, and highest for 7 d ago (Fig. 4f), mirroring the temporal pattern of the $W_{60 ant}$ weights in the $\Psi_B$ model. With respect to the diurnal (half-hourly) variables affecting $\Psi_D$, $\omega$ for $D_{ant}$ was highest for the concurrent half-hour and quickly attenuated thereafter (Fig. 5a), whereas $\Delta D_{ant}$ had the highest $\omega$ for the concurrent half-hour and 3 h ago (Fig. 5b), indicating another potential bimodal timescale response.

**Discussion**

Upon applying the SAM framework to repeated measurements of $\Psi_B$ and $\Psi_D$ and associated atmospheric and soil moisture indices $D$ and $W$, we broadly found that while *Larrea* $\Psi_B$ is governed by the main effects of daily-scale $D$ and $W$, $\Psi_D$ is interactively controlled by $D$ and $W$ at multiple timescales. Furthermore, the response of $\Psi_D$ to subdaily $D$ depends upon past conditions, indicating diurnal hysteresis. However, owing to sampling of plant $\Psi$ primarily during the summer growing season (Fig. S1), our results may reflect this particular study period rather than broader patterns of *Larrea* $\Psi$. In the following we discuss Q1 and Q2 (the effect and temporal scales of environmental drivers of $\Psi$) first for atmospheric moisture, then for soil moisture. We subsequently address Q3 and interpret the interactive influence of antecedent conditions on the regulation of $\Psi_D$.

**Atmospheric moisture controls plant $\Psi$ on multiple timescales**

Higher vapor pressure deficit $D$ increases the driving gradient for transpiration, which increases tension on the water column and is expected to result in more negative plant $\Psi$ (Sperry *et al.*, 2002). Though this expectation generally applies to subdaily variation in $\Psi_D$ (Jarvis, 1976), our analyses indicate an analogous lagged effect of past $D$. Antecedent maximum daily $D$ (max $D_{max}$,
estimated sensitivities ($S_{\Psi, D} = d\Psi/d\Delta D$) of diurnal water potential $\Psi_D$ to changes in antecedent half-hourly vapor pressure deficit $D_{\text{ant}}$ for a range of antecedent shallow soil water ($W_{\text{ant}}^{0.5}$) and antecedent daily maximum $D$ (max $D_{\text{ant}}$) values at three levels of antecedent half-hourly changes in $D$: (a) $\Delta D_{\text{ant}} = 0.5$ kPa (‘morning’), (b) $\Delta D_{\text{ant}} = 0$ kPa (‘midday’), and (c) $\Delta D_{\text{ant}} = -0.5$ kPa (‘afternoon’). $S_{\Psi, D}$ was calculated within the Bayesian Markov chain Monte Carlo simulations to propagate uncertainties in the parameters (i.e. relevant $x$ values). The contours represent the posterior means for $S_{\Psi, D}$ (MPa/kPa), the lighter shaded regions indicate significant negative sensitivities ($S_{\Psi, D} < 0$), whereas the darker shaded regions represent significant positive sensitivities ($S_{\Psi, D} > 0$). The unshaded regions represent neutral sensitivities ($S_{\Psi, D}$ not significantly different from zero).

Research of antecedent shallow soil water ($\Psi = \text{kPa}$); the lighter shaded regions indicate significant negative sensitivities ($S_{\Psi, D} < 0$), whereas the darker shaded regions represent significant positive sensitivities ($S_{\Psi, D} > 0$). The unshaded regions represent neutral sensitivities ($S_{\Psi, D}$ not significantly different from zero).

Hereafter ‘daily $D$’ negatively affected both $\Psi_B$ and $\Psi_D$, indicating that prior exposure to dry (moist) atmospheric conditions resulted in more (less) negative plant $\Psi$. Larrea appears to retain the negative impact of past atmospheric drought for multiple days. Specifically, $\Psi_B$ and $\Psi_D$ exhibited lags of 4 d and 2 d respectively in response to variation in daily $D$, which could possibly reflect hormonal transport times, xylem embolism, or depletion of surface soil moisture. Foliar-derived abscisic acid (ABA) can be transported basally via phloem (Ikegami et al., 2009; Manzi et al., 2015; McAdam et al., 2016) and may impact root growth (McAdam et al., 2016), stomatal conductance (Mitchell et al., 2017), and potentially plant $\Psi$. The observed multi-day lag between daily-scale maximum $D$ and plant $\Psi$ may be due to the relatively slow transport time of foliar ABA to roots (Mencuccini & Hölttä, 2010). Cumulative high-$D$ events could also cause progressive cavitation fatigue (Hacke et al., 2001), which could manifest as a lagged effect of $D$ on plant $\Psi$. Finally, past $D$ could influence plant $\Psi$ through evaporation of surface soil moisture. Although the model directly accounts for the integrated effects of soil moisture from 0 to 30 cm and 30 to 60 cm, a small but significant amount of Larrea’s active roots are found in the top 2 cm of the soil (Ogle et al., 2004), where soil moisture is strongly affected by evaporation (Kidron, 2009). Previously high $D$ could exacerbate evaporation from the surface soil, resulting in apparent lagged declines in plant $\Psi$ in response to daily $D$.

Whereas $\Psi_B$ responded independently to atmospheric and soil moisture stress, $\Psi_D$ responses to daily $D$ were modulated by antecedent soil moisture. The negative effect of daily $D$ is enhanced when either shallow or deep $W$ is (or has been) high, another potential indication of hormone signaling effects. For example, dry soil can trigger an ABA signal that results in stomatal closure (Wilkinson & Davies, 2002), but wet soil may prevent such hormone signaling, thus reducing stomatal sensitivity to $D$ (Tardieu & Davies, 1992). Contrasting signals from wet soil and a dry atmosphere may permit Larrea’s $\Psi$ to decline, as stomata remain open to ensure carbon acquisition under moist soil conditions.

Though we expected a negative relationship between $\Psi_D$ and half-hourly $D$ ($D_{\text{ant}}$, hereafter ‘subdaily $D$’), the significance and direction of the effect depended upon antecedent daily-scale moisture variables (max $D_{\text{ant}}$ and $W_{\text{ant}}^{0.5}$) as well as the directional change in $D$ (as captured by $\Delta D_{\text{ant}}$). Under relatively moist antecedent soil and atmospheric conditions, $\Psi_D$ exhibits the expected negative relationship with subdaily $D$ in the morning ($\Delta D_{\text{ant}} > 0$) and a neutral relationship in the afternoon ($\Delta D_{\text{ant}} < 0$), even when past daily $D$ is high (Fig. 3a,c). This pattern in $\Psi_D$ aligns with Larrea’s natural circadian pattern of photosynthesis, wherein photosynthesis peaks in the morning hours (Bamberg et al., 1975) followed by frequent midday and afternoon depressions (Naumburg et al., 2003). By contrast, under dry antecedent moisture conditions, subdaily $D$ has no impact on $\Psi_D$ in the morning (Fig. 3a), and higher values in the afternoon (Fig. 3c) correspond to less negative $\Psi_D$. It is not uncommon for maximum $\Psi_D$ in Larrea to become less negative than $\Psi_B$ in dry soils (Syvertsen et al., 1975), as occurred on two of our sampling dates (Fig. 1) following 19 consecutive dry days. Such dry
antecedent conditions may prompt ABA production in the guard cells of the stomata (Virlouvet & Fromm, 2015), triggering low rates of morning photosynthesis and stomatal closure in the afternoon, which would allow $\Psi_D$ to recover to less negative values (Tenhunen et al., 1982). The variable sensitivity of $\Psi_D$ to subdaily $D$ highlights how acclimation to antecedent conditions can modify the underlying circadian pattern of stomatal behavior and $\Psi_D$ (Lange et al., 1982; Hennessey & Field, 1991; Mencuccini et al., 2000).

Because circadian controls also affect diurnal carbon and water fluxes in plants (Doughty et al., 2006; Resco de Dios et al., 2016), diurnal hysteresis has often been observed between indices of plant water use and environmental drivers (Jarvis, 1976; O’Grady et al., 1999; Zhang et al., 2014). Hysteresis in $\Psi_D$ was detected in our analysis via significant interactions between the covariate $\Delta D^{\text{ant}}$ (an index of time of day) and both shallow soil moisture $W_{30}$ and subdaily $D$. $W_{30}$ had a stronger positive effect on $\Psi_D$ when $D$ was increasing ($\Delta D^{\text{ant}} > 0$) than when $D$ was

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**Fig. 4** Posterior means and 95% central credible intervals for antecedent weights $\omega$ associated with (a, d) daily max $D$, (b, e) daily $W_{30}$, and (c, f) daily $W_{60}$. (a–c) From the baseline water potential $\Psi_B$ model; (d–f) from the diurnal water potential $\Psi_D$ model. The dotted horizontal line represents the prior mean. See Table 1 for definitions of covariates.
Research acclimation to past atmospheric (Kutsch et al. 2005) dry antecedent conditions over multiple days and respond by decreasing $\Delta D^{\text{ant}} < 0$. This suggests that the effect of past soil moisture varies throughout Larrea’s diurnal course of plant $\Psi$; past soil moisture has a strong effect in the morning, when transpiration, conductance, and photosynthesis are generally the highest, but less impact on $\Psi$ in the afternoon, during midday stomatal closure. Such hysteresis in $\Psi$ matches hysteretic responses of stomata to $D$ in a Populus hybrid (Meinzer et al., 1997), wherein transpiration rates at the same $D$ are higher in the morning vs the afternoon of the same day. Causes of hysteresis in response to changing $D$ are not well understood, but may be driven by the contribution of stored water in the stem, changes in soil-to-leaf hydraulic conductivity (O’Grady et al., 1999), or determined by underlying circadian rhythms (Hennessey & Field, 1991; Resco de Dios et al., 2016).

In general, subdaily $D$ ($D^{\text{ant}}$ and $\Delta D^{\text{ant}}$) affects $\Psi$ through interactions with antecedent daily-scale $D$ and shallow $\Psi$, suggesting that $\Psi$ responses integrate over multiple timescales. $\Psi$ responds to subdaily $D$ in near real time (no lag), such that the conditions occurring in the half-hour concurrent to observed $\Psi$ were the most important. Stomatal conductance of these same shrubs also exhibited a short lag with respect to subdaily $D$ (Ogle et al., 2015), indicating that fast $\Psi$ responses are likely driven by stomata that are tightly coupled to variable atmospheric conditions (Damour et al., 2010). Because the effect of subdaily $D$ interacts significantly with daily-scale moisture variables, $\Psi$ responds to environmental conditions over multiple timescales, from hours to days. This suggests that Larrea can acclimate to dry antecedent conditions over multiple days and respond by decreasing $\Psi$ sensitivity to subdaily $D$, likely through stomatal acclimation to past atmospheric (Kutsch et al., 2001) and soil moisture conditions (Ludlow et al., 1985).

Soil moisture effects on plant $\Psi$ depend on depth and cumulative moisture status

Interestingly, shallow and deep $\Psi$ had opposite effects on plant $\Psi$ ($\Psi_B$ and $\Psi_D$). In both treatments groups (control vs watered), as expected, wetter shallow $\Psi$ is associated with increased (less negative) plant $\Psi$, because additional soil moisture increases the supply of water to the roots and transpiration stream. In many deserts, most rain events primarily recharge surface soil layers, leading to notable temporal variation in shallow $\Psi$, while deep $\Psi$ can remain fairly constant over time (Scanlon, 1994), leading to temporal decoupling between shallow and deep soil moisture (e.g. Fig. S1c–f). In general, Larrea root biomass is confined to shallow or intermediate depths (e.g. 10–30 cm; Montañoa et al., 1995; Briones et al., 1996), and roots in the subsurface (e.g. 0–10 cm) are capable of water uptake following rains (Ogle et al., 2004), which accounts for the positive relationship between plant $\Psi$ and shallow $\Psi$. By contrast, we generally found a negative relationship between plant $\Psi$ and deep $\Psi$ (Fig. 2a,b). Roots at intermediate or deeper depths (20–45 cm) are primarily responsible for water uptake in Larrea at this site (Ogle et al., 2004), and some large shrubs can access relatively stable deeper soil moisture (Franco et al., 1994). Therefore, a reliable supply of deep (30–60 cm) soil water may permit stomata to avoid closure and become less sensitive to $D$ (Hinckley et al., 1983), resulting in more negative $\Psi_B$ and $\Psi_D$, as the plant continues to photosynthesize and transpire in response to ‘available’ deep soil water. Overall, Larrea appears to regulate plant $\Psi$ by responding differently to shallow vs deep soil moisture.

In general, plant $\Psi_B$ and $\Psi_D$ responded to concurrent shallow $\Psi$ but exhibited a lagged (6–7 d) response to deep $\Psi$, which mirrors the timescales of influence uncovered for stomatal conductance in Larrea (Ogle et al., 2015). However, $\Psi_D$ displayed a bimodal lagged response to shallow $\Psi$, which was strongly influential both 1 and 7 d before measurement. Differential lags for shallow vs deep $\Psi$ could be a function of Larrea’s bimodal rooting distribution (Ogle et al., 2004), as well as the dynamics of root conductivity, growth, and mycorrhizal associations. The 1-d lagged responses of both $\Psi_B$ and $\Psi_D$ to shallow $\Psi$ may result from water uptake by existing shallow roots that maintain high conductivity (Hultine et al., 2006). For example, the C4 grass Bouteloua gracilis increased plant $\Psi$ within 1 d of a simulated

![Fig. 5](image-url) Posterior means and 95% central credible intervals for antecedent weights $\omega$ associated with (a) subdaily $D$ and (b) subdaily $\Delta D$ from the diurnal water potential $\Psi_D$ model. The dotted horizontal line represents the prior mean. See Table 1 for definitions of covariates.
5 mm rain event (Sala & Lauenroth, 1982) as the result of water uptake by existing, functional roots (Lauenroth et al., 1987). The 6- and 7-d lagged responses of plant $\Psi_B$ and $\Psi_D$ to deep $W$ could be driven by both recovery of hydraulic conductivity and new growth belowground. In the desert succulent *Agave deserti*, partial recovery of root hydraulic conductivity was achieved after 7 d of rewetting, with full recovery attributed to new root growth (North & Nobel, 1995). New root growth can further aid the absorption of water by increasing root contact with wet soil (Caldwell, 1976), but may lag behind the initial recharge of soil moisture due to high soil temperatures or *Larrea*'s high oxygen requirements for root growth (Lunt et al., 1973). Finally, colonization by arbuscular mycorrhizal fungi following rainfall (Titus et al., 2002) may enhance Larrea's water status, though slow colonization rates (Apple et al., 2005) could also contribute to the 6–7 d lag responses. Soil moisture in deep layers is also less impacted by evapotranspiration and may have a longer residence time (Sala et al., 1992; Ng et al., 2015), resulting in a longer lag effect of deep $W$ on plant $\Psi$.

Different primary drivers of $\Psi_D$ were significant for control and watered shrubs, suggesting prolonged legacy effects of soil moisture availability. Though $\Psi_D$ of both treatment groups increased with wetter shallower $W$, control and watered shrubs had differential $\Psi_D$ responses to daily-scale atmospheric and deep soil moisture (Fig. 2b). Antecedent daily $D$ regulated $\Psi_D$ of control shrubs, whereas $\Psi_D$ of watered shrubs was negatively affected by deep $W$, suggesting that large moisture pulses that infiltrate deeper soil layers can fundamentally alter regulation of plant $\Psi$.

In desert ecosystems, plant physiological responses may only be triggered by ‘biologically important’ amounts of precipitation (Beatley, 1974; Fernández, 2007). Though irrigation was only applied three times during the study period, the magnitudes of the applications exceeded most single precipitation events that occurred during the study period (Fig. S1). The surplus water inputs could push watered shrubs past a threshold $W$ that suppressed the response of watered shrubs’ $\Psi_D$ to antecedent daily $D$. Because antecedent daily $D$ was not a significant driver of $\Psi_D$ in watered shrubs, watered shrubs appeared to have weaker ‘memory’ of past $D$ extremes. The increased deep $W$ may provide a long-term water source for transpiration such that the plant can routinely avoid stomatal closure, rendering $\Psi_D$ insensitive to antecedent daily $D$. Therefore, large irrigation (or rain) events that affect both shallow and deep $W$ can apparently exert a long-term (months–seasons) legacy effect on plant $\Psi$ that is not captured by antecedent daily-scale variables.

The relationship between $\Psi_B$, $\Psi_D$, and environmental drivers ($D$ and $W$) are well understood and can be modeled mechanistically (e.g. Sperry et al., 2016). However, it remains to be seen whether mechanistic models can capture the effect of antecedent conditions through simulation of the biophysical process. Future work could address whether lagged responses emerge from plant hydraulic models that explicitly include mechanisms linking stomatal behavior, plant $\Psi$, soil moisture, and vapor pressure deficit. If lagged responses are not captured through the biophysics of water transport, then additional representation of physiology (e.g. ABA transport, acclimation) may be needed.

Dynamic shifts in water potential regulation

The $\Psi_D$ was positively, negatively, or not significantly correlated with subdaily $D$ depending on time of day and antecedent moisture conditions, suggesting dynamic stomatal regulation of plant $\Psi$ in Larrea. Negative sensitivity to $D$ ($S_{\Psi,D} < 0$) in the mornings ($\Delta D^{\text{mor}} > 0$) suggests weak stomatal regulation such that $\Psi_D$ becomes more negative as $D$ increases. Neutral sensitivity ($S_{\Psi,D} \approx 0$) can occur at any time of day and implies strong stomatal regulation such that $\Psi_D$ does not change in response to changing $D$. Finally, positive sensitivity to $D$ ($S_{\Psi,D} > 0$) in the afternoons ($\Delta D^{\text{am}} < 0$) suggests excessive stomatal closure such that $\Psi_D$ becomes less negative under higher $D$, which we deem as overcompensating behavior. Importantly, our results suggest that weak stomatal regulation and overcompensation are unlikely to occur within the same day. For example, the highlighted (light and dark gray) areas of significant negative and positive $S_{\Psi,D}$ barely overlap for the same daily-scale antecedent variables (Fig. 3). Under moist antecedent conditions, $S_{\Psi,D}$ can shift from negative to neutral during a single day. However, under dry antecedent conditions, $S_{\Psi,D}$ can shift from neutral to positive within a day. Such overcompensating stomatal behavior during dry antecedent conditions may explain how $\Psi_D$ can recover to, and sometimes even exceed, $\Psi_B$ (Syvertsen et al., 1975; Fig. 1). While concurrent environmental conditions are known to influence midday stomatal closure and recovery of $\Psi_D$ (Schulze et al., 1974; Tenhunen et al., 1982), we demonstrate the importance of antecedent moisture status in regulating $\Psi_D$ patterns. Given that $\Psi_D$ lags daily-scale $D$ (max $D$) by 2–4 d and lags $W_{30}$ by 1 and 7 d, shifts in plant $\Psi$ regulation may occur in under 1 wk, which may be advantageous in a mostly dry ecosystem with pulsed moisture inputs (Noy-Meir, 1973; Loik et al., 2004). Larrea's $\Psi$ and stomatal conductance (Ogle et al., 2015) have similar temporal responses to soil and atmospheric moisture conditions, confirming that regulation of plant $\Psi$ is strongly coordinated by stomatal behavior.

We propose that Larrea is able to adjust regulation of plant $\Psi$ as a result of past soil and atmospheric moisture conditions. Furthermore, our analysis revealed an unexpected positive sensitivity of plant $\Psi$ to $D$ ($S_{\Psi,D} > 0$) indicative of overcompensating stomatal regulation; this syndrome could be common to desert shrubs that experience midday stomatal closure and $\Psi$ recovery under high $D$ (Tenhunen et al., 1982; Nilsen et al., 1983). Larrea's ability to dynamically shift between weak, strong, and overcompensating regulation of plant $\Psi$ depending on past moisture conditions could be key to its dominance in the hot deserts of North America (Smith et al., 1997). More generally, we suggest that subdaily measurements of plant $\Psi$ will be invaluable for expanding current conceptions of iso-/anisohydry spectrum (Klein, 2014; Martinez-Vilalta et al., 2014; Hochberg et al., 2018) to encompass overcompensating stomatal regulation and condition-dependent plant $\Psi$ sensitivity to $D$.

Conclusion

Our results suggest that Larrea's baseline and diurnal plant $\Psi$ are interactively controlled by atmospheric and soil...
moisture conditions (D and W respectively) at multiple timescales and well coordinated with temporal patterns of stomatal conductance (Ogle et al., 2015). This is not surprising given the history of research that indicates that plant water status and stomatal behavior are controlled by D and W (Dixon & Joly, 1895; Jarvis, 1976; Sperry et al., 2002). However, we refined the classic understanding of plant Ψ by quantifying the temporal lags of associated atmospheric and soil moisture drivers at two temporal scales: daily and subdaily. We found evidence of a hysteretic effect of subdaily D on diurnal plant Ψ, highlighting the importance of circadian rhythms. The variation in sensitivity of Ψ to subdaily D depends upon antecedent daily-scale D and W conditions, likely reflecting rapid shifts in plant Ψ regulation. We identified a positive sensitivity of Larrea’s Ψ to D, indicating possible overcompensating stomatal regulation of plant Ψ. Changes in plant Ψ sensitivity to D are also evident in the 2–4 d lagged response of baseline and diurnal plant Ψ to maximum daily D. Moreover, the timescales of influence associated with soil moisture depended on the depth at which water is available: shallow W has a shorter lagged effect than deep W, possibly indicative of Larrea’s bimodal rooting distribution, the dynamics of root hydraulic recovery and growth, and/or colonization by mycorrhizae. Finally, drivers of ΨD differed between control and watered shrubs, highlighting a potential long-term legacy effect of large moisture conditions. The variation in sensitivity of Ψ to subdaily D depends upon antecedent daily-scale D and W conditions, likely reflecting rapid shifts in plant Ψ regulation. We identified a positive sensitivity of Larrea’s Ψ to D, indicating possible overcompensating stomatal regulation of plant Ψ. Changes in plant Ψ sensitivity to D are also evident in the 2–4 d lagged response of baseline and diurnal plant Ψ to maximum daily D. Moreover, the timescales of influence associated with soil moisture depended on the depth at which water is available: shallow W has a shorter lagged effect than deep W, possibly indicative of Larrea’s bimodal rooting distribution, the dynamics of root hydraulic recovery and growth, and/or colonization by mycorrhizae. Finally, drivers of ΨD differed between control and watered shrubs, highlighting a potential long-term legacy effect of large moisture conditions. The variation in sensitivity of Ψ to subdaily D depends upon antecedent daily-scale D and W conditions, likely reflecting rapid shifts in plant Ψ regulation. We identified a positive sensitivity of Larrea’s Ψ to D, indicating possible overcompensating stomatal regulation of plant Ψ. Changes in plant Ψ sensitivity to D are also evident in the 2–4 d lagged response of baseline and diurnal plant Ψ to maximum daily D. Moreover, the timescales of influence associated with soil moisture depended on the depth at which water is available: shallow W has a shorter lagged effect than deep W, possibly indicative of Larrea’s bimodal rooting distribution, the dynamics of root hydraulic recovery and growth, and/or colonization by mycorrhizae. Finally, drivers of ΨD differed between control and watered shrubs, highlighting a potential long-term legacy effect of large moisture conditions.

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Author contributions

K.O. conducted the field study, J.S.G. and K.O. both contributed to the design of the research questions and approaches, J.S.G. performed the data analysis, K.O. supervised the data analysis, J.S.G. led the writing of the manuscript, and K.O. contributed to manuscript writing.

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References


**Supporting Information**

Additional Supporting Information may be found online in the Supporting Information tab for this article:

**Fig. S1** Site- and shrub-level environmental conditions, including maximum daily D, soil moisture from 0–30 cm and 30–60 cm, and moisture inputs (precipitation and irrigation).

**Fig. S2** Model fit of observed vs predicted $\Psi_B$ and $\Psi_D$ for individual measurements.

**Fig. S3** Model fit of observed vs predicted $\Psi_B$ and $\Psi_D$ averaged across all shrubs for each round of measurement.

**Fig. S4** Estimates of the intercepts of the $\Psi_B$ and $\Psi_D$ models, representing the expected $\Psi_B$ and $\Psi_D$ at mean or nominal conditions.

**Fig. S5** Interaction plots of the significant interactions in the $\Psi_D$ model.

**Methods S1** Priors for the $\Psi_B$ and $\Psi_D$ models.

**Methods S2** Description of $\Psi_B$ and $\Psi_D$ models without lagged effects.

**Notes S1** Data for the $\Psi_B$ and $\Psi_D$ models.

**Notes S2** JAGS code for the $\Psi_B$ model.

**Notes S3** JAGS code for the $\Psi_D$ model.

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