Differential daytime and night-time stomatal behavior in plants from North American deserts

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Summary

- Night-time stomatal conductance (g\text{night}) occurs in many ecosystems, but the g\text{night} response to environmental drivers is relatively unknown, especially in deserts.
- Here, we conducted a Bayesian analysis of stomatal conductance (g) (N = 5013) from 16 species in the Sonoran, Chihuahuan, Mojave and Great Basin Deserts (North America). We partitioned daytime g (g\text{day}) and g\text{night} responses by describing g as a mixture of two extreme (dark vs high light) behaviors.
- Significant g\text{night} was observed across 15 species, and the g\text{night} and g\text{day} behavior differed according to species, functional type and desert. The transition between extreme behaviors was determined by light environment, with the transition behavior differing between functional types and deserts. Sonoran and Chihuahuan C\text{4} grasses were more sensitive to vapor pressure difference (D) at night and soil water potential (Ψ\text{soil}) during the day, Great Basin C\text{3} shrubs were highly sensitive to D and Ψ\text{soil} during the day, and Mojave C\text{3} shrubs were equally sensitive to D and Ψ\text{soil} during the day and night.
- Species were split between the exhibition of isohydric or anisohydric behavior during the day. Three species switched from anisohydric to isohydric behavior at night. Such behavior, combined with differential D, Ψ\text{soil} and light responses, suggests that different mechanisms underlie g\text{day} and g\text{night} regulation.

Introduction

Night-time stomatal conductance (g\text{night}) and transpiration (E\text{night}) have been observed in several plant functional groups from diverse ecosystems (Barbour et al., 2005; Daley & Phillips, 2006; Caird et al., 2007; Marks & Lechowicz, 2007), including semi-arid settings (Snyder et al., 2003; Dawson et al., 2007). E\text{night} is generally < 15% of daytime transpiration (Caird et al., 2007), but may range up to 30% in deserts, partially reflecting low daytime transpiration as a result of low daytime stomatal conductance (g\text{day}) associated with stomatal closure or constrained maximum conductance (Snyder et al., 2003). Given that g\text{night} varies in time and is substantially higher than cuticular conductance (Caird et al., 2007; Zeppel et al., 2010), this implies the occurrence of guard cell regulation (e.g. Roelfsema & Hedrich, 2005). Indeed, E\text{night} is often positively correlated with the night-time leaf-to-air vapor pressure difference (D), such that E\text{night} is greatest on high-temperature, low-humidity nights, and is less influenced by soil water potential (Ψ\text{soil}) (Phillips et al., 2010; Zeppel et al., 2010). However, Dawson et al. (2007) found that a variety of woody plants maintained low g\text{night} on nights with high D or low Ψ\text{soil} (dry soil), and g\text{night} was enhanced by improved soil water status. Such conflicting patterns make it unclear how D, Ψ\text{soil} and other environmental variables affect g\text{night} and E\text{night}.

Despite substantial work over the last four decades on stomatal control (Cowan & Farquhar, 1977; Buckley et al., 2003; Buckley, 2005; Katul et al., 2009; Medlyn et al., 2011), there is no commonly accepted mechanism for stomatal regulation during the daytime (Mott & Peak, 2010; Pieruschka et al., 2010), and certainly not at night. Numerous mechanisms and consequences have been postulated for g\text{night} (for just a few, see Caird et al., 2007; Dawson et al., 2007), but the most common hypothesis – nutrient resource acquisition in low-nutrient...
environments (Scholz et al., 2007; Snyder et al., 2008; Yoo et al., 2009) – is often not observed (Howard & Donovan, 2010). Studies suggest that \( g_{\text{night}} \) is responsive to natural selection (Christman et al., 2008) and that \( g_{\text{night}} \) and \( g_{\text{day}} \) are under separate genetic control (Caird et al., 2007; Christman et al., 2009), yet the significance of \( g_{\text{night}} \), remains unresolved. Thus, more thorough studies are necessary to evaluate the mechanistic responses of \( g_{\text{night}} \) and \( g_{\text{day}} \) to environmental drivers (Caird et al., 2007).

Stomatal conductance (\( g \)) during the day can be highly variable between co-occurring species (e.g. Tardieu & Simonneau, 1998; Brodribb & Jordan, 2008; Quero et al., 2011), and \( g_{\text{day}} \) of individual species can be characterized along a continuum between extreme isohydric and anisohydric behaviors (e.g. Buckley, 2005; Collins et al., 2010). Isohydric plants regulate \( g_{\text{lay}} \) to maintain relatively constant leaf water potentials (\( \Psi_{\text{leaf}} \)) (Lambers et al., 1998) and may operate at \( \Psi_{\text{leaf}} \) near xylem cavitation thresholds (e.g. Holta et al., 2009). This strategy may increase susceptibility to mortality during prolonged drought (West et al., 2008). Conversely, anisohydric plants exhibit variable diurnal \( \Psi_{\text{leaf}} \) together with decreasing \( \Psi_{\text{leaf}} \) and \( g_{\text{lay}} \) in response to decreasing \( \Psi_{\text{soil}} \), allowing photosynthesis at very low \( \Psi_{\text{soil}} \) (Lambers et al., 1998). Anisohydric and isohydric strategies are infrequently used to describe \( g_{\text{night}} \), because these strategies have rarely been evaluated at night (but, see Rogiers et al., 2009). The characterization of anisohydry and isohydry during both daytime and night-time periods within and between species may lend mechanistic insight into the stomatal control of \( g_{\text{night}} \).

We assessed diel \( g \) and transpiration (\( E \)) in the Chihuahuan, Great Basin, Mojave and Sonoran Deserts. In these deserts, we measured day and night patterns of \( g \) and \( E \) for 16 functionally and physiologically diverse species (C3 and C4 grasses, C3 shrubs and a C3 rosette). We synthesized observed \( g (N = 5013) \) within a hierarchical Bayesian (HB) framework to: assess \( g_{\text{night}} \) and \( E_{\text{night}} \) variation by species, functional type and desert; partition \( g_{\text{night}} \) and \( g_{\text{day}} \) as a mixture of the \( g \) behavior expressed during dark vs high light; evaluate \( g_{\text{night}} \) and \( g_{\text{day}} \) responsiveness to light, \( D \) and \( \Psi_{\text{soil}} \), and explore the variation in \( g_{\text{day}} \) and \( g_{\text{night}} \) along the isohydric to anisohydric continuum.

**Materials and Methods**

**Study sites**

We focused on 16 common plant species (Table 1; Supporting Information Fig. S1). Artemisia tridentata and Purshia tridentata were measured at the Valentine Eastern Sierra University of California Natural Reserve near Mammoth Lakes, CA, USA (Great Basin Desert). Achnatherum hymenoides, Krameria parvifolia, Larrea tridentata, Lycium andersonii, Lycium pallidum and Pleuraphis rigida were measured at the Mojave Global Change Facility, located on the Nevada Test Site, NV, USA (Mojave Desert). Heteropogon contortus and Ergrotris lehmanniana were measured at the Santa Rita Experimental Range near Tucson, AZ, USA (Sonoran Desert). Artemisia ludoviciana, Bouteloua curtipendula, Bouteloua bursa, Dasylirion leiosphyllum, Gutierrezia microcephala, L. tridentata and Nolania texana were measured at Big Bend National Park, TX, USA (Chihuahuan Desert). Larrea tridentata was measured at two sites, resulting in 17 species–desert combinations (hereafter, just ‘species’). Although we used data from all species in the analysis, we focus on the 12 ‘data-rich’ species that had at least five night-time and 20 total observations (see Table 1). Study site details are given elsewhere (Gillespie & Loik, 2004; Barker et al., 2006; Ignace et al., 2007; Patrick et al., 2009).

**Field measurements of leaf and environmental variables**

Leaf-level stomatal conductance (\( g \)), transpiration (\( E \)), ambient leaf-to-air vapor pressure difference (\( D \)), photosynthetically active radiation (PAR) and leaf temperature (\( T \)) were measured with portable, open-flow gas-exchange systems (Model LI-6400; LI-COR Inc., Lincoln, NE, USA) that were cross-calibrated when multiple systems were used concurrently. Data collection varied slightly between sites as a result of site-specific research objectives underlying the original measurements. The \( D \) and air temperature of incoming air approximated external ambient values, the flow rate was maintained near 300 \( \mu mol \) s\(^{-1} \) (27% of observations) or 500 \( \mu mol \) s\(^{-1} \) (68%) and reference CO2 was held constant at 380 \( \mu mol \) mol\(^{-1} \) for each measurement. Most measurements were logged multiple times within 2–3 min for a given leaf (or leaf cluster); values were averaged to obtain a single observation for that leaf and sampling interval. Most often, a single leaf or leaf cluster was repeatedly measured during a particular 24–96-h period. Measurements were leaf area corrected, and only positive-valued \( g \) observations were retained. Most data were collected during sampling periods beginning in the late afternoon and concluding 24 h later, except for an L. tridentata dataset collected over a 96-h period in the Chihuahuan Desert.

At each site, volumetric soil water content (SWC) was recorded at daily to biweekly to monthly intervals, depending on desert and year, using soil moisture probes placed horizontally to a depth of 15 cm. For automated measurements, mean daily SWC was determined by averaging values recorded over 24-h periods; details of the data-logging frequency varied by site (Barker et al., 2006; Ignace et al., 2007; Patrick et al., 2009). Soil water potential (\( \Psi_{\text{soil}} \)), averaged over soil depths from 5 to 15 cm, was estimated using the measured SWC, estimated soil hydraulic properties and measured daily precipitation in a physical-based simulation model, HYDRUS-1D (Simunek et al., 2005). HYDRUS-1D uses the Richards’ equation for saturated and unsaturated water flow to predict a continuous time series of SWC and \( \Psi_{\text{soil}} \) at multiple depths that were used in subsequent analyses.

**Estimates of integrated \( E_{\text{night}} \)**

We explored the implications of \( g_{\text{night}} \) for water loss by calculating the total water transpired during the night (\( E_{\text{night}} \)) for each observed 24-h period; the night-time period was defined as 21:30 h to 06:30 h local time and further constrained to \( \text{PAR} = 0 \mu mol \) m\(^{-2} \) s\(^{-1} \). We compared the estimated \( E_{\text{night}} \) with the total amount of water transpired over 24 h. Total transpiration...
<table>
<thead>
<tr>
<th>Species</th>
<th>Desert</th>
<th>PFT</th>
<th>$g_{\text{day}}$ (mol m$^{-2}$ s$^{-1}$) Median</th>
<th>2.5th</th>
<th>97.5th</th>
<th>n</th>
<th>$g_{\text{night}}$ (mol m$^{-2}$ s$^{-1}$) Median</th>
<th>2.5th</th>
<th>97.5th</th>
<th>n</th>
<th>Ratio night : day</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACHY</td>
<td>Moj.</td>
<td>C grass</td>
<td>0.1856 (0.187, 0.196)</td>
<td>0.1856</td>
<td>0.190</td>
<td>36</td>
<td>0.3417 (0.337, 0.349)</td>
<td>0.337</td>
<td>0.349</td>
<td>6</td>
<td>Y</td>
</tr>
<tr>
<td>KRPA</td>
<td>Moj.</td>
<td>C shrub</td>
<td>0.0868 (0.085, 0.089)</td>
<td>0.0864</td>
<td>0.089</td>
<td>36</td>
<td>0.20</td>
<td>0.03</td>
<td>0.06</td>
<td>36</td>
<td>0.0300 (0.029, 0.031)</td>
</tr>
<tr>
<td>LYAN</td>
<td>Moj.</td>
<td>C shrub</td>
<td>0.0568 (0.058, 0.060)</td>
<td>0.0564</td>
<td>0.060</td>
<td>36</td>
<td>0.1589 (0.158, 0.161)</td>
<td>0.158</td>
<td>0.161</td>
<td>36</td>
<td>0.207 (0.206, 0.208)</td>
</tr>
<tr>
<td>LYPA</td>
<td>Moj.</td>
<td>C shrub</td>
<td>0.0847 (0.082, 0.087)</td>
<td>0.0843</td>
<td>0.087</td>
<td>36</td>
<td>0.3461</td>
<td>0.03</td>
<td>0.346</td>
<td>36</td>
<td>0.3793 (0.377, 0.381)</td>
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<td>PLRI</td>
<td>Moj.</td>
<td>C grass</td>
<td>0.0906 (0.090, 0.091)</td>
<td>0.0902</td>
<td>0.091</td>
<td>36</td>
<td>0.2447</td>
<td>0.03</td>
<td>0.245</td>
<td>36</td>
<td>0.2457 (0.245, 0.246)</td>
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<tr>
<td>ARTR</td>
<td>GB</td>
<td>C shrub</td>
<td>0.0663 (0.065, 0.067)</td>
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<td>0.067</td>
<td>36</td>
<td>0.2096</td>
<td>0.03</td>
<td>0.209</td>
<td>36</td>
<td>0.4156 (0.414, 0.417)</td>
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<td>PUTR</td>
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<td>0.0398 (0.039, 0.040)</td>
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<td>0.040</td>
<td>36</td>
<td>0.1809</td>
<td>0.01</td>
<td>0.181</td>
<td>36</td>
<td>0.6978 (0.697, 0.698)</td>
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<td>ERLE</td>
<td>Son.</td>
<td>C grass</td>
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<td>0.0328</td>
<td>0.034</td>
<td>83</td>
<td>0.1724</td>
<td>0.0084</td>
<td>0.172</td>
<td>83</td>
<td>0.4903 (0.490, 0.491)</td>
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<td>GUMI</td>
<td>Chi.</td>
<td>C shrub</td>
<td>0.0617 (0.061, 0.062)</td>
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<td>0.062</td>
<td>36</td>
<td>0.230</td>
<td>0.02</td>
<td>0.230</td>
<td>36</td>
<td>0.4337 (0.433, 0.434)</td>
</tr>
<tr>
<td>LATR</td>
<td>Chi.</td>
<td>C shrub</td>
<td>0.0214 (0.021, 0.022)</td>
<td>0.0213</td>
<td>0.022</td>
<td>583</td>
<td>0.0633</td>
<td>0.0018</td>
<td>0.063</td>
<td>583</td>
<td>0.4337 (0.433, 0.434)</td>
</tr>
<tr>
<td>NOTE</td>
<td>Chi.</td>
<td>C shrub</td>
<td>0.0021 (0.0020, 0.0021)</td>
<td>0.0020</td>
<td>0.0021</td>
<td>377</td>
<td>0.0282</td>
<td>0.0001</td>
<td>0.028</td>
<td>377</td>
<td>0.4337 (0.433, 0.434)</td>
</tr>
</tbody>
</table>

PFT, plant functional type; Moj., Mojave; GB, Great Basin; Son., Sonoran; Chi., Chihuahuan; ACHY, Achnatherum hymenoides; ARLU, Artemisia ludoviciana; ARTR, A. tridentata; BOCU, Bouteloua curtipendula; BOHI, B. hirsuta; DALE, Dasylirion leiophyllum; ERLE, Eragrostis lehmanniana; GUMI, Gutierrezia microcephala; HECO, Heteropogon contortus; PLRI, Pleuraphis rigida; PUTR, Purshia tridentata; NOTE, Nolina texana; PFT, plant functional type; Moj., Mojave; GB, Great Basin; Son., Sonoran; Chi., Chihuahuan; ACHY, Achnatherum hymenoides; ARLU, Artemisia ludoviciana; ARTR, A. tridentata; BOCU, Bouteloua curtipendula; BOHI, B. hirsuta; DALE, Dasylirion leiophyllum; ERLE, Eragrostis lehmanniana; GUMI, Gutierrezia microcephala; HECO, Heteropogon contortus; PLRI, Pleuraphis rigida; PUTR, Purshia tridentata; NOTE, Nolina texana; Monte Carlo (MC) simulations were conducted to propagate uncertainty in the reported conductance values according to the observation error model for SE2 described with Eqn 2. For each MC simulation, the sample median and 2.5th and 97.5th percentiles were computed based on the sample size (n), and the median values of these statistics (across the 3000 MC simulations) are reported; values in parentheses below the median are the 2.5th and 97.5th percentiles for the median (again, based on the MC simulations). Within each MC simulation, the median $g_{\text{night}}$ divided by the median $g_{\text{day}}$ was computed for data-rich species, and the median 2.5th and 97.5th percentiles across the 3000 MC simulations are reported (ratio night : day). Data rich = Y (yes) if a species is associated with > 5 night-time observations and > 20 total observations, N (no) otherwise.
was estimated by summing the observed transpiration for individual plants over time.

Data synthesis methods

Disentangling night-time and daytime behavior  Stomatal conductance (g) and covariates (D, PAR and Ψsoil) were analyzed within an HB framework (Clark, 2005; Ogle & Barber, 2008) to evaluate gday and gnight patterns. An HB approach was used because it is easily structured to the nested and unbalanced sampling designs associated with this large dataset; can directly propagate uncertainty in the reported g values and accommodate other sources of uncertainty contributing to the observed g patterns; allows for the computation of sensitivity indices and accurate estimates of their uncertainty; and can accommodate a nonlinear model that treats g as a mixture of the behaviors predicted in dark vs high light. The HB model implemented is analogous to a nonlinear, mixed-effects model that would be challenging to implement in a classical statistical framework.

Our data model describes the likelihood of the observed g (gobs). Preliminary analyses suggested that gobs is normally distributed such that, for observation i (i = 1, 2, ..., 5013):

\[
g_{obs,i} \sim \text{Normal}(g_i, \sigma_i^2) \tag{Eqn 1}
\]

where \(g_i\) is the predicted (or mean) conductance; the variance \(\sigma_i^2\) is decomposed into a term that quantifies the gobs values (SEg2); preliminary analyses indicated that the first term depends on D, such that:

\[
\sigma_i^2 = \sigma_i^2 + SE_g^2 \tag{Eqn 2}
\]

where \(\sigma_g^2\) and \(\sigma_D^2\) are parameters we estimated; greater variation in gobs is expected under low D (e.g., Ewers & Oren, 2000), and Eqn 2 allows \(\sigma_g^2\) to increase with decreasing D (e.g. if \(\sigma_D^2 < 0\)). The expected standard error of the multiple logged values used to compute gobs, is represented by SEg, and we propagate uncertainty in SEg from sampling log(CVg), where CVg = SEg/gobs, from a normal distribution with a mean and variance that differ by species and the time index (day vs night; see Table S1).

The gday and gnight behaviors were evaluated by modeling \(\tilde{g}_i\) at PAR = 0 µmol m\(^{-2}\) s\(^{-1}\) (\(\tilde{g}_0\)) and at PAR 5000 µmol m\(^{-2}\) s\(^{-1}\) (\(\tilde{g}_{2000}\)). Thus, \(\tilde{g}_0\) and \(\tilde{g}_{2000}\) can be thought of as extreme ‘end-members’, whereby \(\tilde{g}_0\) is the behavior that emerges in the dark (gnight is only based on \(\tilde{g}_0\)), and \(\tilde{g}_{2000}\) is the behavior under high light. We assumed that g at intermediate light levels is a mixture of these end-members:

\[
\tilde{g}_i = \delta_i \cdot \tilde{g}_0 + (1 - \delta_i) \cdot \tilde{g}_{2000} + \epsilon_{\text{sp}(i) \cdot \text{d}(i)} + \epsilon_{\text{DOY}(i) \cdot \text{d}(i)} + \epsilon_{\text{p}(i)} \tag{Eqn 3}
\]

where \(\delta_i\) (0 ≤ \(\delta_i\) ≤ 1) describes the relative contribution of \(\tilde{g}_0\) to the overall stomatal response (\(\tilde{g}_i\)), and \(\epsilon_{\text{sp}(i)}\), \(\epsilon_{\text{DOY}(i) \cdot \text{d}(i)}\), and \(\epsilon_{\text{p}(i)}\) represent time period (within day and night), day and plot random effects. The random effects describe the uncertainty associated with our inability to account for all temporal and plot-level factors affecting gobs (see Notes S1 for definitions). The notations tp(i), sp(i), DOY(i), d(i) and p(i) denote the time period (tp), species (sp), day of year (DOY), desert (d) and plot (p), respectively, associated with observation i.

We define the mixture weight \(\delta_i\) as a function of PAR, where \(\delta_i = 1\) when PAR = 0 and \(\delta_i = 0\) when PAR ≥ 2000 µmol m\(^{-2}\) s\(^{-1}\), and for 0 ≤ PAR ≤ 2000:

\[
\delta_i = \frac{1 - \exp\left(-\theta_{\text{sp}(i)} \cdot \left[1 - \frac{\text{PAR}}{2000}\right]\right)}{1 - \exp\left(-\theta_{\text{sp}(i)}\right)} \tag{Eqn 4}
\]

The species-specific parameter \(\theta_{\text{sp}(i)}\) describes how quickly the \(\tilde{g}_0\) contribution ‘disappears’ as PAR increases.

Evaluating environmental controls on gnight and gday  A phenomenological model linking g to D (Oren et al., 1999; Ewers et al., 2007; Katul et al., 2009), and incorporating the effects of soil water potential (Ψsoil) analogous to Ogle & Reynolds (2002), was employed for \(\tilde{g}_0\) and \(\tilde{g}_{2000}\):

\[
\tilde{g}_i = \left[ \beta_{\text{sp}(i)} + m_{\text{sp}(i)} \cdot \ln\left(\frac{D_i}{D_{\text{ref}}}\right) \right] \cdot \exp(\theta_{\text{sp}(i)} \cdot \Psi_{\text{soil}}) \tag{Eqn 5}
\]

where t is the end-member index (t = 2000 for \(\tilde{g}_{2000}\); t = 0 for \(\tilde{g}_0\)). The term inside the brackets is the predicted end-member at Ψsoil = 0 MPa, where b is the ‘reference’ g at D = Dref, and, following standard approaches, we set \(D_{\text{ref}} = 1\) kPa, and thus −m is the ‘stomatal sensitivity’ of g to changes in ln(D) (Oren et al., 1999; Ewers et al., 2007). The sensitivity of g to changes in Ψsoil is captured by \(\rho\); b, \(\theta\) and \(\alpha\) are allowed to depend on the species (sp) and t to reflect the possibility that D and Ψsoil may differentially affect species-specific gday and gnight. Importantly, these parameters can be interpreted with respect to potential anisohydric and isohydric behavior.

Eqs 1–5 define a nonlinear, mixed-effects regression; unique to HB is the specification of priors for the parameters, thereby obeying basic probability results to obtain the posterior distribution of the parameters (Gelman et al., 2004; Ogle & Barber, 2008). We specified a hierarchical model for the species-specific parameters in Eqs 4, 5, such that they vary around the associated desert-level parameters; hence, for \(\theta\) and \(\alpha\) = b, m or \(\rho\):

\[
\theta_{\text{sp}(i)} \sim \text{Normal}(\bar{\theta}_{\text{d}(i) \cdot \text{sp}}, \sigma_{\theta}^2) \tag{Eqn 6}
\]

\[
\alpha_{\text{t},\text{sp}(i)} \sim \text{Normal}(\bar{\alpha}_{\text{t},\text{d}(i) \cdot \text{sp}}, \sigma_{\alpha}^2) \tag{Eqn 6}
\]

\(d(\text{sp})\) indicates desert d associated with species sp, t is the end-member index, and \(\bar{\alpha}\) and \(\bar{\theta}\) denote the desert-level parameters. We assigned relatively noninformative, standard priors to all remaining parameters (see Notes S1).

Exploring isohydric and anisohydric behavior during the day and night  We evaluated differences between the \(\tilde{g}_0\) and \(\tilde{g}_{2000}\)
parameters to understand the maximum potential difference between $g_{\text{day}}$ and $g_{\text{night}}$ behavior. For parameters that vary by species ($A_{\text{sp}} = b_{\text{sp}}, m_{\text{sp}}$ or $p_{\text{sp}}$) and desert ($A_r = b_r, m_r, \text{ or } p_r$), we obtained the posterior distributions for the differences $A_{\text{sp}} = A_{2000,sp} - A_{0,sp}$ and $A_r = A_{2000,d} - A_{0,d}$.

We evaluated the reference $g$ and sensitivity of $g$ under different $\Psi_{\text{soil}}$ by computing $b' = b \cdot \exp(\psi_{\text{soil}})$ and $m' = m \cdot \exp(\psi_{\text{soil}})$ (see Eqn 5), illustrating how stomatal behavior differs in dark vs high light. For each posterior sample of $b$, $m$ and $p$, we obtained a posterior value of $b'$ and $m'$ associated with different $\Psi_{\text{soil}}$ values, and we focus on the results for $\Psi_{\text{soil}} = -0.1$ and $-1.0 \text{ MPa}$ (25th and 50th percentiles of observed $\Psi_{\text{soil}}$). We also obtained the standardized sensitivity terms by computing $S = -m/b'$, which represents the slope defining the relationship between $-m$ and $b$ (Oren et al., 1999; Katul et al., 2009). We obtained the posterior distribution of $S$ to determine whether desert species behave similarly to species from more mesic regions (expected $S = 0.6$), and to evaluate daytime and night-time isohydric ($S$ generally $\geq 0.6$) vs anisohydric ($S$ generally $< 0.5$) behavior (Oren et al., 1999).

**Implementation of the HB model**

The HB model was implemented in OpenBUGS (Spiegelhalter et al., 2003; Lunn et al., 2009), and Notes S2 provides the code. Three parallel Markov chain Monte Carlo (MCMC) chains were assigned relatively dispersed starting values and run for a sufficiently long period to achieve convergence and obtain a posterior sample size effectively equivalent to >3000 independent samples (for details on MCMC procedures, see Gelman et al., 2004; Gamerman & Lopes, 2006).

**Results**

**Variation in $g_{\text{night}}$ and $E_{\text{night}}$ across species, functional types and deserts**

We observed substantial $g_{\text{night}}$ in 11 of the 12 ‘data-rich’ species (Fig. 1, Table 1). The magnitude of $g_{\text{night}}$ varied considerably across species and was not related to functional type. For example, *Lycium andersonii* (Mojave C3 shrub) and *Purshia tridentata* (nitrogen-fixing Great Basin C3 shrub) exhibited the highest observed $g_{\text{night}}$ values (97.5th percentile = 0.561 and 0.512 mol m$^{-2}$ s$^{-1}$, respectively; Table 1, Fig. 1); the lowest $g_{\text{night}}$ values occurred for *Dasylirion leiophyllum* (Chihuahuan C3 monocot rosette) and *Larrea tridentata* (C3 evergreen shrub) in the Chihuahuan and Mojave Deserts (2.5th percentile = 0.0002 and 0.002 mol m$^{-2}$ s$^{-1}$, respectively; Table 1). For most species, median $g_{\text{night}}$ ranged from 36% (*H. contortus*) to 73% (*A. hymenoides*) of median $g_{\text{day}}$ (Table 1). The three exceptions were *D. leiophyllum*, *L. pallidum* and *P. rigida*; *D. leiophyllum* had a median $g_{\text{night}}$ value that was an order of magnitude lower than that of most species; *L. pallidum* and *P. rigida* exhibited...
The HB model used to explore \( g_{\text{night}} \) and \( g_{\text{day}} \) behavior fit the field data well (Fig. S2; \( r^2 = 0.74 \) for all data). The goodness-of-fit was slightly better for \( g_{\text{night}} \) vs \( g_{\text{day}} \) (\( r^2 = 0.76 \) vs 0.70) and differed across deserts (\( r^2 = 0.44, 0.80, 0.81 \) and 0.83 for the Sonoran, Great Basin, Chihuahuan and Mojave Deserts, respectively) and species (lowest \( r^2 = 0.18 \) for \( A. ludoviciana \) in the Chihuahuan Desert (\( N = 6 \)); second lowest \( r^2 = 0.37 \) for \( E. lehmanniana \) in the Sonoran Desert (\( N = 972 \)); highest \( r^2 = 0.93 \) for \( L. andersonii \) in the Mojave Desert (\( N = 42 \)); median \( r^2 \) across all 17 species = 0.73).

Sources of unexplained variation

The uncertainty in the observed \( g \) values decreased with increasing \( D \), but the \( \sigma \) (standard deviation describing the residual errors; Eqn 2) vs \( D \) relationship differed across deserts (Fig. 3a–d). The model fit the field data better at high \( D \) relative to low \( D \); the predicted values (posterior median) for \( \sigma \) at \( D = 0 \) kPa were 7.4, 3.7, 1.2 and 9.1 times higher than the predicted values at \( D = 10 \) kPa for the Mojave, Great Basin, Sonoran and Chihuahuan Deserts, respectively (Fig. 3a–d). The variation explained by time period and day of year was generally of similar magnitude to this residual variation, but the plot-to-plot variation was comparatively small (Fig. 3e).

Disentangling night-time and daytime behavior

The relative importance of dark (\( g_0 \)) and high-light (\( g_{2000} \)) end-member behavior, as quantified by \( \delta \) in Eqn 4, differed across species and deserts. Four patterns emerged with respect to how the \( g_0 \) behavior decayed with increasing PAR (Fig. 4). The vast majority of species (\( A. tridentata \), \( K. parvifolia \), \( L. andersonii \), \( P. rigida \), \( P. tridentata \) and \( L. tridentata \) in the Mojave Desert) exhibited a clear distinction between \( g_{\text{day}} \) and \( g_{\text{night}} \), such that \( \delta \equiv 0 \) for \( \text{PAR} \geq 200 \text{ m}^2 \text{ s}^{-1} \) (Fig. 4a). For three of the four C4 grasses (\( B. curtipendula \), \( E. lehmanniana \), \( H. contortus \)), the \( g_0 \) behavior persisted under a range of PAR values, whereby the transition to 100% \( g_{2000} \) occurred gradually with increasing PAR (Fig. 4b). One species (\( D. leiophyllum \)) exhibited intermediate behavior, where the contribution of \( g_0 \) disappeared when \( \text{PAR} \leq 800–1200 \text{ m}^2 \text{ s}^{-1} \) (Fig. 4c). Across these three groups, the decay in the relative contribution of \( g_0 \) with increasing PAR was tightly constrained (see relatively narrow 95% credible intervals (CI) for \( \delta \); Fig. 4a–c). By contrast, \( \delta \) was not well resolved for \( A. hymenoides \) or \( L. tridentata \) in the Chihuahuan Desert, and three ‘data-poor’ species (Fig. 4d).

Environmental controls on \( g_{\text{night}} \) and \( g_{\text{day}} \)

The sensitivity of \( g \) to \( D \) (\( -m \)) was >0 for 11 of the 12 species under high light (for \( g_{2000} \), with \( L. tridentata \) in the Chihuahuan Desert being the exception (Fig. 5; see Table S2-B for posterior estimates). During the night-time (\( g_0 \)), \(-m \) was only statistically
> 0 for seven of the 12 species, and \(-m < 0\) (i.e. stomata open in response to increasing \(D\)) for \(L.\) tridentata in the Chihuahuan Desert (Table S2-B). Moreover, \(-m\) did not differ significantly between dark and high-light conditions for eight of the species, but \(-m\) was higher in the dark for the two Great Basin shrubs (\(A.\) tridentata and \(P.\) tridentata) and for two \(C_4\) grasses (\(H.\) contortus and \(B.\) curtispedula). Uncertainty in the \(-m\) estimates was greater during the night-time for seven of the species (wider CIs; Fig. 5; Table S2-B). Integrating across species, the sensitivity to \(D\) appears to differ across deserts (see Table S3-B for posterior estimates of \(-m\)). Mojave plants tend to have \(-m > 0\) for both day and night (sensitive to \(D\)), Sonoran and Chihuahuan plants appear to be relatively insensitive to \(D\) during both day and night (\(-m \equiv 0\)) and Great Basin plants appear to be sensitive to \(D\) under high light but not at night (Table S3-B).

Reference \(g(b)\) was statistically > 0 for all 12 species under high light (for \(g_0,000\)), and for 10 species during the night-time (\(g_0\)), with the exceptions being two Mojave \(C_4\) shrubs (\(K.\) parvolia and \(L.\) pallidum) (Fig. 5; see Table S2-A for posterior estimates of \(b\)). The \(b\) estimates associated with \(g_0,000\) and \(g_0\) were similar for four Mojave species. Conversely, high-light \(b\) was statistically greater than night-time \(b\) for six species, whereas night-time \(b\) was greater than high-light \(b\) for \(D.\) leiophyllum. The uncertainty in \(b\) was greater for \(g_0\) for six species, but was greater for \(g_0,000\) for five other species (Fig. 5, Table S2-A). Integrating across species, the desert-level reference \(g(b)\) was statistically > 0 for all deserts, during both daytime and night-time. However, Great Basin plants tended to have a higher \(b\) under high light relative to night-time, but \(b\) was similar between day and night for plants in the other deserts (Table S3-A).

Soil water availability affected \(g\) and the response to \(D\) (Fig. 5), such that the effect of \(\Psi_{\text{soil}}\) on \(g_0\) and \(g_0,000\) was statistically significant for eight and seven, respectively, of the 12 species (see Table S2-D for posterior estimates of \(\rho\)). With respect to the high-light (\(g_0,000\)) response, the estimates of \(\rho\) were relatively constrained (fairly narrow CIs; Table S2-D). With the exception of three \(C_4\) grasses (\(B.\) curtispedula, \(E.\) lehmanniana, \(H.\) contortus), more negative values of \(\Psi_{\text{soil}}\) reduced \(g\) (\(\rho > 0\)). With respect to the night-time (\(g_0\)) response, the \(\rho\) estimates were characterized by greater uncertainty, but, in general, \(\rho > 0\), indicating that more negative \(\Psi_{\text{soil}}\) also led to stomatal closure at night. The degree to which \(\Psi_{\text{soil}}\) affected \(g\) differed between \(g_0\) and \(g_0,000\) for seven of the 12 species; \(g_0,000\) was more sensitive than \(g_0\) to \(\Psi_{\text{soil}}\) for the two Great Basin shrubs and \(L.\) andersonii (Mojave Desert), but \(g_0\) was more sensitive to \(\Psi_{\text{soil}}\) for the two Sonoran \(C_4\) grasses, \(L.\) tridentata in the Mojave Desert and \(D.\) leiophyllum. Across species, the desert-level \(\Psi_{\text{soil}}\) effects (\(\rho\); see Table S3-D for posterior estimates) differed across deserts. That is, \(g\) appeared to be insensitive to \(\Psi_{\text{soil}}\) for Sonoran and Chihuahuan plants, and \(g_0,000\), but not \(g_0\), was reduced significantly by lower \(\Psi_{\text{soil}}\) in Mojave and Great Basin plants.

Exploring isohydric and anisohydric behavior during the day and night

We used the normalized sensitivity index (\(S = -m/b\)) to explore isohydric vs anisohydric behavior. With respect to the high-light (\(g_0,000\)) behavior, \(S\) values were relatively constrained (see narrow 95% CIs; Fig. 6, Table S2-C), and the posterior median for daytime \(S\) ranged from 0.27 to 0.93 for 11 species, for which \(S\) was statistically different from zero (Table S2-C). Across all 12 species, \(S\) was indistinguishable from or > 0.6 for five of the species, and \(S\) was significantly < 0.6 for the other seven (Fig. 6). Thus, nearly half of the species (\(A.\) tridentata and all Mojave species, except \(L.\) tridentata) were hypersensitive to \(D\) or
exhibited apparent isohydric behavior ($S \geq 0.6$) under high light. The other species (L. tridentata, P. tridentata and all Sonoran and Chihuahuan species) were relatively insensitive to $D$ or exhibited apparent anisohydric behavior ($S < 0.5$).

In contrast with high-light $S$, night-time $S$ (for $g_{st}$) was associated with greater uncertainty (Fig. 6; Table S2-C). $S$ was only statistically different from zero for six of the species, for which the posterior median ranged from 0.20 to 1.55 (Fig. 6). The two Great Basin shrubs and E. lehmanniana appeared to be hypersensitive to $D$ at night ($S > 0.6$), and they were significantly more sensitive to $D$ during the dark relative to high light. Three other species (L. tridentata in the Mojave, H. cortusus and D. leiophyllum) appeared to be relatively insensitive to $D$, exhibiting apparent anisohydric behavior ($0 < S < 0.6$) during the daytime and night-time.

In general, high-light $S$ differed markedly across species; $S$ differed between species for 65% of the 66 species pair-wise comparisons. Conversely, because of the large uncertainty in night-time $S$ (Fig. 6), only 41% of the pairs yielded significant differences. The differences in high-light $S$ across species resulted in desert-level indices ($\hat{S} = -\hat{m}/\hat{b}$) that were unique to each desert (Table S3-C). Conversely, large uncertainties in species-specific night-time $S$ resulted in large uncertainties in night-time $\hat{S}$, yielding night-time estimates that were indistinguishable between deserts (Table S3-C). Ultimately, $g$ of Mojave plants appeared to be hypersensitive to $D$ under high light (narrow 95% CI for $\hat{S}$ that contains 0.6), but uncoupled to $D$ during the night-time (wide 95% CI for $\hat{S}$ that spans zero). Great Basin plants appeared to be hypersensitive to $D$, especially at night ($\hat{S} > 0.6$). Sonoran plants appeared to approach isohydric-type behavior at night ($\hat{S} = 0.6$), but were relatively insensitive to $D$ under high light ($\hat{S} < 0.5$). A general pattern did not emerge in Chihuahuan plants because of divergent or highly uncertain species-specific $S$ values.

**Discussion**

**Variation in $g_{night}$ and $E_{night}$ across species, functional types and deserts**

In our study, $g_{night}$ was c. 40–75% of $g_{day}$, with the exception of the C₃ monocot (D. leiophyllum), suggesting that substantial night-time stomatal opening may be important in deserts. Most notably, $g_{night}$ exceeded 60% of $g_{day}$ for half of the species studied here, and the occurrence of significant $g_{night}$ appeared to be independent of growth form, photosynthetic pathway or desert (Fig. 1, Table 1). Substantial $g_{night}$ has been reported for a small number of species in semi-arid systems (Snyder et al., 2003) and several species from a variety of ecosystems (Caird et al., 2007; Dawson et al., 2007). Interestingly, we found that several desert grasses exhibited relatively high $g_{night}$, which has not been commonly observed (Caird et al., 2007). Moreover, reference $g$ (i.e. $g$...
Species abbreviations are defined in Table 1.

The contribution of each end-member is assumed to depend on ambient light levels (PAR), representing the potential ability to adjust g in response to daylight conditions.

Disentangling night-time and daytime behavior

Next, we asked whether g_{night} behavior is distinguishable from g_{day} behavior. To address this, we employed a unique analytical framework for partitioning g_{night} and g_{day} by assuming that g is a mixture of two extreme behaviors: g_0 and g_{2000}, the predicted g values at PAR = 0 and 2000 \mu mol m^{-2} s^{-1}, respectively. The contribution of each end-member is assumed to depend on ambient light levels (PAR), representing the potential ability to adjust g in response to daylight conditions.

Three C_4 grasses (B. curtipendula, E. lehmanniana and H. contorta) exhibited g_{day} that was influenced by the dark behavior over a range of PAR levels (Fig. 4b). A potential explanation is that these species exhibit sluggish stomatal responses (e.g. Mott et al., 1999; Kaiser & Kappen, 2001), such that they slowly adjust guard cell turgor in response to increasing PAR (e.g. sunflecks or sunrise) or decreasing PAR (e.g. ephemeral cloud cover or sunset). Conversely, the high-light behavior dominated g_{day} under nearly the full range of PAR levels for all of the ‘data-rich’ species in the Great Basin and Mojave Deserts (Fig. 4a), suggesting that their stomata can rapidly adjust to changes in light (e.g. Mott et al., 1999). Five of six of these species are C_3 plants, including four shrubs. Differences in the responsiveness of g to PAR could be a result of transport times of hormones affecting stomatal aperture (e.g. abscisic acid), and the taller stature of the shrubs may expose their canopies to relatively higher D (Rambo & North, 2009), potentially stimulating more rapid stomatal adjustment under changing PAR (Mott et al., 1999; Kaiser & Kappen, 2001). The shrubs may also have deeper roots and greater access to more stable soil water (e.g. Ogle et al., 2004), improving their ability to maintain turgid guard cells and to enable rapid stomatal responses (Saës, 1979; Roelfsema & Hedrich, 2005). The dissimilar behavior of the C_4 vs C_3 species could also be attributed to the differential roles of direct (changes in g directly attributed to changes in PAR) and indirect (as affected by changes in leaf internal CO_2 concentration) responses to PAR (Huxman & Monson, 2003).

Evaluating environmental controls on g_{night} and g_{day}

As one might expect, g of nearly all species was affected by \Psi_{soil}. The model in Eqn 5 assumes an overall, multiplicative effect of \Psi_{soil} on both reference g (b) and stomatal sensitivity (m). The assumption that both are similarly affected by \Psi_{soil} is supported by the observed tight relationship between reference g and sensitivity (Oren et al., 1999; Katul et al., 2009), and a similar model was successfully applied to L. tridentata in the Chihuahuan Desert (Ogle & Reynolds, 2002). Across most species, lower \Psi_{soil} was associated with reduced g, reference g and sensitivity for both g_{day} and g_{night}, similar to the observation that soil water deficits led to stomatal closure at night in several woody plants from...
diverse ecosystems (Dawson et al., 2007). The negative effects of declining \( \Psi_{\text{soil}} \) on \( g \) were expected because stomata should close under water stress to conserve water, regardless of the time of day (e.g. Caird et al., 2007). However, the magnitude of the \( \Psi_{\text{soil}} \) effect often differed between time periods, species and deserts.

The \( \text{C}_4 \) grasses (\( B. \) curtipendula, \( E. \) lehmanniana and \( H. \) contortus) universally exhibited dual stomatal behavior, such that their night-time responses to environmental drivers (\( D \) and \( \Psi_{\text{soil}} \)) differed from their high-light responses, which facilitated the partitioning of the extreme end-member behaviors. However, the slow decay of the dark behavior contribution with increasing PAR suggests that, during most daytime conditions, these \( \text{C}_4 \) plants experience a spectrum between the extreme \( g \) behaviors. Moreover, compared with the other species, these species are relatively unresponsive to changes in \( D \), PAR and \( \Psi_{\text{soil}} \). Interestingly, the species with the more responsive stomata exhibited behavior specific to their geographic origin. The two Great Basin \( \text{C}_4 \) shrubs exhibited dual stomatal behavior, whereby their dark and high-light responses differed with respect to their reference \( g \) and their sensitivities to \( D \) and \( \Psi_{\text{soil}} \). Although we could partition the two extreme behaviors for the Mojave Desert species, most of these species responded similarly to \( D \) and \( \Psi_{\text{soil}} \) during the daytime and night-time.

Why do our study species generally exhibit different responsiveness to environmental drivers during the night-time relative to the daytime? With respect to the \( \text{C}_4 \) grasses, differential responsiveness to \( D \) and \( \Psi_{\text{soil}} \) may be associated with the relative control of photosynthetic feedbacks and the regulation of \( g \) to maintain leaf internal CO\(_2\) concentrations during the daytime (e.g. Wong et al., 1978; Huxman & Monson, 2003). As the optimization of carbon uptake is not relevant at night-time for \( \text{C}_3 \) and \( \text{C}_4 \) species, night-time stomatal regulation is expected to directly affect water balance, independent of carbon balance. The three \( \text{C}_4 \) grasses were more responsive to environmental drivers during the day, suggesting that the optimization of carbon gain may be more important. By contrast, the Great Basin and Mojave species generally appear to be more responsive during the night-time, suggesting a comparatively greater importance of controlling water balance, potentially to optimize carbon balance over longer time-scales.

The aforementioned stomatal behavior characteristics suggest fundamental differences between \( \text{C}_4 \) grasses and \( \text{C}_3 \) shrubs, but such differences could also be attributed to their geographic associations. Plants in the Mojave Desert, the driest of the four deserts (Reynolds et al., 2004), exhibited \( g \) behavior that was most sensitive to \( D \), perhaps indicating the need for the greater conservation of water. Plants in the Sonoran and Chihuahuan Deserts, which receive notable summer rains (Reynolds et al., 2004), were comparatively insensitive to \( D \), indicating potential alleviation of growing season water stress. The greater diurnal swings in temperature and \( D \) in the high-elevation Great Basin may explain why plants in this desert were sensitive to \( D \) during the daytime (high \( D \)), but were relatively insensitive to \( D \) at night (low \( D \)) (Gillespie & Loik, 2004). In summary, geographic location, photosynthetic pathway and life form all appear to be potentially important for understanding \( g_{\text{day}} \) and \( g_{\text{night}} \) behavior.

Exploring isohydric and anisohydric behavior during the day and night

Here, we used the normalized sensitivity \( (S = -m/b) \) as an index of the potential for a species to possess isohydric vs anisohydric behavior (e.g. Oren et al., 1999; Katul et al., 2009). Seven of the 12 study species exhibited apparent anisohydric behavior (\( S < 0.6 \)) under high light, which is somewhat expected for desert plants (Oren et al., 1999; Ogle & Reynolds, 2002). Surprisingly, five species possessed apparent isohydric behavior (\( S > 0.6 \)) under high light, similar to species from wetter environments (Oren et al., 1999), but the relatively high uncertainty associated with \( S \) for \( P. \) rigid\( a \) and \( A. \) tridentata does not rule out anisohydry (Table S2). The two Great Basin shrubs and a Sonoran \( \text{C}_4 \) grass were clearly associated with two temporally distinct behaviors analogous to an anisohydric strategy under high light and an isohydric strategy at night (Table S2, Fig. 6). Sap flux data from silver birch (\( B. \) pendula) also indicate that nocturnal canopy conductance may be more sensitive to \( D \) at night than during the daytime (Sellin & Lubenets, 2010). Moreover, Barbour & Buckley (2007) evaluated the stomatal behavior of castor bean and observed that the sensitivity to \( D \) of \( g_{\text{night}} \) relative to \( g_{\text{day}} \) depended on prior growth chamber \( D \) conditions. This could partially explain the dual stomatal behavior observed here, because \( D \) preceding the \( g \) measurements probably differed during the daytime vs night-time periods.

For those species that exhibited significant differences in night-time vs daytime \( S \), we ask why might stomata be hypersensitive to \( D \) at night? This could potentially reflect amplified ‘wrong-way’ responses and oscillatory behavior that have been observed in isohydric plants (Buckley, 2005). That is, stomata appeared to respond to changes in \( D \), but they may overshoot their target aperture because other positive or negative feedback mechanisms (e.g. Jones & Sutherland, 1991; Buckley, 2005) may be lacking or muted during the night. The importance of different feedback mechanisms for \( g_{\text{night}} \) has not been rigorously evaluated (but, see Mott & Peak (2010)), and experiments addressing this would lend insight into the mechanisms underlying \( g_{\text{night}} \) behavior.

The occurrence of anisohydry or isohydry has commonly been reported in the literature (e.g. Tardieu & Simonneau, 1998; Franks et al., 2007; McDowell et al., 2008; Rogiers et al., 2009; Collins et al., 2010) and represents different strategies employed during drought stress (McDowell et al., 2008; West et al., 2008). Quero et al. (2011) found that co-occurring Mediterranean woody species possessed daytime strategies spanning different degrees of isohydric to anisohydric behavior. We report similar results for both \( g_{\text{night}} \) and \( g_{\text{day}} \) for co-occurring desert species, but our study is the first to indicate the potential for both isohydric and anisohydric behavior to occur within individuals of the same species growing at a particular site. The employment of a shifting strategy is consistent with other studies (Addington et al., 2006; Barbour & Buckley, 2007); for example, \( P. \) palustris trees growing on xeric soils adjusted their hydraulic architecture to enable a mean \( g \) that was occasionally greater than \( g \) measured on trees growing on more mesic soils (Addington et al., 2006).
The shifting behavior reported here suggests that $g_{\text{night}}$ and $g_{\text{day}}$ may be under different selection pressures (Christman et al., 2008). Katul et al. (2009) conducted a theoretical analysis, which predicted that $S$ should vary between 0.5 and 0.7 to optimize daytime carbon gain and water use. Our study predicted notable differences between daytime and night-time $S$ with respect to the median (three species) and the uncertainty (all species) in the predicted $S$, indicating that the daytime optimization strategy is not appropriate for describing $g_{\text{night}}$. Thus, we ask: what is the physiological strategy underlying $g_{\text{night}}$ behavior? Although empirical studies provide some insight (e.g. Caird et al., 2007), theoretical analyses focus on $g_{\text{day}}$ (e.g. Medlyn et al., 2011), and the coupling of empirical and analytical work is needed to explore nocturnal strategies.

Conclusions

We implemented a novel analytical approach to partition $g_{\text{night}}$ and $g_{\text{day}}$ behaviors, which allowed us to show, within a given species and site, $g_{\text{night}}$ may exhibit both isohydric and anisohydric behavior. We suggest that future studies should explore the mechanisms associated with differential $g_{\text{night}}$ vs $g_{\text{day}}$ responses to environmental drivers, and determine the factors underlying exaggerated isohydric behavior at night. It was beyond the scope of this study to evaluate the direct physiological or genetic mechanisms underlying $g_{\text{night}}$, and it remains unclear whether $g_{\text{night}}$ is an adaptive trait or under indirect selection (Caird et al., 2007; Christman et al., 2008). This study, however, demonstrated that stomata behave differently during the day relative to the night for some North American desert species, suggesting that $g_{\text{night}}$ and $g_{\text{day}}$ may be under different selection pressures.

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References


Supporting Information
Additional supporting information may be found in the online version of this article.

Fig. S1 Map of study sites in the four North American deserts indicating the plant species that were measured at each site.
Fig. S2 Figure of model goodness-of-fit.

Table S1 Statistics used to propagate uncertainty in the reported stomatal conductance values associated with the measurement/observation error model in Eqn 2

Table S2 Posterior medians and 95% credible intervals (CIs) for time- and species-specific parameters in Eqn 5

Table S3 Posterior medians and 95% credible intervals (CIs) for time- and desert-specific parameters in Eqn 6

Notes S1 Description of the random effects models and priors.

Notes S2 OpenBUGS code for the hierarchical Bayesian model of stomatal conductance.

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