Sap flux-scaled transpiration and stomatal conductance response to soil and atmospheric drought in a semi-arid sagebrush ecosystem

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Summary

Arid and semi-arid ecosystems represent a dynamic but poorly understood component of global carbon, water, and energy cycles. We studied a semi-arid mountain big sagebrush (Artemisia tridentata var. vaseyana; hereafter, “sagebrush”) dominated ecosystem to quantify the (1) relative control of surface (0–15 cm) versus deep (15–45 cm) soil moisture on leaf transpiration ($E_L$) and stomatal conductance ($g_S$); (2) response of $E_L$ and $g_S$ to light and soil and atmospheric drought; and (3) physiological mechanisms underlying these responses. The physiological mechanisms were tested using a simple plant hydraulic model for $g_S$, based on homeostatic regulation of minimum leaf water potential ($\Psi_{\min}$) that was originally developed for trees. Our results showed that a combination of atmospheric and surface soil drought controlled $E_L$, whereas $g_S$ was mainly driven by atmospheric drought. Sagebrush displayed greater reference conductance ($g_{SR}@1$ kPa vapor pressure deficit ($D$), $g_{SR}$) and greater sensitivity ($-m$) of $g_S$ to $D$ than mesic trees, reflecting the high average light intensity within the shrub canopy. The slope of $-m/g_{SR}$ was similar to mesic trees ($-0.6$), indicating an isohydric regulation of $\Psi_{\min}$ but different than previously published values for semi-arid shrubs ($-0.4$). Isohydric behavior of sagebrush indicates that well-known forest ecosystem models with greater $g_{SR}$ and $-m$ can be used for modeling water, energy and carbon cycles from sagebrush and similar ecosystems.

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1. Introduction

About 40% of the Earth’s terrestrial surface is covered by arid and semi-arid ecosystems which are expanding globally (Schlesinger, 1997; Reynolds, 2000). Global and regional climate models predict a change in crop productivity in response to changing temperature and precipitation patterns, especially in arid and semi-arid ecosystems (Easterling et al., 2000; NAST, 2001; Bates et al., 2008), which are subjected to strong seasonal cycles of rainfall and extended drought (Smith and Allen, 1996; Sivakumar et al., 2005) and may not be predictable from more intensely studied mesic ecosystems (Ogle and Reynolds, 2002, 2004). Understanding physiological responses of arid and semi-arid vegetation to soil and atmospheric drought and the underlying mechanisms is critical for accurate prediction of long term ecosystem carbon, water and, energy fluxes and will provide a more mechanistic picture of plant response to drought.

Stomatal conductance ($g_S$) couples photosynthesis and transpiration (Cowan and Farquhar, 1977), which makes it a key parameter in climate models for quantifying biosphere–atmosphere interactions (Sellers et al., 1997; Lai et al., 2002; Baldocchi et al., 2002; Schäfer et al., 2003). $g_S$ can be estimated at leaf scales by using instantaneous gas exchange measurements (Jarvis, 1995) and from branch to ecosystem scales by continuous sap flux and eddy covariance techniques (Köstner et al., 1992). Sap flux provides species-specific transpiration rates (Cermák et al., 1995; Ewers et al., 2002; Baldocchi, 2005) and can be used for continuous estimation of leaf and canopy $g_S$ and its response to environmental variables at sub-daily time scales (Köstner et al., 1992; Phillips and Oren, 1998; Ewers et al., 2007). However, prior studies on response of sap flux–scaled transpiration and $g_S$ are heavily biased from forest ecosystems (see Mackay et al., 2010 for a comprehensive list) with few sap flux field studies in arid and semi-arid ecosystems (e.g., Oren et al., 1999; Pataki et al., 2000; Dawson et al., 2007; Qu et al., 2007; Lei et al., 2010). This paucity of sap flux field data for arid and semi-arid shrub ecosystems needs to be addressed to improve current and future prediction of long term ecosystem carbon, water, and energy fluxes.

The current understanding of transpiration suggests that leaf water potential ($\Psi_L$) plays an important role in regulation of transpiration which in turn is dependent on whole plant water status (Meinzer and Grantz, 1991; Mott and Parkhurst, 1991; Salieandra et al., 1995; Cochard et al., 1996; Nardini and Salleo, 2000; Salleo...
Nomenclature

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>D</td>
<td>leaf area index (m²)</td>
</tr>
<tr>
<td>D_max</td>
<td>maximum D</td>
</tr>
<tr>
<td>Dl</td>
<td>drought index</td>
</tr>
<tr>
<td>E_L</td>
<td>leaf transpiration rate (mmol m⁻² s⁻¹)</td>
</tr>
<tr>
<td>E_R</td>
<td>root sap flux (mmol s⁻¹)</td>
</tr>
<tr>
<td>E_Rmax</td>
<td>maximum root sap flux (mmol s⁻¹)</td>
</tr>
<tr>
<td>g_S</td>
<td>stomatal conductance of water vapor (mmol m⁻² s⁻¹)</td>
</tr>
<tr>
<td>g_Smax</td>
<td>theoretical maximum stomatal conductance (mmol m⁻² s⁻¹)</td>
</tr>
<tr>
<td>g_Sref</td>
<td>reference stomatal conductance (mmol m⁻² s⁻¹)</td>
</tr>
<tr>
<td>K_C</td>
<td>conductance coefficient (kPa m³ kg⁻¹)</td>
</tr>
<tr>
<td>K_L</td>
<td>leaf-specific whole-plant hydraulic conductance (kg m⁻² s⁻¹ MPa⁻¹)</td>
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Greek letters

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
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<tbody>
<tr>
<td>Ψ_L</td>
<td>leaf water potential (MPa)</td>
</tr>
<tr>
<td>Ψ_Lmin</td>
<td>minimum leaf water potential (MPa)</td>
</tr>
<tr>
<td>Ψ_S</td>
<td>soil water potential (MPa)</td>
</tr>
<tr>
<td>Ψ_g</td>
<td>gravitational water potential (MPa)</td>
</tr>
<tr>
<td>c0</td>
<td>volumetric soil water content (m³ m⁻³)</td>
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eq\ _{\psi L} - {\psi _S}^{<}\ _{\psi L} - {\psi _S}^{>}

where g_S is stomatal conductance for water vapor, K_L is leaf-specific whole-plant hydraulic conductance, Ψ_L is soil water potential, and Ψ_S is gravitational potential. As soil dries out, K_L declines with declining Ψ_S and this decline in K_L requires further decrease in Ψ_L to sustain increasing transpiration (Sperry et al., 1998). Hydraulic failure occurs when transpiration exceeds the water supply, which drives K_L to zero and is referred to as run-away cavitation (Tyree and Sperry, 1989).

Because the signaling mechanisms which integrate leaf and root controls on g_S are still unknown (Franks et al., 2007; Fujii et al., 2009; Pandey et al., 2010), g_S responses to environmental drivers are still predicted semi-mechanistically with models, such as the Ball–Woodrow–Berry (1987) or the Jarvis (1976) model consisting of multiplicative nonlinear functions of environmental variables:

\[
g_S = g_{Smax} f(D) f(Q) f(T_{air}) f(\Psi_L)
\]

where g_{Smax} is the theoretical maximum g_S observed in fully developed leaves before senescence, in plants growing under optimal water, nutrient, and climatic conditions (Körner, 1994), Q is photosynthetically active photon flux density, and T_{air} is ambient temperature. Oren et al. (1999) used a logarithmic relationship to put a mechanism in the f(D) portion of Eq. (2):

\[
g_S = g_{SR} - m \ln D
\]

where g_{SR} is g_S @ 1 kPa D and m is the stomatal sensitivity to ln D or the slope of stomatal response to logarithmic D (m = Δg_S). This work and others (Oren et al., 1999, 2001; Ewers et al., 2001b; Gunderson et al., 2002; Addington et al., 2004) showed that −m ~ 0.6 g_{SR} for a wide range of environmental conditions in mesic tree species. The 0.6 proportionality can be explained by the homeostatic regulation of Ψ_Lmin to prevent damagably low xylem water potential which leads to cavitation (Eq. (1)). Deviations from 0.6 proportionality can occur when: (1) a species can adjust Ψ_Lmin to decline with increasing D (anisohydric); (2) a species experiences a wide range of D; and (3) boundary layer conductance to g_S is low (Oren et al., 1999). The first two conditions arise due to different drought response mechanisms of species that tolerate high water column tensions, such as arid and semi-arid shrub species (Oren et al., 1999; Ogle and Reynolds, 2002: −m/g_{SR} ~ 0.46), which lowers the 0.6 proportionality; the third condition gives higher proportionality than 0.6 (Oren et al., 1999).

Mencuccini’s (2003) synthesis of the plant hydraulic literature showed that arid/semi-arid shrubs have the highest K_L and g_S of all the plant functional types surveyed. This synthesis coupled with results from arid/semi-arid shrubs showing a proportion between −m and g_{SR} as low as 0.4 led us to test whether the semi-arid shrub, mountain big sagebrush (Artemisia tridentata var. vaseyana (Rydby) Beetle) is similar to other arid/semi-arid shrubs. Sagebrush-steppe is a dominant vegetation type of Intermountain west and covers approximately 630,000 km² of North America (West, 1983). Sagebrush is known for surviving in water limited conditions by physiological adaptations. It displays hydraulic redistribution, the movement of water [upwards (e.g., Richards and Caldwell, 1987), downwards (e.g., Brooks et al., 2006), and laterally (Hultine et al., 2003)] across a gradient of Ψ_S from high Ψ_S (wet soil) to low or more negative Ψ_S (dry soil) (Richards and Caldwell, 1987; Caldwell and Richards, 1989; Caldwell et al., 1998), and uses deep taproots as well as shallow, diffuse roots (Sturges, 1977). In a previous study of sagebrush ecosystem by Kwon et al. (2008), the net ecosystem exchange (NEE) showed greater dependence on deep soil moisture (15–45 cm) than surface soil (4 cm). We tested the hypothesis proposed by Kwon et al. (2008) for NEE to assess if Ε_L and g_S also depend on deep soil moisture. Previous studies on trees (Matsumoto et al., 2005) and crop ecosystems (Irmak and Mutiuibwa, 2010) reported that variability in g_S is explained mostly by Q, T_{air} and relative humidity (RH) and Ψ_S explained the least variation. We tested this hypothesis by quantifying the relative control of Q and soil and atmospheric drought on Ε_L and g_S under field conditions in a sagebrush ecosystem. In addition, we tested a simple plant-hydraulic model (Oren et al., 1999), as described above, to understand underlying mechanisms of hydraulic control and asked the following questions: (1) are Ε_L and g_S controlled more by surface (0–15 cm) or deep (15–45 cm) soil moisture?; (2) what is the relative control of Q and soil and atmospheric drought on Ε_L and g_S?; and (3) is mountain big sagebrush similar to other arid/semi-arid shrubs and different than mesic trees in terms of reference conductance (g_{SR}) and the ratio (−m/g_{SR})?
2. Materials and methods

2.1. Study area

This study was conducted during the growing season (May–October) of 2005 in a semi-arid mountain big sagebrush (A. tridentata var. vaseyana) ecosystem located at ~2270 m elevation (N41°12’21’’; W107°23’33’’) in the northwest of the Sierra Madre Mountain Range, Wyoming, USA. The study area was dominated by mountain big sagebrush with scattered grasses, such as western wheatgrass (Pascopyrum smithii), needle and thread (Hesperostipa comata), Idaho fescue (Festuca idahoensis), and forbs, such as silvery lupine (Lupinus argenteus). The canopy height was about 1 m with 1.2 m² m⁻² leaf area index (LI) and ~39% vegetation cover (Kwon et al., 2008). The site climate was marked with long, cold winters (~7 month snow presence) and warm, dry summers with 259–341 mm annual precipitation and 6.2–7.2 °C annual temperature (Ewers and Pendall, 2008). Surface soil texture was sandy clay loam and deep (below 20 cm) soil texture was clay loam (Cleary et al., 2010).

2.2. Meteorological measurements

\( T_{Air} \) and relative humidity (RH) were measured by a RH probe (Model HMP45C, Vaisala, Helsinki, Finland) and Q was measured by a quantum sensor (Model Li-190SZ, Li-COR) at 2.5 m height. \( D \) was calculated from RH and \( T_{Air} \) measurements using Goff and Gratch (1946) equation. A tipping-bucket rain gauge (Model TE525MM, Texas Electronics, Texas, USA) was used to measure downwelling rainfall or on nights when \( D > 0.6 \) to minimize relative errors (<10%) (Ewers and Oren, 2000). The study area conditions matched these assumptions being windy (large boundary layer conductance) and having an open (canopy height ~1 m) canopy. Daytime and nighttime averages of sap flux and meteorological data were calculated using Q as a filter to assign day (>10 μmol m⁻² s⁻¹) and night (<10 μmol m⁻² s⁻¹). The upwards sap flux (USF) from root sensor was compared with the stem sap flux to check their relationship. Both root and stem sap flux sensors were normalized by the maximum observed sap flux value during July 8–August 24 for the respective sensors and an average of five stem sap flux sensors was compared with one root sap flux sensor.

2.4. Calculations of \( E_l \) and \( g_S \)

Sap flux was divided by the leaf area of the branch to calculate branch transpiration per unit leaf area (\( E_l \); kg m⁻² s⁻¹). \( g_S \) was calculated from \( E_l \) and \( D \) using a simplified inversion of Penman–Monteith model (Monteith and Unsworth, 1990)

\[
g_S = \frac{k_c (T_{Air} E_l)}{D}
\]  

(5)

where \( g_S \) is the stomatal conductance (m s⁻¹) to water vapor; \( k_c \) is conductance coefficient as a function of temperature (115.8 + 0.4236T\(_{Air}\)) kPa m² kg⁻¹ which accounts for temperature effects on the psychrometric constant, latent heat of vaporization, specific heat of air at constant pressure and air density; and \( T_{Air} \) is bulk air temperature (°C) used in calculation of \( k_c \) (Phillips and Oren, 1998). \( g_S \) was converted from m s⁻¹ to mmol m⁻² s⁻¹ using atmospheric pressure of the site (78 kPa) and simultaneous temperature measurements (Peary et al., 1989). The simplified inversion of Penman–Monteith assumes large boundary layer conductance, no vertical gradient of \( D \) and negligible water storage above the sensor (Ewers and Oren, 2000). The study area conditions matched these assumptions being windy (large boundary layer conductance) and having an open canopy (~39%) and short canopy height (~1 m) canopy. Daytime (\( Q \approx 10 \mu\text{mol m}^{-2} \text{s}^{-1} \)) data were used for calculation of \( g_S \) at \( D > 0.6 \) to minimize relative errors (<10%) (Ewers and Oren, 2000).

2.5. Data and statistical analyses

Two approaches were used to analyze the effects of multiple parameters on \( g_S \) and \( E_l \). The first approach analyzed the response...
of half hourly (root sap flux, $E_R$) and daily (stem sap flux, $E_L$) means (day and night separately) of transpiration and $g_S$ to half hourly and daily means of $Q$ and soil and atmospheric drought respectively. $E_R$ was normalized by the observed maximum daytime root sap flux value ($E_{R_{\text{max}}}$) during the growing season (e.g., Dawson et al., 2007) and reported as:

$$E_R[i] = \frac{E_R[i]}{E_{R_{\text{max}}}} \times 100$$

where $E_R[i]$ is the half hourly mean of root sap flux for a given point in time $[i]$. Soil (at both soil depths) and atmospheric drought were calculated using a similar approach from $\theta_V$ (at 0–15 and 15–45 cm depth) and $D$ data that were normalized by the maximum respective values across the growing season. Soil and atmospheric drought were calculated as:

$$\text{Soil Drought}[i] = \left(1 - \frac{\theta_V[i]}{\theta_{V_{\text{max}}}}\right) \times 100$$

where $\theta_V[i]$ is the half hourly mean of the volumetric soil water content (m$^3$ m$^{-3}$) of a given point $[i]$ in time and $\theta_{V_{\text{max}}}$ is the maximum observed $\theta_V$ during the growing season.

$$\text{Atmospheric Drought}[i] = \left(1 - \frac{D[i]}{D_{\text{max}}}\right) \times 100$$

where $D[i]$ is the half hourly mean of $D$ at a given point $[i]$ in time and $D_{\text{max}}$ is the maximum observed $D$ during the growing season. Drought index ($D_i$) was calculated by averaging the soil and atmospheric droughts:

$$D_i = \left(\frac{\text{Soil Drought}[i] + \text{Atmospheric Drought}[i]}{2}\right)$$

The daily values were calculated by averaging half hourly values for day and night hours.

The second approach reduced data to parameters explaining the relationship between $g_S$ and $D$ by performing boundary line analysis under different $Q$, $T_{\text{air}}$, and $\theta_V$ conditions (Chambers et al., 1985; Pezeshki and Hinckley, 1988; Schafer et al., 2000; Ewers et al., 2001a). The boundary line analysis was performed by: (1) partitioning data into seven bins of the $g_S$ response to $D$ by keeping equal number of points within each bin; (2) calculating the mean ($\mu$) and standard deviation ($\sigma$) of $g_S$ within each D bin; (3) removing outliers ($P < 0.05$ Dixon’s test; Sokal and Rohlf, 1995); (4) selecting data more than the “$\mu + \sigma$” of $g_S$ (Schafer et al., 2000; Ewers et al., 2001a) to obtain boundary line data. The boundary line represents the highest (optimum physiological) $g_S$ response under measured conditions in a plant or population (Martin et al., 1997). The binned variables ($D$ and $g_S > "\mu + \sigma"$) were re-gressed to obtain the $g_S$ response parameters (slope ($m$) and intercept ($g_{\text{bin}}$)) for Eq. (3). Mackay et al. (2003) showed that this boundary line approach provides the same interpretation of Eq. (3) as a full process model of $g_S$. We also tested the robustness of boundary line analysis under different bin and sample sizes. R statistical software (R Development Core Team, 2010) was used to perform all statistical analyses and SigmaPlot (Systat Software Inc.) was used for preparing graphs.

3. Results

3.1. Are $E_L$ and $g_S$ controlled more by surface (0–15 cm) or deep (15–45 cm) soil moisture?

A general decline in $\theta_V$ and $\Psi_S$ was observed in both soil layers during the growing season (Fig. 1a). However, the surface soil (0–15 cm) showed greater range of $\theta_V$ and $\Psi_S$. The change in $\Psi_S$ was greater in surface soil than deep soil despite similar absolute changes in the $\theta_V$ (Fig. 1a) due to different soil texture [sandy clay loam in the surface and clay loam below 20 cm (Cleary et al., 2010)]. There were noticeable seasonal trends in $Q$, $D$, and $E_L$ (Fig. 1b and c). The daily average $D$ and sum of $Q$ displayed similar seasonal declining trend during the growing season (Fig. 1b). The mean daily daytime $E_L$ was low (<5 mmol m$^{-2}$ s$^{-1}$) at the beginning of the growing season (late May) and reached the maximum value (<11 mmol m$^{-2}$ s$^{-1}$) in late June–early July with a declining $E_L$ after early August, which continued until September (Fig. 1c).

Daily daytime ($Q > 10$ mmol m$^{-2}$ s$^{-1}$) data were used to quantify the effect of soil drought on $E_L$ and $g_S$ at both soil depths. Surface soil drought explained greater ($R^2 = 0.61$) variability in transpiration than deeper soil ($R^2 = 0.47$) (Table S1 in Supplementary data). In addition, $g_S$ showed a weak ($R^2 = 0.18$) exponential decline with surface soil and no relationship with deep soil drought (Table S1 in Supplementary data). Subsequent analyses were done using surface soil (0–15 cm) moisture to see the effect of soil drought on $E_L$ and $g_S$.

3.2. What is the relative control of $Q$ and soil and atmospheric drought on $E_L$ and $g_S$?

Stem sap flux sensors showed diei $E_L$ closely following $D$ and displayed minimum $E_L$ during early morning (~2 mmol m$^{-2}$ s$^{-1}$) and night (1–5 mmol m$^{-2}$ s$^{-1}$) and maximum (10–22 mmol m$^{-2}$ s$^{-1}$) $E_L$ during mid-day (Fig. 2a and b). Nighttime and early morning $D$ rarely reached zero (e.g., Fig. 2b) which was reflected in similar $E_L$ trends and values greater than zero at nighttime. The USF sensor showed diei trends similar to $D$ and the DSF sensor showed negative sap flow (downward movement of water) only after a rainfall event (Fig. 3a and b). The corresponding $\Psi_S$ showed wetting of surface soil (greater $\Psi_S$ at 0–15 cm) during rain event and gradual drying (lower $\Psi_S$ at 0–15 cm) after the rain event (Fig. 3a and c).
increasing soil drought (Fig. 4e). DSF also showed declining relations with increasing atmospheric drought (Fig. 4a) and decreased with increasing soil moisture deficit between 0–15 cm) at the same time when deeper soil layer (15–45 cm) gradually started wetting (greater $\Psi_S$) (Fig. 3c) at 0–15 and 15–45 cm depth displaying reverse flow after a rain event. Each data point is a 30 min averaged value and error bars are associated standard error of five sapflux sensors.

Both daytime and nighttime USF (half hourly average) increased with increasing atmospheric drought (Fig. 4a) and decreased with increasing soil drought (Fig. 4b). Both stem and root sap flux (30 min average) showed linear increase with increasing Q and displayed a hysteresis effect (30 min lag) in the relationship (Fig. 4c, Table S1 in Supplementary data). The DSF occurred during day and night (Fig. 4d–f) and increased in absolute magnitude with increasing atmospheric drought (Fig. 4d) and declined with increasing soil drought (Fig. 4e). DSF also showed declining relationship with increasing soil moisture deficit between 0–15 cm and 15–45 cm (Fig. 4f) which indicates drying of surface soil. Due to limited sample size (one root) of root sensors we compared the normalized root data with normalized stem sap flux data to check the representativeness of the data from one root. Comparison of root and stem sap flux sensors showed a linear relationship ($R^2 = 0.52$), with stem sap flux higher than root sap flux at low (0–15%) sap flux values and root sap flux higher than stem sap flux at high (60–80%) sap flux values (Fig. S2 in Supplementary data).

The averaged (five sap flux sensors) daily daytime $E_t$ displayed exponentially saturating response to atmospheric and soil (0–15 cm) drought and combined drought index (Fig. 5a–c and Table S1 in Supporting information). Both soil ($R^2 = 0.61$) and atmospheric ($R^2 = 0.60$) drought displayed equal control on daily daytime transpiration (Fig. 5a and b). Combined drought index explained 72% ($R^2 = 0.54$) and showed a weak declining relationship with soil drought (Fig. 5e) and combined drought index (Fig. 5f). There were several outliers at high $g_S$ under maximum soil drought (Fig. 5e) and most of them were under low temperature (daily average <18°C) and low D (daily average <1.5 kPa) (Fig. 5e). Mean daily nighttime transpiration (4–7 mmol m$^{-2}$ s$^{-1}$) varied from 40% to 70% of the maximum daily daytime transpiration (10 mmol m$^{-2}$ s$^{-1}$) (Fig. S3 in Supplementary data). Mean daily nighttime $D$ (0.2–1.5 kPa) was 7–50% of the maximum daily daytime $D$ (3 kPa). Soil and atmospheric drought did not show any relationship with nighttime transpiration ($E_{t_{night}}$), however, atmospheric drought controlled nighttime stomatal response ($R^2 = 0.78$) (Fig. S3 in Supplementary data).

3. Is mountain big sagebrush similar to other arid and semi-arid shrubs and different than mesic trees in terms of reference conductance ($g_{SR}$) and the ratio ($-m/g_{SR}$)?

Our results indicate that boundary line analysis is robust to binning and $-m/g_{SR}$ did not change with changing bin size (Fig. S5 in Supplementary data). However, sample size showed a significant effect on boundary line analysis. $-m/g_{SR}$ ratio declined with smaller sample size (Fig. S5 in Supplementary data). We conducted boundary line analysis on sample size greater than 100 days to avoid the effect of sample size on the ratio. Sagebrush displayed greater $g_{SR}$ and $-m$ than previously reported values for mesic trees and arid/semi-arid shrubs (Fig. 6a). The average ratio of $-m$ and $g_{SR}$ (Eq. (3) and solid line in Fig. 6a–d) was 0.54 (±0.03), which did not differ statistically ($P$ value = 0.109) from the theoretical value (~0.6) for mesic trees. The range of ratio between $-m$ and $g_{SR}$ varied from 0.48 to 0.63 among five sap flux sensors (Fig. 6a). The mean ratio between $-m$ and $g_{SR}$ did not differ significantly under varying values of Q (Fig. 6b, $P$ value = 0.503). $T_{Air}$ (Fig. 6c, $P$ value = 0.155), or $T_v$ (Fig. 6d, $P$ value = 0.756), but data from individual sensors declined with increasing $T_{Air}$ (Fig. 6c) and decreasing $T_v$ (Fig. 6d) (Table S2 in Supplementary data).

4. Discussion

Our results show that surface soil drought explained higher variability in $E_t$ and $g_S$ than deep soil drought (Table S1 in Supplementary data) which suggests the use of surface soil moisture in ecosystem models for arid and semi-arid shrub ecosystems will not introduce biases by ignoring deep soil moisture. Kwon et al. (2008) used 2004–2005 NEE data for 2 months (June and July) of the growing season from eddy covariance tower, with 2004 being a dry year and 2005 being a wet year. We collected data in the relatively wet year (2005) and the timeframe of our data collection was greater (May–October) than Kwon et al. (June–July), which provided a wide moisture gradient from wet early spring to dry late summer. Q displayed weak (30 min average) or no relationship (daily daytime data) with $g_S$ (Fig. 4 and Table S1 in Supplementary data), which can be explained by the open canopy and sunny conditions of the study site. Soil and atmospheric drought showed equal
control (Fig. 5a–c) over $E_L$, whereas atmospheric drought showed more control over $g_S$ than soil drought (non-significant) (Fig. 5d–f). Previous studies from different ecosystems (Matsumoto et al., 2005 [Quercus sarrata]; Irmak and Mutiibwa, 2010 [Zea mays]) tested the importance of different meteorological factors in modeling leaf and canopy stomatal conductance and found that $Q$, $T_{Air}$ and $RH$ contributed the most and $i_t$ contributed the least. Our field results partially supported these modeling results by showing greater control of atmospheric drought over $g_S$, which is calculated by $T_{Air}$ and $RH$, and a weak control of $Q$ over $g_S$, which could be attributed to different canopy structure as explained above. Despite the different ecosystems (trees and crops versus shrubland), our field data support results reported by Matsumoto et al. (2005) and Irmak and Mutiibwa (2010) showing that soil drought is a poor predictor for $g_S$. The relationship between soil drought and $g_S$ becomes weak when soil and atmospheric drought decouple, for instance days when atmospheric drought is low due to low temperature and soil drought is high (Fig. 5e). A previous study on a semi-arid shrub by Ogle and Reynolds (2002) reported an exponential decline in $g_S$ with increasing $D$ and a flat response of $/C_0$ with increasing soil drought, while our data showed a direct effect of soil and atmospheric drought (individually and combined effect) on $E_L$ and $g_S$. Our results showed similar exponential decline in $g_S$ to $D$, but we did not see a flat response of stomatal sensitivity to $D$ at lower soil moisture conditions (see below).

Despite the limitations of sample size (one root) and measurement time (3 months) for root sensors, we observed strong signals of upwards (hydraulic lift) and downwards (reverse hydraulic

Fig. 4. (a–c) Response of upwards sapflux (USF) to soil (0–15 cm) and atmospheric drought and photosynthetic photon flux density ($Q$). (d–f) Response of downwards sapflux (DSF) to soil and atmospheric drought and soil moisture deficit between 0–15 cm and 15–45 cm depth. Closed gray symbols are% daytime and closed black symbols are% nighttime root sapflux standardized by the maximum observed root sapflux during July 9–August 24. Each point is a 30 min averaged value.

Fig. 5. Response of leaf transpiration ($E_L$) and leaf stomatal conductance ($g_S$) to soil (a and d), and atmospheric (b and e) drought and a drought index (c and f). Drought index is an average of soil (0–15 cm) and atmospheric drought. Daily values are calculated from daytime ($Q > 10$ mmol m$^{-2}$ s$^{-1}$) data.
flow) water movement in sagebrush. We use this data as additional evidence to explain the variability in $E_l$ and $g_S$. Comparison of root and stem sap flux sensors showed a positive linear relationship ($R^2 = 0.52$). At relatively low root sap flux (0–15%), stem sap flux was higher (20–40%) suggesting more use of surface water than deep water and, at high root sap flux (80–100%), stem sap flux was relatively low (60–80%) (Fig. S2 in Supplementary data). This pattern could be attributed to stomatal regulation during high transpiration rate or leaky roots (Caldwell et al., 1998). Daytime transpiration from root sensors showed a declining relationship with increasing soil drought (Fig. 4b), whereas stem sensors showed an exponentially saturating response (Fig. 5a). These responses indicate an immediate response of roots to soil drought and a delayed response of stem sensors, in addition to stomatal regulation of leaf transpiration when water supply from roots started declining.

Nighttime transpiration has been reported across a variety of ecosystem types (5–50% of daytime $E_l$; Benyon, 1999; Feild and Holbrook, 2000; Snyder et al., 2003; Bucci et al., 2005; Daley and Phillips, 2006; Cavender-Bares et al., 2007; Dawson et al., 2007; Fisher et al., 2007; Howard and Donovan, 2007; Scholz et al., 2007; Howard et al., 2009) and our results expand the dataset for poorly represented semi-arid shrubs (maximum $E_{night}$ ~70% of the daily maximum $E_{day}$. $E_{night}$ did not show significant relationships with soil and atmospheric drought (Fig. S3 in Supplementary data), which is contrary to prior work by Dawson et al. (2007), showing an increase in nighttime transpiration with increasing soil moisture and $D$ across different ecosystem types. This could be explained by the relationship between $D$ and $\theta_v$ in the study area, where under high soil moisture conditions $T_W$ was very low and, as a result, $D$ was always low (Fig. S4 in Supplementary data).

Sagebrush displayed a similar ratio between $-m$ and $g_{SR}$ (Fig. 6a, 0.54 ± 0.03, Table S2 in Supplementary data) compared to the theoretical value and other mesic trees, which suggests stomatal regulation in sagebrush maintains $\Psi_{s, min}$. Our results did not follow previous findings on two other semi-arid shrubs, Larrea tridentata (0.46, Ogle and Reynolds, 2002 (gas exchange data) and 0.31, Pataki, unpublished data cited in Oren et al., 1999) and Ephedra nevadensis (0.41, Pataki, unpublished data cited in Oren et al., 1999) (Fig. 6a). A different ratio for sagebrush than other semi-arid shrubs could be due to (1) different range of $D$ (0–4.5 kPa) experienced by sagebrush than reported for L. tridentata (Ogle and Reynolds, 2002; 0–10.5 kPa) as the slope of $g_s$ response to $D$ decreases with increased range of $D$; and/or (2) use of different technique (gas exchange in Ogle and Reynolds, 2002) which provides substantially smaller number of datapoints than sap flux technique (e.g., this study). Boundary line analysis seems to be sensitive to the number of datapoints included and tended to decrease the ratio when smaller number of datapoints were included (Fig. S5 in Supplementary data). Environmental conditions, such as $Q$ (Fig. 6b), $T_{air}$ (Fig. 6c), and $\theta_v$ (Fig. 6d) did not change the mean ratio but the values for individual sensors increased under low $T_{air}$ and high $\theta_v$, which is consistent with a previous study by Ewers et al. (2001b).

Loranty et al. (2010) reported a lower $g_{SR}$ for forests with high $L$ and closed canopy, suggesting that competition for light limits the $g_{SR}$ in different stands of mesic forests. Sagebrush (this study) displayed greater $g_{SR}$ and $-m$ than the reported values in literature (Fig. 6a) which can be explained by lower $L$ (1.2 m² m⁻²) and an open canopy (~39% canopy cover) in our study, resulting in less competition for light. Plants with greater $g_{SR}$ have associated cost of greater absolute reduction in conductance with increasing $D$ than plants with low $g_{SR}$ (Oren et al., 1999). Sagebrush can maintain high $g_{SR}$ for a longer time period as the range of $D$ is not as wide as reported in other semi-arid ecosystems (Ogle and Reynolds, 2002; 0–10.5 kPa) and it has access to deeper soil moisture which is being recharged by its roots during wet conditions (Richards and Caldwell, 1987; this study: Figs. 3 and 4). The combination of high $g_s$ and isohydric regulation increases stomatal sensitivity of sagebrush which is useful for normal, seasonal droughts and allows sagebrush to take advantage of high $g_s$ under low atmospheric drought and high light conditions. Sagebrush

![Figure 6](https://example.com/figure6.png)

**Fig. 6.** Relationship between reference stomatal conductance ($g_{SR}$ = $g_s$ @ 1 kPa $D$) and sensitivity ($-m$ of $g_s$ to vapor pressure deficit ($D$). The solid line represents theoretical value of $-m$ versus $g_{SR}$ ratio (0.6) suggesting regulation of minimum leaf water potential ($\Psi_{s, min}$) (Oren et al., 1999). (a) Previous data (Oren et al., 1999; Gunderson et al., 2002; Ewers et al., 2001a,b, 2005) for seven mesic tree species (Trees) from the temperate Chequamegon Ecosystem-Atmosphere Study (ChEAS) closely follow 0.6 line despite changes in water status, defoliation and leaf area dynamics. Species with lower $m$ value at a given $g_{SR}$ (Oren et al., 1999; Larrea tridentata, LATR and Ephedra nevadensis, EPNE; unpublished results), Ogle and Reynolds (2002) (LATR), Ewers et al. (2005) (Picea mariana, PIMA)) have less strict $\Psi_{s, min}$ regulation. This study (Artemisia tridentata var. valseiana, ARTR) follows 0.6 line under (b) low (<10%), and high (>10%) volumetric soil water content ($\theta_{v, LTR}$), (c) low (<1000 mmol m⁻² s⁻¹) and high (>1000 mmol m⁻² s⁻¹) photosynthetic photon flux density ($Q$) and (d) low (<20 °C) and high (>20 °C) air temperature ($T_{air}$). Each filled circle for ARTR represents an individual stem sapflux sensor and empty circle represents an average of five stem sapflux sensors with standard error as error bars.
then relies on deep roots for prolonged and more extensive droughts. This may be one reason why mountain big sagebrush is restricted to areas with snowpack. Among all plant functional types, arid/semi-arid shrubs have the highest hydraulic and stomatal conductance per unit leaf area (Mencuccini, 2003). Arid/semi-arid plants have a wide range of evaporative demands (Ogle and Reynolds, 2002: 0–10.5 kPa; present study: 0–4.5 kPa) compared to other vegetation types (e.g., Loranty et al., 2010: 0–2 kPa). As a result of adaptation to their environment, arid/semi-arid shrubs have reduced leaf area which results in several key changes in plant water relations, such as: (1) increased K_l and g_s with reduced leaf area, (2) increased water supply due to less leaf area per unit root area, and (3) increased photosynthesis by open canopy and increased leaf area exposed to incident radiation (Mencuccini, 2003). Additionally, desert shrubs tend to have short canopies (~1 m in present study) and plant height is negatively related to K_l (Mencuccini, 2003), which further explains high values of K_l observed in arid/semi-arid shrubs. Moreover, the ability to redistribute soil water (hydraulic redistribution: Caldwell et al., 1987, 1998: present study (Fig. 3)) allows desert shrubs to store the excess water in the deep soil layers during wet conditions and access deep soil water during drought to maintain high K_l and –m in addition to regulating irrigation and reverse hydraulic flow help sagebrush to regulate g_s and irrigation and reverse hydraulic flow help sagebrush to regulate g_s and irrigation and reverse hydraulic flow help sagebrush to regulate g_s and –m in addition to regulating, the aforementioned adaptations of arid/semi-arid shrubs make them a potential carbon sink due to increasing CO_2 concentration which will result in increasing assimilation and decreasing g_s ( stomatal optimization theory – Kutul et al., 2009).

Our work has demonstrated that hydraulic mechanisms operating in semi-arid sagebrush ecosystems, such as nighttime transpiration and reverse hydraulic flow help sagebrush to regulate g_s and irrigation and reverse hydraulic flow help sagebrush to regulate g_s and irrigation and reverse hydraulic flow help sagebrush to regulate g_s and –m. This study tested a plant-hydraulic model and showed that sagebrush has a suite of water relation adaptations, which should be considered when modeling ecosystem water loss.

4.1. Implications for ecosystem and hydrologic modeling

Isohydric behavior of sagebrush indicates that well-known forest ecosystem and hydrology models can be used for modeling water, energy and carbon cycles from sagebrush and similar ecosystems. A simple modification (e.g., higher g_s – m) and incorporation of hydraulic redistribution in ecosystem and hydrology models which were designed originally for forest ecosystems (e.g., TREES (Mackay et al., 2003)) may improve future prediction of water, energy and carbon cycles of these widely distributed sagebrush ecosystems and other similar arid and semi-arid shrublands.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jhydrol.2012.07.008.

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