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Stem photosynthesis and hydraulics are coordinated in desert plant species

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Summary

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Key words: chlorophyll fluorescence, cuticular conductance, evaporative flux method, gas exchange, hydraulic conductance, specific bark area, specific stem area, wood density.

- Coordination between stem photosynthesis and hydraulics in green-stemmed desert plants is important for understanding the physiology of stem photosynthesis and possible drought responses. Plants with photosynthetic stems have extra carbon gain that can help cope with the detrimental effects of drought.
- We studied photosynthetic, hydraulic and functional traits of 11 plant species with photosynthetic stems from three California desert locations. We compared relationships among traits between wet and dry seasons to test the effect of seasonality on these relationships. Finally, we compared stem trait relationships with analogous relationships in the leaf economics spectrum.
- We found that photosynthetic and hydraulic traits are coordinated in photosynthetic stems. The slope or intercept of all trait relationships was mediated by seasonality. The relationship between mass-based stem photosynthetic CO₂ assimilation rate (A_{mass}) and specific stem area (SSA; stem surface area to dry mass ratio) was statistically indistinguishable from the leaf economics spectrum.
- Our results indicate that photosynthetic stems behave like leaves in the coordination of multiple traits related to carbon gain, water movement and water loss. Because of the similarity of the stem A_{mass} –SSA relationship to the leaf A_{mass} –specific leaf area relationship, we suggest the existence of a photosynthetic stem economic spectrum.

Introduction

The efficiency of the stem xylem to transport water to photosynthesizing tissue is of paramount importance in the life of plants. We know that water is the resource that most limits terrestrial productivity (Schulze *et al.*, 1987; Chaves & Pereira, 1992), and plants living where water is scarce need a suite of traits that allows them to persist in such harsh environments. Leaf photosynthetic traits, for example, are tightly related to the ability of stems to transport water (Brodribb & Feild, 2000; Brodribb *et al.*, 2002; Santiago *et al.*, 2004). This coordination implies that investment in stem hydraulic capacity is correlated with investment in leaf carbon gain potential in plants where leaves are the main photosynthetic organs. Having high stem hydraulic conductivity is only useful if leaves can capitalize on high water transport capacity in gaining carbon through a high stomatal conductance (g_s). In some foliated plants, photosynthetic green stems are the organs responsible for most of the annual carbon assimilation (Ávila *et al.*, 2014). However, we do not know whether hydraulic capacity and carbon gain are related in the stems of these plants. In this regard, the main goal of this work was to evaluate the relationships between photosynthetic and hydraulic traits in green-stemmed plants from southern California desert ecosystems.

Traits of leaf photosynthetic capacity, such as relative quantum yield of photosystem II (Φ_{PSII}) (Brodribb & Feild, 2000), electron transport rate (ETR) (Brodribb *et al.*, 2002), and maximum leaf photosynthetic rate (A_{max}) (Santiago *et al.*, 2004), have been found to be positively related to leaf-specific stem hydraulic conductivity (K_{L}) in both tropical rainforests and dry forests. Also, soil to leaf hydraulic conductance (K_{plant}) is positively correlated with leaf A_{max} and g_s in *Pinus ponderosa* (Hubbard *et al.*, 2001). All of these studies found positive correlations between leaf photosynthetic rate and stem hydraulic efficiency, and the mechanism coupling these traits appears to be leaf stomatal responses to changes in water potential (Ψ) brought about by changes in stem hydraulic conductance (Sperry, 2000; Hubbard *et al.*, 2001). High rates of stem water transport can maintain high leaf Ψ and g_s , which in turn allow more diffusion of CO₂ to the sites of carboxylation. This physiological coordination may be expected to occur in photosynthetic stems as well. Yet, the functional relationship between stem photosynthesis and hydraulic conductance has not been assessed.

Woody plants with photosynthetic stems are common in dry and hot ecosystems world-wide (Gibson, 1983, 1998; Nilsen, 1995; Ávila *et al.*, 2014) and, as leaf area declines along aridity gradients, many plants increasingly rely on stem photosynthetic

activity (Comstock *et al.*, 1988; Smith *et al.*, 2004). Plants with photosynthetic stems are represented in at least 35 dicotyledonous families and the gymnosperm family Ephedraceae (Gibson, 1996), suggesting that the syndrome could have evolved more than once as an adaptation to life in arid environments (Ávila-Lovera & Ezcurra, 2016). The presence of many species with photosynthetic stems in arid ecosystems suggests that photosynthetic stems confer some physiological advantages to plants bearing them, including: extra carbon gain during periods of water deficit when many plants are leafless, thus extending the period for carbon gain (Osmond *et al.*, 1987; Nilsen *et al.*, 1989; Nilsen & Bao, 1990; Nilsen & Sharifi, 1997); balance of respiratory costs as a result of reassimilation of CO₂ (Smith & Nobel, 1986; Pfanz *et al.*, 2002; Aschan & Pfanz, 2003); and improved water-use efficiency (WUE) because stem photosynthesis often occurs at higher WUE than leaf photosynthesis (Ehleringer *et al.*, 1987; Osmond *et al.*, 1987; Nilsen & Sharifi, 1997). This higher WUE can be critical for plant survival during periods of water stress, which can last several months in most North American warm deserts.

Photosynthetic stems have positive effects on the carbon economy of plants through two main mechanisms. Photosynthetic stems can either assimilate atmospheric CO₂ and contribute to the net carbon gain of the plant through the process of stem net photosynthesis, or decrease respiratory losses by recycling CO₂ previously respired by roots and stems through the process of stem recycling photosynthesis (Ávila *et al.*, 2014). In this work, we focused on foliated plants that have stem net photosynthesis, that is, plants that have green and photosynthetic stems year round and have positive net CO₂ assimilation rates (A_{stem}). There is no doubt that stem photosynthesis contributes to the carbon economy of plants, but little is known about the water use by these organs, and how hydraulic traits scale with stem photosynthesis.

The main questions that we address in this paper are as follows. Are photosynthetic and hydraulic traits coordinated in photosynthetic stems? Are relationships between stem photosynthetic and hydraulic traits mediated by seasonality? How do stem trait relationships compare with analogous relationships in the leaf economics spectrum? We hypothesized that there is a positive relationship between stem hydraulic capacity and stem photosynthesis mediated by g_s and seasonality. In the dry season, when plants are leafless, we expect a tighter relationship between stem hydraulics and photosynthesis. We also expect that photosynthetic stems are similar to leaves in their relationships between carbon acquisition and functional traits.

Materials and Methods

Study sites

This study was conducted in three southern California locations: a Sonoran Desert scrub in Boyd Deep Canyon Desert Research Center (DC), a Mojave Desert–chaparral transitional ecosystem in Morongo Valley (MV), and the University of California, Riverside (UCR) Botanic Gardens Desert Collection (BG), both in wet (winter) and dry (summer) seasons during 2014–2016. Boyd Deep Canyon is located at 299 m above sea level (asl)

(33°41'5"N, 116°22'8"W) and has an annual average temperature of 23.7°C (average minimum of 17.8°C and average maximum of 29.5°C) and an annual precipitation of 135.1 mm for the 1961–2015 period (<http://www.wrcc.dri.edu/weather/ucde.html>). Morongo Valley is located at 1000 m asl (34°2'12"N, 116°37'24"W) and has an annual average temperature of 17.6°C (average minimum of 9.3°C and average maximum of 25.1°C) and an annual precipitation of 184 mm for 1991–2016 (information for Yucca Valley; <http://www.raws.dri.edu/wraws/scaF.html>). The UCR Botanic Gardens is located at 440 m asl (33°58'14"N, 117°19'20"W) and has an annual average temperature of 18.1°C (average minimum of 10.2°C, and average maximum of 26.1°C) and annual precipitation of 257 mm for the 1948–2005 period (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?carvrc>). Wet season measurements were taken between December and February, whereas dry season measurements were taken between May and July in DC, and between July and September for the other two sites. Soils are classified as an eutric fluvisol with loam texture at DC, a luvisol yermosol with sandy loam texture at MV, and a chromic luvisol with sandy clay loam texture at BG based on Batjes (2012).

Plant species

The 11 plant species selected are known to have green photosynthetic stems year round and are frequent in the warm deserts of North America (Table 1). All species are drought-deciduous shrubs or small trees, except for the three species of *Ephedra*, which have scales instead of leaves. The shrubby species are usually rounded bushes of < 3 m height with many thin green twigs (Supporting Information Fig. S1). The thin twigs (0.2–0.5 cm thickness) are the ones used for all the measurements. All species are native to California except *Euphorbia xanti* Engelm. ex Boiss., which is native to central and southern Baja California, Mexico (Table 1).

Stem hydraulic conductance using the evaporative flux method

Stem hydraulic conductance (K_{stem}) was measured in wet and dry seasons on twigs of four to six individuals of each species, using the evaporative flux method, which is commonly used to estimate leaf hydraulic conductance (Sack *et al.*, 2002; Sack & Scoffoni, 2012). Terminal sections of current-year photosynthetic twigs were collected from adult plants, the cut end was wrapped in parafilm, and they were sealed in dark plastic bags inside an ice chest to be transported to the laboratory. In the laboratory, the twigs were cut under 20 mM KCl partially degassed solution. The cut end was submerged in this solution and allowed to fully rehydrate overnight for *c.* 12 h. For wet season measurements, leaves were removed from the twig and the cuts covered with melted wax in order to avoid water loss through the wounds. During the dry season, twigs had no leaves.

Once rehydrated, the twigs were recut under solution to a length of 10–12 cm, and connected to tubing filled with partially degassed 20 mM KCl solution. One end of the tubing was

Table 1 List of species studied per location, family, symbol used in graphs, origin/growth form, and average height from The Jepson Desert Manual (Wetherwax, 2002), except for *Euphorbia xanti*, which was taken from the Baja California Plant Field Guide (Rebman & Roberts, 2012)

Species	Family	Symbol	Origin/growth form	Average height (m)
Boyd Deep Canyon				
<i>Ambrosia salsola</i>	Asteraceae	◆	Native shrub	<2
<i>Bebbia juncea</i>	Asteraceae	●	Native shrub	≤3
<i>Ephedra aspera</i>	Ephedraceae	♂	Native shrub	<1.5
<i>Hoffmannseggia microphylla</i>	Fabaceae	✕	Native shrub	0.5–2
<i>Justicia californica</i>	Acanthaceae	▲	Native shrub	<2
<i>Parkinsonia florida</i>	Fabaceae	▼	Native tree	<8
Morongo Valley				
<i>Ambrosia salsola</i>	Asteraceae	◆	Native shrub	<2
<i>Ephedra californica</i>	Ephedraceae	★	Native shrub	<1.5
<i>Scutellaria mexicana</i>	Lamiaceae	⊕	Native shrub	0.5–1
<i>Thamnosma montana</i>	Rutaceae	♀	Native shrub	0.3–0.6
UCR Botanic Gardens				
<i>Ephedra nevadensis</i>	Ephedraceae	●	Native shrub	<1.3
<i>Euphorbia xanti</i>	Euphorbiaceae	■	Mexican shrub	3
<i>Justicia californica</i>	Acanthaceae	▲	Native shrub	<2
<i>Parkinsonia florida</i>	Fabaceae	▼	Native tree	<8

connected to the base of the twig section, and the other was placed in a reservoir containing the solution on a balance (± 0.1 mg; Denver Instrument P-214; Bohemia, NY, USA). It is important to note that these were terminal twigs with only one cut end, the end connected to the tubing. The twig was positioned on top of a fan and under a light source ($> 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD)), which stimulated stomatal opening. The amount of water evaporated from the surface of the twig was recorded every 60 s on a computer synchronized with the balance. After reaching a maximum steady-state transpiration rate (E_{max}), usually after 30 min in the system, the twig continued transpiring for 10 min before the last E_{max} measurements were recorded. The twig was then removed from the system and sealed in a hermetic plastic bag and placed in the dark for at least 20 min, to allow any Ψ gradients within the twig to equilibrate. After reaching equilibration, Ψ was rapidly measured using a pressure chamber (Model 1000; PMS Instrument Co., Albany, OR, USA). Finally, stem projected area was measured with an area meter (Li-3100; Li-Cor Biosciences, Lincoln, NE, USA). The twig hydraulic conductance on a projected area basis ($K_{\text{stem-area}}$; $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) was calculated as:

$$K_{\text{stem}} = \frac{E_{\text{max}}}{-\Delta\Psi_{\text{stem}}} \quad \text{Eqn 1}$$

(E_{max} , the steady-state transpiration rate per unit of stem projected area ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$); $-\Delta\Psi_{\text{stem}}$ (MPa), the water potential driving flow (where $\Delta\Psi_{\text{stem}} = \Psi_{\text{final}} - 0$ MPa according to Sack & Scoffoni, 2012).) The dry mass of the sample was also measured, so that K_{stem} could be expressed on a mass basis ($K_{\text{stem-mass}}$; $\text{mmol H}_2\text{O g}^{-1} \text{s}^{-1} \text{MPa}^{-1}$).

These measures of hydraulic conductance differ from hydraulic conductivity (K_{H}) measurements, in which only axial flow through a stem segment is measured (Sperry *et al.*, 1988; Kolb *et al.*, 1996), but is more appropriate for evaluating water supply capacity to support stem photosynthesis. As K_{stem} was estimated

through the determination of E_{max} , K_{stem} refers to a total stem hydraulic conductance, which includes xylem conductance (in the axial direction) which moves water vertically, and extra-xylem conductance (in the radial direction) which moves water horizontally from the xylem to the sites of evaporation. This is important for interpreting results for K_{stem} .

From these measurements, it is also possible to estimate maximum g_s ($g_{s-\text{max}}$), g_s associated with maximum K_{stem} , by determining the mole fraction stem-to-air vapor pressure difference (VPD_{stem}). We measured air temperature and air relative humidity near the sample using a traceable digital hygrometer/thermometer (11-661-9; Fisher Scientific, Waltham, MA, USA), and the stem temperature using a laser infrared temperature gun (Minitemp MT6; Raytek, Santa Cruz, CA, USA). With these parameters, VPD_{stem} was determined using the equation in Pearcy *et al.* (2000), and this value was used in the calculation of $g_{s-\text{max}}$ ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) as follows:

$$g_{s-\text{max}} = \frac{E_{\text{max}}}{\text{VPD}_{\text{stem}}} \quad \text{Eqn 2}$$

Stem cuticular conductance

Cuticular conductance, also known as minimum epidermal conductance (g_{min} , *sensu* Kerstiens, 1996), was determined on twigs of six individuals per species during the late wet season and late dry season following the methods of Sack & Scoffoni (2011) on *PrometheusWiki*. One 20-cm-long twig section was chosen from each individual sampled and taken to the lab. Twig samples were cut to a length of 10 cm with a fresh razor blade, and cut ends were sealed with melted candlewax. The samples were taped to a shelf above a bench and placed near a fan, such that they swayed in the breeze for at least 1 h at PPFD of $< 10 \mu\text{mol m}^{-2} \text{s}^{-1}$ to induce stomatal closure. A traceable digital hygrometer/thermometer (11-661-9; Fisher Scientific, Waltham, MA, USA) was

placed next to the samples within the breeze, and air temperature and relative humidity were recorded at the beginning of each weighing cycle to determine the mole fraction air vapor pressure deficit (VPD_{mf}). Samples were weighed for at least eight intervals of 20 min. A graph of sample mass versus time was obtained for each sample. These curves were linear most of the time. When they were not linear, they were concave down and the water lost per unit of time during the late linear portion, when all stomata have closed, was used to calculate g_{min} and taken to represent water loss after full stomatal closure. Values of g_{min} were calculated as transpiration rate ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) divided by VPD_{mf} using the spreadsheet provided with the *PrometheusWiki* protocol, which was modified to estimate the total surface area of stems (Sack & Scoffoni, 2011).

Stem photosynthetic rate

Stem photosynthetic CO_2 assimilation rate (A_{stem}) was measured in the field in wet and dry seasons on intact twigs of six individuals per species using an open system infrared gas analyzer (Li-6400; Li-Cor Biosciences) between 09:00 and 12:00 h. For each individual, A_{stem} was measured in one intact twig of <0.5 cm of diameter using the 2×3 cm leaf chamber and clay-modeled gaskets that allowed a hermetic seal. No leaks were found in the system using this protocol and the measurements were taken to be accurate. Measurements were performed at ambient temperature, which varied from 16.28 to 35.65°C in the wet season and from 22.86 to 44.09°C in the dry season, $400 \mu\text{mol mol}^{-1}$ of CO_2 and $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ of PPFD provided by a red blue light source (6400-02B #SI-710; Li-Cor Biosciences) (Evans & Santiago, 2014). After gas exchange measurements had been taken, the stems were sectioned and transported to the lab, where projected area was measured using an area meter (Li-3100; Li-Cor Biosciences). Total stem surface area was determined by multiplying the projected area by π (3.14). Samples were then dried in an oven at 65°C for at least 48 h to obtain dry mass. Photosynthetic rate was expressed on a total surface area basis (A_{area}) as well as a dry mass basis (A_{mass}).

Stem Chl *a* fluorescence

Fluorescence of Chl *a* in stems was measured in wet and dry seasons on twigs of six individuals per species using a portable chlorophyll fluorometer (mini-PAM; Watz, Effeltrich, Germany) between 09:00 and 12:00 h. Minimum (F_0'), stable (F) and maximum (F_m') fluorescences of light-adapted twigs were measured at the PPFD that induced the maximum electron transport rate ($PPFD_{max}$), which varied between 600 and $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$, depending on the species. Relative quantum yield of photosystem II (Φ_{PSII}) and ETR were calculated using fluorescence data as follows:

$$\Phi_{PSII} = \frac{(F_m' - F)}{F_m'} \quad \text{Eqn 3}$$

$$\text{ETR} = \Phi_{PSII} \times \text{PPFD} \times a \times 0.5 \quad \text{Eqn 4}$$

where a is the fraction of light absorbed by the stem, which we consider to be 0.8, a value typically found in many non-succulent leaves (Demmig & Björkman, 1987; Krall & Edwards, 1992).

Functional traits: specific stem area, specific bark area, wood density, and stem surface area to xylem area ratio

We define specific stem area (SSA) as a new term to represent the ratio between stem photosynthetic surface area and whole-stem dry mass. SSA was measured for each sample stem after each gas exchange measurement. Stems were sectioned and projected area was measured using an area meter (Li-3100). Stem surface area was determined by multiplying the projected area by π (3.14). Samples were then dried in an oven at 65°C for at least 48 h to obtain whole-stem dry mass. SSA ($\text{cm}^2 \text{g}^{-1}$) was calculated as:

$$\text{SSA} = \frac{\text{Stem surface area}}{\text{Whole - stem dry mass}} \quad \text{Eqn 5}$$

We define specific bark area (SBA) as a new term to represent the ratio between stem photosynthetic surface area and bark dry mass. One 4-cm-long twig was selected from six individuals from each species and transported to the lab. Stem surface area was estimated as in SSA. The photosynthetic bark was removed from the twig and dried separately from the wood and pith tissue in an oven at 65°C for at least 48 h to obtain dry mass. Specific bark area ($\text{cm}^2 \text{g}^{-1}$; SBA) was calculated as:

$$\text{SBA} = \frac{\text{Stem surface area}}{\text{Bark dry mass}} \quad \text{Eqn 6}$$

Samples of branches longer than 25 cm were collected at the end of the dry season to estimate wood density (WD) and stem surface area to xylem area ratio, and to establish functional relationships with hydraulic and photosynthetic traits. For WD, a 1-cm-long stem segment was sectioned 25 cm from the tip of the branch, and the bark and pith (if present) were removed. As the wood segments had a regular cylinder shape, the fresh volume was determined by measuring the diameter of the wood segments using a vernier caliper. The fresh volume was calculated as the volume of a cylinder ($\pi r^2 L$, where r is diameter/2, and L is 1 cm) and subtracting the volume of the pith if present. Dry mass was obtained after drying the wood segments in an oven at 100°C for at least 48 h. Wood density was calculated as dry mass divided by fresh volume.

For stem surface area to xylem area ratio measurements, the same 25-cm-long branches were used. Xylem area was estimated by measuring the diameter of the xylem at 25 cm from the tip, and calculating the area of a circle (πr^2 , where r is diameter/2). If pith was present, its area was subtracted from the total xylem area.

Statistical analyses

Cross-species bivariate relationships among the photosynthetic, hydraulic and functional traits were assessed using Pearson's correlation coefficients and a significance level of $P < 0.05$. These analyses were performed using the 'HMISC' library and the 'RCORR' function in R v.3.2.3. The correlation analyses were performed to assess the correlated structure of the data and to choose correlated traits for further analyses. As our data have errors in both the predictor and response variables, we used standard major axis (SMA) regressions in significant bivariate relationships to test whether wet and dry season slopes were significantly different, and, in the case of statistically indistinguishable wet and dry season slopes, to test for shifts in elevation (changes in y -intercept) or shifts along the common slope (changes in x -range and y -range) using SMATR software (Warton *et al.*, 2006). To evaluate the stem A_{mass} -SSA relationship against the analogous relationship in the leaf economic spectrum, the SMA slope and intercept of the leaf A_{mass} -SLA relationship were determined using the leaf 'globamax' data set (Maire *et al.*, 2015), and compared for homogeneity against the SMA regression of stem A_{mass} -SSA. STATISTICA 10 (StatSoft Inc., Tulsa, OK, USA) was used to perform ANOVAs to test the effects of season, species and season \times species interactions within sites for chlorophyll fluorescence traits. All plots were made using SIGMAPLOT 11 (Systat Software, San Jose, CA, USA).

Results

We found substantial evidence for coordination between stem photosynthesis and stem hydraulic conductance. There was a positive relationship between K_{stem} and A_{stem} when the traits were expressed on a dry mass basis ($K_{\text{stem-mass}}$ and A_{mass} ; Fig. 1a). This relationship was found in both wet ($r^2 = 0.420$; $P = 0.017$) and dry seasons ($r^2 = 0.542$; $P = 0.006$), with no difference between slopes but with a significant shift in the y -intercept (Table 2). Values of Φ_{PSII} were also positively related to $K_{\text{stem-mass}}$, but only during the wet season ($r^2 = 0.439$; $P = 0.010$). In contrast, ETR was positively related to K_{stem} , but only when this

was expressed on an area basis and again only during the wet season ($r^2 = 0.339$; $P = 0.029$). Also, there was a positive relationship between $K_{\text{stem-area}}$ and $g_{\text{s-max}}$ in wet ($r^2 = 0.581$; $P = 0.002$) and dry seasons ($r^2 = 0.763$; $P < 0.0001$) (Fig. 1b; Table 2), and between A_{mass} and $g_{\text{s-max}}$ in both wet ($r^2 = 0.296$; $P = 0.055$) and dry seasons ($r^2 = 0.438$; $P = 0.019$) (Fig. 2; Table 2). The coordination between $K_{\text{stem-area}}$ and $g_{\text{s-max}}$ is expected and supports the idea that stomatal opening, and therefore photosynthesis, are constrained by hydraulic conductance in these photosynthetic stems.

Values of $K_{\text{stem-mass}}$ and A_{mass} were positively related to both SSA (Fig. 3a,b) and SBA, with plant species with long and thin twigs (high SSA) having higher values of $K_{\text{stem-mass}}$ (Fig. 3a) and A_{mass} (Fig. 3b). Responses of $K_{\text{stem-mass}}$ and A_{mass} to SBA were similar in their significance, slopes and intercepts to responses of $K_{\text{stem-mass}}$ and A_{mass} to SSA (Table 2). These relationships were found in both wet and dry seasons, with significantly steeper slopes in both cases during the dry season (Table 2).

Maximum stomatal conductance, measured with the evaporative flux method, and A_{area} were positively correlated with the PPF_D inducing maximum ETR (Fig. 4a,b). The relationship between $g_{\text{s-max}}$ and PPF_{Dmax} was found in both wet ($r^2 = 0.557$; $P = 0.002$) and dry seasons ($r^2 = 0.389$; $P = 0.017$) (Fig. 4a), with the slope of the relationship being significantly greater during the wet season (Table 2). The relationship between A_{area} and PPF_{Dmax} was significant only during the dry season ($r^2 = 0.333$; $P = 0.049$) (Fig. 3b).

Traits of chlorophyll fluorescence were not compared across sites because of differences in climate and soil characteristics but also because of different species composition. Within sites, there was no effect of season, species or season \times species interaction in Φ_{PSII} or ETR in DC and MV, while there was a significant effect of season on both traits in BG (for Φ_{PSII} : $F_{1,39} = 45.04$; $P < 0.0001$; for ETR: $F_{1,39} = 47.96$; $P < 0.0001$), with higher values in the dry season than in the wet season (Table 3).

Values of g_{min} ranged from 1.11 $\text{mmol m}^{-2} \text{s}^{-1}$ in *Ephedra nevadensis* in BG in the wet season to 20.49 $\text{mmol m}^{-2} \text{s}^{-1}$ in

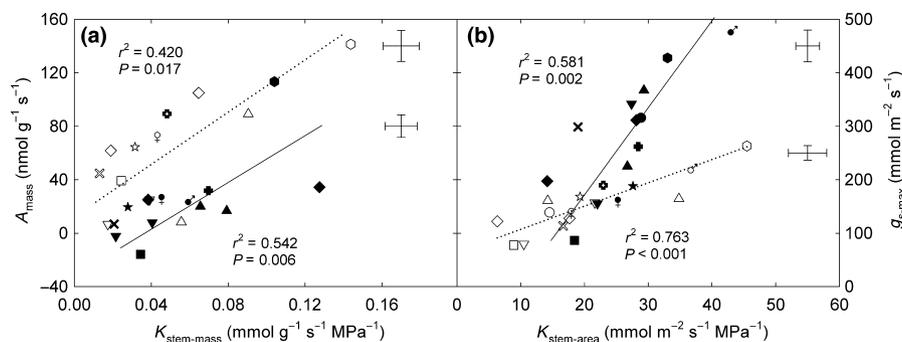


Fig. 1 Relationship between (a) mass-based stem hydraulic conductance ($K_{\text{stem-mass}}$) and mass-based photosynthetic rate (A_{mass}), and between (b) area-based stem hydraulic conductance ($K_{\text{stem-area}}$) and maximum stomatal conductance ($g_{\text{s-max}}$) of green stemmed species from Boyd Deep Canyon, Morongo Valley and the UCR Botanic Gardens during wet (closed symbols) and dry (open symbols) seasons. Species symbols are *Ambrosia salsola* (◆), *Bebbia juncea* (●), *Ephedra aspera* (♂), *Ephedra californica* (★), *Ephedra nevadensis* (●), *Euphorbia xanti* (■), *Hoffmannseggia microphylla* (✱), *Justicia californica* (▲), *Parkinsonia florida* (▼), *Scutellaria mexicana* (⊕), and *Thamnosma montana* (♀). Symbols represent species means, and error bars represent \pm SE in both x and y variables for each season. The standard major axis (SMA) regression lines are also shown: solid for wet season, and dotted for dry season. Results of SMA regression analyses are presented in Table 2.

Table 2 Tests for common slope, shifts in intercept, and shifts along a standardized major axis with a common slope for main relationships among stem traits in wet and dry seasons

y	x	Slope		Heterogeneity of slope	Intercept		Shift in intercept	Shift along common slope
		Wet	Dry		Wet	Dry		
A_{mass}	$K_{\text{stem-mass}}$	936.2	1082.6	$P = 0.654$	-29.26	8.97	$P = 0.0001$	$P = 0.259$
$g_{\text{s-max}}$	$K_{\text{stem-area}}$	15.845	4.472	$P = 0.001$	-148.30	59.56		
A_{mass}	$g_{\text{s-max}}$	0.264	0.802	$P = 0.005$	-47.36	-55.46		
$K_{\text{stem-mass}}$	SSA	9.59×10^{-4}	2.50×10^{-3}	$P = 0.011$	9.50×10^{-5}		-0.07	
A_{mass}	SSA	0.898	2.702	$P = 0.003$	-29.17	-61.95		
$K_{\text{stem-mass}}$	BSA	8.48×10^{-4}	9.54×10^{-4}	$P < 0.001$	-0.02	-0.03		
A_{mass}	BSA	0.794	1.029	$P < 0.001$	-49.54	-12.78		
$g_{\text{s-max}}$	PPFD _{max}	0.579	0.302	$P = 0.034$	-108.93	-50.82		
A_{area}	PPFD _{max}	0.015	0.063	$P = 0.003$	-6.01	-26.75		
A_{area}	Dry season g_{min}	0.488	1.216	$P = 0.006$	-0.65	1.24		
A_{mass}	Dry season g_{min}	4.914	6.659	$P < 0.001$	-23.10	-5.10		

Traits are: maximum stomatal conductance ($g_{\text{s-max}}$; $\text{mmol m}^{-2} \text{s}^{-1}$), photosynthetic photon flux density inducing maximum electron transport rate (PPFD_{max}; $\mu\text{mol m}^{-2} \text{s}^{-1}$), stem photosynthetic rate on an area basis (A_{area} ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), stem photosynthetic rate on a mass basis (A_{mass} ; $\text{nmol g}^{-1} \text{s}^{-1}$), stem hydraulic conductance on a mass basis ($K_{\text{stem-mass}}$; $\text{mmol g}^{-1} \text{s}^{-1} \text{MPa}^{-1}$), stem hydraulic conductance on an area basis ($K_{\text{stem-area}}$; $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$), specific stem area (SSA; $\text{cm}^2 \text{g}^{-1}$), specific bark area (BSA; $\text{cm}^2 \text{g}^{-1}$), and dry-season cuticular conductance on an area basis (g_{min} ; $\text{mmol m}^{-2} \text{s}^{-1}$). Values in bold indicate a statistically significant test.

Ambrosia salsola in MV in the dry season. Mean wet season g_{min} was significantly lower than mean dry season g_{min} for all species (4.37 versus 9.02 $\text{mmol m}^{-2} \text{s}^{-1}$; $t_{13} = -4.33$; $P = 0.0008$). Wet season g_{min} was found to be correlated to dry season g_{min} ($r = 0.84$; $P < 0.001$), so only dry season g_{min} data are shown. Dry season g_{min} was found to be related to stem A_{area} in both wet ($r^2 = 0.566$; $P = 0.003$) and dry ($r^2 = 0.339$; $P = 0.047$) seasons (Fig. 5a). Dry season g_{min} was also related to A_{mass} in both wet ($r^2 = 0.373$; $P = 0.027$) and dry ($r^2 = 0.409$; $P = 0.025$) seasons (Fig. 5b), indicating that the cost of water loss through the permeable cuticle increases with the benefit of high rates of stem photosynthetic CO_2 assimilation.

The SMA slope of the dry season relationship between stem A_{mass} and SSA (2.102) was significantly greater than the SMA slope of the relationship between leaf A_{mass} and SLA of 1.299 derived from the 'globamax' data set ($F = 7.786$; $P = 0.019$). However, the SMA slope of the wet season A_{mass} -SSA relationship (0.898) was not significantly different from the A_{mass} -SLA SMA 'globamax' slope of 1.299 ($F = 4.294$; $P = 0.063$), indicating that, during the wet season, an increase in $1 \text{ cm}^2 \text{g}^{-1}$ of stem dry mass increases photosynthetic rate to a similar degree as $1 \text{ cm}^2 \text{g}^{-1}$ of dry leaf mass.

Wood density was only correlated with stem cross-sectional area ($r = -0.60$; $P = 0.023$) and stem diameter in the dry season ($r = -0.72$; $P = 0.009$), with plants having thick stems also having low-density wood.

Discussion

Our results indicate substantial coordination between photosynthetic capacity and hydraulic efficiency. We found positive relationships between A_{mass} and $K_{\text{stem-mass}}$ and between $g_{\text{s-max}}$ and PPFD_{max}, demonstrating how photosynthetic and hydraulic traits are coordinated in the photosynthetic stems of desert plant species from southern California. We also found that the

relationship between A_{mass} and SSA is similar to the leaf economic spectrum (Wright *et al.*, 2004). The photosynthetic-hydraulic coordination in stems is as important as in leaves because most of these plants rely on their stems for assimilating carbon year round, probably affecting whole-plant carbon balance and performance. When leaves were absent during the dry season, stems continued to assimilate CO_2 at even higher rates than during the wet season, probably because of seasonal acclimation to higher light availability and warmer temperatures (Kitajima *et al.*,

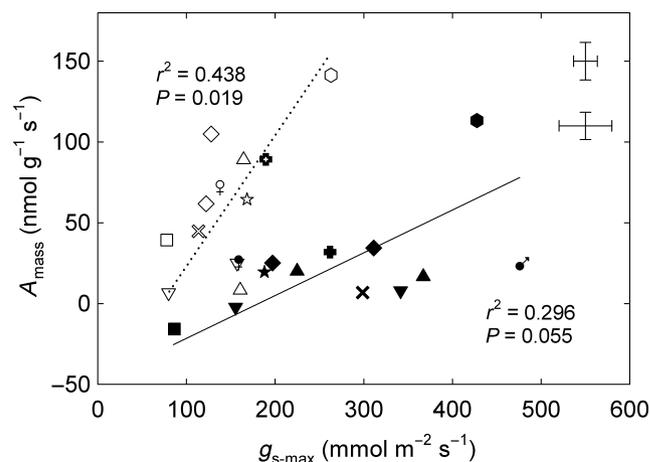


Fig. 2 Relationship between maximum stomatal conductance ($g_{\text{s-max}}$) and mass-based photosynthetic rate (A_{mass}) of green stemmed species from Boyd Deep Canyon, Morongo Valley and the UCR Botanic Gardens during wet (closed symbols) and dry (open symbols) seasons. Species symbols are *Ambrosia salsola* (◆), *Bebbia juncea* (●), *Ephedra aspera* (☆), *Ephedra californica* (★), *Ephedra nevadensis* (■), *Euphorbia xanti* (▲), *Hoffmannseggia microphylla* (✕), *Justicia californica* (▲), *Parkinsonia florida* (▼), *Scutellaria mexicana* (+), and *Thamnosma montana* (⊙). Symbols represent species means, and error bars represent \pm SE in both x and y variables for each season. The standard major axis (SMA) regression lines are also shown: solid for wet season, and dotted for dry season. Results of SMA regression analyses are presented in Table 2.

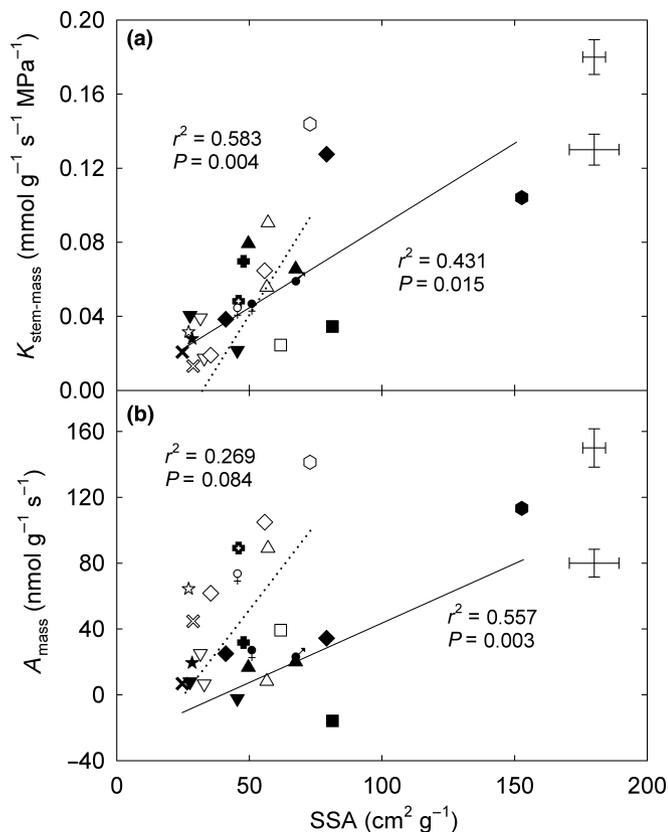


Fig. 3 Relationship between (a) stem specific area (SSA) and mass-based stem hydraulic conductance ($K_{\text{stem-mass}}$), and between (b) SSA and mass-based photosynthetic rate (A_{mass}) of green stemmed species from Boyd Deep Canyon, Morongo Valley and the UCR Botanic Gardens during wet (closed symbols) and dry (open symbols) seasons. Species symbols are *Ambrosia salsola* (◆), *Bebbia juncea* (●), *Ephedra aspera* (σ) *Ephedra californica* (★), *Ephedra nevadensis* (●), *Euphorbia xanti* (■), *Hoffmannseggia microphylla* (✕), *Justicia californica* (▲), *Parkinsonia florida* (▼), *Scutellaria mexicana* (⊕), and *Thamnosma montana* (♀). Symbols represent species means, and error bars represent ± SE in both x and y variables for each season. The standard major axis (SMA) regression lines are also shown: solid for wet season, and dotted for dry season. Results of SMA regression analyses are presented in Table 2.

1997). One of the first works on stem photosynthetic responses to temperature on *Parkinsonia florida* showed that stems maintained their A_{area} near its maximum value over a broad range of temperatures (20–40°C) (Adams & Strain, 1968). This characteristic is significant in the maintenance of metabolism during the leafless period, which is also the period of high temperature, and the decrease in shading after leaf loss increased light interception by the stems, promoting continued CO₂ assimilation. Therefore, our results offer strong support for the conclusion that the principles of investment in photosynthetic capacity and structure in leaves apply to photosynthetic stems as well.

The coordination found between A_{mass} and $K_{\text{stem-mass}}$ and between g_s and $K_{\text{stem-area}}$ is in agreement with previous findings relating stem or whole-plant hydraulic conductance to leaf photosynthesis and g_s in plants from different ecosystems (Meinzer *et al.*, 1995; Brodribb & Feild, 2000; Sperry, 2000; Hubbard *et al.*, 2001; Brodribb *et al.*, 2002; Santiago *et al.*, 2004), suggesting that stem photosynthesis is also constrained by stem water

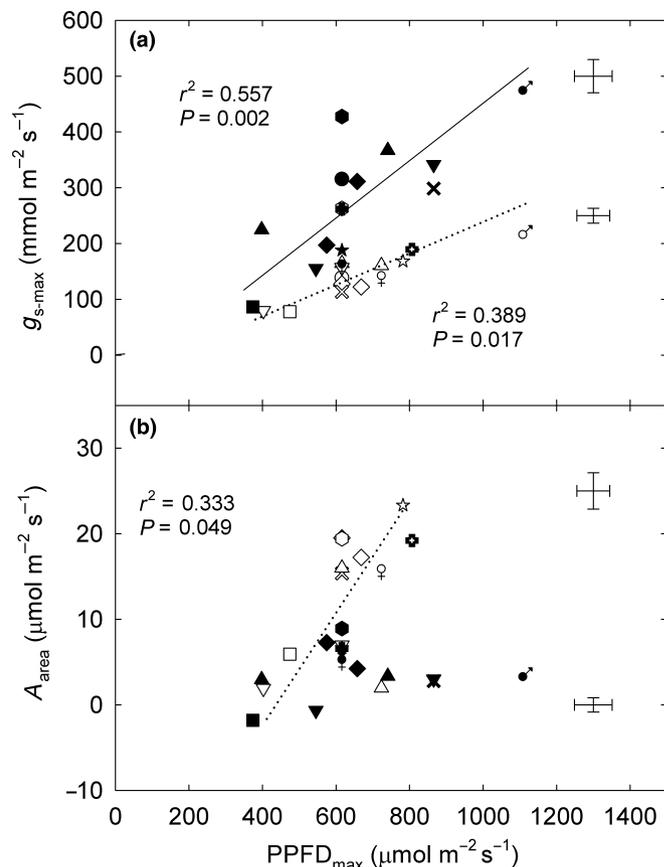


Fig. 4 Relationship between (a) photosynthetic photon flux density inducing maximum electron transport rate (PPFD_{max}) and maximum stomatal conductance ($g_{s\text{-max}}$), and between (b) PPFD_{max} and area-based photosynthetic rate (A_{area}) of green-stemmed species from Boyd Deep Canyon, Morongo Valley and the UCR Botanic Gardens during wet (closed symbols) and dry (open symbols) seasons. Species symbols are *Ambrosia salsola* (◆), *Bebbia juncea* (●), *Ephedra aspera* (σ) *Ephedra californica* (★), *Ephedra nevadensis* (●), *Euphorbia xanti* (■), *Hoffmannseggia microphylla* (✕), *Justicia californica* (▲), *Parkinsonia florida* (▼), *Scutellaria mexicana* (⊕), and *Thamnosma montana* (♀). Symbols represent species means, and error bars represent ± SE in both x and y variables for each season. The standard major axis (SMA) regression lines are also shown: solid for wet season, and dotted for dry season. Results of SMA regression analyses are presented in Table 2.

transport capacity. The coupling between stem A_{mass} and $K_{\text{stem-mass}}$ is expected to be stronger, with different slopes and intercepts during the dry season compared with the wet season, because when leaves are present stems are transporting water both for downstream leaf processes and for local stem photosynthesis. We found that the coefficient of determination (r^2) and the y-intercept of the $A_{\text{mass}}-K_{\text{stem-mass}}$ relationship were higher during the dry season, supporting the idea that relationships among stem photosynthesis and hydraulic function are mediated by seasonality and that stronger coordination exists between stem photosynthetic and hydraulic traits in the dry season than during the wet season, consistent with the need to transport water for both leaf and stem photosynthesis during the wet season, while during the dry season the water moved by the stem is only used in stem photosynthesis. This has implications for plants facing future climate change, because losses of hydraulic conductivity could limit

Table 3 Relative quantum yield of photosystem II (Φ_{PSII}), electron transport rate (ETR), and photosynthetic photon flux density inducing maximum ETR (PPFD_{max}) for the species studied in both wet and dry seasons

Species	Φ_{PSII}		ETR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		PPFD _{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	
	Wet	Dry	Wet	Dry	Wet	Dry
Boyd Deep Canyon						
<i>Ambrosia salsola</i>	0.180 ± 0.026 ^a	0.181 ± 0.020 ^a	45.38 ± 4.25 ^a	46.62 ± 5.05 ^a	657.7 ± 100.1 ^a	616.0 ± 0 ^a
<i>Bebbia juncea</i>	0.176 ± 0.015 ^a	0.150 ± 0.013 ^a	43.25 ± 0 ^a	38.62 ± 3.43 ^a	616.2 ± 111.5 ^a	616.0 ± 0 ^a
<i>Ephedra aspera</i>	0.125	0.187	58.40	87.50	1115.0	1115.0
<i>Hoffmannseggia microphylla</i>	0.115 ± 0.008 ^a	0.131 ± 0.014 ^a	40.43 ± 4.42 ^a	33.77 ± 3.59 ^a	865.5 ± 111.6 ^a	616.0 ± 0 ^a
<i>Justicia californica</i>	0.117 ± 0.015 ^a	0.159 ± 0.039 ^a	33.35 ± 4.33 ^a	35.10 ± 4.30 ^a	740.8 ± 124.7 ^a	616.2 ± 111.5 ^a
<i>Parkinsonia florida</i>	0.142 ± 0.011 ^a	0.142 ± 0.020 ^a	49.12 ± 3.71 ^a	32.80 ± 3.17 ^a	865.5 ± 111.6 ^a	616.2 ± 111.5 ^a
Mean ± SE	0.145 ± 0.008 ^a	0.152 ± 0.010 ^a	48.83 ± 2.15 ^a	38.66 ± 2.44 ^a	760.9 ± 50.1 ^a	632.2 ± 32.6 ^a
Morongo Valley						
<i>Ambrosia salsola</i>	0.106 ± 0.013 ^a	0.114 ± 0.017 ^a	25.15 ± 3.51 ^a	32.90 ± 5.98 ^a	574.5 ± 41.5 ^a	668.7 ± 156.1 ^a
<i>Ephedra californica</i>	0.102 ± 0.015 ^a	0.141 ± 0.020 ^a	26.40 ± 3.86 ^a	34.13 ± 5.91 ^a	616.0 ± 0 ^a	782.3 ± 105.2 ^a
<i>Scutellaria mexicana</i>	0.121 ± 0.028 ^a	0.107 ± 0.028 ^a	31.27 ± 7.17 ^a	31.27 ± 6.88 ^a	616.0 ± 0 ^a	806.5 ± 147.7 ^a
<i>Thamnosma montana</i>	0.125 ± 0.016 ^a	0.115 ± 0.020 ^a	32.23 ± 4.05 ^a	34.20 ± 3.47 ^a	616.0 ± 0 ^a	723.3 ± 135.9 ^a
Mean ± SE	0.114 ± 0.009	0.119 ± 0.010	28.76 ± 2.36	30.94 ± 2.67	605.6 ± 10.4	745.2 ± 65.1
UCR Botanic Gardens						
<i>Ephedra nevadensis</i>	0.097 ± 0.009 ^a	0.248 ± 0.034 ^a	24.92 ± 2.44 ^a	60.37 ± 10.44 ^a	616.0 ± 0 ^a	616.2 ± 111.5 ^a
<i>Euphorbia xanti</i>	0.088 ± 0.011 ^a	0.261 ± 0.065 ^a	13.27 ± 1.81 ^a	45.28 ± 7.95 ^a	373.5 ± 52.9 ^a	474.0 ± 65.4 ^a
<i>Justicia californica</i>	0.051 ± 0.009 ^b	0.262 ± 0.061 ^a	7.62 ± 1.63 ^b	73.23 ± 18.27 ^a	397.5 ± 71.1 ^a	723.3 ± 135.9 ^a
<i>Parkinsonia florida</i>	0.050 ± 0.010 ^b	0.391 ± 0.081 ^a	10.46 ± 1.63 ^b	54.20 ± 10.12 ^a	545.2 ± 70.8 ^a	402.5 ± 97.2 ^a
Mean ± SE	0.072 ± 0.006	0.290 ± 0.032	14.22 ± 1.65	58.27 ± 6.13	480.4 ± 33.8	554.0 ± 55.7

Values are the mean of six replicates ± SE. For *Ephedra aspera*, only one individual was found and it was not included in the one-way ANOVA. Same letters within rows indicate no statistical difference in values between seasons.

carbon gain through the stem and possibly remove the advantage of having this extra photosynthetic organ. In this situation, higher maintenance costs of photosynthetic pigments and enzymes should be expected in plants with photosynthetic stems than in plants without photosynthetic stems. More work on the costs and benefits of having photosynthetic stems in terms of carbon gain and water loss is needed to better understand their physiology and their possible responses to future or present climate change.

A huge body of research suggests that having photosynthetic stems is advantageous for plants living in hot and dry ecosystems (see recent reviews by Ávila *et al.*, 2014; Vandegehuchte *et al.*, 2015; Cernusak & Cheesman, 2015). The stem photosynthetic contribution to whole-plant carbon gain is usually high and this contribution has been measured before in some of the species studied here (Comstock *et al.*, 1988). Two of these species did not rely heavily on stem photosynthesis during most of the year; these were *A. salsola*, in which the contribution of the stem was 0% in late August and reached a maximum of 44% in late May, and *Bebbia juncea*, which had a minimum of 2% during June–October and a maximum of 56% in late March (Comstock *et al.*, 1988). In other species, namely *Scutellaria mexicana* and *Thamnosma montana*, the contribution of the stem was larger and the contribution of leaves was significantly lower than in the other species studied; in *S. mexicana* and *T. montana* the stem contribution ranged from 17% in late August to a maximum of 67% in late May (Comstock *et al.*, 1988). The stem contribution to whole-plant carbon gain in multiple species has been estimated to range from 23 to 100% (Ávila *et al.*, 2014).

In general, stems are thought to have higher WUE than leaves, but this relationship has only been evaluated on a limited amount of available data (Santiago *et al.*, 2016). We did not measure leaves in our study, but an extensive literature review including our stem data suggests that stem intrinsic WUE is higher in stems than in leaves (E. Ávila-Lovera, unpublished data). Also, carbon isotopic composition tends to be higher in stems than in leaves, suggesting that stems may have a higher long-term integrated WUE (Ehleringer *et al.*, 1987; Osmond *et al.*, 1987; Smith & Osmond, 1987; Nilsen & Sharifi, 1997), although some of this effect is probably attributable to within-plant carbon isotopic fractionation (Cernusak *et al.*, 2009). Desert plants with green stems may have access to water year round considering their presence in desert washes (Adams & Strain, 1968; Gibson, 1996). Furthermore, if they access groundwater in spring and fall seasons (M. E. Allen *et al.*, unpublished data), and the stem contribution to whole-plant carbon gain is relatively high, there may be stronger selection on these stems to maximize carbon gain than to minimize water loss (Gibson, 1998). Values of g_s and E are usually lower in stems than in leaves of the same species (Osmond *et al.*, 1987; Smith & Osmond, 1987; Comstock & Ehleringer, 1988; Franco-Vizcaíno *et al.*, 1990; Nilsen & Bao, 1990; Tinoco-Ojanguren, 2008), but the stems may lose more water through the cuticle. In an extensive literature survey (201 species; Kerstiens, 1996), mean leaf g_{min} was estimated to be 5.40 mmol m⁻² s⁻¹, which is lower than the dry season stem g_{min} of 9.02 mmol m⁻² s⁻¹ found in this study, but higher than the wet season stem g_{min} of 4.37 mmol m⁻² s⁻¹. The overall mean stem g_{min} for both seasons of 6.69 mmol m⁻² s⁻¹ in this study was also higher than the periderm permeability found in different

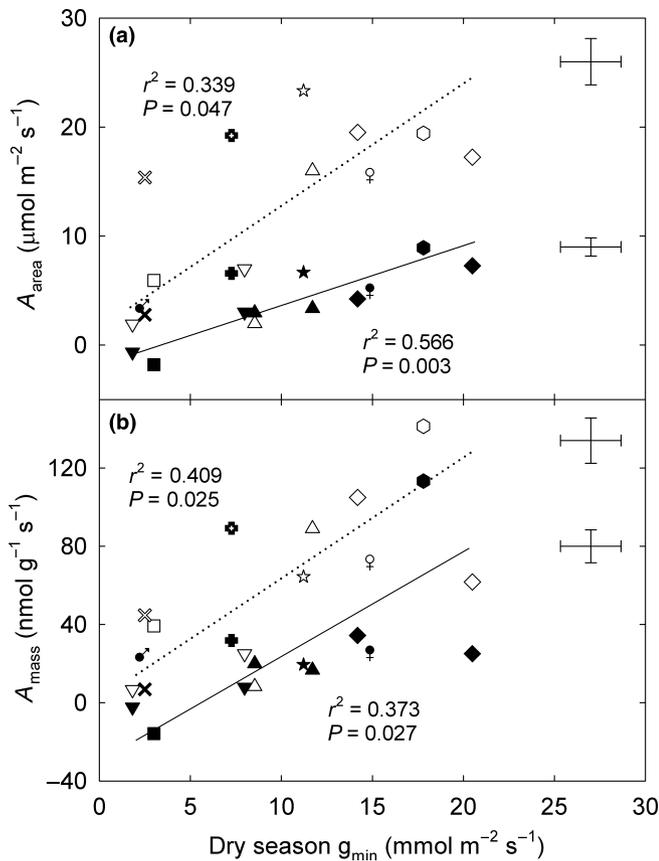


Fig. 5 Relationship between (a) dry-season stem cuticular conductance (g_{\min}) and area-based photosynthetic rate (A_{area}), and between (b) g_{\min} and mass-based photosynthetic rate (A_{mass}) of green-stemmed species from Boyd Deep Canyon, Morongo Valley and the UCR Botanic Gardens during wet (closed symbols) and dry (open symbols) seasons. Species symbols are *Ambrosia salsola* (◆), *Bebbia juncea* (●), *Ephedra aspera* (♂), *Ephedra californica* (★), *Ephedra nevadensis* (●), *Euphorbia xanti* (■), *Hoffmannseggia microphylla* (✕), *Justicia californica* (▲), *Parkinsonia florida* (▼), *Scutellaria mexicana* (⊕), and *Thamnosma montana* (♀). Symbols represent species means, and error bars represent \pm SE in both x and y variables for each season. The standard major axis (SMA) regression lines are also shown: solid for wet season, and dotted for dry season. Results of SMA regression analyses are presented in Table 2.

tree and crop species (mean of $2.42 \text{ mmol m}^{-2} \text{ s}^{-1}$; Schönherr & Ziegler, 1980; Vogt *et al.*, 1983; Garrec & Barrois, 1992; Lulai & Orr, 1994; Lulai *et al.*, 1996; Groh *et al.*, 2002; Schreiber *et al.*, 2005; Kocurek *et al.*, 2015). This suggests that during periods of low water availability where stomata are partially or fully closed, water loss through the stem cuticle can be significant. Although g_{\min} measured here is cuticular conductance to water, CO_2 could possibly move through the cuticle if there is a concentration gradient between the atmosphere and the stem cortex intercellular air spaces. The positive relationships between A_{area} and A_{mass} with dry season g_{\min} partially support this idea (Table 2). Stomatal conductance measured in the field (Table S1) shows small values, usually in the order of magnitude of g_{\min} . With such small values of g_s , g_{\min} might significantly contribute to the movement of CO_2 from the atmosphere to the intercellular air spaces, significantly increasing the rate of photosynthesis.

Most of the relationships between hydraulic and photosynthetic traits with functional traits were significant only when using mass-based values. This has also been found in nine temperate tree species exhibiting stem recycling photosynthesis (Berveiller *et al.*, 2007). Massive and thick stems with low SSA and SBA have a higher proportion of wood and pith tissue than bark, which can explain their lower photosynthetic capacity (Table S2). Thick stems also have relatively low K_{stem} , which may be partly attributable to their higher WD (although the negative relationship between K_{stem} and WD was not statistically significant in this study), and to the low conductance of extra-xylary tissue. The trait K_{stem} as measured here combines conductance of two types of tissue: xylem and cambium/phloem/parenchyma tissues, the latter not being specialized for conducting water. We estimated bark thickness from our measurements of twig and xylem diameter and found that it was negatively related to E_{max} , $g_{s\text{-max}}$ and $K_{\text{stem-area}}$, and recent work has shown the role of other anatomical and functional traits of leaf parenchyma in leaf hydraulic conductance (Aasamaa *et al.*, 2005; Sack *et al.*, 2015).

SSA and SBA are terms that we are introducing in this paper to refer to the ratio of stem photosynthetic surface area to whole-stem dry mass and to bark dry mass, respectively. As with SLA, SSA and SBA reflect investment of mass in capturing light and are expected to be associated with photosynthetic capacity and life span (Reich *et al.*, 1997; Wright *et al.*, 2004). We found a positive relationship between A_{mass} and SSA and SBA, similar to the world-wide leaf economic spectrum, which runs from a fast (high SSA and SBA) to a slow (low SSA and SBA) return on investment of dry mass, and directly influences photosynthetic capacity. Furthermore, the slope of the A_{mass} –SSA relationship during the wet season was similar to the global leaf A_{mass} –SLA relationship, indicating that stems are similar to leaves in terms of investment in structure and function. This is true not only for species with stem net photosynthesis (this work), but also for species with stem recycling photosynthesis (Berveiller *et al.*, 2007). Assuming that life span depends on how the organs are built, we expect that SSA and SBA could be related to stem life span, nitrogen and phosphorus concentrations, and dark respiration (Berveiller *et al.*, 2007).

WD has been found to be negatively correlated with K_L and K_{plant} in some plants (Santiago *et al.*, 2004; Anderegg & Meinzer, 2015) but not in others (Mitchell *et al.*, 2008; Pivovarov *et al.*, 2014; De Guzman *et al.*, 2016). In our study, WD was not correlated with either $K_{\text{stem-area}}$ or $K_{\text{stem-mass}}$. WD determines stem mechanical strength (Zanne *et al.*, 2010), and has been found to be negatively related to the Ψ at which 50% of sapwood-specific hydraulic conductivity (K_S) is lost (P50) (Jacobsen *et al.*, 2007), with species having high WD also having low P50. We did not measure P50 but, based on the global relationship between WD and P50 (Gleason *et al.*, 2016), it is possible that stems with high WD, those with small stem diameters, are also more resistant to xylem cavitation and are able to continue transporting water at low Ψ .

Our results indicate that photosynthetic stems behave like leaves in the coordination of multiple traits related to carbon gain and water movement and loss. Such similarity is potentially advantageous because we may be able to extend our knowledge of

leaf physiology and the leaf economic spectrum to better understand photosynthetic stem physiology. Furthermore, understanding seasonal changes in photosynthetic capacity and hydraulics can help in predicting green-stemmed plant responses to global-change-type droughts. Whereas numerous models are now being parameterized for predicting drought-induced mortality of woody plants (Joetzjer *et al.*, 2014; Christoffersen *et al.*, 2016), most of these do not incorporate the contribution of stems and may benefit from including stem-derived carbon balances for plants during drought.

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Author contributions

E.A.-L. and L.S.S. planned and designed research. E.A.-L. and A.J.Z. conducted field and lab work. E.A.-L. wrote the manuscript with significant input from A.J.Z. and L.S.S.

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Supporting Information

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

Fig. S1 Pictures of the four species with photosynthetic stems studied in Morongo Valley.

Table S1 Data matrix of all traits measured in 11 desert species with photosynthetic stems

Table S2 Morphometric traits of 11 desert species photosynthetic stems measured at the end of the growing season (fall)

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