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The response of sap flow in desert shrubs to environmental variables in an arid region of China

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ABSTRACT

A case study was conducted in a desert–oasis ecotone in the middle of China's Heihe River basin to reveal the response of sap velocity to environmental variables. We measured sap flow in the branches and stems of desert shrubs (*Nitraria sphaerocarpa* and *Elaeagnus angustifolia*) using sap-flow gauges, and simultaneously measured environmental variables at the study site. The relationships between sap velocity and the environmental variables were analysed using redundancy analysis. The diurnal variation in sap velocity was best described by a bimodal curve, except for the branches of *N. sphaerocarpa*, which followed a unimodal curve. Sap flow began about 1 h earlier in the branches than in the stems. The dynamic variations in sap velocity were remarkably similar for the two species at a given position (stem vs branch) but differed between the two positions for each species. Redundancy analysis and Kendall's tau analysis indicated that precipitation had the greatest influence on sap velocity in the stem, whereas precipitation duration significantly affected sap velocity in the branches of the desert shrubs ($R^2 = 0{\cdot}85$ and 0·73, respectively). The variation in sap velocity could be described by a multiple linear regression against the meteorological variables, and the simulated value was significantly linearly correlated with the measured value ($0{\cdot}861 \le R^2 \le 0{\cdot}938$, $P < 0{\cdot}0001$). Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS desert shrubs; sap velocity; environmental variables; redundancy analysis

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INTRODUCTION

Evaluating the response of desert ecosystems to global changes and the associated environmental feedback mechanisms requires a better understanding of transpiration by desert plants and of their carbon assimilation in arid regions (Lebaude *et al.*, 2000; Gibert *et al.*, 2006). These processes depend on sap flow, which drives the physiological responses of desert plants, and sap flow depends on the plant's water balance and on subsurface hydrology (Johnson *et al.*, 2002; Lambs and Berthelot, 2002; Lambs *et al.*, 2002). Small rainfall events (≤5 mm) occur more frequently throughout the year in arid regions than in other climatic regions (Sala and Lauenroth 1982; Loik *et al.*, 2004). As a result, sap flow in this region is more dynamic than in other climatic regions (Yoshifuji *et al.*, 2004; Komatsu *et al.*, 2006; Kume *et al.*, 2006). However, sap flow in desert plants is likely to vary strongly among species or positions within the plants owing to differences in their physiological responses and in aspects of their morphology such as the crown architecture, stem size and shape, and other characteristics (O'Brien *et al.*, 2004). Therefore, accurately estimating the response of sap flow to changes in environmental variables is the basis for comprehending the physiological responses of desert shrubs to their habitats and how variations in sap flow determine the magnitude of any differences in species responses.

Sap flow measurements are the most useful technique for obtaining transpiration data, because other techniques such as the eddy covariance method cannot provide reliable measurements during and after rainfall (Mizutani *et al.*, 1997); in contrast, sap flow measurements have the advantage that the instrumentation can be easily installed at accessible points on the tree, such as at the base of the stem. Since 1990s, the sap flow technique has been widely used to measure plant transpiration (e.g., Barrett *et al.*, 1995; Schiller and Cohen, 1995; Edwards and Jèermák, 1996; Hall *et al.*, 1998; MacNish *et al.*, 2000; Green *et al.*, 2003; O'Brien *et al.*, 2004; Nicolas *et al.*, 2005; Chang *et al.*, 2006; Kume *et al.*, 2006; Kigalu, 2007; McDowell *et al.*, 2008; Xia *et al.*, 2008; Yue *et al.*, 2008). Sap flow data are generally obtained using two main measurement methods to quantify plant transpiration (Swanson, 1994; Kigalu, 2007): the heat-pulse velocity, based on heat compensation theory, can measure the upstream xylem sap velocity and sap-flow rate within a stem section (Dugas, 1990), but this technique is invasive and may damage the plant; the stem heat-balance method is less invasive, and estimates sap velocity (Steinberg *et al.*, 1989; Ishida *et al.*, 1991; Batho *et al.*, 1994; Boersma and Weibel, 1995) using a small heater wrapped around the plant's stem or a branch to supply heat to that section of the plant, and therefore creates less damage to the plants (Kigalu,

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2007). In addition, the approach is less expensive than other methods, including the use of weighing lysimeters (Cermak *et al*., 1973, 1984; Swanson, 1994). For these reasons, we chose the heat-balance method in the present study.

Plants regulate sap flow via changes in stomatal conductance in response to variations in environmental variables such as radiation intensity, vapour pressure deficit (VPD), soil moisture, rainfall, temperature, and wind speed (McDowell *et al*., 2008). Sap flow significantly accelerates, and transpiration and respiration increase, after plants absorb the water provided by rainfall events (Schwinning and Sala, 2004). However, sap flow decreases under conditions of high VPD (Meinzer *et al*., 1993, 1995; Granier *et al*., 1992) due to the development of water stress leading to stomatal closure. In addition, many of the environmental variables that affect sap velocity interact strongly with each other; for example, VPD and radiation often co-vary, but have opposite effects on plant physiology (O'Brien *et al*., 2004). The interactions among environmental variables are less well understood, because the simultaneous impact of multiple variables is what actually drives sap-flow responses; as a result, exploiting the responses of sap flow to these variables can be an effective approach for comparing the species-specific and position-specific responses to environmental changes (Qu *et al*., 2007; O'Brien *et al*., 2004). However, little work has been done on sap flow in desert plants in response to changing environmental variables in arid regions of China (Xia *et al*., 2008), where determining the impact of sap flow patterns is difficult due to the lack of long-term measurements.

The Heihe River Basin is the second largest inland river basin in arid northwestern China, which is one of the country's major grain-producing regions (Chang *et al*., 2006). The environmental degradation, secondary salinization, and desertification that are occurring in this region have become the main obstacles to sustainable development of the desert–oasis ecosystem (Pan and Chao, 2003; Su *et al*., 2007). In general, desert shrubs are the dominant plant species in these regions (Schwinning and Ehleringer, 2001), and *Nitraria sphaerocarpa* and *Elaeagnus angustifolia* are the dominant species on mobile and semi-mobile dunes. Both species can be characterized as light-tolerant, drought- and salinity-resistant species, and can be used for soil and water conservation, as well as for sheltering other vegetation from the wind and serving a sand-fixation function (Qu *et al*., 2007). We hypothesized that variations in sap flow in response to changes in environmental conditions would be involved in the regulation of water demand by desert shrubs. Therefore, we investigated sap flow of desert shrubs in their branches and stems using stem-flow gauges, which are described in detail by Batho *et al*. (1994), Weibel and Devos (1994), Kigalu *et al*. (1995), and Yue *et al*. (2008). Our goals were to confirm the response of sap flow to changes in environmental variables, water use by developing a regression equation for sap velocity as a function of the measured environmental variables, and to examine the pattern of variation in the magnitude of species-specific sap-flow responses. Our results will provide the information required to support cultivation and management of these ecologically important plants in arid regions of northwestern China.

METHODS

Study area

The study area is located in a desert–oasis ecotone in the middle of China's Heihe River basin, in Linze County (between 39°22′N and 39°23′N, and between 100°07′E and 100°08′E) (Figure 1). The environment is characterized as a continental arid temperate climate. The annual precipitation averages 116·8 mm (1965–2000), and about 65% of the total precipitation falls (with a low rainfall intensity) between July and September. The potential evaporation is 2390 mm year^{-1}, and the resulting dryness index is 20·5. The annual temperature averages 7·6 °C, and the lowest and highest temperatures are about −27·3 °C in January and 39·1 °C in July. The wind direction is mainly from the northwest, and the wind speed averages 3·2 m·s^{-1}, with a frequent occurrence of gales (wind speed ≥21 m·s^{-1}). During the growing season (from May to October), the frost-free period is about 165 days. The zonal soil is typically characterized as a desert soil, and is highly susceptible to wind erosion as a result of its coarse texture. The landscape includes fixed, semi-fixed, semi-mobile, and mobile dunes, as well as inter-dune lowlands. Desert shrubs and annual herbaceous species grow on the fixed and semi-fixed dunes. These include *Haloxylon ammodendron, E. angustifolia, Tamarix ramosissima, N. sphaerocarpa, Suaeda glauca*, and *Agriophyllum squarrosum*.

Sap flow and meteorological measurements

We used stem-flow gauges (Flow32 meters, Dynamax Inc., Houston, TX, USA) and the energy-balance method to measure sap flow in the branches and stems of *N. sphaerocarpa* and *E. angustifolia* from June to

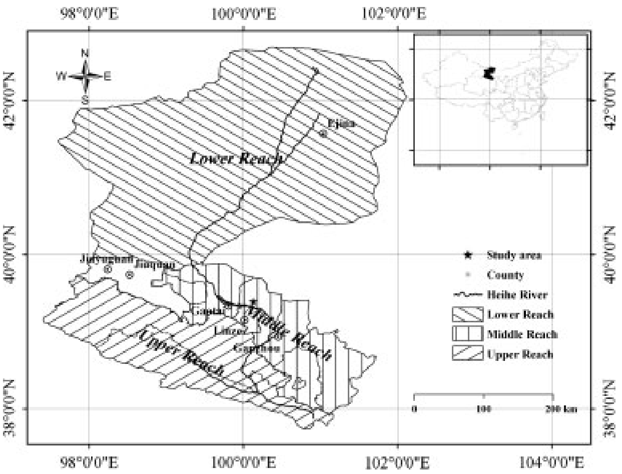

Figure 1. A map of the Heihe River Basin and its location in China.

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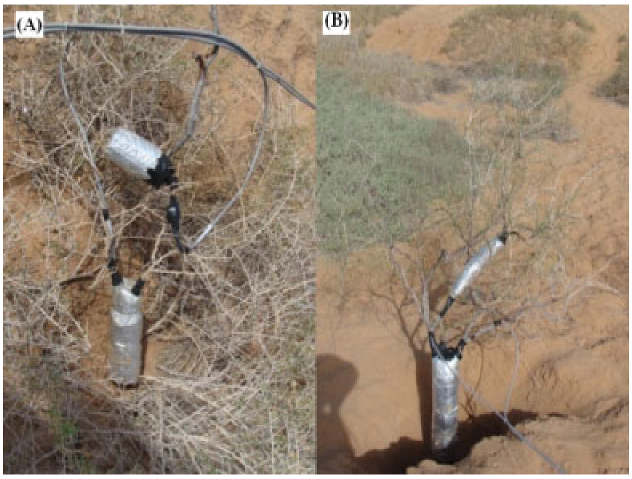

Figure 2. Installation of the sap-flow gauges on the branches and stems of (A) *Nitraria sphaerocarpa* and (B) *Elaeagnus angustifolia*.

October 2008. To determine the influence of the environment on differences in sap flow between species and within species (between positions on a shrub) at the 1 ha study site, we attached model SGB3 and SGB5 gauges to the branches of *N. sphaerocarpa*, and model SGB9 gauges to its stems. We installed model SGB9, SGB13, and SGB19 gauges to the branches of *E. angustifolia*, and model SGB25 and SGB35 gauges to its stems (Figure 2). We used three replicates for each position in each species. The theory and methodology of using sap-flow gauges have been described previously in detail (e.g., Kigalu *et al*., 1995; Yue *et al*., 2008), and we installed the gauges strictly following the manufacturer's instructions. The data were recorded at 10 s intervals and stored as 30 min averages using a CR1000 datalogger (Campbell Scientific, Logan, UT, USA).

The meteorological data were measured using an AG1000 automatic weather station (Onset Computer Corporation, Pocasset, MA, USA), and was used to analyse the responses of sap flow to environmental variables during the study period. The meteorological tower that held the weather station's sensors was installed in a study field surrounded by a large area of desert shrubs. The sensors were installed at two levels above the ground (2 and 3 m), except for the net and photosynthetically active radiation sensors, which were only installed at 2 m above the ground. Wind velocity was measured using a two-dimensional ultrasonic anemometer (Windsonic, Gill, UK). Air temperature and relative humidity were measured with an HMP45D probe (Vaisala, Vantaa, Finland) protected by a radiation shield. Volumetric soil moisture content and soil temperature were measured using ECH_2O-10 dielectric aquameter probes (Decagon Devices, Pullman, WA, USA) buried at eight depths below the soil surface (10, 20, 30, 40, 50, 60, 80, and 100 cm). Atmospheric pressure and water vapour were measured using a barometric pressure sensor (CS100, Setra, UT, USA). Net radiation was measured with a closed-cell thermocouple sensor (NR-lite, Kipp and Zonen, Delft, The Netherlands). Three soil heat-flux plates (model HFP01, Radiation Energy Balance Systems) were buried at a depth of 2 cm in 1×1 m plots separated by 20 m near the base of the tower. Rainfall was measured with a tipping-bucket rain gauge (model TE525, metric; Texas Electronics, Dallas, TX, USA). The meteorological data were measured at a frequency of 10 Hz and recorded every 5 min using a CR1000 datalogger (Campbell Scientific Inc., Logan, UT, USA), then stored as the 30-min-mean data, whereas precipitation and wind data were stored as the 10-min-mean data.

In addition, we revised the data to account for missing or low-quality data. For missing data, we used the gap-filling approach of Falge *et al*. (2001), which involves linear interpolation between the mean diurnal values when the differences between data are large. To remove low-quality data, we excluded rainfall events that lasted longer than 5 days or interpulse periods of less than 1 week.

Statistical analysis

We analysed the differences in sap velocity between species and positions (stem vs branch) by means of ANOVA and Tukey's HSD test using version 13·0 of the SPSS software (SPSS Inc., Chicago, IL, USA), and considered values to be significantly different when $P < 0{\cdot}05$. We used the constrained ordination technique because it provides results similar to those of multivariate multiple regression, and performs well with non-orthogonal data with a collinear gradient (McGarigal *et al*., 2000; Robertson *et al*., 2009). We used redundancy analysis (RDA) to explore the responses of sap flow to changes in the following environmental factors (Canoco 4·5; University of South Bohemia, Ceske Budejovice, Czech Republic): precipitation, precipitation duration, inter-pulse duration between rainfall events, air temperature, wind speed, relative humidity, net radiation, VPD, soil heat flux, and soil moisture (at depths of 10 and 20 cm). Because the results for the other six depths did not differ significantly among measurement periods, we have not presented that data. The data for each parameter was analysed separately from that for the other parameters to determine the possible effects of each environmental variable on sap flow during the measurement period.

RESULTS

Environmental variables

Figure 3 illustrates the dynamic variation in the meteorological variables at the study site. The wind speed averaged 1·80 m s^{-1} during the study period, with maximum and minimum values of 3·88 and 0·88 m s^{-1}, respectively (Figure 3E). The precipitation averaged 4·89 mm per event, with maximum and minimum values of about 21·6 mm and 0·1 mm, respectively. In general, precipitation was greatest and exhibited the shortest inter-pulse period during the summer (Figure 3F). Net radiation, VPD, air temperature, and relative humidity varied throughout the study period, with the minimum values

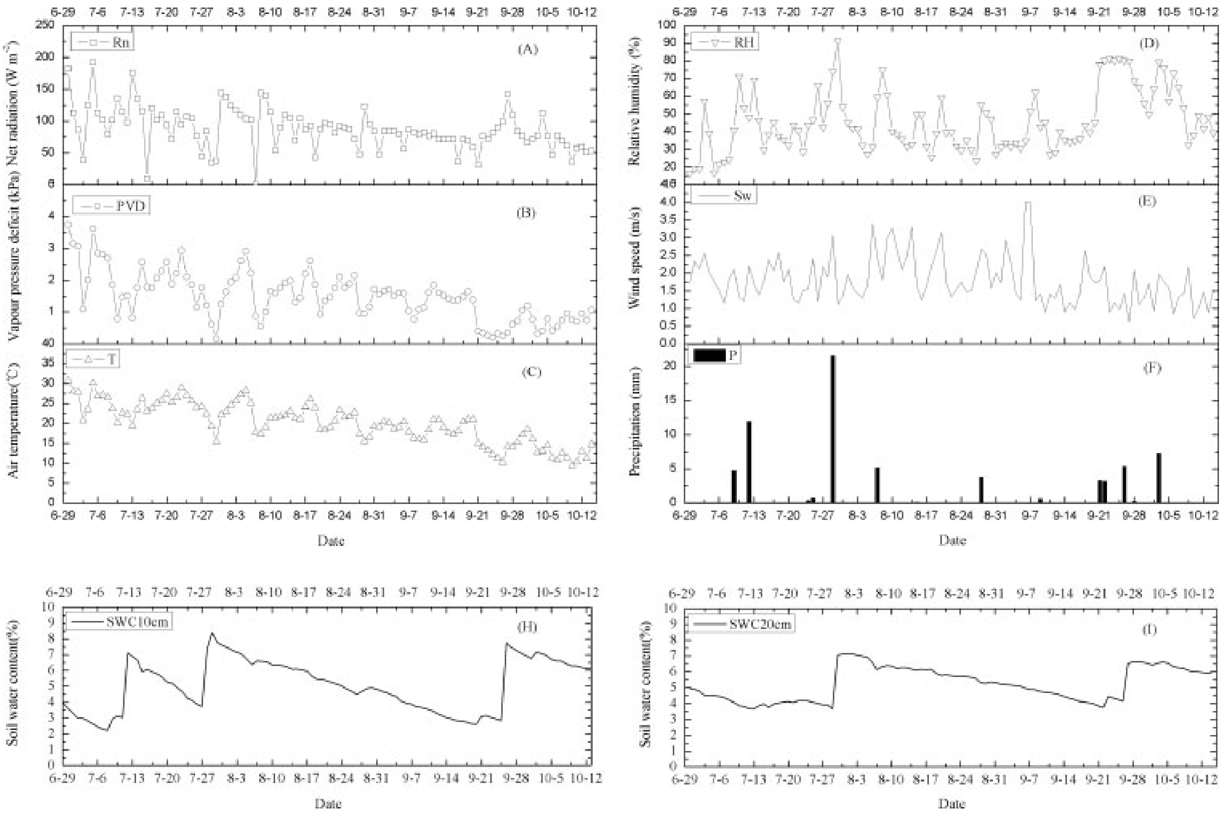

Figure 3. The patterns of variation in the meteorological variables during the study period.

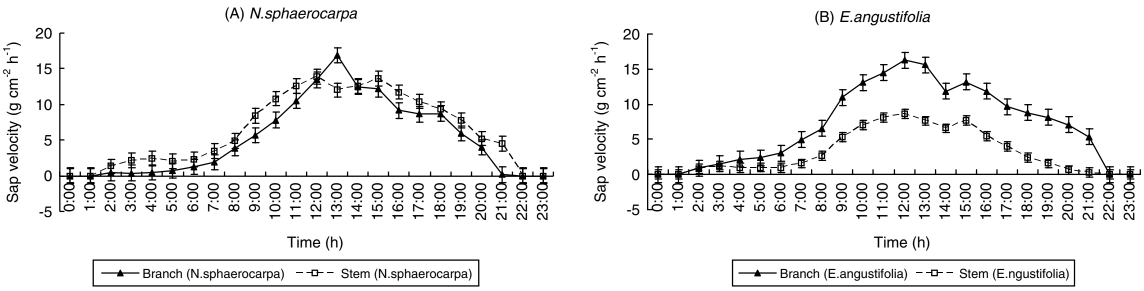

Figure 4. The diurnal variation in sap velocity during the measurement period for (A) *Nitraria sphaerocarpa* and (B) *Elaeagnus angustifolia*.

occurring after a rainfall event followed by increasing values during the inter-pulse periods, and reached the maximum value before the next rainfall. The values averaged 87·61 $W{\cdot}m^{-2}{\cdot}day^{-1}$, 1·49 kPa, 20·14 °C, and 45·8%, respectively (Figure 3A–D). Soil water content was higher after precipitation events, and particularly after large events, and generally ranged from 2·2 to 8·4%. Soil moisture content was higher at a depth of 20 cm than at 10 cm, and differed among seasons, with greater soil moisture during the summer and fall than during the winter and spring (Figure 3G and H). Meteorological variables differed among the seasons, with greater values in the summer than in the fall and spring.

Variation in sap velocity

Diurnal variation in sap velocity. The sap velocity in the branches and stems of *N. sphaerocarpa* and *E. angustifolia* varied greatly during the measurement period because of natural heterogeneity in the hydraulic conductivity of the sapwood and in the responses of the plants to environmental parameters. During the night, sap velocity was slow (nearly zero) and constant, but rapidly accelerated as the solar radiation increased in intensity and the air temperature increased (starting about 06 : 00 to 07 : 00 in the morning), with the highest value occurring at or shortly after noon. The sap velocity subsequently decreased, reaching a value near zero by nightfall (Figure 4).

Sap flow began about 1 h earlier and the peak values were higher in the branches than in the stems in *E. angustifolia*; in contrast, sap flow began earlier in the stems of *N. sphaerocarpa*, and the peak values did not differ greatly between these two positions. The diurnal variation in sap velocity was best described using a bimodal curve, except for the branches of *N. sphaerocarpa*, which followed a unimodal curve. The highest sap-velocity values in the branches and stems of *N. sphaerocarpa* were 16·85 and 12·99 g cm^{-2} h^{-1}, respectively, versus 16·25 and

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Table I. The sap velocity values for the two desert shrubs.

Species	*Nitraria sphaerocarpa*		*Elaeagnus angustifolia*	
	Branch	Stem	Branch	Stem
Sap velocity (g cm^{-2} day^{-1})	45·56 (25·79) d	151·21 (51·78) a	91·35 (57·05) b	63·91 (19·72) c

Values represent means ± SD and means followed by different letters differ significantly (Tukey's HSD, $P < 0.05$).

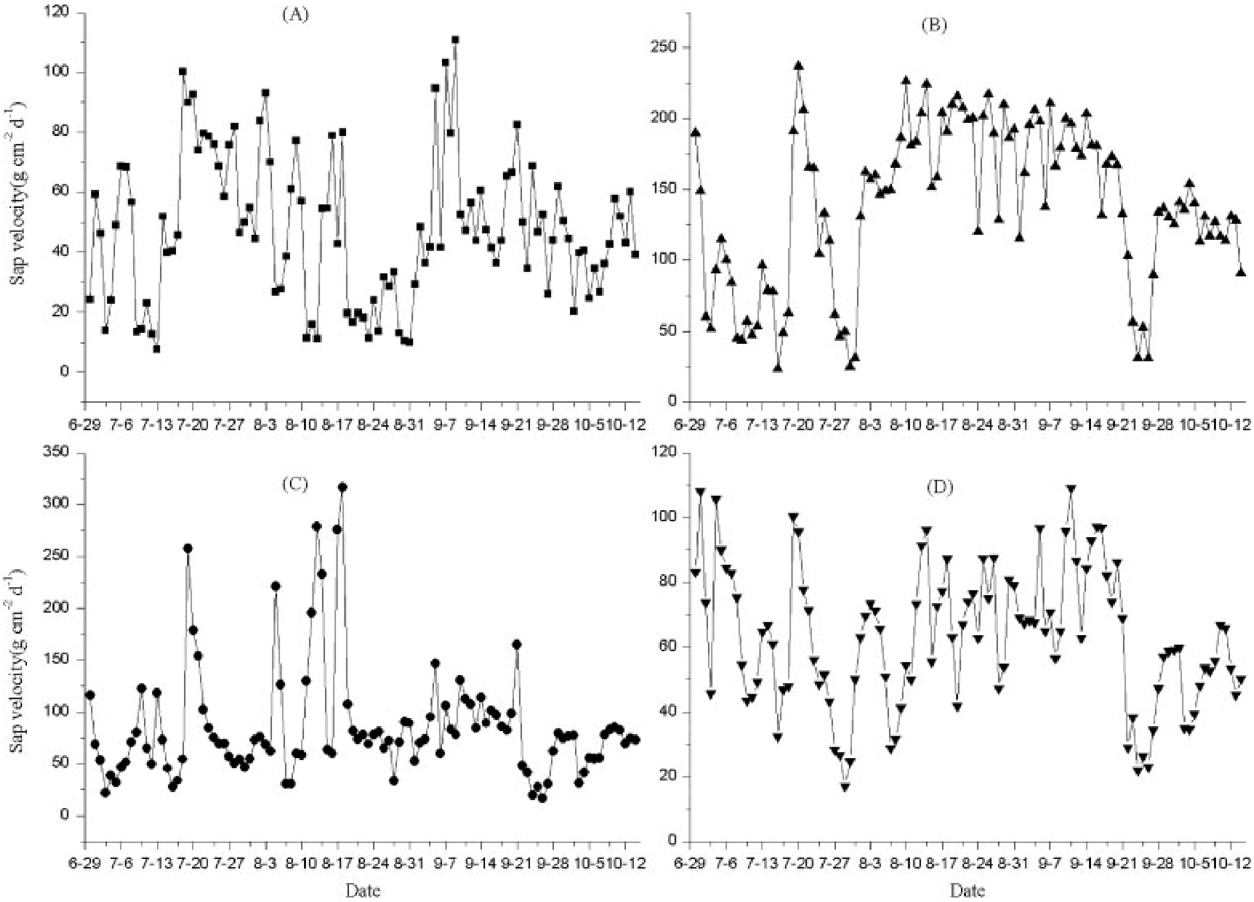

Figure 5. The dynamic variation in mean sap velocity during the study period. (A) Branches and (B) stems of *Nitraria sphaerocarpa*. (C) branches and (D) stems of *Elaeagnus angustifolia*.

8·11 g cm^{-2} h^{-1}, respectively, for *E. angustifolia*, with average values of 5·19, 6·39, 6·99, and 3·09 g cm^{-2} h^{-1}, respectively (Figure 4).

Dynamic variation in sap velocity. Table I summarizes the characteristics of sap velocity in the branches and stems of *N. sphaerocarpa* and *E. angustifolia*. Sap velocity was relatively high and variable in both species, with values of 45.56 ± 25.79 and 151.21 ± 51.78 g cm^{-2} day^{-1}, respectively, for the branches and stems of *N. sphaerocarpa* and 91.35 ± 57.05 and 63.91 ± 19.72 g cm^{-2} day^{-1}, respectively, for the branches and stems of *E. angustifolia*. The differences in sap velocity between species and between positions within a species were all significant; the average sap velocity in the branches was lower than that in the stems for *N. sphaerocarpa*, whereas velocity was higher in the stems in *E. angustifolia*.

The patterns of dynamic variation in sap velocity were remarkably similar for the two species at a given position during the study period, but differed between the two positions for a given species (Figure 5). During the study period, the climate conditions affected sap velocity, which responded particularly significantly to rainfall. For example, sap flow on sunny days was greater than on cloudy days, and sap velocity increased significantly with increasing VPD and solar radiation after a rainfall event. Sap velocity in the branches of *N. sphaerocarpa* reached its maximum (110·89 g cm^{-2} day^{-1}) after 3·8 mm of rainfall (9 September), whereas sap velocity for *E. angustifolia* reached its maximum (316·73 g cm^{-2} day^{-1}) after 5·2 mm of rainfall (18 August). However, sap flow in the stems of both species reached their maximum after 12 mm of rainfall, with values of 236·56 and 100·32 g cm^{-2} day^{-1} for *N. sphaerocarpa* and *E. angustifolia*, respectively (Figure 5).

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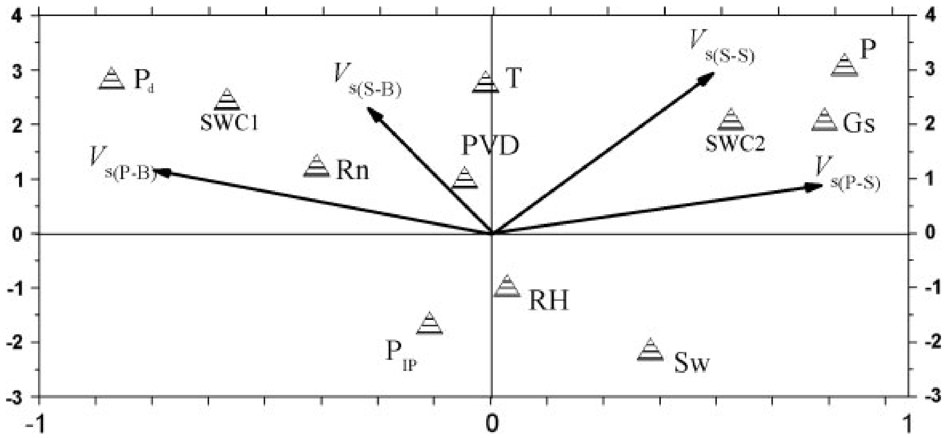

Figure 6. Redundancy analysis (RDA) for the relationship between sap-flow velocity and the meteorological variables. $V_{s(P-B)}$, sap-flow velocity in branches (*Nitraria sphaerocarpa*); $V_{s(P-S)}$, sap-flow velocity in stems (*N. sphaerocarpa*); $V_{s(S-B)}$, sap-flow velocity in branches (*Elaeagnus angustifolia*); $V_{s(S-S)}$, sap-flow velocity of stems (*E. angustifolia*); P, precipitation (mm); P_d, precipitation duration (min); P_{IP}, inter-pulse period between precipitation (days); T, air temperature at 2 m (°C); S_w wind speed at 2 m (m s^{-1}); RH, relative humidity (%); R_n, net radiation (W m^{-2}); VPD, vapour pressure deficit (kPa); G_s, soil heat flux (W m^{-2}); SWC_1, soil moisture at 10 cm (%); SWC_2 soil moisture at 20 cm (%).

Table II. The eigenvalues and intraset correlations in the RDA of the relationship between sap flow and the environmental variables.

Parameter	Axes				Total inertia
	1	2	3	4	
Eigenvalue	0·273	0·066	0·017	0·013	1·000
Correlation between sap velocity and the meteorological variables	0·982	0·668	0·263	0·156	
Cumulative percentage of total variance					
Sap velocity	87·8	89·3	0	0	
Correlation between sap velocity and the meteorological variables	95·0	99·7	100·0	100·0	
Sum of all eigenvalues					1·000
Sum of all canonical eigenvalues					0·368

Response of sap velocity to environmental variables

Environmental variables also influence sap flow through their effects on the physiological characteristics of the plant. The successive decrease in eigenvalues along the first four axes of the RDA based on the relationship between the RDA axes and the environmental variables. Only the first and second axes are shown in Figure 6, as these two axes explain most of the variation in the graphs. Almost all of the RDA graphs had a high correlation between the sap velocity and the meteorological variables, suggesting that most of the environmental variables were important, although there may have been other factors of equal importance that we did not account for in our analysis. The correlation between sap velocity and the meteorological variables was higher for the first two canonical axes (0·982 and 0·668, respectively), and the cumulative variance in this relationship accounted for by the two axes totalled 99·7% (Table II), which suggests that sap velocity was significantly correlated with both axes.

The RDA and Kendall's tau value indicated that precipitation had the strongest influence on sap velocity in the stem, whereas the precipitation duration most significantly affected sap velocity in the branches ($R^2 =$ 0·85 and 0·73, respectively; Figure 6, Table III), which suggested that precipitation is crucial for the survival and growth of these desert plants. The soil heat flux and soil moisture below a depth of 20 cm were significantly positively correlated with sap velocity in the stems ($P < 0{\cdot}01$), and sap velocity was more strongly affected by soil moisture than by soil heat flux. However, net radiation and soil moisture a depth of 10 cm were significantly positively correlated with sap velocity in the branches ($P < 0{\cdot}01$), and sap velocity was more strongly affected by soil moisture than by net radiation. These results suggest that sap velocity depended strongly on the variations in soil moisture. In addition, sap velocity increased significantly with increasing VPD for both species, and sap velocity in *E. angustifolia* also increased with increasing air temperature ($P < 0{\cdot}01$). In contrast, sap velocity decreased with increasing wind speed, relative humidity, and the duration of the inter-pulse period (Figure 6, Table III).

We expressed the variation in sap velocity (V_s) in the two desert shrubs by means of multiple linear regression against the meteorological variables. The resulting model performed well, explaining the 82·4–96·6% of the variation in sap velocity (Table IV).

We carried out a regression analysis between the measured sap velocity values and the values predicted using

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Table III. Kendall's tau correlation matrix between sap velocity and the meteorological variables.

Species	Position	S_w ($m \cdot s^{-1}$)	T (°C)	RH (%)	R_n ($W\ m^{-2}$)	VPD (kPa)	G_s ($W\ m^{-2}$)	SWC_1 (10 cm, %)	SWC_2 (20 cm, %)	P (mm)	P_t (min)	P_{IP} (days)
N. sphaerocarpa	$V_{s(P-B)}$	−0·40	0·19	−0·01	0·52**	0·44**	0·29	0·55**	0·10	0·55	0·85**	−0·19
	$V_{s(P-S)}$	0·16	0·22	−0·42**	0·28	0·38**	0·34**	0·14	0·76**	0·74**	0·30	−0·39
E. angustifolia	$V_{s(S-B)}$	−0·29	0·37**	−0·44**	0·49**	0·42**	0·24	0·58**	0·20	0·54	0·73**	−0·35
	$V_{s(S-S)}$	−0·15	0·28**	−0·68**	0·14	0·47**	0·48**	0·15	0·63**	0·90**	0·29	−0·58

R_n, net radiation; T, air temperature; S_w, wind speed; VPD, vapour pressure deficit; RH, relative humidity; G_s, soil heat flux; SWC_1, soil moisture at 10 cm; SWC_2, soil moisture at 20 cm; P, precipitation; P_t, precipitation duration and P_{IP}, inter-pulse period between precipitation.
* $P < 0.05$; ** $P < 0.01$.

the regression equations in Table IV to determine the predictive value of these equations. For each species and position, the simulated value was significantly linearly correlated with the measured value ($0.861 \leq R^2 \leq 0.938$, $P < 0.0001$), with a y-intercept ranging from 13·80 to 49·24 g cm^{-2} h^{-1} and a slope ranging from 0·74 to 0·85 (Figure 7)

DISCUSSION

The variation in sap flow in plants is related not only to their biological and physiological characteristics, such as canopy structure, stomatal closure, and root hydraulic conductance, but also to environmental variables such as soil moisture and meteorological factors such as wind velocity (McDowell *et al*., 2008; Xia *et al*., 2008; Yue *et al*., 2008). In previous research, sap velocity was also significantly related to the available soil water and VPD (Granier *et al*., 2000), and also increased with increasing VPD and solar radiation on sunny days (Nadezhda, 1999). The significant variation in the pattern of diurnal sap flow has been shown to result mainly from variations in the intensity of solar radiation (Heilman and Ham, 1990; O'Brien *et al*., 2004), and the startup and peak times of sap flow have been shown to be closely related to solar radiation (Qu *et al*., 2007).

Transpiration is influenced indirectly by leaf water potential through its effect on the stomatal aperture of plants (Jones, 1992). For example, cassava responds to drought by closing its stomata to reduce transpiration, thereby protecting leaf tissues from turgor loss and desiccation (El-Sharkawy, 1993; Alves and Setter, 2000). Reductions in transpiration have also been attributed to decreases in leaf conductance in response to an increasing relative humidity (El-Sharkawy, 2006; Oguntunde, and Alatise, 2007). The increasing intensity of solar radiation and increasing air temperatures during the morning induce stomatal opening, thereby accelerating sap flow due to the high evaporative demand from the canopy (O'Brien *et al*., 2004). As a result, sap flow typically begins about 1 h earlier in the branches than in the stems because of the morning lag in the response of stems to light; this can be explained by water capacitance in the stem, a slow stomatal response to light, and boundary layer dynamics (O'Brien *et al*., 2004). Many authors have reported lags between sap flow at the base of tree and transpiration in the crown (e.g., Goldstein *et al*., 1998; Phillips *et al*., 1999). The cells of the plant are provided with water and nutrients after a rainfall, which increases the plant's ability to respond to changes in light intensity, resulting in increased sap velocity. In contrast, low sap velocity can be caused by low air temperature, low solar radiation, and a low VPD in windy weather. High wind speed typically causes stomatal closure to decrease water loss from the canopy. Moreover, a lack of soil moisture will decrease sap velocity, leading to decreases in sap velocity with an increasing inter-pulse period for precipitation, which agrees with the results of our RDA.

Table IV. Regression equations for the relationships between sap velocity (V_s) and the significant meteorological variables.

Species	Position	Df	Regression equation	R^2	F-statistic
N. sphaerocarpa	$V_{s(P-B)}$	8, 77	$V_s = 24{\cdot}68 + 1{\cdot}25\ RH - 0{\cdot}34\ R_n + 2{\cdot}19\ G_s$	0.833	2·23*
	$V_{s(P-S)}$	8, 77	$V_s = 136{\cdot}97 - 1{\cdot}07\ RH + 14{\cdot}41\ SWC_2 - 10{\cdot}96\ SWC_1 + 0{\cdot}31\ R_n$	0.824	12·90***
E. angustifolia	$V_{s(S-B)}$	8, 77	$V_s = 26{\cdot}51 + 45{\cdot}23\ VPD$	0891	26·66***
	$V_{s(S-S)}$	8, 77	$V_s = 122{\cdot}44 - 0{\cdot}81\ RH - 6{\cdot}32\ S_w - 1{\cdot}79\ SWC_1 + 0{\cdot}11\ R_n$	0.966	28·84***

R_n, net radiation; S_w, wind speed; *VPD*, vapour pressure deficit; *RH*, relative humidity; G_s, soil heat flux; SWC_1, soil moisture at 10 cm; SWC_2, soil moisture at 20 cm.
* $P < 0{\cdot}05$; *** $P < 0{\cdot}001$.

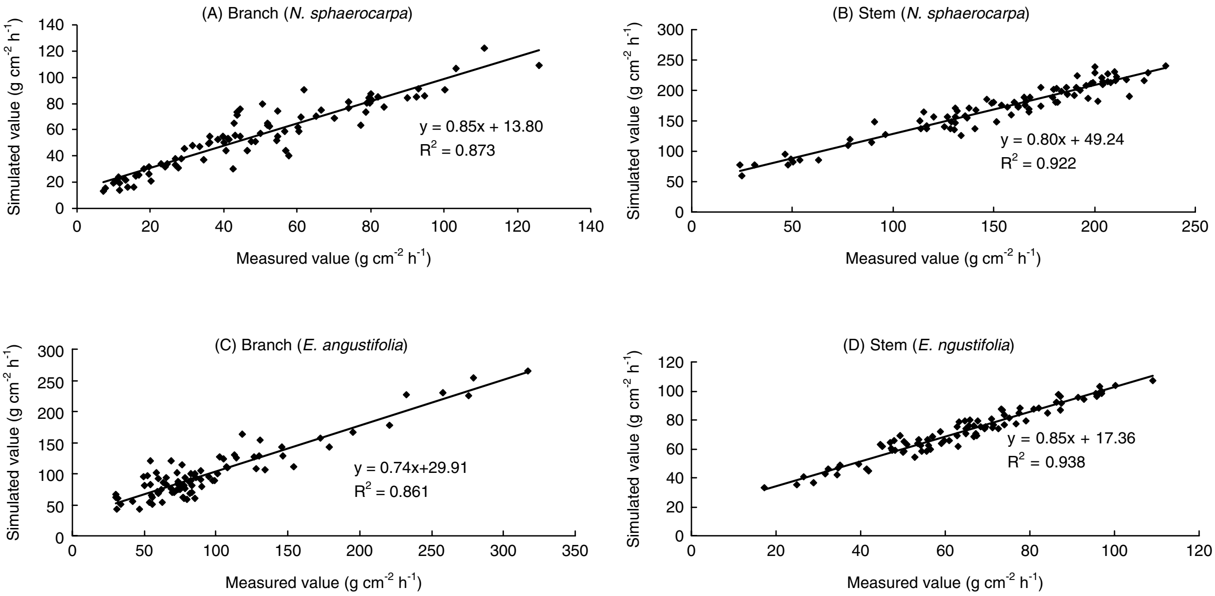

Figure 7. Comparison of the measured and simulated sap velocities during the study period.

Precipitation and precipitation duration were particularly crucial for determining the effect on sap velocity, which depended on the resulting variations in soil moisture. Large rainfall events (≥10 mm) and small precipitation duration had the strongest influence on sap velocity in the stems of *N. sphaerocarpa* and *E. angustifolia*, whereas sap velocity in the branches responded significantly to small rainfall events (≤5 mm) during the rainfall period (Figure 6, Table III). We observed that sap velocity in the two desert plants was positively correlated with net radiation, air temperature, VPD, and soil heat flux, but was negatively correlated with relative humidity, wind speed, and the inter-pulse period for precipitation ($P < 0{\cdot}01$).

The differences in sap velocity were significant between the branches and stems for *N. sphaerocarpa* and *E. angustifolia* (Figure 5), possibly because of intrinsic differences in morphology, anatomy, life history, and architecture between these species. Despite these differences, the two species appear to have converged on a common pattern of response to changes in their environmental conditions. The differences in branch density among desert shrubs may have resulted from heterogeneity in the variation in sap velocity in their branches and stems. Stems of old desert shrubs include a large amount of dead tissue and knots that decrease sap velocity, making it difficult to choose an appropriate location for sensor installation. The combination of morning lags in the response of the stems to light and of afternoon lags in the responses of the branches to VPD produced differences in sap velocity between the two positions in each species. In desert regions, sap velocity was greater and the curve was described by a bimodal curve in the daytime, they suggested that the relationship between sap flow and evaporative demand might show a similar universality among species. During the night, sap velocity differed between the branches and stems in both *N. sphaerocarpa* and *E. angustifolia*, which presumably helps to maintain the water balance within the plant, as roots can actively absorb water from the soil at night to compensate for water losses caused by transpiration during the day (Xia *et al*., 2008). Our results agree with previous findings (e.g., Clark and Gibbs, 1957; Zhang *et al*., 2004; Bai *et al*., 2005).

Global climate change is likely to increase the variability in precipitation patterns. Consequently, desert plants will be forced to endure repetitive cycles of water scarcity followed by rainfall (Smith and Nowak, 1990; Jackson *et al*., 2001). Soil water limitations would then cause decreased transpiration under conditions of high evaporative demand. Morphological and architectural differences among species might cause different responses to these conditions, and differences in the architectural characteristics will determine the effectiveness of their response to changing environmental variables.

CONCLUSIONS

Sap flow drives the physiological responses of desert plants, and is in turn affected by a plant's water balance and the subsurface hydrology (i.e., by the water supply). The variation in sap flow was related to both the biological and physiological characteristics of the plants and also responded to changes in the environmental variables. Sap velocity accelerated significantly under increasing evaporative demand, and sap flow began about 1 h earlier in the branches relative to the stems because of the morning lag in the response of the stems to light. The intrinsic differences in morphology, physiology, and architecture between species may lead to differences in sap velocity between their branches and stems, but the combination of a morning lag in the response of the stems to light and an afternoon lag in the response of the branches to VPD increased the differences in sap velocity between different positions in both species. Soil water limitations would decrease transpiration during periods of high evaporative demand, and the response of sap flow to differences in species architectural characteristics may prove to be more effective than the responses to environmental variables under a scenario of global climate change.

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