



Response of *Populus euphratica* Oliv. sap flow to environmental variables for a desert riparian forest in the Heihe River Basin, Northwest China

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Abstract: Being an important desert riparian forest in the lower reaches of the Heihe River Basin, *Populus euphratica* Oliv. forest functions as a natural barrier in maintaining and preserving the stability of local oases. Accordingly, accurately estimating the water use of *P. euphratica* is important for vegetation protection and water resource allocation. To date, little data are available for evaluating the hysteretic effects between sap flow and environmental variables, and for estimating the water use of desert riparian forest. In this study, we measured the sap flow velocity (V_s) of *P. euphratica* using the heat ratio method during the growing season of 2012. Based on the response of V_s to solar radiation (R_s) and vapor pressure deficit (VPD), we estimated the hourly V_s and daily V_s using the multivariable linear regression and a modified Jarvis-Stewart (JS) model, respectively. Hysteretic response of V_s to environmental variables was then evaluated using a sap flow model. We found the thresholds of V_s responses to R_s and VPD at both hourly and daily scales during the growing season, and successfully estimated the seasonal variations of hourly V_s and daily V_s using the JS model. At an hourly scale, the maximum V_s occurred earlier than the maximum VPD by approximately 0.5 h but later than the maximum R_s by approximate 1.0 h. At a daily scale, the maximum V_s lagged behind the maximum VPD by approximately 2.5 h while occurred earlier than the maximum R_s by approximately 2 h. However, hysteretic response of V_s was weakened when R_s and VPD were measured together using the JS model at both hourly and daily scales. Consequently, short-term and intensive field campaigns, where V_s and environmental variables can be measured, may be used to estimate short-run sap flow and stand transpiration using only two environmental variables.

Keywords: sap flow; solar radiation; vapor pressure deficit; Jarvis-Stewart model; hysteresis

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The exchange of water flux between vegetation and the atmosphere is an important function for both energy transferring and hydrological cycling in forest ecosystems. Accordingly, it is critical to determine water budgets of woody forests, water use of individual trees and water exchanges of stands, either through direct measurements or model predictions (Komatsu et al., 2006; Whitley et al., 2009). Techniques in determining sap flow are characterized by practicality and repeatability.

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They must provide accurate and instantaneous estimations of water flux for plants in their entirety (e.g. trunk, leaves and roots) over relative short-time scales (Dragoni et al., 2009; Steppe et al., 2010). Such techniques are widely used to monitor the water use of tree or stand in various ecosystems for a long period (O'Grady et al., 2008; Sánchez-Costa et al., 2015). However, they are applied to forest stands in arid and semi-arid regions only in recent years (Du et al., 2011; Zheng and Wang, 2014).

Sap flow velocity (V_s), which is similar to plant water use, is driven by available energy, evaporative demand and water availability. For example, David et al. (2004) reported a progressive loss in V_s sensitivity to solar radiation (R_s) from morning to afternoon. V_s increases with increasing vapor pressure deficit (VPD) rates following times of higher water availability, while V_s will be saturated above a certain VPD threshold to prevent catastrophic loss of xylem functions (Granier et al., 1996; Hernández-Santana et al., 2008). V_s is also higher under wetter conditions than under water-limited conditions (O'Grady et al., 2008) because lower soil water availability could increase hydraulic resistance between soil and root systems, preventing water movement from soil to plant leaves and triggering stomatal closure (Tognetti et al., 2009). The relationship between V_s and environmental variables varies normally between species and scales. Limited by lower water availability and higher evaporative demand in arid environments, we hypothesized that larger threshold constrains on V_s was a response of environmental variables at both hourly and daily scales for desert riparian forests.

Furthermore, hourly V_s and daily V_s could be estimated using synthetic environmental variables, and many of these driving environmental variables are highly correlated to one another. Previous studies have applied statistical approaches, including simple linear regression (Hultine et al., 2010) and multiple linear regression (Qu et al., 2007; Si et al., 2007), to estimate sap flow variations. O'Brien et al. (2004) used principle components analysis (PCA) to explore the underlying structure in multiple co-varying meteorological variables to estimate whole-tree sap flux, and applied a simple S-shaped model and composite environmental index to estimate V_s in tropical species. Moreover, for well-coupled forest canopies, V_s could be estimated using some non-linear, multiplicative and independent functions (applied to modify through Jarvis-Stewart (JS) model) (Komatsu et al., 2006).

The modified JS model has been successfully applied to various types of forests (Dierick and Hölscher, 2009; Whitley et al., 2009; Han et al., 2012) with two to four factorial functions for canopy or stand transpiration. However, incongruent patterns in V_s variations to driving variables complicate mechanisms related to the dynamics of whole-tree transpiration. Zeppel et al. (2004) reported an obvious hysteretic response of V_s to photosynthetically active radiation (PAR) and VPD . Moreover, hysteretic patterns that vary from a few minutes to several hours have a significant effect on relationships between hourly V_s and daily V_s and environmental variables (Oren et al., 1999). Zheng et al. (2014) indicated that the hysteretic response of evapotranspiration to temperature (T_a) and VPD would cause certain uncertainties in simply evapotranspiration estimates. However, hysteresis is either eliminated or significantly reduced for half-hourly V_s estimations when it is combined with R_s and VPD in an evaporative demand index (O'Brien et al., 2004). Consequently, whether hysteretic influences the performance of sap flow models at a temporal scale remains uncertain.

In this study, we presented the results of V_s of *Populus euphratica*, R_s , VPD and soil water content (SWC) from a field investigation during the growing season of 2012 in Northwest China. Our objectives were to: (1) detect the responses of V_s to main environmental variables at both hourly and daily scales; (2) compare the performance of a simple linear model and a physically-based non-linear model to estimate hourly V_s and daily V_s of *P. euphratica*; and (3) evaluate the hysteretic responses of V_s to R_s and VPD . Our hypothesis was that a physically-based non-linear model which takes into account R_s and VPD will provide direct and effective V_s estimations during the growing season. Moreover, the hysteretic phenomenon between V_s and environmental variables will play a key role in V_s estimation.

1 Materials and methods

1.1 Study area

This study was conducted at the Alxa Desert Eco-hydrology Experimental Research Station, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences (42°01'N, 101°21'E; 884 m asl) in the lower reaches of the Heihe River Basin, Northwest China. The region is characterized by a continental arid climate, with an average annual precipitation of 37.4 mm, an average annual pan evaporation of >3,390 mm and an annual average temperature of 8.2°C. Prevailing wind directions are northwest in winter and spring, and southwest to south in summer and autumn. Annual average wind speed ranges from 3.4 to 4.0 m/s. Soil physical properties of the study area are provided in Table 1.

Table 1 Soil physical properties of the study area

Soil depth (cm)	Soil bulk density (g/cm ³)	Soil particle composition (%)			Soil field water capacity (cm ³ /cm ³)
		Sand	Silt	Clay	
0–10	1.05	46.74	47.71	5.56	38.93
10–30	1.43	49.17	43.86	6.97	46.53
30–50	1.41	42.13	51.54	6.33	11.39
50–80	1.28	28.45	63.86	7.69	7.81
80–120	1.47	99.00	0.86	0.14	32.92
120–160	1.54	25.37	70.80	3.83	33.66

The experimental field in this study is located at approximately 200 m southwest from the Alxa Desert Eco-hydrology Experimental Research Station. It is protected by a 100 m×100 m fenced enclosure. A detailed field inventory was conducted in July 2011. The dominant overstory species was *P. euphratica*, with the density of 146 trees/hm² and a canopy cover of approximate 42%. The next dominant overstory species was *Tamatis ramosissima* with approximately 42 trees/hm². The understory species was dominated by grasses, including *Sophra alopecutoides*, *Achnatherum splendens* and *Karelinia caspica*. Groundwater depths ranged from 1.93 to 2.65 m during the experimental period (the growing season of 2012). Apart from precipitation, groundwater recharged from the Heihe River provided the main sources of water to sustain the regional ecosystems. The average age of *P. euphratica* forests was 120 years old, the average tree height was 11.17 m, and the tree canopy dimensions in an east to west direction and in a south to north direction were 5.93 and 5.93 m, respectively (Table 2). The average diameter at breast height (DBH) was 45.90 cm. The sapwood area (*SA*, cm²) was determined by the drilling method. In total, 66 cores were extracted from 66 trees based on DBH using an increment borer from which the sapwood empirical formula was established ($SA=1.27 \times DBH^{1.43}$). Thus, the average *SA* was approximately 305.74 cm².

Table 2 Height, diameter at breast height (DBH) and canopy diameter of trees in the enclosed *P. euphratica* site

	Height (m)	DBH (cm)	Canopy diameter (m)	
			East–west	South–north
Quadrat	11.17±2.35	45.90±14.38	5.93±1.59	5.93±1.68
Tree 1	12.9	43.4	5.3	7.8
Tree 2	12.6	52.3	8.2	8.6
Tree 3	16.3	47.3	6.4	8.8

Note: Mean values of the quadrat were calculated from 146 trees; and tree 1, tree 2 and tree 3 were selected as samples to monitor sap flow. Mean±SD.

1.2 Sap flow measurements

We selected three representatives of *P. euphratica* trees by means of tree height and DBH in the experimental field. We used heat ratio method (HRM) to determine the continuous *V_s* during the growing season (June–September, day 168 to 276) of 2012. HRM was used for measuring the ratio of *T_a* increase following the release of a pulse of heat at points equidistant downstream and upstream from center heater. A pair of copper-constantan thermocouples (HRM-30 sap flow

sensors, ICT International Pty Ltd., Armidale, NSW, Australia) were symmetrically installed into the north facing of xylem tissues of stems (1.3-m height) 6 mm above and 6 mm below the center heater probe, respectively. Taking into account the radial distributions of sapwood, each thermocouple had two junctions to measure V_s , which were measured in xylem tissues at 7.5 and 22.5 mm depths from the tip of the needle. A metal guide was used to aid in drilling holes and minimize probe misalignment during insertion. Pulses were sent at an interval of 30 min, and T_a ratios were recorded continuously by a data logger (Smart Logger, ICT, Australia). We calculated the heat pulse velocity (V_h ; cm/h) according to the method of Burgess et al. (2001):

$$V_h = \frac{k}{x} \ln\left(\frac{v_1}{v_2}\right) \times 3600. \quad (1)$$

Where, k (cm^2/s) is the thermal diffusivity of fresh wood; x (cm) is the distance between the heater and the thermocouple; and v_1 and v_2 ($^\circ\text{C}$) are the differences of the initial T_a between the two thermocouples (downstream and upstream of the flow in relation to the position of the heater, respectively). k was initially fixed at $2.50 \times 10^3 \text{ cm}^2/\text{s}$, but this value was adjusted after we determined the thermal properties of wood ($(2.98 \pm 0.21) \times 10^3 \text{ cm}^2/\text{s}$). All wound and misalignment corrections of probes were conducted according to Burgess et al. (2001), and the final V_s was then calculated according to the method of Burgess et al. (2001).

1.3 Soil volumetric water content and meteorological parameters

Soil volumetric water content was monitored by multisensory frequency domain probes (EnviroSCAN; Sentek, Adelaide, Australia) at five soil depths (10, 30, 50, 80 and 140 cm), and recorded at 10-min intervals using a CR1000 data logger (Campbell Inc., USA). Each capacity sensor was frequency-normalized by calibration against air and water in the laboratory to ensure the precision measurement (Yu et al., 2013). R_s (W/m^2) was measured using a pyranometer (CM5, Kipp & Zonen, the Netherlands), and T_a ($^\circ\text{C}$) and relative humidity (RH ; %) were measured using a Rotronic Sensor (RS2, Rotronic, Switzerland). Additionally, VPD was determined by T_a and RH according to the method of Compbell and Norman (1998). Meteorological data, including R_s , T_a , RH and precipitation were recorded by a data logger as mean values of 30-min intervals from an automatic meteorological station.

1.4 Models for estimating V_s

Physiological studies have shown that V_s mainly depends on environmental variables, such as R_s , VPD and SWC (Si et al., 2007; Guan et al., 2012). In this study, we explored two approaches (multiple linear regression analysis (linear model) and modified non-linear JS model) to simulate the hourly V_s and daily V_s . Firstly, the linear model was applied to associate V_s to major environmental variables as follows:

$$V_s = a + bR_s + cVPD. \quad (2)$$

Where, a , b and c are regression coefficients.

Secondly, the JS model was modified from an analytical model of stomatal conductance proposed by Jarvis (1976). Because of the simplicity and the direct calculation of stomatal conductance or canopy conductance as a function of environmental variables of this model, it has been widely used in soil-vegetation-atmosphere-transfer (SVAT) formulations (Oguntunde et al., 2007). Theoretically, stand water use could be calculated from canopy conductance by VPD for a well-coupled forest canopy. Thus, a modified JS model was used to calculate the recent canopy water use (Komatsu et al., 2006; Dierick and Hölscher, 2009; Köhler et al., 2009; Whitley et al., 2009; Han et al., 2012). In this case, V_s , which is similar to water use, was assumed to be calculated by R_s and VPD according to the following equation:

$$V_s = V_{s-\max} \times f(R_s) \times f(VPD). \quad (3)$$

Where, $V_{s-\max}$ is defined as the maximum V_s for each driving variable under non-limiting environmental conditions; and f denoted a series of normalized response functions. Each of these functions had values between 0 and 1 ($0 \leq f \leq 1$). To determine the response functions for V_s in terms of its driving environmental variables, we assumed that the response of V_s to each variable

was independent of all the other variables when values for the other variables were not limiting.

Solar radiation (R_s) response was determined by a hyperbolic-saturating function, which was applied to express the response of canopy transpiration to R_s as follows (Komatsu et al., 2006; Whitley et al., 2009):

$$f(R_s) = \left(\frac{R_s}{R_m}\right) \times \left(\frac{R_m + k_1}{R_s + k_1}\right). \quad (4)$$

Where, R_m is an arbitrary radiation constant often fixed at 1,000 W/m²; and k_1 (W/m²) is the curvature of the relationship between V_s and R_s .

Vapor pressure deficit (VPD) response had three different expressions: (1) a strong S-shaped curve (O'Brien et al., 2004; Dierick and Kohler, 2009); (2) a new three-phrase response shape, which is similar to Boltzmann distribution (Whitley et al., 2009); and (3) an exponential saturation function (Kumagai et al., 2007; Du et al., 2011). We selected the S-shaped curve after a preliminary comparison between these three functions as follows:

$$f(VPD) = 1 / (1 + \exp((k_2 - VPD)/k_3)). \quad (5)$$

Where, k_2 (kPa) is the VPD from which V_s increases to half of the maximum value (R_s non-limiting); and k_3 (kPa) is related to the slope. Parameters k_1 – k_3 were optimized by minimizing the residual sum of squares using the Levenberg-Marquart algorithm (LMA) (Marquardt, 1963).

1.5 Hysteretic response of V_s to environmental variables

Hysteretic effect occurred when an increase in a given independent variable does not cause the same variation in a dependent variable. We used cross-correlation coefficient plots between independent and dependent variables to identify their direct and inverse relationships at different time. Specifically, serial correlation coefficients were respectively calculated between 30-min mean V_s observed at time t and corresponding meteorological variables (both forward and backward time t) at a 30-min time step (for a total of 17 scenarios). When correlation coefficient between V_s and each environmental variable reached optimum, time lags were then regarded as actual hysteresis. Rearranged environmental variables with hysteresis were then used to retrain and recalibrate the sap flow model. We named this method as “hysteresis calibration” in a subsequent study.

1.6 Data sets and statistical analysis

Measurements of V_s were filtered to eliminate hours when R_s was zero. This allowed us to only use daytime (07:00–19:00) sap flow and environmental data for modeling inputs. Days with rainfall were also excluded to avoid wet-canopy conditions. For evaluating the linear and JS models, the pre-selected measurement period (90 days) during the growing season was partitioned into two separate data sets of alternate days. Data of odd days (training data) were used to optimize response parameters of Eqs. 3–5, and data of even days (calibration data) were used to validate the model. No systematic patterns were evident in the data and no changes to model outputs occurred when allocation of each half of the data set to either optimization or validation days were reversed. Finally, root mean square error (RMSE) was used to weigh the deviation between observed value in the i^{th} day (y_i) and predicted value in the i^{th} day (\bar{y}_i):

$$\text{RMSE} = \left(\frac{1}{n} \sum_{i=1}^n (y_i - \bar{y}_i)^2\right)^{\frac{1}{2}}. \quad (6)$$

All procedures were conducted with the SPSS software 17.0 (SPSS Inc., USA) and SigmaPlot software 10.0 (Hearne Scientific Software Plc, Melbourne, Australia).

2 Results

2.1 Variations in V_s and environmental variables

Significant differences were observed for the variations of V_s and environmental variables during

the growing season ($P < 0.001$, $n = 90$; ANOVA). Precipitation during the measurement period was 27.4 mm with only once large precipitation event (15.4 mm) occurring on day 206. This large precipitation event increased SWC significantly at the depth of 0–140 cm by 13.5%, while SWC was increased slightly under the other precipitation events (Fig. 1). Average T_a was 28.03°C, which was consistent with the long-term average T_a from June to September recorded at the Ejina meteorological station. Mean daily V_s changed from 6.66 cm/h on one rainy day (day 206) to 23.37 cm/h on one rain-free day (day 216) and increased 3.5 folds during consecutive days. Daily R_s ranged from 513.75 to 1,061.08 W/m², while mean daily VPD varied from 0.41 to 5.66 kPa. Although the seasonal variations in R_s and VPD were similar to that in V_s during most days, mismatching patterns also occurred on certain periods (Fig. 1).

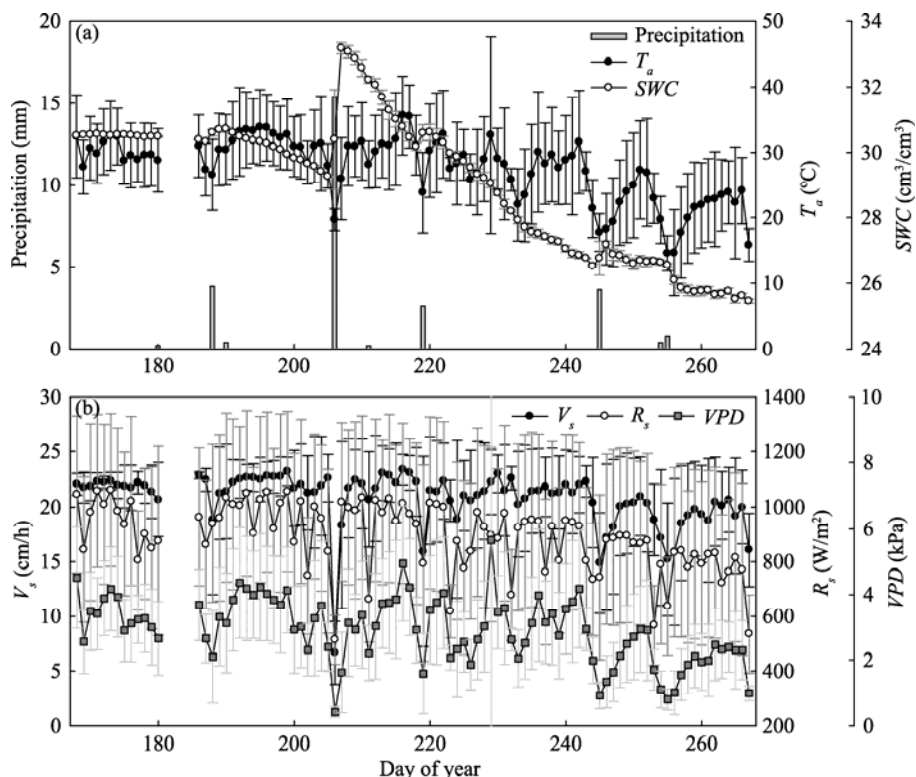


Fig. 1 Seasonal variations in (a) precipitation, temperature (T_a) and soil water content (SWC), and (b) sap flow velocity (V_s), solar radiation (R_s) and vapor pressure deficit (VPD) during the growing season of 2012. Error bar denotes standard deviation at a daily scale. Data between days 181 and 185 missed due to sensor damage.

2.2 Response of V_s to environmental variables

At an hourly scale, V_s was significantly correlated to all environmental variables ($P < 0.01$), with the correlation coefficients of $T_a > VPD > R_s > SWC$ (Table 3). For avoiding the potential effects of T_a and VPD co-variation, we then used partial correlation analysis to determine that R_s , VPD and SWC were the main driving environmental variables. We found that V_s was hyperbolic increased following the increasing R_s until it reached approximately 600 W/m², from that further increasing in R_s did not lead to corresponding increasing in V_s (Fig. 2a). As evaporative demand increased, increasing VPD caused corresponding increases in V_s for lower values of VPD (< 2 kPa), but for higher values of VPD , V_s exhibited a stable trend with increasing VPD (Fig. 2b). Thus, a matching strong sigmoid (“S”) curve was found between V_s and VPD . Unfortunately, no clear correlations were found between V_s and SWC (Fig. 2c).

V_s was also positively correlated with environmental variables (with the correlation coefficients of $VPD > T_a > R_s > SWC$) at a daily scale (Table 3). A hyperbolic-saturating function and a sigmoid function were shown between V_s and R_s , and V_s and VPD , respectively (Figs. 2d and e). However,

the saturation points of R_s (900 W/m^2) and VPD (3.5 kPa) at a daily scale were greater than those at an hourly scale (600 W/m^2 for R_s and 2 kPa for VPD). SWC was weakly linearly correlated to V_s (Fig. 2f). Thus, we selected R_s and VPD to analyze the response of V_s to environmental variables at both hourly and daily scales.

Table 3 Correlation coefficients between V_s and environmental variables during the growing season

	R_s	VPD	T_a	SWC
Hourly V_s	0.651**	0.772**	0.791**	0.336**
Daily V_s	0.545**	0.830**	0.822**	0.388**

Note: ** means significance at $P < 0.01$ level. V_s , sap flow velocity; R_s , solar radiation; VPD , vapor pressure deficit; T_a , temperature; SWC , soil water content.

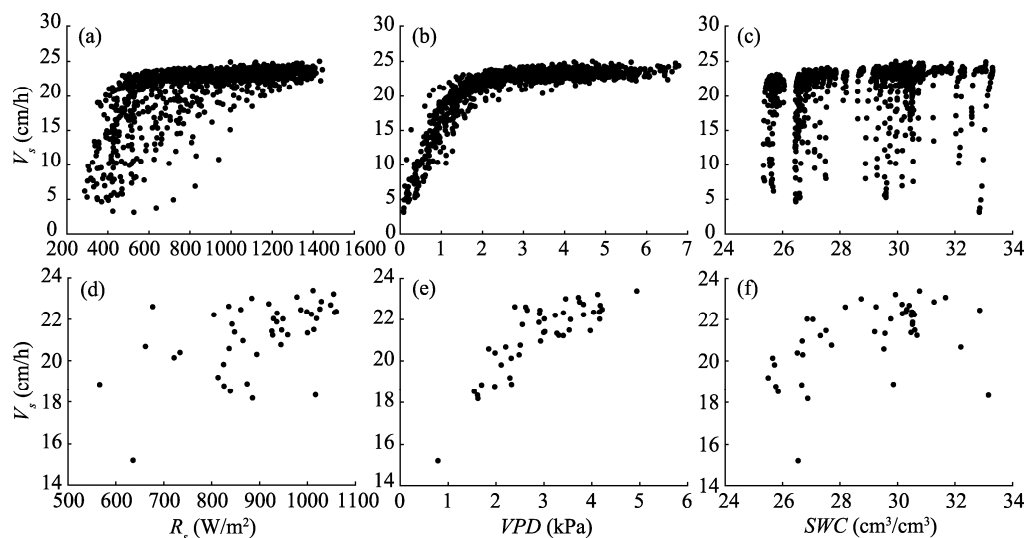


Fig. 2 Relationships of V_s with (a) R_s , (b) VPD and (c) SWC at an hourly scale; and (d) R_s , (e) VPD and (f) SWC at a daily scale based on experimental data

2.3 Modeling V_s based on environmental variables

Compared to the linear model, the coefficient (R^2) was higher but RMSE was lower for the JS model (Fig. 3). At an hourly scale, although V_s was significantly overestimated between 07:00 and 08:00, it could be well-determined between 09:00 and 19:00 using the JS model (Fig. 3a). The slope, R^2 and RMSE of regression of observed V_s and modeled V_s generated by the JS model were 0.98, 0.93 and 1.07, respectively, which were all higher than those generated by the linear model (Fig. 4a). At a daily scale, there was a slight underestimate of V_s from 17 July to 27 July and from 13 August to 21 August for both models, which coincided with the relatively low VPD resulting from precipitation (Fig. 3b). However, compared to the linear model, the JS model showed stronger linear relationships between observed V_s and modeled V_s . Specifically, R^2 and the slope for the JS model (0.91 and 0.99, respectively) were higher than those for the linear model (0.71 and 0.83, respectively), while RMSE for the JS model (0.49) was lower than that for the linear model (0.86; Fig. 4b). It demonstrated that seasonal variations in hourly V_s and daily V_s could be well-estimated using R_s and VPD through physically-based non-linear model.

2.4 Hysteretic response of V_s to environmental variables

The maximum V_s occurred either coincident with or later than the maximum R_s , and earlier than the maximum VPD (Fig. 5). At an hourly scale, the maximum V_s occurred earlier than the maximum VPD by approximately 0.5 h ($R^2=0.79$) but later than the maximum R_s by approximate 1.0 h ($R^2=0.72$; Fig. 6). At a daily scale, the maximum V_s lagged behind the maximum VPD by approximately 2.5 h ($R^2=0.84$) but occurred earlier than the maximum R_s by approximately 2 h ($R^2=0.56$; Fig. 6). At an hourly scale, hysteretic response of V_s to environmental variables unexpectedly weakened when R_s and VPD were combined together due to little increases in $V_{s\text{-max}}$,

R^2 and RMSE. At a daily scale, R^2 increased by approximately 2% (0.85 to 0.88) but RMSE decreased by approximately 10% (0.62 to 0.56) after R_s and VPD hysteretic calibration, demonstrating a slightly improvement in analyzing the response of V_s to environmental variables after taking the hysteretic response of R_s and VPD into account (Table 4).

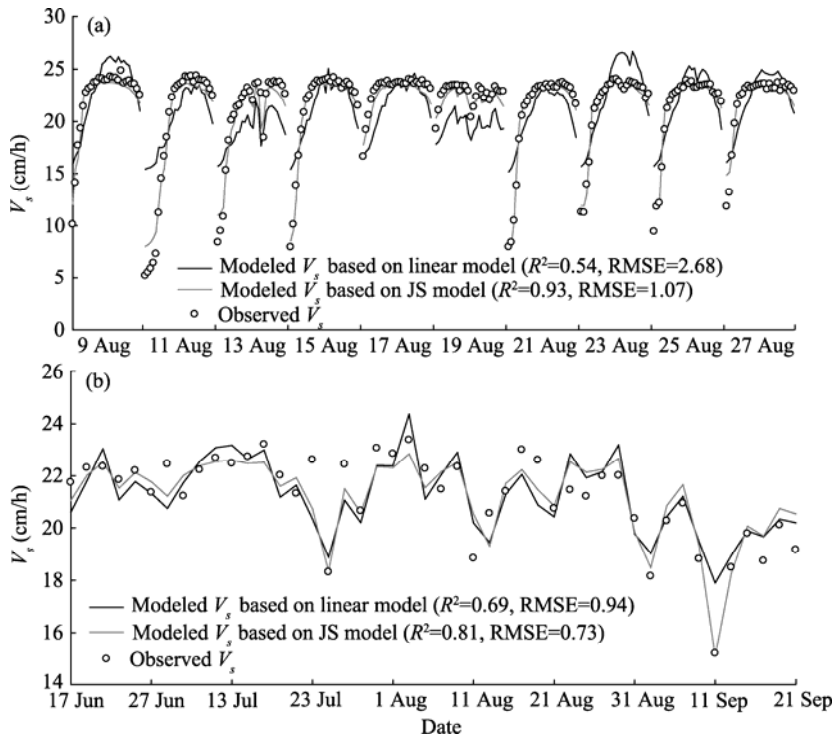


Fig. 3 Comparison between observed V_s and modeled V_s from the linear model and modified Jarvis-Stewart (JS) model for the training data sets in odd days (a) at an hourly scale (07:00–19:00) during 9–27 August 2012 and (b) at a daily scale from 17 June to 21 September, 2012. RMSE, root mean square error. Data in 29 June, 1 July, 3 July and 1 September were omitted due to rainfall events.

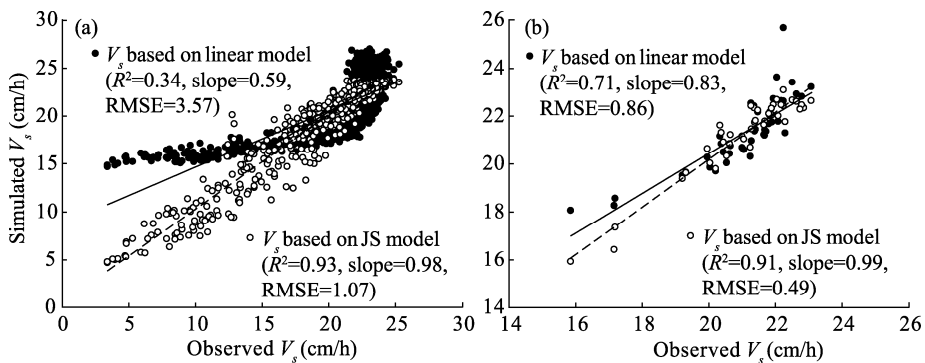


Fig. 4 Relationships between observed V_s and modeled V_s from the linear model and the modified JS model based on calibration data (a) at an hourly scale and (b) at a daily scale

3 Discussion

3.1 Response of V_s to environmental variables

Seasonal variations in V_s of *P. euphratica* were evident, and V_s was significantly positively correlated to environmental variables during the growing season. Previous studies also showed good relationships between V_s and R_s for *Artemisia ordosica* (Huang et al., 2010), *Salix*

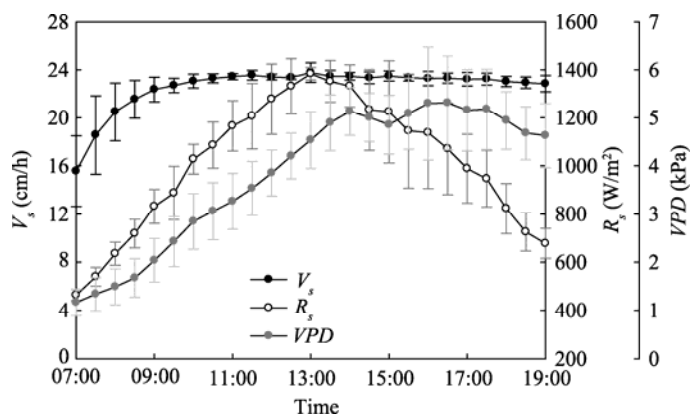


Fig. 5 Daily variations in V_s , R_s and VPD during 10 sunny days

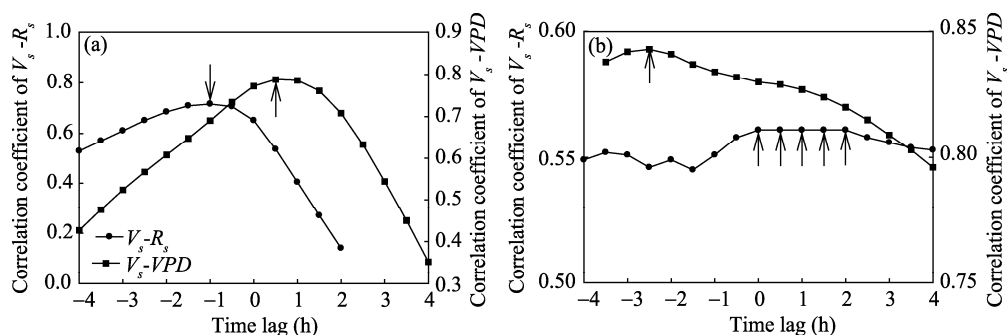


Fig. 6 Cross-correlation of V_s with R_s and VPD (a) at an hourly scale and (b) at a daily scale. Maximum correlation coefficient was retained as the time lag. Values in the horizontal axis higher than zero represent that the maximum V_s occurs earlier than the maximum environmental variables, while values lower than zero represent that the maximum V_s occurs later than the maximum environmental variables. The arrows indicate the maximum correlation coefficients.

Table 4 Comparison between parameter estimations from optimization of the modified Jarvis-Stewart (JS) model for a weighted non-linear least squares regime for non-hysteretic and hysteretic calibration

Time scale	Calibration	V_{s-max} (cm/h)	k_1 (W/m ²)	k_2 (kPa)	k_3 (kPa)	R^2	RMSE
Hourly	Non-hysteresis	23.18±0.03	82.33±3.39	0.53±0.01	0.43±0.01	0.93	1.06
	Hysteresis	23.08±0.03	84.83±3.91	0.49±0.01	0.40±0.01	0.92	1.09
Daily	Non-hysteresis	22.92±0.24	-37.82±24.71	0.14±0.11	1.05±0.11	0.85	0.62
	Hysteresis	23.94±0.22	41.91±24.54	-0.03±0.10	0.88±0.09	0.88	0.56

Note: RMSE, root mean square error.

matsudana (Yin et al., 2014) and *Haloxylon ammodendron* (Zheng and Wang, 2014) in arid regions of Northwest China. However, for *P. euphratica* in this study, VPD was the dominant limiting factor to V_s at both hourly and daily scales due to higher energy and water availability, and large VPD ranges (2–7 kPa) constrained V_s .

As increasing R_s , V_s increased asymptotically. Hyperbolic saturating functions to plant water use or V_s have been extensively applied (Komatsu et al., 2006; Whitley et al., 2009; Han et al., 2012). Different to linear relationship of V_s and R_s under wetter conditions (Rousseaux et al., 2009; Singer et al., 2010; Liu et al., 2012), V_s tended to be stable when R_s was in the neighborhood of 600 and 900 W/m² at hourly and daily scales under arid conditions in this study, respectively (Figs. 2a and d). David et al. (2004) reported a progressive loss in V_s sensitivity to R_s from morning to afternoon and attributed this phenomenon to transpiration saturation above a certain level of VPD by means of gradual stomatal closure. At low R_s ranges, energy supplies limited evaporation; while at high R_s levels, soil moisture and hydraulic resistance between soil and canopy limited evaporation (Whitley et al., 2009).

The response of V_s to VPD was more sensitive than that to R_s (Table 3). V_s exhibited a positive relationship with VPD at lower levels (<2 kPa), while for higher values of VPD (2–7 kPa), V_s showed a plateau-type response to VPD at an hourly scale (Fig. 2e). The response of V_s to increasing VPD compared well with other studies that have found an alternative exponential saturation response, e.g. relationship between V_s (or water use) and VPD for *Camellia japonica* in the Japanese cedar forest watershed on Kyushu Island, Japan (Kumagai et al., 2007) and between V_s and co-variation of VPD and R_s for *Robinia pseudoacacia*, *Quercus liaotungensis* and *Abies sibirica* in the Loess Plateau of China (Du et al., 2011). As VPD increasing, the two-phase behavior of V_s was a feedback between increasing cuticular water loss and declining supply of water to guard cells which resulted in direct stomatal response to VPD . A low decoupling coefficient less than 0.2 indicated that *P. euphratica* was well coupled to the atmosphere and able to exert effective stomatal control over V_s or transpiration in response to environmental stresses (Li et al., 2013). Thus, for avoiding excessive water loss and maintaining water potential above a critical threshold, effective stomatal control and, hence, canopy conductance should be taken on preventing cavitations and irreversible loss of xylem functions (Bush et al., 2008; Tognetti et al., 2009). However, a new three-phase response of stand transpiration to VPD was found for Australia native woodland (dominated by *Eucalyptus crebra* and *Callitris glaucophylla*) in northwestern New South Wales of Australia (Whitley et al., 2009) and *Platanus orientalis* in the Tuqiaogou watershed of China (Han et al., 2012). V_s (or stand scale transpiration) tended to increase and further reached the peak with increasing VPD , and then decreased with gradually increasing VPD later. Naithani et al. (2012) attributed this phenomenon to the stomatal regulation of transpiration for declining the root water supply. Thus strong stomatal regulation was taken effects to control the V_s of *P. euphratica* as evaporative demand increasing. However, *P. euphratica* could use deep SWC and groundwater following well-developed root system to avoid declining hydraulic conductance from soil to atmosphere, therefore, V_s remained at plateau level when undergoing high levels of VPD (>2 kPa) in this study. Moreover, this could also be related to the sensitivity of desert species to VPD and leaf water potential. Finally, V_s showed stable trend with increasing VPD in the range of 2–3.5 kPa in this study, and this range was larger than those observed by Pataki and Oren (2003), Komastu et al. (2006), Oguntunde et al. (2007) and Han et al. (2012), but was similar to that observed by Whitley et al. (2009). This was probably because the site selected for our study was extremely dry, and experienced a large range of VPD (0–7 kPa) and would recover from a long period of drought, compared to those mentioned above.

Bernier et al. (2002) and Ford et al. (2005) indicated that only under very low soil water availability did transpiration show a strong relationship with SWC . Lower soil water availability could increase hydraulic resistance between soil and root systems, prevent water movement from soil to plant leaves, and subsequently trigger stomatal closure, which in turn would obviously reduce transpiration rates (Tognetti et al., 2009). Moreover, Si et al. (2014) indicated that the main water source of *P. euphratica* was from the soil water in the subsoil layer (140–180 cm) and groundwater at a subsurface depth of 2.00–2.65 m. Thus, V_s was slightly constrained by SWC in this study due to the narrow range of SWC and low groundwater availability during the growing season of 2012 (Figs. 2c and f).

3.2 V_s modeling and hysteretic calibration

Compared to the linear model, the JS model could estimate the V_s of *P. euphratica* more accurately for higher R^2 and lower $RMSE$ values both at hourly and daily scales (Fig. 3). Previous studies have developed multiple linear models for analyzing the responses of V_s to the main environmental variables, including R_s , T_a , VPD , wind speed and SWC (Qu et al., 2007; Si et al., 2007). In this study, the linear model only explained 34% and 71% of V_s variation at hourly and daily scales, respectively (Fig. 4). This was possibly caused by disregarding threshold constraints on V_s from driving environmental variables and the interactions between these variables (Table 3). The JS model complied with the primary assumption in which driving environmental variables should be independent from each other, which was defined in the original JS model for estimating

canopy conductance (Macfarlane et al., 2004). Observed hourly V_s varied 4.8 folds over 10 sunny days in August 2012, and the JS model was able to follow the V_s variations accurately (Fig. 3a). The JS model has been successfully used to estimate sap flux density or stand transpiration of Japanese *Cryptomeria japonica* trees (Komatsu et al., 2006), native Australian forests (Whitley et al., 2009), Indonesian *Cacao* and *Gliricidia* trees (Köhler et al., 2009) and Chinese *Platycladus orientalis* trees (Han et al., 2012). However, the JS model failed to detect the measured V_s for low values of R_s and VPD during the morning hours.

At an hourly scale, the maximum V_s occurred earlier than the maximum VPD by approximately 0.5 h but later than the maximum R_s by approximate 1.0 h. At a daily scale, the maximum V_s lagged behind the maximum VPD by approximately 2.5 h while occurred earlier than the maximum R_s by approximately 2 h. Lu et al. (2004) reported that understanding the hysteresis between V_s and environmental variables was a solid foundation in identifying the mechanisms of V_s and whole tree transpiration. Various generations of hysteresis occurring between V_s (or transpiration) and environmental variables have been identified, including progressive (canopy) stomatal closure (Chen et al., 2011; Zheng et al., 2014), declining patterns in soil-to-canopy conductance at a daily scale (Zeppel et al., 2004), and stem water storage capacity (Kumagai et al., 2009). Thus, hysteretic effect could be considered as a means of plant self-protection in avoiding the overlapping of peak transpiration and the maximum meteorological variables to prevent excessive water extraction from stems (Chen et al., 2011). There were many previous studies demonstrated that sap flow (or water use) was mismatched with environmental variables (Oren et al., 1999; Ford et al., 2005), while a few studies discussed the effect of time lag on V_s estimation. O'Brien et al. (2004) reported the morning hysteresis in V_s response to R_s and the afternoon hysteresis in V_s response to VPD , and the result showed that hysteresis was either eliminated or significantly reduced when it was combined with R_s and VPD as the evaporative demand index. Oguntunde et al. (2007) ignored hysteretic effects in transpiration modeling due to the synchronicity of transpiration and potential transpiration. An alternative autoregressive integrated moving average (ARIMA) time series model (with orders of 3, 1 and 1) for synthetic photosynthetically active radiation, VPD and SWC emphasized the importance of hysteresis in hydrological processes related to canopy transpiration modeling (Ford et al., 2005). Unexpectedly, there were no improvements in hourly V_s estimations and only a slight enhancement in daily V_s estimations using the JS model after hysteretic calibration in this study (Table 4). This can be partly explained by the fact that the combination of morning hysteresis that related to V_s - R_s and afternoon hysteresis that related to V_s - VPD would eliminate or reduce the mismatched patterns between V_s and synthetic environmental variables as a whole.

4 Conclusions

In this study, we examined the relationships between V_s and main environmental variables and found that V_s of *P. euphratica* was driven by R_s , VPD and SWC with an order of $VPD > R_s > SWC$ at both hourly and daily scales. Obvious threshold constraints of R_s and VPD on V_s were observed, and they exhibited hyperbolic-saturating and sigmoid functions, respectively, especially at an hourly scale. A multiple linear regression and a newly modified JS model were then used to model V_s according to the responses of V_s to R_s and VPD at both hourly and daily scales during the growing season of 2012. Compared to the linear model, the JS model could estimate the V_s variations more accurately. Although significant hysteresis in V_s - R_s and V_s - VPD relationships was found at both hourly and daily scales, no significant improvements in V_s estimation were detected after hysteretic calibration. This indicated that hysteretic response of V_s to environmental variables would be eliminated when taking the time lag in the morning (for V_s - R_s) and afternoon (for V_s - VPD) into account together. These findings will help us understand the comprehensive mechanisms of seasonal patterns of V_s at hourly and daily scales, as well as provide new insights into evaluating the contribution of *P. euphratica* trees to water use for desert riparian ecosystems in the Heihe River Basin.

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