Response to the reviewers' comments

Ref: doi:10.5194/bg-2016-480
Title: **Soil moisture control on sap-flow response to biophysical factors in a desert-shrub species, *Artemisia ordosica***
Authors: TianShan Zha, Duo Qian, Xin Jia, Yujie Bai, Yun Tian , Charles P.-A. Bourque, Jingyong Ma, Wei Feng, Bin Wu, Heli Peltola

Dear Editor,

Thank you very much for your helpful comments and suggestions for improvement of our manuscript. We have carefully looked at your comments and have revised the manuscript accordingly. Please find below our responses to your comments and/or revisions to the manuscript.

We look forward to your decision and the possible publication of our manuscript in the special issue of BG, *Ecosystem processes and functioning across current and future dryness gradients in arid and semi-arid lands*.

Kind regards,
Tianshan Zha

Comments to the Author:
The manuscript was reasonably well-designed and written if not perhaps a bit standard with limited new insights into the response of sapflux to environmental variables in dryland ecosystems. The discussion was a weak point; mechanistic rigor could be added by noting important lags in the soil-vegetation-atmosphere system that must be taken into account to understand hysteresis behavior (e.g. Bohrer et al. http://onlinelibrary.wiley.com/doi/10.1029/2005WR004181/full or Matheny et al., http://onlinelibrary.wiley.com/doi/10.1002/2014JG002623/full). The discussion of hysteresis loops is interesting but must be framed more mechanistically to have full impact. I also note that the discussion of the decoupling coefficient was somewhat lacking after its introduction in the Methods section nor is it clear how u* was calculated for atmospheric conductance calculations. Please address these and the following minor comments and send a revised manuscript for consideration of publication.

RESPONSE: The discussion on hysteresis has been re-written (see line 338-356). The decoupling coefficient was used in the discussion (see line 350-351). The u* was used as input variable of equation (2) to calculate aerodynamic conductance which is used to calculate decoupling coefficient. (line 182, line 178)

Minor comments:
(All line numbers correspond to the Author's Response manuscript.)

Quantify 'sizeable' on line 455.
RESPONSE: We revised the sentence as “resulting in transpiration 34% lower in 2013 than that in 2014.” (line 52-53)

'and thus less sensitive' on line 461.
RESPONSE: We revised the sentence. (line 58)

I'm not sure what the resultant for line 489 is but I assume that it will be improved by BG editorial services. (The same holds for line 509.)
RESPONSE: There is something wrong with the format. There was no ‘the resultant’ in clear copy of the ms.

502: usually around midday
RESPONSE: We revised the word as suggested. (line 98)

In equation 2 how was friction velocity measured? (and wind speed for that matter, which is described in the following subsection 2.3 that would be better off before the description of the decoupling coefficient.)
RESPONSE: The friction velocity was measured using eddy covariance system (line 184). We switch the order of subsection 2.2 and 2.3, so that the description of environmental measurement appears before the description of stomatal conductance and decoupling coefficient. (see line 183-184).

On line 594, why these definitions of the seasons?
RESPONSE: The reason we defined the seasons is to simply clarify the calendar period of each season (spring, summer, and autumn) that was used in the manuscript.

on line 598, these REW/VWC relationships should approximately hold for different soil types: do the references relate to the soil types found at the site? On line 604 I don't understand how this would vary from year to year.
RESPONSE: The soil types were not described, but the studies were done in forest stands with different soil types in ten European countries including Mediterranean climate, and Australia as well. Therefore, the REW of 0.4 was reasonable as a drought threshold.
The annual precipitation is different, therefore, the maximum and minimum soil water content varies with years.

Ref:

Granier, A., Bréda, N., Biron, P., and Villette, S.: A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. Ecol. Model., 116, 269–283, 1999.

Granier, A., Reichstein M., Bréda N., Janssens I. A., Falge E., Ciais P., Grünwald T., Aubinet M., Berbigier P., Bernhofer C., Buchmann N., Facini O., Grassi G., Heinesch B., Ilvesniemi H., Kerone P., Knohl A., Köstner B., Lagergren F., Lindroth A., Longdoz B., Loustau D., Mateus J., Montagnani L., Nys C., Moors E., Papale D., Peiffer M., Pilegaard K., Pita G., Pumpanen J., Rambal S., Rebmann C., Rodrigues A., Seufert G., Tenhunen J., Vesala T., and Wang Q.: Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. Agr. Forest Meteorol., 143, 123-145, 2007.

Zeppel, M. J. B., Murray, B. R., Barton, C., and Eamus, D.: Seasonal responses of xylem sap velocity to VPD and solar radiation during drought in a stand of native trees in temperate Australia, Funct. Plant Biol., 31, 461-470, 2004.

Zeppel, M. J. B., Macinnis-Ng, C. M. O., Yunusa, I. A. M., Whitley, R. J., and Eamus, D. Long term trends of stand transpiration in a remnant forest during wet and dry years, J. Hydrol., 349, 200-213, 2008.

Should equation 5 be corrected for the clumpiness of shrubs on the landscape? The leaf area index applies for the area near the shrub, but I'm assuming that the space between the shrubs has marginal vegetation which should be accounted for when presenting results on a per-area basis.
RESPONSE: We calculated the leaf area index with allometric equations (see line 164-168) , which was based on measurements of sampled leaf area in the quadrat of the plot, thus clumpiness being corrected.

'Range of daily' should be 'The range of daily' in a few instances in the Results section.
RESPONSE: We revised the sentences. (line 221)

683: peaked
RESPONSE: We revised the sentence. (line 234)

687 wasn't an effective argument: why would you want to remove the influence of Js from the data? Perhaps its diurnal behavior to help understand lag relationships.
RESPONSE: The description in the manuscript was ambiguous, we have deleted it.

On line 766 the counterclockwise hysteresis loop is consistent with capacitance in the soil-plant-atmosphere system: it takes time for water to move up and expand vascular elements during the transition from night to day.
Please justify the statement 'In semi-arid regions, low VWC restricts plant transpiration more than VPD'. I'd assume that they are both important but perhaps at different time scales with VPD playing an important role during the mid-day depression even under high VWC, but low VWC is correlated to low VPD indicating that both water supply via VWC and demand via VPD are important in this case.
RESPONSE: The description is not clear, we have revised the discussions on the hysteresis. (see line 338-355)

I note that the decoupling coefficient was not discussed following its description in the Methods section.
RESPONSE: In the discussion, the Ω supported the result, as "This is further supported by a large Ω, when VWC is high (Fig. 10b). The larger Ω is, the greater is the influence of R_s on J_s. The effect of VWC on time lag varied between 2013 and 2014. " (line 349-350)

In Figure 6 please avoid using red and green simultaneously if possible (or at least choose different symbols so our red-green colorblind colleagues can distinguish them).
RESPONSE: We revised the figure and added different symbols.

Soil moisture control on sap-flow response to biophysical factors in a desert-shrub species, *Artemisia ordosica*

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Short title: **Sap flow in *Artemisia ordosica***

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Author Contribution Statement:

Dr.'s Duo Qian and Tianshan Zha contributed equally to the design and implementation of the field experiment, data collection and analysis, and writing the first draft of the manuscript.

Dr. Xin Jia gave helpful suggestions concerning the analysis of the field data and contributed to the scientific revision and editing of the manuscript.

Prof. Bin Wu contributed to the design of the experiment.

Dr.'s Charles P.-A. Bourque and Heli Peltola contributed to the scientific revision and editing of the manuscript.

Yujie Bai, Wei Feng, and Yun Tian were involved in the implementation of the experiment and in the revision of the manuscript.

Key Message: This study provides a significant contribution to the understanding of acclimation processes in desert-shrub species to drought-associated stress in dryland ecosystems

Conflict of Interest:

This research was financially supported by grants from the National Natural Science Foundation of China (NSFC No. 31670710, No. 31670708), the National Basic Research Program of China (Grant No. 2013CB429901), and by the Academy of Finland (Project No. 14921). The project is related to the Finnish-Chinese collaborative research project, EXTREME (2013-2016), between Beijing Forestry University and the University of Eastern Finland, and USCCC. We appreciate Dr. Ben Wang, Sijing Li, Qiang Yang, and others for their help with the fieldwork. **The authors declare that they have no conflict of interest.**

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Abstract: Current understanding of acclimation processes in desert-shrub species to drought stress in dryland ecosystems is still incomplete. In this study, we measured sap flow in *Artemisia ordosica* and associated environmental variables throughout the growing seasons of 2013-2014 (May-September period of each year) to better understand the environmental controls on the temporal dynamics of sap flow. We found that the occurrence of drought in the dry year of 2013 during the leaf-expansion and leaf-expanded periods caused sap flow per leaf area (J_s) to decline significantly, resulting in transpiration being 34% lower in 2013 than ~~that~~ in 2014.~~a sizable drop in transpiration.~~ Sap flow per leaf area correlated positively with radiation (R_s), air temperature (T), and vapor pressure deficit (VPD), when volumetric soil water content (VWC) was > 0.10 $m^3 m^{-3}$. Diurnal J_s was generally ahead of R_s by as much as 6 hours. This lag time, however, decreased with increasing VWC. Relative response of J_s to the environmental variables (i.e., R_s, T, and VPD) varied with VWC, J_s being more biologically-controlled with a low decoupling coefficient and ~~thus less~~low ~~sensitivity~~ sensitiv~~e~~ity to the environmental variables during periods of dryness. According to this study, soil moisture is shown to control sap-flow (and, therefore, plant-transpiration) response in *Artemisia ordosica* to diurnal variations in biophysical factors. The findings of this study add to the knowledge of acclimation processes in desert-shrub species under drought-associated stress. This knowledge is essential to model desert-shrub-ecosystem functioning under changing climatic conditions.

Keywords: sap flow; transpiration; cold-desert shrubs; environmental stress; volumetric soil water content

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1. Introduction

Due to the low amount of precipitation and high potential evapotranspiration in desert ecosystems, low soil water availability limits both plant water- and gas-exchange and, as a consequence, limits vegetation productivity (Razzaghi et al., 2011). Therefore, it is important to understand the mechanisms controlling the vegetation-water dynamics under rapidly changing environments (Jacobsen et al., 2007). Grass species are gradually being replaced by shrub and semi-shrub species in arid and semi-arid areas of northwestern China (Yu et al., 2004). This progression is predicted to continue under a changing climate (Asner et al., 2003; Houghton et al., 1999; Pacala et al., 2001). This is mostly because desert shrubs are able to adapt to hot-dry environments by modifying their morphological characteristics, e.g., by (1) minimizing plant-surface area directly exposed to sun and hot air, (2) producing thick epidermal hairs, (3) thickening cuticle, (4) recessing stomata into leaves (Yang and Zhu, 2011), and (5) increasing root-to-shoot ratios (Eberbach and Burrows, 2006; Forner et al., 2014). Also, acclimation of physiological characteristics of plants under water stress, by way of e.g., water potential, osmotic regulation, anti-oxidation, and photosynthetic characteristics, assist the plants to maintain a hydrological balance (Huang et al., 2011a). Changes in stomatal conductance and, thus, transpiration may ~~likewise~~ equally affect plant water use efficiency (Pacala et al., 2001; Vilagrosa et al., 2003).

Sap flow can accurately reflect water consumption during plant transpiration. It maintains ecosystem balance through the soil-plant-atmosphere continuum, but is often affected by environment factors (Huang *et al*., 2010; Zhao et al., 2016). In recent studies, sap flow in *Tamarix elongate* has been observed to be controlled by solar radiation and air temperature, whereas in *Caragana korshinskii* vapor pressure deficit and solar radiation

Formatted: Left, Automatically adjust right indent when grid is defined, Space Before: 0 pt, Line spacing: single appear to be more important (Jacobsen et al., 2007; Xia et al., 2008). In *Elaeagnus angustifolia*, transpiration is observed to peak at noon, i.e., just before stomatal closure at mid-day under water-deficit conditions (Liu et al., 2011). In contrast, transpiration in *Hedysarum scoparium* peaks multiple times during the day (Xia et al., 2007). Sap flow has been observed to decrease rapidly when the volumetric soil water content (VWC) is lower than the water loss through evapotranspiration (Buzkova et al., 2015). In general, desert shrubs can close their stomata to reduce transpiration when exposed to dehydration stress around mid-~~-~~day. However, differences exist among shrub species with respect to their stomatal response to changes in soil and air moisture deficits (Pacala et al., 2001). For some shrubs, sap-flow response to precipitation varies from an immediate decline after a heavy rainfall to no observable change after a small rainfall event (Asner et al., 2003; Zheng and Wang, 2014). Sap flow has been found to increase with increasing rainfall intensity (Jian et al., 2016). Drought-insensitive shrubs have relatively strong stomatal regulation and, therefore, tend to be insensitive to soil water deficits and rainfall unlike their drought-sensitive counterparts (Du et al., 2011). In general, understanding ~~of~~ the relationship between sap-flow rates in plants and environmental factors is decidedly ~~highly~~ inconsistent, potentially varying with plant habitat (Liu et al., 2011).

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Artemisia ordosica, a shallow-rooted desert shrub, is the dominant plant species in the Mu Us Desert of northwestern China. The shrubs have an important role in combating desertification and in stabilizing sand dunes (Li et al., 2010). Increases in air temperature and precipitation variability and associated shorter wet periods and longer intervals of periodic drought are expected to ensue with projected climate change (Lioubimtseva and Henebry, 2009). During dry periods of the year, sap flow in *Artemisia ordosica* has been observed to be controlled by VWC at ~~about~~ about a 30-cm depth in the soil (Li et al., 2014). Sap-flow rate is known to be affected by variation in precipitation patterns. Soil water content, in combination with other environmental factors, may have a significant influence on sap-flow rate (Li et al., 2014; Zheng and Wang, 2014). Thus, understanding the controlling mechanisms of sap flow in desert shrubs as a function of variations in biotic and abiotic factors is greatly needed (Gao et al., 2013; Xu et al., 2007).

In this study, we measured stem sap flow in *Artemisia ordosica* and associated environmental variables throughout the growing seasons of 2013-2014 (May-September period of each year) to better understand the environmental controls on the temporal dynamics of sap flow. We believe that our findings will provide further understanding of acclimation processes in desert-shrub species under stress of dehydration.

2. Materials and Methods

2.1 Experimental site

Continuous sap-flow measurements were made at the Yanchi Research Station (37°42′31″ N, 107°13′47″ E, 1530 m above mean sea level), Ningxia, northwestern China. The research station is located between the arid and semi-arid climatic zones along the southern edge of the Mu Us Desert. The sandy soil in the upper 10 cm of the soil profile has a bulk density of 1.54±0.08 g cm^{-3} (mean ± standard deviation, n=16). Mean annual precipitation in the region is about 287 mm, of which 62% falls between July and September. Mean annual potential evapotranspiration and air temperature are about 2,024 mm and 8.1°C based on meteorological data (1954-2004) from the Yanchi County weather station. Normally, shrub leaf-expansion, leaf-expanded, and leaf-coloration stages begin in April, June, and September (Chen et al., 2015), respectively.

2.~~3~~2 Environmental measurements

Shortwave radiation (R_s in W m^{-2}; CMP3, Kipp & Zonen, Netherland), air temperature (T in °C), wind speed (u in m s^{-1}, 034B, Met One Instruments Inc., USA), and relative humidity (RH in %; HMP155A, Väisälä, Finland) were measured simultaneously near the sap-flow measurement plot. Half-hourly data were recorded by data logger (CR3000 data logger, Campbell Scientific Inc., USA). ~~Soil v~~Volumetric soil water content (VWC) at 30-cm depths were ~~monitored~~measured ~~with~~using three ECH$_2$O-5TE soil moisture probes (Decagon Devices, USA). In the analysis, we used half-hourly averages of VWC from the three soil moisture probes. Vapor pressure deficit (VPD in kPa) was calculated from recorded *RH* and *T*.

2.~~2~~3 Measurements of sap flow, leaf area and stomatal conductance

The experimental plot (10 m × 10 m) was located on the western side of Yanchi Research Station in an *Artemisia ordosica*-dominated area. Mean age of the *Artemisia ordosica* was 10-years old. Maximum monthly mean leaf area index (LAI) for plant specimens with full leaf expansion was about 0.1 m^2 m^{-2} (Table 1). Over 60% of their roots were distributed in the first 60 cm of the soil ~~depths of 0-60 cm~~complex (Zhao et al., 2010; Jia et al., 2016). Five stems of *Artemisia ordosica* were randomly selected within the plot as replicates for sap-flow

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measurement. Mean height and sapwood area of sampled shrubs were 84 cm and 0.17 cm^2, respectively. Sampled stems represented the average size of stems in the plot. A heat balance sensor (Flow32-1K, Dynamax Inc., Houston, USA) was installed at about 15 cm above the ground surface on each of the five stems (Dynamax, 2005). Sap-flow measurements from each stem were taken once per minute~~ for each stem~~. Half-hourly data were recorded by a Campbell CR1000 data logger from May 1 to September 30, 2013-2014 (Campbell Scientific, Logan, UT, USA).

Leaf area was estimated for each stem every 7-10 days by sampling about 50-70 leaves from five randomly sampled ~~neighbouring~~neighboring shrubs with similar characteristics to the shrubs used for sap-flow measurements. Leaf area was measured immediately at the station laboratory with a portable leaf-area meter (LI-3000, Li-Cor, Lincoln, NE, USA). Leaf area index (LAI) was measured at roughly weekly intervals on a 4×4 grid of 16 quadrats (10 m ×10 m each) within a 100 m × 100 m plot centered on the flux tower using measurements of sampled leaves and allometric equations (Jia et al., 2014). Stomatal conductance (g_s) was measured *in situ* for three to four leaves on each of the sampled shrubs with a LI-6400 portable photosynthesis analyzer (Li-Cor Inc., Lincoln, USA). The g_s measurements were made every two hours from 7:00 to 19:00 h every ten days from May to September, 2013~~-~~ and 2014.

The degree of coupling between the ecosystem surface and the atmospheric boundary layer was estimated with the decoupling coefficient (Ω). The decoupling coefficient varies from 0 (i.e., leaf transpiration is mostly controlled by g_s) to 1 (i.e., leaf transpiration is mostly controlled by radiation). The Ω was calculated as described by Jarvis and McNaughton

(1986):

$$\Omega = \frac{\Delta + \gamma}{\Delta + \gamma\left(1 + \frac{g_a}{g_s}\right)}, \quad (1)$$

where Δ is the rate of change of saturation vapor pressure *vs*. temperature (kPa K^{-1}), γ is the psychrometric constant (kPa K^{-1}), and g_a is the aerodynamic conductance (m s^{-1}; Monteith and Unsworth, 1990):

$$g_a = \left(\frac{u}{u*^2} + 6.2u*^{-0.67}\right)^{-1}, \quad (2)$$

where u is the wind speed (m s^{-1}) at 6 m above the ground, and $u*$ is the friction velocity (m s^{-1})~~.~~, which was measured using nearby eddy covariance system (Jia et al., 2014).

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~~2.3 Environmental measurements~~

~~Shortwave radiation (R_s in W m^{-2}; CMP3, Kipp & Zonen, Netherland), air temperature (T in °C), wind speed (u in m s^{-1}, 034B, Met One Instruments Inc., USA), and relative humidity (*RH* in %; HMP155A, Väisälä, Finland) were measured simultaneously near the sap-flow measurement plot. Half-hourly data were recorded by data logger (CR3000 data logger, Campbell Scientific Inc., USA). VWC at 30-cm depths were monitored with three ECH$_2$O-5TE soil moisture probes (Decagon Devices, USA). In the analysis, we used half-hourly averages of VWC from the three soil moisture probes. Vapor pressure deficit (VPD in kPa) was calculated from recorded *RH* and *T*.~~

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2.4 Data analysis

In our analysis, March-May represented spring, June-August summer, and September-November autumn (Chen et al., 2015). Drought days were defined as those days with daily mean VWC < 0.1 $m^3 m^{-3}$. This is based on a VWC threshold of 0.1 $m^3 m^{-3}$ for J_s (Fig. 1), with J_s increasing as VWC increased, saturating at VWC of 0.1 $m^3 m^{-3}$, and decreasing as VWC continued to increase. The VWC threshold of 0.1 $m^3 m^{-3}$ is equivalent to a relative extractable soil water (REW) of 0.4 for drought conditions (Granier et al., 1999 and 2007; Zeppel et al., 2004 and 2008; Fig. 2d, e). Duration and severity of 'drought' were defined based on a VWC threshold and REW of 0.4. REW was calculated as ~~according to~~ from equation (3):

$$REW = \frac{VWC - VWC_{\min}}{VWC_{\max} - VWC_{\min}} \qquad (3)$$

where VWC is the specific daily soil water content ($m^3 m^{-3}$), VWC_{min} and VWC_{max} are the minimum and maximum VWC during the measurement period in each year, respectively.

Sap-flow analysis was conducted using mean data from five sensors. Sap flow per leaf area (J_s) was used in this study, i.e.,

$$J_s = \left(\sum_{i=1}^{n} E_i / A_{li} \right) \Big/ n \qquad (4)$$

where, J_s is the sap flow per leaf area (kg m^{-2} h^{-1}) or (kg m^{-2} d^{-1}), E is the measured sap flow of a stem (g h^{-1}), A_l is the leaf area of the sap-flow stem, and "n" is the number of stems used (n = 5).

Transpiration per ground area (T_r) was estimated in this study according to:

$$T_r = \left(\sum_{i=1}^{n} J_s \times LAI \right) \Big/ n \qquad (5)$$

where, T_r is transpiration per ground area (mm d^{-1}), and LAI is the leaf area index (m^2

m^{-2}).

Linear and non-linear regressions were used to analyze abiotic control on sap-flow rate. In order to minimize the effects of different phenophases and rainfall, we used data only from mid-growing season, non-rainy days, and daytime measurements (8:00-20:00), i.e., from June 1 to August 31, with hourly shortwave radiation > 10 W m^{-2}. Relations between mean sap-flow rates at specific times over a period of 8:00-20:00 and corresponding environmental factors from June 1 to August 31 were derived with linear regression (p<0.05; Fig. 3). Regression slopes were used as indicators of sap-flow sensitivity (degree of response) to the various environmental variables (see e.g., Zha et al., 2013). All statistical analyses were performed with SPSS v. 17.0 for Windows software (SPSS Inc., USA). Significance level was set at 0.05.

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3. Results

3.1 Seasonal variations in environmental factors and sap flow

The r~~R~~ange of daily means (24-hour mean) for R_s, T, VPD, and VWC during the 2013 growing season (May-September) were 31.1-364.9 W m^{-2}, 8.8-24.4^{o}C, 0.05-2.3 kPa, and 0.06-0.17 m^{3} m^{-3} (Fig. 2a, b, c, d), respectively, annual means being 224.8 W m^{-2}, 17.7^{o}C, 1.03 kPa, and 0.08 m^{3} m^{-3}. Corresponding range of daily means for 2014 were 31.0-369.9 W m^{-2}, 7.1-25.8^{o}C, 0.08-2.5 kPa, and 0.06-0.16 m^{3} m^{-3} (Fig. 2a, b, c, d), respectively, annual means being 234.9 W m^{-2}, 17.2^{o}C, 1.05 kPa, and 0.09 m^{3} m^{-3}.

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Total precipitation and number of rainfall events during the 2013 measurement period (257.2 mm and 46 days) were about 5.6% and 9.8% lower than those during 2014 (272.4 mm and 51 days; Fig. 2d), respectively. In 2013, more irregular rainfall events occurred than in 2014, with 45.2% of rainfall falling in July and 8.8% in August.

Drought mainly occurred in May, June, and August of 2013 and in May and June of 2014 (Fig. 2d, e). Both years had dry springs. Over one-month period of ~~–~~summer drought occurred in 2013.

The r~~R~~ange of daily J_s during the growing season was 0.01-4.36 kg m^{-2} d^{-1} in 2013 and 0.01-2.91 kg m^{-2} d^{-1} in 2014 (Fig. 2f), with annual means of 0.89 kg m^{-2} d^{-1} in 2013 and 1.31 kg m^{-2} d^{-1} in 2014. Mean daily J_s over the growing season of 2013 was 32%, lower than that of 2014. Mean daily T_r were 0.05 mm d^{-1} and 0.07 mm d^{-1} over the growing season ~~in~~ of 2013 and 2014 (Fig. 2f), respectively, being 34% lower in 2013 than in 2014. The total T_r over the growing season (May 1-September 30) ~~in~~ of 2013 and 2014 were 7.3 mm and 10.9 mm, respectively. Seasonal fluctuations in J_s and T_r corresponded with ~~the~~ seasonal patterns in VWC (Fig. 2d, f). Daily mean J_s and T_r decreased or remained nearly constant during dry-soil periods (Fig. 2d, f), with the lowest J_s and T_r observed in spring and mid-summer (August) of 2013.

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3.2 Sap flow response to environmental factors

In summer, J_s increased with increasing VWC (Fig. 2d, f; Fig. 3d). Soil water was shown to modify the response of J_s to environmental factors (Fig. 4). Sap flow increased more rapidly with increases in R_s, T, and VPD under high VWC (i.e., VWC > 0.1 m^3 m^{-3} in both 2013 and 2014) compared with periods with lower VWC (i.e., VWC < 0.1 m^3 m^{-3} in both 2013 and 2014). Sap flow J_s was more sensitive to R_s, T, and VPD under high VWC (Fig. 4), which coincided with a larger regression slope under high VWC conditions.

Sensitivity of J_s to environmental variables (in particular, R_s, T, VPD, and VWC) varied depending on ~~the ~~time of ~~a ~~day (Fig. 5). Regression slopes for the relations of J_s-R_s, J_s-T, and J_s-VPD were greater in the morning before 11:00 h, and lower during mid-day and early afternoon (12:00-16:00 h). In contrast, regression slopes of the relation of J_s-VWC were lower in the morning (Fig. 5), increasing thereafter, peaking at ~13:00 h, and subsequently decreasing in late afternoon. Regression slopes of the response of J_s to R_s, T, and VPD in 2014 were greater than those in 2013.

3.3 Diurnal changes and hysteresis between sap flow and environmental factors

Diurnal patterns of J_s were similar in both years (Fig. 6), initiating at 7:00 h and increasing thereafter, peaking before noon (12:00 h), and subsequently decreasing thereafter and remaining near zero from 20:00 to 6:00 h. Diurnal changes in g_s were similar to J_s, but peaking about 2 and 1 h earlier than J_s in July and August, respectively (Fig. 6).

There were pronounced time lags between J_s and R_s over the two years (Fig. 7), J_s peaked earlier than R_s and, thus, earlier than either VPD or T. These time lags differed seasonally. For example, mean time lag between J_s and R_s was 2 h during July, 5 h during May, and 3 h during June, August, and September of 2013. However, the time lags in 2014 were generally shorter than those observed in 2013 (Table 2).

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~~Use of normalized variables may remove the influence of J_s and R_s from the data. As a result, ~~C~~c~~lockwise hysteresis loops between J_s and R_s during the growing period were observed (Fig. 7). As R_s increased in the morning, J_s increased until it peaked at ~10:00 h. Sap-flow rate declined with decreasing R_s during the afternoon. Sap flow J_s was higher in the

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morning than in the afternoon, forming a clockwise hysteresis loop.

Diurnal time lag in the relation of J_s-R_s were influenced by VWC (Fig. 8, 9). For example, J_s peaked about 2 h earlier than R_s on days with low VWC (Fig. 8a), 1 h earlier than R_s on days with moderate VWC (Fig. 8b), and at the same time as R_s on days with high VWC (Fig. 8c). Lag hours between J_s and R_s over the growing season were negatively and linearly related to VWC (Fig. 9: Lag (h) =-133.5×VWC+12.24, R^2=0.41). Effect of VWC on time lags between J_s and R_s was smaller in 2014, with evenly distributed rainfall during the growing season, than in 2013, with a pronounced summer drought (Fig. 9). State variables g_s and Ω showed a significantly increasing trend with increasing VWC in 2013 and 2014, respectively (Fig. 10).

4. Discussion and conclusions

4.1 Sap flow response to environmental factors

Drought tolerance of some plants may be related to lower overall sensitivity of plant physiological attributes to environmental stress and/or stomatal regulation (Huang et al., 2011b; Naithani et al., 2012). In this study, large regression slopes between J_s and the environmental variables (R_s, VPD, and T) in the morning indicated that sap flow was more sensitive to variations in R_s, VPD, and T during the ~~less dry~~ drier and hotter period of the day (Fig. 5). Stomatal conductances were the largest in the morning (Fig. 6), which led to increases in water fluxes to the atmosphere as a result of increased R_s, T, and VPD. When R_s peaked during mid-day (13:00-14:00 h), there was often insufficient soil water to meet the atmospheric demand for water, causing g_s to be limited by available soil moisture and making

J_s more responsive to VWC at noon, but less responsive to R_s and T. Similarly, *Hedysarum mongolicum* in a nearby region positively correlated with VWC at noon (Qian et al., 2015), and the evapotranspiration of a Scots pine stand showed higher sensitivity to surface conductance, temperature, vapor pressure deficit, and radiation in the morning than in the afternoon (Zha et al., 2013).

Synergistic interactions among environmental factors influencing sap flow are complex. In general, VWC has an influence on physiological processes of plants in water-limited ecosystems (Lei et al., 2010; She et al., 2013). Our finding regarding lower sensitivity in J_s to environmental factors (R_s, T and VPD) during dry periods was consistent with an earlier study of boreal grasslands (Zha et al., 2010). Also our finding that VWC is the most important factor modifying responses in sap flow in *Artemisia ordosica* to other environmental factors, is in contrast to other shrub species. For example, it has been found that sap flow in *Haloxylon ammodendron* in northwest China, where annual precipitation is 37.9 mm and mean annual temperature is 8.2 °C, was mainly controlled by T (Zhang et al., 2003), while sap flow in *Cyclobalanopsis glauca* in south China, where annual precipitation is 1900 mm and mean annual temperature is 19.3 °C, was controlled by R_s and T, when VWC was not limiting (Huang et al., 2009).

Precipitation, being the main source of VWC at our site, affected transpiration directly. In this sense, frequent small rainfall events (< 5 mm) were important to the survival and growth of the desert plants (Sala and Lauenroth, 1982; Zhao and Liu, 2010). Variations in J_s were clearly associated with the intermittent supply of water to the soil during rainfall events, as revealed ~~indicated~~ at our site (Fig. 2d, f). Reduced J_s during rainy days can be explained by a reduction in incident R_s and water-induced saturation on the leaf surface, which led to a decrease in leaf turgor and stomatal closure. After each rainfall event, J_s increased quickly when soil water was replenished. Schwinning and Sala (2004) showed previously for similar research sites that VWC contributed the most to the response in plant transpiration to post-rainfall events. We showed in this study that *Artemisia ordosica* responded in a different way to wet and dry conditions. In the mid-growing season, high J_s in July were related to rainfall-fed VWC, which increased the rate of transpiration. However, dry soil conditions combined with high T and R_s, led to a reduction in J_s in August of 2013 (Fig. 2). In some desert shrubs, groundwater may replenish water lost by transpiration by having deep roots (Yin et al., 2014). *Artemisia ordosica* roots are generally distributed in the upper 60 cm of the soil (Zhao et al., 2010; Wang et al., 2016), and as a result the plant usually depends on water directly supplied by precipitation because groundwater levels in drylands can be well below the rooting zone, typically, at depths ≥ 10 m at our site.

4.2 Hysteresis between sap flow and environmental factors

Diurnal patterns in J_s corresponded with those of R_s from sunrise until diverging later in the day (Fig. 7), suggesting that R_s was a primary controlling factor of diurnal variation in J_s. According to O'Brien et al. (2004), diurnal variation in R_s could cause change in the diurnal variation in the consumption of water. As an initial energy source, R_s can force T and VPD to increase, causing a phase difference in time lags among the relations J_s-R_s, J_s-T, and J_s-VPD.

We found a consistent clockwise hysteresis loop between J_s and R_s over a diurnal cycle

(Fig. 7).~~, indicating that R_s lagged J_s, and the response of J_s to R_s varied both diurnally and seasonally.~~ This hysteresis m~~ight~~ay be due to stomatal conductance being inherently dependen~~ce~~t on ~~the~~ plant hydrodynamics (Matheny et al. 2014). The ~~A~~ large g_s in the morning promoted higher rates of transpiration (Fig. 6, 7), ~~and~~ while ~~the~~ lower g_s in the afternoon reduced transpiration ~~in the afternoon~~. Therefore, ~~the~~ diurnal curves (hysteresis) were mainly caused by the g_s-induced hydraulic process (Fig. 7). The finding that ~~the~~ hysteresis varied seasonally, decreasing with increasing VWC, further supports the ~~that~~ hydrodynamic explanation of ~~the~~ hysteresis. At our site, dry soils accompanied with high VPD in summer, ~~which lead~~led to a decreased in g_s and ~~In dry and hot conditions, g_s decreased, causing the~~ greater ~~larger~~ control of the stomata on J_s ~~to increase~~ relative to other ~~changes in~~ environmental factors. The result that g_s increased with increasing VWC (Fig. 10a), along with the synchronization of J_s and g_s, suggests that J_s is more sensitive to g_s in low VWC and less so to R_s. Due to the ~~a large~~ incidence of small rainfall events ~~at~~in desert drylands, soil water suppl~~y~~ied by rainfall pulses ~~could not~~was largely insufficient to meet the transpiration demand under high mid-day R_s, resulting in clockwise loops. ~~The l~~Lower Ω values (< 0.4) at our site also ~~indicated~~support the idea that VPD ~~or~~and g_s have a greater control ~~more~~ on transpiration than R_s ~~at this dryland site~~ (Fig. 10). ~~Diurnal trends in J_s and g_s occurred together, both peaking earlier than R_s. The g_s peaked 3-4 h earlier than R_s, leading to a reduction in J_s and an increase in R_s and a clockwise hysteresis loop.~~ Contrary to our findings, counterclockwise hysteresis has been observed to occur between transpiration (J_s) and R_s in tropical and temperate forests (Meinzer et al., 1997; O'Brien et al., 2004; Zeppel et al., 2004), which was reported to be consistent with the capacitance in ~~the~~ soil-plant-atmosphere

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systems~~:~~; ~~–~~it usually takes time for water to move up and expand vascular elements in tree stem during the transition from night to day. ~~A possible reason for this difference may be due to differences in VWC associated with the different regions. According to Zheng and Wang (2014) favorable water conditions after rainfall could render clockwise hysteresis loops between J_s and R_s under dry conditions to counterclockwise loops. In this study, due to a large incidence of small rainfall events, soil water supply by rainfall pulses could not meet the transpiration demand under high mid-day R_s, resulting in clockwise loops even though rainfall had occurred.~~

~~In semi-arid regions, low VWC restricts shrubplant transpiration more than VPD in soil water deficit condition. Water vapor deficits tend to restrict transpiration in forest species in wet regions to a greater extent. According to Zheng et al. (2014), high water availability in alpine shrubland meadows may contribute to weakened hysteresis between evapotranspiration and the environmental variables. Our results showed that hysteresis between J_s and R_s decreased as VWC increased (Fig. 8, 9). The result that g_s increased with increasing VWC (Fig. 10a), along with the synchronization of J_s and g_s, suggests that J_s is less sensitive to g_s in high VWC and more so to R_s. Temporal patterns in J_s became more consistent with those in R_s as VWC increased, leading to a weakened hysteresis between the two variables. In this study, due to a large incidence of small rainfall events, soil water supply by rainfall pulses could not meet the transpiration demand under high mid-day R_s, resulting in clockwise loops even though rainfall had occurred. This is further supported by a large Ω decoupling coefficient, when VWC is high (Fig. 10b). The larger Ω the decoupling coefficient is, the greater is the influence of R_s on J_s. The effect of VWC on time lag varied~~

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~~between 2013 and 2014.~~

4.3. Conclusions

Drought during the leaf-expansion and leaf-expanded periods led to a greater decline in J_s, causing J_s to be lower in 2013 than in 2014. The relative influence of R_s, T, and VPD on J_s in *Artemisia ordosica* was modified by volumetric soil water content, indicating J_s's lessened ~~lower~~ sensitivity to environmental variables (R_s, T and VPD) during dry periods. Sap flow J_s was constrained by soil water deficiency, causing J_s to peak several hours prior to R_s. Diurnal hysteresis between J_s and R_s varied seasonally and was mainly controlled by hydrodynamic stresses. ~~, because of the control by stomatal conductance under low VWC and R_s under high VWC.~~ According to this study, soil moisture controlled sap-flow response in *Artemisia ordosica*. This species is capable to tolerate and adapt to soil water ~~deficiencies~~ deficits and drought conditions during the growing season. Altogether, our findings add to our understanding of acclimation in desert-shrub species under stress of dehydration. The knowledge gain can assist in modeling desert-shrub-ecosystem functioning under changing climatic conditions.

Acknowledgments: This research was financially supported by grants from the National Natural Science Foundation of China (NSFC No. 31670710, 31670708, 31361130340, 31270755), the National Basic Research Program of China (Grant No. 2013CB429901), and the Academy of Finland (Project No. 14921). Xin Jia and Wei Feng are also grateful to financial support from the Fundamental Research Funds for the Central Universities (Proj. No. 2015ZCQ-SB-02). This work is related to the Finnish-Chinese collaborative research project EXTREME (2013-2016), between Beijing Forestry University (team led by Prof.

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Tianshan Zha) and the University of Eastern Finland (team led by Prof. Heli Peltola), and the U.S. China Carbon Consortium (USCCC). We thank Ben Wang, Sijing Li, Qiang Yang, and others for their assistance in the field.

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Table 1 Seasonal changes in monthly transpiration (T_r), leaf area index (LAI), and stomatal conductance (g_s) of *Artemisia ordosica* from 2013 to 2014.

	T_r (mm mon^{-1})		LAI (m^2 m^{-2})		g_s (mol m^{-2} s^{-1})	
	2013	2014	2013	2014	2013	2014
May	0.57	1.59	0.02	0.04	0.07	0.18
June	1.03	2.28	0.05	0.06	0.08	0.13
July	3.36	3.46	0.10	0.06	0.09	0.14
August	1.04	2.45	0.08	0.06	0.10	0.08
September	1.23	1.13	0.05	0.04	0.15	0.05

Table 2 Mean monthly diurnal cycles of sap-flow rate (J_s) response to shortwave radiation (R_s), air temperature (T), and vapor pressure deficit (VPD), including time lags (h) in J_s as a function of R_s, T, and VPD.

Pattern	May		June		July		August		September	
	2013	2014	2013	2014	2013	2014	2013	2014	2013	2014
J_s-R_s	5	2	3	0	2	1	3	1	3	2
J_s-T	8	6	7	4	4	4	6	5	6	6
J_s-VPD	8	5	7	4	6	4	6	5	6	5

Figure captions:

Fig. 1 Sap-flow rate per leaf area (J_s) as a function of soil water content (VWC) at 30 cm depth in non-rainy, daytime hours during the mid-growing period from June 1-August 31 over 2013-2014. Data points are binned values from pooled data over two years at a VWC increment of 0.003 m^3 m^{-3}. Dotted line represents the VWC threshold for J_s.

Fig. 2 Seasonal changes in daily (24-hour) mean shortwave radiation (R_s; a), air temperature (T; b), vapor pressure deficit (VPD; c), volumetric soil water content (VWC; d), relative extractable water (REW; e), daily total precipitation (PPT; d), and daily sap-flow per leaf area (J_s; f), and daily transpiration (T_r, mm d^{-1}; f) from May to September for both 2013 and 2014. Horizontal dash lines (d, e) represent VWC and REW threshold of 0.1 m^3 m^{-3} and 0.4, respectively. Shaded bands indicate periods of drought.

Fig. 3 Relationships between **s**ap-flow rate per leaf area (J_s) and environmental factors [shortwave radiation (R_s), air temperature (T), vapor pressure deficit (VPD), and soil water content at 30-cm depth (VWC)] in non-rainy days between 8:00-20:00 h during the mid-growing season of June 1-August 31 ~~for 2013~~for 2013 and 2014. Data points are binned values from pooled data over two years at increments of 40 W m^{-2}, 1.2 °C, 0.3 kPa, and 0.005 m^3 m^{-3} for R_s, T, VPD and VWC, respectively.

Fig. 4 Sap-flow rate per leaf area (J_s) in non-rainy, daytime hours during the mid-growing season of June 1-August 31 for both 2013 and 2014 as a function of shortwave radiation (R_s), air temperature (T), vapor pressure deficit (VPD) under high volumetric soil water content (VWC > 0.10 m^3 m^{-3} both in 2013 and 2014) and low VWC (< 0.10 m^3 m^{-3}, 2013 and 2014). J_s is given as binned averages according to R_s, T, and VPD, based on increments of 100 W

m^{-2}, 1°C, and 0.2 kPa, respectively. Bars indicate standard error.

Fig. 5 Regression slopes of linear fits between sap-flow rate per leaf area (J_s) in non-rainy days and shortwave radiation (R_s), vapor pressure deficit (VPD), air temperature (T), and volumetric soil water content (VWC) between 8:00-20:00 h during the mid-growing season of June 1-August 31 for 2013 and 2014.

Fig. 6 Mean monthly diurnal changes in sap-flow rate per leaf area (J_s) and stomatal conductance (g_s) in *Artemisia ordosica* during the growing season (May-September) for both 2013 and 2014. Each point is given as the mean at specific times during each month.

Fig. 7 Seasonal variation in hysteresis loops between sap-flow rate per leaf area (J_s) and shortwave radiation (R_s) using normalized plots for both 2013 and 2014. The y-axis represents the proportion of maximum J_s (dimensionless), and the x-axis represents the proportion of maximum R_s (dimensionless). The curved arrows indicate the clockwise direction of response during the day.

Fig. 8 Sap-flow rate per leaf area (J_s) and shortwave radiation (R_s) over consecutive three days in 2013, i.e., (a) under low volumetric soil water content (VWC) and high vapor pressure deficit (VPD; DOY 153-155, VWC=0.064 m^3 m^{-3}, REW=0.025, VPD=2.11 kPa), (b) moderate VWC and VPD (DOY 212-214, VWC=0.092 m^3 m^{-3}, REW=0.292, VPD=1.72 kPa), and (c) high VWC and low VPD (DOY 192-194, VWC=0.152 m^3 m^{-3}, REW=0.865, VPD= 0.46 kPa). REW is the relative extractable soil water. VWC, REW, and VPD are the mean value of the three days.

Fig. 9 Time lag between sap-flow rate per leaf area (J_s) and short wave radiation (R_s) in relation to volumetric soil water content (VWC). Hourly data in non-rainy days during the mid-growing season of June 1-August 31 for 2013 and 2014. The lag hours were calculated by a cross-correlation analysis using a three-day moving window with a one-day time step. Rainy days were excluded. The solid line is based on exponential regression (p<0.05).

Fig. 10 Relationship between volumetric soil water content (VWC) and (a) stomatal conductance (g_s) in *Artemisia ordosica*, and (b) decoupling coefficient (Ω) for 2013 and 2014. Hourly values are given as binned averages based on a VWC-increment of 0.005 m^3 m^{-3}. Bars indicate standard error. Only regressions with p-values < 0.05 are shown.

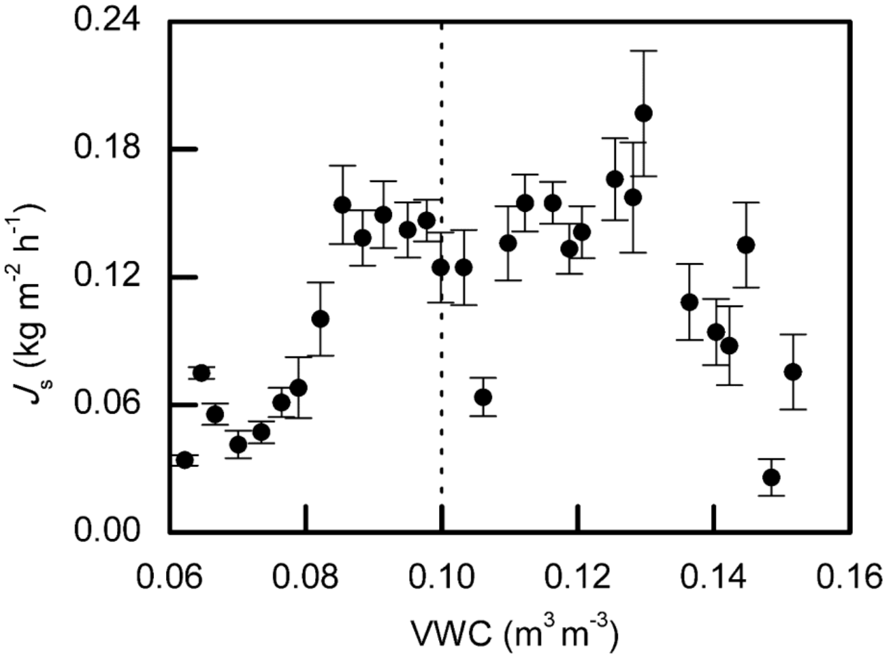

Fig. 1 Sap-flow rate per leaf area (J_s) as a function of soil water content (VWC) at 30 cm depth in non-rainy, daytime hours during the mid-growing period from June 1-August 31 over 2013-2014. Data points are binned values from pooled data over two years at a VWC increment of 0.003 m^3 m^{-3}. Dotted line represents the VWC threshold for J_s.

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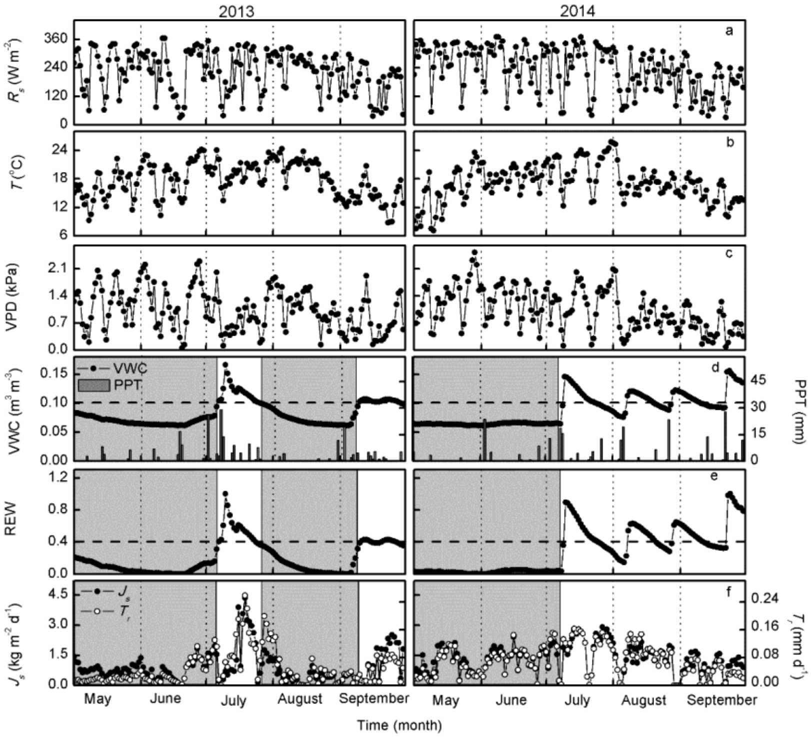


Fig. 2 Seasonal changes in daily (24-hour) mean shortwave radiation (R_s; a), air temperature (T; b), vapor pressure deficit (VPD; c), volumetric soil water content (VWC; d), relative extractable water (REW; e), daily total precipitation (PPT; d), and daily sap-flow per leaf area (J_s; f), and daily transpiration (T_r, mm d^{-1}; f) from May to September for both 2013 and 2014. Horizontal dash lines (d, e) represent VWC and REW threshold of 0.1 m^3 m^{-3} and 0.4, respectively. Shaded bands indicate periods of drought.

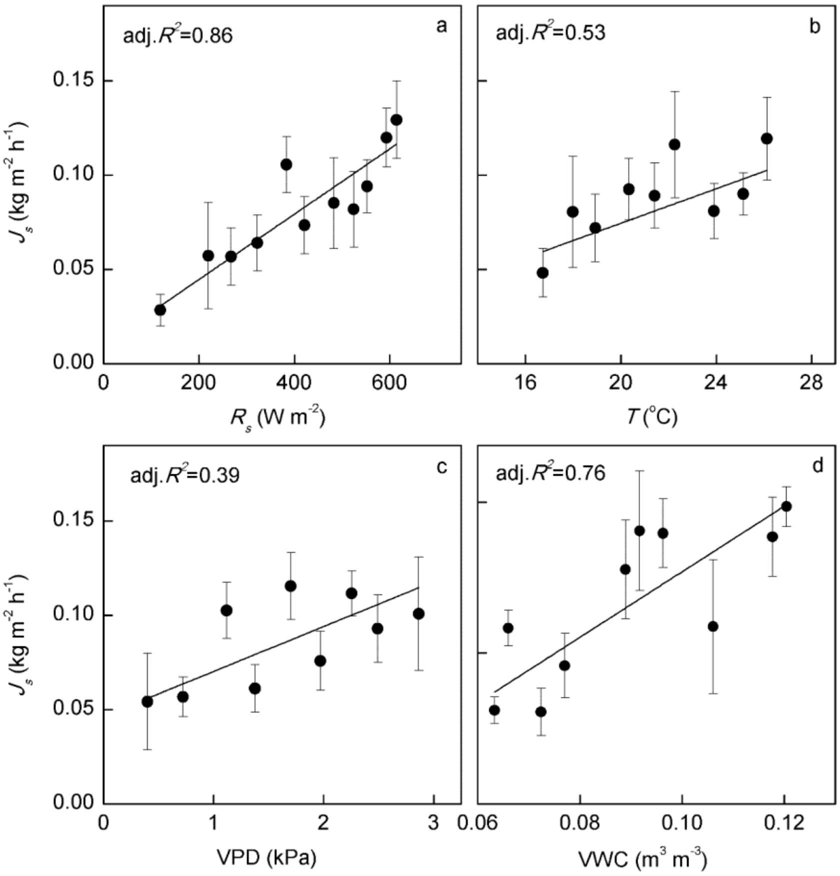


Fig. 3 Relationships between **s**ap-flow rate per leaf area (J_s) and environmental factors [shortwave radiation (R_s), air temperature (T), vapor pressure deficit (VPD), and soil water content at 30-cm depth (VWC)] in non-rainy days between 8:00-20:00 h during the mid-growing season of June 1-August 31 for 2013 and 2014. Data points are binned values from pooled data over two years at increments of 40 W m^{-2}, 1.2 °C, 0.3 kPa, and 0.005 m^3 m^{-3} for R_s, T, VPD and VWC, respectively.

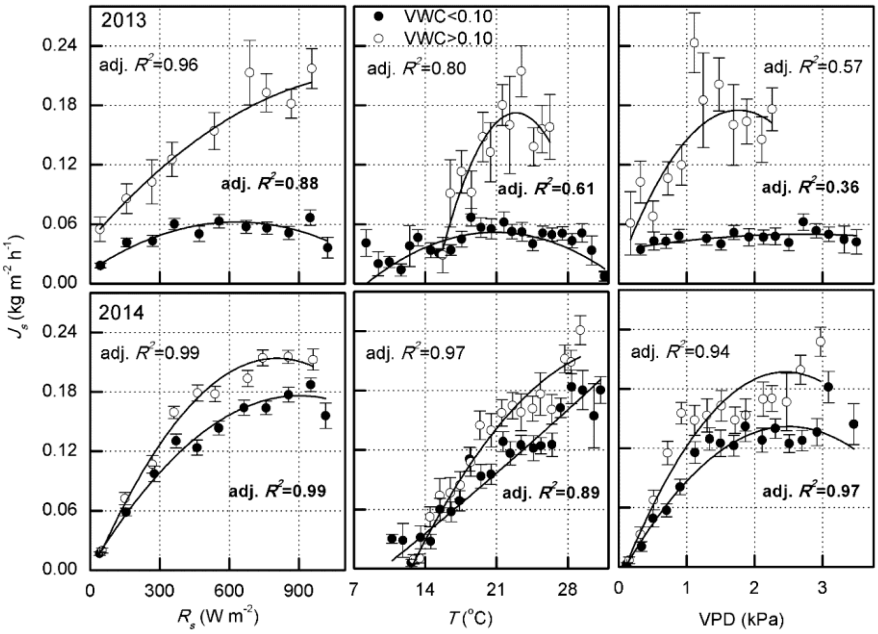


Fig. 4 Sap-flow rate per leaf area (J_s) in non-rainy, daytime hours during the mid-growing season of June 1-August 31 for both 2013 and 2014 as a function of shortwave radiation (R_s), air temperature (T), vapor pressure deficit (VPD) under high volumetric soil water content (VWC > 0.10 m^3 m^{-3} both in 2013 and 2014) and low VWC (< 0.10 m^3 m^{-3}, 2013 and 2014). J_s is given as binned averages according to R_s, T, and VPD, based on increments of 100 W m^{-2}, 1°C, and 0.2 kPa, respectively. Bars indicate standard error.

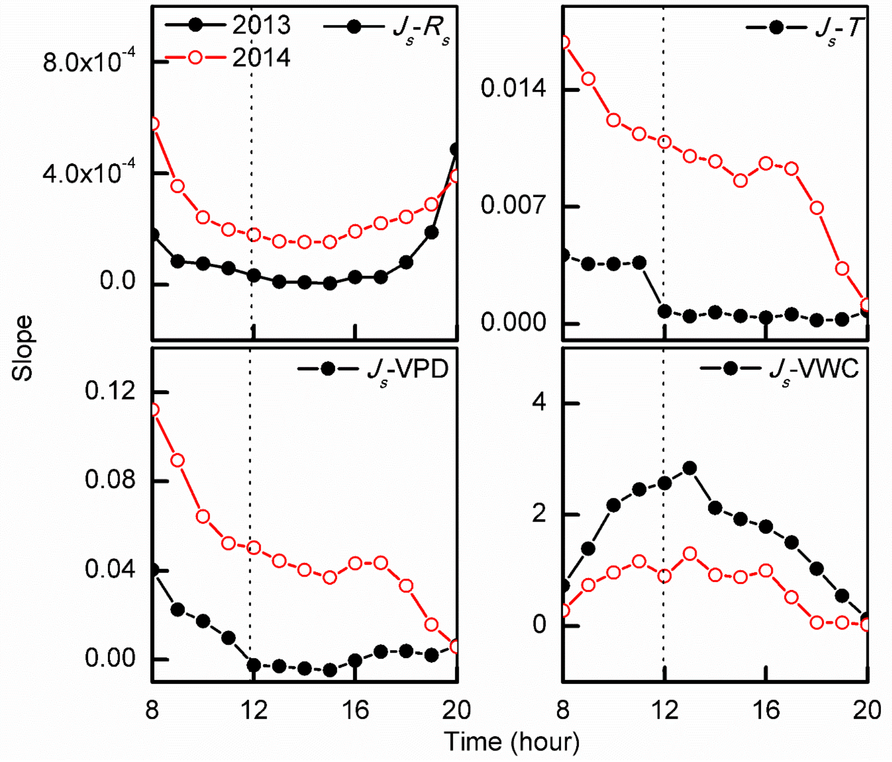
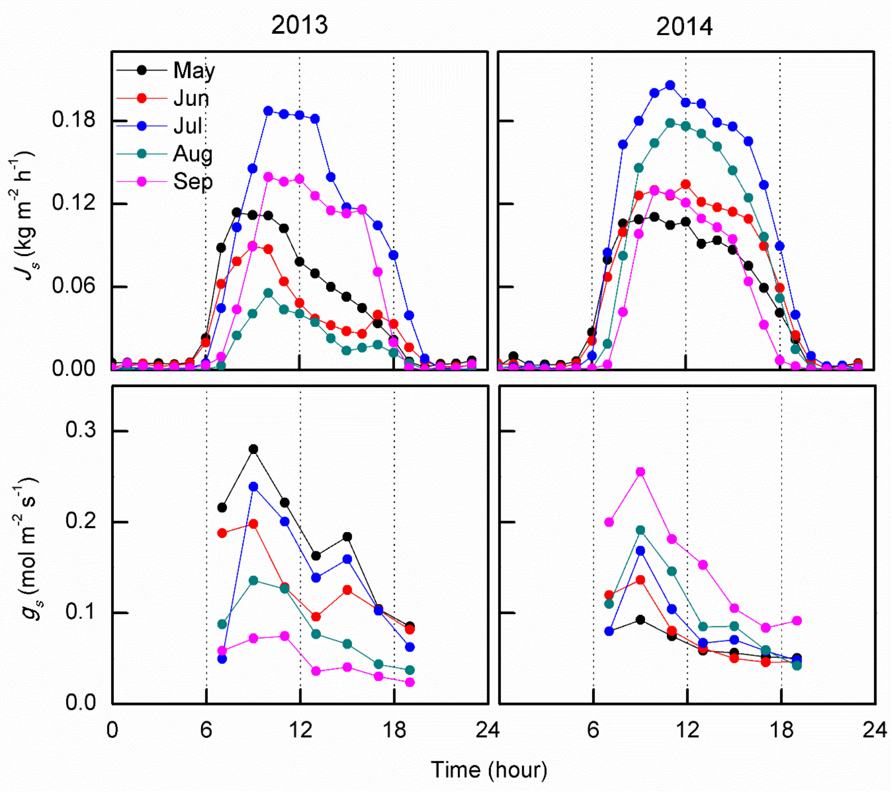
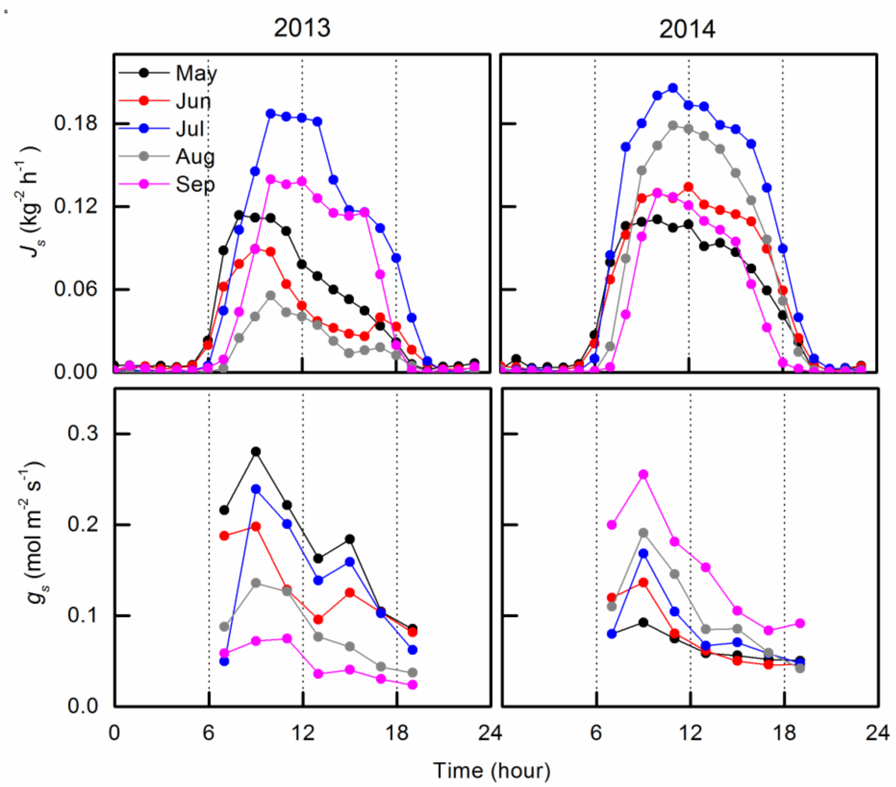


Fig. 5 Regression slopes of linear fits between sap-flow rate per leaf area (J_s) in non-rainy days and shortwave radiation (R_s), vapor pressure deficit (VPD), air temperature (T), and volumetric soil water content (VWC) between 8:00-20:00 h during the mid-growing season of June 1-August 31 for 2013 and 2014.


2013
2014
May
Jun
Jul
Aug
Sep
J_s (kg m^{-2} h^{-1})
0.18
0.12
0.06
0.00
g_s (mol m^{-2} s^{-1})
0.3
0.2
0.1
0.0
0
6
12
18
24
6
12
18
24
Time (hour)



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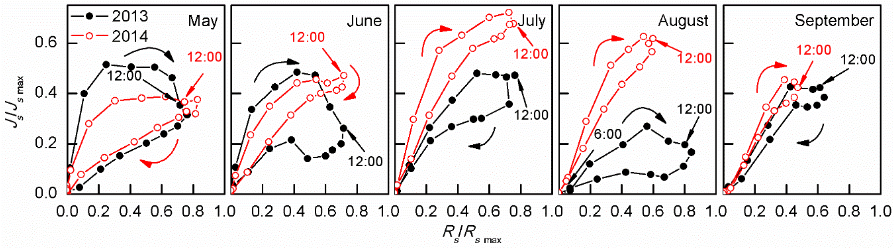

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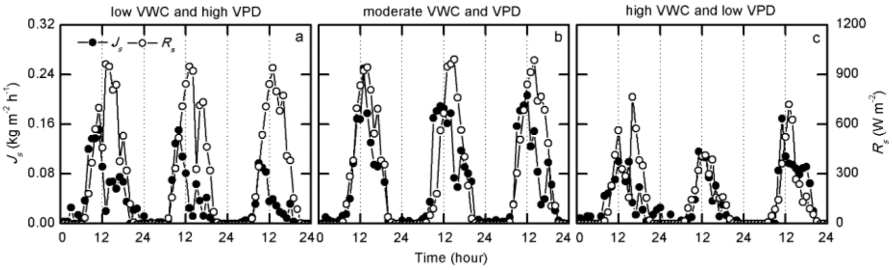

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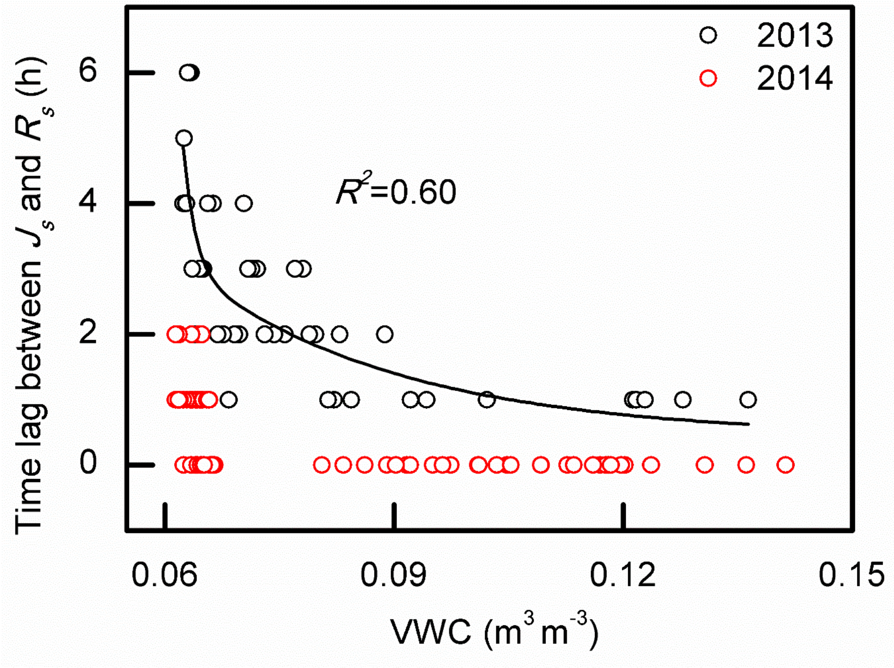

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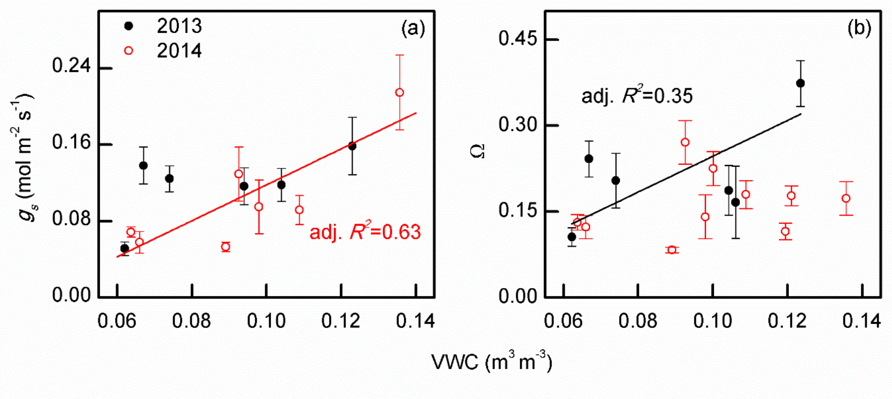

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