Dear Editor,

We greatly appreciate your helpful comments and suggestions for improving this manuscript. We have carefully looked at your comments and revised the manuscript accordingly. Please find below our responses to your comments and/or revisions to the manuscript.

We look forward to a possible publication of the manuscript bg-2016-480 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

Associate Editor Decision: Publish subject to minor revisions (Editor review) (27 Jul 2017) by Paul Stoy

Re: Thank you for your very helpful comments. We have revised the manuscript accordingly. (see a marked-up version enclosed below)

Comments to the Author:

The manuscript represents an improvement but requires further minor edits. Comments are based on the draft with tracked edits and focus on the introduction and discussion sections.

Re: We read the manuscript through and revised manuscript based on the editor's comments. (see a marked-up version enclosed below)

53: Js was just defined in the previous paragraph. (see also line 61 "sap-flow" with hyphen and other abbreviation inconsistency likewise elsewhere; please be consistent with abbreviations.)

Re: We revised all abbreviations consistently throughout text. (check in a marked-up version)

'escaped' on line 62 is too strong a word. Every plant dreams of escaping drought limitation but arid species can't. (I do note that it is used in Briolette et al., but for reproduction timing).

Re: The word 'escaped' was deleted. The sentence was revised accordingly like " This species acclimated to water limitations by invoking a water-conservation strategy……"(see line 63 in marked-up version)

Line 68 can be cut because no models are involved.

Re: The sentence referred to was cut.

Line 91 needs re-wording

Re: The sentence was reworded as "Transpiration maintains ecosystem balanceis controlled by stomatal through changing its conductance and pores,……". (see line 87-90 in marked-up version)

Lines 100-105 should be moved perhaps to the methods, they are a distraction here.

Re: The statements referred to were moved to the methods. (see line 193-196 in marked-

up version)

The paragraph on line 122 is actually informative. This is effective background that educates the reader and motivates the study. (line 127 can be moved to the next paragraph to "funnel" the flow of arguments toward the importance of studying A. odorosica (i.e. undo the change on line 151). Note that it may help to write A. odorosica henceforth for brevity.

Re: This sentence was moved to the next paragraph. (see line 132-134 in in marked-up version)

what is 'steep' on line 345? ('steep' is qualitative).

Re: The ‘steep’ was changed into ‘larger’.(line 309)

sentences like that on 357 provide nice comparisons. But after that, is Picea crassifolia a dryland species? (note bolding/lack of italics in "Caragana korshinskii".

Re: The species Picea crassifolia was deleted. It is not really dryland species.

The gray banding in Fig. 2 is inconsistent if it refers to VWC or REW values below the indicated thresholds (unless there is a time-integrated aspect that is best to describe in the legend).

Re: The gray bandings in figure 2 show the long dry period with low soil moisture that is < 0.1 of VWC or 0.4 of REW.

Soil moisture control on ~~sap flow~~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.

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 and 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 in 2014. J_s ~~Sap flow per leaf area~~ correlated positively with radiation (R_s), air temperature (T), and water vapor pressure deficit (VPD), when volumetric soil water content (VWC) was > 0.10 m^3 m^{-3}. There was a time lag of as much as six hours between d~~D~~iurnal J_s ~~was generally ahead of~~and R_s. ~~by as much as six hours.~~ This ~~time lag~~hysteresis effect, 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 strongly controlled by plant-physiological processes during periods of dryness indicated by a low decoupling coefficient and low sensitivity to the environmental variables. According to this study, soil moisture is shown to control J_s ~~sap flow~~ (and, therefore, plant-transpiration) response in *Artemisia ordosica* to diurnal variations in biophysical factors. This species ~~escaped (~~acclimated to~~)~~ water limitations by invoking a water-conservation strategy with the regulation of stomatal conductance and advancement of J_s peaking time, manifesting in a hysteresis effect. The findings of this study add to the knowledge of acclimation processes in desert-shrub species under drought-associated stress. ~~This knowledge is essential in modeling desert-shrub ecosystem functioning under changing climatic conditions.~~

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

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). Shrub and semi-shrub species are replacing grass species in arid and semi-arid lands in response to ongoing aridification of the land surface (Huang et al., 2011a). This progression is predicted to continue under a changing climate (Houghton et al., 1999; Pacala et al., 2001; Asner et al., 2003). Studies have shown that desert shrubs are able to adapt to hot-dry environments as a result of their small plant-surface area, thick epidermal hairs, and large root-to-shoot ratios (Eberbach and Burrows, 2006; Forner et al., 2014). Plant traits related to water use are likely to adapt differentially with species and habitat type (Brouillette et al., 2014). Plants may select water-acquisition or water-conservation strategies in response to water limitations (Brouillette et al., 2014). Knowledge of physiological acclimation of changing species to water shortages in deserts, particularly with respect to transpiration, is inadequate and, in the context of plant adaptation to changing climatic conditions, is of immense interest (Jacobsen et al., 2007; Huang et al., 2011a). Transpiration ~~maintains ecosystem balance~~is controlled by stomatal through changing its conductance and pores, ~~–the soil-plant-atmosphere continuum~~ and its magnitude and timing is related to the prevailing biophysical factors (Jarvis 1976; Jarvis and McNaughton, 1986).

Sap flow can be used to reflect species-specific water consumption by plants (Ewers et al., 2002; Baldocchi, 2005; Naithani et al., 2012). Sap flow can also be used to continuously monitor canopy conductance~~ (g_s)~~ and its response to environmental variables (Ewers et al., 2007; Naithani et al., 2012). ~~Biotic and abiotic effects on sap flow and transpiration are often interactive and confounded. The decoupling coefficient (Ω) was used to examine the relative contribution of plant control through stomatal regulation of transpiration (Jarvis and McNaughton, 1986). Stomatal regulation becomes stronger as Ω approaches zero.~~ Stomatal conductance~~ (g_s)~~ at the plant scale exerts a large biotic control on transpiration particularly during dry conditions (Jarvis 1976; Jarvis and McNaughton, 1986). Stomatal conductance couples photosynthesis and transpiration (Cowan and Farquhar, 1977), making this parameter an important component of climate models in quantifying biospheric-atmospheric interactions (Baldocchi et al., 2002).

Studies have shown that xylem hydraulic conductivity was closely correlated with drought resistance (Cochard et al., 2008, 2010; Ennajeh et al., 2008). With increasing aridity, trees can progressively lessen their stomatal conductance, resulting in lower transpiration (McAdam et al., 2016). Generally, desert shrubs can close their stomata, reducing stomatal conductance, and reduce their water consumption when exposed to dehydration stresses. However, differences exist among shrub species in terms of their stomatal response to changes in air and soil moisture deficits (Pacala et al., 2001).

In *Elaeagnus angustifolia*, transpiration is observed to peak at noon, i.e., just before stomatal closure under water-deficit conditions (Liu et al., 2011), peaking earlier than radiation, temperature, and water vapor pressure deficit. This response lag or hysteresis effect ~~have~~ has been widely noticed in dryland species (Du et al., 2011; Naithani et al., 2012), but its function is not completely understood. Transpiration in *Hedysarum scoparium* peaks multiple times during the day. ~~During dry periods of the year, sap flow in *Artemisia ordosica* has been observed to be controlled by VWC at about a 30-cm depth in the soil (Li et al., 2014).~~ For other shrubs, sap flow has been observed to decrease rapidly when the volumetric soil water content ~~(VWC)~~ is lower than the water ~~loss~~ lost through evapotranspiration (Buzkova et al., 2015). Sap flow in *Caragana korshinskii* and *Hippophae rhamnoides* has been found to increase with increasing rainfall intensity (Jian et al., 2016), whereas in *Haloxylon ammodendron*, it was found to vary in response to rainfall, from an immediate decline after a heavy rainfall to no observable change after a small rainfall event (Zheng and Wang, 2014). 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). Support for the relationship between sap flow in desert shrubs and prevailing environmental factors is decidedly variable (McDowell et al., 2013; Sus et al., 2014), potentially varying with plant habitat and species (Liu et al., 2011).

Artemisia ordosica, a shallow-rooted desert shrub, is the dominant species in the Mu Us Desert of northwestern China. It plays 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 and longer dry periods are expected to ensue under changing climate change (Lioubimtseva and Henebry, 2009). Sap flow in *Artemisia ordosica* has been observed to be controlled by soil water content at about a 30-cm depth in the soil during dry periods of the year (Li et al., 2014). However, our understanding of the mechanisms of desert-shrub acclimation during periods of water shortage remains incomplete. Questions needing answering from our research include (1) how do changes in sap flow relate to changes in biotic and abiotic factors, and (2) whether *Artemisia ordosica* selects a strategy of water-conservation or water-acquisition under conditions of drought? To attend to these questions, we continuously measured stem sap flow in *Artemisia ordosica* and associated environmental variables *in situ* throughout the growing seasons of 2013 and 2014 (May-September period of each year). Our findings ~~will~~ present ~~lead to~~ insights concerning the main environmental factors affecting transpiration in *Artemisia ordosica*, e.g., optimal temperature, ~~VPD~~water vapor pressure deficit, and ~~VWC~~soil water content. This understanding can lead to improving phytoremediation practices in desert-shrub ecosystems.

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, respectively (Chen et al., 2015).

2.2 Environmental measurements

Shortwave radiation (R_s in W m^{-2}; CMP3, Kipp & Zonen, Netherland), air temperature (T in ^{o}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~~sap flow measurement plot. Half-hourly data were recorded by data logger (CR3000 data logger, Campbell Scientific Inc., USA). Volumetric soil water content (VWC) at a 30-cm depth were measured 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. Water vapor pressure deficit (VPD in kPa) was calculated from recorded RH and T.

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 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~~sap flow 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. Half-hourly data were recorded by a Campbell CR1000 data logger from May 1 to September 30, for both 2013 and 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 neighboring shrubs with similar characteristics to the shrubs being 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 on a weekly basis from a 4 × 4 grid of 16 quadrats (10 m × 10 m each) within a 100 m × 100 m plot centered on a 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.

Biotic and abiotic effects on sap flow and transpiration are often interactive and confounded. The decoupling coefficient (Ω) was used to examine the relative contribution of ~~plant~~biotic control through stomatal regulation of transpiration (Jarvis and McNaughton, 1986). Stomatal regulation becomes stronger as Ω approaches zero. ~~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 zero (i.e., leaf transpiration is mostly controlled by g_s) to one (i.e., leaf transpiration is mostly controlled by radiation). The *Ω* was calculated as described by Jarvis and McNaughton (1986), i.e.,

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

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),

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

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

2.4 Data analysis

In our analysis, 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 2013; Fig. 2d, e). Duration and severity of ‘drought’ were defined based on a VWC threshold and REW of 0.4. REW was calculated with

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

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

~~Sap flow~~Sap flow analysis was conducted using mean data from five sensors. Sap flow per leaf area (J_s, kg m^{-2} h^{-1} or kg m^{-2} d^{-1}~~)~~) was calculated according to

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

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~~sap flow stem, and "n" is the number of stems sampled (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}).

Linear and non-linear regressions were used to analyze abiotic control on sap flow. In order to minimize the effects of different phenophases and rainfall, we only used data from the mid-growing season, non-rainy days, and daytime hours from 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 at specific times over a period of 8:00-20:00 and corresponding environmental factors from June 1 to August 31 were derived from linear regression (p<0.05; Fig. 3). Regression slopes were used as indicators of ~~sap flow~~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.

3. Results

3.1 Seasonal variations in environmental factors and sap flow

The range 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°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°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°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°C, 1.05 kPa, and 0.09 m^3 m^{-3}.

Total precipitation and number of days with 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. More irregular rainfall events occurred in 2013 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 (shaded sections in Fig. 2d, e). Both years had dry springs. Over a one-month period of summer drought occurred in 2013.

The range 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 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) of 2013 and 2014 were 7.3 mm and 10.9 mm, respectively. Seasonal fluctuations in J_s and T_r corresponded with seasonal patterns in VWC (Fig. 2d, f). Daily mean J_s and $\mathrm{T_r}$ 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.

3.2 Sap flow response to environmental factors

In summer, J_s increased with increasing VWC, R_s, T, and VPD (Fig. 2d, f; Fig. 3). 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; Fig. 4) compared with periods with lower VWC (i.e., VWC < 0.1 m^3 m^{-3} in both 2013 and 2014; Fig. 4). J_s ~~Sap flow~~ was more sensitive to R_s, T, and VPD under high VWC (Fig. 4), which coincided with a steeper regression slope under high VWC conditions.

Sensitivity of J_s to environmental variables (in particular, R_s, T, VPD, and VWC) varied depending on time of 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 steeper 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

peaking 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).

Clockwise 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. J_s~~Sap flow~~ declined with decreasing R_s during the afternoon. ~~Sap flow (~~J_s~~)~~ was higher in the morning than in the afternoon.

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). The 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). Variables g_s and Ω showed a significantly increasing trend with increasing VWC in 2013 and 2014 (Fig. 10). This trend was more obvious in the dry year of 2013 than in 2014.

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, ~~steep~~ larger regression slopes between J_s and the environmental variables (R_s, VPD, and T) in the morning indicated that J_s~~sap flow~~ was less sensitive to variations in R_s, VPD, and T during the drier and hotter part of the day (Fig. 5). The lower sensitivity combined with lower g_s~~stomatal conductances~~ led to lower J_s~~sap flow~~, and, thus, lower transpiration (water consumption) during hot mid-day summer hours, pointing to a water-conservation strategy in plant acclimation during dry and hot conditions. When R_s peaked during mid-day (13:00-14:00 h) in summer, there was often insufficient soil water to meet the atmospheric demand, 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, sap flow in *Hedysarum mongolicum* and some other shrubs in a nearby region was positively correlated with VWC at noon (Qian et al., 2015). For instance, ~~sap flow in *Picea crassifolia* peaked at noon (12:00 and 14:00) and then decreased, heightening by increasing R_s, T, and VPD, when R_s < 800 W m^{-2}, T < 18.0°C, and VPD < 1.4 kPa (Chang et al., 2014);~~ sap flow in *Caragana korshinskii* was significantly lower during the stress period, its conductance decreasing linearly after the wilting point (She et al., 2013). The fact that J_s was less sensitive to meteorological variables when VWC < 0.10 m^3 m^{-3}, highlights the water-conservation strategy taken by drought-afflicted *Artemisia ordosica*. The positive linear relationship between g_s and VWC in this study further supports this conclusion.

Precipitation, being the most important source of soil moisture and, thus, VWC, affected transpiration directly. Frequent small rainfall events (< 5 mm) are crucially important to the survival and growth of desert plants (Zhao and Liu, 2010). Variations in J_s were clearly associated with the intermittent supply of water to the soil during rainfall events (see Fig. 2d, f). Reduced J_s during rainy days can be largely explained by a reduction in incident R_s and liquid water-induced saturation of the leaf surface, which led to a decrease in leaf turgor and stomatal closure. After each rainfall event, J_s increased quickly when soil moisture was replenished. Schwinning and Sala (2004) have previously shown that VWC contributed the most to the post-rainfall response in plant transpiration at similar sites. The study shows that *Artemisia ordosica* responded differently to wet and dry conditions. In the mid-growing season, high J_s in July was related to rainfall-fed soil moisture, 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 deep-rooting desert shrubs, groundwater may replenish water lost by transpiration (Yin et al., 2014). *Artemisia ordosica* roots are generally distributed in the upper 60 cm of the soil (Zhao et al., 2010), and as a result the plant usually depends on water directly supplied by precipitation because groundwater levels in drylands can often be below the rooting zone of many shrub species, typically at depths $\geqslant$ 10 m as witnessed at our site. Similar findings regarding the role of rainfall and VWC in desert vegetation is reported by Wang et al. (2017).

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 J_s. As an initial energy source, R_s also can force T and VPD to increase, causing a phase difference in time lags among the relations of J_s-R_s, J_s-T, and J_s-VPD.

The hysteresis effect reflects plant acclimation to water limitations, due to g_s~~stomatal conductance~~ being inherently dependent on plant hydrodynamics (Matheny et al. 2014). The large g_s in the morning promoted higher rates of transpiration (Fig. 6, 7), while lower g_s in the afternoon reduced transpiration. Therefore, diurnal curves (hysteresis) were mainly caused by a g_s-induced hydraulic process (Fig. 7). The finding that hysteresis varied seasonally, decreasing with increasing VWC, further reflects the acclimation to water limitation causing J_s to peak in advance of the environmental factors. At our site, dry soils accompanied with high VPD in summer, led to a decreased g_s and a more significant control of the stomata on J_s relative to the 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 incidence of small rainfall events in drylands, soil water supplied by rainfall pulses was largely insufficient to meet the transpiration demand under high mid-day R_s, resulting in clockwise loops. Lower Ω values (< 0.4) at our site also support the idea that g_s have a greater control on transpiration than R_s under situations of water limitation (Fig. 10).

Altogether, stomatal control on the diurnal evolution of J_s by reducing g_s combined with lower sensitivity to meteorological variables during the mid-day dry hours help to reduce water consumption in *Artemisia ordosica*. Seasonally, plant-moderated reductions in g_s and increased hysteresis, leads to reduced J_s and acclimation to drought conditions. It is suggested here that water limitation invokes a water-conservation strategy in *Artemisia ordosica*. Contrary to our findings, counterclockwise hysteresis has been observed to occur between J_s and R_s in tropical and temperate forests (Meinzer et al., 1997; O'Brien et al., 2004; Zeppel et al., 2004), which is reported to be consistent with the capacitance of the particular soil-plant-atmosphere system being considered. Unlike short-statured vegetation, it usually takes more time for water to move up and expand vascular elements in tree stems during the transition from night to day.

4.3. Conclusions

The relative influence of R_s, T, and VPD on J_s in *Artemisia ordosica* was modified by soil water, indicating J_s's lessened sensitivity to the environmental variables during dry periods. J_s~~Sap flow~~ was constrained by soil water deficits, causing J_s to peak several hours prior to the peaking of R_s. Diurnal hysteresis between J_s and R_s varied seasonally and was mainly controlled by hydraulic stresses. Soil moisture controlled ~~sap ~~J_s~~flow~~ response in *Artemisia ordosica* to meteorological factors. This species ~~escaped and ~~acclimated to water limitations by invoking a water-conservation strategy through ~~hysteresis effect and ~~stomatal regulation, producing a hysteresis effect. Our findings add to our understanding of acclimation in desert-shrub species under stress of dehydration.~~ The information advanced here 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 Key Research and Development Program of China (2016YFC0500905), 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. 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) in *Artemisia ordosica* during the growing seasons (May-September period) of 2013 and 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 (J_s) response to shortwave radiation (R_s), air temperature (T), and water vapor pressure deficit (VPD), including time lag~~ time~~s (h) as a function of R_s, T, and VPD.

Relationship	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 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, 2013 and 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), water 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 sap flow per leaf area (J_s) and environmental factors [shortwave radiation (R_s), air temperature (T), water 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 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~~water 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 per leaf area (J_s) in non-rainy days and shortwave radiation (R_s), water 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.

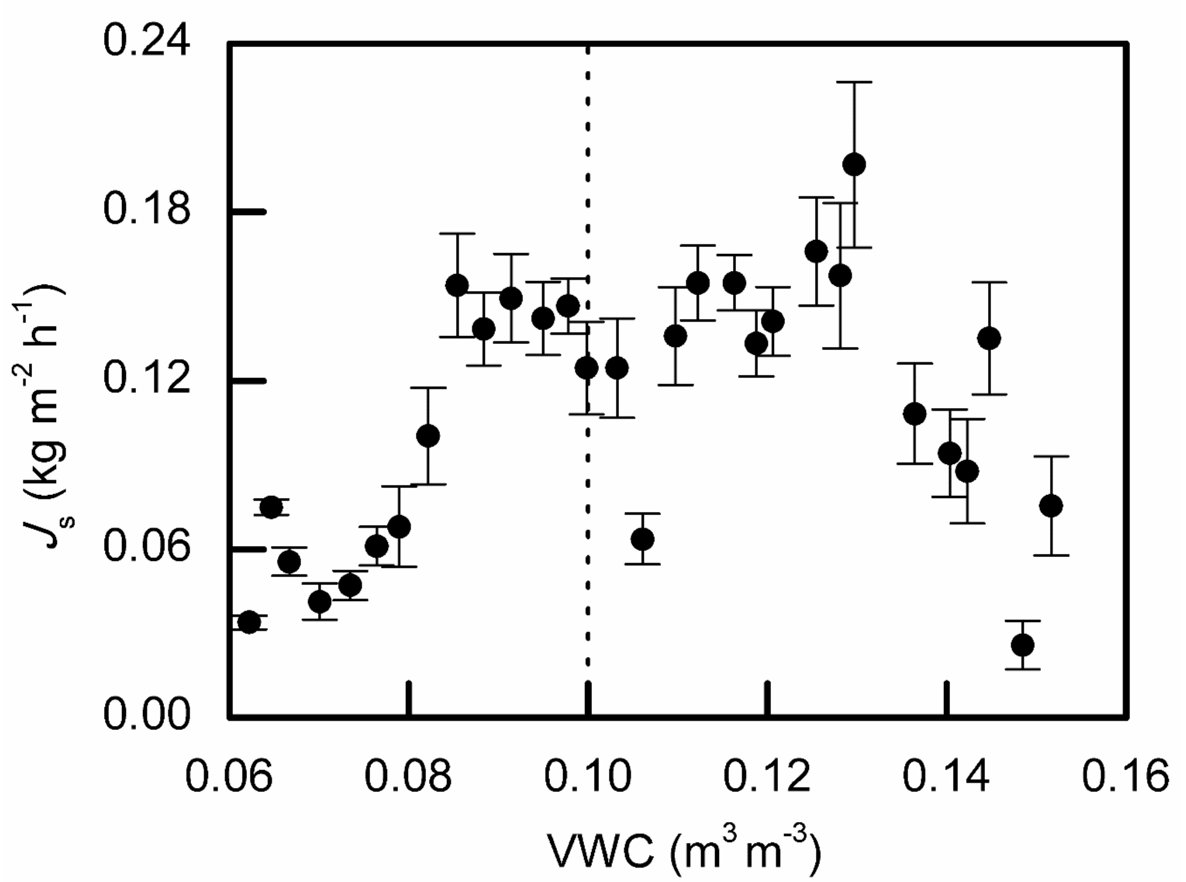
Fig. 6 Mean monthly diurnal changes in sap flow per leaf area (J_s) and stomatal conductance (g_s) in *Artemisia ordosica* during the growing season (May-September period) for both 2013 and 2014. Each point is given as the mean at specific times during each month.

Fig. 7 Seasonal variation in hysteresis ~~loops~~ between sap flow 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 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 water 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 3-day mean value.

Fig. 9 Time lag between sap flow 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 statistically significant regressions (with p-values < 0.05) are shown.



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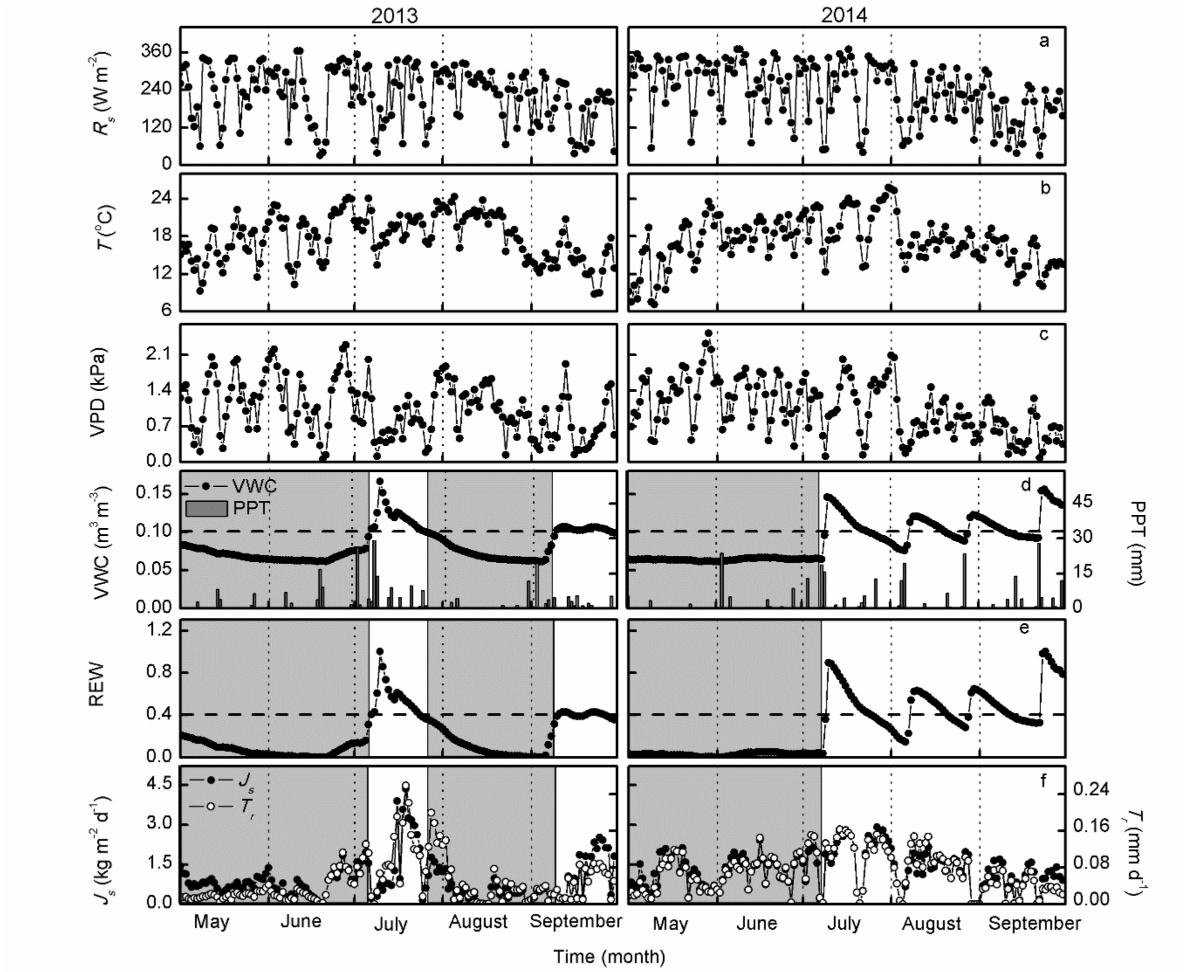

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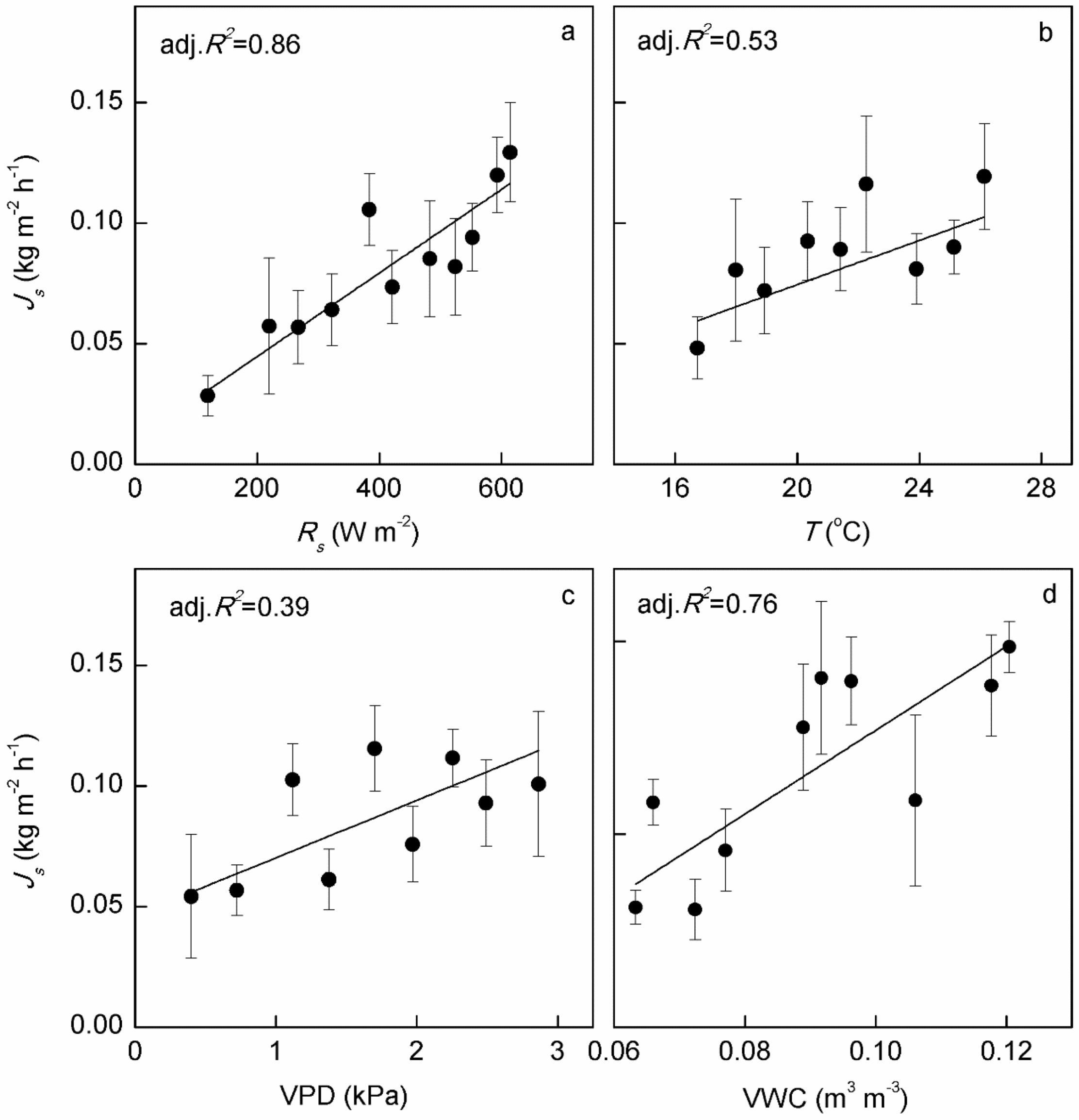

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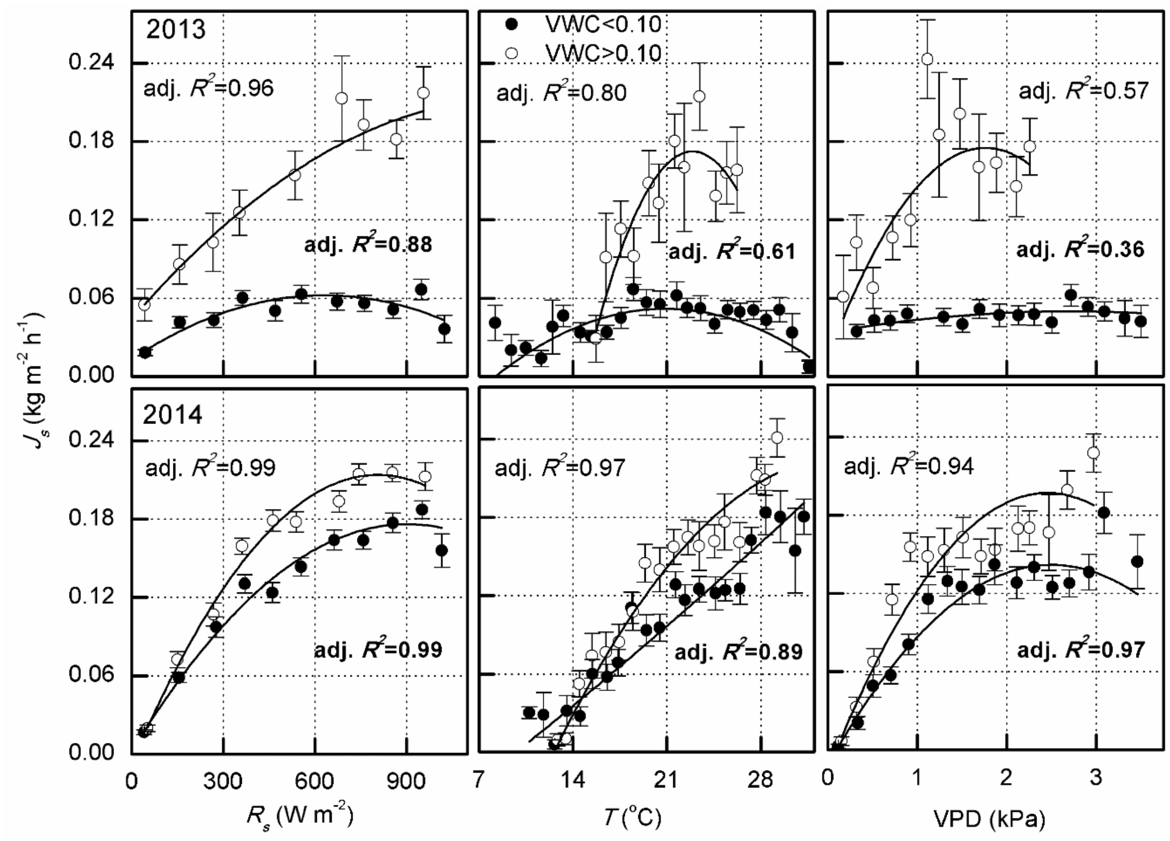


Fig. 4 Sap flow per leaf area (J_S) in non-rainy, daytime hours during the mid-growing season of June 1-August 31 for both 2013 and 2014 as a function of shortwave radiation (R_S), air temperature (T), ~~vapor pressure~~water vapor pressure deficit (VPD) under high volumetric soil water content (VWC > 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.

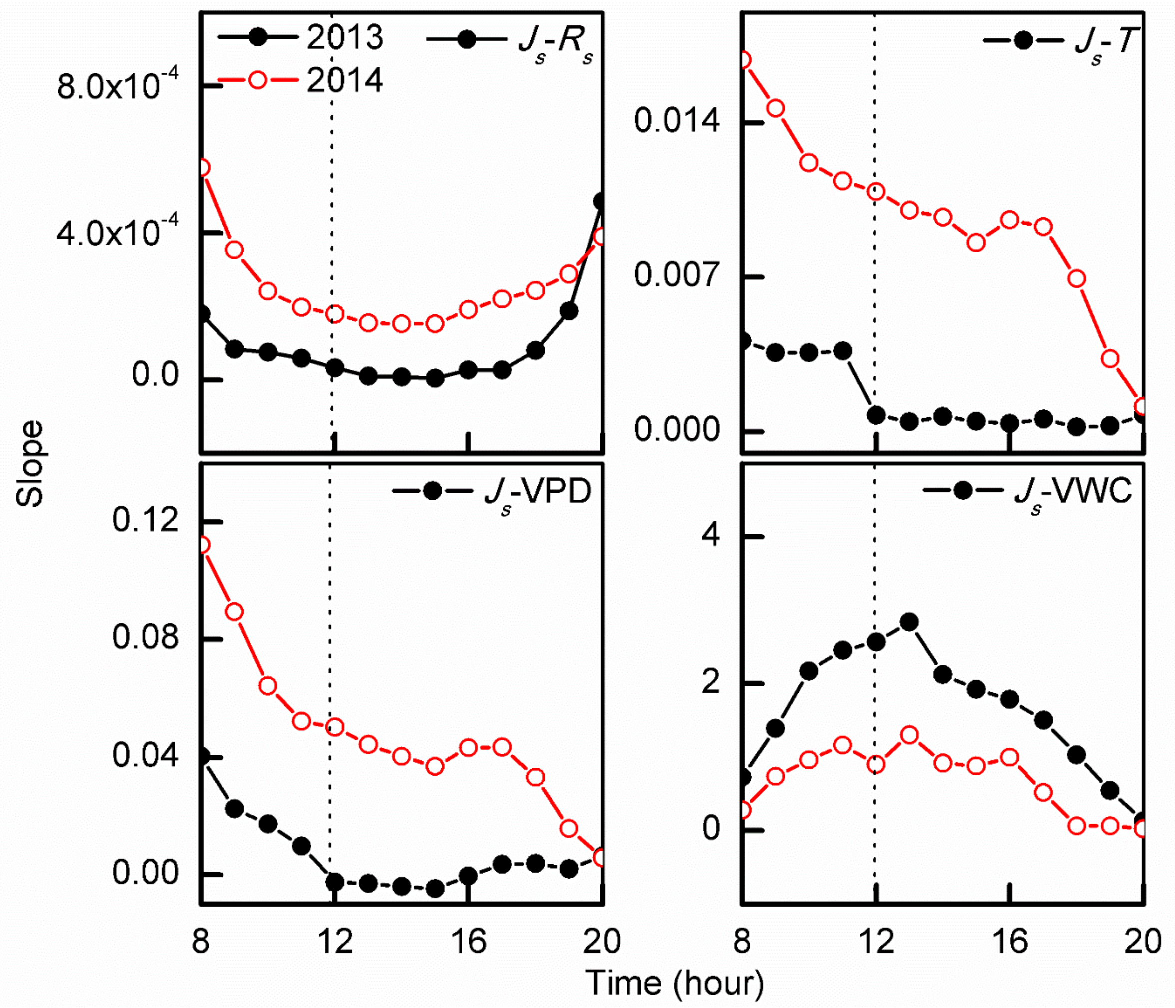
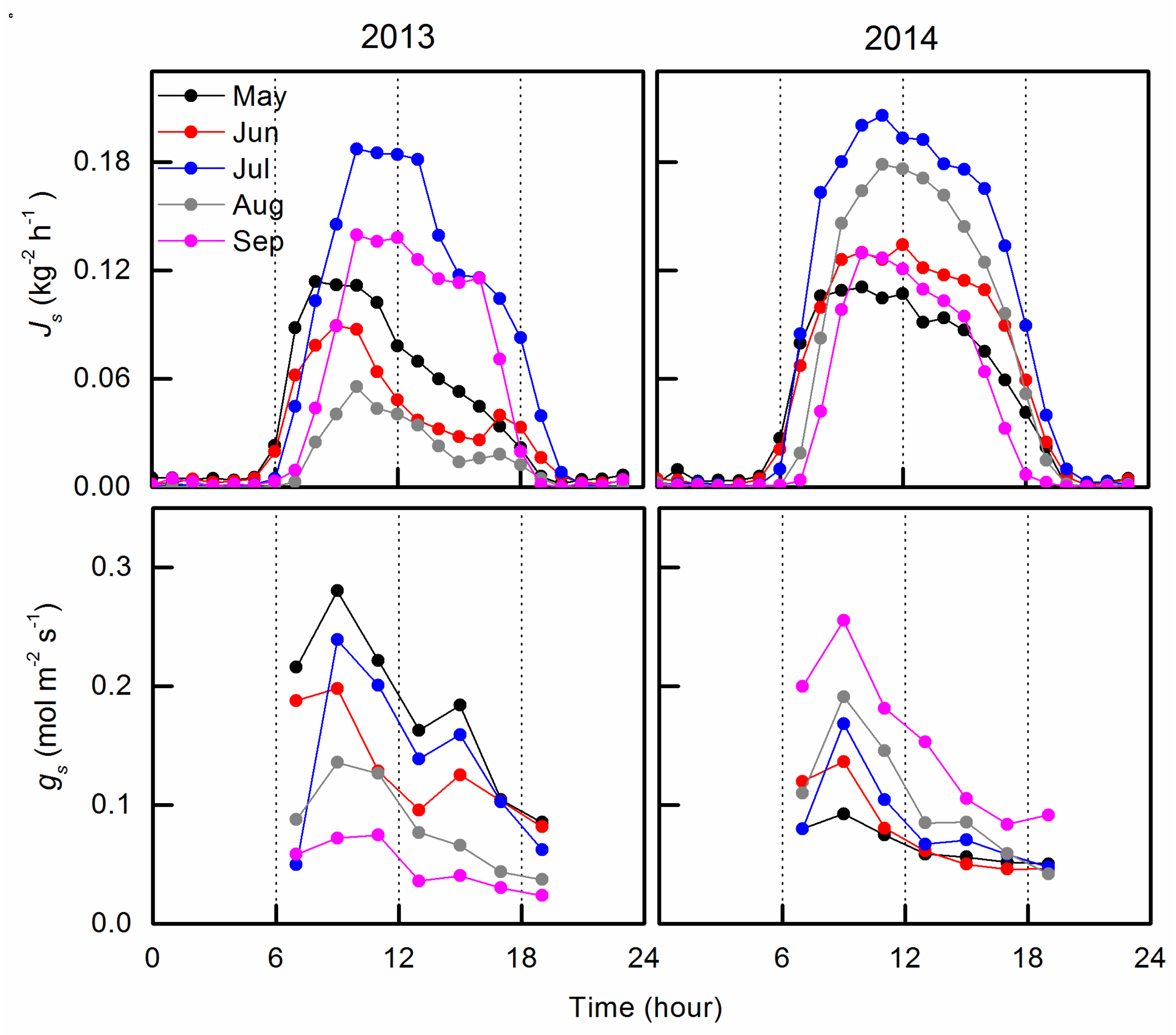


Fig. 5 Regression slopes of linear fits between sap flow per leaf area (J_s) in non-rainy days and shortwave radiation (R_s), ~~vapor pressure~~water vapor pressure deficit (VPD), air temperature (T), and volumetric soil water content (VWC) between 8:00-20:00 h during the mid-growing season of June 1-August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



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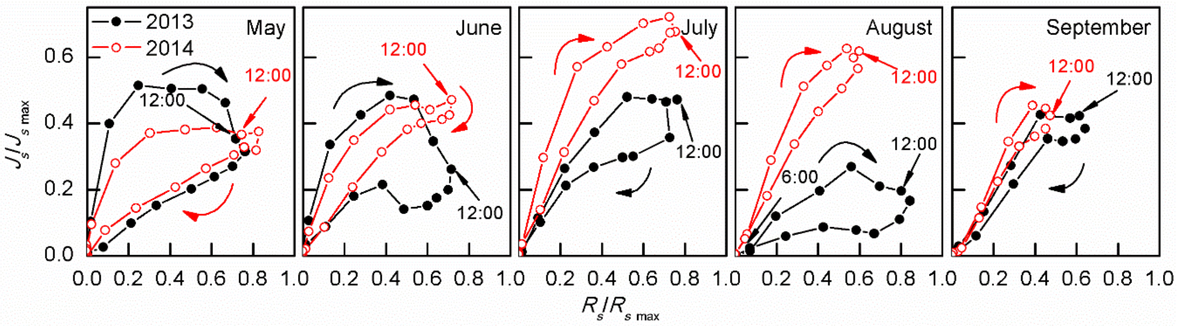

Fig. 7 Seasonal variation in hysteresis ~~loops~~ between sap flow per leaf area (J_s) and shortwave radiation (R_s) using normalized plots for both 2013 and 2014. The y-axis represents the proportion of maximum J_s (dimensionless), and the x-axis represents the proportion of maximum R_s (dimensionless).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

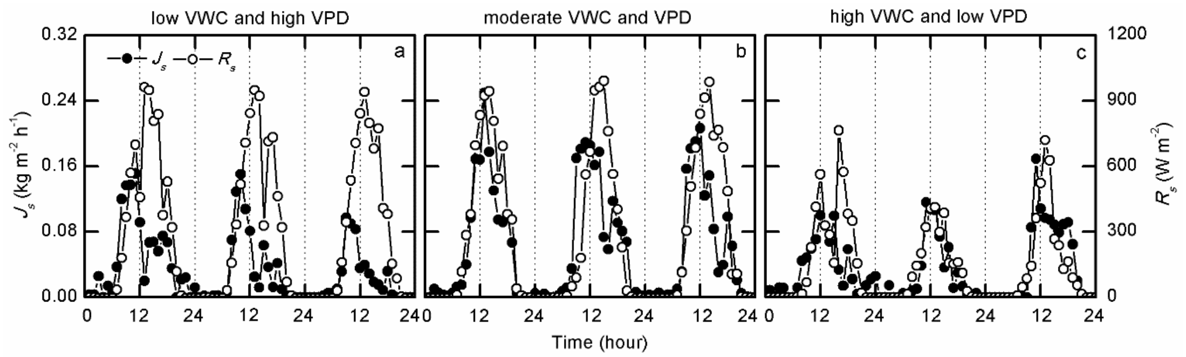

Fig. 8 Sap flow per leaf area (J_s) and shortwave radiation (R_s) over consecutive three days in 2013, i.e., (a) under low volumetric soil water content (VWC) and high ~~vapor pressure~~water vapor pressure deficit (VPD; DOY 153-155, VWC=0.064 m^3 m^{-3}, REW=0.025, VPD=2.11 kPa), (b) moderate VWC and 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 3-day mean value.

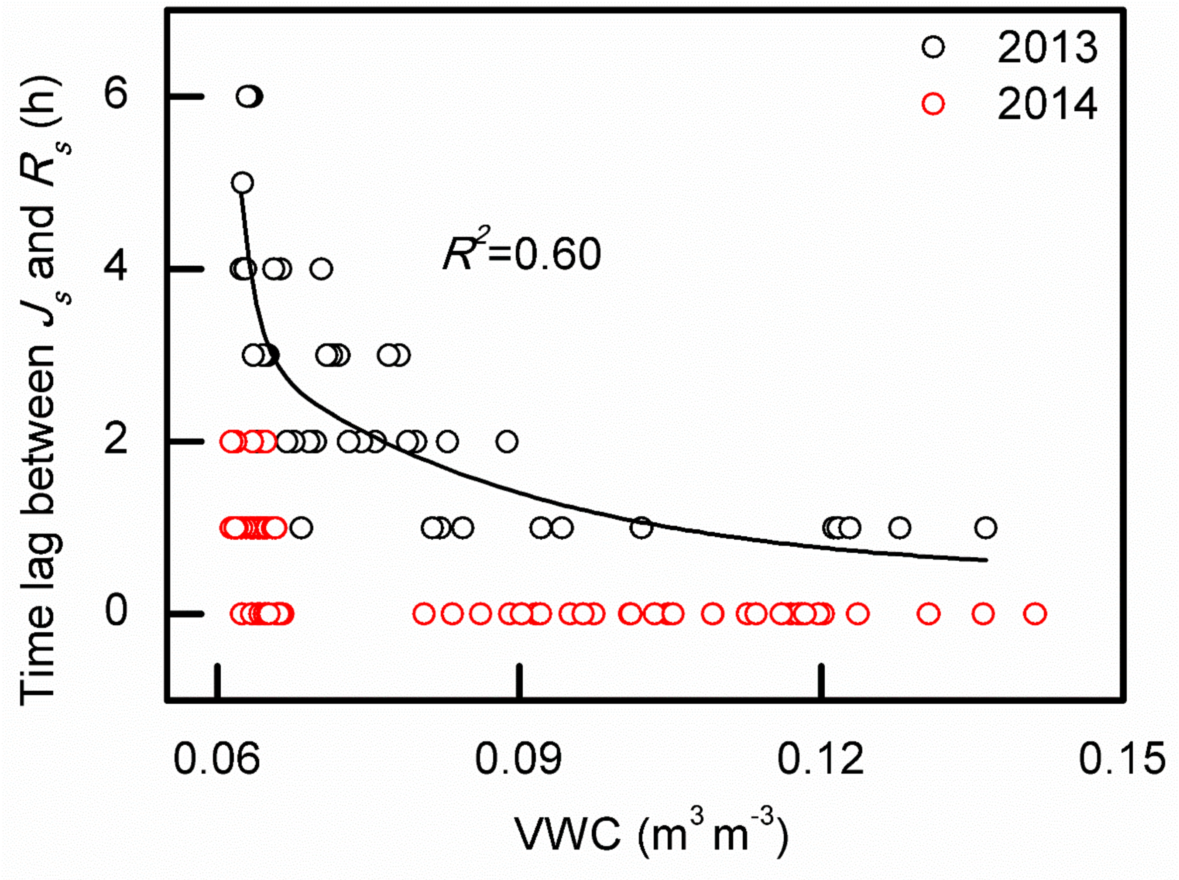

Fig. 9 Time lag between sap flow per leaf area (J_s) and short wave radiation (R_s) in relation to volumetric soil water content (VWC). Hourly data in non-rainy days during the mid-growing season of June 1-August 31 for 2013 and 2014. The lag hours were calculated by a cross-correlation analysis using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

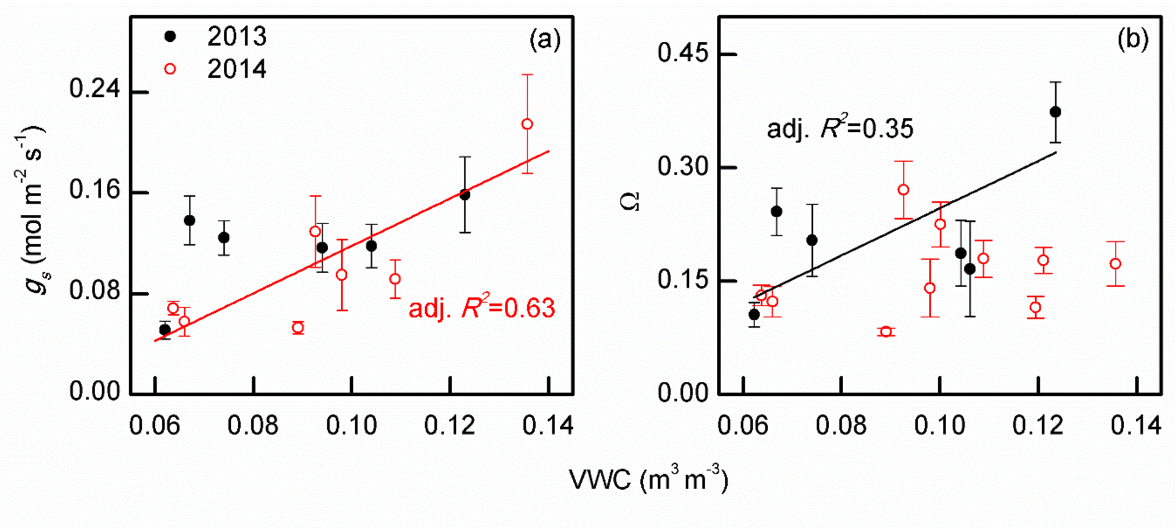

Fig. 10 Relationship between volumetric soil water content (VWC) and (a) stomatal conductance (g_s) in *Artemisia ordosica*, and (b) decoupling coefficient (Ω) for 2013 and 2014. Hourly values are given as binned averages based on a VWC-increment of 0.005 m^3 m^{-3}. Bars indicate standard error. Only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