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 and reviewers' 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

Anonymous Referee #1

General comments

*As the paper is about the soil moisture control on sap-flow and its response to meteorological variables, a physical basis for the definition for drought condition and its severity should be included. Instead, the authors keep on changing their definition of dry conditions for each year and in various figures. What is the reason for using 0.08 m3 m-3, as the threshold to identify drought periods? Is it for severe, moderate or mild drought? The analysis lacks consistency (Example figures 2 6). In section 2.4, they used 0.08 m3 m-3 as the threshold to identify drought conditions. In Figure 2, it is 0.11 $m^3 m^{-3}$ for the drought year 2013 and 0.09 for the wet 2014. Why don't they use 0.08 $m^3 m^{-3}$ in both years? They change threshold, definition of dry condition and VWC values in figure 6. I strongly suggest being consistent in their definition of drought conditions and use the same threshold in all figures. *The root zone depth for this species is around 60 cm (Line 291). The water deep in the root zone can maintain transpiration rates even at low VWC. I think a better way is to define threshold based on root zone soil water content in this paper. Is there any field capacity or wilting point measurements available at the site? If so mention that in the paper and use relative available water content in the root zone. If not, use relative water content (based on maximum and minimum VWC values at the site) in the 30 cm soil layer to identify the drought conditions. The value of VWC shown in Figure 1 indicate that soil drying occurred mainly in shallow layer, not in the deep layer (30 cm), especially during pre and post growing periods.

RESPONSE: We agree with reviewer's suggestion of a consistent threshold of soil water content among years. The soil drought conditions were defined based on relative extractable soil water (REW) at a 30-cm depth during the measurement period (2013-2014) in the revised manuscript. The consistent soil water threshold of 0.10 m^3m^{-3} for sap flow was taken over years in the revised manuscript (Fig. 1). Interestingly, this threshold is equivalent to a drought REW value of 0.4 that was proposed by Granier et al. (1999; 2003). The plant is in drought condition, when VWC at 30 cm depth is $\leq$ 0.10 m^3 m^{-3}. For details relevant to what constitutes drought condition, see the description in the revised text (see L188-195).

Literature that was added in the revised manuscript:

1. Granier et al.: Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. Agricultural and Forest Meteorology, 143,123-145, 2007.

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

*Is it possible to include transpiration (mm) values in this paper? That will add more value to understand the acclimation process of plants to the dry conditions.

RESPONSE: Yes, we have added estimated transpiration values (mm) in the revised manuscript (Fig. 2f). The transpiration has been estimated on the basis of leaf area index (LAI) and sap flow per leaf area (Equation 5, L205-208).

*The methods section reports leaf area measurements, but its values are not mentioned in the paper. Even in conclusion they have mentioned leaf expanded periods, but no data to support it.

RESPONSE: The leaf area measurements were used to calculate the sap flow rate per leaf area, which is a comparative unit with other species. We added the equation to calculate sap-flow rates per leaf area in the revised manuscript (Equation 5, L205-208). Leaf area measurements were added to revised manuscript. (L142, L152-158, Table 1)

We added observations of phenological phases in the revised manuscript (Line 135-137). Observations of phenological phases have been briefly described in section 2.1 relating to the "Experimental site", see Lines 135-137 "Normally, shrub leaf-expansion, leaf-expanded, and leaf-coloration stages begin in April, June, and September, respectively."

*Statistical significance should be evaluated for each figure and include *p*-value along with R2 in figures.

RESPONSE: We added statistical significance and R-square values in the figures of the revised manuscript.

*The 2013-2014 data shown clearly indicate that there is no direct control of VWC on sap flow (Figure 2 first vertical panel). Figure 2 also clearly shows that the relation between Js with Rs , T and VPD are non-linear (check previous comments on p-value). If the relationships are non-linear how can they explain the linear regression slopes shown in Figure 3? Is the linear relationships shown are statistically significant?

RESPONSE: We redefined VWC threshold of sap flow in the revised manuscript using pooled data over two years (Fig. 2). The drought conditions were defined by the VWC threshold and REW of 0.4 for drought conditions (Granier et al., 1999, 2002). The VWC threshold of 0.10 $m^3 m^{-3}$ at our site is equivalent to a REW threshold of 0.4 (Line 188-195). Relations between mean sap-flow rate at specific times over a period of 8:00-20:00 and corresponding environmental factors from Jun. 1 to Aug. 31 period were linear ($p<0.05$; Fig. 3). Regression slopes were, therefore, used to identify the sensitivity of sap flow (degree of response) to the environmental variables (see e.g., Zha et al., 2013). (Line 212-215, Fig. 3)

References:

1. Granier et al.: Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. Agricultural and Forest Meteorology, 143,123-145, 2007.

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

Specific Comments

*Abstract: 0.11 m3 m-3 is only for 2013, not for 2014.

Response: A consistent VWC threshold of 0.10 for both years was defined based on the pooled data over two years. The related statements were revised accordingly in the revised manuscript (Line 188-195, Fig. 1).

*Introduction: The section need to highlight what is the need for sap-flow measurements and how it influence ecosystem water transport and balance. The importance and need for the study is not properly addressed even though the authors explain the effect of environmental variables on sap-flow in this section. In addition to this the section should refer more recent papers on sap-flow measurements.

Response: We added statements addressing the importance and need for sap flow studies in the revised manuscript (Line 86-88, Line 105-107).

*Line 131: Also include root zone depth, and mean leaf area values. Is it possible to include field capacity and wilting point here?

Response: The root zone depth and leaf area values were added in the revised manuscript (Line 141-143, Table 1).

There were no data for field capacity and wilting point available. Therefore, we calculated the relative extractable soil water (REW, Fig. 2) as suggested by one of the reviewers and the literature (Fernández et al., 1997; Zeppel et al., 2008).

$REW=(VWC-VWC_{min})/(VWC_{max}-VWC_{min})$,

where VWC is 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.

References:

1. Fernández, J. E., Moreno, F., Girón I. F., and Blázquez, O. M.: Stomatal control of water use in olive tree leaves, Plant Soil, 190, 179–192, 1997.

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

349, 200-213, 2008.

*Line 140: ‘after dynamax 2005’, what is that?
RESPONSE: The citation ‘after dynamax 2005’ was revised to ‘Dynamax, 2005’ (Line 149).

*Line 141: What is the frequency of measurements?
Response: Sap-flow measurements were taken once per minute for each stem. This was added to the method section in the revised manuscript (L149-150).

*Line 143: What was the mean leaf area? How did it vary with season?
Response: Mean leaf area is based on the mean of estimated leaf areas of five shrubs. The leaf area of each shrub is the product of branch numbers and leaf area per branch. The seasonal changes in LAI was presented in the revised manuscript (Table 1).

*Line 151-155: decoupling coefficient re-expresses gs, and can be removed.
Response: We removed the term “decoupling coefficient” here in the revised manuscript (L166).

*Line 164-171: Be consistent with label style. It is better to italicize all mathematical variable labels. Only u, gs and Js are italicized.
Response: We italicized all labels throughout the text in the revised manuscript.

*Line 178- What is the reason for selecting VWC=0.08 m3 m-3 as the threshold to determine the drought condition. It is not explained in the paper. The time series of VWC (Figure 1) don’t show any severe drought conditions in 30 cm depth. It is useful if the authors can include relative water content within 0-30 cm layer.
Response: We revised the VWC threshold using relative extractable soil water (REW) and VWC at 30-cm depth during the measurement period (2013-2014) using pooled data of two years. Consequently, a consistent VWC threshold of 0.10 was defined for the two years (Line 188-195).

*Line 197: ‘Lower than...’ What is the reduction in percentage?
RESPONSE: We added the statement “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, 1d), respectively.” into revised manuscript. (L228-230)

*Line 205-210: Can you add time series of gs here?
RESPONSE: Yes, we added monthly mean of gs (Table 1).

*Line 215: See general comments above. The threshold to define drought conditions should be the same in both years.
RESPONSE: Yes, we revised VWC threshold as responded to general comments above (Line 188-195).

*Line 222-228: How can you explain the use of the slope of linear regression relationship if the variation of Js with Rs, T and D are non-linear? Use values only when $p<0.05$.

RESPONSE: Each of slope in Fig. 5 (in revised ms) was from a linear regression between sap-flow rates at specific times and corresponding environmental factors over the Jun. 1 to Aug. 31 period. Related linear relations are statistically significant (Fig. 3 in revised ms).

*Line 233-243: What is the reason for this delay?

RESPONSE: The reason for the delay between Js and R_s could be related to available energy. Specific explanation could be that R_s can force T and VPD to increase, causing a phase difference in time lags among the J_s-R_s, J_s-T, and J_s-VPD relations. Stomatal conductance gs peaks earlier than Rs. These delays reflect an acclimation of plant to dry and hot environments. We added this explanation in the revised manuscript (Line 338-343).

*Line 246-252: Figure 6 shows data from three days. What are those days in day number? A meaning full explanation should be given for the use of VWC limits. The first panel shows VWC variation within 0.001 m3 m-3! Is it meaning full considering the errors in VWC measurements? Also use only significant digits while using VWC values. The data is only three days. Is it possible to add more data in this figure, also from both years? Using only three days for this analysis is not conclusive.

RESPONSE: We added the DOY in Fig. 8 caption. This figure compared the degree of soil water control on the hysteresis between J_s and R_s. Therefore, we took three contrasting drought classes (severe, moderate, light) to see corresponding changes in hysteresis to drought (Figure 8).

*Line 252: Figure 8 should be included in the results section.

RESPONSE: Fig.10 in the revised ms was included in the results section, as suggested (L280-282).

*Line 263-265: This is already known. Provide some references here.

RESPONSE: References were added. Similar results were reported by Qian et al., 2015 and Zha et al., 2013) (Line 295-299).

References added:

1. Qian, D., Zha, T., Jia, X., Wu, B., Zhang, Y., Bourque C. P. A., Qin, S., and Peltola, H.: Adaptive, water-conserving strategies in Hedysarum mongolicum endemic to a desert shrubland ecosystem, Environ. Earth. Sci., 74, 6039–6046, 2015.

2. Zha, T., Li, C., Kellomäki, S., Peltola, H., Wang, K.-Y., and Zhang, Y.: Controls of Evapotranspiration and CO2 Fluxes from Scots Pine by Surface Conductance and Abiotic Factors, Plos One, 8, e69027, 2013.

*Line 271: Rewrite this sentence. VWC don't show any direct effect on Js in the figure shown

RESPONSE: The sentence was rewritten as "…VWC is the most important factor modifying the response in sap flow in *Artemisia ordosica* to other environmental factors." (L304-306)

*Line 291: Provide information on root zone depth in the methods section.

RESPONSE: We added information on root zone depth in the methods section of the revised manuscript. Over 60% of the total roots were distributed in the 0-60cm depth (Zhao et al. 2010; Jia et al., 2016). (Line 143-144)

References that added:

1. Zhao, W., Liu, B., Chang, X., Yang, Q., Yang, Y., Liu Z., Cleverly, J., Eamus, Derek.: Evapotranspiration partitioning, stomatal conductance, and components of the water balance: A special case of a desert ecosystem in China. J. Hydrol., 538, 374-386, 2016.

2. Xin Jia, Tianshan Zha, Jinnan Gong, Ben Wang, et al.: Carbon and water exchange over a temperate semi-arid shrublandduring three years of contrasting precipitation and soil moisturepatterns. Agricultural and Forest Meteorology, 228, 120-129, 2016.

*Figure 1: Dotted line is not explained in the figure caption.

RESPONSE: We added an explanation in the caption of Fig. 2 in the revised ms.

*Figure 2: Use the same definition for dry periods in 2013 and 2014 as mentioned above.

RESPONSE: Consistent VWC threshold of 0.1 was used for the dry periods of 2013 and 2014 in the revised manuscript.

*Figure 8: This figure is not mentioned in results sections. Look like p value is low (both N and R2 low) and not statistically significant. If it is below 95.

RESPONSE: Fig.10 (in revised ms) was simply used to explain the hysteresis between sap flow and the environmental factors. We added some results from Fig. 10 in the result section of the revised manuscript. Statistical significance was checked. Only regression lines with p-value < 0.05 are shown in the Fig. of the revised manuscript (Fig. 10; Line 280-282).

Anonymous Referee #2

*General comments

I have some minor comments which should be addressed about the drought classification, soil and vegetation characteristics. Also at the end, I have some minor points about writing. Based on Li et al., 2014 (L108), shrub is shallow rooted. If available/known, it may be good to include root distribution of Artemisia ordosica such as XX% of shrub roots are located within the top 30 cm, and tap root can reach up to 60 cm (Zhao et al., 2010 from L291). This also supports your soil moisture content measurements in the top 10 cm and 30 cm.

RESPONSE:

1) We redefined VWC threshold of sap flow in the revised manuscript using pooled data over two years (Fig. 2). The drought conditions were defined by a VWC threshold and REW-value of 0.4 for drought conditions (Granier et al., 1999, 2002). The VWC threshold of 0.10 m^3m^{-3} at our site is equivalent to a REW threshold of 0.4 (Line 188-195).

References added in the revised manuscript:

- Granier et al.: Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. Agricultural and Forest Meteorology, 143,123-145, 2007.

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

2) Information on root zone depth was added in the methods section of the revised manuscript. Overall, more than 60% of the total roots were distributed within the 0-60 cm depth (Zhao et al. 2010; Jia et al., 2016). (L143-144)

References added in the revised manuscript:

- Zhao, W., Liu, B., Chang, X., Yang, Q., Yang, Y., Liu Z., Cleverly, J., Eamus, Derek.: Evapotranspiration partitioning, stomatal conductance, and components of the water balance: A special case of a desert ecosystem in China. J. Hydrol., 538, 374-386, 2016.
- Xin Jia, Tianshan Zha, Jinnan Gong, Ben Wang, et al.: Carbon and water exchange over a temperate semi-arid shrublandduring three years of contrasting precipitation and soil moisturepatterns. Agricultural and Forest Meteorology, 228, 120-129, 2016.

*If available, it will be good to include stomata closure point, wilting point, and hygroscopic point levels. Hence, the reader can judge the severity of drought. So, there will be some justification based on your drought classification. You used 0.08 (L178), 0.09 (Figure 2), and 0.11 (Figure 2). Is it 0.08 or 0.09?

RESPONSE: There is no value of stomata closure point, wilting point and hygroscopic point available at the moment. We added monthly means of stomatal conductance to Table 1 in the revised manuscript.

We redefined VWC threshold of sap flow in revised manuscript using pooled data over two years (Fig. 1). The drought conditions were defined by VWC threshold and REW value of 0.4 for drought condition (Granier et al., 1999, 2002). The VWC threshold of 0.10 $m^3 m^{-3}$ at our site is equivalent to a REW threshold of 0.4 (Line 188-195).

*Also knowing wilting point and hygroscopic point helps us appreciating the Figure 6. You stratified soil water content based on three limits. How much severe the lowest value. My back of envelope calculation by using Campbell (1974) for sandy soil where porosity is ~0.42 (1-1.54/2.65), the wilting point (15000cm) is ~0.07. It seems your wilting point is much lower. Definitely, to appreciate the Figure 6 and drought severity, giving values are beneficial.

RESPONSE: From our analysis of REW and VWC (Fig. 1, Fig. 2d,e), the plants are in drought conditions, when VWC at a 30-cm depth is < 0.10 m^3 m^{-3}, which is equivalent to a drought REW-value of 0.4 reported by Granier et al. (1999, 2003) (Line 188-195).

*A little more detail about vegetation setting is beneficial. LAI and plant canopy cover of shrub are beneficial. As far as I know, in Mu Us Desert dunes are migrating or semi-migrating depending on canopy cover. So, it will be beneficial for readers.

RESPONSE: We added monthly means of LAI and descriptions of vegetation characteristics in the revised manuscript (Table 1).

*L272-274. In your DISCUSSION, it will be good to include climate for these plant species. Because your ecosystem which is water-limited, most probably different than their study sites!

For example, Huang et al. (2009) study site (L275) is in Guangxi, where annual precipitation is 1900 mm, and mean annual temperature is 19.3 °C. Most probably some/most part of the year, the ecosystem is energy-limited. So, it is not so surprising to see solar radiation control on sap flow. I could not find electronic copy of Zhang et al. (2003) work. Please include prevailing climate in their study area too.
RESPONSE: We added prevailing climate of these species in the revised manuscript. Generally, the present result 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 temperature (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 both radiation and temperature with VWC not limiting (Huang et al. 2009)." (Line 304-310)

*L276-L278. To emphasize the importance of small events on ecological processes, I want to draw authors attention another study by Sala and Lauenroth (1982).
Sala and Lauenroth (1982) showed the ecological importance of small events (<5mm) in semiarid site where dominated by C4 grass. I will be worth to check!
Sala O.E. and W.K. Lauenroth (1982). Small rainfall events: an ecological role in semi-arid regions. Oecologia, 53 (3), 301-304.
RESPONSE: We appreciate the recommendation. We have read the paper and added the relevant findings as a support and generalization of our own results in the revised manuscript (see references in the revised ms).

*Minor Points:
L69. VERB. ....low soil water availability limitS .....,
RESPONSE: We corrected this (Line 70)

L70. VERB. .....limitS vegetation productivity
RESPONSE: We corrected this as well (Line 71)

L73. I recommend citation for: grass replacement by shrubs.
RESPONSE: We added the citation in the sentence "…semi-arid areas of northwestern China (Yu et al., 2004)." in the revised manuscript (Line 74)

L103. Capitalization. ...the Mu Us Desert.....
RESPONSE: The name 'Mu Us desert' was corrected to 'Mu Us Desert' in the revised manuscript. (Line 109)

L125. Capitalization. ...the Mu Us Desert....
RESPONSE: The name 'Mu Us desert' was corrected to 'Mu Us Desert' in the revised manuscript. (Line 131)

L137. VERB. Mean height and sapwood area of sampled shrubs WERE .....
RESPONSE: We corrected this (Line 146)

L156. Replace UPSILON in the equation with lower-case gamma, γ for psychrometric constant.
RESPONSE: We revised as suggested (Line 168-170)

L161. Insert a comma after "ground". ....the ground, and....
RESPONSE: We inserted a comma in the sentence.

L180. VERB. Linear and nonlinear regression WERE .....
RESPONSE: We corrected this (Line 209)

L197. VERB. Total precipitation and number of rainfall events.... WERE lower than THOSE....
RESPONSE: Yes, we corrected this (Line 229)

L266. VERB. Synergistic interactions ..... ARE....
RESPONSE: Corrected (Line 300)

L355-461. Please go through the references. Make sure the unity within the references. Journal names abbreviated some of them (L361, L367, L370 etc.), but not others (L 358, L383, L386 etc.). Choose one of them and stick with it. L424. Typo. Systems... L430. Typo. EcologY... L449. Typo. PLoS ONE. Compare with (L461 and L373). Use lower case for article names. Check (L456, L461, L416 etc.).
RESPONSE: We carefully checked and revised citations and references throughout the manuscript as suggested.

L541. Figure 4. I recommend following some color scheme (pattern) to represent different months such as jet etc. This change will help the readers to follow the figure easier than the current form.
RESPONSE: We replotted Fig. 6 in the revised ms using color, as suggested. (Fig. 6)

L553. Insert a comma after (dimensionless). .... (dimensionless), and ....
RESPONSE: We revised the sentence.

L554. To distinguish from straight arrows, I recommend using 'curved arrows' such as: The CURVED arrowS indicate the clockwise....
RESPONSE: We revised as suggested. (Fig. 7)

L558. I recommend using 'three' instead of '3' days.
RESPONSE: We write "three" instead (Fig. 8)

Track change manuscript version

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), the National Basic Research Program of China (Grant No. 2013CB429901), and by the Academy of Finland (Project No. 14921). ~~It is~~The project is ~~also~~ 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 2013-2014 (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 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.~~11~~ 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~~ biologically-controlled with a low decoupling coefficient and ~~thus being~~ less ~~sensitive~~ sensitivity to the environmental variables during periods of dryness ~~periods~~. 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 ~~is~~are~~have already~~ gradually being~~en~~ 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 affect plant water use efficiency (Pacala et al., 2001; Vilagrosa et al., 2003).

Sap flow ~~measurement~~ can accurately reflect ~~the~~ water consumption ~~estimation~~ ~~of~~~~by~~during plant transpiration~~, water consumption,~~ ~~i~~It ~~has positive influence of~~maintains ecosystem balance ~~by~~through the soil-plant-atmosphere continuum~~ path~~, but is often ~~is~~ ~~influenced~~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 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 all~~In general, understanding~~s~~ ~~Studies~~ o~~n~~f the relationship~~s~~ between ~~the~~ sap~~-~~-flow rate~~s~~ in plants and environmental factors ~~are~~is highly inconsistent, varying with ~~is conducive to understanding vegetal physiological responses to their~~plant habitat~~s~~ (Liu et al., 2011).

Artemisia ordosica, a shallow-rooted desert shrub, is the dominant plant species in the Mu Us ~~desert~~ 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

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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 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 ~~needed~~ ~~on~~of acclimation processes in desert-shrub species under stress of dehydration ~~stress~~.

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 D~~d~~esert. 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

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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 8.1ºC 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.

2.2 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. ~~Annual m~~Maximum monthly mean leaf area index (LAI) ~~is in~~for ~~leaf-expanded stage~~plant specimens with full leaf expansion –was about 0.1 m^2 m^{-2} (Table 1). ~~62.14%~~ Over 60% of ~~the total~~ their roots ~~weight of *Artemisia ordosica*~~ were ~~mainly~~ distributed in ~~the~~ soil depths of 0-60 cm –(Zhao et al., 2010; Jia et al., 2016). Five stems of *Artemisia ordosica* were randomly selected within the plot as replicates for sap-flow measurement. Mean height and sapwood area of sampled shrubs ~~was~~ 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 (~~after~~ Dynamax, 2005). ~~The frequency of s~~Sap--flow measurements w~~as~~ere taken ~~1 record~~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

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from five randomly sampled neighbouring shrubs with similar characteristics ~~as~~ to the shrubs used for ~~sap~~ sap-flow measurements~~, to avoid damaging them~~. 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 ~~at~~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). S~~s~~tomatal 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). ~~Stomatal conductanc~~The g_s~~e~~ measurements were made every two hours from 7:00 to 19:00 h every ten days from May to September, 2013-2014.

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 ~~decoupling coefficient~~ 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

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s^{-1}).

2.3 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 measurement plot. Half-hourly data were recorded by ~~a~~ data logger (CR3000 data logger, Campbell Scientific Inc., USA). VWC at ~~10 and~~ 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*.

2.4 Data analysis

In ~~the~~ 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 ~~with~~as ~~increased~~ VWC increased, ~~saturated~~saturating at VWC of 0.1 m^3 m^{-3}, and ~~then showed a~~ decreasing ~~trend~~ as VWC continued to increase~~d~~. The VWC threshold of 0.1 m^3 m^{-3} is equivalent to a relative extractable soil water (REW) ~~value~~ of 0.4 for drought conditions ~~(by~~ Granier et al., ~~(~~1999~~,~~ and 2007~~) and~~; Zeppel et al., ~~(~~2004~~,~~ and 2008~~) (~~; Fig. 2d, e). Duration and severity of 'drought' were defined based on ~~the~~a VWC threshold and REW ~~value~~ of 0.4. REW was calculated ~~as~~as according to equation (3)~~.:~~

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

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. ~~An extreme dry soil period was defined as the time period when VWC < 0.08 m^3 m^{-3} for both 10- and 30-cm depths for at least 10 consecutive days.~~

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

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

where, J_s is the sap flow per leaf area (kg m^{-2} h^{-1}) or (kg m^{-2} d^{-1})~~, summed over a 24 hour day),~~ E_i 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 ~~replicate~~ ~~sap-flow~~ stems used ~~(, in this case~~ n = 5).

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

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

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 regression 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}. ~~The regression~~ Relations between mean sap-flow rates at specific times over a period of 8:00-20:00 and ~~its~~ corresponding environmental factors ~~over period of~~ from Jun~~.~~e 1 to Aug~~.~~ust 31 ~~can be~~ were fittedderived with, linear regression ($p<0.05$; Fig. 3). Regression TheRegression slopes of linear regression were – therefore used to identify theas indicators of sap-flow sensitivity of sap flow (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

Range of daily means (24-hour mean) for R_s, *T*, R_s, VPD, and VWC during the 2013 growing season (May-September) were 31.1-364.9 W m^{-2}, 8.8-24.4ºC, 31.1-364.9 W m^{-2}, 0.05-2.3 kPa, and 0.06-0.17 m^3 m^{-3} (Fig. 1Fig. 2a, b, c, d), respectively,; annual means for the same yearbeing were 224.8 W m^{-2}, 17.7ºC, 224.8 W m^{-2}, 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}, 7.1-25.8ºC, 31.0-369.9 W m^{-2}, 0.08-2.5 kPa, and 0.06-0.16 m^3 m^{-3} (Fig. 1Fig. 2a, b, c, d), respectively,; annual means were being 234.9 W m^{-2}, 17.2ºC, 234.9 W m^{-2}, 1.05 kPa, and 0.09 m^3 m^{-3}.

Total precipitation and number of rainfall events during the 2013 measurement period (257.2 mm and 46 days) wereaseas about 5.6% and 9.8% lower than thoseat during 2014 (272.4 mm and 51 days; Fig., 21d), respectively. In 2013, more irregular rainfall events occurred than in 2014,. The measurement period in 2013 had many irregular rainfall events compared to 2014, with 45.2% of rainfall falling in July and 8.8% in August., 2013.

Drought condition mainly occurred in May, June, and August of 2013 and in May and June of 2014 (Fig. 1Fig. 2d,e). Both years had dry springs. A nearlyMore than Over one-

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month period of ~~long~~ summer drought occurred in ~~August of~~ 2013.

Range of daily ~~means of~~ 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. ~~1e~~2f)~~;~~ with annual means ~~were~~ 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 ~~was~~were 0.05 mm d^{-1} and 0.07 mm d^{-1} over the growing season in 2013 and 2014 (Fig. 2f), respectively, ~~and it was~~being 34% lower in 2013 than ~~that~~ in 2014. The total T_r over growing season (May 1-September 30) in 2013 and 2014 were 7.3 mm and 10.9 mm, respectively. Seasonal fluctuations in J_s and T_r corresponded with the seasonal pattern in VWC (~~Fig. 1~~Fig. 2d, ~~e~~f). Daily mean J_s and T_r decreased or remained nearly constant during dry-soil periods (~~Fig. 1~~Fig. 2d, ~~e~~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 (Fig. 2d, f; Fig. 3d). ~~(Fig. 2), meanwhile, saturating at VWC ~0.11 m^3 m^{-3} in 2013 and ~0.09 m^3 m^{-3} in 2014, then decreasing with VWC when VWC is greater than the thresholds of 0.11 m^3 m^{-3} in 2013 and 0.09 m^3 m^{-3} in 2014. Ss~~Soil water ~~is~~ was shown to modify the response of J_s to environmental factors (~~Fig. 2~~Fig. 4). Sap flow ~~J_s~~ increased more rapidly with increases in R_s, T, and VPD under high VWC (i.e., VWC > 0.~~11~~1 m^3 m^{-3} ~~both~~ in both 2013 and ~~, VWC > 0.09 m^3 m^{-3} in~~ 2014) compared with periods with lower VWC (i.e., VWC < 0.~~11~~1 m^3 m^{-3} ~~both~~ in both 2013 and~~, VWC < 0.09 m^3 m^{-3} in~~ 2014). Sap flow J_s was more sensitive to R_s, T, and VPD under high VWC (Fig. ~~2~~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, ~~T,~~ and VWC)

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varied depending on the time of a day (Fig. 3Fig. 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. 3Fig. 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. 46), 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 stomatal conductance (g_s) were similar to J_s, but peaking about 2 and 1 h earlier than J_s in July and August, respectively (Fig. 4Fig. 6).

There were pronounced time lags between J_s and R_s over the two years (Fig. 5Fig. 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 12).

Use of normalized variables may remove the influence of J_s and R_s from the data. As a result, clockwise hysteresis loops between J_s and R_s during the growing period were observed (Fig. 57). 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 morning

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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. 6~~Fig. 8, ~~7~~9). For example, J_s peaked about 2 h earlier than R_s on days with low VWC (~~Fig. 6~~Fig. 8a), 1 h earlier than R_s on days with moderate VWC (~~Fig. 6~~Fig. 8b), and at the same time as R_s on days with high VWC (~~Fig. 6~~Fig. 8c). Lag hours between J_s and R_s over the growing season were negatively and linearly related to VWC (~~[~~Fig. 9~~7~~: 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. 7~~Fig. 9). ~~The~~State variables g_s and Ω showed a significantly increas~~ed~~ing trend with increasing VWC in 2013 and 2014, respectively (~~Fig. 8~~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 ~~the~~ plant~~s'~~ physiological attributes to environmental stress and/or stomatal regulation (Huang et al., 2011b; Naithani et al., 2012). In this study, large regression slopes ~~of linear relationships~~ 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 and hot period of the day (Fig. ~~3~~5). Stomatal conductances were the largest in the morning (Fig. ~~4~~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 ~~of~~ for water, causing ~~stomatal conductance~~g_s to be limited by

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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~~the~~ nearby region positively correlated ~~to~~with VWC at noon (Qian et al., 2015), and the evapotranspiration ~~over a~~of a Scots pine ~~forest~~stand showed ~~a~~ higher sensitivity to surface conductance, ~~T~~temperature, ~~VPD~~vapor pressure deficit, and radiation in the morning~~,~~ than in the afternoon (Zha et al., 2013).

Synergistic interactions among environmental factors influencing sap flow ~~is~~ 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~~s~~ regarding lower sensitivity in J_s to environmental factors (R_s, T and VPD) during dry periods was ~~in line~~consistent with ~~a previous~~an earlier study of boreal grasslands (Zha et al., 2010). ~~O~~Also our finding ~~that soil water regulates the response of other environmental factors, suggests~~ that VWC is the most important factor ~~controlling~~ modifying ~~the~~ responses ~~of~~in sap flow in *Artemisia ordosica* ~~response~~ to other environmental factors,~~.~~ ~~This is~~ ~~was~~is in contrast to other shrub species.~~,~~ ~~where~~ ~~for~~ 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

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were clearly associated with the intermittent supply of water to the soil during rainfall events, as ~~we found~~indicated at our site (Fig. ~~1d~~2d, ~~e~~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. ~~This finding is related to a positive response in J_s to R_s, T, and VPD under high VWC (Fig. 2).~~ 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. 1~~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. ~~5~~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

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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. 5~~Fig. 7), indicating that R_s lagged J_s, and the response of J_s to R_s varied both diurnally and seasonally. A large g_s in the morning promoted higher rates of transpiration (~~Fig. 4~~Fig. 6). In dry and hot conditions, g_s ~~stomatal conductance~~ decreased, causing the control of the stomata on J_s to increase relative to changes in environmental factors. Diurnal trends in J_s and g_s occurred together, both peaking earlier than R_s. The g_s~~Stomatal conductance~~ 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). 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 plant transpiration more than VPD. 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. 6~~Fig. 8, ~~7~~9). The result that g_s ~~stomatal conductance~~ increased with increasing VWC (~~Fig. 8~~Fig. 10a), along with the synchronization ~~harmonization~~ of J_s and g_s, suggests that J_s is less sensitive to ~~stomatal conductance (~~g_s~~)~~ in high VWC and more so to R_s. Temporal patterns in J_s became more consistent ~~coherent~~ with those in R_s as VWC increased, leading to a weakened hysteresis between the two variables. This is further supported by a large decoupling coefficient, when VWC is high (~~Fig. 8~~Fig. 10b). The larger the decoupling coefficient is, the greater is the influence of R_s on J_s. The effect of VWC on time lag varied 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 soil water content, indicating J_s's 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, 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 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

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climatic conditions.

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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* in the plot 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 sap-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~~ 30-cm depth (VWC~~))~~)] in non-rainy days between 8:00-20:00 h during the mid-growing ~~period~~ season of June 1-August 31 for ~~over~~ 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 ~~period~~ 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}, ~~both in~~ 2013 and 2014). J_s is given as binned averages according to R_s, T~~-~~, and VPD, based

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on increments of 100 W m^{-2}, 1^{o}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 period season of June 1-August 31 for both 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 ~~period~~ season of June 1-August 31 for ~~both~~ 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 ~~both~~ 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 ~~line~~ with ~~p~~ p-values < 0.05 ~~was~~ are ~~showed~~shown.

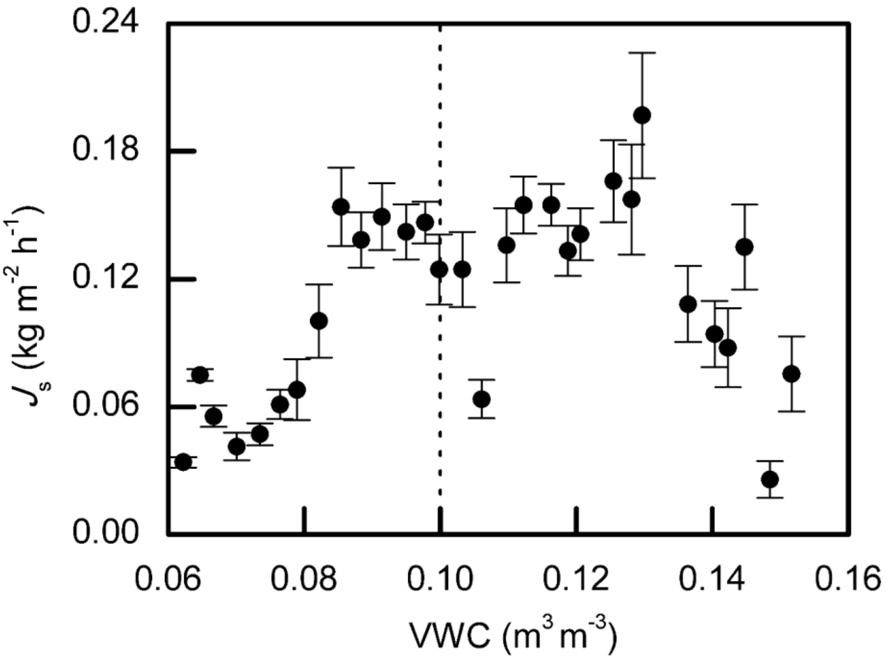

Fig. 1 Sap-flow rate per leaf area (J_s) as a function of soil water content (VWC) at 30 cm depth in non-rainy, daytime hours during the mid-growing period from June 1-August 31 over 2013-2014. Data points are binned values from pooled data over two years at a VWC increment of 0.003 m^3 m^{-3}. Dotted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

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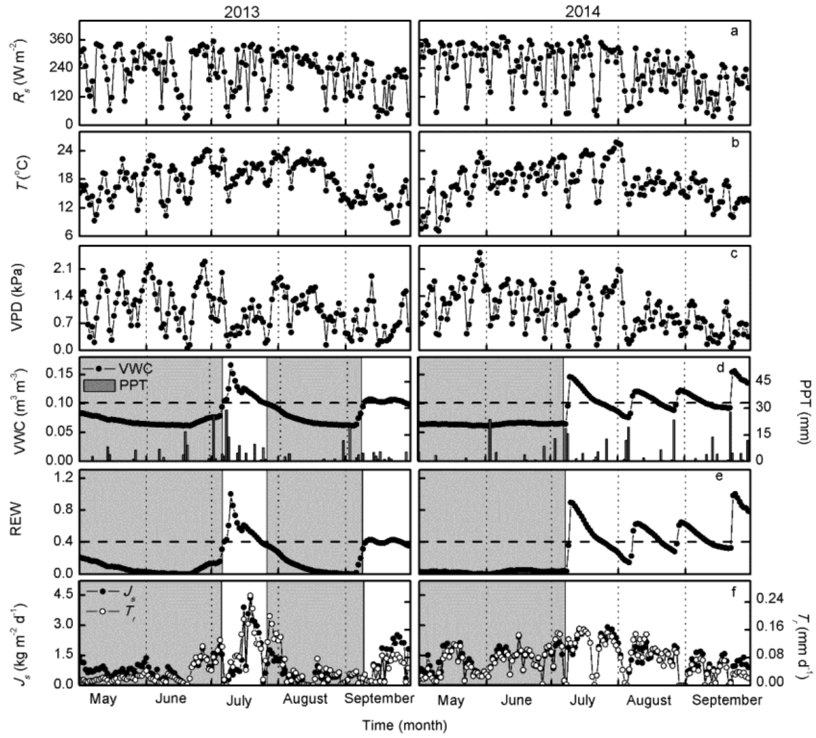

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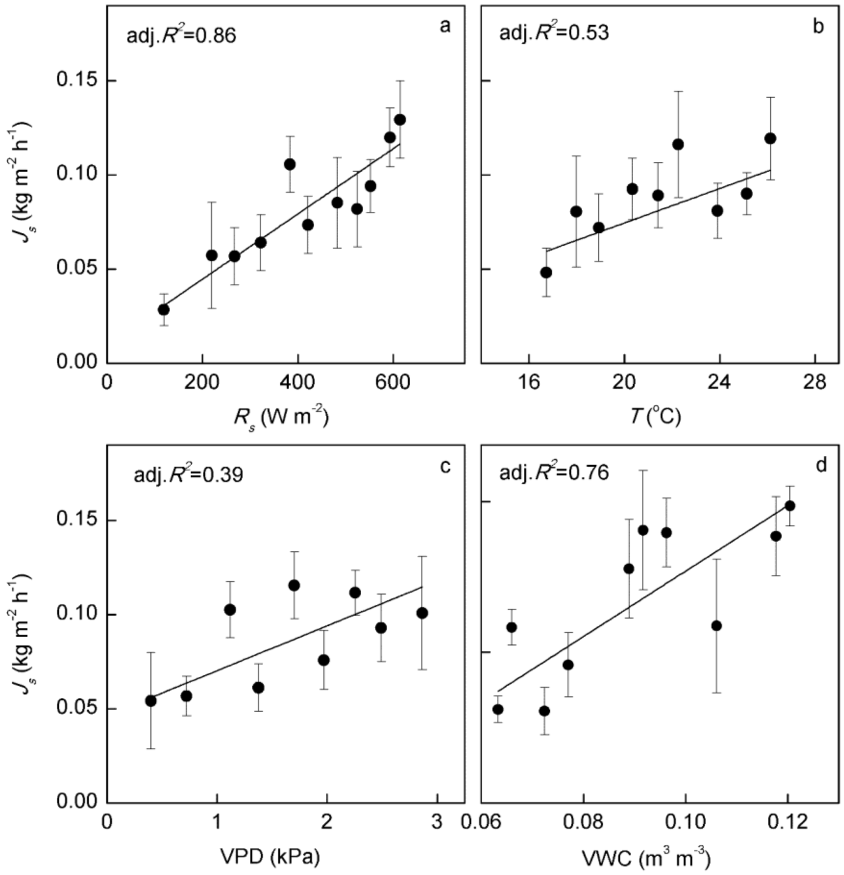

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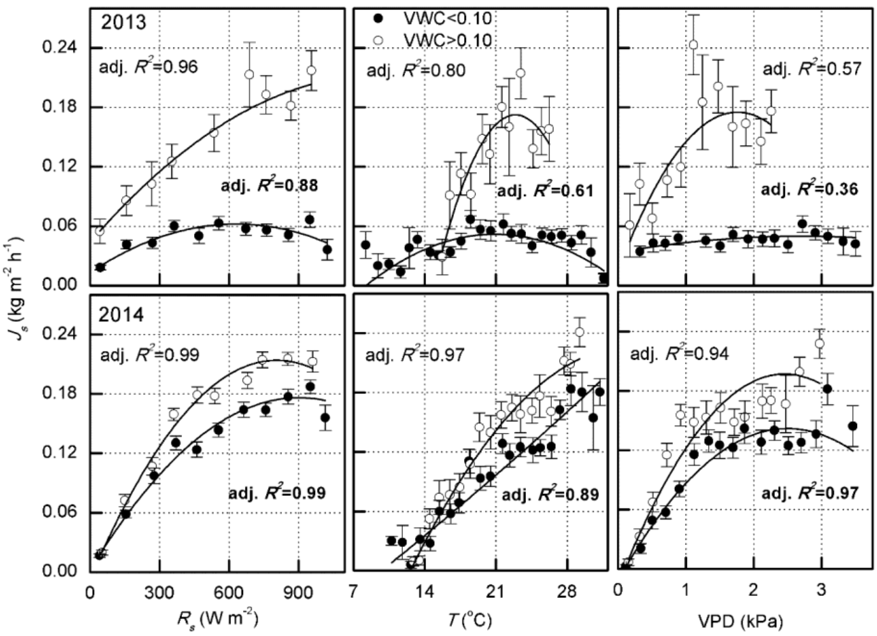

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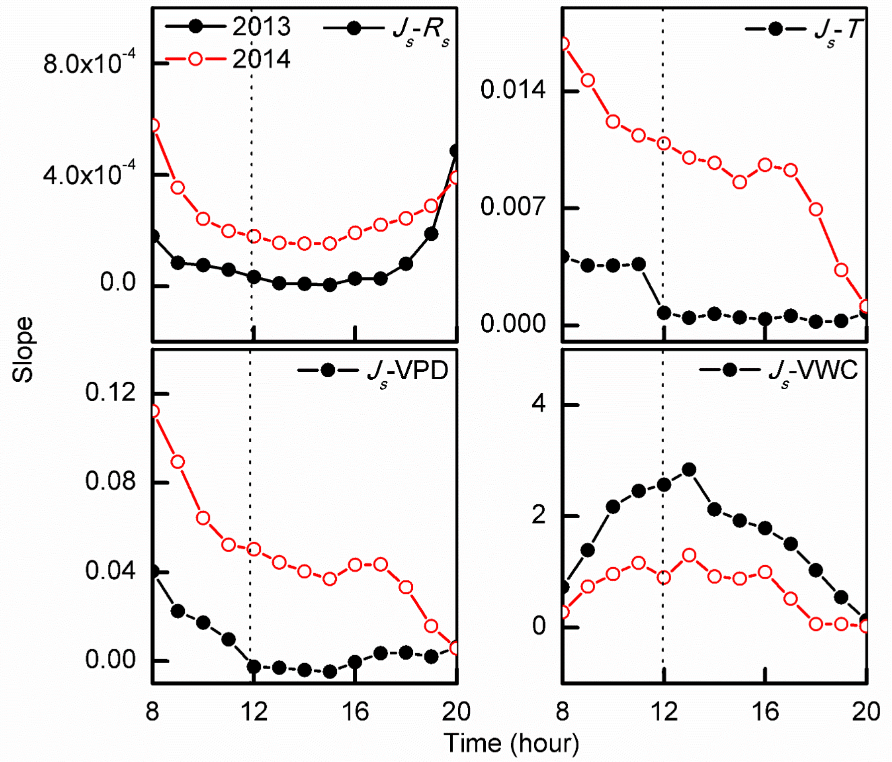

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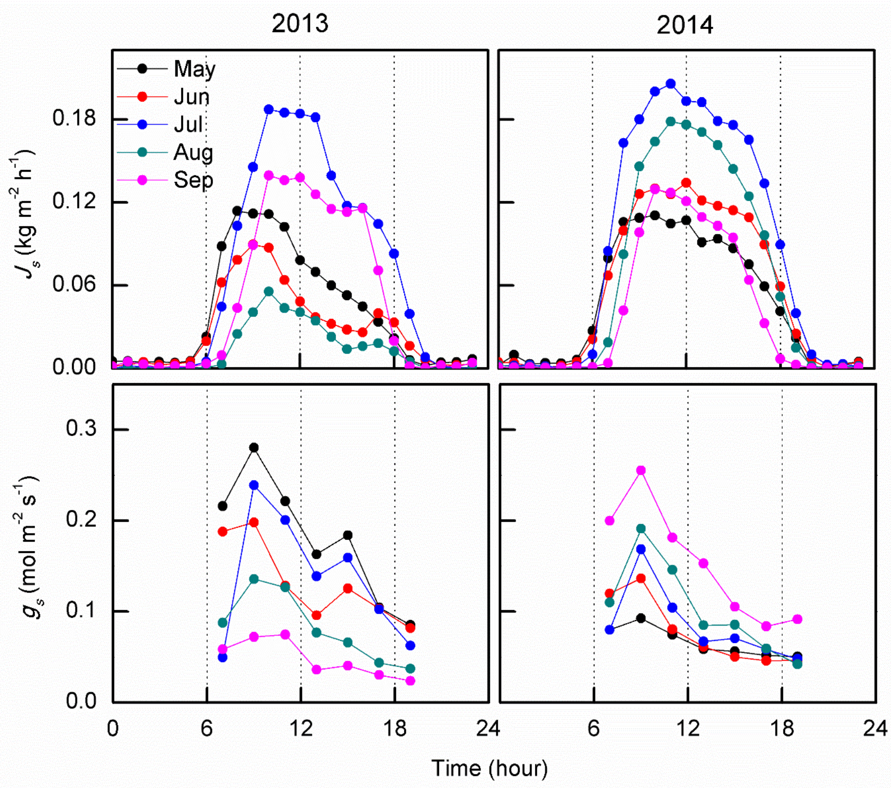

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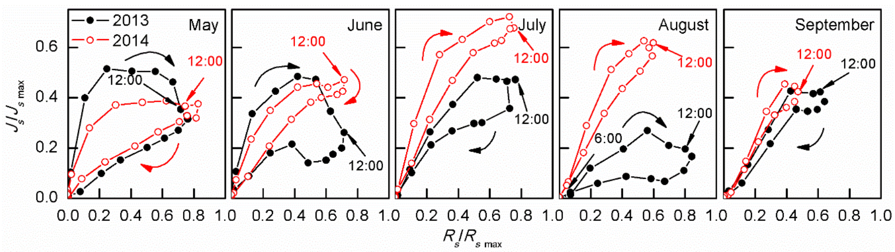

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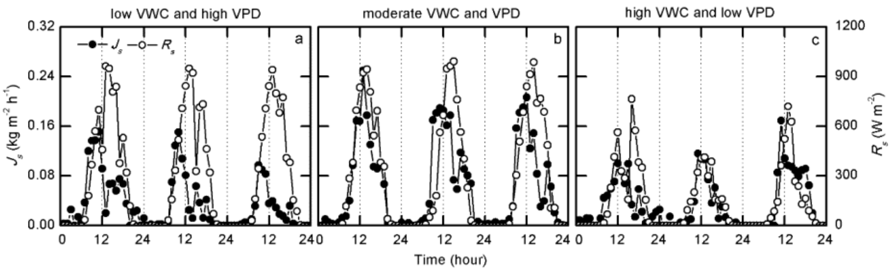

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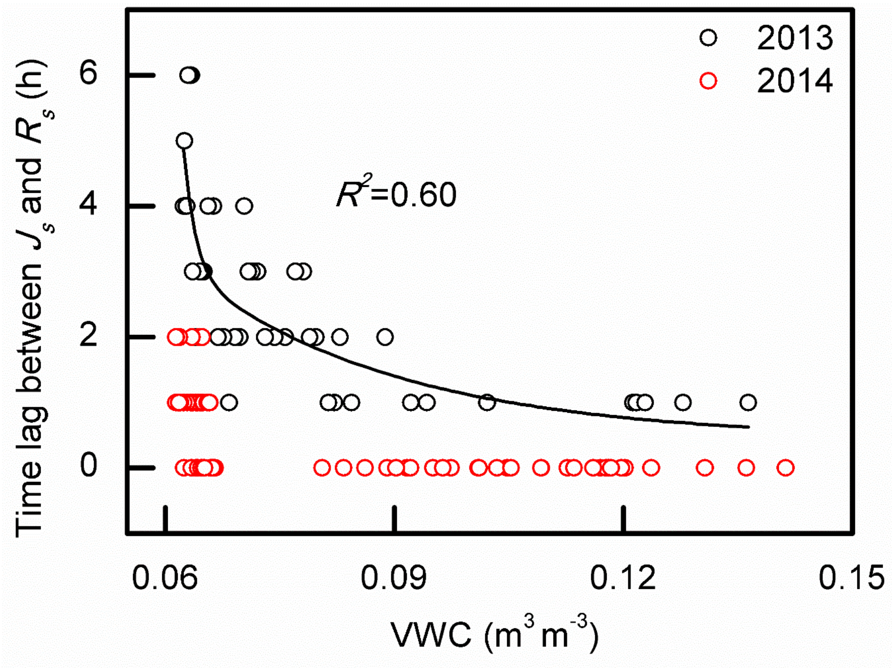

Fig. 9 Time lag between sap-flow rate per leaf area (J_s) and short wave radiation (R_s) in relation to volumetric soil water content (VWC). Hourly data in non-rainy days during the mid-growing season of June 1-August 31 for 2013 and 2014. The lag hours were calculated by a cross-correlation analysis 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).

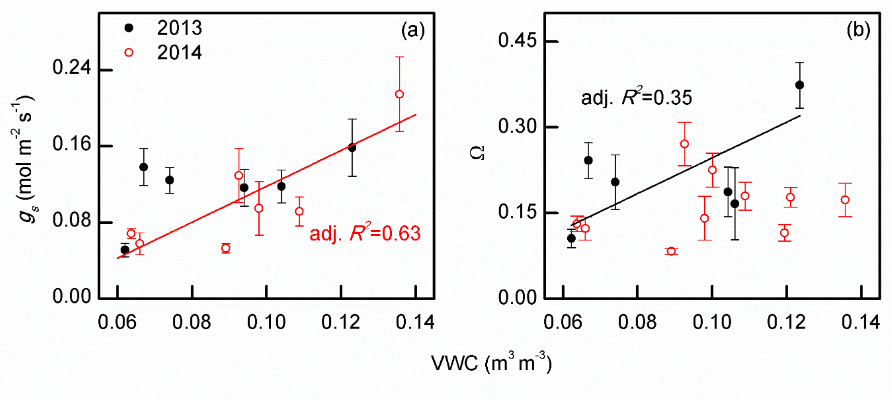

Fig. 10 Relationship between volumetric soil water content (VWC) and (a) stomatal conductance (g_s) in *Artemisia ordosica*, and (b) decoupling coefficient (Ω) for 2013 and 2014. Hourly values are given as binned averages based on a VWC-increment of 0.005 m^3 m^{-3}. Bars indicate standard error. Only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

Marked-up manuscript version

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), 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 2013-2014 (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 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 less sensitivity 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

2. 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 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 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 highly inconsistent, varying with plant habitat (Liu et al., 2011).

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 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 8.1ºC 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.

2.2 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 soil depths of 0-60 cm (Zhao et al., 2010; Jia et al., 2016). Five stems of *Artemisia ordosica* were randomly selected within the plot as replicates for 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 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 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, 2013-2014.

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}).

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.

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 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.,

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

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:

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

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 regression 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.

3. Results

3.1 Seasonal variations in environmental factors and sap flow

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}, 8.8-24.4ºC, 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}, 17.7ºC, 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}, 7.1-25.8ºC, 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}, 17.2ºC, 1.05 kPa, and 0.09 m^3 m^{-3}.

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.

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 in 2013 and 2014 (Fig. 2f), respectively, being 34% lower in 2013 than in 2014. The total T_r over growing season (May 1-September 30) in 2013 and 2014 were 7.3 mm and 10.9 mm, respectively. Seasonal fluctuations in J_s and T_r corresponded with the seasonal pattern 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.

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 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).

Use of normalized variables may remove the influence of J_s and R_s from the data. As a result, 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. Sap-flow rate declined with decreasing R_s during the afternoon. Sap flow J_s was higher in the 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 and hot 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 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. A large g_s in the morning promoted higher rates of transpiration (Fig. 6). In dry and hot conditions, g_s decreased, causing the control of the stomata on J_s to increase relative to changes in environmental factors. 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). 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 plant transpiration more than VPD. 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. This is further supported by a large decoupling coefficient, when VWC is high (Fig. 10b). The larger the decoupling coefficient is, the greater is the influence of R_s on J_s. The effect of VWC on time lag varied 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 soil water content, indicating J_s's 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 $\mathrm{R_s}$. Diurnal hysteresis between J_s and R_s varied seasonally, 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 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.

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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 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.

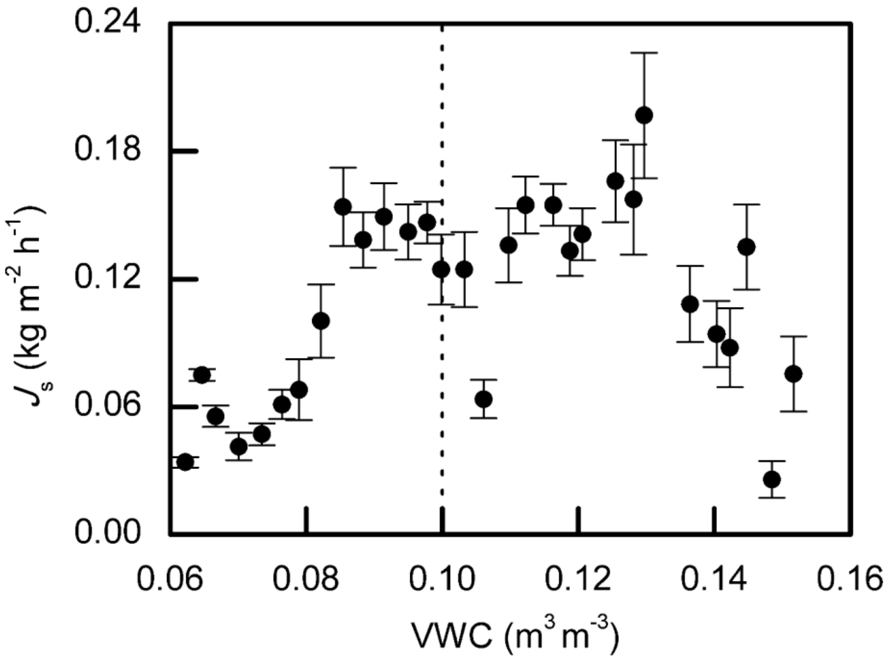
Fig. 6 Mean monthly diurnal changes in sap-flow rate per leaf area (J_s) and stomatal conductance (g_s) in *Artemisia ordosica* during the growing season (May-September) for both 2013 and 2014. Each point is given as the mean at specific times during each month.

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.



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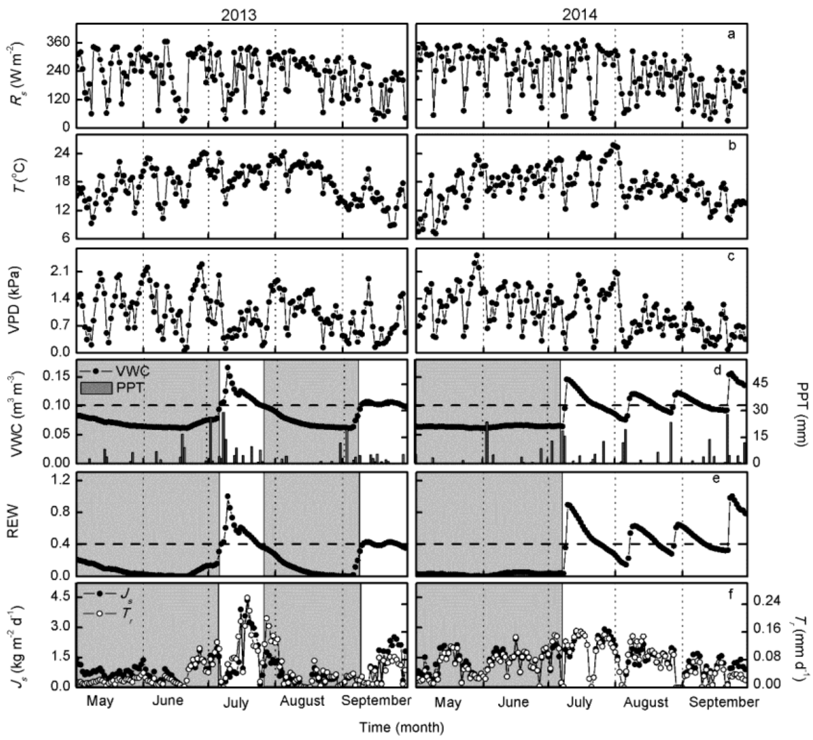

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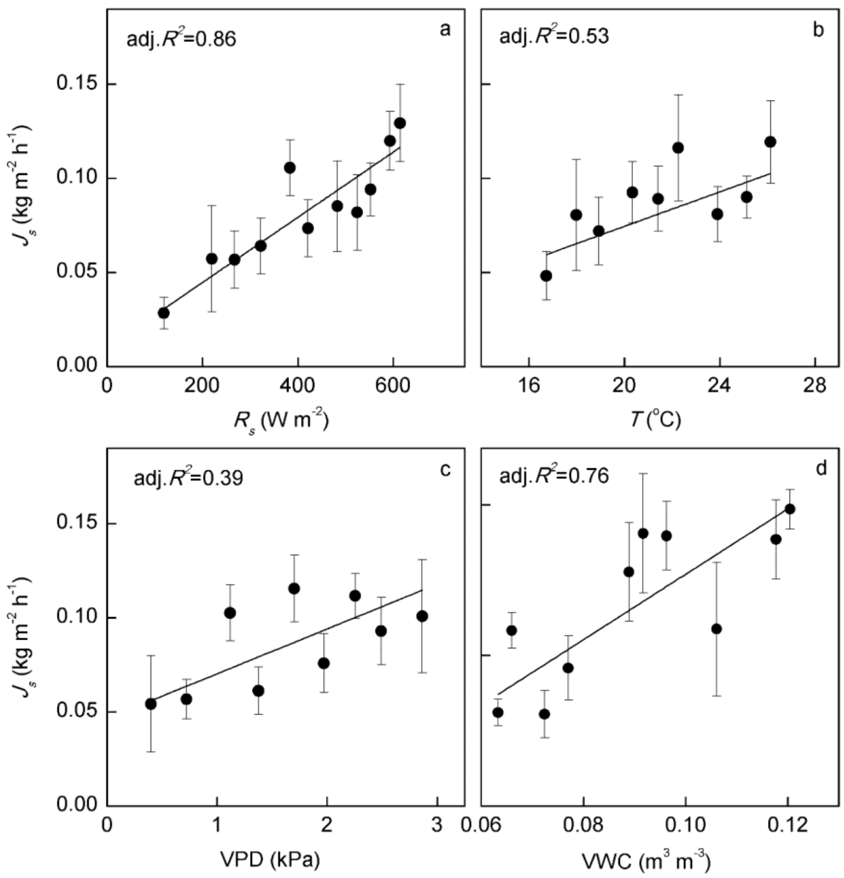

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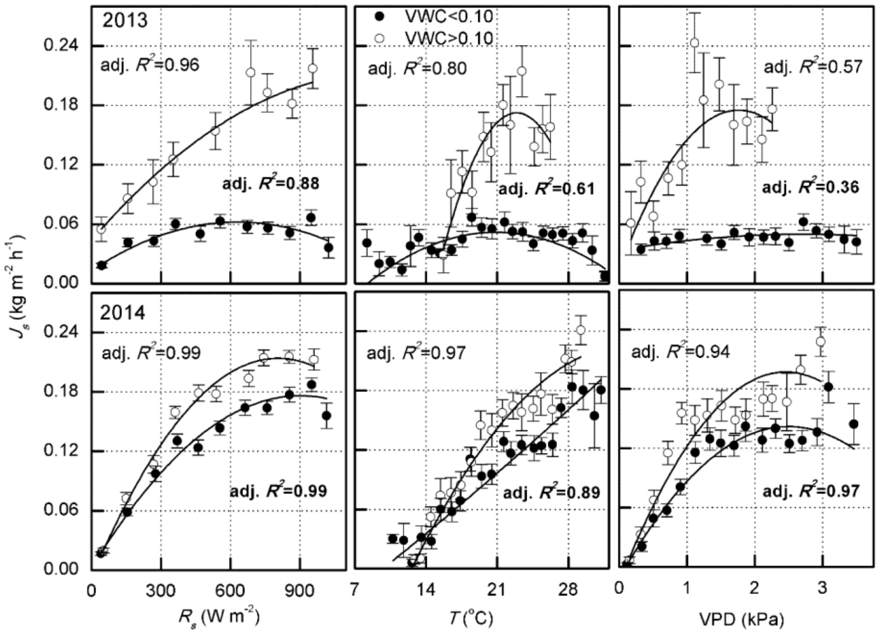

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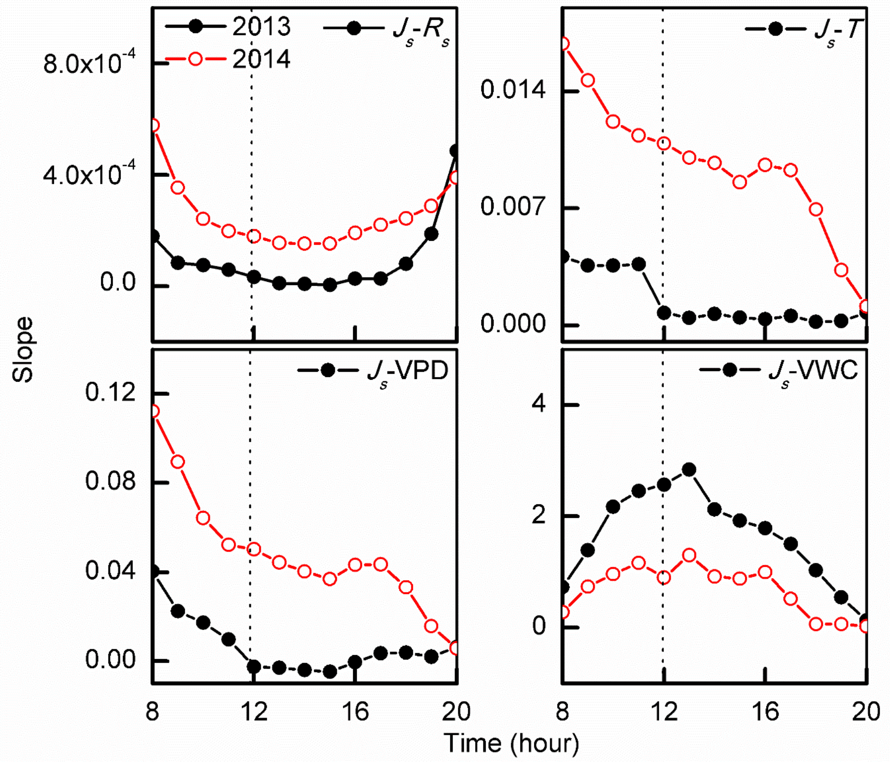

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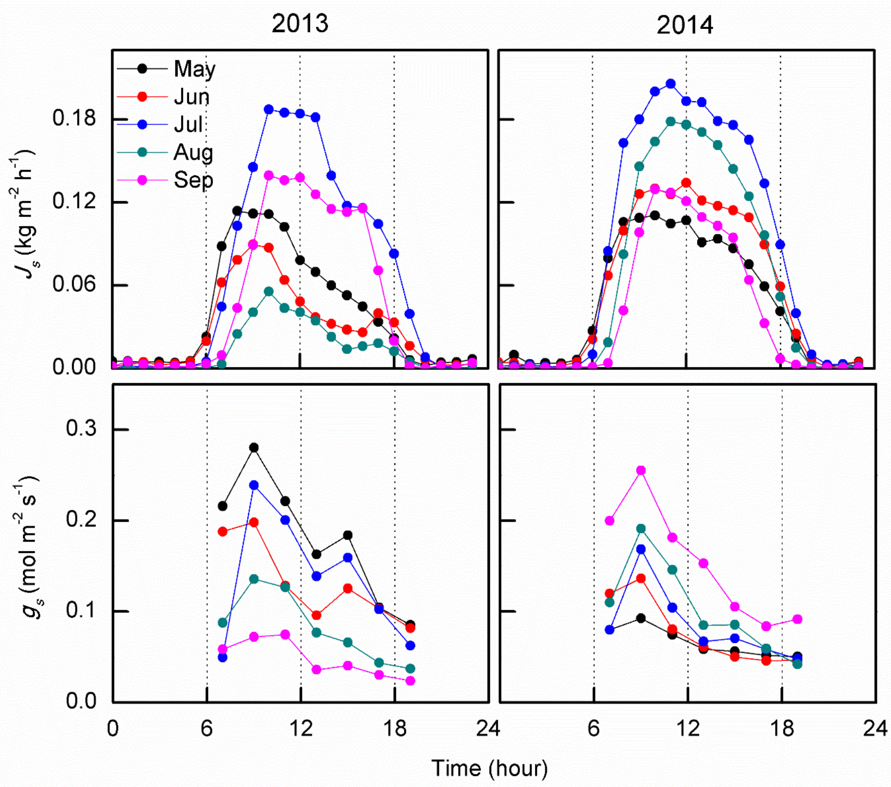

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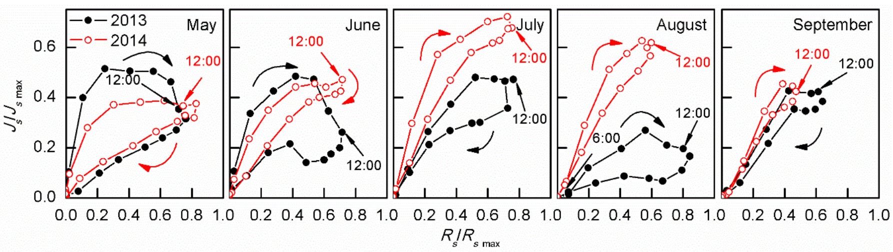

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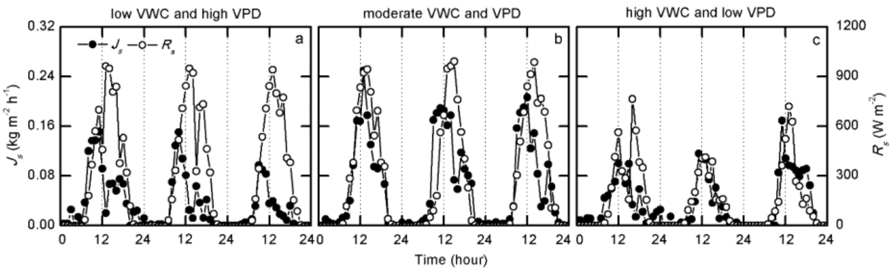

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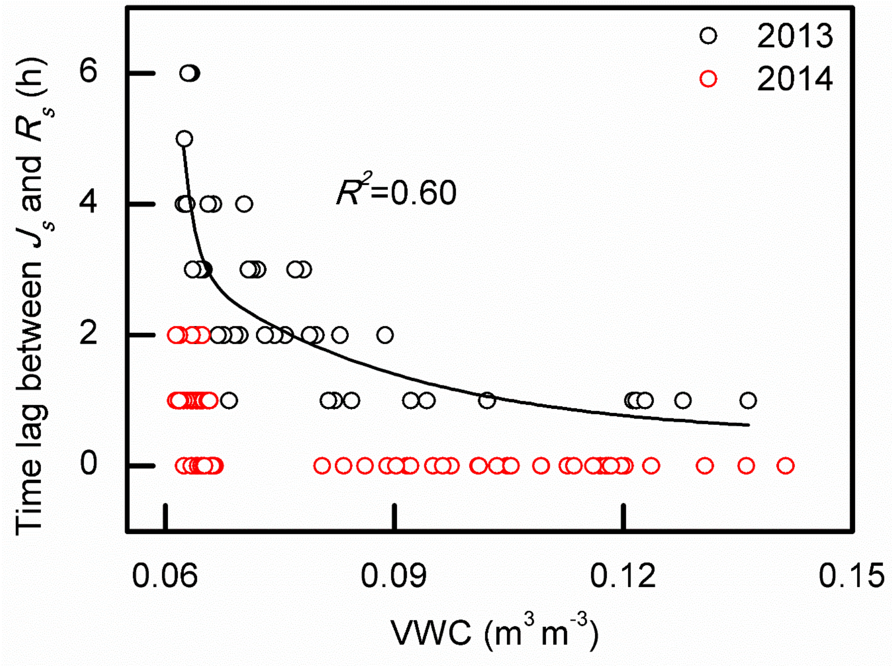

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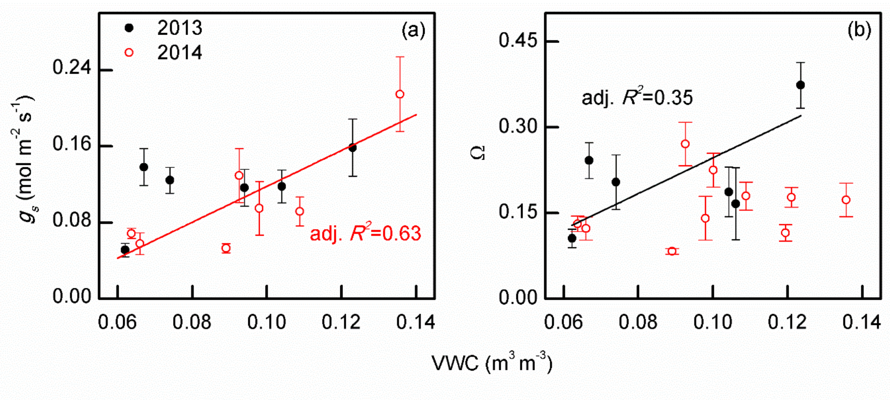

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