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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. Tianshan Zha and Dr. Duo Qian 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, Jingyong Ma, 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:

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Abstract: Current understanding of acclimation processes in desert-shrub species to drought stress in dryland ecosystems is still incomplete. In this study, we measured sap flow in *Artemisia ordosica* and associated environmental variables throughout the growing seasons of 2013-2014 (May-September period of each year) to better understand the environmental controls on the temporal dynamics of sap flow. We found that the occurrence of drought in the dry year of 2013 during the leaf-expansion and leaf-expanded periods caused sap flow per leaf area (J_s) to decline significantly, resulting in 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 $m^3 m^{-3}$. 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 low decoupling coefficient and thus being less sensitive to the environmental variables during dry 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

1. Introduction

Due to the low amount of precipitation and high potential evapotranspiration in desert ecosystems, low soil water availability limit both plant water- and gas-exchange and, as a consequence, limit 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 have already been replaced by shrub and semi-shrub species in arid and semi-arid areas of northwestern China. 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, 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).

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

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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).

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 needed on acclimation processes in desert-shrub species under 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 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, 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. 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 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). 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 neighbouring shrubs with similar characteristics as the shrubs used for sap flow measurement 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). Also 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). Stomatal conductance 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 decoupling coefficient was calculated as described by Jarvis and McNaughton (1986):

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

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

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

where u is 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 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 analysis, March-May represented spring, June-August summer, and September-November autumn. Duration and severity of 'drought' were defined based on mean VWC < 0.08 m^3 m^{-3} measured at 10- and 30-cm depths over the spring-autumn period, from March through November (Fig. 1a). 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.

Data analysis was conducted using hourly mean data from five sensors. Linear and non-linear regression was 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 day, daytime measurements (8:00-20:00), i.e., from June 1 to August 31, with hourly shortwave radiation > 10 W m^{-2}. Regression slopes were used to identify the sensitivity of sap flow (degree of response) to the 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 T, R_s, VPD, and VWC during the 2013 growing season (May-September) were 8.8-24.4^{o}C, 31.1-364.9 W m^{-2}, 0.05-2.3 kPa, and 0.06-0.17 m^3 m^{-3} (Fig. 1a, b, c); annual means for the same year were 17.7^{o}C, 224.8 W m^{-2}, 1.03 kPa, and 0.08 m^3 m^{-3}. Corresponding range of daily means for 2014 were 7.1-25.8^{o}C, 31.0-369.9 W m^{-2}, 0.08-2.5 kPa, and 0.06-0.16 m^3 m^{-3} (Fig. 1a, b, c); annual means were 17.2^{o}C, 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) was lower than that during 2014 (272.4 mm and 51 days; Fig, 1d). 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.

Extreme dry-soil periods with VWC < 0.08 m^3 m^{-3} (at 10- and 30-cm depths) for at least 10 consecutive days occurred in May, June, and August of 2013 and in May and June of 2014 (Fig. 1d). Both years had dry springs. A nearly one-month 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); annual means were 0.89 kg m^{-2} d^{-1} in 2013 and 1.31 kg m^{-2} d^{-1} in 2014. Mean J_s over the growing season of 2013 was 32% lower than that of 2014. Seasonal fluctuations in J_s corresponded with the seasonal pattern in VWC (Fig. 1d, e). Daily mean J_s decreased or remained nearly constant during dry-soil periods (Fig. 1d, e), with the lowest J_s 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. 2), 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. Soil water is shown to modify the response of J_s to environmental factors (Fig. 2). Sap flow J_s increased more rapidly with increases in R_s, T, and VPD under high VWC (i.e., VWC > 0.11 m^3 m^{-3} in 2013, VWC > 0.09 m^3 m^{-3} in 2014) compared with periods with lower VWC (i.e., VWC < 0.11 m^3 m^{-3} in 2013, 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), which coincided with a larger regression slope under high VWC conditions.

Sensitivity of J_s to environmental variables (in particular, R_s, VPD, T, and VWC) varied depending on the time of a day (Fig. 3). 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. 3), 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.4), 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. 4).

There were pronounced time lags between J_s and R_s over the two years (Fig. 5), 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 1).

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.5). 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. 6, 7). For example, J_s peaked about 2 h earlier than R_s on days with low VWC (Fig. 6a), 1 h earlier than R_s on days with moderate VWC (Fig. 6b), and at the same time as R_s on days with high VWC (Fig. 6c). Lag hours between J_s and R_s over the growing season were negatively and linearly related to VWC [Fig.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).

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 plants' 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). Stomatal conductances were the largest in the morning (Fig.4), 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 water, causing stomatal conductance 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.

Synergistic interactions among environmental factors influencing sap flow is 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 findings regarding lower sensitivity in J_s to environmental factors (R_s, T and VPD) during dry periods was in line with a previous study of boreal grasslands (Zha et al., 2010). Our finding that soil water regulates the response of other environmental factors, suggests that VWC is the most important factor controlling sap flow in *Artemisia ordosica*. This is in contrast to other shrub species, where for example it has been found that sap flow in *Haloxylon ammodendron* was mainly controlled by T (Zhang et al., 2003), while sap flow in *Cyclobalanopsis glauca* 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 (Zhao and Liu, 2010). Variations in J_s were clearly associated with the intermittent supply of water to the soil during rainfall events, as we found at our site (Fig.1d, e). 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). 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), 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.

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), 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. 5), 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). In dry and hot conditions, 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. Stomatal conductance peaked 3-4 h earlier than R_s, leading to 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, 7). The result that stomatal conductance increased with VWC (Fig. 8a), along with the 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 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. 8b). 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 climatic conditions.

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References

Asner, G. P., Archer, S., Hughes, R. F., Ansley, R. J., and Wessman, C. A.: Net changes in regional woody vegetation cover and carbon storage in Texas Drylands, 1937–1999, Global Change Biology, 9, 316-335, 2003.

Buzkova, R., Acosta, M., Darenova, E., Pokorny, R., and Pavelka, M.: Environmental factors influencing the relationship between stem CO2 efflux and sap flow, Trees-Struct Funct, 29, 333-343, 2015.

Du, S., Wang, Y.-L., Kume, T., Zhang, J.-G., Otsuki, K., Yamanaka, N., and Liu, G.-B.: Sapflow characteristics and climatic responses in three forest species in the semiarid Loess Plateau region of China, Agricultural and Forest Meteorology, 151, 1-10, 2011.

Dynamax: Dynagage® Installation and Operation Manual, Dynamax, Houston, TX, 2005.

Eberbach, P. L. and Burrows, G. E.: The transpiration response by four topographically distributed Eucalyptus species, to rainfall occurring during drought in south eastern Australia, Physiol. Plant., 127, 483-493, 2006.

Forner, A., Aranda, I., Granier, A., and Valladares, F.: Differential impact of the most extreme drought event over the last half century on growth and sap flow in two coexisting Mediterranean trees, Plant Ecol, 215, 703-719, 2014.

Gao, Q., Yu, M., and Zhou, C.: Detecting the Differences in Responses of Stomatal Conductance to Moisture Stresses between Deciduous Shrubs and Artemisia Subshrubs, PLoS ONE, 8, e84200, 2013.

Houghton, R. A., Hackler, J. L., and Lawrence, K. T.: The U.S. Carbon Budget: Contributions from Land-Use Change, Science, 285, 574-578, 1999.

Huang, H., Gang, W., and NianLai, C.: Advanced studies on adaptation of desert shrubs to environmental stress, Sciences in Cold and Arid Regions, 3, 0455–0462, 2011a.

Huang, Y., Li, X., Zhang, Z., He, C., Zhao, P., You, Y., and Mo, L.: Seasonal changes in Cyclobalanopsis glauca transpiration and canopy stomatal conductance and their dependence on subterranean water and climatic factors in rocky karst terrain, Journal of Hydrology, 402, 135-143, 2011b.

Huang, Y., Zhao, P., Zhang, Z., Li, X., He, C., and Zhang, R.: Transpiration of Cyclobalanopsis glauca (syn. Quercus glauca) stand measured by sap-flow method in a karst rocky terrain during dry season, Ecological Research, 24, 791-801, 2009.

Jacobsen, A. L., Agenbag, L., Esler, K. J., Pratt, R. B., Ewers, F. W., and Davis, S. D.: Xylem density, biomechanics and anatomical traits correlate with water stress in 17 evergreen shrub species of the Mediterranean-type climate region of South Africa, Journal of Ecology, 95, 171-183, 2007.

Jarvis, P. G. and McNaughton, K. G.: Stomatal Control of Transpiration: Scaling Up from Leaf to Region. In: Advances in Ecological Research, MacFadyen, A. and Ford, E. D. (Eds.), Academic Press, 1986.

Jian, S. Q., Wu, Z. N., Hu, C. H., and Zhang, X. L.: Sap flow in response to rainfall pulses for two shrub species in the semiarid Chinese Loess Plateau, J Hydrol Hydromech, 64, 121-132, 2016.

Lei, H., Zhi-Shan, Z., and Xin-Rong, L.: Sap flow of Artemisia ordosica and the influence of environmental factors in a revegetated desert area: Tengger Desert, China, Hydrological Processes, 24, 1248-1253, 2010.

Li, S., Werger, M. A., Zuidema, P., Yu, F., and Dong, M.: Seedlings of the semi-shrub Artemisia ordosica are resistant to moderate wind denudation and sand burial in Mu Us sandland, China, Trees, 24, 515-521, 2010.

Li, S., Zha, T., Qin, S., Qian, D., and Jia, X.: Temporal patterns and environmental controls of sap flow in Artemisia ordosica, Chinese Journal of Ecology, 33, 1-7, 2014.

Lioubimtseva, E. and Henebry, G. M.: Climate and environmental change in arid Central Asia: Impacts, vulnerability, and adaptations, Journal of Arid Environments, 73, 963-977, 2009.

Liu, B., Zhao, W., and Jin, B.: The response of sap flow in desert shrubs to environmental variables in an arid region of China, Ecohydrology, 4, 448-457, 2011.

Meinzer, F. C., Andrade, J. L., Goldstein, G., Holbrook, N. M., Cavelier, J., and Jackson, P.: Control of transpiration from the upper canopy of a tropical forest: the role of stomatal, boundary layer and hydraulic architecture components, Plant, Cell & Environment, 20, 1242-1252, 1997.

Monteith, J. L. and Unsworth, M. H.: Principles of Environmental Physics. Butterworth-Heinemann: Oxford, 1990.

Naithani, K. J., Ewers, B. E., and Pendall, E.: Sap flux-scaled transpiration and stomatal conductance response to soil and atmospheric drought in a semi-arid sagebrush ecosystem, Journal of Hydrology, 464, 176-185, 2012.

O'Brien, J. J., Oberbauer, S. F., and Clark, D. B.: Whole tree xylem sap flow responses to multiple environmental variables in a wet tropical forest, Plant, Cell & Environment, 27, 551-567, 2004.

Pacala, S. W., Hurtt, G. C., Baker, D., Peylin, P., Houghton, R. A., Birdsey, R. A., Heath, L., Sundquist, E. T., Stallard, R. F., Ciais, P., Moorcroft, P., Caspersen, J. P., Shevliakova, E., Moore, B., Kohlmaier, G., Holland, E., Gloor, M., Harmon, M. E., Fan, S.-M., Sarmiento, J. L., Goodale, C. L., Schimel, D., and Field, C. B.: Consistent Land- and Atmosphere-Based U.S. Carbon Sink Estimates, Science, 292, 2316-2320, 2001.

Razzaghi, F., Ahmadi, S. H., Adolf, V. I., Jensen, C. R., Jacobsen, S. E., and Andersen, M. N.: Water Relations and Transpiration of Quinoa (Chenopodium quinoa Willd.) Under Salinity and Soil Drying, Journal of Agronomy and Crop Science, 197, 348-360, 2011.

Schwinning, S. and Sala, O. E.: Hierarchy of responses to resource pulses in arid and semi-arid ecosystems, Oecologia, 141, 211-220, 2004.

She, D., Xia, Y., Shao, M., Peng, S., and Yu, S.: Transpiration and canopy conductance of Caragana korshinskii trees in response to soil moisture in sand land of China, Agroforestry systems, 87, 667-678, 2013.

Vilagrosa, A., Bellot, J., Vallejo, V. R., and Gil‐Pelegrín, E.: Cavitation, stomatal conductance, and leaf dieback in seedlings of two co‐occurring Mediterranean shrubs during an intense drought, Journal of Experimental Botany, 54, 2015-2024, 2003.

Xia, G., Kang, S., Du, T., Yang, X., and Zhang, J.: Transpiration of Hedysarum scoparium in arid desert region of Shiyang River basin, Gansu Province, Chinese Journal of Applied Ecolog, 18, 1194-1202, 2007.

Xia, G., Kang, S., Li, F., Zhang, J., and Zhou, Q.: Diurnal and seasonal variations of sap flow of Caragana korshinskii in the arid desert region of north‐west China, Hydrological Processes, 22, 1197-1205, 2008.

Xu, D. H., Li, J. h., Fang, X. W., and Wang, G.: Changes in soil water content in the rhizosphere of Artemisia ordosica: Evidence for hydraulic lift, Journal of Arid Environments, 69, 545-553, 2007.

Yang, Y. and Zhu, Y.: Plant Ecology (Second Edition), Higher Education Press, Beijing, 2011.

Yin, L., Zhou, Y., Huang, J., Wenninger, J., Hou, G., Zhang, E., Wang, X., Dong, J., Zhang, J., and Uhlenbrook, S.: Dynamics of willow tree (Salix matsudana) water use and its response to environmental factors in the semi-arid Hailiutu River catchment, Northwest China, Environmental earth sciences, 71, 4997-5006, 2014.

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

Zha, T., Barr, A. G., Kamp, G. V. D., Black, T.A., McCaughey, J.H., Flanagan, L.B.: Interannual variation of evapotranspiration from forest and grassland ecosystems in western Canada in relation to drought, Agricultural and Forest Meteorology, 150, 1476-1484, 2010.

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.

Zhang, X., Gong, J., Zhou, M., and Si, J.: A study on the stem sap flow of Populus euphrtaicr and Tamaris spp. By heat pulse technique, J Glaciol Geocryol, 25, 584-590, 2003.

Zhao, W. and Liu, B.: The response of sap flow in shrubs to rainfall pulses in the desert region of China, Agricultural and Forest Meteorology, 150, 1297-1306, 2010.

Zhao, Y., Yuan, W., Sun, B., Yang, Y., Li, J., Li, J., Cao, B., and Zhong, H.: Root Distribution of Three Desert Shrubs and Soil Moisture in Mu Us Sand Land Research of Soil and Water Conservation, 17, 129-133, 2010.

Zheng, C. and Wang, Q.: Water-use response to climate factors at whole tree and branch scale for a dominant desert species in central Asia: Haloxylon ammodendron, Ecohydrology, 7, 56-63, 2014.

Zheng, H., Wang, Q., Zhu, X., Li, Y., and Yu, G.: Hysteresis Responses of Evapotranspiration to Meteorological Factors at a Diel Timescale: Patterns and Causes, PLoS ONE, 9, e98857, 2014.

Table 1 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 Seasonal changes in daily (24-hour) mean air temperature (T; a), shortwave radiation (R_s; b), vapor pressure deficit (VPD; c), volumetric soil water content (VWC; d) at 10- and 30-cm depths, daily total precipitation (PPT; d), and sap-flow rate per leaf area (J_s; e) from May to September for both 2013 and 2014. Shaded bands in plot (d, e) indicate periods of drought.

Fig. 2 Sap-flow rate per leaf area (J_s) in non-rainy, daytime hours during the mid-growing period of June 1-August 31 for both 2013 and 2014 as a function of volumetric soil water content (VWC) at a 30-cm depth, shortwave radiation (R_s), air temperature (T), vapor pressure deficit (VPD) under high VWC (> 0.11 $m^3 m^{-3}$ in 2013 and > 0.09 $m^3 m^{-3}$ in 2014) and low VWC (< 0.11 $m^3 m^{-3}$ in 2013 and < 0.09 $m^3 m^{-3}$ in 2014); J_s is given as binned averages according to VWC, R_s, T, and VPD, based on increments of 0.005 $m^3 m^{-3}$, 100 W m^{-2}, 1°C, and 0.2 kPa, respectively. Bars indicate standard error.

Fig. 3 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 of June 1-August 31 for both 2013 and 2014.

Fig. 4 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. 5 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 arrow indicates the clockwise direction of response during the day.

Fig. 6 Sap-flow rate per leaf area (J_s) and shortwave radiation (R_s) over consecutive 3 days in 2013, i.e., (a) under low volumetric soil water content (VWC) and high vapor pressure deficit (VPD, 0.063 m^3 m-

^{3}<VWC<0.064 m^3 m^{-3}, VPD$_{mean}$=2.07 kPa), (b) moderate VWC and VPD (0.067 m^3 m^{-3}<VWC<0.072 m^3 m^{-3}, VPD$_{mean}$=1.95 kPa) before rainfall, and (c) high VWC and low VPD (0.094<VWC<0.098 m^3 m^{-3}, VPD$_{mean}$= 1.20 kPa) after rainfall; VPD$_{mean}$ is the mean value of the three days.

Fig. 7 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) at a 30-cm depth. Hourly data in non-rainy days during the mid-growing period 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 timestep. Rainy days were excluded. The solid line is based on exponential regression.

Fig. 8 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.

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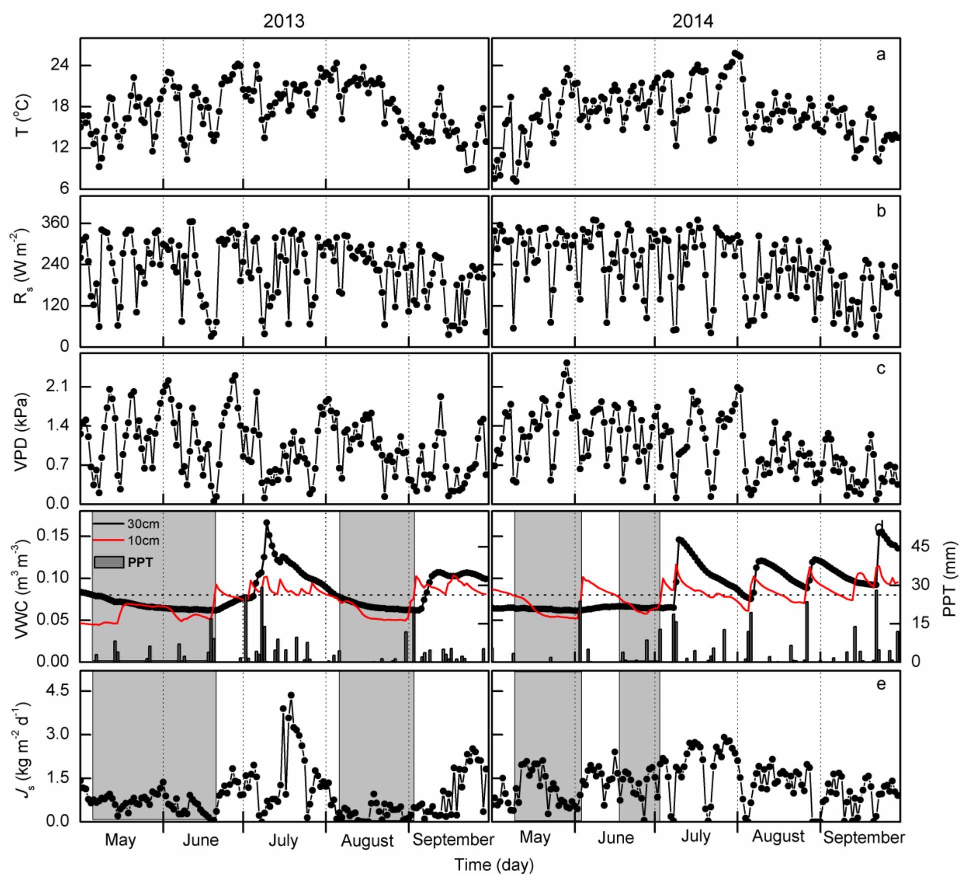

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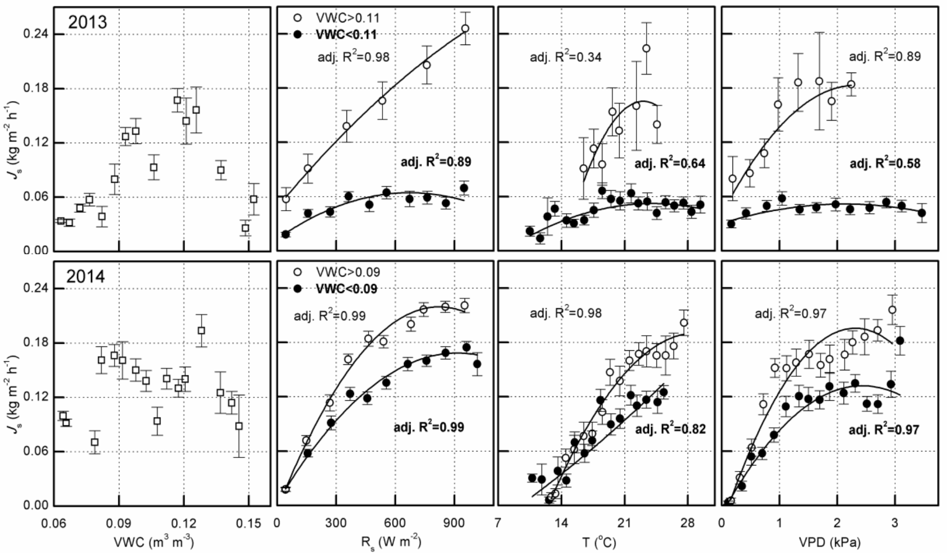

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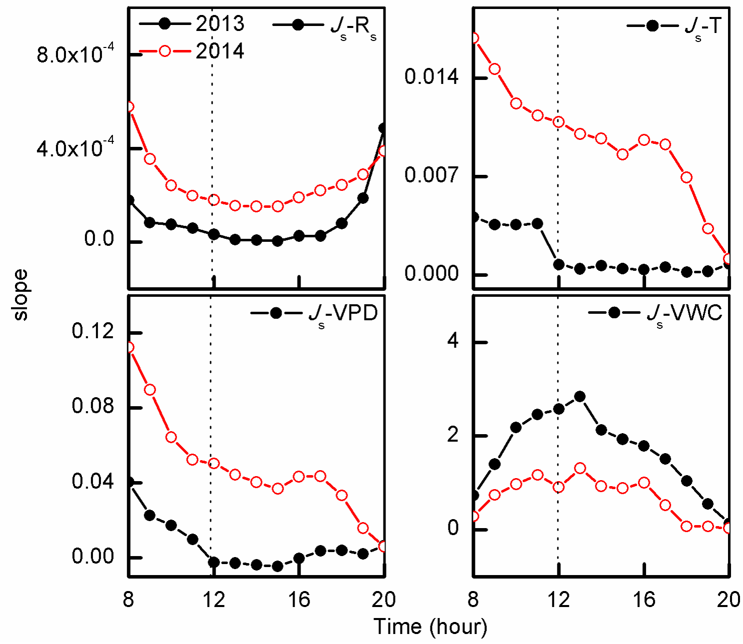

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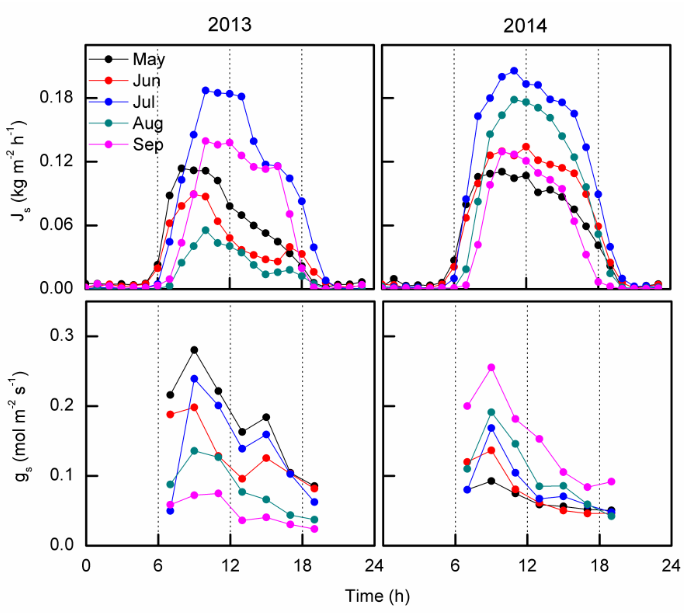

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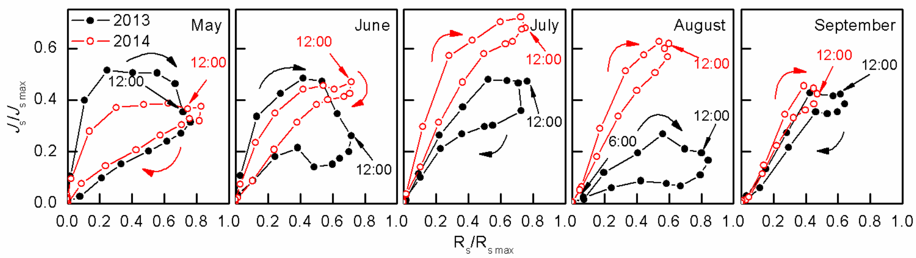

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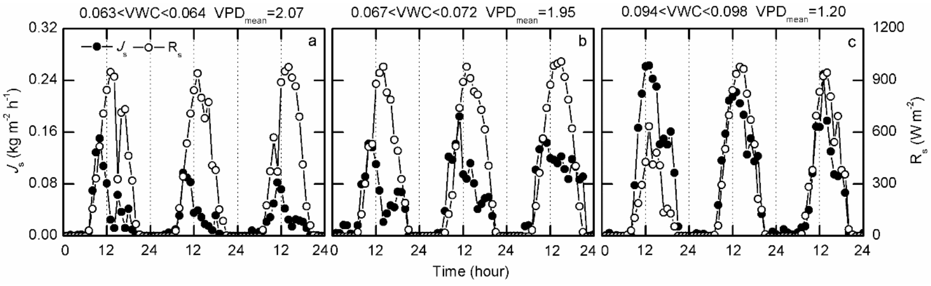

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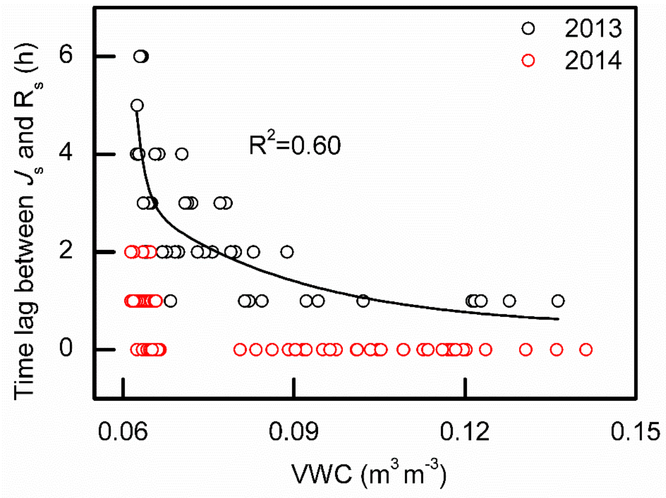

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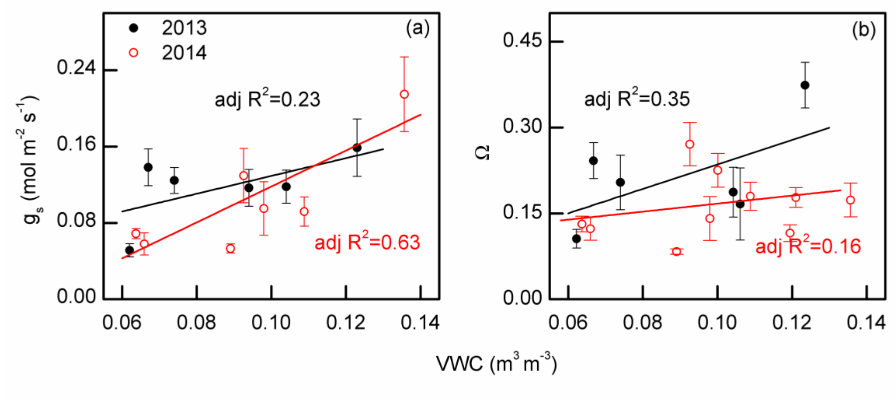

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