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

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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.

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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:

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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 > 0.10 $m^3 m^{-3}$. 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

1. Introduction

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

157 ×10 m each) within a 100 m × 100 m plot centered on the flux tower using measurements of
158 sampled leaves and allometric equations (Jia et al., 2014). Stomatal conductance (g_s) was
159 measured *in situ* for three to four leaves on each of the sampled shrubs with a LI-6400
160 portable photosynthesis analyzer (Li-Cor Inc., Lincoln, USA). The g_s measurements were
161 made every two hours from 7:00 to 19:00 h every ten days from May to September, 2013-
162 2014.

163 The degree of coupling between the ecosystem surface and the atmospheric boundary
164 layer was estimated with the decoupling coefficient (Ω). The decoupling coefficient varies
165 from 0 (i.e., leaf transpiration is mostly controlled by g_s) to 1 (i.e., leaf transpiration is mostly
166 controlled by radiation). The Ω was calculated as described by Jarvis and McNaughton
167 (1986):

168 $$\Omega = \frac{\Delta + \gamma}{\Delta + \gamma\left(1 + \frac{g_a}{g_s}\right)}, \quad (1)$$

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

172 $$g_a = \left(\frac{u}{u*^2} + 6.2u*^{-0.67}\right)^{-1}, \quad (2)$$

173 where u is the wind speed (m s^{-1}) at 6 m above the ground, and $u*$ is the friction velocity (m
174 s^{-1}).

175

176 **2.3 Environmental measurements**

177 Shortwave radiation (R_s in W m^{-2}; CMP3, Kipp & Zonen, Netherland), air temperature (T in

178 ^{o}C), wind speed (u in m s^{-1}, 034B, Met One Instruments Inc., USA), and relative humidity
179 (RH in %; HMP155A, Väisälä, Finland) were measured simultaneously near the sap-flow
180 measurement plot. Half-hourly data were recorded by data logger (CR3000 data logger,
181 Campbell Scientific Inc., USA). VWC at 30-cm depths were monitored with three ECH$_2$O-
182 5TE soil moisture probes (Decagon Devices, USA). In the analysis, we used half-hourly
183 averages of VWC from the three soil moisture probes. Vapor pressure deficit (VPD in kPa)
184 was calculated from recorded RH and T.
185
186 **2.4 Data analysis**
187 In our analysis, March-May represented spring, June-August summer, and September-
188 November autumn (Chen et al., 2015). Drought days were defined as those days with daily
189 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),
190 with J_s increasing as VWC increased, saturating at VWC of 0.1 m^3 m^{-3}, and decreasing as
191 VWC continued to increase. The VWC threshold of 0.1 m^3 m^{-3} is equivalent to a relative
192 extractable soil water (REW) of 0.4 for drought conditions (Granier et al., 1999 and 2007;
193 Zeppel et al., 2004 and 2008; Fig. 2d, e). Duration and severity of 'drought' were defined
194 based on a VWC threshold and REW of 0.4. REW was calculated as according to equation
195 (3):

196 $$REW = \frac{VWC - VWC_{\min}}{VWC_{\max} - VWC_{\min}} \quad (3)$$

197 where VWC is the specific daily soil water content (m^3 m^{-3}), VWC$_{min}$ and VWC$_{max}$ are the
198 minimum and maximum VWC during the measurement period in each year, respectively.
199 Sap-flow analysis was conducted using mean data from five sensors. Sap flow per leaf

200 area (J_s) was used in this study, i.e.,

201 $$J_s = \left(\sum_{i=1}^{n} E_i / A_{li} \right) \Big/ n \quad (4)$$

202 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
203 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
204 (n = 5).

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

206 $$T_r = \left(\sum_{i=1}^{n} J_s \times LAI \right) \Big/ n \quad (5)$$

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

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

219

220 **3. Results**

221 **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

289 environmental variables (R_s, VPD, and T) in the morning indicated that sap flow was more
290 sensitive to variations in R_s, VPD, and T during the less dry and hot period of the day (Fig.
291 5). Stomatal conductances were the largest in the morning (Fig. 6), which led to increases in
292 water fluxes to the atmosphere as a result of increased R_s, T, and VPD. When R_s peaked
293 during mid-day (13:00-14:00 h), there was often insufficient soil water to meet the
294 atmospheric demand for water, causing g_s to be limited by available soil moisture and making
295 J_s more responsive to VWC at noon, but less responsive to R_s and T. Similarly, *Hedysarum*
296 *mongolicum* in a nearby region positively correlated with VWC at noon (Qian et al., 2015),
297 and the evapotranspiration of a Scots pine stand showed higher sensitivity to surface
298 conductance, temperature, vapor pressure deficit, and radiation in the morning than in the
299 afternoon (Zha et al., 2013).

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

311 (Huang et al., 2009).

312 Precipitation, being the main source of VWC at our site, affected transpiration directly.
313 In this sense, frequent small rainfall events (< 5 mm) were important to the survival and
314 growth of the desert plants (Sala and Lauenroth, 1982; Zhao and Liu, 2010). Variations in J_s
315 were clearly associated with the intermittent supply of water to the soil during rainfall events,
316 as indicated at our site (Fig. 2d, f). Reduced J_s during rainy days can be explained by a
317 reduction in incident R_s and water-induced saturation on the leaf surface, which led to a
318 decrease in leaf turgor and stomatal closure. After each rainfall event, J_s increased quickly
319 when soil water was replenished. Schwinning and Sala (2004) showed previously for similar
320 research sites that VWC contributed the most to the response in plant transpiration to post-
321 rainfall events. We showed in this study that *Artemisia ordosica* responded in a different way
322 to wet and dry conditions. In the mid-growing season, high J_s in July were related to rainfall-
323 fed VWC, which increased the rate of transpiration. However, dry soil conditions combined
324 with high T and R_s, led to a reduction in J_s in August of 2013 (Fig. 2). In some desert shrubs,
325 groundwater may replenish water lost by transpiration by having deep roots (Yin et al., 2014).
326 *Artemisia ordosica* roots are generally distributed in the upper 60 cm of the soil (Zhao et al.,
327 2010; Wang et al., 2016), and as a result the plant usually depends on water directly supplied
328 by precipitation because groundwater levels in drylands can be well below the rooting zone,
329 typically, at depths ≥ 10 m at our site.

330

331 **4.2 Hysteresis between sap flow and environmental factors**

332 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 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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530 **Table 1** Seasonal changes in monthly transpiration (T_r), leaf area index (LAI), and stomatal
531 conductance (g_s) of *Artemisia ordosica* from 2013 to 2014.
532

	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

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534

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 ^oC, 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

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

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

569 **Fig. 6** Mean monthly diurnal changes in sap-flow rate per leaf area (J_s) and stomatal
570 conductance (g_s) in *Artemisia ordosica* during the growing season (May-September) for both
571 2013 and 2014. Each point is given as the mean at specific times during each month.

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

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

584 **Fig. 9** Time lag between sap-flow rate per leaf area (J_s) and short wave radiation (R_s) in
585 relation to volumetric soil water content (VWC). Hourly data in non-rainy days during the

586 mid-growing season of June 1-August 31 for 2013 and 2014. The lag hours were calculated
587 by a cross-correlation analysis using a three-day moving window with a one-day time step.
588 Rainy days were excluded. The solid line is based on exponential regression (p<0.05).
589 **Fig. 10** Relationship between volumetric soil water content (VWC) and (a) stomatal
590 conductance (g_s) in *Artemisia ordosica*, and (b) decoupling coefficient (Ω) for 2013 and 2014.
591 Hourly values are given as binned averages based on a VWC-increment of 0.005 m^3 m^{-3}.
592 Bars indicate standard error. Only regressions with p-values < 0.05 are shown.
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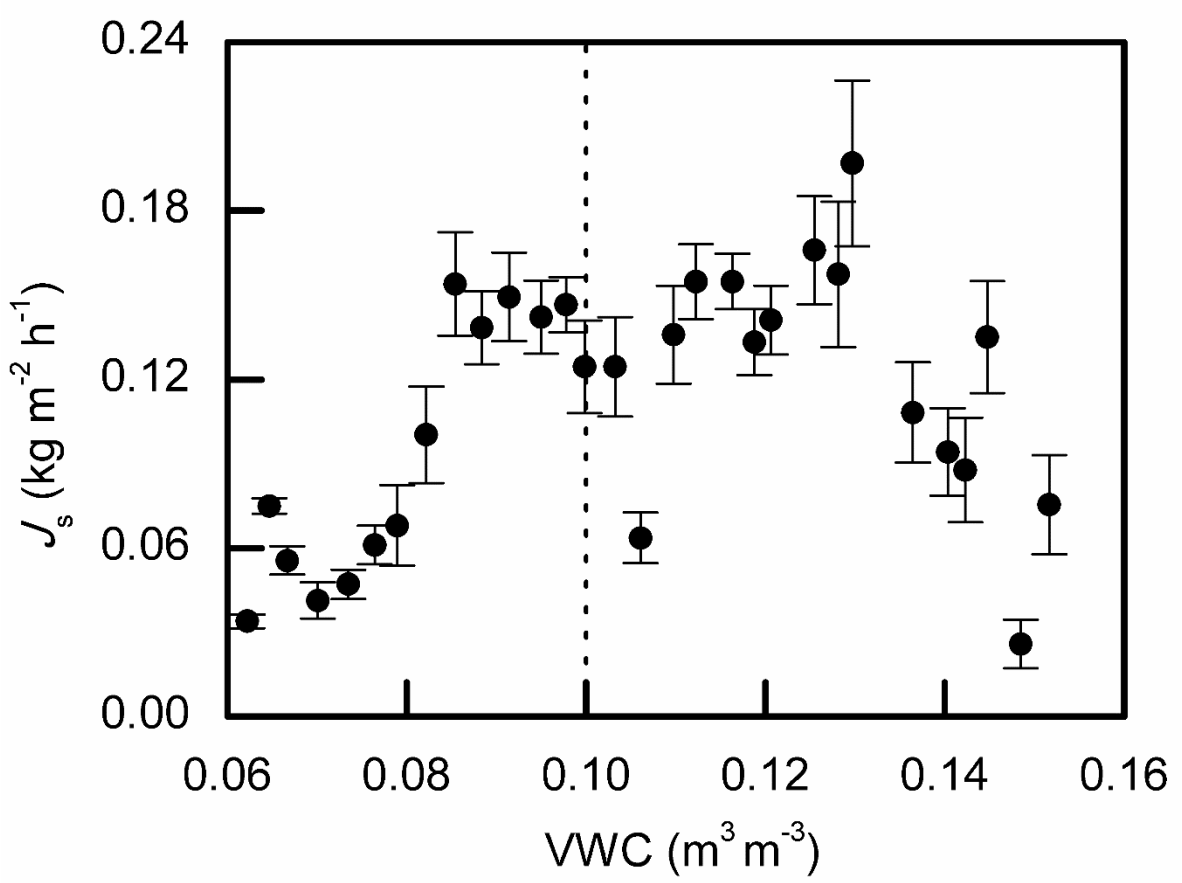

Fig. 1 Sap-flow rate per leaf area (J_s) as a function of soil water content (VWC) at 30 cm depth in non-rainy, daytime hours during the mid-growing period from June 1-August 31 over 2013-2014. Data points are binned values from pooled data over two years at a VWC increment of 0.003 m^3 m^{-3}. Dotted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

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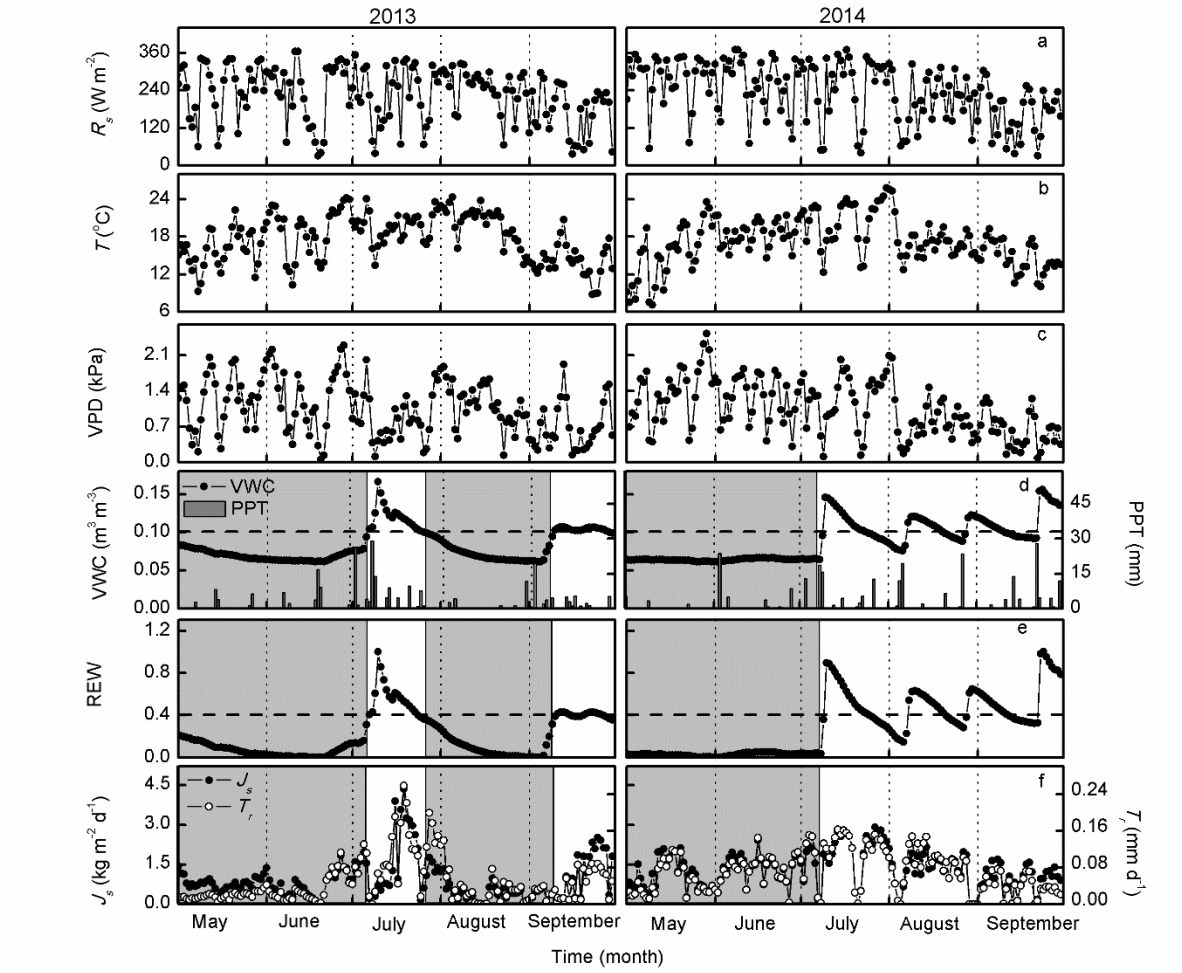

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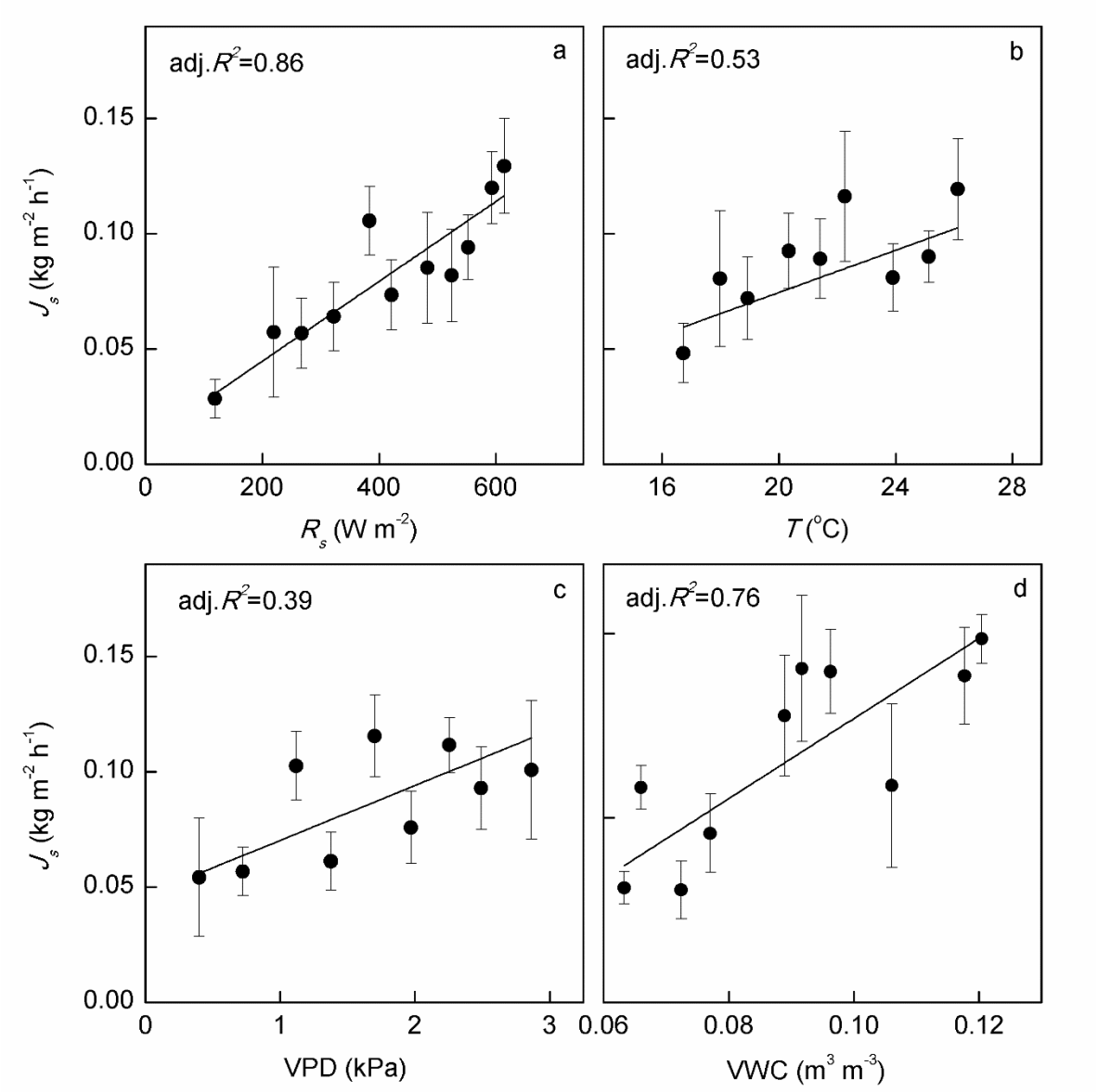

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614 **Fig. 3** Relationships between **s**ap-flow rate per leaf area (J_s) and environmental factors

615 [shortwave radiation (R_s), air temperature (T), vapor pressure deficit (VPD), and soil water

616 content at 30-cm depth (VWC)] in non-rainy days between 8:00-20:00 h during the mid-

617 growing season of June 1-August 31 for 2013 and 2014. Data points are binned values from

618 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

619 R_s, T, VPD and VWC, respectively.

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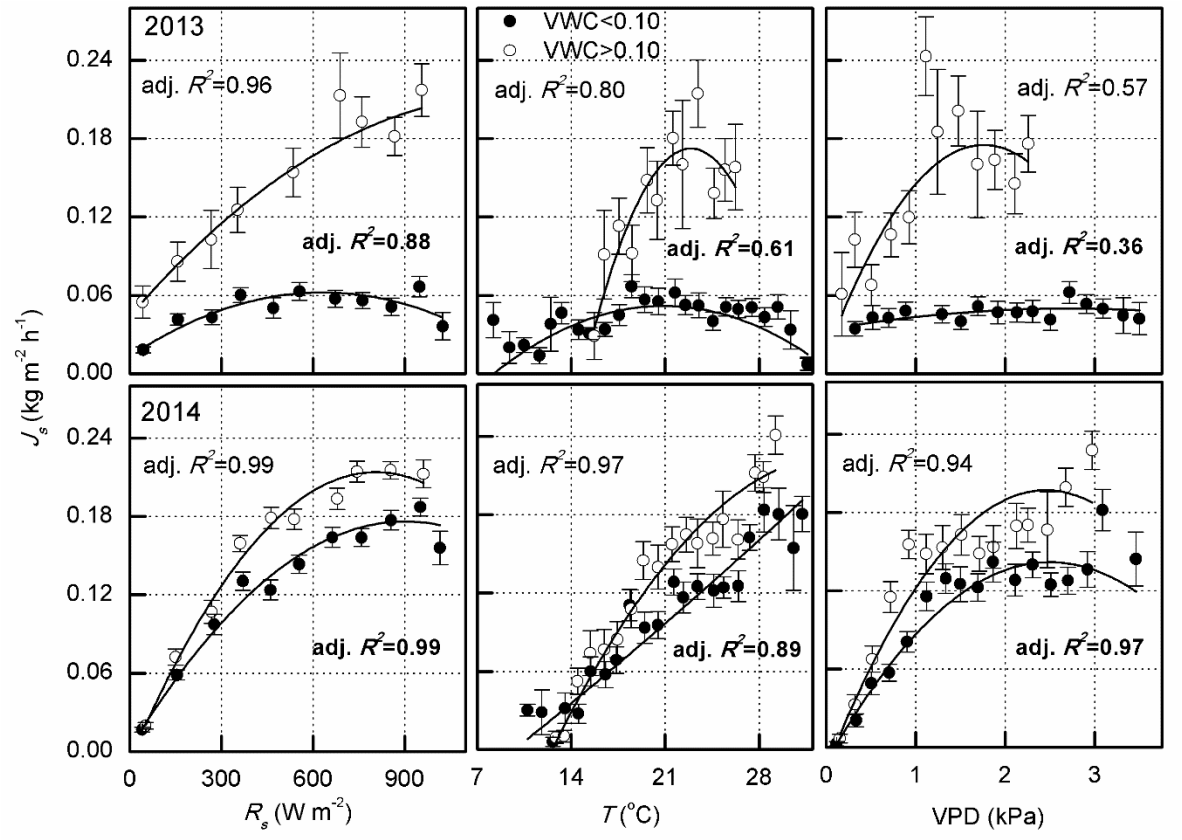

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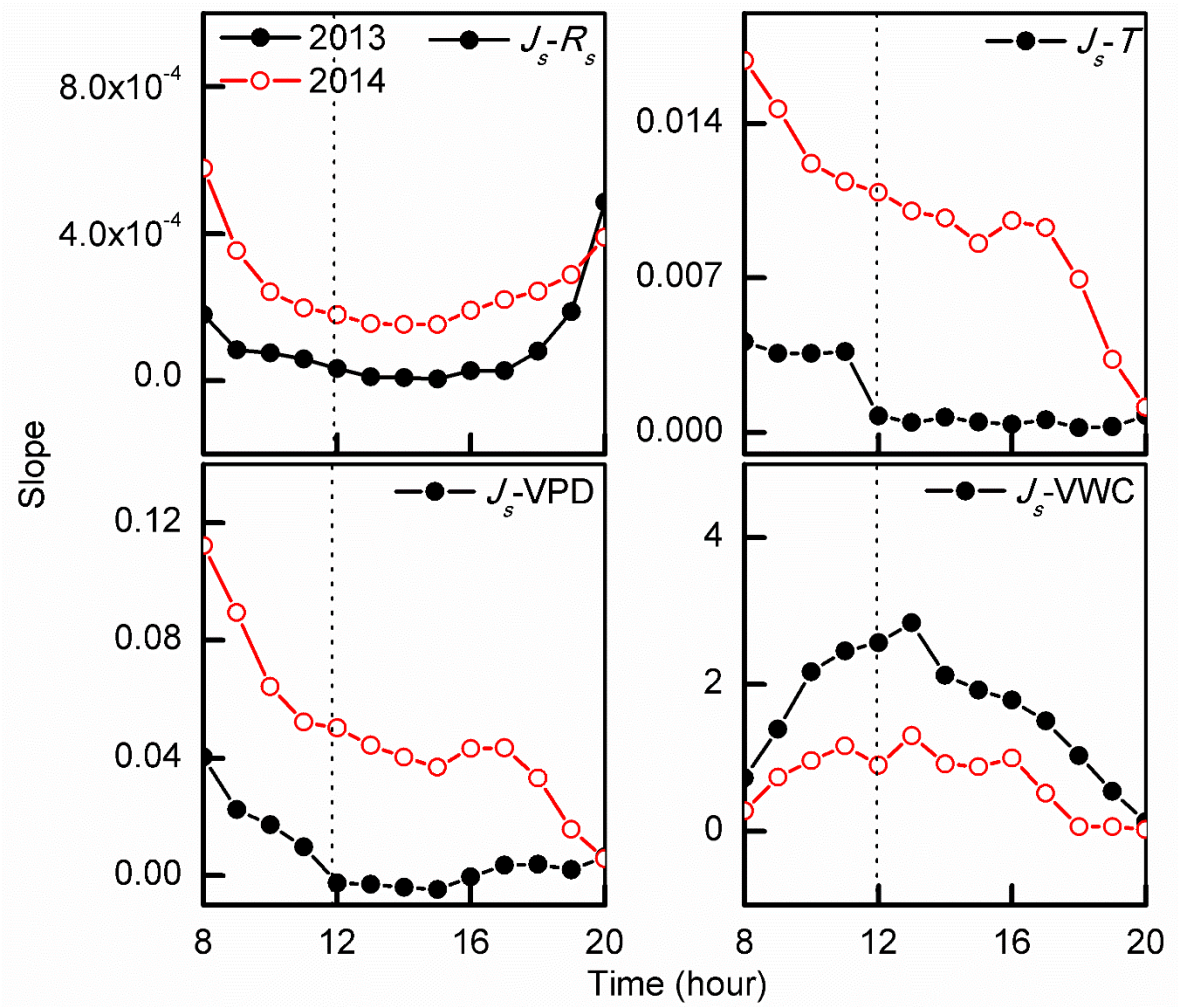
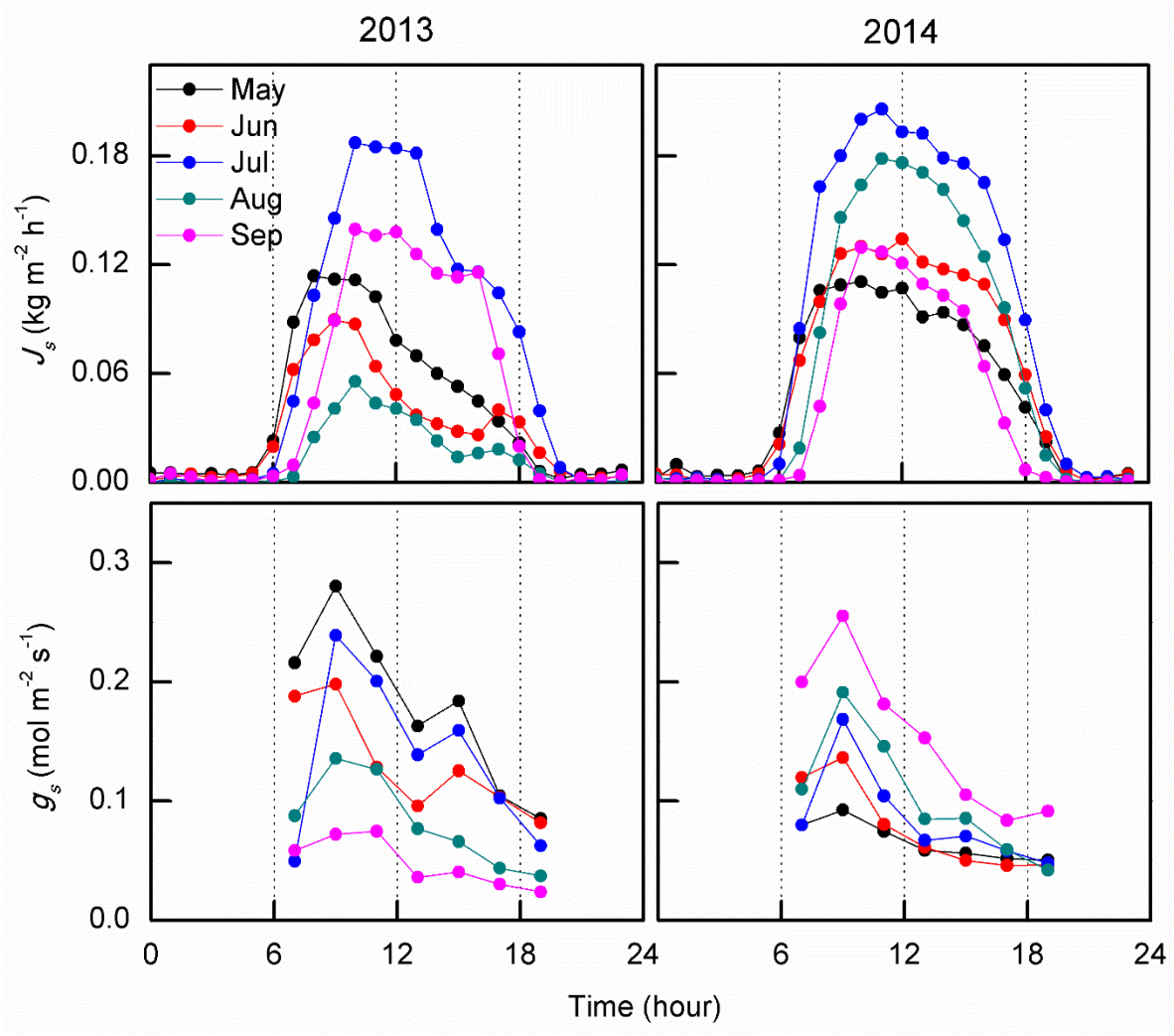


Fig. 5 Regression slopes of linear fits between sap-flow rate per leaf area (J_s) in non-rainy days and shortwave radiation (R_s), vapor pressure deficit (VPD), air temperature (T), and volumetric soil water content (VWC) between 8:00-20:00 h during the mid-growing season of June 1-August 31 for 2013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



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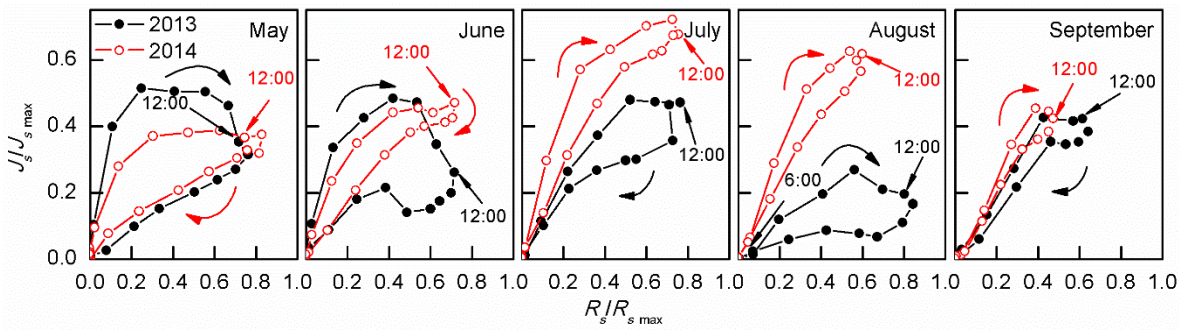

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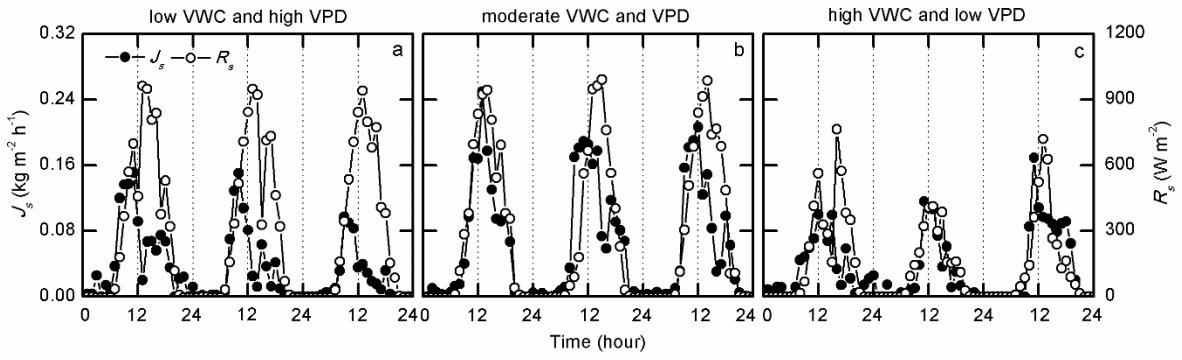

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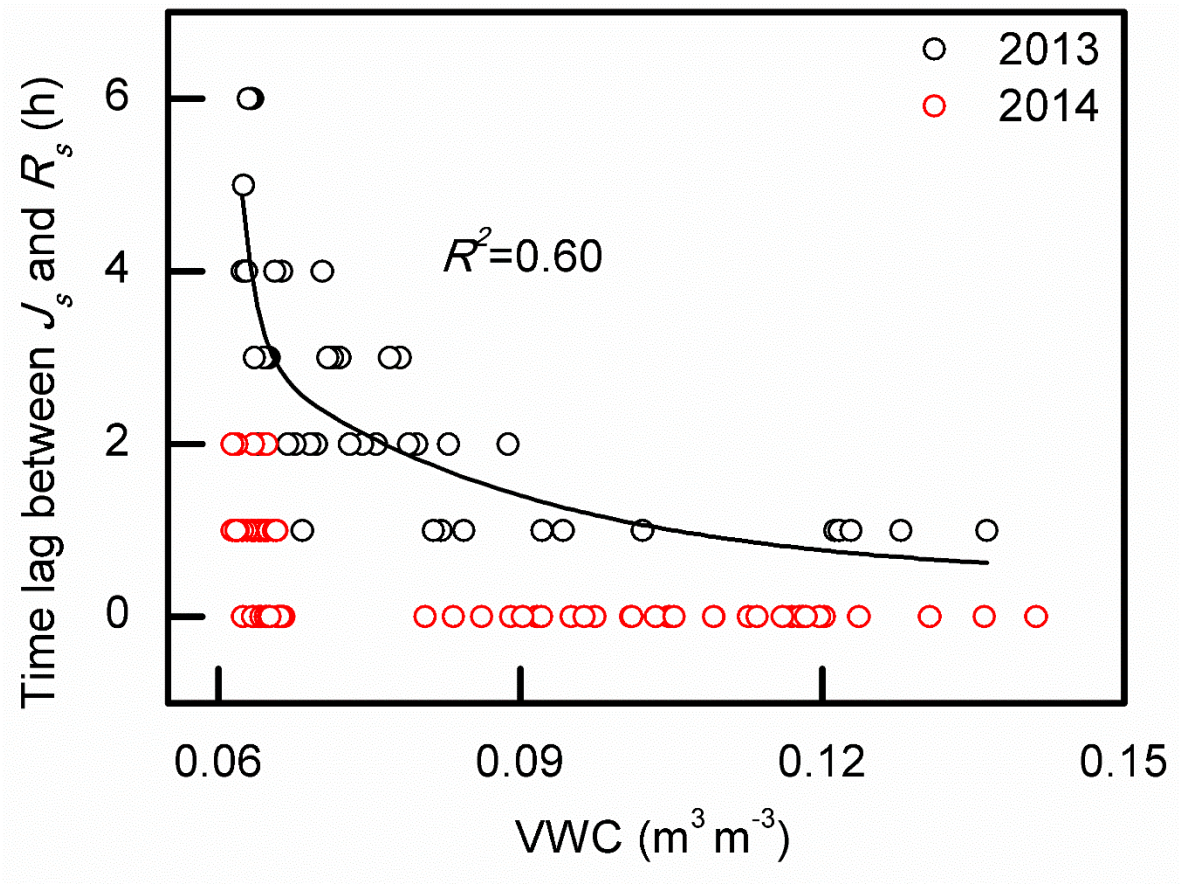

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670 **Fig. 9** Time lag between sap-flow rate per leaf area (J_s) and short wave radiation (R_s) in
671 relation to volumetric soil water content (VWC). Hourly data in non-rainy days during the
672 mid-growing season of June 1-August 31 for 2013 and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

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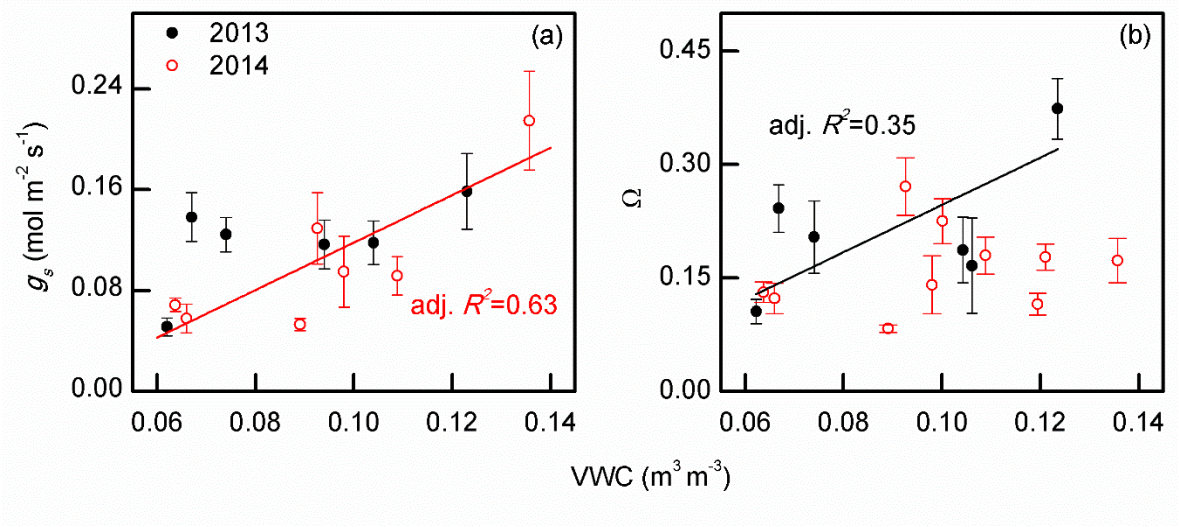

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679 **Fig. 10** Relationship between volumetric soil water content (VWC) and (a) stomatal

680 conductance (g_s) in *Artemisia ordosica*, and (b) decoupling coefficient (Ω) for 2013 and 2014.

681 Hourly values are given as binned averages based on a VWC-increment of 0.005 m^3 m^{-3}.

682 Bars indicate standard error. Only regressions with *p*-values < 0.05 are shown.

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