

1 **Response to the reviewers' comments**

2
3 Ref: doi:10.5194/bg-2016-480

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

6 Authors: TianShan Zha, Duo Qian, Xin Jia, Yujie Bai, Yun Tian , Charles P.-A. Bourque,
7 Jingyong Ma, Wei Feng, Bin Wu, Heli Peltola

8
9 **Dear Editor,**

10
11 **Thank you very much for your and reviewers' helpful comments and suggestions for**
12 **improvement of our manuscript. We have carefully looked at your comments and have**
13 **revised the manuscript accordingly. Please find below our responses to your comments**
14 **and/or revisions to the manuscript.**

15
16 **We look forward to your decision and the possible publication of our manuscript in the**
17 **special issue of BG, *Ecosystem processes and functioning across current and future***
18 ***dryness gradients in arid and semi-arid lands.***

19
20 **Kind regards,**
21 **Tianshan Zha**

22 -----
23 -----
24 **Anonymous Referee #1**

25 General comments

26 *As the paper is about the soil moisture control on sap-flow and its response to
27 meteorological variables, a physical basis for the definition for drought condition and its
28 severity should be included. Instead, the authors keep on changing their definition of dry
29 conditions for each year and in various figures. What is the reason for using 0.08 m³ m⁻³, as
30 the threshold to identify drought periods? Is it for severe, moderate or mild drought? The
31 analysis lacks consistency (Example figures 2 6). In section 2.4, they used 0.08 m³ m⁻³ as
32 the threshold to identify drought conditions. In Figure 2, it is 0.11 m³ m⁻³ for the drought year
33 2013 and 0.09 for the wet 2014. Why don't they use 0.08 m³ m⁻³ in both years? They change
34 threshold, definition of dry condition and VWC values in figure 6. I strongly suggest being
35 consistent in their definition of drought conditions and use the same threshold in all figures.

36 *The root zone depth for this species is around 60 cm (Line 291). The water deep in the root
37 zone can maintain transpiration rates even at low VWC. I think a better way is to define
38 threshold based on root zone soil water content in this paper. Is there any field capacity or
39 wilting point measurements available at the site? If so mention that in the paper and use
40 relative available water content in the root zone. If not, use relative water content (based on
41 maximum and minimum VWC values at the site) in the 30 cm soil layer to identify the
42 drought conditions. The value of VWC shown in Figure 1 indicate that soil drying occurred
43 mainly in shallow layer, not in the deep layer (30 cm), especially during pre and post growing
44 periods.

45 **RESPONSE: We agree with reviewer's suggestion of a consistent threshold of soil water**

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

53
54 Literature that was added in the revised manuscript:

55 1. Granier et al.: Evidence for soil water control on carbon and water dynamics in European
56 forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology*, 143,123-
57 145, 2007.

58 2. Granier, A., Bre´da, N., Biron, P., Villette, S.: A lumped water balance model to evaluate
59 duration and intensity of drought constraints in forest stands. *Ecol. Model.* 116, 269–283,
60 1999.

61
62 *Is it possible to include transpiration (mm) values in this paper? That will add more value
63 to understand the acclimation process of plants to the dry conditions.

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

67
68 *The methods section reports leaf area measurements, but its values are not mentioned in the
69 paper. Even in conclusion they have mentioned leaf expanded periods, but no data to support
70 it.

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

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

79
80 *Statistical significance should be evaluated for each figure and include *p*-value along with
81 R² in figures.

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

84
85 *The 2013-2014 data shown clearly indicate that there is no direct control of VWC on sap
86 flow (Figure 2 first vertical panel). Figure 2 also clearly shows that the relation between Js
87 with Rs, T and VPD are non-linear (check previous comments on p-value). If the
88 relationships are non-linear how can they explain the linear regression slopes shown in Figure
89 3? Is the linear relationships shown are statistically significant?

90 **RESPONSE:** We redefined VWC threshold of sap flow in the revised manuscript using

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

98 99 References:

- 100 1. Granier et al.: Evidence for soil water control on carbon and water dynamics in European
101 forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology*, 143,123-
102 145, 2007.
- 103 2. Granier, A., Bre´da, N., Biron, P., Villette, S.: A lumped water balance model to evaluate
104 duration and intensity of drought constraints in forest stands. *Ecol. Model.* 116, 269–283,
105 1999.

106 107 Specific Comments

108 *Abstract: $0.11 \text{ m}^3 \text{ m}^{-3}$ is only for 2013, not for 2014.

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

112
113 *Introduction: The section need to highlight what is the need for sap-flow measurements and
114 how it influence ecosystem water transport and balance. The importance and need for the
115 study is not properly addressed even though the authors explain the effect of environmental
116 variables on sap-flow in this section. In addition to this the section should refer more recent
117 papers on sap-flow measurements.

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

120
121 *Line 131: Also include root zone depth, and mean leaf area values. Is it possible to include
122 field capacity and wilting point here?

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

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

128 $REW = (VWC - VWC_{min}) / (VWC_{max} - VWC_{min})$,

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

131 References:

- 132 1. Fernández, J. E., Moreno, F., Girón I. F., and Blázquez, O. M.: Stomatal control of water
133 use in olive tree leaves, *Plant Soil*, 190, 179–192, 1997.
- 134 2. Zeppel, M. J. B., Macinnis-Ng, C. M. O., Yunusa, I. A. M., Whitley, R. J., Eamus, D. Long
135 term trends of stand transpiration in a remnant forest during wet and dry years, *J. Hydrol.*,

136 349, 200-213, 2008.

137

138 *Line 140: 'after dynamax 2005', what is that?

139 RESPONSE: The citation 'after dynamax 2005' was revised to 'Dynamax, 2005' (Line 149).

140

141 *Line 141: What is the frequency of measurements?

142 Response: Sap-flow measurements were taken once per minute for each stem. This was

143 added to the method section in the revised manuscript (L149-150).

144

145 *Line 143: What was the mean leaf area? How did it vary with season?

146 Response: Mean leaf area is based on the mean of estimated leaf areas of five shrubs. The

147 leaf area of each shrub is the product of branch numbers and leaf area per branch. The

148 seasonal changes in LAI was presented in the revised manuscript (Table 1).

149

150 *Line 151-155: decoupling coefficient re-expresses g_s , and can be removed.

151 Response: We removed the term "decoupling coefficient" here in the revised manuscript

152 (L166).

153

154 *Line 164-171: Be consistent with label style. It is better to italicize all mathematical variable

155 labels. Only u , g_s and J_s are italicized.

156 Response: We italicized all labels throughout the text in the revised manuscript.

157

158 *Line 178- What is the reason for selecting $VWC=0.08 \text{ m}^3 \text{ m}^{-3}$ as the threshold to determine

159 the drought condition. It is not explained in the paper. The time series of VWC (Figure 1)

160 don't show any severe drought conditions in 30 cm depth. It is useful if the authors can

161 include relative water content within 0-30 cm layer.

162 Response: We revised the VWC threshold using relative extractable soil water (REW) and

163 VWC at 30-cm depth during the measurement period (2013-2014) using pooled data of two

164 years. Consequently, a consistent VWC threshold of 0.10 was defined for the two years (Line

165 188-195).

166

167 *Line 197: 'Lower than...' What is the reduction in percentage?

168 RESPONSE: We added the statement "Total precipitation and number of rainfall events

169 during the 2013 measurement period (257.2 mm and 46 days) were about 5.6% and 9.8%

170 lower than those during 2014 (272.4 mm and 51 days; Fig. 1d), respectively." into revised

171 manuscript. (L228-230)

172

173 *Line 205-210: Can you add time series of g_s here?

174 RESPONSE: Yes, we added monthly mean of g_s (Table 1).

175

176 *Line 215: See general comments above. The threshold to define drought conditions should

177 be the same in both years.

178 RESPONSE: Yes, we revised VWC threshold as responded to general comments above (Line

179 188-195).

180

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

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

186

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

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

193

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

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

204

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

206 **RESPONSE:** Fig.10 in the revised ms was included in the results section, as suggested (L280-
207 282).

208

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

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

212

213 **References added:**

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

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

220

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

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

224

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

226 **RESPONSE:** We added information on root zone depth in the methods section of the revised
227 manuscript. Over 60% of the total roots were distributed in the 0-60cm depth (Zhao et al.
228 2010; Jia et al., 2016). (Line 143-144)

229

230 **References that added:**

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

234 2. Xin Jia, Tianshan Zha, Jinnan Gong, Ben Wang, et al.: Carbon and water exchange over
235 a temperate semi-arid shrubland during three years of contrasting precipitation and soil
236 moisture patterns. *Agricultural and Forest Meteorology*, 228, 120-129, 2016.

237

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

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

240

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

242 **RESPONSE:** Consistent VWC threshold of 0.1 was used for the dry periods of 2013 and
243 2014 in the revised manuscript.

244

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

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

251

252 -----

253 **Anonymous Referee #2**

254 ***General comments**

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

261 **RESPONSE:**

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

266

267 **References added in the revised manuscript:**

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

271 • Granier, A., Bre´da, N., Biron, P., Villette, S.: A lumped water balance model to
272 evaluate duration and intensity of drought constraints in forest stands. *Ecol. Model.*
273 116, 269–283, 1999.

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

277
278 References added in the revised manuscript:

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

285
286 *If available, it will be good to include stomata closure point, wilting point, and hygroscopic
287 point levels. Hence, the reader can judge the severity of drought. So, there will be some
288 justification based on your drought classification. You used 0.08 (L178), 0.09 (Figure 2), and
289 0.11 (Figure 2). Is it 0.08 or 0.09?

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

293 We redefined VWC threshold of sap flow in revised manuscript using pooled data over two
294 years (Fig. 1). The drought conditions were defined by VWC threshold and REW value of
295 0.4 for drought condition (Granier et al., 1999, 2002). The VWC threshold of $0.10 \text{ m}^3 \text{ m}^{-3}$ at
296 our site is equivalent to a REW threshold of 0.4 (Line 188-195).

297
298 *Also knowing wilting point and hygroscopic point helps us appreciating the Figure 6. You
299 stratified soil water content based on three limits. How much severe the lowest value. My
300 back of envelope calculation by using Campbell (1974) for sandy soil where porosity is
301 ~ 0.42 (1-1.54/2.65), the wilting point (15000cm) is ~ 0.07 . It seems your wilting point is
302 much lower. Definitely, to appreciate the Figure 6 and drought severity, giving values are
303 beneficial.

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

307
308 *A little more detail about vegetation setting is beneficial. LAI and plant canopy cover of
309 shrub are beneficial. As far as I know, in Mu Us Desert dunes are migrating or semi-migrating
310 depending on canopy cover. So, it will be beneficial for readers.

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

313
314 *L272-274. In your DISCUSSION, it will be good to include climate for these plant species.
315 Because your ecosystem which is water-limited, most probably different than their study sites!

316 For example, Huang et al. (2009) study site (L275) is in Guangxi, where annual precipitation
317 is 1900 mm, and mean annual temperature is 19.3 °C. Most probably some/most part of the
318 year, the ecosystem is energy-limited. So, it is not so surprising to see solar radiation control
319 on sap flow. I could not find electronic copy of Zhang et al. (2003) work. Please include
320 prevailing climate in their study area too.

321 **RESPONSE:** We added prevailing climate of these species in the revised manuscript.
322 Generally, the present result is in contrast to other shrub species. For example, it has been
323 found that sap flow in *Haloxylon ammodendron* in northwest China, where annual
324 precipitation is 37.9 mm, and mean annual temperature is 8.2 °C, was mainly controlled by
325 temperature (Zhang et al., 2003), while sap flow in *Cyclobalanopsis glauca* in south China,
326 where annual precipitation is 1900 mm and mean annual temperature is 19.3 °C, was
327 controlled by both radiation and temperature with VWC not limiting (Huang et al. 2009).”
328 (Line 304-310)

329
330 *L276-L278. To emphasize the importance of small events on ecological processes, I want
331 to draw authors attention another study by Sala and Lauenroth (1982).

332 Sala and Lauenroth (1982) showed the ecological importance of small events (<5mm) in
333 semiarid site where dominated by C4 grass. I will be worth to check!

334 Sala O.E. and W.K. Lauenroth (1982). Small rainfall events: an ecological role in semi-
335 arid regions. *Oecologia*, 53 (3), 301-304.

336 **RESPONSE:** We appreciate the recommendation. We have read the paper and added the
337 relevant findings as a support and generalization of our own results in the revised manuscript
338 (see references in the revised ms).

339
340 *Minor Points:

341 L69. VERB.low soil water availability limitS,

342 **RESPONSE:** We corrected this (Line 70)

343
344 L70. VERB.limitS vegetation productivity

345 **RESPONSE:** We corrected this as well (Line 71)

346
347 L73. I recommend citation for: grass replacement by shrubs.

348 **RESPONSE:** We added the citation in the sentence “...semi-arid areas of northwestern China
349 (Yu et al., 2004).” in the revised manuscript (Line 74)

350
351 L103. Capitalization.the Mu Us Desert....

352 **RESPONSE:** The name ‘Mu Us desert’ was corrected to ‘Mu Us Desert’ in the revised
353 manuscript. (Line 109)

354
355 L125. Capitalization.the Mu Us Desert....

356 **RESPONSE:** The name ‘Mu Us desert’ was corrected to ‘Mu Us Desert’ in the revised
357 manuscript. (Line 131)

358
359 L137. VERB. Mean height and sapwood area of sampled shrubs WERE

360 **RESPONSE:** We corrected this (Line 146)

361
362 L156. Replace UPSILON in the equation with lower-case gamma, γ for psychometric
363 constant.
364 **RESPONSE: We revised as suggested (Line 168-170)**
365
366 L161. Insert a comma after “ground”.the ground, and....
367 **RESPONSE: We inserted a comma in the sentence.**
368
369 L180. VERB. Linear and nonlinear regression WERE

370 **RESPONSE: We corrected this (Line 209)**
371
372 L197. VERB. Total precipitation and number of rainfall events.... WERE lower than
373 THOSE....
374 **RESPONSE: Yes, we corrected this (Line 229)**
375
376 L266. VERB. Synergistic interactions ARE....
377 **RESPONSE: Corrected (Line 300)**
378
379 L355-461. Please go through the references. Make sure the unity within the references.
380 Journal names abbreviated some of them (L361, L367, L370 etc.), but not others (L 358,
381 L383, L386 etc.). Choose one of them and stick with it. L424. Typo. Systems... L430. Typo.
382 Ecology... L449. Typo. PLoS ONE. Compare with (L461 and L373). Use lower case for
383 article names. Check (L456, L461, L416 etc.).
384 **RESPONSE: We carefully checked and revised citations and references throughout the**
385 **manuscript as suggested.**
386
387 L541. Figure 4. I recommend following some color scheme (pattern) to represent different
388 months such as jet etc. This change will help the readers to follow the figure easier than the
389 current form.
390 **RESPONSE: We replotted Fig. 6 in the revised ms using color, as suggested. (Fig. 6)**
391
392 L553. Insert a comma after (dimensionless). (dimensionless), and
393 **RESPONSE: We revised the sentence.**
394
395 L554. To distinguish from straight arrows, I recommend using ‘curved arrows’ such as: The
396 CURVED arrowS indicate the clockwise....
397 **RESPONSE: We revised as suggested. (Fig. 7)**
398
399 L558. I recommend using ‘three’ instead of ‘3’ days.
400 **RESPONSE: We write “three” instead (Fig. 8)**
401
402

403 **Track change manuscript version**

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

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417 [#]These authors contributed equally to this work.

418

419

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

421

422

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424

425 **Author Contribution Statement:**

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

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

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

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

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

435

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

439

440 **Conflict of Interest:**

441 This research was financially supported by grants from the National Natural Science
442 Foundation of China (NSFC No. 31670710), the National Basic Research Program of China
443 (Grant No. 2013CB429901), and by the Academy of Finland (Project No. 14921). ~~It is~~The
444 project is-also related to the Finnish-Chinese collaborative research project, EXTREME
445 (2013-2016), between Beijing Forestry University and the University of Eastern Finland, and
446 USCCC. We appreciate Dr. Ben Wang, Sijing Li, Qiang Yang, and others for their help with
447 the fieldwork. **The authors declare that they have no conflict of interest.**

448

449 **Abstract:** Current understanding of acclimation processes in desert-shrub species to drought
450 stress in dryland ecosystems is still incomplete. In this study, we measured sap flow in
451 *Artemisia ordosica* and associated environmental variables throughout the growing seasons
452 of 2013-2014 (May-September period of each year) to better understand the environmental
453 controls on the temporal dynamics of sap flow. We found that the occurrence of drought in
454 the dry year of 2013 during the leaf-expansion and leaf-expanded periods caused sap flow
455 per leaf area (J_s) to decline significantly, resulting in a sizable drop in transpiration. Sap flow
456 per leaf area correlated positively with radiation (R_s), air temperature (T), and vapor pressure
457 deficit (VPD), when volumetric soil water content (VWC) was $> 0.14-10 \text{ m}^3 \text{ m}^{-3}$. Diurnal J_s
458 was generally ahead of R_s by as much as 6 hours. This lag time, however, decreased with
459 increasing VWC. Relative response of J_s to the environmental variables (i.e., R_s , T , and VPD)
460 varied with VWC, J_s being more ~~biologically-biologically~~-controlled with a low decoupling
461 coefficient and ~~thus being~~ less ~~sensitive-sensitivity~~ to the environmental variables during
462 ~~periods of dryness-periods~~. According to this study, soil moisture is shown to control sap-
463 flow (and, therefore, plant-transpiration) response in *Artemisia ordosica* to diurnal variations
464 in biophysical factors. The findings of this study add to the knowledge of acclimation
465 processes in desert-shrub species under drought-associated stress. This knowledge is
466 essential to model desert-shrub-ecosystem functioning under changing climatic conditions.

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

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471 **1. Introduction**

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

489 ~~Sap flow measurement can accurately reflect the water consumption estimation~~
490 ~~of~~ ~~by~~ ~~during~~ ~~plant~~ ~~transpiration~~, ~~water~~ ~~consumption~~, ~~it~~ ~~has~~ ~~positive~~ ~~influence~~ ~~of~~ ~~maintains~~
491 ~~ecosystem~~ ~~balance~~ ~~by~~ ~~through~~ ~~the~~ ~~soil~~ ~~plant~~ ~~atmosphere~~ ~~continuum~~ ~~path~~, ~~but~~ ~~is~~ ~~often~~ ~~is~~
492 ~~influenced~~ ~~affected~~ by environment factors (Huang et al., 2010; Zhao et al., 2016). In recent
493 studies, sap flow in *Tamarix elongate* has been observed to be controlled by solar radiation

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494 and air temperature, whereas in *Caragana korshinskii* vapor pressure deficit and solar
 495 radiation appear to be more important (Jacobsen et al., 2007; Xia et al., 2008). In *Elaeagnus*
 496 *angustifolia*, transpiration is observed to peak at noon, i.e., just before stomatal closure at
 497 mid-day under water-deficit conditions (Liu et al., 2011). In contrast, transpiration in
 498 *Hedysarum scoparium* peaks multiple times during the day (Xia et al., 2007). Sap flow has
 499 been observed to decrease rapidly when the volumetric soil water content (VWC) is lower
 500 than the water loss through evapotranspiration (Buzkova et al., 2015). In general, desert
 501 shrubs can close their stomata to reduce transpiration when exposed to dehydration stress
 502 around mid-day. However, differences exist among shrub species with respect to their
 503 stomatal response to changes in soil and air moisture deficits (Pacala et al., 2001). For some
 504 shrubs, sap-flow response to precipitation varies from an immediate decline after a heavy
 505 rainfall to no observable change after a small rainfall event (Asner et al., 2003; Zheng and
 506 Wang, 2014). Sap flow has been found to increase with increasing rainfall intensity (Jian et
 507 al., 2016). Drought-insensitive shrubs have relatively strong stomatal regulation and,
 508 therefore, tend to be insensitive to soil water deficits and rainfall unlike their drought-
 509 sensitive counterparts (Du et al., 2011). ~~In all~~ In general, understandings ~~Studies~~ of the
 510 relationships between the sap-flow rates in plants and environmental factors are highly
 511 inconsistent, varying with is conducive to understanding vegetal physiological responses to
 512 their plant habitats (Liu et al., 2011).

513 *Artemisia ordosica*, a shallow-rooted desert shrub, is the dominant plant species in the
 514 Mu Us desert ~~Desert~~ of northwestern China. The shrubs have an important role in combating
 515 desertification and in stabilizing sand dunes (Li et al., 2010). Increases in air temperature and

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516 precipitation variability and associated shorter wet periods and longer intervals of periodic
517 drought are expected to ensue with projected climate change (Lioubimtseva and Henebry,
518 2009). During dry periods of the year, sap flow in *Artemisia ordosica* has been observed to
519 be controlled by VWC at about 30-cm depth in the soil (Li et al., 2014). Sap-flow rate is
520 known to be affected by variation in precipitation patterns. Soil water content, in combination
521 with other environmental factors, may have a significant influence on sap-flow rate (Li et al.,
522 2014; Zheng and Wang, 2014). Thus, understanding the controlling mechanisms of sap flow
523 in desert shrubs as a function of variations in biotic and abiotic factors is greatly needed (Gao
524 et al., 2013; Xu et al., 2007).

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

530

531 2. Materials and Methods

532 2.1 Experimental site

533 Continuous sap-flow measurements were made at the Yanchi Research Station (37°42'
534 31" N, 107°13' 47" E, 1530 m above mean sea level), Ningxia, northwestern China. The
535 research station is located between the arid and semi-arid climatic zones along the southern
536 edge of the **Mu Us Desert**. The sandy soil in the upper 10 cm of the soil profile has a bulk
537 density of $1.54 \pm 0.08 \text{ g cm}^{-3}$ (mean \pm standard deviation, n=16). Mean annual precipitation

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538 in the region is about 287 mm, of which 62% falls between July and September. Mean annual
539 potential evapotranspiration and air temperature are about 2,024 mm and 8.1°C based on
540 meteorological data (1954-2004) from the Yanchi County weather station. Normally, shrub
541 leaf-expansion, leaf-expanded, and leaf-coloration stages begin in April, June, and
542 September (Chen et al., 2015), respectively.

543

544 2.2 Measurements of sap flow, leaf area and stomatal conductance

545 The experimental plot (10 m × 10 m) was located on the western side of Yanchi Research
546 Station in an *Artemisia ordosica*-dominated area. Mean age of the *Artemisia ordosica* was

547 10-years old. Annual maximum monthly mean leaf area index (LAI) is in for leaf expanded

548 stage plant specimens with full leaf expansion was about 0.1 m² m⁻² (Table 1), 62.14%

549 Over 60% of the total their roots weight of *Artemisia ordosica* were

550 mainly distributed in the soil depths of 0-60 cm (Zhao et al., 2010; Jia et al., 2016). Five

551 stems of *Artemisia ordosica* were randomly selected within the plot as replicates for sap-flow

552 measurement. Mean height and sapwood area of sampled shrubs was were 84 cm and 0.17

553 cm², respectively. Sampled stems represented the average size of stems in the plot. A heat

554 balance sensor (Flow32-1K, Dynamax Inc., Houston, USA) was installed at about 15 cm

555 above the ground surface on each of the five stems (after Dynamax, 2005). The frequency of

556 sap-flow measurements were taken 4 record once per minute for each stem. Half-hourly

557 data were recorded by a Campbell CR1000 data logger from May 1 to September 30, 2013-

558 2014 (Campbell Scientific, Logan, UT, USA).

559 Leaf area was estimated for each stem every 7-10 days by sampling about 50-70 leaves

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560 from five randomly sampled neighbouring shrubs with similar characteristics as to the shrubs
 561 used for sap-sap-flow measurements, to avoid damaging them. Leaf area was measured
 562 immediately at the station laboratory with a portable leaf-area meter (LI-3000, Li-Cor,
 563 Lincoln, NE, USA). Leaf area index (LAI) was measured at roughly weekly intervals at on a
 564 4x4 grid of 16 quadrats (10 m x 10 m each) within a 100 m x 100 m plot centered on the flux
 565 tower using measurements of sampled leaves and allometric equations (Jia et al., 2014).
 566 Stomatal conductance (g_s) was measured *in situ* for three to four leaves on each of the
 567 sampled shrubs with a LI-6400 portable photosynthesis analyzer (Li-Cor Inc., Lincoln, USA).
 568 Stomatal conductance. The g_s measurements were made every two hours from 7:00 to 19:00
 569 h every ten days from May to September, 2013-2014.

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

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

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

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

580 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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581 s⁻¹).

582

583 2.3 Environmental measurements

584 Shortwave radiation (R_s in W m^{-2} ; CMP3, Kipp & Zonen, Netherland), air temperature (T in
585 $^{\circ}\text{C}$), wind speed (μ in m s^{-1} , 034B, Met One Instruments Inc., USA), and relative humidity
586 (RH in %; HMP155A, Väisälä, Finland) were measured simultaneously near the sap-flow
587 measurement plot. Half-hourly data were recorded by a data logger (CR3000 data logger,
588 Campbell Scientific Inc., USA). VWC at 10 and 30-cm depths were monitored with three
589 ECH₂O-5TE soil moisture probes (Decagon Devices, USA). In the analysis, we used half-
590 hourly averages of VWC from the three soil moisture probes. Vapor pressure deficit (VPD
591 in kPa) was calculated from recorded RH and T .

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593 2.4 Data analysis

594 In ~~the our~~ analysis, March-May represented spring, June-August summer, and September-
595 November autumn (Chen et al., 2015). Drought days were defined as those days with daily
596 mean VWC $< 0.1 \text{ m}^3 \text{ m}^{-3}$. This is based on a VWC threshold of $0.1 \text{ m}^3 \text{ m}^{-3}$ for J_e (Fig. 1),
597 with J_e increasing with as increased VWC increased, saturated saturating at VWC of 0.1 m^3
598 m^{-3} , and then showed a decreasing trend as VWC continued to increase. The VWC threshold
599 of $0.1 \text{ m}^3 \text{ m}^{-3}$ is equivalent to a relative extractable soil water (REW) value of 0.4 for drought
600 conditions (by Granier et al., (1999, and 2007) and; Zeppel et al., (2004, and 2008); Fig.
601 2d, e). Duration and severity of 'drought' were defined based on the VWC threshold and
602 REW value of 0.4. REW was calculated as according to equation (3):

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

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where VWC is the specific daily soil water content ($\text{m}^3 \text{m}^{-3}$), 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 $VWC < 0.08 \text{m}^3 \text{m}^{-3}$ for both 10- and 30-cm depths for at least 10 consecutive days.

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Sap-flow data analysis was conducted using hourly-mean data from five sensors.

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Sap flow per leaf area (J_s) was used in this study, i.e.,

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

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where, J_s is the sap flow per leaf area ($\text{kg m}^{-2} \text{h}^{-1}$) or ($\text{kg m}^{-2} \text{d}^{-1}$), summed over a 24-hour day; E_i is the measured sap flow of a stem (g h^{-1}), A_{li} is the leaf area of the sap-flow stem, and "n" is the number of replicate sap-flow stems used (in this case, $n = 5$).

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

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

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

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

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June 1 to August 31, with hourly shortwave radiation $> 10 \text{W m}^{-2}$. 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 June 1 to August 31 can be were

624 ~~fitted derived with linear regression (p<0.05; Fig. 3). Regression~~ The Regression slopes of
625 ~~linear regression~~ were ~~therefore~~ used to identify the indicators of sap-flow sensitivity of
626 ~~sap flow~~ (degree of response) to the various environmental variables (see e.g., Zha et al.,
627 2013). All statistical analyses were performed with SPSS v. 17.0 for Windows software
628 (SPSS Inc., USA). Significance level was set at 0.05.

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630 3. Results

631 3.1 Seasonal variations in environmental factors and sap flow

632 Range of daily means (24-hour mean) for R_s , T , R_s -VPD, and VWC during the 2013 growing
633 season (May-September) were 31.1-364.9 W m⁻², 8.8-24.4°C, 31.1-364.9 W m⁻², 0.05-2.3
634 kPa, and 0.06-0.17 m³ m⁻³ (Fig. 2a, b, c, d), respectively; annual means for the same
635 year being were 224.8 W m⁻², 17.7°C, 224.8 W m⁻², 1.03 kPa, and 0.08 m³ m⁻³. Corresponding
636 range of daily means for 2014 were 31.0-369.9 W m⁻², 7.1-25.8°C, 31.0-369.9 W m⁻², 0.08-
637 2.5 kPa, and 0.06-0.16 m³ m⁻³ (Fig. 2a, b, c, d), respectively; annual means were being
638 234.9 W m⁻², 17.2°C, 234.9 W m⁻², 1.05 kPa, and 0.09 m³ m⁻³.

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639 Total precipitation and number of rainfall events during the 2013 measurement period
640 (257.2 mm and 46 days) ~~were~~ about 5.6% and 9.8% lower than those during 2014 (272.4
641 mm and 51 days; Fig. 2d), respectively. In 2013, more irregular rainfall events occurred
642 than in 2014. ~~The measurement period in 2013 had many irregular rainfall events compared~~
643 ~~to 2014~~, with 45.2% of rainfall falling in July and 8.8% in August, ~~2013~~.

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

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

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647 Range of daily means of J_s during the growing season was 0.01-4.36 kg m⁻² d⁻¹ in 2013

648 and 0.01-2.91 kg m⁻² d⁻¹ in 2014 (Fig. 2f); with annual means were of 0.89 kg m⁻² d⁻¹ in

649 2013 and 1.31 kg m⁻² d⁻¹ in 2014. Mean daily J_s over the growing season of 2013 was 32%

650 lower than that of 2014. Mean daily T_r were 0.05 mm d⁻¹ and 0.07 mm d⁻¹ over the

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651 growing season in 2013 and 2014 (Fig. 2f), respectively, and it was being 34% lower in 2013

652 than that in 2014. The total T_r over growing season (May 1-September 30) in 2013 and 2014

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653 were 7.3 mm and 10.9 mm, respectively. Seasonal fluctuations in J_s and T_r corresponded with

654 the seasonal pattern in VWC (Fig. 2d, ef). Daily mean J_s and T_r decreased or remained

655 nearly constant during dry-soil periods (Fig. 2d, ef), with the lowest J_s and T_r observed

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656 in spring and mid-summer (August) of 2013.

657

658 3.2 Sap flow response to environmental factors

659 In summer, J_s increased with increasing VWC (Fig. 2d, f; Fig. 3d). Fig. 2), meanwhile,

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660 saturating at VWC 0.11 m³ m⁻³ in 2013 and 0.09 m³ m⁻³ in 2014, then decreasing with

661 VWC when VWC is greater than the thresholds of 0.11 m³ m⁻³ in 2013 and 0.09 m³ m⁻³ in

662 2014. Soil water is was shown to modify the response of J_s to environmental factors (Fig.

663 2Fig. 4). Sap flow J_s increased more rapidly with increases in R_s , T , and VPD under high

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664 VWC (i.e., VWC > 0.11 m³ m⁻³ both in both 2013 and VWC > 0.09 m³ m⁻³ in 2014)

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665 compared with periods with lower VWC (i.e., VWC < 0.11 m³ m⁻³ both in both 2013 and

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666 VWC < 0.09 m³ m⁻³ in 2014). Sap flow J_s was more sensitive to R_s , T , and VPD under high

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667 VWC (Fig. 2d), which coincided with a larger regression slope under high VWC conditions.

668 Sensitivity of J_s to environmental variables (in particular, R_s , T , VPD, T_r , and VWC)

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669 varied depending on the time of a day (Fig. 3Fig. 5). Regression slopes for the relations of
670 J_s - R_s , J_s - T , and J_s -VPD were greater in the morning before 11:00 h, and lower during mid-
671 day and early afternoon (12:00-16:00 h). In contrast, regression slopes of the relation of J_s -
672 VWC were lower in the morning (Fig. 3Fig. 5), increasing thereafter, peaking at ~13:00 h,
673 and subsequently decreasing in late afternoon. Regression slopes of the response of J_s to R_s ,
674 T , and VPD in 2014 were greater than those in 2013.

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676 3.3 Diurnal changes and hysteresis between sap flow and environmental factors

677 Diurnal patterns of J_s were similar in both years (Fig. 46), initiating at 7:00 h and increasing
678 thereafter, peaking before noon (12:00 h), and subsequently decreasing thereafter and
679 remaining near zero from 20:00 to 6:00 h. Diurnal changes in stomatal conductance (g_s) were
680 similar to J_s , but peaking about 2 and 1 h earlier than J_s in July and August, respectively (Fig.
681 4Fig. 6).

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682 There were pronounced time lags between J_s and R_s over the two years (Fig. 5Fig. 7), J_s
683 peaking earlier than R_s and, thus, earlier than either VPD or T . These time lags differed
684 seasonally. For example, mean time lag between J_s and R_s was 2 h during July, 5 h during
685 May, and 3 h during June, August, and September of 2013. However, the time lags in 2014
686 were generally shorter than those observed in 2013 (Table 42).

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687 Use of normalized variables may remove the influence of J_s and R_s from the data. As a
688 result, clockwise hysteresis loops between J_s and R_s during the growing period were observed
689 (Fig. 57). As R_s increased in the morning, J_s increased until it peaked at ~10:00 h. Sap-flow
690 rate declined with decreasing R_s during the afternoon. Sap flow J_s was higher in the morning

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

692 Diurnal time lag in the relation of J_s - R_s were influenced by VWC (Fig. 6 Fig. 8, 79). For
693 example, J_s peaked about 2 h earlier than R_s on days with low VWC (Fig. 6 Fig. 8a), 1 h earlier
694 than R_s on days with moderate VWC (Fig. 6 Fig. 8b), and at the same time as R_s on days with
695 high VWC (Fig. 6 Fig. 8c). Lag hours between J_s and R_s over the growing season were
696 negatively and linearly related to VWC (Fig. 97: Lag (h) = -133.5 × VWC + 12.24, R² = 0.41).
697 Effect of VWC on time lags between J_s and R_s was smaller in 2014, with evenly distributed
698 rainfall during the growing season, than in 2013, with a pronounced summer drought (Fig.
699 7 Fig. 9). The state variables g_s and Ω showed a significantly increased trend with
700 increasing VWC in 2013 and 2014, respectively (Fig. 8 Fig. 10).

701

702 4. Discussion and conclusions

703 4.1 Sap flow response to environmental factors

704 Drought tolerance of some plants may be related to lower overall sensitivity of the plants'
705 physiological attributes to environmental stress and/or stomatal regulation (Huang et al.,
706 2011b; Naithani et al., 2012). In this study, large regression slopes of linear relationships
707 between J_s and the environmental variables (R_s , VPD, and T) in the morning indicated that
708 sap flow was more sensitive to variations in R_s , VPD, and T during the less dry and hot period
709 of the day (Fig. 35). Stomatal conductances were the largest in the morning (Fig. 46), which
710 led to increases in water fluxes to the atmosphere as a result of increased R_s , T , and VPD.
711 When R_s peaked during mid-day (13:00-14:00 h), there was often insufficient soil water to
712 meet the atmospheric demand of for water, causing stomatal conductance to be limited by

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713 available soil moisture and making J_s more responsive to VWC at noon, but less responsive

714 to R_s and T . Similarly, *Hedysarum mongolicum* in the nearby region positively correlated

715 with VWC at noon (Qian et al., 2015), and the evapotranspiration over a Scots pine

716 foreststand showed a higher sensitivity to surface conductance, temperature, VPD vapor

717 pressure deficit, and radiation in the morning, than in the afternoon (Zha et al., 2013).

718 Synergistic interactions among environmental factors influencing sap flow ~~is~~ are

719 complex. In general, VWC has an influence on physiological processes of plants in water-

720 limited ecosystems (Lei et al., 2010; She et al., 2013). Our findings regarding lower

721 sensitivity in J_s to environmental factors (R_s , T and VPD) during dry periods was ~~in~~

722 ~~line~~ inconsistent with a previous an earlier study of boreal grasslands (Zha et al., 2010). Also

723 our finding that soil water regulates the response of other environmental factors, suggests

724 that VWC is the most important factor controlling/modifying the responses of in sap flow in

725 *Artemisia ordosica* response to other environmental factors. This ~~is~~ was in contrast to other

726 shrub species, where ~~for~~ For example, it has been found that sap flow in *Haloxylon*

727 *ammodendron* in northwest China, where annual precipitation is 37.9 mm, and mean annual

728 temperature is 8.2 °C, was mainly controlled by T (Zhang et al., 2003), while sap flow in

729 *Cyclobalanopsis glauca* in south China, where annual precipitation is 1900 mm, and mean

730 annual temperature is 19.3 °C, was controlled by R_s and T , when VWC was not limiting

731 (Huang et al., 2009).

732 Precipitation, being the main source of VWC at our site, affected transpiration directly.

733 In this sense, frequent small rainfall events (< 5 mm) were important to the survival and

734 growth of the desert plants (Sala and Lauenroth, 1982; Zhao and Liu, 2010). Variations in J_s

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735 were clearly associated with the intermittent supply of water to the soil during rainfall events,
736 as ~~we found~~indicated at our site (Fig. 4d, e). Reduced J_s during rainy days can be
737 explained by a reduction in incident R_s and water-induced saturation on the leaf surface,
738 which led to a decrease in leaf turgor and stomatal closure. After each rainfall event, J_s
739 increased quickly when soil water was replenished. ~~This finding is related to a positive~~
740 ~~response in J_s to R_s , T , and VPD under high VWC (Fig. 2).~~ Schwinnig and Sala (2004)
741 showed previously for similar research sites that VWC contributed the most to the response
742 in plant transpiration to post-rainfall events. We showed in this study that *Artemisia ordosica*
743 responded in a different way to wet and dry conditions. In the mid-growing season, high J_s
744 in July were related to rainfall-fed VWC, which increased the rate of transpiration. However,
745 dry soil conditions combined with high T and R_s , led to a reduction in J_s in August of 2013
746 (~~Fig. 1~~Fig. 2). In some desert shrubs, groundwater may replenish water lost by transpiration
747 by having deep roots (Yin et al., 2014). *Artemisia ordosica* roots are generally distributed in
748 the upper 60 cm of the soil (Zhao et al., 2010; Wang et al., 2016), and as a result the plant
749 usually depends on water directly supplied by precipitation because groundwater levels in
750 drylands can be well below the rooting zone, typically, at depths ≥ 10 m [at our site](#).

751

752 4.2 Hysteresis between sap flow and environmental factors

753 Diurnal patterns in J_s corresponded with those of R_s from sunrise until diverging later in the
754 day (Fig. 5), suggesting that R_s was a primary controlling factor of diurnal variation in J_s .
755 According to O'Brien et al. (2004), diurnal variation in R_s could cause change in the diurnal
756 variation in the consumption of water. As an initial energy source, R_s can force T and VPD

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757 to increase, causing a phase difference in time lags among the relations J_s - R_s , J_s - T , and J_s -
758 VPD.

759 We found a consistent clockwise hysteresis loop between J_s and R_s over a diurnal cycle
760 (Fig. 5 Fig. 7), indicating that R_s lagged J_s , and the response of J_s to R_s varied both diurnally
761 and seasonally. A large g_s in the morning promoted higher rates of transpiration (Fig. 4 Fig.
762 6). In dry and hot conditions, g_s stomatal conductance decreased, causing the control of the

763 stomata on J_s to increase relative to changes in environmental factors. Diurnal trends in J_s
764 and g_s occurred together, both peaking earlier than R_s . The g_s Stomatal conductance peaked
765 3-4 h earlier than R_s , leading to a reduction in J_s and an increase in R_s and a clockwise
766 hysteresis loop. Contrary to our findings, counterclockwise hysteresis has been observed to
767 occur between transpiration (J_s) and R_s in tropical and temperate forests (Meinzer et al., 1997;
768 O'Brien et al., 2004; Zeppel et al., 2004). A possible reason for this difference may be due to
769 differences in VWC associated with the different regions. According to Zheng and Wang
770 (2014) favorable water conditions after rainfall could render clockwise hysteresis loops
771 between J_s and R_s under dry conditions to counterclockwise loops. In this study, due to a
772 large incidence of small rainfall events, soil water supply by rainfall pulses could not meet
773 the transpiration demand under high mid-day R_s , resulting in clockwise loops even though
774 rainfall had occurred.

775 In semi-arid regions, low VWC restricts plant transpiration more than VPD. Water
776 vapor deficits tend to restrict transpiration in forest species in wet regions to a greater extent.
777 According to Zheng et al. (2014), high water availability in alpine shrubland meadows may
778 contribute to weakened hysteresis between evapotranspiration and the environmental

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779 variables. Our results showed that hysteresis between J_s and R_s decreased as VWC increased
780 (Fig. 6 Fig. 8, 79). The result that g_s stomatal conductance increased with increasing VWC
781 (Fig. 8 Fig. 10a), along with the synchronization harmonization of J_s and g_s , suggests that J_s
782 is less sensitive to stomatal conductance (g_s) in high VWC and more so to R_s . Temporal
783 patterns in J_s became more consistent coherent with those in R_s as VWC increased, leading
784 to a weakened hysteresis between the two variables. This is further supported by a large
785 decoupling coefficient, when VWC is high (Fig. 8 Fig. 10b). The larger the decoupling
786 coefficient is, the greater is the influence of R_s on J_s . The effect of VWC on time lag varied
787 between 2013 and 2014.

789 4.3. Conclusions

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

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801 climatic conditions.

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812

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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

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

966

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

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970 **Figure captions:**

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

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975 **Fig. 2** Seasonal changes in daily (24-hour) mean shortwave radiation (R_s ; a), air temperature
976 (T ; b), vapor pressure deficit (VPD; c), volumetric soil water content (VWC; d), relative
977 extractable water (REW; e), daily total precipitation (PPT; f), and daily sap-flow per leaf
978 area (J_s ; f), and daily transpiration (T_r , mm d^{-1} ; f) from May to September for both 2013 and
979 2014. Horizontal dash lines (d, e) represent VWC and REW threshold of $0.1 \text{ m}^3 \text{ m}^{-3}$ and 0.4 ,
980 respectively. Shaded bands indicate periods of drought.

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

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

993 **Fig. 5** Regression slopes of linear fits between sap-flow rate per leaf area (J_s) in non-rainy
994 days and shortwave radiation (R_s), vapor pressure deficit (VPD), air temperature (T), and
995 volumetric soil water content (VWC) between 8:00-20:00 h during the mid-growing ~~period~~
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997 **Fig. 6** Mean monthly diurnal changes in sap-flow rate per leaf area (J_s) and stomatal
998 conductance (g_s) in *Artemisia ordosica* during the growing season (May-September) for both
999 2013 and 2014. Each point is given as the mean at specific times during each month.

1000 **Fig. 7** Seasonal variation in hysteresis loops between sap-flow rate per leaf area (J_s) and
1001 shortwave radiation (R_s) using normalized plots for both 2013 and 2014. The y-axis
1002 represents the proportion of maximum J_s (dimensionless), and the x-axis represents the
1003 proportion of maximum R_s (dimensionless). The curved arrows indicate the clockwise
1004 direction of response during the day.

1005 **Fig. 8** Sap-flow rate per leaf area (J_s) and shortwave radiation (R_s) over consecutive three
1006 days in 2013, i.e., (a) under low volumetric soil water content (VWC) and high vapor pressure
1007 deficit (VPD): DOY 153-155, $\text{VWC}=0.064 \text{ m}^3 \text{ m}^{-3}$, $\text{REW}=0.025$, $\text{VPD}=2.11 \text{ kPa}$, (b)
1008 moderate VWC and VPD (DOY 212-214, $\text{VWC}=0.092 \text{ m}^3 \text{ m}^{-3}$, $\text{REW}=0.292$, $\text{VPD}=1.72$
1009 kPa), and (c) high VWC and low VPD (DOY 192-194, $\text{VWC}=0.152 \text{ m}^3 \text{ m}^{-3}$, $\text{REW}=0.865$,
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1011 mean value of the three days.

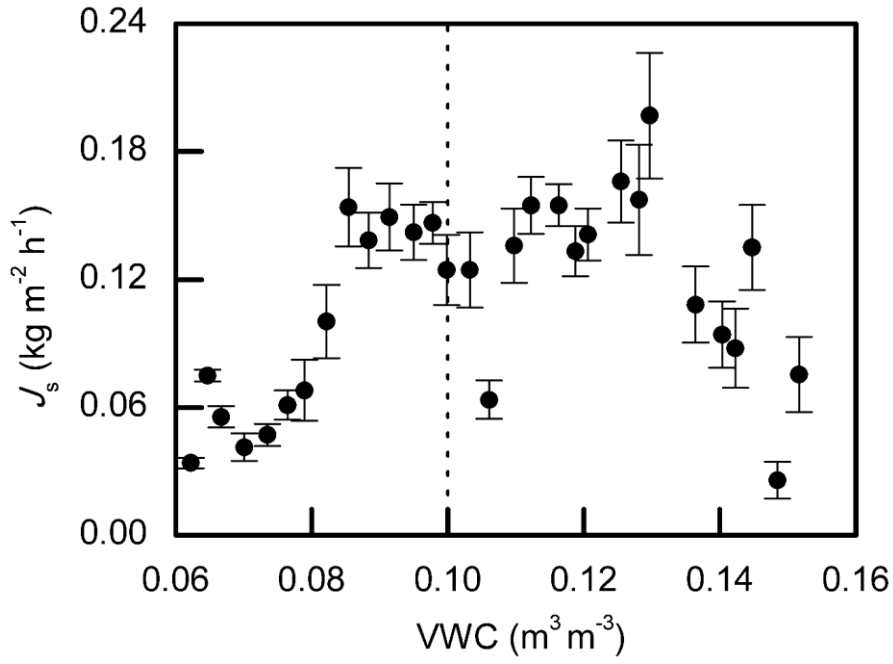
1012 **Fig. 9** Time lag between sap-flow rate per leaf area (J_s) and short wave radiation (R_s) in
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1014 mid-growing ~~period~~ season of June 1-August 31 for ~~both~~ 2013 and 2014. The lag hours were
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1016 time step. Rainy days were excluded. The solid line is based on exponential regression
1017 ($p < 0.05$).

1018 **Fig. 10** Relationship between volumetric soil water content (VWC) and (a) stomatal
1019 conductance (g_s) in *Artemisia ordosica*, and (b) decoupling coefficient (Ω) for ~~both~~-2013 and
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1021 m^{-3} . Bars indicate standard error. ~~Only regressions line with p -values < 0.05 was are~~
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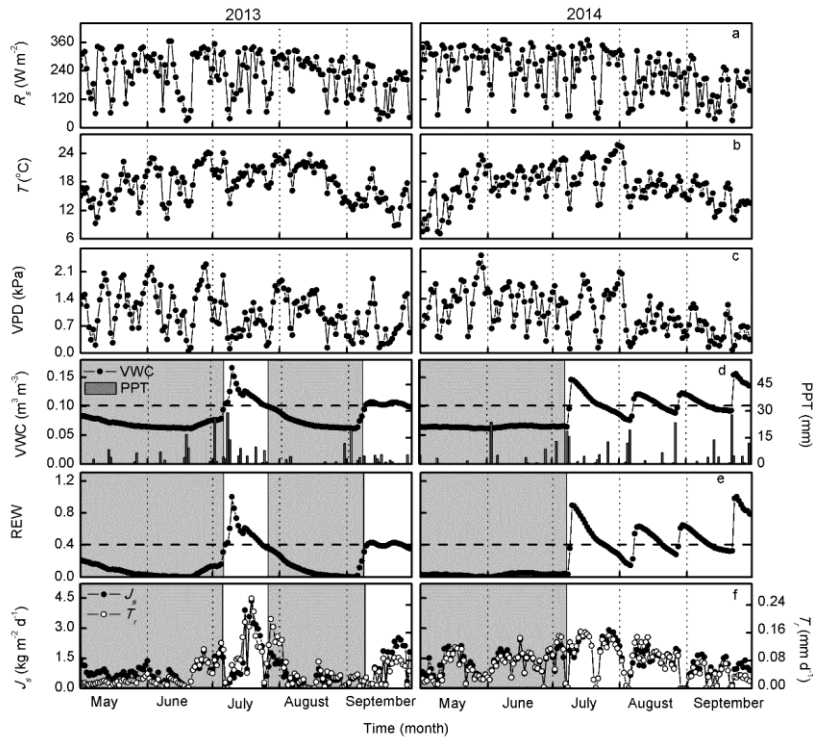
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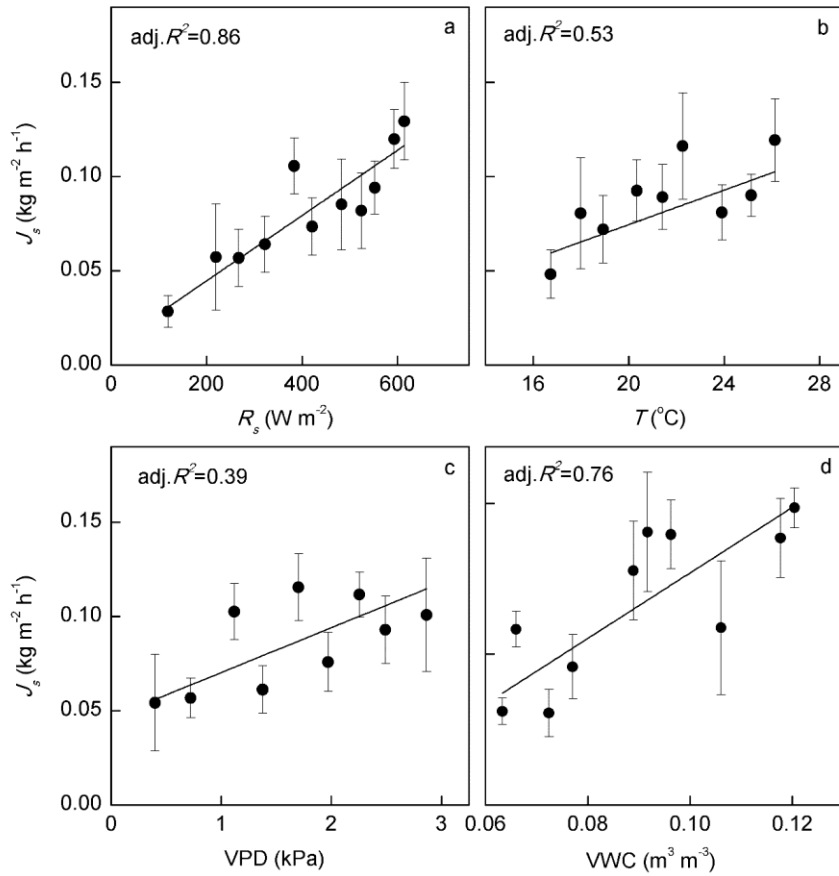


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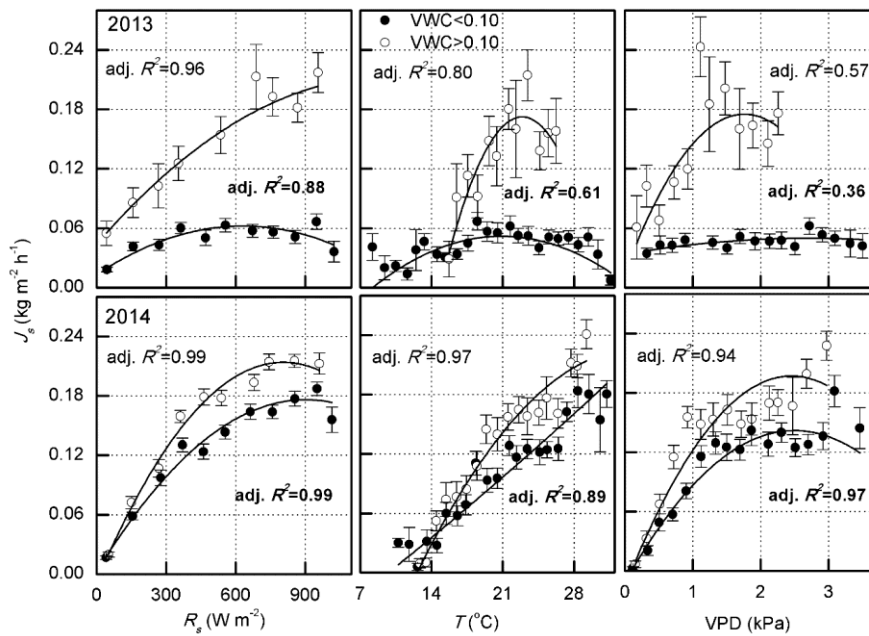
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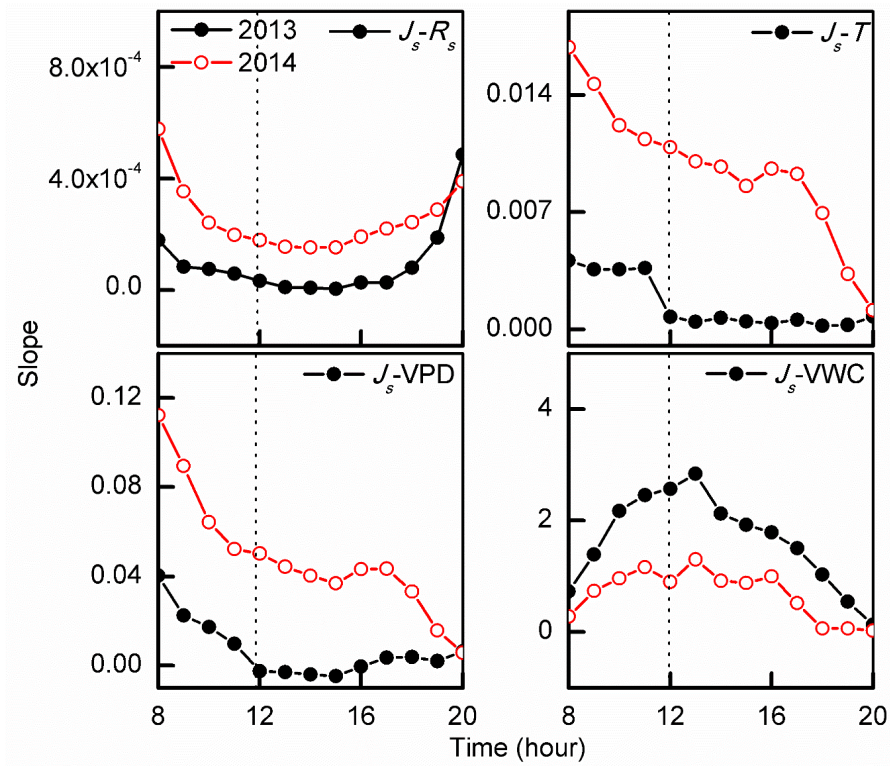


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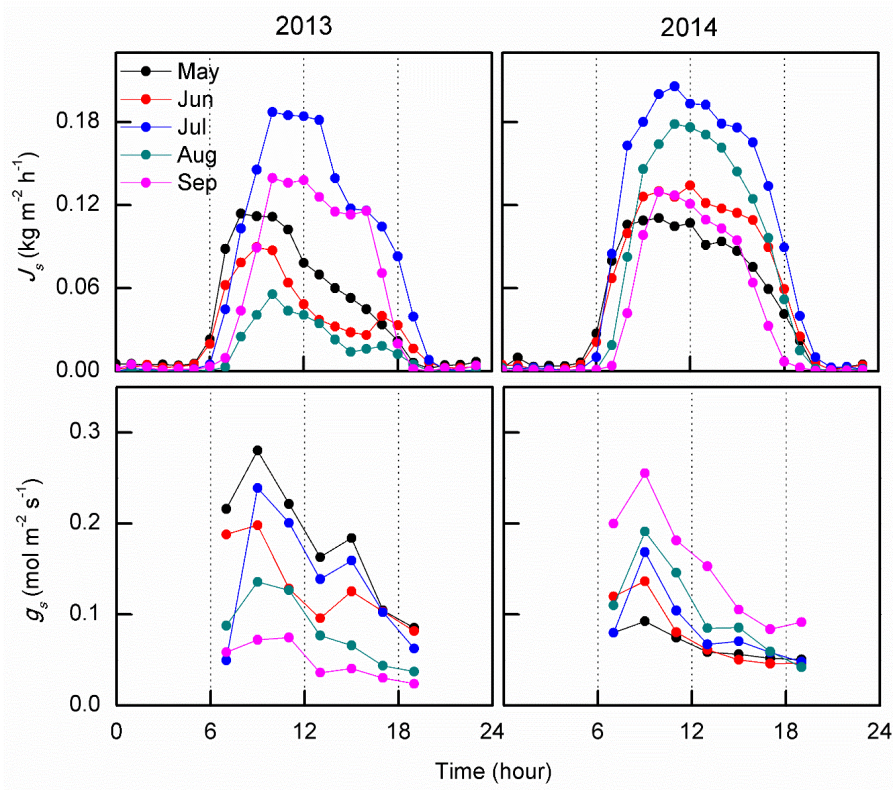
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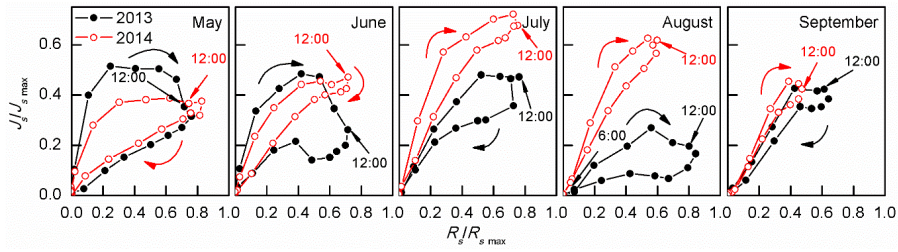
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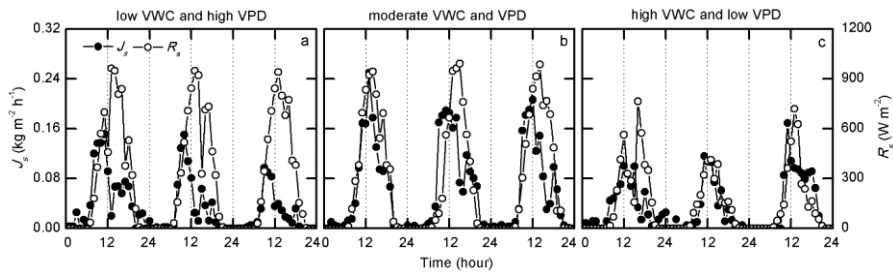
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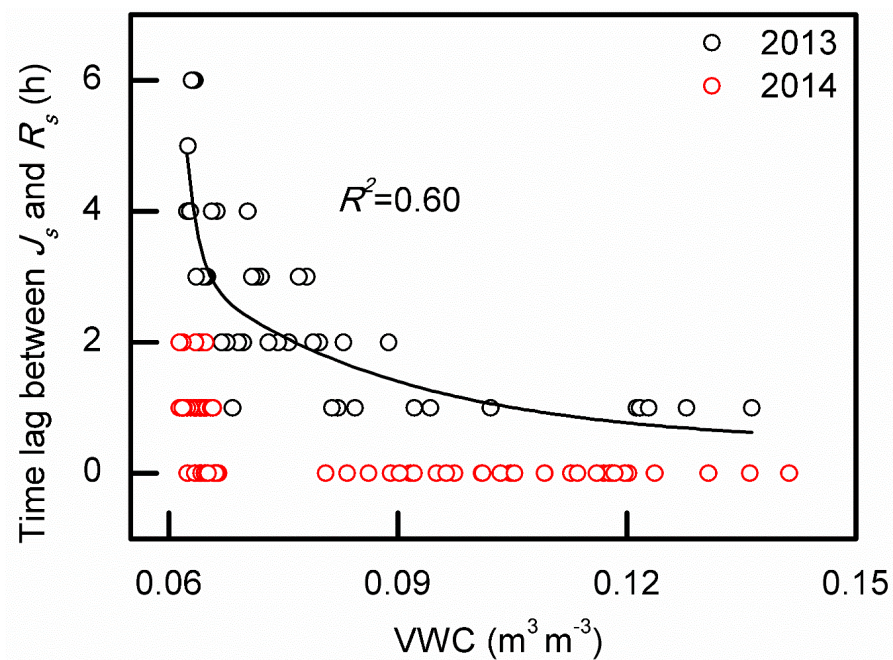


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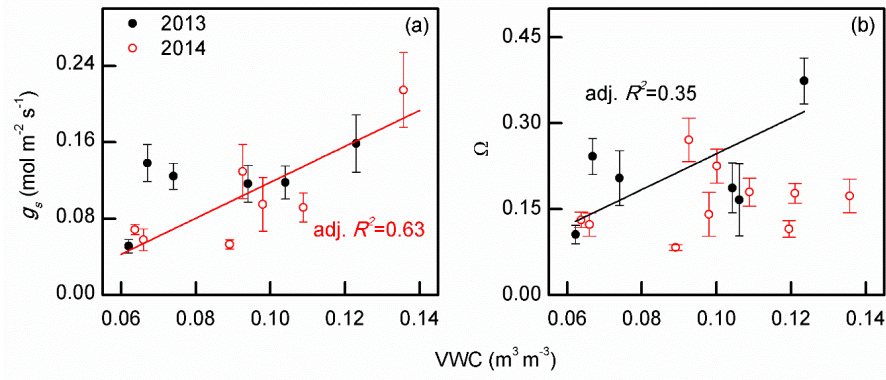
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1114 Bars indicate standard error. Only regressions with p -values < 0.05 are shown.

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Marked-up manuscript version

1117 **Soil moisture control on sap-flow response to biophysical factors in a desert-shrub**

1118 **species, *Artemisia ordosica***

1119 **Authors:** Tianshan Zha^{1,3*#}, Duo Qian^{2#}, Xin Jia^{1,3}, Yujie Bai¹, Yun Tian¹, Charles P.-A.

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1133 **Short title: Sap flow in *Artemisia ordosica***

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1138 **Author Contribution Statement:**

1139 Dr.'s Duo Qian and Tianshan Zha contributed equally to the design and implementation of
1140 the field experiment, data collection and analysis, and writing the first draft of the manuscript.

1141 Dr. Xin Jia gave helpful suggestions concerning the analysis of the field data and contributed
1142 to the scientific revision and editing of the manuscript.

1143 Prof. Bin Wu contributed to the design of the experiment.

1144 Dr.'s Charles P.-A. Bourque and Heli Peltola contributed to the scientific revision and editing
1145 of the manuscript.

1146 Yujie Bai, Wei Feng, and Yun Tian were involved in the implementation of the experiment
1147 and in the revision of the manuscript.

1148

1149 **Key Message:** This study provides a significant contribution to the understanding of
1150 acclimation processes in desert-shrub species to drought-associated stress in dryland
1151 ecosystems

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1153 **Conflict of Interest:**

1154 This research was financially supported by grants from the National Natural Science
1155 Foundation of China (NSFC No. 31670710), the National Basic Research Program of China
1156 (Grant No. 2013CB429901), and by the Academy of Finland (Project No. 14921). The
1157 project is related to the Finnish-Chinese collaborative research project, EXTREME (2013-
1158 2016), between Beijing Forestry University and the University of Eastern Finland, and
1159 USCCC. We appreciate Dr. Ben Wang, Sijing Li, Qiang Yang, and others for their help with
1160 the fieldwork. **The authors declare that they have no conflict of interest.**

1161

1162 **Abstract:** Current understanding of acclimation processes in desert-shrub species to drought
1163 stress in dryland ecosystems is still incomplete. In this study, we measured sap flow in
1164 *Artemisia ordosica* and associated environmental variables throughout the growing seasons
1165 of 2013-2014 (May-September period of each year) to better understand the environmental
1166 controls on the temporal dynamics of sap flow. We found that the occurrence of drought in
1167 the dry year of 2013 during the leaf-expansion and leaf-expanded periods caused sap flow
1168 per leaf area (J_s) to decline significantly, resulting in a sizable drop in transpiration. Sap flow
1169 per leaf area correlated positively with radiation (R_s), air temperature (T), and vapor pressure
1170 deficit (VPD), when volumetric soil water content (VWC) was $> 0.10 \text{ m}^3 \text{ m}^{-3}$. Diurnal J_s was
1171 generally ahead of R_s by as much as 6 hours. This lag time, however, decreased with
1172 increasing VWC. Relative response of J_s to the environmental variables (i.e., R_s , T , and VPD)
1173 varied with VWC, J_s being more biologically-controlled with a low decoupling coefficient
1174 and less sensitivity to the environmental variables during periods of dryness. According to
1175 this study, soil moisture is shown to control sap-flow (and, therefore, plant-transpiration)
1176 response in *Artemisia ordosica* to diurnal variations in biophysical factors. The findings of
1177 this study add to the knowledge of acclimation processes in desert-shrub species under
1178 drought-associated stress. This knowledge is essential to model desert-shrub-ecosystem
1179 functioning under changing climatic conditions.

1180 **Keywords:** sap flow; transpiration; cold-desert shrubs; environmental stress; volumetric soil
1181 water content

1182

1183

1184 **2. Introduction**

1185 Due to the low amount of precipitation and high potential evapotranspiration in desert
1186 ecosystems, low soil water availability limits both plant water- and gas-exchange and, as a
1187 consequence, limits vegetation productivity (Razzaghi et al., 2011). Therefore, it is important
1188 to understand the mechanisms controlling the vegetation-water dynamics under rapidly
1189 changing environments (Jacobsen et al., 2007). Grass species are gradually being replaced
1190 by shrub and semi-shrub species in arid and semi-arid areas of northwestern China (Yu et al.,
1191 2004). This progression is predicted to continue under a changing climate (Asner et al., 2003;
1192 Houghton et al., 1999; Pacala et al., 2001). This is mostly because desert shrubs are able to
1193 adapt to hot-dry environments by modifying their morphological characteristics, e.g., by (1)
1194 minimizing plant-surface area directly exposed to sun and hot air, (2) producing thick
1195 epidermal hairs, (3) thickening cuticle, (4) recessing stomata into leaves (Yang and Zhu,
1196 2011), and (5) increasing root-to-shoot ratios (Eberbach and Burrows, 2006; Forner et al.,
1197 2014). Also, acclimation of physiological characteristics of plants under water stress, by way
1198 of e.g., water potential, osmotic regulation, anti-oxidation, and photosynthetic characteristics,
1199 assist the plants to maintain a hydrological balance (Huang et al., 2011a). Changes in stomatal
1200 conductance and, thus, transpiration may likewise affect plant water use efficiency (Pacala
1201 et al., 2001; Vilagrosa et al., 2003).

1202 Sap flow can accurately reflect water consumption during plant transpiration. It
1203 maintains ecosystem balance through the soil-plant-atmosphere continuum, but is often
1204 affected by environment factors (Huang et al., 2010; Zhao et al., 2016). In recent studies, sap
1205 flow in *Tamarix elongate* has been observed to be controlled by solar radiation and air
1206 temperature, whereas in *Caragana korshinskii* vapor pressure deficit and solar radiation

1207 appear to be more important (Jacobsen et al., 2007; Xia et al., 2008). In *Elaeagnus*
1208 *angustifolia*, transpiration is observed to peak at noon, i.e., just before stomatal closure at
1209 mid-day under water-deficit conditions (Liu et al., 2011). In contrast, transpiration in
1210 *Hedysarum scoparium* peaks multiple times during the day (Xia et al., 2007). Sap flow has
1211 been observed to decrease rapidly when the volumetric soil water content (VWC) is lower
1212 than the water loss through evapotranspiration (Buzkova et al., 2015). In general, desert
1213 shrubs can close their stomata to reduce transpiration when exposed to dehydration stress
1214 around mid-day. However, differences exist among shrub species with respect to their
1215 stomatal response to changes in soil and air moisture deficits (Pacala et al., 2001). For some
1216 shrubs, sap-flow response to precipitation varies from an immediate decline after a heavy
1217 rainfall to no observable change after a small rainfall event (Asner et al., 2003; Zheng and
1218 Wang, 2014). Sap flow has been found to increase with increasing rainfall intensity (Jian et
1219 al., 2016). Drought-insensitive shrubs have relatively strong stomatal regulation and,
1220 therefore, tend to be insensitive to soil water deficits and rainfall unlike their drought-
1221 sensitive counterparts (Du et al., 2011). In general, understanding of the relationship between
1222 sap-flow rates in plants and environmental factors is highly inconsistent, varying with plant
1223 habitat (Liu et al., 2011).

1224 *Artemisia ordosica*, a shallow-rooted desert shrub, is the dominant plant species in the
1225 Mu Us Desert of northwestern China. The shrubs have an important role in combating
1226 desertification and in stabilizing sand dunes (Li et al., 2010). Increases in air temperature and
1227 precipitation variability and associated shorter wet periods and longer intervals of periodic
1228 drought are expected to ensue with projected climate change (Lioubimtseva and Henebry,

1229 2009). During dry periods of the year, sap flow in *Artemisia ordosica* has been observed to
1230 be controlled by VWC at about 30-cm depth in the soil (Li et al., 2014). Sap-flow rate is
1231 known to be affected by variation in precipitation patterns. Soil water content, in combination
1232 with other environmental factors, may have a significant influence on sap-flow rate (Li et al.,
1233 2014; Zheng and Wang, 2014). Thus, understanding the controlling mechanisms of sap flow
1234 in desert shrubs as a function of variations in biotic and abiotic factors is greatly needed (Gao
1235 et al., 2013; Xu et al., 2007).

1236 In this study, we measured stem sap flow in *Artemisia ordosica* and associated
1237 environmental variables throughout the growing seasons of 2013-2014 (May-September
1238 period of each year) to better understand the environmental controls on the temporal
1239 dynamics of sap flow. We believe that our findings will provide further understanding of
1240 acclimation processes in desert-shrub species under stress of dehydration.

1241

1242 **2. Materials and Methods**

1243 **2.1 Experimental site**

1244 Continuous sap-flow measurements were made at the Yanchi Research Station (37°42'
1245 31" N, 107°13' 47" E, 1530 m above mean sea level), Ningxia, northwestern China. The
1246 research station is located between the arid and semi-arid climatic zones along the southern
1247 edge of the Mu Us Desert. The sandy soil in the upper 10 cm of the soil profile has a bulk
1248 density of $1.54 \pm 0.08 \text{ g cm}^{-3}$ (mean \pm standard deviation, n=16). Mean annual precipitation
1249 in the region is about 287 mm, of which 62% falls between July and September. Mean annual
1250 potential evapotranspiration and air temperature are about 2,024 mm and 8.1°C based on

1251 meteorological data (1954-2004) from the Yanchi County weather station. Normally, shrub
1252 leaf-expansion, leaf-expanded, and leaf-coloration stages begin in April, June, and
1253 September (Chen et al., 2015), respectively.

1254

1255 **2.2 Measurements of sap flow, leaf area and stomatal conductance**

1256 The experimental plot (10 m × 10 m) was located on the western side of Yanchi Research
1257 Station in an *Artemisia ordosica*-dominated area. Mean age of the *Artemisia ordosica* was
1258 10-years old. Maximum monthly mean leaf area index (LAI) for plant specimens with full
1259 leaf expansion was about 0.1 m² m⁻² (Table 1). Over 60% of their roots were
1260 distributed in soil depths of 0-60 cm (Zhao et al., 2010; Jia et al., 2016). Five stems of
1261 *Artemisia ordosica* were randomly selected within the plot as replicates for sap-flow
1262 measurement. Mean height and sapwood area of sampled shrubs were 84 cm and 0.17 cm²,
1263 respectively. Sampled stems represented the average size of stems in the plot. A heat balance
1264 sensor (Flow32-1K, Dynamax Inc., Houston, USA) was installed at about 15 cm above the
1265 ground surface on each of the five stems (Dynamax, 2005). Sap-flow measurements were
1266 taken once per minute for each stem. Half-hourly data were recorded by a Campbell CR1000
1267 data logger from May 1 to September 30, 2013-2014 (Campbell Scientific, Logan, UT, USA).

1268 Leaf area was estimated for each stem every 7-10 days by sampling about 50-70 leaves
1269 from five randomly sampled neighbouring shrubs with similar characteristics to the shrubs
1270 used for sap-flow measurements. Leaf area was measured immediately at the station
1271 laboratory with a portable leaf-area meter (LI-3000, Li-Cor, Lincoln, NE, USA). Leaf area
1272 index (LAI) was measured at roughly weekly intervals on a 4×4 grid of 16 quadrats (10 m

1273 $\times 10$ m each) within a 100 m \times 100 m plot centered on the flux tower using measurements of
1274 sampled leaves and allometric equations (Jia et al., 2014). Stomatal conductance (g_s) was
1275 measured *in situ* for three to four leaves on each of the sampled shrubs with a LI-6400
1276 portable photosynthesis analyzer (Li-Cor Inc., Lincoln, USA). The g_s measurements were
1277 made every two hours from 7:00 to 19:00 h every ten days from May to September, 2013-
1278 2014.

1279 The degree of coupling between the ecosystem surface and the atmospheric boundary
1280 layer was estimated with the decoupling coefficient (Ω). The decoupling coefficient varies
1281 from 0 (i.e., leaf transpiration is mostly controlled by g_s) to 1 (i.e., leaf transpiration is mostly
1282 controlled by radiation). The Ω was calculated as described by Jarvis and McNaughton
1283 (1986):

$$1284 \quad \Omega = \frac{\Delta + \gamma}{\Delta + \gamma \left(1 + \frac{g_a}{g_s} \right)}, \quad (1)$$

1285 where Δ is the rate of change of saturation vapor pressure vs. temperature (kPa K⁻¹), γ is the
1286 psychrometric constant (kPa K⁻¹), and g_a is the aerodynamic conductance (m s⁻¹; Monteith
1287 and Unsworth, 1990):

$$1288 \quad g_a = \left(\frac{u}{u_*^2} + 6.2u_*^{-0.67} \right)^{-1}, \quad (2)$$

1289 where u is the wind speed (m s⁻¹) at 6 m above the ground, and u_* is the friction velocity (m
1290 s⁻¹).

1291

1292 **2.3 Environmental measurements**

1293 Shortwave radiation (R_s in W m⁻²; CMP3, Kipp & Zonen, Netherland), air temperature (T in

1294 °C), wind speed (u in m s^{-1} , 034B, Met One Instruments Inc., USA), and relative humidity
1295 (RH in %; HMP155A, Väisälä, Finland) were measured simultaneously near the sap-flow
1296 measurement plot. Half-hourly data were recorded by data logger (CR3000 data logger,
1297 Campbell Scientific Inc., USA). VWC at 30-cm depths were monitored with three ECH₂O-
1298 5TE soil moisture probes (Decagon Devices, USA). In the analysis, we used half-hourly
1299 averages of VWC from the three soil moisture probes. Vapor pressure deficit (VPD in kPa)
1300 was calculated from recorded RH and T .

1301

1302 2.4 Data analysis

1303 In our analysis, March-May represented spring, June-August summer, and September-
1304 November autumn (Chen et al., 2015). Drought days were defined as those days with daily
1305 mean VWC $< 0.1 \text{ m}^3 \text{ m}^{-3}$. This is based on a VWC threshold of $0.1 \text{ m}^3 \text{ m}^{-3}$ for J_s (Fig. 1),
1306 with J_s increasing as VWC increased, saturating at VWC of $0.1 \text{ m}^3 \text{ m}^{-3}$, and decreasing as
1307 VWC continued to increase. The VWC threshold of $0.1 \text{ m}^3 \text{ m}^{-3}$ is equivalent to a relative
1308 extractable soil water (REW) of 0.4 for drought conditions (Granier et al., 1999 and 2007;
1309 Zeppel et al., 2004 and 2008; Fig. 2d, e). Duration and severity of ‘drought’ were defined
1310 based on a VWC threshold and REW of 0.4. REW was calculated as according to equation
1311 (3):

$$1312 \quad REW = \frac{VWC - VWC_{\min}}{VWC_{\max} - VWC_{\min}} \quad (3)$$

1313 where VWC is the specific daily soil water content ($\text{m}^3 \text{ m}^{-3}$), VWC_{\min} and VWC_{\max} are the
1314 minimum and maximum VWC during the measurement period in each year, respectively.

1315 Sap-flow analysis was conducted using mean data from five sensors. Sap flow per leaf

1316 area (J_s) was used in this study, i.e.,

$$1317 \quad J_s = \left(\sum_{i=1}^n E_i / A_{li} \right) / n \quad (4)$$

1318 where, J_s is the sap flow per leaf area ($\text{kg m}^{-2} \text{h}^{-1}$) or ($\text{kg m}^{-2} \text{d}^{-1}$), E is the measured sap flow
1319 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
1320 ($n = 5$).

1321 Transpiration per ground area (T_r) was estimated in this study according to:

$$1322 \quad T_r = \left(\sum_{i=1}^n J_s \times LAI \right) / n \quad (5)$$

1323 where, T_r is transpiration per ground area (mm d^{-1}), and LAI is the leaf area index (m^2
1324 m^{-2}).

1325 Linear and non-linear regression were used to analyze abiotic control on sap-flow rate.

1326 In order to minimize the effects of different phenophases and rainfall, we used data only from

1327 mid-growing season, non-rainy days, and daytime measurements (8:00-20:00), i.e., from

1328 June 1 to August 31, with hourly shortwave radiation $> 10 \text{ W m}^{-2}$. Relations between mean

1329 sap-flow rates at specific times over a period of 8:00-20:00 and corresponding environmental

1330 factors from June 1 to August 31 were derived with linear regression ($p < 0.05$; Fig. 3).

1331 Regression slopes were used as indicators of sap-flow sensitivity (degree of response) to the

1332 various environmental variables (see e.g., Zha et al., 2013). All statistical analyses were

1333 performed with SPSS v. 17.0 for Windows software (SPSS Inc., USA). Significance level

1334 was set at 0.05.

1335

1336 3. Results

1337 3.1 Seasonal variations in environmental factors and sap flow

1338 Range of daily means (24-hour mean) for R_s , T , VPD, and VWC during the 2013 growing
1339 season (May-September) were 31.1-364.9 $W m^{-2}$, 8.8-24.4°C, 0.05-2.3 kPa, and 0.06-0.17
1340 $m^3 m^{-3}$ (Fig. 2a, b, c, d), respectively, annual means being 224.8 $W m^{-2}$, 17.7°C, 1.03 kPa,
1341 and 0.08 $m^3 m^{-3}$. Corresponding range of daily means for 2014 were 31.0-369.9 $W m^{-2}$, 7.1-
1342 25.8°C, 0.08-2.5 kPa, and 0.06-0.16 $m^3 m^{-3}$ (Fig. 2a, b, c, d), respectively, annual means being
1343 234.9 $W m^{-2}$, 17.2°C, 1.05 kPa, and 0.09 $m^3 m^{-3}$.

1344 Total precipitation and number of rainfall events during the 2013 measurement period
1345 (257.2 mm and 46 days) were about 5.6% and 9.8% lower than those during 2014 (272.4 mm
1346 and 51 days; Fig. 2d), respectively. In 2013, more irregular rainfall events occurred than in
1347 2014, with 45.2% of rainfall falling in July and 8.8% in August.

1348 Drought mainly occurred in May, June, and August of 2013 and in May and June of
1349 2014 (Fig. 2d,e). Both years had dry springs. Over one-month period of summer drought
1350 occurred in 2013.

1351 Range of daily J_s during the growing season was 0.01-4.36 $kg m^{-2} d^{-1}$ in 2013 and 0.01-
1352 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 $kg m^{-2}$
1353 d^{-1} in 2014. Mean daily J_s over the growing season of 2013 was 32% lower than that of
1354 2014. Mean daily T_r were 0.05 $mm d^{-1}$ and 0.07 $mm d^{-1}$ over the growing season in 2013 and
1355 2014 (Fig. 2f), respectively, being 34% lower in 2013 than in 2014. The total T_r over growing
1356 season (May 1-September 30) in 2013 and 2014 were 7.3 mm and 10.9 mm, respectively.

1357 Seasonal fluctuations in J_s and T_r corresponded with the seasonal pattern in VWC (Fig. 2d,
1358 f). Daily mean J_s and T_r decreased or remained nearly constant during dry-soil periods (Fig.
1359 2d, f), with the lowest J_s and T_r observed in spring and mid-summer (August) of 2013.

1360

1361 **3.2 Sap flow response to environmental factors**

1362 In summer, J_s increased with increasing VWC (Fig. 2d, f; Fig. 3d). Soil water was shown to
1363 modify the response of J_s to environmental factors (Fig. 4). Sap flow increased more rapidly
1364 with increases in R_s , T , and VPD under high VWC (i.e., $VWC > 0.1 \text{ m}^3 \text{ m}^{-3}$ in both 2013 and
1365 2014) compared with periods with lower VWC (i.e., $VWC < 0.1 \text{ m}^3 \text{ m}^{-3}$ in both 2013 and
1366 2014). Sap flow J_s was more sensitive to R_s , T , and VPD under high VWC (Fig. 4), which
1367 coincided with a larger regression slope under high VWC conditions.

1368 Sensitivity of J_s to environmental variables (in particular, R_s , T , VPD, and VWC) varied
1369 depending on the time of a day (Fig. 5). Regression slopes for the relations of J_s - R_s , J_s - T , and
1370 J_s -VPD were greater in the morning before 11:00 h, and lower during mid-day and early
1371 afternoon (12:00-16:00 h). In contrast, regression slopes of the relation of J_s -VWC were
1372 lower in the morning (Fig. 5), increasing thereafter, peaking at ~13:00 h, and subsequently
1373 decreasing in late afternoon. Regression slopes of the response of J_s to R_s , T , and VPD in
1374 2014 were greater than those in 2013.

1375 **3.3 Diurnal changes and hysteresis between sap flow and environmental factors**

1376 Diurnal patterns of J_s were similar in both years (Fig. 6), initiating at 7:00 h and increasing
1377 thereafter, peaking before noon (12:00 h), and subsequently decreasing thereafter and
1378 remaining near zero from 20:00 to 6:00 h. Diurnal changes in g_s were similar to J_s , but
1379 peaking about 2 and 1 h earlier than J_s in July and August, respectively (Fig. 6).

1380 There were pronounced time lags between J_s and R_s over the two years (Fig. 7), J_s
1381 peaking earlier than R_s and, thus, earlier than either VPD or T . These time lags differed
1382 seasonally. For example, mean time lag between J_s and R_s was 2 h during July, 5 h during

1383 May, and 3 h during June, August, and September of 2013. However, the time lags in 2014
1384 were generally shorter than those observed in 2013 (Table 2).

1385 Use of normalized variables may remove the influence of J_s and R_s from the data. As a
1386 result, clockwise hysteresis loops between J_s and R_s during the growing period were observed
1387 (Fig. 7). As R_s increased in the morning, J_s increased until it peaked at ~10:00 h. Sap-flow
1388 rate declined with decreasing R_s during the afternoon. Sap flow J_s was higher in the morning
1389 than in the afternoon, forming a clockwise hysteresis loop.

1390 Diurnal time lag in the relation of J_s - R_s were influenced by VWC (Fig. 8, 9). For
1391 example, J_s peaked about 2 h earlier than R_s on days with low VWC (Fig. 8a), 1 h earlier than
1392 R_s on days with moderate VWC (Fig. 8b), and at the same time as R_s on days with high VWC
1393 (Fig. 8c). Lag hours between J_s and R_s over the growing season were negatively and linearly
1394 related to VWC (Fig. 9: Lag (h) = -133.5×VWC+12.24, $R^2=0.41$). Effect of VWC on time
1395 lags between J_s and R_s was smaller in 2014, with evenly distributed rainfall during the
1396 growing season, than in 2013, with a pronounced summer drought (Fig. 9). State variables g_s
1397 and Q showed a significantly increasing trend with increasing VWC in 2013 and 2014,
1398 respectively (Fig. 10).

1399

1400 4. Discussion and conclusions

1401 4.1 Sap flow response to environmental factors

1402 Drought tolerance of some plants may be related to lower overall sensitivity of plant
1403 physiological attributes to environmental stress and/or stomatal regulation (Huang et al.,
1404 2011b; Naithani et al., 2012). In this study, large regression slopes between J_s and the

1405 environmental variables (R_s , VPD, and T) in the morning indicated that sap flow was more
1406 sensitive to variations in R_s , VPD, and T during the less dry and hot period of the day (Fig.
1407 5). Stomatal conductances were the largest in the morning (Fig. 6), which led to increases in
1408 water fluxes to the atmosphere as a result of increased R_s , T , and VPD. When R_s peaked
1409 during mid-day (13:00-14:00 h), there was often insufficient soil water to meet the
1410 atmospheric demand for water, causing g_s to be limited by available soil moisture and making
1411 J_s more responsive to VWC at noon, but less responsive to R_s and T . Similarly, *Hedysarum*
1412 *mongolicum* in a nearby region positively correlated with VWC at noon (Qian et al., 2015),
1413 and the evapotranspiration of a Scots pine stand showed higher sensitivity to surface
1414 conductance, temperature, vapor pressure deficit, and radiation in the morning than in the
1415 afternoon (Zha et al., 2013).

1416 Synergistic interactions among environmental factors influencing sap flow are complex.
1417 In general, VWC has an influence on physiological processes of plants in water-limited
1418 ecosystems (Lei et al., 2010; She et al., 2013). Our finding regarding lower sensitivity in J_s
1419 to environmental factors (R_s , T and VPD) during dry periods was consistent with an earlier
1420 study of boreal grasslands (Zha et al., 2010). Also our finding that VWC is the most important
1421 factor modifying responses in sap flow in *Artemisia ordosica* to other environmental factors,
1422 is in contrast to other shrub species. For example, it has been found that sap flow in *Haloxylon*
1423 *ammodendron* in northwest China, where annual precipitation is 37.9 mm and mean annual
1424 temperature is 8.2 °C, was mainly controlled by T (Zhang et al., 2003), while sap flow in
1425 *Cyclobalanopsis glauca* in south China, where annual precipitation is 1900 mm and mean
1426 annual temperature is 19.3 °C, was controlled by R_s and T , when VWC was not limiting

1427 (Huang et al., 2009).

1428 Precipitation, being the main source of VWC at our site, affected transpiration directly.
1429 In this sense, frequent small rainfall events (< 5 mm) were important to the survival and
1430 growth of the desert plants (Sala and Lauenroth, 1982; Zhao and Liu, 2010). Variations in J_s
1431 were clearly associated with the intermittent supply of water to the soil during rainfall events,
1432 as indicated at our site (Fig. 2d, f). Reduced J_s during rainy days can be explained by a
1433 reduction in incident R_s and water-induced saturation on the leaf surface, which led to a
1434 decrease in leaf turgor and stomatal closure. After each rainfall event, J_s increased quickly
1435 when soil water was replenished. Schwinning and Sala (2004) showed previously for similar
1436 research sites that VWC contributed the most to the response in plant transpiration to post-
1437 rainfall events. We showed in this study that *Artemisia ordosica* responded in a different way
1438 to wet and dry conditions. In the mid-growing season, high J_s in July were related to rainfall-
1439 fed VWC, which increased the rate of transpiration. However, dry soil conditions combined
1440 with high T and R_s , led to a reduction in J_s in August of 2013 (Fig. 2). In some desert shrubs,
1441 groundwater may replenish water lost by transpiration by having deep roots (Yin et al., 2014).
1442 *Artemisia ordosica* roots are generally distributed in the upper 60 cm of the soil (Zhao et al.,
1443 2010; Wang et al., 2016), and as a result the plant usually depends on water directly supplied
1444 by precipitation because groundwater levels in drylands can be well below the rooting zone,
1445 typically, at depths ≥ 10 m at our site.

1446

1447 **4.2 Hysteresis between sap flow and environmental factors**

1448 Diurnal patterns in J_s corresponded with those of R_s from sunrise until diverging later in the

1449 day (Fig. 7), suggesting that R_s was a primary controlling factor of diurnal variation in J_s .
1450 According to O'Brien et al. (2004), diurnal variation in R_s could cause change in the diurnal
1451 variation in the consumption of water. As an initial energy source, R_s can force T and VPD
1452 to increase, causing a phase difference in time lags among the relations J_s - R_s , J_s - T , and J_s -
1453 VPD.

1454 We found a consistent clockwise hysteresis loop between J_s and R_s over a diurnal cycle
1455 (Fig. 7), indicating that R_s lagged J_s , and the response of J_s to R_s varied both diurnally and
1456 seasonally. A large g_s in the morning promoted higher rates of transpiration (Fig. 6). In dry
1457 and hot conditions, g_s decreased, causing the control of the stomata on J_s to increase relative
1458 to changes in environmental factors. Diurnal trends in J_s and g_s occurred together, both
1459 peaking earlier than R_s . The g_s peaked 3-4 h earlier than R_s , leading to a reduction in J_s and
1460 an increase in R_s and a clockwise hysteresis loop. Contrary to our findings, counterclockwise
1461 hysteresis has been observed to occur between transpiration (J_s) and R_s in tropical and
1462 temperate forests (Meinzer et al., 1997; O'Brien et al., 2004; Zeppel et al., 2004). A possible
1463 reason for this difference may be due to differences in VWC associated with the different
1464 regions. According to Zheng and Wang (2014) favorable water conditions after rainfall could
1465 render clockwise hysteresis loops between J_s and R_s under dry conditions to counterclockwise
1466 loops. In this study, due to a large incidence of small rainfall events, soil water supply by
1467 rainfall pulses could not meet the transpiration demand under high mid-day R_s , resulting in
1468 clockwise loops even though rainfall had occurred.

1469 In semi-arid regions, low VWC restricts plant transpiration more than VPD. Water
1470 vapor deficits tend to restrict transpiration in forest species in wet regions to a greater extent.

1471 According to Zheng et al. (2014), high water availability in alpine shrubland meadows may
1472 contribute to weakened hysteresis between evapotranspiration and the environmental
1473 variables. Our results showed that hysteresis between J_s and R_s decreased as VWC increased
1474 (Fig. 8, 9). The result that g_s increased with increasing VWC (Fig. 10a), along with the
1475 synchronization of J_s and g_s , suggests that J_s is less sensitive to g_s in high VWC and more so
1476 to R_s . Temporal patterns in J_s became more consistent with those in R_s as VWC increased,
1477 leading to a weakened hysteresis between the two variables. This is further supported by a
1478 large decoupling coefficient, when VWC is high (Fig. 10b). The larger the decoupling
1479 coefficient is, the greater is the influence of R_s on J_s . The effect of VWC on time lag varied
1480 between 2013 and 2014.

1481 **4.3. Conclusions**

1482 Drought during the leaf-expansion and leaf-expanded periods led to a greater decline in J_s ,
1483 causing J_s to be lower in 2013 than in 2014. The relative influence of R_s , T , and VPD on J_s in
1484 *Artemisia ordosica* was modified by soil water content, indicating J_s 's lower sensitivity to
1485 environmental variables (R_s , T and VPD) during dry periods. Sap flow J_s was constrained by
1486 soil water deficiency, causing J_s to peak several hours prior to R_s . Diurnal hysteresis between
1487 J_s and R_s varied seasonally, because of the control by stomatal conductance under low VWC
1488 and R_s under high VWC. According to this study, soil moisture controlled sap-flow response
1489 in *Artemisia ordosica*. This species is capable to tolerate and adapt to soil water deficiencies
1490 and drought conditions during the growing season. Altogether, our findings add to our
1491 understanding of acclimation in desert-shrub species under stress of dehydration. The
1492 knowledge gain can assist in modeling desert-shrub-ecosystem functioning under changing

1493 climatic conditions.

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1646 **Table 1** Seasonal changes in monthly transpiration (T_r), leaf area index (LAI), and stomatal
1647 conductance (g_s) of *Artemisia ordosica* from 2013 to 2014.
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	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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1651 **Table 2** Mean monthly diurnal cycles of sap-flow rate (J_s) response to shortwave radiation
 1652 (R_s), air temperature (T), and vapor pressure deficit (VPD), including time lags (h) in J_s as a
 1653 function of R_s , T , and VPD.

1654

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

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1658 **Figure captions:**

1659 **Fig. 1** Sap-flow rate per leaf area (J_s) as a function of soil water content (VWC) at 30 cm
1660 depth in non-rainy, daytime hours during the mid-growing period from June 1-August 31
1661 over 2013-2014. Data points are binned values from pooled data over two years at a VWC
1662 increment of $0.003 \text{ m}^3 \text{ m}^{-3}$. Dotted line represents the VWC threshold for J_s .

1663 **Fig. 2** Seasonal changes in daily (24-hour) mean shortwave radiation (R_s ; a), air temperature
1664 (T ; b), vapor pressure deficit (VPD; c), volumetric soil water content (VWC; d), relative
1665 extractable water (REW; e), daily total precipitation (PPT; f), and daily sap-flow per leaf
1666 area (J_s ; g), and daily transpiration (T_r , mm d^{-1} ; h) from May to September for both 2013 and
1667 2014. Horizontal dash lines (d, e) represent VWC and REW threshold of $0.1 \text{ m}^3 \text{ m}^{-3}$ and 0.4 ,
1668 respectively. Shaded bands indicate periods of drought.

1669 **Fig. 3** Relationships between sap-flow rate per leaf area (J_s) and environmental factors
1670 [shortwave radiation (R_s), air temperature (T), vapor pressure deficit (VPD), and soil water
1671 content at 30-cm depth (VWC)] in non-rainy days between 8:00-20:00 h during the mid-
1672 growing season of June 1-August 31 for 2013 and 2014. Data points are binned values from
1673 pooled data over two years at increments of 40 W m^{-2} , $1.2 \text{ }^\circ\text{C}$, 0.3 kPa , and $0.005 \text{ m}^3 \text{ m}^{-3}$ for
1674 R_s , T , VPD and VWC, respectively.

1675 **Fig. 4** Sap-flow rate per leaf area (J_s) in non-rainy, daytime hours during the mid-growing
1676 season of June 1-August 31 for both 2013 and 2014 as a function of shortwave radiation (R_s),
1677 air temperature (T), vapor pressure deficit (VPD) under high volumetric soil water content
1678 ($\text{VWC} > 0.10 \text{ m}^3 \text{ m}^{-3}$ both in 2013 and 2014) and low VWC ($< 0.10 \text{ m}^3 \text{ m}^{-3}$, 2013 and 2014).
1679 J_s is given as binned averages according to R_s , T , and VPD, based on increments of 100 W

1680 m^{-2} , 1°C , and 0.2 kPa , respectively. Bars indicate standard error.

1681 **Fig. 5** Regression slopes of linear fits between sap-flow rate per leaf area (J_s) in non-rainy
1682 days and shortwave radiation (R_s), vapor pressure deficit (VPD), air temperature (T), and
1683 volumetric soil water content (VWC) between 8:00-20:00 h during the mid-growing season
1684 of June 1-August 31 for 2013 and 2014.

1685 **Fig. 6** Mean monthly diurnal changes in sap-flow rate per leaf area (J_s) and stomatal
1686 conductance (g_s) in *Artemisia ordosica* during the growing season (May-September) for both
1687 2013 and 2014. Each point is given as the mean at specific times during each month.

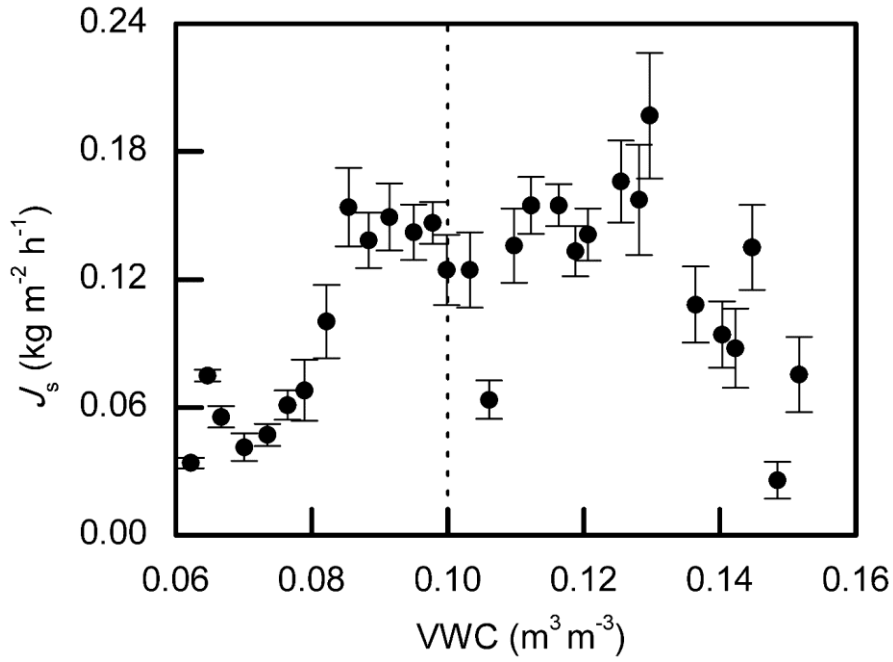
1688 **Fig. 7** Seasonal variation in hysteresis loops between sap-flow rate per leaf area (J_s) and
1689 shortwave radiation (R_s) using normalized plots for both 2013 and 2014. The y-axis
1690 represents the proportion of maximum J_s (dimensionless), and the x-axis represents the
1691 proportion of maximum R_s (dimensionless). The curved arrows indicate the clockwise
1692 direction of response during the day.

1693 **Fig. 8** Sap-flow rate per leaf area (J_s) and shortwave radiation (R_s) over consecutive three
1694 days in 2013, i.e., (a) under low volumetric soil water content (VWC) and high vapor pressure
1695 deficit (VPD; DOY 153-155, $\text{VWC}=0.064 \text{ m}^3 \text{ m}^{-3}$, $\text{REW}=0.025$, $\text{VPD}=2.11 \text{ kPa}$), (b)
1696 moderate VWC and VPD (DOY 212-214, $\text{VWC}=0.092 \text{ m}^3 \text{ m}^{-3}$, $\text{REW}=0.292$, $\text{VPD}=1.72$
1697 kPa), and (c) high VWC and low VPD (DOY 192-194, $\text{VWC}=0.152 \text{ m}^3 \text{ m}^{-3}$, $\text{REW}=0.865$,
1698 $\text{VPD}=0.46 \text{ kPa}$). REW is the relative extractable soil water. VWC, REW, and VPD are the
1699 mean value of the three days.

1700 **Fig. 9** Time lag between sap-flow rate per leaf area (J_s) and short wave radiation (R_s) in
1701 relation to volumetric soil water content (VWC). Hourly data in non-rainy days during the

1702 mid-growing season of June 1-August 31 for 2013 and 2014. The lag hours were calculated
1703 by a cross-correlation analysis using a three-day moving window with a one-day time step.
1704 Rainy days were excluded. The solid line is based on exponential regression ($p < 0.05$).
1705 **Fig. 10** Relationship between volumetric soil water content (VWC) and (a) stomatal
1706 conductance (g_s) in *Artemisia ordosica*, and (b) decoupling coefficient (Ω) for 2013 and 2014.
1707 Hourly values are given as binned averages based on a VWC-increment of $0.005 \text{ m}^3 \text{ m}^{-3}$.
1708 Bars indicate standard error. Only regressions with p -values < 0.05 are shown.
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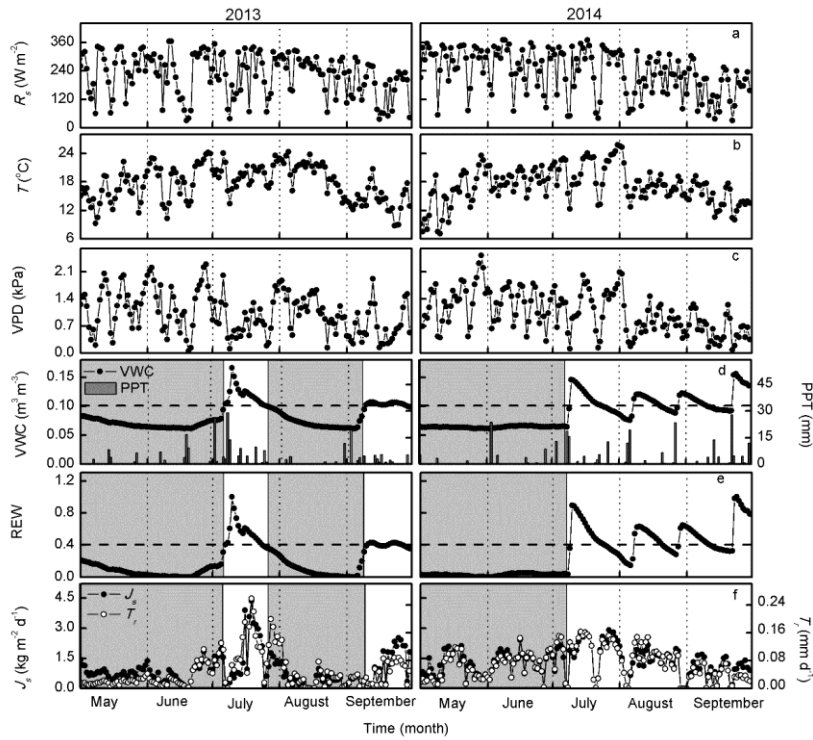


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1712 **Fig. 1** Sap-flow rate per leaf area (J_s) as a function of soil water content (VWC) at 30 cm
1713 depth in non-rainy, daytime hours during the mid-growing period from June 1-August 31
1714 over 2013-2014. Data points are binned values from pooled data over two years at a VWC
1715 increment of $0.003 \text{ m}^3 \text{m}^{-3}$. Dotted line represents the VWC threshold for J_s .

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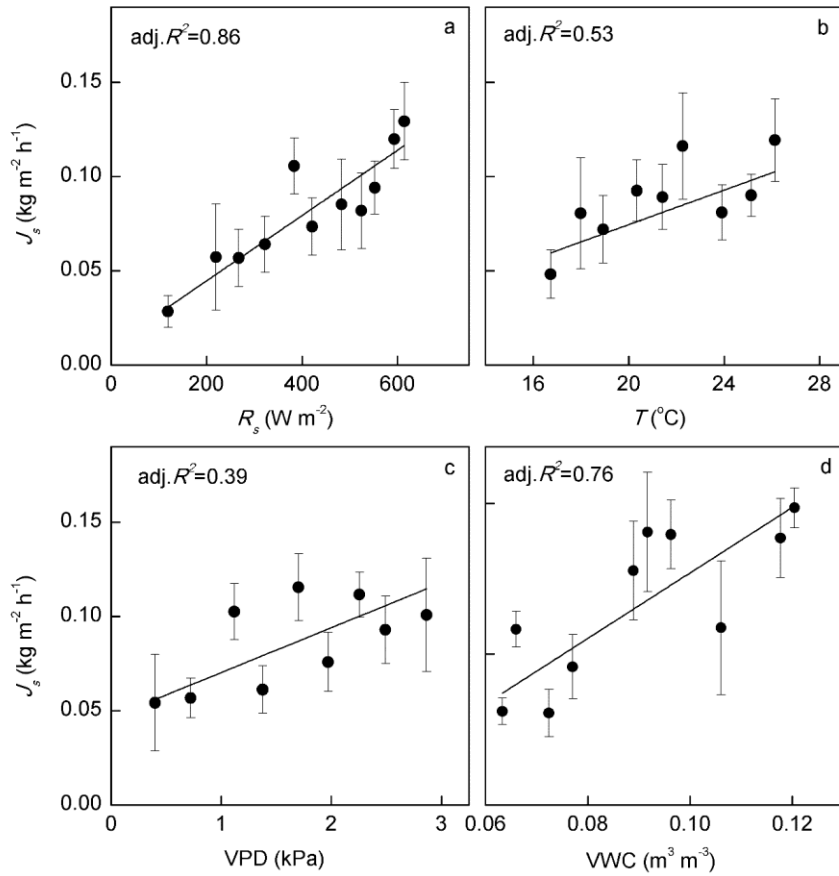


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1721 **Fig. 2** Seasonal changes in daily (24-hour) mean shortwave radiation (R_s ; a), air temperature
 1722 (T ; b), vapor pressure deficit (VPD; c), volumetric soil water content (VWC; d), relative
 1723 extractable water (REW; e), daily total precipitation (PPT; d), and daily sap-flow per leaf
 1724 area (J_s ; f), and daily transpiration (T_r , mm d^{-1} ; f) from May to September for both 2013 and
 1725 2014. Horizontal dash lines (d, e) represent VWC and REW threshold of $0.1 \text{ m}^3 \text{ m}^{-3}$ and 0.4 ,
 1726 respectively. Shaded bands indicate periods of drought.

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1730 **Fig. 3** Relationships between sap-flow rate per leaf area (J_s) and environmental factors

1731 [shortwave radiation (R_s), air temperature (T), vapor pressure deficit (VPD), and soil water

1732 content at 30-cm depth (VWC)] in non-rainy days between 8:00-20:00 h during the mid-

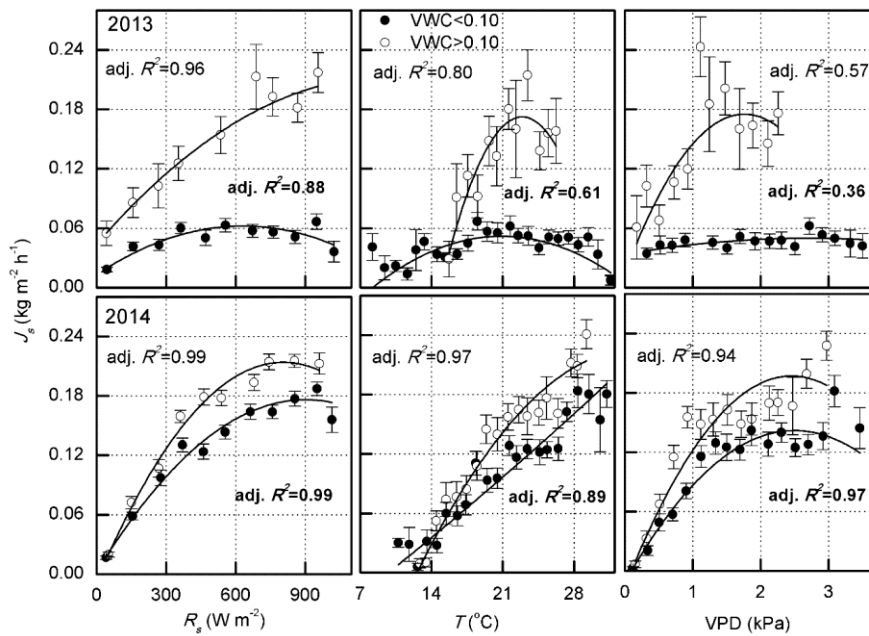
1733 growing season of June 1-August 31 for 2013 and 2014. Data points are binned values from

1734 pooled data over two years at increments of 40 W m^{-2} , $1.2 \text{ }^\circ\text{C}$, 0.3 kPa , and $0.005 \text{ m}^3 \text{ m}^{-3}$ for

1735 R_s , T , VPD and VWC, respectively.

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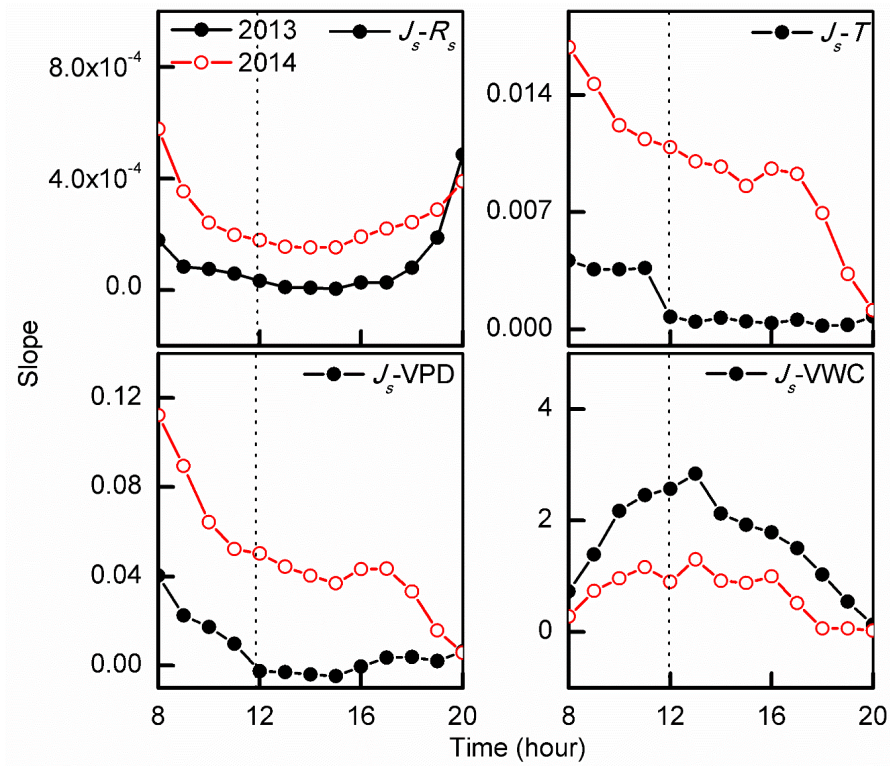
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1740 **Fig. 4** Sap-flow rate per leaf area (J_s) in non-rainy, daytime hours during the mid-growing
 1741 season of June 1-August 31 for both 2013 and 2014 as a function of shortwave radiation (R_s),
 1742 air temperature (T), vapor pressure deficit (VPD) under high volumetric soil water content
 1743 ($\text{VWC} > 0.10 \text{ m}^3 \text{ m}^{-3}$ both in 2013 and 2014) and low VWC ($< 0.10 \text{ m}^3 \text{ m}^{-3}$, 2013 and 2014).

1744 J_s is given as binned averages according to R_s , T , and VPD, based on increments of 100 W

1745 m^{-2} , 1°C , and 0.2 kPa, respectively. Bars indicate standard error.

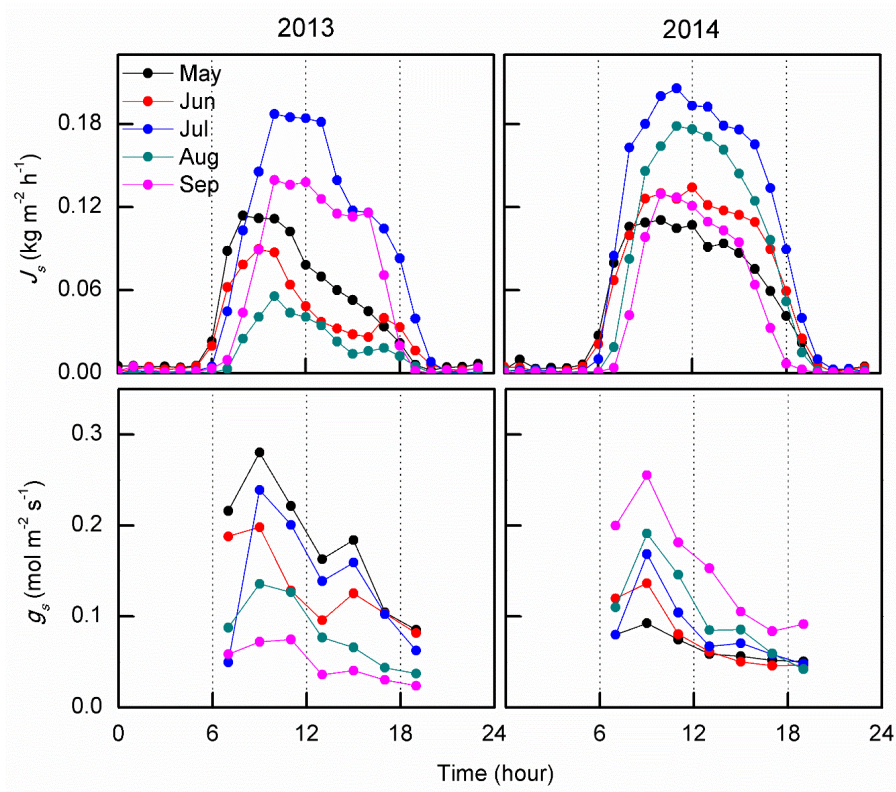
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1749 **Fig. 5** Regression slopes of linear fits between sap-flow rate per leaf area (J_s) in non-rainy
 1750 days and shortwave radiation (R_s), vapor pressure deficit (VPD), air temperature (T), and
 1751 volumetric soil water content (VWC) between 8:00-20:00 h during the mid-growing season
 1752 of June 1-August 31 for 2013 and 2014.

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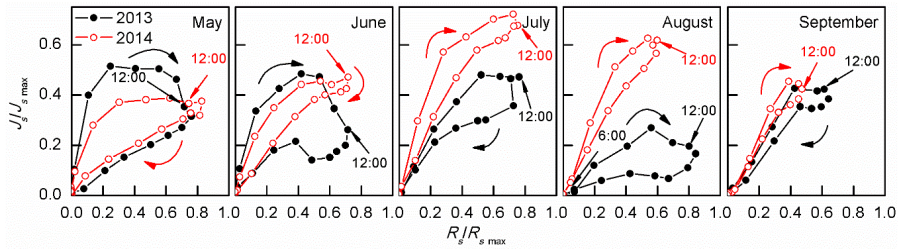
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1757 **Fig. 6** Mean monthly diurnal changes in sap-flow rate per leaf area (J_s) and stomatal
 1758 conductance (g_s) in *Artemisia ordosica* during the growing season (May-September) for both
 1759 2013 and 2014. Each point is given as the mean at specific times during each month.

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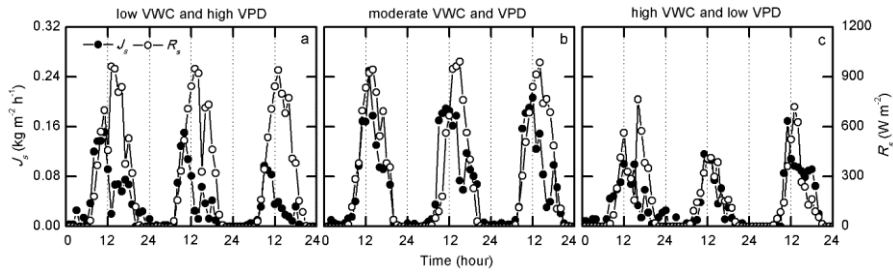
1765 **Fig. 7** Seasonal variation in hysteresis loops between sap-flow rate per leaf area (J_s) and
1766 shortwave radiation (R_s) using normalized plots for both 2013 and 2014. The y-axis
1767 represents the proportion of maximum J_s (dimensionless), and the x-axis represents the
1768 proportion of maximum R_s (dimensionless). The curved arrows indicate the clockwise
1769 direction of response during the day.

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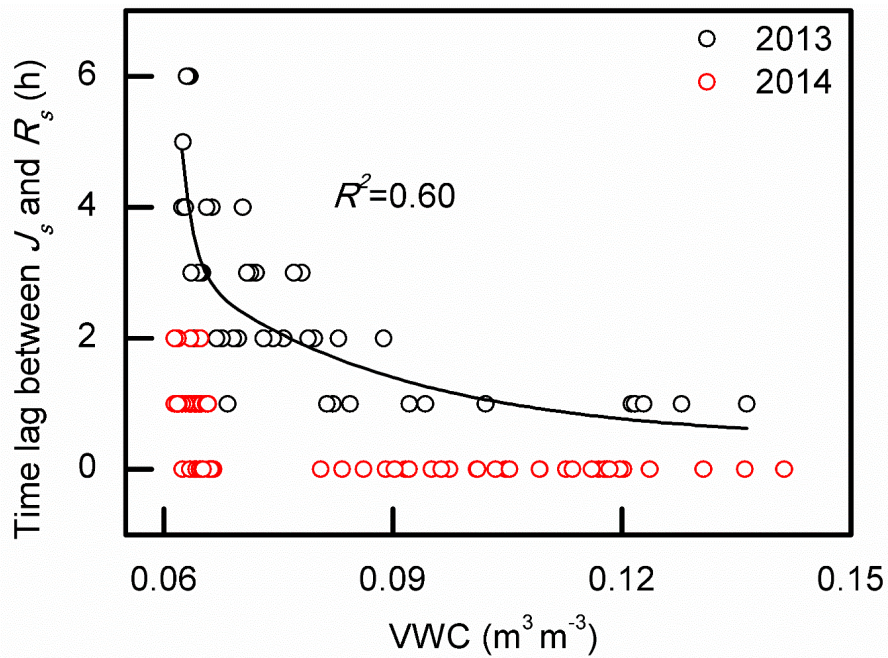


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1776 **Fig. 8** Sap-flow rate per leaf area (J_s) and shortwave radiation (R_s) over consecutive three
1777 days in 2013, i.e., (a) under low volumetric soil water content (VWC) and high vapor pressure
1778 deficit (VPD; DOY 153-155, VWC=0.064 m³ m⁻³, REW=0.025, VPD=2.11 kPa), (b)
1779 moderate VWC and VPD (DOY 212-214, VWC=0.092 m³ m⁻³, REW=0.292, VPD=1.72
1780 kPa), and (c) high VWC and low VPD (DOY 192-194, VWC=0.152 m³ m⁻³, REW=0.865,
1781 VPD= 0.46 kPa). REW is the relative extractable soil water. VWC, REW, and VPD are the
1782 mean value of the three days.

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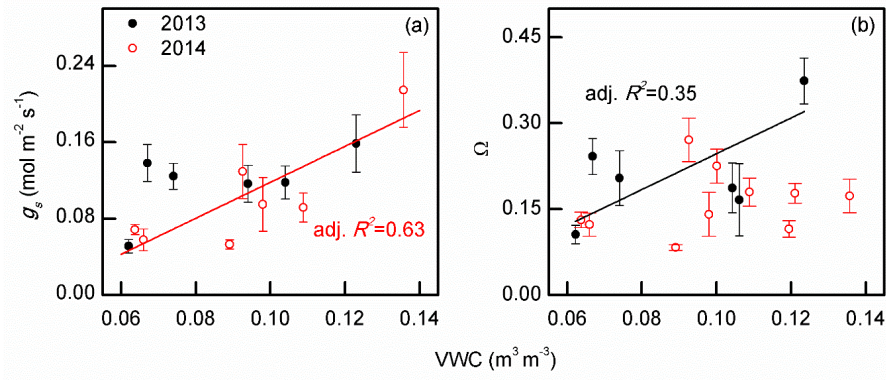
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1786 **Fig. 9** Time lag between sap-flow rate per leaf area (J_s) and short wave radiation (R_s) in
 1787 relation to volumetric soil water content (VWC). Hourly data in non-rainy days during the
 1788 mid-growing season of June 1-August 31 for 2013 and 2014. The lag hours were calculated
 1789 by a cross-correlation analysis using a three-day moving window with a one-day time step.
 1790 Rainy days were excluded. The solid line is based on exponential regression ($p < 0.05$).

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1795 **Fig. 10** Relationship between volumetric soil water content (VWC) and (a) stomatal
1796 conductance (g_s) in *Artemisia ordosica*, and (b) decoupling coefficient (Ω) for 2013 and 2014.
1797 Hourly values are given as binned averages based on a VWC-increment of $0.005 \text{ m}^3 \text{ m}^{-3}$.
1798 Bars indicate standard error. **Only regressions with p -values < 0.05 are shown.**

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