

1 **Annual variations of T/ET in a semi-arid region: implications of plant water use** 2 **strategies**

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8 **Abstract**

9 Understanding the annual variation in the transpiration to evapotranspiration ratio (T/ET) remains a
10 challenge and is essential for a thorough understanding of plant responses to the changing
11 environment. We obtained the annual dynamics of T/ET in a semi-arid area of the southwestern
12 United States based on the medians of monthly T/ET derived from two ET partitioning methods. The
13 variation in monthly T/ET was analysed, and plant water use strategies were discussed based on the
14 water use efficiency evaluated by the transpiration (WUE_T). The results show that physiological
15 changes in plants are vital in the annual dynamics of T/ET . Switches in plant physiological status
16 (growth and dormancy) at the start and end of growing seasons induce two dramatic changes in T/ET .
17 Consequently, there is an annual bimodal dynamic of monthly T/ET , with a maximum of 0.84 in
18 October and a minimum of 0.14 in December. Physiological/biochemical variations of plants
19 indicated by solar-induced chlorophyll fluorescence (SIF) are linearly related to T/ET in growing
20 seasons at a monthly scale ($T/ET = 3.40 \times SIF + 0.36$, $R^2 = 0.987$). Generally, a stable high monthly
21 T/ET occurs under sufficient energy and water conditions and a highly variable monthly T/ET occurs
22 under energy and water deficient conditions. In semi-arid regions, plants can flexibly adjust WUE_T

23 following different water use strategies to survive or gain as much gross primary productivity (*GPP*)
24 to compete. Saving water by greatly elevating *WUE_T* is the main strategy by which plants survive
25 the non-growing season when *WUE_T* is linearly related to *SIF* ($WUE_T = -114.93 \times SIF + 3.25$,
26 $R^2=0.970$). However, *GPP* and not *WUE_T*, becomes the goal of plants in growing seasons when
27 they employ a stable and moderate *WUE_T* (around 2.1 gC kg⁻¹ H₂O) despite the abundant energy
28 and precipitation. There are obvious reductions in *WUE_T* during the transition periods of the plants'
29 'growth-dormancy' cycle. Our study highlights the importance of studying annual *T/ET* variations
30 and water-use efficiency dynamics to better understand water use strategies in plants.

31 **1. INTRODUCTION**

32 Investigation of evapotranspiration (*ET*) partitioning in ecosystems can improve our understanding
33 of the hydrological systems which affect the stream flow, groundwater recharge, and weather
34 conditions, as well as the plant biomass production and associated carbon sequestration (Kool et al.,
35 2014). The dynamics of transpiration (*T*) and the *T/ET* ratio are closely related to the vigour of
36 terrestrial plants playing a crucial role in regulating atmospheric composition and climate (e.g., Suni
37 et al., 2015). The water use efficiency evaluated based on the transpiration ($WUE_T = GPP/T$, *GPP*
38 denotes the gross primary productivity), which describes the intrinsic trade-off between the carbon
39 assimilation and water loss owing to the evaporation from stomas of leaves during CO₂ acquisition,
40 is related to plant water use strategies. Studying the dynamics of *T* and *T/ET* is necessary for
41 obtaining *WUE_T* variations and linking plant-water use strategies to environmental variability
42 (Perez-Priego et al., 2018).

43 The dynamics of *T/ET* during growing seasons have been widely recognised. During growing

44 seasons, shrublands and grasslands in the southern United States display the lowest T/ET in the early
45 growing season, owing to the time lag between precipitation pulses at the beginning of the rainy
46 season, wetted root zone soil, and upregulated plants (Scott and Biederman, 2017). Globally, high
47 T/ET has been observed in the late growing season of agricultural or natural ecosystems (Wang et al.,
48 2014). T/ET and the leaf area index (LAI) increased during the growing seasons of grass, reflecting
49 the surface controls of plants on T/ET (Wang et al., 2013). Recent results also indicate that T/ET may
50 be less sensitive to the LAI than previously assumed, as a part of the covariation of T/ET and LAI
51 could be attributed to other seasonal patterns such as the soil water availability or phenology cycles
52 (Nelson et al., 2020). LAI and growing stage collectively explained 43% of the variation in T/ET
53 (Wang et al., 2014). LAI has been shown to explain only small (20%) variations in the mean annual
54 T/ET of agricultural or natural ecosystems (Li et al., 2019). No significant relationship was found
55 between T/ET and LAI at diel, daily, or annual timescales for a temperate needle leaf forest
56 (Berkelhammer et al., 2016). Fatichi and Pappas (2017) also found that LAI was not a key driver of
57 the spatial variations of T/ET . In growing seasons, T/ET also changed with different precipitation
58 patterns (with regard to the timing, frequency, duration, and intensity), which is considered as a part
59 of water use strategies in a temperate deciduous forest (Gu et al., 2016). It has been reported that
60 following a precipitation event of 9.7 mm, T/ET increased from 63.4 to 88.5% in a growing maize
61 field as the upper soil layer dried out, while the plants accessed the deeper soil water (Hogan et al.,
62 2020). In particular, water management can induce larger T/ET variations during the growing seasons
63 in croplands compared to natural ecosystems (Xiao et al., 2018). However, considering the factors
64 controlling the variations in T/ET , no clear correlation for annual precipitation, soil texture, or
65 ecosystem type was found in drylands worldwide, and T/ET varied most during dynamic

66 wetting-drying episodes (Sun et al., 2019). Studies concerning T/ET in growing seasons have
67 neglected the importance of seasonal T/ET variations to understand the factors controlling the T/ET
68 variation and plant water use strategies. Recently, the annual dynamics of T/ET have been reported.
69 In an annual cycle, variations in water availability strongly influenced not only the T/ET (Scott et al.,
70 2021), but also the water use efficiency (WUE_{ET} , the water use efficiency evaluated based on ET)
71 (Wang et al., 2021). The dynamics of T/ET may become complicated with varying levels of climatic
72 and surface controls (precipitation, evaporative demand, water availability, leaf area, stomatal
73 conductance, etc.). Despite these efforts, elucidating the annual T/ET dynamics and water use
74 efficiency are still challenging, and the water use strategies incorporated in the annual dynamics of
75 T/ET and water use efficiency have not been studied well.

76 Several ET partitioning methods have been developed to achieve reliable T/ET estimates (Kool
77 et al., 2014). The stable isotope technique is a commonly used method, but is costly and laborious
78 (Wang et al., 2010, 2013; Good et al., 2015). A typical uncertainty range for the stable isotope
79 technique was $\pm 21\%$ (Xiao et al., 2018). The combined use of eddy covariance (EC) measurements
80 and sap flow techniques provides a comprehensive method (Scott et al. 2006; Cammalleri et al.,
81 2013). However, sap flow measurements are not representative of all species within the footprint of a
82 flux tower. Scanlon and Kustas (2010) proposed a correlation analysis method based on the
83 similarity theory. However, it requires high-frequency (10 Hz) turbulent data, which are not widely
84 available, and tends to overestimate the soil flux components (E) (Klosterhalfen et al., 2019). Simple
85 EC-based approaches are promising for future use in various ecosystems through the global flux
86 tower networks. Zhou et al. (2014) proposed an underlying water-use efficiency ($uWUE =$
87 $GPP \cdot VPD^{0.5} / ET$) model. Based on $uWUE$, T/ET can be estimated as the ratio of the apparent $uWUE$

88 ($uWUE_a$, estimated using the linear regression between $GPP \cdot VPD^{0.5}$ and ET) over the potential
89 $uWUE$ ($uWUE_p$, estimated using the 95th quantile regression between $GPP \cdot VPD^{0.5}$ and ET ; Zhou et
90 al., 2016). Scott's method for T/ET estimation is applicable when linear regressions between monthly
91 GPP (abscissa) and monthly ET (ordinate) yield positive intercepts for months of the year.
92 Subsequently, monthly T/ET is estimated based on the intercepts (considered as the multi-year
93 average E for the month) along with the monthly ET (Scott and Biederman, 2017). However, the two
94 EC-based methods are constrained by certain assumptions. The $uWUE_p$ is assumed to be relatively
95 constant under steady-state conditions (e.g. relatively constant atmospheric CO_2 and water stress) for
96 a given plant (Zhou et al., 2016 and Zhou et al., 2018). The assumption for Scott's method assumes
97 that monthly GPP is a predictor of monthly ET based on the multi-year flux tower measurements
98 (Scott and Biederman, 2017). Given the uncertainty or bias associated with a single partitioning
99 method, using multiple methods to achieve reliable T/ET estimates is recommended (Hogan et al.,
100 2020; Scott et al., 2021).

101 Based on the eddy covariance measurements in a semi-arid area, we estimated the monthly
102 T/ET ratios using EC-based approaches proposed by Zhou et al. (2016) and Scott et al. (2017) for the
103 growing and non-growing seasons from 2008 to 2015. The major purpose of this study was to reveal
104 the annual variation patterns of T/ET and T in semi-arid regions. The secondary objective was to
105 reveal plant water use strategies for their survival in a changing environment.

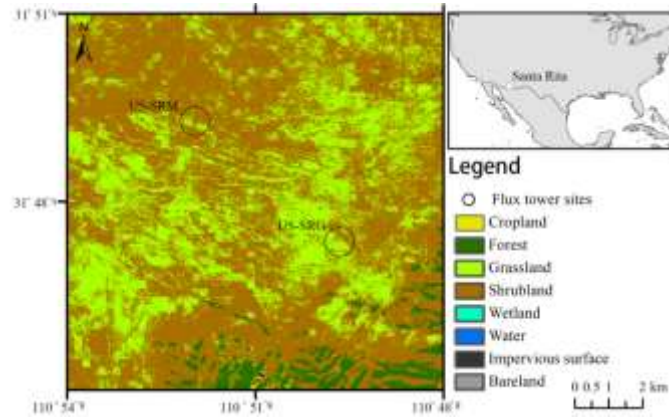
106 **2. DATA and METHODS**

107 **2.1. Sites and data**

108 The study area was Santa Rita, southeast Arizona, USA. Santa Rita is a semi-arid land located

109 between the Chihuahuan and Sonoran deserts. The land cover comprises mainly desert shrublands,
110 grasslands, and savanna lands. The Köppen climate type is 'Bsk', a steppe with warm winters. The
111 long-term mean annual temperature is 17 °C. The annual mean precipitation is approximately 320
112 mm, with an annual potential *ET* of 1400 mm. The rainy season spans from July to September. The
113 growing season spans from March to October. The non-growing seasons span from December to
114 February, namely the winter months.

115 We obtained the EC and meteorological data from two AmeriFlux sites in Santa Rita (US-SRG,
116 grassland with tree and shrub cover, whose data are available from 2008 to 2015; and US-SRM,
117 woody savanna lands with grassland and shrub cover, whose data are available from 2008 to 2015).
118 Vegetation fluorescence is the light emitted from chlorophyll during photosynthesis (Parazoo et al.,
119 2014). Solar-induced chlorophyll fluorescence (*SIF*), measured by satellites, is sensitive to both
120 structural and biochemical variations in vegetation (Yang et al., 2015; Sun et al., 2017; Smith et al.,
121 2018). We used a 0.05° GOSIF product (Li and Xiao, 2019) to indicate variations in the vegetation of
122 Santa Rita. The land cover of Santa Rita and the *SIF* pixels of the two sites were desert shrubs,
123 grasses, and trees (Figure 1). The proportions of grasses, shrubs, and trees were different between the
124 two sites. Despite this difference, the land cover of the two sites is typical to Santa Rita. A pooled
125 dataset of the flux data from the two sites and the *SIF* data of the two pixels approximately represents
126 the dynamics of climate and vegetation in Santa Rita.



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FIGURE 1 Land use and land cover in Santa Rita (land use and land cover data was downloaded from http://data.ess.tsinghua.edu.cn/fromglc10_2017v01.html in January 2021).

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2.2. Methodology

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Based on the half-hourly observations at the two sites, we calculated the *GPP* using the R package

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‘REddyProc’ (Wutzler et al., 2018) and estimated the *ET* from latent heat. A standard and extensible

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EC data post-processing was executed by the package, including uStar-filtering (Papale et al., 2006),

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gap-filling (Reichstein et al., 2005), and flux-partitioning (Lasslop et al., 2010). We pooled the

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meteorological observations, flux data, and *SIF* data of the two sites to gain medians of those

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variables for the months of a year, to obtain representative annual dynamics of the variables in Santa

137

Rita.

138

We calculated the monthly *T/ET* for the two sites using Scott’s and Zhou’s methods, respectively.

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We calculated the monthly *T/ET* using Zhou’s method in three stages of a year: March – June (the

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pre-monsoon phase with high energy and low water availability), July – September (the monsoon

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phase with high energy and high water availability), and October – February (the period with low

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energy and low water availability), respectively. We calculated the monthly *T/ET* ratios using Scott’s

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method when the linear correlation between the monthly *GPP* and *ET* was sufficiently high

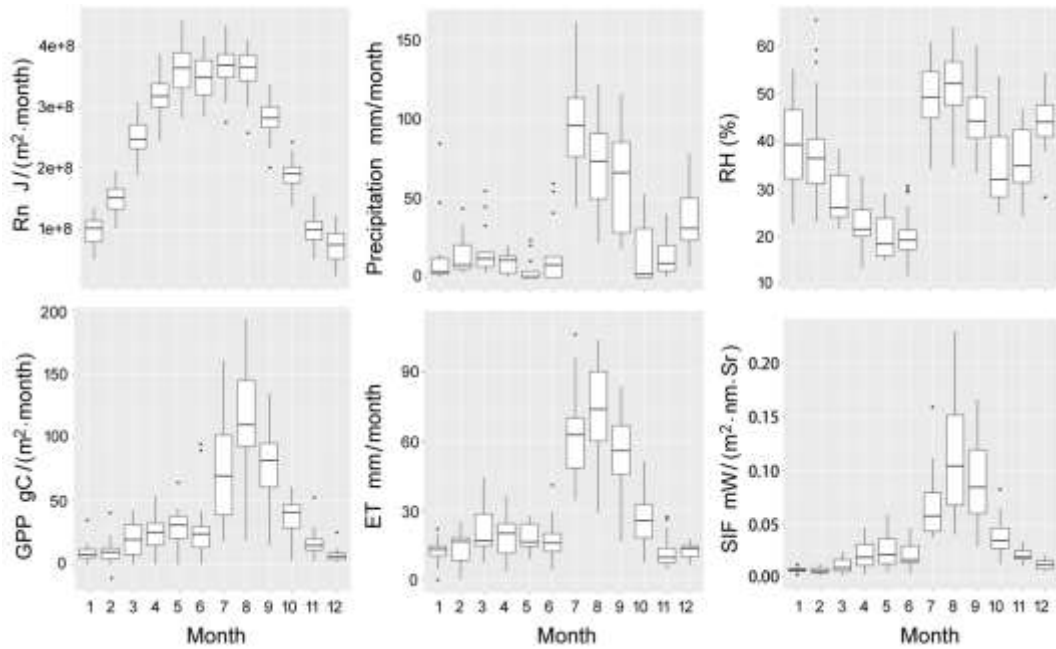
144 (Pearson's $r \geq 0.7$). The results of the two ET partitioning methods were compared, and the Pearson's
145 r of linear regressions between the results was calculated by months of a year. Subsequently, the
146 result of Zhou's method was corrected (the T/ET estimates of Zhou's method as a predictor of the
147 results of Scott's method) to reduce the uncertainty, which is explained in section 3.2. Although both
148 Scott's and Zhou's methods have uncertainty, the corrected T/ET estimates enhance the common
149 variance of T/ET contained in the two results. We grouped the months within a year (stages as
150 mentioned above) during the correction to ensure that the Pearson's r of linear regressions between
151 the results is higher than 0.7. The T/ET from Zhou's method in January, February, and December was
152 directly employed, as explained in section 3.2. Based on the corrected monthly T/ET , the monthly
153 transpiration ($T = ET \cdot T/ET$) and leaf scale water use efficiency were calculated. Finally, the corrected
154 monthly T/ET , calculated monthly T , and WUE_T were obtained, and their medians were calculated
155 for months of the year to represent the responses of mixed vegetation in Santa Rita to the changing
156 environment.

157 **3. RESULTS**

158 *3.1. Annual patterns of climate and surface controls*

159 The annual patterns of net radiation (Rn), precipitation (P), relative humidity (RH), GPP , ET , and
160 SIF are shown in Figure 2. Rn consistently increases until May, reaches a plateau from May to
161 August, and gradually decreases thereafter. Approximately 74% of the precipitation occurs during
162 rainy seasons, which is associated with the North American monsoon system (Perez-Ruiz et al.,
163 2010). Plants gain sufficient energy and water during the rainy season. In May and June,
164 precipitation is almost at its lowest level with an RH below 20%, while Rn is close to its peak value

165 when the study area is in its driest state; namely, the pre-monsoon drought (Figure 2). The study area
 166 is in its wettest state during July and August when the soil moisture content could recover,
 167 accompanied by a humid atmosphere (RH around 50%) due to abundant rainfall in rainy seasons. In
 168 winter, there are obvious energy and water deficiencies. However, *the RH* was relatively high.



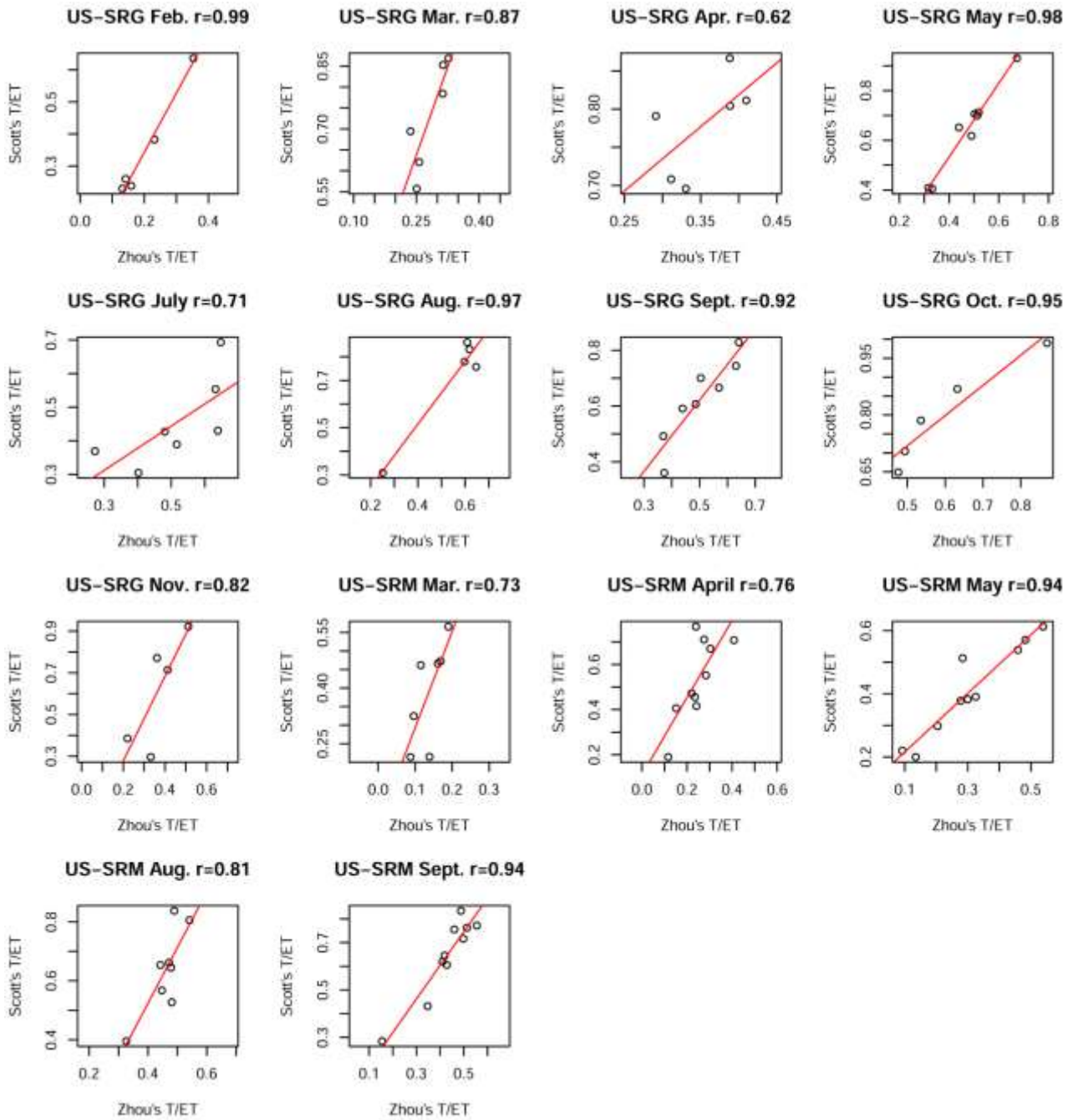
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 170 **FIGURE 2** Box plots of monthly Rn , precipitation, RH , GPP , ET , and SIF in Santa Rita. The
 171 meteorological measurements and flux data are from the two AmeriFlux sites (US-SRM and
 172 US-SRG) from 2008 to 2015. The SIF data of Santa Rita is from the GOSIF product for the same
 173 period. The statistic features of the variables for the months of a year indicate the seasonal variation
 174 of the climatic controls and surface controls in Santa Rita.

175 GPP , ET , and SIF are stimulated by sufficient precipitation and are constrained by insufficient
 176 Rn . Consequently, they are in the high-level stage during the main growing seasons (from July to
 177 October), and in the low-level stage during the pre-monsoon growing seasons (from March to June)
 178 and non-growing seasons, displaying similar seasonal patterns. GPP , ET , and SIF are relatively low
 179 from March to June because of the pre-monsoon drought when the bare ground cover can increase

180 from approximately 45 to 60% (Scott et al., 2015).

181 ***3.2. ET partitioning results and annual dynamics of T/ET***

182 The monthly *T/ET* result from Scott's method was unavailable for several months, including
183 January, February, June, and December, due to the insufficient linear correlation (Pearson's $r < 0.7$)
184 between monthly the *GPP* and *ET*. In the other months, the monthly *T/ET* estimates from Scott's
185 method exhibited a clear linear correlation with those from Zhou's method (Figure 3), indicating that
186 these two methods have grasped the common variations of the monthly *T/ET*.

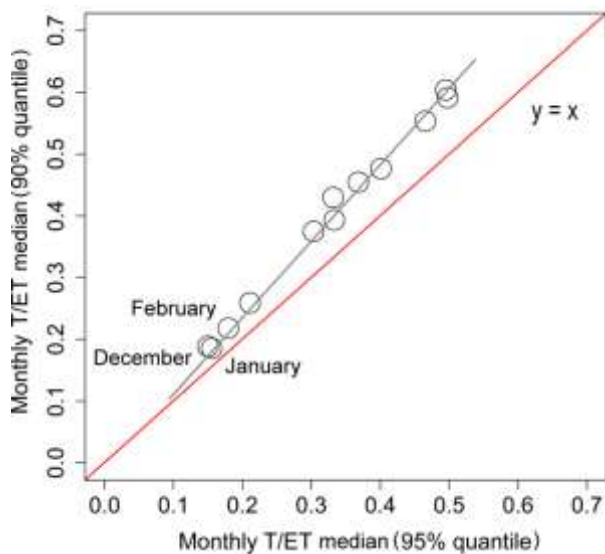


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188 **FIGURE 3** Correlation between the monthly T/ET ratios estimated by Zhou's and Scott's methods,
 189 respectively. The r represents the Pearson linear correlation coefficient. The red lines indicate the
 190 regression lines between Zhou's and Scott's T/ETs, respectively.

191 However, the results of Scott's method were greater than those of Zhou's method (Figure 3).
 192 Given that Scott's method was verified by its comparison with direct measurements at Santa Rita
 193 (Scott and Biederman, 2017), Zhou's method might underestimate T/ET . This is possibly the case in

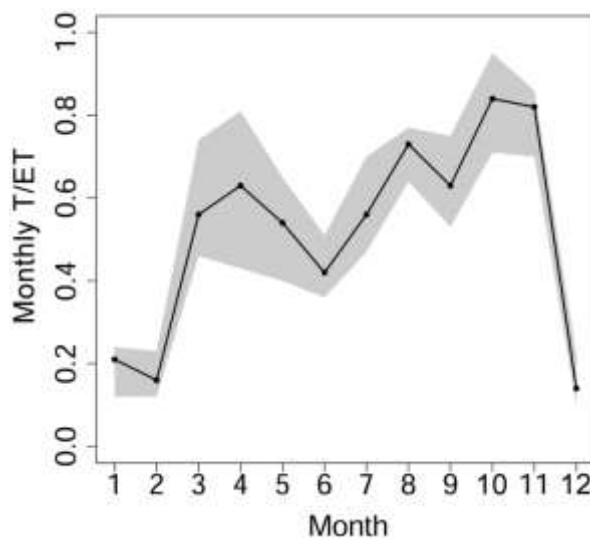
194 dry land. First, $uWUEp$ is generally higher under water stress conditions than under non-stress
 195 conditions. Second, a higher quantile in the quantile regression of Zhou's method produces a greater
 196 estimation of $uWUEp$ and, consequently, an underestimation of T/ET . As shown in Figure 4, the
 197 monthly mean T/ET increases by 22% on average when a 90% quantile is used to calculate the
 198 $uWUEp$, compared to that using the 95% quantile. Our results show less influence of different
 199 quantiles on the T/ET estimation in December, January, and February (Figure 4), indicating the
 200 robustness of the estimation during periods with low T/ET . Therefore, we corrected the results of
 201 Zhou's method according to those of Scott's method to achieve T/ET estimates and enhance the
 202 common variations contained in the two results, with no corrections for December, January, and
 203 February.



204
 205 **FIGURE 4** Comparison of results with different quantiles in Zhou's method. Monthly T/ET medians
 206 derived by a 90% quantile are 22% higher than those by a 95% quantile on average. High quantiles
 207 contribute to the underestimation of T/ET . As indicated by the regression line, the underestimation
 208 increases with an increase in the T/ET ratio. The points of January, February, and December are
 209 closer to the 1:1 line than other months, suggesting that the estimation of T/ET in these months are

210 relatively insensitive to different quantiles.

211 We combined the corrected monthly T/ET with the T/ET estimates from Zhou's method in
212 January, February, and December to represent the T/ET estimates in the months of a year (Figure 5).
213 Scott and Biederman reported that the monthly T/ET of the two sites change from 0.45 – 0.54 in July,
214 0.62 – 0.69 in August, and 0.54 – 0.66 in September, respectively (Scott and Biederman, 2017).
215 These results fall within the scope of our results (average ± 1 standard deviation). Although it is
216 almost impossible to conduct an absolute validation for the partitioning results, it is interesting to
217 achieve an annual dynamic of monthly T/ET based on the medians of monthly T/ET estimates.
218 According to our estimates, the monthly T/ET median reached its maximum (0.84) in October and
219 dropped to its lowest level (0.14) in December. The monthly T/ET ratios were low in non-growing
220 seasons with monthly T/ET medians not more than 0.21. Furthermore, there are two sharp changes in
221 the annual dynamics of the monthly T/ET . The first significant change occurs in March when T/ET
222 sharply rises from 0.16 to 0.56. The second occurs in December, with a quick drop of T/ET
223 to 0.14.

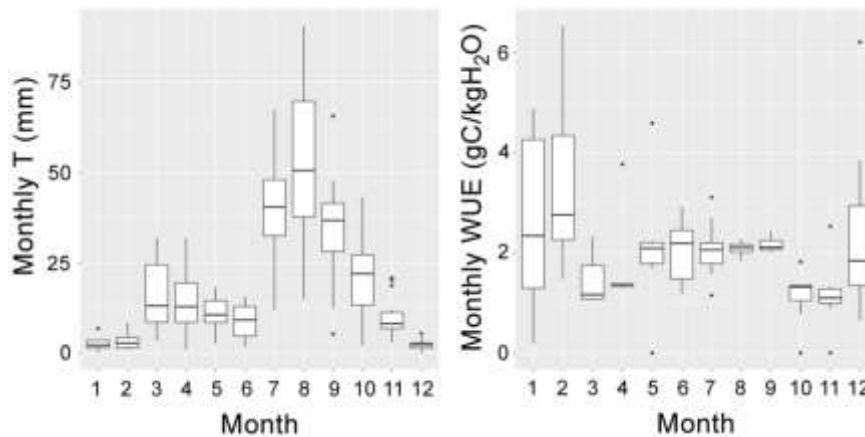


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225 **FIGURE 5** Annual dynamic of the monthly T/ET . Monthly T/ET medians are indicated by black dots.

226 The grey shadow indicates the range from 25 to 75% quantiles of monthly T/ET .

227 **3.3. Annual change of transpiration and leaf scale water use efficiency**

228 Monthly T was calculated as the product of the monthly T/ET estimates and ET . The largest T
229 was 91 mm month⁻¹ during the observation period in Santa Rita, while the lowest was only 0.7 mm
230 month⁻¹. T , as an indicator of physiological/biochemical variations in vegetation, is constrained by
231 the energy input and water availability. Our results showed that vegetation consumes more water
232 (average T of 37 ± 19 mm month⁻¹) during the main growing season when the energy and water
233 inputs were abundant (Figure 6). In the pre-monsoon growing seasons, the energy input is moderate,
234 while precipitation is scarce; thus, T is obviously lower (average T of 12 ± 8 mm month⁻¹) than that
235 in the main growing season. In the non-growing season (winter), T is generally not more than 8.5
236 mm month⁻¹ with an average of 3 ± 2 mm month⁻¹.



237

238 **FIGURE 6** Monthly transpiration and WUE_T in Santa Rita.

239 The monthly WUE_T ranges from 0 to 6.54 gC kg⁻¹ H₂O (Figure 6). Medians of WUE_T for
240 months of a year change between 1.1 and 2.8 gC kg⁻¹ H₂O, which is comparable to the range from
241 0.8 to 2.4 gC kg⁻¹ H₂O across dryland ecosystems in an arid region in Northwest China (Wang et al.,
242 2021). The monthly WUE_T varies greatly in January, February, March, June, and December, when
243 the growth is obviously hindered by insufficient energy and/or water stress which would significantly

244 change ecosystem functions (Gu et al., 2016). Simultaneously, the monthly WUE_T is less variable
245 in the other months than in these five months. According to the monthly WUE_T medians, months of
246 a year can be divided into two groups by the value $1.6 \text{ gC kg}^{-1} \text{ H}_2\text{O}$. The low monthly WUE_T group
247 includes March, April, October, and November which denote the start and end of the growing
248 seasons or the transition periods between non-growing and growing seasons. The high monthly
249 WUE_T group included the other months of the growing and non-growing seasons. It is obvious that
250 the WUE_T of plants is different between winter and summer in the semi-arid area. However, it has
251 been reported that WUE_{ET} does not differ between winter and summer (Biederman et al., 2018).
252 Notably, WUE_T and WUE_{ET} (GPP/ET) might result in opposite results.

253 The annual WUE_T dynamic does not follow the pattern of energy (Rn), water availability (P),
254 or physiological/biochemical activities (SIF), and is thus distinct from T . The amount of water that
255 can be used by plants (i.e. T) can be determined by Rn , P , and SIF ; but how this water is used
256 (namely WUE_T) is influenced by the plant water use strategies. The water use strategies of plants in
257 a changing environment thus provide a deeper understanding of plant adaptability.

258 **4. DISCUSSION**

259 ***4.1. Variations of T/ET in an annual cycle***

260 Reliable estimates of monthly T/ET produced reasonable estimates of the monthly T . There is
261 often a strong relationship between the ET and GPP at water-limited sites (Law et al., 2002). In our
262 case, the linear correlation coefficient between the monthly GPP and ET was 0.92 (Pearson's r).
263 Stomatal conductance critically determines both the photosynthetic uptake of CO_2 and the loss of
264 water transported from the leaf (Zhou et al., 2014). Thus, a better linear correlation between monthly

265 *GPP* and *T* was achieved ($r = 0.96$), suggesting the reliability of *T* and consequently, the *T/ET*
266 estimates.

267 The monthly *T/ET* estimates for the main growing seasons are reasonable. During the main
268 growing seasons, the *T/ET* ratio was 0.58 for the Chihuahuan Desert shrubland (Scott et al., 2006).
269 Schlesinger and Jasechko (2014) found similar *T/ET* ratios of 0.54 ± 0.18 and 0.57 ± 0.19 for
270 temperate grasslands, respectively. The *T/ET* of desert shrubs in northern China was 0.64 during the
271 growing seasons, with groundwater being the main water source for plant transpiration and soil
272 evaporation (Zhao et al., 2016). Rain-fed spring maize transpiration accounted for 59 and 56% of *ET*
273 in the semi-arid Loess Plateau of China (Gao et al., 2018). In the semi-arid Santa Rita, the monthly
274 *T/ET* of the main growing season is 0.68 ± 0.19 for the vegetation, which is consistent with previous
275 estimates ranging from 0.55 to 0.75 for southeast Arizona (Hamerlynck et al., 2014). Furthermore,
276 the monthly *T/ET* median reached a peak in October (0.84) in our case. Similarly, the *T/ET* ratio
277 approached 0.91 at the end of the growing season in a cold semi-arid site in China, wherein grassland
278 and woodland were the dominant land cover types (Li et al., 2016). In October, precipitation was
279 greatly reduced as the rainy season passed, which could trigger a rapid drop in soil evaporation.
280 However, moisture in the deep soil layer has a longer memory than precipitation (Stillman et al.,
281 2014). The antecedent deep soil moisture supports plant *T* to generate a high *T/ET* in the
282 post-monsoon period. We also confirmed that the time-lag induced the low *T/ET* in July. At the
283 beginning of the rainy season, soil moisture gradually recovers, which activates the ecosystem
284 activities (Cable et al., 2013; Biederman et al., 2018). However, precipitation must first satisfy the
285 soil moisture deficit before being absorbed by the roots (Scott et al., 2017). It has been reported that
286 vegetation *T* delays its responses to increased soil moisture for approximately three weeks after the

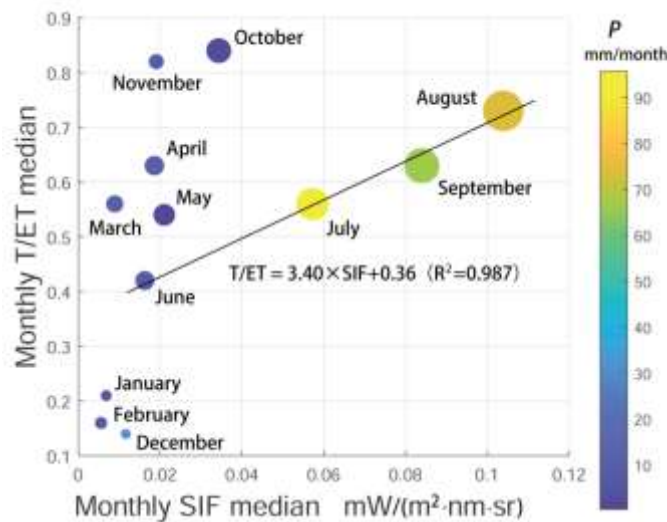
287 onset of the monsoon (Cavanaugh et al., 2011).

288 The monthly T/ET medians change between 0.42 and 0.63 in the pre-monsoon growing seasons
289 and between 0.56 and 0.73 in the main growing seasons, respectively. In the pre-monsoon growing
290 seasons, plants are suppressed by the pre-monsoon drought, as revealed by the low P , SIF , T , and
291 GPP , which induces lower T/ET values than those in the main growing seasons.

292 Changes in the physiological status of plants related to dormancy contribute to two dramatic
293 changes in the monthly T/ET before and after non-growing seasons. The lowest energy input in an
294 annual cycle and limited precipitation forces plants into dormancy (Perez-Ruiz et al., 2010). We
295 confirmed that plants with inactive physiological/biochemical activities become dormant in the
296 winter months, as indicated by the drops in SIF , GPP , and T to their annual minimums. The very low
297 T/ET ratios in non-growing seasons are appropriate for dormant plants. Additionally, plant mortality
298 coinciding with disadvantageous conditions (Hamerlynck et al., 2013) could further limit the T/ET
299 ratios. After the non-growing seasons, the energy input (Rn) sharply increased by 75% in March,
300 which is the largest annual change in monthly Rn . Simultaneously, the precipitation is approximately
301 the sum of the previous two months. The disadvantageous conditions disappeared, and plants were
302 subsequently upregulated out of dormancy, which can be verified by the significant increases in SIF ,
303 T , and GPP in March. The re-upregulated plants produced a large increase in T/ET from February to
304 March. Before the non-growing seasons, plants were suppressed by persisting decreases in energy
305 input and limited precipitation, with a 63 and 64% decrease in T and GPP in November compared to
306 October, respectively. However, the SIF only declined by 45%. Compared to T (GPP), which is
307 controlled by stomata, the relatively weak SIF response indicates that plants struggle to maintain
308 physiological/biochemical activities before falling into dormancy. A fairly high monthly T/ET

309 median is produced by struggling plants. However, plants eventually downregulate and resume
 310 dormancy by suppressing the climate control (Rn , P , and RH). Consequently, T/ET quickly dropped
 311 by 83% in December, relative to November.

312 As shown in Figure 7, there is a strong linear relationship between the monthly SIF and T/ET
 313 from June to September ($T/ET = 3.40 \times SIF + 0.36$, $R^2 = 0.987$). SIF is directly related to the structural,
 314 physiological, and biochemical variations in vegetation (Yang et al., 2015; Sun et al., 2017; Smith et
 315 al., 2018). Therefore, SIF is a good plant metric for T/ET dynamics. According to our results, plants
 316 can have a dominant influence on the ET partitioning during the growing seasons in a semi-arid area.

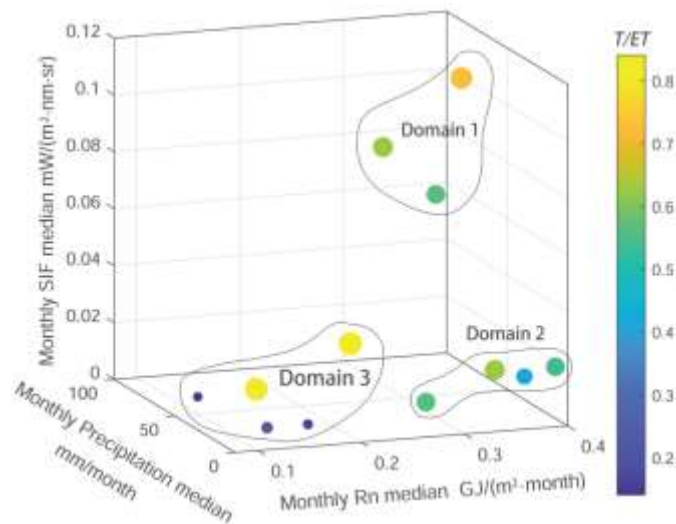


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318 **Figure 7** A scatter plot of SIF and T/ET . The colour of dots indicates the magnitude of monthly
 319 precipitation. The size of dots indicates the magnitude of monthly GPP .

320 However, we could not find a single driving factor solely responsible for the intra-annual
 321 dynamics of T/ET (Figure 7). The seasonal course of T/ET is related to both surface and climatic
 322 controls (Scott et al., 2017). In our case, the annual dynamics of T/ET are closely related to Rn , P ,
 323 SIF , T , and GPP , suggesting the climatic and physiological controls on ET partitioning. Climatic
 324 controls tend to produce a T/ET pattern similar to those of SIF , T , and GPP in the semi-arid area,

325 while physiologic controls of plants probably break the pattern. Therefore, in an annual cycle, the
 326 T/ET ratio does not depend on any single factor. For example, the climate might be similar between
 327 February and November, but the physiological status related to dormancy differs. Hence, the monthly
 328 T/ET medians were obviously different between the two months. We summarized the annual
 329 dynamics of monthly T/ET as follows. When active plants are met with sufficient energy and water,
 330 the monthly T/ET will be high and the mean anomaly will be low, suggesting a stable high monthly
 331 T/ET . For example, in July, August, and September (Domain 1 in Figure 8), the monthly T/ET mean
 332 is 0.64 and the mean anomaly is only 0.06. When suppressed plants are subjected to energy and
 333 water deficiencies, the mean anomaly of monthly T/ET is high, suggesting that it is highly variable.
 334 For example, the mean anomaly of monthly T/ET from October to February is 0.33 (Domain 3
 335 Figure 8).

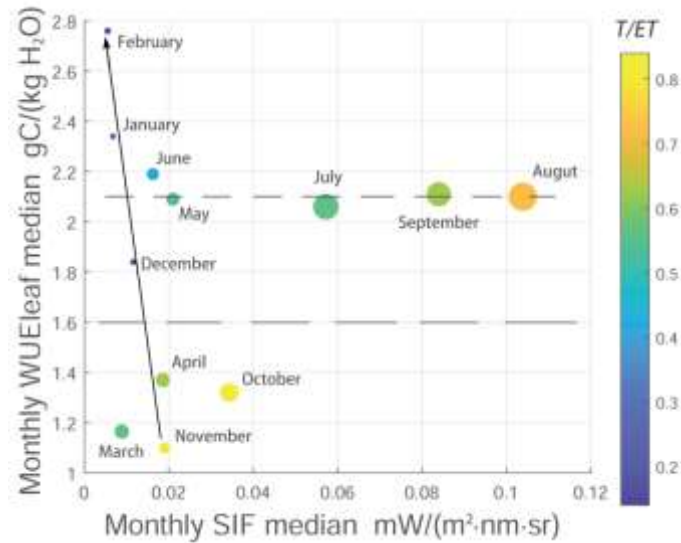


336
 337 **FIGURE 8** Variation of monthly T/ET median along with the Rn , P , and SIF . The color and size of
 338 dots indicate the magnitude of T/ET . The energy and water are sufficient for plants to grow in
 339 Domain 1, where differences of T/ET are small. In Domain 3, where the T/ET differs greatly, small
 340 SIF values with low energy and water inputs represent a disadvantageous stage. The energy input is
 341 high, but the water input is low in Domain 2, where the differences of T/ET are moderate.

342 **4.2. Plant water use strategies**

343 WUE_{ET} variability in arid ecosystems is primarily controlled by physical processes in
344 semi-arid and sub-humid regions (Yang et al., 2016). In our case, WUE_T might be regulated not
345 only by physical processes (water stress and heat stress), but also by biological processes
346 (transpiration, dormancy, germination, senescence, water, and nutrient storage). Plants respond to
347 regulations that reveal a wide range of water use strategies.

348 Plants employ a moderate WUE_T during growing seasons to obtain as much GPP in semi-arid
349 areas. Notably, plants seem to ‘waste’ water by employing a moderate WUE_T in growing seasons
350 (Figure 9). In particular, precipitation can affect leaf-level physiology through the direct dilution of
351 soil nitrogen (Patrick, et al. 2009). Dilution could be obvious in the semi-arid area due to abundant
352 monsoon precipitation. Consequently, excess T is needed for plants to procure sufficient nutrients to
353 obtain as much GPP as possible in the main growing seasons. Moreover, WUE_T begins to decline
354 when the leaf is exposed to temperatures exceeding the optimum (Hatfield and Dold, 2019).
355 Therefore, overshoots in the stomatal opening are common features of plants under heat stress,
356 resulting in water loss to maintain the leaf temperature and maximize the GPP production (Lawson
357 and Violet-Chabrand, 2019). With sufficient energy and water, GPP production and not water use
358 efficiency, has become the main concern for plants.



359

360 **Figure 9** Monthly *SIF* medians versus monthly *WUE_T* medians. The size of the dots is directly
 361 proportional to the magnitude of monthly transpiration medians. The upper and lower dashed lines
 362 indicate 2.1 gC kg⁻¹ H₂O (the average from May to September) and 1.6 gC kg⁻¹ H₂O (dividing the
 363 two groups), respectively.

364 Plants employ an almost constant monthly *WUE_T* during the growing season. Zhou et al.
 365 (2014) demonstrated that the underlying water use efficiency (describing a linear relationship
 366 between $A\sqrt{GPP}$ and *T*; *A* is the rate of CO₂ assimilation) at the leaf scale remains essentially
 367 constant for certain vegetation types during the growing season. In our case, the monthly *WUE_T*
 368 median remained almost unchanged (with an average of 2.1 gC kg⁻¹ H₂O) from May to September,
 369 despite the large variations in the monthly *SIF* (Figure 9), which is obviously different from the
 370 increase in the monthly *T/ET* median (Figure 7). More efforts are required to explain the almost
 371 constant monthly *WUE_T* during the growing seasons. It has been reported that water use efficiency
 372 increases under water-stress conditions (Tong et al., 2019), reflecting the adaptability of plants in
 373 semi-arid areas to water deficiency (Wang et al., 2021). Stomata are key players in the response of
 374 plants to water stress (Gambetta et al., 2020). The reduction in photosynthesis is less than that in

375 stomatal conductance, which explains the increase in water use efficiency under water-deficit stress
376 conditions (Hatfield and Dold, 2019). In our case, the monthly WUE_T median in June was slightly
377 higher than that in other months as a result of the water stress at the end of the pre-monsoon drought.
378 Both GPP and SIF decreased by 23% in June compared to May, indicating a reduction in
379 photosynthesis. Although we did not measure the stomatal conductance, a very dry condition can be
380 confirmed based on limited precipitation and considerably low RH in June, which suggests reduced
381 stomatal conductance (Grossiord et al., 2020).

382 Plants survive the non-growing seasons by greatly enhancing WUE_T . Plants (here evergreen
383 shrubs) have to continue GPP production to survive the non-growing seasons. However, T in
384 non-growing seasons is less than 3 mm month⁻¹ on average and is less variable than that of the
385 growing seasons. To deal with this, plants conduct highly efficient GPP production. According to our
386 result, the monthly WUE_T median greatly increased from 1.10 gC kg⁻¹ H₂O (November) to 2.76 gC
387 kg⁻¹ H₂O (February), with an increment of around 0.42 gC kg⁻¹ H₂O per month (Figure 9). Finally,
388 plants increase the monthly WUE_T by up to 130.8% of the average WUE_T in growing seasons,
389 possibly due to the disappearance of heat stress. The process can be described as $WUE_T =$
390 $-114.93 \times SIF + 3.25$ ($R^2=0.970$), suggesting a high sensitivity of WUE_T to SIF in non-growing
391 seasons. The rapid increase in WUE_T suggests a strong adaptability of plants to the changing
392 environment in semi-arid Santa Rita. Rapid stomatal responses have been reported to greatly
393 improve the water-use efficiency (McAusland et al., 2016). To a certain degree, the strong
394 adaptability could be supported by the rapidity of stomatal responses in the stomatal pore apertures,
395 size, and density in changing environments (Bertolino et al., 2019).

396 Plants employ a low WUE_T during the transition of the ‘growth-dormancy’ physiological cycle,

397 possibly to prepare for the subsequent stage. According to our results, WUE_T changed between 1.1
398 and $1.4 \text{ gC kg}^{-1} \text{ H}_2\text{O}$ in the transition periods, which was significantly lower than that in the growing
399 and non-growing seasons (Figure 9). The decrease in WUE_T in March and April is possibly related
400 to the germination during plant physiological/biochemical upregulation. The decline of WUE_T in
401 October and November might be a result of the grass senescence and water storage in shrubs and tree
402 bodies during low production periods. Further studies are required to explain the decline in WUE_T
403 during the transition of the ‘growth-dormancy’ physiological cycle.

404 5. CONCLUSIONS

405 In an annual cycle, the average monthly T/ET medians of vegetation composed of grasses,
406 shrubs, and savanna is 0.52 ± 0.24 in the semi-arid Santa Rita, Arizona (southwestern USA), with a
407 maximum of 0.84 in October and a minimum of 0.14 in December. There is a bimodal annual
408 dynamic of monthly T/ET medians. The monthly T/ET medians change from 0.42 to 0.63 in the
409 pre-monsoon growing season (March-June) and from 0.56 to 0.84 (July-October) in the main
410 growing season. The monthly T/ET median is at a minimum in June during the growing seasons
411 under the water stress of the pre-monsoon drought. In the non-growing season (from December to
412 February), the monthly T/ET medians are not more than 0.21, forming the other valley. We found a
413 strong linear relationship between SIF and T/ET from June to September ($T/ET = 3.40 \times SIF + 0.36$,
414 $R^2 = 0.987$). SIF is a good plant metric for T/ET dynamics.

415 Climate controls, especially the energy input, stimulate plants’ physiological status, which is
416 crucial in the annual T/ET dynamics. Changes in the plant physiological status related to the
417 dormancy contribute to the two dramatic changes in monthly T/ET . When the energy input increases

418 greatly in spring, plants can quickly revert from dormancy, producing a dramatic increase in T/ET .
419 When the energy input decreases greatly after growing seasons, plants dramatically decrease the
420 biomass production but produce the highest monthly T/ET . A dramatic decrease in T/ET occurred
421 when plants became dormant. Consequently, plants can have a dominant influence on the ET
422 partitioning in semi-arid areas.

423 In semi-arid regions, plants implement different water use strategies to adapt to changing
424 environments. The monthly WUE_T median remained almost unchanged (2.1 gC kg⁻¹ H₂O on
425 average) from May to September in growing seasons, despite the large variations in monthly SIF .
426 However, the monthly WUE_T median greatly increased from 1.10 to 2.76 gC kg⁻¹ H₂O from
427 November to February in non-growing seasons, displaying a high sensitivity to SIF ($WUE_T =$
428 $-114.93 \times SIF + 3.25$, $R^2=0.970$). Highly efficient production under conditions that inhibit
429 transpiration (less than 3 mm month⁻¹) is the core strategy for plant survival in non-growing seasons.
430 However, with abundant energy and precipitation, plants employ only a moderate WUE_T in the
431 growing seasons. On the one hand, focusing on production (and not the water use efficiency)
432 becomes the key strategy for plants with sufficient energy and water. Conversely, the moderate
433 WUE_T is considered to be a result of heat stress. Additionally, low WUE_T values were employed
434 at the start and end of the growing season, which is considered as the transition during the
435 'growth-dormancy' physiological cycle of plants. The reduction of WUE_T during the transition is
436 believed to be a water use strategy for plants to prepare for upregulation/downregulation out of or
437 into dormancy. Further studies are required to address the global variation in T/ET dynamics,
438 WUE_T , and related water use strategies.

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