

Article

# Extrapolation of Leaf Measurements to Obtain the Whole-Canopy Transpiration of C<sub>3</sub> and C<sub>4</sub> Xerophytic Shrubs

Yanxia Jin <sup>1,2</sup>, Xinping Wang <sup>1,\*</sup>, Yafeng Zhang <sup>1</sup>, Yanxia Pan <sup>1</sup> and Rui Hu <sup>1</sup>

<sup>1</sup> Shapotou Desert Research and Experiment Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China; jinyanx526@163.com (Y.J.); zhangyafeng1986@gmail.com (Y.Z.); panyanxia@gmail.com (Y.P.); hurui22831@163.com (R.H.)

<sup>2</sup> College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China

\* Correspondence: xpwang@lzb.ac.cn; Tel.: +86-931-4967175; Fax: +86-931-8273894

Received: 9 May 2018; Accepted: 7 June 2018; Published: 20 June 2018



**Abstract:** Quantifying the water balance within areas with sparse vegetation requires frequent measurement of transpiration in water-limited, arid, desert ecosystems. Field experiments were conducted in Shapotou, northwestern China, to examine the feasibility of up-scaling the transpiration of C<sub>3</sub> and C<sub>4</sub> xerophytic shrubs (*Reaumuria soongorica* and *Salsola passerina*, respectively) from the leaf to the canopy level throughout the growing season in 2015. The large weighing lysimeter method and LI-6400XT portable photosynthesis system were used to make relatively long-term measurements of transpiration. The results indicated that meteorological factors coupled with stomatal conductance affected the transpiration rate of the two shrubs at the leaf level, and that the vapor pressure deficit other than net radiation and the air temperature affected the transpiration rate of *S. passerina* at the canopy level. Precipitation and vegetation characteristics determined the transpiration amount of the C<sub>3</sub> and C<sub>4</sub> xerophytic shrubs. The leaf gas exchange measurements were arithmetically scaled up to the canopy level based on the leaf area. The validity of the extrapolation was evaluated by comparing the upscale values of transpiration with the calculated values obtained from lysimeter measurement. The up-scaling approach accurately ( $\pm 0.005 \text{ mm h}^{-1}$ , RMSE = 35%) obtained canopy transpiration from the leaf measurements. Our study suggests that the up-scaling method based on leaf area can be adopted to determine the canopy transpiration of C<sub>3</sub> and C<sub>4</sub> xerophytic shrubs in arid desert environments.

**Keywords:** transpiration; Lysimeter; LI-6400XT; *Reaumuria soongorica*; *Salsola passerina*

## 1. Introduction

Transpiration (T) is the process whereby water is transported from the soil to the plant, via the roots, and to the atmosphere through the plant. It serves as an important component of evapotranspiration (ET) and is a dominant force in the global water cycle, as it accounts for 61% ( $\pm 15\%$  s.d.) of ET at the ecosystem scale and accounts for more than two-thirds of total surface water ET for 85% of the catchments examined [1,2]. Partitioning T from ET is essential to understanding the links between hydrological and ecological systems, because biological water use is inexorably coupled with ecosystem productivity, yet it is difficult and problematic to use a single method to determine their partitioning [3]. Remarkably, the ratio of T to ET ranged from 6% to 60% due to seasonal patterns of precipitation, the differential water use of different plant types and varying ET contributions in a Chihuahuan Desert shrub-dominated community [4]. The ability to independently measure soil evaporation (E) and canopy T is important for the detection of sparse vegetation water balance [5]. However, areas covered by sparse vegetation, such as the Shapotou area of Tengger

Desert in northwestern China are, which is normally dominated by xerophytic shrubs with fascicular branches without a visible trunk and with a small leaf area. It is difficult to determine the T of these shrubs using the existing mathematical techniques on either the temporal or spatial scale, such as the Penman–Monteith equation, which was not developed for such situations and thus has very poor estimation accuracy. Despite this, the view toward replacing the mathematical paradigm with more direct estimation of vegetation ET based on an understanding of the vegetation- and growth-stage-specific canopy resistance is still a work in progress [6]. The possible mechanisms affecting the magnitude of T were determined by the interaction of external and physiological factors and was controlled by stomata at the landscape scale [7].

A variety of techniques are available to directly or indirectly measure T at different scales under field conditions, such as leaf gas exchange systems at the leaf scale [8,9], sap flow gauges at the individual scale [10], isotopic tracers, weighing lysimeters, the Bowen ratio technique, the FAO-56 (Food and Agriculture Organization) dual crop coefficient method, and the Shuttleworth–Wallace dual model at the canopy scale [2,11]. In general, weighing lysimeters are usually regarded as the standard device and the most accurate method for determining ET, especially in arid environments. The lysimeter data can be used to test, evaluate and further develop hydrological and other models, such as the soil and water assessment tool (SWAT), root zone water quality model II (RZWQM), and the energy and water balance (ENWATBAL) model [6]. Leaf gas exchange systems can simultaneously measure the net carbon assimilation, leaf transpiration, stomatal conductance and some other parameters [12,13]. Particularly, leaf gas exchange systems can make up for the deficiencies of the lysimeter, which usually determines seasonal water use efficiency (WUE) based on a single biomass and water use measurement at the end of season [14]. Nevertheless, leaf gas exchange measurements are complicated due to the temporal variation of environmental factors and of plant physiological processes, e.g., the temporal variation of stomatal conductance [15,16]. Diurnally-varied meteorological conditions exhibit considerable additional variability on the order of minutes, such as scattered cloud cover [17]. Changes in plant water status through the day result in differences in the stomatal limitation of transpiration [18].

Although extensive studies have been carried out on scaling up leaf-level stomatal resistance and photosynthesis to canopy-level resistance and photosynthesis [19,20], few studies paid attention to problems and strategies for up-scaling the transpiration from the leaf to the individual or canopy level in ecosystems dominated by xerophytic shrubs [8,13,17,21,22]. In this study, leaf gas exchange measurements from a LI-6400XT portable photosynthesis system and the lysimeter-measured ET minus calculated soil evaporation (E) method were used to obtain the T at the leaf and canopy scale. Furthermore, the reliability of up-scaling transpiration from the leaf to the canopy level of C<sub>3</sub> and C<sub>4</sub> xerophytic shrubs was evaluated. The specific objectives of the study were: (1) quantifying the daily and seasonal T patterns of *R. soongorica* and *S. passerina* at the leaf level; (2) quantifying the variation of T of *R. soongorica* and *S. passerina* in relation to physiological (e.g., carbon assimilation, stomatal conductance, stomatal limitation) and other meteorological variables; and (3) up-scaling T from the leaf to the canopy level based on leaf area and evaluating the reliability of the extrapolation. Leaf area was expected to be a standard factor for up-scaling T from the leaf to the canopy level of xerophytic shrubs in arid desert areas.

## 2. Materials and Methods

### 2.1. Study Area and Plant Description

Our field experiments were conducted at the Shapotou Desert Research and Experiment Station (SDERS) of the Chinese Academy of Sciences, at an elevation of 1340 m above mean sea level, located at the southeastern margin of the Tengger Desert in northwestern China (37°32' N, 105°02' E). This region is a typical transitional zone of desert and desert oasis. The natural vegetation is *Hedysarum scoparium* and *Agriophyllum squarrosum*, with a cover of approximately 1% [23]. The groundwater is unavailable

for plant roots since it is at a depth of 80 m. Precipitation is dominated by small events (e.g., <5 mm), and few infrequent and highly unpredictable large rainfall events, as in some other arid regions [24]. According to meteorological records from 1956 to 2009, the annual mean precipitation was 188 mm, with 80% of rainfall events occurring between May and September, and large inter-annual variability. The minimum and maximum average monthly relative humidity is 33% (April) and 54.9% (August), respectively. The long-term soil moisture content varies between 3% and 4%, with a field capacity of 6.70% and a wilting coefficient of 0.61% [25,26]. The mean maximum air temperature is 24.3 °C in July and the mean minimum is −6.9 °C in January. The annual mean wind velocity at 2 m height is approximately 2.9–3.5 m s<sup>−1</sup>. The potential evapotranspiration is approximately 2800 mm during the growing season, resulting in a large annual moisture deficit [27,28].

*Reaumuria soongorica* (Pall.) Maxim and *Salsola passerina* Bunge are the zonal vegetation of the southeastern margin of the Tengger Desert, and their nearest natural distribution area is located in Mengjiawan with about 10 km away from SDERS. Thus, the two shrubs used in this study were transplanted from natural vegetation areas. Both were chosen because they are constructive and dominant species of steppes and typical deserts and play a vital role in sustaining the ecological stability of the deserts due to their drought-resistant nature. Furthermore, they are considered to be climax communities in the southeast of the Tengger Desert and are widely distributed across the desert regions of China. *R. soongorica* and *S. passerina* may exist either in individuals or in associated communities, and they survive under severe environmental stresses, including low water availability, extreme temperature fluctuations, high radiation and nutrient deprivation [29]. Water availability is one of the main limiting factors determining their growth [30]. *R. soongorica* can be found in the foothill zones, river terraces and in the Gobi, providing grazing forage for abundant foliar levels of proteins, fats, and micronutrients. *R. soongorica* has many branches, with a height between 10 and 70 cm, characterized by short and cylindrical leaves with a length of 1~5 mm and a width of 0.5~1 mm, with normally 4–6 clusters on shortened branches. In addition, *R. soongorica* leaves have a unique adaptive strategy, entering a state of dormancy during dehydration but reviving when rewetted [31]. *S. passerina* also has many branches, with a height ranging between 15 and 50 cm, with cone- or triangle-shaped leaves 2~3 mm in length and 2 mm in width, and roots that are normally distributed at depths between 0 and 50 cm. *S. passerina* is mainly present in hilly mountain basins and foothill areas with an annual precipitation of 100–200 mm, and they may also be found in the vast foothill zone and the vast Gobi desert, with an annual precipitation <100 mm [32,33].

## 2.2. Methods

### 2.2.1. Experimental Design

In this study, the in situ field experiments lasted from May to October in 2015 at SDERS, which is considered as the peak growth season for plants in this region. Four individuals of *R. soongorica* were transplanted into one high-precision weighing lysimeter with a cross-section area of 4 m<sup>2</sup>. Four individuals of *S. passerina* were transplanted into another lysimeter with the same size and accuracy. The two large weighing lysimeters were located at SDERS. The shrubs' morphological traits are quantified in Table 1. Shrub height and new shoot length were measured with a ruler. The canopy projection area (approximated as an ellipse) was determined by measuring the longer and shorter sides of the plant canopy. The leaf area index (LAI) was measured directly by a LAI-2000 plant canopy analyzer (Li-Cor, Inc., Lincoln, NE, USA). The measurements were carried out at the end of each month during the growing season in 2015. Each lysimeter has two heat flux plates with an 80-mm diameter (HFP015C, Hukseflux Thermal Sensors, Delft, the Netherlands) at 5 cm and 7 cm below the soil surface, respectively. Stevens pF Sensors (for measuring soil matric potential and soil temperature) and TDR (Time Domain Reflectometry) probes (for measuring soil water content) were installed at soil depths of 10, 20, 40, 60, 80, 100, 160, 180, 200, and 220 cm within each lysimeter. The mass, a full suite of micrometeorological variables, soil heat flux, soil matric potential and soil temperature data at

each lysimeter were recorded every 30 min. The accuracy of the lysimeter is  $\pm 0.1000$  kg (equivalent to 0.025 mm water of the 4 m<sup>2</sup> lysimeter). The difference between lysimeter mass losses (from T and E) and gains (precipitation) divided by the lysimeter cross-section area was used to determine hourly and daily ET values of *R. soongorica* and *S. passerina*.

**Table 1.** The values (means  $\pm$  standard errors) of the canopy height, canopy projection area, new shoot length, and leaf area index (LAI) of *R. soongorica* and *S. passerina*.

Month	Shrubs	Height (cm)	Canopy Projection Area ( $\times 100$ cm)	New Shoot Height (cm)	LAI (m <sup>2</sup> m <sup>-2</sup> )
May	<i>S. passerina</i>	20.13 $\pm$ 1.13	6.91 $\pm$ 0.76	1.84 $\pm$ 0.16	1.51 $\pm$ 0.36
	<i>R. soongorica</i>	17.80 $\pm$ 3.03	7.92 $\pm$ 0.84	2.65 $\pm$ 0.37	1.00 $\pm$ 0.19
Jun.	<i>S. passerina</i>	22.68 $\pm$ 1.21	8.77 $\pm$ 0.83	5.91 $\pm$ 1.07	1.71 $\pm$ 0.42
	<i>R. soongorica</i>	21.68 $\pm$ 2.35	10.70 $\pm$ 1.04	6.88 $\pm$ 1.19	1.33 $\pm$ 0.19
Jul.	<i>S. passerina</i>	26.15 $\pm$ 1.50	10.80 $\pm$ 1.47	7.20 $\pm$ 0.86	1.85 $\pm$ 0.46
	<i>R. soongorica</i>	23.30 $\pm$ 3.51	11.87 $\pm$ 1.13	7.74 $\pm$ 1.39	1.51 $\pm$ 0.20
Aug.	<i>S. passerina</i>	29.78 $\pm$ 2.23	13.56 $\pm$ 2.24	10.67 $\pm$ 1.23	1.81 $\pm$ 0.35
	<i>R. soongorica</i>	24.08 $\pm$ 2.99	12.92 $\pm$ 1.25	7.86 $\pm$ 1.44	1.56 $\pm$ 0.26
Sep.	<i>S. passerina</i>	28.48 $\pm$ 2.75	14.71 $\pm$ 1.18	11.13 $\pm$ 1.10	1.72 $\pm$ 0.33
	<i>R. soongorica</i>	23.65 $\pm$ 3.51	12.12 $\pm$ 1.91	7.51 $\pm$ 1.42	1.33 $\pm$ 0.20
Qct.	<i>S. passerina</i>	28.88 $\pm$ 2.42	14.44 $\pm$ 1.14	10.95 $\pm$ 0.69	1.56 $\pm$ 0.37
	<i>R. soongorica</i>	23.75 $\pm$ 3.30	10.86 $\pm$ 0.70	7.23 $\pm$ 1.27	1.26 $\pm$ 0.22

### 2.2.2. Gas Exchange Measurements

Leaf gas exchange measurements were taken on two consecutive days at the end of each month during the growing season in 2015 using the LI-6400XT portable photosynthesis system equipped with a 6400-05 Conifer Chamber (Li-Cor Inc., Lincoln, NE, USA). One leaf gas exchange measurement was completed each 2 h from 7:00 to 19:00 h, that is to say, measurements were taken six times a day. The measurements were repetitively conducted on three mature, healthy and expanded leaves of *R. soongorica* and *S. passerina* per individual under uniform conditions. The parameters recorded included the leaf net carbon assimilation rate ( $A$ ,  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), transpiration rate ( $T_r$ ,  $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ), stomatal conductance ( $g_s$ ,  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ), air temperature ( $T_1$ ,  $^\circ\text{C}$ ), leaf temperature ( $T_{\text{leaf}}$ ,  $^\circ\text{C}$ ), relative humidity ( $\text{RH}_1$ , %), leaf-to-air vapor pressure deficit ( $\text{VPD}_1$ , kPa), intercellular  $\text{CO}_2$  concentration ( $C_i$ ,  $\mu\text{mol CO}_2 \text{ mol}^{-1}$ ), ambient  $\text{CO}_2$  concentration ( $C_a$ ,  $\mu\text{mol CO}_2 \text{ mol}^{-1}$ ), and photosynthetically active radiation (PAR,  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ). The instantaneous water use efficiency (WUE,  $\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$ ) was calculated by  $A$  and  $T_r$  using Equation (1). Stomatal limitation ( $L_s$ ) was calculated by  $C_i$  and  $C_a$  as Equation (2) [34,35].

$$\text{WUE} = A/T_r \quad (1)$$

$$L_s = 1 - C_i/C_a \quad (2)$$

### 2.2.3. Transpiration Calculation Procedures

$T$  was calculated as the difference between  $ET$  and  $E$  using the lysimeter-recorded data. Based on a study finding that the  $E$  rates under the canopy are significantly lower (e.g., 0.53 times) than those measured at the exposed habit [36], we assumed that the  $E$  under the vegetation canopy was negligible. Although the canopy-intercepted evaporative loss is an indispensable part of evapotranspiration, it was neglected in this study due to the small amount. For example, interception loss accounts for 3.2% of the total water consumption during the growing period [37]. The calculation of the  $T$  by the lysimeter is shown in Equations (3) and (4).

$$T_L = ET - k_i E \quad (3)$$

$$k_i = \frac{A - C_i}{A} \times 100\% \quad (4)$$

where  $ET$  is evapotranspiration (mm),  $k_i$  is the coefficient of the soil evaporation ( $i = 5, 6, 7, 8, 9, 10$  represent different months),  $E$  is the soil evaporation (mm),  $A$  is the cross-section area of the lysimeter ( $m^2$ ), and  $C_i$  is the canopy projection area ( $m^2$ ).

Assuming that the leaf transpiration rate of each sample branch did not change obviously during the measurement period, the average transpiration rate of the three standard samples was taken as the canopy transpiration rate of the individual. The hourly average transpiration rate per unit leaf area ( $T_c$ ,  $kg\ m^{-2}\ h^{-1}$ ) was  $T_c = 0.0648 T_r$  after the unit conversion. Based on these conditions, the total transpiration amount of the four individuals within 2 h ( $T_s$ , mm) and during the experimental period (7:00–19:00)  $T_l$  (mm) were obtained as Equations (5) and (6):

$$T_s = \sum_{i=1}^n T_{ci} A_i t \quad (5)$$

where  $T_{ci}$  is individual transpiration rate ( $kg\ m^{-2}\ h^{-1}$ ),  $A_i$  is individual total leaf area ( $m^2$ ),  $t$  is the required measurement time, and  $n$  is the number of individuals.

$$T_l = \sum_{i=1}^n \frac{T_{si}}{\rho A} \quad (6)$$

where  $T_{si}$  is canopy transpiration (kg),  $\rho$  is water density ( $10^3\ kg\ m^{-3}$ ),  $A$  is the cross-section area of lysimeter ( $m^2$ ), and  $n$  is the number of measurements.

To evaluate the quality of the up-scaling of the transpiration, linear regression graphs of the Lysimeter measurements and the LI-6400XT extrapolation were drawn together with the 1:1 line. The root mean squared error (RMSE) was used as a criterion to judge the accuracy and reliability of the simulated values for the leaf levels. As RMSE is an indication of both bias and variance from the 1:1 line, it provides an effective measure of how well the values of two methods compare. Low RMSE values indicate better agreement [38]. The slope and correlation coefficient of the linear regression should be close to one. Points of good quality extrapolation should lie close to the 1:1 line, and assuming there is no model error, the measured and simulated values should be identical and all points should lie on the 1:1 line [8].

#### 2.2.4. Precipitation and Meteorological Variables

The details of the measurement of event-based precipitation and meteorological variables were demonstrated by Wang et al. [39] and Zhang et al. [28]. In order to understand the depth and distribution of precipitation based on the daily time scale in the given year of 2015, we assigned an individual day of recorded precipitation to a rain event.

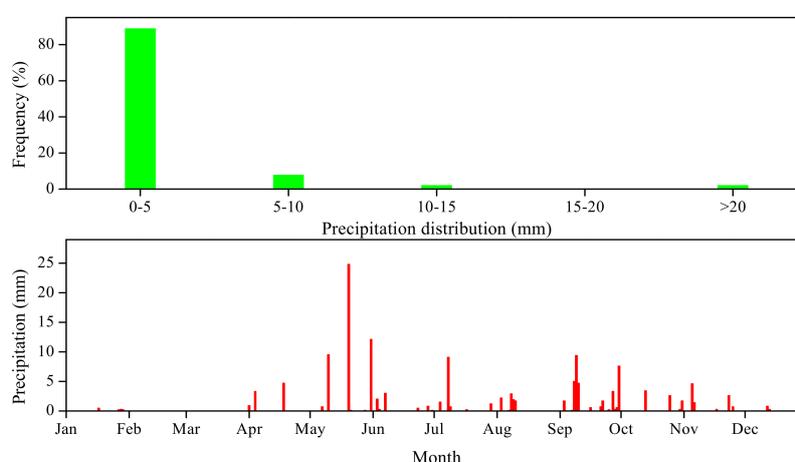
#### 2.2.5. Statistical Analysis

All the descriptive statistics were performed with SAS version 9.2 (SAS Institute Inc., Cary, NC, USA). Paired sample  $t$ -tests were performed to identify whether the soil matric potential, soil temperature,  $L_s$ , WUE and  $T$  rates of *R. soongorica* were significantly different from that of *S. passerina* at the 5% significance level. Correlation between transpiration and meteorological factors was determined using Pearson correlation analysis ( $p < 0.05$ ). We used Origin version 8.1 (OriginLab Corp., Northampton, MA, USA) to fit all curves.

### 3. Results

#### 3.1. Precipitation and Soil Environment

The year 2015 was a relatively dry year with a total precipitation amount of 140.2 mm, which is lower than the long-term average of 188.2 mm, and 59% of its annual precipitation was mainly concentrated during May and September. The highest precipitation occurred in May with 47.3 mm, while the lowest occurred in June with only 6.7 mm. The precipitation was fairly heterogeneous, apparently, in all months during the growing season. The precipitation events between 0–5 mm accounted for 88.7% of the annual precipitation events (53), followed by events between 5–10 mm, 10–15 mm, 15–20 mm, >20 mm, accounting for 7.5%, 1.9%, 0%, 1.9%, respectively. Therefore, May was relatively distinctly moist, with the highest rainfall, and July was a relatively distinct dry period, with higher temperature and lower rainfall input during the growing season (Figure 1).



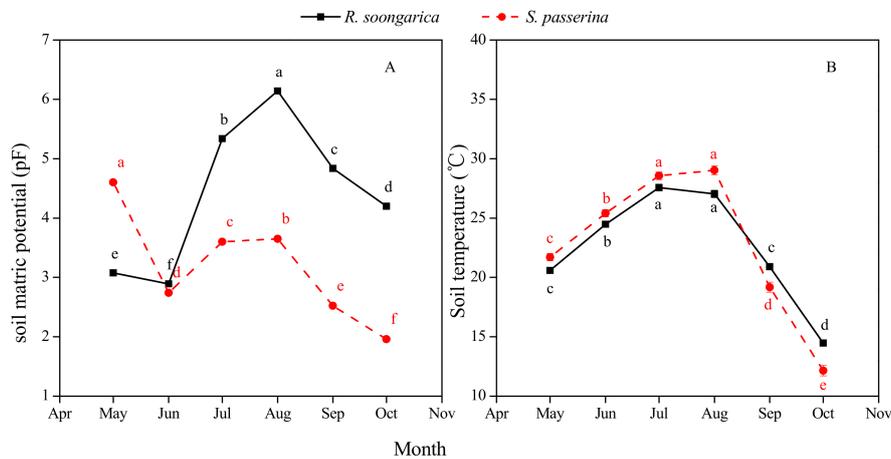
**Figure 1.** Precipitation and precipitation distribution in 2015.

The soil matric potential ( $\psi_m$ ) and soil temperature ( $T_{soil}$ ) at the soil depth 0–40 cm (topsoil) were observed for *R. soongorica* and *S. passerina* during the growing season. As can be seen from Figure 2A,B, the  $\psi_m$  and  $T_{soil}$  in the topsoil soil layer of *R. soongorica* and *S. passerina* showed significant seasonal fluctuation ( $p < 0.05$ ) and a similar trend. The  $\psi_m$  of *R. soongorica* and *S. passerina* gradually increased from the lowest value in June to the highest value in August. Simultaneously, the  $T_{soil}$  gradually increased from the lowest value in May to the highest value in August. Subsequently, due to the high precipitation that occurred in September, the  $\psi_m$  and  $T_{soil}$  decreased significantly until October. However, there was no significant difference between the  $\psi_m$  of *R. soongorica* and the  $\psi_m$  of *S. passerina*, or between the  $T_{soil}$  of *R. soongorica* and the  $T_{soil}$  of *S. passerina*.

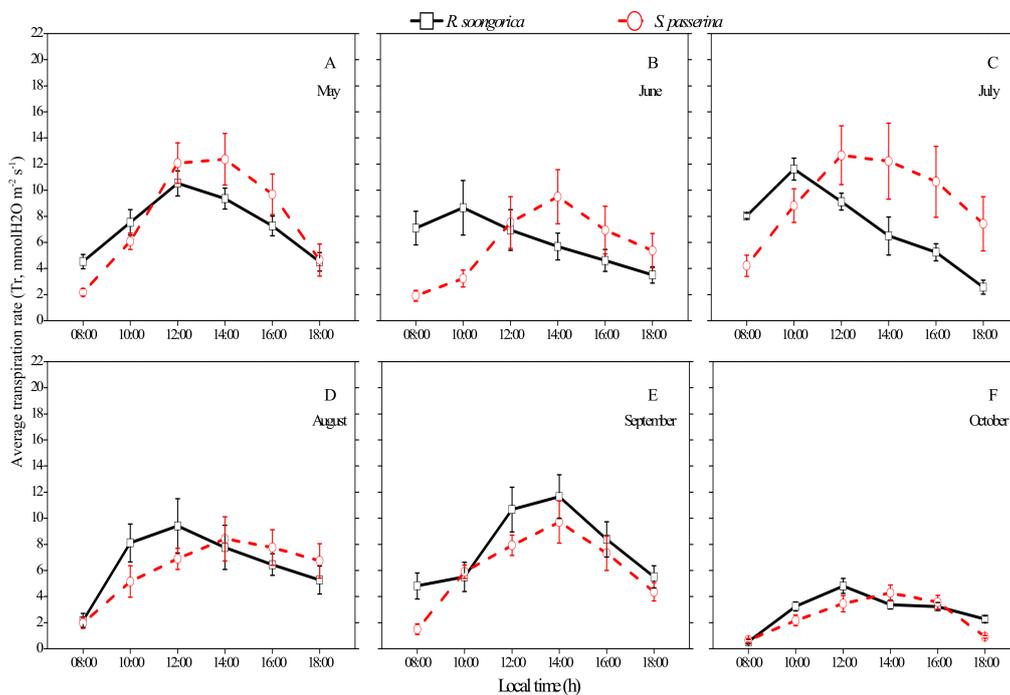
#### 3.2. Daily and Seasonal Patterns of $T_r$

The observed daily leaf  $T_r$  in *R. soongorica* and *S. passerina* exhibited distinct seasonal patterns, with the highest mean values occurring in September and July, respectively. Both generally exhibited an increasing pattern at the beginning of the day and then showed a declining change after reaching the peak at different times (Figure 3). The  $T_r$  of *R. soongorica* was higher than that of *S. passerina*, since it began to increase, but with the passage of time the  $T_r$  of *S. passerina* was gradually higher than that of *R. soongorica* during the later months of the growing season, although the changes were statistically insignificant between *R. soongorica* and *S. passerina*. In contrast, *R. soongorica* maintained a higher  $T_r$  than *S. passerina* in September. Overall, the  $T_r$  for both plants changed with the time of day, with a single-peak curve with various peak appearance times during different stages of growth, which indicates that there was no obvious ‘noon break’ phenomenon or midday depression for *R. soongorica* and *S. passerina*. The  $T_r$  of *R. soongorica* increased gradually before 12:00 a.m. and then decreased with

the same diurnal variation, except in September. The peak of  $T_r$  of *R. soongorica* occurred at 2:00 p.m. in September. However,  $T_r$  of *S. passerina* was increased gradually before 2:00 p.m. and then decreased during the growing season, although it showed a statistically indistinguishable peak of  $T_r$  at 12:00 a.m. in July. The maximum daily mean  $T_r$  of *R. soongorica* and *S. passerina* appeared in September and July, with a value of 7.76 and 9.33  $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ , respectively (Figure 3C,E).



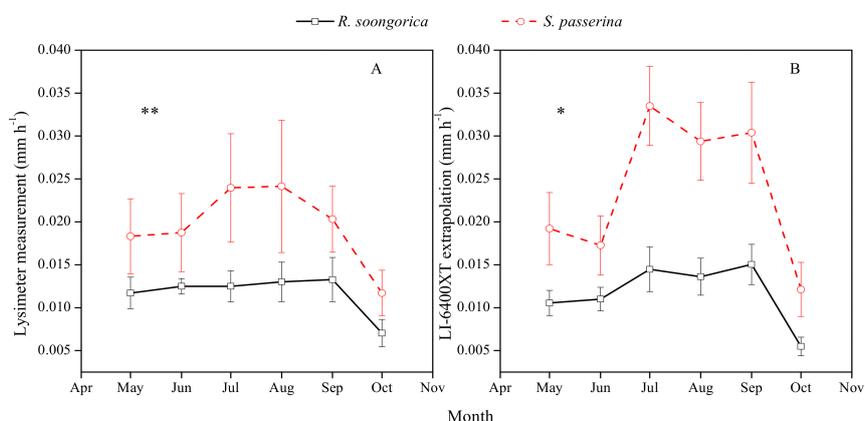
**Figure 2.** Seasonal changes in soil matric potential (A) and soil temperature (B) at a soil depth of 0–40 cm for *R. soongorica* and *S. passerina*. Error bars are standard errors of the mean ( $n = 30$  or  $31$ ). Different lowercase letters indicate significant differences among the months at  $p < 0.05$ .  $pF = \log(-hPa)$ ;  $pF > 4.2$ , no plant-available water;  $pF = 4.2$ , permanent wilting point;  $pF = 1.8$ – $2.5$ , field capacity.



**Figure 3.** Diurnal changes in the average transpiration rate for *R. soongorica* and *S. passerina* during the experimental period.

The seasonal  $T_r$  of *R. soongorica* was significantly ( $p < 0.05$ ) lower than that of *S. passerina* (Figure 4). *R. soongorica* had its maximum value of  $T_r$  in September; for *S. passerina* the maximum value was recorded in July. The maximum average transpiration rates of *R. soongorica* and *S. passerina* were

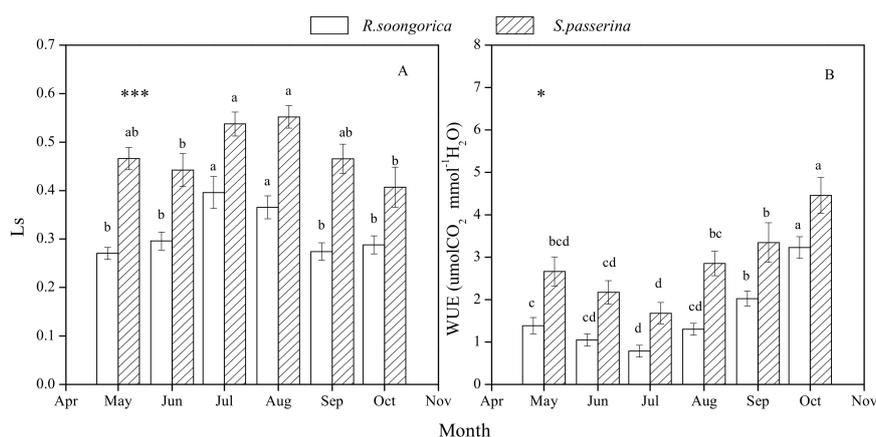
0.015 mm h<sup>-1</sup> and 0.034 mm h<sup>-1</sup> based on LI-6400XT extrapolation, and they were 0.013 mm h<sup>-1</sup> and 0.024 mm h<sup>-1</sup> according to lysimeter measurements, respectively.



**Figure 4.** Seasonal changes of the hourly transpiration rate of *R. soongorica* and *S. passerina* by Lysimeter measurement (A) and LI-6400XT extrapolation (B) during the experimental period. Asterisks indicate significant differences between *R. soongorica* and *S. passerina* during the experimental period: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ .

### 3.3. L<sub>s</sub> and WUE Seasonal Changes

With respect to seasonal changes, there was an apparent trend in L<sub>s</sub> and the instantaneous WUE of *R. soongorica* and *S. passerina* (Figure 5). *S. passerina* had higher L<sub>s</sub> and instantaneous WUE compared to *R. soongorica*. The L<sub>s</sub> value of *R. soongorica* was significantly high in July and August. Although the L<sub>s</sub> value of *S. passerina* was also relatively high in July and August, it was not statistically significant compared to May and September. The instantaneous WUE of *R. soongorica* and *S. passerina* were the lowest in July, with values of 0.78 and 1.68 μmol CO<sub>2</sub> mmol<sup>-1</sup> H<sub>2</sub>O, respectively. *R. soongorica* and *S. passerina* showed different strategies in adapting to the environment, as C<sub>3</sub> and C<sub>4</sub> desert xerophytic shrubs [32]. The C<sub>3</sub> shrub *R. soongorica* was drought resistant type, and the C<sub>4</sub> shrub *S. passerina* was the high water use efficiency type.



**Figure 5.** Seasonal changes in stomatal limitation (A) and instantaneous water use efficiency (B) of *R. soongorica* and *S. passerina*. Different lowercase letters indicate significant differences among the months ( $p < 0.05$ ). Asterisks indicate significant differences between *R. soongorica* and *S. passerina* in stomatal limitation and instantaneous water use efficiency during the experimental period: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ .

### 3.4. Analysis of the Factors Influencing Transpiration at the Leaf and Canopy Scale

Correlation coefficients between the  $T_r$  of the two shrubs and the influencing factors are provided in Tables 2 and 3, respectively.

**Table 2.** Summary of correlations (Pearson) between the transpiration rates ( $T_r$ ,  $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) of *R. soongorica* and other gas exchange parameters.

Month	$g_s$	$T_1$	$T_{\text{leaf}}$	$RH_1$	PAR	VPD <sub>1</sub>	A
May	0.2077	0.7857 ***	0.7952 ***	−0.2137	0.7104 ***	0.6960 ***	−0.1373
Jun.	0.7149 ***	−0.2673	−0.2874	0.5154 *	0.1098	−0.5996 **	0.8189 ***
Jul.	0.5572 **	0.0441	0.0737	0.4360 *	0.5456 **	−0.0287	0.5101 *
Aug.	0.4580 *	0.5642 **	0.5631 **	−0.3076	0.6200 **	0.4411 *	0.7516 ***
Sep.	0.3530	0.7056 ***	0.7205 ***	−0.5480 **	0.5785 **	0.6820 ***	0.7556 ***
Oct.	0.7081 ***	0.8440 ***	0.8629 ***	−0.7627 ***	0.8169 ***	0.8539 ***	0.8845 ***

Asterisks indicate a significant correlation between measurements at: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ .

**Table 3.** Summary of correlations (Pearson) between transpiration rates ( $T_r$ ,  $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) of *S. passerina* and other gas exchange parameters.

Month	$g_s$	$T_1$	$T_{\text{leaf}}$	$RH_1$	PAR	VPD <sub>1</sub>	A
May	0.7807 ***	0.8234 ***	0.8264 ***	−0.3549	0.8397 ***	0.8381 ***	0.7071 ***
Jun.	0.6717 ***	0.6453 ***	0.6654 ***	−0.3065	0.4962 *	0.5554 **	0.7154 ***
Jul.	0.7225 ***	0.5963 **	0.6242 **	−0.0541	0.7028 ***	0.4980 *	0.5786 **
Aug.	0.6735 ***	0.7353 ***	0.7447 ***	−0.4890 *	0.7152 ***	0.6142 **	0.7395 ***
Sep.	0.2939	0.7605 ***	0.7685 ***	−0.5593 **	0.7855 ***	0.6872 ***	0.7084 ***
Oct.	0.6213 **	0.8892 ***	0.8920 ***	−0.6171 **	0.6077 **	0.8639 ***	0.8969 ***

Asterisks indicate a significant correlation between measurements at: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ .

At the leaf level, we found that the factors influencing  $T_r$  changed with the changing seasons, especially for *R. soongorica*, under the stress of high temperatures and drought, and the factors influencing  $T_r$  were obviously different. The relationship between  $T_r$  and environmental factors was obviously different from the other months in June and July, which had higher average temperatures,  $\psi_m$ , and a lower precipitation input. For example, there was a negative correlation between  $T_r$  and  $T_1$  and  $T_{\text{leaf}}$ , a significant positive correlation between  $T_r$  and  $RH$  ( $p < 0.05$ ) and a negative correlation between  $T_r$  and  $VPD_1$  ( $p < 0.01$ ) in June.

At the canopy level, the  $T_r$  of *R. soongorica* was significantly ( $p < 0.05$ ) lower than that of *S. passerina* (Figure 4). As can be seen from Table 4, both the  $T_r$  of *R. soongorica* and *S. passerina* were mainly affected by  $R_n$  and  $T_{\text{air}}$ , and the  $T_r$  of *S. passerina* was also sensitive to changes in vapor pressure deficit (VPD). In addition, the accumulated transpiration of *R. soongorica* showed a significant positive correlation with accumulated rainfall ( $p < 0.01$ ) and canopy height ( $p < 0.05$ ), respectively, whereas the cumulative transpiration of *S. passerina* was positively correlated with cumulative rainfall, canopy height, canopy projection area, and new shoot length (Table 5). The transpiration of *R. soongorica* was negatively correlated with  $\psi_m$ , whereas the transpiration of *S. passerina* was positively correlated with  $\psi_m$ , and the transpiration of *S. passerina* was significantly positively correlated with  $T_{\text{soil}}$  (Table 6).

**Table 4.** Summary of correlations (Pearson) between the transpiration rates ( $T_r$ ,  $\text{mm h}^{-1}$ ) and meteorological factors at the canopy level.

Shrubs	Measurement Methods	$R_n$ ( $\text{W m}^{-2}$ )	Wind Speed ( $\text{m s}^{-1}$ )	$T_{\text{air}}$ ( $^{\circ}\text{C}$ )	RH (%)	VPD (kPa)
<i>R. soongorica</i>	Lysimeter	0.6549 ***	−0.0297	0.4058 *	−0.0762	0.2026
	LI-6400XT	0.5430 ***	−0.2128	0.4177 *	−0.0347	0.2182
<i>S. passerina</i>	Lysimeter	0.7106 ***	0.4763 **	0.6000 ***	−0.5324	0.6923 ***
	LI-6400XT	0.7514 ***	0.1864	0.6220 ***	−0.5623	0.6972 ***

$R_n$ , net radiation;  $RH$ , relative humidity;  $T_{\text{air}}$ , air temperature;  $VPD$ , vapor pressure deficit. Asterisks indicate a significant correlation between measurements at: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ .

**Table 5.** Summary of correlations (Pearson) between the accumulated transpiration (mm) by Lysimeter measurement and the accumulated rainfall and shrubs morphological traits during the experimental period.

Shrubs	Accumulated Rainfall (mm)	Canopy Height (cm)	Canopy Projection Area ( $\times 100 \text{ cm}^2$ )	New Shoot Length (cm)	LAI ( $\text{m}^2 \text{ m}^{-2}$ )
<i>R. soongorica</i>	0.9226 **	0.9042 *	0.7423	0.7935	0.5070
<i>S. passerina</i>	0.9558 **	0.9275 **	0.9842 ***	0.9585 **	0.1482

Asterisks indicate a significant correlation between measurements at: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ .

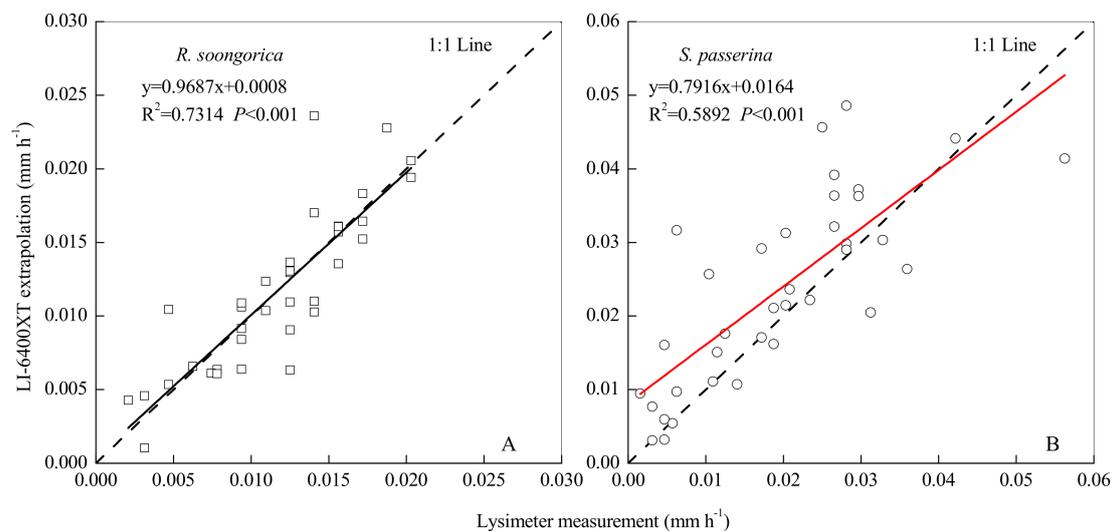
**Table 6.** Summary of correlations (Pearson) between the transpiration ( $\text{mm d}^{-1}$ ) by Lysimeter measurement and the soil matric potential ( $\psi_m$ ) and the soil temperature ( $T_{\text{soil}}$ ) at a depth of 0–40 cm during the experimental period.

Shrubs	Soil Matric Potential (pF)	Soil Temperature ( $^{\circ}\text{C}$ )
<i>R. soongorica</i>	−0.6948	0.3171
<i>S. passerina</i>	0.5977	0.9171 **

Asterisks indicate a significant correlation between measurements at: \*\*  $p < 0.01$ .

### 3.5. Scaling Up Transpiration from Leaf to Canopy Level

The seasonal changes in the hourly T rate of *R. soongorica* and *S. passerina*, as measured by lysimeters and found using Equations (3) and (4), and as approximated by up-scaling the LI-6400XT measurements with Equations (5) and (6), exhibited remarkable agreement. The RMSE was 0.003 and 0.008  $\text{mm h}^{-1}$  for *R. soongorica* and *S. passerina*, respectively (Figure 6). Moreover, the observed versus simulated transpiration values fell around the 1:1 line, which means that the LI-6400XT extrapolation was accurate and reasonable ( $R^2 = 0.7314$  for *R. soongorica* and  $R^2 = 0.5892$  for *S. passerina*,  $p < 0.001$ ). The results of both methods indicated that the average hourly transpiration rate of *S. passerina* throughout the growing season was greater than that of *R. soongorica* (Figure 4).



**Figure 6.** Relationships between Lysimeter measurements (A) and LI-6400XT extrapolation (B).

## 4. Discussion

At the leaf level, our findings indicated how the magnitude of the  $T_r$  of the  $C_3$  shrub *R. soongorica* and the  $C_4$  shrub *S. passerina* changed within a day (Figure 3). This does not agree well with

Su et al. [32], whose study suggested that the C<sub>4</sub> shrub *S. passerina* had advantages over the C<sub>3</sub> shrub *R. soongorica* through lower  $T_r$ , especially when moisture is limited. The potential causes of this are the differences in plant growth status and environmental factors (e.g., meteorological and edaphic factors). Moreover, transpiration was lower in the C<sub>4</sub> than in the C<sub>3</sub> plants for a given photosynthetic capacity [40]. Nevertheless, the results were in line with previous finding by Su et al. [32], that the C<sub>4</sub> shrub *S. passerina* has a higher WUE (Figure 5B), since the C<sub>4</sub> pathway results in a higher WUE, with a higher efficiency utilization of low intercellular CO<sub>2</sub> concentrations at the leaf level [39]. Stomata control determines the WUE of a plant by optimizing the water lost against the carbon gained [41]. Su et al. [32] also showed that the associated growth of the C<sub>3</sub> shrub *R. soongorica* and the C<sub>4</sub> shrub *S. passerina* decreased the  $T_r$  of the whole community, whereas both *R. soongorica* and *S. passerina* existed as individuals in our study. C<sub>3</sub> and C<sub>4</sub> plants have different environmental adaptation strategies, responding differently to environmental factors [42]. C<sub>4</sub> plants had an advantage compared to C<sub>3</sub> plants due to a decrease in transpiration under the same drought conditions [43]. Furthermore, the C<sub>4</sub> photosynthetic mechanism equips plants with a valuable competitive advantage under conditions of high-light intensity, high temperatures and low water availability, exerting a tighter control over water balance [44]. The 'short-term' stomata control responses of plants include stomata aperture changes in response to the availability of water, light, temperature, wind speed, and carbon dioxide [40]. According to the correlations between  $T_r$  and  $g_s$  and environmental factors, we can easily find that the  $T_r$  of the C<sub>3</sub> shrub *R. soongorica* and C<sub>4</sub> shrub *S. passerina* was mainly affected by nonstomatal factors in May and September, respectively. It can be concluded that under the conditions of relatively adequate soil available water, the main influencing factors on the  $T_r$  of the C<sub>3</sub> shrub *R. soongorica* and the C<sub>4</sub> shrub *S. passerina* are nonstomatal factors, i.e., environmental factors. The high temperature response observed in the  $T_r$  of the C<sub>4</sub> shrub *S. passerina* was clearly advantageous for the maintenance of high productivity in the desert, whereas the negative or slightly positive high temperature response observed in the  $T_r$  of the C<sub>3</sub> shrub *R. soongorica* was essential for its survival under harsh conditions (Tables 2 and 3). When the air temperatures were below 35 °C, the average leaf temperatures were above the air temperature by an amount dependent on wind velocity, and the increasing wind diminished transpiration. When air temperatures were above 35 °C, the leaf temperatures were below the air temperatures, and increasing wind markedly increased transpiration [45]. The negative response of the  $T_r$  of the C<sub>3</sub> shrub *R. soongorica* to the leaf-to-air vapor pressure deficit in June and July could be explained as an adaptation of the C<sub>3</sub> shrub *R. soongorica* to long dry periods, during which the shrub was forced to maintain a minimum  $g_s$  to continue functioning [21]. The negative response of the  $T_r$  of the C<sub>3</sub> shrub *R. soongorica* to the net carbon assimilation rate (A) was due to the high evaporative demand as well as the limitation of A by the intercellular CO<sub>2</sub> increases with temperature (Table 3).

At the canopy level, both the  $T_r$  of the C<sub>3</sub> shrub *R. soongorica* and the C<sub>4</sub> shrub *S. passerina* were well associated with the  $R_n$  and  $T_{air}$ , and the  $T_r$  of the C<sub>4</sub> shrub *S. passerina* is also sensitive to changes in VPD (Table 4). Transpiration is controlled by radiation as the rate of production of water vapor inside the leaf is driven by absorbed radiation [46]. Furthermore, rainfall was the main factor influencing the transpiration amount of the C<sub>3</sub> shrub *R. soongorica* and the C<sub>4</sub> shrub *S. passerina* during the growing season. Canopy height had a significant effect on the transpiration of the C<sub>3</sub> shrub *R. soongorica*, and the transpiration of the C<sub>3</sub> shrub *R. soongorica* was influenced by canopy height, canopy projection area and new shoot length (Table 5). As for edaphic influences on the transpiration of the C<sub>3</sub> shrub *R. soongorica* and the C<sub>4</sub> shrub *S. passerina* during the growing season, our study observed the soil matric potential and soil temperature impact on transpiration. The results indicated that the transpiration responses of the C<sub>3</sub> shrub *R. soongorica* and the C<sub>4</sub> shrub *S. passerina* to soil matric potential were opposite, since the C<sub>3</sub> shrub *R. soongorica* had less plant-available soil water compared to the C<sub>4</sub> shrub *S. passerina* (Figure 2). Transpiration was not affected by soil moisture under well-watered conditions [47]. When the soil matric potential exceeds the field capacity (e.g., pF > 2.5), plants start reducing transpiration by closing their stomata to prevent internal water loss [48]. In summary, how the transpiration of xerophytic shrubs responds to soil moisture depends on the

available soil water content. The transpiration of the C<sub>3</sub> shrub *R. soongorica* and the C<sub>4</sub> shrub *S. passerina* responded positively to soil temperature, and this response was statistically significant for *S. passerina* (Table 6). A possible explanation for this may be that the soil water content was negatively correlated with soil temperature at moderate-to-high water contents [49]. Transpiration increases with high soil temperature due to the fact that higher temperature promotes the absorption of soil water by the roots of the plant [50].

The purpose of our study was to demonstrate whether it is feasible to approximately estimate the transpiration of xerophytic shrubs using the scaling approach in the absence of a lysimeter. The results proved successful for up-scaling the transpiration of C<sub>3</sub> and C<sub>4</sub> xerophytic shrubs from the leaf to the canopy level using the unified scaling factor (e.g., leaf area). The results are comparable to Huang et al. [25], Zhao and Zhao [13], and Gitz III et al. [13], whose research involved up-scaling from the leaf to the individual or canopy level. Although long-term transpiration continuously determined by a LI-6400XT portable photosynthesis system is difficult due to the influence of micrometeorological factors and artificial operation, there is no doubt that transpiration can be effectively and accurately measured using the LI-6400XT method within a short time. This may be explained by the high coefficient of determination between the canopy transpiration rate found using the LI-6400XT and that found by lysimeter measurement ( $R^2 = 0.7314$  for *R. soongorica* and  $R^2 = 0.5892$  for *S. passerina*) (Figure 6), between the daily transpiration rate using the LI-6400XT and that found by using stem heat balance measurement ( $R^2 = 0.67$  for *C. korshinskii* and  $R^2 = 0.77$  for *A. ordosica*) [8], between canopy transpiration found using LI-6400XT and that found using the FAO-56 dual crop coefficient method ( $R^2 = 0.66$  for maize) [13], as well as between the canopy transpiration found using the LI-6400XT and that found using the canopy evapo-transpiration and assimilation (CETA) chamber system ( $R^2 = 0.94$  for cotton) [17]. Transpiration up-scaling from leaf-level measurements was much higher than lysimeter measurement due to many errors. For example, a certain error was due to the selected leaves where the leaf transpiration was measured. The leaf area obtained from photograph processing and integration also led to some error. Moreover, the monitored leaf transpiration values often fluctuate during measurement, which also leads to some errors. This discrepancy may also be due to the error caused by the fact that scaling up leaf-level measurements assumes that all leaves within the canopy receive equal ambient radiation [51].

## 5. Conclusions

At the leaf level, the transpiration rates of the C<sub>3</sub> shrub *R. soongorica* and the C<sub>4</sub> shrub *S. passerina* showed unimodal trends throughout the growing season. The dependence of the transpiration rates on stomatal conductance and meteorological factors varied seasonally. At the canopy level, the transpiration rates dependent on net radiation and air temperature and the transpiration rates of the C<sub>4</sub> shrub *S. passerina* were also dependent on the vapor pressure deficit. The transpiration amount depended on rainfall, the morphological traits of the shrubs (e.g., canopy height for C<sub>3</sub> shrub *R. soongorica*, canopy height, canopy projection area and new shoot length for C<sub>4</sub> shrub *S. passerina*), and soil temperature (particularly for the C<sub>4</sub> shrub *S. passerina*). The linearly-fitted regression between the actual measurement and the normalized leaf-area-based extrapolation showed that the leaf area is a reliable up-scaling factor for the transpiration of xerophytic shrubs from the leaf level to the canopy level in desert regions (with low a RMSE value of  $\pm 0.005 \text{ mm h}^{-1}$ ). The reliability of the extrapolated values is evidenced by the significant regression relationship between the measured and the up-scaling values. Our study suggests that canopy transpiration rates can be estimated by up-scaling leaf-level transpiration rates, which is useful for the estimation of whole-plant transpiration for crops and for xerophytic shrubs. Our study not only provides an experimental basis for the transpiration water consumption of potential C<sub>3</sub> and C<sub>4</sub> xerophytic shrubs in the study area, but also provides important data support and methodological references for research into the water balance and ecological water requirements at regional scales.

**Author Contributions:** Y.J. and X.W. conceived and designed the experiments; Y.J. performed the experiments, analyzed the data and wrote the manuscript; Y.Z. contributed significantly to writing and revising the manuscript; Y.P., R.H. helped perform the experiments. All authors reviewed the paper.

**Acknowledgments:** This work was funded by one of National Key Research and Development Program of China (2016YFE0203400), the National Natural Science Foundation of China (Grant Nos. 41771101 and 41530750).

**Conflicts of Interest:** The authors declare no conflict of interest.

## References

- Schlesinger, W.H.; Jasechko, S. Transpiration in the global water cycle. *Agric. For. Meteorol.* **2014**, *189–190*, 115–117. [[CrossRef](#)]
- Jasechko, S.; Sharp, Z.D.; Gibson, J.J.; Birks, S.J.; Yi, Y.; Fawcett, P.J. Terrestrial water fluxes dominated by transpiration. *Nature* **2013**, *496*, 347. [[CrossRef](#)] [[PubMed](#)]
- Good, S.P.; Noone, D.; Bowen, G. Hydrologic connectivity constrains partitioning of global terrestrial water fluxes. *Science* **2015**, *349*, 175–177. [[CrossRef](#)] [[PubMed](#)]
- Reynolds, J.F.; Kemp, P.R.; Tenhunen, J.D. Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the chihuahuan desert: A modeling analysis. *Plant Ecol.* **2000**, *150*, 145–159. [[CrossRef](#)]
- Ham, J.M.; Heilman, J.L.; Lascano, R.J. Determination of soil water evaporation and transpiration from energy balance and stem flow measurements. *Agric. For. Meteorol.* **1990**, *52*, 287–301. [[CrossRef](#)]
- Evetts, S.R.; Howell, T.A.; Schneider, S.; Arland, D.; Copeland, K.S.; Dusek, D.A.; Brauer, D.K.; Tolck, J.A.; Marek, G.W.; Marek, T.M.; et al. The bushland weighing lysimeters: A quarter century of crop et investigations to advance sustainable irrigation. *Trans. ASABE* **2016**, *59*, 163. [[CrossRef](#)]
- Meinzer, F.C. Stomatal control of transpiration. *Trends Ecol. Evol.* **1993**, *8*, 289–294. [[CrossRef](#)]
- Huang, L.; Zhang, Z.S.; Li, X.R. The extrapolation of the leaf area-based transpiration of two xerophytic shrubs in a revegetated desert area in the Tengger Desert, China. *Hydrol. Res.* **2015**, *46*, 389–399. [[CrossRef](#)]
- Ivanova, L.A.; Ivanov, L.A.; Ronzhina, D.A.; Tserenkhand, G.; Tsoog, S.; Bazha, S.N.; Gunin, P.D. Leaf and biomass traits of mongolian forest-steppe shrubs linking to their ecological properties. *Arid Ecosyst.* **2012**, *2*, 45–53. [[CrossRef](#)]
- Barbour, M.M.; Hunt, J.E.; Walcroft, A.S.; Rogers, G.N.D.; McSeveny, T.M.; Whitehead, D. Components of ecosystem evaporation in a temperate coniferous rainforest, with canopy transpiration scaled using sapwood density. *New Phytol.* **2005**, *165*, 549–558. [[CrossRef](#)] [[PubMed](#)]
- Herbst, M.; Kappen, L.; Thamm, F.; Vanselow, R. Simultaneous measurements of transpiration, soil evaporation and total evaporation in a maize field in northern germany. *J. Exp. Bot.* **1996**, *47*, 1957–1962. [[CrossRef](#)]
- Ávila-Lovera, E.; Zerpa, A.J.; Santiago, L.S. Stem photosynthesis and hydraulics are coordinated in desert plant species. *New Phytol.* **2017**, *216*, 1119–1129. [[CrossRef](#)] [[PubMed](#)]
- Zhao, L.W.; Zhao, W.Z. Canopy transpiration obtained from leaf transpiration, sap flow and fao-56 dual crop coefficient method. *Hydrol. Process.* **2015**, *29*, 2983–2993. [[CrossRef](#)]
- Karam, F.; Breidy, J.; Stephan, C.; Roupheal, J. Evapotranspiration, yield and water use efficiency of drip irrigated corn in the bekaa valley of lebanon. *Agric. Water Manag.* **2003**, *63*, 125–137. [[CrossRef](#)]
- Baker, J.T.; Gitz, D.C.; Payton, P.; Wanjura, D.F.; Upchurch, D.R. Using leaf gas exchange to quantify drought in cotton irrigated based on canopy temperature measurements. *Agron. J.* **2007**, *99*, 637–644. [[CrossRef](#)]
- Jones, H.G. Use of thermography for quantitative studies of spatial and temporal variation of stomatal conductance over leaf surfaces. *Plant Cell Environ.* **1999**, *22*, 1043–1055. [[CrossRef](#)]
- Gitz, D.C., III; Baker, J.T.; Lascano, R.J. Scaling leaf measurements to estimate whole canopy gas exchanges of cotton. *Am. J. Plant Sci.* **2016**, *7*, 1952–1963. [[CrossRef](#)]
- Gitz, D.C., III; Baker, J.T.; Lascano, R.J. Relating xylem cavitation to gas exchange in cotton. *Am. J. Plant Sci.* **2015**, *6*, 10. [[CrossRef](#)]
- Kim, J.; Verma, S.B. Modeling canopy photosynthesis: Scaling up from a leaf to canopy in a temperate grassland ecosystem. *Agric. For. Meteorol.* **1991**, *57*, 187–208. [[CrossRef](#)]

20. Irmak, S.; Mutiibwa, D.; Irmak, A.; Arkebauer, T.J.; Weiss, A.; Martin, D.L.; Eisenhauer, D.E. On the scaling up leaf stomatal resistance to canopy resistance using photosynthetic photon flux density. *Agric. For. Meteorol.* **2008**, *148*, 1034–1044. [[CrossRef](#)]
21. Infante, J.M.; Rambal, S.; Joffre, R. Modelling transpiration in holm-oak savannah: Scaling up from the leaf to the tree scale. *Agric. For. Meteorol.* **1997**, *87*, 273–289. [[CrossRef](#)]
22. Van der Zande, D.; Mereu, S.; Nadezhkina, N.; Cermak, J.; Muys, B.; Coppin, P.; Manes, F. 3d upscaling of transpiration from leaf to tree using ground-based lidar: Application on a mediterranean holm oak (*quercus ilex* L.) tree. *Agric. For. Meteorol.* **2009**, *149*, 1573–1583. [[CrossRef](#)]
23. Zhang, Z.S.; Zhao, Y.; Li, X.R.; Huang, L.; Tan, H.J. Gross rainfall amount and maximum rainfall intensity in 60-minute influence on interception loss of shrubs: A 10-year observation in the tengger desert. *Sci. Rep.* **2016**, *6*, 26030. [[CrossRef](#)] [[PubMed](#)]
24. Loik, M.E.; Breshears, D.D.; Lauenroth, W.K.; Belnap, J. A multi-scale perspective of water pulses in dryland ecosystems: Climatology and ecohydrology of the western USA. *Oecologia* **2004**, *141*, 269–281. [[CrossRef](#)] [[PubMed](#)]
25. Huang, L.; Zhang, Z.S. Effect of rainfall pulses on plant growth and transpiration of two xerophytic shrubs in a revegetated desert area: Tengger Desert, China. *Catena* **2016**, *137*, 269–276. [[CrossRef](#)]
26. Li, X.R.; Xiao, H.L.; Zhang, J.G.; Wang, X.P. Long-term ecosystem effects of sand-binding vegetation in the Tengger Desert, Northern China. *Restor. Ecol.* **2004**, *12*, 376–390. [[CrossRef](#)]
27. Li, X.R.; Kong, D.S.; Tan, H.J.; Wang, X.P. Changes in soil and vegetation following stabilisation of dunes in the southeastern fringe of the Tengger Desert, China. *Plant Soil* **2007**, *300*, 221–231. [[CrossRef](#)]
28. Zhang, Y.F.; Wang, X.P.; Hu, R.; Pan, Y.X. Throughfall and its spatial variability beneath xerophytic shrub canopies within water-limited arid desert ecosystems. *J. Hydrol.* **2016**, *539*, 406–416. [[CrossRef](#)]
29. Yin, H.X.; Yan, X.; Shi, Y.; Qian, C.J.; Li, Z.H.; Zhang, W.; Wang, L.R.; Li, Y.; Li, X.Z.; Chen, G.X.; et al. The role of East Asian monsoon system in shaping population divergence and dynamics of a constructive desert shrub *Reaumuria soongarica*. *Sci. Rep.* **2015**, *5*, 15823. [[CrossRef](#)] [[PubMed](#)]
30. Liu, Y.B.; Liu, M.L.; Li, X.R.; Cao, B.; Ma, X.F. Identification of differentially expressed genes in leaf of *Reaumuria soongarica* under peg-induced drought stress by digital gene expression profiling. *PLoS ONE* **2014**, *9*, e94277. [[CrossRef](#)] [[PubMed](#)]
31. He, M.Z.; Zhang, K.; Tan, H.J.; Hu, R.; Su, J.Q.; Wang, J.; Huang, L.; Zhang, Y.F.; Li, X.R. Nutrient levels within leaves, stems, and roots of the xeric species *Reaumuria soongarica* in relation to geographical, climatic, and soil conditions. *Ecol. Evol.* **2015**, *5*, 1494–1503. [[CrossRef](#)] [[PubMed](#)]
32. Su, P.X.; Yan, Q.D.; Xie, T.T.; Zhou, Z.J.; Gao, S. Associated growth of C<sub>3</sub> and C<sub>4</sub> desert plants helps the C<sub>3</sub> species at the cost of the C<sub>4</sub> species. *Acta Physiologiae Plantarum* **2012**, *34*, 2057–2068. [[CrossRef](#)]
33. Yang, H.T.; Li, X.R.; Liu, L.C.; Jia, R.L.; Wang, Z.R.; Li, X.J.; Li, G. Biomass allocation patters of four shrubs in desert grassland. *J. Desert Res.* **2013**, *33*, 1340–1348. [[CrossRef](#)]
34. Youssef, T.; Awad, M.A. Mechanisms of enhancing photosynthetic gas exchange in date palm seedlings (*phoenix dactylifera* L.) under salinity stress by a 5-aminolevulinic acid-based fertilizer. *J. Plant Growth Regul.* **2007**, *27*, 1–9. [[CrossRef](#)]
35. Berry, J.A.; Downton, W.J.S. 9:-Environmental regulation of photosynthesis. In *Photosynthesis*; Academic Press: Cambridge, MA, USA, 1982; pp. 263–343.
36. Kidron, G.J. The effect of shrub canopy upon surface temperatures and evaporation in the Negev Desert. *Earth Surf. Process. Landf.* **2009**, *34*, 123–132. [[CrossRef](#)]
37. Zhao, W.Z.; Liu, B.; Chang, X.X.; Yang, Q.Y.; Yang, Y.T.; Liu, Z.L.; Cleverly, J.; Eamus, D. Evapotranspiration partitioning, stomatal conductance, and components of the water balance: A special case of a desert ecosystem in China. *J. Hydrol.* **2016**, *538*, 374–386. [[CrossRef](#)]
38. Irmak, S.; Howell, T.A.; Allen, R.G.; Payero, J.O.; Martin, D.L. Standardized ASCE penman-monteith: Impact of sum-of-hourly vs. 24-hour timestep computations at reference weather station sites. *Trans. ASABE* **2005**, *48*, 1063. [[CrossRef](#)]
39. Wang, X.P.; Zhang, Y.F.; Hu, R.; Pan, Y.X.; Xu, H.J.; Shi, W.; Jin, Y.X.; Yasuda, H. Revisit of event-based rainfall characteristics at shapotou area in northern china. *Sci. Cold Arid Reg.* **2016**, *8*, 0477–0484. [[CrossRef](#)]
40. Pearcy, R.W.; Ehleringer, J. Comparative ecophysiology of C<sub>3</sub> and C<sub>4</sub> plants. *Plant Cell Environ.* **1984**, *7*, 1–13. [[CrossRef](#)]

41. Haworth, M.; Elliott-Kingston, C.; McElwain, J.C. Stomatal control as a driver of plant evolution. *J. Exp. Bot.* **2011**, *62*, 2419–2423. [[CrossRef](#)] [[PubMed](#)]
42. Ehleringer, J.R.; Sage, R.F.; Flanagan, L.B.; Pearcy, R.W. Climate change and the evolution of C<sub>4</sub> photosynthesis. *Trends Ecol. Evol.* **1991**, *6*, 95–99. [[CrossRef](#)]
43. Yan, W.M.; Zhong, Y.Q.W.; Shangguan, Z.P. A meta-analysis of leaf gas exchange and water status responses to drought. *Sci. Rep.* **2016**, *6*, 20917. [[CrossRef](#)] [[PubMed](#)]
44. Moore, P.D. High hopes for c<sub>4</sub> plants. *Nature* **1994**, *367*, 322. [[CrossRef](#)]
45. Drake, B.G.; Raschke, K.; Salisbury, F.B. Temperature and transpiration resistances of leaves as affected by air temperature, humidity, and wind speed. *Plant Physiol.* **1970**, *46*, 324–330. [[CrossRef](#)] [[PubMed](#)]
46. Pieruschka, R.; Huber, G.; Berry, J.A. Control of transpiration by radiation. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 13372–13377. [[CrossRef](#)] [[PubMed](#)]
47. Vico, G.; Porporato, A. Modelling c<sub>3</sub> and c<sub>4</sub> photosynthesis under water-stressed conditions. *Plant Soil* **2008**, *313*, 187–203. [[CrossRef](#)]
48. Porporato, A.; Laio, F.; Ridolfi, L.; Rodriguez-Iturbe, I. Plants in water-controlled ecosystems: Active role in hydrologic processes and response to water stress: III. Vegetation water stress. *Adv. Water Resour.* **2001**, *24*, 725–744. [[CrossRef](#)]
49. Davidson, E.A.; Belk, E.; Boone, R.D. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Glob. Change Biol.* **1998**, *4*, 217–227. [[CrossRef](#)]
50. Abd El Rahman, A.A.; Batanouny, K.H. Transpiration of desert plants under different environmental conditions. *J. Ecol.* **1965**, *53*, 267–272. [[CrossRef](#)]
51. Amthor, J.S. Scaling CO<sub>2</sub>-photosynthesis relationships from the leaf to the canopy. *Photosynth. Res.* **1994**, *39*, 321–350. [[CrossRef](#)] [[PubMed](#)]



© 2018 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).