

The extrapolation of the leaf area-based transpiration of two xerophytic shrubs in a revegetated desert area in the Tengger Desert, China

L. Huang, Z. Zhang and X. Li

ABSTRACT

Plant transpiration plays a key role in sand-binding zones, but obtaining accurate estimates at an integrated leaf-individual-canopy scale is difficult. In this study, transpiration rates of two typical xerophytic shrubs, *Caragana korshinskii* and *Artemisia ordosica*, were investigated during the growing season (April–October) from 2008 to 2012 in the Tengger Desert, a revegetated desert area in China. Gas exchange techniques, sap flow measurements, and the crop evapotranspiration minus micro-lysimeter method were used to evaluate plant transpiration. Transpiration data were subsequently compared with the dynamical normalized leaf area-based extrapolation. The results indicated that at leaf level, the transpiration rates of *C. korshinskii* and *A. ordosica* were 2.67 and 4.51 mmol H₂O m⁻² s⁻¹, respectively. The sap flow rates were 0.071 and 0.086 g h⁻¹ cm⁻² at the tree level, and the transpiration rates were 0.42 and 0.35 mm d⁻¹ at the stand level. The total seasonal transpiration of the two xerophytic shrubs reached 71.79 and 55.62 mm, representing approximately 48.4 and 37.5% of the total rainfall over this period. Direct measurements of plant transpiration and upscaling transpiration from leaf level to the stand level exhibited good correspondence, which verified that leaf area was a reliable representation of scaled transpiration, especially in arid desert regions.

Key words | *Artemisia ordosica*, *Caragana korshinskii*, sap flow measurement, transpiration, upscaling

INTRODUCTION

Artificial vegetation restoration is considered to be one of the most effective ways to combat desertification and land degradation in arid desert areas (Wang 2004). Xerophytic shrubs, such as *Caragana korshinskii* and *Artemisia ordosica*, have been planted at the southeastern fringe of the Tengger Desert in Western China since 1956 (Li *et al.* 2004). The implementation of this strategy has progressed remarkably over the past years and has played a large role in the control of soil erosion, land degradation, and desertification, as well as in grassland reconstruction (Li *et al.* 2007). However, restoration implementation still faces a number of problems, such as poor understanding of water requirements of desert-living plants. Furthermore,

inappropriate tree selection and planting could lead to a reduction in groundwater and the death of sand-binding vegetation in certain regions (Li 2005; Ford *et al.* 2007; Xia *et al.* 2008). Scientists have sought to solve this problem and have developed reliable techniques for estimating the total amount of water transpired by plants (Kelliher *et al.* 1992; Granier *et al.* 1996; Kumagai *et al.* 2004; Dierick & Holscher 2009). Wang *et al.* (2004a, b) have studied the evapotranspiration of *C. korshinskii* and *A. ordosica* using the auto-weighing lysimeter method, and the results have demonstrated that cumulative precipitation and cumulative evapotranspiration were linearly correlated. Huang *et al.* (2010) have studied the sap flow rate of *A. ordosica* and its

L. Huang (corresponding author)

Z. Zhang

X. Li

Shapotou Desert Research and Experimental Station,

Cold and Arid Regions Environmental and Engineering Research Institute,

CAS, Lanzhou 730000,

China

and

Key Laboratory of Stress Physiology and Ecology in

Cold and Arid Regions Gansu Province, Lanzhou 730000,

China

E-mail: mathecolgy@163.com

correlation with meteorological factors. Such studies are, however, still scattered and unsystematic and, generally, do not involve scaling problems. Evaluating transpiration over a range of temporal and spatial scales remains a challenge (Tanaka *et al.* 2008; Du *et al.* 2011), especially in desert areas, primarily because of the dispersed patchy vegetation distribution and the spatially heterogeneous terrain (Domingo *et al.* 1999).

At present, a number of techniques are available for using field measurements to estimate daily stand transpiration rates through appropriate scaling methodologies (Chabot *et al.* 2005). Transpiration in potted plants (Dugas *et al.* 1993) and herbaceous species (Senock & Ham 1995) is often estimated using leaf-level gas exchange techniques, and stand water use in forests is usually scaled from the sap flow of individual trees by diameter or sapwood area (Hatton & Wu 1995; Granier *et al.* 1996). However, the suitability of these methods in revegetated desert areas remains unknown, and few studies have considered the scaling issues of transpiration estimates from an integrated leaf-individual-canopy scaling perspective. Furthermore, when scaling up an individual plant or tree transpiration to area-average estimates of stand water usage, various scaling factors have been proposed, ranging from tree basal area (Teskey & Sheriff 1996) and stem diameter at breast height (DBH) (Vertessy *et al.* 1997) to leaf area (Hatton & Wu 1995) and sapwood area (Dunn & Connor 1993). Hatton & Wu (1995) suggested that the xylem transfusion cross-sectional area, leaf area, DBH and the area occupied by a single tree are all reliable spatially derived scaling factors, of which the leaf area is the most credible variable for the conversion of water consumption from a single tree to the scale of a forest stand (Oren *et al.* 1999; Granier *et al.* 2000), especially in arid desert areas (Li *et al.* 2013). Furthermore, the deviation in the upscaling transpiration was reduced by almost half using leaf area as a basis compared with the above-mentioned other scaling factors (Ham *et al.* 1990; Nicolas *et al.* 2005). Leaf area is, however, a dynamic variable that depends on the situation and temporal aspects, which have often been ignored in previous studies (Chabot *et al.* 2005; Delzon & Loustau 2005).

This study is based on long-term measurements from April 2008 to October 2012. During this time period, gas exchange techniques with a portable photosynthesis

system, sap flow measurements, and the crop evapotranspiration minus micro-lysimeter method were used to evaluate the transpiration of sand-binding plants at different scales. The specific objectives of the study were: (1) to quantify the daily, seasonal, and annual transpiration patterns of *C. korshinskii* and *A. ordosica*; and (2) to scale up transpiration from the leaf level to the stand level with dynamical leaf area-based extrapolation. We expected that the leaf area would be a standard scaling factor for upscaling transpiration in arid desert regions.

MATERIAL AND METHODS

Study area

The study was conducted in the Soil Water Balance Experimental Fields of the Shapotou Desert Experimental Research Station, Chinese Academy of Sciences. The research station borders the Tengger Desert, the fourth largest desert in China, located in the central part of West China (37°27' N, 104°57' E). The climate at the site is characterized by abundant sunshine and low relative humidity. The minimum average monthly relative humidity is 33% in April, and the maximum is 54.9% in August. The elevation is 1,330 m above sea level, with a mean annual precipitation of 188.2 mm (according to meteorological records from 1956 to 2009), falling predominantly from June to September. The mean annual temperature is 9.6 °C, and the mean monthly temperatures are -6.9 °C in January and 24.3 °C in July. The potential evapotranspiration during the growing season (May–September) is from 2,300 to 2,500 mm (observed by evaporation pan of type E-601). The windy season lasts from September to April, with an average wind velocity of 2.6 m s⁻¹. The soil surface is loose, poorly aggregated mobile sand with a moisture content of 2 to 3%.

To protect the Baotou–Lanzhou railway line from sand burial, a non-irrigated vegetation protection system was established in 1956. After 50 years, the initial shrub plantings (among them *C. korshinskii*, *Artemisia ordosica*, *Hedysarum scoparium*, *C. intermedia*, *Calligonum arborescens*, and *Atraphaxis bracteata*) were gradually replaced with dominant shrubs, such as *A. ordosica*, *C. korshinskii*, *Hedysarum scoparium*, and herbaceous plants (Li *et al.*

2004). Two 10 m × 10 m sample plots in the revegetation system were selected in 2008 to investigate basic plant characteristics, such as species, age, density, height, and crown-width (Table 1).

Plant transpiration measurement

Six *C. korshinskii* and six *A. ordosica* shrubs in our plot were selected for long-term monitoring and local observation. The stem heat balance (SHB) technique was used to measure sap flow rate and to determine whole-plant transpiration (Sakuratani *et al.* 1999; Chabot *et al.* 2005). Twelve sap flow gauges, ranging from SGA2 to SGB19 (Dynamax Inc., Houston, TX, USA), were placed at the base of the stem of each plant to continuously measure transpiration (Table 2). Thirty-minute averages of the flow rate were recorded by a data logger (CR1000; Campbell Scientific, Inc., Logan, UT, USA). During the growing season (April–October) from 2008 to 2012, diurnal transpiration rates were measured monthly from each sensor-wrapped stem using an LI-6400 photosynthesis system (Li-Cor, Lincoln, NE, USA) with a 6 cm² clamp-on leaf cuvette. Two to four leaves adjacent to the quantum sensors were selected and all leaves were from a south-facing canopy position at a height of 0.5 to 1 m. Each diurnal measurement began at 8:00 and ended at 20:00 (Beijing local time), with a 1 h interval. A total of 34 diurnal measurements were made during the 5-year study period.

Leaf area index (LAI) measurement

The leaf areas of the sensor-wrapped plants (Nos. 1–12) were measured twice monthly during the growing season using image analysis. With a standard scale board, the images were obtained using a digital camera (Canon Power Shot A550), as seen in Figure 1. The digital images were processed using Matlab 7.0 (MathWorks, Natick,

MA, USA) software, and the actual measured areas were obtained with the proportional calibrated figure area; for more details refer to Rico-García *et al.* (2009). The whole plant LAI (m²/m²) was measured using LAI-2000 Plant Canopy Analyzer (PCA; Li-Cor). PCA measurements were performed for each plant during our experimental period using the same unit. In each measurement, a measurement cycle consisted of a reference measurement and four below-canopy readings. The reference measurements were collected in large clearings or open areas near the experimental plots at the beginning of each cycle. The below-canopy measurements were carried out for each plant at a fixed position and were taken at the same level as the litter traps. The fish-eye lens of the instrument was covered by a view cap with a 90° opening to ensure that the reference measurements were not influenced by the trees surrounding the clearings or by the operator. Before the measurements were taken, the LAI 2000 was calibrated directly by collecting the whole leaves of plants. The LiCor PCA was used after the sun set every evening to avoid confusing brightly sunlit leaves for gaps, and the data were recomputed with the FV2000 LI-COR software built into the instrument. Finally, the actual LAI value was the difference between measurements during the growing season and those taken before leaf emergence (branch area index).

Meteorological and soil evaporation measurements

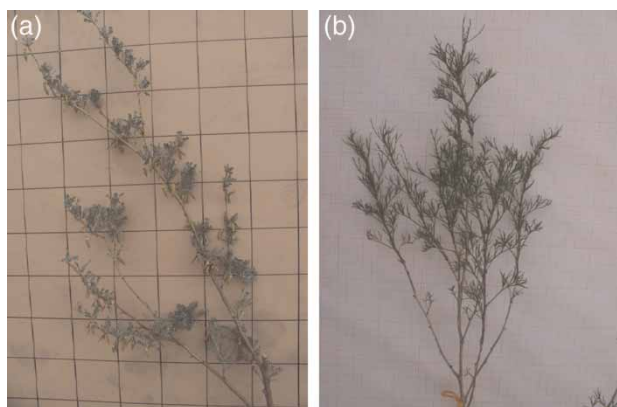
Precipitation was recorded using a tipping bucket-type rain gauge (Casella). Meteorological factors, such as net radiation (CNR-1; Kipp & Zonen, Delft, The Netherlands) at 2 m height, soil heat flux density (HFP-01; Hukseflux Thermal Sensors, Delft, The Netherlands) at 0.05 m below the soil surface, air temperature and relative humidity (HMP45C; Vaisala Inc., Helsinki, Finland) at 2 m height, and wind speed (CSAT3; Campbell Scientific, Inc.) at 2 m height were measured at the micrometeorological

Table 1 | Results of agronomic measurements carried out on 17 May 2008

Vegetation	Age (year)	Density (Individuals/100 m ²)	Height (m)	Crown-width (m ²)	Basal stem diameter (cm)
<i>C. korshinskii</i>	5	25	1.43 ± 0.496	1.6 ± 0.836	4.47 ± 1.349
<i>A. ordosica</i>	2	123	0.68 ± 0.154	0.9 ± 0.261	2.15 ± 0.827

Table 2 | Selected sensor type and stem area

<i>C. korshinskii</i>	Sensors	Wrapped stem area (cm ²)	<i>Artemisia ordosica</i>	Sensors	Wrapped stem area (cm ²)
No. 1	SGA13	1.3287	No. 7	SGA5	0.2229
No. 2	SGB19	3.1212	No. 8	SGB5	0.1877
No. 3	SGB16	2.2981	No. 9	SGA13	1.3369
No. 4	SGA9	0.8507	No. 10	SGA10	1.2099
No. 5	SGB19	1.5628	No. 11	SGA2	0.0669
No. 6	SGA10	0.94985	No. 12	SGA3	0.05723

**Figure 1** | Image capture of the sensor-wrapped stems of *C. korshinskii* (a) and *A. ordosica* (b).

tower, which was located approximately 30 m from the sample plot. The data were measured every 10 min and averaged every 30 min, and recorded on Campbell CR3000 data-loggers. Soil evaporation was measured with micro-lysimeters (Zhang *et al.* 2008), which were made using PVC pipes that were 30 cm high and 10 cm in internal diameter. The bottom of each micro-lysimeter was capped with steel grids permitting the free drainage of water. Three micro-lysimeters were buried in three directions (120°) from each *C. korshinskii* and *A. ordosica* plant. Thus, mean soil evaporation was determined using the variation of average soil column weights. During the no-rainfall period, continuous measurements were taken every day during the growing season of *C. korshinskii* and *A. ordosica*, but during rainy days or missed data, measurements were calculated by interpolation, based on the data before and after the period of missing data.

Simulated canopy transpiration

The reference transpiration (ET) of the plant canopy was calculated following the FAO Penman–Monteith equation, according to standard FAO procedure (Allen *et al.* 1998)

$$ET_0 = \frac{0.408(R_n - G) + \gamma(900/(T + 273))u_2(e_s - e_a)}{\Delta + \gamma(1 + 0.34u_2)} \quad (1)$$

where ET_0 is the reference ET (mm d⁻¹), R_n is the net radiation at the plant surface (MJ m⁻² day⁻¹), G is the soil heat flux density (MJ m⁻² day⁻¹), T is the air temperature at 2 m height (°C), u_2 is the wind speed at 2 m height (m s⁻¹), e_s is the saturation vapor pressure (kPa), e_a is the actual vapor pressure (kPa), $e_s - e_a$ is the saturation vapor pressure deficit (VPD; kPa), Δ is the slope vapor pressure curve (kPa °C⁻¹), and γ is the psychrometric constant (kPa °C⁻¹). ET was calculated following the classical method:

$$ET = K_c ET_0 \quad (2)$$

where K_c is the crop coefficient. K_c was deduced using the auto-weighing lysimeter method to determine the average evapotranspiration rates of *C. korshinskii*, *A. ordosica*, and sand (1.09, 1.01 and 0.68 mm d⁻¹, respectively) for the 6-year intermittent study period (1990–1995). Thus the K_c was 0.38 for *C. korshinskii* and 0.32 for *A. ordosica* in this study (Li *et al.* 2013). Next, the mean transpiration of the plants canopy (T_d' ; mm d⁻¹) was calculated as:

$$T_d' = ET - E_s \quad (3)$$

where E_s (mm d⁻¹) is the mean soil evaporation measured using micro-lysimeters.

Evapotranspiration calculation processes

Sap flow data were analyzed using the DGSF software (Dynamax Inc., USA) to determine hourly sap flow rates and cumulative sap flux. Daily average transpiration per unit leaf area was calculated according to the cumulative sap flux and leaf area. Given the following data processing schedule, the results were then compared to the measurements from the LI-6400 photosynthesis system.

The transpiration rate (Tr) measured using the LI-6400 photosynthesis system was in $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$. Based on unit conversion, the hourly average transpiration per unit leaf area (Tr_{hr} , $\text{g m}^{-2} \text{h}^{-1}$) was $Tr_{hr} = 0.015 Tr$. Then, the diurnal variations in transpiration rate were fitted as the following polynomial:

$$Tr_{hr} = A + \sum B_i t^i \quad (i = 2) \quad (4)$$

where A is a constant, B_i is the coefficient of the polynomial, and t is the time ($8 \leq t \leq 20$). Finally, the diurnal transpiration rate per unit leaf area (Tl) was obtained as:

$$Tl = \int_8^{20} Tr_{hr} dt \quad (5)$$

Stem flow measurements from the individual plants were converted to the transpiration rate of whole trees per unit leaf area using the following expression:

$$T_d = \left[\sum_{i=1}^n \frac{f_i/A_{ij}}{n} \right] LAI_j \quad (i = 1, 2 \dots n; j = 4, 5 \dots 10) \quad (6)$$

where T_d is the plant canopy transpiration ($\text{g h}^{-1} \text{m}^{-2}$), f_i is the sap flow measured in the stem i (g h^{-1}), A_{ij} is the leaf area of the stem i (m^2) at time j (month), n is the number of equipped stems, and LAI_j is the LAI (m^2/m^2) measured above at time j . The daily transpiration rates (ET_d ; $\text{g m}^{-2} \text{d}^{-1}$) were estimated from the cumulative T_d values over 24 h. The equivalent mass of a kilogram of water in one square meter of ground area was subsequently expressed as depth in millimeters (mm) such that transpiration could be given in mm d^{-1} . Next, the direct measurements in Equation (6) were compared with simulation results in Equations (1)–(3).

Scaling model quality evaluation

To evaluate the quality of the scaling-up transpiration simulations, graphs measured against the simulated values were drawn together with the linear regression, the correlation coefficient, and the 1:1 line. Assuming there is no model error, the measured and simulated

values should be identical and all points should lie on the 1:1 line. The points of good quality simulations should lie close to the 1:1 line, the slope of the linear regression should be close to one, and the correlation coefficient should be close to one. A widely used measure of agreement between measured and simulated values is the root mean squared error (RMSE) (Wallach 2006)

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^n (X_{\text{obs},i} - X_{\text{sim},i})^2}{n}}$$

where $X_{\text{obs},i}$ is observed values and $X_{\text{sim},i}$ is simulated values at time i , and n is the sample number.

RESULTS

Daily transpiration rate using the photosynthesis system and sap flow measurements

The diurnal cycle of the transpiration rates of *C. korshinskii* and *A. ordosica* (averages of 34 diurnal transpiration measurements from April 2008 to October 2012) are shown in Figure 2(a). Both species exhibited a single-peak curve, with the peak occurring at 09:00 and 10:00 a.m., respectively. The diurnal variations of *A. ordosica* were slightly different in that the transpiration rate increased gradually at 12:00 a.m. and later decreased after 14:00 p.m. Although it showed a small peak of transpiration, the later peak appears statistically indistinguishable from the three previous hours, which indicates the ‘noon break’ phenomenon or midday depression (Li et al. 2008). Mean transpiration rates of *C. korshinskii* and *A. ordosica*, as seen in Figure 2(a), were 2.67 and 4.51 $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$, respectively.

The sap velocity of *C. korshinskii* and *A. ordosica* had distinct diurnal variations during sunny days from April 2008 to October 2012 (approximately 700 days). As shown in Figure 2(b), the sap flow rate of *C. korshinskii* increased immediately at 6:00 a.m., peaked at 12:00 p.m., and gradually decreased to a minimal sap velocity at night. By contrast, the sap flow rate of *A. ordosica*

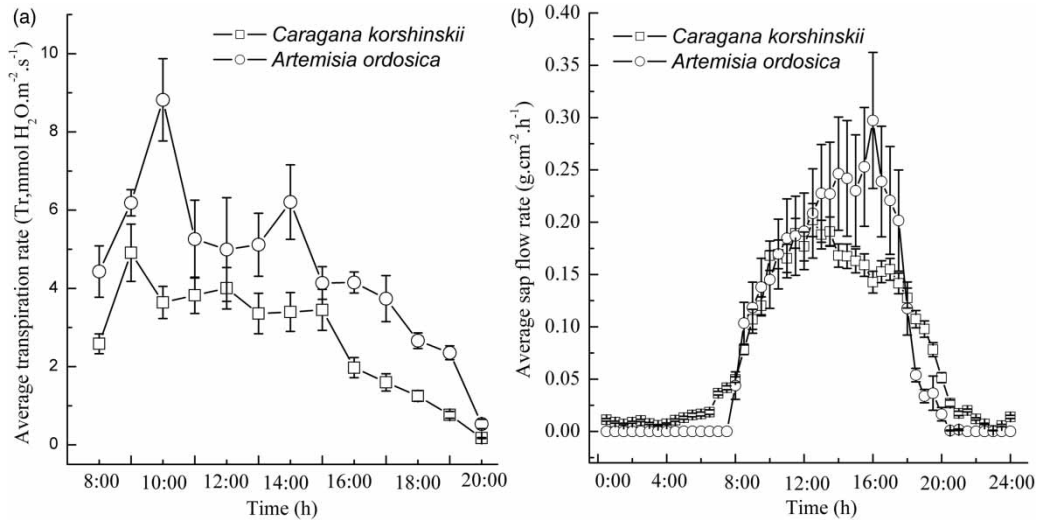


Figure 2 | Diurnal course of transpiration rate Tr (a) and the sap flow rate (b) in *C. korshinskii* and *A. ordosica* during the experimental period (April 2008–October 2012).

gradually increased at 8:00 a.m., and peaked at 14:00 to 16:00 p.m., 2 h later than in *C. korshinskii*, and then immediately decreased to zero after 20:00 p.m. No sap flow was observed at night or before dawn, which indicates that no transpiration occurred or that the transpiration was too small to measure. The average sap flow rate in *C. korshinskii* was $0.071 \text{ g h}^{-1} \text{ cm}^{-2}$, and that in *A. ordosica* was

$0.086 \text{ g h}^{-1} \text{ cm}^{-2}$, which were mainly determined by R_s , VPD, and RH, respectively (Huang *et al.* 2010).

LAI variations

The monthly variations in LAI and precipitation during the experimental period are illustrated in Figure 3. LAI varied

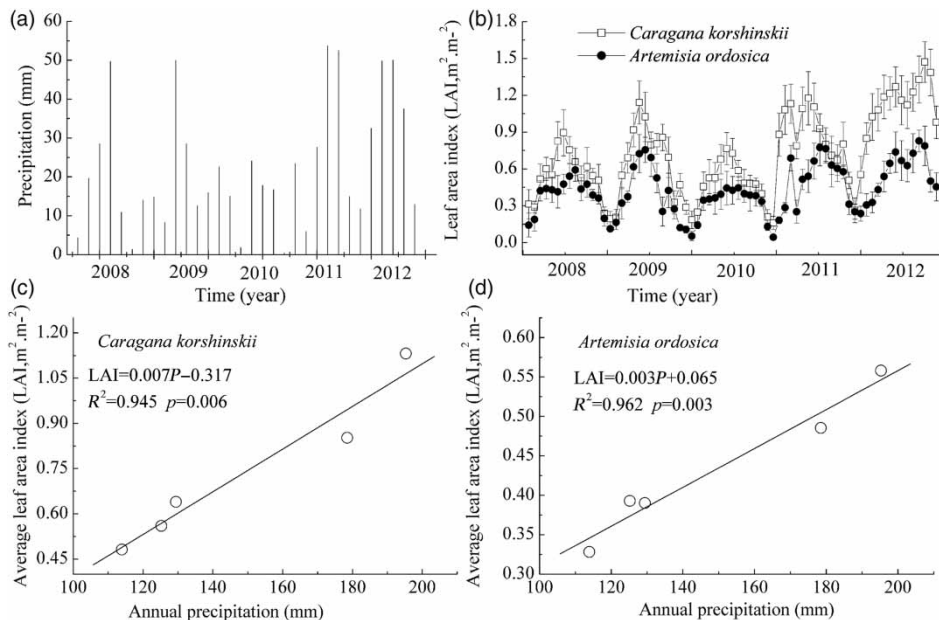


Figure 3 | Precipitation (a), LAI dynamics (b) and its corresponding linear regression relationship with annual precipitation in *C. korshinskii* (c) and *A. ordosica* (d) during the experimental period (April 2008–October 2012).

with precipitation as seen in Figures 3(a) and 3(b), especially in 2010, during which the precipitation was only 113.9 mm, resulting in a significant decrease in LAI. However, the opposite was true in 2011 and 2012, when the precipitation was 178.5 and 195.3 mm, respectively, and the LAI showed a correspondingly significant increase. During each year, the buds started to burst and the LAI increased in April and peaked in June. Then, the decreased precipitation and higher air temperatures in July caused a decrease in LAI; by August or September, *C. korshinskii* and *A. ordosica* often went through a second growing stage, even with little precipitation. Thereafter, the leaves began to fall and LAI gradually decreased to a low level. Figures 3(c) and 3(d) show that the mean LAI during the growing season (April–October) had a significant positive linear correlation with annual precipitation. During study years of heavy rainfall, such as in 2008 and 2009, the total amount of annual precipitation was approximately the same (125.2 and 127.4 mm), although the number of rain days was 23 in 2008 and 29 in 2009; results have shown that the LAI of *C. korshinskii* was 0.55 in 2008 and 0.64 in 2009, which indicates that rain frequency had a positive effect on LAI. On the other hand, rain frequency had little effect on the LAI of *A. ordosica*, which was 0.39 in 2008 and 0.38 in 2009. Thus, we could hypothesize that under certain situations, such as among different plant species or rainfall amounts, rainfall intermittency and frequency could cause differences in the LAI dynamics; this means that temporal rainfall intermittency could result in relatively higher LAIs and longer plant-growing periods compared with constant precipitation.

Scaling up transpiration from leaf to stand

To compare different plants, the sap flow values from SHB measurements were divided by leaf area to obtain transpiration per leaf unit. Average daily transpiration rates of *C. korshinskii* and *A. ordosica* with the sap flow measurements during our experimental period were 0.81 and 1.45 g cm⁻² d⁻¹, and the simulation results with Equations (4) and (5) were 0.64 and 1.38 g cm⁻² d⁻¹, respectively. The observed data with sap flow measurement versus simulated values from the Li-6400 extrapolation transpiration rate during the 34 diurnal measurements are shown in Figure 4. The result

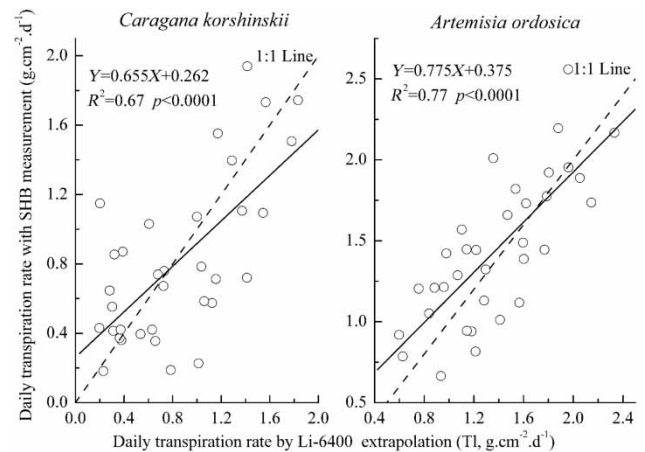


Figure 4 | Comparisons of *C. korshinskii* and *A. ordosica* daily transpiration rates by Li-6400 extrapolation and SHB measurement during the experimental period (April 2008–October 2012).

indicates that the model can estimate transpiration with reasonable accuracy ($R^2 = 0.67$ for *C. korshinskii* and $R^2 = 0.77$ for *A. ordosica*), although the simulated values were generally lower than measured values. The statistical analysis of the results showed that both the relative error was $<10\%$, and the RMSE was 0.38 and 0.31 g cm⁻² d⁻¹ for *C. korshinskii* and *A. ordosica*, respectively. Furthermore, simulated versus observed transpiration values fell around the 1:1 line for combined data, which means that the extrapolation model was accurate and reasonable.

Plant canopy transpiration on a per unit ground area basis was calculated using Equation (6), and then compared with the actual ET minus soil evaporation as calculated by Equations (1)–(3). During our experimental period from April 2008 to October 2012 (909 days), mean soil evaporation in the *C. korshinskii* and *A. ordosica* community was 0.72 and 0.83 mm d⁻¹, respectively. Furthermore, soil evaporation of the two shrubs in wet years (such as 195.3 mm rainfall in 2012) was 0.86 and 0.97 mm d⁻¹, which was significantly greater than 0.41 and 0.59 mm d⁻¹ in the dry years (such as 113.9 mm rainfall in 2010). The daily transpiration rates of *C. korshinskii* and *A. ordosica* communities were 0.36 and 0.28 mm d⁻¹ with the sap flow extrapolation, respectively, whereas direct measurements from the crop evapotranspiration method were 0.42 and 0.35 mm d⁻¹. Comparisons between the two methods are presented in Figure 5. The linearly fitted regression equation also indicated a notably good upscaling process. The value

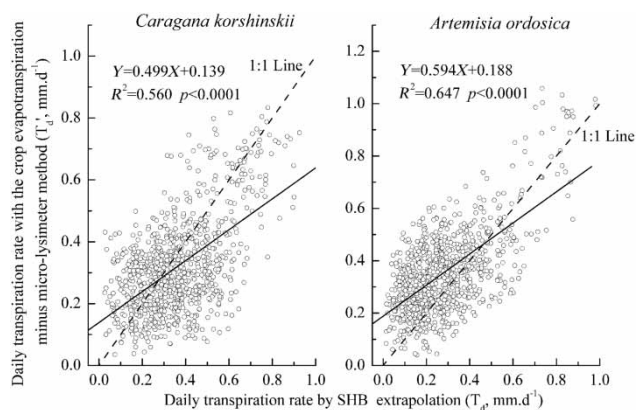


Figure 5 | Comparisons of *C. korshinskii* and *A. ordosica* daily transpiration rates with SHB extrapolation and the crop evapotranspiration minus micro-lysimeter method during the experimental period (April 2008–October 2012).

of the coefficient of determination ($R^2 = 0.560$ for *C. korshinskii* and $R^2 = 0.647$ for *A. ordosica*) indicated that a good correlation exists between the simulated and observed stand transpiration. The RMSE was 0.16 and 0.15 mm d⁻¹ for *C. korshinskii* and *A. ordosica*, respectively. Stand transpiration values of the two methods were distributed around the 1:1 line for combined data, which also means that the sap flow extrapolation model is accurate and reasonable. The transpiration of *C. korshinskii* was higher than *A. ordosica* and total seasonal transpiration (April–October) amounted to 71.79 and 55.62 mm, respectively, representing approximately 48.4 and 37.5% of the total rainfall over this period.

DISCUSSION

Estimating plant transpiration is highly complex due to the unique, sparse vegetation cover in arid and semiarid zones (Noilhan et al. 1997; Ramirez et al. 2006). Compared with the continuous coverage observed in forests and on cropland, the soil heterogeneity and vegetation boundary differences in the desert make upscaling difficult. Researchers have their own scaling methods at different scales, but the results of their research are not always comparable. In this study, leaf area was used as a unified scaling factor that shifted from one scale to another, mainly because of the biological features of desert plants, such as low biomass or growth in the stems. Our scaled measurements have

proven successful for scaling up transpiration from the leaf to the stand level. The LAI dynamics of *C. korshinskii* and *A. ordosica* are illustrated in Figure 3. LAI was significantly dependent on the precipitation. In the wet years, the LAI of *C. korshinskii* and *A. ordosica* was 0.85 and 0.39, larger than in the dry years at 0.48 and 0.32, respectively. However, the sensitivity of LAI to decreasing precipitation was greater in *C. korshinskii* than in *A. ordosica*, which may indicate that *A. ordosica* communities display a greater drought tolerance in arid desert regions. During rainfall years, rainfall intermittency and frequency caused differences in the LAI dynamics. This phenomenon also agrees with other studies showing that plants from desert ecosystems are favored by less frequent rainfall events for the same total seasonal rainfall volume (Sher et al. 2004), as a minimal amount of water is in fact needed to activate biological processes such as reproduction or seed germination. If precipitation is concentrated in time, this minimum amount of soil water is intermittently exceeded and vegetation can persist. If rainfall is more uniformly spread across the growing season, soil moisture never exceeds the threshold needed to activate plant reproduction and germination, and the vegetation tends to disappear (Baudena et al. 2007).

Considering that transpiration is a fundamental part of ET, the sap flow-scaled method is the main method used for upscaling transpiration from the leaf level to the canopy level. Plant transpiration within a short period can be accurately measured using a Li-6400 photosynthesis system, but the total amount of long-term transpiration is difficult to determine continuously because of the influence of microclimate factors. The difference between the average simulated daily transpiration rate and the direct sap flow measurement was readily discernible through the polynomial fit and integration of data from the experimental period, but the results of the simulation were slightly lower than the direct measurements, as indicated by the regression coefficients (both are <1). This discrepancy may be due to the different measuring instruments: the photosynthesis system only measures leaf transpiration, whereas the sap flow sensors measure both leaf transpiration and stem transpiration. The discrepancy may also be because leaf transpiration was only measured from 8:00 a.m. to 20:00 p.m., but sap flow was measured for 24 h. Determining actual transpiration based on a combination of the

Penman–Monteith reference ET (ET_0) and the crop coefficient (K_c) method is a simple and effective method that has gained wide acceptance in agricultural water management (Suyker & Verma 2009). In this study, the K_c values were obtained from other publications as a constant; however, these values varied significantly during the growing season (Zhang *et al.* 2012). Thus, more accurate parameterizations using new techniques should be developed to estimate the stand transpiration. The regression coefficients for the leaf level to tree level and the tree level to stand level of *C. korshinskii* were both lower than those of *A. ordosica*, which indicates that the leaf area-based extrapolation method is more appropriate for *A. ordosica* shrubs. Based on Figure 5, the sap flow extrapolation was also less than that from the crop evapotranspiration minus the lysimeter results, especially during the growing seasons. This differs from the laboratory experiments in that the sap flow sensors overestimated 13.5% of the total transpiration (Chabot *et al.* 2002). This discrepancy is mainly observed because certain annual and perennial herbs inhabit and reproduce on the soil surface after the re-establishment of vegetation, and their contribution to transpiration cannot be distinguished from those observed under the crop evapotranspiration method.

The transpiration values of the *C. korshinskii* stand were higher than those of the *A. ordosica* stand during the growing season because of the large difference in tree size. The seasonal (April–October) total transpiration reached 71.79 and 55.62 mm, respectively, representing approximately 48.4 and 37.5% of the total rainfall over this period. Species differences in water use per unit of leaf area were smaller, but sometimes statistically significant, especially during rainy days. A small amount of precipitation increased the sap flow and transpiration; however, large amounts of precipitation decreased sap flow and transpiration (Huang *et al.* 2010). *A. ordosica* is more likely to be affected by this phenomenon because its roots are found primarily in the uppermost soil layers, especially in the case of coarse roots, which are concentrated in the 0.2 m soil layer and are more easily influenced by rainfall. However, for *C. korshinskii*, the roots are primarily concentrated in the 0.6 to 1 m soil layer (Zhang *et al.* 2009), and the influence is relatively smaller as the water is redistributed in the soil. Further

analysis showed that the percentage of soil evaporation was very high after precipitation, and it was also different at different experimental plots, although in most cases (61%) there was no significant difference ($p > 0.05$). However, during the rainy days, the transpiration of *C. korshinskii*, *A. ordosica* and soil evaporation was 0.72, 0.75 and 0.61 mm d⁻¹, respectively, but during the drier days, the daily transpiration and soil evaporation were 0.12, 0.13 and 0.24 mm d⁻¹. There was a significant difference ($p < 0.01$) between them. The ratio of transpiration to ET decreased as annual precipitation declined, while the ratio of evaporation to ET increased. This would mean that drought stress decreased transpiration and ET and increased precipitation loss due to evaporation, which, in turn, led to a large decrease in available water for plant growth, and so less drought-tolerant plants, such as *C. korshinskii*, would disappear or degrade with future vegetation succession.

CONCLUSIONS

A long-term transpiration study was conducted during the growing seasons from April 2008 to October 2012 using two xerophytic shrubs typically used in revegetation: *C. korshinskii* and *A. ordosica*. Gas exchange techniques (using an infrared gas analyzer), sap flow measurements, and the crop evapotranspiration minus lysimeter method were used to evaluate plant transpiration at the leaf level, tree level, and stand level. Simultaneous measurements using the three methods were made diurnally and were compared with the normalized leaf area-based extrapolation. The results show that leaf area is a reliable scaling factor for upscaling transpiration from the leaf level to the stand level in desert regions. At the leaf level, the transpiration rates of *C. korshinskii* and *A. ordosica* were 2.67 and 4.51 mmol H₂O m⁻² s⁻¹, respectively, showing a single-peak curve with meteorological factors as the key limiting factors. The sap flow rates were 0.071 and 0.086 g h⁻¹ cm⁻² at the tree level, and the transpiration rates were 0.42 and 0.35 mm d⁻¹ at the stand level with precipitation and LAI as the main limiting factors. Direct measurement and extrapolation during non-rainfall periods showed very good correlations. The results provide a key

link for designing management strategies to improve water use efficiency and to determine the appropriate plant density in revegetated areas with limited soil water capacity.

ACKNOWLEDGMENTS

This work was supported by the National Key Basic Research program (2013CB429905-03) and Chinese National Natural Scientific Foundation (41201084; 31170385).

REFERENCES

- Allen, R. G., Pereira, L. S., Raes, D. & Smith, M. 1998 Crop evapotranspiration-guidelines for computing crop water requirements. FAO Irrigation and Drainage Paper 56. Food and Agricultural Organization of the United Nations, Rome, Italy.
- Baudena, M., Boni, G., Ferraris, L., von Hardenberg, J. & Provenzale, A. 2007 Vegetation response to rainfall intermittency in drylands: results from a simple ecohydrological box model. *Adv. Water Resour.* **30**, 1320–1328.
- Chabot, R., Bouarfa, S., Zimmer, D., Chaumont, C. & Duprez, C. 2002 Sugarcane transpiration with shallow water-table: sap flow measurements and modeling. *Agric. Water Manage.* **54**, 17–36.
- Chabot, R., Bouarfa, S., Zimmer, D., Chaumont, C. & Moreau, S. 2005 Evaluation of the sap flow determined with a heat balance method to measure the transpiration of a sugarcane canopy. *Agric. Water Manage.* **75**, 10–24.
- Delzon, S. & Loustau, D. 2005 Age-related decline in stand water use: sap flow and transpiration in a pine forest chronosequence. *Agric. Forest Meteorol.* **129**, 105–119.
- Dierick, D. & Holscher, D. 2009 Species-specific tree water use characteristics in reforestation stands in the Philippines. *Agric. Forest Meteorol.* **149**, 1317–1326.
- Domingo, F., Villagarcia, L., Brenner, A. & Puigdefábregas, J. 1999 Evapotranspiration model for semi-arid shrublands tested against data from SE Spain. *Agric. Forest Meteorol.* **95**, 67–84.
- Du, S., Wang, Y. L., Kume, T., Zhang, J. G., Otsuki, K., Yamanakac, N. & Liu, G. B. 2011 Sap flow characteristics and climatic responses in three forest species in the semiarid Loess Plateau region of China. *Agric. Forest Meteorol.* **151** (1), 1–10.
- Dugas, W. A., Wallace, J. S., Allen, S. J. & Roberts, J. M. 1993 Heat balance, porometer, and deuterium estimates of transpiration from potted trees. *Agric. Forest Meteorol.* **64**, 47–62.
- Dunn, G. M. & Connor, D. J. 1993 Analysis of sap flow in mountain ash (*Eucalyptus regnans*) forests of different age. *Tree Physiol.* **13**, 321–336.
- Ford, C. R., Hubbard, R. M., Kloeppel, B. D. & Vose, J. M. 2007 A comparison of sap flux-based evapotranspiration estimates with catchment-scale water balance. *Agric. Forest Meteorol.* **145**, 176–185.
- Granier, A., Huc, R. & Barigah, S. T. 1996 Transpiration of natural rain forest and its dependence on climatic factors. *Agric. Forest Meteorol.* **78**, 19–29.
- Granier, A., Loustau, D. & Breda, N. 2000 A generic model of forest canopy conductance dependent on climate, soil water availability and leaf area index. *Ann. Forest Sci.* **57**, 755–765.
- Ham, J., Heilman, J. L. & Lascano, R. J. 1990 Determination of soil water evaporation and transpiration from energy balance and stem flow measurements. *Agric. Forest Meteorol.* **52**, 287–301.
- Hatton, T. J. & Wu, H. I. 1995 Scaling theory to extrapolate individual tree water use to stand water use. *Hydrolog. Process.* **9**, 527–540.
- Huang, L., Zhang, Z. S. & Li, X. R. 2010 Sap flow of *Artemisia ordosica* and the influence of environmental factors in a revegetated desert area: Tengger Desert, China. *Hydrolog. Process.* **24**, 1248–1253.
- Kelliher, F. M., Kostner, B. M. M., Hollinger, D. Y., Byers, J. N., Hunt, J. E., McSeveny, T. M., Meserth, R., Weir, P. L. & Schulze, E. D. 1992 Evaporation, xylem sap flow, and tree transpiration in a New Zealand broad-leaved forest. *Agric. Forest Meteorol.* **62**, 53–73.
- Kumagai, T., Saitoh, T. M., Sato, Y., Morooka, T., Manfroi, O. J., Kuraji, K. & Suzuki, M. 2004 Transpiration, canopy conductance and the decoupling coefficient of a lowland mixed dipterocarp forest in Sarawak, Borneo: dry spell effects. *J. Hydrol.* **287**, 237–251.
- Li, X. R. 2005 Influence of variation of soil spatial heterogeneity on vegetation restoration. *Science in China Series D: Earth Sciences* **48**, 2020–2031.
- Li, X. R., Xiao, H. L., Zhang, J. G. & Wang, X. P. 2004 Long-term ecosystem effects of sand-binding vegetation in Shapotou Region of Tengger Desert, Northern China. *Restor. Ecol.* **12**, 376–390.
- Li, X. R., He, M. Z., Duan, Z. H., Xiao, H. L. & Jia, X. H. 2007 Recovery of topsoil physicochemical properties in revegetated sites in the sand-burial ecosystems of the Tengger Desert, northern China. *Geomorphology* **88**, 254–265.
- Li, Q. H., Zhao, Y. M., Liu, J. F., Zhao, X. L. & Jiang, Z. P. 2008 The differences of growth and photosynthetic traits of five shrubs species from two origins in the northeastern Ulanbuh Desert. *Forest Res.* **3**, 357–361.
- Li, X. R., Zhang, Z. S., Huang, L. & Wang, X. P. 2013 Review of the ecohydrological processes and feedback mechanisms controlling sand-binding vegetation systems in sandy desert regions of China. *Chinese Sci. Bull.* **58**, 1483–1496.
- Nicolas, E. A., Torrecillas, M. F., Domingo, O. R. & Alarcon, J. J. 2005 Evaluation of transpiration in adult apricot trees from sap flow measurements. *Agric. Water Manage.* **72**, 131–145.
- Noilhan, J., Lacarrere, P., Dolman, A. J. & Blyth, E. M. 1997 Defining area-average parameters in meteorological models

- for land surfaces with mesoscale heterogeneity. *J. Hydrol.* **190**, 302–316.
- Oren, R., Phillips, N., Ewers, B. E., Pataki, D. E. & Mezonigal, J. P. 1999 Sap-flux-scaled transpiration responses to light, vapor pressure deficit, and leaf area reduction in a flooded *Taxodium distichum* forest. *Tree Physiol.* **19**, 337–347.
- Ramirez, D. A., Valladares, F., Blasco, A. & Bellot, J. 2006 Assessing transpiration in the tussock grass *Stipa tenacissima* L.: the crucial role of the interplay between morphology and physiology. *Acta Oecol.* **30** (3), 386–398.
- Rico-García, E., Hernández-Hernández, F., Soto-Zarazúa, G. & Herrera-Ruiz, G. 2009 Two new methods for the estimation of leaf area using digital photography. *Int. J. Agric. Biol.* **11**, 397–400.
- Sakuratani, T., Aoe, T. & Higuchi, H. 1999 Reverse flow in roots of *Sesbania rostrata* measured using the constant power heat balance method. *Plant Cell Environ.* **22**, 1153–1160.
- Senock, R. S. & Ham, J. M. 1995 Measurement of water use by prairie grasses with heat balance sap flow gauges. *J. Range Manage.* **48**, 150–158.
- Sher, A. A., Goldberg, D. E. & Novoplansky, A. 2004 The effect of mean and variance in resource supply on survival of annuals from Mediterranean and desert environments. *Oecologia* **141** (2), 353–362.
- Suyker, A. E. & Verma, S. B. 2009 Evapotranspiration of irrigated and rainfed maize-soybean cropping systems. *Agric. Forest Meteorol.* **149**, 443–452.
- Tanaka, N., Kume, T., Yoshifuji, N., Tanaka, K., Takizawa, H., Shiraki, K., Tantasirin, C., Tangtham, N. & Suzuki, M. 2008 A review of evapotranspiration estimates from tropical forests in Thailand and adjacent regions. *Agric. Forest Meteorol.* **148**, 807–819.
- Teskey, R. O. & Sheriff, D. W. 1996 Water use by *Pinus radiata* trees in a plantation. *Tree Physiol.* **16**, 273–279.
- Vertessy, R. A., Hatton, T. J., Reece, P., Sullivan, S. K. & Benyon, R. G. 1997 Estimating stand water use of large mountain ash trees and validation of the sap flow measurement technique. *Tree Physiol.* **17**, 747–756.
- Wallach, D. 2006 Evaluating crop models. In: *Working with Dynamic Crop Models: Evaluation, Analysis, Parameterization, and Applications*. Elsevier, Amsterdam, The Netherlands, pp. 11–50.
- Wang, T. 2004 Progress in sandy desertification research of China. *J. Geogr. Sci.* **14** (4), 387–400.
- Wang, X. P., Kang, E. S., Zhang, J. G. & Li, X. R. 2004a Evapotranspiration of *Artemisia ordosia* vegetation in stabilized arid desert dune in Shapotou, China. *Arid Land Res. Manag.* **18**, 63–76.
- Wang, X. P., Brown-Mitic, C. M., Kang, E. S., Zhang, J. G. & Li, X. R. 2004b Evapotranspiration of *Caragana korshinskii* communities in a revegetated desert area: Tengger Desert, China. *Hydrol. Process.* **18**, 3293–3303.
- Xia, G. M., Kang, S. Z., Li, F. S., Zhang, J. H. & Zhou, Q. Y. 2008 Diurnal and seasonal variations of sap flow of *Caragana korshinskii* in the arid desert region of north-west China. *Hydrol. Process.* **22**, 1197–1205.
- Zhang, Z. S., Liu, L. C., Li, X. R., Zheng, J. G., He, M. Z. & Tan, H. J. 2008 Evaporation properties of a revegetated area of the Tengger Desert North China. *J. Arid Environ.* **72**, 964–973.
- Zhang, Z. S., Li, X. R., Liu, L. C., Jia, R. L., Zhang, J. G. & Wang, T. 2009 Distribution, biomass, and dynamics of roots in a revegetated stand of *Caragana korshinskii* in the Tengger Desert, northwestern China. *J. Plant Res.* **122**, 109–119.
- Zhang, F., Zhou, G. S., Wang, Y., Yang, F. L. & Nilsson, C. 2012 Evapotranspiration and crop coefficient for a temperate desert steppe ecosystem using eddy covariance in Inner Mongolia, China. *Hydrolog. Process.* **26**, 379–386.

First received 24 October 2013; accepted in revised form 5 February 2014. Available online 13 March 2014