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# Regulation of the water status in three co-occurring phreatophytes at the southern fringe of the Taklamakan Desert

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## Abstract

### Aims

We investigated the regulation of the water status in three predominant perennial C3 phreatophytes (*Alhagi sparsifolia*, *Populus euphratica*, *Tamarix ramosissima*) at typical sites of their occurrence at the southern fringe of the hyperarid Taklamakan Desert (north-west China).

### Methods

In the foreland of the river oasis of Qira (Cele), we determined meteorological variables, plant biomass production, plant water potentials ( $\Psi_L$ ) and the water flux through the plants. We calculated the hydraulic conductance on the flow path from the soil to the leaves ( $k_{SL}$ ) and tested the effects of  $k_{SL}$ ,  $\Psi_L$  and the leaf-to-air difference in the partial pressure of water vapour ( $\Delta w$ ) on stomatal regulation using regression analyses.

### Important Findings

Despite high values of plant water potential at the point of turgor loss, all plants sustained  $\Psi_L$  at levels that were high enough to maintain transpiration throughout the growing season. In *A. sparsifolia*, stomatal resistance ( $r_s$ ; related to leaf area or leaf mass) was most closely correlated with  $k_{SL}$ ; whereas in *P. euphratica*, ~70% of the variation in  $r_s$  was explained by  $\Delta w$ . In *T. ramosissima*, leaf area-related  $r_s$  was significantly correlated with  $\Psi_L$  and  $k_{SL}$ . The regulation mechanisms are in accordance with the growth patterns and the occurrence of the species in relation to their distance to the ground water.

**Keywords:** aboveground growth • extreme aridity • stomatal conductance • transpirational demand • vapour pressure deficit

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## INTRODUCTION

The Taklamakan Desert, located in the Central-Asian Tarim Basin (Xinjiang province, north-west China), is a hyper-arid desert exhibiting a ratio of mean annual precipitation to mean annual evapotranspiration of  $<0.03 \text{ mm mm}^{-1}$  (cf. Whitford 2002). In the central part of its southern fringe, mean annual

precipitation is ~33 mm (Thomas *et al.* 2000), and potential annual evaporation ~2600 mm (Xia *et al.* 1993). There, river oases exist that are supplied with water by the melting of snow and glaciers in the adjacent Kunlun mountain range. In the transition zone between the oases and the open desert, perennial species form stands of varying density and composition (Bruelheide *et al.* 2003; Walter and Box 1983). These species bear ecological

and economical importance for the human population because they constitute a shelter for the oases from sand drift (Xia *et al.* 1993) and are used for grazing, forage, construction and fuel (cf. Thomas *et al.* 2000). Among the perennial plants, the C3 species *Alhagi sparsifolia* Shap. (Fabaceae), *Tamarix ramosissima* Ledeb. (Tamaricaceae) and *Populus euphratica* Oliv. (syn. *Populus diversifolia* Schrenk; Salicaceae) represent the most abundant life forms around the oases, i.e. clonal herbs/sub-shrubs, shrubs and trees. Detailed information on these species is provided by Gries *et al.* (2005), Thomas *et al.* (2000) and Thomas *et al.* (2006).

Within the framework of a larger research project, evidence was provided that all perennial species in the transition zone between oasis and desert are phreatophytes, i.e. plants that meet their water demand by water uptake from the ground water or its capillary fringe (Gries *et al.* 2005; Li *et al.* 2002; Thomas *et al.* 2006; Zeng *et al.* 2002). The nitrogen requirements of the plants are also met by uptake from the ground water as has been revealed in a simultaneous study at the same sites (Arndt *et al.* 2004a). As an outcome of this research project, previous publications on plant water relations have focused on diurnal and seasonal courses of leaf water relations in *A. sparsifolia* (Li *et al.* 2002; Zeng *et al.* 2002), growth and water relations of *P. euphratica* and *T. ramosissima* along gradients of the ground water distance (Gries *et al.* 2003), effects of experimental flooding (Thomas *et al.* 2006; Zeng *et al.* 2006) and water use by the vegetation (Thomas *et al.* 2006). The present study concentrates on comparing regulation mechanisms of the plant water status in three of the predominating C3 phreatophytes (*A. sparsifolia*, *P. euphratica* and *T. ramosissima*), which occur within the same stand or in close-by stands. A strict regulation of water loss by transpiration and/or an effective water supply through the roots and the shoot axes is necessary due to the high transpirational demand that is caused by the large water vapour pressure deficit of the air (VPD) during the greatest part of the growing season. The large distance to the ground water (up to 16 m in level stands, Thomas *et al.* 2006, and up to 24 m on the top of sand dunes, Gries *et al.* 2003) renders such regulation mechanisms even more decisive. The water relations of the above-mentioned species were studied during the growing season at sites that are typical for their distribution in the transition zone between oases and desert. It was hypothesized that (i) in *A. sparsifolia*, which can form monospecific stands at a large distance to the ground water (~16 m at the study site), stomatal regulation is mainly governed by the leaf-specific hydraulic conductance on the flow path from ground water to leaf ( $k_{SL}$ ); (ii) in *P. euphratica*, which is a typical tree species of the floodplain forests along rivers (Walter and Box 1983), stomatal regulation is mainly determined by the leaf-to-air difference in the partial pressure of water vapour ( $\Delta w$ ) that, at light saturation, is the driving force of transpiration (e.g. Meinzer 2003; Oren *et al.* 1999) and (iii) in *T. ramosissima*, the leaf water potential that can assume lower (more negative) values in this salt-tolerant species is significantly correlated with stomatal regulation.

In the latter species, a less tight correlation between stomatal regulation and  $k_{SL}$  than in *A. sparsifolia* was expected because the extensive system of roots (Xu and Li 2006; Xu *et al.* 2007) and buried parts of the shoot (Qong *et al.* 2002) provide a high potential of tapping into ground water, but, at the same time, increases the length of the flow path from the ground water to the leaves.

## MATERIALS AND METHODS

### Study sites

The study was conducted at the southern fringe of the Taklamakan Desert, Xinjiang-Uighur Autonomous Region, China, in the foreland of the river oasis of Qira (Cele; N 37° 01', E 80° 48'; 1365 m a.s.l.) in the growing season of 1999. Mean annual temperature is 11.9 °C and mean annual precipitation 33 mm. At sites that were typical for the distribution of the respective species (cf. Bruelheide *et al.* 2003), one rectangular, level study plot per species was fenced, which was almost exclusively covered by *A. sparsifolia* Shap. (maximum height: 1.5 m, maximum leaf area index (LAI): 1.7), *P. euphratica* Oliv. (syn. *P. diversifolia* Schrenk) (average height: 6 m; maximum LAI: 2.6) or *T. ramosissima* Ledeb. (average height: 2 m; maximum LAI: 2.8) (for details, see Foetzki 2003; Thomas *et al.* 2000, 2006). At the *Populus* and the *Tamarix* plots, the distance to ground water was 3.6 and 5.7 m, respectively, as was proven by manual drilling. On the basis of the water table in a nearby well, the ground water distance was estimated to be 16 m at the *Alhagi* plot. One automatic weather station (Campbell Scientific, Shepshed, UK) each at the *Alhagi* and the *Tamarix* site was installed to continuously record climatic variables: air temperature, air humidity, global solar radiation, photosynthetically active radiation (PAR) and wind speed. According to a comparison conducted for 2 years (1999 and 2000), the data of both stations were nearly interchangeable.

Within the framework of a larger study (cf. Thomas *et al.* 2000), the contribution of natural inundations—which occur, on average, every 2–3 years in summer—to the plants' water supply was assessed. To this end, the plots were artificially flooded in summer 1999. As the flooding had no measurable effect on the water relations of the investigated species (Thomas *et al.* 2006), it can be neglected in the context of the present study.

### Plant biomass and productivity

The aboveground biomass of the plants was calculated by means of allometric regressions (Gries *et al.* 2005). In *A. sparsifolia*, we established correlations between the aboveground biomass, which had been determined through preliminary harvests, and the spherical crown volume. In *P. euphratica* and *T. ramosissima*, aboveground biomass was computed from regressions with the basal area diameter. Growth was determined on the basis of these allometric regressions by repeated surveys of the diameters of marked stems (Gries *et al.* 2005). Leaf mass per unit leaf area (LMA) was calculated through leaf area measurements

with a scanner using Delta-T SCAN software (Version 2.04nc; Delta-T Devices Ltd., Burwell, Cambridge, UK).

### Plant water relations

In six ramets per species of similar size, diurnal courses (~from 7:00 to 19:00 h, including predawn measurements) of the leaf water potential ( $\Psi_L$ ) were measured at intervals of 4–6 weeks from early May until the end of September using pressure chambers (Model 1000, PMS Co, Corvallis, OR, USA) with three replicates per ramet and time of measurement. Coinciding with these measurements, diurnal courses (approximately from 8:00 to 19:00 h) of transpiration ( $E$ ) and stomatal conductance to water vapour ( $g_s$ ) were monitored using a porometer (LI-1600, LI-COR, Lincoln, NE, USA) with equal numbers of ramets and replicates. Measurements of PAR were conducted using a quantum sensor (LI-COR LI-190S-1) that was coupled to the porometer. The water-vapour gradient (leaf-to-air difference in the partial pressure of water vapour,  $\Delta w$ ) was calculated from leaf temperature, air temperature and air humidity measured during porometry and the tabulated value for air pressure at an altitude of 1365 m (86.17 kPa). From April to October, at intervals of 3–5 weeks, water-relation parameters of shoots were measured by establishing pressure–volume curves (pV curves) in three ramets per plot according to Thomas (2000). The osmotic pressure at the turgor loss point ( $\Psi_{\pi}^0$ , which, at this point, equals the tissue water potential) was determined from the pV curves.

In six ramets of *A. sparsifolia* and *T. ramosissima* of similar size within each species, xylem sap flow was continually measured during the growing season at the stem base using the heat-balance method (sap-flow meter T693.2, EMS, Brno, Czech Republic; cf. Lindroth *et al.* 1995). Transpiration and sap flow were related to the area or to the dry matter of the leaves. The hydraulic conductance on the flow path from the soil to the leaves ( $k_{SL}$ ) was calculated according to

$$k_{SL} = J_{H_2O} / (\Psi_{soil} - \Psi_L - \Psi_G),$$

where  $J_{H_2O}$  is the mass of liquid water translocated from the soil to the leaves per unit leaf area (or leaf dry matter) and time,  $\Psi_{soil}$  is the water potential of the soil and  $\Psi_G$  is the gravitational potential along the distance between ground water level and the leaves of the upper canopy (0.01 MPa  $m^{-1}$ ). Because the plants were presumed to have contact with the ground water (see Study sites),  $\Psi_{soil}$  was set to the osmotic potential of the moderately saline ground water (–0.3 MPa, according to the concentrations of inorganic ions analysed in the ground water at the *Populus* site; Arndt *et al.* 2004a). In *P. euphratica*,  $E$  was used instead of  $J_{H_2O}$  for calculating  $k_{SL}$ . This was possible because the decoupling coefficient  $\Omega$  (calculated according to Jarvis and McNaughton 1986) was below 0.2, indicating a relatively close coupling between the conditions at the leaf surface and those in the free airstream (Herbst 1995; Thomas *et al.* 2006). Daily maximum  $k_{SL}$  values were computed for the time of the day with the greatest quotient of  $J_{H_2O}$  or  $E$ , respectively (measured at light saturation of  $g_s$ ) and the differ-

ence  $\Psi_{soil} - \Psi_L - \Psi_G$ . To consider the different distances to the water table,  $k_{SL} \times$  path length was also calculated using ground water depth plus canopy height for the path length.

### Data analyses

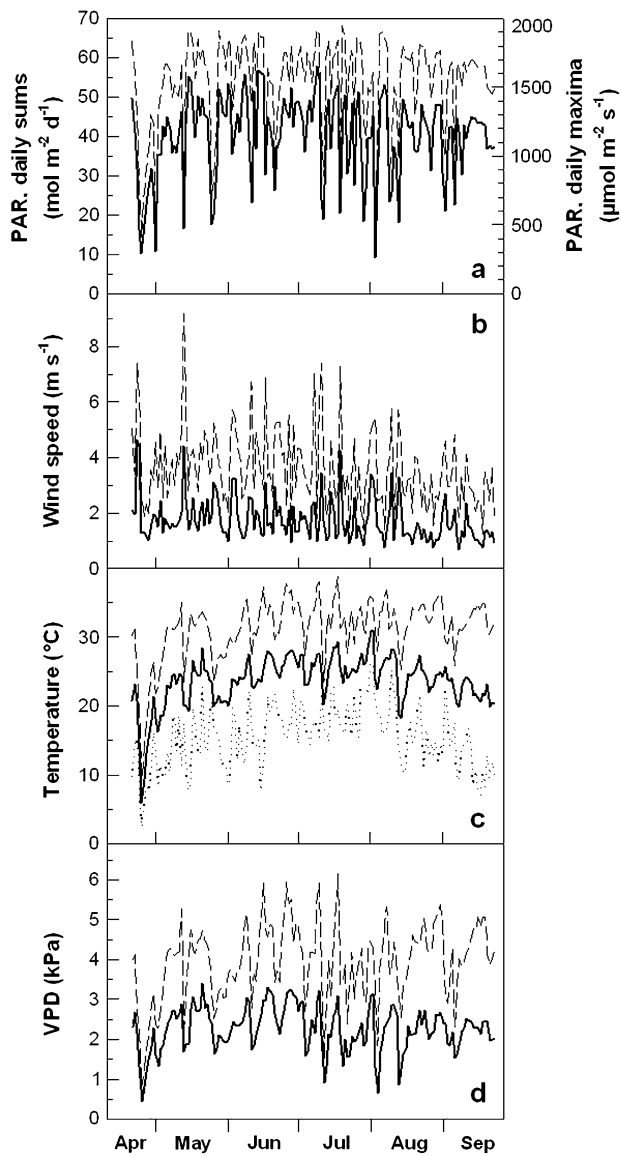
Mean values and standard errors are given in the presentation of the results. Differences among the species in their diurnal and seasonal courses of water relation parameters were tested using the Friedman test, followed by multiple pairwise comparisons according to the Student–Newman–Keuls method ( $P < 0.05$ ). Multiple regressions including the predictor variables  $\Delta w$ ,  $\Psi_L$  and  $k_{SL}$ , and  $r_s$  as the response variable, were calculated with SPSS 13.0.1 (SPSS Inc., Chicago, IL, USA). Leaf area-related and leaf mass-related  $r_s$  ( $m^2 s mol^{-1}$  or  $g s mmol^{-1}$ )—the inverse value of stomatal conductance ( $g_s$ )—were chosen because of their linear relationship with the vapour pressure deficit, whereas the relationship between the vapour pressure deficit and  $g_s$  is curvilinear (cf. Meinzer 2003). Only those values were included that were measured at light-saturating  $g_s$  and at the same time of the day of measurement. Air temperature and air humidity were not considered as additional predictor variables as they were significantly correlated with  $\Delta w$  ( $R^2 > 0.5$ ).

For a more detailed analysis of stomatal regulation, we calculated boundary lines for the relationship between stomatal conductance ( $g_s$ ) and  $\Delta w$  according to Schäfer *et al.* (2000): within the range between 20 and 65 Pa  $kPa^{-1}$ ,  $\Delta w$  data were partitioned to classes with a width of 2.5 Pa  $kPa^{-1}$  (assuring that each class comprised at least five data points); from each class, the outliers were removed using Dixon's test according to Sachs (1984; pp. 279 f); for the remaining data, the mean value and the standard deviation of  $g_s$  were computed class wise; and data falling above the mean value plus one standard deviation were averaged. From these average values of  $g_s$  and the corresponding  $\Delta w$  values, the upper boundary lines were constructed for each species. To avoid effects of rapid growth in spring and of different irradiation, this analysis was performed on time periods when the aboveground biomass of the species had reached at least 80% of peak aboveground biomass, and when light saturation of  $g_s$  was provided, irrespective of the time of the day (*A. sparsifolia*: PAR > 980  $\mu mol m^{-2} s^{-1}$ ; *P. euphratica*: PAR > 240  $\mu mol m^{-2} s^{-1}$ ; *T. ramosissima*: PAR > 510  $\mu mol m^{-2} s^{-1}$ ; light saturation was determined by plotting stomatal conductance against PAR).

## RESULTS

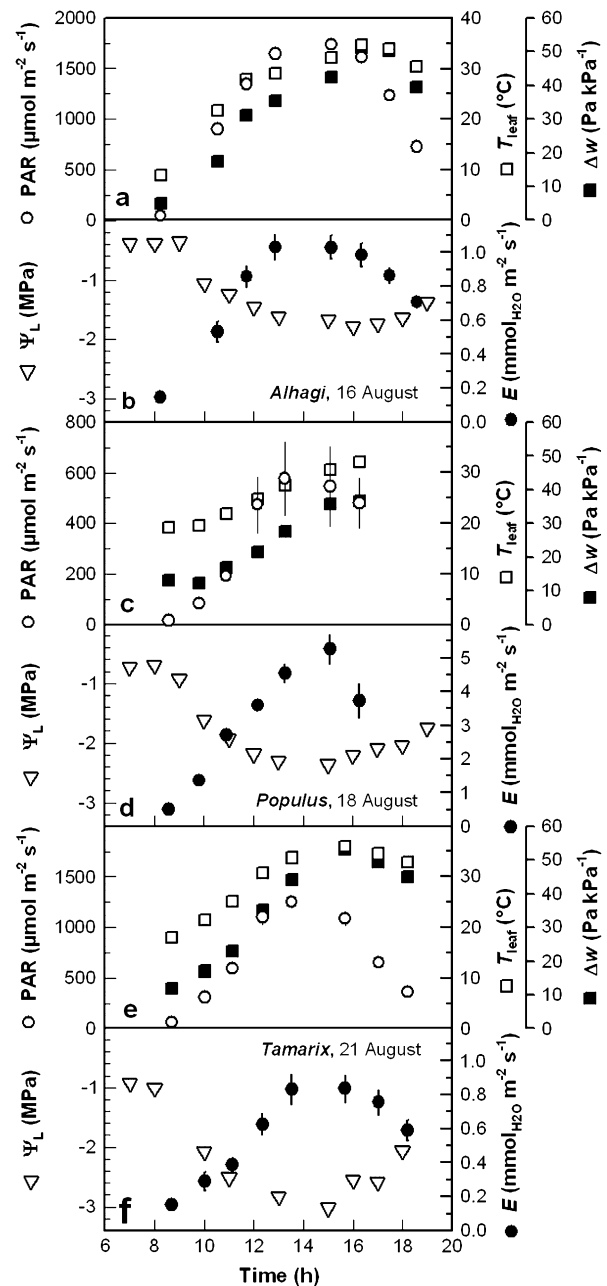
### Meteorological variables and plant water status

The PAR reached peak values from mid-May to the beginning of August, whereas the highest temperatures were confined to a period from mid-June to mid-July (Fig. 1). On >90% of the days in the period from mid-April to the end of September, the daily average VPD exceeded 1.5 kPa, and on >80% of the days, the daily maximum exceeded 3 kPa. Peak values of >5.5 kPa were reached in June and July.



**Figure 1:** seasonal courses of (a) PAR (daily sums, solid line; daily maxima, broken line), (b) wind speed (daily means, solid line; daily maxima, broken line), (c) temperature (daily means, solid line; daily maxima, broken line; daily minima, dotted line) and (d) VPD (daily means, solid line; daily maxima, broken line) in the growing season of 1999, measured in the foreland of Qira oasis (*Tamarix* study site). The values were calculated from hourly means.

Typical examples of diurnal courses of  $\Psi_L$  and  $E$  in mid-August, when complete data sets could be obtained from all species within 5 days, are shown in Fig. 2. *Alhagi sparsifolia* exhibited the highest  $\Psi_L$  values and *T. ramosissima* the lowest. The leaf area-related values of  $E$  were highest in *P. euphratica*. During the growing season, the minimum diurnal water potential of the photosynthetically active plant parts ( $\Psi_{\min}$ ) decreased except for *T. ramosissima* in which, after reaching a minimum in August, it increased slightly towards the end of September (Fig. 3). During the seasonal course, the  $\Psi_{\min}$



**Figure 2:** diurnal courses of leaf water potential ( $\Psi_L$ ) and leaf area-related transpiration ( $E$ ) (b, d, f), and diurnal courses of PAR, leaf temperature ( $T_{\text{leaf}}$ ) and the leaf-to-air difference in the partial pressure of water vapour ( $\Delta w$ ) (a, c, e) in *Alhagi sparsifolia* (a, b), *Populus euphratica* (c, d) and *Tamarix ramosissima* (e, f) in August. The  $\Psi_L$  and  $E$  data are mean values ( $\pm 1$  SE) from six ramets (note the differing scaling for  $E$  of *Populus*). Time is given as the official Beijing time (Greenwich mean time + 8 h). Sunrise was at  $\sim 8:00$  h and sunset at  $\sim 21:00$  h. The weather conditions were similar on all 3 days (sunny with maximum air temperature of  $30.6\text{--}33.5$   $^{\circ}\text{C}$ , maximum wind speed of  $2.6\text{--}3.9$   $\text{m s}^{-1}$  and maximum VPD of  $3.8\text{--}4.5$  kPa [hourly means]). The diurnal courses of  $\Psi_L$  differed significantly among all species (*A. sparsifolia* > *P. euphratica* > *T. ramosissima*). In *P. euphratica*,  $E$  was significantly higher than in *A. sparsifolia* and *T. ramosissima* during the day (Friedman test).

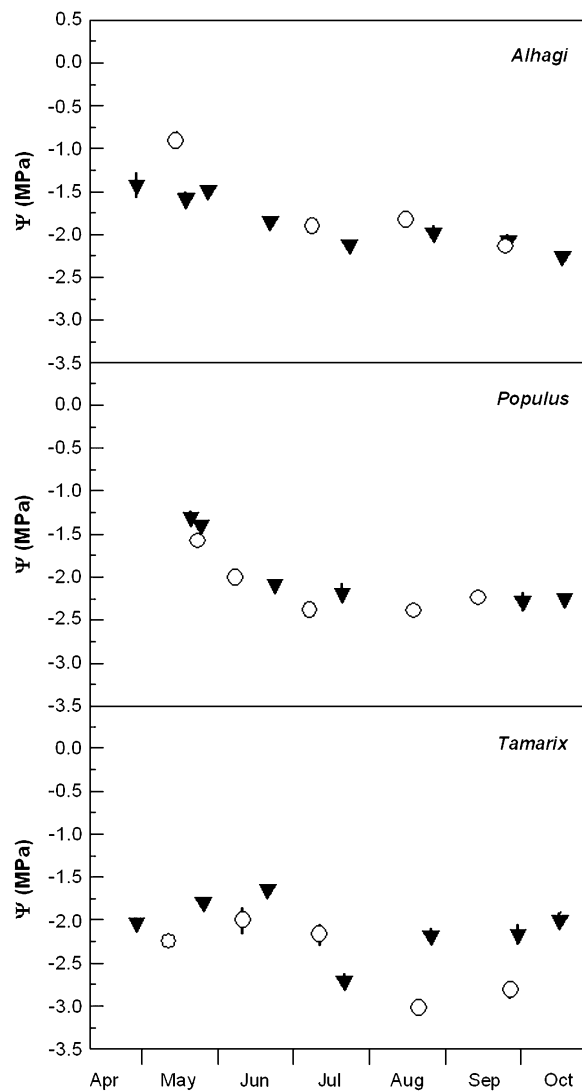
values of *A. sparsifolia* were significantly higher than in *P. euphratica* and *T. ramosissima*. Only in *T. ramosissima* did  $\Psi_{\min}$  fall below  $-2.5$  MPa. The course of the relatively high water potentials at the point of turgor loss ( $\Psi_{\pi}^0$ ) was parallel to that of  $\Psi_{\min}$ .

### Biomass formation, water translocation and hydraulic conductance

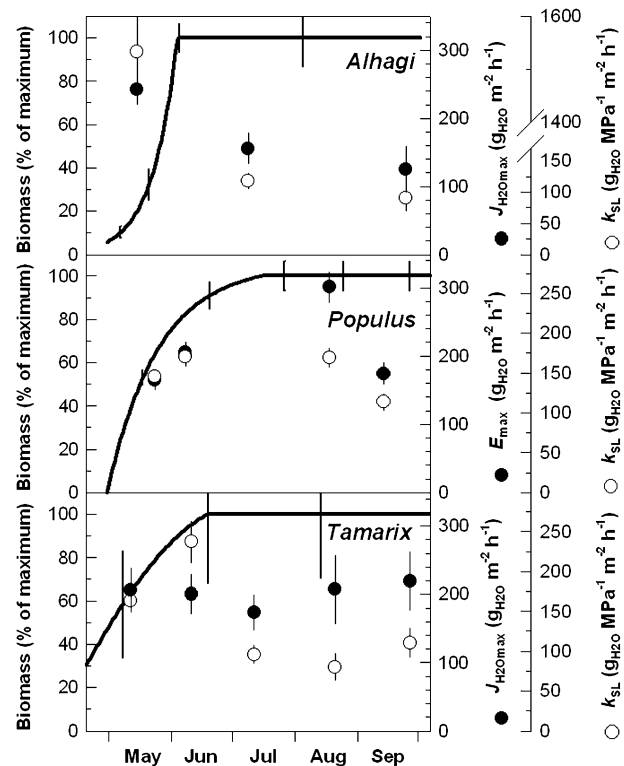
From the first transpiration measurements in May to the last ones in September, LMA increased from 100.3 to 218.4 g m<sup>-2</sup> in *A. sparsifolia*, from 119.0 to 141.7 g m<sup>-2</sup> in *P. euphratica* and from 124.1 to 156.0 g m<sup>-2</sup> in *T. ramosissima*. *Alhagi sparsifolia* reached its peak aboveground biomass within considerably

shorter time than did the other species: starting from 1% of initial aboveground biomass, 100% aboveground biomass were formed within only 56 days; whereas in *P. euphratica* and *T. ramosissima*, maximum photosynthetically active biomass was developed after 77 and 79 days, respectively (Fig. 4). In *A. sparsifolia*, the almost exponential course of aboveground biomass formation coincided with high daily maximum values of  $J_{H_2O}$  and very high maximum hydraulic conductance on the flow path from the soil to the leaves ( $k_{SL}$ ), due to high  $\Psi_L$  at that time. Once the peak aboveground biomass had been reached, these values declined drastically (Fig. 4). In *P. euphratica* and *T. ramosissima*, the maximum values of  $k_{SL}$  and of  $E$  or  $J_{H_2O}$  started from a much lower level and exhibited only a slight to moderate decrease ( $k_{SL}$ ) or no distinct seasonal trend at all ( $E$  and  $J_{H_2O}$ ). The maximum values of leaf area-related  $g_s$  were 706 mmol<sub>H<sub>2</sub>O</sub> m<sup>-2</sup> s<sup>-1</sup> in *A. sparsifolia* (May), 208 mmol<sub>H<sub>2</sub>O</sub> m<sup>-2</sup> s<sup>-1</sup> in *P. euphratica* (July and August) and 194 mmol<sub>H<sub>2</sub>O</sub> m<sup>-2</sup> s<sup>-1</sup> in *T. ramosissima* (May).

In Fig. 4, the maximum values of  $J_{H_2O}$ ,  $E$  and  $k_{SL}$  are related to unit leaf area. When normalized by unit leaf dry matter, the decrease in *Alhagi*'s  $J_{H_2Omax}$  and  $k_{SL}$  was even steeper (from



**Figure 3:** minimum diurnal water potential ( $\Psi_{\min}$ ; open circles) and water potential at the point of turgor loss ( $\Psi_{\pi}^0$ ; triangles) in photosynthetically active parts of *Alhagi sparsifolia*, *Populus euphratica* and *Tamarix ramosissima* during the growing season (means  $\pm$  1 SE). In the seasonal course,  $\Psi_{\min}$  values were significantly higher in *A. sparsifolia* than in *P. euphratica* and *T. ramosissima* (Friedman test).



**Figure 4:** development of aboveground (*Alhagi sparsifolia*) or leaf biomass (*Populus euphratica*, *Tamarix ramosissima*) in per cent of maximum biomass (solid lines; means  $\pm$  1 SE at the dates of biomass determination); leaf area-related daily maximum sap flow ( $J_{H_2Omax}$ ) or transpiration ( $E_{max}$ ), respectively (solid circles; means  $\pm$  1 SE), and leaf area-related daily maximum hydraulic conductance on the flow path from the soil to the leaves ( $k_{SL}$ , open circles; means  $\pm$  1 SE) during the growing season. For details of biomass determination, see Gries et al. (2005).

May to September:  $J_{H_2O}$ , 2.42–0.57  $g_{H_2O} g_{DM}^{-1} h^{-1}$ ;  $k_{SL}$ , 15.28–0.42  $g_{H_2O} MPa^{-1} g_{DM}^{-1} h^{-1}$ ), due to the larger increase in LMA. In the other species, the seasonal patterns of  $J_{H_2O}$  or  $E$  and of  $k_{SL}$  were similar to those derived from the leaf area-related values.

In May, the differences in  $k_{SL}$  among the species were even larger when the path length from the ground water table to the canopy was considered. Corresponding with the high  $J_{H_2O}$  in May, and due to the large estimated distance to the ground water level (16.7 m including the aboveground part of the stem), the leaf area-related  $k_{SL} \times$  path length was especially high in *A. sparsifolia* (maximum value:  $25.6 \pm 1.1 g_{H_2O} m MPa^{-1} m^{-2} h^{-1}$ ), but decreased to the level of *T. ramosissima* ( $\sim 1.7 g_{H_2O} m MPa^{-1} m^{-2} h^{-1}$ ) after peak aboveground biomass was reached. In *P. euphratica*, maximum  $k_{SL} \times$  path length was  $1.6 \pm 0.1 g_{H_2O} m MPa^{-1} m^{-2} h^{-1}$ .

### Effects of $\Delta w$ , $\Psi_L$ and $k_{SL}$ on stomatal regulation

In *A. sparsifolia*,  $k_{SL}$  was the strongest single predictor variable and, together with  $\Delta w$ , explained  $\sim 60\%$  of the total variance in  $r_s$  (Table 1). By contrast,  $\Psi_L$  and  $\Delta w$  had only low prediction value when applied as single variables. In *P. euphratica*,  $\Delta w$  was the variable with the highest prediction value, whereas  $k_{SL}$  and  $\Psi_L$  had much lower predictive power. In *T. ramosissima*, the regression model yielded significant results only when  $r_s$  and  $k_{SL}$  were related to leaf area instead of dry matter (Table 1). In this case,  $\Psi_L$  and  $k_{SL}$  were the strongest predictor variables. There was no significant relationship between  $r_s$  and  $\Delta w$ , but together with  $\Psi_L$  or  $k_{SL}$ ,  $\Delta w$  contributed significantly to explaining the variance in  $r_s$  due to a significant correlation between  $\Delta w$  and  $\Psi_L$  ( $r^2 = 0.666$ ;  $P < 0.001$ ).

In *P. euphratica*, maximum  $g_s$  was much more responsive to  $\Delta w$  than in *T. ramosissima* (Fig. 5). The different thresholds of light saturation of  $g_s$  (see Data analyses) did not affect the result because a computation with values of *P. euphratica* obtained at higher irradiance ( $\geq 510 \mu mol m^{-2} s^{-1}$ ) yielded a slope that did not differ significantly from the one calculated for the lower threshold. In the case of *A. sparsifolia*, no boundary line with a significant linear or simple non-linear regression could be calculated, probably due to the only small effect of  $\Delta w$  on  $g_s$ .

## DISCUSSION

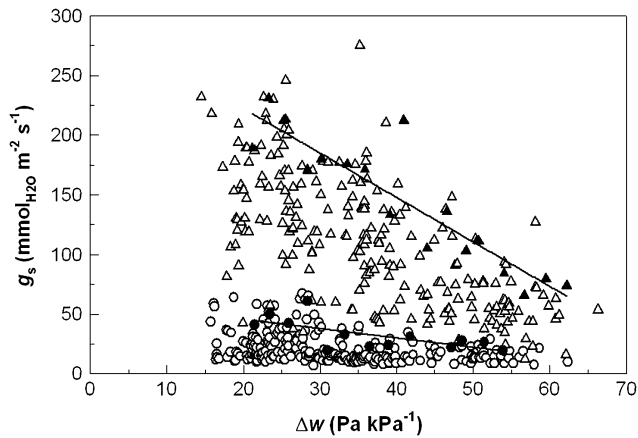
### Plant water relations under hyperarid conditions

The  $\Psi_{min}$  values measured in our study were high (greater than or equal to  $-3$  MPa) compared to typical desert plants. The lowest  $\Psi_{min}$  values were detected in *T. ramosissima* that accumulates salt (Arndt *et al.* 2004a). Desert shrubs of north-western America exhibited minimum stem water potentials between  $-3$  and  $-6$  MPa (Sperry and Hacke 2002), and minimum water potentials of  $-4.2$  MPa were measured in the chamaephyte *Anabasis articulata* in interdune corridors of the Negev Desert (Veste 2008). In desert plants, minimum values as low as  $-14$  MPa can be found (Schulze *et al.* 2005). Even in semi-arid environments like in south-eastern Spain, minimum water potentials

**Table 1:**  $R^2$  values resulting from multiple regression analysis of the leaf-to-air difference in the partial pressure of water vapour ( $\Delta w$ ), the water potential of photosynthetically active plant parts ( $\Psi_L$ ), and the hydraulic conductance on the flow path from the soil to the leaves ( $k_{SL}$ ) (predictor variables) on the stomatal resistance to water vapour ( $r_s$ ; response variable) in *Alhagi sparsifolia*, *Populus euphratica* and *Tamarix ramosissima*. The analysis was separately performed for  $r_s$  and  $k_{SL}$  values related to leaf area and to leaf dry matter. It was restricted to periods when aboveground biomass was at least 80% of peak aboveground biomass and to conditions of light saturation of  $g_s$ .  $n$ , number of measurements.  $P$  values  $< 0.1$  are printed in boldface

Predictor variables	$r_s$ , $k_{SL}$ related to leaf area		$r_s$ , $k_{SL}$ related to leaf mass	
	$R^2$	$P$	$R^2$	$P$
<i>A. sparsifolia</i> ( $n = 11$ )				
$k_{SL}$	0.507	<b>0.014</b>	0.311	<b>0.075</b>
$\Psi_L$	0.329	0.065	0.173	0.204
$\Delta w$	0.042	0.547	0.000	0.979
$k_{SL}$ , $\Delta w$	0.589	<b>0.028</b>	0.618	<b>0.021</b>
$k_{SL}$ , $\Psi_L$	0.512	<b>0.057</b>	0.316	0.218
$\Psi_L$ , $\Delta w$	0.332	0.199	0.219	0.372
$k_{SL}$ , $\Delta w$ , $\Psi_L$	0.606	<b>0.075</b>	0.683	<b>0.036</b>
<i>P. euphratica</i> ( $n = 18$ )				
$\Delta w$	0.738	<b>&lt;0.001</b>	0.693	<b>&lt;0.001</b>
$k_{SL}$	0.304	<b>0.018</b>	0.201	<b>0.062</b>
$\Psi_L$	0.035	0.460	0.006	0.766
$\Delta w$ , $k_{SL}$	0.960	<b>&lt;0.001</b>	0.962	<b>&lt;0.001</b>
$\Delta w$ , $\Psi_L$	0.738	<b>&lt;0.001</b>	0.701	<b>&lt;0.001</b>
$k_{SL}$ , $\Psi_L$	0.359	<b>0.036</b>	0.279	<b>0.086</b>
$\Delta w$ , $k_{SL}$ , $\Psi_L$	0.965	<b>&lt;0.001</b>	0.978	<b>&lt;0.001</b>
<i>T. ramosissima</i> ( $n = 14$ )				
$\Psi_L$	0.481	<b>0.006</b>	0.032	0.542
$k_{SL}$	0.447	<b>0.009</b>	0.037	0.509
$\Delta w$	0.159	0.158	0.040	0.490
$\Psi_L$ , $\Delta w$	0.565	<b>0.010</b>	0.041	0.794
$\Psi_L$ , $k_{SL}$	0.492	<b>0.024</b>	0.037	0.812
$k_{SL}$ , $\Delta w$	0.447	<b>0.039</b>	0.049	0.760
$k_{SL}$ , $\Psi_L$ , $\Delta w$	0.569	<b>0.032</b>	0.067	0.868

distinctly below  $-4$  MPa were measured during drought (almost  $-5$  MPa in the shrub *Anthyllis cytisoides*, Domingo *et al.* 2003;  $-8.4$  MPa in the perennial tussock grass *Stipa tenacissima*, Balaguer *et al.* 2002). However, similar minimum leaf water potentials as in our study were found in woody phreatophytes at a high elevation in arid south-eastern Wyoming ( $-2.7$  MPa in *Populus angustifolia*, *Salix monticola* and *Salix exigua*; Foster and Smith 1991). Owing to the relatively high water potentials at the point of turgor loss ( $\Psi_{\pi}^0$ ), the range of water potentials that allow stomatal opening is rather narrow in the plants of our study. However, our diurnal measurements of  $E$ ,  $g_s$  and  $J_{H_2O}$  demonstrate that although  $\Psi_{min}$  was close to  $\Psi_{\pi}^0$  in all



**Figure 5:** leaf area-related stomatal conductance ( $g_s$ ) versus leaf-to-air difference in the partial pressure of water vapour ( $\Delta w$ ) in *Populus euphratica* (triangles) and *Tamarix ramosissima* (circles). All values have been measured at light saturation of  $g_s$ . Solid symbols depict the values that have been calculated according to Schäfer *et al.* (2000) for constructing the boundary lines (*P. euphratica*:  $n = 17$ ;  $g_s = 296.7 - 3.724 \cdot \Delta w$ ;  $r^2 = 0.816$ ;  $P < 0.0001$ ; *T. ramosissima*:  $n = 13$ ;  $g_s = 61.4 - 0.786 \cdot \Delta w$ ;  $r^2 = 0.451$ ;  $P < 0.01$ ). The slopes of the regression lines differ significantly ( $t = 4.396$ ;  $P < 0.001$ ).

but one instances during the daylight period, stomata did not close completely during daylight. Thus, all investigated plant species were capable of maintaining their water potentials high enough to ensure transpiration and, in return,  $\text{CO}_2$  uptake throughout the growing season.

Especially in *A. sparsifolia*, high  $\Psi_L$  allowed maximum values of leaf area-related  $g_s$  (up to  $700 \text{ mmol}_{\text{H}_2\text{O}} \text{ m}^{-2} \text{ s}^{-1}$ ) that were considerably higher than in typical desert shrubs ( $220 \text{ mmol}_{\text{H}_2\text{O}} \text{ m}^{-2} \text{ s}^{-1}$ ) and even desert annuals ( $300 \text{ mmol}_{\text{H}_2\text{O}} \text{ m}^{-2} \text{ s}^{-1}$ ) (Körner 1994). High  $g_s$  in May facilitated high rates of biomass production during that time, before temperature and VPD increased in summer. However, the maximum value of  $J_{\text{H}_2\text{O}}$  in *A. sparsifolia* ( $243 \text{ g}_{\text{H}_2\text{O}} \text{ m}^{-2} \text{ h}^{-1}$ ) is not particularly high when compared to values from other shrub species with small or highly divided leaves in arid regions. In a floodplain in southern Nevada with a distance to the ground water of 0–3 m, average values of  $370\text{--}460 \text{ g}_{\text{H}_2\text{O}} \text{ m}^{-2} \text{ h}^{-1}$  were measured with sap-flow gauges in *T. ramosissima*, *Pluchea sericea*, *Prosopis pubescens* and *S. exigua* (Sala *et al.* 1996). In the small-leaved, drought-deciduous shrub *Guiera senegalensis* of the Nigerian Sahel, a maximum value as high as  $490 \text{ g}_{\text{H}_2\text{O}} \text{ m}^{-2} \text{ h}^{-1}$  has been obtained (Allen and Grime 1995). Nevertheless,  $J_{\text{H}_2\text{O}}$  in *A. sparsifolia* was high enough to enable a production of aboveground biomass of up to  $3.9 \text{ Mg ha}^{-1} \text{ a}^{-1}$  (Gries *et al.* 2005), which is higher than the maximum net primary productivity of typical desert scrub vegetation (up to  $2.5 \text{ Mg ha}^{-1} \text{ a}^{-1}$ ; Lieth 1975).

In *P. euphratica* and *T. ramosissima*, maximum  $g_s$  ( $\sim 200 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) was similar to that determined in woody species growing in a floodplain of the arid region of the Lower Colorado River ( $150\text{--}250 \text{ mmol m}^{-2} \text{ s}^{-1}$  in *Populus fremontii*,

*T. ramosissima* and *Salix gooddingii*; Busch and Smith 1995). However, at high elevation (2300 m a.s.l.) with low atmospheric pressure, woody phreatophytes (*P. angustifolia*, *S. monticola*, *S. exigua*) may also exhibit high maximum values of  $g_s$  ( $800\text{--}900 \text{ mmol m}^{-2} \text{ s}^{-1}$ ; Foster and Smith 1991). In the present study, the leaf area-related average daily sums of transpiration in *P. euphratica* ( $1.20\text{--}2.35 \text{ kg}_{\text{H}_2\text{O}} \text{ m}^{-2} \text{ d}^{-1}$ ) were similar to those determined by measuring xylem sap flow in the mesic tree species *Betula pendula* that is well known for its high transpirational rates compared to other mesic trees (daily mean value measured in a warm and dry growing season:  $2.1 \text{ kg}_{\text{H}_2\text{O}} \text{ m}^{-2} \text{ d}^{-1}$ ; Backes 1996). The high transpiration rates of *P. euphratica* were coupled with relatively high rates of annual biomass production (up to  $6.5 \text{ Mg ha}^{-1} \text{ a}^{-1}$ ; Gries *et al.* 2005), which is similar to the lower margin of the productivity of warm temperate mixed forests ( $6\text{--}25 \text{ Mg ha}^{-1} \text{ a}^{-1}$ ; Lieth 1975).

### Regulation of the plant water status

A close correlation between stomatal conductance (or stomatal resistance, respectively) and parameters of vapour pressure deficit as was established in *P. euphratica* in the present investigation has also been detected in other studies on plants in arid environments. Bucci *et al.* (2005) found a sharp decline of  $g_s$  with increasing VPD—from the wet to the dry season—in eight isohydric woody species of the Brazilian savannah that exhibited only small differences in the daily  $\Psi_{\text{min}}$  between the seasons. A seasonal change in the sensitivity of stomatal conductance to VPD was also observed in a population of the phreatophytic *Prosopis glandulosa* that grew at a ground water distance of 4–6 m in the Sonoran desert and was interpreted as an adaptation to avoid drought stress (Nilsen *et al.* 1983). In a semi-arid region of Southeastern Spain,  $g_s$  was negatively correlated with VPD in the shrub *Retama sphaerocarpa* (Brenner and Incoll 1997; Domingo *et al.* 2003). *Populus euphratica*, a characteristic species of Central-Asian floodplain forests, is not only restricted to sites with small ground water distances but also forms natural *Tamarix*–*Populus euphratica* forests with a ground water distance of  $>10$  m (Wang *et al.* 1996). A study along a gradient of increasing ground water distance revealed that *P. euphratica* is able to grow with accumulating sand up to a distance of the canopy to the water table that was as large as 23 m; at this distance, however, aboveground growth as well as stomatal conductance were significantly reduced (Gries *et al.* 2003). This ability of *P. euphratica* to tolerate larger ground water distances might be connected with the close correlation between  $r_s$  and  $\Delta w$  that was found in the present study: a high responsiveness of the stomatal resistance to changes in  $\Delta w$  decreases the risk of xylem cavitation under high transpirational demand at a given conducting efficiency (McDowell *et al.* 2008). In *P. euphratica*,  $\Delta w$  was also closely correlated with  $g_s$ , the inverse value of  $r_s$  ( $R^2 = 0.817$  when related to leaf area,  $R^2 = 0.844$  when related to leaf mass;  $P < 0.001$  in both cases). The correlation between  $\Delta w$  and  $g_s$  seems to be less tight in *Populus* species that are more restricted to small ground water distances: in *P. fremontii*, an obligate riparian tree, linear

regression models including VPD explained <29% of the variation in  $g_s$  (Horton *et al.* 2001; Pockman and Sperry 2000).

In *A. sparsifolia*, stomatal regulation is related to the leaf-specific hydraulic conductance on the flow path from ground water to leaf ( $k_{SL}$ ) more than to the leaf-to-air difference in the partial pressure of water vapour ( $\Delta w$ ). This is true at least for the largest part (beginning of June to September) of the growing season, when the aboveground biomass had reached at least 80% of its peak value. Water transport from the ground water level obviously is achieved through long shoot sections that extend from the soil surface vertically through the soil, with roots formed immediately at the threshold of the capillary fringe as could be observed on vertically eroded river banks (F. M. Thomas, personal observation). Thus, in *A. sparsifolia*, a high hydraulic conductance is a prerequisite for sustaining high levels of  $\Psi_L$ ,  $g_s$  and growth at large distances to the ground water.

Together with  $\Psi_L$ ,  $k_{SL}$  also affected stomatal resistance ( $r_s$ ) in *T. ramosissima* (the lack of significance in the model that used leaf dry matter-related data possibly was due to the smaller range of  $r_s$  values: minimum and maximum values differed by a factor of 2.4, as opposed to a factor of 3.5 in the case of leaf area-related  $r_s$  values). The figure of  $\sim 100 \text{ g}_{\text{H}_2\text{O}} \text{ MPa}^{-1} \text{ m}^{-2} \text{ h}^{-1}$  (computed as leaf-specific apparent hydraulic conductance from measurements of  $\Psi_L$  and transpiration) in *T. ramosissima* growing in the Gurbantonggut Desert (north-west China; Xu and Li 2006) fits to the  $k_{SL}$  values calculated in our study ( $80\text{--}237 \text{ g}_{\text{H}_2\text{O}} \text{ MPa}^{-1} \text{ m}^{-2} \text{ h}^{-1}$ ). The correlation between  $k_{SL}$  and  $r_s$  was somewhat surprising because, due to the plant's complex belowground structure (Gries *et al.* 2003; Qong *et al.* 2002; Xu and Li 2006), the flow path from the soil to the leaves should be considerably longer and, in addition, more variable than in the other species that have a more direct vertical connection to the ground water. Accordingly, no correlation was found between ground water distance on the one hand and leaf water potential and stomatal conductance on the other (Gries *et al.* 2003; Mounisif *et al.* 2002). Possibly, at a moderate distance to the ground water like in our study, the water translocation to the canopy is restricted to some few main paths, in which water flux is immediately controlled by  $\Psi_L$ . Low  $\Psi_L$  that, together with  $k_{SL}$ , sensitively control  $r_s$  might help *T. ramosissima* to maintain water uptake and growth under high transpirational demand during the entire growing season and might be one reason of this species' capability of extending farther into the desert than other perennial species (Bruehlheide and Jandt 2004; Walter and Box 1983).

In conclusion, our study has revealed that the mechanisms of water status regulation differ among the investigated phreatophytes. In the sub-shrub *A. sparsifolia* that can grow at ground water distances of as much as 16 m, stomatal conductance is mainly governed by the hydraulic conductance on the flow path from the ground water to the canopy. In *T. ramosissima*, a salt-accumulating shrub that exhibits the lowest  $\Psi_L$  values,  $\Psi_L$  contributes significantly to stomatal regulation. In *P. euphratica*, a typical species of floodplain forests, stomatal conductance is most sensitive to  $\Delta w$ . However, all

species are capable of maintaining  $\Psi_L$  within a range that allows transpiration throughout the growing season. Continuous transpiration facilitates  $\text{CO}_2$  uptake and, hence, sustains carbon assimilation, which may promote the growth of belowground shoots even after the peak of aboveground biomass formation has been reached. Belowground growth forms the basis of an extensive clonal growth, which has been observed in *A. sparsifolia* and *P. euphratica* (Bruehlheide *et al.* 2004). This clonal growth obviously is the basis of the occupation of space and of vegetative regeneration once the ground water distance is too large to be bridged from the soil surface.

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