Growth and water relations of *Tamarix ramosissima* and *Populus euphratica* on Taklamakan desert dunes in relation to depth to a permanent water table

D. GRIES[1], F. ZENG[3], A. FOETZKI[1], S. K. ARNDT[2]*, H. BRUELHEIDE[1], F. M. THOMAS[1], X. ZHANG[3] & M. RUNGE[1]

[1]*Albrecht-von-Haller-Institute for Plant Sciences, Department of Ecology and Ecosystems Research, University of Goettingen, 37073 Goettingen, Germany,* [2]*Institute of Ecology and Conservation Biology, University of Vienna, A-1090 Vienna, Austria* and [3]*Institute of Ecology and Geography, Chinese Academy of Science, Urumqi 830011, Xinjiang, P.R. China*

ABSTRACT

The hypothesis that water relations and growth of phreatophytic *Tamarix ramosissima* Ledeb. and *Populus euphratica* Oliv. on dunes of varying height in an extremely arid Chinese desert depend on vertical distance to a permanent water table was tested. Shoot diameter growth of *P. euphratica* was inversely correlated with groundwater depth (GD) of 7 to 23 m (adj. $R^2 = 0.69$, $P = 0.025$); growth of *T. ramosissima* varied independent of GD between 5 and 24 m ($P = 0.385$). Pre-dawn (pd) and midday (md) water potentials were lower in *T. ramosissima* (minimum pd − 1.25 MPa, md −3.6 MPa at 24 m GD) than in *P. euphratica* (minimum pd −0.9 MPa, md −3.05 MPa at 23 m GD) and did not indicate physiologically significant drought stress for either species. Midday water potentials of *P. euphratica* closely corresponded to GD throughout the growing season, but those of *T. ramosissima* did not. In both species, stomatal conductance was significantly correlated with leaf water potential (*P. euphratica*: adj. $R^2 = 0.84$, $P < 0.0001$; *T. ramosissima*: adj. $R^2 = 0.64$, $P = 0.011$) and with leaf-specific hydraulic conductance (*P. euphratica*: adj. $R^2 = 0.79$, $P = 0.001$; *T. ramosissima*: adj. $R^2 = 0.56$, $P = 0.019$); the three variables decreased with increasing GD in *P. euphratica*. Stomatal conductance of *P. euphratica* was more strongly reduced (> 50% between −2 and −3 MPa) in response to decreasing leaf water potential than that of *T. ramosissima* (30% between −2 and −3 MPa). Tolerance of lower leaf water potentials due to higher concentrations of leaf osmotically active substances partially explains why leaf conductance, and probably leaf carbon gain and growth, of *T. ramosissima* was less severely affected by GD. Additionally, the complex below-ground structure of large clonal *T. ramosissima* shrub systems probably introduces variability into the assumed relationship of xylem path length with GD.

Correspondence: Dirk Gries. E-mail: dgries@gwdg.de

*Present address: Department of Botany, University of Western Australia, Nedlands, WA, 6009, Australia.

INTRODUCTION

Indigenous vegetation in the foreland of river oases at the extremely arid southern margin of the Taklamakan desert in Xinjiang, NW China, is dominated by a few perennial phreatophytes, primarily *Tamarix ramosissima* Ledeb., *Populus euphratica* Oliv., *Alhagi sparsifolia* Shap. and *Phragmites australis* (Cav.) Steudel (Bruelheide *et al*. 2003; Qong, Takamura & Hudaberdi 2002). Due to permanent access to groundwater at depths from 3 to more than 10 m (Thomas *et al*. 2000a), stands of *T. ramosissima* and *P. euphratica* can be nearly as productive as typical vegetation of mesic climates (D. Gries, unpublished), even though mean annual precipitation is less than 50 mm throughout the region (Zhou 1993; Qong *et al*. 2002). The population of the oases exploits the vegetation by harvest of construction wood, fuel and livestock feed, and by grazing of sheep and goats; it thus plays an important role in the agro-economic system of the oases (Runge *et al*. 2001).

The productivity of dominant species varies considerably at small spatial scales in the foreland of the oasis (D. Gries, unpublished). Differences in nutrient supply can be ruled out as a reason because plants are uniformly supplied with most nutrients by the groundwater (S.K. Arndt, unpublished). Patterns of stand production in relation to position on dunes or in dune valleys suggest that stand growth is affected by distance to groundwater (D. Gries, unpublished). Greater groundwater depth could also explain why the size of *P. euphratica* trees generally decreases with increasing elevation on the dunes.

Groundwater depth could affect growth by at least two mechanisms:

1 Inevitably, more below-ground biomass per unit leaf area is required to reach groundwater from higher dunes, leaving less carbon available for above-ground growth; in this respect the situation may be similar to age-related

decline of tree productivity due to a shift of allocation from leaves to transport tissue (Magnani, Mencuccini & Grace 2000).

2   Lower leaf conductance of *T. ramosissima* on high dunes than in a dune valley, indicated by higher leaf $\delta^{13}C$ during the growing season (S.K. Arndt, unpublished results), suggested that effects of groundwater depth on growth may be mediated by plant water status. This may be anticipated, because as xylem transport distance increases at greater groundwater depth, lower leaf water potentials are required for water uptake and may in turn cause stronger stomatal limitation of photosynthetic carbon gain, similar to mechanisms operative in tall trees (Yoder *et al.* 1994; Mencuccini & Grace 1996; Ryan & Yoder 1997; Hubbard, Bond & Ryan 1999; Schäfer, Oren & Tenhunen 2000; Hubbard *et al.* 2001; McDowell *et al.* 2002).

The effects of groundwater depth on performance of *T. ramosissima* and related *Tamarix* species summarized as *Tamarix chinensis* Lourd., have been widely studied in riparian vegetation in the south-western US (Smith *et al.* 1998); however, most studies focused on the consequences of temporal depressions of groundwater tables induced by human alteration of riparian hydrology, rather than steady-state effects of different depths to a permanent groundwater table. Some results were unclear with respect to tolerance of deep groundwater: reduced gas exchange and increased canopy dieback was found if groundwater levels decreased below 3 m (*T. chinensis*, Horton, Kolb & Hart 2001a), whereas occurrence of vigorous *T. chinensis* stands at 7–8 m groundwater depth was reported by Stromberg (1998). This just indicates that in riparian ecosystems with seasonally variable precipitation, surface flow and groundwater tables, the water sources of facultative phreatophytes such as *T. ramosissima* are difficult to track; detailed isotope analyses are normally required in order to quantify temporally varying contributions from various sources to plant water supply (Busch, Ingraham & Smith 1992; Smith *et al.* 1998; Zencich *et al.* 2002).

The ecological situation at the margin of the Taklamakan desert is unusual and especially well suited for studying growth and water relations of facultative or obligate phreatophytes in relation to groundwater depth because the influence of other water sources, such as precipitation or water stored in the soil, can be ruled out. Annual precipitation is insignificant for plant growth; and typically no water is stored in the soils down to the capillary fringe (Thomas *et al.* 2000a; F.M. Thomas, unpublished). Moreover, in contrast to typical riparian situations, groundwater levels remain largely stable throughout the year (Thomas *et al.* 2000a; Bruelheide *et al.* 2002b; A. Foetzki, unpublished results).

We hypothesize that water relations and productivity of *P. euphratica* and *T. ramosissima* growing on dunes at varying elevations above a permanent groundwater table depend on distance to the water table. This distance is likely to affect (1) the whole-plant carbon economy, in particular above-to-below-ground allocation patterns and leaf area ratios, as well as (2) leaf-specific hydraulic conductance, leaf water relations and therefore potentially per-leaf area carbon gain. In order to test our hypothesis, we established elevation transects along depths of groundwater ranging from 7 to 23 m for *P. euphratica* and from 5 to 24 m for *T. ramosissima* within two dune complexes in the foreland of Qira oasis. The situation in Qira is typical for oases and riparian dunes along tributaries and ephemeral rivers at the margin of the Taklamakan, the largest desert in China and one of the largest ergs (sand dune deserts) in the world (Zhou 1993). At different elevations along the transects we measured daytime courses of leaf transpiration rate and conductance as well as pre-dawn and midday leaf water potentials on several days during the growing season, and measured the annual basal area increment of stems or shoots. Leaf analyses will be published in a related paper (Arndt *et al.* in preparation).

METHODS

Study site

The study was carried out near Qira (Cele) oasis (population 130 000), at 37°01′ N, 80°48′ E and at an elevation of 1365 m a.s.l. Qira is located 90 km east of Hotan at the southern fringe of the Taklamakan desert in Xinjiang Uighur Autonomous Region, NW China. Due to its location in the Tarim basin, surrounded by the alpine mountain ranges of the Pamir to the west, the Tian Shan to the north and the Kunlun to the south, the climate in the Taklamakan is extremely arid. Mean annual temperature is 11.9 °C, annual potential evaporation is approx. 2600 mm and the annual sum of precipitation is 35.1 mm (Zhou 1993). Tributaries and ephemeral rivers, fed by snow melt in the mountains during the summer months, allowed the establishment of river oases along the desert margins, which mark the course of the ancient silk road. The oasis is surrounded by a 5–10 km belt of sparse vegetation dominated by woody phreatophytic species (Bruelheide *et al.* 2003; Qong *et al.* 2002). As there is no rainy season, typically no annual species occur in the foreland.

Meteorological variables (Table 1) were recorded by a weather station located nearby in the foreland (Campbell Scientific, Shepshed, Leicestershire, UK). In 2000, the last day of spring with frost was 26 March and the first frost in autumn was recorded on 14 October (–0.15 °C). The lowest air temperature recorded in the foreland vegetation of Qira in 2000 was –18.7 °C on 18 January; the highest air temperature was 40.6 °C on 13 July. Solar noon is about 1430 h Beijing time, which is the official time in Xinjiang. Photosynthetic photon flux density (PPFD) is frequently reduced by dust. Relative humidity is usually very low and no dewfall was recorded in 1999 and 2000.

Silt is the predominant grain size fraction of the soil down to 7.5 m depth, with more than 87%, in 35 plots sampled around Qira oasis (H. Bruelheide, unpublished). Soil chem-

Date	PPFD (μmol m^{-2} s^{-1})	Air temperature (°C)	Relative humidity (%)	VPD (kPa)
P. euphratica				
2 June	682	26.7 (14.3–32.3)	20.7 (12–54)	2.98 (0.8–4.3)
10 July	742	30.3 (19.6–35.1)	23.4 (13–57)	3.52 (1.0–4.9)
24 August	875	26.6 (16.0–30.7)	30.8 (20–66)	2.60 (0.6–3.5)
9 October	609	16.6 (6.0–20.9)	33.3 (24–70)	1.35 (0.3–1.9)
T. ramosissima				
26 May	656	20.5 (14.3–25.2)	50.3 (29–82)	1.33 (0.3–2.3)
1 July	971	31.4 (16.9–37.7)	22.0 (10–58)	3.95 (0.8–5.8)
12 October	592	13.0 (6.1–17.1)	27.4 (17–54)	1.14 (0.4–1.6)

Means during daylight hours, and 24 h minimum and maximum (in parentheses), of 10 min average values recorded by a nearby weather station.

ical properties are uniform among the study sites, except for a higher sodium content in the uppermost soil layer underneath *T. ramosissima* stands (unpublished results).

Dune gradients and groundwater depths

We selected two sites where *P. euphratica* and *T. ramosissima* grew naturally in the foreland of Qira oasis. Just one gradient per species was considered because of the great homogeneity of the vegetation. The *Tamarix ramosissima* dune complex is 3 km north-west of the oasis (37°04.862′ N, 080°43.388′ E) and is never reached by surface water even during extreme summer floods. The dune height at the base of each sampled shrub group was determined with a laser surveying device. The difference in height between the highest dune top and the lowest point was 18.7 m and the horizontal difference between the two points was 55 m. *Tamarix ramosissima* shoots of 0.5–1.5 m height, clustered in groups of varying area and density, covered the tops and some slopes of the dunes, but less so in the valleys. The dune tops at lower elevations were covered more uniformly and densely. According to Qong *et al*. (2002) and our observations, clonal shrubs of *Tamarix* spp. cause the formation of cone-shaped dunes by fixing wind-blown sand and silt with their leaf and shoot litter. As a consequence of this accumulation, the dune surface constantly rises and the shrubs are forced to grow upward, forming dune cones of up to 15 m height, but always stay in contact with groundwater. The oldest *Tamarix* cones date back (^{14}C) to 4200 B.P. (Qong *et al*. 2002).

The *Populus euphratica* dune complex is 5 km west of the oasis (37°00.663′ N 080°40.166′ E) near an old, now dry, bed of the Qira river.; it is reached by surface water every few years, when an occasional extreme summer flood of the Qira river exceeds the capacity of the oasis' irrigation system and water is diverted into the foreland. The height difference between the highest dune top and the old river bed is 16 m. Consistent with clonal growth of *P. euphratica* trees, shoots are scattered in groups of varying size over the crests, slopes and saddles of the dune complex. Shoot groups are sparser at higher elevations; but sometimes form nearly closed canopies at the lowest elevations. The maxi-mal shoot height is 2 m at the highest top and more than 10 m near the dry riverbed. Excavations have shown that the woody parts of the *P. euphratica* trees buried in the dunes are stems, not roots (M. Runge, personal obs.). This is in agreement with our hypotheses about the establishment of these plant stands in the foreland of the oasis which suggest that these trees began growth, through germination after a flood or as root suckers, when the landscape surface was much lower and closer to the groundwater than today, and the trees then grew to greater height along with the dunes that were created by the accumulation of wind-blown silt.

The depth of groundwater was measured in the old riverbed at the *P. euphratica* site, and in a low dune valley 55 m east of the highest dune at the *T. ramosissima* site. We used a 7.5-m-long hand auger. Water-saturated soil was detected at a depth of 7.25 m at the *P. euphratica* site and at a depth of 5.0 m at the *T. ramosissima* site. Groundwater levels fluctuate little at the field sites. According to time domain reflectometry (TDR) measurements at a range of depths in nearby field sites, groundwater levels did not decrease during the growing season in 1999 (Thomas *et al*. 2000a) or 2000 (A. Foetzki, unpublished). Soil samples were collected throughout the range of depth and soil water content was determined gravimetrically (data not shown). Soil water content was less than 3% throughout the profiles to a depth of approximately 6.5 m at the *P. euphratica* site and 4.2 m at the *T. ramosissima* site and only increased close to the nominal groundwater level. It was not possible to determine the exact groundwater level for the higher dunes due to the length of the auger but previous drilling at other sites had shown that groundwater level varied little over short horizontal distances.

Along the gradients, trees or shrubs at similar groundwater depths (GD) are spatially closer to each other than to those at different GD, suggesting lower variability of site conditions such as soil nutrient supply or microclimate. However, soil nutrient supply does not play a significant role because plants are uniformly supplied with most nutrients by the groundwater. Furthermore, vegetation structure and relief are such that significant differences in microclimate between GD are not likely to occur.

Growth measurement

Growth was measured as annual increase of stem or shoot basal area (BA) between April 2000 and 2001. Natural logarithms of basal area and dry weight were shown previously to be closely correlated with each other in *T. ramosissima* and *P. euphratica* ($r^2 = 0.98$ and 0.96, respectively, $P < 0.0001$) (D. Gries, unpublished). To reduce bias from different initial stem or shoot diameters, relative basal area increments were calculated to give the annual increment of basal area as percentage of the initial basal area.

At each of six dune heights (Table 2), *P. euphratica* stems were selected to span the range of diameters at the respective height and were marked in 1.3 m height. Diameters of less than 6 cm were measured with a vernier caliper rule, and circumferences of larger trees were measured with a steel tape measure. At each of 10 dune heights (Table 2) shoots of *T. ramosissima* were selected to span the range of diameters at the respective height and were marked at 0.1 m height, where one diameter was measured in the N–S direction and one in the E–W direction. Several shoots died or were lost to harvest by oasis farmers between April 2000 and 2001 (Table 2).

Water relations

It is recognized that 'leaves' of *T. ramosissima* are actually short shoots bearing scale-like leaves; however, the term 'leaves' will sometimes be used for green short shoots for simplicity. All transpiration and leaf water potential measurements were made on fully expanded, sunlit leaves on sunny, cloudless days (Table 1). *Populus euphratica* leaves were sampled at 1.5 m height above ground at 23 m GD and at 3 m height at the other GD.

Transpiration and conductance measurements were made with two Licor Li1600 porometers (LiCor Inc., Lincoln, NE, USA) equipped with a broad leaf chamber for *P. euphratica* and a conifer chamber for *T. ramosissima*. Five to seven times during a day, three leaves of each of four trees of *P. euphratica,* or three short-shoots of each of four long-shoots of *T. ramosissima* were measured at each groundwater level. It is acknowledged that transpiration rates inside the well-stirred Li1600 chamber are probably higher than those in free air because at low wind speed, boundary layer conductances in free air are lower than those in the chamber. However, this is not likely to affect the comparison between GD. Leaf temperatures are not likely to have risen during measurements because the Li1600 chamber, which is double-shielded and ventilated to minimize radiative heating was kept in the shade between measurements; also, measurement periods were short because steady-state transpiration was rapidly attained for both species. Mass of short-shoots per area (LMA) was calculated by dividing sample dry weight, determined after oven-drying to constant weight, by one-sided leaf area measured with a flat-bed scanner and DT-Scan software (Delta-T, Cambridge, UK). Leaf water potentials were measured with pressure chambers (PMS, Corvallis, OR, USA). At each groundwater level, pre-dawn and midday leaf water potentials were measured on three leaves of each of four trees of *P. euphratica,* or three short-shoots of each of four long-shoots of *T. ramosissima*. The transpiration, conduc-

Table 2. Study design

Depth of groundwater (m)	No. shoots in growth measurement	Dates of water status measurements
P. euphratica		
22.7	11	2 June/10 July/24 August/9 October
17.9	10	–
14.0	10	2 June/10 July/24 August
11.6	10	2 June/10 July/24 August
8.7	11	–
7.3	11	2 June/10 July/24 August/9 October
T. ramosissima	marked in 2000/ remaining in 2001	
23.7	30/25	26 May/1 July/12 October
19.5	26/25	–
16.8	25/17	26 May/1 July
13.0	25/14	–
12.7	25/25	–
12.2	25/20	26 May/1 July
9.8	37/23	26 May/1 July/12 October
7.5	25/11	–
5.9	30/11	–
5.0	25/13	–

On 26 May, transpiration data of *T. ramosissima* at 12 and 10 m groundwater depth (GD) were lost due to equipment failure. In August no measurements could be made on *T. ramosissima* because all shrubs in the area were defoliated by beetles; complete recovery was attained in mid-September On 9 and 12 October, only two GD could be sampled due to logistic constraints.

tance and leaf water potential data from the three leaves of a *P. euphratica* tree or from the three short-shoots of a *T. ramosissima* long-shoot were averaged. For calculation of daily mean transpiration rate and conductance, all rates of a plant measured during a day were averaged separately for each of the four plants, and then the mean and standard deviation of the four plants was calculated. Midday conductance was calculated as average of measurements between 1400 and 1700 h.

Leaf-specific hydraulic conductance of the flow path from soil to leaf (K_L) was calculated according to

$$K_L = F_L/(\Psi_{soil} - \Psi_{leaf} - \Psi_{gravitation})$$

where F_L is the flux of liquid water per unit leaf area in the xylem tissue. Under steady-state conditions, F_L is approximately equal to transpiration per unit leaf area. Ψ_{soil}, Ψ_{leaf} and $\Psi_{gravitation}$ are soil and leaf water potentials and gravitational potential (-0.01 MPa m^{-1}, Scholander *et al.* 1965), respectively. Soil water potentials are assumed to be zero near the groundwater table.

In order to test whether changes in K_L with GD were fully explained by changes of path lengths, path length-specific K_L, or hydraulic conductivity (Sperry 1995), was calculated for each GD by multiplying K_L with path length (l), namely the sum of nominal GD at the stem base plus the canopy height of the leaf sample. Changes of path length-specific K_L ($l\,K_L$) with GD should indicate changes of leaf area: sapwood area ratios or sapwood permeability k_s, because

$$lK_L = Ak_s/\eta$$

(Pothier, Margolis & Waring 1989), where η is the viscosity of xylem water and A is the sapwood cross-sectional area per unit leaf area.

Statistical analyses

Growth and water status data were tested for normal distribution by calculating the Shapiro–Wilk W statistics (SAS proc UNIVARIATE, SAS version 6.12; The SAS Institute, Cary, NC, USA) for each sample ($n = 4$ for water status variables, $n = 10$–11 for growth of *P. euphratica* and $n = 11$–25 for growth of *T. ramosissima*). If $P(W) < 0.1$ for more than one sample for each variable, the assumption of normal distribution was rejected and data were tested for general differences between groundwater depths using the Kruskal–Wallis *H*-test (SAS proc NPAR1WAY). Nonnormally distributed variables were analysed for correlations with groundwater depth using Spearman rank correlation analysis (SAS proc CORR). Otherwise, normal distribution was assumed and ANOVA (SAS proc GLM) and Pearson correlation analysis (SAS proc REG or SigmaPlot 2000; SPSS Inc., Chicago, IL, USA) were used.

RESULTS

Growth

Relative basal area increments of *P. euphratica* differed significantly between GD (ANOVA: d.f. = 62, $F = 3.20$,

$P = 0.013$) and were inversely correlated with GD (Fig. 1a). Absolute basal area increments also differed between groundwater depths (*H*-test: $P = 0.0001$, $n = 10$–11).

Most of the stems sampled at the lowest elevation were much older and taller than all other stems and were therefore likely to respond differently to GD (see Discussion).
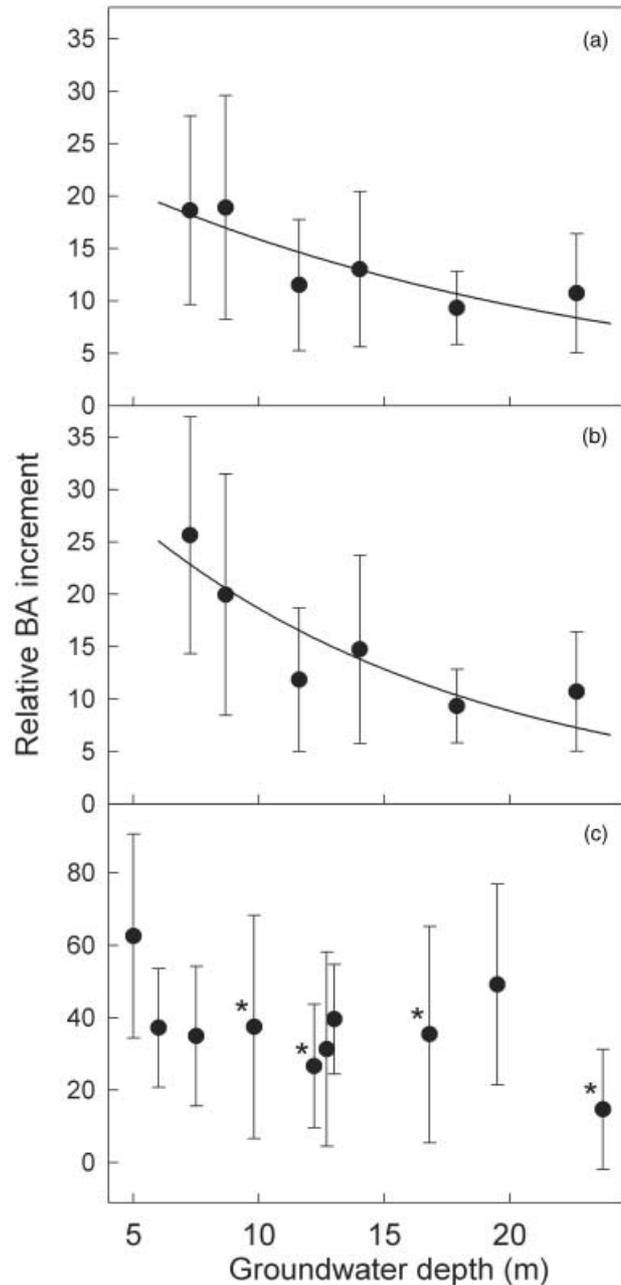
Figure 1. Relative basal area increment in relation to groundwater depth. Values are means ± 1 SD. (a) *Populus euphratica*, all trees, $n = 10$–11; (b) *Populus euphratica*, trees with up to 70 cm^2 basal area, $n = 3$–11; (c) *Tamarix ramosissima*, $n = 11$–25. Asterisks mark shrub groups at which water status measurements were made. Regression equations are (a) relative BA increment = 26.3 exp(-0.0503 GD), adj. $r^2 = 0.69$, $P = 0.025$; (b) relative BA increment = 39.2 exp(-0.0742 GD), adj. $r^2 = 0.72$, $P = 0.020$.

Median stem diameter at the lowest elevation was 14.0 cm (maximum 19.9 cm), median at the highest elevation was 3.7 cm (maximum 8.8 cm). If only stems with basal areas of up to 70 cm^2 were included in the analysis, reducing the sample size from 11 to 3 at the lowest elevation, the relationship between GD and growth was even clearer (Fig. 1b).

Growth of *T. ramosissima* did not correspond to GD (Fig. 1c) but differed significantly between shrubs at different GD (*H*-test for basal area increment: $P = 0.0001$, $n = 11$–25; relative basal area increment, $n = 11$–25, $P = 0.0001$). Spearman rank correlation coefficients for correlations between GD and absolute or relative basal area increments were –0.309, $P = 0.385$, and –0.297, $P = 0.405$, respectively ($n = 10$). The mean relative basal area increment across all GD was 36%.

Physiological measurements

The pre-dawn leaf water potentials of *P. euphratica* differed significantly between GD ($P < 0.0001$ for all dates) and clearly corresponded to GD, but did not decrease below – 0.90 ± 0.10 MPa at any GD (Fig. 2a) even during high evaporative demand in July. The midday leaf water potentials also differed significantly between GD and were clearly correlated with GD, but never decreased below –3.05 MPa. Differences between pre-dawn and midday potentials were essentially similar at 7, 12 and 14 m GD but were slightly larger at 23 m GD (maximum, –0.79 MPa).

Mean leaf conductance of *P. euphratica* was significantly lower at greater GD on all dates except in June (Table 3). The daily maximum of leaf conductance was lower at greater GD on all dates (Fig. 2b). Midday leaf conductance was also lower at greater GD, and decreased more strongly during the high evaporative demand in July than at smaller GD. In August, the conductance at low GD almost reached June levels again, but it remained lower at higher GD. In October the conductance was comparably low at all GD.
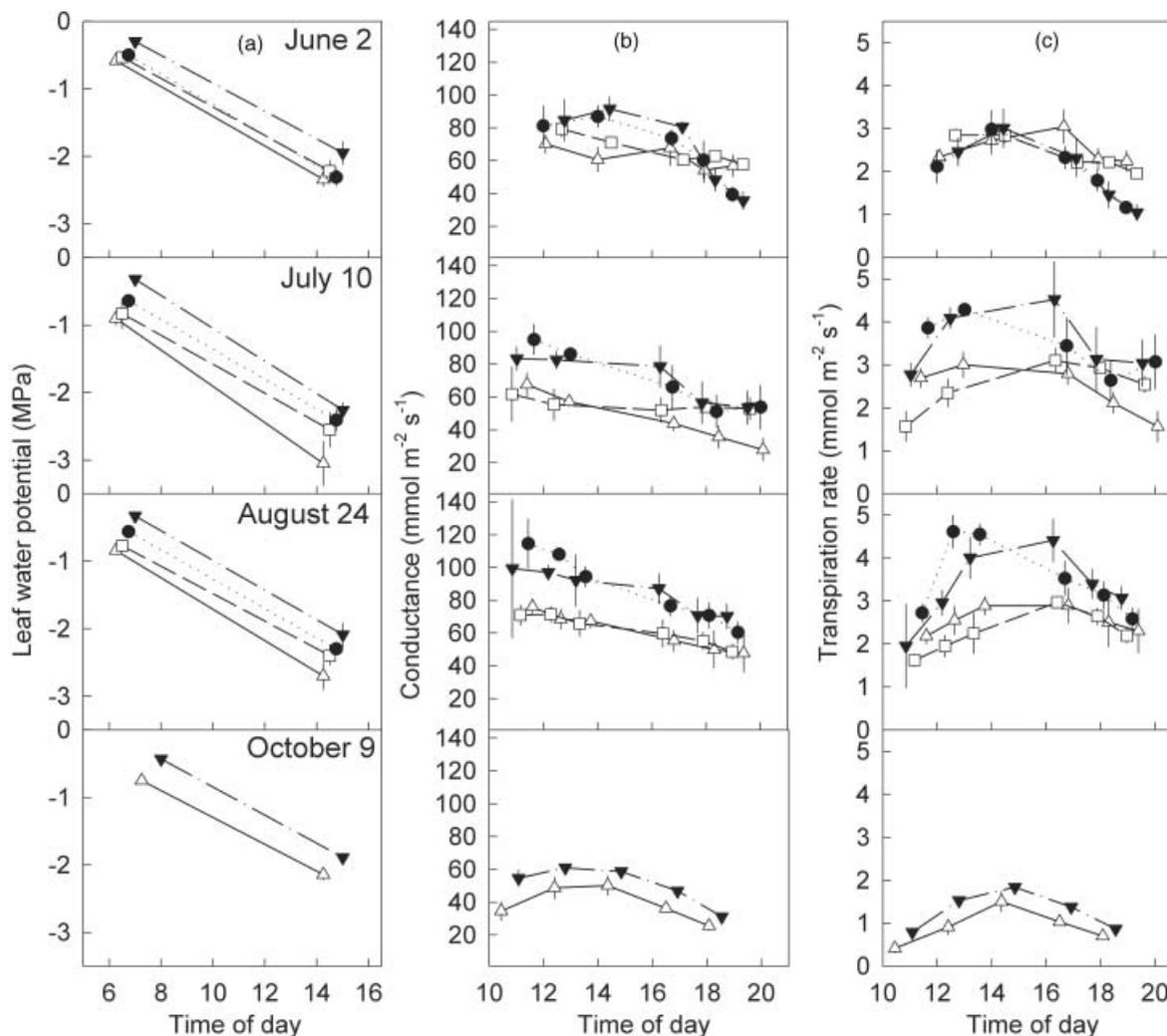
Figure 2. (a) Daily courses of leaf water potentials (b) leaf conductances and (c) transpiration rates of *Populus euphratica* at different GD in June, July, August, and October (from top to bottom row). Values are means ± 1 SD of four trees, with three leaves per tree. Groundwater depths: ▼, 7 m (dry river bottom); ●, 12 m; □, 14 m; △, 23 m (dune top). Note: *x*-axis shows Beijing time.

Table 3. Mean conductance and transpiration rates of *P. euphratica* and *T. ramosissima*

Date	GD (m)	Transpiration (mmol m^{-2} s^{-1})	P_{Trans}	Conductance (mmol m^{-2} s^{-1})	P_{cond}
Populus euphratica					
2 June	22.7	2.53 ±0.25 b	0.0059	62.0 ±7.3 b	0.1994
	14.0	2.42 ±0.01 ab		66.4 ±0.6 ab	
	11.6	2.08 ±0.17 a		68.4 ±4.0 a	
	7.3	2.06 ±0.20 a		68.2 ±2.6 a	
10 July	22.7	2.44 ±0.17 b	0.0003	46.5 ±3.7 b	0.001
	14.0	2.50 ±0.21 b		55.2 ±7.8 ab	
	11.6	3.46 ±0.37 a		70.4 ±9.0 a	
	7.3	3.52 ±0.42 a		71.0 ±7.6 a	
24 August	22.7	2.57 ±0.20 b	0.0001	60.8 ±4.6 b	0.0006
	14.0	2.27 ±0.17 b		62.0 ±5.4 b	
	11.6	3.52 ±0.28 a		87.5 ±6.2 a	
	7.3	3.30 ±0.31 a		86.1 ±13.9 a	
9 October	22.7	0.91 ±0.12 b	0.0009	39.1 ±4.0 b	0.0016
	7.3	1.28 ±0.02 a		50.5 ±1.1 a	
Tamarix ramosissima					
26 May	23.7	1.13 ±0.29 a	0.5703	41.1 ±12.4 a	0.3119
	16.8	1.23 ±0.16 a		48.5 ±5.0 a	
1 July	23.7	1.24 ±0.21 b	0.0062	28.8 ±5.4 b	0.0082
	16.8	1.43 ±0.25 ab		32.1 ±5.7 ab	
	12.2	1.24 ±0.09 b		28.5 ±2.9 b	
	9.8	1.72 ±0.08 a		40.1 ±2.0 a	
12 October	23.7	0.72 ±0.18 a	0.5345	31.2 ±7.5 a	0.3146
	9.8	0.80 ±0.19 a		39.1 ±12.3 a	

Values are means ± SD of daily means of four shoots. Letters indicate significant differences between groundwater depths (GD) for each date (Scheffe test, $n = 4$); P-values are for ANOVA among GD for each sampling date.

Daily means (Table 3) and maxima (Fig. 2c) of transpiration rates of *P. euphratica* were lower at greater GD in July, August and October At the first sampling date in June, leaves at smaller GD had lower transpiration rates than leaves at greater GD despite higher conductance at smaller GD; this was explained by lower leaf temperatures at the lower GD, probably caused by differences in irradiance due to temporal shading by neighbouring trees.

A clear relationship exists between midday leaf water potential and midday leaf conductance of *P. euphratica* (Fig. 3a). Leaf conductance gradually decreased with decreasing leaf water potential over the range of midday water potentials that were observed (–1.95 to –3.05 MPa), indicating anisohydric regulation. The reduction of conductance between –2 and –3 MPa leaf water potential was more than 50%: The October measurements basically confirmed the dependence of leaf conductance on leaf water potential in Fig. 3a, but deviated from the summer measurements, due to progressing leaf senescence.

Leaf-specific hydraulic conductance of *P. euphratica* was significantly lower at greater GD except in the June measurement (Table 4), and was significantly correlated with stomatal conductance (Fig. 4). Path length-specific K_L was higher at greater GD in June and October but was statistically equal among GD in July and August with a slight tendency for higher values at greater GD.

Pre-dawn water potentials of *Tamarix ramosissima* were always near –1 MPa, varied little between GD and were inconsistently related with GD (Fig. 5a). Annual maximum and minimum values were –0.68 and –1.25 MPa at 10 and 24 m GD, respectively. Pre-dawn potentials differed more between GD in May and October (ANOVA: $P < 0.0001$) but less during the strongest decrease of midday water potentials in July ($P = 0.0836$).

Midday water potentials of *T. ramosissima* (Fig. 5a) responded less clearly to GD than those of *P. euphratica*. The only consistent agreement with GD was that water potentials were always significantly lower at 24 m GD than at 10 m GD, whereas values at 17, 12 and 10 m varied independently of GD in May (Fig. 5a) and did not differ significantly in July The largest difference of midday leaf water potentials between high and low elevation (10 and 24 m) was –0.76 MPa and occurred in July

Leaf water relations of *T. ramosissima* generally differed from those of *P. euphratica* by lower mean and minimum midday leaf water potentials, throughout the season (ANOVA: $F = 43.33$, $P = 0.0001$) and especially in July during intense transpiration (ANOVA: $F = 93.13$, $P = 0.0001$).

Mean daily leaf conductances and transpiration rates of *T. ramosissima* significantly differed between GD (Table 3), but did not consistently correspond to GD (Fig. 5b & c); conductance and transpiration of shrubs growing at 24, 17 and 10 m GD increased with decreasing GD in accordance with expectations, but at 12 m GD the values were as low as at 24 m GD. This ranking was similar to that of growth of these four shrub complexes (Fig. 1c).
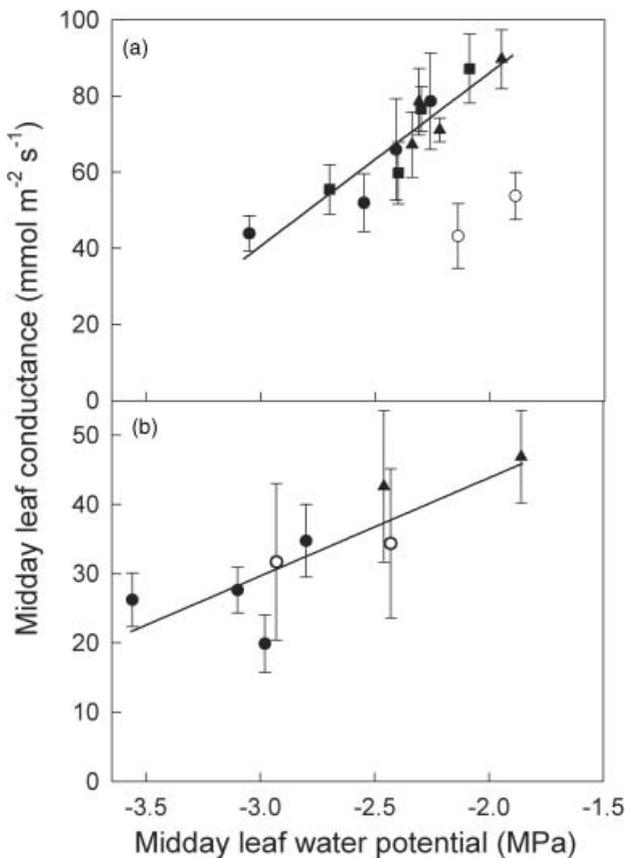
Figure 3. Relationship between midday leaf water potential and midday means of leaf conductance in (a) *Populus euphratica*, and (b) *Tamarix ramosissima* at different groundwater depths during the growing season 2000. Values are means ± SD of four trees. Labels: ▲, May/June; ●, July; ■, August; ○, October. Linear regression for *Populus euphratica*: $y = 177.3 + 45.55x$, adj. $r^2 = 0.84$, $P < 0.0001$, $n = 12$ (October measurement not included); for *Tamarix ramosissima*: $y = 72.22 + 14.18x$, adj. $r^2 = 0.64$, $P = 0.0109$, $n = 8$. Note: *y*-axis scales differ between diagrams.

In the May and October measurements, at moderate vapour pressure deficit (VPD), leaf conductance was relatively constant during the days (Fig. 5b). Only in July, when at high VPD transpiration was intense and leaf water potentials strongly decreased, the daily courses suggested a reduction of conductance during midday in comparison to morning and evening hours at all GD, but especially at 12 m GD. In accordance with the daily courses of conductance, transpiration (Fig. 5c) described an optimum curve in May and in October, following the course of VPD, with 1.5-times higher maximal values in May than in October In July, due to stronger stomatal limitation, transpiration did not follow VPD but was relatively constant during the day.

Similar to *Populus euphratica*, midday leaf conductance of *Tamarix ramosissima* was significantly correlated to midday leaf water potentials over the range of midday potentials measured (–1.86 to –3.56 MPa) across all dates and GD (Fig. 3b). The slope of this relationship (14.2 ± 3.9) was

smaller than that for *P. euphratica* (45.6 ± 6.0), and this difference between slopes was larger than would be expected, based on the lower overall level of leaf conductance in *T. ramosissima*. Consequently, *T. ramosissima* lost only about 30% conductance between –2 and –3 MPa (Fig. 3b).

K_L was highest at the smallest GD in July but did not differ between GD in May and October (Table 4). Path length-specific K_L was higher at greater GD in July and October K_L was significantly correlated with stomatal conductance (Fig. 4). This correlation also existed when stomatal conductance did not correspond to GD.

DISCUSSION

Populus euphratica

In agreement with expectations, consistently lower pre-dawn and midday leaf water potentials at greater GD in *P. euphratica* demonstrate the adverse effects of greater xylem path length. This relationship holds true for a nearby *P. euphratica* stand at only 4.5 m GD, where leaf water potentials during the summer months were higher than those reported here (Thomas *et al.* 2000b; A. Foetzki unpublished).

The decrease of leaf-specific hydraulic conductance, calculated from transpiration rates and leaf water potentials, with GD also demonstrates the effect of xylem path lengths. Trees may alleviate hydraulic constraints imposed by greater heights by down-regulation of leaf area: sapwood area ratios (Schäfer *et al.* 2000; McDowell *et al.* 2002); the tendency for higher path length-specific K_L at greater GD suggests such adjustments in *P. euphratica*; they deserve further study.
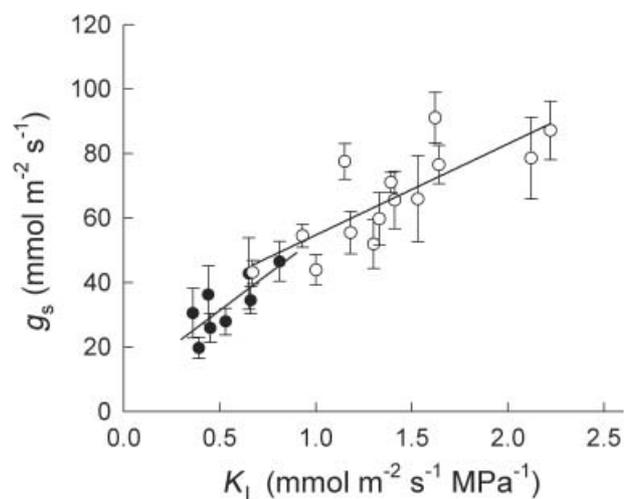
Figure 4. Midday stomatal conductance versus leaf-specific hydraulic conductance K_L of *P. euphratica* (○) and *T. ramosissima* (●) for all dates and GD. Values are means ± SD of four plants. Regression equations are $g_s = 9.0 + 44.8 \times K_L$ adj. $r^2 = 0.56$, $P = 0.019$ for *T. ramosissima*, and $g_s = 26.5 + 28.28 \times K_L$, adj. $r^2 = 0.79$, $P = 0.0007$, $P_{intercept} = 0.013$, for *P. euphratica*.

Table 4. Mean K_L and path length-specific K_L of *P. euphratica* and *T. ramosissima*

Date	GD (m)	K_L (mmol m^{-2} s^{-1} MPa^{-1})	P (K_L)	$K_L \times$ path length (m mmol m^{-2} s^{-1} MPa^{-1})	P (l K_L)
P. euphratica					
2 June	22.7	1.41 ±0.18 ab	0.0367	34.1 ±4.3 a	0.0001
	14.0	1.39 ±0.16 ab		23.7 ±2.7 b	
	11.6	1.15 ±0.12 b		16.8 ±1.7 bc	
	7.3	1.62 ±0.28 a		16.6 ±2.9 c	
10 July	22.7	1.00 ±0.10 b	0.003	24.2 ±2.3 a	0.8369
	14.0	1.30 ±0.11 b		22.2 ±1.9 a	
	11.6	1.53 ±0.37 ab		22.4 ±5.4 a	
	7.3	2.12 ±0.52 a		21.7 ±5.4 a	
24 August	22.7	1.18 ±0.21 c	0.0001	28.6 ±5.0 a	0.0609
	14.0	1.33 ±0.07 bc		22.7 ±1.3 a	
	11.6	1.64 ±0.18 b		23.9 ±2.6 a	
	7.3	2.22 ±0.21 a		22.8 ±2.2 a	
9 October	22.7	0.67 ±0.08 b	0.0017	16.2 ±2.0 a	0.0008
	7.3	0.93 ±0.05 a		9.6 ±0.5 b	
T. ramosissima					
26 May	23.7	0.65 ±0.12 a	0.1067	16.0 ±2.9 a	0.4599
	16.8	0.81 ±0.13 a		14.5 ±2.4 a	
1 July	23.7	0.45 ±0.08 b	0.0016	11.1 ±2.0 a	0.0001
	16.8	0.53 ±0.06 ab		9.4 ±1.1 ab	
	12.2	0.39 ±0.05 b		5.1 ±0.7 c	
	9.8	0.66 ±0.10 a		7.1 ±1.0 bc	
12 October	23.7	0.36 ±0.09 a	0.273	8.8 ±2.2 a	0.0144
	9.8	0.44 ±0.10 a		4.7 ±1.0 b	

Values are means ± SD of midday means of four shoots. Letters indicate significant differences between groundwater depths (GD) for each date (Scheffe test, $n = 4$); *P*-values are for ANOVA among GD for each sampling date.

The dependence of stomatal conductance of *P. euphratica* on leaf water potential is probably caused by the well-known fine-scale feedback loop between mesophyll water potential and guard cell turgor (Nonami, Schulze & Ziegler 1990). Because the pressure bomb gives only a volume-averaged estimate of leaf water potential, it is surprising that this relationship is so clear; it may indicate that transpiration rates and leaf water potentials were at a steady state at constant hydraulic conductance even during high evaporative demand. The characteristics of stomatal regulation strongly suggest a lower threshold and wider safety margin for xylem cavitation in *P. euphratica* than, for example in *Populus fremontii* (no loss of xylem conductivity at −1.5, fully cavitated at −1.6 MPa; Pockman, Sperry & O'Leary 1995) or *Populus balsamifera* (50% loss at −1.8 MPa, 90% loss at −2.8 MPa; Hacke & Sauter 1995).

Data from a nearby *P. euphratica* stand at 4.5 m GD studied by Thomas *et al.* (2000a) corroborate and extend the relationship between leaf water potential and leaf conductance: higher midday leaf water potentials than those in the present study allowed for leaf conductances of 140–170 mmol m^{-2} s^{-1} during the summer months (A. Foetzki unpublished), which are much higher than those observed in the present study.

Because stomata also control the flux of CO_2 into the leaf, lower stomatal conductance suggests lower per leaf area carbon gain in *P. euphratica* stems at greater GD. This largely explains the observed relationship between groundwater depth and shoot growth rates.

The effect of xylem path length on stomatal conductance via leaf water potentials may also be illustrated as a close correlation between stomatal conductance and K_L across a range of VPD and water potential gradients for both species, which is however, partly due to autocorrelation because transpiration rates enter calculations for both variables. Yet it is clear in the present study that this correlation is not based on any direct effect of K_L or on root signalling but on the correlation between stomatal conductance and leaf water potential in both species.

At a given GD, growth rates of small shoots were somewhat higher than those of tall shoots (Fig. 1a & b) but this may be expected because in tall trees a longer above-ground xylem path adds to the nominal GD at the stem base. This does not affect water relations measurements, which were made at a defined height above ground, but growth rates integrate effects of xylem path lengths for all leaves.

Below-ground stems that extend from roots near the water table to the dune surface are inevitably longer on taller dunes, and shoots and canopies of *P. euphratica* were visibly much smaller on tall dunes, suggesting that leaf area ratios strongly decreased with dune height. For example, the typical canopy length was 1.5 m at 23 m GD versus 10 m in some trees at 7 m GD. Theoretically, the effects of higher below-ground carbon allocation for longer below-ground
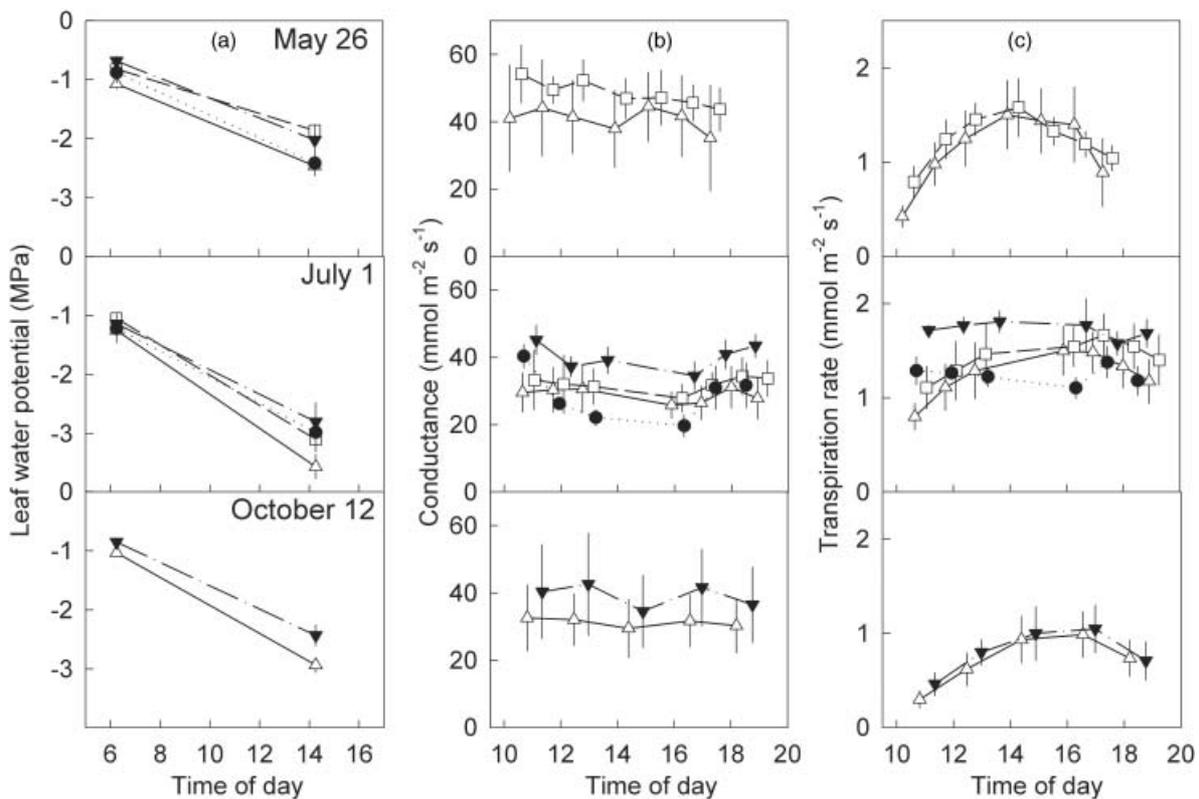
Figure 5. Daily courses of (a) leaf water potentials; (b) leaf conductances and (c) transpiration rates of *Tamarix ramosissima* at different GD in May, July, and October (from top to bottom row). Values are means ± 1 SD. of four shoots (three samples per shoot). Groundwater depths: ▼, 10 m; ●, 12 m; □, 17 m; △, 24 m. Note: *x*-axis shows Beijing time.

stems should add to the adverse effects of limited water supply on growth rates at greater GD; causing a stronger decrease of growth rates than observed. However, an excavation at the study site showed that the buried stem section of a typical *P. euphratica* shoot was thinner than the unburied stem section above it and, after removal of the mechanical support by the dune, was not able to bear the weight of the above-ground shoot and broke spontaneously (M. Runge, personal obs.). As it is known that stem radial growth, taper and wood density respond to mechanical stress in *Populus* genotypes (Pruyn, Ewers & Telewski 2000), this observation suggests that less carbon is invested into diameter growth and wood density of buried stem sections mechanically supported by the dunes than is normally required for mechanical support in standing trees of similar height. Thus, consequences of longer below-ground stems for below-ground carbon allocation may be partially alleviated by lower carbon requirements for mechanical strength of these below-ground stems. In conclusion, growth at greater GD may be less strongly reduced by unfavourable plant architecture than we expected, but may be more strongly reduced by a smaller carbon gain per unit leaf area due to unfavourable water relations.

We demonstrated that *P. euphratica* tolerates large GD up to 23 m that result from height growth of above-ground shoots and a rising landscape surface. On the other hand, recent large-scale destruction of *P. euphratica* stands along

the Tarim river caused by groundwater drawdown (Meckelein 1988; Zhou 1993) strongly suggests that *P. euphratica* is not able to follow rapidly decreasing groundwater tables by downward root growth, even if total soil-to-leaf distances remain within the 23 m range shown to be tolerated in the present study.

Tamarix ramosissima

Similar to *P. euphratica*, the stomatal conductance of *T. ramosissima* was correlated with leaf water potential and with leaf-specific hydraulic conductance. Stomatal regulation kept leaf water potentials of *T. ramosissima* (minimum: −3.56 MPa) well above reported cavitation threshold and safety margin values for this species (50% cavitation at −4.5 MPa, fully cavitated at −7.0 MPa, Pockman & Sperry 2000). This wide safety margin is in agreement with comparably low stomatal sensitivity to water potential in *T. ramosissima* in the present study (Blake *et al.* 1996). Area-based stomatal conductance was generally low in comparison with values reported by Horton *et al.* (2001a, b) for similar water potentials, probably reflecting the difficulty of defining the effective transpiring surface area of *T. ramosissima*, due to needle-like leaf anatomy, overlapping leaf positioning and variable short-shoot branching patterns.

Differences in stomatal conductance between the four shrub complexes investigated for water status resembled

significant differences of growth rates between them, suggesting that growth, although not correlated with GD, was to some degree limited by stomatal conductance. Inconsistency in the relationship between leaf water potential and stomatal conductance of the four shrubs could be explained by varying leaf concentrations of osmotically active substances (2100–2800 μmol g^{-1} dry mass; S.K. Arndt, unpublished), which alter the relationship of leaf water potential with leaf turgor.

The lack of correlation of both leaf water variables and growth rates with GD could be partly explained by adjustments of leaf area : sapwood area ratios suggested by larger path length-specific K_L at greater GD, which could partially alleviate the effects of GD on leaf water status. Small differences of pre-dawn potentials between GD support this. Furthermore, the xylem path length may not be as closely correlated with GD as thought because of the complex and variable below-ground structure of clonal *T. ramosissim* shrub systems, due to developmental history (Qong *et al*. 2002). This was also suggested by excavations showing variably oriented shoots and erratic branching patterns, but few vertically oriented shoots that would support a clear correlation of xylem path length with elevation above groundwater (personal obs.). Rather, variable tortuosity of flow paths and number of branch junctions, which have lower conductivity compared with the rest of the flow path (Zimmerman 1983), may be expected. These ideas are supported by a much clearer response of growth and water relations of *T. ramosissima* to GD in a previous study in which the growth of entire stands consisting of many shrubs was determined and averaged over larger areas. A stand at 10–15 m GD was less productive (D. Gries, unpublished), and had lower transpiration rates and higher δ^{13}C values than a nearby stand at 5 m GD (S.K. Arndt and A. Foetzki, unpublished results).

Independent of water relations, growth rates should decrease with increasing GD because of increased below-ground carbon allocation. The lack of a clear growth response to the wide range of GD suggests that below-ground carbon costs are smaller than assumed, possibly because plants invest mostly into below-ground conducting tissue, but not into expensive mechanical support. We also speculate that carbon costs for growth and respiration of fine roots may be much lower for these phreatophytes, which do not only take up water, but also nutrients from the groundwater table. This deserves further study.

Tolerance of lower leaf water potentials by *T. ramosissima* is explained by generally higher concentrations of osmotically active substances than in *P. euphratica* (approx. 2400 and 1700 μmol g^{-1} dry mass in *T. ramosissima* and *P. euphratica*, respectively; S.K. Arndt, unpublished). These enable *T. ramosissima* to maintain positive turgor and higher stomatal conductance at lower leaf water potential (Busch & Smith 1995), which helps to overcome hydraulic constraints imposed by long xylem paths with probably less stomatal limitation of carbon dioxide uptake.

Horton *et al*. (2001a) reported much lower pre-dawn potentials of *T. ramosissima* than in the present study, at

much shallower GD (below –3.5 MPa at approximately 2.5 m GD). This suggests that *T. ramosissima* had established a shallow root system in response to a higher frequency of surface water supply at the site, relied more on water uptake from unsaturated soil than from groundwater (Busch *et al*. 1992), and its root system was slow to react to that soil drying out. In the present study, stable pre-dawn water potentials and high growth rates in the absence of other water sources indicate that groundwater at up to 24 m depth is readily used and permanently available, and that its depth does not fluctuate much. Thus, root systems of both *T. ramosissima* and *P. euphratica* are probably concentrated in a narrow depth range near the groundwater table. Our results agree with the view that present stands of both species were established through germination or sprouting in lowland areas, and then grew to great heights above groundwater with the rising landscape surface (Bruelheide *et al*. 2003; Qong *et al*. 2002). Tolerance of great groundwater depths that were largely attained by upward growth of above-ground shoots should, however, not be misinterpreted as large capacity for growing roots downward over similar distances. We thus predict that a decline of groundwater tables may have deleterious consequences for the foreland vegetation dominated by *P. euphratica* and *T. ramosissima*. A future drawdown of the groundwater table that underlies the foreland is to be expected, as according to local authorities, groundwater use for irrigation of arable land is being intensified and already causes groundwater tables within the oasis to fluctuate by several metres during the growing season.

CONCLUSIONS

The effect of groundwater depth on leaf-specific hydraulic conductance and leaf water relations of these phreatophytic plants is similar to that of height in free-standing trees. Decreasing growth rates of *P. euphratica* at greater GD are probably a consequence of lower hydraulic conductance. Tolerance of lower leaf water potentials due to higher concentrations of leaf osmotica, and a less conservative stomatal regulation explain why leaf conductance, and therefore probably leaf carbon gain and growth of *T. ramosissima* was less severely affected by GD. Additionally, the variable and complex structure of old *T. ramosissima* clones probably introduces variability in the relationship of xylem path length with groundwater depth.

Access to a permanent water table at up to 24 m depth explains the absence of physiologically significant water stress and the vigorous growth of *T. ramosissima* and *P. euphratica* under high evaporative demand in virtually dry soil. Both species seem productive enough to tolerate a moderate removal of biomass, but will probably not be able to adapt to a rapid decrease of the groundwater table.

ACKNOWLEDGMENTS

REFERENCES

Blake T.J., Sperry J.S., Tschaplinski T.J. & Wang S.S. (1996) Water relations. In *Biology of Populus and its Implications for Management and Conservation* (eds R.F. Stettler, H.D. Bradshaw, P.E. Heilman Jr & T.M. Hinckley), pp. 401–422. NRC. Research Press, Ottawa, Canada.

Bruelheide H., Jandt U., Gries D., Thomas F.M., Foetzki A., Buerkert A., Wang G., Zhang X. & Runge M. (2003) Vegetation changes in a river oasis on the southern rim of the Taklamakan Desert in China between 1956 and 2000. *Phytocoenologia* **33**, in press.

Busch D.E. & Smith S.D. (1995) Mechanisms associated with decline of woody species in riparian ecosystems of the southwest U.S. *Ecological Monographs* **65**, 347–370.

Busch D.E., Ingraham N.L. & Smith S.D. (1992) Water uptake in woody riparian phreatophytes of the Southwestern United States: a stable isotope study. *Ecological Applications* **2**, 450–459.

Hacke U. & Sauter J.J. (1995) Vulnerability to embolism in relation to leaf water potential and stomatal conductance in *Fagus sylvatica* f. purpurea and *Populus balsamifera*. *Journal of Experimental Botany* **46**, 1177–1183.

Horton J.L., Kolb T.E. & Hart S.C. (2001a) Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. *Plant, Cell and Environment* **24**, 293–304.

Horton J.L., Kolb T.E. & Hart S.C. (2001b) Leaf gas exchange characteristics differ among Sonoran Desert riparian tree species. *Tree Physiology* **21**, 233–241.

Hubbard R.M., Bond B.J. & Ryan M.G. (1999) Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. *Tree Physiology* **19**, 165–172.

Hubbard R.M., Ryan M.G., Stiller V. & Sperry J.S. (2001) Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. *Plant, Cell and Environment* **24**, 113–121.

Magnani F., Mencuccini M. & Grace J. (2000) Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. *Plant, Cell and Environment* **23**, 251–263.

McDowell N., Barndard H., Bond B.J., *et al.* (2002) The relationship between tree height and leaf area: sapwood area ratio. *Oecologia* **132**, 12–20.

Meckelein W. (1988) Naturbedingte und anthropogen bedingte Morphodynamik am Beispiel der innerasiatischen Trockengebiete Chinas. *Abhandlungen der Akademie der Wissenschaften Göttingen, Mathematisch-Physikalische Klasse* **41**, 328–343.

Mencuccini M. & Grace J. (1996) Developmental patterns of above-ground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. *Plant, Cell and Environment* **19**, 939–948.

Nonami H., Schulze E.D. & Ziegler H. (1990) Mechanisms of stomatal movement in response to air humidity, irradiance, and xylem water potential. *Planta* **183**, 57–64.

Pockman W.T. & Sperry J.S. (2000) Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany* **87**, 1287–1299.

Pockman W.T., Sperry J.S. & O'Leary J.W. (1995) Sustained and significant negative water pressure in xylem. *Nature* **378**, 715–716.

Pothier D., Margolis H.A. & Waring R.H. (1989) Patterns of change of saturated sapwood permeability and sapwood conductance with stand development. *Canadian Journal of Forest Research* **19**, 432–439.

Pruyn M.L., Ewers B.J. III & Telewski F.W. (2000) Thigmomorphogenesis: changes in the morphology and mechanical properties of two *Populus* hybrids in response to mechanical perturbation. *Tree Physiology* **20**, 535–540.

Qong M., Takamura H. & Hudaberdi M. (2002) Formation and internal structure of Tamarix cones in the Taklimakan Desert. *Journal of Arid Environments* **50**, 81–97.

Runge M., Arndt S.K., Bruelheide H., Foetzki A., Gries D., Huang J., Popp M., Thomas F.M., Wang G. & Zhang X. (2001) Contributions to a sustainable management of the indigenous vegetation in the foreland of Cele oasis – a project report from the Taklamakan desert. In *Sustainable Land Use in Deserts* (eds S.W. Breckle, M. Veste & W. Wucherer), pp. 343–349. Springer, Berlin, Germany.

Ryan M.G. & Yoder B.J. (1997) Hydraulic limits to tree heights and tree growth. *Bioscience* **47**, 235–242.

Schäfer K.V.R., Oren R. & Tenhunen J.D. (2000) The effect of tree height on crown level stomatal conductance. *Plant, Cell and Environment* **23**, 365–375.

Scholander P.R., Hammel H.T., Bradstreet E.D. & Hemmingsen E.A. (1965) Sap pressure on vascular plants. *Science* **148**, 339–346.

Smith S.D., Devitt D.A., Sala A., Cleverly J.A. & Busch D.E. (1998) Water relations of riparian plants from warm desert regions. *Wetlands* **18**, 687–696.

Sperry J.S. (1995) Limitations on stem water transport and their consequences. In *Plant Stems Physiology and Functional Morphology* (ed. B.L. Gartner), pp. 105–124. Academic Press, San Diego, CA, USA.

Stromberg J. (1998) Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. *Journal of Arid Environments* **40**, 133–155.

Thomas F.M., Arndt S.K., Bruelheide H., Foetzki A., Gries D., Huang J., Popp M., Wang G., Zhang X. & Runge M. (2000a) Ecological basis for a sustainable management of the indigenous vegetation in a central Asian Desert: presentation and first results. *Journal of Applied Botany* **74**, 212–219.

Thomas F.M., Arndt S.K., Bruelheide H., Foetzki A., Gries D., Li X., Zeng F., Zhang X. & Runge M. (2000b) Wasserhaushaltsparameter von vier Gehölzbeständen (*Alhagi sparsifolia*, *Calligonum caput-medusae*, *Populus diversifolia*, *Tamarix ramosissima*) im Vorland einer zentralasiatischen Flussoase. *Verhandlungen der Gesellschaft für Ökologie* **30**, 60.

Yoder B.J., Ryan M.G., Waring R.H., Schoettle A.W. & Kaufmann M.R. (1994) Evidence of reduced photosynthetic rates in old trees. *Forest Science* **40**, 513–527.

Zencich S.J., Froend R.H., Turner J.V. & Gailitis V. (2002) Influence of groundwater depth on the seasonal sources of water accessed by *Banksia* tree species on a shallow, sandy coastal aquifer. *Oecologia* **131**, 8–19.

Zhou X. (1993) Features of the deserts and changes in the desert surrounding in Xinjiang. In *Desertification and Control of Blown Sand Disasters in Xinjiang* (eds X. Xia, C. Li, X. Zhou, P. Huang & B. Pan), pp. 1–63. Science Press, Beijing, China.

Zimmermann M.H. (1983) *Xylem Structure and the Ascent of Sap*. Springer, New York, USA.