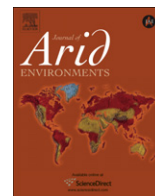


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On the run for water – Root growth of two phreatophytes in the Taklamakan Desert

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ABSTRACT

Desert phreatophytes require extremely fast root growth for a successful establishment. We measured the speed of seedling root growth of two phreatophytic plant species, *Alhagi sparsifolia* and *Karelinia caspia*, which form dominant or codominant stands around the river oases at the southern fringe of the Taklamakan Desert. As *A. sparsifolia* occurs at sites with deeper groundwater, we expected the roots of this species to reach down more rapidly than those of *K. caspia*. Furthermore, we expected seedlings experiencing no irrigation and low fertilization to have deeper reaching roots than seedlings with irrigation and fertilization. Seeds of both species were sown into 1 and 2 m long tubes in a glasshouse and in a field experiment, respectively. After 16 weeks of growth in the field roots of *K. caspia* and *A. sparsifolia* reached down 2.2 m and 1.7 m, respectively. In accordance with a faster growth, *K. caspia* had a higher water use, which resulted in a faster decrease of water content in the tubes. Species differences in the vertical reach of roots in the glasshouse experiment were comparable to those in the field experiment. After 12 weeks without irrigation, *A. sparsifolia* had a higher rooting depth (0.45 m) than with irrigation (0.30 m), while root depths of *K. caspia* showed the opposite pattern with 0.62 m and 0.72 m, respectively. Fertilizing increased total biomass of both species, while low level of fertilization had the tendency to increase the root: shoot ratio and the specific root lengths (SRL), most likely a response to acquire nutrients at lower costs. However, plants of *K. caspia* showed an increase in SLR already after 12 weeks, while it took 16 weeks for *A. sparsifolia* to increase SRL in the low fertilization level. Our results show clearly that both species are able to reach the groundwater table in the river valleys (6.5 m) within a time span of five to six months after germination. However, the encountered vegetation pattern is probably not caused by differences in the speed of rooting depth, but might be the result of a higher capability of growing up with sand accumulation of *A. sparsifolia*. As additional irrigation and fertilization did not enhance rooting depth in both species, these factors will have little impact in restoration procedures.

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1. Introduction

The spatial and temporal variation in water availability is the main driver of plant development in arid environments. In deserts where water occurs in form of short pulses in limited amount, perennial plant species rely on access to water in deep soil layers (Padilla and Pugnaire, 2007; Sala and Lauenroth, 1982). To tap this soil water at great depths, desert plants must have deep-reaching roots, which makes them record holders of maximum rooting depth compared to plants from all other ecosystems (Canadell et al., 1996; Jackson et al., 1996; Schenk and Jackson, 2005; Seyfried et al.,

2005). Nevertheless, the deep root system can only sustain limited aboveground biomass. Thus, these plant species are also characterized by a high root: shoot ratio (Jackson et al., 1996; Schulze et al., 1996; Schwinning and Ehleringer, 2001) and a high specific root length (SRL), defined as the unit root length per unit mass (m g^{-1}) (Nicotra et al., 2002). SRL characterizes the roots' growth economy, giving the cost (mass) per potential return (length) (Ryser, 2006) and is assumed to be high under growth limiting conditions when the construction costs per root length should be minimized to exploit large soil volumes at small costs. Accordingly, Poot and Lambers (2003) found a higher SRL during early development in narrowly endemic *Hakea* species that are adapted to shallow soil habitats with summer drought compared to widespread congeners that occur on deeper soils. A high root: shoot ratio and high SRL are particularly important during establishment of desert phreatophytes, which have only a short time window to

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follow declining water tables after germination. Phreatophytes can only establish themselves on river banks at a time when the surface layers down to the groundwater table are water-saturated, which is only the case at or shortly after sporadic flooding events. As the surface dries, the seedlings face the challenge to follow the decreasing groundwater level with their roots in order to survive and to become established (Padilla and Pugnaire, 2007).

Such phreatophytes are the only perennial life form of the natural vegetation belts around river oases at the southern fringe of the Taklamakan Desert (Bruelheide et al., 2003, 2010). Groundwater distance outside these flooding events is usually several meters, e.g. 6.5 m in case of the river valley in the foreland of Qira oasis (Vonlanthen et al., in press). The vegetation in the oases forelands is composed mainly of *Populus euphratica*, *Tamarix ramosissima*, *Alhagi sparsifolia*, *Karelinia caspia* and *Phragmites australis*. Successful establishment is a rare event, which is reflected in low seedling densities and low survival rates (Vonlanthen et al., in press).

As the different phreatophytic species exhibit different realized niches according to different depths to the groundwater table (Bruelheide et al., 2010), they might differ in their root growth and their ability to deal with receding water tables in the period of establishment. For example, mean groundwater distance of populations of *A. sparsifolia* was 14.62 m, which was higher than 10.07 m of populations of *K. caspia* ($df = 11, p = 0.05$, for the method of drilling groundwater observation holes see Bruelheide et al., 2010). It is possible that the ability to become established at great groundwater depths is related to a species' ability of fast rooting depth. In consequence, roots of *A. sparsifolia* would be expected to exhibit faster relative growth in depth ($m\ m^{-1}\ d^{-1}$) than those of *K. caspia*. In this context, *A. sparsifolia* would also be expected to exploit soil water contents more effectively and to maintain a more relaxed water status.

A flooding event of longer duration or additional irrigation does not necessarily increase the establishment success of phreatophytes. This has been shown by von Willert (1994), who examined rooting depth during early development of *Welwitschia mirabilis*, a phreatophyte of the Namibian Desert. von Willert (1994) tested the effect of irrigation on rooting depth and found a lower rooting depth by the end of the experiment of irrigated plants compared to non-irrigated plants. Accordingly, Padilla et al. (2007) also described increased root lengths of non-irrigated plants compared to irrigated plants from three Mediterranean shrubland species. At higher soil moisture, plants might have less need to invest in roots and tend to allocate more biomass to shoot growth resulting in a lower root: shoot ratio (Bargali and Tewari, 2004; Chapin et al., 1987; Li et al., 2008; Padilla et al., 2009). Thus the photosynthetic activity and the potential carbon gain might increase, resulting in a higher total dry biomass (Cortina et al., 2008). For phreatophytes, this shift in allocation patterns would result in a decreased ability to follow declining water tables.

In natural environments, limitation of a single resource is uncommon or might lead to the limitation of another resource, because the uptake of different resources might be coupled (Ryser, 2006). For example, at low moisture levels the soil nutrient availability is reduced due to the decrease in nutrient diffusion (Kramer, 1988; Passioura, 1988). Therefore, we expected that plants experiencing low nutrient and low water supply display increased overall root length (Trubat et al., 2006), higher root: shoot ratio (Schippers and Olff, 2000; Wu et al., 2008) and a higher SRL (Schippers and Olff, 2000; Trubat et al., 2006). However, the results of nutrient limitation on SRL are not unequivocal. In contrast to our expectation, SRL has also been found to increase with higher nutrient availability (e.g. Elberse and Berendse, 1993). Ryser (2006) explained this phenomenon with the ability for faster and more

efficient acquisition of resources of fine roots compared with roots with a larger diameter.

Root growth is not only relevant in the initial phase of establishment but also during the whole lifetime of a genet. Once the species in the oasis foreland are established, they spread vegetatively and form extensive clones, which in the case of *P. euphratica* can reach a size of up to 121 ha (Vonlanthen et al., 2010). These clones have to produce new roots to reach the groundwater when expanding horizontally. These roots have to reach deeper and deeper because, with time, the plants accumulate silt and sand, which is continuously deposited in the oases and their surroundings by frequent dust storms. In this way, plants also grow vertically with accumulated sediment and finally form nebkhas. By trapping these sediments, the peripheral vegetation belt has an essential function for the oases' sustainability (Danin, 1996; Walls, 1982; Xia et al., 1993; Zhang et al., 2001). Even though the vegetation has been shown to be of prominent importance for the oases' functionality, the vegetation is severely threatened by human activities, as it serves as a major source of fuel and construction material and provides forage for sheep, donkeys and camels (Thomas et al., 2000).

The objectives of this study are to analyse species-specific differences in root growth in water availability and nutrient supply to draw conclusions on the species' success of establishment in the oases forelands. We addressed these issues experimentally and set up a field experiment and a glasshouse experiment. While the field experiment may be considered more realistic, as it was carried out at the original growth locations in the Taklamakan Desert, the laboratory conditions offered more options of manipulations. We used the same two species in these experiments (*A. sparsifolia* and *K. caspia*), employed a similar experimental set-up and focused on the same root growth variables of the early stages of establishment. We hypothesized that (1) the species that occurs naturally at greater distance from groundwater (i.e. *A. sparsifolia*) has higher rooting depth (distance from the soil surface) and a higher SRL ($m\ g^{-1}$); (2) irrigated plants attain lower rooting depths and have lower root: shoot ratios ($g\ g^{-1}$) and a lower SRL ($m\ g^{-1}$); and (3) fertilized plants show responses similar to irrigation. Finally, based on the differences in realized niches observed for the two species, we hypothesized that (4) *A. sparsifolia* as a legume with symbioses with N_2 -fixing bacteria (Arndt et al., 2004), makes less use of increased N supply and better use of increased water supply.

2. Material and methods

2.1. Study area

The study area is located in the western foreland of Qira Oasis (37°01' N, 80°48' E and 1365 m a.s.l.) at the southern rim of the Taklamakan Desert (Xingjiang Uyghur Autonomous Region, China). The climate is continental with cold dry winters and hot, dry summers and extremely arid. Mean annual temperature is 11.9 °C, mean annual precipitation is 33.2 mm and potential evaporation is more than 2570 mm (Runge et al., 2001; Zeng et al., 2004).

2.2. Study species

Initially, the experiments had been planned with all dominant species in the oasis foreland. However, seeds of *P. euphratica*, *T. ramosissima* and *P. australis* did not germinate in sufficient amount to be used in these experiments. We obtained sufficient seedlings from two study species, *A. sparsifolia* Shab. (Fabaceae) and *K. caspia* Less. (Asteraceae). Both species are perennial shrubs. Their shoots die over winter and resprout again in spring. Both species

are phreatophytes (McGinnies, 1968; Wickens, 1998). The main reproduction mode is clonal spread with below-ground tillers.

A. sparsifolia Shab. (camelthorn) is probably synonymous to *A. maurorum* Medik., *A. pseudoalhagi* (M: Bieb.) Desv., and *A. kirghisorum* Schrenk (Foetzki, 2003). *A. sparsifolia* flowers in June and July and sets fruits in September to October (pers. obs). Seeds are dispersed by mammals and weigh between 4 and 5 mg. *Alhagi* species grow in salinized and arid regions in northwestern China, Central Asia, India, Middle and Near East (Kurban et al., 1998).

K. caspia Less. (Asteraceae) flowers between July and September and sets fruits in September and October. The fruits are wind dispersed and have a weight between 0.06 and 0.08 mg. It grows in rock and sand deserts as well as in saline meadows in Central and Southwest Asia (Wu and Raven, 1994).

In autumn 2005, seeds of eight populations of *A. sparsifolia* and *K. caspia* were collected in the oasis foreland of Qira Oasis, Xingjiang province, China. The seeds were kept separately by population and stored at room temperature at the research station. The station was not inhabited in the wintertime; therefore the temperatures could have dropped to about +4 °C.

2.3. Field experiment

The root experiment was conducted at the Qira research station 37° 00' 56.36" N, 80° 43' 45.03" E, Xingjiang Uyghur Autonomous Region, China. PVC waste water tubes with a diameter of 0.11 m and 2 m in length were cut lengthwise in two halves, then reassembled and duct-taped together and closed at the bottom with a cap. This preparation was done to simplify the later harvest of the plants. At the end of April 2006, two sets of tubes, which were designated for two different harvest sets at two different developmental stages of the seedlings, were inserted in a 2 m deep pit and buried completely up to 2 cm below the rim of the tubes. The tubes were covered with shading net with 5 mm mesh size, which reduced incident radiation by approximately 50%, and thus, reduced desiccation of seedlings. Maximum values of photosynthetically active radiation (PAR) rarely exceed 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Zeng et al., 2006) because of a high atmospheric dust load. Thus, the reduction by shading nets provided maximum PAR of about 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

The tubes were filled with coarse silt with the prevailing particle size between 0.020 and 0.063 mm (Bruehlheide et al., 2010) from a typical growth location of the target species in the oasis foreland. The tubes were watered for two days and, at the beginning of May 2006, several seeds either of *A. sparsifolia* or *K. caspia* were sown into the tubes. Seeds were used from eight different populations, thus accounting for genetic variation among the different populations. In each treatment combination, two individuals from each population were used, resulting in 16 replicates. To enhance germination of *A. sparsifolia* seeds, they were scarified for 20 min in 98% sulfuric acid (Baskin and Baskin, 2004) prior to sowing. Germinated seedlings were watered regularly with 200 ml three times per week and, after 10 days, thinned out to one seedling per tube. The plants were fertilized with 5 ml of 14 ppm of $\text{CO}(\text{NH}_2)_2$ (70 $\mu\text{g N}$ per tube) at the end of May and the watering continued to the 15th of June. The first set of plants was harvested between 3rd and 5th of July when seedlings were 8 weeks old, the second between 28th and 30th of August when seedlings were 16 weeks old. At the two harvest dates, shoot length and the number of leaves of 16 individual plants per species were recorded. The shoots were cut at the soil surface and the midday water potential was measured in a pressure chamber (Plant Moisture Systems, Corvallis, Oregon, USA). The soil core from each tube was divided in ten sections of 0.2 m each. For each section, volumetric soil water content was measured with time domain reflectometry (TDR) (sensor type TRIME-P2D, IMCO, Ettlingen, Germany) and roots were

separated from the substrate. All plant material was dried for 24 h at 72 °C and dry root and shoot biomasses of all fractions were determined. Specific root length (SRL, m g^{-1}) was calculated as the length of the main root axis divided by the total root biomass, according to Cornelissen et al., (2003). Root: shoot ratio (g g^{-1}) was calculated as the dry root biomass divided by the dry shoot biomass.

2.4. Glasshouse experiment

The root experiment in Germany was conducted in the experimental glasshouse in the Botanical Garden in Halle (Saale), Germany. At the beginning of September 2006, seedlings of *K. caspia* and *A. sparsifolia* were raised in plastic trays with 3 × 3 × 3 cm pots, using sand obtained from a quarry at Ploetz 51° 38' 15.24" N, 11° 57' 04.56" E, 15 km north of Halle. This fine to medium sized sand had a particle size between 0.045 and 0.63 mm. We used a slightly coarser substrate than in the field experiment to allow for a faster decrease of water content under the less extreme glasshouse conditions. Seeds of *A. sparsifolia* were scarified as described in the experiment in China. They grew under simulated early summer conditions with 13 h light at 25 °C and 11 h dark at 15 °C. Additional light was provided by greenhouse lamps, which resulted in a PAR of 230 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the height of the plants.

Tubes, 0.11 m in diameter and 1 m in length, were prepared in the same manner as in the field experiment in China. Instead of being buried, the tubes were placed in basins and stabilized with gravel. The basins ensured drainage of the tubes and held 12 tubes each. In the middle of September 2006, seedlings were transplanted into the tubes. As in the field experiment, we controlled for the effect of genetic variation within species by using seeds from different populations as replicates of the treatment combinations. Thus, the effect of genetic variation has been pooled with the overall error term. The tubes were watered with 50 ml twice a week. A fertilizer treatment was applied from the 3rd to the 13th of November with two levels; plants at the high level received fertilizer five times, each with 50 ml of 100 ppm N (1000 $\mu\text{g N}$ per tube), while in the low level treatment the plants were fertilized five times each with 50 ml of 5 ppm N (50 $\mu\text{g N}$ per tube). The fertilizer used was Wuxal Universaldünger (Native Plants, Burgebrach; Germany). The nitrogen in the fertilizer was composed of 29% of NO_3 , 46% NH_4 and 25% $\text{CO}(\text{NH}_2)_2$. In addition, the fertilizer contained P_2O_5 and K_2O_2 as well as micronutrients such as B, C, Fe, Mn, Mo and Zn. Watering continued until the 22nd of November, when the irrigation treatment was started. Plants at the high irrigation treatment received 50 ml water twice a week, while a control remained without irrigation and was allowed to dry out. In total, we had 96 tubes (2 different harvest dates, corresponding to two different stages of seedling development × 2 species × 2 irrigation levels × 2 fertilizer levels × 6 replicates). Six tubes per species, i.e. 12 in total, were placed in one basin. To avoid water and nutrient transfer among the different treatments, all 12 tubes in each of the eight basins received the same treatment combination.

In the middle of December 2006, when seedlings were 12 weeks old, and in the middle of January 2007, when seedlings were 16 weeks old, a total of 48 plants (six plants from each combination of species, water and fertilizer) were harvested in the same way as in the field experiment. The measurements on plants were essentially the same as in the field experiment, except for the determination of the water potential. At the second harvest date, we additionally measured specific leaf area (SLA, $\text{cm}^2 \text{g}^{-1}$) on all seedlings. One fresh leaf per seedling was scanned and subsequently analysed for area with Win-Folia (Regent Instruments Inc., Quebec, Canada). After the leaf had been dried for 24 h at 72 °C the leaf biomass was assessed using the protocol of Cornelissen et al. (2003).

2.5. Statistical Analysis

The data were analysed with SAS 9.1 (SAS Institute Inc. 2002. Cary, NC, USA) and plotted with SigmaPlot 8.0. In the absence of normal distribution of the variables the data were rank transformed.

In the field experiment, we used a two-factorial ANOVA to test for the effects of the two different developmental stages of the seedlings, the two different species and the interaction of species and stages of development. In the glasshouse experiment, a mixed model was applied, using the effects of developmental stage, species, irrigation and fertilizer and their interactions as fixed effects. Differences among all treatment combinations were tested with a post-hoc test after Tukey. In addition, a random factor was included, accounting for the fact that tubes of one irrigation and fertilization treatment combination were always placed together in the same basin, thus, the random basin effect was nested within the irrigation and fertilizer treatment. Tested variables were rooting depth (i.e. distance the roots extended down the tube), total dry biomass, root: shoot ratio, SRL and relative growth rate (RGR) of rooting depth, RGR of shoot biomass, water potential (only in the field experiment) and SLA (only in the glasshouse experiment). The RGRs for the first interval (from the start of the experiment to the first time of harvest) were calculated using additional individuals from the thinning in the field experiment and from individuals transplanted into the tubes in the glasshouse experiment. RGRs for the second interval were based on the mean rooting depth and mean shoot biomass within each treatment combination at the first time of harvest. To analyse the vertical biomass distribution of the roots we fitted the biomasses by depth sections to the asymptotic equation $Y = 1 - \beta^d$, where Y is the cumulative root fraction, calculated as proportion of cumulative root biomass, summed up from the surface to the depth d , and the regression coefficient β indicates the steepness of declining cumulative root fraction with depth (Jackson et al., 1996). Higher values of β indicate a more evenly distributed root biomass over the length of the root. ANOVAs were carried out with β as response variable, using the same model as described above. The decrease in mean volumetric soil water content per tube, expressed as the ratio of difference in water content between the first and second time of harvest to the water content at the first time of harvest, was first tested with a linear mixed model, including the fixed covariables RGR of rooting depth and RGR of shoot biomass, respectively, the fixed factors species, irrigation and fertilizer and the random factor basin nested within the irrigation and fertilizer treatment. Subsequently, the full model was optimized based on AIC values. In a first step, the random term was optimized based on restricted maximum likelihood estimation, then the fixed factors

and their interaction were dropped from the model based on maximum likelihood estimation. For both continuous covariables (RGR of rooting depth and RGR of shoot biomass), the best model included species, fertilizer and their interaction as fixed factors and basin nested within fertilization as random factor. This final model was finally tested once more with a restricted maximum likelihood estimation procedure to find the correct p-values. The amount of variance explained was assessed by regressing the predicted values of the models against the observed values.

Using the mean RGR of the rooting depth of each species in the field experiment, we extrapolated the number of days needed to grow to 6.5 m, which is the depth to the groundwater in the river valley outside the flooding season (based on drilling groundwater holes, see Vonlanthen et al., 2010). We also extrapolated the number of days needed to grow to the mean depth of the groundwater table in stands of *A. sparsifolia* (14.62 m) and of *K. caspia* (10.07 m).

3. Results

3.1. Field experiment

Alhagi sparsifolia and *K. caspia* differed significantly in root growth characteristics (Table 1). *Karelinia caspia* had deeper reaching roots (Fig. 1a) than *A. sparsifolia*. In addition, the root: shoot ratio was lower (Fig. 1c) and RGR of shoot biomass was higher (Fig. 1e) than of *A. sparsifolia*. The deeper reaching roots and the higher RGR of shoot biomass were more pronounced after 16 than after 8 weeks, indicated by the significant interaction between species and developmental stage for these two variables (Table 1). *K. caspia* also had a higher total dry biomass (Fig. 1b) and a higher RGR of rooting depth (Fig. 1d) at the second harvest date. *A. sparsifolia* had lower water potentials than *K. caspia* (Fig. 1f) (Table 1). The mean volumetric water content was significantly lower in the tubes of *K. caspia* ($5.2\% \pm 4.9$ s.d.) than in those of *A. sparsifolia* ($10.2\% \pm 6.9$ s.d.) (Table 1), indicating that the faster growing species had a higher water usage. The relative change in soil water content between the two harvest dates was not correlated with any growth variable (RGR of rooting depth, $p = 0.66$ and RGR of shoot biomass, $p = 0.44$).

With a mean RGR of rooting depth of $0.041 \text{ m m}^{-1} \text{ day}^{-1}$ *A. sparsifolia* would need 158 days to reach the groundwater table in the river valley (6.5 m), whereas *K. caspia* with an RGR of rooting depth of $0.044 \text{ m m}^{-1} \text{ day}^{-1}$ would need 147 days. The time difference between the species to reach groundwater increases when calculated with the groundwater distances at the species sites; *A. sparsifolia* needs 178 days to reach 14.62 m at the *Alhagi* sites and *K. caspia* 157 days for 10.07 m at the *Karelinia* sites.

Table 1

F-values of the ANOVA of the field experiment, with stage of development, species and their interaction as predictor variables. The variables total dry biomass, SRL and RGR of rooting depth were rank transformed prior to analysis. Nominator df of all factors equals one.

	Harvest		Species		Harvest × species		Error df
Rooting depth [m]	171.9	***	4.20	*	5.48	*	45
Total dry biomass ^a [g]	81.06	***	0.05		5.65	*	44
Root: shoot ratio [g g ⁻¹]	27.38	***	4.59	*	0.74		44
SRL ^a [m g ⁻¹]	6.53	*	3.60		3.65		45
RGR of root length ^a [m m ⁻¹ day ⁻¹]	209.62	***	4.72		9.36	**	45
RGR shoot biomass [m m ⁻¹ day ⁻¹]	0.7		4.07	*	7.87	**	44
Beta	98.48	***	1.74		2.77		43
Vol water content [%]	0.21		8.34	**	0.95		44
Water potential [MPa]	16.2	***	23.13	***	7.94	*	44

Significance levels * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

^a Analysis with rank transformed data.

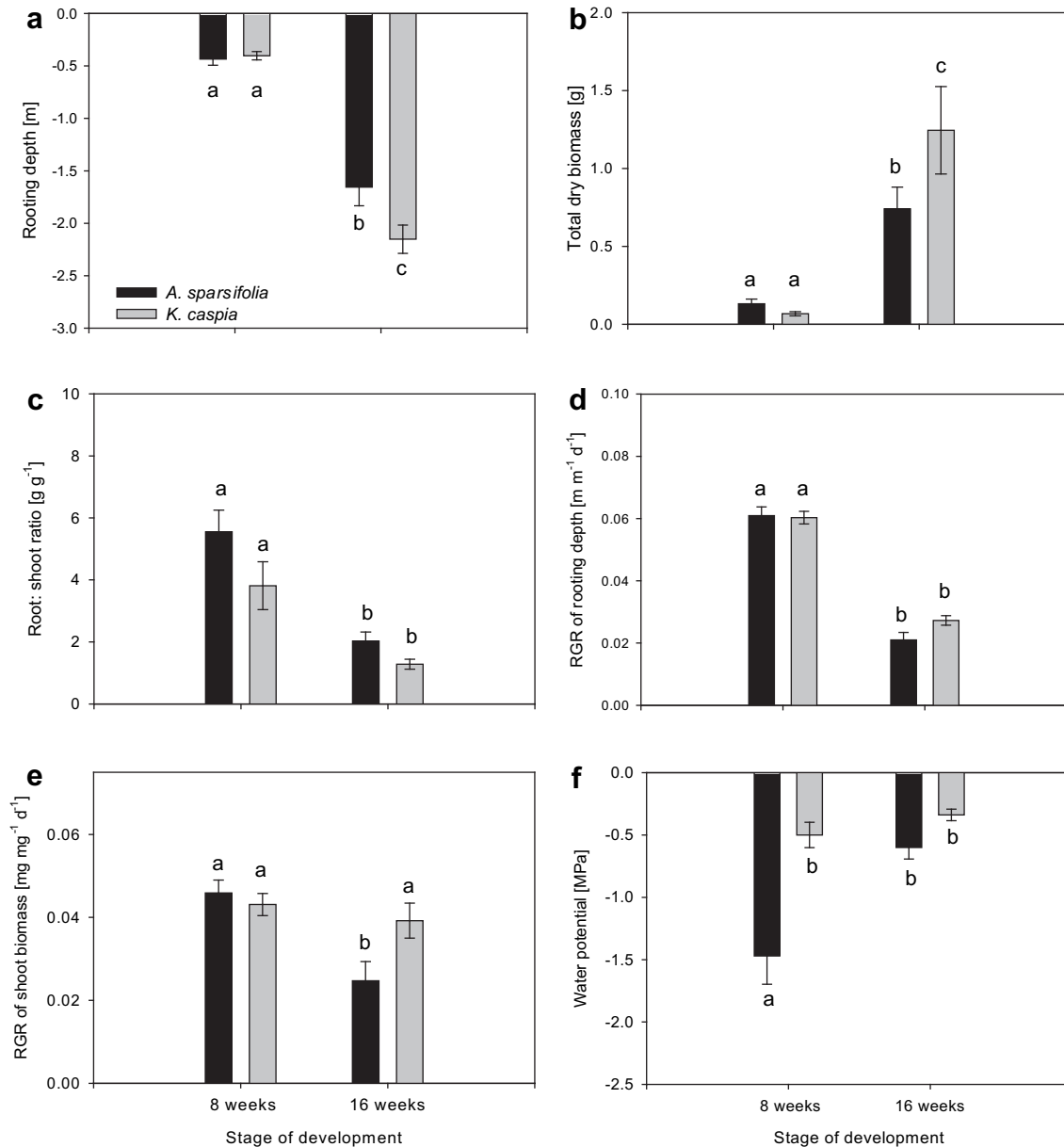


Fig. 1. Mean and SE of a) rooting depth, b) total dry biomass, c) root: shoot ratio d) RGR of rooting depth e) RGR of shoot biomass and f) water potential of *A. sparsifolia* and *K. caspia* at the two developmental stages (1 = after 8 weeks, 2 = after 16 weeks) in the field experiment. The tests for statistically significant differences for all factors are given in Table 1. Different small letters indicate significant differences between all four treatment combinations.

3.2. Glasshouse experiment

Consistent with the results of the field experiment, there were species-specific differences in almost all response variables (Table 2). Accordingly, *K. caspia* had deeper reaching roots (Fig. 2a), higher total dry biomass (Fig. 2b), lower SRL (Fig. 2d) and higher RGR of shoot biomass (Fig. 2f) than *A. sparsifolia*. The SLA of *K. caspia* was only marginally significant higher than the SLA of *A. sparsifolia* (Fig. 2g). After 16 weeks, *K. caspia* had lower SRL and lower RGR of rooting depth than *A. sparsifolia* (Fig. 2d, e). In contrast, while *K. caspia* had a higher RGR of shoot biomass than *A. sparsifolia* after 12 weeks, these differences became insignificant after 16 weeks (Fig. 2f). Furthermore, there were significant differences between the two species in their root biomass distribution (Table 2). *Karelinia caspia* had overall significantly higher β values (0.964) than *A. sparsifolia* (0.933) (Table 2),

indicating that *K. caspia* had a more equal root biomass distribution than *A. sparsifolia* (Fig. 3). As in the field experiment we also found lower soil water contents in the tubes of *K. caspia*. These differences become more pronounced with time, indicated by a significant interaction of species and developmental stage (Table 2). At the second harvest date, volumetric soil water contents in the high and low water treatment in tubes with *K. caspia* were $15.2\% \pm 3.9$ (s.d.) and $11.2\% \pm 3.7$ (s.d.), respectively, and in tubes with *A. sparsifolia* $17.9\% \pm 1.9$ (s.d.) and $16.8\% \pm 2.8$ (s.d.), respectively. The volumetric soil water content in the tubes decreased linearly with increasing RGR of rooting depth ($p = 0.004$) and RGR of shoot biomass ($p = 0.02$) (Table 3, Fig. 4). This indicates that the increased root extension and increased shoot growth were realized by a higher water consumption. These relationships were species-specific, indicated by a significant interaction between species and RGR of rooting

Table 2
 F-values of the ANOVA of the glasshouse experiment with stage of development, species, water and fertilizer and the interactions as fixed factors and basin nested within the interaction of water and fertilizer as random factor. Basin had no significant effect on the measured variables. Z-values correspond to the F-value in the Wald Z-statistics. The variables total dry biomass, SRL and beta were rank transformed prior to analysis. Please note that SLA was only measured at the second harvest date. Nominator df of the factors equals one.

	Rooting depth [m]		Total dry biomass ^a [g]		Root: shoot ratio [g g ⁻¹]		SRL ^a [m g ⁻¹]		RGR rooting depth [m m ⁻¹ day ⁻¹]		RGR shoot biomass [mg mg ⁻¹ day ⁻¹]		Beta ^a		Vol water content [%]		SLA [cm ² g ⁻¹]	
	Den	F	Den	F	Den	F	Den	F	Den	F	Den	F	Den	F	Den	F	Den	F
Harvest	74	142.9 ***	73	388.3 ***	73	24.67 ***	74	234.9 ***	74	123.4 ***	73	249.9 ***	66	72.4 ***	58	183 ***	31	3.61 (*)
Species	74	49.8 ***	73	103.1 ***	73	1.09	74	34.8	74	0.09	73	36.6	66	54.3 ***	58	13.9	31	
Harvest × species	74	0.03	73	2.44	73	1.95	74	10.6	74	41.28 ***	73	13.2	66	0.56	58	13.9 ***	4	2.23
Water	4	0.00	4	0.07	4	6.56	4	0.84	4	0.57	4	0.24	4	2.05	4	11.4 *	4	
Harvest × water	74	0.71	73	0.33	73	0.45	74	1.52	74	3.21	73	1.92	66	0.07	58	1.42	31	0.07
Species × water	74	1.37	73	0.69	73	0.98	74	0.26	74	6.86 *	73	1.44	66	0.31	58	2.17	31	
Harvest × species × water	74	4.01 *	73	1.74	73	2.97	74	0.27	74	27.27 ***	73	16.7	66	1.76	58	1.06	4	0.11
Fertilizer	4	3.28	4	12.15 *	4	1.25	4	4.47	4	0.29	4	3.04	4	0.58	4	1.26	4	
Harvest × fertilizer	74	1.80	73	4.06 *	73	1.79	74	0.07	74	22.12 ***	73	52.4 ***	66	0.01	58	0.01	31	1.51
Species × fertilizer	74	0.09	73	0.10	73	1.70	74	0.08	74	0.66	73	0.06	66	0.00	58	0.60	4	0.12
Harvest × species × fertilizer	74	0.73	73	3.07	73	4.01 *	74	8.61 **	74	0.59	73	0.47	66	0.11	58	1.90 **	4	
Water × fertilizer	4	3.03	4	0.57	4	0.36	4	0.78	4	1.82	4	0.10	4	1.78	4	0.90	4	
Harvest × water × fertilizer	74	5.96 *	73	0.35	73	0.14	74	2.98	74	59.55 ***	73	3.44	66	0.87	58	10.5	31	0.14
Species × water × fertilizer	74	0.19	73	0.16	73	1.46	74	0.89	74	0.04	73	0.53	66	2.36	58	2.51	31	
Harvest × species × water × fertilizer	74	0.11	73	0.06	73	3.43	74	0.15	74	1.73	73	3.80	66	0.00	58	1.11	4	
Basin (water × fertilizer)		Z-value 0.96		Z-value 1.06		Z-value 0.00		Z-value 1.02		Z-value 0.93		Z-value 0.94		Z-value 0.00		Z-value 0.00		Z-value 0.15

Significance levels **p* < 0.05, ***p* < 0.01, ****p* < 0.001.
^a Analysis with rank transformed data.

depth and RGR of shoot biomass (Table 3). In the tubes with *K. caspia* the soil water content decreased faster than those with *A. sparsifolia* (Fig. 4).

Irrigation had no consistent effect on root growth (Table 2). After 12 weeks without irrigation, *A. sparsifolia* had higher rooting depth (0.45 m) than with irrigation (0.30 m), while root depths of *K. caspia* showed the opposite pattern with 0.62 m and 0.72 m, respectively (Fig. 5a). However, the irrigation effect disappeared after 16 weeks. At this second harvest date, RGR of rooting depth and RGR of shoot biomass were enhanced for *A. sparsifolia* in the irrigation treatment and for *K. caspia* in the dry treatment (Fig. 5b and c).

Fertilizer had a positive effect on total dry biomass in both species (Table 2). There were also significant interactions of developmental stage, species and fertilization on SRL and root: shoot ratio (Table 2). After 8 weeks, *K. caspia* had a much higher SRL in the low than in the high fertilization treatment, whereas *A. sparsifolia* displayed almost no differences. In contrast, after 16 weeks, *A. sparsifolia* had a higher SRL at low fertilization and *K. caspia* no longer showed any difference in SRL (Fig. 6a). We also found a significant effect of developmental stage, species and fertilizer interaction on root: shoot ratio. Generally, root: shoot ratio tended to be higher in the low compared to the high fertilization level, indicating that plants allocated more biomass to the root system in the low nutrient level. Only *A. sparsifolia* had a lower root: shoot ratio at the low fertilization level at the first harvest date (Fig. 6b).

4. Discussion

The results from the experiments in the field and in the glasshouse were similar, although there were differences in several response variables. We had expected that the lower levels of radiation in the glasshouse compared to field conditions in the desert resulted in lower photosynthetic rates, and thus, in less biomass production, which was not the case. Higher nutrient supply and higher air humidity in the glasshouse might have compensated for the lower radiation in the greenhouse. Thus, there certainly was a higher pressure for rapid rooting depth in the field experiment, which might have resulted in a slightly higher RGR of rooting depth and higher root: shoot ratio compared to the glasshouse experiment.

The question arises as to which degree our experimental root growth data correspond to the natural situation in the field. It is a common practice to use PVC tubes to conduct root experiments (Mosena and Dillenburg, 2004; Stave et al., 2005), because it minimizes the soil heterogeneity and prevents root loss at harvest. However, water retention in tubes might be higher than under real field conditions, which should result in lower root growth of the plants. Therefore, our study plants should be expected to exhibit even larger rates in rooting depth than what we have found experimentally. Compared to other experiments, the rooting depths of *A. sparsifolia* and *K. caspia* were considerably faster than those reported for *W. mirabilis* (von Willert, 1994). Within eight months *W. mirabilis* developed roots to a depth of 1 m, whereas in half of the time *A. sparsifolia* and *K. caspia* reached 1.7 m and 2.2 m, respectively. In contrast, rooting depth of both species was lower than values described for *Acacia tortilis* and *Faidherbia albida*. After 56 days, Stave et al. (2005) measured a rooting depth of 1.2 m for *A. tortilis* and 0.8 m for *F. albida*, which was considerably deeper than the 0.4 m for our two study species at the first harvest date (after 56 days) in the field experiment. However, from this comparison we can conclude that the growth rates we have described are not completely way beyond natural field conditions.

The first hypothesis of a higher rooting depth of *A. sparsifolia* has to be rejected. The two species differed consistently over both

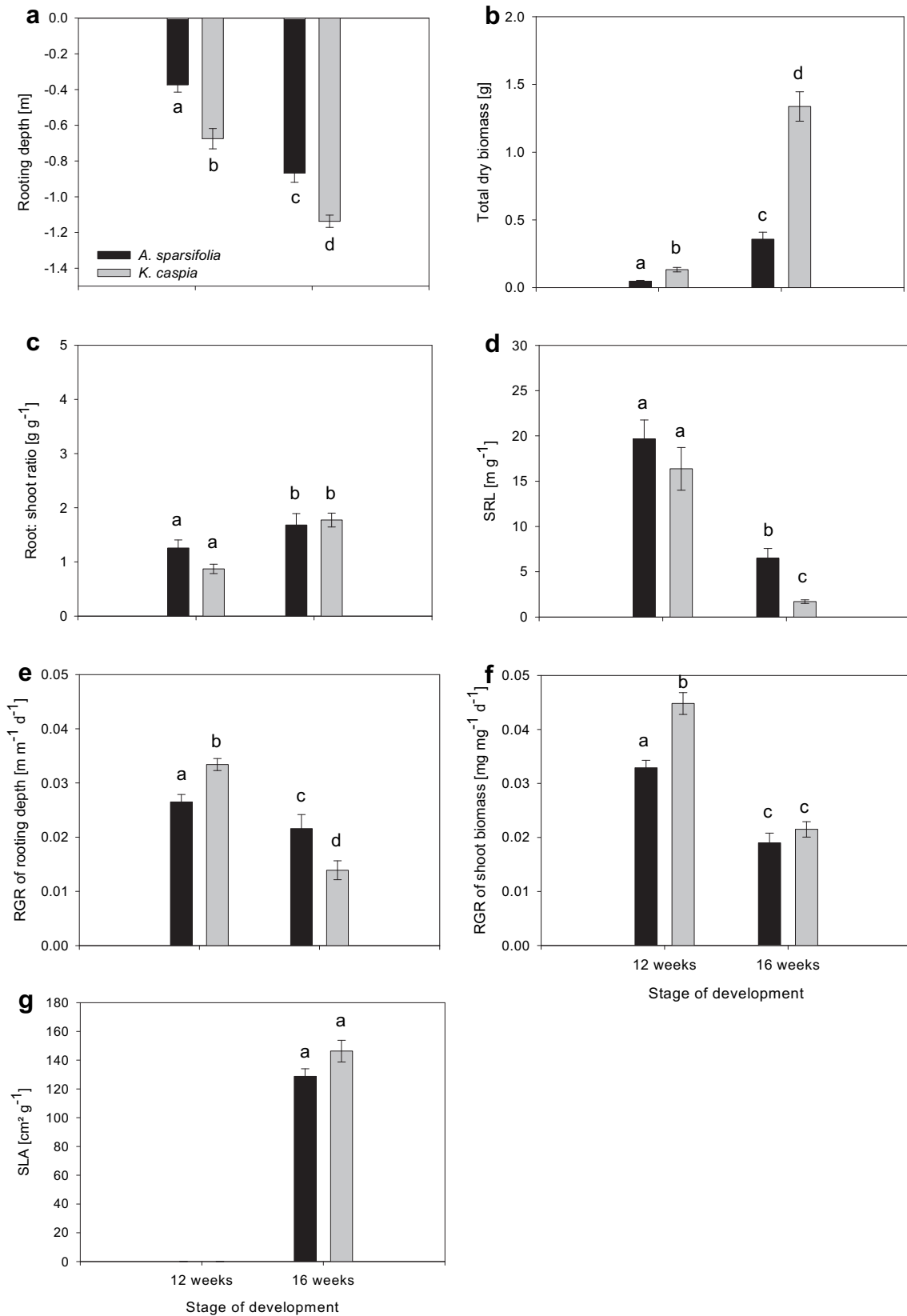


Fig. 2. Mean and SE of the a) rooting depth, b) total dry biomass, c) root: shoot ratio d) SRL e) RGR of rooting depth, f) RGR of shoot biomass and g) SLA of *A. sparsifolia* and *K. caspia* at the two different developmental stages (1 = after 12 weeks, 2 = after 16 weeks) in the glasshouse experiment. Please note that SLA was only measured at the second time of harvest. The tests for significant differences for all factors are given in Table 2. Different small letters indicate significant differences between all four treatment combinations.

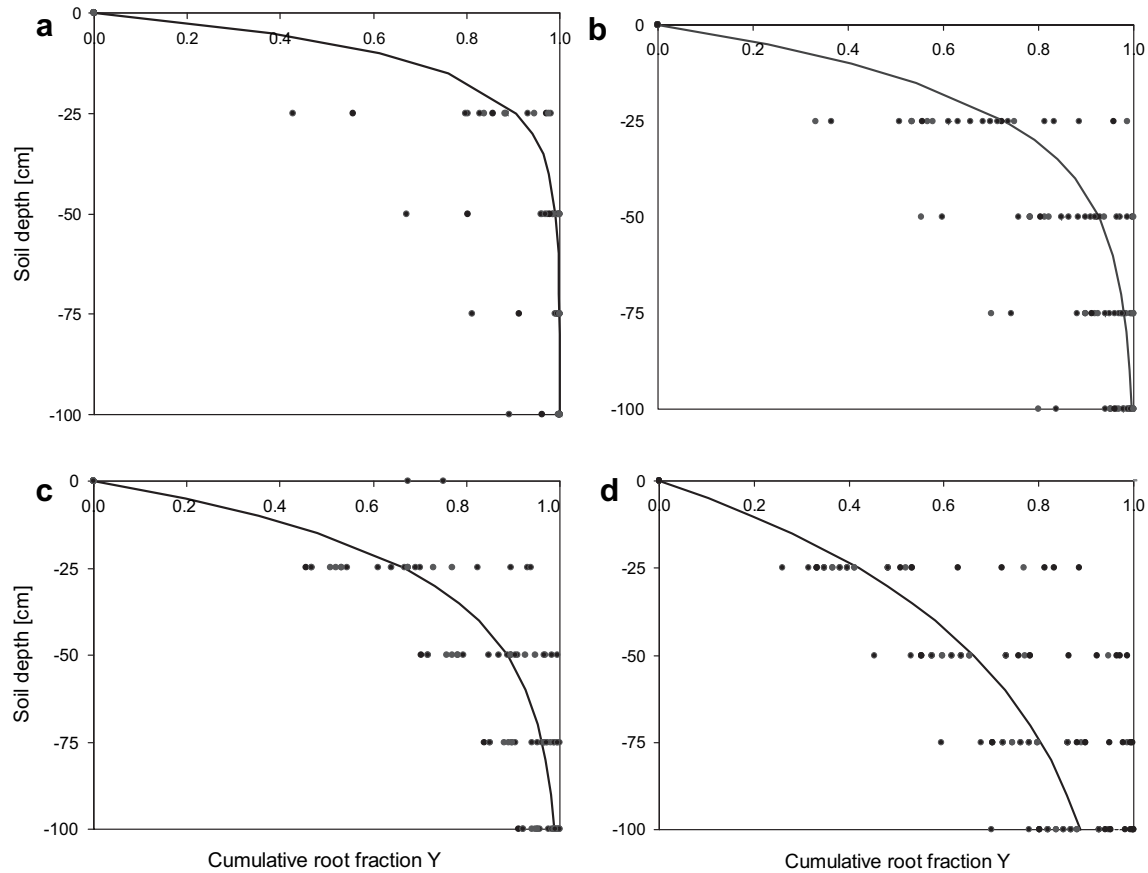


Fig. 3. Cumulative root fraction, calculated as proportion of cumulative root biomass, summed up from the surface to the depth d , using the formula $Y = 1 - \beta^d$. Y is the cumulative root fraction. The regression coefficient β indicates the steepness of declining root proportions with depth in the glasshouse experiment for the first developmental stage of a) *A. sparsifolia* and b) *K. caspia* and the second developmental stage of c) *A. sparsifolia* and d) *K. caspia*. The regression line represents the mean cumulative biomass distribution along the soil profile and the points represent the observed values for each single plant.

experiments, however against our expectations, we found that roots of *K. caspia* grew faster in depth than *A. sparsifolia*. Consistently with the faster growth, *K. caspia* took up more water from the substrate and maintained higher xylem water potentials. The range in water potentials of *A. sparsifolia* and *K. caspia* seedlings in our experiment was between -0.1 and -2.7 MPa, which is in the range of the values observed in established vegetation in the field (Zeng

et al., 2006). In accordance with our results, Zeng et al. (2006) also encountered lower water potentials in *A. sparsifolia* than in *K. caspia*. As in emerging relationships in global data sets (Reich et al., 1997), the higher growth rates of *K. caspia* also corresponded to the higher SLA found in this species. Furthermore, the higher water potentials of *K. caspia* explain the species-specific responses to the irrigation treatment. *K. caspia* apparently used more water, and thus, in the low irrigation treatment was probably compelled to increase RGR in rooting depth to follow the sinking water fringe for survival. Conversely, *A. sparsifolia* used less water and probably is able to persist in drier soils. This might be crucial in the ability to grow up with drift sand and might explain why *K. caspia* and *A. sparsifolia* co-dominate at sites with distances to the groundwater table up to 12 m, but only *A. sparsifolia* occurs at distances up to 17 m. Thus, due to a tolerance of low water potentials, *A. sparsifolia* might persist longer at sites that become increasingly unfavourable than *K. caspia*.

The second hypothesis of lower rooting depths with irrigation was only partly confirmed. Only one species, *A. sparsifolia* had deeper roots without than with irrigation, and only at the first monitoring date. In this respect our results confirm those of von Willert (1994) for *Welwitschia mirabilis* and of Stave et al. (2005) for *Faidherbia alba*. However, the irrigation effect had vanished at the end of the experiment after 16 weeks. There was also no effect of irrigation on root: shoot ratio and SRL. One explanation for this unexpected outcome might be that the difference in volumetric water content between irrigated and non-irrigated tubes might not have been substantial enough to invoke different responses of the

Table 3

F-values of the mixed ANCOVA model of the glasshouse experiment predicting the relative decrease in soil water content with RGR of rooting depth or RGR of shoot biomass as covariables, species and fertilizer and their interaction as fixed factors, and basin nested within fertilizer as random factor. The model was optimized starting from a full model with all interactions based on AIC values. *Z*-values show the significance of the random factor and are based on the Wald *Z*-statistics.

	RGR of rooting depth		RGR of shoot biomass			
	Den	<i>F</i>	df	<i>F</i>		
RGR of rooting depth/ shoot biomass	30	9.98	**	31	5.97	*
Species	30	0.03		31	1.10	
Fertilizer	6	2.51		6	0.49	
RGR × species	30	6.90	*	31	5.65	*
Species × fertilizer	30	6.52	*	31	6.06	*
Basin (fertilizer)	Z-value 0.00		Z-value 0.78			

Significance levels * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

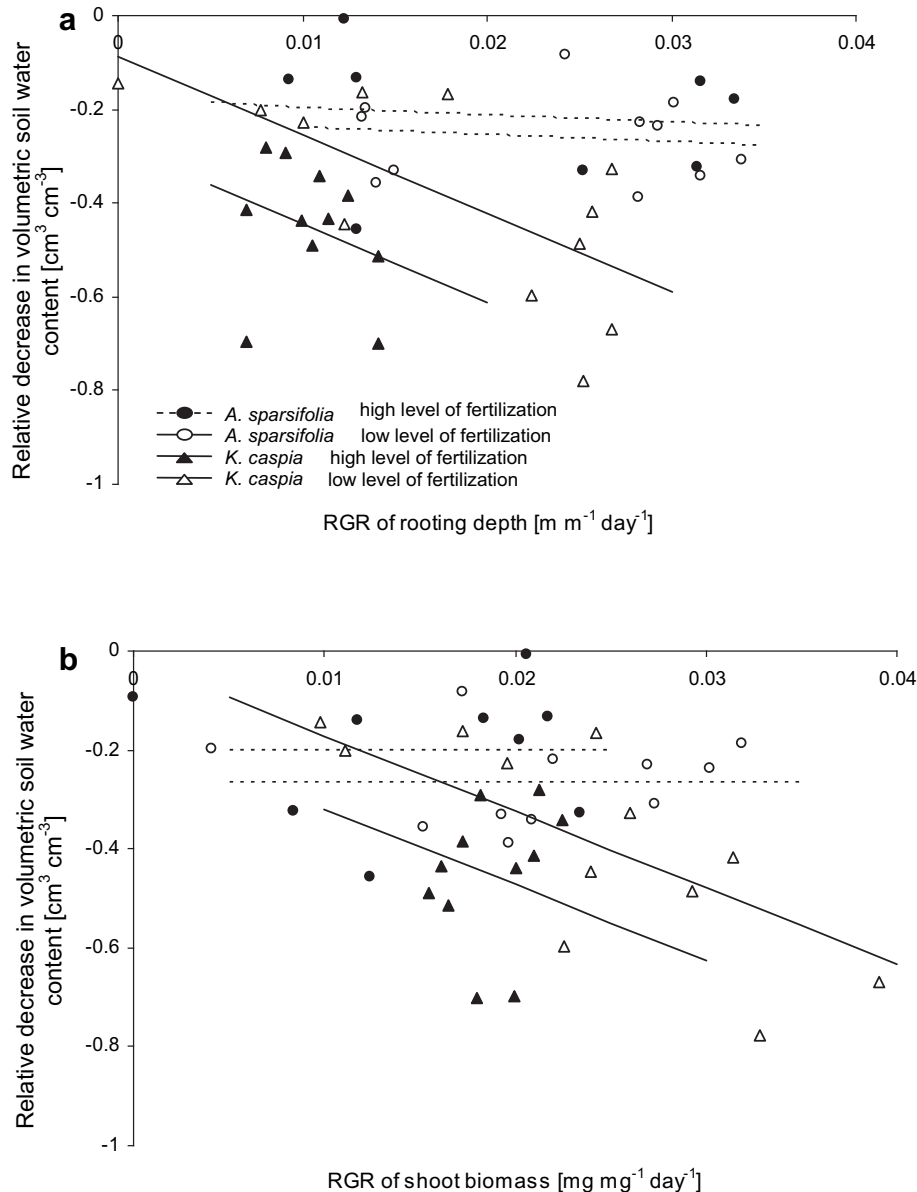


Fig. 4. Relationship between relative decrease in volumetric soil water content (calculated as difference in water content [$\text{cm}^3 \text{cm}^{-3}$] between first and second harvest divided by water content at first time of harvest) and a) RGR of the rooting depth and b) RGR of shoot biomass of the two study species at the two levels of fertilization in the glasshouse experiment. The regression lines are based on the least square means parameters obtained from the optimized mixed models shown in Table 3. The amount of variance explained for a) and b) is $R^2 = 0.50$ and $R^2 = 0.59$, respectively.

plants. This interpretation is supported by the results of Li et al. (2008). They studied root growth of plants grown under five different water regimes (100, 80, 60, 40 and 20% water field capacity) and found no difference in root: shoot ratio in the three driest treatments. Our water contents were certainly in the range of these dry treatments, and although being significant, the absolute differences between irrigated and non-irrigated tubes were only small. In consequence, a higher root: shoot ratio as found by Li et al. (2008) in comparison to the moist treatments, could not be detected in our study. Nevertheless, the range of water contents in our study might also have been more realistic to the conditions the plants encounter in the field.

The third hypothesis of fertilization having similar effects as irrigation can also be partly confirmed. Fertilizer increased the total dry biomass (Schippers and Olf, 2000) and, showed the tendency of a lower SRL (Schippers and Olf, 2000; Trubat et al., 2006). In

a review on specific root length, Ryser (2006) concluded that SRL can increase, decrease or stay constant with nutrient limitation. These inconsistent results might have their cause in a different response of different parts of the root system. Nicotra et al. (2002) described increasing SRL of the main root axis with decreasing precipitation. However, the SRL of the entire root system decreased with decreasing precipitation. The same differences might occur at different nutrient levels. Our results of an increased SRL in the low fertilization treatment most likely reflect the primary need of reaching down to deep layers and getting down to the groundwater. This has to be realized at lower costs per unit root length when nutrients are limited. We also found a higher root: shoot ratio in the unfertilized treatment, which is a common result in studies with different nutrient levels (e.g. Agren and Franklin, 2003; Ingestat and Agren, 1991; Schade and Lewis, 2006; Schippers and Olf, 2000). This result is also supported by a review of Reynolds

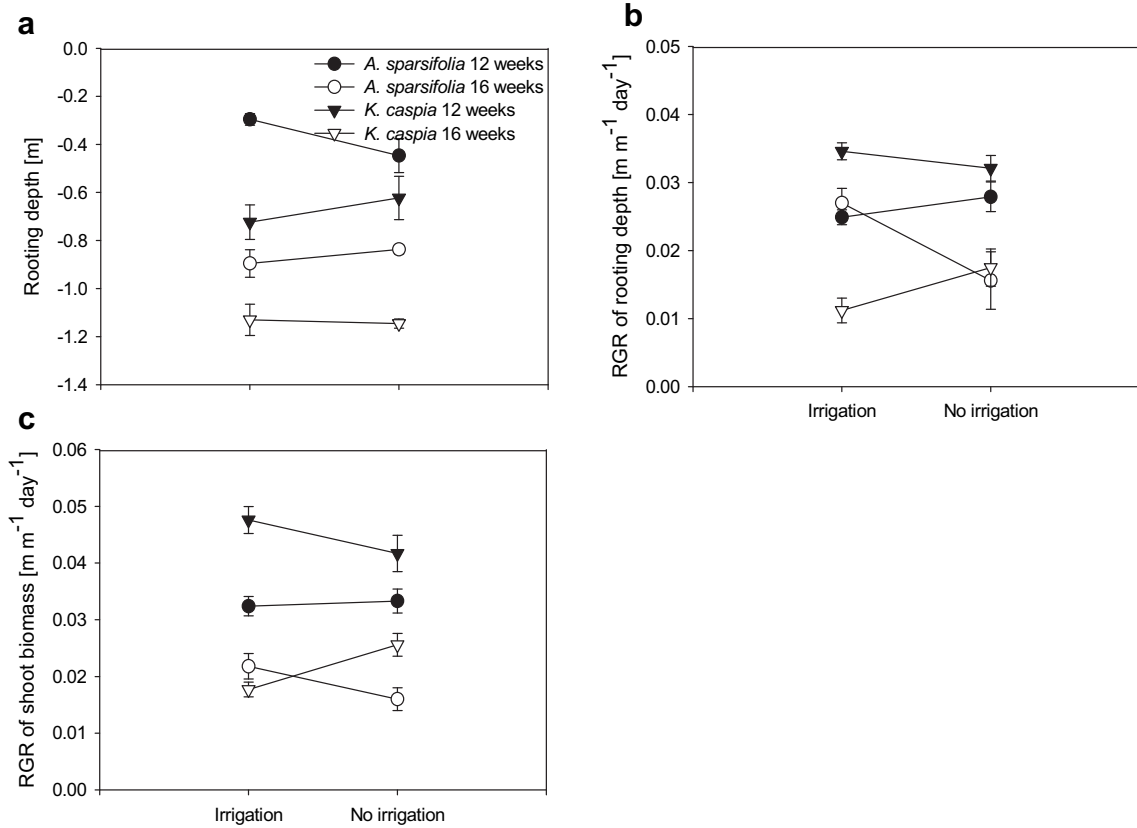


Fig. 5. Mean and SE of a) rooting depth, b) RGR of rooting depth and c) RGR of shoot biomass of the two study species at the two developmental stages and the two irrigation treatments in the glasshouse experiment. The tests for significant differences for all factors are given in Table 2.

and D'Antonio, (1996), who described a decrease in root: shoot ratio with increased nitrogen supply in 56 out of 77 studies. Nitrogen supply might also be considered to explain the lower root growth rates of *A. sparsifolia* compared to *K. caspia*. As a legume *A. sparsifolia* is able to utilize atmospheric N_2 (Arndt et al., 2004). In 41% of the studied *A. sparsifolia* plants, N_2 -fixation contributed more than 80% of the total leaf N (Arndt et al., 2004). This might explain the lower root: shoot ratio of *A. sparsifolia* compared to *K. caspia* in the lower level of fertilization because there would be no need for increased root growth in nutrient limited environment.

In conclusion, both species displayed an extremely rapid rooting depth, which allows them to follow declining water tables during

the period of establishment. Depths to the groundwater of 6.5 m, as encountered in the river plains, can be easily reached by the roots within five to six months. *K. caspia* has a faster rooting depth in accordance with a higher water use than *A. sparsifolia*. Although *K. caspia* might become established more successfully, the higher water use might be disadvantageous at later stages. Further studies, focusing on later stages of plant development such as i.e. the ability to grow with sand accumulation and water use efficiency might provide further explanations for the current species distribution in the oasis foreland.

Against the background of the specific adaptations to this extreme environment, it is a tragedy that these species are severely

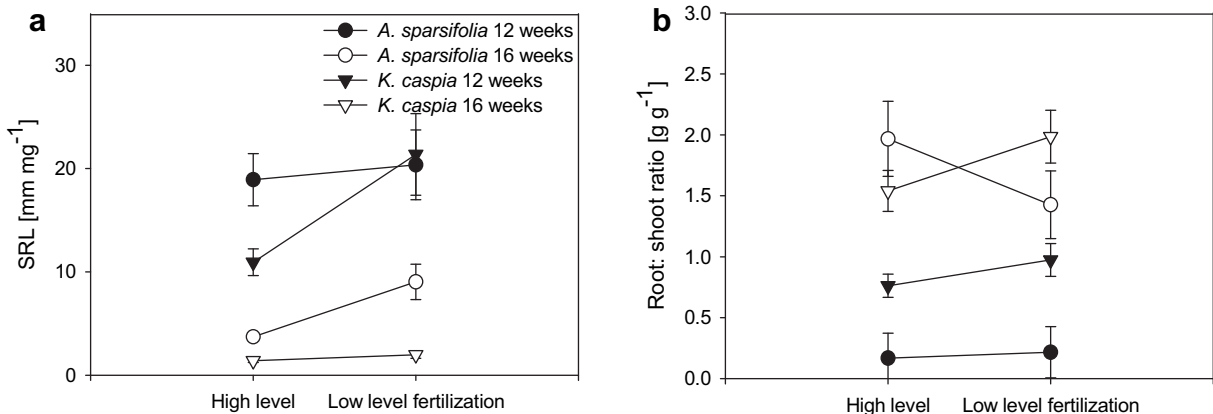


Fig. 6. Mean and SE of the a) SRL and b) root: shoot ratio of the two study species at the two developmental stages and the two fertilization levels in the glasshouse experiment. The tests for significant differences for all factors are given in Table 2.

endangered by human activities. At present, the depth to the groundwater table in many oases is declining due to the increasing water demand of a growing population in China (Ma et al., 2007). In consequence, vegetation dies back because the plants fail to follow the sinking water fringes with their roots (Cui and Shao, 2005). The construction of water reservoirs and the expansion of the oasis' water systems decrease the amount and frequency of floodings which are needed for new sexual establishment. Therefore, it is uncertain how far in the future the vegetation can fulfil its multifunctionality.

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References

- Agren, G.I., Franklin, O., 2003. Root: shoot ratios, optimization and nitrogen productivity. *Annals of Botany* 92, 795–800.
- Arndt, S.K., Kahmen, A., Arampatsis, C., Popp, M., Adams, M., 2004. Nitrogen fixation and metabolism by groundwater-dependent perennial plants in a hyperarid desert. *Oecologia* 141, 385–394.
- Bargali, K., Tewari, A., 2004. Growth and water relation parameters in drought-stressed *Coriaria nepalensis* seedlings. *Journal of Arid Environment* 58, 505–512.
- Baskin, C.C., Baskin, J.M., 2004. Seeds, Ecology, Biogeography, and Evolution of Dormancy and Germination, third ed. Academic Press, San Diego.
- Bruelheide, H., Jandt, U., Gries, D., Thomas, F.M., Foetzki, A., Buerkert, A., Gang, W., Zhang, X.M., 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, 801–818.
- Bruelheide, H., Vonlanthen, B., Jandt, U., Thomas, F.M., Foetzki, A., Gries, D., Wang, G., Zhang, X.M., Runge, M., 2010. Life on the edge – which type of water source sustains vegetation in the periphery of the Taklamakan Desert? *Journal of Vegetation Science* 13, 56–71.
- Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108, 583–595.
- Chapin, F.S., Bloom, A.J., Field, C.B., Waring, R.H., 1987. Plant responses to multiple environmental factors. *Bioscience* 37, 49–57.
- Cortina, J., Green, J.J., Baddeley, J.A., Watson, C.A., 2008. Root morphology and water transport of *Pistacia lentiscus* seedlings under contrasting water supply: a test of the pipe stem theory. *Environmental and Experimental Botany* 62, 343–350.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, E., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., et al., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51, 335–380.
- Cui, Y., Shao, J., 2005. The role of groundwater in arid/ semiarid ecosystems, Northwest China. *Groundwater* 43, 471–477.
- Danin, A., 1996. *Plants of Desert Dunes*. Shaker Verlag, Berlin.
- Elberse, W.T., Berendse, F., 1993. A comparative study of the growth and morphology of eight grass species from habitats with different nutrient availabilities. *Functional Ecology* 7, 223–229.
- Foetzki, A., 2003. Wasserhaushalt und Wassernutzungseffizienz in vier perennierenden Pflanzenarten im Vorland einer zentralasiatischen Flussoase Forschungszentrum Waldökosysteme. University of Göttingen, Göttingen.
- Ingestat, T., Agren, G.I., 1991. The influence of plant nutrition on biomass allocation. *Ecological Applications* 1, 168–174.
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, A., Schulze, E.D., 1996. A global analysis of root distribution for terrestrial biomes. *Oecologia* 108, 389–411.
- Kurban, H., Saneoka, H., Nehira, K., Adilla, R., Fukita, K., 1998. Effect of salinity on growth and accumulation of organic and inorganic solutes in the leguminous plants *Alhagi pseudoalhagi* and *Vigna radiata*. *Soil Science and Plant Nutrition* 44, 589–597.
- Kramer, P.J., 1988. Changing concepts regarding plant water relations. *Plant Cell and Environment* 11, 565–568.
- Li, F., Bao, W.K., Wu, K., You, C., 2008. Growth, biomass partitioning, and water-use efficiency of a leguminous shrub (*Bauhinia faberi* var. *microphylla*) in response to various water availabilities. *New Forests* 36, 53–65.
- Ma, Y., Fan, S., Zhou, L., Dong, Z., Feng, J., 2007. The temporal change of driving factors during the course of land desertification in arid region of North China: the case of Minqin county. *Environmental Geology* 51, 999–1008.
- McGinnies, W.G., 1968. Appraisal of research on vegetation of desert environments. In: McGinnies, W.G., Goldman, B.J. (Eds.), *Deserts of the World*. University of Arizona Press, Tucson, pp. 381–566.
- Mosena, M., Dillenburg, L.R., 2004. Early growth of Brazilian pine (*Araucaria angustifolia* [Bertol.] Kuntze) in response to soil compaction and drought. *Plant and Soil* 258, 293–306.
- Nicotra, A.B., Babicka, N., Westoby, M., 2002. Seedling root anatomy and morphology: an examination of ecological differentiation with rainfall using phylogenetically independent contrasts. *Oecologia* 130, 136–145.
- Padilla, F.M., de Dios Miranda, J., Pugnaire, F.I., 2007. Early root growth plasticity in seedlings of three Mediterranean woody species. *Plant and Soil* 296, 103–113.
- Padilla, F.M., Pugnaire, F.I., 2007. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Functional Ecology* 21, 489–495.
- Padilla, F.M., de Dios Miranda, J., Jorquera, M.J., Pugnaire, F.I., 2009. Variability in amount and frequency of water supply affects roots but not growth of arid shrubs. *Plant Ecology* 204, 261–270.
- Passioura, J.B., 1988. Changing concepts regarding plant water relations. *Plant Cell and Environment* 11, 569–571.
- Poot, P., Lambers, H., 2003. Are trade-offs in allocation pattern and root morphology related to species abundance? A congeneric comparison between rare and common species in the south-western Australian flora. *Journal of Ecology* 91, 58–67.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences* 94, 13730–13734.
- Reynolds, H.L., D'Antonio, C., 1996. The ecological significance of plasticity in root weight ratio in response to nitrogen: opinion. *Plant and Soil* 185, 75–97.
- Runge, M., Arndt, S., Bruelheide, H., Foetzki, A., Gries, D., Hunag, J., Popp, M., Thomas, F.M., Wang, G., Zhang, X.M., 2001. Contributions to a sustainable management of the indigenous vegetation in the foreland of Cele oasis. A project report from the Taklamakan Desert. In: Breckle, S., Veste, M., Wucherer, W. (Eds.), *Sustainable Land Use in Deserts*. Springer Verlag, Berlin, pp. 343–349.
- Ryser, P., 2006. The mysterious root length. *Plant and Soil* 286, 1–6.
- Sala, O.E., Lauenroth, W.K., 1982. Small rainfall events: an ecological role in semi-arid regions. *Oecologia* 53, 301–304.
- Schade, J.D., Lewis, D.B., 2006. Plasticity in resource allocation and nitrogen-use efficiency in riparian vegetation: implications for nitrogen retention. *Ecosystems* 9, 740–755.
- Schenk, H.J., Jackson, R.B., 2005. Mapping the global distribution of deep roots in relation to climate and soil characteristics. *Geoderma* 126, 129–140.
- Schippers, P., Olff, H., 2000. Biomass partitioning, architecture and turnover of six herbaceous species from habitats with different nutrient supply. *Plant Ecology* 149, 219–231.
- Schulze, E.D., Mooney, H.A., Sala, O.E., Jobbagy, E., Buchmann, N., Bauer, G., Canadell, J., Jackson, R.B., Loreti, J., Oesterheld, M., Ehleringer, J.R., 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia* 108, 503–511.
- Schwinnig, S., Ehleringer, J.R., 2001. Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology* 89, 464–480.
- Seyfried, M.S., Schwinnig, S., Walvoord, M.A., Pockman, W.T., Newman, B.D., Jackson, R.B., Phillips, E.M., 2005. Ecohydrological control of deep drainage in arid and semiarid regions. *Ecology* 86, 277–287.
- Stave, J., Oba, G., Eriksen, A.B., Nordal, I., Stenseth, N.C., 2005. Seedling growth of *Acacia tortilis* and *Faidherbia albida* in response to simulated groundwater tables. *Forest Ecology and Management* 212, 367–375.
- Thomas, F.M., Arndt, S.K., Bruelheide, H., Foetzki, A., Gries, D., Huang, J., Popp, M., Wang, G., Zhang, X.M., Runge, M., 2000. Ecological basis for a sustainable management of the indigenous vegetation in a Central-Asian desert: presentation and first results. *Journal of Applied Botany- Angewandte Botanik* 74, 212–219.
- Trubat, R., Cortina, J., Vilagrosa, A., 2006. Plant morphology and root hydraulics are altered by nutrient deficiency in *Pistacia lentiscus* (L.). *Trees – Structure and Function* 20, 334–339.
- Vonlanthen, B., Zhang, X.M., Bruelheide, H., 2010. Clonal structure and genetic diversity of three desert phreatophytes. *American Journal of Botany* 97 (2), 234–242.
- Vonlanthen, B., Zhang, X.M., Bruelheide, H. Establishment and early survival of five phreatophytes of the Taklamakan Desert. *Flora*, in press.
- von Willert, D.J., 1994. *Welwitschia mirabilis* Hook. fil. – das Überlebenswunder der Namibwüste. *Naturwissenschaften* 81, 430–442.
- Walls, J., 1982. Combating desertification in China. *United Nation Environmental Program*, 1–70.
- Wickens, G.E., 1998. *Ecophysiology of economic plants in arid and semi-arid lands*. Springer Verlag, Berlin.
- Wu, F.Z., Bao, W.K., Li, F.L., Wu, N., 2008. Effects of drought stress and N supply on the growth, biomass partitioning and water-use efficiency of *Sophora davidii* seedlings. *Environmental and Experimental Botany* 63, 248–255.
- Wu, Z.Y., Raven, P.H., 1994. *Flora of China*. Science Press, Beijing/Missouri Botanical Garden (St. Louis).

- Xia, X., Zhou, X., Zhang, H., Huang, P., Pan, B., 1993. Desertification and control of blown sand disasters in Xingjiang. Science Press, Beijing.
- Zeng, F.J., Li, X., Zhang, X.M., 2004. Seasonal variation in the water potential of four desert plant species at the Qira oasis. In: Runge, M., Zhang, X.M. (Eds.), *Ecophysiology and habitat requirements of perennial plant species in the Taklamakan Desert*. Contributions to a "Workshop on sustainable management of the shelterbelt vegetation of river oasis in the Taklamakan Desert", 2003. Shaker Verlag, Urumqi/Aachen, pp. 49–58.
- Zeng, F.J., Bleby, T.M., Landman, P.A., Adams, M.A., Arndt, S.K., 2006. Water and nutrient dynamics in surface roots and soils are not modified by short-term flooding of phreatophytic plants in a hyperarid desert. *Plant and Soil* 279, 129–139.
- Zhang, X.M., Li, X., Zhang, H., 2001. The control of drift sand on the southern fringe of the Taklamakan Desert – an example from Cele oasis. In: Breckle, S., Veste, M., Wucherer, W. (Eds.), *Sustainable Land Use in Deserts*. Springer Verlag, Berlin, pp. 350–356.