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ORIGINAL ARTICLE

Physiological acclimation strategies of riparian plants to environment change in the delta of the Tarim River, China

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Abstract The occurrence and development of riparian forests, which were mainly dominated by mesophytes species related closely with surface water. Since there was no water discharged to the lower reaches of Tarim River in the past three decade years, the riparian forests degrade severely. The groundwater table, the saline content of the groundwater, as well as the content of free proline, soluble sugars, plant endogenous hormones (abscisic acid (ABA), and cytokinins (CTK)) of the leaves and relative rates of sap flow of the *Populus euphratica* Oliv. (arbor species), *Tamarix ramosissima* Ldb. (bush species), and *Apocynum venetum* L. (herb species) were monitored and analyzed at the lower reaches of the Tarim River in the study area where five positions on a transect were fixed at 100 m intervals along a sampling direction from riverbank to the sand dunes before and after water release. The physiological responses and acclimation strategies of three species to variations in water and salinity stress were discussed. It was found that *A. venetum* population recovered to groundwater table ranging from −1.73 to −3.56 m, and when exposed to saline content of the groundwater ranging from 36.59 to 93.48 m mol/L; *P. euphratica* appeared to be more sensitive to the elevation of groundwater table than the *A. venetum* and *T. ramosissima* at groundwater table ranging from −5.08 to −5.80 m, and when exposed to saline content of the groundwater ranging from 42.17 to 49.55 m mol/L. *T. ramosissima* tended to be the best candidate species for reclamation in this hyper-arid area because it responded to groundwater table ranging from −1.73 to −7.05 m, and when exposed to saline content of the groundwater ranging from 36.59 to 93.48 m mol/L. These results explained the distribution patterns of desert vegetation in the lower reaches of the Tarim River. Understanding the relationships among ecological factors variables, physiological response and acclimation strategies of plant individuals could provide guidance to sustainable management, reclamation and development of this and similar regions.

Keywords Soluble sugars · Free proline · Endogenous abscisic acid · Cytokinins · Groundwater table · Water and saline stress

Introduction

The natural vegetation of arid environments is characterized by low diversity, sparse cover and dominance by perennial species. This is thought to be responsible for their fragility and predispose them to desertification under human influences. The vascular plants of many arid areas furnish a scant ground cover of discrete and widely spaced units. Both biotic and abiotic factors are thought to influence the distributive patterns and ranges of different plants (Tongway and Ludwig 1994). Interrelationships between plant communities and environmental factors are complex, reflecting simultaneous changes in factors such as groundwater depth, soil moisture, salt content and soil

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stability. Plants grown in arid environments are usually subject to salt stress and drought stress conditions caused by high evaporative demand, low water availability, and high mineral content of groundwater. They have evolved various physiological processes in response and acclimation to the changes of environments. A better understanding of the strategies of desert plant adaptation to changes may help to improve water resources utilization and environmental restoration efficient.

Osmotic adjustment (OA) is one of the drought-avoidance mechanisms involved in counteracting the loss of turgor by increasing and maintaining a higher amount of intracellular compatible solutes. It proved to be most effective among all stress adaptation mechanisms (Cushman 2001). Soluble sugars (Rekika et al. 1998) and proline (Mattioni et al. 1997 level increased under water stress and were potentially important contributors to OA. Drought adversely affected many physiological and biochemical processes in plants, including mechanisms that regulated stomatal responses. In some plants, the suppression in leaf stomatal conductance during drought had been reported to be independent of changes in water flux, and accumulating abscisic acid (ABA) might be responsible for these responses (Aguilar et al. 2000). Many authors, however, had reported negative exponential relationships between leaf stomatal conductance and ABA content. Tardieu and Davies (1992) and Jarvis and Davies (1997) had noted that this relationship could be largely dominated by decreasing water flux as stomata close. In addition to ABA, the work of Blackman and Davies (1985a) suggest that a continuous supply of cytokinins (CTK) from roots was necessary to sustain maximal stomatal opening in plants growing in drying soil, the role of CTK as negative signals in root to shoot communication under drought conditions had remained controversial. Itai and Vaadia (1965) concluded that a reduced supply of CTK was a sensitive “signal” of root stress, a view substantiated by Hubick et al. (1986) in sunflower, which showed a significant reduction in total CTK activity in the xylem sap. The most comprehensive analysis of CTK as a putative negative root messenger was in Phaseolus vulgaris (Fußeder et al. 1992).

The Tarim River is the longest continental river in China with a length of 1,321 Km. Water resources of the river system sustain the growth of desert plants and associated ecological system. The natural forests of *P. euphratica* in the Tarim River watershed account for 89% of the total area in China and 54% worldwide. This watershed is the largest gene base of *P. euphratica* (Yang 2002). Due to worldwide changes in climate and irrational utilization of water resources in the upper and middle reaches (Ragab and Prudhomme 2002), a cut-out of more than 320 km of the riverbed in the lower reaches of river occurred in the late 1970s, groundwater levels had dropped to 5–8 m below the surface and the groundwater had become salinized (Wang et al. 2007), resulting in the withering of forest areas and degradation of ecological environment along both the riverbanks. The lower Tarim river valley had become one of the hot-spots for eco-environmental protection in china. The central and local governments of China recognized this problem and invested RMB ¥10.7 billion (US \$1 $\approx$ RMB ¥8.2) to restore and reconstruct the ecological environment of this district. One of the most important measures implemented was the ecological engineering of water release from the Bositen Lake to the lower reaches of the Tarim River. The project was launched on 15 September 2000. It ensured the transfer of 3.50×10^8 m^3 of water from the Bositen Lake to the lower reaches of the Taitema Lake every year (Chen et al. 2004). One study, conducted in patterned riverbank forests in the lower Tarim River demonstrated that the distribution of riverbank forests were mainly determined by the moisture and soil salinity gradient (Pan 2001). Zhang et al. (2005) used canonical correspondence analysis (CCA) and correspondence analysis (CA) to investigate the floristics of plant communities and patterns in species distribution relative to environmental factors variables in the lower reaches of the Tarim River. Chen et al. (2003) investigated free proline accumulation in *P. euphratica* in response to variable groundwater table in the lower reaches of the Tarim River.

The aim of the present work was to study the physiological responses and acclimation strategies of three desert species along the lower reaches of the Tarim River, *P. euphratica* (arbor species), *T. ramosissima* (bush species), and *A. venetum* (herb species), in two periods: before water release and after water release; and to determine how these physiological processes were influenced by changes in (1) groundwater table, and (2) saline content of groundwater. The chosen transect was at Yhepumahan of the lower reaches of the Tarim River. Five sampled positions were fixed at 100 m intervals along a sampling direction from riverbank to the sand dunes. The groundwater table, the saline content of the groundwater, as well as the content of free proline, soluble sugars, plant endogenous hormones [abscisic acid (ABA), and cytokinins (CTK)] of the leaves and relative rates of sap flow of three species were monitored and analyzed before and after water release. The main purpose of this research was to realize the physiological response and acclimation strategies of the natural vegetation to the changes of environmental factors, to determine the optimum ecological requirements of the natural vegetation for devising means of recovery and reconstruction of the ecological environment in this and similar regions.

Materials and methods

Study area

The study areas are located on the section from the Daxihaizi Reservoir to the Taitema Lake in the lower reaches of the Tarim River (Lat. 40°36′N; Long. 87°12′E) between the Taklamakan Desert and Kuluke Desert (see Fig. 1). The total annual solar radiation varies from 5,692 to 6,360 MJ/m^2 with 2,780–2,980 cumulative sunlight hours. Annual-accumulated temperature (10°C) is from 4,040°C to 4,300°C with an average diurnal temperature range from 13 to 17°C. The annual precipitation varies in a range of 17.4–42.0 mm and occurs between June and August. The mean pan-evaporation is more than 2,700–3,100 mm annually and exceeds the precipitation by 50–60 times. The climatic conditions make the north of the Tarim Basin a typical hyper-arid region. Due to the low and highly erratic precipitation, the water content of soils in the Taklamakan is low and seldom exceeds 1% (V/W) until groundwater is reached (Thomas et al. 2000). Groundwater is consequently the only reliable source of moisture and nutrients available to plants.

The riverbank vegetation provides a natural defense against wind by obstructing sand movement. The flora of the region includes 14 families, 24 genera, and about 40 species of vascular plants. The plant cover includes: (1) *Populus. euphratica–Phragmites communnis* communities (with the associates *Tamarix ramosissima, Glycyrrhiza inflate, Poacynum hendersonii, Karelinia caspia*), (2) *Tamarix ramosissima–Phragmites communis* communities (with the associates *P. hendersonii*, *G. inflata*, *Asparagus neglectus*), and (3) *Tamarix ramosissima–Halostachys caspia* communities (with the associates *P. communis*, *P. hendersonii*, *K. caspia*, *Lycium ruthenicum*). Due to the construction of reservoirs and development of irrigation in the upper and middle reaches for 30 years, the water flow into the lower reaches was reduced and the groundwater level was lowered greatly, down to 8–12 m deep. The natural vegetation, such as the shrub–grass vegetation, dominated by *T. chinensis*, *P. communis*, and the *P. euphratica* forest, rely on groundwater for their survival and growth. They have seriously degenerated, and the sand dunes in the sand soils between the forests have become active (Wang et al. 2007).

Plant source

The first sampling (before water release) was conducted from 1 July to 20 July 2000, and after that, sampling (after water release) was conducted from 1 July to 20 July, every year thereafter. The data of years 2000 and 2007 were compared and analyzed. The studied species were *P. euphratica* (arbor species), *T. ramosissima* (bush species), and *A. venetum* (herb species). All plants selected were healthy and without infection. Care was taken to select three species, plants individual close to each other, and make mark on them. Southwards-facing leaves and branches (receiving maximum light during the day), being located in the middle layer of the canopies were used for measurements.

Measurements of groundwater table

Five positions on a transect at Yhepumahan were selected at 100 m intervals along a sampling line with an average of 500 m long from riverbank to sand dune in the area. Within each position, three wells were established for investigation. The positions and distances between the sample points were determined according to the GPS (GPS 12XL, Garmin Olathe, KS, USA). The height of the positions was 1 ± 0.1 m above the river water table and 2.5 ± 0.1 m above the river bottom. The groundwater table in these wells was monitored. The collected water and plant samples were analyzed in laboratory.

Estimation of salinity of groundwater

The mean salinity of the groundwater was estimated through its electrical conductivity. After digestion by HNO_3, K^+, Mg^{2+}, Ca^{2+} and Na^+ analyzes was carried out using an inductively coupled argon plasma emission spectrophotometer (Jobin-Yvon JY 48). Cl^- was colorimetrically determined with ferric ammonium sulfate and mercuric thiocyanate following the procedure of Guerrier and Patolia (1989). The total sulfate in the water was analyzed using ion-chromatography.

Psychrometric measurements of three species

The objective of psychrometric measurements was to test the possibility of determining the leaf water potentials by measuring the rate of sap flow of stem in three species. Leaf water potentials and the rate of sap flow of stem were tested under water deficient and water-logging conditions in laboratory. Sap flow measurements in response to variable groundwater table in study area were also carried out from 1 to 20 July 2000 and 2007, respectively.

Seedlings of three species were transplanted into 95-mm-diameter plastic pots filled with general purpose peat-based ‘Levington’ (Fisons, Ipswich, UK) compost containing a slow-release fertilizer (Osmocote, Grace Sierra UK, Nottingham, UK) and grown in a Fisons 1550 controlled environment room. Day/night temperatures were 25 and 20°C; the photoperiod was 16 h at 400 mmol m^{-2} s^{-1} PPFD with a relative humidity of 50%.

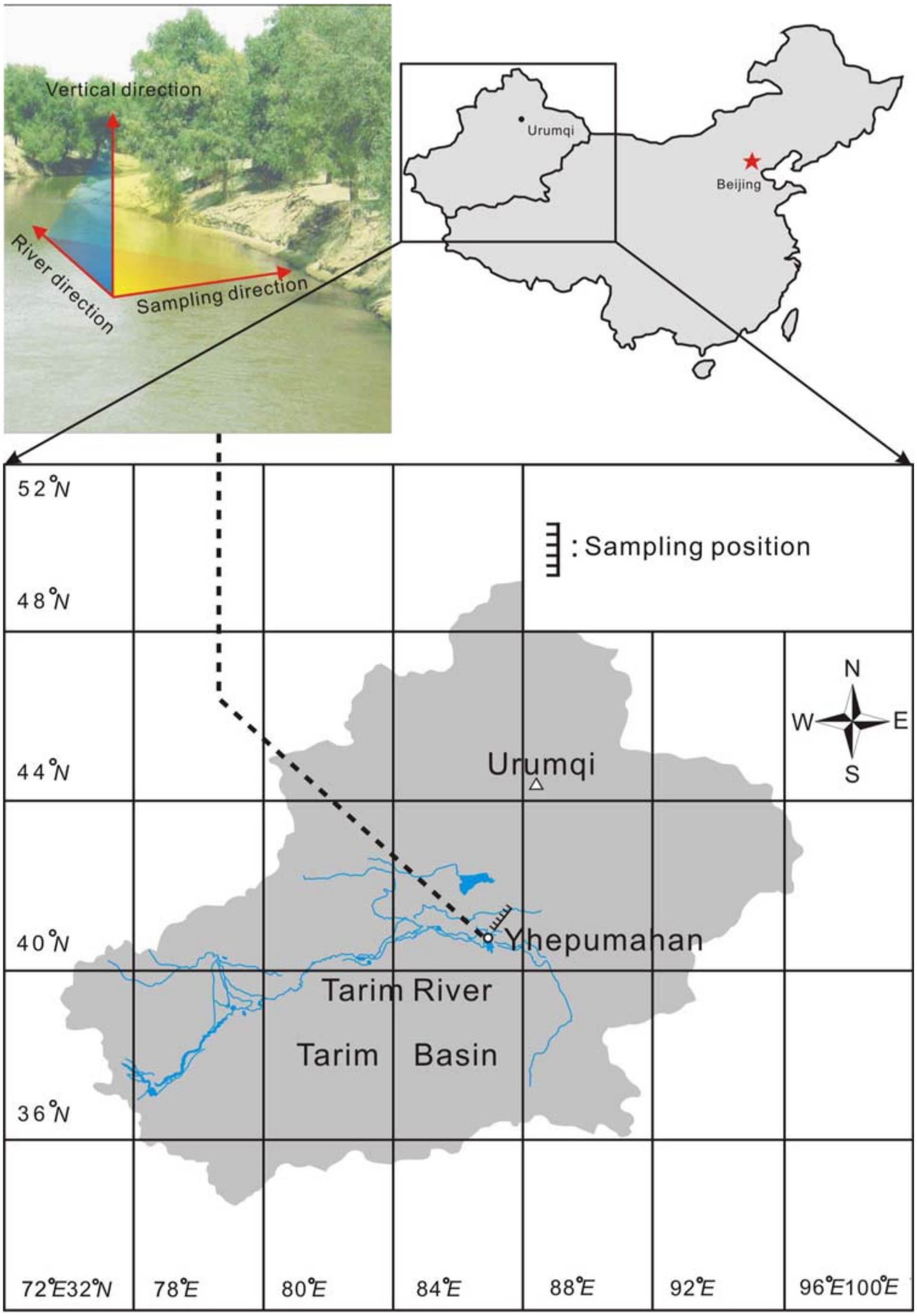

Fig. 1 Map showing the studied transect in the lower reaches of the Tarim River

All pots were irrigated automatically and side shoots of the plants removed regularly. Five-week-old plants were flooded for 0, 6, 24 or 48 h by placing the pots into larger plastic pots (1.2×10^{-3} m^3) filled with tap water, and then were in-irrigated for 25 days. Leaf water potentials and the rate of sap flow of stem were tested once every 3 days and each data was presented as the means of three replicates.

Leaf water potentials (ψ_L) were measured using a Scholander-type pressure chamber. Excised leaflets were immediately placed into the chamber and pressurized slowly until the meniscus was visible at the cut surface when viewed with an illuminating magnifier.

Sap flow measurements were based on the concepts proposed by Granier (1985). The gauges were installed following the manufacturer's instructions (Phytalk User Manual, PhyTech Ltd.). The signals from the gauges were recorded every 20 s and stored as 15-min averages with an automatic data logger. Three sap flow gauges [Stem Flux Relative Rate Remote Sensor (RS-SF-8PR)] were used to measure sap flow relative rates continuously from three branches, being located in the middle layer of the canopies of three selected species of similar leaf area, respectively. Leaf area was measured using a LAI-2000 Plant Canopy Analyzer (Li-Cor, Lincoln, NE, USA) (Patakas and Noitsakis 1999). Using Total Irradiance (solar radiation) Remote Sensor (RS-TIR-4PR), Wind Velocity Gauge Remote Sensor (RS-WSW-1PR), Air Temperature and Humidity Gauge Remote Sensor (RSD-ATH-5R), meteorological parameters such as total solar radiation, wind speed, air temperature and air humidity were measured simultaneously.

Proline extraction

The proline content was estimated using the method of Troll and Lindsley (1995). The plant material was homogenized in 3% aqueous sulfosalicylic acid, and the homogenate was centrifuged for 10 min at 8,000*g*. The supernatant was used for estimating proline content. The reaction mixture consisted of 0.2 mL supernatant, 2 mL acid ninhydrin, and 2 mL glacial acetic acid, which was boiled at 100°C for 1 h. After termination of the reaction in an ice bath, the reaction mixture was extracted with 4 mL of toluene. The absorbance was at 520 nm.

The proline stimulation (Sanchez et al. 2004): $\Delta[\text{proline}] = [\text{proline}]_{\text{after water release}} - [\text{proline}]_{\text{before water release}} / [\text{proline}]_{\text{before water release}}$.

Analysis of soluble sugars

Freeze-dried leaves (50 mg) were grounded and extracted in 1 mL of 80% (v/v) ethanol. For recovery purposes, a known amount of ribitol was added to the extracts at an internal standard. The extracts were then boiled for 15 min and centrifuged for 5 min at 10,000*g*. The supernatant was removed and the pellet was extracted twice as above. The extracts were vaccum-dried at 45°C. The dried extracts were re-dissolved in 1.0 mL distilled water and purified using anion exchange (Sephadex QAE-A-25, Pharmacia Biotech, Sweden). The eluates (1.0 mL extract and 2 mL water washings) were vacuum-dried and re-dissolved in 300 µl of water. Hexose (glucose × fructose) and sucrose were analyzed at 35°C using an HPLC equipped with a 300 × 7.8 mm column (carbohydrate-H^+, HYDERSIL, UK). H_2SO_4 (0.005 M) was used as the solvent at a flow rate of 0.6 mL/min.The soluble sugar stimulation (Sanchez et al. 2004):$\Delta[\text{sugar}] = [\text{sugar}]_{\text{after water release}} - [\text{sugar}]_{\text{before water release}} / [\text{sugar}]_{\text{before water release}}$.

Extraction and quantification of ABA using HPLC

Leaves (0.5 g) were grounded with liquid nitrogen. Abscisic acid was extracted in 250 µL of methanol at 4°C while being shaken overnight. Samples were centrifuged, and the supernatant was collected and vacuum-dried and subsequently dissolved in 30 µL of 10% CH_3CN. The ABA content was determined using HPLC analysis. An LC-10A TVP photodiode and ray detector (PDA), and a Shim pack CLC-C_8 (0.15 m × 6.0φ) were used. The flow rate was 1.5 mL min^{-1}. Detection was at 250 nm, at 30°C. The solvent for the pump A was 10% CH_3CN after the pH value was adjusted to 3.0 with CF_3COOH. The solvent for pump B was 60% CH_3CN. The abscisic acid (ABA) standard was purchased from Aldrich. The peak was identified and quantified against the external standard.

ELISA analysis of cytokinins

Cytokinins were extracted with 70% ethanol from the green parts of leaves (0.5 g). The extracts were evaporated to the water phase at 45°C under vacuum. The aqueous phase was made alkaline to pH 8–9 with 2 N NaOH and then extracted with *n*-hexane. The hexane phases were extracted two times with *n*-butanol. The resulting extracts were evaporated to dryness, dissolved in 400 µl ethanol, treated for 30 min with polyvinylpyrrolidone, and passed through a 0.45 µm membrane filter.

Detection using antibody kits for zeatin (Z), zeatin riboside (ZR), dihydrozeatin (DZ), and dihydrozeatin riboside (DZR) was carried out according to the method of Vonk et al. (1986). The following cross-reactivity was found: Z/ZR kit-31.25 for Z, 100.00 for ZR, 7.87 for DZ; DZ/DZR kit-1.75 for Z, 1.60 for ZR, 39.50 for DZ and 100.00 for DZR. The concentration of total cytokinins is calculated as the sum of the four types of compound (Z, ZR, DZ and DZR).

Statistical analysis

Statistical analysis was carried out using the SPSS statistical computer package (SPSS for windows, standard version, release 6.1); Statistical difference among positions on transect were analyzed by one-way analysis of variance (ANOVA).

Results

Groundwater table and salinity of groundwater

The Data of groundwater table and salinity of groundwater before and after water release are shown in Table 1. The groundwater table had been obviously raised by the water release program in this area. The groundwater table at the position of 100 m to the riverbank increased from −5.82 to −1.73 m, and the total saline content of the groundwater increased from 43.61 to 72.54 m mol/L (66.34% increase from before water release). Similarly, at the position of 300 m, the groundwater table increased from −7.66 to −3.56 m, and the total saline content of groundwater increased from 71.02 to 93.48 m mol/L (31.62% increase from before water release). In contrast to both these positions, the groundwater table at the position of 200 m increased from −7.25 to −3.39 m, while the total saline content of groundwater decreased from 38.56 to 36.59 m mol/L (−5.11% increase from before water release). At the same time, the plants that were exposed to the various salinity of groundwater: the largest at 300 m, and the lowest at 200 m.

At the positions of 400 and 500 m, the groundwater table increased from −6.64 to −5.08 m and from −7.05 to −5.80 m, respectively. Total saline content of the groundwater also slightly increased from 41.15 to 42.17 m mol/L and from 49.33 to 49.55 m mol/L, respectively (2.48 and 0.45% increase from before water release). Changes in total saline content of the groundwater were not significant at these two positions after water release.

Water status of three species

The major meteorological parameters such as wind speed, air temperature, air humidity and maximum diurnal sap flow rates of three species were recorded, before and after water release. The major meteorological parameters variation was insignificant at the same periods of the year. On 20 days, maximum diurnal sap flow relative rates were observed and exhibited a clear diurnal pattern during the mid-day hours from 11 to 13 O'clock (Civil time) (Fig. 2). The maximum diurnal sap flow rates measured under similar meteorological parameters conditions were selected to be averaged and shown in Table 2. Sap flow was monitored continuously, thus providing a continuous record of plant water status in response to groundwater table variables. Psychrometric measurements showed that sap flow varied in parallel to leaf water potential in laboratory. Maximum diurnal sap flow rates ranging from 0.05 to 0.20 L/h in *A. venetum*, from 0.15 to 0.37 L/h in *T. ramosissima* and from 0.18 to 0.46 L/h in *P. euphratica*, of the three species were under lethal leaf water potentials conditions, respectively. In response to increased groundwater table after water release at the position of 400 m, the maximum diurnal sap flow rates in *P. euphratica* increased from 0.294 to 0.445 L/h, in *T. ramosissima* from 0.203 to 0.338 L/h, and in *A. venetum* from 0.108 to 0.162 L/h; At the position of 500 m, the maximum diurnal sap flow rates in *P. euphratica* increased from 0.250 to 0.383 L/h, in *T. ramosissima* from 0.142 to 0.237, and in *A. venetum* from 0.058 to 0.156 L/h. However, at the positions of 400 and 500 m the maximum diurnal sap flow rates in three

Table 1 Groundwater table and salinity of groundwater at different positions (a, b indicate before and after water release)

Distance (m)	Groundwater table (m)[a]	HCO_3	Cl^-	SO_4^{2-}	Ca^{2+}	Mg^{2+}	Na^+	K^+	Total[b]
100	5.82a	7.08 ± 1.32^A	11.32 ± 1.85^C	3.57 ± 0.37^E	1.85 ± 0.32^C	3.08 ± 0.29^D	16.33 ± 2.29^C	0.38 ± 0.05^D	43.61 ± 1.41^D
	1.73b	3.65 ± 0.69^B	22.14 ± 3.53^B	10.00 ± 1.14^B	2.83 ± 0.33^B	6.42 ± 2.28^{BC}	26.65 ± 0.84^B	0.85 ± 0.05^A	72.54 ± 0.61^B
200	7.25a	2.56 ± 0.18^{BC}	10.87 ± 1.60^C	5.52 ± 1.02^D	1.60 ± 0.17^{CD}	3.50 ± 0.54^D	14.13 ± 1.74^C	0.38 ± 0.05^D	38.56 ± 2.04^{EF}
	3.39b	1.19 ± 0.39^C	10.99 ± 1.90^C	5.10 ± 0.89^D	0.83 ± 0.14^E	2.75 ± 0.41^D	15.22 ± 1.97^C	0.51 ± 0.15^{BCD}	36.59 ± 1.23^F
300	7.66a	7.13 ± 1.11^A	20.45 ± 2.48^B	8.13 ± 0.99^C	2.08 ± 0.24^C	7.04 ± 0.97^B	25.57 ± 1.55^B	0.62 ± 0.12^{ABC}	71.02 ± 2.20^B
	3.56b	7.02 ± 0.98^A	29.52 ± 2.62^A	11.56 ± 1.16^A	3.99 ± 0.36^A	10.79 ± 2.14^A	29.91 ± 2.29^A	0.69 ± 0.29^{AB}	93.48 ± 6.11^A
400	6.64a	7.04 ± 0.90^A	10.37 ± 0.77^C	3.54 ± 0.07^E	1.65 ± 0.23^C	2.92 ± 0.44^D	15.22 ± 1.84^C	0.41 ± 0.11^{CD}	41.15 ± 0.55^{DEF}
	5.08b	6.52 ± 1.35^A	9.72 ± 1.31^C	4.57 ± 0.35^{DE}	1.15 ± 0.18^{DE}	4.25 ± 0.67^{CD}	15.22 ± 1.57^C	0.41 ± 0.14^{CD}	42.17 ± 2.37^{DE}
500	7.05a	3.58 ± 0.52^B	10.64 ± 2.26^C	10.10 ± 0.99^{AB}	2.93 ± 0.37^B	7.29 ± 1.79^B	14.00 ± 2.38^C	0.79 ± 0.08^A	49.33 ± 3.07^C
	5.80b	3.65 ± 0.94^B	10.64 ± 1.26^C	10.01 ± 1.12^B	2.83 ± 0.42^B	6.42 ± 2.24^{BC}	15.15 ± 1.26C	0.85 ± 0.17^A	49.55 ± 3.24^C

Values are mean ± SD. A, B, C, D, E and F denote significant differences at $a = 0.05$ level in the process of LSD multiple comparisons

[a] The values of groundwater table are means of three replications

[b] The concentration of total salt was calculated on the basis of these seven ions. The values of salinity groundwater in each position are means of three replications

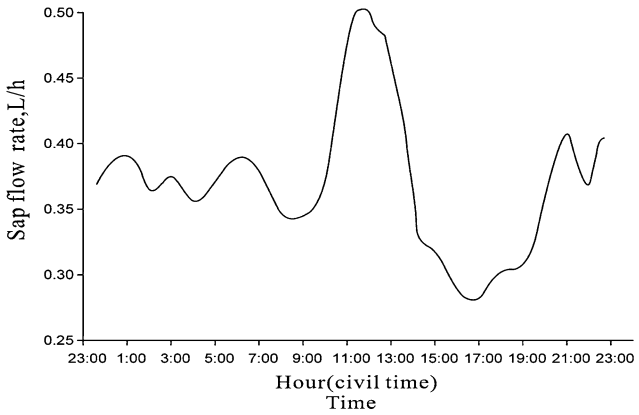

Fig. 2 Sap flow relative rates measured in individual stems of *P. euphratica* on 10 July 2007 (the maximum sap flow rate value means maximum diurnal sap flow rate. The leaf area of *P. euphratica* is 100 cm^2)

species fluctuated under values of lethal leaf water potentials, the three species were exposed to the water stress conditions. Whereas, the maximum diurnal sap flow rates in *P. euphratica* increased from 0.465 and 0.572 to 0.823 L/h, in *T. ramosissima* increased from 0.384 and 0.485 to 0.654 L/h, and in *A. venetum* increased from 0.218 and 0.234 to 0.343 L/h from position 300 to 100 m, the three species were exposed to the decreased water stress progressively after water release.

Growth state of three species

The data of the growth state of three species in response to the changes of environment are shown in Table 3. Before the water release, the population of *A. venetum* was destroyed greatly because the groundwater table was

Table 2 Average of maximum diurnal sap flow rates of three species at different postions (a, b indicate before and after water release)

Distance (m)	Groundwater table (m)	Species	Maximum diurnal sap flow rate (L/h)
100	5.82a	*A. venetum*	0.135 ± 0.010
		T. ramosissima	0.263 ± 0.008
		P. euphratica	0.347 ± 0.012
	1.73b	*A. venetum*	0.343 ± 0.012
		T. ramosissima	0.654 ± 0.010
		P. euphratica	0.823 ± 0.007
200	7.25	*A. venetum*	0.087 ± 0.010
		T. ramosissima	0.176 ± 0.008
		P. euphratica	0.201 ± 0.009
	3.39b	*A. venetum*	0.234 ± 0.013
		T. ramosissima	0.485 ± 0.006
		P. euphratica	0.572 ± 0.008
300	7.66a	*A. venetum*	0.058 ± 0.002
		T. ramosissima	0.154 ± 0.006
		P. euphratica	0.192 ± 0.005
	3.56b	*A. venetum*	0.218 ± 0.011
		T. ramosissima	0.384 ± 0.006
		P. euphratica	0.465 ± 0.007
400	6.64a	*A. venetum*	0.108 ± 0.011
		T. ramosissima	0.203 ± 0.008
		P. euphratica	0.294 ± 0.009
	5.08b	*A. venetum*	0.162 ± 0.006
		T. ramosissima	0.338 ± 0.011
		P. euphratica	0.445 ± 0.008
500	7.05a	*A. venetum*	0.058 ± 0.001
		T. ramosissima	0.142 ± 0.007
		P. euphratica	0.250 ± 0.009
	5.80b	*A. venetum*	0.156 ± 0.004
		T. ramosissima	0.237 ± 0.003
		P. euphratica	0.383 ± 0.005

Values are means ± SD of 12 replicates

Table 3 Data of the growth state of the three desert species in response to the groundwater table change

Species	Distributing depth of main-root/m	Groundwater table of promoting growth/m	Groundwater table of inhibiting growth/m	Groundwater table of lethal growth/m
A. venetum	2–3	1.5–4	>4	>6
T. ramosissima	<5	1–5	>6	>10
P. euphratica	<7	1–4	4–5	>8

Data were collected by our group. The method of measurement of the parameters could be seen in Liu et al. (2004)

beyond the distributing depth of the main root and close to the lethal depth of growth. *P. euphratica* also degraded severely due to low availability of water, the groundwater table had decreased to the degree of inhibiting the plant's growth. After water release, as the groundwater table rose, the recovery of the population of three species (especially *A. venetum*) was rapid within the extent of 300 m and the vegetation development was improved.

Soluble sugars and proline accumulation in three species

Free proline and soluble sugars were determined to check if these compatible solutes were accumulated with changes of groundwater table and salinity of groundwater. Figure 3 showed the soluble sugar concentration as a function in response to groundwater table and salinity of groundwater among three species. Within the 300 m extent, as the groundwater table rose, total saline content of the groundwater increased. The total saline contents increase at the positions of 100 and 300 m was about 66.34 and 31.62%, respectively. Increased total saline contents of groundwater dramatically increased soluble sugar concentration of the three species and was found to be more elevated at positions of 100 and 300 m than those at 200 m. Differences in sugar accumulation were determined among the species over the extent from 100 to 300 m; the variability in *A. venetum* and *T. ramosissima* was greatest at the positions of 100 and 300 m, respectively. At these two positions, the variability in *P. euphratica* was closed and the greatest. On the other hand, soluble sugar concentration tended to be more significantly increased due to low availability of groundwater in *P. euphratica* than that in *T. ramosissima* and *A. venetum* within 400–500 m.

The free proline concentration in *T. ramosissima* and *P. euphratica* accumulated more in the 300–500 m extent than that in the 100–200 m extent after water release, and it also underwent a decrease with various degrees of elevation of the groundwater table. At the positions of 200, 400 and 500 m, the free proline concentration in *A. venetum* decreased in response to elevation of groundwater table, whereas it increased remarkably at the positions of 100 and 300 m (from 5.42 to 7.12 μg g^{-1} DW and from 7.06 to 12.37 μg g^{-1} DW, respectively) in response to the high total saline content of groundwater (Fig. 4). Figure 6 showed the relationship between free proline stimulation and soluble sugar stimulation in leaves of three species at different positions.

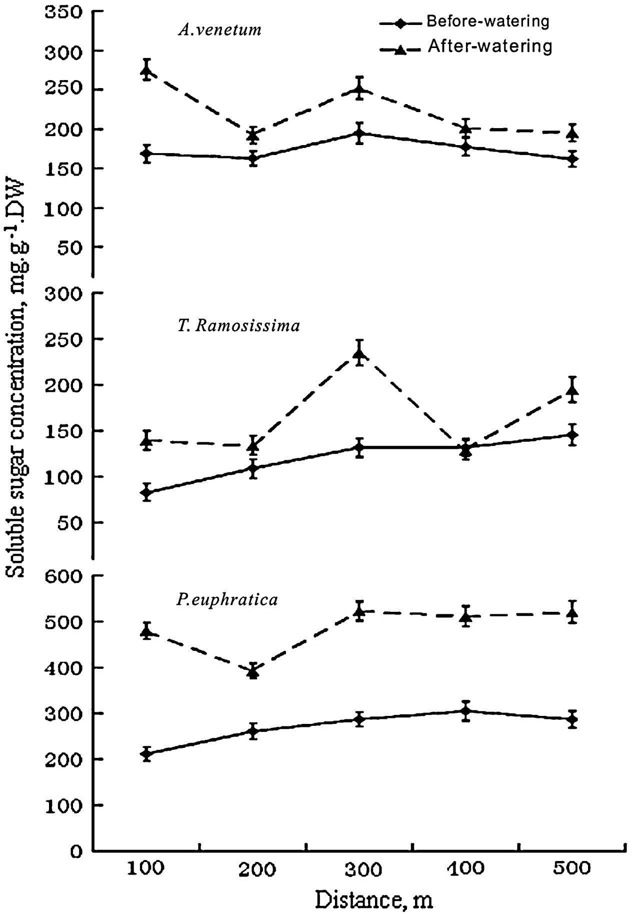

Fig. 3 Changes of soluble sugar concentration in leaves of the three species at different positions (each *point* represents the average of ten measurements ± SD)

Changes of ABA and CTK in the three species

Changes in the concentration increase of ABA and CTK in the leaves of three species after water release are shown in Fig. 5. The trend of changes in *A. venetum* over different positions were similar to those in *T. ramosissima*, and there was a positive increase in concentrations of ABA and CTK

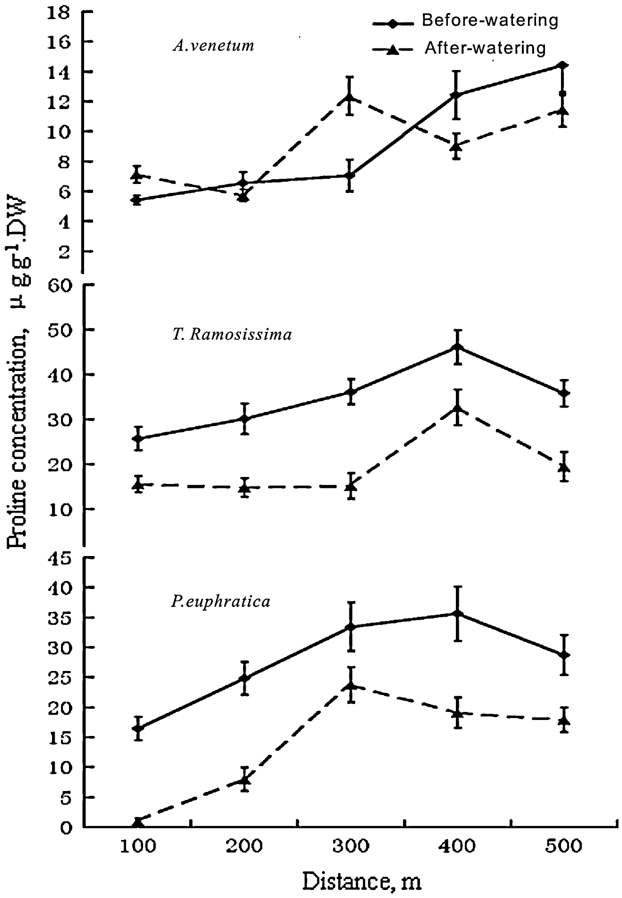

Fig. 4 Changes of free proline concentration in leaves of the three species (each *point* represents the average of ten measurements ± SD)

at positions 100 and 300 m in contrast to negative increase at positions 200, 400, and 500 m. It showed a different pattern in *P. euphratica* when compared with that in *A. venetum* and *T. ramosissima*. There were positive increases in the concentration of CTK and negative increases in that of ABA over all five positions. The concentration of ABA decreased, whereas that of CTK increased after the water release. Figure 7 showed the relationship between ABA concentration increment, free proline stimulation and soluble sugar stimulation in leaves of three species at different positions.

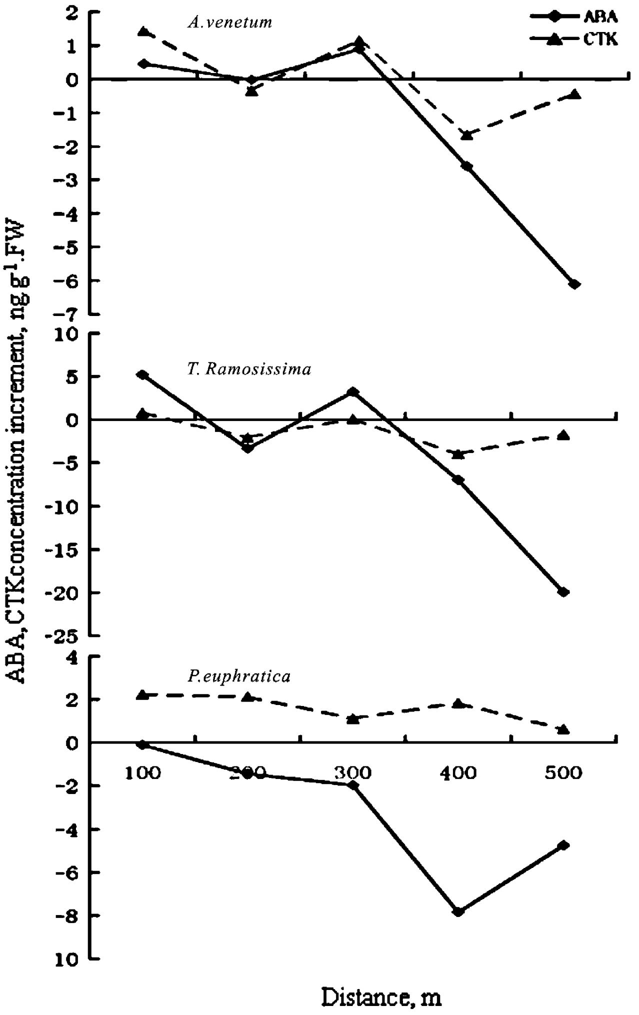

Fig. 5 Changes in concentration and increase of ABA and CTK in leaves of the three species at different positions (each *point* represents the average of ten measurements ± SD)

Discussion

Osmotic adjustment (OA) was considered an important component of drought-tolerance mechanisms in plants (Serraj and Sinclair 2002; Zhang et al. 1999), and operated only under severe water deficit when survival was threatened. It had also been suggest that OA decreased lethal water potential and postponed dehydration (Basnayake et al. 1993). It involved the active accumulation of organic and inorganic solutes in a cell, in response to a fall in the water potential of the cell's environment. Consequently, the osmotic potential of the cell was lowered, which in turn attracted water into the cell, thereby maintaining turgor pressure. Plants under different environmental stresses accumulated low-molecular weight organic solutes generically termed compatible solutes, which included free proline and soluble sugars. Synthesis of solutes could increase the osmotic potential of cells to stabilize the water status of tissues. Soluble sugars and proline contributed to osmoregulation of leaf samples in different plants (Elhaak et al. 1993). For survival in hyper water-deficient environments, the three desert species had evolved physiological processes to maintain tissue water status to some extent. For instance, *P. euphratica* had been exposed to water stress under groundwater table from −3.63 to −5.14 m (Chen et al. 2003). A moderate content of 50 m mol/L salinity, as recorded for this groundwater, could be detrimental to

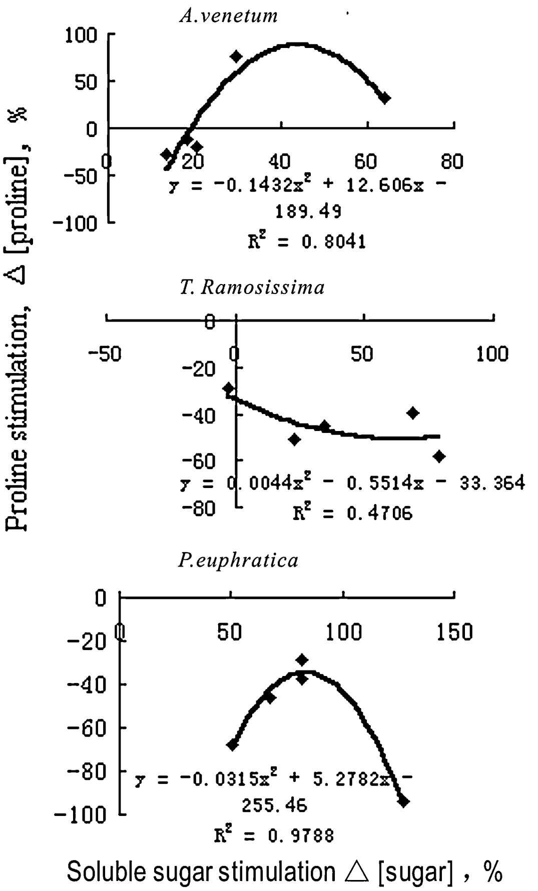

Fig. 6 Relationship between free proline stimulation and soluble sugar stimulation in leaves of the three species at different positions (each *point* represents the average of ten measurements ± SD)

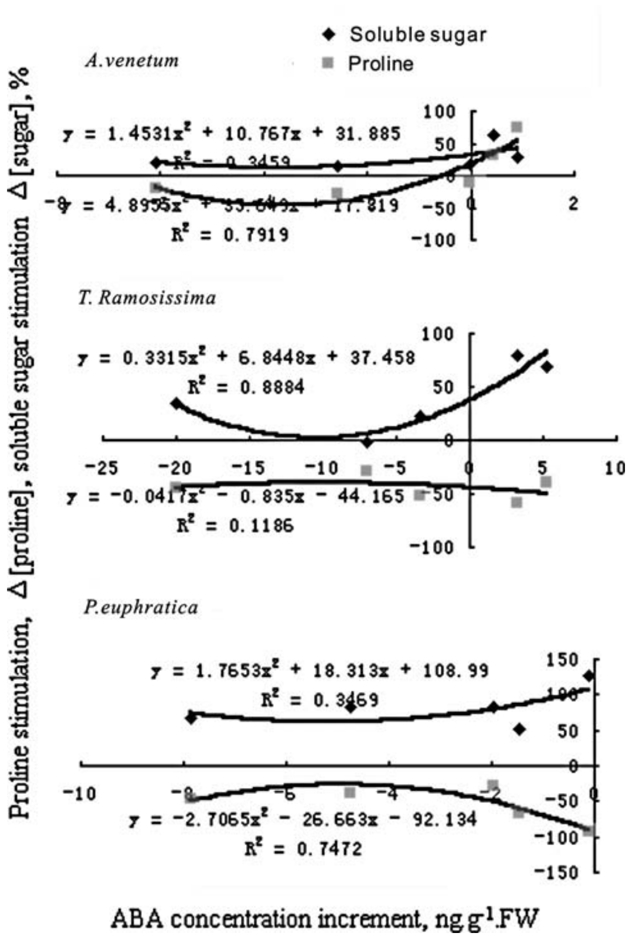

Fig. 7 Relationship between ABA concentration increase and free proline stimulation and soluble sugar stimulation in leaves of the three species at different positions (each *point* represents the average of ten measurements ± SD)

plants that were not adaptable to saline environments (Marschner 1995). However, an important operational question was that how best to select the measurements needed in hyper water-deficient environments to evaluate plant water status. The most widely used approach for evaluating plant water status had been to determine leaf water potential (ψ_L) using a pressure bomb (Hsiao 1990; Améglio et al. 1999). Recent technological developments allowed the use of alternative indices of the plant water status, such as those derived from continuous measurement sap flow. In this investigation, measuring the rate of sap flow of stem of three species in laboratory and in fields were proved as a simpler and more precise alternative method to express the plant water status in hyper-environment.

The findings suggest that the three desert species had present different water and salt resistance strategies: The reduction of osmotic potential due to soluble sugar accumulation in response to a high level of total saline content of groundwater was a well-established mechanism whereby the three species adjusted to low-water availability at positions 100, and 300 m. Over the whole study area, the proline concentration of the leaves of *T. ramosissima* and *P. euphratica* decreased with water stress relief due to the elevation of the groundwater table. In addition, both proline concentration in *A. venetum* in response to salt stress at positions 100, and 300 m and soluble sugar concentration in *P. euphratica* in response to water stress at positions 400, and 500 m increased to amplify salt and water- deficient resistance of these two species (Figs. 3, 4). When soluble sugar and proline concentration of the leaves were measured over the whole study area for the three species, the stimulation in the sugar level ranged from 13.58 to 63.71%, −2.49 to 78.75%, and from 50.52 to 127.04% for *A. venetum*, *T. ramosissima*, and *P. euphratica,* respectively. The stimulation in the proline level was also ranged from −12.40 to 75.21%, −39.44 to −58.12%, and from −28.91 to −94% for the three species. The soluble sugar stimulation was significantly related to the proline stimulation in *A.venetum* and *P. euphratica*, but not in *T. ramosissima* (Fig. 6). It seemed that *A. venetum* was less influenced by salinity concentration while it overcame the impact of salt stress on soluble sugars and proline accumulation.

However, its growth was restricted by the low availability of water because of the depth of groundwater table beyond the main root distributing depth (Tables 1, 3). In field observation, it was shown that *A. venetum* recovered better than *T. ramosissima* and *P. euphratica* within the range of 300 m to riverbank. The results also indicated that *P. euphratica* accumulated higher levels of soluble sugars than *A. venetum* and *T. ramosissima* under the same water and saline stress condition. *P. euphratica* appeared to be more sensitive to the elevation of groundwater table, because the increasing soluble sugar concentration or decreasing proline concentration was more rapid here than that for *A. venetum* and *T. ramosissima*, The recovery effect of the forest of *P. euphratica* appeared better than the other two species while the groundwater table rose after water release at positions 400 and 500 m (Figs. 3, 4). This was also in agreement with field observation in study area.

In contrast to *A. venetum* and *P. euphratica*, there was least correlation between the soluble sugar and proline stimulation in *T. ramosissima* (Fig. 6). It was strongly suggested that *T. ramosissima* developed a different strategy to accumulate organic solutes to adapt to stress environment. The soluble sugars and proline accumulation in leaves responded to changes of groundwater table independently: the soluble sugar accumulation occurred under salt stress (at position 300 m), whereas proline accumulation was more significant under drought stress (over position 400 and 500 m) (Figs. 3, 4). *T. ramosissima* tended to be a suitable candidate species for reclamation in this hyper-arid area, where water stress was usually accompanied by salt stress.

A common response to various stressors affecting the water status on plants was stomatal closure to minimize water loss. It was believed that the chemical information generated when only part of the root system of plants was exposed to drying soil was sufficient to influence stomatal behavior (Davies and Zhang 1991; Davies et al. 1994). Hormonal substance might be involved in transmitting information about the water status of soil and roots to the shoot (Masia et al. 1994). ABA and CTK were likely candidates for chemical messages moving from drying roots to leaves. Endogenous ABA concentrations were necessary to affect leaf stomatal conductance. CTK had been investigated in drought stress studies (Blackman and Davies 1985b; Incoll and Jewer 1987). It was believed that water stress might strongly influence the concentration of CTK in plants because CTK was predominantly synthesized in roots, although its role as a signal in root-to-shoot communication had not been clearly demonstrated. Masia et al. (1994) had suggested that a decrease in CTK transport from root-to-shoot occurred during the onset of drought stress. It had been reported that drought could result in the reduction of leaf CTK concentrations in drought-susceptible cultivars of tomato (Pillay and Beyl 1990) and in seedlings of rice (Bano et al. 1993). That was in agreement with the results obtained in this study on *P. euphratica*, in which there were positive increases of CTK concentration in leaves and negative increases of ABA concentration over the whole study area, thereby warranting the conclusion that CTK favored stomatal opening (Jewer and Incoll 1980; Incoll and Jewer 1987). An increase in leaves might amplify the effect of the ABA signal after water release. At the same time, proline accumulation declined with elevation of groundwater table and a significant correlation was found between ABA accumulation and Δ[proline] (Figs. 4, 7). Proline accumulation in response to change of the groundwater table was one way to maintain turgor, and the stomatal behavior of *P. euphratica* depended on the sensitivity to ABA. The interactions of CTK and ABA were similar in *A. venetum* and *T. ramosissima*, there were positive increases of the concentrations of ABA and CTK at positions 100 and 300 m in contrast to negative increases at positions 200, 400, and 500 m. Changes in CTK and ABA concentrations at positions 100 and 300 m would result in a new endogenous hormone balance that could be favorable to the plant's response to salt stress, because increasing CTK impaired the effect of the ABA signal, maintained the stomatal activity to some degree, and thus increased the plant's tolerance to salt stress (Fig. 5). In this case, the differential sensitivity of soluble sugars and proline responding to ABA could be seen from the relationships presented in Fig. 7. Both species showed the variable solute accumulation in response to the groundwater table when expressed as a function of ABA concentration increase in leaves, and a significant correlation was found between ABA accumulation and Δ[proline] in *A. venetum,* and between ABA accumulation and Δ[sugar] in *T. ramosissima*.

Conclusions

In the course of recovery and restoration of the ecological environment in this district by the water release program, we found that *A. venetum* population recovered to groundwater table ranging from −1.73 to −3.56 m, and when exposed to saline content of the groundwater ranging from 36.59 to 93.48 m mol/L; *P. euphratica* appeared to be more sensitive to the elevation of groundwater table than that of *A. venetum* and *T. ramosissima* at groundwater table ranging from −5.08 to −5.80 m, and when exposed to saline content of the groundwater ranging from 42.17 to 49.55 m mol/L. *T. ramosissima* tended to be the best candidate species for reclamation in this hyper-arid area because it responded to groundwater table ranging from

−1.73 to −7.05 m, and when exposed to saline content of the groundwater ranging from 36.59 to 93.48 m mol/L.

These results agreed with and could explain the distribution patterns of desert vegetation in the lower reaches of the Tarim River. Understanding the relationships among ecological factors variables, physiological response and acclimation strategies of plant individuals and distribution of plant communities could provide guidance to sustainable management, reclamation and development of this and similar regions. The results would also provide a theoretical base for the restoration of degenerated vegetation in this area. Understanding the indicator of environmental factors of a given site lead us to recommend adaptable species for reclamation and improvement of that site and similar sites.

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References

Améglio T, Archer P, Cohen M, Valancogne C, Daudet F, Daudet FA, Dayau S, Cruiziat P (1999) Significance and limits in the use of predawn leaf water potential for tree irrigation. Plant Soil 207:155–167

Aguilar ML, Espadas FL, Coello J, Maust BE, Trejo C, Robert ML, Santamaria JM (2000) The role of abscisic acid in controlling leaf water loss, survival and growth of micropropagated *Tagetes erecta* plants when transferred directly to the field. J Exp Bot 51:1861–1866

Bano A, Dprffling K, Bettin D, Hahn H (1993) Abscisic acid and cytokinins as possible root-to-shoot signals in xylem sap of rice plants in drying soil. Aust J Physiol 20:109–115

Basnayake J, Ludlow MM, Cooper M, Henzell RG (1993) Genotypic variation of osmotic adjustment and desiccation tolerance in contrasting sorghum inbred lines. Field Crops Res. 35:51–62

Blackman PG, Davies WJ (1985a) Root to shoot communication in maize plants of the effects of soil drying. J Exp Bot 36:39–48

Blackman PG, Davies WJ (1985b) Cytokinins, abscisic acid and the control of plant water balance. Acta Hortic 171:255–261

Chen YN, Chen YP, Li WH (2003) Response of proline accumulation to the change of groundwater table in lower reaches of Tarim River. Chin Sci Bull 48:958–961

Chen YN, Zhang XL, Cui WC (2004) Ecological problems and proposals in Tarim River Basin Xinjiang. J Chin Acad Sci 3:191–195 (in Chinese)

Cushman JC (2001) Osmoregulation in plants: implications for agriculture. Am Zool 41:758–769

Davies WJ, Zhang J (1991) Root signals and the regulation of growth and development of plants in drying soil. Annu Rev Plant Physiol Plant Mol Biol 42:55–76

Davies WJ, Tardieu F, Trejo CL (1994) How do chemical signals work in plants that grow in drying soil. Plant Physiol 104:309–314

Elhaak MA, El-Din AS, Sammour RH (1993) Response of *Phragmites australis* to water stress from flooding to drought. Pak J Bot 25:41–46

Fußeder A, Wartinger A, Hartung W, Schulze ED, Heilmeier H (1992) Cytokinins in the xylem sap of desert grown almond (*Prunus dulcis*) trees: daily courses and their possible interactions with abscisic acid and leaf conductance. New Phytol 122:45–52

Granier A (1985) Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. Ann Sci For 42:193–200

Guerrier G, Patolia JS (1989) Comparative salt responses of excised cotyledons and seedlings of pea to various osmotic and ionic stresses. J Plant Physiol 135:330–337

Hsiao TC (1990) Measurements of plants water status. In: Stewart BA, Nielsen DR (eds) Irrigation of agricultural crops, agronomy monograph 30, ASA, CSSA, SSSA. Madison, WI, pp 243–279

Hubick KT, Taylor JS, Reid DM (1986) The effect of drought on levels of abscisic acid, cytokinins, gibberellins and ethylene in aeroponically grown sunflower plants. Plant Growth Regul 4:139–151

Itai C, Vaadia Y (1965) Kinetin like activity in root exudate of water stressed sunflower plants. Physiol Planta 18:941–944

Incoll L, Jewer PC (1987) Cytokinins and the water relations of whole plants. In: Horgan R, Jeffcoat B (eds) Cytokinins: plant hormones in search of a role, monograph 14. British Plant Growth Regulator Group, Bristol, pp 85–97

Jarvis AJ, Davies WJ (1997) Whole plant ABA flux and the regulation of water loss in *Cedrella odorata*. Plant Cell Environ. 20:521–527

Jewer PC, Incoll LD (1980) Promotion of stomatal opening in the grass *Anthephora pubescens* Nees. by a range of natural and synthetic cytokinins. Planta 150:218–281

Liu JZ, Chen YN, Li WH, Chen YP (2004) Analysis on the distribution and degraded succession of plant communities at lower reaches of Tarim River. Acta Ecol Sin 24(2):379–383 (in Chinese)

Marschner H (1995) Mineral nutrition of higher plants. Academic Press, London, 889 pp

Masia A, Pitacc O, Braggio L, Giulivo C (1994) Hormonal responses to partial drying of the root system of *Helianthus annuus*. J Exp Bot 45:69–76

Mattioni C, Lacerenza NG, Troccoli A, De Leonardis AM, Di Fonzo N (1997) Water and salt stress-induced alterations in proline metabolism of *Triticum durum* seedlings. Physiol Plant 101:787–792

Pan YL (2001) Multivariate analysis and environmental interpretation of desert bank forest plant communities in Tarim basin, Xinjiang. Acta Botanica Boreali-Occidentalia Sinica 21:247–251

Patakas A, Noitsakis B (1999) An indirect method of estimating leaf area index in cordon trained spur pruned grapevines. Sci Hortic 80:299–305

Pillay I, Beyl C (1990) Early responses of drought-resistant and -susceptible tomato plants subjected to water stress. Plant Growth Regul 9:213–220

Ragab R, Prudhomme C (2002) Climate change and water resources management in arid and semi-arid regions: prospective and challenges for the 21st century. Bio Syst Eng 81(1):3–34

Rekika D, Nachit MM, Araus JL, Monneveux P (1998) Effects of water deficit on photosynthetic rate and osmotic adjustment in tetraploid wheats. Photosynthetica 35:129–138

Sanchez FJ, de Andres EF, Tenorio JL, Ayerbe L (2004) Growth of epicotyls, turgor maintenance and osmotic adjustment in pea plants (*Pisum sativum* L.) subjected to water stress. Field Crops Res 86:81–90

Serraj R, Sinclair TR (2002) Osmolyte accumulation: can it really help increase crop yield under drought conditions? Plant Cell Environ 25:333–341

Tardieu F, Davies WJ (1992) Stomatal response to abscisic acid is a function of current plant water status. Plant Physiol 98:540–545

Thomas FM, Arndt SK, Bruelheide H, Foetzki A, Gries D, Huang J, Popp M, Wang G, Zhang X, Runge M (2000) Ecological basis for a sustainable management of the indigenous vegetation in a central-Asian desert: presentation and first results. J Appl Bot 74:212–219

Tongway DJ, Ludwig JA (1994) Small-scale patch heterogeneity in semi-arid landscapes. Pac Conserv Biol 1:201–208

Troll W, Lindsley J (1995) A photometric method for the determination of proline. J Biol Chem 215:655–660

Vonk CR, Davelaar E, Ribot SA (1986) The role of cytokinins in relation to flower-bud blasting in Iris cv. Ideal: cytokinin determination by an improved enzyme-linked immunosorbent assay. Plant Growth Regul 4:65–74

Wang Q, Ruan X, Chen YN, Li WH (2007) Eco-physiological response of *Populus euphratica* Olivto. water release of the Lower Reaches of the Tarim River China. Environ Geol 53:349–357

Yang JP (2002) Study on the ecological construction problem in Tarim River valley. Forest Economy 2:1–10 (in Chinese)

Zhang J, Nguyen HT, Blum A (1999) Genetic analysis of osmotic adjustment in crop plants. J Exp Bot 50:291–302

Zhang YM, Chen YN, Pan BR (2005) Distribution and floristics of desert plant communities in the lower reaches of Tarim River, southern xinjiang, People's Republic of China. J Arid Environ 63:772–784