RESEARCH ARTICLE

Physiological response of riparian plants to watering in hyper-arid areas of Tarim River, China

RUAN Xiao[1], WANG Qiang (✉)[1], CHEN Yaning[2], LI Weihong[2]

1 Ningbo Institute of Technology, Zhejiang University, Ningbo 315100, China
2 Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi 830011, China

Abstract The physiological responses and adaptive strategies of *Populus euphratica* Oliv. (arbor species), *Tamarix ramosissima* Ldb. (bush species), and *Apocynum venetum* L. (herb species) to variations in water and salinity stress were studied in the hyper-arid environment of the Tarim River in China. 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 of the three species were monitored and analyzed at the lower reaches of the Tarim River in the study area where five transects were fixed at 100 m intervals along a vertical sampling line before and after water release. Saline stress dramatically increased soluble sugar concentration of the three species. Differences in sugar accumulation were determined among the species at different transects. The free proline concentration of the leaves of *T. ramosissima* and *P. euphratica* showed a proportional decrease with various degrees of elevation of the groundwater table after water release. There was a least correlation between the soluble sugars and proline stimulation in *T. ramosissima*. It was strongly suggested that *T. ramosissima* developed a different strategy to accumulate organic solutes to adapt to the stress environment. The soluble sugars and proline accumulation responded to the changes of groundwater table independently: the former occurred under salt stress, whereas the latter was more significant under drought stress. The concentration and the increase in concentration of ABA and CTK involved in stress resistance of the three species were also determined. This increase in the hormone concentration in *P. euphratica* was different from that of the other two species. Expressed as a function of increase of ABA concentration in leaves, *A. venetum* and *T. ramosissima* showed a different solute accumulation in response to groundwater table. There was a significant correlation between ABA accumulation and Δ [proline] in *A. venetum* as well as between ABA accumulation and Δ [sugar] in *T. ramosissima*.

Keywords soluble sugars, free proline, endogenous abscisic acid, cytokinins, groundwater table, water and saline stress

1 Introduction

The Tarim River is the longest continental river in China, with a length of 1 321 km. It flows south of Urumqi, the capital of the Xinjiang autonomous region in China. This area displays a climate typical of hyper-arid environments. Water resources of the river system sustain the growth of desert plants and the associated ecological system. 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 300 km of the riverbed in the lower reaches of the Tarim River occurred in the late 1970s, resulting in the withering of forest areas and degradation of the ecological environment along both riverbanks. The central and local governments of China recognized this problem and invested RMB ¥10.7 billion to restore and reconstruct the ecological environment of this district. One of the most important measures 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 ensures the transfer of $3.50 \times 10^8 \, m^3$ of water from the Bositen Lake to the lower reaches of the Taitema Lake every year (Chen et al., 2003). Desert plants in both riverbanks of the Tarim River have evolved various physiological processes in response to the changes of groundwater table, which rises when water is released. A better understanding of the strategies of desert plant adaptation to changes may help to improve water release management.

Osmotic adjustment (OA) is one of the drought-avoidance mechanisms involved in counteracting 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 (Munns and Weir, 1981; Kameli and Lösel, 1995; Johnson et al., 1984; Rekika et al., 1998) and proline (Tan and Halloran, 1982; Ali et al., 1994; Mattioni et al., 1997) level increase under water stress and are potentially important contributors to OA. Drought adversely affects many physiological and biochemical processes in plants, including mechanisms that regulate stomatal responses. In some plants, the suppression in leaf stomatal conductance during drought has been reported to be independent of the changes in water flux, and accumulating abscisic acid (ABA) may be responsible for these responses (Correia and Pereira, 1995; Dodd et al., 1996; Aguilar et al., 2000). Many authors, however, have reported negative exponential relationships between leaf stomatal conductance and ABA content. Tardieu and Davies (1992) and Jarvis and Davies (1997) have noted that this relationship can be largely dominated by decreasing water flux as stomata close. In addition to ABA, since the work of Blackman and Davies (1985) suggesting that a continuous supply of cytokinins (CTK) from roots was necessary to sustain maximal stomatal opening in plants growing in drying soil, a view substantiated by Hubick et al. (1986) in sunflower showed a significant reduction in total CTK activity in the xylem sap. Worldwide, research has been concerned with OA mechanisms, which is an important physiological adaptation for minimizing the detrimental effects of water deficits in the cultivation of plants. However, a few studies have been made on the physiological response to salt and water stress, which occurred in native riparian plants surviving in hyper-arid environments. Chen (2003) investigated free proline accumulation in *P. euphratica* in response to variable groundwater table in the lower reaches of the Tarim River. Francisco (2001) and Matthew (2001) reported on the effects of pulse floods on regeneration of native trees and tolerance of vegetation in the delta region of the Colorado River, respectively.

The aim of the present work was to study the physiological responses and adaptation strategies of the three typical desert species, *P. euphratica* (arbor species), *T. ramosissima* (bush species), and *A. venetum* (herb species), in two periods: during very limited water availability and during 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 area was at Yhepumahan of the lower reaches of the Tarim River. Five transects were fixed at 100-m intervals along a vertical sampling line. The groundwater table, saline content of groundwater, as well as the content of proline, soluble sugars, and plant endogenous hormones (ABA, and CTK) of leaves, were monitored and analyzed before and after water release. The purpose was to find the optimum niche of ecology when vegetation is exposed to severe salt stress and drought stress, and the results of an ecosystem biodiversity's rapid recovery, following reasonable water release.

2 Materials and methods

2.1 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, China (40°36′N, 87°12′E) between the Taklamakan Desert and Kuluke Desert. The total annual solar radiation varies from 5 692 to 6 360 MJ/m^2, with 2 780 to 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°C 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 precipitation by 50–60 times. The climatic conditions make the north of the Tarim Basin a typical hyper-arid region.

2.2 Plant source

The first sampling (before water release) was conducted from July 1–20 2000, and after that, sampling (after water release) was conducted from July 1–20 2002. 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 the three kinds of plants close to each other and made marks on them, respectively. In each of the species, a representative sample of 15 plants was chosen. South-facing plants leaves (receiving maximum light during the day) were used for measurements.

2.3 Measurements of groundwater table

Five transects were selected at 100 m intervals along a vertical sampling line with an average distance of 500 m from the riverbank to sand dune in the study area. Within each transect, three wells were established for investigation. The groundwater table in these wells was monitored. The collected water and plant samples were analyzed in our laboratory.

2.4 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$^+$ analysis was carried out using an inductively coupled argon plasma emission spectrophotometer (Jobin-Yvon JY 48). Cl$^-$ was colorimetrically determined with ferric ammonium sulphate and mercuric thiocyanate following the procedure of Guerrier and Patolia (1989). The total sulfate in the water was analyzed using ion-chromatography.

2.5 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 of 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: $\Delta[\text{proline}] = [\text{proline}]_{\text{after water release}} - [\text{proline}]_{\text{before water release}} / [\text{proline}]_{\text{before water release}}$

2.6　Analysis on soluble sugars

Freeze-dried leaves (50 mg) were ground and extracted in 1 mL 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 vacuum-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 or fructose) and sucrose were analyzed at 35°C using a high performance liquid chromatography (HPLC) equipped with a 300 mm × 7.8 mm column (carbohydrate-H⁺, HYDERSIL, UK). H_2SO_4 (0.005M) was used as the solvent at a flow rate of 0.6 mL/min.

The soluble sugar stimulation: $\Delta[\text{sugar}] = [\text{sugar}]_{\text{after water release}} - [\text{sugar}]_{\text{before water release}} / [\text{sugar}]_{\text{before water release}}$

2.7　Extraction and quantification of plant hormones using HPLC

Leaves (0.5 g) were ground with liquid nitrogen. Plant hormones were 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 and CTK content was determined using HPLC analysis. An LC-10A TVP (Author: please spell out TVP) photodiode and ray detector, and a Shim pack CLC-C₈ (0.15 m × 6.0 φ) were used. The flow rate was 1.5 mL/min. Detection was at 250 nm at 30°C. The solvent for 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) and cytokinins (CTK) standard were purchased from Aldrich. The peak was identified and quantified against the external standard.

2.8　Statistical analysis

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

3　Results

3.1　Groundwater table and salinity of groundwater

The changes of groundwater table and salinity of groundwater before and after water release to the Yhepumahan area 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 transect 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 mmol/L (66.34% increase from before water release). Similarly, at the transect of 300 m, the groundwater table increased from −7.66 to −5.56 m, and the total saline content of groundwater increased from 71.02 to 93.48 mmol/L (31.62% increase from before water release). In contrast to both these transects, the

Table 1　Groundwater table and salinity of groundwater at different transects from the riverbank

Distance/m	Groundwater table/m*	HCO_3^-	Cl^-	SO_4^{2-}	Ca^{2+}	Mg^{2+}	Na^+	K^+	Total**
					$/\text{mmol} \cdot \text{L}^{-1}$				
100	5.82 a	7.08	11.32	3.57	1.85	3.08	16.33	0.38	43.61
	1.73 b	3.65	22.14	10.00	2.83	6.42	26.65	0.85	72.54
200	7.25 a	2.56	10.87	5.52	1.60	3.50	14.13	0.38	38.56
	3.39 b	1.19	10.99	5.10	0.83	2.75	15.22	0.51	36.59
300	7.66 a	7.13	20.45	8.13	2.08	7.04	25.57	0.62	71.02
	3.56 b	7.02	29.52	11.56	3.99	10.79	29.91	0.69	93.48
400	6.64 a	7.04	10.37	3.54	1.65	2.92	15.22	0.41	41.15
	6.08 b	6.52	9.72	4.90	1.15	4.25	15.22	0.41	42.17
500	7.05 a	3.58	10.64	10.10	2.93	7.29	14.00	0.79	49.33
	6.80 b	3.65	10.64	10.01	2.83	6.42	15.15	0.85	49.55

a, b indicate before and after water release; *: The values of groundwater table are means of three replications;

**: The concentration of total salt was calculated on the basis of these seven ions. The values of salinity groundwater in each transect were means of three replications

Table 2 Data of the growth state of the three desert species in response to the groundwater table change (Data are collected by our group)

| Species	Distributing depth of main-root/m	Groundwater table of promoting growth/m	Groundwater table of inhibiting growth/m	Lethal groundwater table of 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

groundwater table at the transect 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 mmol/L (−5.11% increase from before water release). *P. euphratica*, *T. ramosissima* and *A. venetum*, which were exposed to the water stress, decreased progressively from 300 to 100 m after water release. At the same time, the plants that were exposed to the saline stress increased: the largest at 300 m, and the lowest at 200 m.

At the transects of 400 and 500 m, the groundwater table increased slightly from −6.64 to −6.08 m, and −7.05 to −6.80 m, respectively. Total saline content of the groundwater also increased from 41.15 to 42.17 mmol/L, and 71.83 to 72.55 mmol/L, respectively (2.48% and 1.00% increasing of before water release). Changes of groundwater table and increase of total saline content of the groundwater were not significant at this point after water release. Table 2 shows us the growth state of the three species to the groundwater table.

3.2 Soluble sugars and proline accumulation in the 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 1 shows the soluble sugar concentration as a function in response to groundwater table and salinity of groundwater among the three kinds of species. Within the 300 m extent, the groundwater table rose rapidly as water is released to the lower reaches of the Tarim River. However, total saline content of the groundwater increased, especially at the transects of 100 and 300 m, and the total saline contents of the groundwater increase were about 66.34% and 31.62% of before water release value, respectively. Saline stress dramatically increased soluble sugar concentration of the three species and was found to be more elevated in the leaves at transects 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. This variability in *A. venetum* and *T. ramosissima* was greatest at the transects of 100 and 300 m, respectively. At these two transects, 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* increased more in the 300–500 m extent than that
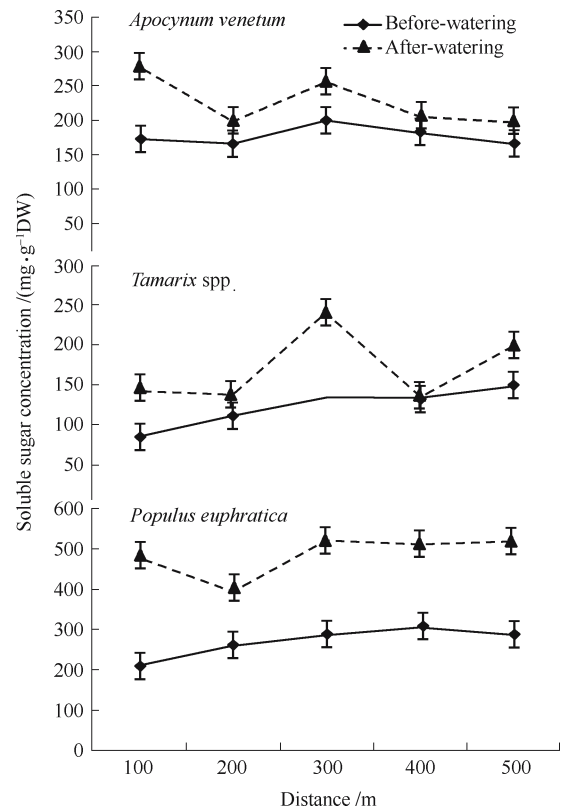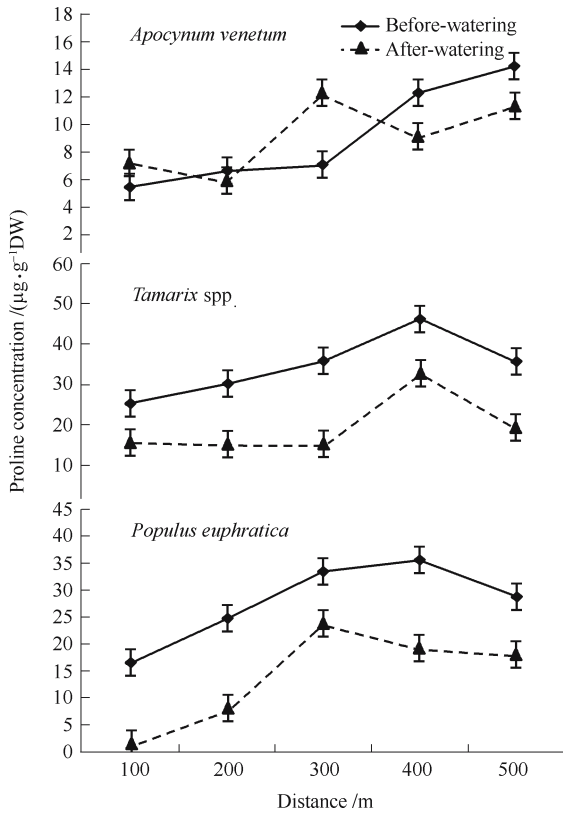

Each point represented the average of 10 measurements ± S.D.
Fig. 1 Changes of soluble sugar concentration in leaves of the three species at different transects of the study area with watering

in the 100–200 m extent whenever water was released to the lower reaches of the Tarim River, and it also underwent a proportional decrease with various degrees of elevation of the groundwater table. At the transects of 200, 400 and 500 m, the free proline concentration in *A. venetum* decreased due to elevation of groundwater table after water release, whereas it increased remarkably at the transects of 100 and 300 m due to the high total saline content of the groundwater (Fig. 2). Figure 3 shows us the relationship between free proline stimulation and soluble sugar stimulation in leaves of the three species at different transects.

3.3 Changes of ABA and CTK in the three species

Changes of the concentration increase of ABA and CTK in the leaves of the three species after water release are shown in Fig. 4. The changes in *A.venetum* over different transects were similar to those in *T. ramosissima*, and there were
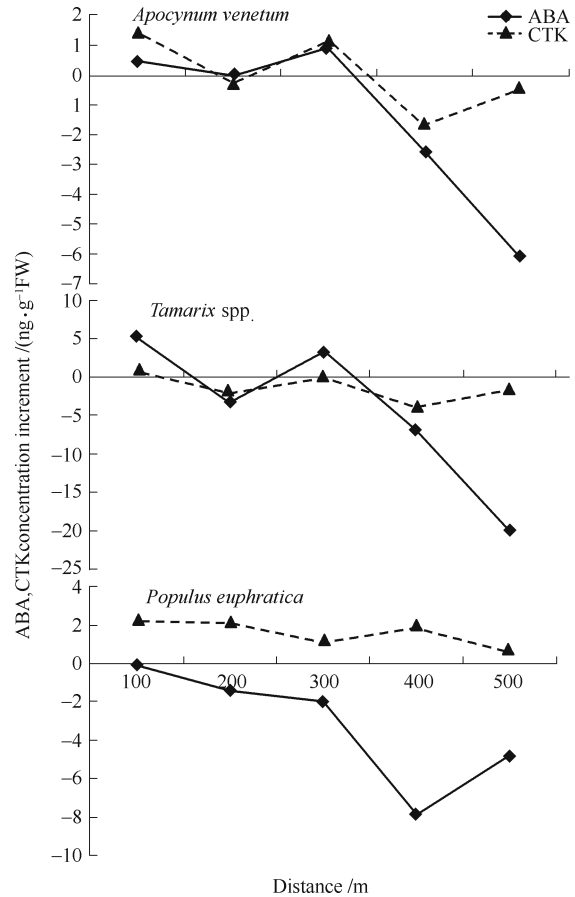
58

Each point represented the average of 10 measurements ± S.D.
Fig. 2 Changes of free proline concentration in leaves of the three species

Each point represented the average of 10 measurements ± S.D.
Fig. 3 Changes of concentration increase of ABA and CTK in leaves of the three species at different transacts

positive increasing in concentrations of ABA and CTK in both species at transects 100 and 300 m in contrast to negative increase at transects 200, 400, and 500 m. These changes showed a different pattern in *P. euphratica* 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 transects. The concentration of ABA decreased, whereas that of CTK increased after the water release program. Figure 5 shows us the relationship between ABA concentration increment and free proline stimulation and soluble sugar stimulation in leaves of three species at different transects.
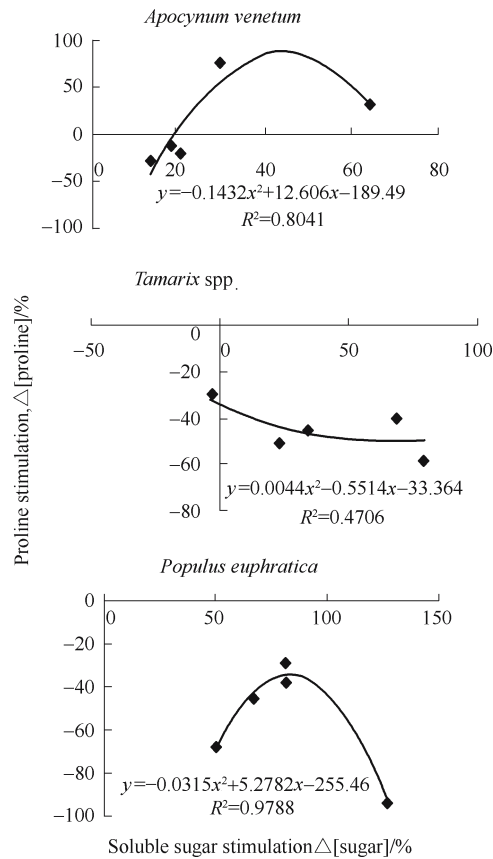
4 Discussion

The data of the growth state of the three desert species in response to the groundwater table are shown in Table 2. Before the water release program, the population of *A. venetum* in the area where the groundwater table was beyond the distributing depth of the main-root and close to the lethal depth of growth was destroyed greatly. *P. euphratica*, having the largest natural vegetation population in these areas, also degraded severely due to low availability of water, because the groundwater table had decreased to the degree of inhibiting the plant's growth. After water release, the groundwater

table rose quickly. Recovery of the population of the three species (especially *A. venetum*) in response to the changes of groundwater table was rapid within the extent of 300 m because the groundwater table at this range was elevated to the appropriate degree, and because the vegetation growth was improved.
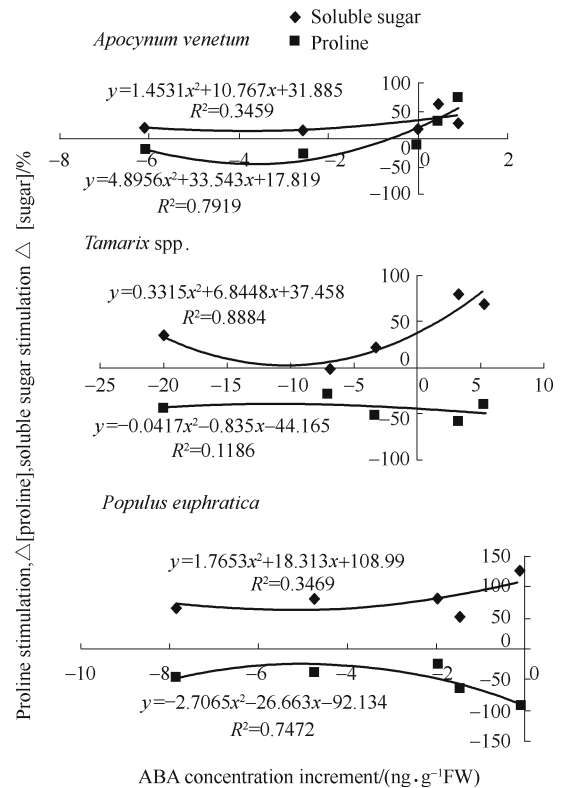
Osmotic adjustment (OA) is considered an important component of drought-tolerance mechanisms in plants (Serraj and Sinclair, 2002; Zhang et al., 1999), and operates only under severe water deficit when survival is threatened. It has also been suggested that OA decreases lethal water potential and postpones dehydration (Basnayake et al., 1993). It involves 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 is lowered, which in turn attracts water into the cell, thereby maintaining turgor pressure. Plants under different environmental stresses accumulate low-molecular weight organic solutes generically termed compatible solutes, which include free proline and soluble sugars. Synthesis of solutes can increase the osmotic potential of cells to stabilize the water status of tissues. Soluble sugars and proline contribute to osmoregulation of leaf samples in different plants (Elhaak et al., 1993). For survival in hyper water-deficient environments, the three desert species have evolved physiological

Apocynum venetum

$y=-0.1432x^2+12.606x-189.49$
$R^2=0.8041$

Tamarix spp.

$y=0.0044x^2-0.5514x-33.364$
$R^2=0.4706$

Populus euphratica

$y=-0.0315x^2+5.2782x-255.46$
$R^2=0.9788$

Soluble sugar stimulation△[sugar]/%

Each point represents the average of 10 measurements ± S.D.
Fig. 4 Relationship between free proline stimulation and soluble sugar stimulation in leaves of the three species at different transects

◆ Soluble sugar
■ Proline

Apocynum venetum

$y=1.4531x^2+10.767x+31.885$
$R^2=0.3459$

$y=4.8956x^2+33.543x+17.819$
$R^2=0.7919$

Tamarix spp.

$y=0.3315x^2+6.8448x+37.458$
$R^2=0.8884$

$y=-0.0417x^2-0.835x-44.165$
$R^2=0.1186$

Populus euphratica

$y=1.7653x^2+18.313x+108.99$
$R^2=0.3469$

$y=-2.7065x^2-26.663x-92.134$
$R^2=0.7472$

ABA concentration increment/(ng·g⁻¹FW)

Each point represents the average of 10 measurements ± S.D.
Fig. 5 Relationship between ABA concentration increase and free proline stimulation, soluble sugar stimulation in leaves of the three species at different transects

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 mmol·L⁻¹ salinity, as recorded for this groundwater, can be detrimental to plants that are not adaptable to saline environments (Marshner, 1995). Our findings suggest that the three desert species could 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 is a well-established mechanism whereby the three desert species adjust to low water availability at transects 100, and 300 m. Over the whole study area, the proline concentration of the leaves of *T. ramosissima* and *P. euphratica* proportionally decreased with stress relief due to the progressive elevation of the groundwater table. In addition, both proline concentration in *A. venetum* in response to salt stress at transects 100, and 300 m and soluble sugar concentration in *P. euphratica* in response to water stress at transects 400, and 500 m increased to amplify salt and water-deficient resistance of these two species (Figs. 2, 3). When soluble sugar concentration and proline concentration of the leaves were measured over the whole study area for the three species, a rise in the sugar level was seen from 13.58% to 63.71%, −2.49% to 78.75%, and 50.52% to 127.04%, for

A. venetum, *T. ramosissima*, and *P. euphratica*, respectively. An increase in the proline level was also observed from −12.40% to 75.21%, −39.44% to −58.12%, and −28.91% to −94% for the three species. The soluble sugar stimulation was significantly correlated with the proline stimulation in *A. venetum* and *P. euphratica*, but not in *T. ramosissima* (Fig. 4). 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, 2). In our study, it is shown that *A. venetum* recovers better than *T. ramosissima* and *P. euphratica* within the range of 300 m to riverbank. The results also indicate that *P. euphratica* accumulate higher levels of proline and soluble sugars than *A. venetum* and *T. ramosissima* under the same water and saline stress condition. *P. euphratica* appears to be more sensitive to the elevation of groundwater table, because the increasing soluble sugar concentration or decreasing proline concentration is more rapid here than that for *A. venetum* and *T. ramosissima*, the former recovering better than the latter after water was released to the transects 400 and 500 m (Figs. 2, 3). In contrast to *A. venetum* and *P. euphratica*, there is least correlation between the soluble sugar and proline stimulation in *T. ramosissima* (Fig. 4). It is strongly suggested that *T. ramosissima* develops a different strategy to accumulate

organic solutes to adapt to stress environment: the soluble sugar accumulation occurs under salt stress (at transect 300 m), whereas proline accumulation is more significant under drought stress (over transect 400 and 500 m) (Figs. 2, 3). *T. ramosissima* tends to be a suitable candidate species for reclamation in this hyper-arid area, where water stress is usually accompanied by salt stress.

A common response to various stressors affecting the water status on plants is stomatal closure to minimize water loss. It is believed that the chemical information generated when only part of the root system of plants is exposed to drying soil is sufficient to influence stomatal behavior (Davies and Zhang, 1991; Davies et al., 1994). Hormonal substance may be involved in transmitting information about the water status of soil and roots to the shoot (Masia et al., 1994). ABA and CTK are likely candidates for chemical messages moving from drying roots to leaves. Endogenous ABA concentrations are necessary to affect leaf stomatal conductance. CTK has been investigated in drought stress studies (Blackman and Davies, 1985b; Incoll and Jewer, 1987). It is believed that water stress may strongly influence the concentration of CTK in plants because CTK is predominantly synthesized in roots, although its role as a signal in root-to-shoot communication has not been clearly demonstrated. Masia et al. (1994) have suggested that a decrease in CTK transport from root-to-shoot occurs during the onset of drought stress. It has 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). This is in agreement with the results obtained in our study on *P. euphratica*, in which there are positive increases of CTK concentration in leaves and negative increases of ABA concentration over the whole study area, thereby warranting the conclusion that CTK favors stomatal opening (Jewer and Incoll, 1980; Incoll et al., 1987). An increase in leaves may amplify the effect of the ABA signal after water is released to the study area. At the same time, proline accumulation declines with elevation of groundwater table and a significant correlation is found between ABA accumulation and Δ [proline]. Proline accumulation in response to change of the groundwater table is one way to maintain turgor, and the stomatal behavior of *P. euphratica* depends on the sensitivity to ABA. The interactions of CTK and ABA are similar in *A. venetum* and *T. ramosissima*, there were positive increases of the concentrations of ABA and CTK at transects 100 and 300 m in contrast to negative increases at transects 200, 400, and 500 m. Changes in CTK and ABA concentrations at transects 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 impairs the effect of the ABA signal, maintains the stomatal activity to some degree, and thus increases the plant's tolerance to salt stress (Fig. 3). In this case, the differential sensitivity of soluble sugars and proline responding to ABA can be seen from the relationships presented in Fig. 6. Both species show 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 is found between ABA accumulation and Δ [proline] in *A. venetum,* and between ABA accumulation and Δ [sugar] in *T. ramosissima*.

5 Conclusions

In the course of recovery and restoration of the ecological environment in this district by the water release program, we find that *A. venetum* population recovers to groundwater table ranging from −1.73 to −5.56 m, and when exposed to saline content of the groundwater ranging from 36.39 to 93.48 mmol·L^{-1}. *P. euphratica* appears to be more sensitive to the elevation of groundwater table than that of *A. venetum* and *T. ramosissima* at groundwater table ranging from −6.08 to −6.80 m, and when exposed to saline content of the groundwater ranging from 42.17 to 72.55 mmol·L^{-1}. *T. ramosissima* tends to be the best candidate species for reclamation in this hyper-arid area because it responds to groundwater table ranging from −1.73 to −7.05 m, and when exposed to saline content of the groundwater ranging from 36.39 to 93.48 mmol·L^{-1}.

References

Aguilar M L, Espadas F L, Coello J, Maust B E, Trejo C, Robert M L, Santamaria J M (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

Ali Dib T, Monneveux P, Acevedo E, Nachit M M (1994). Evaluation of proline analysis and chlorophyII fluorescence quenching measurements as drought tolerance indicators in durum wheat (*Triticum turgidum* L. var. durum). Euphytica, 79: 65–73

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

Blackman P G, Davies W J (1985a). Root to shoot communication in maize plants of the effects of soil drying. Journal of Experimental Botany, 36: 39–48

Blackman P G, Davies W J (1985b). Cytokinins, abscisic acid and the control of plant water balance. Acta Hort, 171: 255–261

Chen Y N, Chen Y P, Li W H (2003). Response of proline accumulation to the change of groundwater table in lower reaches of Tarim River. Chinese Science Bulletin, 48: 958–961 (in Chinese)

Correia M J, Pereira J S (1995). The control of leaf conductance of white lupin by xylem ABA concentration decreases with the severity of water deficits. J Exp Bot, 46: 101–110

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

Davies W J, Tardieu F, Trejo C L (1994). How do chemical signals work in plants that grow in drying soil. Plant Physiology, 104: 309–314

Davies W J, Zhang J (1991). Root signals and the regulation of growth and development of plants in drying soil. Annual Review of Plant Physiology and Plant Molecular Biology, 42: 55–76

Dodd I C, Stikic R, Davies W J (1996). Chemical regulation of gas exchange and growth of plants in drying soil in the field. J Exp Bot, 47: 1475–1490

Elhaak M A, El-Din A S (1993). Sammour R H, Response of *Phragmites australis* to water stress from flooding to drought. Pak J Bot, 25: 41–46

Francisco Z A, Pawela L N, Mark B (2001). Regeneration of native trees in response to flood releases from the United States into the delta of the Colorado River, Mexico. J Arid Environment, 49: 49–64

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

Hubick K T, Taylor J S, Reid D M (1986). The effect of drought on levels of abscisic acid, cytokinins, gibberellins and ethylene in aeroponically grown sunflower plants. Plant Growth Regulation, 4: 139–151

Incoll L, Jewer P C (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. Bristol: British Plant Growth Regulator Group, 85–97

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

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

Johnson R C, Nguyen H T, Croy L I (1984). Osmotic adjustment and solute accumulation in two wheat genotypes differing in drought resistance. Crop Sci, 24: 957–962

Kameli A, Lösel D M (1995). Contribution of carbohydrates and other solutes to osmotic adjustment in wheat leaves under water stress. J Plant Physiol, 145: 363–366

Marschner H (1995). Mineral Nutrition of Higher Plants. London: Academic Press, 889

Masia A, Pitacco B L, Giulivo C (1994). Hormonal responses to partial drying of the root system of *Helianthus annuus.* Journal of Experimental Botany, 45: 69–76

Matthew W V, Edward P G, James L W (2001). Tolerance of five riparian plants from the lower Colorado River to salinity drought and inundation. J Arid Environment, 49: 147–159

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

Munns R, Weir R (1981). Contribution of sugars to osmotic adjustment in elongating and expanded zones of wheat during moderate water deficits at two light levels. Aust J Plant Physiol, 8: 93–105

Pillay I, Beyl C (1990). Early responses of drought-resistant and— susceptible tomato plants subjected to water stress. Plant Growth Regulation, 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-systems Engineering, 81(1): 3–34

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

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

Tan B H, Halloran G M (1982). Variation and correlations of proline accumulation in spring wheat cultivars. Crop Sci, 22: 459–463

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

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

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