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BRIEF COMMUNICATION

Responses of dominant desert species *Artemisia ordosica* and *Salix psammophila* to water stress

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Abstract

Morphology, biomass accumulation and allocation, gas exchange, and chlorophyll fluorescence were compared for one-year-old seedlings of *Salix psammophila* and *Artemisia ordosica*, two dominant desert species, in response to two water supplies (equivalent to 315.0 mm for present precipitation in growing season and to 157.5 mm for future decreasing precipitation) during 105 d. For both species, photochemical efficiency of photosystem 2 (F_v/F_m), net photosynthetic rate, transpiration rate, stomatal conductance, biomass accumulation in different organs, tree height, number of leaves, and leaf area were reduced in response to the decrease in water supply. For both species, instantaneous water use efficiency was not affected by the water deficit. However, diurnal patterns of gas exchange and biomass allocation were affected in different ways for the two species, with notably a decrease in specific leaf area and an increase in root : shoot ratio for *S. psammophila* only. Overall, *S. psammophila* was more responsive to the decreasing precipitation than *A. ordosica*.

Additional key words: biomass allocation; chlorophyll fluorescence; gas exchange; morphology; specific leaf area; stomatal conductance; water supply; water use efficiency; transpiration rate.

Precipitation in arid regions will be obviously decreased by global climate change as a result of the impacts of human population growth (Fu and An 2002). Hence it is necessary to find out how arid dominant communities might respond and be adapted to future decrease in precipitation. Long term effects of drought result essentially in changes in carbon allocation between plant organs: roots sometimes are furthered at the expense of leaves and shoots. Consequences of this phenomenon are an overall leaf area reduction, linked to decreases in both number and individual size of the leaves, and increases in root : shoot and root : leaves ratios (Chen *et al.* 1997, Tschaplinski *et al.* 1998). These changes have the double advantage to improve water uptake in a dry ground and to reduce transpiring foliar area (Tschaplinski *et al.* 1994). Leaf structure is also modified by water deficit. A decrease of the specific leaf area (SLA, indicator of density and/or thickness of the leaves) has often been observed with a subsequent increase of water retention due to an accentuation of the resistance to water transfer in the leaf (Niinemets 2001, Nautiyal *et al.* 2002). The degree of adaptation to water stress is extremely variable within genera and species (Torrecillas *et al.* 1996).

Maowusu sandland, a semi-arid area, is located in the middle of the northern Chinese desert (37°30'–39°20'N, 107°20'–113°30'E). *Salix psammophila* C. Wang *et* Ch. Y. Yang and *Artemisia ordosica* Krasch. are the dominant desert species that mainly occur in the semi-fixed and fixed dunes in Maowusu sandland (Zhang 1994, Xiao *et al.* 2003). In Maowusu sandland, mean

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Abbreviations: Chl – chlorophyll; E – transpiration rate; F_v/F_m – photochemical efficiency of photosystem 2; g_s – stomatal conductance; P_N – net photosynthetic rate; RSR – root : shoot ratio; SLA – specific leaf area; SWC – volumetric soil water content; WUE_i – instantaneous water use efficiency.

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annual temperatures are 6–9 °C and mean annual precipitation is 388 mm, over 70 % of which occurs within plant growth season (Zhang 1994). Recently measured precipitation often is about 200 mm (Xu and Yan 2003), representing an about 50 % decrease compared with the mean annual precipitation. The objectives of this study were to investigate how a 50 % decrease in precipitation (315.0 mm for present precipitation and 157.5 mm for suspected future decreasing precipitation) affects growth and physiology of the two desert species, and how they adjust their physiology and structure to the low precipitation conditions.

The experiment was conducted at Ordos Sandlad Ecological Station (OSES) (39°29.66'N, 110°11.47'E, 1 295 m above sea level), Institute of Botany, the Chinese Academy of Sciences. One-year-old seedlings of *Salix psammophila* C. Wang *et* Ch. Y. Yang and *Artemisia ordosica* Krasch. were collected from dunes near to OSES. Forty seedlings per species were randomly divided into two groups of twenty seedlings. Then, within each group of twenty per species, the individuals were randomly planted in two sand-pools ($0.67\times1.50\times2.00$ m^3) in a greenhouse on May 1, 1999. The top of the greenhouse was covered with tarps when it rained, and was totally exposed to sunshine. Therefore, the seedlings did not receive any ambient rainfall during the experiment. The sand matrix of each pool was from dunes near to OSES, and its depth was 60 cm. Seedlings were grown in sand pools with two water supplies, *i.e.* equivalent to 315.0 mm as control (representing present precipitation) and 157.5 mm as water stress (representing a 50 % decrease in precipitation) from May 24 to September 5, 1999 (105 d). To reach these conditions, water was supplied once every second day after 17:30, and each water supply was 9.0 and 4.5 mm for the two sand pools, respectively. All sand pools were weeded and splashed with insecticide once a week.

Volumetric soil water content (SWC) was measured at 15-d-intervals during the experiment. For each measurement, seven sand matrix columns were randomly excavated in each pool, and samples from four different depths (0–15, 15–30, 30–45, and 45–60 cm) were made and labelled. A total of 28 samples were made for each pool. SWC of each sample was determined after oven drying at 85 °C during 3 d. Therefore, SWC of each pool was calculated as the moisture average of the 28 samples.

Leaf chlorophyll (Chl) fluorescence was used to assess the photochemical efficiency of photosystem 2 (F_v/F_m). Five uppermost fully expanded leaves per treatment and per species were selected for Chl fluorescence measurements. Leaves were dark adapted in aluminium foil during 30 min at noon in July 23, 1999. Minimal fluorescence (F_0) and maximal fluorescence (F_m) were determined with a Plant Efficiency Analyzer (*PEA*, *Hansatech*, Kings Lynn, UK). F_v/F_m was calculated as: $F_v/F_m = 1 - F_0/F_m$, where F_v is the variable fluorescence.

Gas exchanges measurements were made for *S. psammophila* on July 31, 1999 and for *A. ordosica* on August 11, 1999. The transmitted maximal photon flux density in the photosynthetically active radiation and the air temperature were close for the two days. Net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) were determined at one-hour intervals from 07:00 to 18:00 (local time) with a portable photosynthesis system (*LCA4*, *ADC*) on the five leaves per treatment and per species used for Chl fluorescence measurements. Instantaneous water use efficiency (WUE_i) was calculated as the ratio of P_N to E.

At the end of the experiment (September 5, 1999), height and number of leaves of the seedlings (leaves ≥ 5 mm in length) were determined and then a destructive harvest was carried out. Ten seedlings of each species and treatment were randomly sampled. Leaf area was measured using a *CI-203* area meter (*CID*, USA). Leaves, shoots, and roots were dried at 85 °C during 48 h. Specific leaf area of the whole plant (SLA) [m^2 kg^{-1}] and root : shoot ratio (RSR: total root biomass to total stem and branches biomass) were calculated according to Beadle (1993).

Data management and statistical analyses were performed using *SPSS* software (*SPSS*, Chicago, IL, USA). Means were expressed with their standard error (± SE) and compared by ANOVA. All statistical tests were considered significant at $p\leq0.05$.

Seasonal patterns of SWC were similar for *S. psammophila* and *A. ordosica* under the two water supplies, *i.e.* control and stressed. SWC increased and reached a maximum at day 15 (June 7) for the low water treatment of *A. ordosica* and at day 30 (June 21) for the high water treatment of *A. ordosica* and both treatments of *S. psammophila,* and then decreased. Decreasing watering significantly decreased SWC ($p\leq0.01$): on average, SWC was decreased by 19.7 % for *S. psammophila* and by 17.7 % for *A. ordosica* as compared to their respective high water regimes. However, the average SWC was not significantly different between the two species at control and stressed treatments, respectively ($p\geq0.05$).

Decreasing water supply significantly decreased F_v/F_m of *S. psammophila* ($p\leq0.01$) and *A. ordosica* ($p\leq0.05$) (Table 1). F_v/F_m decreased by 7.4 % for *S. psammophila* and 6.1 % for *A. ordosica*. However, F_v/F_m was not significantly different between the two species at control and stressed treatments, respectively ($p\geq0.05$).

Whatever the water supply, P_N increased quickly, reached a maximum at 08:00 for *A. ordosica* and at 10:00 h for *S. psammophila,* and decreased slowly until 18:00 (Fig. 1*A,B*). There was a short midday depression at 12:00, significant under low water supply for *S. psammophila* only. Decreasing water supply significantly decreased P_N of the two species ($p\leq0.001$): on average, P_N was decreased by 33.9 % in *S. psammophila* and by 43.2 % in *A. ordosica*.

Diurnal patterns of E were similar for both species under the two water supplies (Fig. 1*C,D*). *S. psammo-*

Table 1. Parameters of photochemical efficiency of photosystem 2 (F_v/F_m) and growth of *S. psammophila* and *A. ordosica* seedlings grown under two water supplies, *i.e.* control and stressed at final harvest (September 5, 1999). Means ± SE, $n = 10$ seedlings. Significant differences between the treatments are indicated as: NS = not significant at $p>0.05$, $^{*}p\leq0.05$, $^{**}p\leq0.01$, $^{***}p\leq0.001$.

Parameter	*S. psammophila*		*A. ordosica*	
	Control	Stressed	Control	Stressed
F_v/F_m	0.758±0.011	0.702±0.008***	0.768±0.013	0.721±0.009**
Height [cm]	113.0±5.1	76.9±6.0***	66.0±2.1	50.8±1.9***
Number of leaves	390.2±41.3	175.3±20.2***	2737.6±319.0	1170.3±127.3***
Leaf area [cm^2]	895.9±90.7	397.2±54.6***	8077.3±880.0	3238.4±310.0***
SLA [m^2 kg^{-1}]	14.17±0.32	12.80±0.33**	47.20±2.99	42.72±2.45^{NS}
Leaf biomass [g]	6.3±0.5	3.1±0.4***	16.8±1.2	7.7±0.9***
Shoot biomass [g]	10.8±1.4	3.3±0.4***	28.7±2.1	12.6±1.1***
Root biomass [g]	8.1±1.1	3.5±0.4***	12.9±0.5	6.7±0.8***
Total biomass [g]	25.2±2.9	9.9±1.1***	58.5±3.4	27.0±2.1***
RSR [kg kg^{-1}]	0.75±0.04	1.14±0.10**	0.47±0.04	0.53±0.04^{NS}

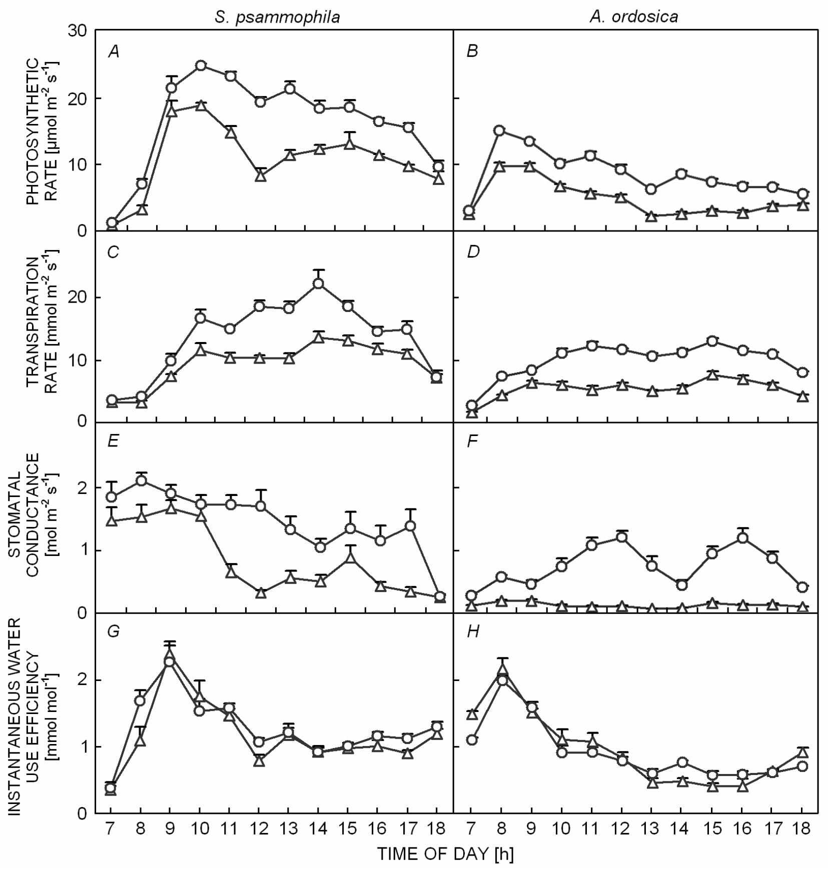

Fig. 1. Diurnal patterns of photosynthetic rate (*A, B*), transpiration rate (*C, D*), stomatal conductance (*E, F*), and instantaneous water use efficiency (*G, H*) for *S. psammophila* (*A, C, E, G*) and *A. ordosica* (*B, D, F, H*) seedlings grown under two water supplies, *i.e.* control (○) and stressed (Δ). Means ± standard error, $n = 5$ leaves.

phila showed a peak under the two water supplies at 14:00. Decreasing water supply significantly affected *E* of the two species ($p\leq0.001$): on average, *E* was decreased by 30.6 % for *S. psammophila* and by 44.5 % for *A. ordosica*.

Diurnal patterns of g_s were different for both species under the two water supplies (Fig. 1*E,F*). For the high water supply of *S. psammophila*, g_s slowly decreased until 18:00 while for the low water supply, the decrease in g_s was steep between 10:00 and 12:00. Under high water supply of *A. ordosica*, g_s peaked at 12:00 and 16:00, respectively, while under low water supply, g_s was negligible. Decreasing water supply significantly decreased g_s of the two species ($p \leq 0.001$): on average, g_s was decreased by 42 % for *S. psammophila* and by 82.1 % for *A. ordosica*. WUE_i quickly increased and reached a maximum at 09:00 for *S. psammophila* and at 08:00 for *A. ordosica*, then slowly decreased until 12:00, and finally was stabilised (Fig. 1*G,H*). Decreasing water supply did not significantly affect WUE_i of the two species ($p > 0.05$).

In comparison of the two species, *S. psammophila* had higher average P_N, E, g_s, and WUE_i than *A. ordosica* at control and stressed treatments, respectively ($p \leq 0.05$).

At the end of the experiment, tree height, number of leaves, leaf area, and leaf, shoot, root, and total biomasses of the two species were significantly decreased by decreasing water supply ($p \leq 0.001$) (Table 1). Decreasing water supply significantly decreased SLA in *S. psammophila* only. Total biomass was decreased by 60.6 % for *S. psammophila* and by 53.9 % for *A. ordosica*. RSR was significantly increased by decreasing water supply for *S. psammophila* only ($p \leq 0.01$). All growth characteristics mentioned above were significantly different between the two species at control and stressed treatments, respectively ($p \leq 0.01$).

Decreasing precipitation strongly decreased P_N of the two species. One possible reason is a decrease of the CO_2 supply due to the stomatal closure caused by water stress for both species. Similar results were observed for various species (Ramanjulu *et al.* 1998, Ashraf *et al.* 2002, Ranjbarfordoei *et al.* 2002). However, F_v/F_m at noon was also decreased in response to water stress for both species, reflecting that photosynthetic apparatus was affected by drought. Fluorescence indices provide indications on the ability of a plant to tolerate environmental stresses by measuring the extent to which the photosynthetic apparatus is damaged (Fracheboud *et al.* 1999, Maxwell and Johnson 2000). Similar decrease in F_v/F_m in response to water stress was observed by Ogaya and Peñuelas (2003).

E and P_N decreased in response to water shortage, but WUE_i was not affected because stomatal closure reduced proportionally both P_N and E for the two species. Under water stress, contrasted WUE_i responses have been reported: decreases for species like okra (Ashraf *et al.* 2002) or increases for species like Douglas-fir, lodgepole pine, heather, bracken, and *Populus davidiana* (Smit and van den Driessche 1992, Gordon *et al.* 1999, Zhang *et al.* 2004).

The decrease in carbon assimilation under water stress involves a reduction of biomass accumulation for both species. Decrease in biomass in response to water stress is a commonly observed phenomenon (Guenni *et al.* 2002, Singh and Singh 2003). For the two tested species, tree height, number of leaves, and leaf area were also decreased by water limitation. This is in agreement with a mechanism minimizing water losses and irreversible damages linked to xylem cavitation (sap column breaking) when the air evaporating demand is high during water stress by limiting the produced transpiring leaf area (Harvey and van den Driessche 1997, Ruiz-Sánchez *et al.* 2000).

Decreasing precipitation decreased SLA for *S. psammophila* only. Decrease in SLA in response to water stress is often observed in various species (Fernández *et al.* 2002, Marron *et al.* 2003, Zhang *et al.* 2004). Reduction of SLA is assumed to be a way to improve WUE (Araus *et al.* 1997). This is because thicker and/or denser leaves usually have a higher content of Chl and proteins per unit leaf area and, hence, have a greater photosynthetic capacity than thinner and/or less dense leaves. This was not the case in our study where WUE for *S. psammophila* was unaffected by decreasing precipitation. However, decrease in SLA is also supposed to improve water retention during water stress by increasing leaf density and resistance to water losses (Niinemets 2001). Drought tolerant species or cultivars exhibit denser leaves both under well-watered conditions and under drought than the drought sensitive ones (Marron *et al.* 2003).

Effects of decreasing precipitation on biomass allocation were also different for the two species: RSR significantly increased for *S. psammophila*, indicating that a larger proportion of photosynthates is allocated to the belowground plant parts when water supply is limiting. Plants with more roots will explore more efficiently soil in such a way that they can grow and survive better under water stress (van Hees 1997, Fernández *et al.* 2002). Because the change in RSR has been considered as one of the mechanisms involved in the adaptation of plants to water stress (Turner 1986), we could predict that *S. psammophila* will adapt more easily than *A. ordosica* in future decreasing precipitation patterns in Maowusu sandland.

In conclusion, this experiment showed that seedling responses to decreasing precipitation in the future altered climate will be species-specific. Changes in gas exchanges were similar for both species but morphological response of *S. psammophila* to the decreasing precipitation was more pronounced than that of *A. ordosica*. *S. psammophila* seems to be more able than *A. ordosica* to adapt its morphology to lower water supply. Furthermore, these results help to predict how the two species would change their ecological adaptive strategies through eco-physiological and structural adjustments under the future decreasing precipitation.

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