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Abstract: Soil–plant water relations are crucial for understanding the mechanisms by which plants adapt to their environments. An experiment was conducted to understand the responses of 4 dominant psammophyte shrub species to different sandy environments. Pots were filled with tap water or sand, and pots planted with different species and filled with sand with and without pot covers were kept in 4 growth cabinets at 15/25 °C and with a water supply of 75 mm per month. Soil water content; dry weights of roots, shoots, and leaves; and leaf area were measured. The relative growth rate (0.039–0.042 g g^{-1} day^{-1}) was higher for the 2 *Artemisia* Krasch. species and lower for *Caragana korshinskii* Kom. and *Hedysarum laeve* Maxim. (0.016–0.023 g g^{-1} d^{-1}). The final soil water content of the 2 *Artemisia* species (1.3%–2.7%) was lower than that of *H. laeve* and *C. korshinskii* (14.7%–18.4%). Soil water content increased from the top of the profile to deeper levels for *H. laeve* and *C. korshinskii*. However, for the 2 *Artemisia* species, soil water was lower in the deeper profile compared with the upper profile. Considering water consumption, the 2 *Artemisia* species were similar while *C. korshinskii* and *H. laeve* were similar; this result was different from our hypothesis.

Key words: Biomass allocation, growth, microlysimeter, semiarid regions, plant–water relations

1. Introduction

Soil water deficit is common in arid and semiarid areas and has significant effects on the productivity, composition, and diversity of terrestrial plant communities (Maun, 1998; Bates et al., 2006). Global warming may enhance the soil water deficit and affect the dynamics of soil–plant water relations in semiarid rangelands (Alvalá et al., 2002; Lawrence and Slingo, 2004; Nelson et al., 2004). High soil water deficits are factors that limit seedling establishment and growth in arid environments (Maun, 1998) and have a major effect on plant growth and yield (Repellin et al., 1997; Saeidnejad et al., 2013). Water deficits could affect photosynthesis, stomatal conductance, and plant growth even in species adapted to arid conditions (Greenway and Munns, 1980; Cornic, 2000; Poorter et al., 2010; Silva et al., 2013). Tezara et al. (1999) and Lawlor (2002) suggested that drought could affect the mesophyll metabolism, reducing photosynthetic capacity.

Under field conditions, high soil moisture deficits commonly occur near the soil surface, whereas moisture levels deeper in the soil profile may be sufficient for seedling survival. Root depth in sandy soils determines the amount of moisture available for transpiration (Hays et al., 1991; Carrow, 1996). Plants with a well-established root system can use sporadic supplies of available soil moisture, maintaining stomatal conductance and leaf turgor despite large portions of the root system being in dry soil (Kirkham, 1980; Gallardo et al., 1994). Plants tend to allocate more biomass to root systems in dry desert environments, improving their survival (Maun, 1998). Plants respond differently morphologically and physiologically to water deficits. Therefore, plants can tolerate a variety of drought conditions and distributions across diverse microenvironments, resulting in different soil–plant water relations (Poorter, 1999).

Under laboratory and field conditions, numerous experimental studies have investigated the response of plant growth to soil water content (Llorens et al., 2004; Korkmaz and Özçelik, 2013; Salama et al., 2013). Lysimeters offer an effective way to monitor soil–plant water relations (Kato et al., 2007), but this method is a time- and labor-consuming process (Boast, 1982).

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Artemisia sphaerocephala Krasch. and *A. ordosica* Krasch. (Asteraceae), *Hedysarum laeve* Maxim. (Leguminosae), and *Caragana korshinskii* Kom. (Leguminosae) are dominant species in the inland sandy areas on the Ordos Plateau, Inner Mongolia, China. *H. laeve* and *A. sphaerocephala* are mainly distributed in drifting dunes and semifixed dunes, while *C. korshinskii* and *A. ordosica* are mainly distributed in fixed dunes. Therefore, these 4 species potentially have different drought-tolerance strategies to various sandy environments and subsequent soil water status (Zhang, 1994). These 4 species also have significant ecological and practical value for vegetation rehabilitation (Zhang, 1994; Zheng et al., 2003) in Inner Mongolia, where significant desertification occurs (Zha and Gao, 1997). However, in some habitats the transplanting of these 4 species has resulted in variable success of seedling establishment (Qi, 1998). Therefore, it is necessary to understand the seedling growth response of these commonly used species to water-limited conditions. Growth response to soil water availability has been investigated for one of these species, *C. korshinskii* (Xiao et al., 2002). However, to our knowledge, there are no studies demonstrating detailed temporal monitoring of the soil water profile and soil water dynamics under the current regional temperature/precipitation regime. Considering the expense of lysimeters, special pots were made to allow this study to investigate the temporal effects of soil–plant water relations using soil moisture sensors and electronic balances that continually record weight data.

The objective of this study was to understand the response of plant growth, transpiration, biomass allocation, and the temporal effect of soil-plant water relations. We hypothesized that species distributed in drifting dunes consumed more soil water than those in fixed dunes.

2. Materials and methods

2.1. Plant materials

In 2002, seeds of the 4 species *Caragana korshinskii*, *Hedysarum laeve*, *Artemisia sphaerocephala*, and *Artemisia ordosica* were collected from the Mu Us Sandyland, part of the Ordos Plateau (Zheng et al., 2003). The seeds were transported to the National Institute for Environmental Studies, Japan, and stored at 4 °C until sown. After sowing, the seedlings emerged within 15 days and were transferred to pots (11.2 cm in diameter and 20 cm in height), and were then left for 100 days. Seedling heights of *C. korshinskii*, *H. laeve*, *A. sphaerocephala*, and *A. ordosica* were 14.3 ± 0.8, 5.5 ± 1.1, 20.8 ± 1.4, and 22 ± 3.3 cm, respectively, prior to treatment application.

Sand used in this experiment was collected from riverbeds in Japan, washed several times, oven-dried for 3 days at 80 °C, and sifted to remove debris. The sand was separated into 4 groups based on particle size: >0.5

mm, 0.5–0.25 mm, 0.25–0.1 mm, and 0.1–0.05 mm. The sand from different particle-sized groups was then mixed into proportions similar to those in the study area. The composition percentages (percent of gravimetric content) for the 4 size groups (>0.5, 0.5–0.25, 0.25–0.1, and 0.1–0.05 mm) were 3.3 ± 1.1%, 45.0 ± 3.7%, 47.3 ± 2.4%, and 2.4 ± 0.5%, respectively.

Special PVC pots (16 cm in diameter and 20 cm in height) were made with the drainage outlets at the bottom of the pots covered with strips of nylon mesh to prevent sand loss but allow excess water drainage. The experiments were conducted in 2004.

2.2. Experimental design

The experiments were carried out using automatic temperature- and light-controlled growth chambers (KG-50HALS-W, Koito Co. Ltd., Japan). The chambers were set for 55%/75% relative humidity (day/night), with daily photoperiods (450 µmol m⁻² s⁻¹) of 14 h, using cool white fluorescent lights.

Air temperature treatments (15/25 °C) and water supply, equivalent to 75 mm per month, were applied to all treatments based on the monthly average precipitation/temperature level that plants encounter during the main growing season (75 mm precipitation, 15/25 °C temperature in July) in the Mu Us Sandyland. This climate regime is based on a 30-year average (Qi, 1998). Soil–plant water relations for the 4 plant species were determined with the following 4 treatments: 1) PVC pots were filled with tap water such that the distance between the water's surface and the top of the pot was 0.5 cm. This water level was maintained daily throughout the experiment to replace water lost through evaporation. This procedure was designed to test whether potential evaporation was same for every treatment. 2) PVC pots were filled with the dry sand mix and irrigated every 3 days with 7.5 mm. 3) PVC pots were filled with sand with one seedling transplanted into each pot. 4) The final treatment was similar to treatment 3, but the pot was covered to reduce soil evaporation.

To measure the soil moisture level in the different soil layers for each species in the fourth treatment, 4 narrow holes were made in side of every pot. A soil moisture sensor (ECH₂O-10, Decagon Devices, Inc., USA) was put into each hole, and then every hole was enclosed with silica gel to stop water loss. The sensors recorded data every 10 min. To monitor the water loss in treatment 4, every pot in treatment 4 was placed onto its own electronic balance (Mettler ID1, Mettler Instruments AG, Germany) with recordings taken at 10-min intervals. For all treatments, weight was measured using an electronic balance (Mettler PK36, Mettler Instruments) every day to determine water loss. In treatments 2, 3, and 4, the pots were watered until drainage occurred, ensuring seedling survival prior to

treatment application. After 1 week, the pots were watered once every 3 days with tap water (7.5 mm each time). Each treatment contained 3 replicates with pots randomly allocated within the 4 growth chambers. The locations of pots with seedlings were changed daily. Individual plants were sufficiently spaced to prevent a shading effect (Clifton-Brown and Lewandowski, 2000). The experiment ran for 4 weeks. The soil moisture data were changed into gravimetric water content in accordance with the regression model (Zheng et al., 2005) used to calculate the percentage of gravimetric content of the soil samples.

After 4 weeks, the plants were harvested. Plants were separated into roots, shoots, and leaves. The roots were washed to remove soil. The dry weights of roots, shoots, and leaves were determined after oven-drying at 80 °C for 3 days using an electronic balance (Mettler PC 440, Mettler Instruments). Leaf area was measured using a planimeter (LI-COR 3100, LI-COR, USA).

2.3. Growth analysis

The net assimilation rate (NAR) and the relative growth rate (RGR) of each plant was estimated using the following equations:

$$\mathrm{NAR} = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{1}{s} \frac{dW}{dt} dt = \frac{(w_2 - w_1)(\ln s_2 - \ln s_1)}{(s_2 - s_1)(t_2 - t_1)}, \qquad (1)$$

$$\mathrm{RGR} = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} d(\ln w) = \frac{\ln w_2 - \ln w_1}{t_2 - t_1}, \qquad (2)$$

where w_1 and s_1 are plant dry mass and total leaf area, respectively, at the initial time (t_1), and w_2 and s_2 are plant dry mass and total leaf area at the final harvest (t_2) (Hunt, 1990; Xiong et al., 2000).

2.4. Statistical analysis

To ensure homogeneity of variance, all data were log-transformed prior to analysis (Carey et al., 1998). The transformed values were analyzed using a 2-way analysis of variance (ANOVA). Where significant differences occurred, Tukey's test was used to determine the mean differences between treatments (Chen and Maun, 1999). All statistical analyses, including the test for homogeneity of variance, were performed using SPSS 10.0 (SPSS Inc., USA).

3. Results

In general, for growth variables, F-statistic values were significant for species but not for the pot treatment with and without cover (Table).

3.1. Biomass and leaf area

There was no significant difference in the biomass of leaves, shoots, and roots between *Artemisia ordosica* and *A. sphaerocephala* or within these 2 species in treatments with and without covers (Figure 1). However, the leaf, shoot, and root biomass of the 2 *Artemisia* species was several times greater than that of *Caragana korshinskii* and *Hedysarum laeve*, with the latter 2 species showing no significant difference in leaf, shoot, and root biomass (Figure 1). Generally, the leaf area increase was highest for *A. ordosica*, followed by *A. sphaerocephala*, *H. laeve*, and *C. korshinskii* (Figure 2).

3.2. Dry matter allocation

The ratio of below-ground to above-ground dry matter partitioning was lower in the 2 *Artemisia* species (0.13–0.18 to 1) and higher in *Caragana korshinskii* and *Hedysarum laeve* (0.32–0.46 to 1). Although there were no significant differences between treatments of pots with and without covers, the ratios of dry matter partitioning of the covered treatments were lower than those of uncovered treatments for all 4 species (Figure 3).
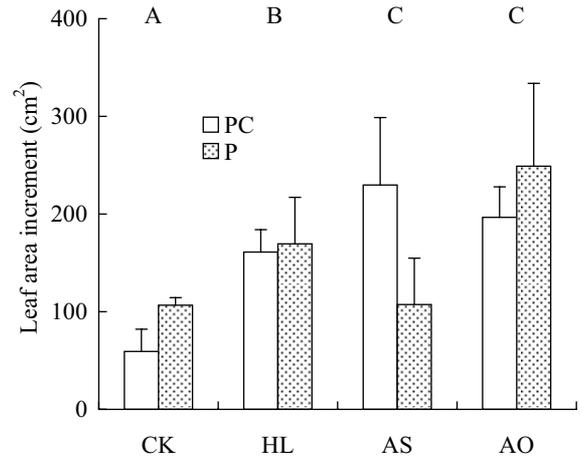
3.3. Relative growth rate

The RGR was similar for the 2 *Artemisia* species (0.039–0.042 g g^{-1} d^{-1}), which was significantly higher compared with *Caragana korshinskii* and *Hedysarum laeve* (0.016–0.023 g g^{-1} d^{-1}), and the RGR was also similar for *C. korshinskii* and *H. laeve*. There was no significant difference for the RGR within any species in treatments with and without cover (Figure 4).

Table. Results of 2-way ANOVA of characteristics of biomass increment of leaves, shoots, and roots; the ratio of below-ground to above-ground dry matter; leaf area increment; NAR; and RGR in relation to species, pot treatment, and their combinations. Seedlings of 4 species were cultured in 2 types of pots, with covers to prevent evaporation or without covers in a growth cabinet. Significance levels: ***, $P < 0.001$; *, $P < 0.05$; ns, $P \geq 0.05$.

| Effect	DF	Dry matter				Leaf area	NAR	RGR
		Leaf	Shoot	Root	Ratio			
		F	F	F	F	F	F	F
Species (S)	3	18.59***	98.68***	16.49***	10.39***	24.70***	31.58***	124.50***
Pot (P)	1	0.02 ns	0.28 ns	3.73 ns	1.45 ns	0.03 ns	1.12 ns	0.50 ns
S × P	3	1.68 ns	3.12 ns	1.62 ns	0.26 ns	5.05*	3.62*	0.50 ns
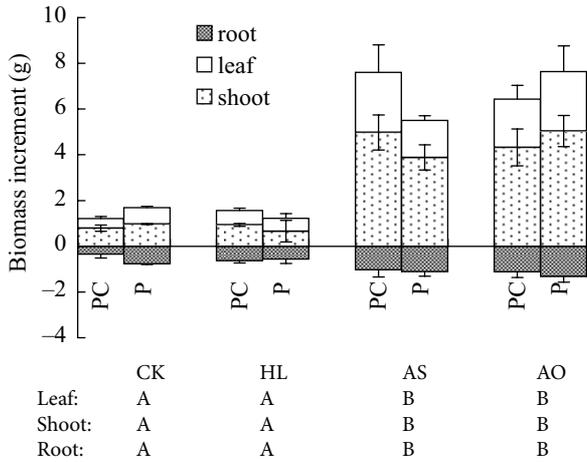
Figure 1. Biomass increment (±SE) of *Caragana korshinskii* (CK), *Hedysarum laeve* (HL), *Artemisia sphaerocephala* (AS), and *Artemisia ordosica* (AO) under alternating temperatures (15/25 °C, night/day) and water availability of 75 mm per month in a growth cabinet. Each bar represents the mean of 3 replicates. Bars with different capital letters underneath them indicate significant difference between species at P < 0.05 (Tukey's test). PC and P denote treatment with and without covers, respectively.

Figure 2. Leaf area increment (±SE) of 4 species. Other descriptions are the same as is Figure 1.
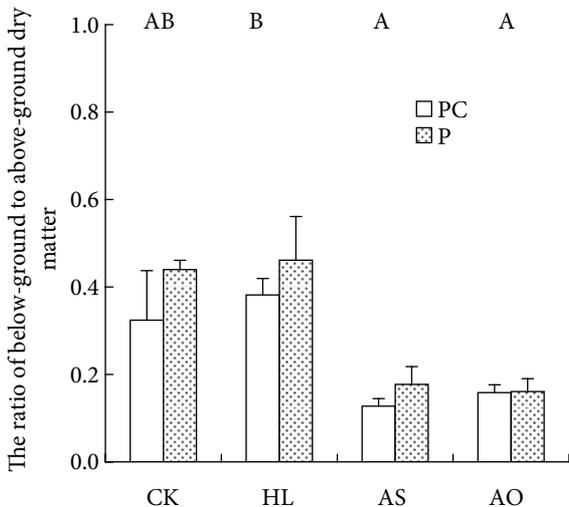
Figure 3. The ratio of below-ground to above-ground dry matter (±SE) of 4 species. Other descriptions are the same as in Figure 1.
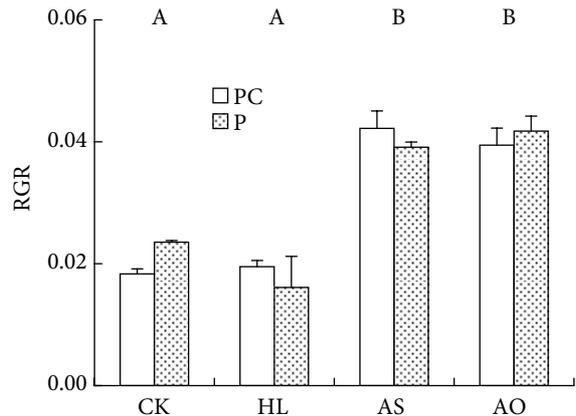
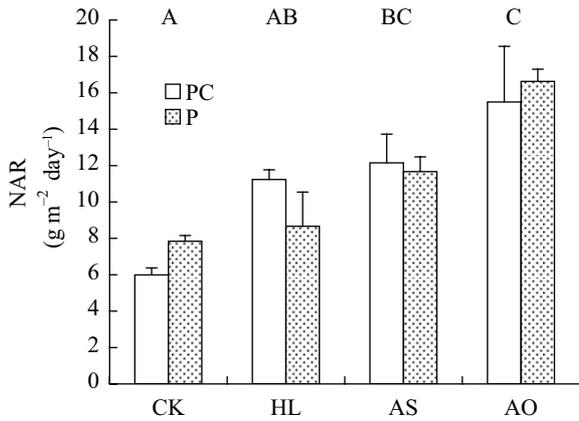**Figure 4.** Relative growth rate (±SE) of 4 species. Other descriptions are the same as in Figure 1.

3.4. Net assimilation rate
The NAR was highest for *Artemisia ordosica*, followed by *A. sphaerocephala* and *Hedysarum laeve*, with the lowest NAR being seen for *Caragana korshinskii* (Figure 5).

3.5. Soil–plant water relations
Water loss from water only and bare sand only (F = 3.5, n = 3, P > 0.05 and F = 2.7, n = 3, P > 0.05, respectively) in the growth chambers showed no significant difference (F = 3.5,

n = 3, P > 0.05). Water loss from treatment pots with and without covers were significantly different for the 4 species (F = 210.2, n = 3, P < 0.001). The 2 *Artemisia* species had similar water losses when compared with each other, but these were significantly higher than those of *Hedysarum laeve* and *Caragana korshinskii* (Figure 6). There was similar loss of water content between covered and uncovered pot treatments for *H. laeve* and *C. korshinskii* (Figure 6).
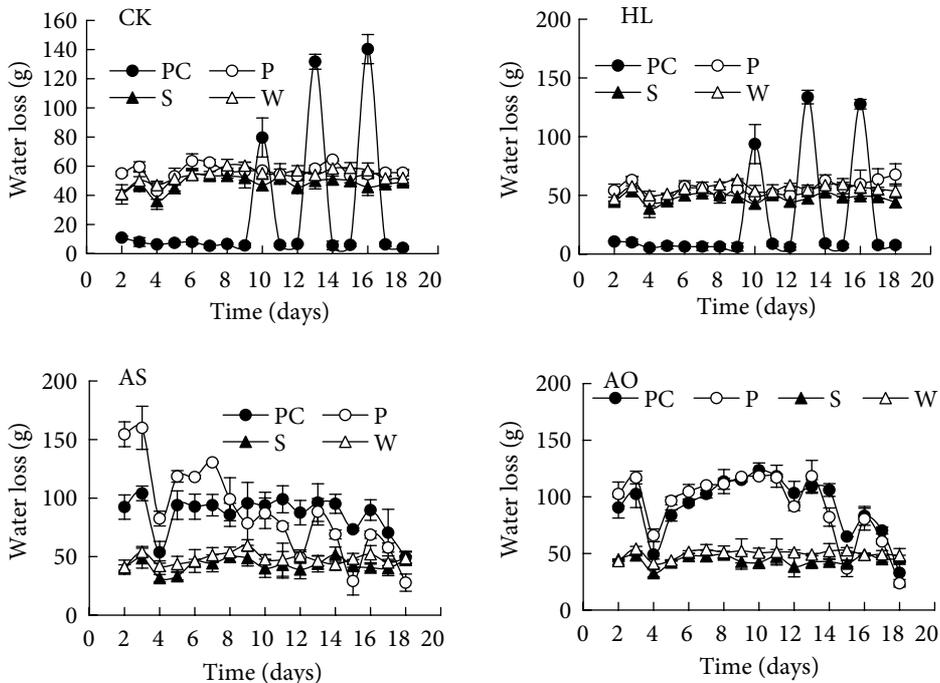
Figure 5. Net assimilation rate (±SE) of 4 species. Other descriptions are the same as in Figure 1.

< 0.001). However, the final soil water content showed no significant differences between treatments for *Artemisia ordosica* (F = 2.3, n = 3, P > 0.05) and *A. sphaerocephala* (F = 3.1, n = 3, P > 0.05). Soil water content increased in the soil profile from the top to lower layers. For *H. laeve* and *C. korshinskii*, the soil water content was greatest at 16 cm, decreasing closer to the soil surface (12, 8, and 4 cm respectively). After irrigation, the soil water content was greater at deeper soil levels (12 and 16 cm) compared with the upper levels (4 and 8 cm). However, for the 2 *Artemisia* species, there was a gradual decrease of the soil water content in deeper layers compared with the shallower layers (Figure 9).

4. Discussion

Plants distributed in areas where limited water availability occurs are expected to have the ability to adjust their water use to either increase biomass production or drought tolerance (Jones, 1993; Heilmeier, 2002). In desert environments, water availability is a major environmental factor affecting the growth and yield of plants (Waring and Schlesinger, 1985; Wilson, 1988). Our results indicated that although there were no significant differences in leaf biomass and area, RGR and NAR showed a positive association with water availability for *Artemisia sphaerocephala*, because there was less water loss when pots were covered. In contrast, these growth variables showed a negative association for *Caragana korshinskii*

The final soil water content of bare sand in the growth chambers showed no significant difference (F = 2.5, n = 3, P > 0.05). The final soil water content of the 2 *Artemisia* species was significantly lower in both pot treatments (with covers: F = 1381.5, n = 3, P < 0.001; without covers: F = 331.7, n = 3, P < 0.001) compared with *Hedysarum laeve* and *Caragana korshinskii* (Figures 7 and 8). Comparing the final soil water content of cover/no cover treatments, there was a significant difference for *H. laeve* (F = 232.2, n = 3, P < 0.001) and *C. korshinskii* (F = 2130.4, n = 3, P

Figure 6. Water loss (g) over the experimental time. W and S denote pots filled with tap water and pots filled with sand, respectively. Other descriptions are the same as in Figure 1.
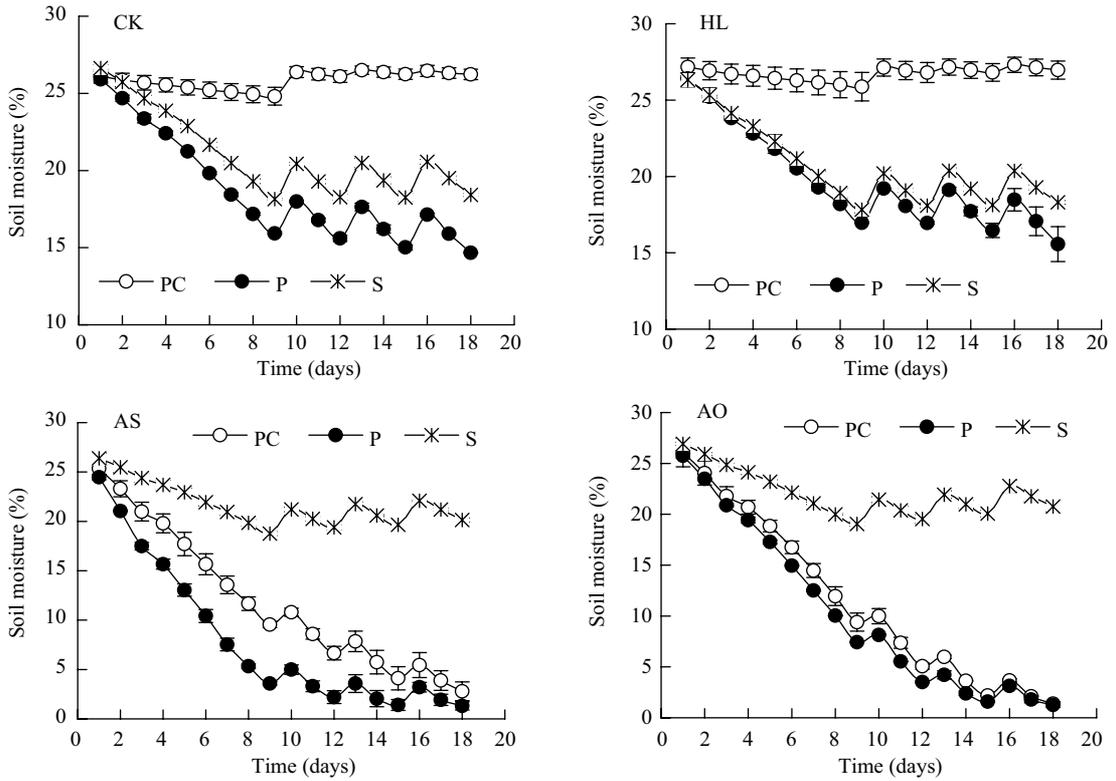
Figure 7. Gravimetric soil water content (%) over the experimental time. Other descriptions are the same as in Figure 1.
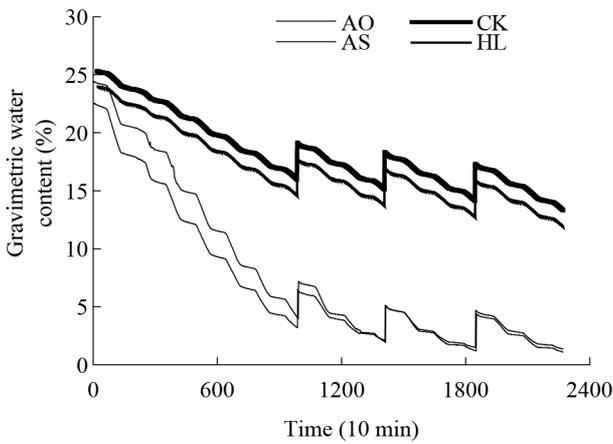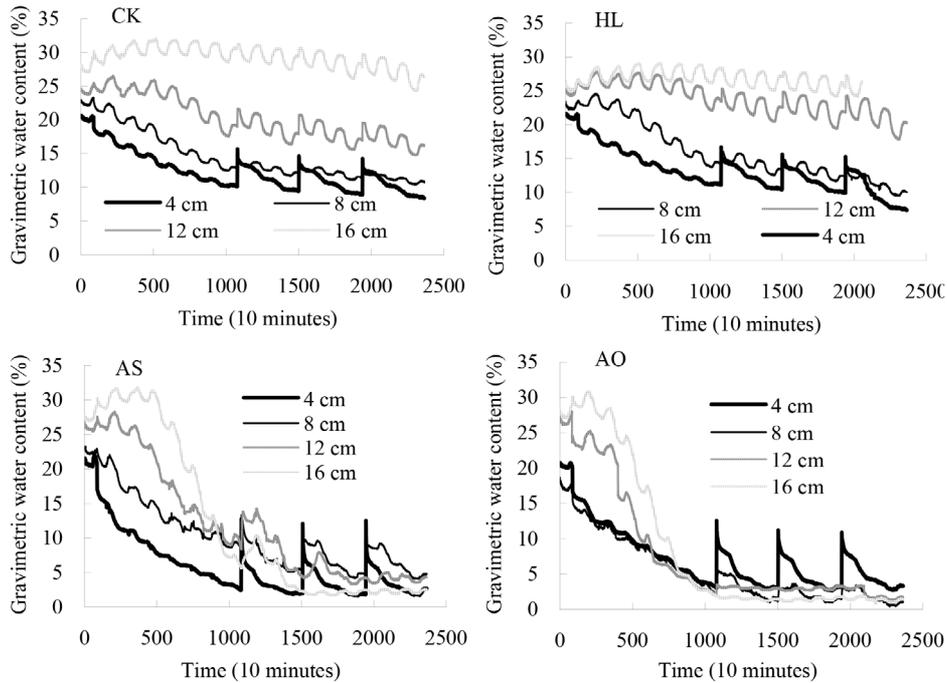

Figure 8. Gravimetric soil water content (%) of treatments with plants grown in pots without covers recorded by electronic balance continually over the experimental time at 10-min intervals when 7.5 mm of water was supplied every 3 days. Other descriptions are the same as in Figure 1.

and *Artemisia ordosica*. For *Caragana korshinskii*, water availability for seedlings was higher compared with the mature plants growing in situ at identical levels of water availability, probably from differing rates of transpiration.

The results for *C. korshinskii* are consistent with findings of Xiao et al. (2002) that demonstrated that when the water supply was increased by 50% above mean (precipitation) in the Mu Us Sandyland, the biomass of *C. korshinskii* was reduced. This phenomenon is seen with *C. korshinskii* because regeneration and distribution of this species occur in more arid, rather than wet, areas (Zhang, 1994; Zheng et al., 2003) (Figures 1, 2, 4, and 5).

Species may adapt to soil water deficits with different mechanisms (Gill et al., 2001; Lehmeier et al., 2005). Changes in biomass allocation can affect the plant–soil water relations (Kirkham, 1980; Gallardo et al., 1994). In our study, all 4 species tended to increase biomass allocation to the roots when water availability decreased in the uncovered pot treatment compared with the covered treatment (Figure 3).

Two contrasting water-use strategies have been reported for plants (Passioura, 1982; Heilmeier, 2002). The more conservative strategy should be advantageous for plants growing without the influence of competitors. The second strategy of prodigal water use should be advantageous under competitive situations. This latter strategy is related to high stomatal conductance associated with high water loss, high carbon gain, and thus growth.

Figure 9. Gravimetric soil water content (%) in 4 layers of treatments with plants grown in pots without covers recorded by ECH$_2$O-10 soil moisture sensors over the experimental time at 10-min intervals when 7.5 mm of water was supplied every 3 days. Other descriptions are the same as in Figure 1.

These 2 strategies are only the extremes; plants' strategies occur across a wide spectrum and plants could respond to changes in the microenvironment and water availability because of precipitation fluctuations within and between years (Cowan, 1986). There was no significant difference for RGR under limited water availability for all 4 species. Therefore, we speculate that species response was related to soil water availability; however, we would expect that *A. sphaerocephala* and *H. laeve* probably use the first strategy, and *C. korshinskii* and *A. ordosica* tend to use the second (Figure 4).

Considering water consumption, our result indicated that the 2 *Artemisia* species were similar, while *C. korshinskii* and *H. laeve* were also similar. This result was different from our hypothesis and indicated that water demand of species in this region was mainly determined by their biological characteristics, because vegetation in sandy land environment is azonal and experiences a relatively short evolution period (Zhang, 1994).

The Ordos Plateau is characterized by relatively low annual precipitation (150–400 mm). Successful establishment of seedlings in revegetation programs is dependent on the species used being suited to the sandy environment. Generally, species with low transpiration and relative high RGR and NAR values are expected to

tolerate sandy environments. Furthermore, a high ratio of below-ground to above-ground dry matter means that plants are more efficient at water uptake from the soil and dune system stabilization. Therefore, this high ratio is a desirable criterion when selecting species for revegetation programs in sandy environments (Zhang, 1994; Maun, 1998). Our results indicated that the 2 *Artemisia* species had high NAR and RGR values. However, these 2 species had the highest transpiration rate and lowest ratio of below-ground to above-ground dry matter, whereas *H. laeve* and *C. korshinskii* had relatively low RGR, NAR, and transpiration levels and a high ratio of below-ground to above-ground biomass. Further, transpiration was the main factor leading to water loss in the 2 *Artemisia* species. Evaporation in *H. laeve* and *C. korshinskii* resulted in the most water loss. However, drainage loss continued to occur after irrigation stopped in the covered treatments, suggesting that less water occurred compared with the 2 *Artemisia* species (Figure 6). Therefore, these species could be used according to the relative microenvironment, with the 2 *Artemisia* species used in sites where water availability is higher and fast growth is necessary to restore a degraded environment. *H. laeve* and *C. korshinskii* could be used in sites where the water deficit is severe.

Suitable coverage for revegetation is important to avoid depleting soil water in arid and semiarid environments (Zhang, 1994). The water loss and soil water content trials in our experiments indicated that available soil water could significantly differ when different species are used (Figures 6 and 7). Water loss was almost 2 times greater with the 2 *Artemisia* species compared with bare sand. The final soil water content of bare sand was about 15 times greater when compared with the treatments in which the *Artemisia* species were used (Figures 6 and 7). Our results support those of Qi (1998), who found that a dry surface layer of bare sand reduced evaporation from deeper soil layers. Therefore, large areas of bare sand in arid areas where the annual precipitation reaches 300–400 mm could store a large volume of water, potentially acting as a reservoir in the sandy lands (Qi, 1998). It could be expected that

differences of vegetation coverage and species composition may induce changes in water use. Furthermore, high densities of *Artemisia* plant communities may increase the chance of vegetation instability because of higher plant transpiration, maximizing the probability of complete soil-drying causing plant death (Cowan, 1986). However, we cannot suggest an appropriate density for the plant community and species composition of the 4 species used in this study. Further investigation is needed to clarify this issue.

Acknowledgments

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