Elevated CO$_2$ accelerates net assimilation rate and enhance growth of dominant shrub species in a sand dune in central Inner Mongolia

Yuanrun Zheng [a,*], Zhixiao Xie [b], Glyn M. Rimmington [c], Yuanjiang Yu [d], Yong Gao [d], Guangsheng Zhou [a], Ping An [e], Xiangjun Li [e], Wataru Tsuji [e], Hideyuki Shimizu [d]

[a] State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Beijing 100093, China
[b] Geosciences Department, Florida Atlantic University, Boca Raton, FL 33431, USA
[c] Office of Global Learning, Wichita State University, Wichita, KS 67260-0142, USA
[d] National Institute for Environmental Studies, Tsukuba 305-8506, Japan
[e] Arid Land Research Center, Tottori University, 1390 Hamasaka, Tottori 680-0001, Japan

ABSTRACT

It has been reported that elevated CO$_2$ can enhance plant growth and water use, and that desert plants in particular will show the strongest response to rising atmospheric CO$_2$ due to the strong water stress on these plants. In this study experiments were conducted to understand the responses of seedlings from four species, which are dominant in different successional stages in the semi-arid sandy grassland of central Inner Mongolia, to rising temperature and elevated CO$_2$. Seedlings of the four species were grown for 8 weeks at two air temperatures and two CO$_2$ concentration regimes in growth chambers. It was found that for the two *Artemisia* species and *Hedysarum laeve* elevated CO$_2$ level resulted in increased relative growth rates (RGR) (6–12%), height increments (24–106%), net assimilation rates (20–45%) and water use efficiencies (WUE) (43–105%), and decreased transpiration (16–55%). For *Caragana korshinskii*, the elevated CO$_2$ significantly increased the ratio of below ground to above ground biomass (16–23%), height increment (31–65%) and WUE (79–84%). At elevated CO$_2$ level and the higher temperature, the two *Artemisia* species showed decreased RGR and height increments, while for, *C. korshinskii* and *H. laeve* increased RGR and height increments were observed. For *A. sphaerocephala* the higher temperature also resulted in increased WUE, but decreased WUE for the other three species. Obvious differences were observed between the two *Artemisia* species and *C. korshinskii*, with the *Artemisia* species characterized by higher RGR, lower ratio of below ground to above ground biomass and lower WUE. These findings should be applicable to similar shrub species located in other arid and semi-arid environments.

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1. Introduction

The atmospheric CO$_2$ concentration has increased from 280 μmol mol^{-1} before the industrial revolution to around 365 μmol mol^{-1} currently (Wall et al., 2006), and is projected to exceed 600 μmol mol^{-1} by the end of this century (IPCC, 2001). Anthropogenic increases in atmospheric CO$_2$ are inevitably coupled with global climate change (IPCC, 2001). General circulation models have predicted average global surface air temperature increases of 1.5–5.2 °C, if the ambient CO$_2$ concentration doubles (Saralabai et al., 1997). Increased atmospheric CO$_2$ in combination with climate change may directly or indirectly affect ecosystem productivity (Riedo et al., 2001). Studies of plant responses to global climate changes are essential to understand both plant impacts and

potential feedback to the global change systems (Diaz and Cabido, 1997).

There is a vast amount of literature on the direct effects of elevated CO$_2$ concentrations on plants and ecosystems, and it is clear that elevated CO$_2$ may contribute to increased plant productivity (Drake et al., 1997; Centritto et al., 2002; Yoon et al., 2009). Most terrestrial plants increase the rate of photosynthesis under elevated CO$_2$ (Geissler et al., 2009) but growth responses vary from zero to 50% gain per season depending on the plant age, duration of observations and growth conditions (Beismann et al., 2002). A common response of plants to elevated atmospheric CO$_2$ is decreased stomatal conductance (Bazzaz, 1990). This can result in reduced transpiration per unit leaf area and higher soil water content compared with non-CO$_2$ enriched plant communities (Field et al., 1995). At the stand level, stomatal responses to CO$_2$ often lead to higher plant biomass and water use efficiency in CO$_2$ enriched environments (Morgan et al., 2001). Increasing the atmospheric CO$_2$ stimulates root biomass in many plant species more than above

ground biomass or leaf area production (Bernacchi et al., 2000). For desert plants, especially those in the seedling stage, CO_2 induced increases in root system size and the rate of root deployment may increase water acquisition by these plants and enhance their survival in arid and semi-arid environments (Obrist and Arnone, 2003). Moreover, elevated CO_2 may lead to an increase in plant water potential and a delay in the onset of water stress, thus improving growth. It has been reported that elevated CO_2 increased biomass production in water stressed plants (Centritto et al., 2002; Yoon et al., 2009) and resulted in higher integrated water use efficiency. These observations show that water limited ecosystems would be the most responsive to increasing CO_2 concentrations (Melillo et al., 1993; Centritto et al., 2002; Morgan et al., 2004).

Arid and semi-arid ecosystems occupy 40% of the Earth's land surface (Dregne, 1991) and an understanding of the responses of component species to increasing atmospheric CO_2 is critical (Lecain et al., 2003; Zavaleta et al., 2003). However, desert ecosystems have received comparatively little attention with respect to elevated CO_2 (Naumburg et al., 2003).

The objective of this study was to investigate the response of growth, biomass allocation, transpiration and water use efficiency of four species to the combined effects of air temperature and elevated CO_2. These four species: *Artemisia sphaerocephala* Krasch. (Asteraceae); *Hedysarum laeve* Maxim. (Leguminosae); *Artemisia ordosica* Krasch.; and *Caragana korshinskii* Kom. (Leguminosae), are indigenous species in the semi-arid area of Inner Mongolia in China. They are often used in restoring the degraded sandy grassland in the Mu Us Sandy land in Inner Mongolia (Qi, 1998) where desertification significantly affects social and economic development. These species are of significant ecological and practical value for vegetation rehabilitation (Zheng et al., 2003). The four species are dominant in different successional stages of the local ecosystem, i.e., mobile dunes, semi-fixed dunes and fixed dunes. These different successional stages have different micro-environments, particularly soil moisture, and hence the four species may show different responses to elevated CO_2. The effect of increased temperature on growth in dominant plant species from the Mu Us Sandy land, including *H. Laeve* and *A. ordosica*, and their growth response to soil water availability have already been investigated separately (Xiao et al., 2003). However, there are no studies on the combined effects of CO_2 enrichment and increased temperature on the four species selected. Therefore, it is necessary to understand the response of seedling growth in these species to the combination of CO_2 enrichment and global warming. The following question was specifically addressed in this study: what are the differences in growth responses of the four species located in different successional stages to elevated CO_2 and increasing temperature?

2. Materials and methods

2.1. Plant materials

Seeds of the four species, *A. sphaerocephala*, *H. laeve*, *A. ordosica*, and *C. korshinskii*, were collected in the Mu Us Sandy land, and were randomly chosen with 20 replicates from sampling quadrants of the whole plant population to get an adequate representation of genetic variation (Zheng et al., 2003). The seeds were collected in 2002, then transported to Japan and stored at $4\,°C$ until they were sown. The seedlings emerged within 15 days and were then transferred to pots made of PVC (11.2 cm in diameter and 20 cm in height). Previous investigations indicated that pots of this size had no significant effect on root growth for the studied plants. After transfer to the pots, the seedlings were left for 30 days before the experiment began.

The pots were filled with prepared sand, which was collected from river beds in Japan, and washed several times with tap water.

The prepared sand used for the experiments was mixed from different particle size groups with proportions similar to the field conditions in the study area (Qi, 1998). The percentage composition (percent of gravimetric content) for the four particle 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. Finally, the mixed sand containing the four particle size groups was mixed with artificial clay (20% of the total volume) and this mixture was used as the soil for the experiment. The soil used in this experiment contained 3.47 g/kg organic matter, 0.65 g/kg total nitrogen, 0.26 g/kg available P (P_2O_5), and 21.25 g/kg available K (K_2O). This nutrient composition was prepared to simulate natural conditions. The drainage outlet at the bottom of the pots was covered with strips of nylon mesh to prevent the loss of soil while allowing drainage of excess water. The experiments were conducted in Japan in 2004.

2.2. Experimental design

The growth experiments were carried out within automatic temperature, humidity and light controlled growth chambers (KG-50HALS-W, Koito Co. Ltd., Japan). The chambers were set for 50/70% relative humidity (day/night) and daily photoperiods of 14 h ($600\,\mu mol\,m^{-2}\,s^{-1}$), using cool white fluorescent lights for the light conditions.

Two air temperature treatments ($15/25\,°C$ and $17.5/27.5\,°C$ – night/day) were distributed among four growth chambers with two chambers for each temperature regime. CO_2 concentrations of 400 and $800\,\mu mol\,mol^{-1}$, relating to reference and elevated CO_2 levels respectively, were maintained for each temperature treatment using an infrared gas analyzer (ZRH1DZY1-OAZYY, Fuji Electric Co. Ltd., Japan). A water supply regime of 11.25 mm every 3 days was applied for each treatment, which is equivalent to 112.5 mm per month. The control levels for the ambient temperature ($15/25\,°C$ night/day) and water supply (112.5 mm per month) regimes were set in accordance with the monthly average conditions during the main growing season ($15/25\,°C$ temperature and 112.5 mm rainfall per month from July to August) in the Mu Us Sandy land, based on the 30 year average of micro-environmental data (Qi, 1998). The $17.5/27.5\,°C$ increased temperature regime is based on predictions for this region from the general circulation models (Gao et al., 2003).

There were eight replicates (each replicate had one pot, one seedling per pot) per treatment for each species. At the beginning of the experiment, eight plants of each species were harvested immediately to provide initial growth values for each species to be used in the final growth analysis for each treatment (Xiong et al., 2000). Pots with seedlings were randomly assigned to each treatment. The pots were well watered then they were placed in the different growth chambers for the experiment (Machado and Paulsen, 2001). After the first week, seedlings in all treatments were watered every 3 days with tap water, and the locations of the seedlings were changed every 3 days. Plants had sufficient space to prevent the shading of smaller plants by larger ones (Clifton-Brown and Lewandowski, 2000). The experiment lasted for 8 weeks.

Two days before the final harvest, all replicates for each treatment were weighted using an electronic balance and then the soil surface and bottom of half of the pots were sealed to prevent soil evaporation. One day later, all pots were weighted again, so that transpiration could be determined. The height of each seedling was measured weekly throughout the experiment. After 8 weeks, the plants were harvested. Plants were divided into roots, shoots and leaves. Soil was washed from the roots by hand. The fresh weight of the leaves was measured using an electronic balance (Mettler PC 440, Mettler Instrument AG, Switzerland) and the leaf area was measured using a planimeter (Li-Cor 3100, Lincoln, NE, USA). Dry weights were determined after oven drying at $80\,°C$ for 3 days.

2.3. Parameter calculations

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

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

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

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

From the primary data the following variables were derived: leaf mass ratio (LMR; leaf mass/total plant mass, in $g\,g^{-1}$); leaf area ratio (LAR; leaf area/total plant mass, in $m^2\,kg^{-1}$); and water use efficiency (WUE; plant biomass increment/transpiration, in $g\,kg^{-1}$) (Poorter, 1999); height increment (presented for the time interval of 8 weeks).

2.4. Statistical tests

All observed values were log transformed before statistical analysis to achieve normality and homogeneous variances (Carey et al., 1998). The transformed values were analyzed using a three-way analysis of variance (ANOVA). If significant differences were found, Tukey's test was used to determine the mean differences between the treatments (Chen and Maun, 1999). All statistical analyses, including the test for homogeneity of variance, were performed using the SPSS 10.0 package (SPSS, 2000).

3. Results

The F values were significant for species, temperature and elevated CO_2 for all growth variables. The F values were insignificant for RGR, below ground to above ground biomass ratio (BAMR), NAR and WUE for all interactions, while the F values were significant for other growth variables for most interactions (Table 1).

3.1. Relative growth rate (RGR)

The RGR was highest for *A. ordosica* ($0.08\,g\,g^{-1}\,day^{-1}$ with the treatment of 15/25 °C and elevated CO_2) followed by *A. sphaerocephala*, then *H. laeve* and lowest for *C. korshinskii*. Elevated CO_2 levels significantly increased RGR for *A. sphaerocephala* at 15/25 °C,
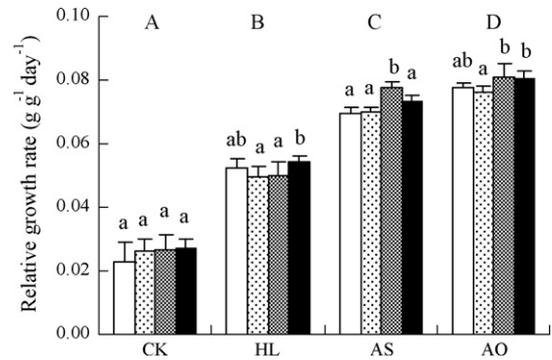

Fig. 1. Relative growth rate (±SE) of *Caragana korshinskii* (CK), *Hedysarum laeve* (HL), *Artemisia sphaerocephala* (AS), *Artemisia ordosica* (AO) under CO_2 concentration (400 μmol mol^{-1} (C1), 800 μmol mol^{-1} (C2)), and alternating temperatures (15/25 °C (T1), 17.5/27.5 °C (T2)) (night:day) in growth chamber. (□) C1T1, (⊡) C1T2, (▩) C2T1, (■) C2T2. Each bar represents the mean of eight replicates; bars with different lowercase letters are significantly different from each other for same species under various treatments, and different capital letters indicate difference among species at $P < 0.05$ (Tukey test).

and for *A. ordosica* and *H. laeve* at 17.5/27.5 °C, while it had no significant effect on *C. korshinskii*. The increased temperature combined with elevated CO_2 significantly increased the RGR for *H. laeve* and decreased the RGR for *A. sphaerocephala* (Fig. 1).

3.2. Dry matter allocation

The BAMR was lower for the two *Artemisia* species (0.2–0.3:1), but higher for *C. korshinskii* and *H. laeve* (0.8–1.6:1). Neither CO_2 nor temperature significantly affected the BAMR for the two *Artemisia* species. Elevated CO_2 significantly increased the BAMR at 17.5/27.5 and 15/25 °C for *C. korshinskii* and *H. laeve*, respectively (Fig. 2).

The LMR was higher for the two *Artemisia* species than for *C. korshinskii* and *H. laeve*. Neither CO_2 nor temperature significantly affected the LMR for *C. korshinskii* and the two *Artemisia* species, but the interaction of CO_2 and temperature affected the LMR for *A. sphaerocephala*. Elevated CO_2 decreased the LMR at the lower temperature for *H. laeve*. The higher temperature combined with elevated CO_2 increased the LMR for *H. laeve* (Table 1, Fig. 3).

3.3. Leaf morphological traits

The LAR was higher for *A. ordosica*, *A. sphaerocephala* and *C. korshinskii*, and lower for *H. laeve*. Neither CO_2 nor temperature alone significantly affected the LAR for *C. korshinskii* and *A. ordosica*

Table 1
Results of a three-way ANOVA with species, CO_2 concentration and temperature.

Variables	Effect						
	Species (S)	Elevated CO_2 (C)	Temperature (T)	S × C	S × T	C × T	S × C × T
RGR	4.7***	0.03**	0.02*	0.01^{ns}	0.01^{ns}	0.003^{ns}	0.01^{ns}
BAMR	108.4***	3.6*	3.7*	0.6^{ns}	2.2^{ns}	0.7^{ns}	1.3^{ns}
LMR	55.9***	5.5*	6.0*	1.1^{ns}	0.6^{ns}	0.0^{ns}	5.8**
LAR	12.0***	31.4***	16.2***	3.5*	0.7^{ns}	7.9**	2.8*
Height increment	502.7***	55.7***	54.2***	4.1*	29.0***	12.0***	0.7^{ns}
NAR	204.9***	35.2***	4.3*	0.7^{ns}	0.8^{ns}	3.4^{ns}	0.3^{ns}
Transpiration	314.8***	52.1***	3.9*	3.7*	7.4***	0.8^{ns}	4.9**
WUE	46.2***	70.1***	3.2*	1.1^{ns}	1.9^{ns}	0.2^{ns}	0.2^{ns}
DF	3	1	1	3	3	1	3

F-values were shown. Seedlings of four species were exposed to two levels of CO_2 concentration (400, 800 μmol mol^{-1}) and two levels of temperature (15/25, 17.5/27.5 °C) in growth chamber.

Note: Significance levels: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, $P \geq 0.05$.

Abbreviations: relative growth rate, RGR; below ground to above ground biomass ratio, BAMR; leaf mass ratio, LMR; leaf area ratio, LAR; net assimilation rate, NAR; water use efficiency, WUE.
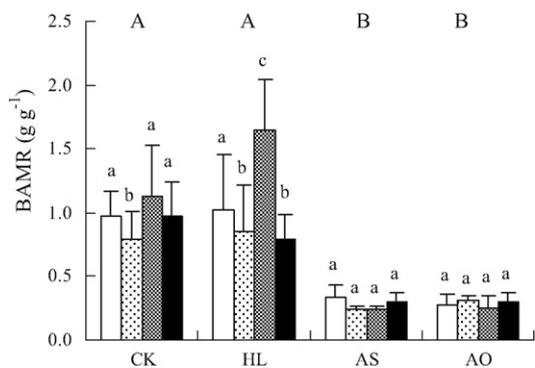
Fig. 2. Below ground to above ground biomass ratio (BAMR) (±SE) of four species. Other description is same as Fig. 1.
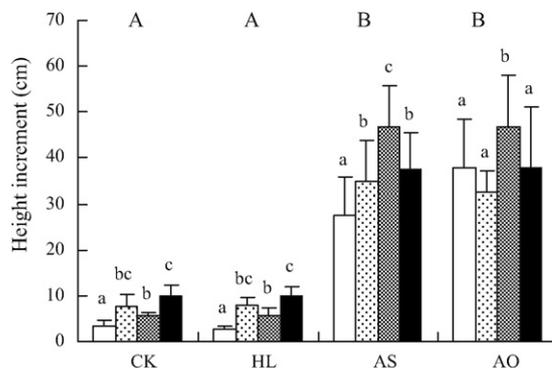

Fig. 3. Leaf mass ratio (±SE) of four species. Other description is same as Fig. 1.

Fig. 5. Height increment (presented for the time interval of 8 weeks) (±SE) of four species. Other description is same as Fig. 1.
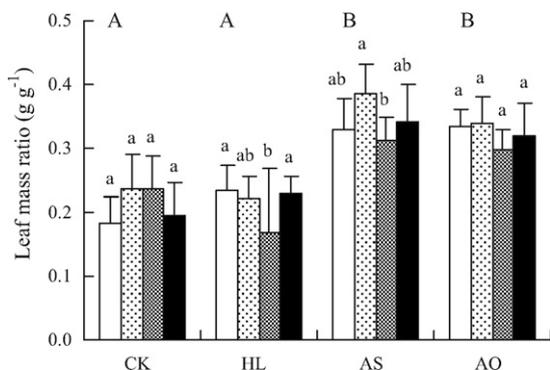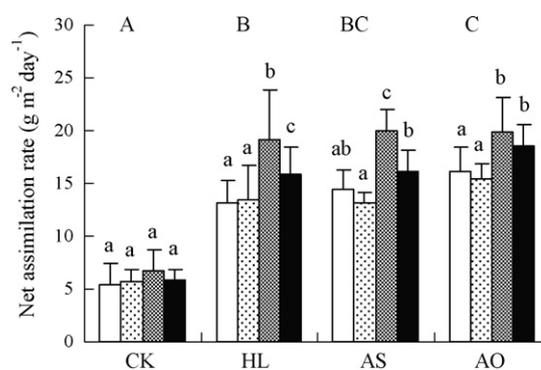

Fig. 6. Net assimilation rate (±SE) of four species. Other description is same as Fig. 1.

although their interaction affected the LAR for *A. ordosica*. Elevated CO_2 decreased the LAR at the lower temperature for *H. laeve* and *A. sphaerocephala*, while the higher temperature increased the LMR when combined with elevated CO_2 for *H. laeve* (Table 1, Fig. 4).

3.4. Growth height

The height increment was higher for *A. ordosica* (46.9 cm) and *A. sphaerocephala* (46.8 cm), and lower for *C. korshinskii* (10.0 cm) and *H. laeve* (10.1 cm). For all four species at the lower temperature (15/25 °C), elevated CO_2 significantly increased the height increment. At the higher temperature an increased height increment for *C. korshinskii* and *H. laeve* was observed under both CO_2 concentrations, an increased height increment was noted for *A. sphaerocephala* under current CO_2 conditions. The positive effect of the elevated CO_2 was decreased under higher temperature for the two *Artemisia* species (Fig. 5).
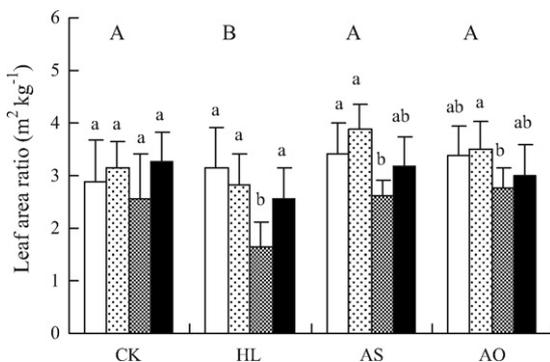

Fig. 4. Leaf area ratio (±SE) of four species. Other description is same as Fig. 1.

3.5. Physiological traits

The NAR was highest for *A. ordosica* and *A. sphaerocephala*, moderate for *H. laeve*, and lowest for *C. korshinskii*. The elevated CO_2 level significantly increased the NAR for all species except *C. korshinskii*. The higher temperature (17.5/27.5 °C) and elevated CO_2 significantly decreased the NAR for *A. sphaerocephala* and *H. laeve* (Fig. 6).

The transpiration was highest for *A. sphaerocephala* and *A. ordosica*, moderate for *H. laeve*, and lowest for *C. korshinskii*. Neither CO_2 nor temperature alone significantly affected transpiration, but their interaction had a significant effect on *C. korshinskii*. Elevated CO_2 at the higher temperature significantly decreased transpiration for *A. sphaerocephala* while elevated CO_2 at the lower temperature significantly decreased transpiration for *H. laeve* and *A. ordosica*. The higher temperature combined with elevated CO_2 decreased transpiration for *A. sphaerocephala* and increased transpiration for *H. laeve* (Tables 1 and 2).

The WUE was highest for *C. korshinskii*, and there was no significant difference between *A. ordosica*, *H. laeve* and *A. sphaerocephala*. The temperature had no significant effect on the WUE for all species except *C. korshinskii*. Elevated CO_2 significantly increased the WUE at lower temperature for all four species, but at the higher temperature it only significantly increased the WUE for *C. korshinskii*, and *A. sphaerocephala* (Table 3).

4. Discussion

It has been shown that arid and semi-arid vegetation shows growth increments of 0–40% under elevated CO_2 conditions (Morgan et al., 2001), so dryland plants were predicted to demonstrate a large relative increment in primary productivity (Melillo et al., 1993), which may aid the early survival of seedlings (Housman

Table 2
Results of multi-variable comparison of temperature and CO_2 effects on transpiration (g day^{-1}) (mean ± SE) of four species (Tukey test).

Species	400 μmol mol^{-1} CO_2, 15/25 °C	400 μmol mol^{-1} CO_2, 17.5/27.5 °C	800 μmol mol^{-1} CO_2, 15/25 °C	800 μmol mol^{-1} CO_2, 17.5/27.5 °C
Caragana korshinskii	4.5 ± 0.7[ab]	5.7 ± 1.2[a]	2.8 ± 1.2[b]	4.0 ± 0.7[ab]
Hedysarum laeve	18.6 ± 0.5[a]	18.3 ± 2.1[a]	8.4 ± 1.2[b]	14.3 ± 1.8[c]
Artemisia sphaerocephala	24.5 ± 3.5[a]	24.3 ± 3.3[a]	23.9 ± 2.1[a]	15.6 ± 4.2[b]
Artemisia ordosica	26.7 ± 3.2[a]	25.2 ± 4.7[ab]	22.6 ± 3.7[b]	23.0 ± 3.9[b]

Seedlings of four species were exposed to two levels of CO_2 concentration and two levels of temperature in growth chamber. Different lowercase letters indicate significant differences in transpiration between different temperature and CO_2 treatments for same species, $P < 0.05$.

et al., 2003). Morgan et al. (2001) reported a 26–47% increase in above ground biomass in elevated CO_2 plots and the increased growth increment was even more obvious during a drought year with a biomass increment of 95%. Gifford (1979) proposed that elevated CO_2 could compensate for drought induced reductions in growth, and it was further suggested that the beneficial effects of elevated CO_2 on plant growth would increase progressively with increasing water deficit (Centritto et al., 2002). Although the measured growth increment in this experiment was smaller than in some previous results, our results showed similar trends, i.e., elevated CO_2 increased the RGR for three of the studied species (Fig. 1), especially the two *Artemisia* species which have higher transpiration demands compared with *C. korshinskii* and *H. laeve* (Table 2) and therefore might encounter a greater soil water deficit.

The beneficial effect of elevated CO_2 on plant production may result from various reasons, including direct photosynthetic enhancements due to CO_2 enrichment (Geissler et al., 2009; Niklaus and Körner, 2004) and an increase in the amount of photosynthate available for the development of resource acquisition structures due to enhanced water use efficiency (Bazzaz, 1990). Mbikayi et al. (1983) reported that the increased production of biomass with CO_2 enrichment was associated with an increased net assimilation rate and relative growth rate. Our results indicate that elevated CO_2 induced a significant increase in net assimilation rate and water use efficiency for the two *Artemisia* species, which therefore resulted in an increased RGR although this was not significant for some treatments.

It is often assumed that the leaf area increment (LAI) will be higher in a CO_2 enriched atmosphere (Norby et al., 2003), but Drake et al. (1997) concluded that at canopy closure the LAI of field grown crops is not generally affected by CO_2. The LAI of a native grassland has also been unaffected by elevated CO_2 (Niklaus and Körner, 2004). Our results showed that the leaf area ratio and leaf mass ratio did not increase significantly with elevated CO_2 in most conditions, which indicates that the RGR increment for the four species is not the result of an increased LAI.

Increasing the atmospheric CO_2 level stimulates root biomass and root length production in many plant species (Pritchard and Rogers, 2000) and has led to increased soil exploration and increased water capture (Obrist and Arnone, 2003). Nijs et al. (1989) reported that the promoted allocation towards the root system under CO_2 enrichment became greater in the course of canopy development with *Lolium perenne*. Our results showed similar behavior for *C. korshinskii* and *H. laeve*, but not for the two *Artemisia* species. The first two species had a higher BAMR with

elevated CO_2 (Fig. 2), which provides the ability to enable them to acquire more water when the soil water is limited and reduce the effect of water deficit. Therefore, *C. korshinskii* and *H. laeve* are more adaptive to dry environments given the scenario of CO_2 enrichment.

It has been identified that a complete water balance in the semi-arid grassland of Israel showed a 10% decrease in evapotranspiration at elevated CO_2, compared with pre-industrial levels, during the wet part of the growing season (Morgan et al., 2004). Morgan et al. (1994) reported that stomatal conductance was reduced by 27 and 36%, and transpiration was reduced 24 and 20% in leaves of *Pascopyrum smithii* and *Bouteloua gracilis* respectively under elevated CO_2 levels. The decline in transpiration was also observed in our experiment for all species except *C. korshinskii* as the other species had comparatively higher transpiration rates.

The change in transpiration inevitably affected the water use efficiency. Lecain et al. (2003) observed improvements in WUE, soil water conservation and plant water relationships in a semiarid ecosystem under elevated CO_2 conditions, and concluded that, although a 14% improvement in soil water content was small, the effect might be larger in a water limited ecosystems. Jones et al. (1985) observed an approximate twofold increase in water use efficiency when the CO_2 level doubled. The four species in our study showed increased water use efficiencies under elevated CO_2 conditions especially at the current temperature regime (15/25 °C). Because water is the primary limiting factor in desert ecosystems (Smith et al., 2000), increasing water use efficiency under elevated CO_2 conditions may be especially important in arid lands (Nowak et al., 2004). However, the observed effect of mitigation of the water stress by elevated CO_2 could depend on water status of the plants. Additional experiment with more precisely controlled irrigation and experiment that soil and plant water status is monitored should be performed when one would like to seriously address water stress mitigation by elevated CO_2.

The effect of CO_2 on growth may be temperature dependent (Overdieck et al., 1998), so the interactions between CO_2 and temperature must be taken into account in the interpretation of results (Saralabai et al., 1997). This was also observed in interpreting the results of our experiments. For the two *Artemisia* species, which had the highest transpiration, increasing the temperature decreased the RGR under both CO_2 concentrations and the RGR showed decreasing trends under elevated CO_2 levels when the temperature increased from 15/25 to 17.5/27.5 °C (meaning that soil moisture decreased) although these differences were not significant for most treatments (Fig. 1). As increasing temperature may enhance soil

Table 3
Results of multi-variable comparison of temperature and CO_2 effects on water use efficiency (g kg^{-1}) (mean ± SE) of four species (Tukey test).

Species	400 μmol mol^{-1} CO_2, 15/25 °C	400 μmol mol^{-1} CO_2, 17.5/27.5 °C	800 μmol mol^{-1} CO_2, 15/25 °C	800 μmol mol^{-1} CO_2, 17.5/27.5 °C
Caragana korshinskii	8.2 ± 3.0[ab]	5.8 ± 0.7[a]	14.6 ± 3.0[c]	10.7 ± 2.5[b]
Hedysarum laeve	3.1 ± 0.4[a]	2.7 ± 0.9[a]	6.4 ± 1.9[b]	4.2 ± 0.6[ab]
Artemisia sphaerocephala	3.3 ± 0.9[a]	3.4 ± 0.7[a]	5.5 ± 0.3[b]	6.3 ± 1.6[b]
Artemisia ordosica	3.1 ± 0.6[a]	3.0 ± 0.6[ab]	4.4 ± 0.2[b]	4.1 ± 0.9[ab]

Seedlings of four species were exposed to two levels of CO_2 concentration and two levels of temperature in growth chamber. Different lowercase letters indicate significant differences in water use efficiency between different temperature and CO_2 treatments for same species, $P < 0.05$.

water stress and thus alleviate the benefit of elevated CO_2 levels, care should be taken when evaluating the effects of elevated CO_2 levels on semi-arid ecosystems.

In conclusion, elevated CO_2 level alone may increase biomass, net assimilation rate, and water use efficiency, while decreasing transpiration for the two *Artemisia* species and *H. laeve* species of mobile and semi-fixed dune environments. However, elevated CO_2 combined with increased temperature tend to decrease the RGR and height increment for the two *Artemisia* species.

Acknowledgments

References

Bazzaz, F.A., 1990. The response of natural ecosystems to rising global CO_2 levels. Annu. Rev. Ecol. Sci. 21, 167–196.

Beismann, H., Schweingruber, F., Speck, T., Körner, C., 2002. Mechanical properties of spruce and beech wood grown in elevated CO_2. Trees 16, 511–518.

Bernacchi, C.J., Coleman, J.S., Bazzaz, F.A., McConnaughay, K.D.M., 2000. Biomass allocation in old-field annual species grown in elevated CO_2 environments: no evidence for optimal partitioning. Glob. Change Biol. 6, 855–863.

Carey, E.V., Callaway, R.M., DeLucia, E.H., 1998. Increased photosynthesis offsets cost of allocation to sapwood in an arid environment. Ecology 79, 2281–2291.

Centritto, M., Lucas, M.E., Jarvis, P.G., 2002. Gas exchange, biomass, whole-plant water-use efficiency and water uptake of peach (*Prunus persica*) seedlings in response to elevated carbon dioxide concentration and water availability. Tree Physiol. 22, 699–706.

Chen, H., Maun, M.A., 1999. Effects of sand burial depth on seed germination and seedling emergence of *Cirsium pitcheri*. Plant Ecol. 140, 53–60.

Clifton-Brown, J.C., Lewandowski, I., 2000. Water use efficiency and biomass partitioning of three different *Miscanthus* genotypes with limited and unlimited water supply. Ann. Bot. 86, 191–200.

Diaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in relation to global change. J. Veg. Sci. 8, 463–474.

Drake, B.G., Gonzalez-Meler, M.A., Long, S.P., 1997. More efficient plants: a consequence of rising atmospheric CO_2. Annu. Rev. Plant Physiol. Plant M. Biol. 48, 609–636.

Dregne, H.E., 1991. Global status of desertification. Ann. Arid Zone 30, 179–185.

Field, C.B., Jackson, R.B., Mooney, H.A., 1995. Stomatal responses to increased CO_2: implications from the plant to the global scale. Plant Cell Environ. 18, 1214–1225.

Gao, X.J., Ding, Y.H., Zhao, Z.C., 2003. Climate change due to greenhouse effects in China as simulated by a regional climate model. Part II. Climate change. Acta Meteor. Sinica 61, 29–38.

Geissler, N., Hussin, S., Koyro, H.W., 2009. Interactive effects of NaCl salinity and elevated atmospheric CO_2 concentration on growth, photosynthesis, water relations and chemical composition of the potential cash crop halophyte *Aster tripolium* L. Environ. Exp. Bot. 65, 220–231.

Gifford, R.M., 1979. Growth and yield of CO_2-enriched wheat under water-limited conditions. Aust. J. Plant Physiol. 6, 367–378.

Housman, D.C., Zitzer, S.F., Huxman, T.E., Smith, S.D., 2003. Functional ecology of shrub seedlings after a natural recruitment event at the Nevada Desert FACE Facility. Glob. Change Biol. 9, 718–728.

Hunt, R., 1990. Basic Growth Analysis. Unwin Hyman Limited, London, UK.

IPCC Work Group 1, 2001. Third Assessment Report. Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge, UK.

Jones, P., Allen Jr., L.H., Jones, J.W., 1985. Responses of soybean canopy photosynthesis and transpiration to whole-day temperature changes in different CO_2 environments. Agron J. 77, 242–249.

Lecain, D.R., Morgan, J.A., Mosier, A.R., Nelson, J.A., 2003. Soil and plant water relations determine photosynthetic responses of C_3 and C_4 grasses in a semi-arid ecosystem under elevated CO_2. Ann. Bot. 92, 41–52.

Machado, S., Paulsen, G.M., 2001. Combined effects of drought and high temperature on water relations of wheat and sorghum. Plant Soil 233, 179–187.

Mbikayi, N.T., Hileman, D.R., Bhattacharya, N.C., Ghosh, P.P., Biswas, P.K., 1983. Effects of CO_2 enrichment on the physiology and biomass production in cowpeas (*Vigna unguiculata* L.) grown in open top chambers. In: Proceedings of the International Congress of Plant Physiology, New Delhi, pp. 640–645.

Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore III, B., Vörösmarty, C.J., Schloss, A.L., 1993. Global climate change and terrestrial net primary production. Nature 363, 234–240.

Morgan, J.A., Hunt, H.W., Monz, C.A., LeCain, D.R., 1994. Consequences of growth at two carbon dioxide concentrations and two temperatures for leaf gas exchange in *Pascopyrum smithii* (C_3) and *Bouteloua gracilis* (C_4). Plant Cell Environ. 17, 1023–1033.

Morgan, J.A., LeCain, D.R., Mosier, A.R., Milchunas, D.G., 2001. Elevated CO_2 enhances water relations and productivity and affects gas exchange in C_3 and C_4 grasses of the Colorado shortgrass steppe. Glob. Change Biol. 7, 451–466.

Morgan, J.A., Pataki, D.E., Körner, C., Clark, H., del Grosso, S.J., Grünzweig, J.M., Knapp, A.K., Mosier, A.R., Newton, P.C.D., Niklaus, P.A., Nippert, J.B., Nowak, R.S., Parton, W.J., Polley, H.W., Shaw, M.R., 2004. Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. Oecologia 140, 11–25.

Naumburg, E., Housman, D.C., Huxman, T.E., Charlet, T.N., Loik, M.E., Smith, S.D., 2003. Photosynthetic responses of Mojave Desert shrubs to free air CO_2 enrichment are greatest during wet years. Glob. Change Biol. 9, 276–285.

Nijs, I., Impens, I., Behaeghe, T., 1989. Leaf and canopy responses of *Lolium perenne* to long-term atmospheric carbon-dioxide concentrations. Planta 177, 312–320.

Niklaus, P.A., Körner, C., 2004. Synthesis of a six year study of calcareous grassland responses to in situ CO_2 enrichment. Ecol. Monogr. 74, 491–511.

Norby, R.J., Sholtis, J.D., Gunderson, C.A., Jawdy, S.S., 2003. Leaf dynamics of a deciduous forest canopy: no response to elevated CO_2. Oecologia 136, 574–584.

Nowak, R.S., Zitzer, S.F., Babcock, D., Smith-Longozo, V., Charlet, T.N., Coleman, J.S., Seemann, J.R., Smith, S.D., 2004. Elevated atmospheric CO_2 does not conserve soil water in the Mojave Desert. Ecology 85, 93–99.

Obrist, D., Arnone, J.A., 2003. Increasing CO_2 accelerates root growth and enhances water acquisition during early stages of development in *Larrea tridentate*. New Phytol. 159, 175–184.

Overdieck, D., Kellomaki, S., Wang, K.Y., 1998. Do the effects of temperature and CO_2 interact? In: Jarvis, P.G. (Ed.), European Forests and Global Change. Cambridge University Press, Cambridge, pp. 236–273.

Poorter, L., 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. Funct. Ecol. 13, 396–410.

Pritchard, S.G., Rogers, H.H., 2000. Spatial and temporal deployment of crop roots in CO_2-enriched environments. New Phytol. 147, 55–71.

Qi, J., 1998. Aerial Sowing for Sand Control in China. Science Press, Beijing.

Riedo, M., Gyalistras, D., Fuhrer, J., 2001. Pasture responses to elevated temperature and doubled CO_2 concentration: assessing the spatial pattern across an alpine landscape. Clim. Res. 17, 19–31.

Saralabai, V.C., Vivekandan, M., Sureshbabu, R., 1997. Plant responses to high CO_2 concentration in the atmosphere. Photosynthetica 33, 7–37.

Smith, S.D., Huxman, T.E., Zitzer, S.F., Charlet, T.N., Housman, D.C., Coleman, J.S., Fenstermaker, L.K., Seemann, J.R., Nowak, R.S., 2000. Elevated CO_2 increases productivity and invasive species success in an arid ecosystem. Nature 408, 79–82.

SPSS, 2000. SPSS 10.0 for Windows. SPSS Inc., USA.

Wall, G.W., Garcia, R.L., Kimball, B.A., Hunsaker, D.J., Pinter, P.J., Long Jr., S.P., Osborne, C.P., Hendrix, D.L., Wechsung, F., Wechsung, G., Leavitt, S.W., LaMorte, R.L., Idso, S.B., 2006. Interactive effects of elevated carbon dioxide and drought on wheat. Agron J. 1982, 354–381.

Xiao, C.W., Zhou, G.S., Ceulemans, R., 2003. Effects of elevated temperature on growth and gas exchange in dominant plant species from Maowusu sandland, China. Photosynthetica 41, 565–569.

Xiong, F.S., Mueller, E.C., Day, T.A., 2000. Photosynthetic and respiratory acclimation and growth response of Antarctic vascular plants to contrasting temperature regimes. Am. J. Bot. 87, 700–710.

Yoon, S.T., Hoogenboom, G., Flitcroft, I., Bannayan, M., 2009. Growth and development of cotton (*Gossypium hirsutum* L.) in response to CO_2 enrichment under two different temperature regimes. Environ. Exp. Bot. 67, 178–187.

Zavaleta, E.S., Shaw, M.R., Chiariello, N.R., Thomas, B.D., Cleland, E.E., Field, C.B., Mooney, H.A., 2003. Grassland responses to three years of elevated temperature, CO_2, precipitation, and N deposition. Ecol. Monogr. 734, 585–604.

Zheng, Y.R., Xie, Z.X., Gao, Y., Shimizu, H., Jiang, L.H., Yu, Y., 2003. Ecological restoration in northern China: germination characteristics of 9 key species in relation to air seeding. Belg. J. Bot. 136, 129–138.