

Chun-Wang Xiao · Osbert J. Sun ·
Guang-Sheng Zhou · Jing-Zhu Zhao · Gang Wu

Interactive effects of elevated CO₂ and drought stress on leaf water potential and growth in *Caragana intermedia*

Received: 3 November 2004 / Accepted: 7 April 2005 / Published online: 5 May 2005
© Springer-Verlag 2005

Abstract We studied the responses of leaf water potential (Ψ_w), morphology, biomass accumulation and allocation, and canopy productivity index (CPI) to the combined effects of elevated CO₂ and drought stress in *Caragana intermedia* seedlings. Seedlings were grown at two CO₂ concentrations (350 and 700 $\mu\text{mol mol}^{-1}$) interacted with three water regimes (60–70%, 45–55%, and 30–40% of field capacity of soil). Elevated CO₂ significantly increased Ψ_w , decreased specific leaf area (SLA) and leaf area ratio (LAR) of drought-stressed seedlings, and increased tree height, basal diameter, shoot biomass, root biomass as well as total biomass under the all the three water regimes. Growth responses to elevated CO₂ were greater in well-watered seedlings than in drought-stressed seedlings. CPI was significantly increased by elevated CO₂, and the increase in CPI became stronger as the level of drought stress increased. There were significant interactions between elevated CO₂ and drought stress on leaf water potential, basal diameter, leaf area, and biomass accumulation. Our results suggest that elevated CO₂ may enhance drought avoidance and improved water relations, thus weakening the effect of drought stress on growth of *C. intermedia* seedlings.

Keywords Biomass allocation · Canopy production index · Morphology · Specific leaf area · *Caragana intermedia*

Introduction

Atmospheric carbon dioxide concentration has been predicted to double its current level before the end of this century as a result of human activities (Bazzaz 1990; Watson et al. 1990; Keeling et al. 1995; Morison and Lawlor 1999; Houghton et al. 2001). A doubling of the atmospheric CO₂ and rises in other greenhouse gases, such as methane, nitrous oxide, and CFCs, could increase the average global temperature by 1.4–5.8°C and change precipitation patterns in the next 100 years (Houghton et al. 2001). Global warming and altered precipitation patterns due to increases in atmospheric CO₂ concentrations are of major international concerns for both policy-makers and scientific communities (Ottman et al. 2001). Further, the elevated CO₂ may bring about increased aridity in some areas of the planet (Gregory et al. 1997; Houghton et al. 2001). Therefore, it is of great importance to elucidate the effects of elevated CO₂ in conjunction with drought stress on plants.

In the past decades, the effects of elevated CO₂ on plants have been documented in numerous papers and review articles, and the consensus of most of these reports is that elevated CO₂ increases plant growth (Ceulemans and Mousseau 1994; Poorter et al. 1996; Drake and Gonzalez-Meler 1997; Jach and Ceulemans 1999; Norby et al. 2001; Calfapietra et al. 2003; Janssens et al. 2005). However, only relatively few investigations have considered the direct consequences of soil water deficits imposed on plants that are exposed to elevated CO₂ atmospheres (Serraj et al. 1999). In studies concerned with the interactive effects of elevated CO₂ and water stress, some found that elevated CO₂ significantly increased plant growth (Kimball et al. 1995; Centritto et al. 1999; Serraj et al. 1999; Ottman et al. 2001; Wall et al. 2001), possibly because plants growing in elevated CO₂ improved water relations under drought stress and were able to withstand the drought stress better (Grant et al. 1999; Wall 2001; Wall et al. 2001; Wullschleger et al. 2002). However, there were also studies finding no positive effects of elevated CO₂ on plant growth under drought-stressed conditions (Mo et al. 1992; Ward et al. 1999; Derner et al. 2003).

C.-W. Xiao (✉) · O. J. Sun · G.-S. Zhou
Laboratory of Quantitative Vegetation Ecology, Institute of Botany, The Chinese Academy of Sciences,
Beijing 100093, P.R. China
e-mail: cw-xiao@ibcas.ac.cn
Tel.: +86-10-62836289
Fax: +86-10-82595962

J.-Z. Zhao · G. Wu
Department of Systems Ecology, Research Center For Eco-Environmental Sciences, The Chinese Academy of Sciences,
Beijing 100085, P.R. China

Maowusu sandland is located in the middle of the northern China with a semi-arid climate (37°30'–39°20' N; 107°20'–113°30' E). *Caragana intermedia* Kuanget H.C. Fu is a dominant desert shrub of the region, occurring mainly in the semi-fixed and fixed dunes of Maowusu sandland. The plant is used by local people as feed for livestock, and as shelter for protection of soils against desertification (Zhang 1994). At present, desertification, coupled with rapid soil erosion, is becoming a critical issue in Maowusu sandland. As water is often a limiting resource for plant recruitment, growth, physiology, nutrient dynamics, and net ecosystem productivity in the semi-arid area (Zhang 1994; Danin 1996), most of the previous researches on desert plants in Maowusu sandland have been mainly concerned with drought stress tolerance (Xiao and Zhou 2001; Xiao et al. 2002). However, with the perception of decreasing precipitation with the global climate change scenarios in much of the semi-arid regions (Fu and An 2002), the interactive effects between elevated CO₂ and drought stress may be more detrimental to changes in vegetation than the effect of either elevated CO₂ or drought stress alone.

In order to determine if exposure to elevated CO₂ would allow desert plants to better withstand drought stress, we investigated the effects of elevated CO₂ on leaf water potential, morphology, biomass accumulation and allocation, and canopy productivity index of *C. intermedia* with varying soil moisture. Our study was carried out in the context of scientifically predicting the changes of dominant plant community and effectively preventing desertification in Maowusu sandland as part of ecosystem restoration project of arid and semi-arid lands of north-western China (Zhang et al. 2000).

Materials and methods

Plant species and growth conditions

Caragana intermedia Kuanget H.C. Fu belongs to the family of *Fabaceae*, and is a deciduous shrub that occurs in Inner Mongolia, Ningxia, and Shanxi in China. The shrub is typically about 0.7–3.0 m tall and has odd, plumose, compound leaves. It is one of the dominant shrubs that fix soil and reduce wind speed, thus actively mitigating desertification in Maowusu sandland.

Seeds of *C. intermedia* were collected from a single tree at Maowusu sandland (39°29.66' N and 110°11.47' E, altitude 1295 m) in 2000. In April 2001, seeds were germinated in sand and seedlings were transplanted individually into black plastic pots (10 cm in diameter and 10 cm in height) filled with sand. The volume of the pot was sufficient to avoid pot-binding effects. The pots remained in the open field under natural environmental conditions until the start of the experiment. A slow releasing fertilizer (14% N, 14% P, 14% K) was added to the sand at the rate of 1 g per pot in end May.

Experimental design

The experiment consisted of two CO₂ concentrations interacting with three levels of watering regimes. On 2 June 2001, seedlings of similar size were transferred into two identical greenhouse compartments (6 m × 3 m × 3 m): one with elevated CO₂ that doubled the current level (700 ± 10 μmol mol⁻¹ for day and night), and another with ambient CO₂ (350 ± 5 μmol mol⁻¹ for day and night). Pure CO₂ was supplied from storage tanks with vaporization facilities. A slight airflow was maintained with fans that provided an outgoing air stream in each compartment. The concentrations of CO₂ inside the chambers were continuously monitored with infrared gas analyzer (Fuji ZSB, Japan) and controlled by a computer.

Each CO₂ treatment contained 60 seedlings randomly divided into groups of 20 and subjected to three soil water regimes. Pots in both compartments were placed on racks to ensure proper drainage and to avoid interference from groundwater. The pots were spaced 20 cm apart in all directions to minimize competition for light, and rows were oriented in a north-south direction.

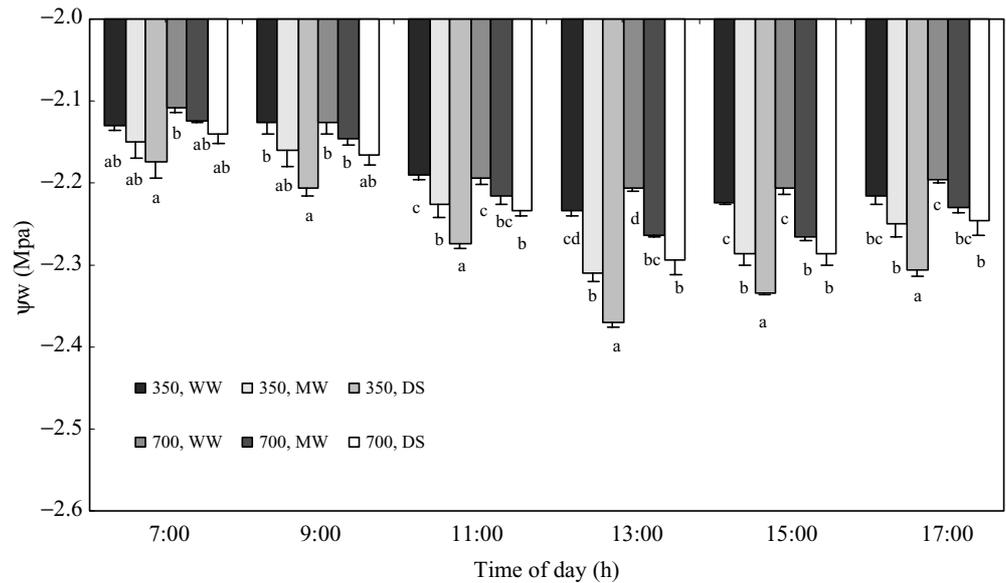
The three water regimes were 60–70%, 45–55%, and 30–40% of soil water content soil at field capacity, simulating well-watered (WW), moderate-watered (MW), and drought-stressed (DS) conditions. The soil water contents were determined by weighing the pots daily and calculated based on the pot weight, soil dry weight, and the expected soil water holding capacity. Water was added following at the time of weighing to maintain the predetermined water content in each pot. Additionally, in the last stage of the experiment, the wet weight per seedling was estimated and added to the pot weight.

The photosynthetic photon flux density (PPFD) in both compartments was measured with a LCA-4 portable photosynthesis system (ADC, Hoddesdon, UK) at the start of the experiment, and was not found to differ between the two compartments. Due to light interception by the greenhouse covers, PPFD inside the compartments was reduced to approximately 90% of the level outside. No artificial light was used in the experiment. Temperature and relative humidity in both compartments were recorded continuously with WHM3 thermo-hygrometer (Tianjin, China), and were found to be similar between the two compartments. Therefore, the climatic conditions in both compartments were assumed to be identical.

Measurements of leaf water potential

Leaf water potential (Ψ_w) was determined with a modified HR-33T dewpoint microvoltmeter (Wescor, Logan, UT, USA). Three uppermost fully expanded sunlit leaves within each treatment were collected for Ψ_w measurement at 2-h intervals from 7:00 to 17:00 on 7 September 2001.

Fig. 1 Diurnal change of leaf water potential (Ψ_w) for *C. intermedia* seedlings exposed to ambient and elevated CO_2 (350 and 700 $\mu\text{mol mol}^{-1}$) under well-watered (WW), moderate-watered (MW), and drought-stressed (DS) conditions on 7 September 2001. Boxes represent treatment means \pm standard error. Treatments with different letters are significantly different ($P < 0.05$) according to post-ANOVA Duncan's test



Growth measurements

At the end of the experiment (17 September 2001), basal diameter, height, and number of leaves ≥ 5 mm in length were measured on each seedling. Twelve seedlings of each treatment were randomly chosen and used for measurements of leaf area and dry mass. Leaf area was measured with an automatic leaf area meter (Hayashi-Denkoh AAM-8, Tokyo, Japan). Leaves, shoots, and roots were separated and dried at 85°C for 48 h and weighed. Leaf area ratio (LAR: leaf area to total biomass, $\text{cm}^2 \text{g}^{-1}$), root mass ratio (RMR: root biomass to total biomass, g g^{-1}), root:shoot ratio (RSR: total root biomass to total stem and branches biomass, g g^{-1}), and specific leaf area (SLA: leaf area to leaf biomass, $\text{cm}^2 \text{g}^{-1}$) were calculated according to Beadle (1993). Also, canopy productivity index (CPI: total growth per unit leaf area, g cm^{-2}) was estimated according to Sigurdsson et al. (2001).

Statistical analysis

Data management and statistical analyses were performed using SPSS software (SPSS, Chicago, IL). The data were analyzed with three-way ANOVA, using sample times, CO_2 concentrations, and water regimes as main effects for leaf

water potential, and with two-way ANOVA, using CO_2 concentrations and water regimes as main effects for growth characteristics. Interactions among the effects were also analyzed. All statistical tests were considered significant at $P \leq 0.05$ and Duncan's post-ANOVA pairwise analysis was used to determine significant differences between means.

Results

Leaf water potential

The diurnal patterns of Ψ_w were similar among the treatments: Ψ_w was highest in morning, and decreased until reaching its minimum at midday, and then increased in the afternoon (Fig. 1). The Ψ_w varied significantly with time ($P < 0.001$; Table 1). Seedlings exposed to elevated CO_2 had less negative Ψ_w under all three water regimes, especially at midday, but significant effects were only observed under drought-stressed conditions (Fig. 1). Drought decreased Ψ_w significantly in both ambient CO_2 and elevated CO_2 (Fig. 1). There was a significant interaction between sample time and water, and between CO_2 and water in the effect on Ψ_w ($P < 0.01$; Table 1), but not between sample time and CO_2 , and sample time, CO_2 , and water on Ψ_w ($P > 0.05$; Table 1).

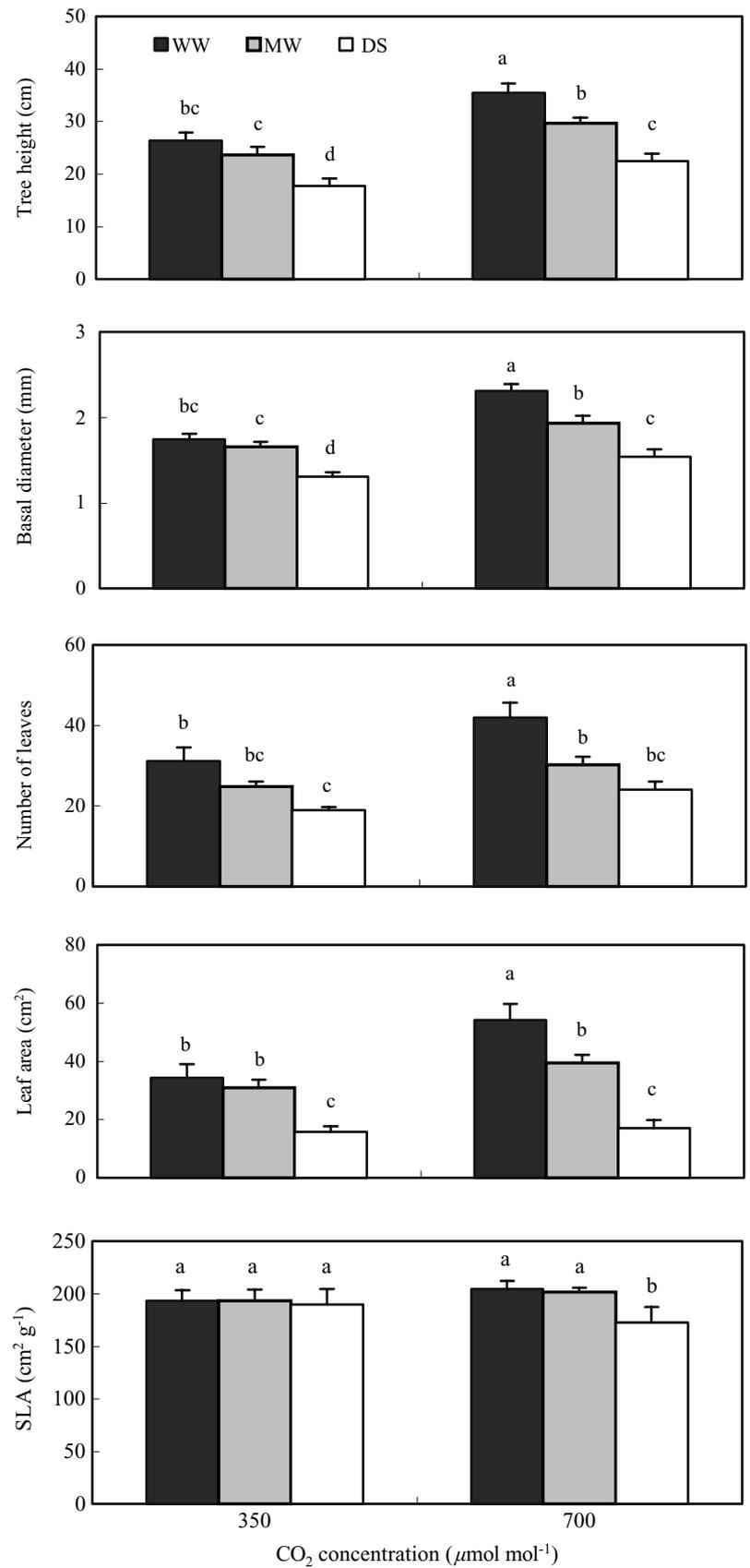
Table 1 *F*-values of three-way ANOVA for leaf water potential (Ψ_w) of *C. intermedia* seedlings measured at six sample times (time), two CO_2 concentrations of 350 and 700 $\mu\text{mol mol}^{-1}$ (CO_2), and three

water regimes of well-watered, moderate-watered, and drought stress conditions (water)

Source	Time	CO_2	Water	Time \times CO_2	Time \times Water	$\text{CO}_2 \times$ Water	Time \times $\text{CO}_2 \times$ Water
df	5, 72	1, 72	2, 72	5, 72	10, 72	2, 72	10, 72
Ψ_w	139.1***	50.1***	107.5***	1.6 ^{NS}	2.6**	6.9**	0.2 ^{NS}

Significance level: NS: not significant $P > 0.05$. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fig. 2 Tree height, basal diameter, number of leaves, leaf area, and specific leaf area (SLA) of *C. intermedia* seedlings exposed to ambient and elevated CO₂ (350 and 700 $\mu\text{mol mol}^{-1}$) under well-watered (WW), moderate-watered (MW), and drought-stressed (DS) conditions. Boxes represent treatment means \pm standard error. Treatments with different letters are significantly different ($P < 0.05$) according to post-ANOVA Duncan's test



Morphology

Elevated CO₂ significantly increased the seedling height and basal diameter under the three water regimes (Fig. 2). Elevated CO₂ only increased number of leaves and leaf area under the well-watered condition and decreased SLA under the drought-stressed condition (Fig. 2). Drought significantly decreased the seedling height, basal diameter, number of leaves, and leaf area at both ambient and elevated CO₂, but only decreased SLA at elevated CO₂ (Fig. 2). There was a significant interaction between CO₂ and water in the effect on basal diameter and leaf area ($P < 0.05$; Table 2), but not for tree height, number of leaves, and SLA ($P > 0.05$; Table 2).

Biomass accumulation

Elevated CO₂ significantly increased shoot biomass, root biomass, and total biomass under the three water regimes, but increased the leaf biomass significantly only under the well-watered condition (Fig. 3). Elevated CO₂ increased total biomass by 79% under the well-watered condition, by 61% under moderate-watered condition, and by 53% under drought-stressed condition. Drought significantly decreased the leaf biomass, shoot biomass, root biomass, and total biomass at both ambient and elevated CO₂ (Fig. 3). There was a significant interaction between CO₂ and water in the effect on leaf biomass, shoot biomass, and total biomass ($P < 0.05$, $P < 0.01$, and $P < 0.01$, respectively; Table 2), but not on root biomass ($P > 0.05$; Table 2).

Biomass allocation

Elevated CO₂ only significantly decreased the LAR under the drought-stressed condition (Fig. 4). Drought decreased LAR at elevated CO₂, and significantly increased RMR and RSR at both ambient and elevated CO₂ (Fig. 4). There were no significant interactions between CO₂ and water on LAR, RMR, and RSR ($P > 0.05$; Table 2).

Canopy productivity index

CPI was significantly increased by elevated CO₂ ($P < 0.01$; Table 2; Fig. 5). The CO₂-induced increase in CPI became stronger as drought stress increased (Fig. 5). At the ambient

CO₂, there was no significant effect of drought stress on CPI (Fig. 5). There was no significant interaction between CO₂ and water on CPI ($P > 0.05$; Table 2).

Discussion

In this study, we found that elevated CO₂ led to lower internal water deficits as the soil-water content became depleted, indicating improved plant water relations at elevated CO₂. This finding is consistent with other studies examining the interaction between elevated CO₂ and water stress in the effect on plant water relations (e.g. Wall et al. 2001). Our finding of increased Ψ_w by elevated CO₂ under varying water regimes is consistent with results for many other species (Sionit et al. 1980; Bhattacharya et al. 1990; Kirkham et al. 1991; Prior et al. 1991; Wall et al. 2001). Moreover, a significant interaction between elevated CO₂ and drought in the effect on Ψ_w was observed in our study. Our results indicate that elevated CO₂ would enhance drought avoidance and improve water relations for *C. intermedia* seedlings in future climate. Improved water relations would alleviate the deleterious effects of water stress on physiological process, such as photosynthesis, and enhance growth during a drought (Hsiao and Jing 1987; Nelson and MacAdam 1989).

Idso (1988) suggested that elevated CO₂ would have more beneficial effects on plants experiencing non-lethal drought conditions than when they were well watered. In the present study, elevated CO₂ significantly increased shoot biomass, root biomass, and total biomass under three different water regimes, and total biomass responses to elevated CO₂ were greater in well-watered plants than under drought stress. This finding contradicts the work of Idso (1988). In our study there was a significant interaction between elevated CO₂ and drought stress in the effect on seedling height, basal diameter, number of leaves, leaf area, and biomass of the plant tissues. These are in agreement with several similar studies (Townend 1993, 1995; Guehl et al. 1994; Tschaplinski et al. 1995). However, some studies with crop plants demonstrated that growth responses to elevated CO₂ were greater in drought-stressed plants than in well-watered plants (Sionit et al. 1980; Morison and Gifford 1984; Marks and Strain 1989; Clifford et al. 1993; Kimball et al. 1995; Pinter et al. 1996; Clark et al. 1999; De Luis et al. 1999).

Table 2 *F*-values of two-way ANOVA for tree height, basal diameter, number of leaves, leaf area, specific leaf area (SLA), leaf biomass, shoot biomass, root biomass, total biomass, leaf area ratio (LAR), root mass ratio (RMR), root:shoot ratio (RSR), and canopy

productivity index (CPI) of *C. intermedia* seedlings measured at two CO₂ concentrations of 350 and 700 $\mu\text{mol mol}^{-1}$ (CO₂) and three water regimes of well-watered, moderate-watered, and drought-stressed conditions (water)

Source	df	Tree height	Basal diameter	Number of leaves	Leaf area	SLA	Leaf biomass	Shoot biomass	Root biomass	Total biomass	LAR	RMR	RSR	CPI
CO ₂	1, 66	30.1***	35.5***	13.1***	11.8***	0.4 ^{NS}	15.6***	56.5***	57.6***	62.0***	13.2***	1.4 ^{NS}	0.5 ^{NS}	9.5**
Water	2, 66	27.4***	33.7***	19.7***	31.8***	1.6 ^{NS}	37.5***	40.1***	20.3***	45.2***	1.7 ^{NS}	9.2***	6.6**	4.2*
CO ₂ × Water	2, 66	1.2 ^{NS}	3.2*	0.9 ^{NS}	3.4*	1.0 ^{NS}	3.6*	5.4**	2.9 ^{NS}	5.0**	1.5 ^{NS}	0.8 ^{NS}	0.01 ^{NS}	2.3 ^{NS}

Significance level: NS: not significant $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Fig. 3 Leaf biomass, shoot biomass, root biomass, and the total biomass of *C. intermedia* seedlings exposed to ambient and elevated CO₂ (350 and 700 $\mu\text{mol mol}^{-1}$) under well-watered (WW), moderate-watered (MW), and drought-stressed (DS) conditions. Boxes represent treatment means + standard error. Treatments with different letters are significantly different ($P < 0.05$) according to post-ANOVA Duncan's test

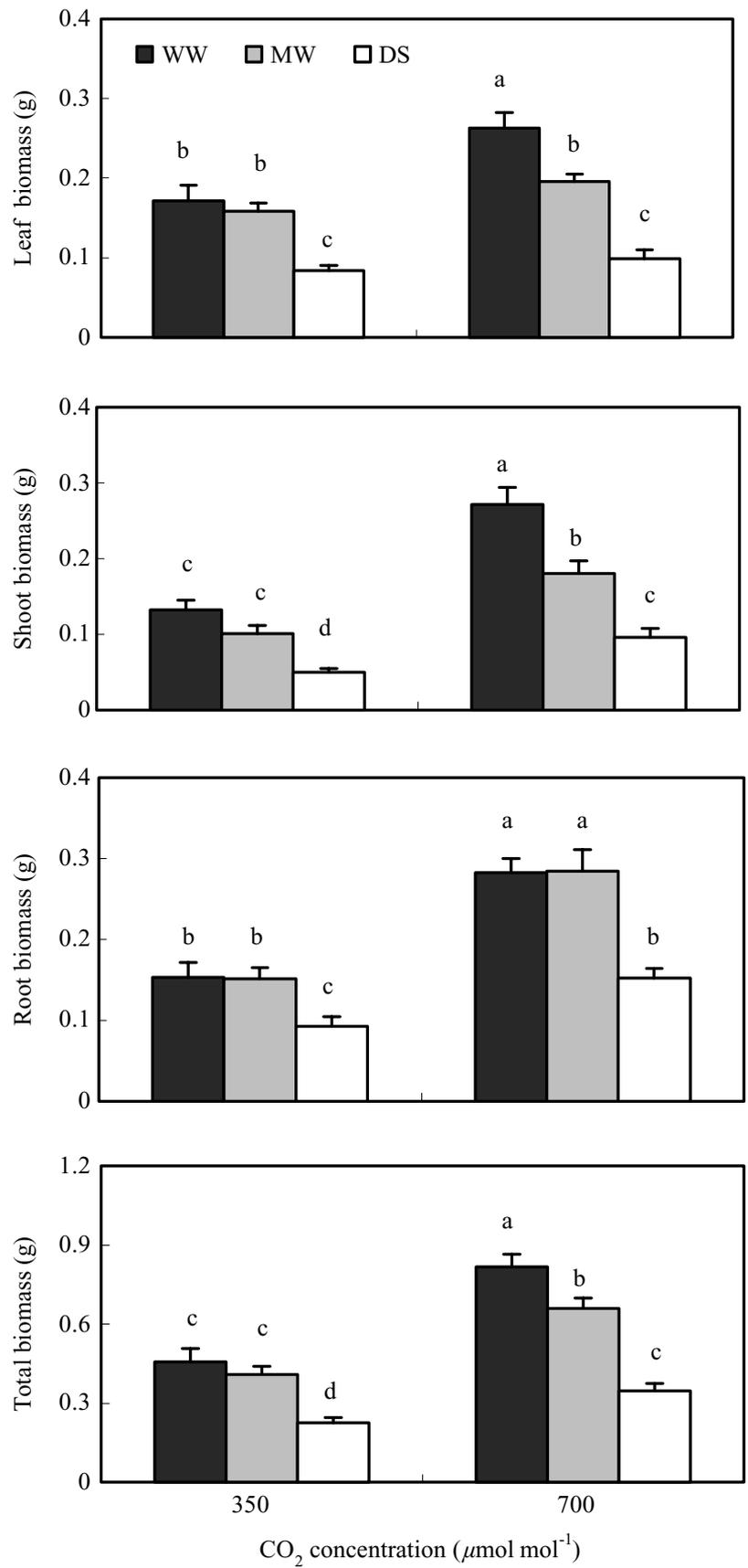


Fig. 4 Leaf area ratio (LAR), root mass ratio (RMR), and root:shoot ratio (RSR) of *C. intermedia* seedlings exposed to ambient and elevated CO₂ (350 and 700 $\mu\text{mol mol}^{-1}$) under well-watered (WW), moderate-watered (MW), and drought-stressed (DS) conditions. Boxes represent treatment means + standard error. Treatments with different letters are significantly different ($P < 0.05$) according to post ANOVA Duncan's test

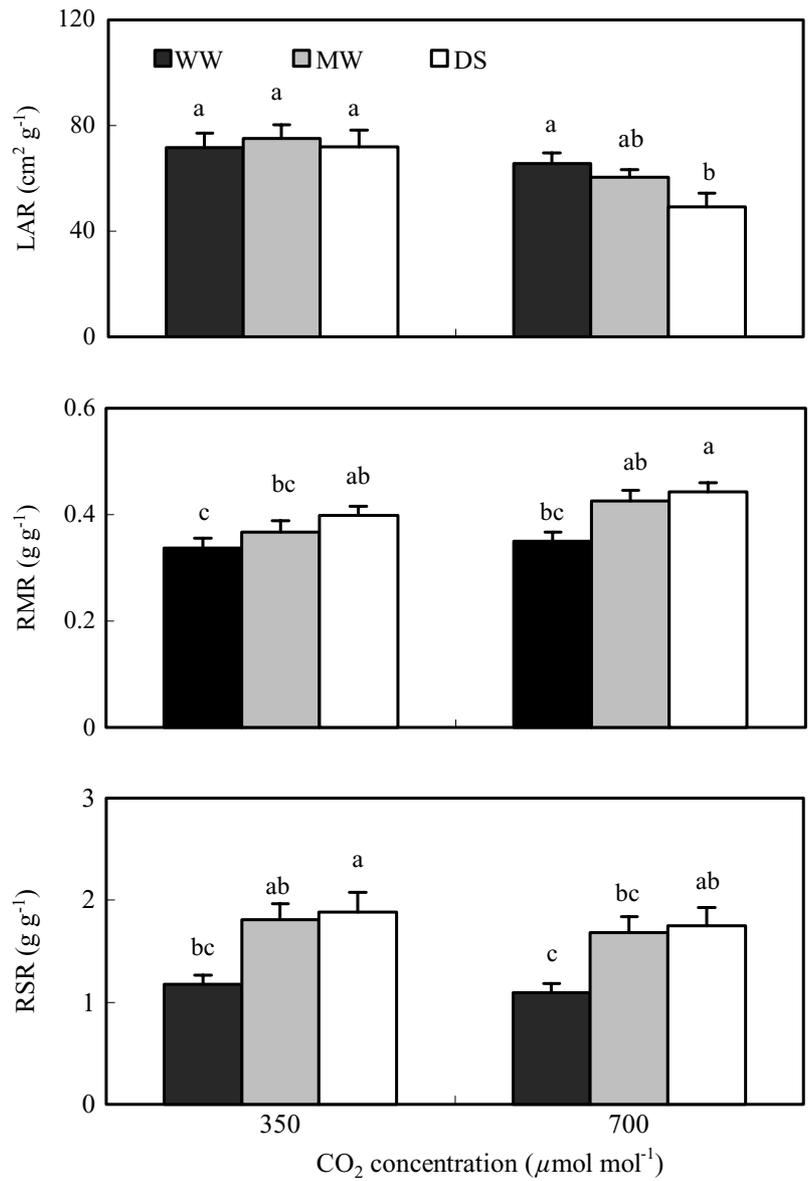
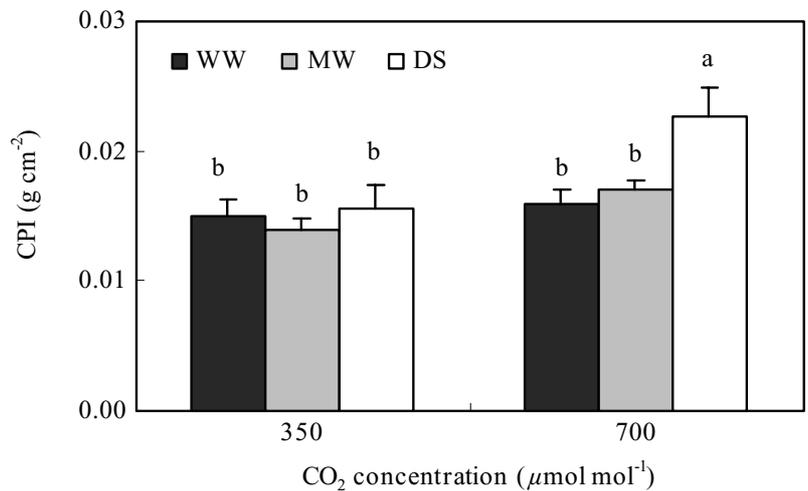


Fig. 5 Canopy productivity index (CPI) of *C. intermedia* seedlings exposed to ambient and elevated CO₂ (350 and 700 $\mu\text{mol mol}^{-1}$) under well-watered (WW), moderate-watered (MW), and drought-stressed (DS) conditions. Boxes represent treatment means + standard error. Treatments with different letters are significantly different ($P < 0.05$) according to post ANOVA Duncan's test



Drought adapted tissue generally has lower SLA because of xeromorphic features such as thicker cuticles, mesophyll, and epidermal cells, or higher trichome density (Hsiao and Acevedo 1974; Turner and Kramer 1980; Kramer 1983; Fernández et al. 2002; Marron et al. 2003; Zhang et al. 2004). No significant drought effects were observed in SLA at ambient CO₂ in this study. This may be because *C. intermedia* is a desert plant species and preadapted to drought conditions, thus is morphologically less plastic. It has compound leaves that are very small and thick (Xiao et al. 2002). Elevated CO₂ significantly decreased SLA under drought stress, indicating that elevated CO₂ increased carbohydrate content per unit leaf area during a drought. We postulate that an increase in carbohydrate supply in elevated CO₂ could enhance adaptation of leaf tissue of *C. intermedia* seedlings to drought stress in favor of minimizing water loss.

The biomass allocation also showed a significant interaction between elevated CO₂ and drought stress. Elevated CO₂ significantly decreased the proportion of leaf area to total biomass (LAR) under drought-stressed condition, indicating that elevated CO₂ might lead to improved productivity of a smaller photosynthetic area under drought-stressed condition. In other words, the seedlings grown at elevated CO₂ were more efficient photosynthetically compared with seedlings grown at ambient CO₂ under drought-stressed condition. This hypothesis was strongly supported by our findings that elevated CO₂ significantly enhanced CPI, and the increase in CPI was greatest at the lowest water availability.

Generally, the greatest increase in biomass in the elevated CO₂ treatment has been found belowground in the roots (Norby and O'Neill 1991; El Kohen et al. 1992; El Kohen and Mousseau 1994; Rogers et al. 1996; Jach et al. 2000). In this study, however, there were no significant effects on RMR and RSR in response to elevated CO₂ under different water regimes, similar to the results of several other studies (e.g. Townend 1993; Centritto et al. 1999). Such lack of increased RMR and RSR has been shown to be an effect of sufficient or high nutrient availability (e.g. Sigurdsson et al. 2001).

Drought stress significantly increased RMR and RSR, consistent with results in our previous study with the same species (Xiao and Zhou 2001). The present study is in agreement with the theory of the functional balance proposed by Brouwer (1963), which predicts that plants would react to a limited water availability with a relative increase in the flow of assimilates to the root, leading to an increased RMR. Plants with more roots are able to explore the soil water more efficiently and therefore grow and survive better under water stress (Chartzoulakis et al. 1993; van Hees 1997; Fernández et al. 2002).

In conclusion, the results of this study confirmed the beneficial effects of elevated CO₂ on *C. intermedia* seedlings exposed to drought-stressed conditions. This finding helps to understand how the species would change its ecological adaptive strategies through ecophysiological and structural adjustments under future elevated CO₂ and changed precipitation patterns.

Acknowledgements The work was financially supported by the Knowledge Innovation Project of the Chinese Academy of Sciences (KZCX1-SW-01-12) and the Project was sponsored by SRF for ROCS, SEM. The authors are very grateful to Prof. Xin-Shi Zhang, Prof. Lian-Min Wang, and Dr. Zhen-Zhu Xu for their constructive comments and help with the research.

References

- Bazzaz FA (1990) The response of natural ecosystems to the rising global CO₂ levels. *Annu Rev Ecol Syst* 21:167–196
- Beadle CL (1993) Growth analysis. In: Hall DO, Scurlock JMO, Bolhar-Nordenkamp HR, Leegood RC, Long SP (eds) Photosynthesis and production in a changing environment, a field and laboratory manual. Chapman and Hall, London, pp 36–46
- Bhattacharya NC, Hileman DR, Ghosh PP, Musser RL, Bhattacharya S, Biswas PK (1990) Interaction of enriched CO₂ and water stress on the physiology of and biomass production in sweet potato grown in open-top chambers. *Plant Cell Environ* 13:933–940
- Brouwer R (1963) Some aspects of the equilibrium between overground and underground plant parts. *Jaarboek IBS, Wageningen*
- Calfapietra C, Gielen B, Galema ANJ, Lukac M, De Angelis P, Moscatelli MC, Ceulemans R, Scarascia-Mugnozza G (2003) Free-air CO₂ enrichment (FACE) enhances biomass production in a short-rotation poplar plantation. *Tree Physiol* 23:805–814
- Centritto M, Lee HSJ, Jarvis PG (1999) Interactive effects of elevated [CO₂] and drought on cherry (*Prunus avium*) seedlings I. Growth, whole-plant water use efficiency, and water loss. *New Phytol* 141:129–140
- Ceulemans R, Mousseau M (1994) Tansley Review no. 71: Effects of elevated atmospheric CO₂ on woody plants. *New Phytol* 127:425–446
- Chartzoulakis K, Noitsakis B, Therios I (1993) Photosynthesis, plant growth, and dry matter distribution in kiwifruit as influenced by water deficits. *Irrig Sci* 14:1–5
- Clark H, Newton PCD, Barker DJ (1999) Physiological and morphological responses to elevated CO₂ and soil moisture deficit of temperate pasture species growing in an established plant community. *J Exp Bot* 50:233–242
- Clifford SC, Stronach IM, Mohamed AD, Azam-Ali SN, Crout NMJ (1993) The effects of elevated atmospheric carbon dioxide and water stress on light interception, dry mass production, and yield in stands of groundnut (*Arachis hypogaea* L.). *J Exp Bot* 44:1763–1770
- Danin A (1996) *Plants of desert dunes*. Springer, Berlin Heidelberg New York
- De Luis I, Irigoyen JJ, Sanchez-Diaz M (1999) Elevated CO₂ enhances plant growth in droughted N₂-fixing alfalfa without improving water status. *Physiol Plant* 107:84–89
- Derner JD, Johnson HB, Kimball BA, Pinter PJ Jr, Polley HW, Tischler CR, Boutton TW, Lamorte RL, Wall GW, Adam NR, Leavitt SW, Ottman MJ, Matthias AD, Brooks TJ (2003) Above- and below-ground responses of C₃-C₄ species mixtures to elevated CO₂ and soil water availability. *Global Change Biol* 9:452–460
- Drake BG, Gonzalez-Meler MA (1997) More efficient plants: a consequence of rising atmospheric CO₂? *Annu Rev Plant Physiol Plant Mol Biol* 48:609–639
- El Kohen A, Mousseau M (1994) Interactive effects of elevated CO₂ and mineral nutrition on growth and CO₂ exchange of sweet chestnut seedlings (*Castanea sativa*). *Tree Physiol* 14:697–690
- El Kohen A, Rouhier H, Mousseau M (1992) Changes in dry weight and nitrogen partitioning induced by elevated CO₂ depend on soil nutrient availability in sweet chestnut (*Castanea sativa* Mill). *Ann Sci For* 49:83–90
- Fernández RJ, Wang MB, Reynolds JF (2002) Do morphological changes mediate plant responses to water stress? A steady-state experiment with two C₄ grasses. *New Phytol* 155:79–88

- Fu CB, An ZS (2002) Study of aridification in northern China—A global change issue facing directly the demand of nation. *Earth Sci Front* 9:271–275
- Grant RF, Wall GW, Kimball BA, Frumau KFA, Pinter PJ Jr, Hunsaker DJ, LaMorte RL (1999) Crop water relations under different CO₂ and irrigation: testing of *ecosys* with the free air CO₂ enrichment (FACE) experiment. *Agric For Meteorol* 95:27–51
- Gregory JM, Mitchell JFB, Brady AJ (1997) Summer drought in northern midlatitudes in a time-dependent CO₂ climate experiment. *J Climate* 10:662–686
- Guehl JM, Picon C, Aussenac G, Gross P (1994) Interactive effects of elevated CO₂ and soil drought on growth and transpiration efficiency and its determinants in two European trees species. *Tree Physiol* 14:707–724
- Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (2001) IPCC 2001: climate change 2001: the scientific basis. Cambridge University Press, New York
- Hsiao TC, Acevedo E (1974) Plant responses to water deficits, water use efficiency, and drought resistance. *Agric For Meteorol* 14:69–84
- Hsiao TC, Jing J (1987) Leaf and root expansion growth in response to water deficits. In: Cosgrove DJ, Kniewel DP (eds) *Physiology of cell expansion during plant growth*. American Society of Plant Physiology, Rockville, MD, pp 180–192
- Idso SB (1988) Three phases of plant response to atmospheric CO₂ enrichment. *Plant Physiol* 87:5–7
- Jach ME, Ceulemans R (1999) Effects of elevated atmospheric CO₂ on phenology, growth, and crown structure of Scots pine (*Pinus sylvestris*) seedlings after two years of exposure in the field. *Tree Physiol* 19:289–300
- Jach ME, Laureysens I, Ceulemans R (2000) Above- and below-ground production of young Scots pine (*Pinus sylvestris* L.) trees after three years of growth in the field under elevated CO₂. *Ann Bot* 85:789–798
- Janssens IA, Medlyn B, Gielen B, Laureysens I, Jach ME, van Hove D, Ceulemans R (2005) Carbon budget of *Pinus sylvestris* saplings after four years of exposure to elevated atmospheric carbon dioxide concentration. *Tree Physiol* 25:325–337
- Keeling CD, Whorf TP, Wahlen M, van der Plicht J (1995) Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature* 375:660–670
- Kimball BA, Pinter PJ, Garcia RL, LaMorte RL, Wall GW, Hunsaker DJ, Wechsung G, Wechsung F, Kartschall T (1995) Productivity and water use of wheat under free-air carbon dioxide enrichment. *Global Change Biol* 1:429–442
- Kirkham MB, He H, Bolger TP, Lawlor DJ, Kanemasu ET (1991) Leaf photosynthesis and water use of big bluestem under elevated carbon dioxide. *Crop Sci* 31:1589–1594
- Kramer PJ (1983) Water relations of plants. Academic, New York, 489pp
- Marks S, Strain BR (1989) Effects of drought and CO₂ enrichment on competition between two old-field perennials. *New Phytol* 111:181–186
- Marron N, Dreyer E, Boudouresque E, Delay D, Petit JM, Delmotte FM, Brignolas F (2003) Impact of successive drought and re-watering cycles on growth and specific leaf area of two *Populus canadensis* (Moench) clones, 'Dorskamp' and 'Luisa_Avanzo'. *Tree Physiol* 23:1225–1235
- Mo G, Nie D, Kirkham MB, He H, Ballou LK, Caldwell FW, Kanemasu ET (1992) Root and shoot weight in a tallgrass prairie under elevated carbon dioxide. *Environ Exp Bot* 32:193–201
- Morison JIL, Gifford RM (1984) Plant growth and water use with limited water supply in high CO₂ concentrations. I. Plant dry weight, partitioning, and water-use efficiency. *Aust J Plant Physiol* 11:375–384
- Morison JIL, Lawlor DW (1999) Interactions between increasing CO₂ concentration and temperature on plant growth. *Plant Cell Environ* 22:659–682
- Nelson CJ, MacAdam JW (1989) Cellular dynamics in the leaf growth zone. *Curr Top Plant Biochem Physiol* 8:207–223
- Norby RJ, O'Neill EG (1991) Leaf area compensation and nutrient interactions in CO₂-enriched seedlings of yellow poplar (*Liriodendron tulipifera* L.). *New Phytol* 117:515–528
- Norby RJ, Todd DE, Fults J, Johnson DW (2001) Allometric determination of tree growth in a CO₂-enriched sweetgum stand. *New Phytol* 150:477–487
- Ottman MJ, Kimball BA, Pinter PJ, Wall GW, Vanderlip RL, Leavitt SW, LaMorte RL, Matthias AD, Brooks TJ (2001) Elevated CO₂ increases sorghum biomass under drought conditions. *New Phytol* 150:261–273
- Pinter PJ Jr, Kimball BA, Garcia RL, Wall GW, Hunsaker DJ, LaMorte RL (1996) Free-air CO₂ enrichment: responses of cotton and wheat crops. In: Koch GW, Mooney HA (eds) *Carbon dioxide and terrestrial ecosystems*. Academic, San Diego, CA, pp 215–264
- Poorter H, Roument C, Campbell BD (1996) Interspecific variation in the growth response of plants to elevated CO₂: a search for functional types. In: Körner C, Bazzaz FA (eds) *Carbon dioxide, populations, and communities*. Academic, San Diego, CA, pp 375–411
- Prior SA, Roger HH, Sionit N, Patterson RP (1991) Effects of elevated atmospheric CO₂ on water relations of soyabean. *Agr Ecosyst Environ* 35:13–25
- Rogers HH, Prior SA, Runion GB (1996) Root to shoot ratio of crops as influenced by CO₂. *Plant Soil* 187:229–248
- Serraj R, Allen LH, Sinclair TR (1999) Soybean leaf growth and gas exchange response to drought under carbon dioxide enrichment. *Global Change Biol* 5:283–291
- Sigurdsson BD, Thorgeirsson H, Linder S (2001) Growth and dry-matter partitioning of young *Populus trichocarpa* trees during three years of elevated CO₂ and fertilisation. *Tree Physiol* 21:941–950
- Sionit N, Hellmers H, Strain BR (1980) Growth and yield of wheat under CO₂ enrichment and water stress. *Crop Sci* 20:687–690
- Townend J (1993) Effects of elevated carbon dioxide and drought on the growth and physiology of clonal Sitka spruce plants (*Picea sitchensis* (Bong.) (Carr.)). *Tree Physiol* 13:389–399
- Townend J (1995) Effects of elevated CO₂, water, and nutrient on *Picea sitchensis* (Bong.) Carr. seedlings. *New Phytol* 130:193–206
- Tschaplinski TJ, Stewart DB, Hanson PJ, Norby RJ (1995) Interactions between drought and on elevated CO₂ growth and gas exchange of seedlings of three deciduous tree species. *New Phytol* 129:63–71
- Turner NC, Kramer PJ (1980) Adaptation of plants to water and high temperature stress. Wiley, New York, 482
- van Hees AFM (1997) Growth and morphology of pedunculate oak (*Quercus robur* L) and beech (*Fagus sylvatica* L) seedlings in relation to shading and drought. *Ann Sci For* 54:9–18
- Wall GW (2001) Elevated atmospheric CO₂ alleviates drought stress in wheat. *Agr Ecosyst Environ* 87:261–271
- Wall GW, Brooks TJ, Adam NR, Cousins AB, Kimball BA, Pinter PJ Jr, LaMorte RL, Triggs J, Ottman ML, Leavitt SW, Matthias AD, Williams DG, Webber AN (2001) Elevated atmospheric CO₂ improved sorghum plant water status by ameliorating the adverse effects of drought. *New Phytol* 152:231–248
- Ward JK, Tissue DT, Thomas RB, Strain BR (1999) Comparative responses of model C₃ and C₄ plants to drought in low and elevated CO₂. *Global Change Biol* 5:857–867
- Watson RT, Rodhe H, Oeschger H, Seigenthaler U (1990) Greenhouse gases and aerosols. In: Houghton JT, Jenkins GJ, Ephraums JJ (eds) *Climate change. The IPCC scientific assessment*, Cambridge University Press, Cambridge, pp1–40
- Wullschlegel SD, Tschaplinski TJ, Norby RJ (2002) Plant water relations at elevated CO₂—implications for water-limited environments. *Plant Cell Environ* 25:319–331
- Xiao CW, Zhou GS (2001) Effect of simulated precipitation change on growth, gas exchange, and chlorophyll fluorescence of *Caragana intermedia* Kuanget H.C.Fu in Maowusu sandland. *Chin J Appl Ecol* 12:692–696

- Xiao CW, Zhou GS, Ma FY (2002) Effect of water supply change on morphology and growth of dominant plants in Maowusu sandland. *Acta Phytoecol Sin* 26(1):69–76
- Zhang P, Shao G, Zhao G, Master DCL, Parker GR, Dunning JB, Li Q (2000) China's forest policy for the 21st century. *Science* 288:2135–2136
- Zhang X, Zang R, Li C (2004) Population differences in physiological and morphological adaptations of *Populus davidiana* seedlings in response to progressive drought stress. *Plant Sci* 166:791–797
- Zhang XS (1994) The ecological background of the Maowusu sandland the principles and optimal models for grass land management. *Acta Photoecol Sin* 18:1–6