Effects of elevated temperature on growth and gas exchange in dominant plant species from Maowusu sandland, China

Chun-Wang XIAO[*,+], Guang-Sheng ZHOU[*], and R. CEULEMANS[**]

Laboratory of Quantitative Vegetation Ecology, Institute of Botany, The Chinese Academy of Sciences, Beijing 100093, P.R. China[*]
Department of Biology, Research Group of Plant and Vegetation Ecology, University of Antwerpen (UIA), Universiteitsplein 1, B-2610 Wilrijk, Belgium[**]

Abstract

We compared the effect of elevated temperature on morphological development, biomass accumulation and allocation, and gas exchange of three dominant plants (*Caragana intermedia* Kuanget H.C. Fu, *Hedysarum mongolicum* Turcz., and *Artemisia ordosica* Krasch.) growing in Chinese Maowusu sandland. Plants were grown in two temperature chambers (25/20, 28/23 °C, day/night) during 60 d. Tree height, number of leaves, and leaf area were increased in *C. intermedia* and *H. mongolicum* seedlings, while in *A. ordosica* temperature only affected tree height. Elevated temperature increased biomass and reduced the root : shoot ratio in *C. intermedia* and *H. mongolicum* seedlings, but not in *A. ordosica* seedlings. The net photosynthetic rate (P_N) and transpiration rate (E) were increased at days 40 and 60 in *C. intermedia* and *H. mongolicum* seedlings, while in *A. ordosica* seedlings no significant effects on E were observed, and P_N was increased only at day 60. Water use efficiency (WUE) was reduced at days 40 and 60 in *H. mongolicum* seedlings, and at day 60 in *C. intermedia* seedlings. No temperature effect on WUE was observed in *A. ordosica* seedlings. These different responses indicate that climate change could alter plant communities in Maowusu sandland.

Additional key words: biomass allocation; net photosynthetic rate; root : shoot ratio; transpiration rate; water use efficiency.

Introduction

It is now predicted that future increases in greenhouse gas emissions are projected to increase global atmospheric temperature by 1.4–5.8 °C in the next 100 years as a result of the impacts of human population growth (Houghton *et al*. 2001). Change in the exchange of mass, energy, and momentum resulting from atmospheric warming will influence the establishment, survival, and reproduction of plants (Woodward 1992). In the past decades, some of these responses to climate warming have been studied in various terrestrial species (*e.g*. Chapin 1983, Farrar 1989, DeLucia *et al*. 1992, Harte and Shaw 1995, Schwarz *et al*. 1997, Gunn and Farrar 1999, Loik *et al*. 2000). Plant morphology, biomass, and physiology for most of these species were affected by climate warming.

Maowusu sandland, located on the middle part of Chinese north desert (37º30'–39º20'N, 107º20'–113º30'E) (Yao *et al*. 1992), contains typical deserts, desertified grasslands, as well as typical grassland. And Maowusu sandland is one of the shrub and sub-shrub 'kingdoms' in the global temperature arid zones, where *Caragana intermedia* Kuanget H.C.Fu, *Hedysarum mongolicum* Turcz., and *Artemisia ordosica* Krasch. are the dominant shrubs and sub-shrub, and they have been used by local people as feed for livestock as well as to protect against desertification (Zhang 1994). At present, climate is warming in the Chinese north desert, such that these ecosystems may already be experiencing climate stress (Chi 1994). Field studies and simulated drought effects on growth and gas exchange in the three dominant species have been reported previously (*e.g*. Jiang and He 1999, Xiao and Zhang 2001, Xiao and Zhou 2001), but the temperature effects associated with climate warming have not been reported. The main objective of this study was to assess how elevated temperature affects morphology, biomass, and gas exchange in the three dominant species, and how they adapt to elevated temperature by different eco-physiological and structural adjustments.

Received 22 September 2003, *accepted* 7 November 2003.
[+]Fax: +86-10-82595962, e-mail: cwxiao@ns.ibcas.ac.cn
Abbreviations: E – transpiration rate; P_N – net photosynthetic rate; WUE – water use efficiency.
Acknowledgements: The authors are very grateful to Prof. Zhang Xinshi and Prof. Ivan Janssens for their help in the research. The work was financially supported by the Knowledge Innovation Project of the Chinese Academy of Sciences (KZCX1-SW-01-12) and the Project-sponsored by SRF for ROCS, SEM.

Materials and methods

Plant species and experimental design: *Caragana intermedia* Kuanget H.C. Fu belongs to the family of Fabaceae, and is a deciduous shrub that occurs in the Inner Mongolia Autonomous Region, Ninxia Autonomous Region and Shanxi Province of China. The shrub is typically about 0.7–3.0 m tall and has odd, plumose, compound leaves. It is one of the dominant shrub species that fixes soil and reduces wind speed, and thus actively mitigates desertification in Maowusu sandland. *Hedysarum mongolicum* Turcz. belongs to the family of Fabaceae, and is a deciduous sub-shrub occurring in Northeast China, Inner Mongolia Autonomous Region, Xinzang Autonomous Region, and Shanxi Province of China. This species is about 1.5–2.0 m tall with odd, plumose, compound leaves. It is one of the dominant plants in fixed dune and semi-fixed dune in Maowusu sandland. *Artemisia ordosica* Krasch. belongs to the family of Asteraceae, and is a deciduous sub-shrub and occurs in Inner Mongolia Autonomous Region, Ningxia Autonomous Region, and Shanxi Province of China. The species is about 0.6–1.0 m tall with plumose, full split leaves. It is also one of the dominant plants in the semi-fixed and fixed dunes in Maowusu sandland.

Seedlings were grown for 60 d in two *CMP3000* chambers (1.5×0.8×1.5 m), in Beijing, China. Seeds of *C. intermedia*, *H. mongolicum*, and *A. ordosica* were collected randomly from one mother tree per species at Maowusu sandland (39º29.66'N and 110º11.47'E, altitude 1295 m) in 1999. Seeds were germinated separately in sand and then transplanted into pots. The pots were filled with sand collected from Maowusu sandland and 10 granules of slow releasing fertiliser (14 % N, 14 % P, 14 % K) was added at the start of the experiment. Physical and chemical properties of the sand are as follows: diameter of grain size 0.5±0.063 mm; water capacity 5.73 %; pH 8.3; organic matter 0.462 %; total N 0.0337 %; total P 0.0261 %; total K 0.0385 %. After two weeks, 25 seedlings per species were transferred to the chambers.

The mean growing-season temperature in the area of origin of the seeds was about 25 °C during daytime and 20 °C at night. Therefore, chamber temperatures were maintained at 25/20 °C (day/night) in the ambient treatment and 28/23 °C in the elevated treatment. In the two chambers, temperature was examined using a thermocouple sensor. The photosynthetically active radiation in both chambers was about 300 µmol m^{-2} s^{-1} and frequently checked using a *LCA-4* portable photosynthesis system (*ADC*, Hoddesdon, UK). Soil water content was about 4.0 %, which is the mean growing-season moisture content in the area of origin.

Measurements: Net photosynthetic rate, P_N [µmol m^{-2} s^{-1}] and transpiration rate, E [mmol m^{-2} s^{-1}] were measured at days 40 and 60 with a portable photosynthesis system (*LCA4, ADC*) on the uppermost, fully expanded leaf of *C. intermedia*, *H. mongolicum*, and *A. ordosica* seedlings. Water use efficiency, WUE [mmol mol^{-1}] was defined as the ratio of P_N to E.

Ten seedlings were non-destructively sampled, and height and number of leaves (leaves ≥ 5 mm long) at 10 day intervals, and leaf area (using a *CI-203* area meter, *CID*, USA) were determined. After 60 d, ten seedlings were harvested to assess biomass. Roots were carefully excavated with a spray gun, and the sand was recollected and checked thoroughly for living roots that had broken off. Root, branch, and leaf dry masses were determined after 48 h in an oven at 85 °C.

Statistical analysis: Data were processed separately for the three species. Standard error (SE) of each treatment was calculated. To test for temperature effects, *t*-test was performed for each species.

Results

Morphological development: The three species showed different responses of tree height, number of leaves, and leaf area to elevated temperature (Fig. 1). Tree height of *C. intermedia* and *H. mongolicum* seedlings was significantly enhanced already at day 40, while in *A. ordosica* seedlings, changes were only observed at day 60 (Fig. 1*A*). Elevated temperature increased the number of leaves in *C. intermedia* and *H. mongolicum* seedlings from day 40 onwards, but in *A. ordosica* seedlings, no significant changes were observed (Fig. 1*B*). Elevated temperature increased leaf area in *C. intermedia* and *H. mongolicum* seedlings from 30 d onwards, but leaf area of *A. ordosica* seedlings was never stimulated (Fig. 1*C*).

Biomass distribution: At the end of the experiment, elevated temperature enhanced total tree biomass in *C. intermedia* and *H. mongolicum* seedlings, but not in *A. ordosica* seedlings (Fig. 2). Elevated temperature enhanced shoot growth more than root growth in both *C. intermedia* and *H. mongolicum* seedlings, and reduced the root : shoot ratios (Fig. 3). In *A. ordosica* seedlings, neither root biomass nor shoot biomass was affected by the elevated temperature.

Gas exchange: Leaf P_N, E, and WUE were determined at days 40 and 60 of the experiment. P_N was significantly increased at days 40 and 60 in *C. intermedia* and *H. mongolicum* seedlings, while in *A. ordosica* seedlings only at day 60 (Fig. 4). A significant increase of E in elevated temperature was obtained at days 40 and 60 in *C. intermedia* and *H. mongolicum* seedlings, but not in *A. ordosica* seedlings (Fig. 4). In *C. intermedia* seedlings, WUE was not affected by elevated temperature at day 40, but decreased at day 60. In *H. mongolicum* seedlings, WUE was significantly reduced both at days 40 and 60, while in *A. ordosica* seedlings, WUE was never affected by the elevated temperature treatment (Fig. 4).

Discussion

The tree height, number of leaves, leaf area, and total biomass of *C. intermedia* and *H. mongolicum* seedlings exposed to elevated temperature were significantly increased. This is agreement with similar works

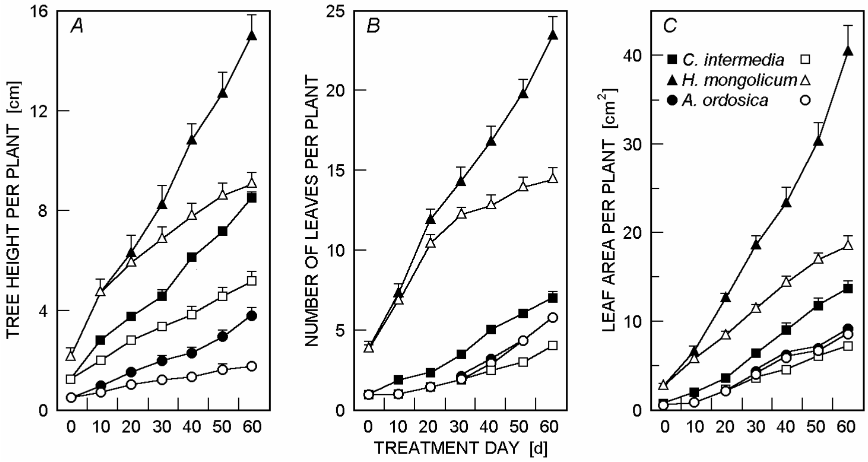

Fig. 1. Developmental changes of *C. intermedia* (Δ, ▲), *H. mongolicum* (□, ■), and *A. ordosica* (○, ●) grown at 25/20 (Δ, □, ○) and 28/23 °C (▲, ■, ●) for 60 d. (*A*) Tree height per plant, (*B*) number of leaves per plant, and (*C*) leaf area per plant. *Points* represent treatment means, *standard error bars* are shown one-sided.

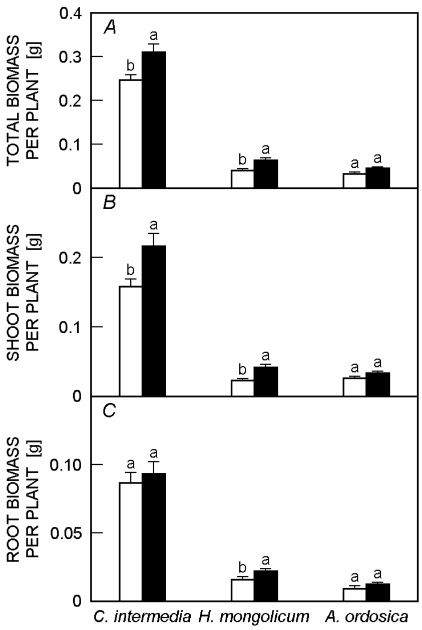

Fig. 2. Biomass per plant of *C. intermedia*, *H. mongolicum*, and *A. ordosica* grown at 25/20 (*white bars*) and 28/23 °C (*black bars*) after day 60 of treatment. (*A*) Total, (*B*) shoot, and (*C*) root biomass per plant. Boxes represent treatment means, *standard error bars* are shown one-sided. Treatments with the different letters are significantly different ($p<0.05$) according to *t*-test.

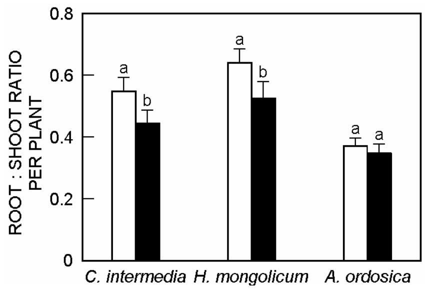

Fig. 3. Root : shoot ratio per plant of *C. intermedia*, *H. mongolicum*, and *A. ordosica* grown at 25/20 (*white bars*) and 28/23 °C (*black bars*) for 60 d. *Boxes* represent treatment means, *standard error bars* are shown one-sided. Treatments with the different letters are significantly different ($p<0.05$) according to *t*-test.

(Clarkson *et al.* 1986, DeLucia *et al.* 1992, Mitchell *at al.* 1993, Harte and Shaw 1995, Henry and Molau 1997, Gunn and Farrar 1999). No significant temperature effects on number of leaves, leaf area, and biomass were observed in *A. ordosica* seedlings all through the experiment, and similar result was observed by Chapin and Shaver (1996), Jones *et al.* (1997), and Stenström *et al.* (1997). However, under the elevated temperature treatment, biomass accumulation was decreased for shrubs and herbaceous perennial species (Harte and Shaw 1995) and drought-tolerant tree species (He and Dong 2003).

The biomass allocation is greatly affected by temperature change (Farrar 1989, DeLucia *et al.* 1992, Rawson 1992, Gunn and Farrar 1999). In this study, the elevated temperature significantly decreased root : shoot ratio in *C. intermedia* and *H. mongolicum* seedlings. Obviously a large proportion of photosynthates of the two desert species will be allocated to the above-ground plant parts, which maintains these species to capture more photons. However no significant temperature effects on root : shoot ratio were found in *A. ordosica* seedlings. Because biomass allocation patters will often affect the competitive relationship among species in plant communities (Aerts *et al.* 1991), we could estimate that *C. intermedia* and *H. mongolicum* seedlings will possibly increase their competitive ability in plant communities of the Maowusu sandland under elevated temperature. This interpretation, however, is made cautiously, since the elevated temperature treatment concerns only two months.

The responses of P_N to elevated temperature varied largely for different species (Chapin 1983, Sun and Sweet 1996, Schwarz *et al.* 1997, Leverenz *et al.* 1999, Sheu and Lin 1999, Loik *et al.* 2000, He and Dong 2003). In this study, significantly positive temperature effects on leaf P_N were observed in *C. intermedia* and *H. mongolicum* seedlings at days 40 and 60 of this experiment. P_N responses of the two species to elevated temperature explained the temperature effects on their growth very well. We can thus estimate that there is a positive feedback among photosynthetic products, biomass, and leaf development of the two species under the elevated temperature range of this experiment. In *A. ordosica*, responses of P_N were significant at day 60 but not significant at day 40. Obviously the different morphological and physiological characteristics had no integrated response to the elevated temperature, but there would probably be temperature lag effects on growth of *A. ordosica* seedlings. Similarly, *Polygonum bistorta* also had internal lags that would delay the response to temperature changes (Chapin *et al.* 1995, Diggle 1997).

We expected that evapotransporation would increase under elevated temperature and the upper sand strata would become drier, leading to lower *E* and higher WUE in the three species. However, the expected changes in *E* and WUE were not observed in this experiment. *E* was significantly increased at days 40 and 60 and WUE was significantly decreased at day 60 in *C. intermedia* and *H. mongolicum* seedlings. No significant temperature effects on *E* and WUE were observed in *A. ordosica* seedlings. Based on these results, we can estimate that the positive elevated temperature effect on the two species might change under more drought environments. For plants exposed to soils dried by elevated atmospheric temperatures, water potential may be decreased, leading to reductions in photosynthetic CO_2 fixation (Loik *et al.* 2000). In fact, a significant decrease in P_N for the two species was observed under drought environment (Xiao and Zhang 2001, Xiao and Zhou 2001). In addition, some characteristics of the two species, such as lower WUE and lower root/shoot ratio, increased soil water consumption under elevated temperature possibly to enhance the drought effect on their growth.

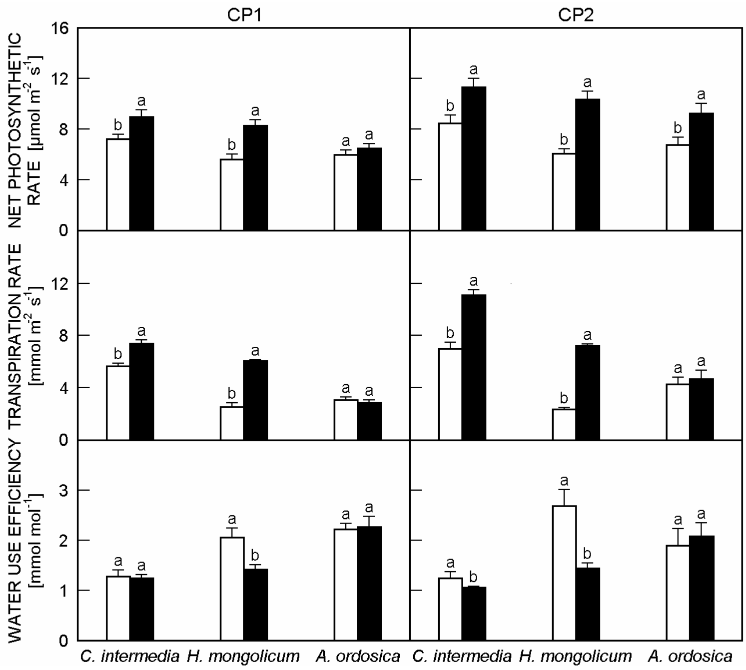

Fig. 4. Net photosynthetic rate, transpiration rate, and water use efficiency of *C. intermedia*, *H. mongolicum*, and *A. ordosica* grown at 25/20 (*white bars*) and 28/23 °C (*black bars*) at day 40 (CP1) and day 60 (CP2). *Boxes* represent treatment means, *standard error bars* are shown one-sided. Treatments with different letters are significantly different (p<0.05) according to *t*-test.

Overall, the results of this experiment indicated different responses of the three dominant desert species to elevated temperature. Furthermore, the results help to predict how these species would change their ecological strategies through eco-physiological and structural adjustments under the climate change of elevated temperature in the future.

References

Aerts, R., Boot, R.G.A., Vanderaart, P.J.M.: The relation between above- and belowground biomass allocation patterns and competitive ability. – Oecologia **87**: 551-559, 1991.

Chapin, F.S., III: Direct and indirect effects of temperature on arctic plants. – Polar Biol. **2**: 47-52, 1983.

Chapin, F.S., III, Shaver, G.R.: Physiological and growth responses of arctic plants to a field experiment simulating climatic change. – Ecology **77**: 822-840, 1996.

Chapin, F.S., III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.G., Laundre, J.A.: Effect of climate change on arctic tundra: Response of arctic tundra to experimental and observed changes in climate. – Ecology **76**: 694-711, 1995.

Chi, L.J.: [The impact of global change on the desertification in China.] – J. natur. Resour. **9**: 289-303, 1994. [In Chin.]

Clarkson, D.T., Hopper, M.J., Jones, L.H.P.: The effect of root temperature on the uptake of nitrogen and the relation size of the root system in *Lolium perenne*. I. Solutions containing both NH_4 and NO_3. – Plant Cell Environ. **9**: 535-545, 1986.

DeLucia, E.H., Heckathorn, S.A., Day, T.A.: Effects of soil temperature on growth, biomass allocation and resource acquisition of *Andropogon gerardii* Vitman. – New Phytol. **120**: 543-549, 1992.

Diggle, P.K.: Extreme preformation in alpine *Polygonum viviparum*: an architectural and developmental analysis. – Amer. J. Bot. **84**: 154-169, 1997.

Farrar, J.F.: Temperature and the partitioning and translocation of carbon. – In: Long, S.P., Woodward, F.I. (ed.): Plants and Temperature. Pp. 203-235. Cambridge University Press, Cambridge 1989.

Gunn, S., Farrar, J.F.: Effects of a 4 °C increase in temperature on partitioning of leaf area and dry mass, root respiration and carbohydrates. – Funct. Ecol. **13**(Suppl. 1): 12-20, 1999.

Harte, J., Shaw, M.R.: Shifting dominance within a montane vegetation community: results of a climate warming experiment. – Science **267**: 876-880, 1995.

He, W.M., Dong, M.: Plasticity in physiology and growth of *Salix matsudana* in response to simulated atmospheric temperature rise in the Mu Us Sandland. – Photosynthetica **41**: 297-300, 2003.

Henry, G.H.R., Molau, U.: Tundra plants and climate change: the International Tundra Experiment (ITEX). – Glob. Change Biol. **3**: 1-9, 1997.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A.: IPCC 2001: Climate Change 2001: The Scientific Basis. – Cambridge University Press, New York 2001.

Jiang, G.N., He, W.M.: [Species- and habitat-variability of photosynthesis, transpiration and water use efficiency of different plant species in Maowusu sand area.] – Acta bot. sin. **41**: 1114-1124, 1999. [In Chin.]

Jones, M.H., Bay, C., Nordenhall, U.: Effects of experimental warming on arctic willows (*Salix* sp.): A comparison of responses from the Canadian High Arctic, Alaskan Arctic, and Swedish Subarctic. – Glob. Change Biol. **3**: 55-60, 1997.

Leverenz, J., Bruhn, D., Saxe, H.: Responses of two provenances of *Fagus sylvatica* seedlings to a combination of four temperature and two CO_2 treatments during their first growing season: gas exchange of leaves and roots. – New Phytol. **144**: 437-454, 1999.

Loik, M.E., Redar, S.P., Harte, J.: Photosynthetic responses to a climate-warming manipulation for contrasting meadow species in the Rocky Mountains, Colorado, USA. – Funct. Ecol. **14**: 166-175, 2000.

Mitchell, R.A.C., Mitchell, V.J., Driscoll, S.P., Franklin, J., Lawlor, D.W.: Effects of increased CO_2 concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. – Plant Cell Environ. **16**: 521-529, 1993.

Rawson, H.M.: Plant response to temperature under conditions of elevated CO_2. – Aust. J. Bot. **40**: 473-490, 1992.

Schwarz, P.A., Fahey, T.J., Dawson, T.E.: Seasonal air and soil temperature effects on photosynthesis in red spruce *(Picea rubens*) saplings. – Tree Physiol. **17**: 187-194, 1997.

Sheu, B.H., Lin, C.K.: Photosynthetic response of seedlings of the sub-tropical tree *Schima superba* with exposure to elevated carbon dioxide and temperature. – Environ. exp. Bot. **41**: 57-65, 1999.

Stenström, M., Gugerli, F., Henry, G.H.R.: Response of *Saxifraga oppositifolia* L. to simulated climate change at three contrasting latitudes. – Glob. Change Ecol. **3**: 44-54, 1997.

Sun, O.J., Sweet, G.B.: Genotypic variation in light and temperature response of photosynthesis in *Nothofagus solandri* var. *cliffortioides* and *N. menziesii*. – Aust. J. Plant Physiol. **23**: 421-428, 1996.

Woodward, F.I.: A review of the effects of climate on vegetation: ranges, competition, and composition. – In: Peters, R.L., Lovejoy, T.E. (ed.): Global Warming and Biological Diversity. Pp. 105-123. Yale University Press, New Haven 1992.

Xiao, C.W., Zhang, X.S.: [Study on the effect of simulated precipitation change on the eco-physiological process for *Artemisia ordosica* seedlings in Maowusu sandland.] – Sci. silvae sin. **37**: 15-22, 2001. [In Chin.]

Xiao, C.W., Zhou, G.S.: [Effect of simulated precipitation change on growth, gas exchange and chlorophyll fluorescence of *Caragana intermedia* in Maowusu sandland.] – Chin. J. appl. Ecol. **12**: 692-696, 2001. [In Chin.]

Yao, H.L., Wei, C.T., Miao, M.C.: [An introduction on the Ordos Plateau sands exploitation and control research center.] – In: Wang, J.Q. (ed.): Collected Papers of the Ordos Plateau Sands Exploitation and Control Research Center (First Vol.). Pp. 1-7. Inner Mongolia University Press, Huhhut 1992. [In Chin.]

Zhang, X.S.: [The ecological background of the Maowusu sandland: the principles and optimal models for grass land management.] – Acta phytoecol. sin. **18**: 1-6, 1994. [In Chin.]