

Photosynthesis and growth responses of *Parthenocissus quinquefolia* (L.) Planch to soil water availability

Z.J. ZHANG^{*}, L. SHI^{*,***}, J.Z. ZHANG^{***}, and C.Y. ZHANG^{**}

Institute of Botany, Chinese Academy of Sciences, 20 Nanxincun, 100093, Beijing, P.R. China^{}*
*National Climate Center, China Meteorological Administration, 100081, Beijing, P.R. China^{**}*

Abstract

Photosynthesis and growth characteristics of *Parthenocissus quinquefolia* were measured under differing soil water availability within a pot. Decreased soil moisture significantly reduced the leaf relative water content (RWC) and the above- and below-ground biomass. However, more biomass was allocated to the root than to the leaf. Net photosynthetic rate (P_N), stomatal conductance (g_s), and transpiration rate (E) were also significantly decreased but water use efficiency (WUE) was increased. Midday depressions in P_N and g_s were not evident for the well-irrigated plants. With the lower water availability, midday reductions in P_N and g_s were much more marked and the duration of the depression was longer. Additionally, the P_N -irradiance response curves also indicated that water supply affected photosynthesis capacity. The growth and photosynthetic response of *P. quinquefolia* to water supply indicated that this species could resilient to water availabilities and adapt to Hunshandak conditions very well.

Additional key words: biomass allocation; diurnal courses; leaf moisture status; net photosynthetic rate; stomatal conductance; transpiration rate.

Introduction

The Hunshandak sandland (HS), a semi-arid area of China, is one of the serious desertified sandlands suffering from the frequent disturbance (Jiang *et al.* 2003). The success of biological restoration (Singh and Rathod 2002) largely depends upon the delicate balance between the availability of soil nutrients/moisture and their use for biomass production. So the selection of plant adapting to the severe environment by some special mechanisms was necessary.

Up to now, a number of studies have focused on the morphological (Bradford and Hsiao 1982, Rascio *et al.* 1990) and physiological (Tyree *et al.* 1998, Terwilliger *et al.* 2001) adaptation mechanisms of species to water stressed environment. Both avoidance (*e.g.* deep rooting, leaf loss) and tolerance (*e.g.* osmotic adjustment, stomatal control) mechanisms may contribute to drought responses in plant species (Chaves *et al.* 2000). The extent to which these mechanisms are invoked may change significantly

according to their drought adaptation ability.

Parthenocissus quinquefolia is an excellent liane of the family Vitaceae that has been widely planted in the north of China. It is an important part of city green and will play important role in the environment management (Zhang *et al.* 2001). To support the selection of *P. quinquefolia* for the bio-restoration of degraded sandland, knowledge of photosynthesis and of the adaptation strategies employed when water stress occurs is essential. The aim of this work was to investigate whether photosynthetic capacity and growth characteristics of *P. quinquefolia* could resilient to water conditions in this area. We hypothesized that *P. quinquefolia* would maintain photosynthetic capacity at the drier site whilst minimizing transpiration water loss. Both growth and physiology characters would change accordingly to adapt to the changing water conditions.

Received 2 January, 2004, accepted 16 February 2004.

***Corresponding author: fax: (+8610-62590348), e-mail: shilei 67@263.net

Abbreviations: E – transpiration rate; g_s – stomatal conductance; HS – Hunshandak Sandland; P_N – net photosynthetic rate; RWC – relative water content; WUE – water use efficiency.

Acknowledgements: This work was supported by the Project of National Science and Technology in Preventing and Managing Sand (FS2000-009, 2002BA517A09-04-04), Key Innovative Project of the Chinese Academy of Science (KSCX1-08-02), and Agriculture Project of the Chinese Academy of Science (NK15-C-16).

Materials and methods

Study area: The experiment was conducted in the grass cultivation station in Zhenlan Banner, Inner Mongolia, China (42°16'N, 115°57'E), which is a part of Hunshandak Sandland (HS). The prevailing climate is of the temperate semiarid type, with the average annual temperature and July and January temperatures of 1.7, 16.6, and -24.1 °C, respectively. The annual total radiation time is 3 000–3 200 h and the above 10 °C accumulated temperature per year is 2 000–2 600 °C. The frostless period is approximately 100 d. It receives annual precipitation of about 250–350 mm, with uneven distribution throughout the year. The maximum values were observed from June to August and the minimum values from March to May, and the rainfall fluctuated among years greatly, from 150 mm in drought year to 400 mm in abundant precipitation year.

Plants: *Parthenocissus quinquefolia* (L.) Planch, an important species of the family Vitaceae, is a perennial woody liane (Flora of China 1998). It has been widely cultivated in the Northeast of China. It has strong resistance to cold and endures barren soil. Due to its high absorption ability, great leaf area, and rapid growth, *P. quinquefolia* is prospective to prevent wind and fix sand.

Experiment design: The experiment was carried out on 2-years-old *P. quinquefolia* seedlings from nursery. Eighty individual seedlings of uniform appearance were randomly divided into five groups, and then every two were planted in one sand pool (0.4 m width×0.4 m length×0.6 m depth) on 2 June 2002. The seedlings were sparsely for one seedling one pool on 20 June. There was a pipe in each pool bottom just for draining enough water from the pools. All pools were placed in greenhouse. The top of the greenhouse was covered with repellent when it rains (every side of the greenhouse leaks out) and exposed in sunshine on clear days. The sand matrix for experiment was taken from a near dune.

Based on the natural precipitation during 1960–2000, we designed five water supply levels, *i.e.* 72.6 (WS1), 147.4 (WS2), 220.0 (WS3), 292.6 (WS4), and 367.4 (WS5) mm during the experiment. These water supply levels were simulated as corresponding to much less, less, equal to, more, and much more than the mean precipitation in the growing season in HS. Water was supplied once every 10 d from the beginning of 20 June to 29 August. Each time water supply was consistent or kept proportion with the precipitation at the same period. All sand pools of the experiment were managed well.

Soil water content was measured by oven drying method once every 14 d. Each sand matrix column was sampled every 10 cm from surface to bottom. The sand matrix moisture percentage was calculated as Soil Water Content

(SWC) = (fresh mass – dry mass)/fresh mass × 100 [%]. There were significant differences among five water supply treatments in terms of sand matrix moisture percentage, and water supply significantly increased the soil moisture (Fig. 1).

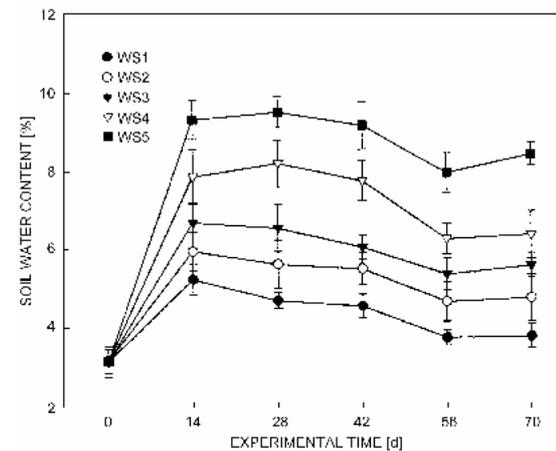


Fig. 1. Effects of different water supplies on soil water content during the experiment period. Error bars are \pm S.E.

Dry mass determination: Eight seedlings of each water supply treatment were harvested on 29 August, 2002. The above-ground parts were separated into leaves and stems; roots were excavated from pool and subsequently washed by water. Then masses of all the parts were determined after 48 h in an oven at 85 °C.

Leaf relative water content (RWC) was estimated 4 d before the end of experiment (on 25 August 2002). RWC was measured in leaf discs similar to those used for photosynthesis measurements by determining fresh mass and the mass at full turgor after 24 h in distilled water: $RWC = (\text{fresh mass} - \text{dry mass}) / (\text{full turgor mass} - \text{dry mass})$ (Kumar and Singh 1998).

Photosynthesis: Three seedlings of each water treatment were measured every hour from 06:00 to 19:00 on 6 August, 2002 to determine net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s). They were measured using a portable gas exchange system (*LCA-4*, *ADC*, Hoddesdon, England). The leaf area was measured using an area meter *AM100* (*ADC*, UK). Water use efficiency (WUE) was calculated as P_N/E . For measurements the fully expanded leaves of upper shoots were selected. Three replications were done for each species at each time.

Irradiance response of P_N : The response of P_N to changes in photosynthetic photon flux density (PPFD) was examined in the field using the method of Jiang and He (1999). A series of PPFD was produced by gradually

altering the angle of leaf chamber. Each angle (*i.e.* the PPFD condition) was maintained for at least 5 min. P_N was recorded after steady value was reached. P_N -PPFD curves were plotted using the mean values of P_N measured at each PPFD. Three replications were made.

Data analysis: Analysis of variance (ANOVA) of leaf traits was conducted on each measurement and the sig-

Results

Leaf RWC: Soil water availability greatly influenced leaf RWC. It was ever increased along with the increasing water supply (Fig. 2), with the highest value (92 %) in WS5 and the lowest one (55 %) in WS1. The values were significantly different from each other among the five treatments except that between WS2 and WS3, and between WS3 and WS4 ($p>0.05$).

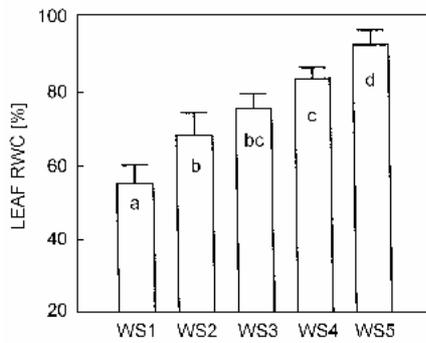


Fig. 2. Leaf relative water content (RWC) of *P. quinquefolia* seedlings under five levels of water supply. Different letters indicate significant differences between water treatments ($p<0.05$). Error bars are \pm S.E.

Biomass accumulation in different water treatments over the same period was increased with the enhancing of water supply both on the above ground parts and root. However, leaf and root biomass were increased more significantly than shoot biomass (Fig. 3A), with 218 % increase in leaf biomass and 62 % increase in root biomass between WS1 and WS5. Under lower water supplies, root growth constituted the largest proportion of the biomass gain while the above ground portion was significantly reduced (Fig. 3B). Averaged over the five water supply treatments, the ratio of root/above ground part dry matter partitioning was highest for WS1 (1.02), intermediate for WS3 (0.85), and the lowest for WS5 (0.63).

Photosynthetic characteristics: The daily maximum P_N measured after 47 d of treatments was 59 % higher in WS5 than in WS1 (Fig. 4A). g_s and E were also significantly increased from WS1 to WS5 (Fig. 4B) with the increase of 39 and 65 %, respectively (Fig. 4C). However, water supply decreased WUE especially during the period from 08:00 to 16:00 with the higher values in WS1 and

nificance of plant mean square determined by testing against the error mean square. The least significant differences (LSD) between the means were estimated at 95 % confidence level. The ultimate value of each characteristic for comparison was the mean of 3-d measurements. All statistical analyses were performed using the SPSS 10.0 package (SPSS, Chicago, USA).

WS2 and the lower ones in WS5 and WS4 (Fig. 4D).

Also water availability greatly changed the diurnal pattern of gas exchange. The midday depression was most serious under WS1 and WS2 with 30 and 26 % decrease in P_N compared with the maximum values. It was more gentle under WS3 and WS4, with 22 and 19 % decrease, while there was no obvious depression under WS5. The depression appeared 2 h earlier in WS1 and WS2 than in the other water treatments. g_s and E changed in the similar patterns similar with that of P_N (Fig. 4B,C).

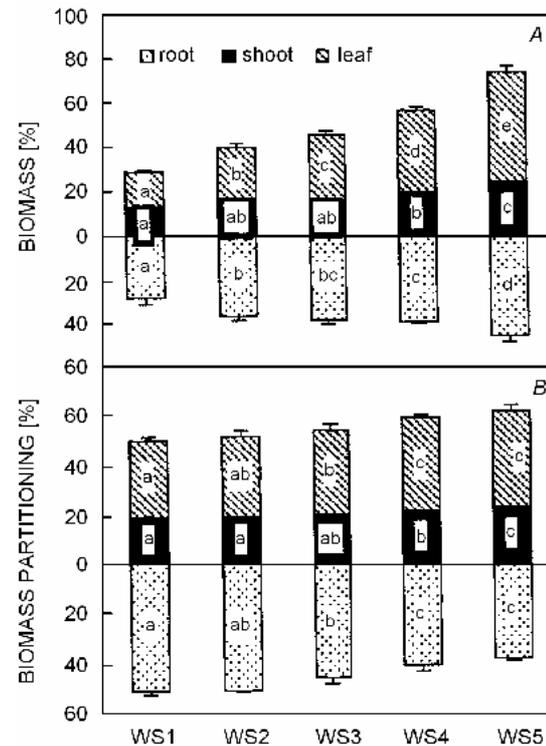


Fig. 3. Biomass (A) and biomass partitioning (B) for *P. quinquefolia* seedlings grown under different water supplies measured at the final harvest time. Different letters indicate significant differences between water treatments ($p<0.05$). Error bars are \pm S.E.

PPFD- P_N response curves under five water supply treatments showed that water supply influenced the maximum P_N and initial slope of the curves (Fig. 5). P_N was saturated at $1\ 600\ \mu\text{mol}\ \text{m}^{-2}\ \text{s}^{-1}$ under WS5, while at $1\ 200$

$\mu\text{mol m}^{-2} \text{s}^{-1}$ under the other four treatments. However, the slopes were different among these four treatments and they increased with the increasing water supply. Seed-

lings responded rapidly from 0 to $400 \mu\text{mol m}^{-2} \text{s}^{-1}$. At each PPFD, P_N in higher water supply treatments was larger than that in lower water supply.

Discussion

RWC is the mass of water in the sample divided by the potential maximum values of water in the sample. It reflects the water content in plant tissue and is often used as a parameter to assess the severity of drought (Tardieu and Simmonneau 1998). In our study, leaf RWC was significantly reduced by the decreasing water supplies (Fig. 2), which reflected the sensitive response of *P. quinquefolia* to soil water moisture. RWC plays an important role in photosynthesis regulating g_s and P_N (Cornic and Massacci 1996, Lawlor and Cornic 2002). So, the sensitive response of RWC to soil moisture in *P. quinquefolia* indicated its higher regulation capability for photosynthesis.

The change of root/above ground part biomass

reflects the adaptation strategies in biomass distribution pattern under different water supply (Zhang *et al.* 2003). Under lower soil water availability, the seedlings invested more biomass in root growth (Fig. 3) in order to absorb more water for higher survival competitive capacity under water stress (Rodrigues *et al.* 1995). The seedlings grown under high water supply invested more biomass in branch and leaf (Fig. 3B) in order to capture more photons for higher photosynthesis. Other studies brought similar results (*e.g.* Hsiao 1993, Spollen *et al.* 1993). The mechanisms underlying the sustained root growth under low water supply include osmotic adjustment (Saab *et al.* 1992) and an increase in the loosening capacity of the cell wall (Hsiao and Xu 2000).

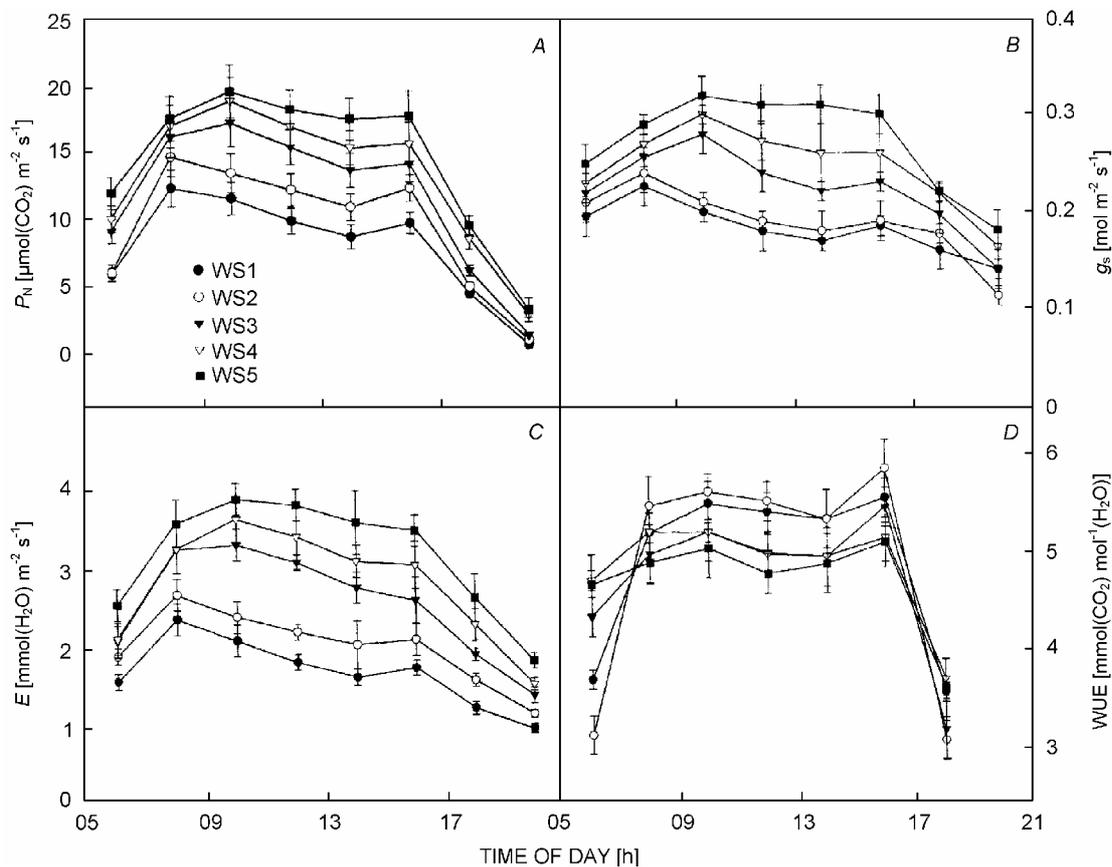


Fig. 4. Diurnal changes in (A) net photosynthetic rate (P_N), (B) stomatal conductance (g_s), (C) transpiration rate (E), and (D) water use efficiency (WUE) in *P. quinquefolia* seedlings under five levels of water supply. Error bars are \pm S.E.

The rainfall in WS1 and WS2 of our experiment was significantly less than the average rainfall in HS. It posed a drought effect on plants during the period of our study at which P_N and g_s were greatly reduced (Fig. 4A). The

increased water supply significantly enhanced P_N in both diurnal gas exchange and P_N -PPFD response curves (Figs. 4A and 5). The large decrease in P_N (Fig. 4A) under lower water availability was in part due to stomata

closure which restricts water loss, *i.e.* the stomatal limitation worked in *P. quinquefolia*. This was reflected by the synchronous changes of P_N and g_s (Fig. 4A,B). The stomatal limitation is a protective mechanism against water loss in water-stressed conditions (Flexas and Medrano 2002). Plants with stomatal control ability survive well in the drought environments (Saliendra *et al.* 1995). In our study, the occurrence of stomatal response in the face of lower water availability and the higher WUE in WS1 and WS2 support the notion that *P. quinquefolia* conserves moisture through effective stomatal control, which is common in the native species in HS (Liu *et al.* 2003, Niu *et al.* 2003). This may act as an important physiological mechanism ensuring the growth of this species in this field.

In addition, to avoid deleterious transpiration water loss under high irradiance and heat, plants tend to close their stomata during midday hours at the cost of photosynthetic CO_2 exchange (Tenhunen *et al.* 1984, Matsumoto *et al.* 2000), especially under arid environment (Jiang and Zhu 2001). In HS, where plants are exposed to drought, high irradiance, hot air, and water stress during the midday time (Niu *et al.* 2003; Fig. 2), *P. quinquefolia* had the similar or even less depression compared with the typical species in this area (Li *et al.* 2003). This reflected its photosynthetic avoidance of heat and high irradiance stress at midday.

Based on our results, we recommend that water supply has a positive effect on growth, biomass partitioning, and photosynthesis of *P. quinquefolia* seedlings in

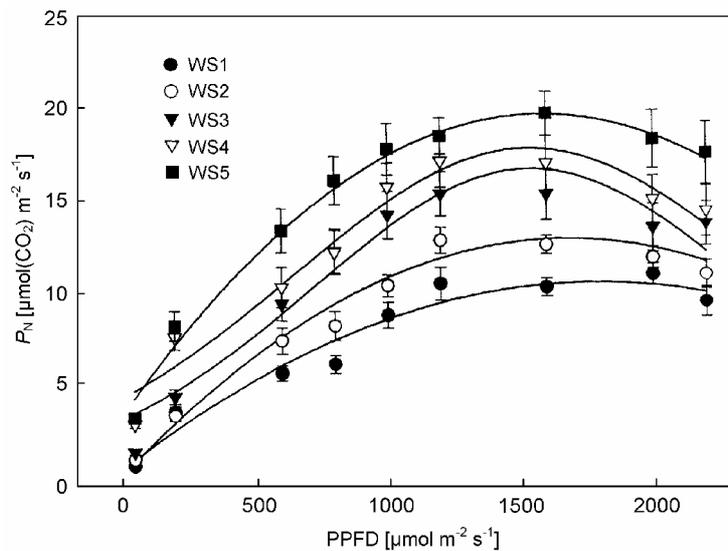


Fig. 5. Irradiance (PPFD) response curves of net photosynthetic rate (P_N) of *P. quinquefolia*. Error bars are \pm S.E.

the range of water supply from 72.6 to 367.4 mm. In addition, the seedlings adapt to the varied water resource environment by changing growth strategies. Lower water supply decreased g_s and E , and plants had relatively higher investment in root growth in order to reduce tissue losing ratio and consumption of water resource, so to improve WUE. However, the seedlings growing under high

water conditions increased their stomatal opening and P_N and had relatively higher investments in branch and leaf growth in order to improve the capacity of capturing photons. In short, water supply caused the different ecological adaptation strategies of *P. quinquefolia* seedlings growing under different water resource environments in HS and so made them grow well in sandlands.

References

- Bradford, K.J., Hsiao, T.C.: Physiological responses to moderate water stress. – In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (ed.): *Physiological Plant Ecology II*. Pp. 263-324. Springer-Verlag, Berlin – Heidelberg – New York 1982.
- Chaves, M.M., Pereira, J.S., Maroco, J., Rodrigues, M.L., Ricardo, C.P.P., Osorio, M.L., Carvalho, I., Faria, T., Hsiao, T.C., Xu, L.K.: Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. – *J. exp. Bot.* **51**: 1595-1616, 2000.
- Cornic, G., Massacci, A.: Leaf photosynthesis under drought stress. – In: Baker, N.R. (ed.): *Photosynthesis and the Environment*. Pp. 347-366. Kluwer Academic Publ., Dordrecht – Boston – London 1996.
- Flexas, J., Medrano, H.: Drought-inhibition of photosynthesis in C_3 plants: Stomatal and non-stomatal limitations revisited. – *Ann. Bot.* **89**: 183-189, 2002.
- Flora of China. 48th Book. Vol. 2. – Pp. 20-21. Science Press, Beijing 1998.
- Hsiao, T.C.: Effects of drought and elevated CO_2 on plant water use efficiency and productivity. – In: Jackson, M.B., Black, C.R. (ed.): *Interaction Stresses on Plants in a Changing*

- Climate. Pp. 435-465. Springer-Verlag, Berlin 1993.
- Hsiao, T.C., Xu, L.V.K.: Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. – *J. exp. Bot.* **51**: 1595-1616, 2000.
- Jiang, G.M., He, W.M.: A quick and effective method for determining photosynthesis-light response curves under field conditions. – *Chin. Bull. Bot.* **21**: 11-15, 1999.
- Jiang, G.M., Liu, M.Z., Han, N.Y., Zhang, Q., Li, W.J.: Potential for restoration of degraded steppe in the Xilingol Biosphere reserve through urbanization. – *Environ. Conserv.* **30**: 304-310, 2003.
- Jiang, G.M., Zhu, G.J.: Different patterns of gas exchange and photochemical efficiency in three desert shrub species under two natural temperatures and irradiances in Mu Us Sandy Area of China. – *Photosynthetica* **39**: 257-262, 2001.
- Kumar, A., Singh, D.P.: Use of physiological indices as a screening technique for drought tolerance in oilseed *Brassica* species. – *Ann. Bot.* **81**: 413-420, 1998.
- Lawlor, D.W., Cornic, G.: Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. – *Plant Cell Environ.* **25**: 275-294, 2002.
- Li, Y.G., Jiang, G.M., Niu, S.L., Liu, M.Z., Peng, Y., Yu, S.L., Gao, L.M.: Gas exchange and water use efficiency of three native tree species in Hunshandak Sandland of China. – *Photosynthetica* **41**: 227-232, 2003.
- Liu, M.Z., Jiang, G.M., Li, Y.G., Gao, L.M., Niu, S.L., Cui, H.X., Ding, L.: Gas exchange, photochemical efficiency and leaf water potential in three *Salix* species. – *Photosynthetica* **41**: 393-398, 2003.
- Matsumoto, J., Muraoka, H., Washitani, I.: Ecophysiological mechanisms used by *Aster kantoensis*, an endangered species, to withstand high light and heat stresses of its gravelly floodplain Habitat. – *Ann. Bot.* **86**: 777-785, 2000.
- Niu, S.L., Jiang, G.M., Li, Y.G., Gao, L.M., Liu, M.Z., Peng, Y., Ding, L.: Comparison of photosynthetic traits between two typical shrubs: legume and non-legume in Hunshandak Sandland. – *Photosynthetica* **41**: 111-116, 2003.
- Rascio, A., Cedola, M.C., Toponi, M., Flagella, Z., Wittmer, G.: Leaf morphology and water status changes in *Triticum durum* under water stress. – *Physiol. Plant.* **78**: 462-467, 1990.
- Rodrigues, M.L., Pacheco, C.M.A., Chaves, M.M.: Soil-plant water relations, root distribution and biomass partitioning in *Lupinus albus* L. under drought conditions. – *J. exp. Bot.* **46**: 947-956, 1995.
- Saab, I.N., Sharp, R.E., Pritchard, J.: Effects of inhibition of abscisic acid accumulation on the spatial distribution of elongation in the primary root and mesocotyl of maize at low water potentials. – *Plant Physiol.* **99**: 26-33, 1992.
- Saliendra, N.Z., Sperry, J.S., Comstock, J.P.: Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in *Betula occidentalis*. – *Planta* **196**: 357-366, 1995.
- Singh, G., Rathod, T.R.: Plant growth, biomass production and soil water dynamics in a shifting dune of Indian desert. – *Forest Ecol. Manage.* **171**: 309-320, 2002.
- Spollen, W.G., Sharp, R.E., Saab, I.N., Wu, Y.: Regulation of cell expansion in roots and shoots at low water potentials. – In: Smith, J.A.C., Griffiths, H. (ed.): *Water Deficits: Plant Responses from Cell to Community*. Pp. 37-52. Bios, Oxford 1993.
- Tardieu, F., Simmonneau, T.: Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. – *J. exp. Bot.* **49**: 419-432, 1998.
- Tenhunen, J.D., Lange, O.L., Gebel, J., Beyschlag, W., Weber, J.A.: Changes in photosynthetic capacity, carboxylation efficiency, and CO₂ compensation point associated with midday stomatal closure and midday depression of net CO₂ exchange of leaves of *Quercus suber*. – *Planta* **162**: 193-203, 1984.
- Terwilliger, V.J., Kitajima, K., Le Roux-Swarthout, D.J., Mulkey, S., Wright, S.J.: Intrinsic water-use efficiency and heterotrophic investment in tropical leaf growth of two Neotropical pioneer tree species as estimated from δ¹³C values. – *New Phytol.* **152**: 267-281, 2001.
- Tyree, M.T., Velez, V., Dalling, J.W.: Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to differing light regimes. – *Oecologia* **114**: 293-298, 1998.
- Zhang, X.L., Zang, R.G., Li, C.Y.: Population differences in physiological and morphological adaptations of *Populus davidiana* seedlings in response to progressive drought stress, – *Plant Sci.*, available online 12 December 2003.
- Zhang, Y.G., Ma, B.Z., Liu, Y.: A primary study on making green by planting *Parthenocissus quinquefolia* at barren mountains. – *J. Mountain – Agr. Biol.* **20**: 110-113, 2001.