BRIEF COMMUNICATION

Characterization of photosynthesis of *Populus euphratica* grown in the arid region

Y.P. CHEN, Y.N. CHEN*, W.H. LI, and C.C. XU

Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Xinjiang, 830011, P.R. China

Abstract

Net photosynthetic rate (P_N), stomatal conductance (g_s), intercellular CO_2 concentration (C_i), transpiration rate (E), water use efficiency (WUE), and stomatal limitation (L_s) of *Populus euphratica* grown at different groundwater depths in the arid region were measured. g_s of the trees with groundwater depth at 4.74 m (D_4) and 5.82 m (D_5) were lower and a little higher than that at 3.82 m (D_3), respectively. Compared with C_i and L_s of the D_3 trees, C_i decreased and L_s increased at 4.74 m, however, *C*i increased and L_s decreased at D_5. Hence photosynthetic reduction of *P. euphratica* was attributed to either stomatal closure or non-stomatal factors depending on the groundwater depths in the plant locations. P_N of the D_3 trees was significantly higher than those at D_4 or D_5. The trees of D_4 and D_5 did not show a significant difference in their P_N, indicating that there are mechanisms of *P. euphratica* tolerance to mild and moderate drought stress.

Additional key words: drought stress; intercellular CO_2 concentration; stomatal conductance; transpiration rate.

Drought is one of the most important environmental factors limiting growth and yield of crops (Boyer 1982, Chaves *et al*. 2003). Usually a significant reduction of photosynthesis of plants under drought stress is detected (Sharkey and Seemann 1989, Lauriano *et al*. 2004, Tezara *et al*. 2005). The reduction of net photosynthetic rate (P_N) of a plant subjected to drought is considered a result of stomatal closure (Sharkey and Seemann 1989, Lal *et al*. 1996, Sánchez-Rodríguez *et al*. 1999) and metabolic impairment (Boyer 1976, Lawlor and Cornic 2002). Under a mild or moderate drought stress, stomatal closure is usually predominant (Sharkey 1990, Chaves 1991, Cornic and Massacci 1996). However, the non-stomatal effects are mostly attributed to the reduction in activity of some enzymes in the Calvin cycle, and the inhibition of photosynthetic electron transport as well as the impairment of photophosphorylation capacity (Sharkey and Seemann 1989, Kicheva *et al*. 1994).

Populus euphratica is a tree species growing at the edge of barren deserts or semi-barren deserts (Gu *et al*. 2004). Its high survival and biomass production in the arid areas of Mongolia, China, Pakistan, Iraq, and Iran is acclaimed (Sharma *et al*. 1999). Thanks to its tolerance to severe drought and high salinity and alkalinity in soils, *P. euphratica* is very important in maintaining ecosystem function in arid and semi-arid regions (Chen *et al*. 2004). The responses of *P. euphratica* to salt stress have also attracted a lot of attention (Ma *et al*. 1997, 2002, Chen *et al*. 2004). However, the mechanisms of *P. euphrarica* tolerance to drought stress are not well understood.

The river flow at the lower reaches of the Tarim River has been cut off since the 1970's, hence the groundwater depths in that region have decreased significantly. *P. euphratica* has never been subject to the most severe drought stress and consequently to degradation of its natural forests. To characterize photosynthesis of *P. euphratica* under such severe drought is not only an attempt to study acclimation mechanisms of plants to drought

---

Received 9 January 2006, *accepted* 14 February 2006.

*Corresponding author; fax: +86-991-7885320, e-mail: chenyn@ms.xjb.ac.cn

Abbreviations: C_i – intercellular CO_2 concentration; E – transpiration rate; g_s – stomatal conductance; L_s – stomatal limitation; P_N – net photosynthetic rate; PAR – photosynthetically active radiation; SI – saturating irradiance; T_{leaf} – leaf temperature; WUE − water use efficiency.

Acknowledgements: We thank Mr. X.M. Hao and Ms. X. Hang for their assistance in field measurements. This study is jointly supported by the Knowledge Innovation Project of the Chinese Academy of Sciences (Water Resources Utilization and Integrated Management Demonstration in Tarim River Basin) and the National Natural Science Foundation of China (grant Nos. 90502004, 30500081).

stress, but also an incentive to maintain *P. euphratica* natural forests in the arid and semi-arid regions.

15 trees (*P. euphratica*) studied were about 50–55 years old, 8–10 m in height, healthy and free of diseases and pest damages. For experiments, study area was located in Yhepumahan along the lower reaches of Tarim River. Trees grown at different groundwater depth were chosen at transects of 50, 150, and 250 m from the riverbank, respectively. Yahepumahan (40°29'N, 87°50'E, 845 m a.s.l.) is located in the lower reaches of the Tarim River between the Taklamakan Desert and the Kuluke Desert in northwestern China, where the annual precipitation varies in a range of 17.4–42.0 mm, annual mean evaporation capacity is 2 714.6 mm, and strong wind occurs frequently. Total annual solar radiation varies from 5 692 to 6 360 MJ m^{-2} and annual sunshine time is from 2 780 to 2 980 h, the accumulated temperature (≥10 °C) is from 4 040 to 4 300 °C, and an average diurnal temperature range is 13–17 °C (Chen *et al*. 2003a).

Gas exchange was measured on 8, 10, and 12 August, 2005 which were all clear days. The highest photosynthetically active radiation (PAR) was 2 000 µmol m^{-2} s^{-1}, the ambient concentration of CO_2 was 375 µmol mol^{-1}, and air temperature was 28 °C. Photosynthetic parameters were studied with a portable gas exchange system (*Li 6400*, *LiCOR*, Lincoln, NE, USA). The fully expanded, healthy and mature leaves in the middle part of crown were closed in the chamber (2×3 cm) for measurements. All the measurements had three replications. P_N, transpiration rate (E), and stomatal conductance (g_s) were automatically recorded by the machine. Water use efficiency (WUE) was calculated from the ratio P_N/E. On 9, 11, and 14 August 2005, diurnal course of gas exchange for the trees with different groundwater depths were measured at approximately 2-h intervals from 08:00 to 20:00 on clear days. Meanwhile, environmental conditions such as PAR, humidity, air temperature, and CO_2 concentration were also recorded. Three typical and functional leaves in every tree were used in diurnal measurements. The leaf surface was held perpendicularly to the radiation direction. Every measurement had three replications. Stomatal limitation (L_s) was calculated as $1 - C_i/C_a$, where C_i and C_a are intercellular and ambient CO_2 concentrations, respectively (Berry and Downton 1982).

Three transects parallel to the Tarim River were selected at 100-m intervals along a vertical sampling line from the riverbank to sand dune in Yhepumahan. Within each transect, an 8–10 m depth well was installed for monitoring the depths to groundwater by conductometry method.

Statistical analysis of all data obtained in this study was conducted by a paired-sample *t*-test using SPSS 11.0 for windows, p=0.05. Results were presented as means ± SE (n = 5). The graphs were processed by *Sigma-Plot 9.0*.

Availability of undergroundwater affected photosynthesis of *P. euphratica* under various PAR (Fig. 1*A*). The saturation irradiances (SI) for the trees with groundwater depth at 3.82, 4.74, and 5.82 m down from soil surface were about 1 900, 1 400, and 1 800 µmol m^{-2} s^{-1}, respectively. Photosynthetic rates of *P. euphratica* changed little when the irradiation was above SI. P_N values of the D_3 trees were significantly higher than those of the D_4 or D_5 trees (p<0.05) when PAR was above 500 µmol $m^{-2}s^{-1}$, while P_N at different groundwater depths was similar under 300 µmol m^{-2} s^{-1}. When PAR was 2 000 µmol m^{-2} s^{-1}, P_N values of the D_3 trees were 41.2 and 48.7% higher than those of the D_4 and D_5 trees. However, the D_4 and D_5 trees did not show significant differences in dependence of P_N on PAR.

g_s was positively correlated with PAR. In D_4 trees, g_s was extremely low and decreased by 68 %, compared with that of the D_3 trees. In D_5 trees, however, g_s was a little higher than in the D_3 trees (Fig. 1*D*). This result was further proved by the L_s in PAR treatment (Fig. 1*E*).

E increased with increasing PAR and groundwater depths (Fig. 1*B*). However, when PAR was less than 1 500 µmol m^{-2} s^{-1}, the average *E* of the D_5 trees was about 1.7-fold higher than that of the D_3 trees. WUE of the trees growing much near the river was significantly higher than those of trees far away the river under various PAR conditions (Fig. 1*C*). At 1 500 µmol m^{-2} s^{-1}, WUE of the D_3 trees was 1.8-fold and 2.4-fold higher than those of the D_4 and D_5 trees, respectively. In particular, in the D_3 and D_5 trees a significant increase in WUE was found (p<0.05) when PAR was less than 1 500 µmol m^{-2} s^{-1}. In D_4 trees, the WUE increased to maximum when PAR was 1 000 µmol m^{-2} s^{-1}.

The amount of carbon dioxide within the leaves decreased along with the increased PAR at three different groundwater depths (Fig. 1*F*). However, C_i did not always decrease along with increasing groundwater depth. C_i initially declined with increased groundwater depth and then increased as groundwater depth farther increased. For instance, at 1 500 µmol m^{-2} s^{-1}, C_i decreased by 17.4 µmol mol^{-1} while the groundwater depth decreased from 3.82 to 4.74 m. But it increased by 43.4 µmol mol^{-1} when the groundwater depth further increased to 5.82 m.

The highest PAR, 1 840 µmol m^{-2} s^{-1}, occurred at 12:00 in all experimental days (Fig. 2*A*). The daytime variations of leaf temperature, T_{leaf} of *P. euphratica* with different groundwater depths were similar, but T_{leaf} of the D_5 plants was obviously higher than that of the D_3 trees during daytime (Fig. 2*B*). P_N of the D_3 trees was significantly higher (p<0.05) than those of the D_4 and D_5 trees all day long (Fig. 2*C*). Daily maximum photosynthetic rate, P_{max}, of the D_3 trees occurred around 12:00 (PAR was around 1 840 µmol m^{-2} s^{-1} at that time, and T_{leaf} was about 27 °C), and then their P_N decreased till 14:00. When PAR reached 1 770 µmol m^{-2} s^{-1} and leaf temperature was about 30 °C, the P_{max} of D_4 trees occurred around 14:00, and decreased afterwards.

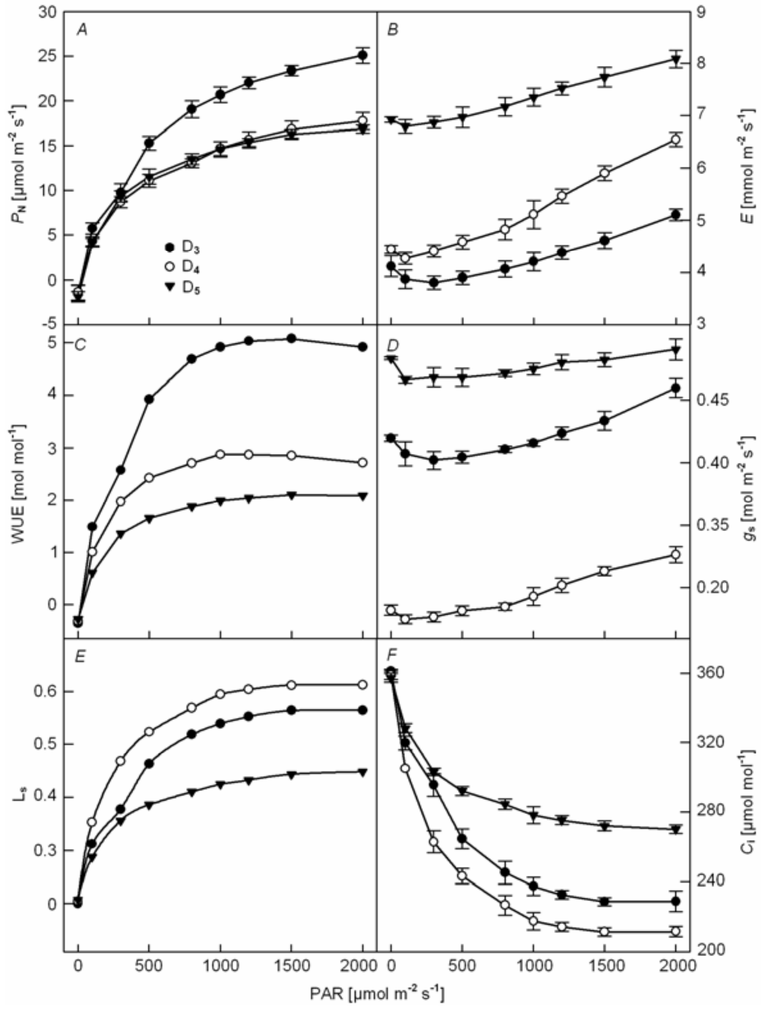

Fig. 1. Net photosynthetic rate, P_N (*A*), transpiration rate, *E* (*B*), water use efficiency, WUE (*C*), stomatal conductance, g_s (*D*), stomatal limitation, L_s (*E*), and intercellular CO_2 concentration, C_i (*F*) of *P. euphratica* under three different groundwater depths (D_3, D_4, and D_5). Means ± SE (*n* = 5).

However, for the D_5 trees P_N peaked at 12:00 (PAR was around 1 840 μmol m^{-2} s^{-1} at that time, and T_{leaf} was about 29 °C), and decreased thereafter (Fig. 2*A,B,C*). The g_s values at 4.74 and 5.82 m obtained at noon decreased by 5 and 6 %, respectively, compared with those obtained in the morning (10:00). Interestingly, while groundwater depth was 3.82 m, g_s at noon was 13 % higher than that at 10:00. However, at the same groundwater depth, the diurnal changes of g_s and P_N showed similar patterns (Fig. 2*C,F*). *E* shared the same trend with T_{leaf} (Fig. 2*B,D*) but also seemed to be influenced by vapour pressure deficit at leaf surface (VpdL) (data not shown), and *E* of D_3 trees was significantly lower than that of D_5 trees during the period of 10:00–16:00 (Fig. 2*D*), because T_{leaf} and VpdL of the D_3 trees were lower than those of D_5 trees at the same time. WUE in *P. euphratica* with different groundwater availabilities came to maximum at 10:00, and decreased from then on, although a little fluctuation existed (Fig. 2*E*). However, the average WUE value of the trees with groundwater depth at 3.82 m was 56 and 72 % higher than those of the D_4 and D_5 trees, respectively. This was consistent with the findings that the D_3 trees displayed a higher P_N and lower *E* compared with those of D_4 and D_5 trees (Fig. 2*C,D*).

The *P. euphratica* trees selected in this study were located along the riverbank of the Tarim River. Availability of groundwater for the trees varied due to different groundwater depths below the soil surface. During a growing season, groundwater is the most important water source for the trees grown in that region because of a huge water deficit resulted from very limited rainfall and enormous water evaporation. According to Chen *et al.* (2003b, 2004), groundwater depths at 3.82, 4.74, or 5.82 m below the ground surface in the lower reaches of the Tarim River are non-water limited, mild, and moderate drought stress to *P. euphratica*, respectively.

Reduction of P_N under water stress has been noted by Kaiser (1987), Chaves (1991), and Ramanjulu *et al.* (1998). Therefore it is reasonable that P_N of D_3 plants of *P. euphratica* was notably higher than that in D_4 and D_5 trees with increased PAR (Fig. 1*A*), indicating a distinct difference in carbon assimilation capacity among the *P. euphratica* trees with different groundwater availabilities. Both stomatal and non-stomatal factors contribute to the effects of drought on the reduction of photosynthesis (Calatayud *et al.* 2000). Farquhar and Sharkey (1982) as

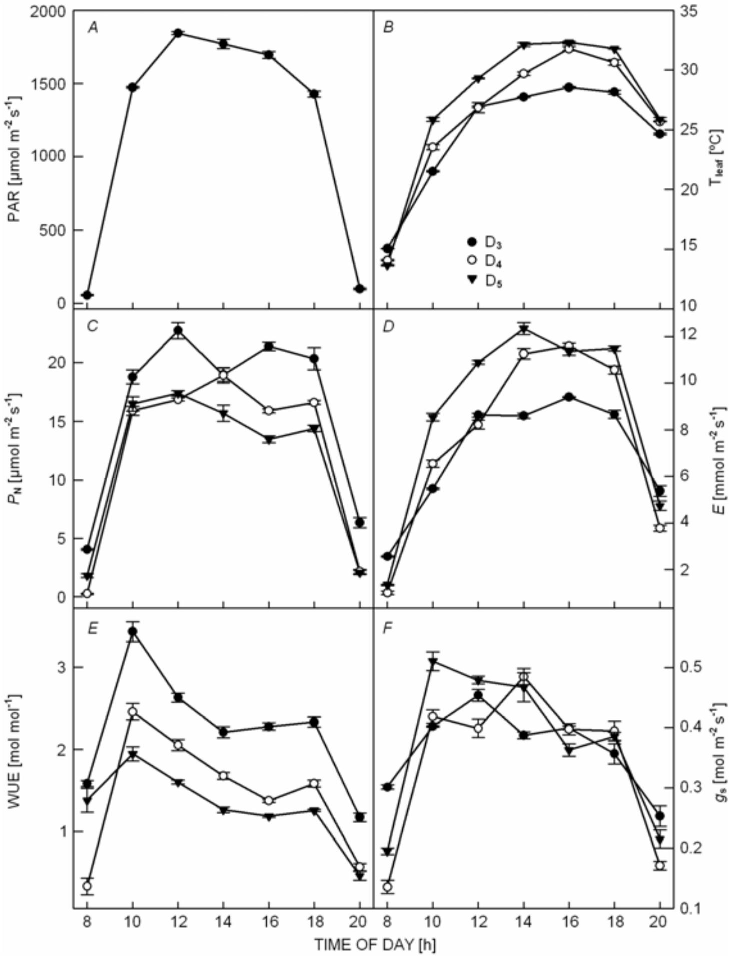

Fig. 2. Diurnal patterns in photosynthetically active radiation, PAR (*A*), leaf temperature, T_{leaf} (*B*), net photosynthetic rate, P_N (*C*), transpiration rate, *E* (*D*), water use efficiency, WUE (*E*), and stomatal conductance, g_s (*F*) of *P. euphratica* under three different groundwater depths (D_3, D_4, and D_5). Means ± SE (*n* = 5).

well as Xu (1997) pointed out that the reduction of P_N is the result of decrease in g_s, only if there is a reduction in C_i and an increase in L_s. On the other hand, if P_N decreases accompany an increase of intercellular CO_2 concentration and a reduction of stomatal limitation as well, the main constraint of photosynthesis is the result of the non-stomatal factors. Thereforethe P_N reduction of the trees with groundwater depth at 4.74 and 5.82 m below ground surface may be due to the reasons above mentioned. The different change trends of C_i and L_s at different groundwater depths could give farther evidence (Fig. 1*E*,*F*). Compared with the C_i and L_s of the trees with groundwater depth at 3.82 m down, trees with poorer accessibility to groundwater at 4.74 m had lower C_i and higher L_s, but higher C_i and lower L_s at 5.82 m groundwater depth throughout irradiances. Hence, the main reasons for the reduction of P_N when groundwater depths were 4.74 and 5.82 m were the decrease of g_s and non-stomatal factors, respectively. This suggests that primary constraint factors for photosynthesis of *P. euphratica* are different and related with drought stress. Stomatal control of water losses has been identified as an early event of plant responses to water deficit under field condition, leading to a limitation of carbon uptake by the leaves (Chaves 1991, Cornic and Massacci 1996). However, as drought stress continues, metabolic impairment becomes the dominant limitation and inhibits photosynthetic CO_2 assimilation (Flexas and Medrano 2002). We found that the dominant factors inhibiting photosynthesis in *P. euphratica* were stomatal closure and non-stomatal factors at mild and moderate drought, respectively.

P_N declines as leaf water stress increases (Kramer and Boyer 1995). However, we found that P_N in *P. euphratica* was not all decreased along with increasing drought stress. Although the P_N of D_4 and D_5 trees sharply decreased compared with the D_3 trees, the P_N at 4.74 m of groundwater depth is similar to that at 5.82 m groundwater depth in both daily course and various PAR conditions (Figs. 1*A*, 2*C*). This suggests that *P. euphratica* could maintain P_N as drought stress increased from mild to moderate level, which is consistent with the research results about grapevine under drought stress by Guan *et al*. (2004). The maintenance of P_N in plants under drought stress depends on osmotic adjustment (Morgan *et al*. 1993, Rekika *et al*. 1998, Shangguan *et al*. 1999), so we may speculate that *P. euphratica* under moderate drought stress maintains P_N by osmotic adjustment that enables the plant to continuously function.

References

Berry, J.A., Downton, W.J.S.: Environmental regulation of photosynthesis. – In: Govindjee (ed.): Photosynthesis. Vol. II. Pp. 263-343. Academic Press, New York – London – Paris – San Diego – San Francisco – São Paulo – Sydney – Tokyo – Toronto 1982.

Boyer, J.S.: Photosynthesis at low water potentials. – Phil. Trans. roy. Soc. London B **273**: 501-512, 1976.

Boyer, J.S.: Plant productivity and environment. – Science **218**: 443-448, 1982.

Calatayud, P.-A., Llovera, E., Bois, J.F., Lamaze, T.: Photosynthesis in drought-adapted cassava. – Photosynthetica **38**: 97-104, 2000.

Chaves, M.M.: Effects of water deficits on carbon assimilation. – J. exp. Bot. **42**: 1-16, 1991.

Chaves, M.M., Maroco, J.P., Pereira, J.S.: Understanding plant responses to drought – from genes to the whole plant. – Funct. Plant Biol. **30**: 239-264, 2003.

Chen, S.L., Moitaba, Z., Eberhard, F., Wang, S.S., Aloys, H.: Hydrogel modified uptake of salt ions and calcium in *Populus euphratica* under saline conditions. – Trees **18**: 175-183, 2004.

Chen, Y.N., Chen, Y.P., Li, W.H., Zhang, H.F.: Response of the accumulation of proline in the bodies of *Populus euphratica* to the change of ground water level at the lower reaches of Tarim River. – Chin. Sci. Bull. **48**: 1995-1999, 2003a.

Chen, Y.N., Li, W.H., Xu, H.L., Liu, J.Z., Zhang, H.F., Chen, Y.P.: [The influence of groundwater on vegetation in the lower reaches of Tarim River, China.] – Acta geogr. sin. **58**: 542-549, 2003b. [In Chin.]

Chen, Y.N., Wang, Q., Ruan, X., Li, W.H., Chen, Y.P.: Physiological response of *Populus euphratica* to artificial water-recharge of the lower reaches of Tarim River. – Acta bot. sin. **46**: 1393-1401, 2004.

Chen, Y.P., Chen, Y.N., Li, W.H., Zhang, H.F.: [Effect of ecological water input on MDA of *Populus euphratica* leaf in the lower reaches of the Tarim River.] – Chin. J. appl. environ. Biol. **10**: 408-411, 2004. [In Chin.]

Cornic, G., Massacci, A.: Leaf photosynthesis under drought stress. – In: Baker, N.R. (ed.): Photosynthesis and the Environment. Pp. 347-366. Kluwer Academic Publishers, Dordrecht – Boston – London 1996.

Farquhar, G.D., Sharkey, T.D.: Stomatal conductance and photosynthesis. – Annu. Rev. Plant Physiol. **33**: 317-345, 1982.

Flexas, J., Medrano, H.: Drought-inhibition of photosynthesis in C_3 plants: stomatal and non-stomatal limitations revisited. – Ann. Bot. **89**: 183-189, 2002.

Gu, R.S., Liu, Q.L., Pei, D., Jiang, X.N.: Understanding saline and osmotic tolerance of *Populus euphratica* suspended cells. – Plant Cell Tiss. Org. **78**: 261-265, 2004.

Guan, X.Q., Zhao, S.J., Li, D.Q., Shu, H.R.: Photoprotective function of photorespiration in several grapevine cultivars under drought stress. – Photosynthetica **42**: 31-36, 2004.

Kaiser, W.M.: Effects of water deficit on photosynthetic capacity. – Physiol. Plant. **71**: 142-149, 1987.

Kicheva, M.I., Tsonev, T.D., Popova, L.D.: Stomatal and non-stomatal limitations to photosynthesis in two wheat cultivars subjected to water stress. – Photosynthetica **30**: 107-116, 1994.

Kramer, P.J., Boyer, J.S.: Water Relations of Plants and Soils. – Academic Press, San Diego 1995.

Lal, A., Ku, M.S.B., Edwards, G.E.: Analysis of inhibition of photosynthesis due to water stress in the C_3 species *Hordeum vulgare* and *Vicia faba*: Electron transport, CO_2 fixation and carboxylation capacity. – Photosynth. Res. **49**: 57-69, 1996.

Lauriano, J.A., Ramalho, J.C., Lidon, F.C., Matos, M. do C.: Peanut photosynthesis under drought and re-watering. – Photosynthetica **42**: 37-41, 2004.

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.

Ma, H.C., Lindsay, F., Wang, S.S., Altman, A., Hüttermann, A.: Photosynthetic response of *Populus euphratica* to salt stress. – Forest Ecol. Manage. **93**: 55-61, 1997.

Ma, T.J., Liu, Q.L., Li, Z., Zhang, X.J.: Tonoplast H^+-ATPase in response to salt stress in *Populus euphratica* cell suspensions. – Plant Sci. **163**: 499-505, 2002.

Morgan, J.A., Lecain, D.R., McCaig, T.N., Quick, J.S.: Gas exchange, carbon isotope discrimination, and productivity in winter wheat. – Crop Sci. **33**: 178-186, 1993.

Ramanjulu, S., Sreenivasalu, N., Kumar, S.G., Sudhakar, C.: Photosynthetic characteristics in mulberry during water stress and rewatering. – Photosynthetica **35**: 259-263, 1998.

Rekika, D., Nachit, M.M., Araus, J.L., Monneveux, P.: Effects of water deficit on photosynthetic rate and osmotic adjustment in tetraploid wheats. – Photosynthetica **35**: 129-138, 1998.

Sánchez-Rodríguez, J., Pérez, P., Martínez-Carrasco, R.: Photosynthesis, carbohydrate levels and chlorophyll fluorescence-estimated intercellular CO_2 in water-stressed *Casuarina equisetifolia* Forst. & Forst. – Plant Cell Environ. **22**: 867-873, 1999.

Shangguan, Z., Shao, M., Dyckmans, J.: Interaction of osmotic adjustment and photosynthesis in winter wheat under soil drought. – J. Plant Physiol. **154**: 753-758, 1999.

Sharkey, T.D.: Water stress effects on photosynthesis. – Photosynthetica **24**: 651, 1990.

Sharkey, T.D., Seemann, J.R.: Mild water stress effects on carbon-reduction-cycle intermediates, ribulose bisphosphate carboxylase activity, and spatial homogeneity of photosynthesis in intact leaves. – Plant Physiol. **89**: 1060-1065, 1989.

Sharma, A., Dwivedi, B.N., Singh, B., Kumar, K.: Introduction of *Populus euphratica* in Indian semi-arid trans Gangetic plains. – Ann. forest. **7**: 1-8, 1999.

Tezara, W., Marín, O., Rengifo, E., Martínez, D., Herrera, A.: Photosynthesis and photoinhibition in two xerophytic shrubs during drought. – Photosynthetica **43**: 37-45, 2005.

Xu, D.Q.: [Some problems in stomatal limitation analysis of photosynthesis.] – Plant Physiol. Commun. **33**: 241-244, 1997. [In Chin.]