BRIEF COMMUNICATION

Photosynthetic response to soil water contents of an annual pioneer C_4 grass (*Agriophyllum squarrosum*) in Hunshandak Sandland, China

M.Z. LIU, G.M. JIANG*, S.L. NIU, Y.G. LI, L.M. GAO, L. DING, and Y. PENG

Laboratory of Quantitative Vegetation Ecology, Institute of Botany, the Chinese Academy of Science, 20 Nanxincun, Xiangshan, 100093, Beijing, P.R. China

Abstract

Net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and leaf water potential (Ψ_l) of an annual pioneer C_4 grass (*Agriophyllum squarrosum*) were compared under different simulated precipitation events in a field of Hunshandak Sandland, China. The increase of soil water content (SWC) had significant effect on these physiological traits ($p<0.001$). In the vegetative stage, the values of P_N, E, and g_s went up sharply when SWC increased at the beginning, while they went down with continuous increase of SWC. P_N, E, and g_s increased 1.4, 1.7, and 1.7 fold, respectively, with SWC range from 6.7 to 11.6 %. In the reproductive stage, similar trends were found, except for the climate with a higher SWC. This indicated that *A. squarrosum* was very sensitive to the small increment of SWC which might have a large photosynthetic potential. Ψ_l increased by about 8 % as the SWC changed from 6.7 to 8.8 %, and then maintained a steady level when the SWC was higher than 8.8 %, while the values of P_N, E, and g_s kept increasing even after this SWC. This might indicate that the adjustment of Ψ_l response to the changes of SWC lagged that of the photosynthetic parameters.

Additional key words: leaf water potential; net photosynthetic rate; stomatal conductance; transpiration rate.

Although there have been some investigations on the photosynthetic response to soil water availability of desert plants in arid area around the world (Terwilliger and Zeroni 1994, Singh *et al*. 1996, Szente *et al.* 1996, Deng *et al*. 2002), the response of sand-fixation pioneer plants in sand lands was seldom reported. Hunshandak Sandland is one of the five large sandlands in China (Han *et al.* 2002). It was once the best grassland before 1960's, but now most of it has degraded severely, with the shifting sand dunes amounting to 70 % of total area (Ma *et al.* 1998). It is very urgent to regenerate the degraded grassland in this area, the key being fixation of shifting sand dunes. Therefore, the pioneer plant species in the shifting sand dunes should be firstly taken into account.

Agriophyllum squarrosum, a therophyte of sandy soils (see Wang 2002), is one of the pioneer annual C_4 grasses in shifting sand dunes in Hunshandak Sandland. Its seeds germinate quickly with only a little rainfall in the beginning of June (Chen 1986), its vegetative stage lasts to the end of July, and it begins to bloom and go to seed in the middle of August. Its roots grow very fast. The main root is 3.5 cm long when the cotyledon comes up the soil, while it is 7.8 cm long one week later. After maturing, the rooting depth is about 70 cm and the horizontal scope is about 100 cm. The frond is 30 cm high (Chen 1986). *A. squarrosum* can dominate most of the shifting sand dunes which were fenced, with the highest coverage of about 60 % in the first year. In the second year, other

Received 19 February 2003, *accepted* 14 April 2003.
*Corresponding author; fax: 86-10-62590843, e-mail: jgm@ht.rol.cn.net
Abbreviations: E — transpiration rate; g_s — stomatal conductance; P_N — net photosynthetic rate; PPFD — photosynthetic photon flux density; SWC — soil water contents; T_l — leaf temperature; Ψ_l — leaf water potential.
Acknowledgements: This work was founded by the Key Project of the Chinese Academy of Sciences (KSCX1-08-02). The authors thank Mr. Liu Guohou, the leader of Zhenlan Banner (located in Hunshandak Sandland), and Mr. Wutunasen, the chairman of the village, for their field assistance.

species such as *Corispermum heptapotamicum* can join in. By this way, shifting sand dunes can be fixed gradually. So, *A. squarrosum* is considered as the best indicator of the beginning of community succession in shifting sand dunes. Therefore we compared P_N, E, g_s, and Ψ_l of *A. squarrosum* under different simulating precipitation events. The experiment should help full understanding of the eco-physiological reactions of such pioneer species under different precipitation and explore the relationship between gas exchange and soil water contents.

The experiment was conducted at Hunshandak Sandland Ecosystem Research Station (43º56′47"N, 116º08′15"E) of the Chinese Academy of Sciences, based in Xilingel league of Inner Mongolia Autonomous Region of China. The prevailing climate is of the temperate arid and semi-arid type. The average annual temperature is about 1.7 °C, annual precipitation is about 250-350 mm, with uneven distribution throughout the year. The annual transpiration is 2 000-2 700 mm. The annual total radiation time is 3 000-3 200 h. Photosynthetic photon flux density (PPFD) at 10:00 ranged from 1 625-1 716 μmol m^{-2} s^{-1} during our experiments (Fig. 1*A*); the leaf temperature (T_l) changed from 33.4 to 35.6 °C (Fig. 1*B*).

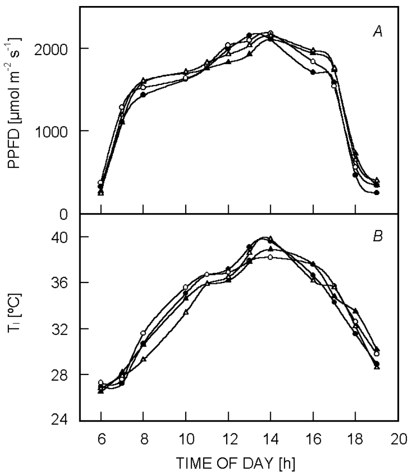

Fig. 1. Average incident photosynthetic flux density (PPFD) (*A*) and leaf temperature (T_l) (*B*) of *A. squarrosum* on the measuring days in vegetative stage (8 July: ●; 9 July: ○) and reproductive stage (17 August: ▲; 18 August: Δ) of 2002 at Hunshandak Sandland, China.

The field experimental plots were circular with a radius 0.5 m aluminium frame (height was 10 cm) containing only *A. squarrosum*, without other plants. The upedge of frames was 3 cm above the sand surface. The sizes of target plants were similar and the distances between two plots were at least 1 m. Each experiment included five water events. On 7 July and 16 August, all plots were watered with 10, 15, 20, 25, and 30 mm of water, respectively. Water was applied to the entire plot area with a handheld sprinkler as uniformly as possible. The application rate was as slow as possible to minimise runoff. In each treatment, three individuals of *A. squarrosum* were chosen. There were three additional plants for the control experiment. P_N, E, g_s, and Ψ_l were measured during 2 d (8-9 July and 17-18 August 2002) after watering, at about 10:00, *i.e.* at the peak of photosynthesis.

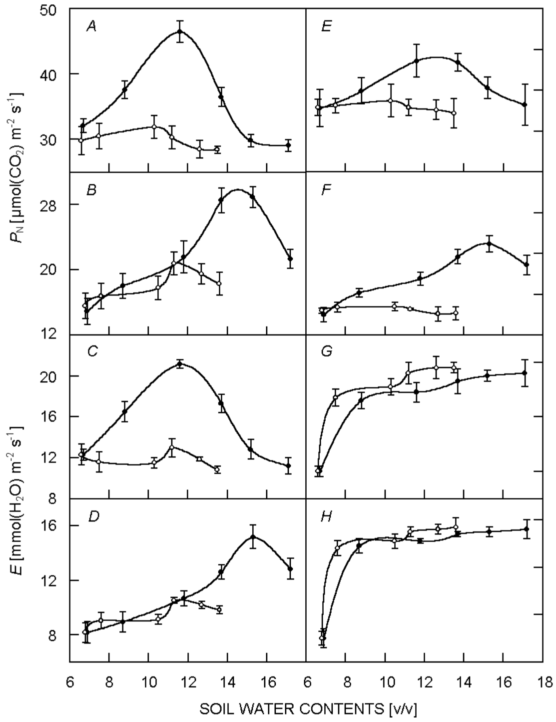

Fig. 2. Net photosynthetic rate (*A, B*), transpiration rate (*C, D*), stomatal conductance (*E, F*), and leaf water potential (*G, H*) of *A. squarrosum* in response to different soil water content in vegetative stage (*A, C, E, G*: 8 July: ●; 9 July: ○) and reproductive stage of 2002 (*B, D, F, H*: 17 August: ●; 18 August: ○) in Hunshandak Sandland, China. Means ± SE.

All experiment days were clear. Prior to both experiments, about 10 d were without rainfall in the area. Three replicate samples of current foliage from each treated plant were measured using a *LCA4* Portable Photosynthetic System (*ADC*, Hoddesdon, UK). After gas exchange measurements, Ψ_l was measured with a *WP4* Dewpoint Potential Meter (*Decagon Devices*, Pullman, WA, USA). Three replications were made for each treatment. Soil moisture contents at 18 experiment plots were investigated with a *Delta-T* Moisture Meter (Profile Probe, type *PR1/6*, UK) by means of one probe buried in soil. The *HH2* moisture meter was connected to the equipment to show readings. The test depth was 10, 20, 30, and 40 cm.

The large data set was entered into an *EXCEL* spreadsheet. Analysis of variance (*ANOVA*) was used to test for statistic evaluation of the impact of amount of precipitation on physiological characteristics (*SPSS 10.0 for*

Windows, Chicago, USA).

Simulated precipitation significantly affected P_N of *A. squarrosum* (p<0.001). At the vegetative stage, P_N increased with SWC from 6.7 to 11.6 % and then decreased gradually as SWC continuously increased. At SWC of 11.6 %, P_N was 1.4 fold that in control plants (SWC of 6.7 %) (Fig. 2*A*), while in the reproductive period, the highest P_N was noted at SWC of 15.3 % (Fig. 2*B*). When SWC decreased in the second experiment day, P_N of all treated plants decreased to the normal levels (Fig. 2*A,B*).

E and g_s were significantly affected by SWC changes (p<0.001). *E* went up quickly and was highest at SWC of 11.6 % in the vegetative stage (Fig. 2*C*), while it increased slowly and was highest at 15.3 % in the reproductive stage (Fig. 2*D*). Similar trends of g_s were found in both growth periods (Fig. 2*E,F*). Ψ_l increased by about 8.0 % quickly when SWC varied from 6.7 to 8.8 %, and then was stable with SWC increasing continuously in both growth periods (Fig. 2*G,H*). The control plants had the lowest Ψ_l. There was no significant difference in Ψ_l among the treatments. Ψ_l only decreased slightly when SWC decreased on the second experiment day (Fig. 2*G,H*).

Photosynthesis is mainly limited by stomata closure that is affected by external environmental factors such as irradiance, temperature (Kaiser 1987), air humidity, and wind speed (Cornic and Briantais 1991, Quick *et al.* 1992). We found that P_N of *A. squarrosum* quickly responded to change of SWC, especially during the vegetative stage (Fig. 2*A*). This is consistent with the results of Tenhunen *et al*. (1990) and Zunzunegui *et al*. (1999) who found that P_N in seedlings of some desert plants was higher in the wet environment than in the drought one. This might indicate that *A. squarrosum* is very sensitive to precipitation in the vegetative stage and has a high photosynthetic potential. In fact, the high P_N was more meaningful for annual grasses in the vegetative stage than in the reproductive stage. From the aspects of energy storage, it must accumulate enough nutrients to produce a large number of seeds in relatively short growth period (from 10 June to 30 August). In our experiment, small increment of SWC led to great increment of P_N. This reflects that xerophytes can start-up the photosynthetic apparatus responding to the increase of SWC more quickly than mesophytes (Ensinger *et al*. 2000, Voils *et al.* 2002). Our results reflected the stomata opened wider under high SWC than under normal conditions (Fig. 2*E,F*). This might suggest that xerophytes usually respond to change of water availability by stomata control (Monteith 1995, Comstock and Mencuccini 1998).

SWC decreased on the second day after watering, which may be due to a good penetration of sandy soil in our experiment site. Correspondingly, the values of P_N, *E*, and g_s were greatly reduced. This agrees with the report of Jones (1993) who suggested that desert plants usually slow down the use of soil water when surplus water is supplied. And some of this water may be used later (Cowan 1982, Schulze *et al.* 1996). Our results may indicate that *A. squarrosum* adopts such conservative water use strategy (Ehleringer *et al*. 1991) since it has both shallow and deep root systems (Chen 1986). Shallow roots (0-15 cm) may absorb a small amount of precipitation, while the deep root systems (20-70 cm) can take up water from the deep soil layer during drought period because the water in sands penetrates into the deep soil layers easily but evaporates with difficulty. These morphological and physiological characteristics might contribute to its strong adaptive ability to the severe condition in shifting sand dunes.

Ψ_l positively influences P_N (Stewart *et al*. 1995). However, we found that gas exchange of *A. squarrosum* increased immediately (Fig. 2*A,B*) *via* stomatal adjustment (Fig. 2*E,F*), instead of Ψ_l (Fig. 2*G,H*), responding to instantaneous elevation of SWC. Similar results were found with desert plants (Cavender-Bares and Bazzaz 2000, Schwinning *et al.* 2002). Additionally, Ψ_l did not decrease when the SWC declined on the second day after watering (Fig. 2*G,H*). This suggests that the adjustment of Ψ_l responding to the SWC might lag that of the photosynthetic parameters (Yao *et al.* 2001, Voils *et al.* 2002).

In conclusion, *A. squarrosum* was sensitive to the small increment of soil water contents and had high photosynthetic potential especially in the vegetative stage. P_N, g_s, and *E* greatly increased with the SWC increase at first, but they decreased when SWC increased continuously. However, the response of leaf water potential to changes of soil water content lagged that of the photosynthetic parameters.

References

Cavender-Bares, J., Bazzaz, F.A.: Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. – Oecologia **124**: 8-18, 2000.

Chen, S.H.: [Root Types of Plants in Inner Mongolia Grassland.] – Inner Mongolia People Press, Hohhot 1986. [In Chin.]

Comstock, J., Mencuccini, M.: Control of stomatal conductance by leaf water potential in *Hymenoclea salsola* (T. & G.), a desert subshrub. – Plant Cell Environ. **21**: 1029-1038, 1998.

Cornic, G., Briantais, J.-M.: Partitioning of photosynthetic electron flow between CO_2 and O_2 reduction in a C_3 leaf (*Phaseolus vulgaris* L.) at different CO_2 concentrations and during drought stress. – Planta **183**: 178-184, 1991.

Cowan, I.R.: Regulation of water use in relation to carbon gain in higher plants. – In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (ed.): Physiological Plant Ecology II. Pp. 589-613. Springer-Verlag, Berlin – Heidelberg – New York 1982.

Deng, X., Li, X.M., Zhang, X.M., Ye, W.H.: [A study of the gas exchange characteristics of four desert plants.] – Acta phytoecol. sin. **26**: 605-612, 2002. [In Chin.]

Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F., Sandquist, D.R.: Differential utilization of summer rains by desert plants. – Oecologia **88**: 430-434, 1991.

Ensinger, I., Hagen, C., Braune, W.: Strategies providing success in a variable habitat. II. Ecophysiology of photosynthesis of *Cladophora glomerata*. – Plant Cell Environ. **23**: 1129-1136, 2000.

Han, N.Y., Jiang, G.M., Li, W.J.: Management of the Degraded Ecosystems in Xilingol Biosphere Reserve. – Tsinghua University Press, Beijing 2002.

Jones, H.G.: Drought tolerance and water-use efficiency. – In: Smith, J.A.C., Griffiths, J. (ed.): Water Deficits: Plant Responses from Cell to Community. Pp. 193-203. BIOS, Oxford 1993.

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

Ma, S.W., Ma, Y.M., Yao, H.L., Wang, L.H., Yao, Y.F.: [Eromology.] – Inner Mongolia People Press, Hohhot 1998. [In Chin.]

Monteith, J.L.: A reinterpretation of stomatal responses to humidity. – Plant Cell Environ. **18**: 357-364, 1995.

Quick, W.P., Chaves, M.M., Wendler, R., David, M., Rodrigues, M.L., Passaharinho, J.A., Pereira, J.S., Adcock, M.D., Leegood, R.C., Stitt, M.: The effect of water stress on photosynthetic carbon metabolism in four species grown under field conditions. – Plant Cell Environ. **15**: 25-35, 1992.

Schulze, E.D., Mooney, H.A., Sala, O.E., Jobbagy, E., Buchmann, N., Bauer, G., Cannadel, J., Jackson, R.B., Loreti, J., Oestrheld, M., Ehleringer, J.R.: Rooting depth, water availability and vegetation cover along an aridity gradient in Patagonia. – Oecologia **108**: 503-511, 1996.

Schwinning, S., Davis, K., Richardson, L., Ehleringer, J.R.: Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. – Oecologia **130**: 345-355, 2002.

Singh, M., Chaturvedi, R., Sane, P.V.: Diurnal and seasonal photosynthetic characteristics of *Populus deltoides* Marsh. leaves. – Photosynthetica **32**: 11-21, 1996.

Stewart, J.D., Zine et Abidine, A., Bernier, P.Y.: Stomatal and mesophyll limitations of photosynthesis in black spruce seedlings during multiple cycles of drought. – Tree Physiol. **15**: 57-64, 1995.

Szente, K., Nagy, Z., Tuba, Z., Fekete, G.: Photosynthesis of *Festuca rupicola* and *Bothriochloa schaemum* under degradation and cutting pressure in a semi-arid loess grassland. – Photosynthetica **32**: 399-407, 1996.

Tenhunen, J.D., Serra, A.S., Harley, P.C., Dougherty, R.L., Reynolds, J.F.: Factors influencing carbon fixation and water use by mediterranean sclerophyll shrubs during summer drought. – Oecologia **82**: 381-393, 1990.

Terwilliger, J., Zeroni, M.: Gas exchange of a desert shrub (*Zygophyllum dumosum* Boiss.) under different soil moisture regimes during summer drought. – Vegetatio **115**: 133-144, 1994.

Voils, S., Mendlinger, S., Ward, D.: Adaptive traits of wild barley plants of Mediterranean and desert origin. – Oecologia **133**: 131-138, 2002.

Wang, R.Z.: The C_4 photosynthetic pathway and life forms in grassland species from North China. – Photosynthetica **40**: 97-102, 2002.

Yao, C., Moreshet, S., Alon, B.: Water relations and hydraulic control of stomatal behaviour in bell pepper plant in partial soil drying. – Plant Cell Environ. **24**: 227-235, 2001.

Zunzunegui, M., Fernandez Baco, L., Barradas, M.C.D., Garcia Novo, F.: Seasonal changes in photochemical efficiency in leaves of *Halimium halimifolium*, a mediterranean semideciduous shrub. – Photosynthetica **37**: 17-31, 1999.