BRIEF COMMUNICATION

Enhanced water use efficiency in dry loess grassland species grown at elevated air CO_2 concentration

K. SZENTE, Z. NAGY and Z. TUBA

Department of Botany and Plant Physiology, Agricultural University of Gödöllő, H-2103 Gödöllő, Hungary

Abstract

Net CO_2 assimilation rate (P_N), stomatal conductance (g_s), transpiration rate (E), and water use efficiency (WUE) in four perennial C_3 species (grasses: *Dactylis glomerata, Festuca rupicola,* dicots: *Filipendula vulgaris, Salvia nemorosa*) grown for 231 d in open-top chambers at ambient (CA, 350 μmol mol^{-1}) or elevated (CE, 700 μmol mol^{-1}) CO_2 concentrations were compared. When measured at CE, P_N was significantly higher in CE plants of all four species than in the CA ones. The increase in P_N was less prominent in the two grasses than in the two dicots. The E was significantly higher in the CE-grass *F. rupicola* and CE-dicot *F. vulgaris* than in the CA plants. There was no change in E owing to CE in the other grass and dicot. The g_s in *F. vulgaris* and *F. rupicola* increased, while there was a decrease in *D. glomerata* and no change in *S. nemorosa*. WUE increased in all species grown in CE: four- to five-fold in the dicots and less than two-fold in the grasses. The increase in WUE was primarily due to an increase in P_N and not to a decrease in E.

Additional key words: acclimation; gas exchange; net photosynthetic rate; stomatal conductance; transpiration rate.

One of the most remarkable impacts on plants of long-term exposure to CE environment is the increase of WUE (Morison 1985, Jarvis 1993, Amthor 1995, Beerling and Woodward 1995, Pearson and Brooks 1995, Šantrůček and Sage 1996,

---

Received 23 December 1997, *accepted* 5 February 1998.
Fax: (+36)-28-410 804; e-mail: tuba@fau.gau.hu
Dedicated to Academician Prof. Pal Jakucs on the occasion of his 70th birthday.
Acknowledgements: The present study was carried out in the framework of the ESPACE-Grass Project (EU Brussels, Contract No. EV5V-CT93-0292) and was supported by the ECOCRAFT Environment R&D Programme (EU Brussels), the Hungarian Scientific Research Foundation (OTKA T22723, OTKA T18595), National Committee for Technical Development (OMFB E0031), and Research Development in Higher Education (FKFP 0472/97).

Drake *et al.* 1997; for review see Saralabai *et al.* 1997), which is mainly caused by a decrease in g_s and E. WUE can increase even in plants with downward acclimation of photosynthesis (Tuba *et al.* 1996). We report here examples where an increase in WUE of dry grassland species occurred at unchanged or increased E. The P_N, g_s, E, and WUE in four C_3 perennial species (*D. glomerata, F. rupicola, F. vulgaris, S. nemorosa*) from a loess grassland growing at CA or CE were compared.

The investigated loess grassland (steppe) vegetation (*Salvio-Festucetum rupicolae pannonicum* Zólyomi) and the tested species are described in Zólyomi and Fekete (1994), Nagy *et al.* (1994), and Tuba *et al.* (1996). The climate is a temperate continental with hot dry summers; mean annual precipitation 500 mm or less; annual mean temperature of 11 °C; and large annual amplitude of temperature changes (22 °C). The CO_2 exposure was carried out in the Global Climate Change and Plant Research Station (Gödöllő, 28 km east of Budapest) for 231 d using open top chambers (Tuba *et al.* 1994, 1996). The CE was maintained at 700 µmol mol^{-1} and the CA at 350 µmol mol^{-1}. Leaf gas-exchange measurements were carried out *in situ*, in the open top chambers in the morning hours in seven to nine replicates per species. The measurements and calculations were carried out as described in Tuba *et al.* (1994, 1996). WUE is given as P_N/E.

Table 1. Net photosynthetic rate, P_N [µmol(CO_2) m^{-2} s^{-1}], transpiration rate, E [µmol(H_2O) m^{-2} s^{-1}], stomatal conductance, g_s [mmol m^{-2} s^{-1}], and water use efficiency, WUE [mmol(CO_2) mol^{-1}(H_2O)] in leaves of the investigated loess grassland species grown in open top chambers for 231 d under the ambient (CA, 350 µmol mol^{-1}) and elevated (CE, 700 µmol mol^{-1}) air CO_2 concentrations. The parameters were measured *in situ* at an irradiance of 1200 µmol m^{-2} s^{-1}, temperature 20 °C, air humidity 40 %, and CA or CE. Mean values (n = 7-9) ± standard deviations are given. $^{*}p = 0.05$, $^{**}p = 0.01$, $^{*}p = 0.001$.

		F. rupicola	*D. glomerata*	*F. vulgaris*	*S. nemorosa*
P_N	CA	1.63±0.44	4.64±0.71	1.61±0.17	1.87±0.37
	CE	5.21±1.89***	7.06±0.99***	8.41±1.04***	12.13±0.63***
E	CA	2.97±0.25	6.03±0.50	5.55±0.41	6.62±1.55
	CE	5.06±0.38***	5.76±0.20^{ns}	6.74±0.54***	7.63±0.26^{ns}
g_s	CA	159.56±21.08	335.71±47.41	426.31±75.11	705.00±137.45
	CE	289.84±27.16***	279.69±13.13**	622.36±92.04***	863.77±165.79^{ns}
WUE	CA	0.55±0.17	0.77±0.11	0.29±0.04	0.32±0.09
	CE	1.01±0.32*	1.23±0.18***	1.26±0.25***	1.59±0.05***

P_N was significantly higher (Table 1) in all four species in the CE plants than in the CA ones. The highest increase was found in *S. nemorosa* (six-fold) and *F. vulgaris* (four-fold) while the grasses increased their P_N only by less than three-fold. This was in agreement with our earlier finding (Tuba *et al.* 1996) that as concerns P_N, the broad leaved dicots benefit more from the doubling of the CO_2 concentration than the narrow leaved monocots. This corresponds with the reported types of acclimation of the species: the ratio of P_N to internal CO_2 concentration (C_i)

indicates a downward acclimation of photosynthesis in the two grasses and an upward acclimation in the two dicots (Tuba *et al.* 1996). In the present study the upward acclimation of the two dicots was also indicated by the significantly higher P_N in the CE plants than in the CA plants (Table 1).

The g_s in the dicot *F. vulgaris* and in the grass *F. rupicola* increased, while there was a decrease in the grass *D. glomerata* and no change in the dicot *S. nemorosa* (Table 1). E was significantly higher in the CE-grown *F. rupicola* and *F. vulgaris* than in their controls (Table 1). There was no change in E due to the CE environment in the two other species. The acclimation of g_s in plants under CE is mostly downwarded with the consequence of decreased g_s and E (Drake *et al.* 1997). However, increased g_s and E similar to that in our study are less frequently documented even in herbaceous species. The above changes in P_N and E in the CE environment increased WUE in all species (Table 1). The increase was four- to five-fold in the dicots and less than two-fold in the monocots. The increase in WUE in these plants occurred at unchanged or increased E, and the highest increase occurred in species with the highest increase in E. The increase in WUE in the present study was primarily due to the increase in P_N and not to a decrease in E. The CE and increased temperature favourably affected WUE in the investigated loess grassland. Plant growth at CE causes increases leaf area (Dugas *et al.* 1994) which can increase whole plant canopy E even at reduced E of individual leaves (Nijs *et al.* 1988, also see the review by Newton 1991), and also a loss of hysteresis in WUE at growing irradiance (Greiner de Mothes 1996). This process can be accelerated if E is enhanced even if only for shorter periods. This can lead to a rapid exhaustion of soil water reserves, especially under more dry climate and in arid areas. The main conclusion of our study is that the type and degree of physiological acclimation to CE can vary among species and from time to time probably more considerably than it is known, even within the same community.

References

Amthor, J. S.: Terrestrial higher-plant response to increasing atmospheric [CO_2] in relation to the global carbon-cycle. - Global Change Biol. **1**: 243-274, 1995.

Beerling, D.J., Woodward, F.I.: Leaf stable carbon isotope composition records increased water-use efficiency of C-3 plants in response to atmospheric CO_2 enrichment. - Funct. Ecol. **9**: 394-401, 1995.

Drake B.G., Gonzalez Meler, M.A., Long, S.P., Ackerson, R.E.: More efficient plants: A consequence of rising atmospheric CO_2. - Annu. Rev. Plant Physiol. Plant mol. Biol. **48**: 609-639, 1997.

Dugas, W.A., Heuer, M.L., Hunsaker, D., Kimball, B.A., Lewin, K.F., Nagy, J., Johnson, M.: Sap flow measurements of transpiration from cotton grown under ambient and enriched CO_2 concentrations. - Agr. Forest Meteorol. **70**: 231-245, 1994.

Greiner de Mothes, M.A.: Effects of enhanced CO_2 concentration on wheat photosynthesis and long- and short-term stomatal behaviour. - Photosynthetica **32**: 193-202, 1996.

Jarvis, P.G.: Global change and plant water relations. - In: Borghetti, M., Grace, J., Raschi, A. (ed.): Water Transport in Plants under Climatic Stress. Pp. 1-13. Cambridge University Press, Cambridge 1993.

Morison, J.I.L.: Sensitivity of stomata and water use efficiency to high CO_2. - Plant Cell Environ. **8**: 467-474, 1985.

Nagy, Z., Tuba, Z., Szente, K., Uzvölgyi, J., Fekete, G.: Photosynthesis and water use efficiency during degradation of a semiarid loess steppe. - Photosynthetica **30**: 307-311, 1994.

Newton, P.C.D.: Direct effects of increasing carbon dioxide on pasture plants and communities. - New Zeal. J. agr. Res. **34**: 1-24, 1991.

Nijs, I., Impens, I., Behaeghe, T.: Effects of rising atmospheric carbon dioxide concentration on gas exchange and growth of perennial ryegrass. - Photosynthetica **22**: 44-50, 1988.

Pearson, M., Brooks, G.L.: The influence of elevated CO_2 on growth and age-related-changes in leaf gas-exchange. - J. exp. Bot. **46**: 1651-1659, 1995.

Šantrůček, J., Sage, R.F.: Acclimation of stomatal conductance to a CO_2-enriched atmosphere and elevated-temperature in *Chenopodium-album*. - Austr. J. Plant Physiol. **23**: 467-478, 1996.

Saralabai, V.C., Vivekanandan, M., Suresh Babu, R.: Plant responses to high CO_2 concentration in the atmosphere. - Photosynthetica **33**: 7-37, 1997.

Tuba, Z., Szente, K., Koch, J.: Response of photosynthesis, stomatal conductance, water use efficiency and production to long-term elevated CO_2 in winter wheat. - J. Plant Physiol. **144**: 661-668, 1994.

Tuba, Z., Szente, K., Nagy, Z., Csintalan, Z., Koch, J.: Responses of CO_2 assimilation, transpiration and water use efficiency to long-term elevated CO_2 in perennial C_3 xeric loess steppe species. - J. Plant Physiol. **148**: 356-361, 1996.

Zólyomi, B., Fekete, G.: The Pannonian loess steppe: differentiation in space and time. - Abstr. Bot. **18**: 29-41, 1994.