BRIEF COMMUNICATION

Photosynthesis, transpiration, and water use efficiency of *Leymus dasystachys* on the Hunshandake desert

R.Z. WANG[*], X.Q. LIU[*], Q. XING[**], and Y. BAI[***]

Laboratory of Quantitative Vegetation Ecology, Institute of Botany, the Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Beijing, 100093, China[*]
Beijing Botanical Garden, Institute of Botany, the Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Beijing, 100093, China[**]
Department of Plant Sciences, University of Saskatchewan, 51 Campus Drive, Saskatoon, Sask. S7N 5A8, Canada[***]

Abstract

Net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) declined from upper leaves to the lower ones during dry and rainy seasons, indicating that long-term carbon budget should take into account P_N variations for different leaf types. Relatively greater P_N in the dry season suggested that this species is more able to maintain higher P_N under drought, but the relatively higher E in the dry season might reduce water use efficiency (P_N/E) for the species. Significant correlations between P_N and g_s indicated that g_s may be the critical factor for P_N variability in the desert region.

Additional key words: dry and rainy seasons; leaf age and insertion; stomatal conductance.

Inter- and intra-specific variations in rates of net photosynthesis (P_N) and transpiration (E), and in water use efficiency (WUE) as well as the effects of leaf age on photosynthesis have been well documented for tree species (*e.g*. Hirose and Werger 1987, Kitajima *et al*. 1997, Sobrado 1992), vines (Ackerly 1992, Hikosaka *et al*. 1994), and grasses (*e.g*. Anderson *et al*. 1995, Schwarz and Redmann 1989, Wang and Gao 2001, Wang and Yuan 2001). These studies proved that P_N after full leaf expansion generally exhibits a monotonic decline (*e.g*. David *et al*. 1998, Kitajima *et al*. 1997, Šesták 1985, Wang and Gao 2001, Subrahmanyam and Rathore 2004), and this decline is accompanied by the redistribution of resources from old leaves to younger ones (*e.g*. Field and Mooney 1983, Hirose *et al*. 1987, Hikosaka *et al*. 1994, Kitajima *et al*. 1997). Studies on the effects of leaf type or leaf age on plant photosynthesis are necessary for estimating the long-term carbon budget at leaf, canopy, community, and region scales (*e.g.* Kitajima *et al*. 1997, Wang and Yuan 2001). The studies on P_N and E of different leaf types are also important for evaluating plant WUE in dry regions, *e.g*. grasslands, steppes, and deserts (*e.g*. Kimenov *et al*. 1989, Hamid *et al*. 1990, Wang and Yuan 2001).

Leymus dasystachys (Trin.) Nevski is a perennial C_3 grass species, widespread on the grasslands and deserts in North China. Because of its higher tolerance to environmental stresses (*e.g*. dry and poor soil), dual reproduction (seeds and rhizomes), and relatively high palatability, the species is ideal for the restoration of deteriorated lands. But its physiological responses to desert environmental conditions remain unclear. This is why we studied variations in gas exchanges and WUE of different leaf types of *L. dasystachys* under dry and rainy conditions.

The study was carried in the Hunshandake desert (42°07'~43°52'N, 111°35'~117°44'E), located in the middle of Mongolian Plateau, North China. Local landscape comprises large areas of sand-covered land, 60 % desertified land, and 30 % mobile dune, mixed with steppes, meadows, and farmlands, varying from 1 050 to 1 350 m. Because of serious desertification, the region has become one of the sand storm sources in North China. Typical

Received 21 October 2004, *accepted* 28 January 2005.
Fax: 01186-10-82591781; e-mail: wangrenzh@sohu.com
Acknowledgments: We thank the staff of the Grassland Station of Duolun County, Inner Mongolia for permission to study on its property. We are grateful for the funding provided by Key Projects of Knowledge Innovation of the Chinese Academy of Sciences (KSCX2-SW-107, KSCX1-08-03).

natural vegetation is the desertified steppe dominated by xerophytes, *e.g*. *Stipa grandis* P. Smirn., *S. krylovii* Roshev., and *L. dasystachys*. Most of the region, *e.g*. dune and disturbed and cultivated land have sandy soil with gravel, while light chestnut and chernozem occur on steppes. For at least 10 years, the study sites were fenced for restoration. Study site has a typical continental climate with low annual precipitation. Mean annual air temperature ranged from –0.2 °C to 2.0 °C, varying from –21.6 °C in January to 19.6 °C in July. Annual precipitation varied from 100 mm in the west to 380 mm in the east, 70 % fell between the late of June and the late of August (Wang 2002).

Table 1. Leaf net photosynthetic rate, P_N [μmol(CO_2) m^{-2} s^{-1}], transpiration rate, *E* [mmol(H_2O) m^{-2} s^{-1}], stomatal conductance, g_s [mol(H_2O) m^{-2} s^{-1}], and water use efficiency, WUE of *Leymus dasystachys* in Hunshandake desert, North China. L_2 = second leaf, L_3 = third leaf, L_4 = fourth leaf. Differences between means (*ANOVA*): $^{**}p<0.01$, $^{*}p<0.05$.

			June	July
P_N	vegetative	L_2	6.85±0.31	4.46±0.33
		L_3	8.50±0.43**	6.79±0.56**
		L_4	8.67±0.56	7.44±0.64*
	reproductive	L_2		7.40±0.46
		L_3		8.06±0.57*
		L_4		5.51±0.61**
E	vegetative	L_2	4.68±0.38	2.75±0.23
		L_3	5.06±0.44*	4.50±0.38**
		L_4	6.00±0.34*	5.21±0.29**
	reproductive	L_2		5.52±0.45
		L_3		5.94±0.22
		L_4		7.84±0.53**
g_s	vegetative	L_2	0.11±0.01	0.08±0.00
		L_3	0.11±0.01	0.12±0.01**
		L_4	0.14±0.01*	0.17±0.02**
	reproductive	L_2		0.14±0.01
		L_3		0.16±0.00
		L_4		0.30±0.00**
WUE	vegetative	L_2	1.44±0.01	1.59±0.05
		L_3	1.62±0.01*	1.43±0.01*
		L_4	1.44±0.01	1.53±0.00
	reproductive	L_2		1.34±0.02
		L_3		1.36±0.03
		L_4		0.77±0.02**

Gas exchange was measured in 5–8 plants of *L. dasystachys*. P_N, *E*, and stomatal conductance (g_s) were determined on fully expanded leaves of the selected plants every 2 h (from 08:00 to 18:00) on clear days, by using a *Li-Cor 6400* CO_2 and H_2O analyzer. The measurements started from the lower leaf (2nd leaf) to the top one (4th leaf) with 3–4 replicates for each leaf type, and data for each leaf were taken 4–7 times in each hour. In order to reduce variations between sample plants, the same plants were re-sampled over the day. The measurements were taken in dry season (6–9 June) and in rainy season (7–9 July), respectively. WUE was calculated as P_N/E (*e.g*. Hamid *et al*. 1990, Wang 2001). The differences in mean P_N, *E*, g_s, and WUE among leaf types were statistically analyzed with *ANOVA* (MINITAB). All results are shown in Table 1.

P_N varied significantly among leaves, decreasing from the 4th to the 2nd leaves of vegetative shoots in both dry and rainy seasons. P_N of the 3rd and 4th leaves of vegetative shoot were 24 and 27 % greater than those of the 2nd leaf in dry season ($p<0.01$), and 52 and 67 % greater in rainy season ($p<0.001$). P_N of reproductive shoot leaves, however, did not decrease from the 4th to the 2nd leaf. P_N of the 2nd, 3rd, and 4th leaf of vegetative shoots in the dry season was 54, 25, and 17 % greater than those in the rainy season ($p<0.01$), respectively. The average P_N of reproductive shoot leaves was about 12 % greater than that of vegetative shoot ones in rainy season, indicating that the variations of P_N for vegetative and reproductive shoots were different in the desert condition. This supports the observations that plant photosynthetic capacity declines with leaf age or from upper leaves to lower ones (Kitajima *et al*. 1997, Wang and Yuan 2001). Many previous studies proved that the decline of plant photosynthetic capacity with leaf age may be due to the redistribution of resources, especially leaf nitrogen content from older to the younger leaves (*e.g*. Field and Mooney 1983, Hirose and Werger 1987, Hikosaka *et al*. 1994, Kitajima *et al*. 1997, Wang and Gao 2001). The leaf life span between the younger leaves and the adjacent older ones of the species was less than 10 d, and the redistribution of resources to new leaves may not be as significant as predicted. Soil water availability and g_s may be the critical factors for the decrease in leaf photosynthetic capacity in plants of desert environments.

E of the species decreased from the 4th leaf to the 2nd leaf. *E* of the vegetative shoot leaves varied little in dry season, while in rainy season the difference was significant for both vegetative and reproductive shoots. *E* for each leaf type in the dry season was also greater than in the rainy one ($p<0.01$). The average *E* was 55 % greater for reproductive shoot leaves than for the vegetative shoot ones in rainy season. In general, *E* was about 10–80 % greater for the younger leaves than for the older ones. *E* probably depends on stomata changes, because *E* of all leaf types of the species was positively correlated with g_s. The g_s of vegetative shoot leaves varied little in dry season, and the 4th leaf had significantly greater g_s than the 2nd and the 3rd ones ($p<0.05$). In rainy season, g_s of the 4th leaf was 40–120 % greater than those of the 2nd and 3rd leaves ($p<0.01$) for both vegetative and reproductive shoots. The g_s was 63 % greater for reproductive shoot leaves than for vegetative shoot leaves in the rainy season. Unlike P_N and *E*, g_s of each leaf type was generally greater in rainy season than in the dry one.

WUE for the species exhibited little variations in both dry and rainy seasons. WUE of 3rd leaf of the vegetative shoot was 13 % greater than that of the 2nd and 4th leaves in dry season ($p<0.05$), while it was about 7 and 10 % lower than for the 2nd and 4th leaves in rainy season ($p<0.05$). The differences of WUE between the dry and rainy seasons for each leaf type were lower. The average WUE was about 24 % lower for the reproductive shoot leaves than for the vegetative shoot leaves in rainy season. Unlike P_N, E, and g_s, WUE did not decline from the 4th leaf to the 2nd one. Relatively high WUE is an important feature of desert plants, because water availability is one of the critical factors for plant survival in dry conditions. *L. dasystachys* in desert region had lower WUE than grasses (*e.g.* *Leymus chinensis*, *Puccinellia tenuiflora*, *P. chinampoensis*) in meadow regions during drought (Wang and Gao 2001, Wang and Yuan 2001). Leaf cooling in the desert species during hot dry season may increase leaf E, resulting in a decline of WUE.

Most studies estimating the long-term carbon budget were oriented on the canopy (or its top leaves) photosynthetic capacity, which had a fairly high P_N. This might enlarge carbon assimilation and introduce a false estimation in long-term carbon budget at population, community, and ecosystem scales (Kitajima *et al*. 1997, Wang and Yuan 2001). Significant differences in P_N between upper and lower leaves of *L. dasystachys* in desert region indicated that long-term carbon budget should take into account P_N variations among leaves of various ages.

References

Ackerly, D.D.: Light, leaf age, and leaf nitrogen concentration in a tropical vine. – Oecologia **89**: 596-600, 1992.

Anderson, J.E., Nowak, R.S., Rasmuson, K.E., Tott, N.L.: Gas exchange and resource-use efficiency of *Leymus cinereus* (Poaceae): diurnal and seasonal responses to naturally declining soil moisture. – Amer. J. Bot. **82**: 699-708, 1995.

David, M.M., Coelho, D., Barrote, I., Correia, M.J.: Leaf age effects on photosynthetic activity and sugar accumulation in droughted and rewatered *Lupinus albus* plants. – Aust. J. Plant Physiol. **25**: 299-306, 1998.

Field, C.B., Mooney, H.A.: Leaf age and seasonal effects on light, water and nitrogen use efficiency in a California shrub. – Oecologia **56**: 348-355, 1983.

Hamid, A., Agata, W., Kawamitsu, Y.: Photosynthesis, transpiration and water use efficiency in four cultivars of mungbean, *Vigna radiata* (L.) Wilczek. – Photosynthetica **24**: 96-101, 1990.

Hikosaka, K., Terashima, I., Katoh, S.: Effects of leaf age, nitrogen nutrition and photon flux density on the distribution of nitrogen among leaves of a vine (*Ipomoea tricolor* Cav.) grown horizontally to avoid mutual shading of leaves. – Oecologia **97**: 451-457, 1994.

Hirose, T., Werger, M.J.A.: Maximum daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. – Oecologia **72**: 520-526, 1987.

Kimenov, G.P., Markovska, Y.M., Tsonev, T.D.: Photosynthesis and transpiration of *Haberlea rhodopensis* FRIV. in dependence on water deficit. – Photosynthetica **23**: 368-371, 1989.

Kitajima, K., Mulkey, S.S., Wright, S.J.: Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. – Amer. J. Bot. **84**: 702-708, 1997.

Schwarz, A.G., Redmann, R.E.: Photosynthetic properties of C_4 grass (*Spartina gracilis* Trin.) from northern environment. – Photosynthetica **23**: 449-459, 1989.

Šesták, Z. (ed.): Photosynthesis During Leaf Development. – Academia, Praha; Dr W. Junk Publ., Dordrecht – Boston – Lancaster 1985.

Sobrado, M.A.: The relationship between nitrogen and photosynthesis in relation to leaf age in a tropical xerophytic tree. – Photosynthetica **26**: 445-448, 1992.

Subrahmanyam, D., Rathore, V.S.: $^{14}CO_2$ assimilation and ^{14}C-photosynthate translocation in different leaves of sunflower. – Photosynthetica **42**: 313-316, 2004.

Wang, R.Z.: Photosynthesis, transpiration, and water use efficiency of vegetative and reproductive shoots of grassland species from northeastern China. – Photosynthetica **39**: 569-573, 2001.

Wang, R.Z.: Photosynthetic pathways, life forms and reproductive types for forage species along desertification gradient on Hunshandake desert, North China. – Photosynthetica **40**: 321-329, 2002.

Wang, R.Z., Gao, Q.: Photosynthesis, transpiration and water use efficiency in two divergent *Leymus chinensis* populations from Northeast China. – Photosynthetica **39**: 123-126, 2001.

Wang, R.Z., Yuan, Y.Q.: Photosynthesis, transpiration and water use efficiency in two *Puccinellia* species on the Songnen grassland, northeastern China. – Photosynthetica **39**: 283-287, 2001.