Photosynthesis, transpiration, and water use efficiency of vegetative and reproductive shoots of grassland species from north-eastern China

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Abstract

The differences in net photosynthetic rate (P_N), transpiration rate (E), and water use efficiency (WUE) between the vegetative and reproductive shoots of three native grass species from the grassland of northeastern China [grey-green and yellow green populations of *Leymus chinensis* (Trin.) Tzvel., *Puccinellia tenuiflora* (Griseb) Scrib & Merr, *Puccinellia chinampoensis* Ohwi] were compared. The two type shoots experienced similar habitats, but differed in leaf life-span and leaf area. The leaf P_N and WUE for the vegetative shoots were significantly higher than those for the reproductive shoots in the grasses, while their E were remarked lower in the dry season. Relative lower leaf P_N and WUE for the reproductive shoots of grassland grasses may explain the facts of lower seed production and the subordinate role of seed in the grassland renewal in north-eastern China.

Additional key words: grasses; *Leymus*; physiological differences; plant water relations; *Puccinellia*.

Introduction

The studies on P_N, E, and WUE have received much attention as means of studying the water plant relations and the response of photosynthesis and transpiration to environmental changes (Du and Yang 1988, Kimenov *et al.* 1989, Hamid *et al.* 1990, Bowman and Turner 1993, Anderson *et al.* 1995, Pugnaire and Haase 1996, Jiang and He 1999, Jiang *et al.* 1999, Wang *et al.* 1999). Mostly theoretical studies by Du and Yang (1988), Schwarz and Redmann (1989), Hamid *et al.* (1990), Bowman and Turner (1993), Anderson *et al.* (1995), Valladares *et al.* (1997), Cabrera *et al.* (1998), and Jiang *et al.* (1999) examined the responses of photosynthesis and transpiration to temperature, radiation, or CO_2, and determined WUE. Some studies tested the relations of photosynthesis to leaf age and to nitrogen and chlorophyll contents (Du and Yang 1988, Ackerly 1992, Sobrado 1992, Kitajima *et al.* 1997, Manuela *et al.* 1998, Wang and Gao 2001, Wang and Yuan 2001). Few studies observed the intraspecific and interspecific variations in photosynthesis, transpiration, and WUE for grass species (Pugnaire and Haase 1996, Wang and Gao 2001, Wang and Yuan 2001). None, however, has looked at the physiological differences between vegetative and reproductive shoots of native grasses from grasslands.

Leymus chinensis (Trin.) Tzvel., *Puccinellia tenuiflora* (Griseb) Scrib & Merr, and *Puccinellia chinampoensis* Ohwi are native perennial grass species, widespread on saline-sodic low-lying grasslands and the surrounding lakes on the Songnen grassland, north-eastern China. Both vegetative shoots and reproductive shoots are attached to the same rhizome (*L. chinensis*) or root system (*P. tenuiflora* and *P. chinampoensis*), and experience a similar habitat, but differ in leaf area (Table 1) and leaf life-span (Jia 1989, Wang and Yuan 2001). Intraspecific and interspecific variations in photosynthesis and transpiration were tested (Wang *et al.* 1998, Yan *et al.* 1998, Wang and Gao 2001, Wang and Yuan 2001) as well as the appropriateness of species for improvement of salinised grasslands (Wang *et al.* 1998, Wang and Yuan 2001). However, the differences in P_N, E, and WUE between vegetative and reproductive shoots of these native grassland plants remain unclear. The objective of this study was to investigate these differences in the plants from native grassland region of north-eastern China. The results could be important for determining the physiological differences between vegetative and reproductive shoots and the reproductive effort of reproductive shoots to the growth and reproduction in grassland plants.

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Materials and methods

Study site and climate: The study was conducted on a native grassland near the Grassland Ecology Field Station of Northeast Normal University, on the Changling Horse Breeding Farm, Jilin province, China in 1998. The site (44°45'N, 123°45'E) is in a flat, low-lying southern part of the Songnen plain. The grassland, dominated by *L. chinensis* with good palatability and high forage value, provides the principal grazing and mowing pasturage in the area. There has, however, been deterioration and salinisation of the grassland since the 1960s, and halophytes (*e.g. P. tenuiflora* and *P. chinampoensis*) became the dominant species in salinised pastures. There are two divergent *L. chinensis* populations, the grey-green (GG) and the yellow-green (YG), distributed in the area. The two divergent *L. chinensis*, *P. tenuiflora* (PT), and *P. chinampoensis* (PC) can form consociations (Wang *et al.* 1998). The grassland is at an average elevation of about 141 m and is surrounded by sand dune about 26 m above this level. Most area of the grassland has a saline meadow soil and the soil pH can be as high as 10 in the spring. For at least 10 years prior to 1998, the grassland was only mowed annually in the middle of August. It had never been ploughed, fertilised, but transient floods often occur in the grassland in August.

The area has a continental monsoon climate, with large seasonal temperature variations (from –34 to +37 °C). The main characteristics of the climate are: a dry, windy spring; a warm, rainy summer; a cool autumn with early frosts; and a long cold winter with little snow. The mean annual air temperature is about 5 °C, with monthly changes ranging from –18 °C in January to 23 °C in July. The annual precipitation ranges between 300-600 mm, falling mainly during the summer monsoon (70 %). There is a clear drought period in the first half of growing season (from middle April to early June). A more detailed description of the climate for the area may be found in Domros and Peng (1988) and Ripley *et al.* (1996).

Methods: In the study site, 6-10 plants for each species were selected. Only in clear days, P_N and E of each fully expanded, attached leaf for sample plants were measured simultaneously every 2 h from 07:00 to 17:00, using a *CID-301PS* CO_2 and H_2O analyser (*CID Scientific Instrument Co.*, Vancouver, USA). The measurements begun from the lower leaves to the top with two replicates for each leaf type. In order to reduce the individual differences between sample plants, the same plants were resampled over the day. The measurements were taken in the dry season (early June) and in the rainy season (middle June). The instrument was calibrated against a CO_2 standard of 390 μmol mol^{-1} each month before the field measurements.

The leaf area of each leaf used for P_N and E measurements was determined by *CI-203* Leaf Area Meter. 6-8 samples of top layer of soil (0-20 cm) were collected from the place of plant sample, and soil moisture was measured gravimetrically.

Data analysis: WUE was calculated as P_N/E (Hamid *et al.* 1990). The differences in leaf area, mean P_N, E, and WUE between the two type shoots for each species were statistically analysed with *ANOVA*.

Results

P_N differed significantly between vegetative and reproductive shoots in the four grass populations (Fig. 1*A,B*), likely due to the different leaf life-span. P_N of the vegetative shoots for the two divergent *L. chinensis* populations were significantly greater than those of their reproductive shoots in both dry and rainy seasons ($p < 0.001$), except for YG which was lower in the dry season. The average P_N of vegetative shoot in GG was 29 % greater than that of reproductive shoots in the dry season, and those in the rainy season were 24 and 48 % greater for GG and YG, respectively. The P_N values of vegetative shoots for the two *Puccinella* species were remarkably higher than those of their reproductive shoots in both dry and rainy seasons ($p < 0.01$), with the average P_N of vegetative shoots 82 and 28 % greater in the dry season, and 28 and 59 % greater in the rainy season for *P. tenuiflora* and *P. chinampoensis*, respectively.

E: The differences in E between vegetative and reproductive shoots for the four grass populations were considerable in the dry and rainy seasons (Fig. 1*C,D*). In the dry season, E values of reproductive shoots for the four grasses were greater than those of the vegetative shoots. The E between the vegetative and reproductive shoots for both GG *L. chinensis* and *P. tenuiflora* did not differ significantly in the dry season ($p > 0.05$). The average E values for reproductive shoots were 3 and 10 % higher than those for vegetative shoots, respectively. The differences in E for YG *L. chinensis* and *P. chinampoensis* were significant in the dry season ($p < 0.05$), and the average E values of the reproductive shoots were 32 and 44 % greater than those of the vegetative shoots for the two species, respectively. Unlike those in the dry season, the differences in E between vegetative and reproductive shoots were significant in the rainy season for the four grasses ($p < 0.05$). The average E values of vegetative shoots were 69, 16, and 49 % higher than those of the reproductive shoots for GG *L. chinensis*, *P. teniuflora*, and *P. chinampoensis*, respectively, except for the YG *L. chinensis* that was 27 % lower.

WUE values of vegetative shoots for the two divergent *L. chinensis* populations were significantly greater than those of the reproductive shoots in both dry and rainy seasons ($p < 0.05$), except that for YG *L. chinensis* in the dry season which was 2 % lower ($p > 0.05$) (Fig. 1*E,F*). The WUE of vegetative shoots was 37 % higher in the dry season for GG *L. chinensis*, and 10 and 12 % higher in the rainy season for both GG *L. chinensis* and YG *L. chinensis*, respectively. The WUE of vegetative shoots was 96 and 83 % of that of reproductive shoots in the dry season for *P. teniuflora* and *P. chinampoensis*, respectively. In the rainy season, the WUE between the vegetative and reproductive shoots for *P. teniuflora* did not differ significantly ($p > 0.05$), while that of vegetative shoots for the *P. chinampoensis* was 31 % greater than that of the reproductive shoots ($p < 0.05$).

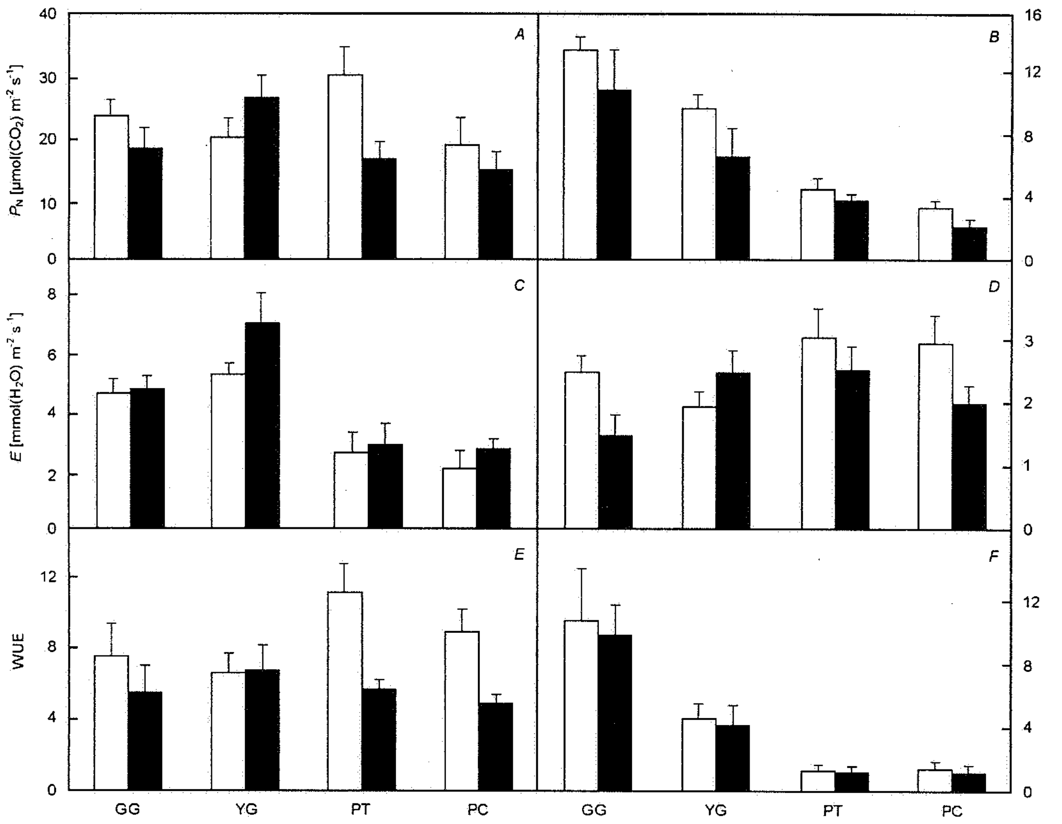

Fig. 1. The differences in net photosynthetic rate (P_N), transpiration rate (E), and water use efficiency (WUE) between the vegetative shoots (*empty columns*) and reproductive shoots (*full columns*) of the four grasses in the dry season (*A, C, E*) and rainy season (*B, D, F*) from north-eastern China. GG = grey-green *Leymus chinensis*; YG = yellow-green *L. chinensis*; PT = *Puccinellia tenuiflora*; PC = *P. chinampoensis*, respectively.

Discussion

The significant differences in leaf P_N between vegetative shoots and reproductive shoots resulted probably from intra-specific differences in morphology, anatomy, and physiology. Although the vegetative shoots and reproductive shoots are attached to the same root system, there are some morphological differences (*e.g.* leaf life-span and leaf area) between the two type shoots (Table 1, Wang and Yuan 2001). Lesser leaf P_N for the reproductive shoots in these grasses was primarily due to shorter leaf life-span. Short leaf life-span is significantly related to the decline of leaf photosynthesis (Kitajima *et al.* 1997). The reproductive shoots for the grasses in the region stop growth in the middle of July when the process of seed production is finished, and the leaf life-span is about 10-20 d shorter than that of vegetative shoots (Wang and Yuan 2001). The relative lower leaf P_N for reproductive shoots may be caused by the N reallocation from the leaves to seed, but this was not tested. Anderson *et al.* (1995) and Hikosaka *et al.* (1994) have proved that the decline in leaf P_N was caused by reallocation to newer leaves or seed of nitrogen resources. High leaf P_N for vegetative shoots suggests that this type of shoots is more able to maintain greater P_N under drought. Lower leaf P_N for the reproductive shoots in plants indicated that their reproductive effort is lower than that of vegetative shoots. The lower reproductive effort by leaf photosynthesis for reproductive shoots in these grasses may in part explain the facts of lower seed production and its subordinate role in grassland renewal (Wang *et al.* 2001).

Table 1. Leaf area [cm^2] of grey-green *Leymus chinensis* (GG), yellow-green *L. chinensis* (YG), *Puccinellia tenuiflora* (PT), and *P. chinampoensis* (PC) and soil moisture [%] in study sites on the grassland in north-eastern China.

		GG	YG	PT	PC
Shoots	Vegetative shoot	3.84 ± 0.29	3.46 ± 0.23	0.71 ± 0.14	1.23 ± 0.09
	Reproductive shoot	2.60 ± 0.18	2.67 ± 0.18	0.73 ± 0.09	1.76 ± 0.17
Soil moisture	Dry season	8.16 ± 0.33	8.42 ± 0.25	10.58 ± 1.01	9.05 ± 1.12
	Rainy season	15.25 ± 1.59	14.58 ± 1.23	21.12 ± 1.89	19.59 ± 2.03

The considerable variations of E between vegetative and reproductive shoots indicate the morphological and physiological differences between the two types of shoots. The relatively greater E for reproductive shoots of these grasses in the dry season suggests that this type of shoot needs more water for reproductive growth (Fig. 1*C,D*). The previous studies proved that the leaf E was related with stomatal resistance (Wang *et al.* 1998, Yan *et al.* 1998, Wang and Gao 2001). The relatively lower E of reproductive shoots for these grasses in the rainy season was primarily due to their shorter leaf life-span, for the leaf colour of reproductive shoots have turned into yellow-brown, while those of the vegetative shoots were still green. Higher leaf E for reproductive shoots indicated that the density of this type of shoots in populations should be lower in order to adapt the dry condition, for their high water consume and the severe water deficit in the region. This hypothesis is supported by the observation that biomass allocation of reproductive shoots in these grasses was much lower than that of vegetative shoots (Wang *et al.* 2001).

The differences of WUE between the vegetative and reproductive shoots can be used to determine economic use of the water resources in the process of vegetative growth and reproduction. The WUE varied remarkably between vegetative and reproductive shoots for these grasses from the grasslands of north-eastern China. The WUE for vegetative shoots in these grasses was higher than that for reproductive shoots in both dry and rainy seasons (Fig. 1*E,F*). This indicated that the water use by vegetative shoots could be more economic in this semi-arid grassland region, because the water deficit was very severe in the early growing season. The lower density and reproductive effort for reproductive shoots in these grass species may result from their lower WUE in growing season, and this is the result of adaptation to dry condition of the grassland region.

The lower P_N and WUE for reproductive shoots in the four grasses from the grassland of north-eastern China, compared with vegetative shoots, may explain the fact of lower seed production and subordinate role of seed in grassland renew. This and other previous researches (Wang and Gao 2001, Wang and Yuan 2001, Wang *et al.* 2001) suggest that the reproductive shoots of these grasses should be removed in the grassland management.

References

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

Anderson, J.E., Robert, S.N., Kaylie, E.R., Nancee, N.T.: 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.

Bowman, W.D., Turner, L.: Photosynthetic sensibility to temperature in populations of two C_4 *Bouteloua* species native to different altitudes. – Amer. J. Bot. **80**: 369-374, 1993.

Cabrera, H.M., Rada, F., Cavieres, L.: Effects of temperatures on photosynthesis of two morphologically contrasting plant species along an altitudinal gradient in tropical high Andes. – Oecologia **114**: 145-152, 1998.

Domros, M., Peng, G.B.: The Climate of China. – Springer-Verlag, Berlin 1988.

Du, Z., Yang, Z.: [A preliminary study on light photosynthetic characteristic in the leaves at various age for *Aneurolepidium chinense*.] – Acta bot. sin. **30**: 196-206, 1988. [In Chin.]

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.

Jia, S.X.: Chinese Flora of Forage Plants. – Pp. 161-174. Chi-

nese Agriculture Press, Beijing 1989.
Jiang, G.M., He, W.M.: Species and habitat variability of photosynthesis, transpiration and water use efficiency of different plant species in Maowusu sand area. – Acta bot. sin. **41**: 1114-1124, 1999.
Jiang, G.M., Tang, H.P., Yu, M., Dong, M.: Response of photosynthesis of different plant functional types to environmental changes along Northeast China Transect. – Trees **14**: 72-82, 1999.
Kimenov, G.P., Markovska, Y.K., Tsonev, T.D.: Photosynthesis and transpiration of *Heberlea 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.
Manuela, M.D., Dulce, C., Isabel, B., Maria, J.C.: Leaf age effects on photosynthetic activity and sugar accumulation in droughted and rewatered *Lupinus albus* plants. – Aust. J. Plant Physiol. **25**: 299-306, 1998.
Pugnaire, F.I., Haase, P.: Comparative physiology and growth of two perennial tussock grass species in a semi-arid environment. – Ann. Bot. **77**: 81-86, 1996.
Ripley, E.A., Wang, R.Z., Zhu, T.C.: The climate of the Songnen plain, northeast China. – Int. J. ecol. environ. Sci. **22**: 27-32, 1996, 1996.
Schwarz, A.G., Redmann, R.E.: Photosynthetic properties of C_4 grass (*Spartina gracilis* Trin.) from northern environment. – Photosynthetica **23**: 449-459, 1989.
Sobrado, M.A.: The relationship between nitrogen and photosynthesis in relation to leaf age in a tropical xerophytic tree. – Photosynthetica **26**: 445-448, 1992.
Valladares, F., Allen, M.T., Pearcy, R.W.: Photosynthetic responses to dynamic light under field conditions in six tropical rain forest shrubs occurring along a light gradient. – Oecologia **111**: 505-514, 1997.
Wang, D.L., Wang, Z.W., Zhang, X.J.: The comparison of photosynthetic physiological characteristics between the two divergent *Aneurolepidium chinense* types. – Acta ecol. sin. **19**: 837-843, 1999.
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., Gao, Q., Li, J.D.: The comparison study on water ecology of two *Puccinellia* communities in Songnen grassland. – Acta ecol. sin. **18**: 107-112, 1998.
Wang, R.Z., Ripley, E.A., Zu, Y.G., Nie, S.Q.: Demography of reproductive and biomass allocation of grassland and dune *Leymus chinensis* on the Songnen plain, northeastern China. – J. Arid Environ. **49**: 289-299, 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.
Yan, X.F., Sun, G.R., Xiao, X.: A comparative study on photosynthetic abilities of *Puccinellia tenuiflora* of different growth years. – Acta phytoecol. sin. **22**: 231-236, 1998.