Photosynthesis, transpiration, and water use efficiency of two *Puccinellia* species on the Songnen grassland, northeastern China

R.Z. WANG and Y.Q. YUAN

Laboratory of Quantitative Vegetation Ecology, Institute of Botany, the Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Beijing 100093, China

Abstract

The intra- and inter-specific variations in net photosynthetic (P_N) and transpiration (E) rates and water use efficiency (WUE) of *Puccinellia tenuiflora* and *Puccinellia chinampoensis* leaves were compared. The two species experienced a similar habitat, but differed in leaf area, leaf colour, and nitrogen contents. Leaf P_N and E for both reproductive and vegetative shoots of the two species declined with leaf age. P_N for reproductive shoots was less than for vegetative shoots, but their E was greater than that of vegetative shoots in the dry season. The average P_N and E for reproductive shoots of *P. tenuiflora* were lower than those of *P. chinampoensis*, but higher for vegetative shoots.

Additional key words: intra- and inter-specific variations; leaf age; net photosynthetic rate; plant and water relations.

Introduction

The diurnal and seasonal variations in photosynthesis and transpiration have been well documented for many grass species (Du and Yang 1988, Schwarz and Redmann 1989, Anderson *et al.* 1995, Yan *et al.* 1998, Kobayashi *et al.* 1999, Wang *et al.* 1999, Wang and Gao 2001). Many studies focused on the responses of grass photosynthesis and transpiration to environment factors, such as temperature, radiation, and CO_2 (*e.g.*, Du and Yang 1988, Schwarz and Redmann 1989, Bowman and Turner 1993, Anderson *et al.* 1995, Jiang and He 1999, Jiang *et al.* 1999). Some have looked at the relations of plant photosynthesis to leaf age (*e.g.*, Field and Mooney 1983, Šesták 1985, Du and Yang 1988, Hikosaka *et al.* 1994, Yan *et al.* 1998). Few papers have tested the intra- and inter-specific variations of photosynthesis and transpiration for grass species (Pugnaire and Haase 1996, Wang *et al.* 1999), although it was well documented for many tree and bean species (*e.g.*, Kimenov *et al.* 1989, Hamid *et al.* 1990, Bassow and Bazzaz 1997, Kitajima *et al.* 1997, Valladares *et al.* 1997, Cabrera *et al.* 1998).

Puccinellia tenuiflora (Griseb) Scrib & Merr and *Puccinellia chinampoensis* Ohwi are two perennial tussock grass species, widespread on saline-sodic low-lying grasslands and the surrounding lakes on the Songnen grassland. Because of their high palatability in early spring and fall, the two species are ideal for animal grazing, and have been sown for the salinised grassland improvements. The two species experience a similar habitat, but differ in leaf area (Table 1), leaf colour, and nitrogen contents (Jia 1989). Together with *Puccinellia distans* (Tang and Zhang 1999) they belong to C_3 plants. Few studies were conducted to test their photosynthesis (Yan *et al.* 1998) and transpiration (Wang *et al.* 1998), and responses to grassland salinisation (Wang *et al.* 1998). The objectives of this study were to investigate intra- and interspecific variations in net photosynthetic (P_N) and transpiration (E) rates and water use efficiency (WUE) of the two *Puccinellia* species on the Songnen grassland, northeastern China. The results could be important for selecting appropriate species for salinised grassland improvements in the semi-arid grassland region.

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 is

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E-mail address: wangrenzh@sohu.com
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Table 1. The leaf area [cm^2] of *P. tenuiflora* and *P. chinampoensis*, and soil moisture in study site on the Songnen grassland. Means ± S.E. L2, L3, L4, and FL represent the 2nd, 3rd, 4th, and flag leaf, respectively. Differences between means (F-test): n.s. – not significant, *** $p < 0.001$.

	Leaf	*P. tenuiflora*	*P. chinampoensi*
Reproductive shoot	L2	0.532 ± 0.092	1.642 ± 0.088***
	L3	0.862 ± 0.091	1.792 ± 0.172***
	L4	0.798 ± 0.085	1.839 ± 0.240***
	FL	0.207 ± 0.036	0.351 ± 0.069***
Vegetative shoot	L2	0.178 ± 0.088	1.030 ± 0.060**
	L3	0.882 ± 0.130	1.409 ± 0.099***
	L4	1.058 ± 0.200	1.244 ± 0.110***
Soil moisture [%]	Dry season	10.58 ± 1.01	9.05 ± 1.12 n.s.
	Rainy season	21.12 ± 1.89	19.59 ± 2.03 n.s.

located at latitude 44°45'N and longitude 123°45'E. The grassland, dominated by *Leymus 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. There are two *Puccinellia* species [*P. tenuiflora* (Griseb) Scrib & Merr and *P. chinampoensis* Ohwi] distributed in the area, and each species 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 in the middle of August annually. It had never been ploughed, fertilised, but transient floods often occur in the grassland in fall.

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 from 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, by using a *CID-301PS* CO_2 and H_2O analyser (*CID Scientific Instrument Co.*, Vancouver, USA). The measurements begun from the lower to the top leaves 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 leaf area of each leaf used for P_N and E determination was measured by *CI-203* Leaf Area Meter. 6 to 8 samples of top layer of soil (0-20 cm) were collected from the place of plant sample, and soil moisture was measured gravimetrically.

Analysis of values: Water use efficiency (WUE) was calculated as P_N/E (Hamid *et al.* 1990). The differences in mean P_N, E, and WUE for each leaf type between the two species were statistically analysed with *ANOVA* (*MINITAB*).

Results

Intra-specific variations in P_N and E: P_N declined significantly with leaf age in both *P. tenuiflora* and *P. chinampoensis* (Table 2). In the dry season, the flag leaves had the greatest P_N for reproductive shoots in both species, while the second leaves had the least one (only 1/2 of those for flag leaves). But those for flag leaves were much lower in rainy season, mainly due to leaf decrepitude. The leaf life spans of flag leaves in two species were less than 30 d. P_N for vegetative shoots also declined with leaf age in the two species (Table 2). The P_N of top leaves was 1.5~10 times higher than in the lower ones in the dry and rainy seasons. The P_N values for every leaf type in the rainy season were much lower than values for its corresponding leaf type in the dry season for both species.

E exhibited relatively little differences between the leaves in each species, but also declined with leaf age (Table 3). Flag leaves had the greatest leaf E, which was about 31~120 % greater than in the least one in each species. But E of the 2nd leaf of reproductive shoots was

Table 2. The comparison of diurnal average net photosynthetic rate [μmol(CO_2) m^{-2} s^{-1}] of *P. tenuiflora* (PT) and *P. chinampoensis* (PC) on the Songnen grassland. Means ± S.E.. Differences between means (F-test): n.s. – not significant, *$p < 0.05$, **$p < 0.01$.

		Dry season		Rainy season	
		PT	PC	PT	PT
Reproductive shoot	L2	14.40 ± 2.89	12.27 ± 3.24*	0.42 ± 0.21	1.29 ± 0.40**
	L3	15.22 ± 2.46	16.17 ± 3.71 n.s.	5.15 ± 0.96	1.97 ± 0.47**
	L4	19.95 ± 3.05	15.60 ± 4.72 n.s.	4.83 ± 0.76	2.67 ± 0.63**
	FL	20.63 ± 2.86	27.51 ± 9.83*	0.88 ± 0.14	0.97 ± 0.26**
Vegetative shoot	L2	22.13 ± 6.08	14.23 ± 3.55*	0.28 ± 0.15	1.41 ± 0.45**
	L3	33.80 ± 10.10	19.94 ± 4.66*	3.24 ± 0.61	2.58 ± 0.35**
	L4	34.18 ± 9.15	22.05 ± 4.90*	4.55 ± 0.70	4.19 ± 0.63**
	FL	–	–	5.51 ± 1.11	4.40 ± 0.75**

greater than E of the 3rd leaves in the dry season for both species. The intra-specific differences of leaf E for the vegetative shoots were relatively little in the dry season for both species, the E values of the top leaves were only 8~20 % greater than those of the 2nd leaves. That, however, can be up to 3 times higher in the rainy season. The average leaf E values for reproductive shoots were about 19~68 % greater than those for vegetative shoots in the dry season, but 10~27 % lower in the rainy season.

Inter-specific variations in P_N and E: The differences of leaf P_N between the two species were considerable in both reproductive and vegetative shoots (Table 2). In the dry season, the 2nd leaf P_N for reproductive shoots of *P. tenuiflora* was 17 % greater than that of *P. chinampoensis*, but those for flag leaves were 25 % lower. P_N of the 3rd and 4th leaf of reproductive shoots did not differ signifi-cantly between the two species. The leaf P_N for vegetative shoots, however, differed significantly, the average leaf P_N for *P. tenuiflora* being 60 % greater. In the rainy sea-son, the leaf P_N for both vegetative and reproductive shoots differed significantly between the two species, with the average leaf P_N for *P. tenuiflora* 8 and 63 % greater, respectively.

Table 3. Comparison of diurnal average transpiration rate [mmol(H_2O) m^{-2} s^{-1}] of *P. tenuiflora* (PT) and *P. chinampoensis* (PC) on the Songnen grassland. Means ± S.E. Differences between means (F-test): n.s. – not significant, *$p < 0.05$, **$p < 0.01$.

		Early June		Middle July	
		PT	PC	PT	PT
Reproductive shoot	L2	2.98 ± 0.99	2.86 ± 0.92 n.s.	2.45 ± 0.58	1.52 ± 0.37*
	L3	2.28 ± 0.68	2.64 ± 0.92 n.s.	2.68 ± 0.54	2.40 ± 0.66 n.s.
	L4	3.39 ± 1.14	3.64 ± 1.12 n.s.	2.81 ± 0.53	2.07 ± 0.47*
	FL	3.90 ± 1.21	4.84 ± 1.46 n.s.	3.20 ± 0.53	3.35 ± 0.95 n.s.
Vegetative shoot	L2	2.37 ± 0.70	2.02 ± 0.84 n.s.	1.61 ± 0.31	1.59 ± 0.35*
	L3	2.66 ± 0.76	2.04 ± 0.89 n.s.	2.48 ± 0.35	2.03 ± 0.33*
	L4	2.85 ± 0.78	2.18 ± 0.62 n.s.	3.82 ± 1.05	4.13 ± 1.24 n.s.
	FL	–	–	4.41 ± 1.18	4.13 ± 0.9*

The leaf E for both reproductive and vegetative shoots did not differ significantly between the two species in the dry season (Table 3). The average leaf E for reproductive shoots of *P. tenuiflora* was about 10 % lower than that of *P. chinampoensis*, but that for the vegetative shoots was about 26 % higher. In the rainy season, E of the 2nd and 4th leaf of reproductive shoots of *P. tenuiflora* was significantly greater than those of *P. chinampoensis*, but those for the 3rd and flag leaves did not differ between the two species. Values of E of the 2nd, 3rd, and 5th leaf for vegetative shoots of *P. tenuiflora* were also remarkably greater than those of *P. chinampoensis*, however, the difference for the 4th leaf E between the two species was not significant. The average leaf E for reproductive shoots and vegetative shoots was about 19 and 4 % greater in *P. tenuiflora*, respectively.

WUE between the two species varied considerable (Table 4). In the dry season, the 2nd, 3rd, and 4th leaf WUEs for reproductive shoots of *P. tenuiflora* were 9~37 % greater than those of *P. chinampoensis*, but those for flag leaves were significantly lower. Leaf WUE values for vegetative shoots of *P. tenuiflora* were 19~32 % greater than those of *P. chinampoensis*, respectively, and the differences were significant. In the rainy season, WUE of the 3rd, 4th, and 5th leaf of vegetative shoots did not differ significantly between the two species, nor did the WUE for flag leaves. The 2nd leaf WUE for both reproductive and vegetative shoots of *P. tenuiflora* was significantly lower than that of *P. chinampoensis* (80 and 81 %, respectively).

Table 4. Average water use efficiency (P_N/E) of the leaves of *P. tenuiflora* and *P. chinampoensis* on the Songnen plain. Means ± S.E. Differences between means (F-test): n.s. – not significant, *$p < 0.05$, **$p < 0.01$.

		Early June		Middle July	
		PT	PC	PT	PT
Reproductive shoot	L2	4.83 ± 0.53	4.29 ± 0.46 n.s.	0.17 ± 0.11	0.85 ± 0.34**
	L3	6.68 ± 0.48	6.13 ± 0.51 n.s.	1.92 ± 0.36	0.82 ± 0.51*
	L4	5.88 ± 0.71	4.29 ± 0.58*	1.72 ± 0.40	1.29 ± 0.29*
	FL	5.29 ± 0.46	7.75 ± 0.82**	0.28 ± 0.13	0.29 ± 0.18 n.s.
Vegetative shoot	L2	9.34 ± 1.24	7.04 ± 0.98*	0.47 ± 0.13	0.89 ± 0.27**
	L3	12.71 ± 2.15	9.77 ± 1.21*	1.31 ± 0.35	1.27 ± 0.42 n.s.
	L4	11.99 ± 1.36	10.11 ± 1.37*	1.19 ± 0.47	1.01 ± 0.39 n.s.
	FL	–	–	1.25 ± 0.54	1.07 ± 0.38 n.s.

Discussion

Leaf P_N of the two *Puccinellia* species declined from top leaves (young leaves) to the low layer leaves (old leaves) in the Songnen grassland. The decline in P_N with leaf age was primarily caused by reallocation to newer leaves of resources, such as nitrogen supply and chlorophyll (Chl) content (Du and Yang 1988, Kitajima *et al.* 1997, David *et al.* 1998). Jia (1989) and Yan *et al.* (1998) proved that the N and Chl contents declined with increasing leaf age for *Puccinellia* species during the growing season. Leaf colour turned from green in top leaves to yellow-brown in low ones with N reallocation in the two *Puccinellia* species, and leaf P_N decreased from top to low leaves (Table 2). P_N of top leaves was 1.5~3.0 times greater than that of the lower ones for the two species in the dry season.

Previous research proved that the intra-specific differences in leaf P_N between the reproductive and vegetative shoots were fairly large (Wang and Gao 2001). The average leaf P_N for vegetative shoots of *P. tenuiflora* was 20~70 % greater than that for reproductive shoots, and that of *P. chinampoensis* was 5~82 % greater. Less leaf P_N for reproductive shoots was primarily due to the shorter leaf spans (about 30 d) in the two species. Shorter leaf spans are significantly related to the decline of leaf photosynthesis (Kitajima *et al.* 1997). This suggests that reproductive effort by photosynthesis for reproductive shoots is lower than that for vegetative shoots in the two species.

Leaf P_N for *P. tenuiflora* was greater than that for *P. chinampoensis*, with average leaf P_N 8~60 % greater, except for reproductive shoots in the dry season. In the latter case, the average leaf P_N for reproductive shoots of *P. chinampoensis* was 2 % greater. The inter-specific differences in leaf P_N were primarily caused by the differences in physiology and morphology between the two species, such as Chl and N contents and stomata numbers (Pugnaire and Haase 1996, Wang and Gao 2001). Jia (1989) proved that the N contents of *P. tenuiflora* were 2.5 times higher than N contents of *P. chinampoensis* in growing season. The greater P_N of *P. tenuiflora* indicated its greater ability to maintain higher P_N over growing season, especially in the drier season. But the relatively smaller leaf area for *P. tenuiflora* may reduce plant production (Table 1).

Leaf E decreased from top leaves to lower leaves for both reproductive shoots and vegetative shoots in the two species. The stomatal variations with leaf age may cause the decline of leaf E in the two species (Jia 1989, Wang *et al.* 1998), but this was not tested. The average leaf E for reproductive shoots was 19 and 68 % greater than that for vegetative shoots in *P. tenuiflora* and *P. chinampoensis* in the dry season, while that in the rainy season was about 9 and 21 % lower for the two species, respectively.

The average leaf E for reproductive shoots of *P. chinampoensis* was greater than that of *P. tenuiflora* (16 %) in the dry season, but E for vegetative shoots was 21 % lower. In the rainy season, leaf E for both reproductive and vegetative shoots of *P. tenuiflora* was greater. This was indirectly proved by previous research (Wang *et al.* 1998).

The average WUE for both reproductive and vegetative shoots of *P. tenuiflora* was relative greater (1~27 %) than that of *P. chinampoensis*, especially in the drier season. Relatively high WUE indicated that the water use of *P. tenuiflora* may be more economic in the Songnen grassland, even though its average leaf E was a little greater. This and other previous studies (Wang *et al.* 1998, Yan *et al.* 1998) suggested that *P. tenuiflora* may more fit for the salinised grassland improvements in this climate region, because the water deficit was very severe at the beginning of growing season. Relatively higher P_N and WUE is the advantage for plants to survive the drier conditions in the Songnen grassland region.

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