

Photosynthesis, transpiration, and water use efficiency in two divergent *Leymus chinensis* populations from Northeast China

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Abstract

The net photosynthetic rate (P_N), transpiration rate (E), and water use efficiency (WUE) of two divergent *Leymus chinensis* populations from the grassland region of Northeast China were compared. The two populations experienced the similar habitats, but differed in leaf colour, stomata numbers, and chlorophyll contents. The leaf P_N for the grey-green (GG) population was greater than that for the yellow-green (YG) population, while the leaf E for GG population was lower than that for the YG population. The greater WUE for the GG population suggests that this type is more able to maintain higher P_N under drought and is more fit for the rangeland use in this climate region.

Additional key words: grassland; physiological differences; plant water relations.

The inter- and intra-specific variations in net photosynthetic rate (P_N), transpiration rate (E), and water use efficiency (WUE) have been well documented for many plant populations (Kimenov *et al.* 1989, Schwarz and Redmann 1989, Bowman and Turner 1993). Most of these studies have focused on the response of these characteristics to water deficit (Kimenov *et al.* 1989, Anderson *et al.* 1995), leaf age, nitrogen concentration, and chlorophyll (Chl) contents (Sobrado 1992, Kitajima *et al.* 1997, Yan *et al.* 1998, Wang *et al.* 1999), as well as to temperature and irradiance (Schwarz and Redmann 1989, Hamid *et al.* 1990, Bowman and Turner 1993), but only a few studies observed the physiological differences between divergent populations in native grasses (Schwarz and Redmann 1989, Yang *et al.* 1997, Ren *et al.* 1999, Tang and Zhang 1999).

Grasslands dominated by *Leymus chinensis* (Trin.) Tzvel. are widely distributed at the eastern end of the Eurasian steppe, with the locations in China being the Songnen plain and Inner Mongolian plateau (Xiao *et al.* 1995). The high palatability of *L. chinensis* and herbage production superior both in quality and quantity make the grasslands ideal for grazing and forage production. Beginning with Wang and Lou (1987), several studies have documented the intra-specific variations in anatomy,

morphology, and genetics of the species from native grassland. Wang and Lou (1987) and Jia (1989) demonstrated that the differences between the divergent *L. chinensis* populations were significant in stomata numbers, epidermal hair, leaf colour, leaf types, and seed production. Wang and Lou (1987) proved that the leaf N in GG population was about 23 % greater than in the YG one. Ren *et al.* (1999) and Cui *et al.* (2000) showed that large variations in genetic differentiation exist within the divergent *L. chinensis* populations. However, the differences in P_N , E , and WUE within the divergent populations from native grassland remain unclear. The objective of this study was to investigate these differences in plants from the native grassland region of Northeast China.

The study was conducted on a native *Leymus chinensis* grassland near the Grassland Ecology Field Station of Northeast Normal University, on the Changling Horse Breeding Farm, Jilin province, China. The site (44°45'N, 123°44'E) is in a flat, low-lying southern part of the Songnen plain. The grassland is at an average elevation of about 141 m and is surrounded by sand dunes about 26 m above this level. The soil is a meadow characteristics because of restricted drainage, and the soil pH can be as high as 10 in the spring. There are two chernozem, having 3.5 to 6.0 % organic matter in the sur-

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face layer, that has developed saline-sodic divergent *L. chinensis* populations, the GG and the YG, distributed in the area, and the latter population exists only in small patches (for detail see Wang 1999).

In winter, the area is dominated by the Mongolian anticyclone, which produces a westerly flow of cold, dry air over the region, and little snowfall. As the anticyclone breaks in spring, the region comes increasingly under the influence of moist pacific air masses, reaching a climax in the summer monsoon, which lasts 2-3 months in Northeast China. 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, with uneven distributed over the growing season (Ripley *et al.* 1996).

In the grassland, 6-8 plants for each divergent *L. chinensis* populations were selected. Only in clear days, P_N , E , and stomata resistance (r_s) of each fully expanded leaf for the sample plants were measured simultaneously every hour from 06:00 to 18:00 by using a *CID-301PS* CO_2 and H_2O analyser, an open system (*CID Scientific Instrument Co.*, Vancouver, WA, USA). The measurements started from the lower leaf to the top one with two replicates for each leaf. In order to reduce the individual differences between sample plants, the same plants were re-sampled over the day. Measured was in the dry season (the early June) and in the rainy season (the early July).

Leaf WUE was calculated as P_N/E . The r_s was calculated by the software provided by *CID*. The differences in mean values of P_N , E , WUE, and r_s for each leaf type between two divergent populations were statistically analysed with *ANOVA* (*MINITAB*).

Leaf P_N of the vegetative shoots between the two populations differed significantly in both June and July. Leaf P_N for the vegetative shoots of the GG population were 6 to 42 % greater, but about 3 % lower for the fourth leaf in July (Table 1). The 2nd and 3rd leaf P_N of reproductive shoots for the GG population were 7 and 58 % lower in June, however, in July they were 102 and 105 % greater (Table 1). Flag leaf P_N between the two populations differed significantly in both June and July, with flag leaf P_N for the GG population 24 and 22 % lower, respectively. However, the inflorescence P_N for the GG population was about 82 and 49 % greater in both June and July. The leaf P_N of the vegetative shoots between the two populations differed significantly in both June and July. This probably resulted from the population differences in anatomy, morphology, genetics, and physiology, because the two populations were sampled from the same site. In previous experiments the GG population had relatively higher chlorophyll *a* and *b* contents (30 and 29 %) than the YG one (Wang *et al.* 1999). Similar differences were found for leaf N contents (Wang and Lou 1987). Wang *et al.* (1999) also proved that the GG type has higher saturation irradiance than the YG type. The higher leaf P_N of the vegetative shoots of the GG population

indicated that it had a larger ability to maintain higher P_N over growing season, especially in the drier conditions in June. The effects of relative lower leaf P_N of the reproductive shoots for the GG on the total P_N of the population in June was rather less because the reproductive shoot differentiation was less than 12 % in this type (Wang 1999).

Leaf E of vegetative shoots between the two populations exhibited relatively little variation in June and July (Table 1). The leaf E of vegetative shoots for GG population was 3 to 18 % lower than for the YG population in June, but the differences were not significant. However, they differed considerably in July, with the leaf E of vegetative shoots for the GG populations 19 to 41 % higher from the 2nd to the 5th leaf. The 2nd and 3rd leaf E of reproductive shoots for the GG population was 17 to 84 % lower than those for the YG population in both June and July (Table 1). The flag-leaf E for the GG population was 34 % lower than that for the YG population in June, but about 69 % greater in July. Although the inflorescence E for the GG population was a little higher than those for the YG population in both June and July, the differences between the two populations were not significant in July.

The remarkable variations of leaf E between the two populations also imply the physiological differences between the two types from the grassland region (Table 1). The relative lower leaf E for both vegetative and reproductive shoots of GG population in June suggested this type may fit better for the grassland environments, because water deficit in this period was serious (Ripley *et al.* 1996, Wang 1999). This result is somewhat different from the work conducted in the water sufficient crop region by Wang *et al.* (1999). The lower leaf E for GG population may result from its relative higher r_s , especially in the drier season. Although the r_s between the two populations did not differ significantly in both June and July, those for GG population in June were relatively higher (Table 1). The variation in stomata numbers and leaf structures between the two populations is also possible (Wang and Lou 1987, Jia 1989). Less leaf E for the GG population under drier season is advantage for this type to survive the seasonal drought in the grassland region.

Leaf WUE (P_N/E) varied significantly between the two divergent populations in both June and July (Table 1). The leaf WUE of vegetative shoots for the GG population was about 6 to 16 % greater than those for the YG population in June, but these differences were not significant. However, leaf WUE for the GG population was about two times as high as for the YG in July. WUE of the 2nd and 3rd leaves of reproductive shoots for the GG population was more than four times greater than for the YG in July. However, flag-leaf WUE for the YG population was about 126 and 30 % greater than for the GG population in June and July. WUE of inflorescence for the GG population was about 6 % lower than that for

YG in June, but about 20 % greater in July.

WUE for the GG population was higher than for the YG population (Table 1), which suggests that the GG type is more able to maintain higher P_N under drought. This and other previous studies (Wang 1999) showed that

the GG type may more fit for the rangeland use in this climate region, because the water deficit was very severe in the early growing season. This may also explain the fact that much less YG type is distributed in the region.

Table 1. Leaf net photosynthetic rate, P_N [$\mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$], transpiration rate, E [$\text{mmol}(\text{H}_2\text{O}) \text{ m}^{-2} \text{ s}^{-1}$], water use efficiency, WUE (P_N/E), and stomata resistance, r_s [m s mol^{-1}] of the two divergent *Leymus chinensis* populations in grassland region from Northeast China (mean \pm S.E.). Divergent populations: GG = grey-green, YG = yellow-green. Leaf P_N : L2 = the second leaf, L3 = the third leaf, L4 = the fourth leaf, L5 = the fifth leaf, FL = flag leaf, INFL = inflorescence. Differences between means (ANOVA) indicated by ** for $p < 0.01$ and * for $p < 0.05$.

		Shoot	June	July		
			GG	YG	GG	YG
P_N	vegetative	L2	22.21 \pm 2.34**	18.04 \pm 2.05	8.76 \pm 0.95**	8.24 \pm 0.83
		L3	23.30 \pm 2.28**	21.94 \pm 3.06	9.17 \pm 0.87**	6.48 \pm 0.61
		L4	25.90 \pm 2.65**	20.81 \pm 3.54	7.06 \pm 0.69**	7.26 \pm 1.14
		L5			7.29 \pm 0.85**	6.83 \pm 0.71
	reproductive	L2	22.71 \pm 2.82**	24.33 \pm 2.96	11.16 \pm 1.33**	5.53 \pm 1.33
		L3	11.06 \pm 3.08**	26.60 \pm 4.14	15.23 \pm 3.16**	7.44 \pm 1.01
		FL	21.41 \pm 3.98**	28.32 \pm 3.91	14.75 \pm 2.87**	18.95 \pm 2.78
		INFL	13.54 \pm 2.96**	7.46 \pm 2.78	14.00 \pm 3.03**	9.40 \pm 2.09
E	vegetative	L2	3.77 \pm 0.39	4.42 \pm 0.44	1.96 \pm 0.15**	1.65 \pm 0.16
		L3	4.70 \pm 0.41	5.73 \pm 0.32	2.61 \pm 0.25**	2.10 \pm 0.24
		L4	5.57 \pm 0.59	5.72 \pm 0.33	3.08 \pm 0.35**	2.18 \pm 0.31
		L5			2.55 \pm 0.24**	1.89 \pm 0.28
	reproductive	L2	4.58 \pm 0.85**	5.55 \pm 1.47	0.96 \pm 0.32**	2.58 \pm 0.56
		L3	3.42 \pm 0.52**	5.69 \pm 1.59	0.48 \pm 0.09**	3.07 \pm 0.67
		FL	6.41 \pm 0.85**	9.75 \pm 2.84	3.25 \pm 0.91**	1.92 \pm 0.43
		INFL	4.36 \pm 0.51**	4.19 \pm 1.20	1.36 \pm 0.31	1.35 \pm 0.29
WUE	vegetative	L2	8.85 \pm 2.02	8.36 \pm 1.34	12.52 \pm 2.63**	6.53 \pm 1.35
		L3	7.04 \pm 1.94	6.07 \pm 0.85	9.61 \pm 1.72**	4.04 \pm 1.10
		L4	6.91 \pm 1.51	6.19 \pm 0.95	7.25 \pm 1.51**	3.00 \pm 0.35
		L5			5.67 \pm 1.24*	3.04 \pm 0.36
	reproductive	L2	7.50 \pm 1.90**	7.29 \pm 1.50	13.49 \pm 3.73**	3.74 \pm 1.40
		L3	4.59 \pm 1.53**	6.66 \pm 1.30	30.71 \pm 4.31**	4.34 \pm 1.07
		FL	4.53 \pm 1.05**	10.24 \pm 1.34	8.09 \pm 1.71*	10.54 \pm 2.63
		INFL	6.28 \pm 2.13*	6.67 \pm 1.46	10.56 \pm 2.10*	8.80 \pm 1.64
r_s	vegetative	L2	7.73 \pm 1.03	7.60 \pm 0.89	10.11 \pm 1.19	13.48 \pm 1.98
		L3	5.67 \pm 0.81	5.17 \pm 0.71	11.39 \pm 1.56	11.83 \pm 1.28
		L4	6.00 \pm 0.95	5.87 \pm 0.92	10.82 \pm 1.14	11.22 \pm 1.76
		L5			14.39 \pm 1.98	14.14 \pm 1.75
	reproductive	L2	6.40 \pm 0.77	6.28 \pm 1.10	7.81 \pm 1.50	7.76 \pm 0.89
		L3	6.36 \pm 0.72	5.19 \pm 0.97	9.12 \pm 2.79	7.23 \pm 0.88
		FL	5.40 \pm 0.83	5.03 \pm 1.12	11.78 \pm 2.29	12.23 \pm 1.44
		INFL	6.30 \pm 0.39	6.48 \pm 0.82	16.99 \pm 2.66	16.33 \pm 2.73

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