BRIEF COMMUNICATION

Physiological divergences between two rhizomatous grasses from a desertification steppe, North China

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Abstract

The inter- and intra-specific physiological differences, *e.g.* rates of net photosynthesis (P_N) and transpiration (E), stomatal conductance (g_s), and water use efficiency (WUE), were compared between two grasses, *Calamagrostis epigeios* (L.) Roth. and *Psammochloa villosa* (Trin.) Bor., and between their leaf types in a desertification steppe in North China. The two species had a similar habitat, but differed in leaf area and rhizome depth. Leaf P_N, E, and g_s for *P. villosa* were significantly greater than those for *C. epigeios* in the growing season, but WUE for the former species was only 50 and 80 % of that for the latter one in dry and rainy seasons, respectively. In general, leaf P_N, E, g_s, and WUE for both vegetative and reproductive shoots of the two species exhibited little variations between leaf types or with leaf age, even though there were some remarkable differences between dry and rainy seasons. The mean leaf P_N and E in reproductive shoots of *P. villosa* were significantly lower than those in its vegetative shoots in rainy season, while these differences were much smaller for those of *C. epigeios*. *P. villosa* with deeper rhizome roots has relative higher leaf P_N, E, and g_s, but a smaller WUE in the arid desertification steppe region.

Additional key words: adaptation to drought; *Calamagrostis epigeios*; net photosynthetic rate; *Psammochloa villosa*; stomatal conductance; transpiration; water relations.

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Research on plant responses to drought is becoming increasingly popular, for most climate change scenarios suggest an increase in aridity in many areas in the world (Chaves *et al*. 2003, Wang and Gao 2003). On a global scale, droughts, in conjunction with coincident high temperature and radiation, are the critical environmental factors limiting plant photosynthesis, growth, and survival, even for the plant species well adapted to arid conditions in steppes and deserts, *e.g. Stipa grandis* P. Smirn., *Leymus chinensis* (Trin.) Tzvel. (Liu 1993, Wang and Gao 2001). Many studies were conducted over the past decades, covering plant strategies and physiological and biochemical responses to drought or water deficits (Schwarz and Redmann 1989, Hamid *et al*. 1990, Meyer *et al*. 2001, Flexas *et al*. 2002). Some studies proved that rates of photosynthesis after full expansion of a leaf generally exhibit a monotonic decline (David 1998, Wang and Yuan 2001), and this decline is mainly due to the redistribution of resources from old leaves to young ones (Field and Mooney 1983, Hikosaka *et al*. 1994, Anderson *et al*. 1995). But there is a long-standing controversy on the decline of photosynthesis due to droughts mainly through stomatal closure, resources redistribution, or by metabolic impairment (Kimenov *et al*. 1989, Tezara *et al*. 1999, Flexas and Medrano 2002, Lawlor and Cornic 2002). Moreover, few studies have tested the intra- and inter-specific variations in plant physiology for grass species (Schwarz and Redmann 1989, Wang 2001, Wang and Yuan 2001), especially the physiological divergences among the grasses under droughts in arid environments, although they were well documented for many tree and bean species (*e.g.* Kimenov *et al*. 1989, Hamid *et al*. 1990). This knowledge is essential for better understanding plant responses to droughts and for predicting the fate of natural vegetation under global changes.

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Calamagrostis epigeios (L.) Roth. and *Psammochloa villosa* (Trin.) Bor., two perennial C_3 grasses, are widespread from semi-arid steppes to dry deserts in North China. Their greater tolerance of environmental stresses (*e.g.* drought, high temperature, radiation, and poor soil) and high productivity and palatability in growing season make the species ideal for grazing in range regions. In desertification steppes, the two species with developed rhizomes can form patches of consociations in dry sandy soil, where the surface soil (0–30 cm) moisture is only about 4 % in dry season (from May to early June). Few studies have looked at the distributions and photosynthetic pathway types of the two species (Liu 1993, Wang 2002), but the physiological divergences of the two species and their adaptations under the dry desert environments remain unclear. The objectives of the present study were to compare inter- and intra-specific variations, *e.g.* net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and water use efficiency (WUE) of the two species in a similar dry desert habitat (*e.g.* precipitation, temperature, and irradiance) in North China. The following questions were addressed: (*1*) How do the two species differ in physiology? (*2*) How do physiological divergences relate to rhizome depth for the two species in similar arid environments? (*3*) What are the relationships of leaf P_N, E, g_s, and WUE with leaf types or leaf age for arid plant species?

The study was carried out in a desertification steppe, Inner Mongolia, North China. The site, located at 42° 07'N, 116°28'E, is a semi-fixed dune at the southeast of Xilingol steppe and eastern end of Otindag sand-land. Local landscape comprises large areas of fixed and semi-fixed dunes, with 80 % desertification lands and 10 % mobile dunes, mixed with steppes, shrubs, woods, and farmlands, on average 1 275 m above sea level, varying from 1 050 to 1 350 m. The typical natural vegetation in the region is desertification steppe, dominated by xerophytes, *e.g. Stipa grandis* P. Smirn., *S. krylovii* Roshev., *Leymus dasystachys* (Trin.) Nevski., and *Calamagrostis epigeios* (L.) Roth. Most of the region, *e.g.* dunes, disturbed and cultivated lands, have sandy soil with gravel, while light chestnut and chernozem occur on steppes and farmlands. For at least 10 years prior to 2004, the site, selected for the study, was fenced for restoration, and has never been grazed, ploughed, fertilized, and burned; the only disturbance or management of the area was annual mowing in mid-August.

The site is in the middle of the Mongolian Plateau, which leads to a typical continental climate and low annual precipitation. Air temperature averages 1.9 °C annually, and monthly mean temperature ranges from −17.8 °C in January to 18.8 °C in July, while the extreme air temperature ranges from −39.8 °C in January to 35.4 °C in July. Annual precipitation averages 389 mm, varying from 255 to 512 mm. Precipitation is not distributed evenly over the growing season, of which 70 % falls between the late June and the late August. Windy

days average 71 d annually, and wind speeds vary from 3.0 to 4.8 m s^{-1}. For at least 3 years prior to 2004, droughts were very severe in the region, with annual precipitation of 50–134 mm being lower than normal. These droughts would have been accentuated in the spring and early summer because of strong winds in the desert region. The main characteristics of the climate in the region are cold, dry, and frequently windy spring, cool and short summer, early autumn frosts, and long cold winter, with little snowfall. A more detailed description of the climate in the region can be found in Wang (2002).

In the study site, 6–8 well growth plants of each of the two species were selected for physiological measurements. Only on clear days, P_N, E, g_s of each fully expanded and attached leaf of the sample plants were measured simultaneously every 2 h between 07:00–18:00, by using *Li-6400* CO_2 and H_2O analyzer (*Li–COR*, USA). The measurements begun from the low to the top leaves (or from the 2nd to the 4th leaves) with 3–4 replicates for each leaf type. In order to reduce the individual differences between sample plants, the plants were re-sampled over the days. The measurements were taken in dry season (6–9 June) and in rainy season (7–9 July), respectively.

Soil samples were collected from the site at 30 cm increments (0–30, 30–60 cm), with 5–6 replicates, and soil moisture was measured gravimetrically. Total soil nitrogen contents were determined by Auto-Kjeldahl method (*Kjektec System 1026 Distilling Unit*, Sweden). Rhizome depths for the two species were measured simultaneously. Plant water use efficiency (WUE) was calculated as P_N/E (Hamid *et al*. 1990, Wang 2001). The differences in mean P_N, E, g_s, and WUE between the two species and leaf types were statistically analyzed with *ANOVA* (MINITAB).

The differences of leaf P_N and E between the two species were significant in both vegetative and reproductive shoots (Fig. 1). In the dry season, mean leaf P_N for the vegetative shoots of *P. villosa* was 18.1 μmol(CO_2) m^{-2} s^{-1}, ranging from 17.5 to 18.8 μmol(CO_2) m^{-2} s^{-1} from the 2nd leaf to the 4th leaf, but that for *C. epigeios* was 9.0 μmol(CO_2) m^{-2} s^{-1}, ranging from 8.2 to 10.1 μmol(CO_2) m^{-2} s^{-1}. In the rainy season, the mean leaf P_N for the vegetative shoots of *P. villosa* dropped by 25 %, but that for *C. epigeios* dropped by 3 % only (Fig. 1*A*), compared with the dry season, and the difference between the two species was significant ($p<0.01$). However, the differences in the 2nd and 4th leaf P_N for reproductive shoots were not significant between the two species ($p>0.05$), while that for the 3rd leaf of *P. villosa* was considerable greater (Fig. 1*E*).

Leaf E and g_s for both vegetative and reproductive shoots differed significantly between the two species in the dry and rainy seasons (Fig. 1). In the dry season, the mean leaf E of vegetative shoots for *P. villosa* was 15.0 mol(H_2O) m^{-2} s^{-1}, ranging from 14.2 mol(H_2O) m^{-2} s^{-1} of the 2nd leaf to 15.5 mol(H_2O) m^{-2} s^{-1} of the 4th leaf, and
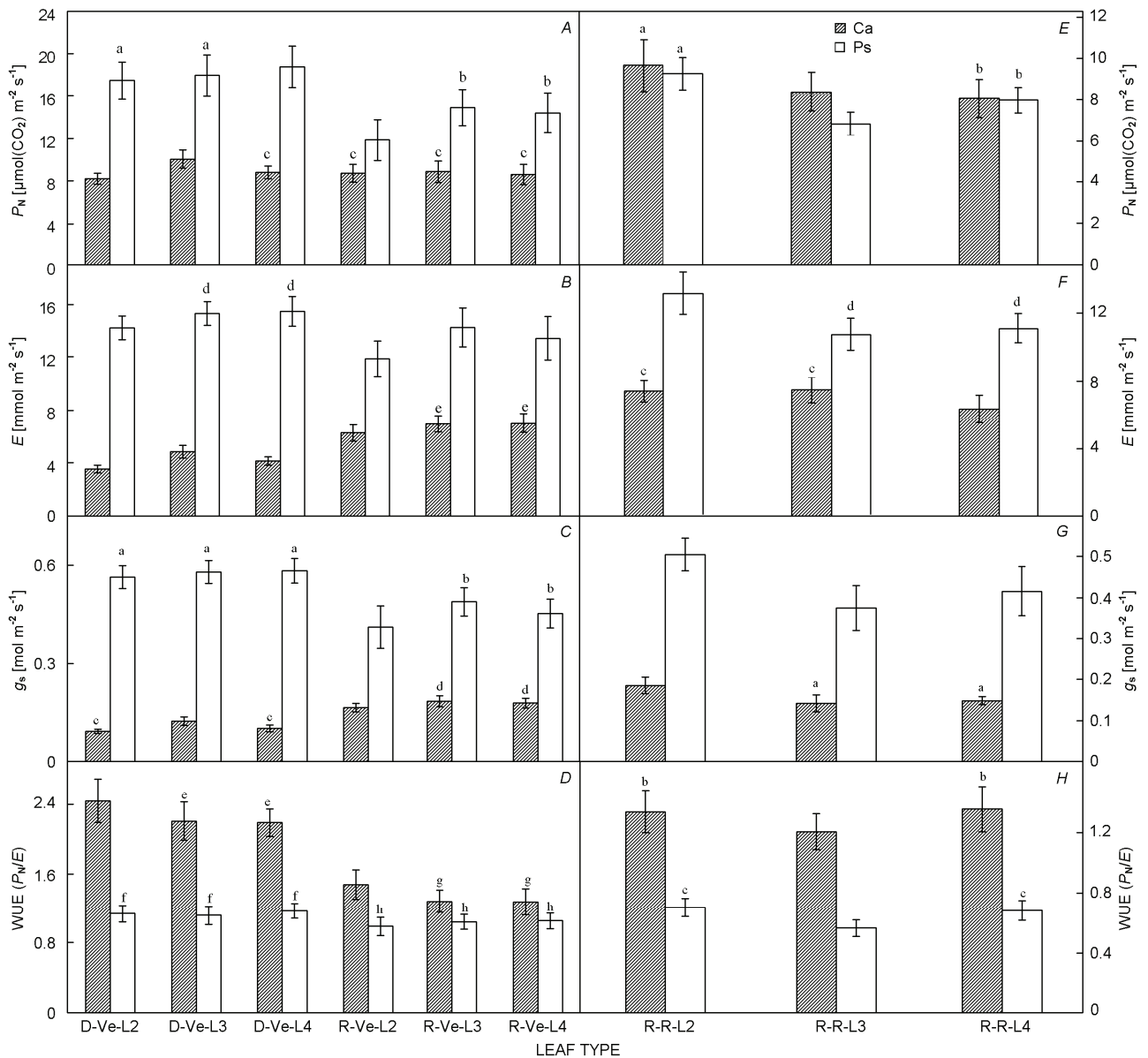
Fig. 1. The differences in rates of leaf photosynthesis, P_N (*A, E*) and transpiration, *E* (*B, F*), stomatal conductance, g_s (*C, G*), and water use efficiency, WUE (*D, H*) of vegetative (*A–D*) and reproductive (*E–H*) shoots between *Psammochloa villosa* (Ps) and *Calamagrosyis epigeios* (Ca), and leaf types in a desertification steppe, North China. D–Ve–L_{2-4} and R–Ve–L_{2-4} represent the 2nd, 3rd, and 4th leaves of vegetative shoots in dry and rainy season, respectively. *Bars with the same lowercase letters* are not significantly different between species and leaf types (*p*>0.05). Means ± standard errors.

about 3.6 times of those for *C. epigeios* (*p*<0.01). In the rainy season, mean leaf *E* for vegetative and reproductive shoots of *P. villosa* were about 2.0 times and 1.6 times those for *C. epigeios*, respectively (Fig. 1*B,F*), and the differences were significant (*p*<0.01). Like that of leaf *E*, values of leaf g_s for both vegetative and reproductive shoots of *P. villosa* were greater than those of *C. epigeios* (Fig. 1*C,G*). The mean leaf g_s of vegetative shoots for the former species were 5.4 times that for the latter species in dry seasons, and 2.6 times and 2.7 times in the rainy season for vegetative and reproductive shoots, respect-

ively (*p*<0.01). Relatively higher leaf *E* and g_s for *P. villosa* indicated there should be larger water supply for the species to maintain higher P_N under arid desertification steppe.

WUE differed significantly between the two grass species (Fig. 1*D,H*). For the vegetative shoots of *P. villosa*, the mean WUE was 1.14, which was only about 50 % of that for *C. epigeios* in the dry season (*p*<0.01). Those for vegetative and reproductive shoots of *P. villosa* in the rainy season were 80 and 50 % of those for *C. epigeios*, respectively (*p*<0.01).

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Leaf P_N and E between leaf types for both species exhibited little variations in the growing seasons (Fig. 1A,B). Even though leaf P_N for vegetative shoots of *P. villosa* declined with leaf age (from the 2nd leaf to the 4th leaf) in both dry and rainy seasons (Fig. 1A), the differences between the 2nd and 3rd leaves in the dry season and between the 3rd and 4th leaves in the rainy season were not significant ($p>0.05$). For *C. epigeios*, leaf P_N for the 2nd leaf was remarkably lower than those for the other type leaves ($p<0.05$), and that for the 3rd leaf was about 20 % greater in the dry season ($p<0.01$). However, there were no significant differences among the other leaf types in the growing season ($p>0.05$). The leaf P_N for the reproductive shoots of both grass species increased significantly ($p<0.05$) with age or dropped from the top leaves to low leaves (Fig. 1E). Leaf P_N for the reproductive shoots of *P. villosa* was only 60 % of those for its vegetative shoots, and the differences were significant ($p<0.01$), while those between the two shoot types for *C. epigeios* were not significant ($p>0.05$).

Leaf E for the two species varied considerably in both dry and rainy seasons (Fig. 1B). In general, leaf E for vegetative shoots was much greater for the top leaves than for the low leaves. The leaf E for vegetative shoots of *P. villosa* in the rainy season was significantly lower than that in the dry season ($p<0.01$), on the contrary that for *C. epigeios* was considerable greater ($p<0.05$). The mean leaf E of reproductive shoots for *P. villosa* in the rainy season was about 11.5 % greater than that of vegetative shoots ($P<0.05$), but there were no significant differences between vegetative and reproductive shoots for *C. epigeios* in the rainy season ($p>0.05$).

The changing pattern of leaf g_s for the two species was much similar to those of leaf E (Fig. 1C). Values of g_s were significantly correlated with leaf P_N ($r^2 = 0.961$, $p<0.01$; 0.913, $p<0.01$) and leaf E ($r^2 = 0.8459$, $p<0.01$; 0.801, $p<0.01$) for *P. villosa* and *C. epigeios*, respectively, suggesting that g_s was the critical factor for leaf P_N and E variations in the arid steppe.

There were only small differences in WUE among leaf types for vegetative shoots of the two species (Fig. 1D). WUE for the 2nd leaf of *P. villosa* were about 10 and 13 % greater than those of the other leaf types in both dry and rainy seasons, and the differences were significant ($p<0.05$). In the other cases, there were no significant differences for the two species in both dry and rainy seasons, respectively ($p>0.05$). However, WUE for vegetative shoots in rainy season dropped by 41 and 10 % for *P. villosa* and *C. epigeios*, respectively, compared with those in the dry season. WUE for reproductive shoots of *P. villosa* was significantly lower than that for vegetative shoots ($p<0.01$), while those for *C. epigeios* were not remarkable (Fig. 1H).

There has been tremendous success in recent years in demonstrating the plant responses to water deficit in whole plant, in morphology, physiology, and at molecular levels (Cellier *et al*. 1998, 2000, Comstock and Mencuccini 1998, Casper *et al*. 2001, Wang and Gao 2001, Chaves *et al*. 2002, 2003, Lawlor and Cornic 2002). Most of relevant research focused on crop plants, which are mainly annual species or are grown in relatively sufficient water supply environments (Bruce *et al*. 2002, Bunce 2004). Studies on physiological divergences or adaptation differences for xerophyte plants from arid and semi-arid regions have not received much attention (Comstock and Mencuccini 1998, Casper *et al*. 2001, Wang and Gao 2003). This knowledge is essential for better understanding plant adaptation, plant and water relationships, and predicting the fate of natural plants under global changes. In this study, the two grass species experienced a similar habitat, but differed significantly in P_N, E, g_s, and WUE, especially for the vegetative shoots (Fig. 1). *P. villosa* had higher gas exchange than *C. epigeios* in growing season, but its WUE was much smaller than that of the latter species, and these differences would have been accentuated in the dry season because of less rainfall. The physiological differences between the species were mainly due to their divergence in rhizome root depths (Table 1). Rhizome roots of *P. villosa* can reach as deep as 35–40 cm and their mean value is about 1.7 times that for *C. epigeios* in the region ($p<0.001$). Soil moisture in deeper layer (30–60 cm) was about 2 times that in the surface layer (0–30 cm). This demonstrates that the species with deeper root systems, such as *P. villosa*, have greater capacity in water uptake from the deeper layer of soil than the species with shallow root systems. Deeper rhizome roots and relatively sufficient soil water supplies for *P. villosa* may well explain the facts that the species has greater P_N, E, and g_s, and a smaller WUE than *C. epigeios* in the arid desertification steppe. Many factors are important for determining plant distributions and physiological variables, such as temperature, irradiance, drought, and resource-use efficiency as well as edaphic characteristics (Field and Mooney 1983, Anderson *et al*. 1995, Wang and Yuan 2001, Chaves *et al*. 2003), but air and soil droughts are particularly important for plants in arid regions (Casper *et al*. 2001, Wang 2002, Maurel *et al*. 2004). In the desertification steppe ecosystem, water limitation is important for determining growth and survival, for average annual precipitation is no more than 389 mm. Relatively less leaf P_N, E, g_s, and higher WUE in *C. epigeios* may be advantageous for the species to fit the arid steppe. Physiological differences between the two species suggest that physiological divergences are related with plant adaptation and survival in the arid desertification steppe.

Unlike for the species from moist environments, *e.g.* meadows, wood, and forests, the leaf P_N, E, g_s, and WUE for each of the two species exhibited little variation among leaf types in both dry and rainy seasons (Fig. 1), even though there were some differences between the dry and rainy seasons. Relatively little physiological variations with leaf types for the plants from the arid steppe may be mainly due to the morphological and

Table 1. Morphological traits of *Calamagrostis epigeios* (L.) Roth. and *Psammochloa villosa* (Trin.) Bor., edaphic, topographic, and climatic characteristigs of the study site in the desertification steppes, North China. Differences between means (plant morphological traits and seasonal climates): n.s. – not significant ($p > 0.05$), [**]$p < 0.01$, [***]$p < 0.001$ (F-test).

		Calamagrostis epigeios	*Psammochloa villosa*
Shoot height [cm]		68.63 ± 14.51	103.91 ± 18.45[***]
Leaf area [cm^2]		5.93 ± 0.89	8.67 ± 1.32[***]
Rhizome depth [cm]		22.44 ± 3.51	37.36 ± 4.64[***]
Soil moisture	0–30 cm	36.00 ± 3.42 %	38.00 ± 4.56 % n.s.
	30–60 cm	82.00 ± 6.71 %	80.00 ± 7.67 % n.s.
Soil N content [%]		0.12 ± 0.04	0.12 ± 0.05 n.s.
Soil type		Sandy soil	
Location		42° 07'N, 116 °28'E	
Elevation [m]		1 275	
Seasonal precipitation	Dry season	22 % of the total	
	Rainy season	63 % of the total[***]	
Mean temperature [°C]	Dry season	17.2	
	Rainy season	20.0[**]	

physiological adaptations to long period drought. There are only 4–6 leaves for a shoot of either species in the arid steppe, which is about 2/3 of those from moist grasslands and meadows. However, leaf life span increased, leaf turnover was reduced and standing leaf crop increased, compared with the meadow species. This was supported by the observations on the *Cryptantha flava* (Casper *et al*. 2001). Prolonged leaf life span and reduced leaf turnover can reduce above-ground biomass allocation (Casper *et al*. 2001, Wang and Gao 2003), which leads to less transpiration and increased WUE in water limited environments. This suggests that the leaf age (cf. Šesták 1985) and the redistribution of resources may not be the critical factor for leaf P_N variation in some desert plant species, except those in final senescent phase. Strong correlations of g_s with both leaf P_N and E for the two species suggested that leaf g_s was the main critical factor regulating physiological variation in the dry desert conditions. We cannot provide direct evidence to explain relations between leaf g_s and plant leaf and soil water potential for the species in the region. Previous studies had proved that air and soil drought affect plant leaf g_s by altering leaf and soil water potential (Comstock and Mencuccini 1998, Wang and Gao 2001, Chaves *et al*. 2002, 2003, Flexas and Medrano 2002).

WUE for plants in arid environments has received considerable attention in the last few decades (David *et al*. 1998, Tezara *et al*. 1999, Casper *et al*. 2001, Chaves *et al*. 2003). The differences in WUE between leaf types and between shoot types (vegetative shoot and reproductive shoot) for desert and grassland species were tested by Wang and Gao (2001) and Wang and Yuan (2001). Unlike in grassland species, there were smaller differences in WUE between leaf types for both *P. villosa* and *C. epigeios* in the dry and rainy seasons, respectively (Fig. 1). This indicated that all leaf types of both species had a great ability to maintain photosynthesis over the drought season, and water use of these plants may be more economic in the arid steppe.

Because of the confounding factors, *e.g.* air and soil droughts, fertility, molecular and physiological differences, and water and chemical signalling between root and shoot (Meyer *et al*. 2001, Flexas *et al*. 2002, Bunce 2004, Maurel *et al*. 2004), studies of reciprocal transplanting, manipulation of water, and greenhouse cultivation are needed to explore the fundamental bases of plant physiological differences in the arid environments, such as stomatal movements and chemical signals controlling the plant water relationships.

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