Are plants more responsive to decreased than to increased rainfall on the Tibetan Plateau? Evidence from *Carex duriuscula* subsp. *stenophylloides*

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Carex duriuscula subsp. *stenophylloides* is a sedge species in alpine grassland ecosystems on the Tibetan Plateau. Here we examine its physiological and growth responses to variation in simulated rainfall in a growing season. Compared with the present local rainfall, increased rainfall had no effect on any measured trait except for long-term water use efficiency, and decreased rainfall significantly reduced total leaf area and biomass production, while only severe limitation of rainfall decreased net photosynthetic rate, stomatal conductance, transpiration rate, and apparent carboxylation efficiency. Net photosynthetic rate was significantly correlated with stomatal conductance, transpiration rate, apparent carboxylation efficiency, and leaf water potential. Total plant dry weight was significantly correlated with net photosynthetic rate, total leaf area, and leaf area ratio. These findings suggest that stomatal limitation and degraded activity of mesophyll cells result in a decrease in net photosynthesis, and that decreased net photosynthesis and total leaf area lead to a decrease in plant production. Based on our measurements, sedge-dominated ecosystems of the Tibetan Plateau are more likely to be impacted by decreases in growing season rainfall than by increases.

Key words: biomass production, *Carex duriuscula* subsp. *stenophylloides*, grassland ecosystems, photosynthesis, rainfall change

Introduction

The Tibetan Plateau, the highest plateau in the world with a mean altitude of more than 4000 m, covers about 2.5 million km² (Li & Zhou 1998, Zhang *et al.* 2002). Due to its perceptible climate change and profound consequences on circumjacent and global climate change (cf. Beniston *et al.* 1997, Zheng *et al.* 2002, Wei *et al.* 2003), the Tibetan Plateau is one of the most sensitive areas

to respond to global climate change (Watson *et al.* 1996, Liu & Chen 2000, Zheng *et al.* 2002). As an important aspect of climate change, significant spatio-temporal changes of rainfall result in changes in run-off at the local and regional scale (Watson 1999). The patterns of rainfall are characterized by a high degree of uncertainty at high elevation sites (Beniston *et al.* 1997). The observational data indicate that over the Tibetan Plateau there are great temporal and spatial variations in rainfall (Lin & Zhao 1996, Zheng *et al.* 2002, Wei *et al.* 2003). Researchers studying the "sensitivity" of the Tibetan Plateau mainly focused on the local climate change and its interactions with the global climate change (Zheng & Li 1999, Liu & Chen 2000, Zheng *et al.* 2002, Xiao & Sun 2003). Very little is known about whether native plants and terrestrial ecosystems on the Tibetan Plateau are sensitive to changing rainfall.

One of the core areas of research on global change is to detect the effect of the climate change on vegetation in terrestrial ecosystems (Fu *et al.* 2005). Alpine and montane grasslands, mainly composed of *Carex* and *Stipa*, are the representative vegetation on the hinterland of the Tibetan Plateau (Zhang 1988). Due to uncertain spatial and temporal variations in future rainfall, plants in a given region may experience either increased or decreased rainfall, and those located in different regions may experience extreme rainfall in whole or part of their life spans. Response patterns and the degree of sensitivity of plants in response to future changing rainfall will affect the structure and function of alpine grassland ecosystems, and consequentially influence the dynamics of vegetation systems in future climate change.

Available soil water, which is largely related to the variations and quantity of rainfall in a region, is an important environmental factor influencing leaf gas exchange (Turner 1986, Sadras & Milroy 1996), plant growth and biomass accumulation (O'Connor *et al.* 2001, Souza *et al.* 2004). Most of the researchers studying gas exchange and plant growth on the Tibetan Plateau have focused on field measurements (Li & Zhou 1998), while fewer investigators used controlled experiments to investigate the responses of plants from alpine grassland to changing environmental factors.

Water use efficiency reflects the relationship between plant yield and consumed water (Kramer & Kozlowski 1979). Instantaneous water use efficiency (IWUE) is calculated as the ratio of photosynthetic rate (P_n) to transpiration rate (E) and long-term water use efficiency (LWUE) is defined as the ratio of dry matter production to water use (Hubick *et al.* 1986). We calculated the water use by subtracting the water remaining in the pots at harvest from all water supplied during the experimental period, thus we approximated the water use as evapotranspiration.

Plants respond to environmental factors differentially at different hierarchies (Chen 1997). We studied the responses of grasses to varying levels of simulated rainfall, mainly using instantaneous gas exchange traits at peak growth and some lifetime traits at harvest. Accordingly, we set up a controlled experiment in Lhasa, Tibet. In this experiment, plants of a sedge species *Carex duriuscula* subsp. *stenophylloides* were subjected to four levels of water supply, simulating future possible rainfall changes at the local and regional scale in a growing season on the Tibetan Plateau. Our main objective was to detect the plant response patterns to increase and decrease of rainfall. We also analyzed correlations between the traits to understand differences in biomass production.

Materials and methods

The species

Carex duriuscula C.A. Mey. subsp. *stenophylloides* (V. Krecz.) S.Y. Liang (hereafter referred to as *Carex stenophylloides*), a clonal perennial sedge, often grows in grasslands, sand and gravel areas along riversides, and is distributed across Inner Mongolia, Shanxi, Gansu, Xinjiang and Tibet in China, also some areas in Russia, Korea and Mongolia (DFRPS 2000). The species reproduces from April to June and proliferates in the field by forming perennial rhizome systems. The species has a strong capacity to resist cold, drought and soil infertility, and due to the long period during which it remains green, rapid reproduction, and trample-resistance, it is not only palatable forage but also a promising lawn grass (Li *et al.* 1996).

Experimental design

The plant materials were collected along the riversides of the Lhasa River near the Lhasa Plateau Ecological Research Station (LPERS, 91°20´37´´E, 29°40´40´´N, 3688 m a.s.l.) of the Chinese Academy of Sciences. The vegetation of the grassland is mainly composed of *Carex stenophylloides* and some other species including *Kobresia pygmaea*, *Potentilla* spp. and *Poa* spp. *Carex stenophylloides* accounts for more than 80% of the vegetation cover.

Ten *Carex stenophylloides* plants were collected from the grassland on 10 June 2004. The distances between two plants were in all cases greater than 5 m, and every plant included many similar-sized ramets. Four similar-sized ramets from every plant were selected and were assigned randomly to four levels of water supply. We planted each ramet into a plastic pot (35 cm diameter and 25 cm height) filled with river sand and 3–4 cm of loam on the surface, and every pot was fertilized with 4 g of a controlled release fertilizer (Osmocote [14% N, 14% P_2O_5, 14% K_2O], the Scotts Company, USA) before cultivation. The experiment was conducted in a greenhouse that was built from laths and colorless EVA (Ethylene Vinyl Acetate Copolymers, 0.12 mm of thickness) film and the film reduced photosynthetic active radiation (PAR) to about 70% of full sunlight. The average temperature and relative humidity in the greenhouse during the experimental period were about 18.2 °C and 68%, respectively, while in the field in the corresponding period 13.9 °C and 71% were recorded (data from the Weather Bureau of Lhasa).

The annual precipitation over the Tibetan Plateau decreases from the southeast (600–800 mm yr^{-1}) to the northwest (17.6 mm yr^{-1}). The rainy and dry seasons are very clearly demarcated and more than 80% of annual precipitation is concentrated in the rainy season, particularly in July and August (Dai 1990, Wei *et al*. 2003). According to the data of rainfall in Lhasa from 1998 to 2003, the mean rainfall between July and August was 290.15 mm. If the pot (35 cm diameter) in the experiment were placed in field, it would receive a sum of 27 901 ml (calculated by multiplying the area of pot by amount of rainfall) rainwater in the period of the two months (62 days), and then a mean of 450 ml rainwater daily would be expected. Based on the assumption, we applied 450 ml pot^{-1} day^{-1} as a level of water supply corresponding to present local rainfall, and increased 40% and decreased 40% and 80% of the water supply. The four levels of water supply were 630, 450, 270 and 90 ml of water per pot per day. These levels correspond to the rainfall in the wet, semi-wet, semi-arid and arid regions on the Tibetan Plateau (cf. Dai 1990, Li & Zhou 1998, Wei *et al*. 2003).

After 20 days of plant establishment time (equal water was supplied to each pot during this period), the watering treatments ran from 1 July to 31 August. During the experiment, we fertilized each plant with 90 ml diluted solution (0.463 mg ml^{-1}) of a water soluble fertilizer (Peters Professional [20% N, 20% P_2O_5, 20% K_2O], the Scotts Company) once a week, besides adding 4 g of a controlled release fertilizer as mentioned above. The nutrition solution was added to the calculation of the total water supply. The pots were weekly assigned to new random positions to compensate for the possible effect of spatial light heterogeneity in the greenhouse. All plants were watered between 09:00 and 10:00 or between 18:00 and 19:00.

Measurements

During the experiment, a few plants died or grew abnormally, and those were excluded from the final harvest. Thus the final analyses included nine replicates for each treatment. Five leaf blades were selected from each water treatment to determine leaf water potential (Ψ_l) using a PSYPRO Water Potential System (Wescor Inc., USA) on a sunny day from 13:00 to 15:00 on 11 August, for plant leaf water potential is relatively constant during this period (cf. Ben *et al*. 1993). All pots were weighed to calculate the water remaining in the pots (20 kg per pot at the start of the experiment) and then on 1 September 2004 all available plants were harvested. Three representative leaf blades were selected from each plant, and leaf area was measured with AM100 leaf-area meter. All plant parts were oven-dried at 65 °C to constant mass and weighed. Total leaf blade (TLDW) and total

plant dry weight (TPDW) of each pot were then measured. Specific leaf area (SLA, leaf area per unit of dry weight) was calculated, then total leaf area (TLA) and leaf area ratio (LAR, leaf area per total plant dry mass) were estimated as TLDW × SLA and TLA/TPDW, respectively.

Net photosynthetic rate (P_n), stomatal conductance to water vapor (g_s), transpiration rate (E) and sub-stomatal CO_2 concentration (C_i), were measured in a climate leaf chamber, at constant leaf temperature (25 °C) and constant water vapour pressure deficit based on leaf temperature (2.0 KPa), with an open gas exchange system, LI-6400 Portable Photosynthesis System (Li-Cor Inc., USA) fitted with a LI-6400-02B LED light source. Considering that photosynthetic capacity of a leaf increases to a maximum at or before full leaf expansion (Henson *et al.* 1990), we selected three to five of the youngest fully expanded leaves (only one leaf was selected from one pot) from each treatment for gas exchange measurements. Inside the chamber, the photosynthetic active radiation (PAR) was gradually elevated from 200 to 2000 μmol m^{-2} s^{-1} at an increment interval of 200 μmol m^{-2} s^{-1}, but only light saturated photosynthesis was used to calculate the mean. All leaf gas exchange measurements were conducted from 11:00 to 15:00 on three sequential sunny days in mid-August 2004. The leaf blades used for gas exchange were cut from plants to determine specific leaf mass (SLM, leaf dry mass per unit of fresh leaf area). Instantaneous water use efficiency (IWUE), long-term water use efficiency (LWUE) and apparent carboxylation efficiency (ACE) (as P_n/C_i) (Flexas *et al.* 2001) were calculated.

Statistical analyses

One-way analysis of variance (ANOVA) with SNK test (Dytham 1998) was employed to reveal differences in responses between treatments. Before analyses, all data were tested for normality and homogeneity of variance. If necessary, data were logarithmically transformed to achieve normality and homoscedasticity. Pearson's simple correlation was applied to assess the relationship between traits. All analyses were performed with the statistical package SPSS 10.0.

Results

All the traits, except for specific leaf mass (SLM), were significantly affected by water supply (Figs. 1 and 2). Gas exchange showed no significant differences among the treatments of 270, 450, and 630 ml pot^{-1} d^{-1} (Fig. 1) (thereafter pot^{-1} d^{-1} was omitted); while in the treatment of 90 ml, P_n, g_s, E, IWUE and ACE declined dramatically (Fig. 1a–b, d–f), and C_i increased significantly (Fig. 1c), and leaf water potential (Ψ_l) was lower than that in the treatments of 450 and 630 ml (Fig. 1h).

Water treatment had significant effects on the lifetime plant traits (Fig. 2). Total leaf blade and total plant dry weight (TLDW and TPDW), total leaf area (TLA) and leaf area ratio (LAR) gradually increased along with increase of water supply from 90 to 450 ml, and there was no significant difference between the treatments of 450 and 630 ml (Fig. 2a, c and d). Long-term water use efficiency (LWUE) showed no significant difference between the treatments of 270 and 450 ml, and no significant difference among the treatments of 90, 270 and 630 ml (Fig. 2b).

There were significantly positive correlations between P_n and g_s, E, ACE, IWUE, Ψ_l (Table 1). TPDW correlated significantly with P_n, g_s, E, ACE and Ψ_l, as well as with TLDW, TLA and LAR (Table 1). IWUE correlated significantly with P_n, E and ACE, but did not correlate with LWUE (Table 1). C_i, SLM and LWUE showed no significant correlations with any considered traits (Table 1).

Discussion

Our results suggest that increased and decreased rainfall have different effects on plant performance in terms of the instantaneous and lifetime traits. Generally, whole plants are more sensitive to changing rainfall than are plant parts. As compared with the average rainfall, decrease in water supply had more profound effects on plant growth than increase in water supply.

There have been very significant changes in the rainfall patterns over the Tibetan Plateau (Lin & Zhao 1996, Zheng *et al.* 2002, Wei *et al.* 2003), leading to changes in run-off at the local
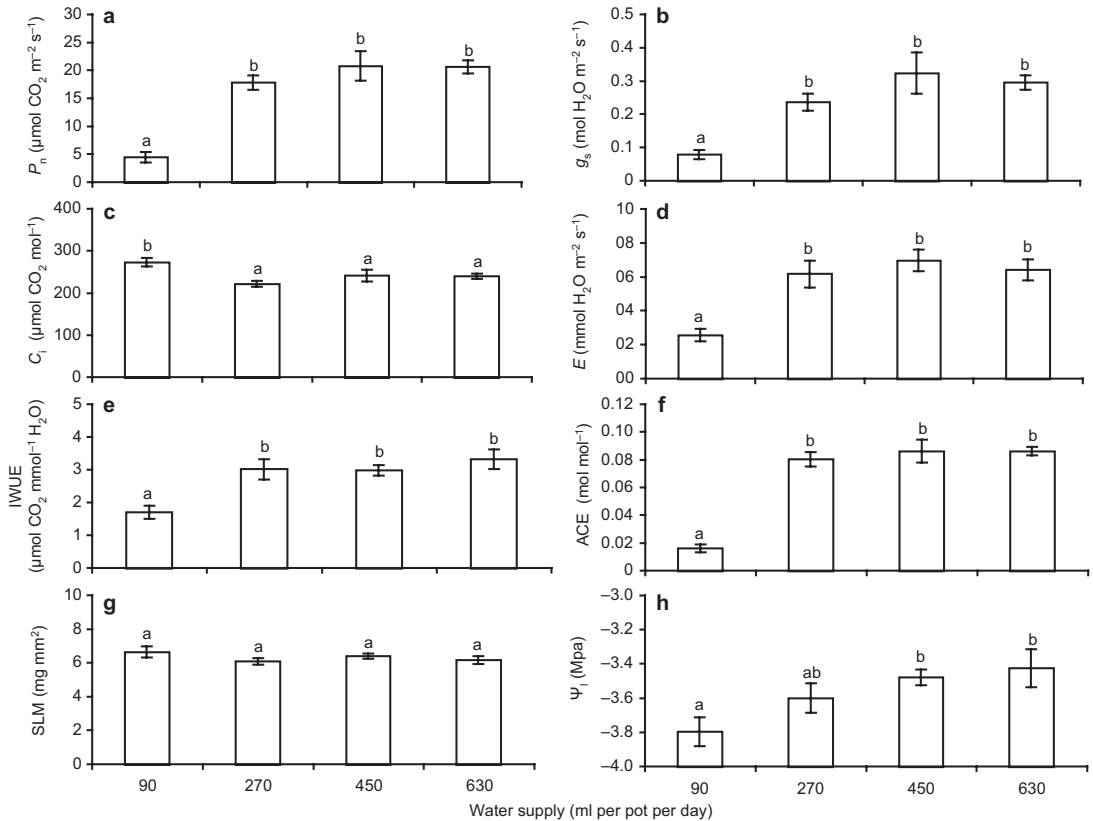
Fig. 1. Variations in (**a**) net photosynthetic rate (P_n), (**b**) stomatal conductance to water vapor (g_s), (**c**) intercellular CO_2 concentration (C_i), (**d**) transpiration rate (E), (**e**) instantaneous water use efficiency (IWUE), (**f**) apparent carboxylation efficiency (ACE), (**g**) specific leaf mass (SLM), and (**h**) leaf water potential (Ψ_l) in the leaves of *Carex stenophylloides* plants along four levels of water supply. Data are means ± S.E. (n = 3–5). The bars sharing the same letter are not significantly different at P = 0.05.

Fig. 2. Variations in (**a**) leaf blades and total dry weight per plant, (**b**) long-term water use efficiency (LWUE), (**c**) total leaf area (TLA), and (**d**) leaf area ratio (LAR) in *Carex stenophylloides* plants along four levels of water supply. Data are means ± S.E. (n = 9). The bars sharing the same letter are not significantly different at P = 0.05.
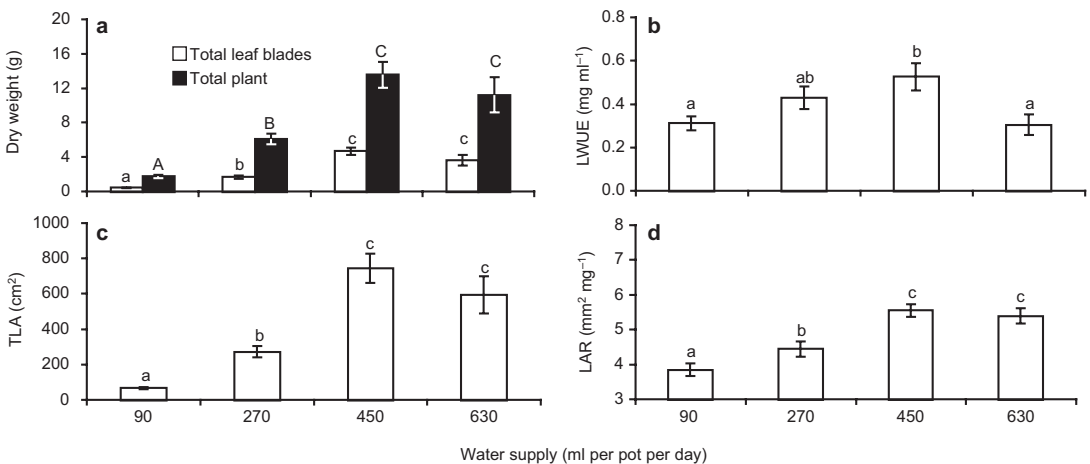
and regional scales (Watson 1999). Increased rainfall at the local scale may not alter performance of the grasses, thus the structure and function of the alpine grassland ecosystems will remain relatively unchanged. Decreased rainfall reduces leaf area and productivity, although only severely decreased rainfall markedly affects leaf gas exchange, which implies that the function of the sedge plants in alpine grassland ecosystems will be weakened, and the grasslands may evolve towards reducing dominance of the sedge plants. An earlier experiment (Shen *et al.* 2002) showed that clonal sedges in alpine meadow on the Tibetan Plateau are slightly sensitive to simulated 20%–40% changing rainfall and suggested that sedge plants would be relatively stable in changed climate. This is different from our results. Great decrease in rainfall is more likely to occur at regional scale. In the northwest Tibetan Plateau, where there is a large area of arid and semi-arid alpine steppe and desert steppe, arid climate severely affects growth and development of local plants (Zhang 1988, Li & Zhou 1998). With the increase in evapotranspiration caused by climate warming, further decreasing rainfall may destructively impact the grasses, and in turn affect the alpine steppe ecosystems, which may lead to alpine steppe ecosystems being drier and more desertified.

Net photosynthesis was significantly correlated with g_s, but not with C_i (Table 1). Lower g_s might lead to decreased P_n through limiting the supply of CO_2. If the supply of CO_2 causes the differential P_n, there must be linear relationship between P_n and C_i (Farquhar & Sharkey 1982). However, such a significant relationship was not detected in our study, indicating the role of stomatal limitation may be evened out by other factor(s) causing low P_n. Under the conditions of moderate decreased rainfall, the photosynthesis was not significantly affected (Brestic *et al.* 1995); while under severe water deficit, the photosynthetic capacity is markedly reduced due to impairment of photosynthetic components and enzymes (Farquhar *et al.* 1982, Brodribb 1996), which was reflected in a significant increase in C_i (Fig. 1c) and a sharp decrease in ACE (Fig. 1f). Therefore, we infer that lower P_n may be mainly caused by the damaged photosynthetic apparatus and decreased assimilatory capacity of mesophyll cells, in addition to stomatal closure. We should point out that gas exchange measurements in our study were made only once during the growing season. Relationships among the variables may change over time, but we selected peak growth as the most logical time to take the physiological measurements.

It is generally assumed that water deficit

Table 1. Correlation matrix of all measured traits in *Carex stenophylloides* plants subjected to four levels of water supply simulating rainfall changes. P_n = Net photosynthetic rate, g_s = stomatal conductance to water vapor, C_i = intercellular CO_2 concentration, E = transpiration rate, IWUE = instantaneous water use efficiency, ACE = apparent carboxylation efficiency, TLDW = total leaf blade dry weight, TPDW = total plat dry weight, LWUE = long-term water use efficiency, SLM = specific leaf mass, Ψ_l = leaf water potential, TLA = total leaf area, and LAR = leaf area ratio. * Correlation is significant at $P < 0.05$, ** significant at $P < 0.01$.

	P_n	g_s	C_i	E	IWUE	ACE	SLM	Ψ_l	TLDW	TPDW	LWUE	TLA
g_s	0.985*	–										
C_i	−0.824	−0.727	–									
E	0.992**	0.980*	−0.847	–								
IWUE	0.976*	0.929	−0.857	0.952*	–							
ACE	0.995**	0.965*	−0.876	0.992**	0.981*	–						
SLM	−0.777	−0.656	0.928	−0.757	−0.879	−0.825	–					
Ψ_l	0.957*	0.965*	−0.647	0.920	0.940	0.927	−0.538	–				
TLDW	0.965*	0.996**	−0.661	0.958*	0.898	0.937	−0.588	0.965*	–			
TPDW	0.980*	0.999**	−0.710	0.975*	0.920	0.958*	−0.635	0.964*	0.998**	–		
LWUE	0.404	0.494	−0.285	0.498	0.208	0.392	0.067	0.271	0.514	0.507	–	
TLA	0.864	0.937	−0.443	0.852	0.765	0.812	−0.367	0.918	0.965*	0.951*	0.547	–
LAR	0.890	0.948	−0.475	0.865	0.815	0.840	−0.440	0.956*	0.971*	0.955*	0.448	0.993**

decreases leaf net photosynthesis, stomatal conductance, transpiration rate and productivity (Turner 1986, Chaves 1991, Souza *et al.* 2004). However, our results showed that only severe water deficits significantly influenced leaf gas exchange, though plant production decreased conspicuously with gradually decreasing water supply. Plant production is related not only to photosynthesis, but also to the total number of leaves per plant, mean leaf surface area and leaf thickness (Pereira 1995). Our results indicate that biomass production (TLDW and TPDW) correlated significantly with P_n, TLA and LAR, but did not correlate with SLM (Table 1), which suggests that plant productivity mainly depends on leaf photosynthesis, total leaf area and leaf area per unit of total plant biomass, but not leaf thickness.

Increased rainfall did not significantly increase transpiration rate (Fig. 1d) or total leaf area (Fig. 2c), and did not significantly decrease TPDW (Fig. 2a), but significantly decreased LWUE (Fig. 2b). This indicates that surplus water must mainly be evaporated and the native plants may not be able to utilize increasing rainfall to produce more biomass. IWUE correlated significantly with P_n, E and ACE, which indicates that photosynthetic activity of mesophyll cells may be the primary factor to determine IWUE. Possibly due to evaporation, a plant cannot utilize the superfluous water, thus no correlation between IWUE and LWUE was detected. Although leaf water potential (Ψ_l) determined in the afternoon was very low and no marked difference was detected among the three higher water treatments (Fig. 1h), significant correlations were detected between Ψ_l and P_n, g_s, LAR, TLDW, TPDW, indicating that leaf water potential in response to rainfall changes may have certain functions on modifying photosynthesis and productivity.

Initially, water stress reduced leaf growth (Fig. 2a) but not photosynthesis (Fig. 1a). However, as the levels of water stress increase, both leaf growth and photosynthesis decline. Plants decrease photosynthesis and productivity in response to decrease in rainfall through limiting stomatal conductance, declining leaf water potential and reducing transpiration surfaces. Considering that *Carex stenophylloides* has a very wide distribution from wet through arid regions (DFRPS 2000), it may be a representa-

tive *Carex* species chosen to conduct such an experiment. The alpine grassland ecosystems dominated by sedge plants may be more sensitive to decreasing rainfall and less sensitive to increasing rainfall. Thus the structures of the ecosystems will be altered and functions will be weakened with decreasing rainfall, particularly in arid and semi-arid regions.

We should point out that the conclusion is preliminarily based on the fact that our experimental design was asymmetrical, as the treatment of 80% increased water supply was not applied. However, the present experiment simulated the range of rainfall change on the Tibetan Plateau. Moreover, the largely increased simulated rainfall will go beyond the soil field capacity, and the results would not be the real reflection if the treatment of 80% increase were applied. Since in our experiment only one species was used and there are very few data of such kind available from the Tibetan Plateau, a multi-species experiment should be conducted to better understand the changes of grassland ecosystems on the Tibetan Plateau in response to rainfall change.

Acknowledgements

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