Plasticity of the clonal growth in the wetland sedge *Carex brevicuspis* along a small-scale elevation gradient in Dongting Lake wetlands, China

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To determine the growth strategies of the clonal wetland sedge *Carex brevicuspis* under different conditions, we measured the ramet density and biomass; numbers of total rhizomes (TR), long rhizomes (LR), and short rhizomes (SR); and environmental factors along a small-scale elevation gradient (23–26 m) in Dongting Lake wetlands, China. Ramet density and biomass were higher at low elevations as compared with those at intermediate and high elevations. There was no significant difference in the number of SR per ramet among the three elevations. However, the number of LR per ramet was higher at high and intermediate elevations as compared with that at low elevation. These results indicate that *C. brevicuspis* can adapt to increasing environmental stress (i.e., decreasing soil moisture contents) along an elevation gradient by producing more long rhizomes. Plasticity of the *C. brevicuspis* clonal growth through the modification of its meristem allocation patterns may allow for wide distribution of the species.

Introduction

Clonal plants are widespread in many ecosystems, including grasslands, wetlands, and even forests (Harper & Ogden 1970, Nabe-Nielsen & Hall 2002, Klimešová & Klimeš 2007). Many rhizomatous or stoloniferous clonal plants exhibit three growth strategies (guerrilla, phalanx, and mixed), which represent different spatial arrangements of ramets arising from differ-

ent below-ground meristems, i.e., rhizomes or other perennating organs (Lovett Doust 1981, Bernard 1990). Plants with a guerrilla growth strategy produce long rhizomes or stolons that spread ramets some distance from the parent shoot, allowing them to escape poor conditions and to obtain more resources in favorable patches (Hutchings & de Kroon 1994, de Kroon & Hutchings 1995, Humphrey & Pyke 1998, von Kleunen & Fischer 2001). In contrast, plants

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with a phalanx growth strategy produce short rhizomes or stolons to form clumps of ramets around the parent shoot, allowing them to better utilize resources and thus consolidate or maintain their place in favorable patches (Lovett Doust 1981, Macdonald & Lieffers 1993, Song & Dong 2002). Clonal plants usually modify their growth strategy by adjusting meristem allocation patterns to adapt to stressful or heterogeneous environments (de Kroon & Schieving 1991, Bonser & Aarssen 1996, 2003, Dalgleish & Hartnett 2006, Klimešová & Klimeš 2007, Zhang *et al.* 2008, Chen *et al.* 2011).

It is well known that modifications of phalanx–guerrilla growth strategies is usually triggered by heterogeneity of soil nutrients (Macdonald & Lieffers 1993, de Kroon & Hutchings 1995, Hutchings & Wijesinghe 1997, Gough *et al.* 2012), and a trade-off between phalanx and guerrilla growth strategies has also been detected under different nutrient regimes (Ye *et al.* 2006). However, in freshwater wetlands or floodplains, the nutrient status may not be a limiting factor for plant growth, as seasonal flooding tends to bring a plentiful supply of nutrients (Odum *et al.* 1979, Megonigal *et al.* 1997). Instead, in these habitats, plant growth and distribution are closely related to water-level gradients, which are closely associated with the elevation at which the plants occur (Menges & Waller 1983). Soil moisture content gradually decreases with increasing elevation, directly affecting aeration and the physical structure of the soil which, in turn, determine species distribution boundaries (Mal *et al.* 1997, Castelli *et al.* 2000, Hefting *et al.* 2004, Dwire *et al.* 2006). For wetland clonal sedges, both low-elevation (wet meadow) and high-elevation (dry meadow) environments represent stressful conditions for plant growth and reproduction due to the anaerobic environment at low elevations, and drought and compacted soil at high elevations; in contrast, intermediate-elevation (mesic meadow) environments provide favorable conditions, e.g., a relatively moderate soil moisture content, soil aeration, and soil bulk density (Castelli *et al.* 2000, Hefting *et al.* 2004, Wang *et al.* 2008).

It has been documented that a change in strategy from phalanx to guerrilla is an effective way to adapt to stressful conditions, e.g., high

sedimentation or low nutrient availability (Ye *et al.* 2006, Chen *et al.* 2011). However, it remains unclear whether the phalanx–guerrilla growth strategy continuum is effective in coping with increasing environmental stress in flooded wetlands caused by decreasing soil moisture with increasing elevation.

The sedge *Carex brevicuspis* is a typical rhizomatous clonal plant that is distributed across a wide small-scale elevation gradient (23–30 m a.s.l.) in Dongting Lake wetlands, China (Wu *et al.* 2005). The below-ground meristems of *C. brevicuspis* consist of two types of rhizomes: long rhizomes (LR) and short rhizomes (SR) (Bernard 1990, Chen *et al.* 2011). In this study, we investigated the effect of environmental conditions on rhizome production in *C. brevicuspis* at three elevations (low, 23–24 m; intermediate, 24–25 m; high, 25–26 m) in Dongting Lake wetlands as an initial step to understanding the clonal growth strategies of this species in freshwater wetlands. Since SR are better at utilizing resources in favorable patches and LR may be more capable of obtaining resources under stressful conditions, we hypothesized that more SR would be produced by plants at intermediate elevations where conditions are favorable, whereas more LR would be produced at high and low elevations where soil moisture contents are lower and higher, respectively. Thus, plasticity of the clonal growth of *C. brevicuspis* through the modification of its meristem allocation pattern may contribute to the species' adaptation to different soil moisture levels along small-scale elevation gradients in wetlands.

Material and methods

Study species

Carex brevicuspis (Cyperaceae), a dominant herbaceous species, grows in a modular pattern and reproduces vegetatively by rhizomes (Bernard 1990). The pseudo-culm of the plant, which is made up of a series of overlapping leaf sheaths, is usually 20–55 cm in height. The below-ground rhizome consists of two distinct types of rhizomes, i.e., long rhizomes (LR; usually 2–25 cm long) and short rhizomes (SR;

usually < 1 cm long and clumping around the ramets). Plants of this species form communities that are either mono-dominant or co-dominant with other *Carex* species or *Miscanthus sacchariflorus* (Chen *et al*. 2011). Following the periodic flooding of Dongting Lake during May–October, *C. brevicuspis* displays rapid vegetative growth from October to December, remains relatively dormant from January to February, sprouts in March, and flowers and fruits from April to May. *Carex* vegetation is of particular importance in the maintenance of ecosystem processes in Dongting Lake wetlands (Chen *et al*. 2011).

Site description

Our study area is located at East Dongting Lake, Hunan Province, China. This region has a north subtropical monsoon climate. The average annual air temperature is 17 °C and the average annual precipitation is 1302 mm (Xie & Chen 2008). Since Dongting Lake is connected to the Yangtze River, its water level usually fluctuates seasonally: flooding occurs from May to September and water recedes again from October to May of the following year, when the shores become exposed. *Carex brevicuspis* is usually distributed adjacent to the waterbody and extends to the embankment, along a mild slope of 5–10°, which provides an ideal elevation gradient for this investigation. We selected Junshan (29°22´16.1´´N, 112°59´28.4´´E), Matang (29°12´06.0´´N, 113°04´52.3´´E), and Dingzidi (29°25´25.8´´N, 112°56´45.8´´E) as our study sites, because they all have similar elevations and slopes, and a vegetation that is primarily dominated by *C. brevicuspis*.

Elevation gradient and sample transects

In this study, we separated the elevation gradient into three categories: high elevation (25–26 m), a relatively dry environment due to a deep below-ground water table; intermediate elevation (24–25 m), a favorable environment for plant growth due to its moderate below-ground water table; and low elevation (23–24 m), adjacent to the waterbody. In total, nine transects (150 × 20 m) were run parallel to the waterbody (one per elevation per site) (Table 1). At each site, the transects were 500 m apart.

Sampling methods

Ramets of *C. brevicuspis* were sampled every two months from November 2010 to May 2011 (representing four different stages of the growing season), using a permanent plot sampling method. In November 2010, three permanent mono-dominant plots (2 × 2 m) were established 50 m apart on each transect at each site. In addition to *C. brevicuspis*, plots contained some low annual herbs, but no other perennial species or tall herbs, and shoots of *C. brevicuspis* accounted for more than 95% of above-ground shoots in each plot. The corners of each plot were marked with durable plastic tubes hammered into the soil. On each sampling occasion, one square (25 × 25 cm) was randomly excavated in each permanent plot, giving a total of 27 squares being sampled per sampling occasion. In each square, all living (> 50% green, potentially photosynthetic tissue) above-ground ramets were counted, clipped and dried in an oven at 60 °C for 48 hours to obtain dry weight. Ramet biomass was

Table 1. Elevation, depth of the below-ground water table, and soil characteristics for each elevation category. The data are means ± SEs (n = 36). Different letters indicate significant differences between elevations ($p < 0.05$, Tukey's HSD).

Elevation category	Elevation (m)	Below-ground water table (cm)	Soil moisture content (%)	Bulk density (g cm^{-3})	Soil organic matter (SOM) (%)	pH
Low	23–24	53.5 ± 10.5[c]	42.1 ± 2.2[a]	0.79 ± 0.02[b]	4.4 ± 0.3[a]	5.8 ± 0.1[a]
Intermediate	24–25	92.9 ± 11.3[b]	35.3 ± 0.5[b]	0.80 ± 0.03[b]	3.8 ± 0.1[b]	6.1 ± 0.2[a]
High	25–26	144.8 ± 11.1[a]	32.9 ± 0.3[b]	0.93 ± 0.02[a]	4.7 ± 0.1[a]	6.0 ± 0.2[a]

defined as the dry weight of total alive above-ground ramets per m^2, and ramet density was defined as the number of ramets per m^2. Undisturbed soil within squares was then excavated to a depth of 15 cm (Benson *et al.* 2004) using a shovel, and was immediately transported to the laboratory for collection of the rhizomes. In addition, from an area adjacent to each square, soil samples were collected from 10 cm depth using two cutting rings: one for measuring soil moisture content and bulk density, and the other for measuring soil organic matter content (SOM) and pH. On each sampling occasion, the depth of the below-ground water table was also measured at a single point on each transect by digging a hole in the ground, and after two hours, when the water table stabilized, measuring the distance from the water surface to the ground surface.

Sample processing

Below-ground tissue samples were carefully washed free of soil to protect the integrity of the rhizomes. Rhizomes were then classified into two types, according to Chen (2011): (1) short rhizomes (SR), which produce the daughter ramet clumping around the parent shoot with a shortened spacer length (< 1 cm); and (2) long rhizomes (LR), which grow horizontally and produce the daughter ramet at some distance (2–25 cm) from the parent shoot. For each square, rhizomes of each type were counted, and these values were then added together to give the total number of rhizomes (TR) per ramet. The numbers of LR, SR, and TR per ramet served as indexes of the ability of the population to carry out vegetative propagation (Wang *et al.* 2008), while the proportions of LR and SR to TR (LR/TR × 100% and SR/TR × 100%, respectively) served as indexes of guerilla and phalanx growth strategies, respectively (Chen *et al.* 2011).

Fresh weights of the soil samples were measured using an electronic balance (Ohaus Scout SE, accuracy 0.01 g), after which the soil samples were dried at 105 °C for 48 hours to obtain the soil moisture content, which was defined as: $(W - D)/W \times 100\%$, where W is the soil fresh weight and D is the soil dry weight. Soil bulk density was defined as soil dry weight per cm^3.

The soil from the other cutting ring was air-dried, and then powdered through a 60-mesh screen to measure SOM and through a 20-mesh screen to measure pH. SOM was determined using the potassium dichromate method (Yeomans & Bremner 1988). For pH measurements, 10 g of air-dried soil was mixed of with 25 ml of CO_2-free water, stirred for one minute, and pH of the mixture was measured with pH meter (Mettler Toledo FE20).

Data analysis

We tested the significance of differences in the numbers of LR, SR, and TR per ramet, ramet density, and ramet biomass at different elevations and during different sampling periods using linear mixed models, with elevation and sampling period included as main factors, and sample site included as a random factor (McKone & Lively 1993). Multiple comparisons of means between elevations were performed using Tukey's test. Homogeneity of variances was tested using Levene's test, and the data were $\log_{10}$-transformed where necessary to reduce the heterogeneity of variances. The relationships between the numbers of LR, SR, and TR per ramet and soil environmental factors in November, January, and March were analyzed using a stepwise multiple linear regression. To account for multiple comparison effect, where needed significance levels (p) were adjusted using the Bonferroni method. All statistical analyses were performed using the statistical software SPSS ver. 18.0 (SPSS Inc., USA).

Results

Environmental characteristics and elevation

During all four sampling periods, the below-ground water table was significantly deeper at high elevations than at intermediate and low elevations (all differences being significant, *see* Table 1). Soil moisture content was significantly higher at low elevations than at intermediate and high elevations (Table 1), while soil bulk den-

sity was significantly higher at high elevations than at intermediate and low elevations (Table 1). SOM was significantly higher at low and high elevations than at intermediate elevations (Table 1). There was no significant difference in soil pH among the three elevations (Table 1).

Ramet density, biomass, and elevation

Ramet density and biomass were significantly affected by elevation in all sampling periods, with higher ramet densities (1507–3333 per m^2) and biomasses (327–999 g per m^2) at low elevations, and relatively lower densities (952–2080 per m^2) and biomasses (142–773 g per m^2) at both intermediate and high elevations (Fig. 1). Ramet density and biomass also varied significantly between the four sampling periods (Table 2 and Fig. 1), with densities being at their lowest in November and then increasing from January to May, and biomasses being at their lowest in January and then increasing from March to May (Fig. 1).

Rhizome production and elevation

There was no significant difference in the number of TR and SR per ramet among the three elevations in any of the sampling periods except for January, when the numbers were significantly higher at high elevations (65.58 × 10^{-2} per ramet) than at intermediate (34.43 × 10^{-2} per ramet) and low elevations (31.95 × 10^{-2} per ramet) (Table 2, Fig. 2A and B). In contrast, the number of LR per ramet was significantly higher at high elevations (2.37–10.01 × 10^{-2} per ramet) and intermediate elevations (2.85–4.21 × 10^{-2} per ramet) than at low elevations (0.66–2.55 × 10^{-2} per ramet) in all sampling periods except for May (Fig. 2C), when very few rhizomes were produced at the three elevations.

Rhizome production and soil characteristics

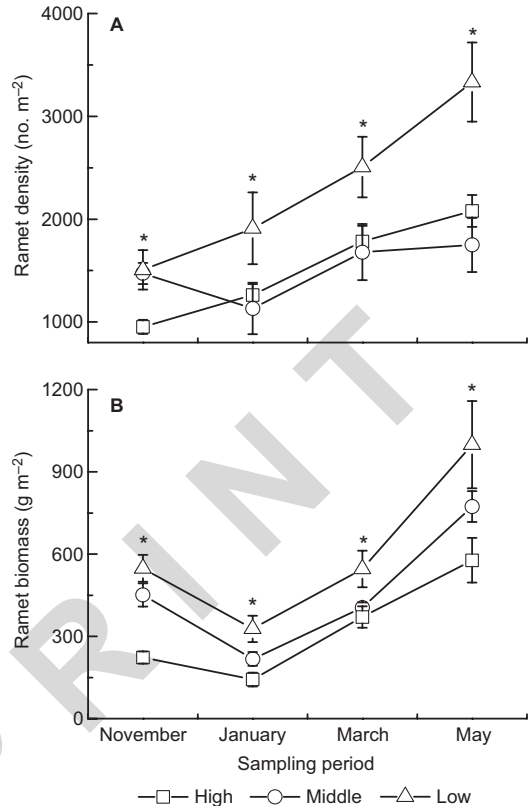Since hardly any rhizomes were produced in May, we did not analyze the relationship

Fig. 1. *Carex brevicuspis* ramet (**A**) density and (**B**) biomass at three elevations in four sampling periods. The data are means ± SEs (*n* = 9). * *p* < 0.05.

between rhizome production and soil characteristics in that month. The number of LR per ramet was mainly affected by soil water moisture and pH in November and March, and by bulk density in January (Table 3). The numbers of SR and TR

Table 2. Linear mixed models analysis (*F* values) of ramet density, and the numbers of LR, SR, and TR per ramet. Sampling period and elevation were included as fixed factors, and site was included as a random factor.

Dependent variables	Sampling period (S)	Elevation (E)	S × E
Ramet density	12.22***	8.21**	2.25*
Ramet biomass	46.04***	24.95***	1.36ns
TR per ramet	31.58***	3.21*	2.86*
SR per ramet	27.16***	2.55ns	3.06*
LR per ramet	19.07***	18.42**	9.02**
df	3	2	6

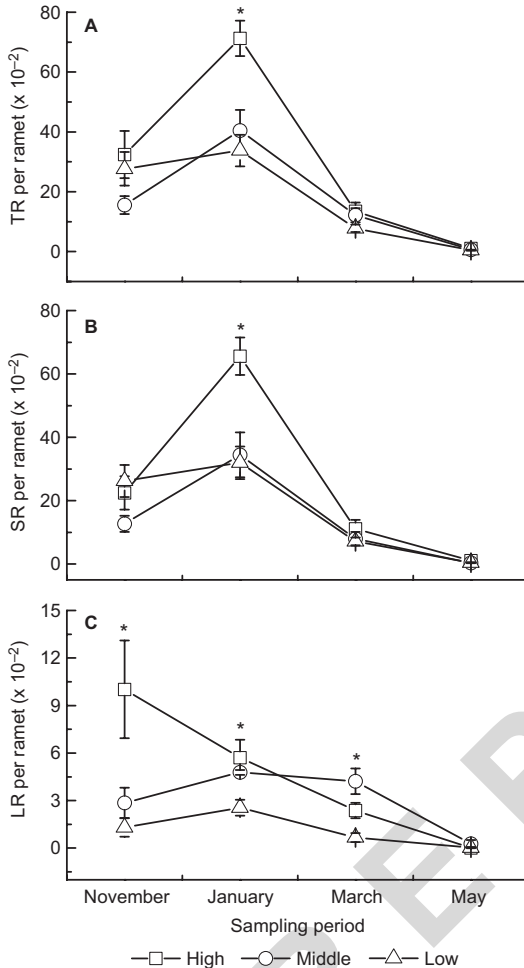***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, ns$p > 0.05$.

Fig. 2. Numbers of (**A**) all rhizomes (TR) per ramet, (**B**) short rhizomes (SR), and (**C**) long rhizomes (LR) per ramet per ramet in *Carex brevicuspis* at three elevations in four sampling periods. The data are means ± SEs (*n* = 9). * *p* < 0.05.

per ramet were affected by soil moisture content only in March, by bulk density in January, and by soil organic matter in November (Table 3).

Growth strategy and elevation

Since very few rhizomes were produced in May (Fig. 2), we only used data from November, January, and March to analyze the proportion of LR to TR at the three elevations. In November, the proportion of LR to TR was highest at high elevations (32.21% ± 6.49%), intermediate

at intermediate elevations (16.06% ± 4.09%), and lowest at low elevations (9.75% ± 5.24%), whereas the proportion of SR to TR showed the opposite trend, being highest at low elevations (90.25% ± 5.24%) and lowest at high elevations (67.79% ± 6.49%) (Fig. 3A). However, in January and March, the proportion of LR to TR was higher at intermediate elevations (17.6%–39.3%) than at low elevations (5.63%–10.23%) (Fig. 3B and C).

Discussion

The number of SR per ramet was not influenced by elevation in any month except for January, when the numbers were higher at high elevations than at intermediate and low elevations. In contrast, the number of LR per ramet was higher at intermediate and high elevations than at low elevations. These results contradict our original hypothesis that more SR would be produced by plants at intermediate elevations where conditions are expected to be more favorable, whereas more LR would be produced at high and low elevations in response to stressful conditions. In *Carex* populations, environmental stress may increase with increasing elevation, e.g., due to an increase in below-ground water table depth and a decrease in soil moisture, which may directly trigger *C. brevicuspis* to produce more LR to spread daughter ramets into favorable patches in the microtopographically heterogeneous environment. We also found that throughout the growing season, ramet density and biomass were higher at low elevations than at intermediate and high elevations. These results suggest that low elevations may in fact be favorable for plant growth, while intermediate and high elevations represent stressful habitats. It is possible that *C. brevicuspis* has successfully adapted to wet conditions through the well-developed aerenchyma in its root system (Moog 1998, Visser *et al.* 2000, Qin *et al.* 2010), allowing this species to grow better under high soil moisture conditions (Smith & Huston 1989).

Many clonal plants can spread their daughter ramets away from the parent shoot by producing elongated rhizomes or stolons in patchy or stressful habitats, e.g., low nutrient levels,

shaded or cool soils (Macdonald & Lieffers 1993, Hutchings & de Kroon 1994, Ye *et al*. 2006). In *Carex* stands, the habitat is usually highly heterogeneous across all elevations due to the habit of many sedge species to form tussocks or microtopographical heterogeneity (Vivian-Smith 1997, Lawrence & Zedler 2011). We found that more LR were produced at intermediate- and high-elevation sites in response to decreasing soil moisture content or increasing bulk density, which may be an effective strategy to escape stressful conditions and find more favorable patches. Thus, the decreasing soil moisture content and increasing bulk density with increasing elevation may determine the upper boundary of this species' distribution. We also found that rhizomes of *C. brevicuspis* were mainly produced from November (after flooding) to January (winter). The higher rhizome density (particularly of short rhizomes) in January may be caused by energy translocation into below-ground organs to survive cold winter and prepare for spring sprouting in the following year (Bernard 1990).

The proportion of LR to TR was higher at intermediate and high elevations than at low elevations in November, January and March, indicating modification of the clonal growth strategy with increasing environmental stress along an elevation gradient. The proportion of SR to TR decreased with increasing elevation, indicating that there is a trade-off between the phalanx and guerilla growth forms in different soil
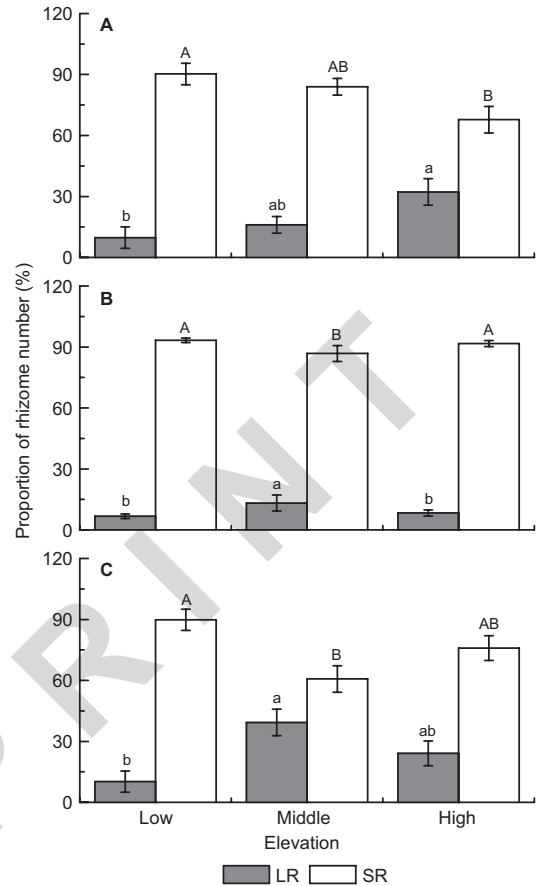

Fig. 3. The proportion of long rhizomes (LR) and short rhizomes (SR) to total rhizomes (TR) at three elevations in (**A**) November, (**B**) January and (**C**) March. The data are means ± SEs ($n = 9$). Different letters indicate significant differences between elevations ($p < 0.05$, Tukey's HSD).

Table 3. The standardized coefficients (β values) of the multiple linear regression between soil moisture content, bulk density, soil organic matter content, and pH; and the numbers of LR, SR, and TR per ramet for the three sampling periods ($n = 27$).

Month		β values				Adj. r^2
		soil moisture	bulk density	soil organic matter	pH	
November	LR per ramet	−2.10*	−	−	1.72*	0.60
	SR per ramet	−	−	0.91*	−	0.82
	TR per ramet	−	−	0.91*	−	0.83
January	LR per ramet	−	0.90*	−	−	0.80
	SR per ramet	−	0.90*	−	−	0.82
	TR per ramet	−	0.91*	−	−	0.84
March	LR per ramet	−1.37*	−	−	2.07*	0.58
	SR per ramet	0.82*	−	−	−	0.67
	TR per ramet	0.86*	−	−	−	0.72

*$p < 0.016$ (after Bonferroni correction).

moisture conditions along an elevation gradient. This result is consistent with the findings of an indoor experiment on *C. brevicuspis* growing in a sedimentation gradient (Chen *et al.* 2011), and on *Leymus secalinus* under different soil nutrient conditions (Ye *et al.* 2006). Through guerilla growth strategy plants spread their modules and/ or ramets more widely than through phalanx growth strategy, enabling them to escape less favorable habitats, which may further facilitate acclimation of *C. brevicuspis* to intermediate- and high-elevation conditions (Song & Dong 2002, Ye *et al.* 2006, Thomas & Hay 2010). Thus, plasticity of this species' growth strategy through the modification of its meristem allocation pattern may contribute to the wide distribution of *C. brevicuspis* along elevation gradients in wetlands.

Acknowledgements

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