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A change from phalanx to guerrilla growth form is an effective strategy to acclimate to sedimentation in a wetland sedge species *Carex brevicuspis* (Cyperaceae)

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ABSTRACT

The rhizomatous sedge *Carex brevicuspis* can produce clumping ramets from shortened rhizomes (phalanx) and spreading ramets from elongated rhizomes (guerrilla) to form a combined clonal growth form. In this paper, changes in clonal growth and biomass allocation pattern of *C. brevicuspis* in response to sedimentation were studied. Four sedimentation depths (0, 3, 6, and 9 cm) were applied to 48 ramets in a randomized block design. Plants were harvested after 20 weeks. With increasing sedimentation depth, the proportion of spreading ramets to total ramets increased from 19.6% in 0 cm to 92.9% in 9 cm sedimentation treatments, whereas that of clumping ramets decreased from 80.4% to 7.1%, indicating a change of clonal growth form from phalanx to guerrilla as a response to sedimentation. With increasing sedimentation depth, biomass allocation to shoots and roots did not change, but rhizome mass ratio increased from 2.7% in 0 cm to 7.2% in 9 cm sedimentation treatments, suggesting that production of long rhizomes changes biomass allocation pattern. The results show that plasticity of clonal growth forms, by which more spreading ramets are produced, is an effective strategy to avoid sedimentation stress under our experimental conditions.

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Introduction

Clonal plants are widespread in all biomes and biogeographical regions, especially in cold, wet or shaded environments (Klimeš et al., 1997). The growth strategies of clonal plants can be categorized as phalanx type and guerrilla type, which represent the endpoints in a continuum of possible growth forms (Cheplick, 1997; de Kroon and Hutchings, 1995; Lovett-Doust, 1981). Clonal plants with the phalanx strategy produce a compact structure of closely spaced ramets, termed clumping ramets or tillers, while those with guerrilla strategy produce a loosely arranged group of widely spaced ramets, termed spreading ramets or tillers (Bernard, 1990; Cheplick, 1997; Lovett-Doust, 1981).

The two growth strategies may have special importance to the ecology and evolution of clonal plant populations (Cheplick, 1997). Guerrilla strategy enables plants to escape from less favorable patches where resource levels are low or where competitive stress is high, whereas phalanx strategy enables plants to con-

solidate or maintain favorable patches (Bernard, 1990; Cheplick, 1997; de Kroon and Hutchings, 1995; Humphrey and Pyke, 1998, 2001; Lovett-Doust, 1981). Consequently, the guerrilla growth form is very common in early successional stages and in heterogeneous habitats, while the phalanx growth form is more favored in late successional stages and in homogeneous, predictable habitats (Lovett-Doust and Lovett-Doust, 1982; Schmid and Bazzaz, 1987).

Growth form of a plant species is genetically determined but can be modified by its environmental conditions (Amiaud et al., 2008; Cheplick, 1997; Ikegami et al., 2007; Lovett-Doust, 1981; Ye et al., 2006). In the perennial grass *Leymus secalinus*, the plants are more phalanx-like under high nutrient supply and more guerrilla-like in low nutrient conditions (Ye et al., 2006). In tidal wetlands, *Elymus repens* changed its colonizing strategy from a guerrilla strategy to a phalanx strategy when it was released from grazing pressure and submitted to competitive stress (Amiaud et al., 2008). To date, most studies examined the changes of clonal growth forms in response to resource availability or biotic competition (Cheplick, 1997; Navas and Garnier, 1990; Schmid and Harper, 1985; Ye et al., 2006). However, few studies examine the plasticity of growth forms to abiotic stress, such as sedimentation, a common phenomenon in coastal areas and wetland ecosystems.

Sedimentation decreases the concentration of oxygen in the root zone and creates a physical overburden over apical meris-

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tems of buried plants (Maun, 1998). Caulescent grasses emerge by an increase in the number of nodes per culm and the elongation of internodes (Maun, 1998). Elongation of petioles, leaf sheaths, leaves, spacers and rhizomes, as well as plagiotropic growth has been recorded for non-stem plants to acclimate to sedimentation stress (Li and Xie, 2009; Maun, 1998; Yu et al., 2004). Here, we investigated the plasticity of clonal growth forms in a rhizomatous sedge *Carex brevicuspis*, as an initial step towards understanding the growth strategies that plants use to adapt to abiotic stress. *C. brevicuspis* is one of the dominant species in the Dongting Lake wetland, the second largest freshwater lake in China, where sediment can accrete 3–7 cm annually during flooding time (Li et al., 2008). *C. brevicuspis* produces both spreading and clumping ramets, resulting in a combined growth form. In this growth form, spreading ramets are first initiated at the end of long rhizomes, then, clumping ramets developed from short rhizomes of spreading ramets (Bernard, 1990). Specifically, we tested the following hypotheses: (1) the proportion of spreading ramets and spacer length will increase with increasing sedimentation depth, i.e. a guerrilla strategy will be favored in conditions with sediment burial since guerrilla strategy has an advantage in escaping from stressful environment; (2) biomass allocation to rhizomes will increase with burial depth because of the demand of producing long rhizomes to form guerrilla ramets. To test the two hypotheses, four levels of sedimentation were applied to *C. brevicuspis* plants to investigate the changes of clonal growth forms and biomass allocation.

Materials and methods

The study species

The genus *Carex* L. is made up of about 2000 species and some are particularly important in wetlands (Bernard, 1990). *Carex brevicuspis* (Cyperaceae) is a perennial rhizomatous sedge distributed in eastern mainland China and Taiwan (Delectis Florae Reipublicae Popularis Sinicae Agendae Academiae Sinicae Edita, 2000). The pseudoculm of the plant, made up of a series of overlapping leaf sheaths, is usually 20–55 cm in height. This species forms monodominant communities or is co-dominated with other *Carex* species or *Miscanthus sacchariflorus*. *C. brevicuspis* is flowering and fruiting from April to May in the Dongting Lake wetland. However, seedlings are scarce in the field because the plant recruits mainly by producing vegetative ramets from rhizomes (Hou et al., 2009). The plants can produce two types of ramets, i.e. clumping ramets produced from buds of shortened rhizomes and spreading ramets from buds of long rhizomes.

Experimental design

Plants were excavated (about 5 m²) from Chunfeng Village of East Dongting Lake wetlands on 31st March 2009. Plants were cut into small patches and transported to the greenhouse (ca. 50% of full sun) of Institute of Subtropical Agriculture, the Chinese Academy of Sciences. Plant fragments with roots were placed into plastic buckets, which were watered every day, to germinate new ramets. On 17th May, 48 ramets with similar size (5–8 leaves and ca. 22 cm in height) were selected and planted in plastic containers (18 cm in height and 25 cm in diameter, one plant per container), which were filled with 6 cm soil (containing 1.20% organic matter, 0.09% total nitrogen, and 0.06% total phosphorus). The soil was collected from the upper layer of natural *Carex* vegetation stands in Junshan, East Dongting Lake. Every four containers with similar plant size were placed in randomized pattern into one bigger plastic tank (70 cm × 52 cm × 37 cm) to form a block. Water level was maintained at 6 cm in the tank (surface for the plant). On 29th May,

0 cm (referred as control), 3 cm, 6 cm, or 9 cm sediment were added to the plants in each block. The sediment consisted of 1.20% organic matter, 0.09% total nitrogen, and 0.06% total phosphorus. The replication was 12. Tap water was supplied as needed and surplus water was removed after rains to control water level. We checked the plants each week and marked new ramets with plastic tags.

Harvest and measurement

The plants were harvested on 16th October, 20 wk after the treatment. The plants were carefully removed from the containers to keep the connection between ramets. Then, the plants were cleaned with tap water and brought to laboratory for measurement. Number of ramets produced by each original plant and the distance from each ramet to the original plants (spacer length) were measured. Each plant was then separated into shoots, roots and rhizomes. Biomass of each plant part was measured after drying at 80 °C for 48 h in an oven. Clumping ramets were defined as ramets produced from shortened rhizomes (spacer length usually less than 1 cm), while spreading ramets were those produced from the distal part of long rhizomes. We define plants with any live aboveground material as live.

Statistics

The data were analyzed by using General Linear Model (GLM) due to unbalanced sample size among treatments (some buried plants died during the experiment). Least-significant difference (LSD) tests were used to investigate the differences among the four burial treatments.

Results

Plant survival and biomass allocation

Upon sediment burial, partially buried leaves withered gradually from the tips and no elongation of leaf sheaths or leaves was observed. New leaves emerged from apical meristems of the original shoots and new ramets emerged from rhizomes of the original plants. All individuals survived in 0 cm burial, 91.7% of the plants in 3 cm burial, 83.3% in 6 cm burial, and 58.3% in 9 cm burial. For the surviving plants, total dry biomass and shoot, root, or rhizome mass did not differ significantly among the four burial treatments ($P > 0.05$). Biomass allocation to shoots and roots did not differ significantly, whereas rhizome mass ratio increased with increasing burial depth. The biomass allocation to rhizomes with 9 cm burial was significantly higher than that in the 0 cm burial treatment (7.2% vs. 2.7%; $P < 0.05$, Fig. 1).

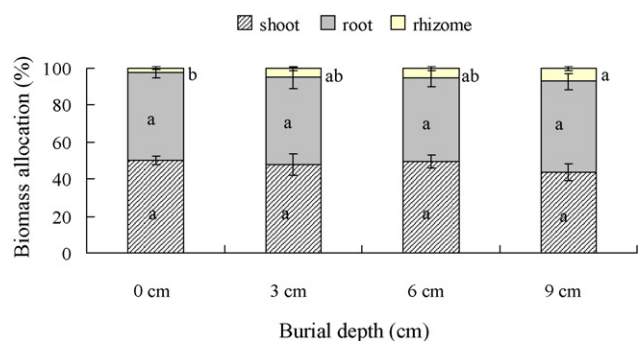


Fig. 1. Percentage biomass allocation in *Carex brevicuspis* under four sediment burial treatments. For each compartment, standard error bars sharing the same letters are not significantly different at $P > 0.05$.

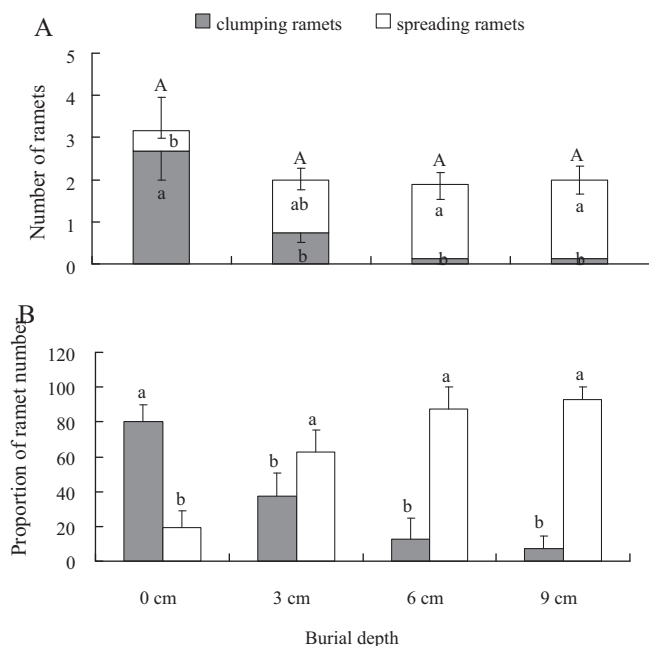


Fig. 2. (A) Number of spreading and clumping ramets and (B) the proportion of spreading and clumping ramets to total number of ramets in *Carex brevicuspis* under the four sediment burial treatments. For each compartment, standard error bars sharing the same letters are not significantly different at $P > 0.05$.

Clumping vs. spreading ramets produced by the initial plant

The total number of new ramets produced by the surviving plants did not differ among treatments (Fig. 2A). However, the number of spreading ramets increased with burial depth, whereas the number of clumping ramets decreased ($P < 0.05$, Fig. 2A). The proportion of spreading ramets to total ramets increased with burial depth, while that of clumping ramets decreased ($P < 0.05$, Fig. 2B). Without sediment burial, 19.6% of the ramets produced by the original plants were spreading ones. With 3 cm burial, the proportion of spreading ramets increased (62.5%). With 6 or 9 cm burial, plants mainly produced spreading ramets (87.5% and 92.9%, respectively). The proportion of spreading or clumping ramets was not significantly different among 3 cm, 6 cm and 9 cm burial treatments.

Spacer length

For the surviving plants, mean spacer length between original plants and ramets increased with burial depth (Fig. 3). Mean spacer length was 6.6 cm in the 9 cm burial but only 1.42 cm in the 0 cm burial treatments. Mean spacer length for the plants in 6 cm or 9 cm burial was significantly longer than that in 0 or 3 cm burial treatments ($P < 0.05$, Fig. 3). There were insignificant differences

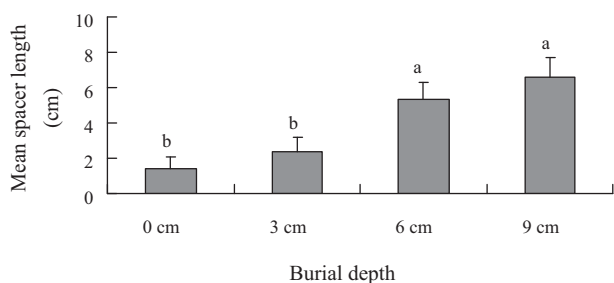


Fig. 3. Mean spacer length in *Carex brevicuspis* under four sediment burial treatments. Standard error bars sharing the same lower-case letters are not significantly different at $P > 0.05$.

between 6 and 9 cm treatments and between 0 and 3 cm treatments ($P > 0.05$, Fig. 3).

Discussion

In response to sediment burial, *C. brevicuspis* cannot emerge by accelerated vertical growth as do caulescent species, or by the elongation of leaf sheaths or leaves found in other non-stem species (Maun, 1998). A change from phalanx to guerrilla growth form is the primary strategy used by *C. brevicuspis* to escape from sedimentation stress.

Growth forms of *Carex* species are determined in large part by the behavior of the rhizomes produced (Bernard, 1990). Two rhizome types (long and short) give rise to three major growth form patterns in *Carex* species: matted type (guerrilla strategy), clumped type (mixed strategy) and tussock type (phalanx strategy): Bernard (1990). *C. brevicuspis* belongs to the clumped type which has a mixed strategy. With increasing sedimentation depth, mean spacer length between the original plant and the ramets increased. Consequently, a relatively loosely-arranged architecture is formed under sedimentation conditions, suggesting a plastic modification from a phalanx towards a guerrilla growth form (Cheplick, 1997).

Ye et al. (2006) suggested that a trade-off between phalanx and guerrilla growth forms exists in *Leymus secalinus*, a rhizomatous grass with a combined growth form, under different nutrient supplies. With higher nutrient supply, *L. secalinus* produced a higher proportion of clumping ramets and a lower proportion of spreading ramets (more phalanx-like) making good use of locally abundant resources (Ye et al., 2006). In response to sedimentation stress, we also found a trade-off between the two growth forms in *C. brevicuspis*, i.e. the proportion of spreading ramets in *C. brevicuspis* increased greatly (more guerrilla-like), whereas the proportion of clumping ramets decreased sharply with increasing sediment burial. The result supports our first hypothesis that the guerrilla growth form has an advantage in escaping from sedimentation stress and will be favored under such conditions.

Biomass allocation to shoots and roots did not differ significantly among the four burial treatments, whereas biomass allocation to rhizomes increased with increasing sediment burial, due to their increased lengths. This result supports our second hypothesis, which predicts that production of long rhizomes involves more energy costs. Upon sedimentation, especially when most of the green plant parts were buried, the energy needed for rhizome growth and elongation mainly depends on carbohydrate reserves. Cabaço and Santos (2007) documented the translocation of nutrients from leaves to rhizomes to meet the energetic requirement of rhizome growth. In the vegetatively stem-less tussock plant *C. brevicuspis*, apical meristems are near or below the soil surface, so they are more easily buried by sedimentation than this is the case in other species. Therefore, this species needs to allocate more energy and substances to produce costly longer rhizomes to escape sedimentation stress. With 3 cm of sedimentation, the survival rate of *C. brevicuspis* decreased and growth forms significantly changed, indicating that this species is not very tolerant to sedimentation. This is consistent with our field observation that *C. brevicuspis* does not grow vigorously in areas with high rates of sedimentation such as the innermost parts of banks in the Dongting Lake (Xie and Chen, 2008).

In our experiment, the number of ramets produced and total biomass accumulated were not different among treatments, indicating that the strategy of producing more guerrilla ramets is a normal and efficient way responding to sedimentation. However, production of more spreading ramets may be at the cost of competitive capacity of the plant. Sutherland and Stillman (1990) showed that the production of long rhizome internodes, as for "guerrilla"

species, was insufficient to confer a strong competitive capacity. In the rhizomatous grass *Amphibromus scabrivalvis*, guerrilla genotypes were more adversely affected than phalanx-like genotypes in response to severe competitive stress induced by a phalanx species (Cheplick, 1997). Therefore, the competitive capacity of *C. brevicuspis* may be reduced as the growth form changes from phalanx to guerrilla after emergence from sedimentation.

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