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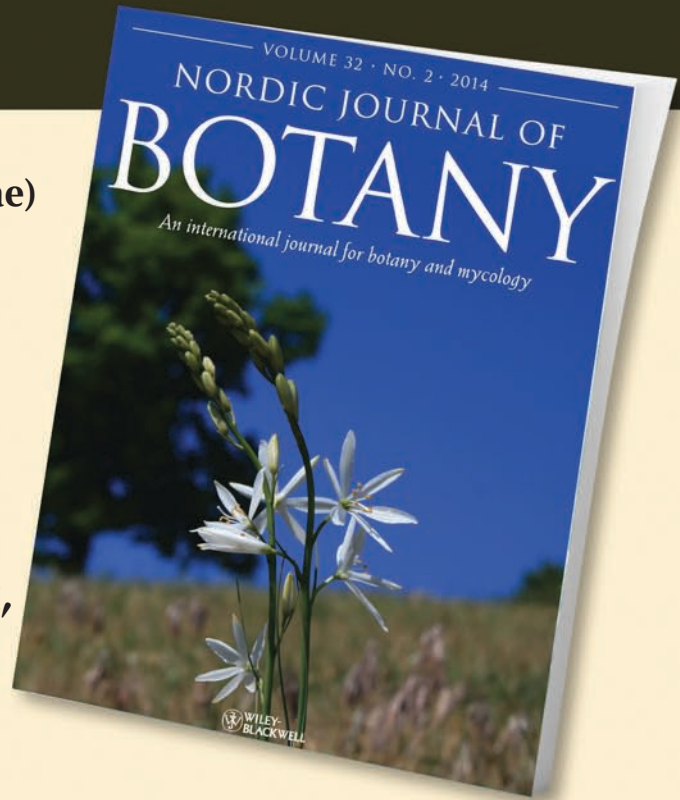
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Demography of *Carex brevicuspis* (Cyperaceae) rhizome populations: a wetland sedge that produces both elongated and shortened rhizomes

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The wetland sedge *Carex brevicuspis* reproduces vegetatively by producing short rhizomes to form clumping ramets (phalanx) and long rhizomes to form spreading ramets (guerrilla), resulting in a combined growth form. As an initial step towards understanding the adaptation of *Carex* growth strategies to seasonal fluctuations in wetland habitats, we investigated the density and composition of *C. brevicuspis* rhizome populations immediately after flooding (November), in winter (January), in spring (March), and before flooding (May) in the Dongting Lake wetlands, China. The total rhizome density peaked in winter and was lowest before flooding. A large rhizome population in winter may enable *C. brevicuspis* to survive the seasonal cold weather and recruit a shoot population in the spring. A small rhizome population before flooding may optimize reproductive allocations and be a strategy for enduring the long flooding season. Regardless of date, short rhizomes comprised the majority of the rhizome population (73.0% in March to 98.2% in May). This indicates that *C. brevicuspis* primarily uses a phalanx growth strategy to utilize locally abundant resources in wetlands. The percentage of long rhizomes in the rhizome population varies significantly between seasons (1.8% in May to 27.0% in March), indicating that growth form also changes with seasonal fluctuation of wetland habitats. The results show that *C. brevicuspis* may adapt to seasonal changes in wetland habitats through changes in demography of rhizome populations.

Clonal plants are widespread in all biomes and biogeographical regions, especially in cold, wet or shaded environments (Klimeš et al. 1997). The plant organs involved in clonal growth can be classified into different types according to their origin, placement and storage function (Klimeš et al. 1997, Klimeš and Klimešová 1999, Klimešová and Klimeš 2008). Rhizomes, tubers, corms and stems are common clonal growth organs (Klimešová and Klimeš 2008, Sosnová et al. 2010). Clonal growth organ type is correlated with many functional traits, including multiplication rate, lateral spread, and persistence of connections (Grace 1993, van Groenendael et al. 1996, Klimešová and Klimeš 2008, Sosnová et al. 2010, Klimešová et al. 2011). Therefore, the composition of clonal growth organs may determine the growth strategy of clonal plants (Šmilauerová and Šmilauer 2007).

The genus *Carex* is composed of about 2000 species, some of which are particularly important in wetlands. Although most *Carex* species can flower and fruit, many mainly reproduce vegetatively by rhizomes and other asexual means (Bernard 1990). Rhizome form is determined in large part by the growth strategy of *Carex* species (Bernard 1990). Long rhizomes, which have many and/or long internodes, grow away from the parent shoot and produce only

spreading ramets. Short rhizomes, which have few and/or short internodes, tend to clump around the parent shoot and produce only clumping ramets. These two rhizome types (long and short) give rise to three major growth forms in *Carex* species: guerrilla, phalanx and mixed growth forms (Bernard 1990).

Carex species often form tufts, clumps, or tussocks of various sizes, and the microtopographic heterogeneity of *Carex* stands is high (Lawrence and Zedler 2011). These growth forms may have special importance for the ecology and evolution of *Carex* populations. Short rhizomes enable *Carex* plants with phalanx growth form to consolidate or maintain a favorable microsite (Lovett-Doust 1981, Bernard 1990, de Kroon and Hutchings 1995, Cheplick 1997, Humphrey and Pyke 1998, 2001). In contrast, long rhizomes enable *Carex* plants with guerrilla growth form to spread quickly, such that they can more readily escape from stressful microsites and find favorable sites in a spatially heterogeneous habitat (Lovett-Doust 1981, Bernard 1990, de Kroon and Hutchings 1995, Cheplick 1997). Thus, the patterns of belowground rhizomes in *Carex* populations may reflect the growth strategies they use to cope with the surrounding environment.

Most *Carex* species produce both long and short rhizomes, resulting in a mixed growth form (Bernard 1990). Clonal species with a mixed growth form may respond to environmental gradients, such as resource or stress levels, through modification of their growth form (Cheplick 1997, Ye et al. 2006, Amiaud et al. 2008, Chen et al. 2011a). In natural habitats, *Carex* vegetation faces seasonal changes in the abiotic environment, such as changes in soil moisture and temperature, and the biotic environment, such as intra- and inter-specific competition. The ways in which *Carex* species modify their growth forms, i.e. the type and number of produced rhizomes, to adjust for seasonal fluctuations in the environment have rarely been studied.

In the present study, we investigated the demography of *C. brevicuspis* rhizome populations in the Dongting Lake wetlands, as an initial step towards understanding the clonal growth strategy that *Carex* species use to cope with wetland habitats. Because the wetlands are usually flooded between June and October, *C. brevicuspis* can only grow and reproduce during non-flooding periods (November–May). We tested the following hypotheses: 1) rhizome density should be relatively high after flooding because a large number of rhizomes is necessary for aboveground population recruitment, and density should be relatively low before flooding because this period is at the end of the growing season and most of the rhizomes have already sprouted; 2) plants should produce a relatively high proportion of short rhizomes after flooding, to utilize favorable resources at the beginning of the growing season, and a relatively high proportion of long rhizomes before flooding, to locate new resources at the end of the growing season.

To test these hypotheses, we sampled *C. brevicuspis* rhizome and shoot populations immediately after flooding (November), in winter (January), in spring (March), and before flooding (May) in order to investigate the rhizome demography over one whole growing season.

Material and methods

Study site

Dongting Lake (111°40′–113°10′E, 28°30′–30°20′N), the second largest freshwater lake in China, is located in northern Hunan Province. It lies in a basin to the south of the Yangtze River and is connected to the Yangtze by distributary channels. The wetlands are characterized by large seasonal fluctuations in water levels. The wetlands are typically completely flooded between June and October and exposed between November and May. The mean annual temperature is 16.4–17.0°C. The coldest month is January (3.9–4.5°C) and the hottest month is July (28.6–29.1°C). The annual precipitation is 1382 mm, with more than 60% falling between April and August.

Study species

Carex brevicuspis (Cyperaceae) is a perennial rhizomatous sedge distributed in eastern mainland China and Taiwan

(Dai et al. 2010). The plant pseudoculm, made up of a series of overlapping leaf sheaths, is usually 20–55 cm in height. In the Dongting Lake wetlands, this species forms mono-dominant communities or is co-dominant with other *Carex* species. During the flood season, *Carex* vegetation is completely submerged and aboveground shoots senesce. *Carex brevicuspis* shoots emerge immediately after flooding (November) and grow into vegetative ramets before January. In January, plants remain relatively dominant, but shoots partially wither because of low temperature. New ramets sprout in March and plants grow rapidly. Plants flower and fruit from April to May, but seedlings are scarce in the field (Hou et al. 2009). This species forms tiller clumps or tussocks of various sizes, and the microtopographic heterogeneity of the stands is high in the Dongting Lake wetlands (authors pers. obs.).

Aboveground and belowground sampling

Carex brevicuspis populations were selected for study from a monitoring plot (112°47′29″E, 29°27′46″N) at the Dongting Lake Station for Wetland Ecosystem Research, a member of the Chinese Ecosystem Research Network. The plot (2000 × 1000 m) is relatively flat and the long edge of the study site was parallel to the lakeshore. In November 2010, when the plot was accessible, 15 permanent quadrats (2 × 2 m) dominated by *C. brevicuspis* were established in a 300 × 1000 m experimental area within the plot. The corners of each quadrat were marked by hammering durable plastic tubes into the soil. The distance between each quadrat was at least 50 m. On each sampling occasion, 1 subquadrat (25 × 25 cm) was randomly excavated from each permanent quadrat, for a total of 15 subquadrat samples per sampling occasion. In each random subquadrat, all ramets within a sampling frame (25 × 25 cm) were counted and clipped. A preliminary experiment indicated that most rhizomes of *C. brevicuspis* are distributed within the uppermost 10 cm of the soil. To ensure that all rhizomes were collected, the soil within the frame was excavated to a depth of 15 cm. Each sample was placed in a plastic bag and brought to the laboratory. Samples were collected in early November 2010 (about 1 week after flooding), middle January 2011 (the coldest month), early March 2011 (after spring sprout), and early May 2011 (before flooding). The newly emerging ramets in March 2011 were calculated as the difference in ramet density between March 2011 and January 2011. To determine the status of the soil resources after and before flooding, a soil sample was taken from the top 15 cm of the soil in 5 of the 15 quadrats. Soil moisture, organic matter, total nitrogen, and total phosphorous were measured in each soil sample.

Sample processing

After carefully washing away the soil by using tap water, the roots and rhizomes in each sample were separated. The rhizomes, with many nodes, are distinct from root parts. Axillary buds at rhizome nodes are inconspicuous, especially in short rhizomes, and contribute little to shoot populations (Bernard 1990). Therefore, only rhizomes with apical

buds, which have the potential to sprout into ramets, were classified and counted. Rhizome types were classified according to Bernard (1990). Rhizomes growing horizontally and farther than 1 cm from the parent shoot were considered to be long rhizomes (Chen et al. 2011a). Rhizomes growing vertically and clumped around the parent shoot were considered to be short rhizomes. Rhizome density was calculated as the number of rhizomes per m².

After weighing the fresh soil samples, 50 g of fresh soil from each sample was dried at 105°C for 48 h to determine the soil moisture content, which was calculated as $((W - D)/W) \times 100\%$, where W is soil fresh weight and D is soil dry weight. The remainder of each soil sample was air-dried and then was ground into a fine powder to pass through a 250- μ m screen (i.e. the soil fraction was less than 250 μ m) to measure organic matter, total nitrogen and total phosphorous. Soil organic matter was determined using the potassium dichromate method (Yeomans and Bremner 1988). Soil total nitrogen was extracted by boiling soil samples in concentrated sulfuric acid and assayed using a fully automated flow injection system (FIAstar 5000, Liu et al. 1996). Soil total phosphorous was extracted by dissolving soil samples in sodium hydroxide and placing in a muffle furnace at 700°C for 30 min. Phosphorous was measured using an ultraviolet and visible spectrophotometer (UV-2450, Liu et al. 1996).

Data analysis

Differences in shoot densities, rhizome densities, and the proportion of each type of rhizome to the whole rhizome population between sampling periods were evaluated using repeated measures analysis of variance (ANOVA). ANOVA was performed using the PROC mixed analysis package in SAS 8.2, and sampling period was treated as a repeated measure. Multiple comparisons of mean values between sampling periods were performed at the 0.05 significance level by using SAS mixed procedure Lsmmeans. Differences in soil characteristics after flooding and before flooding were tested using an independent t-test. The heterogeneity of variances was reduced, if necessary, by log₁₀-transforming data. Levene's test was used to examine the homogeneity of variances. The relationship between rhizome and shoot densities was analyzed using linear regression. All statistical analyses were performed using SAS 8.2.

Results

Soil characteristics after flooding and before flooding

The moisture content of soil sampled after flooding was not significantly different from that sampled before flooding

($p > 0.05$, Table 1). Soil organic matter, total N, and total P content were significantly higher after flooding than before flooding ($p < 0.05$, Table 1).

Seasonal changes in the density of short and long rhizomes

Carex brevicuspis short rhizome density peaked in January 2011 (471 ± 45 rhizomes m⁻²). Short rhizome density dramatically decreased in March (99.2 ± 8.7 rhizomes m⁻²) and was lowest in May (44.8 ± 8.0 rhizomes m⁻²) ($p < 0.001$, Fig. 1). Long rhizome density also peaked in January (94.9 ± 16.3 rhizomes m⁻²) and decreased significantly in March (42.7 ± 8.1 rhizomes m⁻²; $p < 0.001$, Fig. 1). *Carex brevicuspis* produced very few long rhizomes in May (2.13 ± 2.13 rhizomes m⁻²; Fig. 1).

The proportion of long and short rhizomes produced in each sampling period

Short rhizomes represented the majority of the rhizome population throughout the growing season (73.0% in March, 98.2% in May). However, the ratio of each rhizome type to the total rhizome density varied significantly between sampling periods ($p < 0.01$, Fig. 2). The proportion of long rhizomes to total rhizome density increased from January (16.4%) to March (27.0%), and then dramatically decreased in May (1.8%; $p < 0.01$, Fig. 2). The proportion of short rhizomes to total rhizomes had a seasonal pattern that was opposite that of long rhizomes.

Seasonal density changes in total rhizomes and shoots

The seasonal pattern of total rhizome density was similar to that of short rhizomes (Fig. 1, 3). Shoot density was lowest in November (1060 ± 76 shoots m⁻²) and increased almost linearly afterwards (1600 ± 73 shoots m⁻² in May; $p < 0.01$, Fig. 3). Regression analysis revealed a significant relationship between newly emerging ramets in March and total rhizome density in January ($R^2 = 0.41$, $p < 0.05$, $n = 15$, Fig. 4).

Discussion

The seasonal dynamics of the total rhizome density, long rhizomes, and short rhizomes peaked in winter (January) and was lowest before flooding (May). The rhizome density was relatively low after flooding (November). These results are inconsistent with our first hypothesis, which predicted that the rhizome density should be higher after flooding. This may be due to the rapid development and sprouting of rhizomes (especially short rhizomes) after flooding, or

Table 1. Soil nutrient contents of plots dominated by *Carex brevicuspis* at Dongting Lake wetlands after flooding (early November) and before flooding (early May). The data represent means \pm SE ($n = 5$). Different letters indicate significant differences between sampling periods ($\alpha = 0.05$, independent t-test).

Sampling period	Soil moisture (%)	Soil organic matter (%)	Total N (%)	Total P (%)
November	27.38 \pm 2.10 ^a	3.67 \pm 0.16 ^a	0.15 \pm 0.01 ^a	0.072 \pm 0.002 ^a
May	26.19 \pm 2.70 ^a	1.72 \pm 0.13 ^b	0.083 \pm 0.008 ^b	0.016 \pm 0.001 ^b

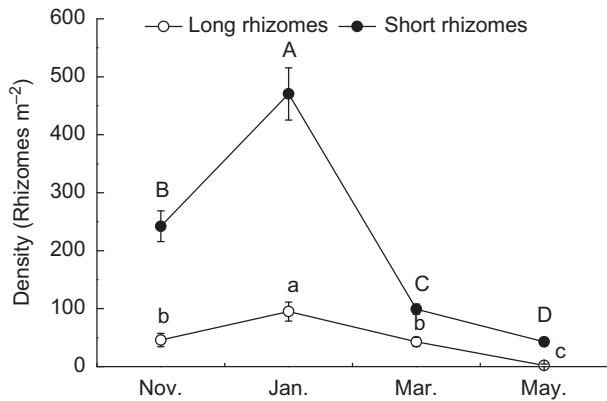


Figure 1. Density changes of short and long *Carex brevicuspis* rhizomes from November 2010 to May 2011. The data are mean values (\pm SE), $n = 15$. Different letters indicate significant differences between seasons ($\alpha = 0.05$, Lsmeans).

even when still covered by shallow water (Chen et al. 2011a). This explanation is supported by the high shoot density in the after-flood samples (1060 ± 76 shoots m^{-2} in November) that were collected when the water surface had declined to about 20 cm belowground (authors pers. obs.). In winter (January), energy, such as carbohydrates, may be translocated from aboveground shoots to belowground storage organs (rhizomes) as low temperatures constrain the growth of aboveground shoots (Roseff and Bernard 1979, Bernard 1990). This translocation of energy may explain the increase in the rhizome population between November and January, even though some rhizomes sprouted during this period. A large reserve of belowground rhizomes in winter may enable *C. brevicuspis* to avoid chilling injury by the cold weather because temperature of the rhizosphere would be relatively higher than that of the atmosphere (Song and Wang 2006). Besides, a large reserve of belowground rhizomes can also facilitate shoot population recruitment in spring as supported by a positive relationship between newly emerging ramets in March and total rhizome density in January (Fig. 4).

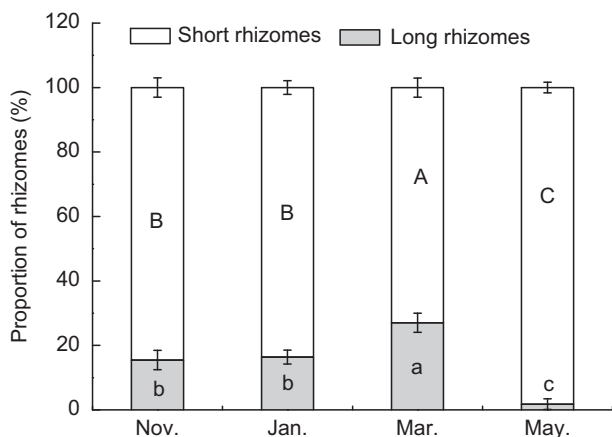


Figure 2. The percentage of long and short *Carex brevicuspis* rhizomes that were sampled between November 2010 and May 2011. The data are mean values (\pm SE), $n = 15$. Different letters indicate significant differences between seasons ($\alpha = 0.05$, Lsmeans).

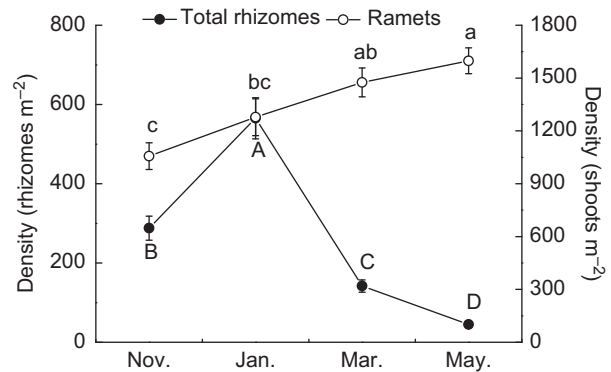


Figure 3. Seasonal density changes in total rhizomes and shoots of *Carex brevicuspis* in the Dongting Lake wetlands between November 2010 and May 2011. The data are mean values (\pm SE), $n = 15$. Different letters indicate significant differences between seasons ($\alpha = 0.05$, Lsmeans).

The rhizome population of *C. brevicuspis* dramatically decreased after spring (March), and it did not increase again before flooding (May). After the spurt of shoot emergence and growth that occurs in spring, carbohydrates stored in belowground rhizomes may be depleted (Roseff and Bernard 1979, Bernard 1990). In addition, *C. brevicuspis* flowers and fruits from April to May (Chen et al. 2011a). During this period, energy and nutrients may be allocated to inflorescence development rather than to the formation of new rhizomes (Bernard 1990). Furthermore, to survive the long and deep submergence of the flood season, *C. brevicuspis* likely chooses a tolerance strategy that involves the use of stored carbohydrates (Chen et al. 2009, Huber et al. 2009, Manzur et al. 2009). As a result, plants may allocate more energy to established organs, such as roots, than to the production of new meristems, such as rhizomes, in the period leading to the flood season (Chen et al. 2011b). Therefore, a small rhizome population before flooding may optimize reproductive allocations and be a strategy for enduring a long flooding season.

Regardless of date, a majority of rhizomes were short rhizomes (over 70%). This indicates that *C. brevicuspis* has primarily adopted a phalanx growth strategy in a natural habitat in the Dongting Lake wetlands. A previous experimental

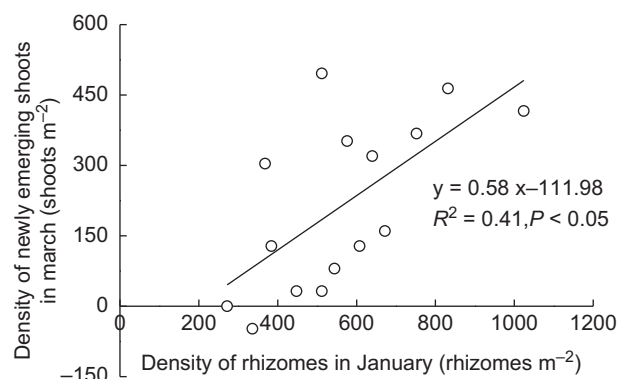


Figure 4. Relationship between total *Carex brevicuspis* rhizome density in January and the density of newly emerging shoots in March in a population at Dongting Lake wetlands, ($n = 15$).

study indicated that *C. brevicuspis* growth form is highly plastic and can change from phalanx to guerrilla as plants acclimate to sedimentation (Chen et al. 2011a). However, in response to seasonal fluctuations in the wetland environment, *C. brevicuspis* primarily exhibits a phalanx growth form. This growth form may enable *C. brevicuspis* to monopolize locally abundant resources in the wetlands and to compete efficiently with other species (de Kroon and Schieving 1990, Derner 1999). Furthermore, the optimal period for *C. brevicuspis* growth is relatively short because of the long flooding season and cold winter. Short rhizomes can sprout rapidly to recruit shoot populations and make the best use of the limited growing season (Zhang et al. 2009).

Long rhizomes are not numerous and constitute less than 30% of the whole *C. brevicuspis* rhizome population during the growing season. However, the percentage of long rhizomes in the whole population varies significantly between seasons; the percentage was highest after spring sprout (27% in March) and was lowest before flooding (1.8% in May). This result did not support our second hypothesis, which predicted a relatively high proportion of long rhizomes before flooding. In March, the shoot population is composed of both overwintering shoots and newly emerging shoots. Therefore, resource competition inside the tussocks/tiller clumps may be intense in spring. Production of a greater proportion of long rhizomes during this period may be a spreading strategy that enables plants to expand into new areas and avoid competition for resources between new shoots and the parent plant (Bernard 1990, Humphrey and Pyke 1998, Wang et al. 2008, Zhang et al. 2009). Unexpectedly, *C. brevicuspis* produced almost no long rhizomes before flooding, even though the soil nutrient content was low at that time. This may be related to plant developmental rhythms and a high energy cost involved in the production of long rhizomes (Lehtila and Larsson 2005).

The demography of *C. brevicuspis* rhizome populations may reflect an ecological adaptation of this species to the seasonal changes of wetland habitats. *Carex brevicuspis* produces a large rhizome population prior to the cold winter and recruits shoot populations in spring. A small population of rhizomes is produced prior to flooding in order to optimize allocation of resources for reproduction and to facilitate plant survival through the long flooding season. *Carex brevicuspis* produces primarily short rhizomes throughout the growing season in order to monopolize locally abundant resources in the wetlands (Lovett-Doust 1981, Bernard 1990, Cheplick 1997). Moreover, *C. brevicuspis* produces a higher proportion of long rhizomes during spring than in other seasons in order to forage new resources or to avoid competition with parent shoots (Lovett-Doust 1981, Bernard 1990, de Kroon and Hutchings 1995).

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