

DIFFERENTIAL GROWTH AND VEGETATIVE REPRODUCTION OF TWO CO-OCCURRING EMERGENT MACROPHYTES ALONG A WATER TABLE GRADIENT

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Abstract

Differential responses of growth and vegetative reproduction among coexisting species to water-level fluctuation might explain their distribution patterns in wetlands. In the present study, we investigated the effect of water-level, ranging from dry to flooded conditions, on the vegetative reproduction of 2 coexisting rhizomatous species, *Carex brevicuspis* C. B. Clarke and *Polygonum hydropiper* Linnaeus, at Dongting Lake wetlands, China. *Carex brevicuspis* exhibited optimal growth and vegetative reproduction when the aboveground parts were not submerged (at -40 cm to 0 cm water level), but remained quiescent under flooded conditions (at 20cm and 40cm water level). In comparison, *P. hydropiper* was sensitive to changes in water level, with an almost linear decline in biomass and rhizome production as the water level increased from -40cm to 40cm. In general, there was less change in biomass production, biomass allocation, and vegetative reproduction for *C. brevicuspis* compared to *P. hydropiper* at different water levels. This result indicates that *C. brevicuspis* is more tolerant of water stress than *P. hydropiper*; therefore, *C. brevicuspis* is likely to have a wider distribution in wetlands, with the latter species embedding in the stands of the former species.

Introduction

The segregation of species ranges is commonly observed along the water table gradients of rivers, lakes, and salt marshes (Lenssen & de Kroon, 2005). Differential tolerance to flooding determines the lower boundaries of species, while drought appears to constrain their upper boundaries (Blom & Voeselek, 1996; Lenssen *et al.*, 2000; Lenssen & de Kroon, 2005). However, it is more common for dominant species to coexist within a certain zone. Normally, species occupy a similar elevation range along a water level gradient, but are distributed in different areas (Lu, 2011). A few studies have suggested that differential growth and morphological responses to flooding levels may reflect species distribution patterns, i.e., one species is distributed within the range of another species (Li *et al.*, 2011; Lu, 2011). However, most of these studies did not consider the effect of water level gradients on vegetative reproduction, which is an essential life-history phase for wetland perennials, and may play a decisive role in plant distribution (Lenssen *et al.*, 2000).

Vegetative reproduction predominates over sexual reproduction in wetland perennials, which may be attributed to phylogeny, life-history constraints, or the consequences of adaptation to wet habitats (Sosnová *et al.*, 2010; Chen *et al.*, 2014). The ability to form rhizomes or other perennating organs is essential for the expansion and persistence of plants in flooded environments (Lenssen *et al.*, 2000; Benot *et al.*, 2011; Yuan *et al.*, 2012). A previous study on the effects of flooding showed that the extent of vegetative reproduction (including rhizome biomass, number, and size of rhizomes) by 2 common wetland species, *Mentha aquatica* and *Epilobium hirsutum*, corresponds to their lower hydrological boundaries (Lenssen *et al.*, 2000). Field observations have also indicated differences in the ability of wetland species to produce vegetative organs in

response to declining or rising water levels, which might account for changes in the structure of wetland vegetation (Barnes, 1999; Tian *et al.*, 2004). However, further experimental studies are required to clarify the effect of water level gradients, ranging from dry to flooded conditions, on the vegetative reproduction of coexisting species, and how this affects plant distribution.

In the present study, we investigated the effect of water level gradients on the growth and vegetative reproduction of 2 rhizomatous species, *Carex brevicuspis* C.B. Clarke and *Polygonum hydropiper* Linnaeus, at Dongting Lake wetlands in China. The wetlands are characterized by large seasonal fluctuations in water level, being completely flooded from May to October, and exposed from November to the following April. Both *C. brevicuspis* and *P. hydropiper* are dominant species that are distributed in the same vegetation zone adjacent to the water body (Xie & Chen, 2008). Typically, *C. brevicuspis* is widely distributed in the vegetation zone, while *P. hydropiper* patches are embedded in stands of *C. brevicuspis* (Peng *et al.*, 1984). We evaluated whether the distribution patterns of the 2 species in the wetlands could be explained by differences in growth tolerance and vegetative reproduction in response to flooding and drought stress. Tolerance is defined as the ability of a species to avoid displacement during periods of stress, with more tolerant species usually undergoing small changes in growth and vegetative reproduction after disturbance (Fritz & Dodds, 2004). We hypothesized that *C. brevicuspis* would be more tolerant to flooding and drought stress than those of *P. hydropiper*, in terms of growth and vegetative reproduction, since the former species has a wider distribution range. Hence, the growth and vegetative reproduction of both species were evaluated in relation to 5 different water table levels; specifically, dry (water level at -40 and -20cm), waterlogged (0 cm), and flooded (20 and 40cm).

Materials and Methods

The study species: *Carex brevicuspis* is a perennial rhizomatous sedge that is distributed in the wetlands of eastern mainland China and Taiwan (Dai *et al.*, 2010). The pseudoculm of the plant, which is made up of a series of overlapping leaf sheaths, is usually 20–55 cm in height. *Polygonum hydropiper* (Polygonaceae) is an annual herb that has a world-wide distribution (Li *et al.*, 2003). However, *P. hydropiper* produces overwintering belowground rhizomes, as the aboveground parts die during the winter at Dongting Lake wetlands (Fig. 1). The rhizomes of this species germinate into new plants the following March. The branched stems of this species are usually 40–70 cm in height. At Dongting Lake wetlands, *C. brevicuspis* forms large patches of monodominant communities, or co-dominates with *P. hydropiper*, while *P. hydropiper* usually co-dominates areas of wetland with *Carex* species. Both species flower and fruit within the wetland habitat; however, seedlings of either species are rarely found in the field (Hou *et al.*, 2009; Chen *et al.*, 2011).

Experimental procedure: On April 20, 2010, plants were removed from a mixed community containing both species (approx. 5 m²) at Chunfeng beach (29°13'49.72"N, 113°02'32.79"E) in East Dongting Lake wetlands, when the water table was approximately 0 cm. The plants were transplanted into plastic basins with 3 cm sand, after being transported to the Institute of Subtropical Agriculture, the Chinese Academy of Sciences. Plant fragments with roots and rhizomes were placed into plastic buckets, which were watered daily, to germinate new ramets. On July 12, 2010, for each species, 30 ramets of similar size (5–7 leaves and *ca.* 28 cm in height for *C. brevicuspis* and 6–8 leaves and *ca.* 30 cm in height for *P. hydropiper*) were selected and planted into separate PVC tubes (45 cm in height and 25 cm in diameter), which were filled with 40 cm soil collected from a mixed community of both species at Junshan beach, East Dongting Lake. The soil contained 1.20% organic matter, 0.09% total nitrogen, and 0.06% total phosphorus. Five ramets of each species were weighed, after drying for at least 48 h, to determine the initial biomass. PVC tubes containing 25 individuals of each species were randomly placed into 5 outdoor concrete pits (130 × 110 × 100 cm, 1 ramet per species per treatment per pit) at the Meteorological Station of Hunan Agricultural University, where mean annual temperature is 17.2°C and annual precipitation is 1361.6 mm. The ramets were grown in moist soil for 1 week, after which 5 water level treatments were implemented: -40 cm, -20 cm, 0 cm, 20 cm and 40 cm (relative to the soil surface). The water level in the concrete pits was maintained at 80 cm (40 cm above the soil surface in the 40 cm water level treatment). Different water level treatments within a concrete pit were created by placing the PVC tubes on concrete benches of different heights (0 cm, 20 cm, 40 cm, 60 cm and 80 cm). The ramets of both species were completely submerged to the 40 cm water level, and partially submerged to the 20 cm water level; hence, these water levels were referred to as

flooding treatments. In the field, most of the roots of both species are distributed in the 20 cm soil layer, and rarely reach 40 cm below the ground. Therefore, the -40 cm and -20 cm water levels were referred to as drought treatments. The 0 cm water level (waterlogged) was the control. The water level was maintained manually by adding tap water (containing 0.511 µg L⁻¹ NH₄⁺-N, 1.760 µg L⁻¹ NO₃-N, and 0.527 µg L⁻¹ PO₄³⁻-P; pH 7.2). Water in the concrete pits was replaced twice weekly, and filamentous algae were removed manually at regular intervals.

Growth measurements: The plants were harvested on December 16, 2010, 17 weeks after the treatment was started, which was at the end of the growing season for *P. hydropiper*. The plants were carefully removed from the tubes by cutting the tubes in half to keep the root and rhizome structure intact. The plants were then cleaned with tap water, and transferred to the laboratory for measurements. The number of modules (ramets for *C. brevicuspis* and the first-order branch for *P. hydropiper*), rhizomes, and axillary rhizome buds was counted. Axillary buds were examined under a microscope, and counted with a hand press counter. Each plant was then separated into shoots, roots, and rhizomes. The biomass of each plant part was measured after drying at 80°C for 48 h in an oven. Biomass production was calculated as the biomass at the end of the experiment minus the biomass at the beginning of the experiment.

Data analysis: The influence of water level on biomass allocation and vegetative traits was tested using one-way ANOVA. Multiple comparisons of means were performed using Tukey's test at the 0.05 significance level. Data were log₁₀ transformed, if necessary, to reduce heterogeneity of variances. Homogeneity was tested using Levene's test.

Results

Shoot length: Drought conditions (-20 cm and -40 cm water levels) did not significantly change the shoot length of *C. brevicuspis*, but the length was reduced by flooding (20 cm and 40 cm water levels) (Fig. 2A). The shoot length of *P. hydropiper* became slightly elongated at the -20 cm and 20 cm water levels; however, it significantly elongated at the -40 cm water level, and significantly shorter at the 40 cm water level (Fig. 2B).

Biomass production: Flooding treatment reduced the biomass production of both species, whereas each species responded differently to the drought treatment (Fig. 2C, 2D). *Carex brevicuspis* biomass at the 20 and 40 cm water levels was just 7.5% and 3.8% greater than that at the 0 cm water level. *Polygonum hydropiper* exhibited negative growth at the 40 cm water level (-0.41 g). *Polygonum hydropiper* biomass at the 20 cm water level was 28.4% greater than that at the 0 cm water level. Overall, *P. hydropiper* biomass increased with drought level, while that of *C. brevicuspis* did not respond to drought.



Fig. 1. Belowground rhizomes of *Polygonum hydropiper* at Dongting Lake wetlands, China.

Biomass allocation: Water level did not have a significant effect on the allocation of biomass to the roots and shoots in *C. brevicuspis* (Fig. 2E); however, flooding reduced the rhizome mass ratio (from 9.06% at the 0 cm water level to zero at the 40 cm water level). The allocation of biomass to the roots, shoots, and rhizomes of *P. hydropiper* was significantly affected by water level ($p < 0.05$; Fig. 2F). In *P. hydropiper*, a higher amount of biomass was allocated to the rhizomes in the drought treatments (67.4–69.4%) compared to the flooding treatments (26.8–39.4%). In contrast, a lower amount of biomass was allocated to the roots and shoots by *P. hydropiper* in the drought treatments (2.6–4.5% for roots and 28.0–28.1% for shoots) compared to the flooding treatments (7.4–15.9% for roots and 53.2–57.3% for shoots).

Number of modules (ramets or branches) produced per plant: Flooding reduced the number of modules produced by both species; however, the 2 species responded differently to drought (Fig. 3A, 3B). Fewer ramets were produced by *C. brevicuspis* in the flooding treatments (0.2 and 0.8 ramets per plant in the 40 and 20 cm water levels, respectively) compared to the control (4.4 ramets per plant). However, the number of ramets produced by *C. brevicuspis* in the drought treatments (4–4.2 ramets per plant) did not differ from the control plants (Fig. 3A). *P. hydropiper* did not produce branches when the water level

was 40 cm, but produced 0.4 branches per plant at the 20 cm water level, which was not significantly different to the control (1.8 branches per plant) (Fig. 3B). *P. hydropiper* produce more branches (9.2–15.8 branches per plant) in the drought treatments compared to the control.

Number of rhizomes and axillary rhizome buds produced per plant: Fewer rhizomes and axillary rhizome buds were produced by either species in the flooding treatments; however, the 2 species responded differently to drought (Fig. 3C, 3D, 3E, 3F). *Carex brevicuspis* did not produce rhizomes in the flooding treatments. The number of rhizomes and axillary rhizome buds produced by *C. brevicuspis* in the drought treatments did not differ from control ($p > 0.05$; Fig. 3C, 3E). *Polygonum hydropiper* produced significantly more rhizomes and axillary rhizome buds in the drought treatments (8.8–13.6 rhizomes and 106.8–305 buds) compared to the flooding treatments (1–3.8 rhizomes and 2.2–16.4 buds) (Fig. 3D, 3F). The number of rhizomes produced by *P. hydropiper* at the -40 cm water level treatment was higher compared to the control, but was not significantly different to the -20 cm water level treatment. More axillary rhizome buds were produced by *P. hydropiper* in the drought treatments (for both the -20 cm and -40 cm water levels) compared to the control ($p < 0.05$).

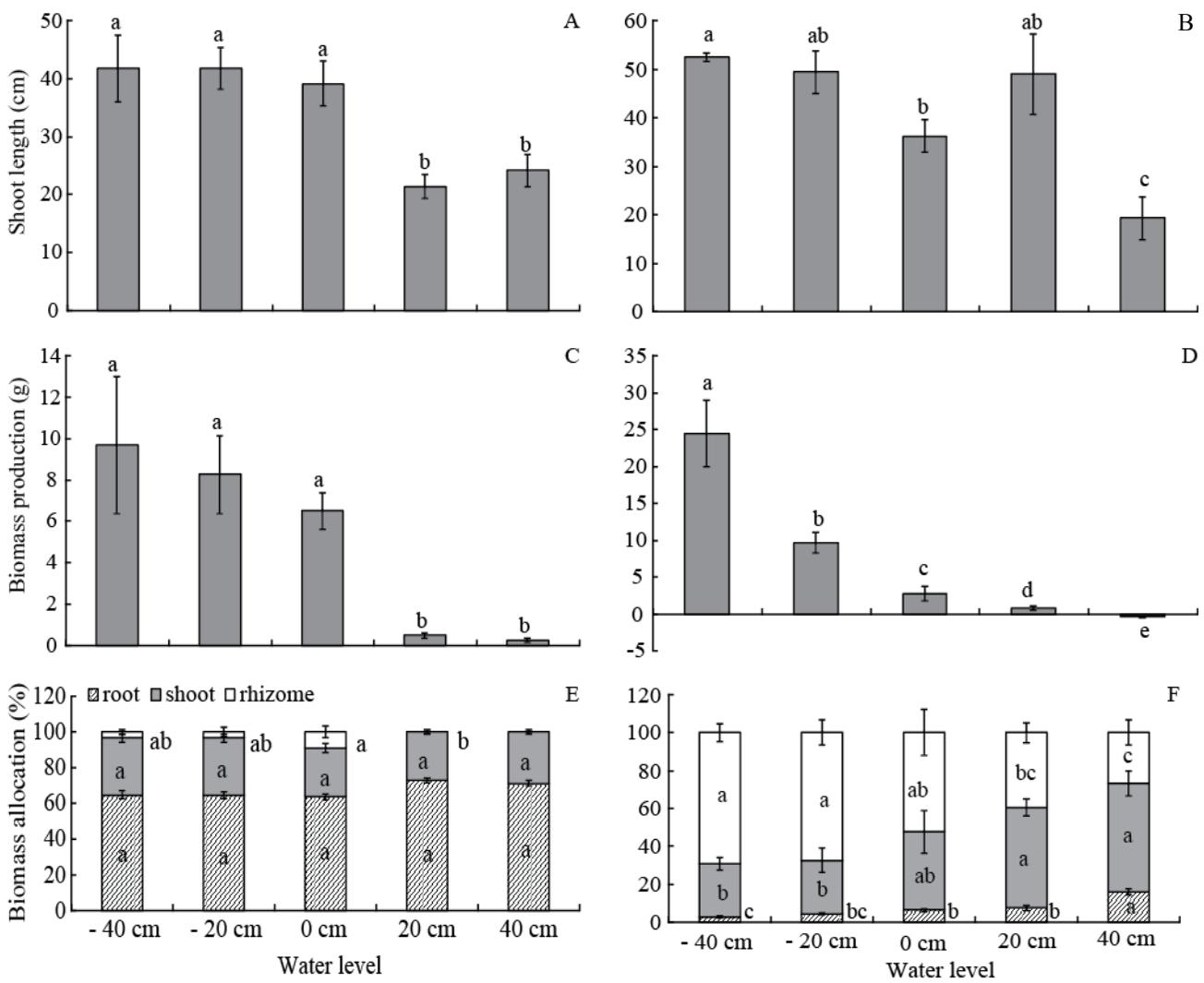


Fig. 2. Shoot length, biomass production, and biomass allocation of *Carex brevicuspis* (A, C, E) and *Polygonum hydropiper* (B, D, F) grown at 5 different water depths. Different letters indicate significant differences among treatments at the 0.05 significance level.

Discussion

The 2 study species exhibited very different growth and vegetative reproduction responses as the water level increased from -40 cm to 40 cm. *Carex brevicuspis* exhibited optimal growth and vegetative reproduction in dry and waterlogged conditions (from -40 cm to 0 cm water levels), whereas growth was suspended under flooded conditions (20 cm and 40 cm water level). In comparison, *P. hydropiper* was more sensitive to water level gradients, with biomass and rhizome production declining as water levels increased from -40 cm to 40 cm.

Under flooded conditions, the growth and vegetative reproduction of both *C. brevicuspis* and *P. hydropiper* were significantly reduced. Emergent macrophytes, such as *C. brevicuspis* and *P. hydropiper*, usually lack the ability to sustain photosynthetic activity when submerged in water (Macek *et al.*, 2006). Extended periods of anoxic conditions may eventually result in the reduction of plant growth and total biomass (Edwards *et al.*, 2003). However, the 2 species exhibited different specific responses to flooding. As a non-stem sedge, *C. brevicuspis* produced very little biomass or vegetative organs when flooded conditions were at 20 cm and 40 cm. Leaf elongation and the emergence of new leaves was not observed in *C. brevicuspis*. *Carex brevicuspis* primarily remains quiescent

when subject to flooding (Manzur *et al.*, 2009). The response of *P. hydropiper* depends on the depth of submergence. For instance, under partial submergence, *P. hydropiper* produced some biomass and rhizomes, although the shoots did not elongate significantly. However, under complete submergence, biomass production declined, and shoot length was shorter. These results indicate that *P. hydropiper* is less tolerant to high levels of flooding (complete submergence) compared to *C. brevicuspis*.

Experimental drought conditions did not affect the growth and vegetative reproduction of *C. brevicuspis*; however *P. hydropiper* responded positively. The growth of typical marsh plants, particularly those distributed at relative low elevations, is usually constrained by drought (Wang *et al.*, 2007; Luo *et al.*, 2008; Touchette *et al.*, 2007, 2008). The limited effects of drought on *C. brevicuspis* may be attributed to its developed root systems. Under all water conditions, *C. brevicuspis* consistently allocated high amounts of total biomass to the roots (63.56–71.15%), which indicates a greater tolerance to drier or drought conditions (Geoff *et al.*, 2007). Furthermore, the negligible changes in biomass production, biomass allocation, and vegetative reproduction under drought conditions also supported the hypothesis that *C. brevicuspis* is tolerant to drought stress (Fritz & Dodds, 2004; Wang *et al.*, 2008).

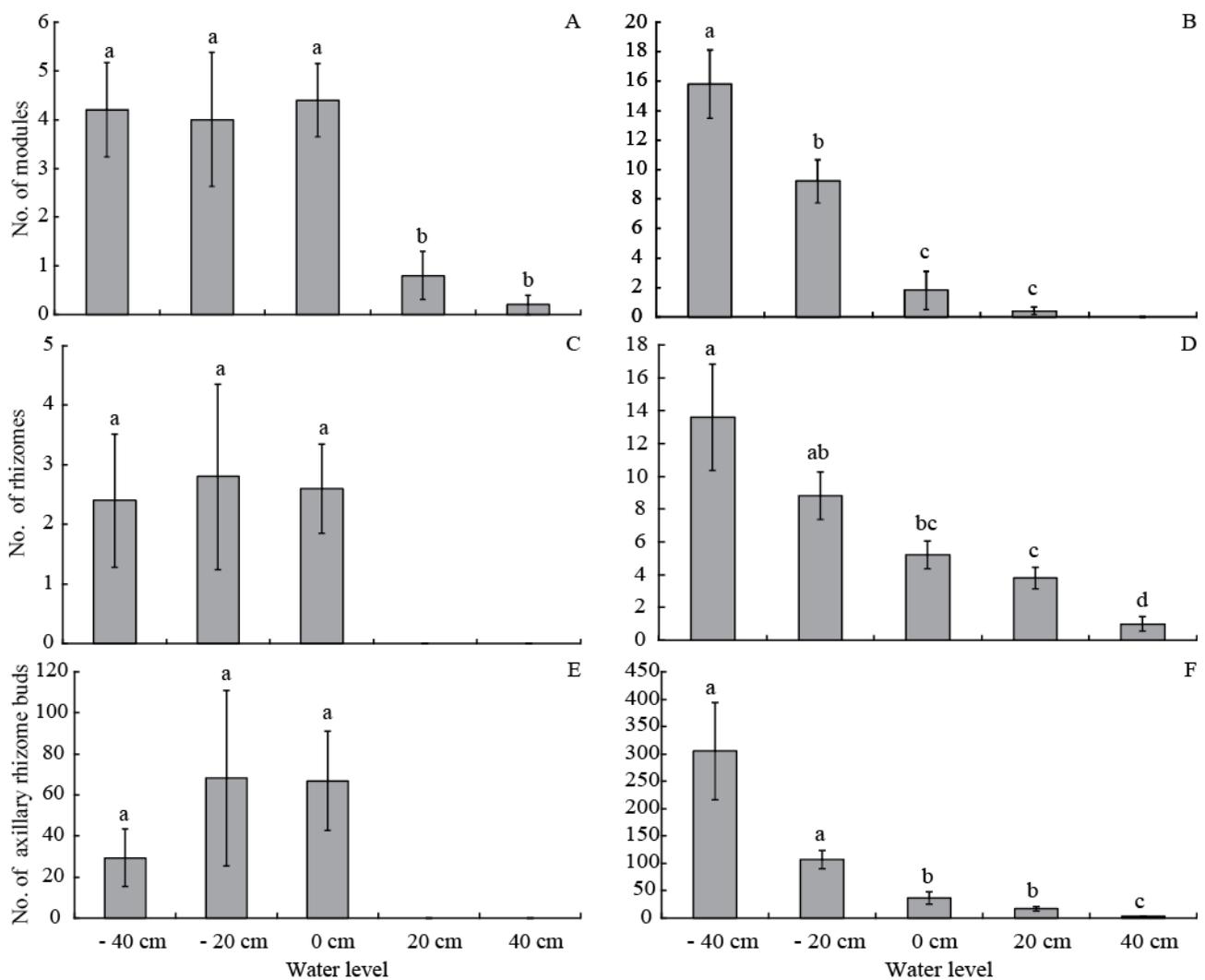


Fig. 3. Number of modules, rhizomes, and axillary rhizome buds produced by *Carex brevicuspis* (A, C, E) and *Polygonum hydropiper* (B, D, F) grown at 5 different water depths. Different letters indicate significant differences among treatments at the 0.05 significance level.

The major increase in growth and vegetative reproduction of *P. hydropiper* in the drought treatments indicates that it has high tolerance to drought stress (Dinler & Aksoy 2014). *P. hydropiper* grows in both terrestrial and shallow flooded habitats, including riverbanks, adjacent to streams, and wet valleys (Li *et al.*, 2003). Similar to other terrestrial plants that inhabit wet habitats, *P. hydropiper* is not specifically adapted to anoxic conditions, generally inhabiting elevated sites over shallow flooded habitats, where anoxic conditions commonly prevail (Šrútek, 1997; Altay *et al.*, 2013). Therefore, enhanced growth and propagule reproduction of *P. hydropiper* under drought conditions are probably attributed to its lower tolerance of excess water. Furthermore, dramatically changed biomass and propagule production among different water levels also indicates that *P. hydropiper* is not tolerant to water stress (Fritz & Dodds, 2004).

While the experimental water level conditions created in our experiment did not cover the full range of water level fluctuations in the field, the 2 species exhibited different responses. *Carex brevicuspis* grows vigorously, as long as the aboveground parts are not submerged. In comparison, *P. hydropiper* exhibits optimal growth when the water level is low, and appears

less tolerant to water excess. Therefore, *C. brevicuspis* has a wider optimal hydrological niche compared to *P. hydropiper*. This observation is consistent with the distribution pattern of these two species; *C. brevicuspis* being more widely distributed than *P. hydropiper* in wetlands. A moderately dry habitat benefits the growth of both species, whereas increased water levels exert more negative impacts on the growth of *P. hydropiper* compared to *C. brevicuspis*. Consequently, extreme climatic events, such as drought or flooding, could potentially alter the distribution patterns of these 2 species in wetland environments, due to their different levels of tolerance to water stress.

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