

Article

The Effects of Water Levels and Interspecific Competition on Two *Carex* Species in a Temperate Wetland of Northeast China

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Abstract: Zonation along a water level is the main spatial distribution characteristic of wetland plants. This is mainly because of the influences of hydrological conditions and interspecific competition, which finally narrow the fundamental niche of a species to its realized niche. In the present study, a controlled experiment was conducted in order to analyze the relationship between *Carex lasiocarpa*/*Carex pseudocuraica* and *Glyceria spiculosa*, in conditions of three competitive treatments at four water levels. The results showed that in no competition, *C. lasiocarpa* preferred low water levels, but this preference receded when competing with *G. spiculosa*. In contrast, *C. pseudocuraica* had greater preference for low water level when competing with *G. spiculosa*. The root/shoot ratios of the two *Carex* species decreased with increasing water levels, but they were almost unaffected by different competition treatments. With the increase in water level during full competition with *G. spiculosa*, the competitive ability of *C. lasiocarpa* showed an increasing trend, whereas a contrary trend was observed in *C. pseudocuraica*. Our results suggested the effects of water levels and their interactions with interspecific competition varied between the two *Carex* species and played an important role in determining spatial distribution patterns and potential community succession of wetland plants.

Keywords: *Carex lasiocarpa*; *Carex pseudocuraica*; interspecies competition; water level; *Glyceria spiculosa*

1. Introduction

The spatial distribution of wetland plants generally shows zonation along environmental gradients [1], which could mainly be attributed to the influences of hydrological and biotic factors [2–5]. However, because multiple factors often function together, there is still no clear consensus on the mechanism of the formation of zonation patterns and plant community development in natural wetlands. On one hand, flooding causes excessive depletion of soil oxygen, which changed soil redox conditions [6]. As a consequence, leaf stomatal conductance, photosynthesis, and biomass were influenced by inundation directly or indirectly [7–9]. On the other hand, the effects of the interactions between different wetland species are numerous. Ellenberg [2] demonstrated that, when interactions with other plant species were prevented, all species had very similar hydrological optima, but in contrast, in the presence of interspecific interactions, optimal growth considerably shifted to different positions along the hydrological gradient. This finding was also supported by the concept of niche presented by Hutchinson [10]. Further research by Silvertown [11] suggested that the fundamental niche of a species is narrowed to the realized niche as a consequence of interspecific competition and natural

enemies. In fact, the extent to what hydrological and biotic factors affect plant species distribution could be dependent on many factors. For example, Lenssen et al. [12] found that species distribution and richness along a freshwater flooding gradient were mainly dependent on hydrology in the frequently flooded zone, whereas at higher elevations, they were mainly dependent on plant interactions.

During the process of growth and development, plants compete with adjacent individuals for water, light, and nutrients. Competition, a ubiquitous phenomenon in plant communities, has long been considered as a major force shaping plant communities [13]. However, the role of competition in community composition remains controversial, and this was discussed in the debate between Grime and Tilman on the role of competition in the formation of plant community structure [14]. The conclusions of this debate have been included in a new conceptual model of stress-gradient hypothesis which predicts a shift of plant interaction from competition to facilitation with increasing physical stress [15,16]. To date, there are still many different opinions on the competition or facilitation relationships of plants along environmental gradients [17].

The Sanjiang Plain lies in northeast China and it was once the largest national distribution area of freshwater marsh wetlands. Although the area has experienced dramatic reduction in wetland areas because of agricultural conversions, it is still an important distribution area of natural freshwater wetlands and it plays an important role in maintaining regional biodiversity. The distribution of plant communities in the wetlands of the Sanjiang Plain generally exhibits distinct plant zonation patterns along the water level gradients [6,18]. Typical plant species in these wetlands include *Carex lasiocarpa* Ehrh., *Carex pseudocuraica* F. Schmidt, and *Glyceria spiculosa* (Schmidt.) Roshev., and they generally occupy niches with similar hydrological conditions [19]. As a result, individuals of these species are influenced by hydrological fluctuations as well as species interactions [8]. In recent years, research was conducted on the distribution of wetland plants of the Sanjiang Plain under different water levels [5,20,21], but studies focusing on the competition between *Carex* species and *G. spiculosa* at different water levels are still quite limited. Considering the fact that the water level of the typical inundated freshwater wetlands in the Sanjiang Plain generally varies from 0 to 40 cm above the soil surface [6,20,21], we designed a controlled experiment in order to investigate the effect of different water levels (0–30 cm) on species interactions between *C. lasiocarpa* and *G. spiculosa*, and between *C. pseudocuraica* and *G. spiculosa*. The aims of this study were to: (1) investigate the response strategies of wetland plants to flooding, (2) investigate the effect of water level on interspecific competition, and (3) compare the interspecific relationships under different competition treatments. We aimed to discuss the mechanism of wetlands species distribution driven by interspecific competition and hydrological factors.

2. Materials and Methods

2.1. Study Site

This study was conducted at the National Observation and Research Station of Wetland Ecology, Sanjiang Plain, northeast China (hereafter referred to as the Sanjiang Station, 47°35′10.66″ N, 133°29′57.06″ E, 55 m a.s.l.). The climate of the area is the temperate continental monsoon climate type in the seasonally frozen zone. The mean annual temperature (1990–2010) is 2.5 °C with monthly mean temperature ranging from −20.4 °C in January to 21.6 °C in July. The mean annual precipitation is 566 mm, with 80% of precipitation occurring from May to September, and the frost-free period is 125 days. About 150 ha of natural wetlands, which are representative of the pristine wetlands in the Sanjiang Plain, were protected by the station and these wetlands can mostly be classified as permanently and seasonally inundated wetlands. The water level in the permanently inundated wetlands generally varies from 10 to 40 cm during the growing season, and the water and soil are frozen during the non-growing season. Dominant plants in the permanently inundated wetlands are *C. pseudocuraica*, *C. lasiocarpa*, *G. spiculosa*, and *Carex appendiculata* (Trautv.) Kukenth., which account for more than 90% of the above ground biomass. *C. lasiocarpa* and *C. pseudocuraica* are the two closely related species

living in similar hydrological conditions with water levels 10–30 cm during the full growing seasons, and they often co-occur in the same habitats [8,21]. In the permanently inundated wetlands, *G. spiculosa* is an important accompanying species in the *C. lasiocarpa* and *C. pseudocuraica* communities. Due to the long term anaerobic environment and the relatively low temperature, the plant residues in the wetland decomposed slowly, and piled up a 0 to 45 cm thick floating peat mat with moss in it. For most plants in the permanently inundated wetland, their roots and part of shoots were unemerged during the growing seasons.

2.2. Experimental Design

A controlled outdoor experiment was set up at the end of April 2017 at the Sanjiang Station. The experimental site was about 500 m away from the permanently inundated wetland and was undisturbed during the study period. We designed the experiment to investigate the responses of *C. lasiocarpa* and *C. pseudocuraica* when competing with *G. spiculosa* in three competitive modes (no competition, shoot competition, and full competition) at four water levels.

For the purpose of allowing and preventing root interactions, rectangular tubes made of polymethyl methacrylate of two sizes (height 20 cm, width 5 cm, and length 10 cm for no competition and full competition, and height 20 cm, width 5 cm, and length 5 cm for shoot competition) were used as containers. Each rectangular tube (hereafter referred to as tube) was filled with a volumetric mixture of wetland soil and sand (1:1) so that the roots could be collected more accurately [22]. Ramets of similar sizes (3–4 leaves, 5–8 cm height) of *C. lasiocarpa*, *C. pseudocuraica*, and *G. spiculosa* were carefully collected in early May 2017 from the permanently inundated wetland of the Sanjiang Station (with the permission of the Station for scientific research), and the same species were collected in a 30 × 30 m plot. We identified the ramets carefully by referring to Flora of China (<http://www.iplant.cn/foc>). The three competitive modes were set as follows: (1) two ramets of *C. lasiocarpa* or two ramets of *C. pseudocuraica* or two ramets of *G. spiculosa* were planted in a 10 cm long tube (no competition; Figure 1a); (2) two 5 cm long tubes were first connected by their single surfaces as one tube group, and one ramet of *C. lasiocarpa* or *C. pseudocuraica* was planted with one ramet of *G. spiculosa* in each of the two tubes (shoot competition; Figure 1b); (3) one ramet of *C. lasiocarpa* or *C. pseudocuraica* was planted with one ramet of *G. spiculosa* in a 10 cm long tube (full competition; Figure 1c). There were six repetitions for each competition treatment. Every six replicate tubes or tube groups of each competitive mode were arranged in one plastic tank (height 50 cm, width 40 cm, length 45 cm; Figure 2).

According to McPhee and Aarssen [23], the main partition techniques of root and shoot competitions could be classified as: the divided pot technique, the row technique, and the target technique. Row technique is arrangement of partitions in aerial portion and soil portion of competition box: (1) no competition contains two units of soil and two units of aerial portion; (2) full competition contains one unit of each; (3) root competition contains one unit of soil portion and two units of aerial portion; (4) shoot competition contains two units of soil portion and one unit of aerial portion. In this study, we chose the simplified way of row technique and planted two herbaceous individuals in each tube. The advantage of this simplified row technique is that, in the shoot competition and full competition modes, each genetic individual competes only with another different genetic individual.

In order to investigate the effect of water level on interspecific competition, we included four water levels of 0, 10, 20, and 30 cm for each competitive mode in our experimental design. As a result, there were 28 tanks in total. Water taken from the permanently inundated wetland nearby was added to the tanks until water surface was flush with (0) or 10, 20, or 30 cm higher than the soil surface of the tube. During the experimental period, we measured water levels in each tank every two days and added water if needed in order to keep the water level constant. The nutrients concentration was consistent for each tank since we collected the soil and water from the same place. Light availability was also the same for each individual as enough room was retained for each tube and the east-west direction of each competitive group avoided shadow to the greatest degree (Figure 2).

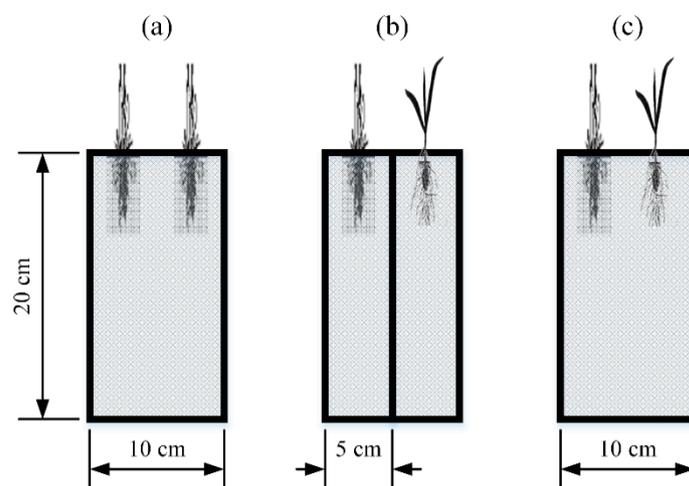


Figure 1. Illustration of the experimental design. (a) No competition with two ramets of same plant (*Carex lasiocarpa*, *Carex pseudocuraica* or *Glyceria spiculosa*) planted in one 10 cm long tube; (b) Shoot competition with two species (one *C. lasiocarpa* or *C. pseudocuraica* and one *G. spiculosa*) planted in two 5 cm long tubes; (c) Full competition with two species (one *C. lasiocarpa* or *C. pseudocuraica* and one *G. spiculosa*) planted in one 10 cm long tube.

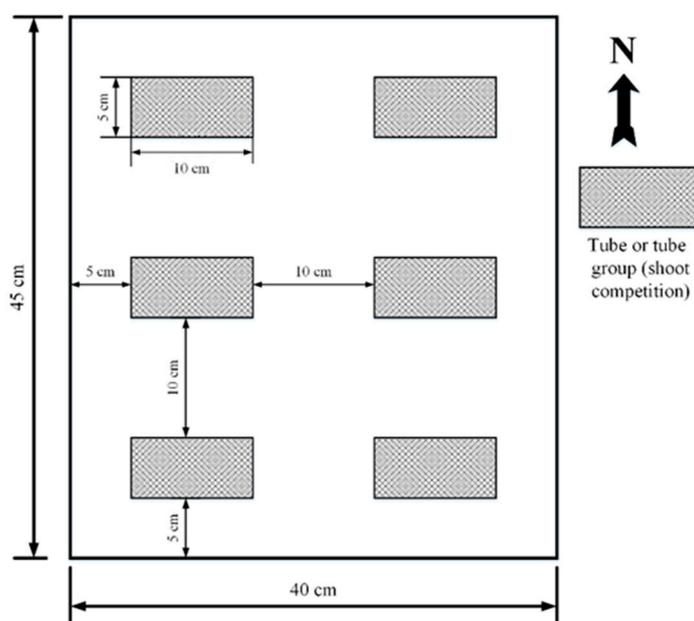


Figure 2. Sketch of the tubes or tube-group arrangement in a plastic tank. There were 28 tanks for the whole experiment, which included 2 species (*C. lasiocarpa* and *C. pseudocuraica*) \times 3 competitive modes \times 4 water levels, and 4 water levels of *G. spiculosa* in no competitive mode.

According to the phenology of wetland plants, the experiment lasted for the whole growing season from early May to the end of September 2017. At the end of the experiment, we counted the ramet amount for ramets with no less than three leaves and propagule amount (including all ramets, buds, and rhizomes) of all the six tubes in each tank and calculated the average value. All plants from each tank were then collected, divided into root and shoot parts, and dried at 65 °C. The average dry weight and root/shoot ratio were then calculated.

2.3. Data Analysis

Biomass can be an important index for explaining the differences caused by different competitive ability [24], and it is especially useful when all species are clonal herbs, as in the present experiment. We selected three parameters to represent the fitness of different species: (1) total dry biomass of the whole plant; (2) single shoot dry biomass, mean shoot biomass of single ramets that had more than three leaves, and (3) propagule amount, including all ramets, buds, and rhizomes, representing clonal growth ability. In order to further evaluate the relative competition ability of two species, we used relative yield (RY, [9,25]) as follows:

$$RY_A = Y_{AB}/(p \times Y_A) \quad (1)$$

$$RY_B = Y_{BA}/(q \times Y_B) \quad (2)$$

where Y_{AB} is the yield of species A growing with species B, Y_{BA} is the yield of species B growing with species A, Y_A is the yield of species A growing in pure culture, Y_B is the yield of species B growing in pure culture, p is the initial proportion of species A in mixed culture, and q is the initial proportion of species B in the mixed culture, with $p + q = 1$.

If a species grows in competition as well as grown in no competition, RY value of the species is 1.0. In order to investigate the relative competitive ability between two species, RY_A values were plotted against RY_B values in space, and there were six main areas of interest in the graph ([25], Figure 3).

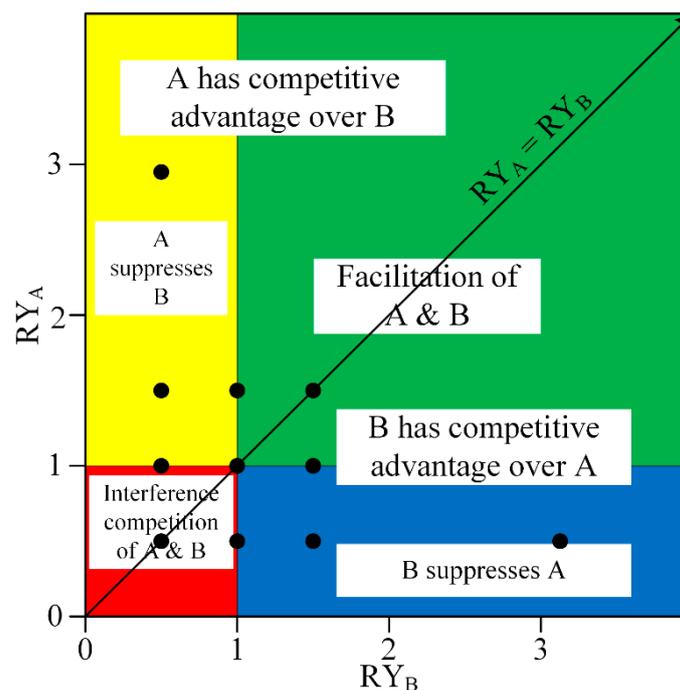


Figure 3. Graphic representation of all possible outcomes of a competition situation between two species (from Williams and McCarthy [25]). The 11 points on the figure are the relative yield (RY) values. Note that these dots span a wide range of outcomes. The diagonal reference line denotes the area of the graph in which species A has competitive advantage over species B (above the line $RY_A = RY_B$) and the area where B has a competitive advantage over A (below the line $RY_A = RY_B$). The area of red indicates both species A and B were suppressed in competition. The area of yellow indicates species B was reduced in competition, but species A performed better in competition, so species A had a clear advantage over species B. The area of green indicates both species performed better in the competition than they did in no competition, showing facilitation of both species. The area of blue indicates species B performed better in competition and suppressed species A.

All data analyses were conducted in R (R Development Core Team, 2019). The normality of the data and the homogeneity of variances were tested by Shapiro–Wilk test and Bartlett’s test, respectively. Data that did not satisfy the normal distribution or the homogeneity of variance were square-root-transformed ($X = \sqrt{x}$) to make sure the prerequisites of the analysis of variance (ANOVA) were met. Two-way ANOVA was used to test the effects of water level and competition treatment using the “Anova” function (type III) in “car” package [26]. One-way ANOVA was used to test the effect of water level in each competition mode and the effect of competition at each water level. Tukey multiple comparisons using “HSD.test function” in “agricolae” package [27] were used to group differences of each treatment when the results of one-way ANOVA were significant. All figures were plotted using “ggplot2” package [28].

3. Results

3.1. Influence of Water Level and Competition on Plant Biomass

Both water level and competitive mode had a significant effect on total biomass of *C. lasiocarpa* and *C. pseudocuraica*, but their interaction only affected total biomass of *C. pseudocuraica* significantly (Figure 4). Total biomass of *C. lasiocarpa* decreased with the increasing of water level in no competition and shoot competition (Figure 4a, Tables A7 and A8). Different to *C. lasiocarpa*, water level had a significant effect on total biomass of *C. pseudocuraica* in shoot competition and full competition (Figure 4b, Tables A9 and A10), and competitive mode had significant effects at 20 cm and 30 cm water levels (Figure 4b, Tables A1 and A2).

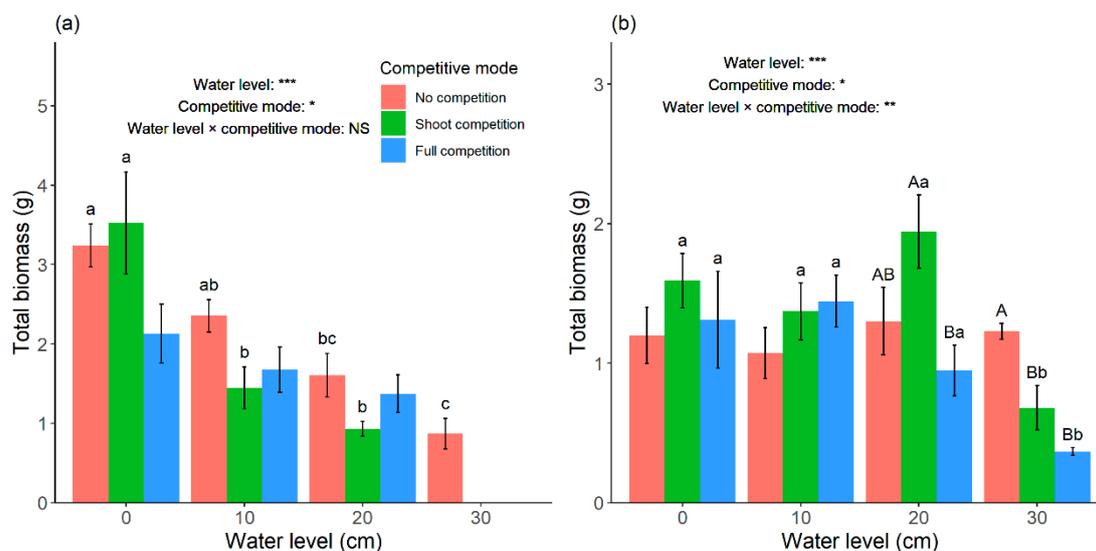


Figure 4. Total biomass (mean \pm SE) of (a) *C. lasiocarpa* and (b) *C. pseudocuraica* under different competition and water level conditions. As few individuals of *C. lasiocarpa* survived at 30 cm water level with the presence of competition, these data are not shown. Significance symbols of two-way ANOVA: ***, $p < 0.001$, **, $p < 0.01$, *, $p < 0.05$, and NS, no significance. Capital letters represent the differences between competitive modes at the same water level at $p < 0.05$. Lower cases represent the differences between water levels in the same competitive mode at $p < 0.05$.

Water level, competitive mode and their interaction had no significant effect on single shoot biomass of *C. lasiocarpa*, while water level and its interaction with competitive mode had a significant effect on single shoot biomass of *C. pseudocuraica* (Figure 5). There was no significant difference in single shoot biomass of *C. lasiocarpa* between competitive modes at each water level or between water levels in each competitive mode (Figure 5a). Water levels had a significant effect on single shoot biomass of

C. pseudocuraica in all competitive modes (Figure 5b, Tables A11–A13), and competitive mode had a significant effect at 30 cm water level (Figure 5b, Table A3).

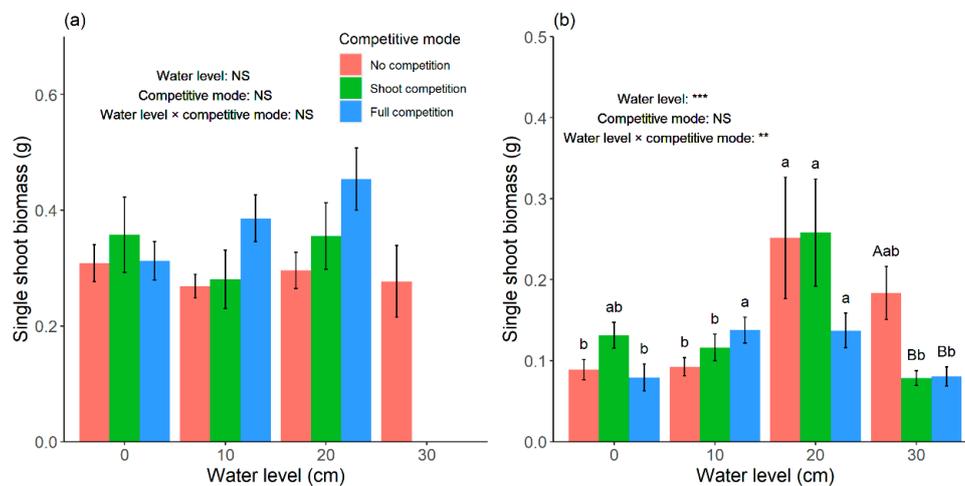


Figure 5. Single shoot biomass (mean \pm SE) of (a) *C. lasiocarpa* and (b) *C. pseudocuraica* under different competition and water level conditions. As few individuals of *C. lasiocarpa* survived at 30 cm water level with the presence of competition, these data are not shown. Significance symbols of two-way ANOVA: *** $p < 0.001$, ** $p < 0.01$, NS no significance. Capital letters represent the differences between competitive modes at the same water level at $p < 0.05$. Lower cases represent the differences between water levels in the same competitive mode at $p < 0.05$.

3.2. Influence of Water Level and Competition on Clonal Growth

Water level and competitive mode had a significant effect on propagule amount of *C. lasiocarpa*, while only water level had a significant effect on propagule amount of *C. pseudocuraica* (Figure 6). Propagule amount of *C. lasiocarpa* decreased significantly with increasing water levels in no competition and shoot competition (Figure 6a, Tables A14 and A15), and differed significantly in different competitive modes at 0–20 cm water levels (Figure 6a, Tables A4–A6). As to propagule amount of *C. pseudocuraica*, water level had a significant effect only in full competitive mode (Figure 6b, Table A16).

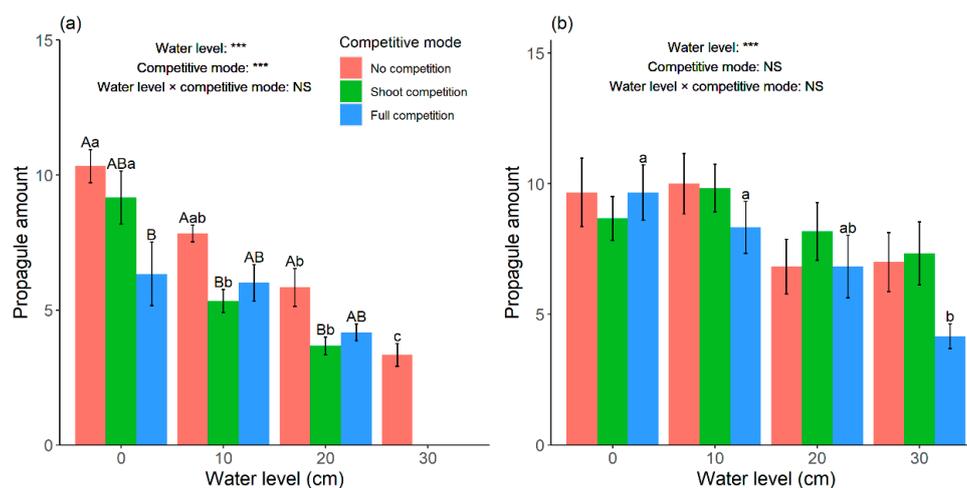


Figure 6. Propagule amount (mean \pm SE) of (a) *C. lasiocarpa* and (b) *C. pseudocuraica* under different competition and water level conditions. As few individuals of *C. lasiocarpa* survived at 30 cm water level with the presence of competition, these data are not shown. Significance symbols of two-way ANOVA: *** $p < 0.001$, NS no significance. Capital letters represent the differences between competitive modes at the same water level at $p < 0.05$. Lower cases represent the differences between water levels in the same competitive mode at $p < 0.05$.

3.3. Influence of Water Level and Competition on Biomass Allocation

Root/shoot ratio of both *C. lasiocarpa* and *C. pseudocuraica* was only significantly affected by water level (Figure 7). Root/shoot ratio of both *C. lasiocarpa* and *C. pseudocuraica* decreased significantly with increasing water level at each competitive mode (Figure 7, Tables A17–A22).

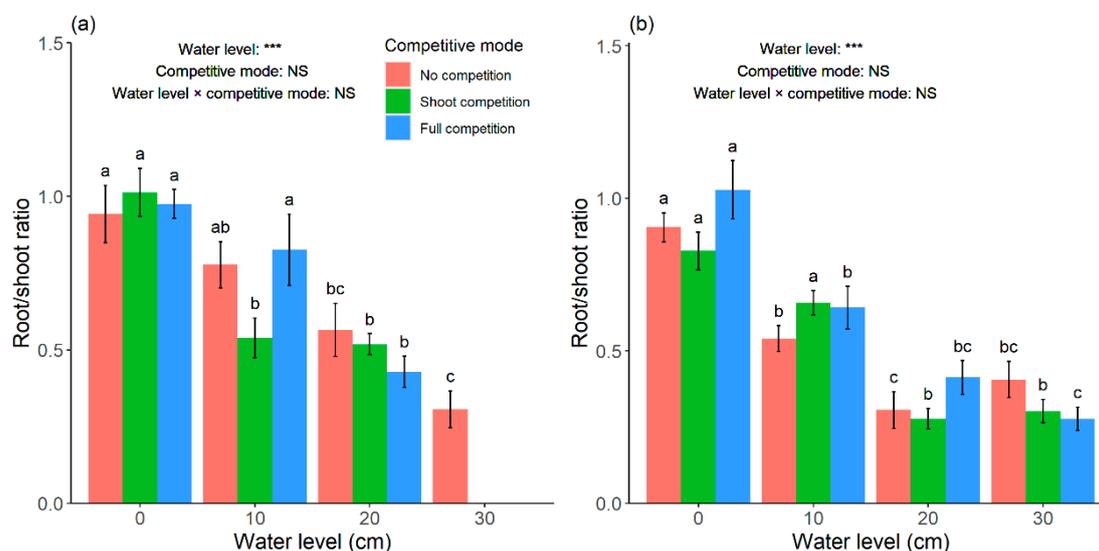


Figure 7. Root/shoot ratio (mean \pm SE) of (a) *C. lasiocarpa* and (b) *C. pseudocuraica* under different competition and water level conditions. As few individuals of *C. lasiocarpa* survived at 30 cm water level with the presence of competition, these data are not shown. Significance symbols of two-way ANOVA: *** $p < 0.001$, NS no significance. Lower cases represent the differences between water levels in the same competitive mode at $p < 0.05$.

3.4. Influence of Water Level on the Competitive Ability of Plants

In full competition, the competitive ability of *C. lasiocarpa* was strengthened with the increase in water level, whether evaluated by relative total biomass or relative single shoot biomass (Figure 8a,c). The competitive ability of *C. lasiocarpa* was always weaker than that of *G. spiculosa* when evaluated by relative total biomass (Figure 8a), whereas the competitive ability of *C. lasiocarpa* varied from weaker to greater than that of *G. spiculosa* when evaluated by relative single shoot biomass (Figure 8c). Different from *C. lasiocarpa*, *C. pseudocuraica* only beat *G. spiculosa* at 10 cm water level when evaluated by both relative total biomass and relative single shoot biomass (Figure 8b,d).

In shoot competition, the relative competitive ability of *C. lasiocarpa* to *G. spiculosa* had no regular trends, whether evaluated by relative total biomass or relative single shoot biomass (Figure 8a,c). The relative competitive ability of *C. pseudocuraica* was always superior to that of *G. spiculosa*, except at 30 cm water level (Figure 8b,d).

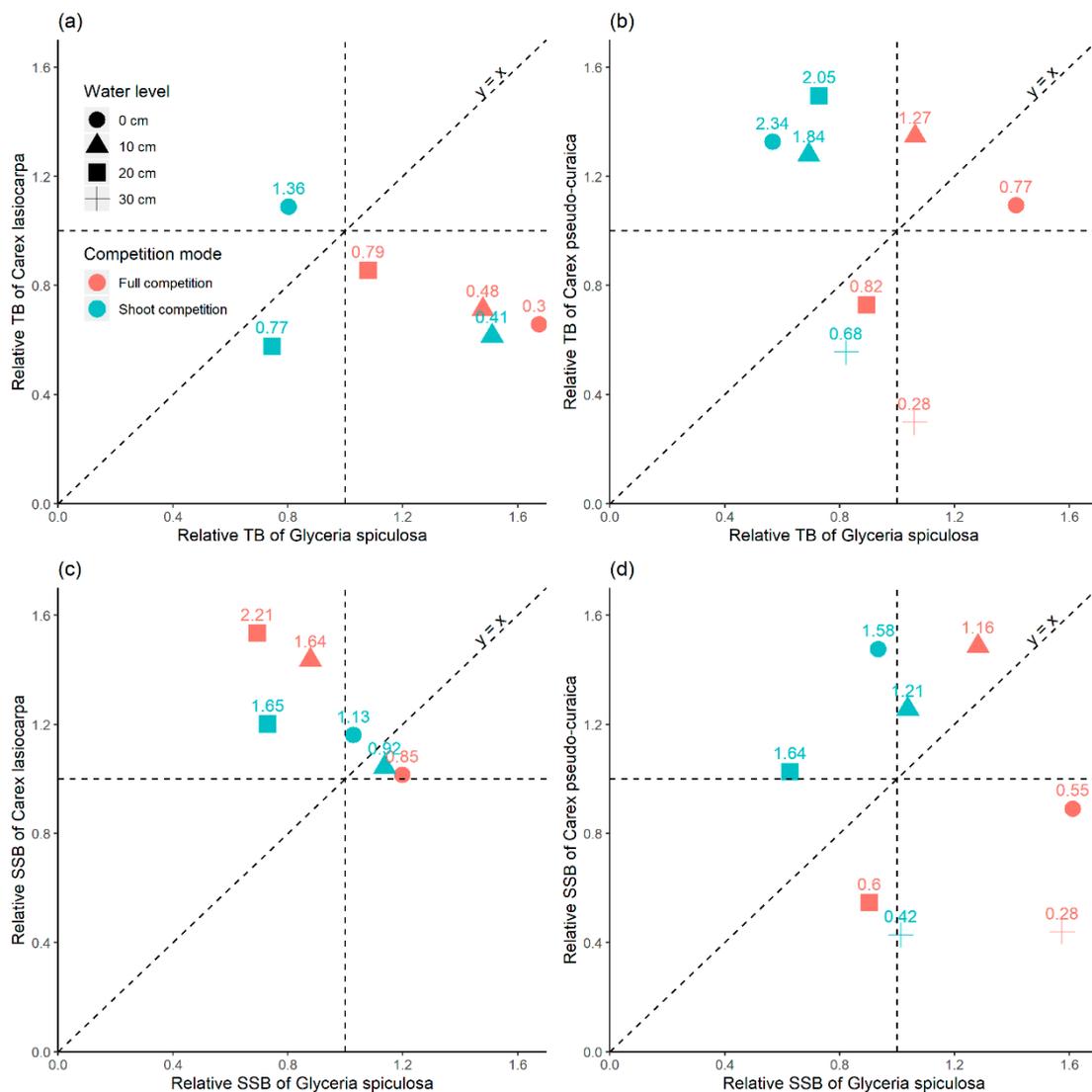


Figure 8. Relative competitive ability of (a) *C. lasiocarpa* vs. *G. spiculosa* evaluated by relative total biomass, (b) *C. pseudocuraica* vs. *G. spiculosa* evaluated by relative total biomass, (c) *C. lasiocarpa* vs. *G. spiculosa* evaluated by relative single shoot biomass, and (d) *C. pseudocuraica* vs. *G. spiculosa* evaluated by relative single shoot biomass. The numbers next to the symbols are their slopes, indicating the relative competitive ability.

4. Discussion

C. lasiocarpa, and *C. pseudocuraica* are typical plant species in Sanjiang Plain wetlands, and they generally occupy niches with similar hydrological conditions [19]. In the present research, a controlled experiment was set up to explore the influence of water level and interspecific competition with *G. spiculosa* on these two *Carex* species.

According to our results, total biomass of *C. lasiocarpa* decreased as the water level increased in no competition conditions, which was consistent with the results of Luo et al. [8] and Zhang et al. [9]. The effects of water level on total biomass and propagule amount of *C. lasiocarpa* were similar (Figure 4a and Figure 6a). This indicated the fundamental water level niche of *C. lasiocarpa* was no more than 0 cm when evaluated by the total biomass and propagule amount indices. However, no significant differences in single shoot biomass of *C. lasiocarpa* were observed among the four water levels (Figure 5a). As *C. lasiocarpa* is clonal plant, total biomass and propagule amount could represent the characteristics of a genetic individual, while single shoot biomass could represent the characteristics

of a physiological individual [29]. Our results suggested that the physiological individual and the whole genetic individual of *C. lasiocarpa* use different trade-off strategies for surviving flooding stress. Genetic individuals were inhibited by deep water, whereas physiological individuals were not.

Unlike *C. lasiocarpa*, there was no significant difference in total biomass and propagule amount of *C. pseudocuraica* in no competition among the four water levels ($p > 0.05$). When evaluated by single shoot biomass, *C. pseudocuraica* preferred a deeper water level (Figure 5b), which indicated that it had better resistance ability than *C. lasiocarpa* under flooding stress. As the stems and leaves of *C. pseudocuraica* are functionally plastic, e.g., they can have an increased number and thickness of vascular bundles in stems and leaves, elongated internode length, and more air cavities under flooding stress [30–32]. Thus, *C. pseudocuraica* is capable of adapting to large water level amplitude [33]. Furthermore, because of the opposite trends of single shoot biomass and propagule amount of *C. pseudocuraica* in this study, it could be inferred that in conditions of increased water levels, more resources were used for the preservation of physiological individuals than for clonal reproduction. This could also help to explain why *C. pseudocuraica* was better adapted to the deep water conditions than *C. lasiocarpa* during the experimental period.

Root/shoot ratio showed a downward trend in the two *Carex* species with the increase in water level in no competition (Figure 7), which was similar to the results of Shi et al. [22] and Zhang et al. [9]. Interspecific competition did not significantly affect root/shoot ratio (Figure 7), indicating that plants allocated more resources or energy to the shoots than to the roots in order to acquire more light and air, which aids photosynthesis [34]. According to Cahill [35], plants can alter root–shoot allocation in response to environmental conditions under certain conditions, which is also supported by the growth–balance hypothesis (optimal foraging theory), which states that plants prioritize resource allocation to organs responsible for acquiring the most limited resources [36]. These resource allocation characteristics could explain, to some extent, the variations of root/shoot ratio under flooding stress in the present study.

In the natural inundated wetlands of the Sanjiang Plain, the optimum water level niche of *C. lasiocarpa* generally varied from 13 to 29 cm with an optimal growing point of 21 cm [20]. Similar to *C. lasiocarpa*, *C. pseudocuraica* was mostly distributed in the water level niche of 13–30 cm [19]. Therefore, the realistic water level niches of *C. lasiocarpa* and *C. pseudocuraica* largely overlapped. This could not be the actual situation when competitions exist. In the current research, although total biomass of *C. lasiocarpa* was not significantly influenced by competition modes, there existed the trend that competitive suppression by *G. spiculosa* in full competition was decreasing along increasing water level (Figure 4a). By contrast, total biomass of *C. pseudocuraica* was relatively constant along water levels under no competition, but the competitive suppression by *G. spiculosa* increased when water level was higher than 10 cm (Figure 4b). Therefore, we could infer that the physiological niche of *C. lasiocarpa* is emerged habitats, where the water level is 0 cm or lower; however, in a field environment, the coexistence of competitors and the relatively better adaptation of *C. lasiocarpa* drive it away from emerged habitats. On the contrary, the actual water level niche of *C. pseudocuraica* could tend to be far away from deep water. The interspecific competition could thus play an important role in the spatial differentiation of the actual water level niche of the two *Carex* species.

According to the variations of propagule amount under different competition modes along the increase in water level (Figure 6a), *C. lasiocarpa* tended to modulate resources allocation by reducing clonal reproduction to survive in the competition with *G. spiculosa*. The slope change of relative single shoot biomass and relative total biomass between *C. lasiocarpa* and *G. spiculosa* also indicated that the stress imposed by *G. spiculosa* on *C. lasiocarpa* showed a decreasing trend with increasing water level (Figure 8a,c), and this is consistent with the actual distribution of these species in natural wetland ecosystems [19,20]. The performances of *C. lasiocarpa* and *G. spiculosa* are in accordance with Ellenberg's rule which states that competition can drive the distribution of a species away from its physiological optimum [37]. Our results showed that based on its competitive ability and individual physiological performance, *C. lasiocarpa* tended to choose a deeper water level niche in competition with *G. spiculosa*

compared to that in no competition. The hydrological niche segregation could mediate the coexistence of plants with similar hydrological niches and finally determine their actual distribution in wetlands.

At full competition (*C. pseudocuraica* vs. *G. spiculosa*), the slopes of relative total biomass and relative single shoot biomass at 0, 20 and 30 cm were smaller than 1 (Figure 8b,d), indicating that shallow (0 cm) or relatively deep (>10 cm) water level are not optimal for the survival of *C. pseudocuraica*. However, *C. pseudocuraica* has greater adaptability than *G. spiculosa* at 10 cm water level, which has been suggested by the high slopes (>1) of relative total biomass and relative single shoot biomass (Figure 8b,d). According to our field observations, *C. pseudocuraica* communities tend to be the first plants that colonize the waterlogged area after trampling disturbances, and their tangled roots (dead and alive) could gradually form floating organic layers, which often perform the similar function of soil. Considering the clonal reproduction mode of *C. pseudocuraica* and the fact that it could be suppressed by *G. spiculosa* in deep water level, we infer that *C. pseudocuraica* often acts as the pioneer plant in natural wetlands and could further benefit the growth of other plants.

The stress-gradient hypothesis predicts a shift from net negative interactions in benign environments to net positive interactions in harsh environments [15], which means that in Figure 3, in cases when the flooding stress was strong enough, the relative indices should be located in top green area (Facilitation of A and B). As evaluated by relative total biomass, in the relationship between *C. lasiocarpa* and *G. spiculosa*, only *G. spiculosa* was facilitated. Generally, in this research, facilitation changed to competition with the increase in flooding stress (Figure 8). This may be because flooding is a non-resource stress in permanently inundated wetlands of the Sanjiang Plain. Although in permanently flooded wetlands, water availability is not a limited resource, other resources, such as rhizosphere air, could be limited by flooding. Our results were consistent with an alternative of stress-gradient hypothesis of that facilitation generally switches to competition in highly flooding stressed conditions [17].

Competitive response is associated with traits related to resource acquisition [38]. As root competition is more size-symmetric than shoot competition and involves multiple resources [39], root competition and shoot competition will show different characteristics. Here, we inferred root competition ability from the difference between the slope of full competition. At 0 cm water level, shoot competitive ability of *C. lasiocarpa* was greater than that of *G. spiculosa*, and root competition ability weaker than that of *G. spiculosa* (Figure 8a). However, it was the opposite at 10 and 20 cm water level. The relative changes in root competition abilities between *C. lasiocarpa* and *G. spiculosa* along water levels could be the main reason why the realistic niche of *C. lasiocarpa* was quite different from its physiological one. When comparing the relative competitive abilities between *C. pseudocuraica* and *G. spiculosa*, we found the shoot competitive ability of *C. pseudocuraica* was greater than that of *G. spiculosa*, and root competitive ability was weaker than that of *G. spiculosa* at 0–20 cm water levels. At 30 cm water level, both shoot and root competitive abilities of *C. pseudocuraica* were weaker than those of *G. spiculosa* (Figure 8b). These results suggested that the relatively weak position of *C. pseudocuraica* when competing with *G. spiculosa* could mainly be ascribed to its low root competition ability.

5. Conclusions

The species *C. lasiocarpa* and *C. pseudocuraica* are two dominant *Carex* species with similar niches inhabiting the inundated wetlands of the Sanjiang Plain. Our experiments indicated that the two *Carex* species generally exhibited similar survival strategies in response to the change in water levels in the absence of interspecific competition. Both *Carex* species tended to preserve their physiological individuals to adapt to flooding environment. In full competition with *G. spiculosa*, the increase in hydrological stress weakened the suppression of *G. spiculosa* on *C. lasiocarpa*, whereas it enhanced the suppression of *G. spiculosa* on *C. pseudocuraica*, which could explain to a large extent the actual spatial distribution difference of the two *Carex* species in the inundated wetlands of the Sanjiang Plain. As our experiment lasted for only one growing season, the response of wetland plants to varying water levels and interspecific competition could be different at larger time scales under more complex conditions,

and more observations are undoubtedly needed to further unveil the underlying mechanisms of the zonation characteristics of wetland plants.

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Appendix A

Table A1. Effects of competitive modes on the total biomass of *Carex pseudocuraica* at 20 cm water level.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	21.3597	1	902.6277	<0.001
Competition Mode	0.2203	2	4.6555	0.02674
Residuals	0.355	15		

Table A2. Effects of competitive modes on the total biomass of *Carex pseudocuraica* at 30 cm water level.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	13.8368	1	1063.238	<0.001
Competition Mode	0.3886	2	14.931	0.00027
Residuals	0.1952	15		

Table A3. Effects of competitive modes on the single shoot biomass of *Carex pseudocuraica* at 30 cm water level.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	3.9722	1	996.9008	<0.001
Competition Mode	0.07	2	8.7795	0.00299
Residuals	0.0598	15		

Table A4. Effects of competitive modes on the propagule amount of *Carex lasiocarpa* at 0 cm water level.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	73.638	1	1780.7348	<0.001
Competition Mode	0.41	2	4.9621	0.02218
Residuals	0.62	15		

Table A5. Effects of competitive modes on the propagule amount of *Carex lasiocarpa* at 10 cm water level.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	61.154	1	4103.6181	<0.001
Competition Mode	0.191	2	6.4106	0.009724
Residuals	0.224	15		

Table A6. Effects of competitive modes on the propagule amount of *Carex lasiocarpa* at 20 cm water level.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	48.5	1	2654.6789	<0.001
Competition Mode	0.2	2	5.4701	0.01644
Residuals	0.274	15		

Table A7. Effects of water level on the total biomass of *Carex lasiocarpa* in no competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	13.0246	1	583.739	<0.001
Water level	1.0131	3	15.134	<0.001
Residuals	0.4462	20		

Table A8. Effects of water level on the total biomass of *Carex lasiocarpa* in shoot competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	13.1397	1	300.5627	<0.001
Water level	0.8418	2	9.6277	0.002043
Residuals	0.6558	15		

Table A9. Effects of water level on the total biomass of *Carex pseudocuraica* in shoot competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	8.0228	1	343.7193	<0.001
Water level	0.5012	3	7.1577	0.001885
Residuals	0.4668	20		

Table A10. Effects of water level on the total biomass of *Carex pseudocuraica* in full competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	6.6914	1	318.5568	<0.001
Water level	0.5755	3	9.1324	<0.001
Residuals	0.4201	20		

Table A11. Effects of water level on the single shoot biomass of *Carex pseudocuraica* in no competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	1.16708	1	138.097	<0.001
Water level	0.11532	3	4.5486	0.0138
Residuals	0.16902	20		

Table A12. Effects of water level on the single shoot biomass of *Carex pseudocuraica* in shoot competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	1.51934	1	250.8466	<0.001
Water level	0.11495	3	6.3261	0.003416
Residuals	0.12114	20		

Table A13. Effects of water level on the single shoot biomass of *Carex pseudocuraica* in full competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	1.05173	1	271.899	<0.001
Water level	0.04638	3	3.997	0.02214
Residuals	0.07736	20		

Table A14. Effects of water level on the propagule amount of *Carex lasiocarpa* in no competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	28.3592	1	1610.124	<0.001
Water level	1.5811	3	29.924	<0.001
Residuals	0.3523	20		

Table A15. Effects of water level on the propagule amount of *Carex lasiocarpa* in shoot competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	25.8904	1	1194.154	<0.001
Water level	0.8983	2	20.716	<0.001
Residuals	0.3252	15		

Table A16. Effects of water level on the propagule amount of *Carex pseudocuraica* in full competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	26.8495	1	640.1095	<0.001
Water level	0.907	3	7.2081	0.00182
Residuals	0.8389	20		

Table A17. Effects of water level on the root/shoot ratio of *Carex lasiocarpa* in no competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	5.3267	1	139.111	<0.001
Water level	1.3621	3	11.858	<0.001
Residuals	0.7658	20		

Table A18. Effects of water level on the root/shoot ratio of *Carex lasiocarpa* in shoot competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	6.1534	1	267.465	<0.001
Water level	0.9406	2	20.442	<0.001
Residuals	0.3451	15		

Table A19. Effects of water level on the root/shoot ratio of *Carex lasiocarpa* in full competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	5.7064	1	157.847	<0.001
Water level	0.9594	2	13.269	<0.001
Residuals	0.5423	15		

Table A20. Effects of water level on the root/shoot ratio of *Carex pseudocuraica* in no competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	4.9107	1	288.668	<0.001
Water level	1.2337	3	24.173	<0.001
Residuals	0.3402	20		

Table A21. Effects of water level on the root/shoot ratio of *Carex pseudocuraica* in shoot competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	4.1117	1	346.326	<0.001
Water level	1.318	3	37.005	<0.001
Residuals	0.2374	20		

Table A22. Effects of water level on the root/shoot ratio of *Carex pseudocuraica* in full competition.

	Sum of Squares	Degree of Freedom	F Value	Probability (>F)
(Intercept)	6.3417	1	230.559	<0.001
Water level	1.9427	3	23.543	<0.001
Residuals	0.5501	20		

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