NOTE

Effect of clone size on submergence tolerance and post-submergence growth recovery in *Carex brevicuspis* (Cyperaceae)

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ABSTRACT

Clonal plants are prevalent in wetlands and play important roles in maintaining the functions of the ecosystem. In the present study, we determined the effect of clone sizes (R1, R2, and R3 comprising 1, 3, and 5clumping ramets) on the tolerance of *Carex brevicuspis* growing under 30-cm-deep water to three different periods (one, two, and three months) of submergence and its growth recovery one month after de-submergence. Our results showed that the relative growth rate (RGR) of *C. brevicuspis* significantly declined with increasing submergence time, and was higher in R3 and R5 than in R1 plants under both submergence and post-submergence conditions. The concentration of water-soluble carbohydrates (WSCs) was highest in R3, intermediate in R5, and the lowest in R1 plants during the first two months of submergence, indicating an optimal trade-off between energy investment and vegetative growth (*i.e.*, buds and ramets production) in *C. brevicuspis*. WSCs were significantly reduced with increasing submergence time, while the starch content was significantly reduced only during the third month of submergence, implying that WSCs were a direct energy source for *C. brevicuspis* during submergence. The number of buds was higher in R5 than in R3 and R1 plants after two and three months of submergence, which directly resulted in a significantly higher post-submergence ramet production in R5 plants. These results indicated that plants with relatively larger clone sizes display better tolerance to submergence stress and post-submergence growth recovery. Therefore, we speculate that the large clone size in *C brevicuspis* might be an effective adaptive mechanism to survive under submergence stress in floodplain wetlands.

Key words: Clone size; growth recovery; submergence; stress; tolerance.

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INTRODUCTION

Clonal plants are the dominant plant species in many ecosystems, especially in grasslands and wetlands. Clonal integration through interconnected ramets is not only advantageous for resource acquisition and habitat expansion (Bernard, 1990; Dong and Pierdominici, 1995; Alpert, 1999), but also plays an important role in enhancing competition abilities leading to increased population dominance in plant communities (Schmid and Harper, 1985; Kleunen *et al.,* 2001). In recent years, numerous studies have been conducted to investigate the effects of clone size on plants growing in stressful environments. These studies reported that the plants with relatively larger clone sizes displayed significantly increased expansion abilities, such as sprouting and branching, than those with smaller clone sizes, when facing sediment burial or nutrient shortage (Kleunen *et al.,* 2001; Deng *et al.,* 2013a; Li *et al.,* 2015). This indicated that the clone size might be an important factor influencing the resistance of clonal plants to environmental stresses.

In floodplain wetlands, flooding regimes are considered as key factors regulating vegetation development (Luo *et al.,* 2008; Li *et al.,* 2013). Under flooding conditions, wetland plants generally sustain their anaerobic metabolism by consuming carbohydrates such as water-soluble carbohydrates (WSCs) and starch (Blom *et al.*, 1994; Macek *et al.*, 2006). Therefore, the carbohydrate content in plants, especially in their roots, might directly control their fate under adverse conditions. Plants with relatively larger clone sizes, which can accumulate more photosynthetic carbohydrates, might be more efficient in resisting flooding stress than those with smaller clone sizes (Colmer and Voesenek, 2009; Manzur *et al.*, 2009). Additionally, carbohydrates are more efficiently transferred from the 'source' (*i.e.*, mother plant) to the 'sink' (*i.e.*, ramets) in relatively larger clones owing to the clonal integration of the ramets, which in turn enhances the energy-use efficiency and spreads the risk of mortality in whole plants growing under environmental stresses (Dong, 1996).

Rapid post-submergence growth recovery is a typical characteristic of most floodplain wetland plants (Parolin *et al.,* 2010). Similar to flood tolerance, the recovery ability of plants depends upon their carbohydrate content because carbohydrate shortage can severely restrict plant

growth and even cause plant death (Panda *et al.*, 2008). In contrast, high carbohydrate content provides energy for rapid compensatory growth of plants after de-submergence (Roseff and Bernard, 1979; Qin *et al.*, 2013). Additionally, the ability of clonal plants to recover their growth is depends on their bud bank size (Chalwell and Ladd, 2005; Deng *et al.*, 2013b). Plants with relatively larger clone sizes might allocate more carbohydrates to their bud banks (Zhao *et al.*, 2007), thereby enhancing their growth-recovery ability, which might be one of the ecological roles of tussock formation in clonal plants. However, further experimental studies are required to clarify the relations among energy content, bud bank allocation, and plant growth-recovery ability in various clonal plants with different clone sizes.

Carex brevicuspis C.B. Clarke (Cyperaceae), a dominant non-stem species, grows in a modular fashion and reproduces vegetatively by rhizomes (Bernard, 1990). The clonal structure of *C. brevicuspis* comprises a population of ramets formed by rhizomes and the plant height is usually 20-55 cm (Chen *et al.*, 2011), and the clonal size is 10-20 cm in diameter (comprising 200-300 ramets) by the end of the growing season (ZD, personal observation). After the periodic flooding of Dongting Lake from May to October, *C. brevicuspis* displays rapid vegetative growth from October to December, remains dormant with plenty of rhizomes from January to February, sprouts in March, and flowers and fruits from April to May. In the present study, the submergence tolerance and recovery ability of *C. brevicuspis* with different clone sizes (R1, R3, and R5 comprising 1, 3, and 5 ramets respectively) were studied to test whether plants with relatively large clone sizes can more effectively resist submergence stress and show faster post-submergence growth recovery. We hypothesized that: i) under submergence, plants with relatively large clone sizes are more efficient in tolerating environmental stress. Specifically, the relative growth rate (RGR), and WSC and starch contents would be the lowest in R1, intermediate in R3, and the highest in R5 plants; ii) plants with relatively large clone sizes would exhibit rapid growth recovery after de-submergence than those with smaller clone sizes. Specifically, the RGR, and WSC and starch contents would increase more rapidly in plants with relatively large clone sizes; iii) the plants with relatively large clone sizes would produce more buds during submergence and, therefore, produce more new daughter ramets after de-submergence.

METHODS

Experimental design

Approximately 200 ramets were collected randomly from the sampling site (29°30′ N, 112°48′ E) of the Dongting Lake Station for Wetland Ecosystem Research, a member of the Chinese Ecosystem Research Network (CERN). The ramets were transported to a greenhouse maintained at a temperature of 25±2°C during the day and 17±2°C during the night, and illuminated by 400W SON-T ARGO sodium lamps (Philips, Guildford, UK) at a photon flux density of 600 µmol m^{-2} s^{-1} (PAR) with a 14-h photoperiod. Each ramet was detached and transplanted into a separate polyvinyl chloride (PVC) tube (20 cm in height and 11 cm in diameter) that was filled with 20-cm soil from the habitat of *C. brevicuspis* (containing 1.86% organic matter, 0.19% total N, and 0.08% total P). These plants were watered daily, and after the regeneration of new ramets (approximately 15 cm in height), they were classified into three types according to the total number of ramets: R1 (one ramet), R3 (three ramets), and R5 (five ramets).

Before treatment, three tubes for each plant type were selected to measure the plant biomass and non-structural carbohydrate (WSC and starch) contents as an initial point (*i.e.*, control). Subsequently, 18 PVC tubes (six tubes for each plant type) were transferred into a plastic tank (88 × 67 × 63 cm), and completely submerged in 30-cm-deep water above the soil surface. Each treatment was repeated six times (*i.e.*, six tanks and 108 PVC tubes in total). During submergence, two tubes of each plant type *per* tank were de-submerged each month. One was used to measure the submergence tolerance (as evaluated by RGR, and number of buds) and non-structural carbohydrate (WSC and starch) contents, and the other was used to evaluate the growth recovery by putting it into a tank with 0-cm water level (relative to the soil surface). One month after the recovery, the plants were harvested to determine their growth-recovery ability [as evaluated by biomass per ramet (RGR), and number of new ramets] and non-structural carbohydrate (WSC and starch) contents. The experiment was started on May 6, 2012, and ended on September 6, 2012.

Harvest and determination of the biomass and RGR

The ramets were carefully harvested from the PVC tubes, and the soil and dead tissues were removed by rinsing under running tap water. Each ramet was separated, and the number of buds *per* plant and ramet were recorded. Subsequently, all plant parts (leaves, roots, and buds) were separately dried in an oven at 65°C for 48 h, and their dry mass was measured. Because the plant biomass was significantly different among the three plant types initially, the relative growth rate (RGR) was used to elucidate the growth response under submergence and post-submergence conditions

$$\text{RGR} = \frac{\ln(w_2) - \ln(w_1)}{t_2 - t_1} \qquad \text{(eq. 1)}$$

where w_2 represents the biomass at harvest, and w_1 is the biomass of the last month.

Non-structural carbohydrate analysis

The soluble sugar content was determined by using the total hydrolysable reducing sugars method (Yemm and Willis, 1954). In brief, the root samples were dried in an oven at 65°C for 48 h, ground into fine powder, and extracted three times with 80% ethanol (vv^{-1}). The extract was used for soluble sugar analysis after the addition of anthrone reagent, followed by the measurement of absorbance at 630 nm using a spectrophotometer. The residue remaining after soluble sugar extraction was dried and extracted using 30% perchloric acid, and analyzed for starch (as glucose equivalent) content by adding anthrone reagent and measuring the absorbance at 630 nm.

Statistical analysis

The number of buds, RGR, and WSC and starch contents under submergence conditions were analyzed by repeated-measures ANOVA using time as the repeated-measures factor and clone size as the main factor. The number, RGR, and WSC and starch contents of new ramets after one month of growth recovery were analyzed by using two-way ANOVA, with submergence period and clone size as fixed factors. The data were $\log_{10}$-transformed, if necessary, to reduce the heterogeneity of variances, and homogeneity was assessed using Levene's test. Multiple comparisons of means between different clone sizes were performed by Tukey's test at the 0.05 significance level. A P-value <0.05 was considered significant. All statistical analyses were performed using the SPSS software v 18.0 (SPSS Inc., USA).

RESULTS

Plant growth, bud production, and non-structural carbohydrate content under submergence

Submergence time and clone size had a significant effect on the RGR of new ramets, and the interaction between both factors was significant (repeated-measures ANOVA, P<0.01; Tab. 1). The RGR of R1 plants was significantly lower than that of R3 and R5 plants during the first and the second months of submergence, with -0.028±0.002 g g^{-1} d^{-1} and -0.016±0.002 g g^{-1} d^{-1}, respec-

tively (P<0.001; Fig. 1). However, no significant difference was observed in the RGR of the three plant types during the third month of submergence (P>0.05; Fig. 1).

Submergence time and clone size had also a significant effect on the total number of buds and displayed a significant interaction (P<0.01; Tab. 1). The total number of buds increased significantly with increasing submergence time in R5 plants; however, it did not significantly change in R1 and R3 plants under submergence (Fig. 2). The number of buds was significantly higher in R5 plants than in R1 and R3 plants after two and three months of submergence (P<0.01; Fig. 2).

The WSC and starch contents were significantly reduced during submergence in all plant types (P<0.01; Tab. 1; Fig. 3). The WSC content was the highest in R3 plants, intermediate in R5, and the lowest in R1 plants after one month of submergence. However, these differences disappeared after two months of submergence (P>0.05; Fig. 3a). In contrast to the WSC content, the starch content slowly declined during the first two months after submergence
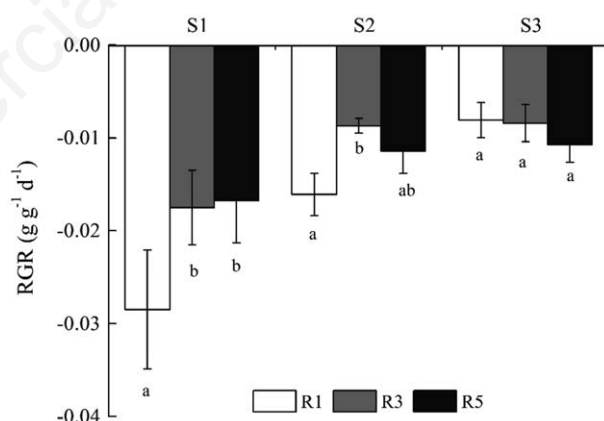
Fig. 1. Relative growth rate (RGR) (g g^{-1} d^{-1}) of R1, R3, and R5 plants under submergence. The data are presented as the mean ±SE (n=6). S1, submerged for one month; S2, submerged for two months; S3, submerged for three months. Different letters (a, b, and ab) represent significant differences among three clone sizes, and *ns* represents no significant difference among three clone sizes (α=0.05, Tukey's test).

Tab. 1. Summary of the repeated-measures ANOVA under submergence (*F* values).

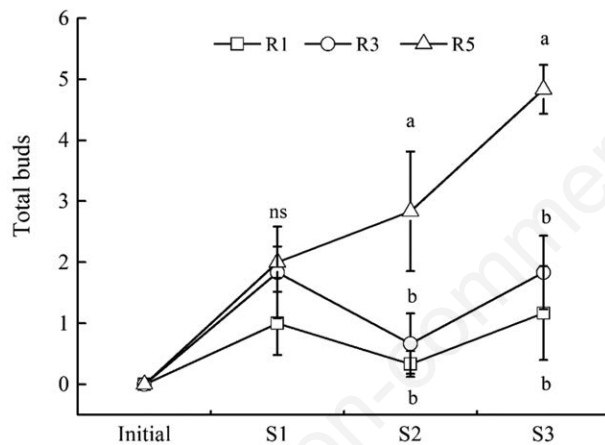| Variables	Time	Clone size	Time*Clone size
RGR	35.48**	4.22*	4.51**
Total buds	4.57*	16.87**	2.41[ns]
WSC content	137.64**	45.51**	54.73**
Starch content	275.06**	3.87*	2.01[ns]
df	2	2	4

*RGR, relative growth rate; WSC, water-soluble carbohydrate; *P<0.05; **P<0.01; ns, not significant; df: degrees of freedom.*

and sharply decreased after three months of submergence (P<0.01; Fig. 3b). The clone size of a plant had a significant effect on its starch content at one month after submergence, which was the highest in R1 and R3 plants and the lowest in R5 plants (P<0.05; Tab. 1; Fig. 3b).

Post-submergence plant growth response

Clone size and the submergence time had a significant effect on the RGR after one month of post-submergence growth recovery (P<0.05; Tab. 2). The RGRs of R3 and R5 plants were significantly higher than that of R1 plants, and increased with increasing submergence period (P<0.05; Fig. 4).

At the end of the one-month growth-recovery period following two months of submergence, the number of new ramets was significantly higher in R5 plants (2.8±0.7) that that in both R1 and R3 plants (1.4±0.4)

(P<0.05; Fig. 5a). After one month of growth recovery following three months of submergence, the number of new ramets was the highest in R5 plants (4.3±0.4), intermediate in R3 plants (2.7±0.5), and the lowest in R1 plants (1.6±0.2) (P<0.01; Fig. 5a). However, the biomass per ramet was the highest in R3 plants (0.41-0.49 g per ramet), intermediate in R5 plants (0.29-0.35 g per ramet)
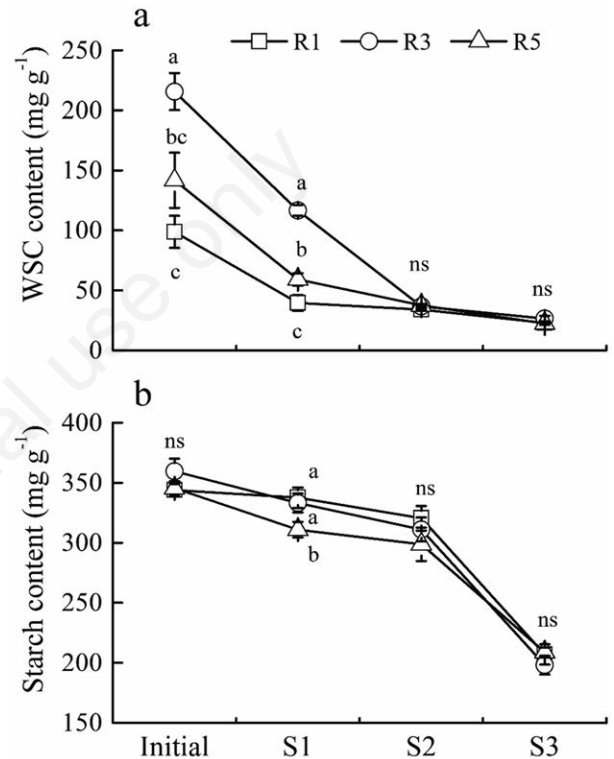
Fig. 3. Water-soluble carbohydrate (WSC; mg g^{-1}) (a) and starch content (mg g^{-1}) (b) of R1, R3, and R5 plants under submergence. The data are presented as the mean ±SE (n=6). S1, submerged for one month; S2, submerged for two months; S3, submerged for three months. Different letters (a, b, c, and bc) represent significant differences among three clone sizes, and *ns* represents no significant difference among three clone sizes (α=0.05, Tukey's test).

Fig. 2. Number of buds produced in R1, R3, and R5 plants under submergence. The data are presented as the mean ±SE (n=6). S1, submerged for one month; S2, submerged for two months; S3, submerged for three months. Different letters (a and b) represent significant differences among three clone sizes, and *ns* represents no significant difference among three clone sizes (α=0.05, Tukey's test).

Tab. 2. Summary of the Two-way ANOVA post-submergence (*F* values).

Variables	Submergence period (P)	Clone size (S)	P * S
RGR	45.04**	6.53*	0.10[ns]
New ramets	3.95*	5.22*	0.52[ns]
Biomass per ramet	0.26[ns]	20.25**	0.19[ns]
WSC content	4.07*	69.62**	2.38[ns]
Starch content	169.10**	3.36*	1.42[ns]
df	2	2	4

*RGR, relative growth rate; WSC, water-soluble carbohydrate; *P<0.05; **P<0.01; ns, not significant; df: degrees of freedom.*

and the lowest in R1 plants (0.25-0.29 g per ramet) at the end of the one-month period of post-submergence growth recovery (P<0.05; Fig. 5b).

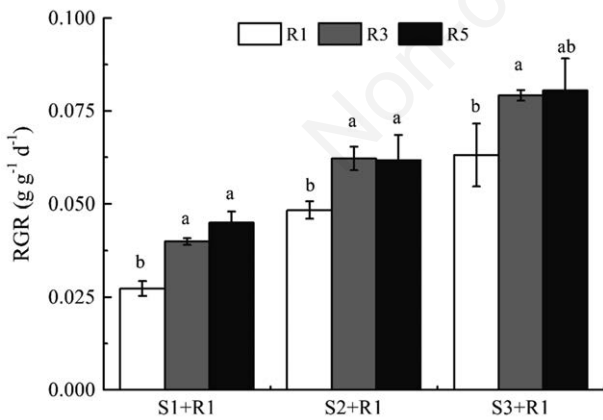### Non-structural carbohydrates content under post-submergence conditions

Regardless of the duration of the submergence period, the WSC content after recovery was significantly higher in R3 plants than in R1 and R5 plants (P<0.01; Fig. 6a). The accumulation of WSCs was significantly affected by the duration of the submergence period only in R5 plants (P=0.03; Fig. 6a). However, the starch content was significantly affected by the duration of the submergence period (Tab. 2; Fig. 6b). At the end of the one-month growth-recovery period, a sharp decrease in the starch content was observed for all plant types after both two and three months of submergence (P<0.01; Fig. 6b). The clone size had little effect on the post-submergence starch accumulation (P=0.05; Tab. 2; Fig. 6b).
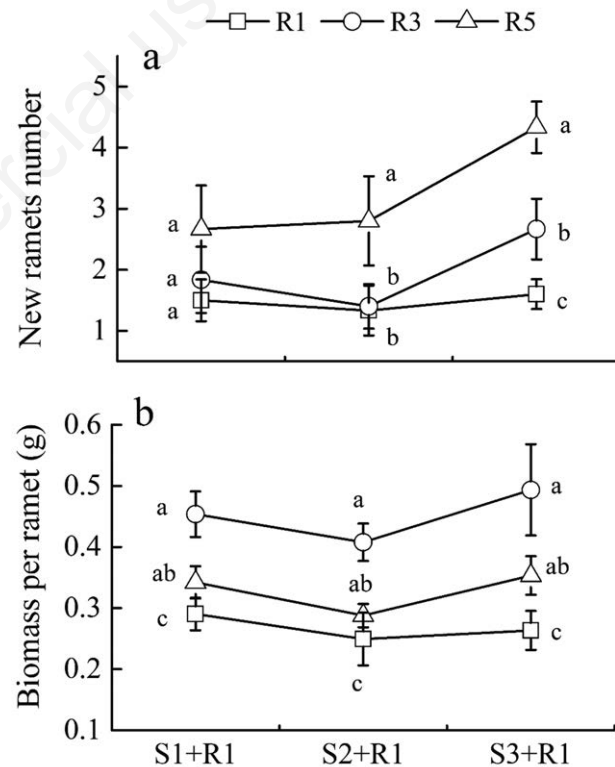
DISCUSSION

Our study showed that in *C. brevicuspis*, the plants with relatively large clone sizes can lead to tussock formation, which is advantageous not only for resource acquisition and habitat expansion, but also for environmental stress resistance and post-stress growth recovery. This might be the new ecological significance of

tussock formation in *Carex* populations, which has been neglected before.

Under submerged conditions, the RGR was significantly reduced in all plant types, indicating that the growth of *C. brevicuspis* was largely inhibited by submergence. The decreasing WSC and starch contents in all plant types under submergence indicated that these carbohydrates were consumed for metabolic maintenance and survival under submergence stress (Manzur *et al.*, 2009). The RGR of R1 plants was significantly lower than that of R3 and R5 plants during the first two months of submergence, indicating that the relatively large clone sizes offer a comparative advantage under submergence stress. However, no difference was observed in the RGRs of R3 and R5 plants during the first and the second months of submergence, while they were significantly higher than that of R1 plants, indicating the existence of

Fig. 5. Number of new ramets (a) and biomass accumulation per ramet (b) in R1, R3, and R5 plants after one month of post-submergence growth recovery. The data are presented as the mean ±SE (n=6). S1+R1, one month growth recovery after one month of submergence; S2+R1, one month of growth recovery after two months of submergence; S3+R1, one month of growth recovery after three months of submergence. Different letters (a, b, c, and ab) represent significant differences among three clone sizes, and *ns* represents no significant difference among three clone sizes (α=0.05, Tukey's test).
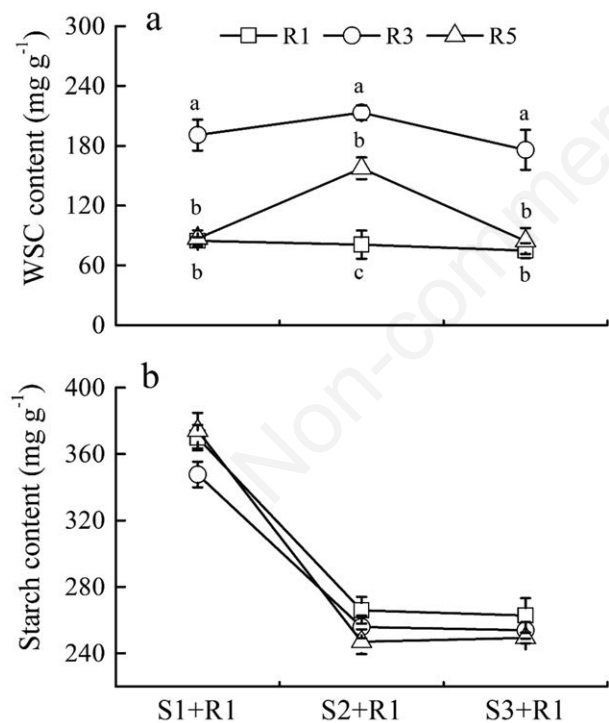

Fig. 4. Relative growth rate (RGR) of R1, R3, and R5 plants after one month of post-submergence growth recovery. The data are presented as the mean ± SE (n=6). S1+R1, one month growth recovery after one month of submergence; S2+R1, one month of growth recovery after two months of submergence; S3+R1, one month of growth recovery after three months of submergence. Different letters (a, b, and ab) represent significant differences among three clone sizes, and *ns* represents no significant difference among three clone sizes (α=0.05, Tukey's test).

an optimal trade-off between energy investment in plant growth and vegetative reproduction in *C. brevicuspis*. As the production of rhizomes, buds, and ramets consumes a lot of energy, the energy investment increases with increasing number of ramets (Suzuki and Stuefer, 1999; Marbà *et al.,* 2006; Ye *et al.,* 2006; Deng *et al.,* 2013a), which is in agreement with our study showing reduced WSC content and increased bud number in R5 plants. The differences in the RGRs of the three plant types disappeared during the third month of submergence, indicating that the perishable plant tissues might have decomposed during the first two months of submergence, and the remaining tissues would be less likely to decompose due to their active metabolism.

Plants usually consume carbohydrates to survive in stress conditions. Our study showed that the WSC content in all plant types rapidly decreased during the first two months of submergence, while the starch content sharply decreased during the third month of submergence. These

Fig. 6. Water-soluble carbohydrate (WSC; mg g^{-1}) (a) and starch content (mg g^{-1}) (b) of R1, R3, and R5 plants after one month of post-submergence growth recovery. The data are presented as the mean ±SE (n=6). S1+R1, one month growth recovery after one month of submergence; S2+R1, one month of growth recovery after two months of submergence; S3+R1, one month of growth recovery after three months of submergence. Different letters (a, b, and c) represent significant differences among three clone sizes, and *ns* represents no significant difference among three clone sizes (α=0.05, Tukey's test).

results indicated that the tolerance to submergence was related to the WSC content in plants as suggested by Qin *et al.* (2013). The observation that the starch content decreased only at a later period during submergence might be ascribed to the fact that starch cannot be directly utilized by the plants, and must first be transformed to soluble sugar (Zeeman *et al.,* 2010; Deng *et al.,* 2013a). Therefore, the higher ability of plants with relatively larger clone sizes to tolerate submergence stress might be attributed to their higher WSC contents.

After de-submergence, the RGR and the number of new ramets were significantly higher in R3 and R5 plants than in R1 plants, indicating higher growth-recovery ability in plants with relatively large clone sizes, which is consistent with our hypothesis. The starch content decreased sharply in all plant types at the end of the growth recovery period following two months of submergence, suggesting that starch might be the main energy source for plant growth during recovery as WSCs are exhausted during submergence (Zeeman *et al.,* 2010; Qin *et al.,* 2013). The number of new buds was significantly higher in R5 than in R1 and R3 plants, suggesting that the clonal plants with relatively larger clone sizes can allocate more energy for bud production, resulting in rapid post-submergence growth recovery. In fact, new ramets formed during recovery were shown to originate mainly from the bud bank formed under submergence conditions. However, the WSC content was higher in R3 plants than that in R5 plants after de-submergence, which was inconsistent with our hypothesis. Generally, the WSC content in plant tissues depends on the rates of carbon synthesis and consumption in plants (Wang, 2009).

Our experiment showed that R5 plants produced more ramets than R3 plants, but the biomass accumulation per ramet in R5 plants was significantly lower than that of R3 plants (Fig. 5), which suggested that R3 plants actually had a relatively higher carbon synthesis rate than R5 plants. These results also indicated the existence of a genotypic trade-off between the number and size of ramets in *C. brevicuspis* in a manner somewhat similar to a stoloniferous herb, *Potentilla reptans* L., which exhibits genotypic trade-off between the number and size of clonal offspring under different light-availability environments (Stuefer *et al.,* 2002).

CONCLUSIONS

Compared to the plants with smaller clone sizes, the plants with relatively larger clones showed better tolerance to submergence and better post-submergence growth recovery. This might be attributed to the high-energy contents in plants with large clones. Additionally, the plants with relatively larger clones produced more buds under submergence, which also directly improved their growth

recovery after de-submergence. Therefore, clone size expansion in *C.brevicuspis* may be an effective adaptive mechanism to survive under flooding conditions in floodplain wetlands.

REFERENCES

Alpert P, 1999. Effects of clonal integration on plant plasticity in *Fragaria chiloensis*. Plant Ecol. 141:99-106.

Bernard JM, 1990. Life history and vegetative reproduction in *Carex*. Can. J. Bot. 68:1441-1448.

Blom CWPM, Voesenek LaCJ, Banga M, Engelaar WMHG, Rijnders JHGM, Van De Steeg HM, Visser EJW, 1994. Physiological ecology of riverside species: adaptive responses of plants to submergence. Ann. Bot. 74:253-263.

Chalwell STS, Ladd PG, 2005. Stem demography and post fire recruitment of *Podocarpus drouynianus*: a resprouting non-serotinous conifer. Bot. J. Linn. Soc. 149:433-449.

Chen X, Xie Y, Deng Z, Li F, Hou Z, 2011. A change from phalanx to guerrilla growth form is an effective strategy to acclimate to sedimentation in a wetland sedge species *Carex brevicuspis* (Cyperaceae). Flora 206:347-350.

Colmer TD, Voesenek LaCJ, 2009. Flooding tolerance: suites of plant traits in variable environments. Funct. Plant Biol. 36:665-681.

Deng Z, Chen X, Xie Y, Li X, Pan Y, Li F, 2013a. Effects of size and vertical distribution of buds on sprouting and plant growth of the clonal emergent macrophyte *Miscanthus sacchariflorus* (Poaceae). Aquat. Bot. 104:121-126.

Deng Z, Chen X, Xie Y, Pan Y, Li F, Hou ZY, Li X, Xie Y, 2013b. Plasticity of the clonal growth in the wetland sedge *Carex brevicuspis* along a small-scale elevation gradient in Dongting Lake wetlands, China. Annal. Bot. Fenn. 50:151-159.

Dong M, 1996. Plant Clonal Growth in Heterogeneous Habitats: Risk-spreading. Acta Phytoecologica Sinica 20:543-548.

Dong M, Pierdominici MG, 1995. Morphology and growth of stolons and rhizomes in 3 clonal grasses, as affected by different light supply. Vegetatio 116:25-32.

Kleunen M, Fischer M, Schmid B, 2001. Effects of intraspecific competition on size variation and reproductive allocation in a clonal plant. Oikos 94:515-524.

Li F, Qin X, Xie Y, Chen X, Hu J, Liu Y, Hou Z, 2013. Physiological mechanisms for plant distribution pattern: responses to flooding and drought in three wetland plants from Dongting Lake, China. Limnology 14:71-76.

Li F, Zhu L, Xie Y, Chen X, Deng Z, Pan B, 2015. Colonization by fragments of the submerged macrophyte *Myriophyllum spicatum* under different sediment type and density conditions. Sci. Rep. 5:11821.

Luo WB, Song FB, Xie YH, 2008. Trade-off between tolerance to drought and tolerance to flooding in three wetland plants. Wetlands 28:866-873.

Macek P, Rejmánková E, Houdková K, 2006. The effect of long-term submergence on functional properties of *Eleocharis cellulosa* Torr. Aquat. Bot. 84:251-258.

Manzur M, Grimoldi A, Insausti P, Striker G, 2009. Escape from water or remain quiescent? *Lotus tenuis* changes its strategy depending on depth of submergence. Ann. Bot. 104:1163-1169.

Marbà N, Hemminga M, Duarte C, 2006. Resource translocation within seagrass clones: allometric scaling to plant size and productivity. Oecologia 150:362-372.

Panda D, Sharma SG, Sarkar RK, 2008. Chlorophyll fluorescence parameters, CO_2 photosynthetic rate and regeneration capacity as a result of complete submergence and subsequent re-emergence in rice (*Oryza sativa* L.). Aquat. Bot. 88:127-133.

Parolin P, Lucas C, Piedade MTF, Wittmann F, 2010. Drought responses of flood-tolerant trees in Amazonian floodplains. Ann. Bot. 105:129-139.

Qin X, Li F, Chen X, Xie Y, 2013. Growth responses and non-structural carbohydrates in three wetland macrophyte species following submergence and de-submergence. Acta Physiol. Plant. 35: 2069-2074.

Roseff SJ, Bernard JM, 1979. Seasonal changes in carbohydrate levels in tissues of *Carex lacustris*. Can. J. Bot. 57:2140-2144.

Schmid B, Harper JL, 1985. Clonal growth in grassland perennials: I. Density and pattern-dependent competition between plants with different growth forms. J. Ecol. 73:793-808.

Stuefer J, Van Hulzen J, During H, 2002. A genotypic trade-off between the number and size of clonal offspring in the stoloniferous herb *Potentilla reptans*. J. Evol. Biol. 15:880-884.

Suzuki JI, Stuefer J, 1999. On the ecological and evolutionary significance of storage in clonal plants. Plant Spe. Biol. 14:11-17.

Wang KY, 2009. [The synthesis and degradation of carbohydrates].[Article in Chinese]. Chemistry of Life 29:155-161.

Ye XH, Yu FH, Dong M, 2006. A trade-off between guerrilla and phalanx growth forms in Leymus secalinus under different nutrient supplies. Ann. Bot. 98:187-191.

Yemm E, Willis A, 1954. The estimation of carbohydrates in plant extracts by anthrone. Biochemical 57:508-514.

Zeeman SC, Kossmann J, Smith AM, 2010. Starch: its metabolism, evolution, and biotechnological modification in plants. Ann. Rev. Plant Biol. 61:209-234.

Zhao L, Zhi Y, Li L, An S, Deng Z, Zhou C, 2007. [Effects of initial clonal number on morphological plasticity and biomass allocation of the invasive *Spartina anglica*].[Article in Chinese]. J. Plant Ecol. 31:607-612.