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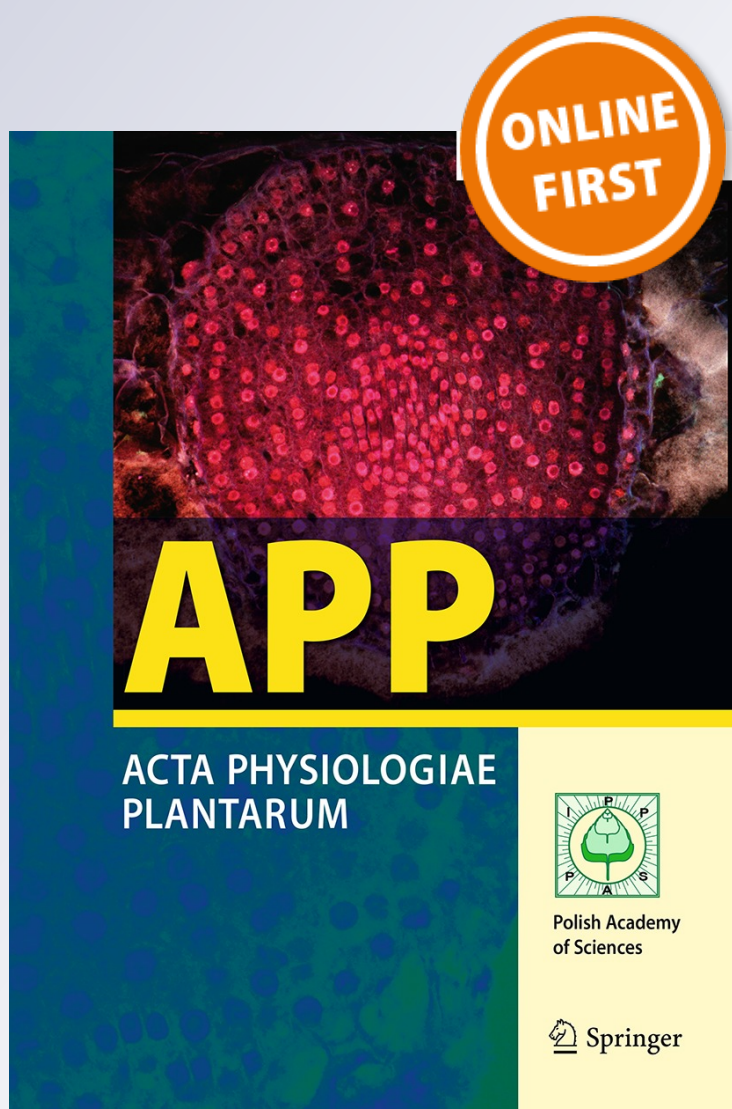
Xiyan Qin, Feng Li, Xinsheng Chen & Yonghong Xie

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Growth responses and non-structural carbohydrates in three wetland macrophyte species following submergence and de-submergence

Xianyan Qin · Feng Li · Xinsheng Chen ·
Yonghong Xie

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Abstract We investigated the responses of growth and non-structural carbohydrates to submergence and de-submergence in three wetland macrophyte species. Survival rate, recovery ability, and soluble sugar and starch contents of flood-tolerant *Polygonum hydropiper* and of flood-sensitive *Phalaris arundinacea* and *Carex argyi* from Dongting Lake wetlands were investigated after 20, 40, and 60 days of complete submergence without light and 10 days after de-submergence. Plant dry weight and soluble sugar and starch contents decreased in all species during the submergence period. The decreases were slowest in *P. hydropiper*, intermediate in *C. argyi*, and most rapid in *P. arundinacea*. After 60 days of submergence, survival rates were 100, 50, and 0 % in *P. hydropiper*, *C. argyi*, and *P. arundinacea*, respectively. After recovery, plant dry weight increased in *P. hydropiper* and in *C. argyi*, but decreased in *P. arundinacea*. Compared to pre-submergence, soluble sugar contents generally increased and then remained relatively constant after recovery in all species, while starch content increased in *P. hydropiper* and decreased in *P. arundinacea* with increasing submergence time. For *C. argyi*, starch content decreased after recovery from the 20-day submergence, but increased after

recovery from the 40- and 60-day submergences. These data illustrate mechanisms behind the flood tolerance of *P. hydropiper* and the sensitivity to flooding in *P. arundinacea* and *C. argyi*. These mechanisms include lower consumption and quicker accumulation of non-structural carbohydrates in flood-tolerant plants.

Keywords Wetland macrophytes · Submergence · Flood tolerance · Carbohydrate dynamics

Introduction

Flooding is a primary factor that regulates the growth, distribution, and composition of wetland macrophytes (Braendle and Crawford 1999; Li et al. 2011). Complete submergence over long periods is a primary selective pressure for plant distribution in seasonal floodplains, primarily because of lower oxygen availability in the root zone. During submergence, plant metabolism converts to anaerobic pathways and carbohydrate supplies are depleted during fermentation processes (Loreti et al. 2003; Gibbs and Greenway 2003). Plants growing in environments that are flooded for significant periods can thus be faced with a severe energy crisis (Colmer and Voesenek 2009).

Flood tolerance indicates the ability of organisms to resist the detrimental effects of flooding (Fritz and Dodds 2004; Luo et al. 2008), and is an important determinant of plant survival and distribution that can be reflected by changes in plant morphology and physiology. Pre-stored carbohydrate is the primary energy source for maintaining necessary physiological and biochemical processes in anaerobic environments (Vriezen et al. 2003; Li et al. 2007). The content of non-structural carbohydrates (e.g., soluble sugars and starch) is an important measure for

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X. Qin · F. Li · X. Chen · Y. Xie (✉)
Key Laboratory of Agro-ecological Processes in Subtropical
Region, Institute of Subtropical Agriculture,
The Chinese Academy of Sciences, Hunan 410125, China
e-mail: yonghongxie@163.com

X. Qin · F. Li · X. Chen · Y. Xie
Dongting Lake Station for Wetland Ecosystem Research,
Institute of Subtropical Agriculture, The Chinese
Academy of Sciences, Changsha 410125, China

evaluating a plant's tolerance to flooding (Vartapetian and Jackson 1997; Kawano et al. 2009). Carbohydrate is depleted faster in flood-sensitive than in flood-tolerant species (van Eck et al. 2005). Compared to susceptible cultivars, a tolerant rice cultivar can survive submergence in part because of the higher content of non-structural carbohydrates in shoot tissues (Panda et al. 2008). Therefore, higher flood tolerance might be reflected by a higher non-structural carbohydrate content or by a lower rate of carbohydrate depletion during submergence. However, the ways in which changes in non-structural carbohydrates content may reflect flood tolerance in macrophytes remain to be clarified.

In addition to flooding, plants in floodplains and river-connected lakes are rapidly re-exposed to high light and oxygen conditions as floodwaters recede (Panda et al. 2008). Plant recovery from flooding may also be restricted by tissue carbohydrate content, particularly during the initial stages of inundation (Mommer et al. 2006; Sarkar et al. 2006), when low carbohydrate concentrations can restrict plant growth or result in death (Sarkar et al. 2006; Panda et al. 2008). In contrast, plant growth processes may recover quickly in flood-tolerant species, in which the carbohydrate content can be restored or can display a more rapid compensative response (Bond and Midgley 2001; Ma et al. 2007). Compared to flood tolerance, the relationship between plants' ability to recover from submergence and the non-structural carbohydrate content of tissues is poorly understood.

In order to elucidate the carbohydrate mechanisms involved in flood tolerance, survival rate, and recovery ability, we examined the soluble sugar and starch contents of the three dominant emergent macrophytes from Dongting Lake after 20, 40, and 60 days of complete submergence and after 10 days of recovery. Dongting Lake, the second largest freshwater lake in China, lies south of the Yangtze River, to which it is connected by three channels. The wetlands in this lake are characterized by large annual seasonal fluctuations in water level (approximately 12–14 m) and are generally flooded from May to October and are dry from November to April (Pan et al. 2012a). The dominant emergent macrophyte species in the wetlands are flood-tolerant *Polygonum hydropiper* and flood-sensitive *Phalaris arundinacea* and *Carex argyi* (Zheng et al. 2009; Pan et al. 2012b). Here, we tested the following hypotheses: (1) plant dry weight and soluble sugar and starch contents will decrease more slowly in flood-tolerant *P. hydropiper* than in flood-sensitive *P. arundinacea* and *C. argyi*, and will be dependent on the duration of submergence; (2) dry weight and soluble sugar and starch contents will increase more in *P. hydropiper* than in *P. arundinacea* and *C. argyi* after recovery from submergence.

Materials and methods

Plant material

In February 2009, rhizomes were collected from stands of *P. arundinacea*, *P. hydropiper*, and *C. argyi* in East Dongting Lake, Junshan County, China (29°22'17"N, 112°59'40"E). The rhizomes were cut into 20 × 20 cm blocks and transported to the Institute of Subtropical Agriculture, Chinese Academy of Sciences (approximately 150 km from the plant collection site). Rhizome blocks were cut between internodes and planted separately into plastic buckets containing 15 cm of soil excavated from Junshan County. The soils contained 14.5 mg g⁻¹ organic matter, 4.04 μg g⁻¹ exchangeable N, and 0.88 μg g⁻¹ exchangeable P. The buckets were watered daily until the soils were visibly moist.

Experimental design

On May 10, 2009, 72 ramets (24 ramets per species) of similar height (~20 cm for *P. hydropiper* and ~25 cm for *C. argyi* and *P. arundinacea*) were planted in individual plastic pots (11.0 × 9.5 × 8.5 cm, 1 ramet per pot) containing Junshan County soils. Each plant was randomly placed into one of four plastic bins (78 × 56 × 60 cm, 6 ramets per species per bin). The bins were placed in an open room and covered with one layer of nylon netting to create light conditions that approximated 50 % full sun. After 2 weeks, the plants were submerged by filling each bin with 50 cm of tap water. To prevent plants from photosynthesizing under water, we shaded the bins with one layer of 2-mm paperboard. 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) was supplied as needed to maintain a constant water level in the bins and was completely replaced once per week to prevent the growth of algae. Four plants of each species were removed from the submerged bins after 20, 40, and 60 days of submergence, to receive the recovery treatments as follows: one plant of each species from each bin was then placed into a separate bin (78 × 56 × 60 cm) with the water level maintained at the soil surface for 10 days in approximately 50 % full-sun conditions, after which the number of living plants was determined. A plant was judged to be alive if new leaves had emerged (minimum 0.5 cm in length, Li et al. 2007).

Harvest and recovery

Four plants of each species were sampled to determine initial biomass prior to the submergence treatment. Four

plants of each species (1 of each species per bin) were harvested after 20, 40, and 60 days of submergence. Plants were carefully cleaned using tap water; divided into leaves, stems, rhizomes and roots; oven dried at 85 °C for 48 h; and then weighed to obtain dry weights (± 0.0001 g). Dry root materials were then ground with a mortar and pestle for measurement of soluble sugar and starch contents. For plants receiving the recovery treatment, dry weight and soluble sugar and starch contents were measured according to the methods described above.

Non-structural carbohydrates

The content of non-structural carbohydrates (e.g., starch and soluble sugar) was analyzed using a modification of the method of Yemm and Willis (1954). Dry root samples were ground to fine powder and extracted three times using 80 % ethanol (v/v). Then, 0.5 ml of anthrone reagent and 5 ml oil of vitriol were added to the extract. The mixture was then heated for 10 min in boiling water and cooled quickly in an ice bath, followed by the measurement of absorbance at 630 nm using a spectrophotometer (Shimadzu, Japan). The residue remaining after soluble sugars were extracted was dried, extracted with 30 % perchloric acid, and analyzed for starch (as glucose equivalent) using the anthrone reagent.

Statistical analysis

All statistical analyses were performed using the software SPSS 16.0 (SPSS Inc., USA). Prior to analysis, bin effects on total plant dry weight, survival rate, and non-structural carbohydrate content were analyzed using Tukey's test at the 0.05 significance level. If bin effects were insignificant, multiple comparisons of biomass, survival rate, and non-structural carbohydrate content during each experimental period were performed using Duncan's test at the 0.05 significance level. Data were \log_{10} -transformed if necessary to reduce the heterogeneity of variances. Normality and homogeneity of variance were tested using Liljefors and Levene's tests, respectively.

Results

Plant dry weight during submergence

Total dry weight of each of the three species decreased significantly with time of submergence ($P < 0.05$, Fig. 1). Compared to day 0, the dry weight of *P. hydro Piper* decreased by approximately 23, 17, and 52 % in the 20-, 40- and 60-day submergence treatments, respectively. Dry weight of *C. argyi* and *P. arundinacea* decreased more than

that of *P. hydro Piper* (e.g., 52 and 66 %, respectively, in the 40-day treatment, compared to 17 % in *P. hydro Piper*) (Fig. 1).

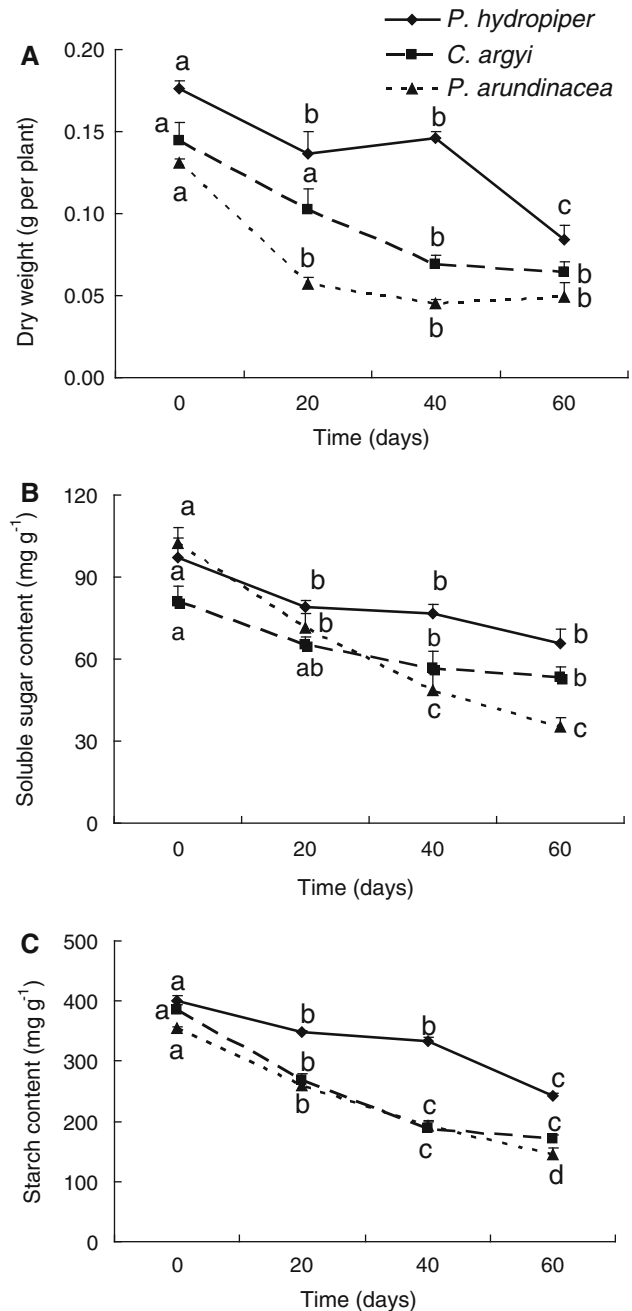


Fig. 1 Plant dry weight and soluble sugar and starch contents (mean \pm SE, $n = 4$) of three emergent species (*Polygonum hydro Piper*, *Carex argyi*, and *Phalaris arundinacea*) during the complete submergence period. Different letters indicate significant differences at 0, 20, 40, and 60 days of submergence. Multiple comparisons among different submergence periods were performed using Duncan's test at the 0.05 significance level

Carbohydrate content during submergence

The soluble sugar content of the three species was significantly reduced during the submergence period ($P < 0.05$, Fig. 1) and decreased considerably more in *P. arundinacea* than in *P. hydro Piper* and *C. argyi*. For instance, the soluble sugar content of *P. hydro Piper* and *C. argyi* decreased by 32 and 34 %, respectively, after 60 days of submergence, compared to a decrease of 65 % in *P. arundinacea* in the same treatment.

Starch content displayed patterns similar to soluble sugar content in the three species, decreasing significantly with increasing submergence time ($P < 0.05$, Fig. 1). The starch content decreased much less in *P. hydro Piper* than in the other two species in all submergence treatments. For example, after 40 days of submergence, starch content in *P. hydro Piper* was reduced by 17 %, while starch content was reduced by 51 and 46 %, respectively, in *C. argyi* and *P. arundinacea*.

Survival rate and plant dry weight after recovery

Survival rate differed significantly among the three species ($P < 0.05$, Table 1). The survival rate of *P. hydro Piper* was 100 % after recovery from all submergence treatments. However, survival rates were 100, 75, and 50 % for *C. argyi*, and 75, 50, and 0 % for *P. arundinacea* after recovery from 20, 40, and 60 days of submergence, respectively.

The mean dry weight of *P. hydro Piper* increased from 0.18 g prior to recovery to 0.19, 0.23, and 0.25 g per plant after recovery from 20, 40, and 60 days of submergence, respectively (Table 1). Mean dry weight of *C. argyi* only

increased after recovery from 20 and 40 days of submergence. However, the dry weight of *P. arundinacea* decreased during each recovery period. The recovery ability observed for the three species, in decreasing order, was: *P. hydro Piper* > *C. argyi* > *P. arundinacea*.

Carbohydrate content after recovery

Compared to pre-submergence, the contents of soluble sugar and starch after recovery differed among the three species. The soluble sugar content generally increased after recovery in comparison to pre-submergence content, and increased more in *P. hydro Piper* than in the other two species ($P < 0.05$, Table 1). The starch content increased with increasing submergence time in *P. hydro Piper*, but decreased in *P. arundinacea* ($P < 0.05$, Table 1). In *C. argyi*, the starch content decreased after recovery from the 20-day submergence, but increased after recovery from the 40- and 60-day submergences ($P < 0.05$, Table 1). Therefore, starch content accumulated most rapidly in *P. hydro Piper*, at an intermediate rate in *C. argyi*, and slowest in *P. arundinacea*.

Discussion

Carbohydrates are more rapidly depleted to satisfy physiological energy requirements under anoxic, compared to aerobic, conditions (Webb and Armstrong 1983), and anaerobic respiration generates considerably less energy than does aerobic respiration (Vartapetian and Jackson 1997). Plant resistance to flooding is related to the control and utilization of carbohydrate reserves (Peña-Fronteras

Table 1 Survival rate, plant dry weight, and soluble sugar and starch contents (mean \pm SE, $n = 4$) of three emergent species (*Polygonum hydro Piper*, *Carex argyi*, and *Phalaris arundinacea*) after recovery from submergence

	Species	N	0 days	20 days	40 days	60 days
Survival rate (%)	<i>P. hydro Piper</i>	4	100.0 \pm 0.0a	100.0 \pm 0.0a	100.0 \pm 0.0a	100.0 \pm 0.0a
	<i>C. argyi</i>	4	100.0 \pm 0.0a	100.0 \pm 0.0a	75.0 \pm 25.0a	50 \pm 28.9a
	<i>P. arundinacea</i>	4	100.0 \pm 0.0a	75.0 \pm 25.0a	50 \pm 28.9a	0.0 \pm 0.0
Dry weight (g per plant)	<i>P. hydro Piper</i>	3	0.18 \pm 0.01c	0.19 \pm 0.02bc	0.23 \pm 0.02ab	0.25 \pm 0.01a
	<i>C. argyi</i>	3	0.13 \pm 0.01c	0.15 \pm 0.01ab	0.16 \pm 0.01a	0.10 \pm 0.00c
	<i>P. arundinacea</i>	3	0.13 \pm 0.00a	0.09 \pm 0.01b	0.06 \pm 0.01b	
Soluble sugar content (mg g ⁻¹)	<i>P. hydro Piper</i>	3	97.33 \pm 7.07b	131.69 \pm 10.31a	143.21 \pm 5.29a	148.98 \pm 7.71a
	<i>C. argyi</i>	3	80.99 \pm 5.75b	104.44 \pm 5.37ab	119.30 \pm 8.50a	119.04 \pm 4.23a
	<i>P. arundinacea</i>	3	102.57 \pm 5.76a	117.63 \pm 8.20a	119.34 \pm 11.54a	
Starch content (mg g ⁻¹)	<i>P. hydro Piper</i>	3	400.56 \pm 7.66c	443.60 \pm 7.56b	471.74 \pm 5.18a	489.34 \pm 4.77a
	<i>C. argyi</i>	3	384.62 \pm 9.00a	285.57 \pm 10.11b	315.53 \pm 12.30b	357.40 \pm 5.65a
	<i>P. arundinacea</i>	3	355.26 \pm 2.78a	328.40 \pm 6.22b	280.13 \pm 10.80c	

Different letters indicate significant differences after recovery from 0, 20, 40, and 60 days of submergence. Multiple comparisons of recovery among different submergence periods were performed using Duncan's test at the 0.05 significance level

et al. 2009), and pre-stored carbohydrates can supply the energy required to satisfy necessary physiological activity (Vartapetian and Jackson 1997). Some studies have shown that low rates of sugar metabolism and the ability to use stored carbohydrates effectively are inherent characteristics of some anoxia-tolerant species (Schlüter and Crawford 2001; Ye 2010). In our experiment, the quantity of soluble sugar and starch contents among 3 emergent macrophyte species was, from highest to lowest, *P. hydro Piper* > *C. argyi* > *P. arundinacea*, which indicated that flood-tolerant *P. hydro Piper* could provide sufficient energy to survive submergence and that more energy was depleted in the flood-sensitive *P. arundinacea*. These results are consistent with our first hypothesis.

After recovery from submergence, plant dry weight increased in *P. hydro Piper* and in *C. argyi*, but decreased in *P. arundinacea*, suggesting that the ability to recover from flooding among the three species examined is, in descending order: *P. hydro Piper* > *C. argyi* > *P. arundinacea*. Soluble sugar contents increased more in *P. hydro Piper* than in the other two species, whereas starch content increased after recovery in *P. hydro Piper* and decreased in *P. arundinacea* with increasing submergence time. These results are consistent with our second hypothesis, with the exception of starch content. A previous study also found the non-structural carbohydrate content of plants to be positively associated with tolerance of, and regeneration after, submergence (Panda et al. 2008). A study on rice seedlings has shown that survival from submergence is strongly dependent upon carbohydrate reserves (Das et al. 2005). Therefore, the relatively higher soluble sugar and starch contents in the flood-tolerant species *P. hydro Piper* may provide more energy for regeneration during recovery from submergence. Compared to pre-submergence, the higher soluble sugar contents observed after recovery in each of the three species may indicate that compensative accumulation of soluble sugar occurs after recovery, as was shown by Luo et al. (2011). Compensative response after recovery from environmental stress is common in nature (Bond and Midgley 2001; Ma et al. 2007). In this study, changes in starch content after recovery from inundation may reflect differences in compensative ability among the three plant species. Reduced starch content after recovery in the flood-sensitive *P. arundinacea* might indicate that this species is not efficient in providing energy for regeneration compared to the other species, as was also suggested by the decrease in dry weight in *P. arundinacea* after the 10-day recovery from submergence.

In conclusion, our study indicates that the contents of soluble sugars and starch in *P. hydro Piper* decreased most slowly among the three species during the submergence period, but accumulated most rapidly during the recovery

period. These data suggest that *P. hydro Piper* has higher tolerance and recovery abilities than the other 2 species in response to flooding, which may also be reflected by changing patterns of biomass accumulation and survival rate. Flooding can be described by the depth, duration, frequency, and rate of filling and drying, and also by the timing and predictability of flooded and dry phases in a wetland (Langhans and Tockner 2006). How the non-structural carbohydrates change under these water regimes is far from clear. Therefore, more studies are still needed.

Author contribution X. Qin contributed to all the experimental process, data analysis and results interpretation as well as manuscript preparing. F. Li and X. Chen were involved in non-structural carbohydrates analysis. Y. Xie was responsible for the experimental design and supervised the experimental work. All authors read and approved the final manuscript.

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