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SURVIVAL AND CARBOHYDRATE STORAGE IN TWO TOLERANT PLANT SPECIES EXPOSED TO PROLONGED FLOODING IN THE THREE GORGES RESERVOIR REGION

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Abstract: High survival rate of long-term flooding was observed in *Arundinella anomala* and *Salix variegata*, two riparian plant species in the Yangtze River water fluctuation zone. Survival of flooding is supposed to be associated with carbohydrate utilization. Survival rate and carbohydrate (soluble sugar and starch) concentration of these two plants were investigated in a simulated flooding experiment lasting up to six months. Three water level treatments (waterlogging, 2 m deep water submergence, and non-flooded control) and four flooding durations (40, 90, 120 and 180 days) were set. Plants death only occurred to *A. anomala* after 120 days and *S. variegata* after 180 days which were submerged in 2 m deep water, while all the waterlogged plants of both species survived after 180 days. Carbon storage was found mainly in stems of *A. anomala* and stems and coarse roots of *S. variegata* plants. Carbohydrate concentration was very low in roots of *A. anomala* and in fine roots of *S. variegata* plants. Waterlogging slightly decreased biomass production and soluble sugar and total starch concentration compared with non-flooded plants. In contrast, 2 m submergence treatments lead to a gradually decrease in biomass while a sharp decrease in soluble sugar and starch concentration in all tissues within 90 days in both species; and then the carbohydrate mobilization slowed down. The results suggested that mortality of long-term submergence might be caused by disabled carbon storage mobilization in the later stages of prolonged flooding. The high flooding tolerance in the two species can be explained by the ability to mobilize carbohydrate storage in the beginning and later when exposed to carbon starvation. Differences of the responses to flooding between *A. anomala* and *S. variegata* could be ascribed to their different carbohydrate storage distribution patterns.

Key words: *Arundinella anomala*; *Salix variegata*; Flood-tolerance; Survival rate; Carbohydrate storage; The Three Gorges Reservoir region

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Annual summer flooding often occurs in Yangtze River in the Three Gorges Reservoir (Yangtze River, China) region. Such natural flooding is characterized by temporary but high water table rise. *Arundinella anomala* and *Salix variegata* are two of the flood-tolerant species growing in riverside. Our previous results showed these two species could survival at least three months complete submergence [1]. The contrasting short natural river flooding regimes and high survival rate in artificially prolonged flooding suggest these species have a capable of resisting unexpected flooding stress.

When terrestrial plants are flooded, one of the most remarkable stresses is reduced gas exchange between plants and the environments due to much slower gas diffusion rates in water than in air [2, 3]. Shortage of CO_2 and O_2 will directly influence the carbon budget of the whole plants at this site. Upon flooding, carbon availability becomes one of the critical factors for plant survival. Photosynthetic assimilation rate can be either decreased in mild waterlogging conditions [4, 5] or almost inhibited in submergence conditions [6]. Even though potential of underwater photosynthesis has been shown in some riparian species, the realized carbon assimilation performance is limited by the low light and low carbon dioxide concentration in water [7]. Carbohydrate utilization efficiency is further lowered by shortage of oxygen. Some studies reported that sugar oxidation by glycolysis in anoxia condition yields only two mol ATP per glucose,

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compare to thirty-six mol ATP in aerobic conditions [8], which suggests plants have to accelerate sugar utilization if the same amount ATP is demanded. Adapatations to reduce energy requirements and distribute energy to essential processes are highly valued in plants anoxia tolerance [9]. It is commonly recognized that flood tolerance can be mostly explained by oxygen deficiency tolerance [10]. The capacity to mobilize carbohydrate pool has been implicated in the mechanisms of oxygen deficiency tolerance in some wetland plants [11, 12]. Hence we hypothesize that plants which can survive during long-term flooding have to tolarate carbon starvation. One of the mechanisms on long-term flooding tolerance of species is the capacity of carbon storage mobilization. More generally, carbon starvation was considered as the key to reed decline in eutrophic lakes [13]. However, few studies focus on carbohydrate metabolism in relation to flood tolerance under more natural conditions [14], with exception of rice plants, anyhow, with a very limited submergence tolerance [15, 16].

Up to now, quite a lot of plant species have been reported to be flood-tolerant in the Three Gorges Reservoir region [1, 17—19]. However, little is known how survival in prolonged flooding couples with carbohydrate concentration in these species. In our previous work, simulated flooding decreased soluble sugar concentration and starch concentration of *S. variegata* plants within 60 days treatments; complete submergence caused larger reduction of sugar concentration and starch concentration than waterloging [20]. Further research showed that *S. variegata* could survive to 180 days of complete submergence; *A. anomala* plants could also keep high photosynthetic capacity after 60 days of flooding treatments [1]. How carbohydrate concentration in these two tolerant species changes with prolonged flooding and how it is related to survive rate need further investigation.

In this paper, *A. anomala* and *S. variegata* plants were exposed to simulated and prolonged flooding conditions with three water levels. Survival rate after long-term flooding was examined and carbohydrate dynamics during the whole flooding period was characterized. We aimed to find out whether carbohydrate pool in these two species can be mobilized and what the possible relationship between carbohydrate level and survival rate of long-term flooding conditions.

1 Materials and Methods

1.1 Plant materials and growth conditions

In May 2005, clones of *A. anomala* and one-year old *S. variegata* seedlings were collected from riverside of Jialing River, one of the largest branches of Yangtze River. To homogenise the initial plants size, single ramets *A. anomala* with shoot length of 10 to 15 cm and seedlings of *S. variegata* with shoot height of 5—7 cm were selected and grown in plastic pots (15 cm tall, 20 cm diameter) filled with a 1∶4 (*v*∶*v*) of mixture of humus and loam. All the plants were placed inside in the ecology experimental garden in Southwest China University (Chongqing, China). The seedlings were growing under ambient climate conditions with sufficient tapwater supply.

1.2 Treatments

Treatments started in the greenhouse at the end of January 2006, with the same experiment design for the both species as the following: Before initiation of the experiments, 8 plants from the stock plants were harvested for biomass and carbohydrate analysis. The remaining plants were randomly allocated to three groups with twenty-eight plants in each group. One group plants were put in a concrete water basin (2.5 m × 2.0 m × 2.5 m) filled with tap water. The water depth was kept 2 cm above soil surface and only the belowground of the plants was flooded (waterlogging), a second group plants were completely submerged in an identical basin, with the water depth remaining at 2 m (submergence). The third group plants were left growing in well drained soils but well watered (controlled plants, CK). Seven plants from each group were harvested after 40, 90, 120 and 180 days treatments. The water in the basins was replaced once a week; for complete submerged plants, exposure to air by shoots was avoided by keeping the stable water depth.

1.3 Survival rate determination

At each harvesting time, for survival rate estimation, 12 plants from each of the two flooding treatments (waterlogging and submergence) were returned to the same normal conditions as control plants. After two months of recovery, the number of living plants and dead plants were recorded. Plants without initiation of buds and green leaves were considered dead. The survival rate was calculated as the ratio of the number of living plants to the total number of 12 plants in each treatment.

1.4 Carbohydrate extraction and determination

For soluble sugar analysis, additional seven plants from each treatment were harvested at day 40, 90, 120 and 180. The plants were washed under tap water and divided into leaves, stems and roots, freeze-dried for 48h and ground to fine powder. About 30 mg powder from each sample was extracted in boiling 80% ethanol for 30min for three times. All the extracts from each sample were pooled together and final volume was made 25 mL. Soluble sugar concentration in each extract was determined with DNS (3, 5-dinitrosalicylic acid) at 540 nm using a spectrometer (UV-2550, SHIMADZU), according to the method by Miller [21]. For starch analysis, the residues leaved from soluble extraction were hydrolyzed using 4 mL demi and 2 mL 8 M HCl (1h, 100℃), according to van Eck, *et al.* [22]. The glucose released from starch were measured with the same method above.

1.5 Data analysis

All the statistical analysis was conducted in SPSS11.0. The average soluble sugar concentration and starch concentration in stem, leaf and root (for *S. variegata*, fine root and coarse root) were calculated. Two-way ANOVA was used to test the two fixed factor flooding water depth treatments (Control, waterlogging and submergence) and flooding duration effects (40d, 90d, 120d and 180d) on soluble sugar and starch concentration. When it was necessary, a Post Hoc multiple comparison with Least Significant Difference test (LSD, $P = 0.05$) was conducted.

2 Results

2.1 The effects of flooding on survival rate, biomass and carbohydrate concentration in *A. anomala* plants

All waterlogged *A. anomala* plants survived 180 days treatment; about one quarter of the complete submerged plants survived 120 days treatment but all died when submerged for 180 days (Tab. 1).

Both flooding duration and water depth had significant effects on plant biomass accumulation, except for stems (Tab. 2). As flooding duration prolonged, dry mass of the roots, leaves and whole plants of the non-flooded plants and waterlogged plants kept increasing, while for submerged plants, dry mass of the roots remained almost stable (Fig. 1a), and dry mass of the stems, leaves and whole plants kept decreasing (Fig. 1). Waterlogging did not decrease biomass accumulation rate compared with non-flooded plants, except at 180d (Fig. 1), while submergence decreased dry mass of all the three tissues significantly starting from day 90, compared with the control and waterlogging treatments ($P < 0.05$) (Fig. 1). Significant effects of interaction between flooding duration and water depth on dry mass occurred for root, leaf and whole plant, but not for stem (Tab. 2).

Flooding duration and water depth also imposed significant effects on carbohydrate concentration in the plants (Tab. 3). Generally, waterlogging only led to slight reduction of soluble sugar and starch concentration ($P > 0.05$, Fig. 2). Significant reduction of soluble sugar and starch concentration occurred in submerged plants starting from day 90, compared with non-flooded and waterlogged treatments ($P<0.05$, Fig. 2). In submerged plants, in stems and leaves, after a reduction at day 40, soluble sugar concentration remained relatively stable ($P>0.05$, Fig. 2c & e), while in roots, soluble sugar concentration kept decreasing until to a much low level at the end of the treatment ($P<0.05$, Fig. 2a). Significant effects of interaction between flooding duration and water depth occurred for both sugar and starch in all the tissues (Tab. 3).

Tab. 1 Survival rate (%) of *A. anomala* and *S. variegata* plants in non-flooding (control), waterlogging (2 cm water above soil surface) and submergence (2 m deep water) treatments. $n = 12$

Flooding duration	*Arundinella anomala*			*Salix variegata*		
	Control	Waterlogging	Submergence	Control	Waterlogging	Submergence
40d	100	100	100	100	100	100
90d	100	100	100	100	100	100
120d	100	100	25	100	100	100
180d	100	100	0	100	100	0

Tab. 2 *F*-values and significance of a two-way ANOVA of dry mass of *A. anomala* and *S. variegata* plants in 3 water depth treatments: non-flooding (control), waterlogging (2 cm water above soil surface) and submergence (2 m deep water) after 40 days, 90 days, 120 days and 180 days of treatments.

Species	Tissues	Main factors		Interaction (flooding duration × water depth)
		Flooding duration	Water depth	
Degrees of freedom		4	2	8
Arundinella anomala	Root	7.778^{***}	14.080^{***}	3.940^{**}
	Stem	2.013^{ns}	12.613^{***}	1.752^{ns}
	Leaf	3.609^{*}	21.772^{***}	3.224^{*}
	Whole plant	3.396^{*}	18.048^{***}	2.762^{*}
Salix variegata	Fine root	3.342*	0.349^{ns}	0.520^{ns}
	Coarse root	7.550^{***}	4.089^{**}	1.538^{ns}
	Stem	8.201^{***}	5.346^{**}	2.780^{*}
	Leaf	7.262^{***}	5.874^{**}	3.324^{*}
	Whole Plant	6.476^{***}	4.145^{**}	1.980^{ns}

Note: ns- not significant, *- $P < 0.05$, **- $P < 0.01$, ***- $P < 0.001$

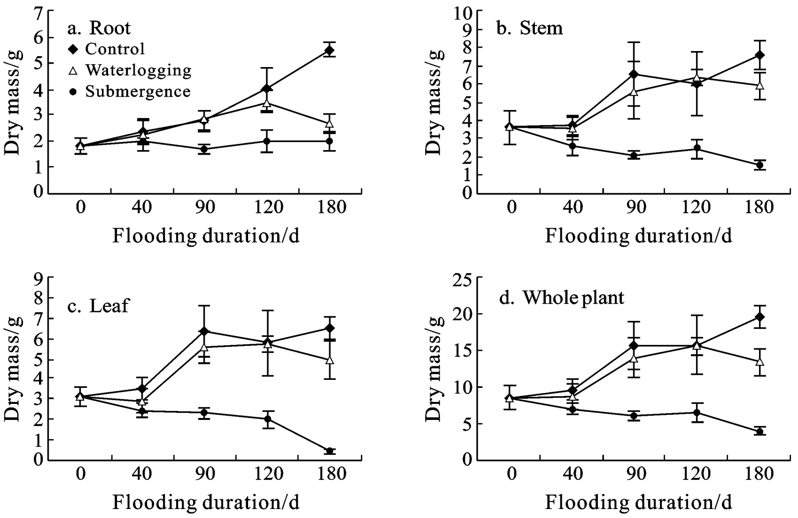

Fig. 1 Dry mass (g) in non-flooded (control), waterlogged (2 cm deep water above soil surface) and completely submerged (2 m deep water) *A. anomala* plants after 40, 90, 120 and 180 days of treatments. Points = means ± SE, *n* = 7

2.2 The effects of flooding on survival rate, dry mass accumulation and carbohydrate concentration in *S. variegata* plants

The flooded *S. variegata* plants survived all the treatments except for 180 days complete submergence (Tab. 1).

There were great variation of dry mass of all tissues between flooding duration and water depth treatments in the *S. variegata* plants (Fig. 3). Both flooding duration and water depth had significant effects on the dry mass accumulation (Tab. 2), except for the dry mass of the fine roots, which were not sensitive to the water depth treatments (Fig. 3b). Generally, as flooding duration prolonged, dry mass of the non-flooded plants and waterlogged plants kept increasing; for submerged plants, dry mass of the coarse roots, stems and whole plants remained almost stable (Fig. 3b, c & e), while it decreased significantly for the leaf ($P < 0.05$, Fig. 3d). There were significant effects of interaction between flooding duration and water depth on biomass of stems and leaves, but not on biomass of coarse roots, fine roots and whole plant (Tab. 2).

Carbohydrate concentration dynamics in flooded *S. variegata* plants was very similar to those in *A. anomala* plants (Fig. 2 and Fig. 4). With the exception of fine roots, waterlogging only decreased soluble sugar and starch concentration after 40 days in various plant parts and later recovered to the level in non-flooded plants (Fig. 4). In fine roots, waterlogging caused a larger reduction of both soluble sugar and starch concentration (Fig. 4a & b, $P < 0.05$). Complete submergence treatment reduced remarkably soluble sugar and starch concentration in all tissues. In roots and stems, the decrease of soluble sugar (Fig. 4a, c & e) lasted during the whole flooding treatments while decrease of starch concentration (Fig. 4b, d & f) seemed slowed down in the late period. After 90 days treatment, all the submerged plants shed their leaves; therefore no carbohydrate measurements were made (Fig. 4g & h). There were significant effects of interaction between flooding duration and water depth for both sugar and starch in all tissues, except for starch in the roots (Tab. 3).

3 Discussion

Our results indicated high flooding tolerance in these two species, as shown in the high survival rate of long-term submergence (Tab. 1). The high flood tolerance in these two species was comparable to some riparian species reported earlier [17—19, 23]. The two species could also accumulate a large amount of carbohydrate in non-flooded plants (Fig. 2 and Fig. 4). It might be that the large carbohydrate pool can be mobilized in the incoming annual summer flooding.

The results indicated that submergence had more detrimental effects on the two species than waterlogging, which did not lead to mortality in both plant, neither did it also reduce biomass accumulation (Fig. 1 and Fig. 3, $P < 0.05$) and carbohydrate availability (Fig. 2 and Fig. 4), compared with non-flooded plants. In contrast, submergence reduced survival rate, hindered biomass accumulation and reduced carbohydrate concentration. This suggested that shoot exposure to air [24] and gas exchange of both CO_2 and O_2 were the dominate factors [7] for these two species in control of the responses to flooding, since submergence decreases photosynthetic carbon fixation[6] and leads to inefficient of carbohydrate consumption owing to insufficient oxygen supply [9], which were critical for growth and survival for the plants under water. The results also indicated significant interaction effects of flooding duration and water depth. This showed different dynamics of biomass and carbohydrate concentration in the different flooding treatments. Partly, this could be due to increasing air temperature from January to July. In another study, it has been found that higher water temperature led to faster carbohydrate consumption in submerged *A. anomala* plants under controlled water temperature conditions (data not shown). The responses to air or water temperature may be different from non-flooded, waterlogged and submerged plants. In another study on the non-structural carbohydrate concentration in dynamics in roots of *S. variegata* plants conducted from August to October [20], it was found that waterlogging and submergence decreased carbohydrate concentration to a greater extent compared to the results in our study;

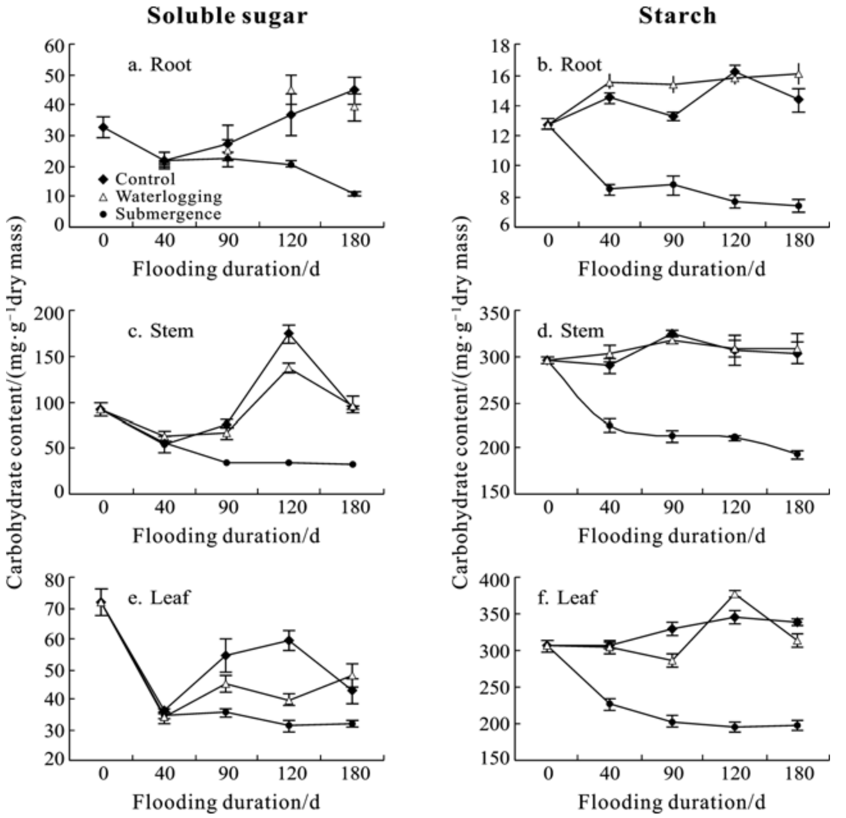

Fig. 2 Soluble sugar and starch concentration (mg/g dry mass) in non-flooded (control), waterlogged (2 cm deep water above soil surface) and completely submerged (2 m deep water) *A. anomala* plants after 40, 90, 120 and 180 days of treatments. Points = means ± SE, *n* = 7

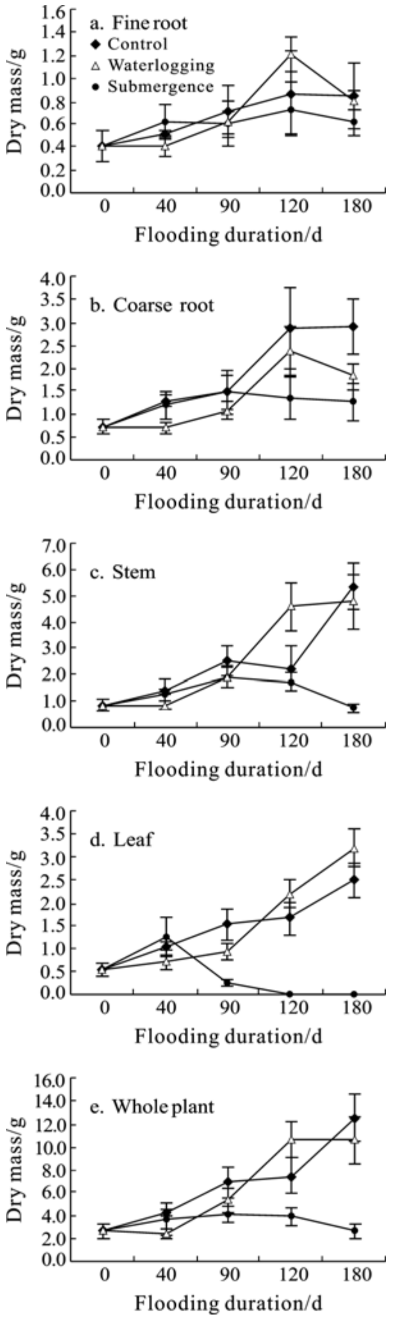

Fig. 3 Dry mass (g) in non-flooded (control), waterlogged (2 cm deep water above soil surface) and completely submerged (2 m deep water) *S. variegata* plants after 40, 90, 120 and 180 days of treatments. Points = means ± SE, *n* = 7

furthermore, their results [20] also showed a much larger effects of waterlogging and submergence duration effects on carbohydrate concentration. This may also due to the air temperature difference in the two studies. Since the flooding treatments in our study started from end January to end of July, which had a lower mean air temperature, much mild effects of flooding on *S. variegata* could be due to lower air temperature. It has been shown that winter flooding had less negative effects on several plant species than winter flooding [22].

Low survival rate was coupled with large biomass loss and decreased of carbohydrate concentration with prolonged submergence. Biomass loss during the flooding period could be partly due to shedding of leaves (Fig. 1c and Fig. 2d) and partly due to consumption of carbohydrate (Fig. 3 and Fig. 4). Biomass loss was reported to be a characteristic of some flood-tolerant species [18, 23]. Probably, this loss of biomass is a consequence of replacement of old tissues by new tissues formation, which can be more adaptive to the new anaerobic conditions, for example new leaves [7] or adventitious roots [25]. However if the submergence is too long, the energy costs paid by biomass loss can not be compensated by the benefits of new tissue formation. If we consider the total amount of carbohydrates in a particular tissue (carbohydrate concentration × tissues dry mass), it will be evident that the carbohydrate storage in most tissues was greatly reduced in the submerged plants (data was not shown), since submergence caused a large reduction of carbohydrate concentration and more biomass loss. Therefore, reduced carbohydrate availability as well as much biomass loss could be the cause of mortality in the prolonged submergence treatment. Studies on other species showed that higher carbohydrate status was associated with higher flood-tolerance in tolerant sorghum varieties [26] and some bottomland tolerant tree species [27].

Generally, in the three Gorges Reservoir region, there were more flood-tolerant herbaceous species than woody

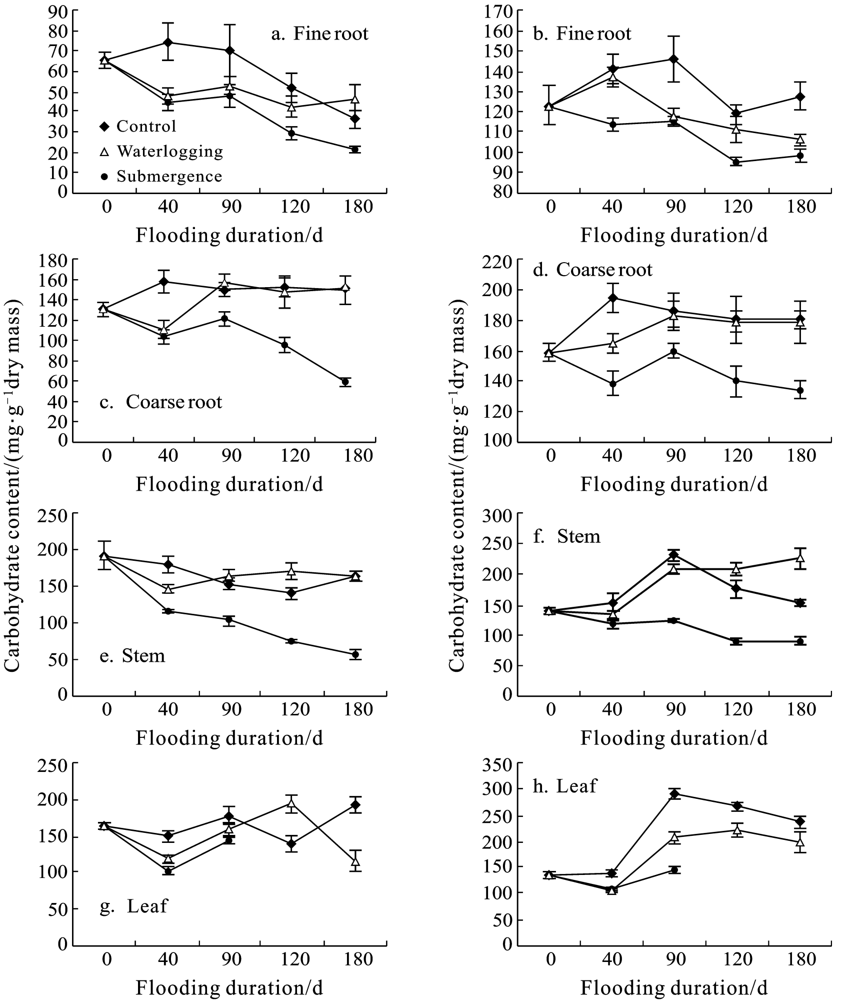

Fig. 4 Soluble sugar concentration and starch concentration (mg/g dry mass) in non-flooded (control), waterlogged (2 cm deep water above soil surface) and completely submerged (2 m deep water) *S. variegata* plants after 40, 90, 120 and 180 days of treatments. Points = means ± SE, *n* = 7

plant species, probably due to the advantage of clonal growth for survival rate in the former group [28]. Up to now, it has been shown that *Arundinella anomala*[1], *Hemarthria altissima*, *Cynodon dactylon*, *Capillipedium assimile*, *Paspalum distichum* [17, 19] and *Polygonum hydropiper* [29] are all flood tolerant, while only three riparian shrubs was reported to be flood-tolerant: *Myricaria laxiflora* [18], *Salix variegata* [30] and *Distylium chinense*[31]. However, in this study, *S. variegata* plants survived a little longer than *A. anomala* plants (Tab. 1). Part of the reasons might be different carbohydrate distribution in the two species. *S. variegata* is a shrub species which stored high amount of carbohydrate in coarse roots and stems (Fig. 4c—f); in *A. anomala* plants, the carbohydrate storage was only in stems (Fig. 3c & d), while in the roots the carbohydrate concentration was much lower compared with that of *S. variegata* roots (Fig.2a & b, Fig.4a—d). Furthermore, after 180 days submergence, the soluble sugar or starch concentration in the roots of *A. anomala* plants was near to or quite below 10 mg/g dry mass (Fig. 2a & b), while sugar or starch concentration was much higher in the fine roots of *S. variegata* (Fig. 4a&b, sugar: 20 mg/g dry mass; starch: 100 mg/g

Tab. 3 *F*-values and significance of a two-way ANOVA of soluble sugar concentration and starch in *A. anomala* and *S. variegata* plants in 3 water depth treatments: non-flooding (control), waterlogging (2 cm water above soil surface) and submergence (2 m deep water) after 40 days, 90 days, 120 days and 180 days of treatment

Species	Tissues	Main factors		Interaction (flooding duration × water depth)
		Flooding duration	Water depth	
Degrees of freedom		4	2	8
Arundinella anomala	Root sugar	7.479***	16.506***	5.855***
	Stem sugar	35.884***	78.367***	18.632***
	Leaf sugar	59.143***	14.827***	4.005***
	Root starch	1.125^{ns}	259.470***	20.036***
	Stem starch	5.850***	148.408***	12.076***
	Leaf starch	12.167***	236.945***	23.701***
Salix variegata	Fine root sugar	12.905***	11.315***	2.157*
	Coarse root sugar	3.085*	38.991***	7.686***
	Stem sugar	30.990***	89.240***	10.597***
	Leaf sugar	33.114***	11.301***	3.241*
	Fine root starch	7.734***	15.560***	1.800^{ns}
	Coarse root starch	1.609^{ns}	20.219***	2.162*
	Stem starch	15.911***	86.967***	13.845***
	Leaf starch	141.865***	42.589***	23.658***

Note: ns- not significant, *- $P < 0.05$, ***- $P < 0.001$

dry mass). Under complete submer-gence conditions, carbon storage might be important to supply sugar for non-storage tissues for survival; when flooding recedes, new roots and leaves initiation for recovery growth also might depend on mobilization of carbohydrate storage. It was very likely that transportation of sugar from stems to roots were blocked in the *A. anomala* plants due to oxygen deficiency [32]. The cease of recharge of soluble sugar pool in the roots might finally lead to exhaustion of sugar and earlier death of *A. anomala* plants.

4 Conclusions

The results showed both *A. anomala* and *S. variegata* plants are very tolerant of long-term flooding. Both species are capable of mobilizing and utilizing carbohydrate storage up to at least 3 months of complete submergence. Coupling of biomass loss, reduction in carbohydrate concentration and mortality rate with increasing submergence duration suggest that high survival rate in these species might be closely associated with the limited but remarkable capacity to mobilize carbohydrate storage.

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三峡库区两种耐水淹植物的存活率和碳水化合物储备关系

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摘要: 野古草和秋花柳是三峡库区消落带两种强水淹耐受能力的植物物种。以往研究显示植物的水淹耐受性和体内碳水化合物储备有关。为了探明野古草和秋花柳水淹下的高存活率是否和碳水化合物储备有关, 研究了在室外 6 个月的模拟水淹条件下两个物种在不同水淹时间(40、90、120 和 180d)和不同水淹深度下(不水淹、根部水淹和完全淹没)的生物量积累、存活率和碳水化合物含量和分布。结果表明: (1)野古草和秋花柳对长期水淹具有很高的耐受性, 根部水淹植物 6 个月处理后完全存活; 而完全淹没条件下, 野古草仅在 4 个月, 秋花柳仅在 6 个月处理后才开始死亡; (2)碳水化合物主要储备在野古草的茎和秋花柳的茎与主根中, 野古草的根和秋华柳的细根中碳水化合物含量很低; (3)水淹深度和水淹时间对植物生物量积累和碳水化合物含量影响显著($P < 0.05$)∶与未水淹植株相比, 根部水淹仅略微降低了生物量积累以及可溶性糖和淀粉含量 ($P > 0.05$), 且保持基本稳定或增加的趋势, 而完全淹没的植株生物量随水淹时间逐渐降低, 碳水化合物含量在前 90 天快速下降 ($P < 0.05$), 之后缓慢下降或保持不变。研究结果表明, 野古草和秋花柳强的水淹耐受性是和它们高的碳水化合物储备以及水淹条件下对碳水化合物的动用能力有关, 后期的死亡率增加与碳水化合物储备消耗殆尽有关, 野古草和秋花柳对碳水化合物储备对水淹的响应的差异可能和它们的碳水化合物储备在不同组织中的分配模式有关。

关键词: 野古草; 秋花柳; 水淹耐受性; 存活率; 碳水化合物储备; 三峡库区