

RESEARCH ARTICLE

Growth and Physiological Responses to Water Depths in *Carex schmidtii* Meinsh.

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Abstract

A greenhouse experiment was performed to investigate growth and physiological responses to water depth in completely submerged condition of a wetland plant *Carex schmidtii* Meinsh., one of the dominant species in the Longwan Crater Lake wetlands (China). Growth and physiological responses of *C. schmidtii* were investigated by growing under control (non-submerged) and three submerged conditions (5 cm, 15 cm and 25 cm water level). Total biomass was highest in control, intermediate in 5 cm treatment and lowest in the other two submerged treatments. Water depth prominently affected the first-order lateral root to main root mass ratio. Alcohol dehydrogenase (ADH) activity decreased but malondialdehyde (MDA) content increased as water depth increased. The starch contents showed no differences among the various treatments at the end of the experiment. However, soluble sugar contents were highest in control, intermediate in 5 cm and 15 cm treatments and lowest in 25 cm treatment. Our data suggest that submergence depth affected some aspects of growth and physiology of *C. schmidtii*, which can reduce anoxia damage not only through maintaining the non-elongation strategy in shoot part but also by adjusting biomass allocation to different root orders rather than adjusting root-shoot biomass allocation.

Introduction

Water regime is one of the major determinants in plant community dynamics and species zonation in wetlands [1,2]. The water regime can be described by the depth, duration, frequency, rate of filling and drying, and timing and predictability of flooded and dry phases in a wetland [1]. Among these, water depth is considered to be one of the key factors controlling the establishment of wetland species [3]. However, water depth in many wetland systems is not always constant. Current climate models have predicted a much greater frequency of sudden storm events accompanied by rapid water depth increases in lowland wetland habitats [4], which could lead to complete submergence and thus could have severe effects on the growth of wetland plants. Increased water depth can directly increase the time needed for gas exchange to

aerate the submerged parts of wetland plants [5,6]. An indirect effect of increased water depth is the attenuation of light in the water column; partial submergence can reduce irradiance to organs and thus reduce carbon assimilation and oxygen production [7]. Therefore, water depth might be one of the key factors in determining wetland species distribution and survival in a completely submerged condition. A number of studies have focused on how wetland plants cope with complete submergence [8–12]. Submergence is detrimental for most plants because it hampers growth and can result in premature death [8]. The negative impact on submerged plants is closely related to the low diffusion rates of gases and the relatively low solubility of oxygen in water [13], which jointly lead to anoxia or hypoxia in plant tissues [14].

Many wetland plants can reduce damage from oxygen deficiency and enhance their ability to tolerate flooding through morphological adjustments [15], such as biomass reallocation [16,17] or adjusting their shoot morphology [5,18]. During floods, some wetland plants can allocate more biomass to aboveground to acquire-oxygen [19], and less biomass to belowground parts in order to reduce oxygen depletion [20]. Changes in shoot morphology are another important strategy in wetland plants when partially or completely submerged [18]. For example, some wetland species can elongate shoot organs such as internodes and petioles during flooding [21], which can help plants bring leaves closer to the surface into better illuminated water layers, and eventually above the water surface. Generally, there are two opposing types of shoot strategies to cope with flooding: shoot elongation (the low-oxygen escape) and non-shoot elongation (the quiescence strategy) [22]. It is suggested that the non-elongation strategy is more advantageous for temporary or deep-flooding events that cannot be outgrown, whereas fast underwater elongation increases fitness mainly during prolonged, but relatively shallow floods [23,24]. Include fast elongation of the shoot is an essential attribute of flooding tolerance in wetland species, which keeps leaves above water in response to rising water level [11,25]. However, increased cell division rates and synthesis of new cell walls during fast cell elongation require substantial amounts of energy and carbohydrates [26], and this strategy is beneficial only if the contact between leaf blades and the atmosphere is restored. Thus, fast elongation under water will be a high-risk strategy during flooding events of short duration and when submergence depths exceed the elongation capacity of the plant [18]. Therefore, submergence depths might be one of the key factors in determining which strategies species adopt in submerged conditions. However, few papers have focused on the responses of wetland species to water depth in submerged conditions [27].

Wetland plants under the flooding conditions can also reduce anoxia damage through physiological adjustments [28]. For instance, enhancing alcohol dehydrogenase (ADH) activity can alleviate damage in plant tissues from oxygen deficiency by maintaining carbohydrate metabolism [29]. Malondialdehyde (MDA) content, a marker for lipid peroxidation, is often used as an indicator of cellular membrane damage [30].

All mechanisms are important for wetland plants to meet the energy requirement of some crucial physiological activities under anoxic conditions [31], so that the starch stored in plants as the primary reserve carbohydrate can be transformed into soluble sugar, such as glucose and fructose, to be used for further metabolism [31]. Thus, accumulation of carbohydrates prior to flooding in plant tissues may also be important for plant survival in flooding environments.

The aim of this study was to identify the role of water depth in affecting the growth and physiology of a wetland plant. For this purpose, *Carex schmidtii* Meinsh. was chosen as the target species for growth in three completely submerged conditions, quantified by water depths of 5 cm, 15 cm and 25 cm for 28 days. *C. schmidtii* (a perennial grass, with typical adventitious root system) is one of the dominant species in wet meadows and marsh communities in the Longwan Crater Lake wetlands, the largest Crater Lake marsh in China.

Here, we tested the following hypotheses: First, water depth might have negative effects on plant growth when the plant is completely submerged, and more biomass will be allocated to shoots and less to roots in submerged treatments. Second, plants will adopt the non-elongation strategy in 25 cm submergence conditions, which is advantageous for deep-flooding events that cannot be outgrown. Third, the plant will store more starch at 25 cm submergence, as it is important for wetland species to maintain metabolism when submerged.

Materials and methods

PLANT materials

Ramets of *C. schmidtii* were chosen in October 2009, from Longwan Freshwater Marsh Field Observation Station (N 42°20', E 126°21'), of Northeast Normal University. We also collected soil from the *C. schmidtii* population in the Longwan Freshwater Marsh Field Observation Station. The major soil types are peats. All plants and soil were taken back to a greenhouse at Northeast Normal University, where the temperature was controlled at $25 \pm 2^\circ\text{C}$ in the day and $17 \pm 2^\circ\text{C}$ at night and light was provided by 400 watt sodium lamps (Guangming Company, China) at a photon flux density of $400/0 \mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR) in a 14 h light/10 h dark cycle. Plant cuttings were then placed into plastic buckets containing 10 cm soil (500 g) and 2 cm water, to germinate new ramets.

Experimental treatment

A total of 36 plants of similar size (3–4 leaves, about 20 cm in height) were cut from plant cuttings and planted in plastic pots (8 cm in height and 10 cm in diameter, one plant per pot). Each pot was filled with soil, a mixture of 0–30 cm surface soil collected from the same site where the *C. schmidtii* population was located (N 42°20', E 126°21'). Four pots were placed into one larger plastic bucket (300L, 65 cm in height) to control water level (three pots per water level). Nine plastic buckets were used in the experiment and were randomly placed in the greenhouse. Every week these plastics buckets were moved randomly. Considering the field observations, we chose 0 cm, 5 cm, 15 cm and 25 cm water levels as experimental flooding levels. The four water levels relative to the soil surface were 0 cm (control), 25 cm (5 cm treatment, completely submerged 5 cm), 35 cm (15 cm treatment, completely submerged 15cm) and 45 cm (25 cm treatment, completely submerged 25 cm) (Fig 1). Tap water was supplied daily to maintain water level.

Harvest

For each treatment, 9 plants were harvested after 28 days. Before harvest, we recorded the height of each plant (natural height), and after harvest, all plants were divided into shoots and roots to determine fresh weight, respectively. Adventitious roots in each group were then divided into main roots and, first-order laterals (no plants had second-order laterals in submerged conditions at the end of the experiment) and were weighed separately [17]. Half of the shoot and root mass was weighed, oven dried at 80°C for 48 h, and then weighed again to calculate a wet-to-dry conversion factor for each tissue type, which was used for calculated the dry weights (S1 File). After that, the dried tissues were used to determine the carbohydrate content. Another half of the samples were kept in a refrigerator prior to being analyzed for ADH activity, and MDA content [28]. Carbohydrate content, ADH activity and Malondialdehyde (MDA) were measured following the procedure of Wignarajah et al. [32], Cakmak and Horst [33] and Yoshida et al. [34], respectively (S1 File).

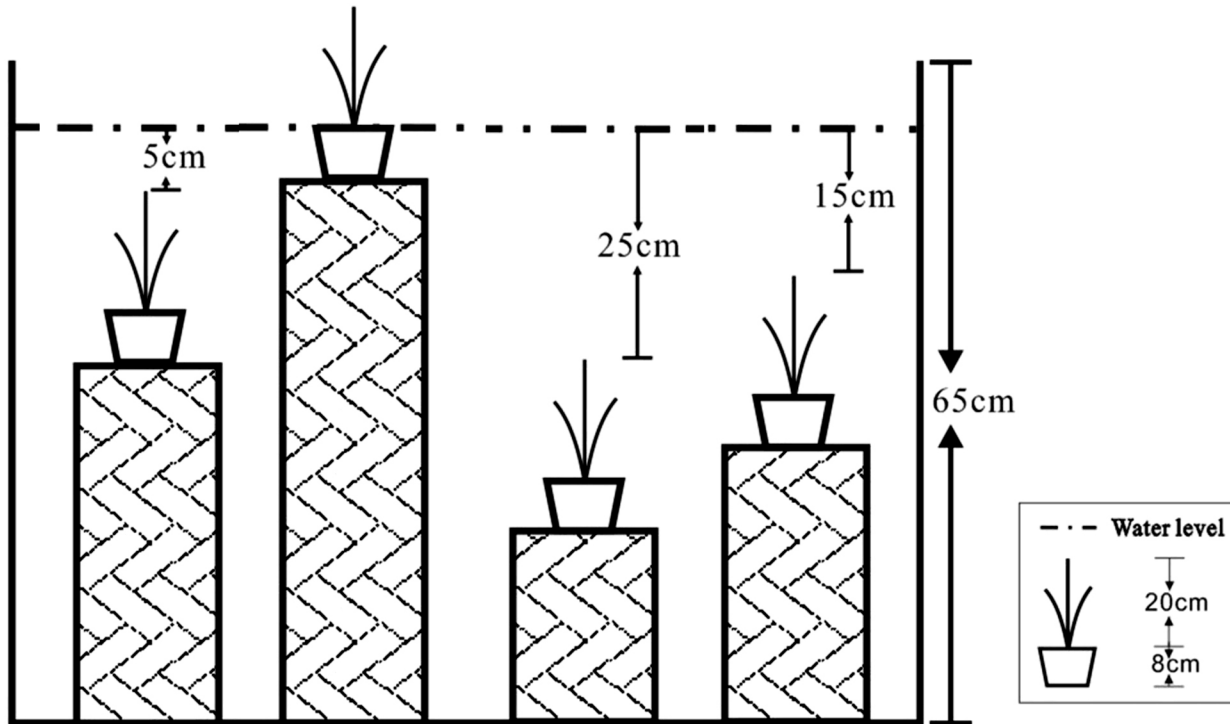


Fig 1. The schematic diagram of the experimental set-up.

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Total biomass and partitioning

Total biomass was calculated using the follow formula: Total biomass = Shoot mass + Root mass. Relative growth rate (RGR) was calculated using the follow formula: $RGR = [\ln(w_2) - \ln(w_1)] / (t_2 - t_1)$ [35,36], where w_2 and w_1 are plant dry weights at the end of the experiment (t_2) and plant dry weight at the beginning of the experiment (t_1), respectively. Relative shoot growth rate (RSR) was calculated using the follow formula: $RSR = [\ln(h_2) - \ln(h_1)] / (t_2 - t_1)$, where h_2 and h_1 are plant heights at the end of the experiment and at the beginning of the experiment, respectively.

Statistical analysis

All statistical analyses were performed using SPSS 20.0 software (SPSS Inc., USA). Treatment effects on total biomass, shoot mass, root mass, root to shoot ratio, first-order laterals to main roots ratio, relative growth rate (RGR), relative shoot growth rate (RSR), ADH activity, MDA content, and carbohydrate content were tested by the analysis of one-way ANOVA. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level. Heterogeneity was tested using Levene's test and data were log₁₀-transformed if necessary to reduce the heterogeneity of variances.

Results and Discussion

Relationship between total biomass, shoot mass, root mass, and water level

Water level had significant effects on total biomass and shoot mass, but had no significant effects on root mass and the root to shoot ratio (Table 1). Total biomass and shoot mass

Table 1. Summary of one-way ANOVAs for total biomass, ADH activity, and carbohydrates contents of *Carex schmidtii* in different water-level conditions.

	n	Treatment (F- statistics)	Treatment (P-values)
Total biomass (g)	9	18.223 ^{***}	0.000
Shoot mass (g)	9	19.007 ^{***}	0.000
Root mass (g)	9	2.888 ^{ns}	0.510
Root to shoot ratio (%)	9	2.838 ^{ns}	0.530
First-order laterals to main roots ratio (%)	9	4.184 [*]	0.013
Relative growth rate (d ⁻¹)	9	18.424 ^{***}	0.000
Relative shoot growth rate (d ⁻¹)	9	62.696 ^{***}	0.000
ADH activity (μ g ⁻¹ fw)	5	7.707 ^{**}	0.003
MDA content (μ mol g ⁻¹)	5	4.486 [*]	0.018
Starch content (mg g ⁻¹)	3	0.633 ^{ns}	0.617
Soluble sugar content (mg g ⁻¹)	3	41.400 ^{***}	0.000

^{ns} $P > 0.05$

^{*} $P < 0.05$

^{**} $P < 0.01$

^{***} $P < 0.001$

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decreased significantly with increasing water depth (Fig 2). At end of the experiment, the total biomass were highest in control (0.16 g), intermediate in 5 cm submergence level (0.12 g), and lowest in other submergence levels (0.06 g in 15 cm treatment and 0.05 g in 25 cm treatment). The total biomass and RGR in our experiment showed that water depth might have negative effects on plant growth under the condition of complete submergence, a result that partly supported our first hypothesis. In particular, optimal partitioning models and theories suggested that plants can respond to resource availability by adjusting biomass allocation patterns to optimize resource capture (e.g. nutrients, light) in a manner that maximizes plant growth [37]. Oxygen is one of the limiting resources in wetland ecosystems. Wetland species could reallocate biomass patterns when flooding, allocating more biomass to shoot parts in order to get more oxygen and allocating less biomass to root parts in order to reduce oxygen depletion [19,20]. Therefore, adjustment in biomass allocation is also an important strategy to enable wetland plants to survive during flooding periods [16].

Relationship between first-order laterals to main roots ratio and water level

The first-order laterals to main roots ratio showed the same trend as total biomass, indicating a significant effect of water depth (Table 1). At the end of the experiment, the first-order laterals to main roots ratios were higher in control and 5 cm treatment than the other treatments (Fig 3). However, root to shoot ratio was not altered in our experiment, which partly contradicted our first hypothesis that more biomass will be allocated to shoots and less to roots in submerged treatments. However, an interesting finding was that *C. schmidtii* can allocate less biomass to first-order laterals as water depth increase. Xie et al. reported that the wetland plant *Myriophyllum spicatum* could reduce the damage from anoxia by adjusting root structure and biomass allocation to different root orders rather than through root morphology [17]. During submerged conditions, the decreased biomass allocation to lateral roots could also reduce the total root numbers or root lengths, which in turn could reduce radial oxygen loss or reduce oxygen depletion by root system, so a low mass fraction of lateral roots is favorable for survival in submerged

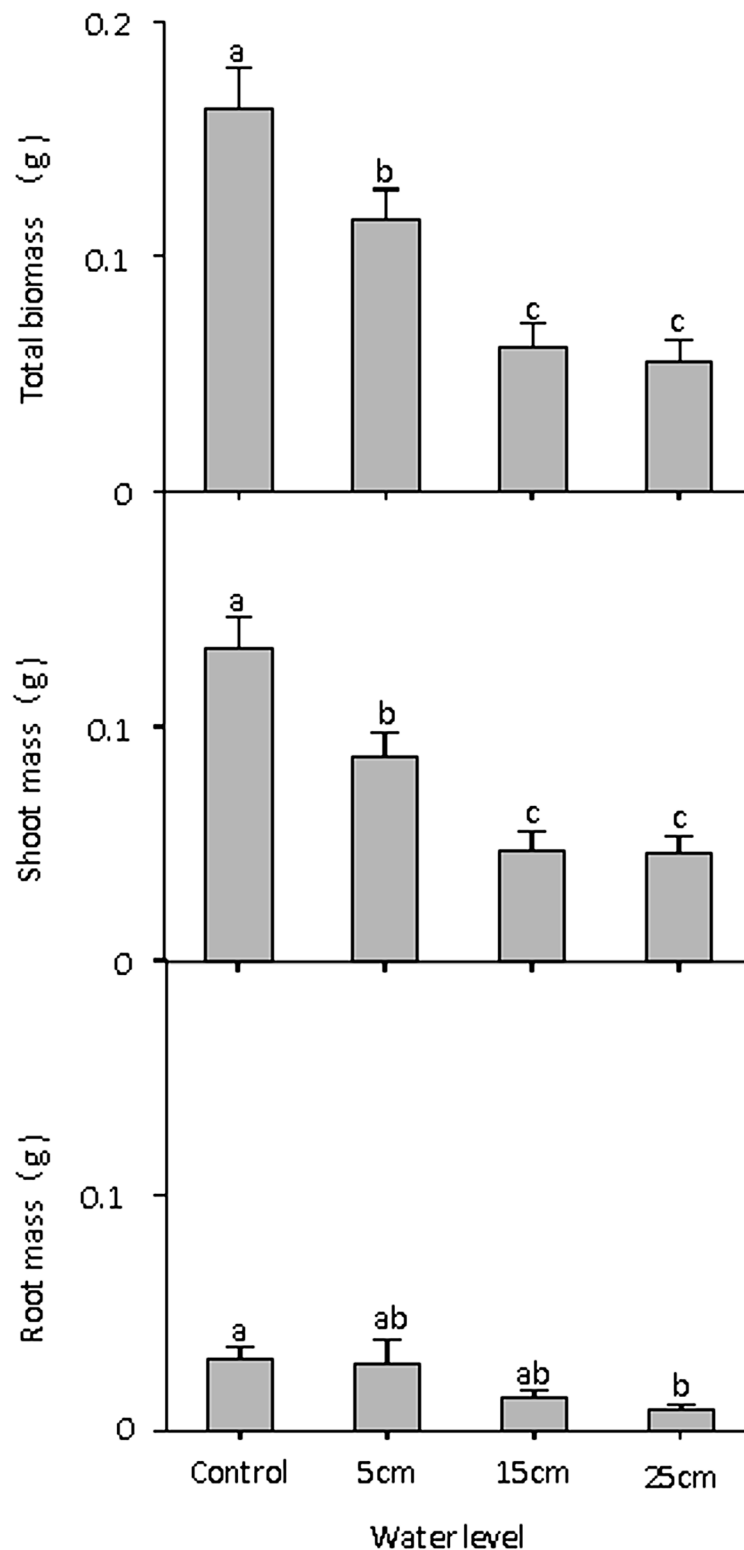


Fig 2. Total biomass, shoot mass, and root mass of *Carex schmidtii* in different treatments (one control: 0 cm water level, and three submerged conditions: 5 cm, 15 cm, and 25 cm water level). Different letters indicate significant differences among treatments ($P < 0.05$).

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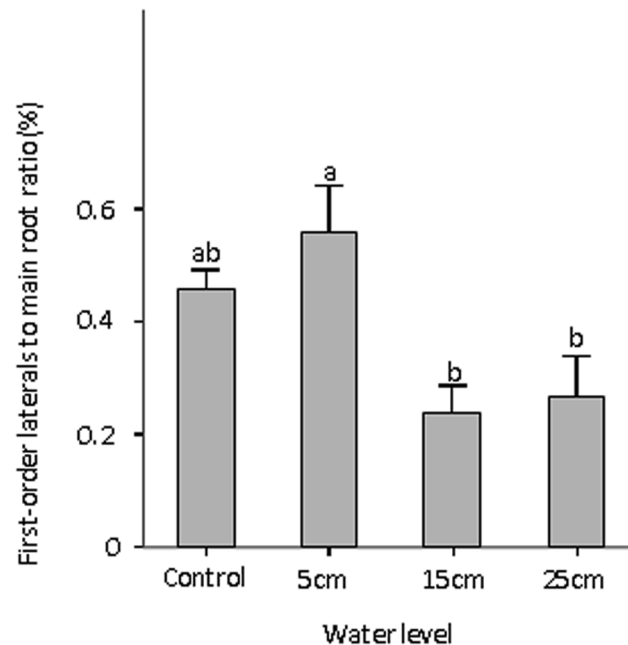


Fig 3. First-order laterals to main roots ratio (%) of *Carex schmidtii* in different treatments (one control: 0 cm water level, and three submerged conditions: 5 cm, 15 cm, and 25 cm water level). Different letters indicate significant differences among treatments ($P < 0.05$).

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environments. Therefore, these data indicated that reallocating biomass to different root orders rather than shoot parts might be a strategy used by *C. schmidtii* when completely submerged.

Relationship between relative growth rate, relative shoot growth rate, and water level

Relative growth rate (RGR) was higher in control and 5 cm treatments but lower in others (Table 1, Fig 4). The relative shoot growth rate (RSR) was higher in control than the other treatments for *C. schmidtii* (Fig 4). Rapid stem elongation occurs mainly to minimize reduction of photosynthesis, which concomitantly increases O_2 production, which can be internally transported by aerenchyma to submerged tissues in an otherwise anoxic environment. However, in our experiment, RSR was lower in submerged treatments than that in control. This result indicates that the stems of *C. schmidtii* did not elongate in all submerged conditions and submergence might be stressful for plant growth, which confirmed our second hypothesis that *C. schmidtii* would adopt non-elongation strategy in 25 cm submerged conditions. Therefore, we can find a positive relationship between RGR and RSR in *C. schmidtii* (Fig 4). They were all higher in control but lower in 15 cm and 25 cm treatments (Fig 4). Shoot elongation underwater requires energy and carbohydrates for cell divisions as well as the synthesis of new cell-wall material [5,23]. Therefore, reduced energy consumption in submerged environment might be a survival strategy for *C. schmidtii*, which confirmed the hypothesis that the non-elongation strategy might be more advantageous for temporary or deep-flooding events that cannot be outgrown [23,24]. However, the mechanisms by which the plants determine whether the water depth can be overcome or not still need further study.

Relationship between ADH, MDA, and water level

ADH activity decreased with increasing water depth (Table 1, Fig 5). At the end of the experiment, ADH activity was higher in control and 5 cm treatments and lower in 15 cm and 25 cm

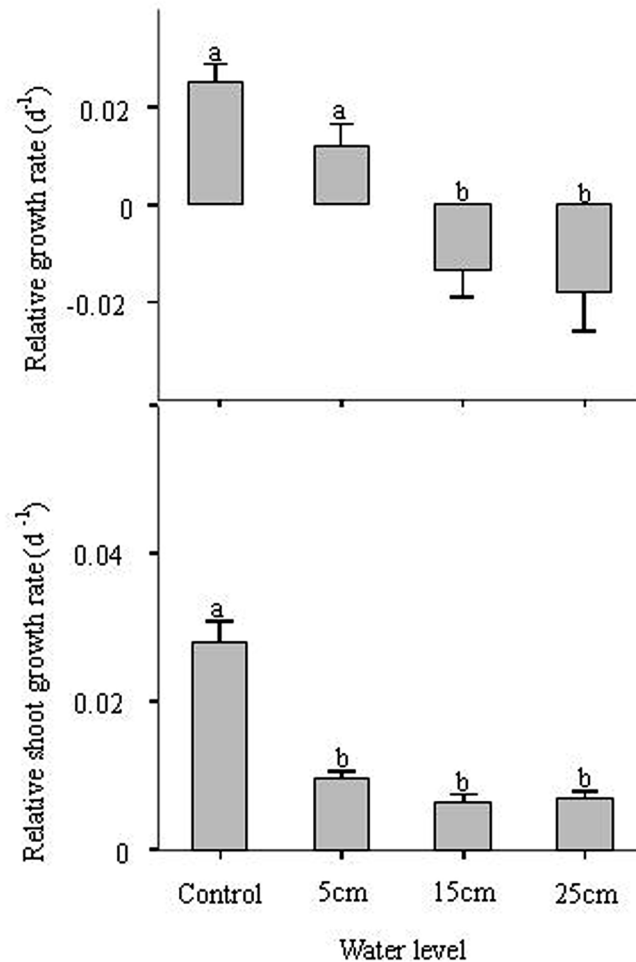


Fig 4. Relative growth rate and relative shoot growth rate of *Carex schmidtii* in different treatments (one control: 0 cm water level, and three submerged conditions: 5 cm, 15 cm, and 25 cm water level). Different letters indicate significant differences among treatments ($P < 0.05$).

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treatments (Fig 5). MDA content was significantly and positively affected by water depth (Table 1, Fig 5). In general, ADH activity is usually enhanced when the oxygen supply to roots is limited [17], allowing wetland plants to survive flooding conditions. However, ADH in *C. schmidtii* decreased as water depth increased. MDA content in plant tissues can indicate the degree of damage caused by severe stress [38,39]. The higher MDA content in 15 cm and 25 cm treatments suggested that water depth had particularly severe impacts on plant growth in submerged conditions. More importantly, aerobic metabolism in submerged or flooding conditions enables plants to tolerate oxygen deficiency at the cellular level [40,41]. Flooding can lead to a switch of aerobic metabolism into less efficient anaerobic fermentation, causing a fast depletion of carbohydrate reserves [8]. In other words, pre-stored non-structural carbohydrates (including starch and soluble sugar) are important for wetland plant survival in anoxic environments [42].

Relationship between starch content, soluble sugar content, and water level

Water level did not have significant effects on starch content (Table 1). However, soluble sugar content was significantly and negatively affected by water level (Table 1, Fig 6). There were no

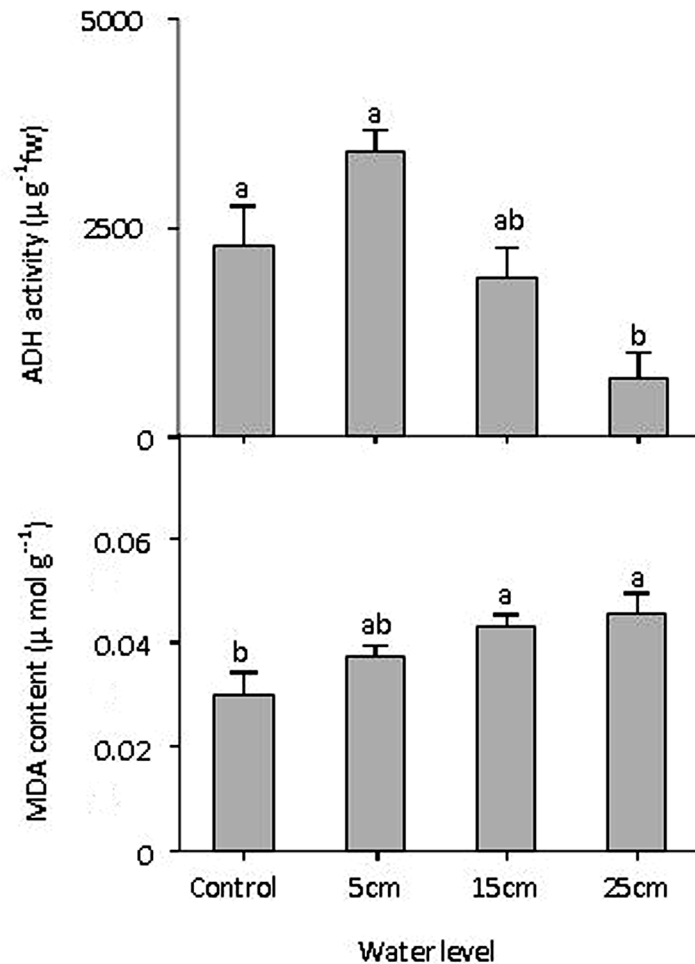


Fig 5. ADH activity and MDA content of *Carex schmidtii* in different treatments (one control: 0 cm water level, and three submerged conditions: 5 cm, 15 cm, and 25 cm water level). Different letters indicate significant differences among treatments ($P < 0.05$).

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differences in starch content among different submerged treatments in our experiment, which contradicted our third hypothesis that *C. schmidtii* might store more starch in the 25 cm submerged treatment. Therefore, it seems that *C. schmidtii* might have stored enough starch to maintain metabolism when submerged. But under anoxic conditions, many more carbohydrates were depleted to satisfy the energy requirement of crucial physiological activity [43,44], so starch must be transformed into soluble sugar for normal anoxic metabolism [31]. This could indicate that the ability to transform starch to soluble sugar might be crucial for plant survival in anoxic conditions. However, in our experiment the lower soluble sugar content in the 25 cm submerged condition suggested that *C. schmidtii* might not be capable of producing enough soluble sugar for anoxic metabolism. In summary, our experiment indicates that submergence depth might affect total biomass and anoxic metabolism, but adaptations, such as the non-elongation strategy in the shoot part or adjustments in the root structures, allow *C. schmidtii* to survive complete submergence.

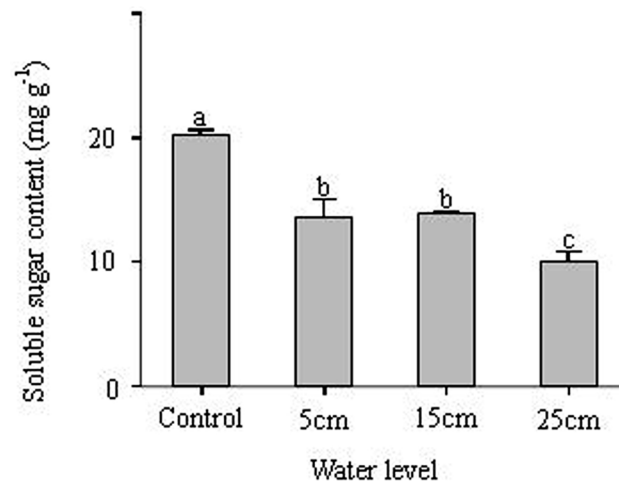


Fig 6. Soluble contents of *Carex schmidtii* in different treatments (one control: 0 cm water level, and three submerged conditions: 5 cm, 15 cm, and 25 cm water level). Different letters indicate significant differences among treatments ($P < 0.05$).

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Conclusions

Total biomass was highest in control, intermediate in 5 cm treatment, and lowest in the other two submerged treatments. Water depth prominently affected the first-order lateral root so as to main root mass ratio. Alcohol dehydrogenase (ADH) activity decreased but malondialdehyde (MDA) content increased as water depth increased. The starch contents showed no differences among different treatments at the end of the experiment. However, soluble sugar contents were highest in control, intermediate in 5 cm and 15 cm treatments, and lowest in 25 cm treatment. Our data suggest that submergence depth affected some aspects of growth and physiology of *C. schmidtii*, which can reduce anoxia damage not only through maintaining the non-elongation strategy in shoot part but also by adjusting biomass allocation to different root orders rather than adjusting root-shoot biomass allocation.

Supporting Information

S1 File. Original data.
(XLSX)

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Author Contributions

Conceived and designed the experiments: HY WL LS. Performed the experiments: RL ZL XW. Analyzed the data: HY WL. Contributed reagents/materials/analysis tools: HY WL. Wrote the paper: HY WL LS.

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