

The effects of complete submergence on the morphological and biomass allocation response of the invasive plant *Alternanthera philoxeroides*

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Abstract Climate change may lead to more intense and frequent flooding. *Alternanthera philoxeroides* is a perennial that grows rapidly in both terrestrial and aquatic habitats. However, there is a lack of information about whether this species survive or not under flooded conditions, especially when completely submerged. In this study, the effect of submergence at depths of 0, 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m on the growth of *A. philoxeroides* was investigated. The results showed that submergence decreased the growth of *A. philoxeroides* but allowed 100% survival. Because of increased shoot length when submerged at the 0.5 m depth for 2 weeks, 62.5% of plants grew above the water. Elongation of shoots and internodes, higher specific leaf area ratio, the leaf weight ratio and stem diameters, development of new leaves (not at depths deeper than 1.0 m), and adventitious roots at all depths were tolerance strategies of *A. philoxeroides* in response to submergence. These strategies suggest that this species is highly tolerant to flooding even

when it is completely submerged at 3.0 m depth. This may contribute greatly to the invasiveness of *A. philoxeroides* and make it very adaptable to habitats that are heavily disturbed (such as by flooding).

Keywords *Alternanthera philoxeroides* · Submergence · Tolerance strategy · Flood invasive

Introduction

In many cases, biotic invaders can inflict enormous environmental damage (Mack et al., 2000) and cause huge economic losses (Pimentel et al., 2005; Xu et al., 2006). Biotic invasions have been recognized as major agents of human-driven global change (Vitousek et al., 1997; Mack et al., 2000). Furthermore, other commonly recognized elements of global change (such as climate change, increased nitrogen (N) deposition, and altered disturbance regimes) can affect species distribution and resource dynamics in terrestrial and aquatic ecosystems, and consequently, can interact with biological invasions (Dukes & Mooney, 1999). Climate change is expected to have a major impact on hydrology, which may lead to even more intense and frequent floods and droughts (IPCC, 2001). For example, in critical regions of Europe, flood events with an intensity of today's 100-year floods and droughts may recur every 50 years or less by the 2070s (Lehner et al., 2006). It is well known that invasions

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can be provoked by disturbance (Mack et al., 2000; Hobbs & Huenneke, 2002; Buckley et al., 2007). Floods are an important natural disturbance (Mack et al., 2000; Lockwood et al., 2007). Many researchers found that floods can facilitate invasion with exotic plants (Sher et al., 2000; Kercher & Zedler, 2004; Diez et al., 2012), mainly because of their tolerance to flooding, which is another highly relevant factor for the success of invasive plant species (Dalmagro et al., 2013).

Adaptive strategies of plants are directed toward survival in flooded conditions (Blom & Voesenek, 1996; Vartapetian & Jackson, 1997). Some plant species avoid flood stress through life history tactics and survive during a period of flooding as dormant seeds or quiescent perennating organs (Voesenek et al., 2004). Furthermore, many flood-resistant plants are able to develop avoidance mechanisms to survive long-term floods based on rapid changes in physiological processes, often characterized by shifts in anatomical and morphological characteristics (Blom & Voesenek, 1996). There are primarily two contrasting strategies: escape or quiescence (Vartapetian & Jackson, 1997; Bailey-Serres & Voesenek, 2008; Akman et al., 2012). Plants that exhibit an escape strategy respond to flooding by enhanced elongation of petioles, stems, or leaves, which can restore the contact of the plant with the atmosphere (Mommer & Visser, 2005; Bailey-Serres & Voesenek, 2008). In contrast, plants that exhibit a quiescence strategy are characterized by limited underwater growth and conservation of energy and carbohydrates to counteract harmful cellular changes associated with flooding (Bailey-Serres & Voesenek, 2008; Yu et al., 2012).

Apart from the frequency, duration, and timing of floods, different depths of flooding can be distinguished, ranging from soil flooding or waterlogging to submergence of the vegetation (Blom & Voesenek, 1996). Submergence occurs when floodwaters rise to a level at which shoots are completely under water (Colmer & Voesenek, 2009). Complete submergence imposes considerable stress or negative impact on nearly all plant characteristics (except shoot length) (Webb et al., 2012), severely influences photosynthesis (Blom & Voesenek, 1996; Jackson & Colmer, 2005), and even causes the death of intolerant species (Jackson & Colmer, 2005; Mommer & Visser, 2005; Bailey-Serres & Voesenek, 2008). Furthermore, some species immediately cease growing upon submergence, while

others maintain or even increase biomass production (Blom & Voesenek, 1996), depending on species type and survival strategy (Bailey-Serres & Voesenek, 2008). Although many researchers have investigated the effects of flooding on population dynamics and the growth of exotic plants (Chen et al., 2002; Stokes, 2008; Gandiaga et al., 2009; Lunt et al., 2012), we know comparatively little about the responses of the invasive plants to complete submergence caused by heavy flooding.

Alternanthera philoxeroides (Mart.) Griseb is an invasive weed originally from South America (Vogt et al., 1979). This species is distributed extensively in all continents except Africa (Julien, 1995; Garbari & Pedulla, 2001). *A. philoxeroides* is a stoloniferous and rhizomatous perennial species that propagates mainly through vegetative propagules (Julien, 1995; Sainty et al., 1998). It grows rapidly in a range of habitats from dry terrestrial to aquatic beginning in the spring, where it may be rooted into the bank or the substrate beneath shallow water or may form dense interwoven free-floating mats on the water's surface (Vogt et al., 1979; Buckingham, 1996; Sainty et al., 1998; Bassett et al., 2012). The mats are composed of both leaf-bearing erect and prostrate stems (Pan et al., 2006). Aquatic growth is characterized by larger hollow stems, providing great buoyancy, which root at closely spaced nodes (Julien et al., 1995; Buckingham, 1996). Depending on water currents and wind conditions, stems often break and float away to begin a new mat elsewhere (Julien, 1995; Buckingham, 1996). Morphological and physiological adaptations, the plant's over-wintering strategy, clonal integration, and recovery capacity after de-submergence may explain the survivability of *A. philoxeroides* during the change from a dry to a flooded environment (Geng et al., 2006; Wang et al., 2008a, b; Liu & Yu, 2009; Luo et al., 2009, 2011; Wang et al., 2009). In brief, *A. philoxeroides* is common on flood-plains and poorly drained agricultural land, and thrives in areas that have high summer rainfall (Sainty et al., 1998).

Currently, *A. philoxeroides* is distributed widely in terrestrial and aquatic habitats in China. In particular, *A. philoxeroides* grows and spreads quickly in rice fields, ditches, rivers, lake shores, or ponds. *A. philoxeroides* is mainly distributed in the warm temperate and subtropical regions of China and especially spreads explosively in the Yangtze River Basin (Xu et al., 2005). The wetter region of southern

China experiences more rainfall than the northeastern China during both summer and winter (Piao et al., 2010) and is subjected to high frequency of extreme precipitation in the Yangtze River Basin, which indicates that the possibility of a flood disaster might be aggravated (Su et al., 2008; Xu et al., 2009). Thus, terrestrial or rooted-aquatic *A. philoxeroides* encounters flooded conditions there and inevitably becomes completely submerged under various depths of water. A previous study found that *A. philoxeroides* could survive under a depth of 2 m (Wang et al., 2008a, b) and a depth of 1 m (Luo et al., 2009, 2011). However, only one depth was examined in these studies. As a highly invasive plant in China, little is known about the response of *A. philoxeroides* to complete submergence at various water depths. Does *A. philoxeroides* survive under these conditions? If *A. philoxeroides* survived at all submergence depths, this species should display adaptability or tolerance to a particular target-submerged environment.

In the summer months, the experiments involving complete submergence of 0, 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m depths was carried out to evaluate survival, morphological responses, changes in biomass, and biomass allocation to discover adaptations of *A. philoxeroides*. We predicted that (1) complete submergence would decrease the growth of *A. philoxeroides* but allow survival even at a deep depth of 3.0 m, and morphological adaptations that help this species tolerate submergent stress would emerge; (2) escape (shoot elongation) and quiescence strategies (limited underwater growth) would be observed in shallow water and deep water, respectively; (3) adventitious roots would develop in response to submergence.

Materials and methods

Study site

This experiment was conducted in The National Field Station of the Freshwater Ecosystem of Liangzi Lake, Hubei Province, China (30°50′–30°180′N, 114°210′–114°390′E). Liangzi Lake was a middle, mesotrophic, and shallow lake located on the middle reaches of the Yangtze River Basin with an area of 304.3 km². The mean depth varied from 2.5 to 10 m. Previous study found that water level increases gradually during May

along with increasing precipitation and that the maximal water level occurred during the July flood season in most lakes in the middle and lower reaches of Yangtze River. The maximal variation in the water level was approximately 3 m compared with that in June (Yang et al., 2000; Li et al., 2007; Hu et al., 2010). In our study site at Liangzi Lake, water level increased gradually during May due to increasing precipitation. Water depth in July was approximately 2 m higher than that in June, which was caused by extreme precipitation in 2010; half a month later, the water level decreased gradually because of the action of a flood discharge pump.

Experimental design

On 18 May, 150 tip cuttings of *A. philoxeroides* were collected in field populations of Liangzi Lake, and then planted vertically into three pots with sand and 2 cm water. After 3 days, all plants were rooted. A total of 105 shoots of *A. philoxeroides* were planted, and the mean fresh weight of the shoots was 0.18 ± 0.004 g; three nodes were selected. At the beginning of the experiment, two shoots were randomly planted into a pot (13.0 cm depth, 14.0 cm up diameter and 7.5 cm down diameter) filled with fine-textured, homogeneous sediment soil. Plants were grown for a further 30 days before the submergence treatments were applied. Plants were watered when needed. After 30 days growth (on 20 June), seven plants were harvested. The mean length and dry weight were 35.39 ± 1.67 cm and 2.27 ± 0.30 g, respectively. Then, 84 plants were submerged under water at depths of 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 m. Another 14 plants served as controls (unsubmerged: termed “0 m”). Among the treatments, half of the plants were randomly selected for submergence for 1 week (until 27 June) and half for 2 weeks (until 4 July). Forty-two pots were placed in each of seven concrete ponds (4 m × 4 m × 4 m deep), where they could be individually adjusted vertically by ropes tied to steel bars lying on top of the ponds. The pots in each pond were randomly allocated to the six treatments, with two replicates per pond. Another 7 unsubmerged pots were laid on the top of concrete pond walls, and plants were watered when needed. Water temperature was 29.4–33.1°C, pH 7.7–8.4, conductivity 175–201 $\mu\text{s cm}^{-1}$, dissolved oxygen concentration 4.77–6.88 mg l⁻¹, and turbidity 0–5 NTU.

Measurements

At harvest, the leaf number, node number, stem diameter, and internode length were recorded and measured. Shoot length was measured from the base of the plant to the tip of its longest leaf. When *A. philoxeroides* was submerged, new adventitious roots developed from the submerged stems (termed “water roots” in this paper, to distinguish them from the roots that grew in sediment, which were termed “sediment roots” in this paper). The plants were separated into stems, leaves, water roots, and sediment roots to analyze biomass allocation. Total biomass was obtained after drying plants in an oven at 80°C for 48 h. The leaf weight ratio (LWR), stem weight ratio (SWR), adventitious water root weight ratio (WRWR), and sediment root weight ratio (SRWR) were calculated as the ratios between the biomass of the leaves, stems, water roots or sediment roots, and the total biomass, respectively. Leaf areas were measured with a leaf area meter (LI-3000; Li-Cor). After measurements, leaves were dried at 80°C for 48 h. Specific leaf area ratio (SLA, leaf area divided by the leaf DW, cm² g⁻¹) was derived.

Statistical analyses

Two-way ANOVA, with water depth and submergence duration as the main factors, was performed to determine main effects and interactions on morphological traits, total biomass, and biomass allocation. If a significant treatment effect was detected, post hoc pair-wise comparisons of means were made to examine differences between treatments using the Studentized Tukey’s HSD for multiple comparisons. Data were log₁₀-transformed if necessary to reduce heterogeneity of variances, and homogeneity was tested using Levene’s test. All data analyses were conducted using SPSS 18.0 (SPSS, Chicago, IL, USA).

Results

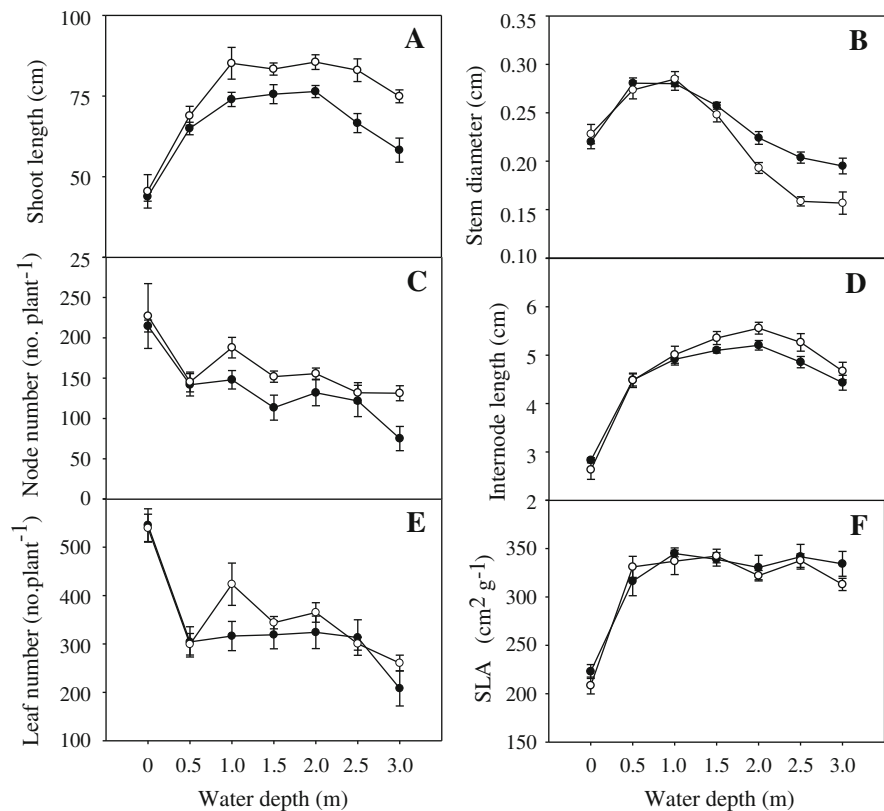
Survival and morphological traits

Plant survival was 100% during both 1 and 2 weeks of complete submergence at the various water depths. 85.7% of plants at 0.5 m depth reached the water

Table 1 *F* and *P* values for two-way ANOVA analysis for morphological, biomass, and biomass allocation traits of *A. philoxeroides*

Variable	df	<i>F</i>	<i>P</i>
Shoot length			
Water depth	6	26.663	<0.001
Duration	1	35.414	<0.001
Water depth × duration	6	1.796	0.111
Stem diameter			
Water depth			
Duration	6	73.124	<0.001
Water depth × duration	1	19.115	<0.001
Node number	6	3.799	0.002
Water depth	6	10.370	<0.001
Duration	1	8.645	0.004
Water depth × duration	6	0.964	0.455
Internodes length			
Water depth	6	84.108	<0.001
Duration	1	3.072	0.083
Water depth × duration	6	1.174	0.328
Leaf number			
Water depth	6	17.310	<0.001
Duration	1	3.232	0.077
Water depth × duration	6	1.166	0.335
SLA			
Water depth	6	33.055	<0.001
Duration	1	1.037	0.312
Water depth × duration	6	0.752	0.609
Total biomass			
Water depth	6	28.347	<0.001
Duration	1	12.871	<0.001
Water depth × duration	6	0.823	0.556
LWR			
Water depth	6	17.761	<0.001
Duration	1	1.655	0.894
Water depth × duration	6	3.876	0.018
SWR			
Water depth	6	6.107	<0.001
Duration	1	0.114	0.678
Water depth × duration	6	2.144	0.361
WRWR			
Water depth	5	2.358	0.050
Duration	1	3.452	0.068
Water depth × duration	5	0.243	0.942
SRWR			
Water depth	6	11.859	<0.001
Duration	1	20.435	<0.001
Water depth × duration	6	4.899	<0.001

Fig. 1 Morphological changes of *A. philoxeroides* of control and submerged plants after 1 and 2 weeks ($n = 7$; bars indicate SE). Filled circle submerged for 1 week; open circle submerged for 2 weeks



surface and did not grow out of the water after submergence for 1 week. In contrast, 62.5% of plants emerged and floated above the water surface because of increased shoot elongation when submerged in 0.5 m depth for 2 weeks. At the other depths, all plants remained submerged.

Both water depth and submergence duration had a significant effect on the shoot length (Table 1). After 1 and 2 weeks submergence, shoot length was significantly elongated (Fig. 1A). When plants grew at submergence from 0 to 1.0 m depth, the length was significantly increased with increasing water depth. The lengths assumed a relatively higher value at depths of 1.0–2.5 m. On the other hand, shoot elongation was inhibited by submergence at 3.0 m depth, and there was no significant difference in shoot length between 3.0 m depth and 0.5 m depth (Fig. 1A). Duration had no significant effects on shoot length of unsubmerged plants and plants at 0.5 m depth, while the length of plants submerged at depths of 1.0–3.0 m was significantly increased (Fig. 1A).

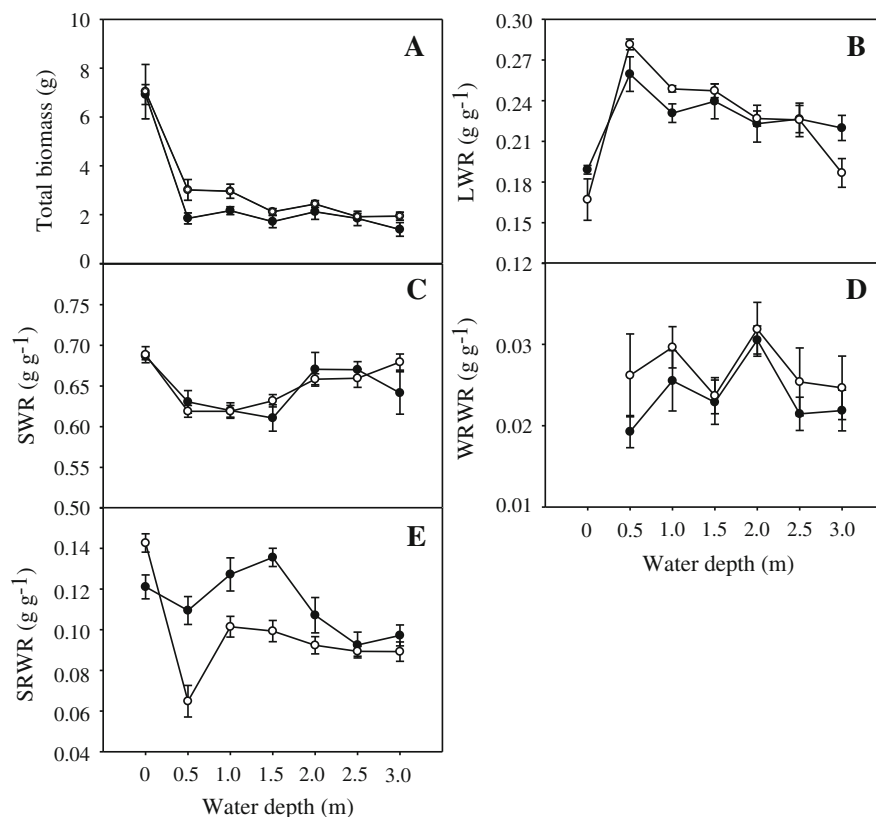
Both water depth and submergence duration had a significant effect on stem diameter, and the interaction

between the two factors was also significant (Table 1). A similar trend was observed for the stem diameter during two submergence durations (Fig. 1B). The stem diameters of plants initially increased with submergence, and the maximum values were reached at 0.5 m depth for the 1-week duration and 1.0 m depth for the 2-week duration. Then, the values decreased gradually, finally attaining minimum values at 3.0 m depth (Fig. 1B). Though the stem diameter of plants submerged from 0 to 1.5 m depth did not change with increasing submergent time, the stem diameter of plants submerged from 2.0 to 3.0 m depth was decreased significantly (Fig. 1B).

Both water depth and submergence duration had a significant effect on node number (Table 1). After 1 and 2 weeks submergence, node numbers decreased significantly with increasing depth, and the minimum values were observed at 3.0 m depth (Fig. 1C). Node number of plants at 1.0 and 3.0 m depth increased significantly with increasing submergent time, but not at the other depths (Fig. 1C).

Water depth, but not submergent duration, had a significant effect on the internode length (Table 1).

Fig. 2 Biomass and biomass allocation of *A. philoxeroides* of control and submerged plants after 1 and 2 weeks ($n = 7$; bars indicate SE). Filled circle submerged for 1 week; open circle submerged for 2 weeks



Compared with the unsubmerged plants, submergence increased internode length significantly, and the maximum values were observed at 2.0 m depth (Fig. 1D). Furthermore, no significant differences of internode length of plants among the water depths from 1.0 to 2.5 m were found (Fig. 1D).

Only water depth had significant effect on leaf number (Table 1). During the two submergent durations, compared with the unsubmerged plants, observations showed that submergence decreased leaf number, and the minimum values were observed at 3.0 m depth (Fig. 1E). After submergence for 1 week, there were no significant differences in leaf number among the water depths from 0.5 to 3.0 m. However, after submergence for 2 weeks, leaf number at 1.0 m depth was significantly higher than that for 0.5, 2.5, and 3.0 m depth, but showed no significant differences with leaf numbers at 1.5 and 2.0 m depths (Fig. 1E).

Water depth, but not submergence duration, had a significant effect on SLA (Table 1). Compared with the unsubmerged plants, SLA increased significantly when the plants were submerged (Fig. 1F). However,

there were no differences in SLA among depths from 0.5 to 3.0 m (Fig. 1F).

Biomass and biomass allocation

Both water depth and submergent duration had a significant effect on total biomass (Table 1). During the two submergent durations, submergence decreased total biomass significantly compared with the unsubmerged plants. However, there were no significant differences in total biomass among depths at 0.5–3.0 m (Fig. 2A). With increased submergence duration, the total biomass of plants increased significantly at the 0.5 and 1.0 m depths, but not at other depths (Fig. 2A).

Water depth, but not submergence duration, had a significant effect on LWR and SWR (Table 1). Furthermore, the interaction of water depth and duration on LWR was also significant (Table 1). The LWR of unsubmerged plants was lower than that of all submerged plants, while the significant difference was only observed in plants at depths from 0.5 to 1.5 m

after submergence for 1 week and at depths from 0.5 to 2.0 m after submergence for 2 weeks (Fig. 2B). After submergence for 1 week, the SWR of unsubmerged plants showed no significant difference compared with submerged plants except for 1.5-m depth plants. After submergence for 2 weeks, shallow submergence (0.5–1.5 m) significantly decreased SWR, while deeper water depths (from 2.0 to 3.0 m) had no significant effect on SWR (Fig. 2C). After submergence for 1 week, no significant differences in LWR and SWR were observed for plants submerged from 0.5 to 3.0 m (Fig. 2B, C). After submergence for 2 weeks, LWR and SWR of plants started to decrease and increase with increasing submergence depth, and the value of LWR of plants at 0.5 m was significantly higher than that for other submerged plants, and SWR of plants at 3.0 m was significantly higher than that for other submerged plants except at 2.0 and 2.5 m (Fig. 2B, C).

Both water depth and submergence duration had no significant effects on WRWR but on SRWR (Table 1, Fig. 2D, E). After submergence for 1 week, submergence had no significant effects on plants SRWR except for plants at 2.5 m depth compared with unsubmerged plants. Furthermore, when plants were submerged deeper than 1.5 m depth, SRWR was decreased significantly with the increasing depth (Fig. 2E). SRWR significantly decreased in all the treatments after submergence for 2 weeks. The SRWR value of plants at 0.5 m depth was the minimum and was significantly lower than for the other treatments. No significant differences were found in SRWR for plants among depths from 1.0 to 3.0 m (Fig. 2E).

Discussion

Our results show that complete submergence did not lead to death but allowed *A. philoxeroides* survival even at a deep 3.0 m depth after 2 weeks flooding duration. Complete submergence imposes considerable stress on plant function traits, predominantly due to oxygen deprivation, and rapidly results in loss of biomass and ultimately the death of many plant species (Mommer & Visser, 2005). However, some plants maintain or even show increased biomass because not all species are equally vulnerable to submergence (Blom & Voeselek, 1996; Mommer & Visser, 2005). A previous study

found that *A. philoxeroides* could survive at 100% in a 1 m depth for 20 or 30 days, respectively (Luo et al., 2009, 2011), and in a 2 m for 30 and 60 days, respectively (Wang et al., 2008a, b). This species may have evolved many of the traits to reduce the negative effects of submergence.

Shoot elongation was the plant response to submergence, in order to restore contact between the leaves and air above the water surface (Voeselek et al., 2004; Jackson & Colmer, 2005; Mommer & Visser, 2005; Bailey-Serres & Voeselek, 2008; Banach et al., 2009; Pierik et al., 2009). Shoot elongation was classified as an escape trait, one of the main strategies to adapt to complete submergence (Bailey-Serres & Voeselek, 2008). Our experiments found that plants in all submergent treatments had significantly increased shoot length, which illustrated that escape traits in response to submergence also existed in *A. philoxeroides*. Furthermore, 62.5% plants emerged and floated above the water surface because of increased shoot elongation when submerged at 0.5 m depth for 2 weeks. Total biomass of plants at 0.5 m depth was higher than that at deeper water depths, these results illustrated that shoot elongation above the surface is associated with fitness benefits; plants emerging above the water had greater biomass production than plants that were kept below the surface (Pierik et al., 2009). On the other hand, shoot elongation may be associated with costs in a severely photosynthesis-limited environment (Voeselek et al., 2004; Kawano et al., 2009; Pierik et al., 2009). If a plant fails to regain contact with the air, then it inevitably gives rise to serious carbohydrate depletion (Kawano et al., 2009), and even causes plant death if resource reserves are depleted before emergence (Das et al., 2005; Bailey-Serres & Voeselek, 2008; Kawano et al., 2009). Therefore, fast shoot elongation under water seems to be a favorable trait only in environments with shallow, prolonged flooding events, while this response was generally absent in sites with deep floods (Voeselek et al., 2004). In our experiments, further increases in shoot length ceased when the submergence depth was deeper than 1.0 m. This illustrated that an alternative strategy for avoiding carbohydrate depletion was a quiescence strategy, characterized by the absence of quick elongation in response to deep submergence (Bailey-Serres & Voeselek, 2008; Kawano et al., 2009). Plants with an escape strategy respond to submergence by

enhanced shoot elongation to regain contact with the atmosphere, whereas those with the quiescence strategy conserve energy and carbohydrate by restraining growth (Luo et al., 2011; Akman et al., 2012).

In this study, compared with unsubmerged plants, shallow submergence (not deeper than 1.5 m) led to higher stem diameters, which is consistent with that *A. philoxeroides* in aquatic habitats had significantly thicker stems, compared with terrestrial habitats (Julien et al., 1992; Geng et al., 2006), and this strategy might be more adaptive in aquatic habitats because thicker and hollow stems could provide buoyancy (Julien et al., 1992). The plants grown in deep water did not exhibit increased stem diameters, which may also suggest that, under deep water submergence, plants with a quiescence strategy conserve energy and carbohydrates by restraining growth (Luo et al., 2011). Submergent duration significantly decreased stem diameter of plants submerged at 2.0–3.0 m depth, which illustrated that with the increasing submergence duration, the effects of deeper submergence were significant.

Our experiments found that all submergent treatments significantly decreased node numbers and increased internode length compared with unsubmerged plants. This was consistent with the result that submergence strikingly enhanced elongation of internodes in *A. philoxeroides* (Wang et al., 2008a, b; Luo et al., 2009), and a report that increased elongation up to 140% of growing internodes of an invasive *Phragmites australis* was caused by submergence (Mauchamp et al., 2001). Increase in the length of the internodes produced during the submergence phase is part of a strategy to expose photosynthetic tissues and ensure efficient carbon acquisition (Mauchamp et al., 2001).

Because underwater photosynthesis was the straightforward way to reduce shortage of both oxygen and carbohydrates, alleviating considerable stress under completely submerged conditions (Mommer & Visser, 2005), flood-tolerant species generally continued to develop new leaves to increase survival during complete submergence (Mommer & Visser, 2005). The development of new leaves of *A. philoxeroides* was observed in our experiment and in the research of Wang et al. (2008a, b). Photosynthesis by these new leaves would contribute to survival and elongation of shoot length of *A. philoxeroides*.

Light intensity underwater was decreased significantly and generally produced shaded environments

(Sand-Jensen, 1989). A major adjustment of the plants induced by complete submergence was a change in leaf morphology and anatomy (Voesenek et al., 2006). For example, previous studies found that some plants developed underwater have a higher SLA (Vervuren et al., 1999; Mommer et al., 2005; Voesenek et al., 2006). In our experiments, submergence led to a higher SLA in *A. philoxeroides*, which at least partly compensated for the unfavorable gas exchange conditions under water by increasing the relative flux of carbon dioxide and oxygen from the water column into the plant (Mommer & Visser, 2005), and as a consequence, increased the potential for gas exchange, resulting in increased leaf longevity and plant survival (Mommer et al., 2006).

In the present experiments, submergence led to a significant reduction in total biomass compared with unsubmerged plants of *A. philoxeroides*, which was consistent with a previous study that showed that submergence largely decreased biomass production of wetland plants (Mauchamp et al., 2001; Chen et al., 2002). This also illustrated that complete submergence could decrease growth of *A. philoxeroides* (Wang et al., 2008a, b; Luo et al., 2011). In aquatic plants, increasing water level would decrease species biomass (Strand & Weisner, 2001; Yang et al., 2004; Zhu et al., 2012). However, increasing water level did not cause differences in total biomass among different depths of submergence in the present experiments, which might be because the experimental duration was not long enough. For example, the mean weight of the submerged *Scirpus* plants decreased with increased water depth after 3 months (Weisner et al., 1993).

Plants will allocate relatively more biomass to shoots if the limiting factor is above ground (e.g., light, CO₂) due to functional equilibrium, which most likely increases plant growth by enhancing the uptake of the most limiting factor (Poorter et al., 2012). Under complete submergence, plants not only face reduced gas exchange but also changed light conditions (Blom & Voesenek, 1996). Light intensity was decreased significantly by submergence (Banach et al., 2009) and was generally considered to be a shaded environment (Sand-Jensen, 1989). An increase of biomass allocation to leaf or stem tissue in a shaded environment will decrease biomass allocation to other tissues (e.g., roots and seeds) (Bloom et al., 1985; Poorter et al., 2012). On the other hand, thickened and storage roots were developed in *A. philoxeroides* when grown

in a terrestrial environment (Shen et al., 2005; Schooler, 2012), while under submergent conditions, gas diffusion and the physical status of soils were changed (Blom & Voesenek, 1996), which would frequently affect roots or other underground organs directly (Vartapetian & Jackson, 1997). The cost of maintaining below-ground biomass under anoxic conditions may have a significantly higher respiratory cost than the maintenance of aerial biomass (Mau-champ et al., 2001), so the growth of roots of *A. philoxeroides* would be inhibited significantly (Wang et al., 2008a, b). In our study, submergence increased *A. philoxeroides* biomass allocation to leaves and decreased biomass allocation to stems and sediment roots, this biomass allocation pattern especially existed during shallow submergence (not deeper than 1.5 m). This may contribute to light harvesting and submergence tolerance in *A. philoxeroides*.

Upon flooding, the initial effects in plants are in the root system (Blom & Voesenek, 1996). The formation of adventitious roots is a morphological acclimation to flooding in many wetland plants (Armstrong et al., 1994; Visser et al., 1996; Chen et al., 2002; Pedersen et al., 2006). This is one of the important adaptive mechanisms of wetland plants to replace existing roots asphyxiated by oxygen shortage in the soil (Vartapetian & Jackson, 1997), therefore, these new roots have a positive role in supporting plant growth during prolonged flooding (Armstrong et al., 1994; Pedersen et al., 2006; Colmer & Voesenek, 2009). In our experiments, all submerged *A. philoxeroides* developed adventitious roots on the nodes of stems in water. This mechanism in this species may contribute to submergence adaptation, especially when caused by a deep, long flood.

Because our findings were related to the early stage (not more than 2 weeks) of development of *A. philoxeroides* in response to complete submergence, submergence but not submergent duration had significant effects on all traits including morphological, biomass, and biomass allocation of *A. philoxeroides*. In conclusion, our results confirmed the hypothesis that complete submergence decreases growth but allows *A. philoxeroides* to survive even when submerged at a deep 3.0 m depth for 2 weeks. The data for shoot length suggests that *A. philoxeroides* adopts an escape strategy (shoot elongation) at shallow water depths and a quiescence strategy in deep water. Though node number, leaf number, and total biomass decreased due to submergence compared with

unsubmerged plants, the plasticity, including shoot elongation, higher SLA, LWR, and stem diameter, the development of new leaves involved in tolerance to shallow depths (not deeper than 1.5 m), may enable *A. philoxeroides* to survive complete submergence. Furthermore, adventitious aquatic root development in completely submerged *A. philoxeroides* was an important contribution to submergence tolerance regardless of the submergence depth. Thus, *A. philoxeroides* appears to be a plant that exhibits plasticity to tolerate or survive complete submergence but not to grow well at depths deeper than 1.5 m. This may be an adaptation to flooded habitats where water level fluctuations are characteristic.

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