Chapter 5

Flooding impact disentangled: water pressure affects the survival and growth of the terrestrial plant *Alternanthera philoxeroides* upon deep submergence more than low light or oxygen availability

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Abstract

Flooding imposes stress upon terrestrial plants, and causes the death of intolerant species. Consequently, there is a steep decline in species richness with water depth in many wetlands and river forelands. The depth range a species occupies is determined by its tolerance to the gradient of factors that vary with water depth, notably light regimes, dissolved oxygen availability and water pressure. However, no previous study has disentangled the effects of these three main factors on plant growth and survival upon complete submergence. We set up a unique full factorial experiment with three factors each at two levels: 2 light regimes × 2 dissolved oxygen concentrations × 2 water pressure levels (i.e. depths), and used Alternanthera philoxeroides (Mart.) Griseb., a submergence-tolerant terrestrial species as a model. We quantified the interactive effects of water pressure, light and dissolved oxygen on the growth and survival of this terrestrial species under complete submergence at different depths. The results demonstrated that water pressure has the largest influence on the growth and survival of deeply submerged plants. High water pressure decreased stem elongation and adventitious root growth, increased the biomass and carbohydrate loss. At the same time, plants under higher dissolved oxygen had more and longer adventitious roots; however the different light regimes did not significantly affect the growth or survival of the plants. These findings advance our understanding of the drivers and mechanisms of flooding impact on terrestrial plants and invite research to test whether the responses seen in A. philoxeroides can be generalized to other terrestrial species in flooding-prone environments.
High water pressure affects the growth and survival of plants

Introduction

Flooding by fresh water profoundly affects a wide range of natural ecosystems and managed land, e.g. in river floodplains worldwide, with often damaging impact on agricultural production (Smith 2013). Moreover, as a consequence of climate change, the frequencies and intensities of floods are expected to increase in the future (Hirabayashi et al., 2013; IPCC, 2013), thereby also increasing the frequency of complete submergence events of terrestrial plant species. A better understanding of plant survival and growth performances in response to different submergence conditions will help to anticipate and perhaps mitigate negative effects of flooding on vegetation performance and diversity.

A prominent feature of wetlands, lakeshores and river forelands is depth zonation, with terrestrial species (including riparian species such as helophytes) occupying different positions relative to the water level (Ellery et al., 1991). A decline in species richness with depth has been seen in many wetlands and river forelands. The depth range a species occupies is determined by its tolerance to the gradient of factors that vary with water depth, notably light regimes, dissolved oxygen availability and water pressure (Sorrell et al., 2012). These respective factors are considered to have profound influences on the growth and survival of plants under submerged conditions.

Under complete submergence, light availability is considered to be an important factor to plant survival because of its role in (underwater) photosynthesis, which may improve the internal carbohydrates status. The plants submerged in close to full light (compared to ambient light above the water) always contained more soluble carbohydrates and starch compared to plants under shaded submerged condition (Ram et al., 2002; Mommer & Visser, 2005b). Indeed, oxygen produced by photosynthesis may improve the aeration status of submerged plant organs, aiding these organs to continue aerobic respiration; as a result, the depletion of the carbohydrate store in submerged plants will also be slowed down considerably (Mommer & Visser, 2005b). Light quality also directly affects plant survival; light levels attenuate steeply with the increase of water depth, in which the intensity of red light absorbed by photosystem II also decreases more steeply than other wavelengths in the visible light regime (Lambers et al., 2008). These different
light regimes with increasing water depth may result in slower photosynthetic rate and compromise survival of submerged plants.

For terrestrial species, complete submergence also imposes stress because the supply of O$_2$ to plants in the water column diminishes (Jackson, 1985). Many terrestrial plants have evolved adaptations to low oxygen environments to absorb oxygen from the water column by leaves or adventitious roots (Mommer et al., 2004; 2005a; 2007; Ayi et al., 2016). For instance, leaves with gas films can easily take up oxygen via stomata, since the gas films on leaves enlarges the water-gas interface. This adaptation of leaves improves the gas exchange with the water column and the internal aeration during complete submergence, (Pedersen et al., 2009). Acclimated leaves of terrestrial plants that develop under water are thinner, have a higher specific leaf area (SLA), have thinner cuticles and cell walls, sometimes retain gas films; these traits facilitate O$_2$ absorption from the surrounding water (Mommer et al., 2004). The internal oxygen status of submerged plants is highly affected by the concentration of dissolved oxygen in the water column (Pedersen et al., 2006; Rich et al., 2013). However, the concentration of dissolved oxygen in the water column, especially in still water, generally varies and often decreases with the water depth because of slow diffusion from the atmosphere, the respiration of organisms, temperature variation and salt content in water (Wetzel, 2001).

Another important but much less understood factor which also changes greatly with water depth is water pressure. Depth in the water column may affect plant survival independently from light, through hydrostatic pressure, which may largely change the total air space (aerenchyma) in submerged plant organs (Adkins et al., 1990). Till now, to our knowledge, all the studies about flooding tolerance of terrestrial plants involving water depth have been limited to shallow submergence (e.g. down to 3 meters depth). Owing to climate change leading to increased flooding regimes (see above), and to the increasing dependence on dams leading to water fluctuation belts upstream (Mallik & Richardson, 2009; Su et al., 2013), plants will experience more and more deep submergence (e.g. down to 10 meters below the surface) in the future. Under such conditions the plants are likely to suffer from the much higher water pressure. However, it is not clear yet whether or how high water pressure affects the performance of terrestrial plants under complete submergence; and how the effects of water pressure interact with or are
confounded with those of light regime and oxygen availability. Indeed, it has been pointed out that the depth extension of emergent vegetation is determined by a complex of interacting external and internal variables (Coops et al., 1994; Sorrell & Hawes, 2010). This calls for a quantification of plant survival and growth responses to the interacting effects of the key environmental drivers associated with variation in water depth.

The aim of this study was therefore to quantify the interacting effects of water pressure, light and dissolved oxygen on the growth and survival of terrestrial plants under complete submergence at different depths. To achieve our aim, we set up an unique full factorial experiment with three factors at two levels: 2 light regimes × 2 dissolved oxygen concentrations × 2 water pressure levels (i.e. depths), and quantified effects of these treatments on growth and survival of Alternanthera philoxeroides (Mart.) Griseb., a submergence-tolerant terrestrial model species.

Materials and methods

Species and plant preparation

Alternanthera philoxeroides (Mart.) Griseb., a perennial terrestrial plant of the Amaranthaceae family, originates in South America, but has spread to many parts of the world and is considered as an invasive species in many countries. This species has a very high flooding tolerance, upon which it usually produces adventitious roots on the nodes of the submerged stems.

In the early spring season, the A. philoxeroides plants used in the experiment were cultivated from cuttings that had been collected from plants growing along the banks of Jialing River in the subtropical Chongqing District, southwest of China (29°49’N, 106°25’E). Unbranched plants with stem length of ca. 30 cm were selected and cut at the stem base. Each cutting was planted in a 20cm diameter and 20cm deep plastic pot (with bottom drainage holes) containing a soil mixture of 40% clay, 40% humus soil and 20% sand. Three stem nodes of the cutting were buried in the soil for rooting. All these plantlets were put in an open field of the experimental garden of the Key Laboratory of Three Gorges Reservoir Region at Southwest University, Chongqing (i.e. close to the collecting site), and cultivated under the same conditions of temperature (around 10-15 °C in day-time), relative
humidity (75-85%), light (daily max. 600-800 µmol·m⁻²·s⁻¹), and water provision (around 80%-90% of soil water-holding capacity). After growing for about two months, all plants had rooted and were in good health, around 50 cm tall, ready for the submergence experiments.

**Experimental set-up**

Before the submergence experiment, 24 plants were harvested as the initial harvest group for measuring the total leaf number, stem diameter, and stem height of each plant. The dry mass of leaves, stem, rhizome, and roots were also quantified. Regression equations between the total number of leaves and dry mass of leaves, between the volume of stem and dry mass of stem, and between the dry mass of above ground parts (leaves + stem) and dry mass of below ground parts (rhizome + roots) were constructed; these equations were used to estimate the initial dry mass of the remaining plants based on their total leaf number, stem height and stem diameter (for analysis of relative growth rate; see below) before complete submergence. In this study, dry mass of each tissue was determined by weighing after oven-drying at 60°C for 72h.

The remaining plants were subjected to eight treatments (shown in Table 1). The treatments were allocated to four concrete pools (two with length × width × height: 5m × 5m × 2.5m; and two with length × width × height: 5m × 5m × 10.5m) located in the experimental garden. Each pool was split in half by a black board which completely stopped the light transmission to the neighboring side. One side

<table>
<thead>
<tr>
<th>Water pressure</th>
<th>Dissolved Oxygen</th>
<th>Light intensity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shallow submergence (2 m depth)</td>
<td>High (≈ 19.6 Kpa)</td>
<td>High (≈ 6 mg/L)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Low (≈ 1 mg/L)</td>
</tr>
<tr>
<td>Deep submergence (10 m depth)</td>
<td>Low (≈ 98 Kpa)</td>
<td>High (≈ 6 mg/L)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Low (≈ 1 mg/L)</td>
</tr>
</tbody>
</table>

Table 1 Experimental treatments. See the main text for details.
of each pool was kept completely dark, while the other side was given 120 µmol·m⁻²·s⁻¹ of PAR light by fluorescent lamps which were hung in the water 25 cm above the top of the plants. In addition, all tops of these four pools were covered by six layers of black shading net to prevent the solar light from affecting the light conditions under water. Light intensity under water was measured by underwater quantum sensors (LI-192, LI-COR Biosciences, USA). In order to create two different water pressure levels for the submerged plants, two pools were filled with the tap water until the water surface reached two meters above the bottom of the pools (i.e. the ‘shallow submergence group’); the other two pools were also filled with tap water, but the depth of water reached ten meters above the bottom of the pools (i.e. the ‘deep submergence group’), since the water pressure equation indicates that pressure is the product of water depth, density of water and acceleration of gravity. For each water depth treatment one pool was randomly selected to be maintained at high dissolved oxygen concentration of the water column. These two pools were bubbled with air twice every day, and the oxygen concentration was monitored at every one meter point under water to ensure it stayed at around 6-7 mg/L throughout the water column. The other two pools were kept at low dissolved oxygen concentration. To achieve this, two additional concrete pools were used to produce water of this low oxygen concentration water. Before starting the submergence experiments, these two extra pools were filled with tap water and covered by six layers of black shading net to darken the water column completely. The oxygen concentration in the water column, which was determined every day, decreased to around 0.5 mg/L after two weeks. The low dissolved oxygen water was then smoothly diverted by tubes into the two pools and subsequently kept at about 1 mg/L during our study. Afterwards, silicone oil was poured onto the water surface of these two pools to prevent the oxygen in air from dissolving into the water. During the submergence experiment, the dissolved oxygen concentration also was determined twice a day in these two pools. If the oxygen concentration was higher than 1 mg/L, water was exchanged with the low oxygen water from the extra pools, until the oxygen concentration was back to 1 mg/L. The dissolved oxygen concentration was measured by a multi-parameter water quality analyzer (HYDROLab, Hach, USA).
Growth and survival status testing

The complete submergence experiment lasted for 28 days, after which all plants were harvested. The stem height, number and total length of adventitious roots were measured, and total dry mass of each plant was determined after drying at 60°C for 72h. In addition, the nonstructural carbohydrates (NSC), including both soluble sugar and starch, in stem and underground organs of these harvested plants were analyzed. For methodological details on the NSC assay see Wong (1979) and Hoch et al. (2003).

Data analysis

The relative growth rate (RGR) of dry mass of each individual plant was calculated as:

$$\text{RGR} = \frac{\ln A_2 - \ln A_1}{t_2 - t_1}$$

where $A_1$ was the estimated dry mass of each plant before complete submergence (see above), calculated as the sum of the estimated dry masses of leaves, stem, rhizome and roots; $A_2$ was obtained from the final harvest of each plant after complete submergence, while $t_1$ and $t_2$ represented the start and end dates of complete submergence, respectively.

Three-way ANOVAs were run to determine the differences in RGR of stem height, RGR of biomass, total number of adventitious roots, total length of adventitious roots and content of non-structural carbohydrates, with water depth and dissolved oxygen as between-subject factors and light regime as within-subject factor. Also a one-way ANOVA across all water depth treatments was carried out separately and followed by a Tukey post-hoc test, to test the differences in RGR of stem height, total number of adventitious roots, total length of adventitious roots, RGR of biomass, and content of non-structural carbohydrates between the light condition and dissolved oxygen treatments. Data transformation was performed to equalize variances when necessary; significant differences were reported at $P < 0.05$. All analyses were performed using SPSS 23.
Results

*RGR of stem height and total biomass*

For these plants the number or length of adventitious roots and non-structural carbohydrates in tissues could not be analyzed.

Under complete submergence, the relative growth rates (RGR) of stem height and total biomass of *A. philoxeroides* were significantly affected (*P* < 0.001) by water depth, dissolved oxygen and light regimes, respectively (Table 2, Figure 1). However, the influence of water depth on RGR of stem height and total biomass was the strongest, followed closely by dissolved oxygen. Light regimes had a much weaker effect on RGR.

Additionally, these factors interacted on RGR of stem height and total biomass (Table 2, Figure 1). The RGR of stem height was significantly affected by the interaction between dissolved oxygen and light regime: The combination of shallow submergence, high oxygen and high light conditions stimulated stem elongation. The RGR of total biomass was significantly affected by the interaction between water depth and dissolved oxygen; between water depth and light regimes and between water depth, dissolved oxygen and light regimes. In this study, all plants lost total biomass under both shallow and deep submergence (Fig. 1B). Under shallow submergence, the plants under low dissolved oxygen and dark conditions lost more biomass compared to the plants under other treatments. Under deep submergence, there were no significant differences between the RGR of biomass under low dissolved oxygen no matter whether it was light or dark. However, under high dissolved oxygen concentration, the relative decrease of biomass of plants at high light regime was significantly lower than that of plants under dark condition (*P* < 0.001).

*Growth of adventitious roots*

During submergence, plants produced a number of adventitious roots on the nodes, and the production of adventitious roots was affected by environmental conditions (Table 2, Figure 2). The number of adventitious roots was significantly affected by water depth, dissolved oxygen, light regimes, the interaction between water depth and dissolved oxygen, and the interaction between water depth and light regime (Table 2, Figure 2). Under shallow submergence and low dissolved oxygen
Table 2. The results of Three-way ANOVA for effects of water depth, dissolved oxygen, light regimes, and their 2-way and 3-way interactions, on the RGR of stem height, RGR of biomass, total number of adventitious roots and total length of adventitious roots of *A. philoxeroides*; η² values and their significance are presented.

<table>
<thead>
<tr>
<th></th>
<th>RGR of stem height</th>
<th>RGR of total biomass</th>
<th>Total number of adventitious roots</th>
<th>Total length of adventitious roots</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>η²</td>
<td>P</td>
<td>η²</td>
<td>P</td>
</tr>
<tr>
<td>Water depth</td>
<td>0.783</td>
<td>&lt; 0.001</td>
<td>0.734</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>0.764</td>
<td>&lt; 0.001</td>
<td>0.714</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Light regimes</td>
<td>0.220</td>
<td>&lt; 0.001</td>
<td>0.219</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Water depth × dissolved</td>
<td>0.003</td>
<td>0.583</td>
<td>0.505</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>dissolved oxygen</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water depth × light</td>
<td>0.026</td>
<td>0.098</td>
<td>0.122</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>regimes</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dissolved oxygen × light</td>
<td>0.258</td>
<td>&lt; 0.001</td>
<td>0.001</td>
<td>0.787</td>
</tr>
<tr>
<td>regimes</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Water depth × dissolved</td>
<td>0.258</td>
<td>0.519</td>
<td>0.133</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>oxygen × light regimes</td>
<td></td>
<td></td>
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</tbody>
</table>

Degrees of freedom (d.f.) were one for all main effects and interactions.
High water pressure affects the growth and survival of plants

**Figure 1.** Relative growth rate (RGR) of stem height (A) and total biomass (B) of *A. philoxeroides* under shallow and deep submergence treatments with different light regimes and dissolved oxygen concentration in the water column. Means ± s.e. (*n*=15), bars that share the same letter are not significantly different from one another (Tukey tests) in each water depth submergence, significance levels are *P* < 0.05. The plants at low oxygen under deep submergence all died during the experiment.
Figure 2. Total number of adventitious roots (A) and total length of adventitious roots (B) of *A. philoxeroides* under shallow and deep submergence treatments with different light regimes and dissolved oxygen concentration in the water column. Means ± s.e. (*n*=15), bars that share the same letter are not significantly different from one another (Tukey tests) in each water depth submergence, significance levels are *P* < 0.05. The plants at low oxygen under deep submergence all died and did not produce adventitious roots.
High water pressure affects the growth and survival of plants

Table 3. The results of Three-way ANOVA for effects of water depth, dissolved oxygen, light regimes, and their 2-way and 3-way interactions, on the nonstructural carbohydrates in roots and stems of *A. philoxeroides*; \( \eta^2 \) values and their significance are presented.

<table>
<thead>
<tr>
<th></th>
<th>Soluble sugar in roots</th>
<th>Starch in roots</th>
<th>Soluble sugar in stems</th>
<th>Starch in stems</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \eta^2 )</td>
<td>( P )</td>
<td>( \eta^2 )</td>
<td>( P )</td>
</tr>
<tr>
<td>Water depth</td>
<td>0.916</td>
<td>&lt; 0.001</td>
<td>0.949</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>0.968</td>
<td>&lt; 0.001</td>
<td>0.913</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Light regimes</td>
<td>0.028</td>
<td>0.380</td>
<td>0.334</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>Water depth \times dissolved oxygen</td>
<td>0.944</td>
<td>&lt; 0.001</td>
<td>0.971</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Water depth \times light regimes</td>
<td>0.008</td>
<td>0.634</td>
<td>0.006</td>
<td>0.691</td>
</tr>
<tr>
<td>Dissolved oxygen \times light regimes</td>
<td>0.001</td>
<td>0.900</td>
<td>0.004</td>
<td>0.753</td>
</tr>
<tr>
<td>Water depth \times dissolved oxygen \times light regimes</td>
<td>0.074</td>
<td>0.145</td>
<td>0.344</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>

Degrees of freedom (d.f.) were one for all main effects and interactions.

concentration, there was no significant difference between the number of adventitious roots for plants between light and dark conditions. However, when the concentration of dissolved oxygen was high, the plants in the dark produced significantly more adventitious roots \((P < 0.001)\). Under deep submergence After the 28 days of deep submergence, the plants under different treatments showed different responses. The plants at high water pressure and low oxygen had
completely died; both the aboveground and belowground parts were fragmented. With high dissolved oxygen, the number of adventitious roots was not

Figure 3. Nonstructural carbohydrates (starch and soluble sugar) in underground organs (A) and stem (B) of *A. philoxeroides* under shallow and deep submergence treatments with different light regimes and dissolved oxygen concentration in the water column. Means ± s.e. (*n*=15), bars that share the same letter are not significantly different from one another (Tukey tests) in each water depth submergence, significance levels are $P < 0.05$. The plants at low oxygen under deep submergence all died and were not tested for NSC.
High water pressure affects the growth and survival of plants

significantly different between the plants at different light regimes \((P = 0.561)\) (Fig. 2A).

The total length of adventitious roots was significantly affected by water depth, dissolved oxygen and the interaction between water depth and dissolved oxygen (Table 2, Figure 2). Plants under high dissolved oxygen produced significantly longer adventitious roots than plants under low dissolved oxygen. However, light condition had no significant influence on the total length of adventitious roots \((P = 0.771)\).

**Non-structural carbohydrates in plant tissues**

Water pressure, dissolved oxygen in the water column and their interaction significantly affected the concentration of sugars in stem and underground organs \((P < 0.001)\) (Table 3). The total amount of non-structural carbohydrates in underground organs was higher than that in stems (Fig. 3). Additionally, the content of starch in stem \((P < 0.05)\) and roots \((P < 0.001)\) significantly depended on the light regime; submerged at high light had higher starch content in these tissues.

**Discussion**

This is, to the best of our knowledge, the first study to have experimentally disentangled the confounded effects of the three main factors that tend to vary simultaneously with water depth (water pressure), dissolved oxygen and light regime. The key role for water pressure and its interactions with oxygen and, partly, light regimes with respect to mortality, biomass losses, adventitious root formation and carbohydrate depletion is not only a novel finding. It is also important in relation to the still increasing numbers of dams and water level rises worldwide, which will increase the likelihood and duration of deep (> 5 m) submergence of terrestrial plants.

**Water pressure largely affects plant survival and stem elongation under deep complete submergence**

In our study, the biomass of plants deceased under any submergence treatment, but water pressure had the greatest negative influence on the biomass decrease (Table 2), while the non-structural carbohydrates were greatly affected by the interaction
between water depth and dissolved oxygen. Notwithstanding the strong single effect of dissolved oxygen level, these results clearly highlight that water pressure is the main factor affecting the survival and performance of plants under deep complete submergence. In marine research, it has frequently been shown that exposure to high water pressure can result in mechanical distortion and tissue compression, especially in gas-filled spaces in the body of most animals (Alam et al., 2016). In our research, the studied plant species had also developed air space, i.e. in aerenchyma in the stem and adventitious roots for transportation of oxygen to the lower parts (Ayi et al., 2016). Whether the dimensions and proportion of air spaces in the stem and in adventitious roots significantly change under deep submergence, i.e. with high water pressure, and whether and how that affects the amount of absorbed oxygen from the water column as well as the extent of internal oxygen transport are not clear; they are our targets for follow-up investigation. Additionally, it has already been pointed out that high pressure affects proteins and other biomolecules structure, especially in membranes (Heremans, 1982; Mozhaev et al., 1996); so it is likely that the biochemistry in our studied species was also affected by high water pressure, with possible knock-on effects on energy production in plant cells. This will be another intriguing issue in need of further investigation.

Shoot elongation is a common response of terrestrial plants to submergence to allow contact via a “snorkel” with the atmosphere to reestablish gas exchange (Voosenek et al., 2004). In our study, plants increased their stem length during the prolonged submergence, but the RGR of stem height was different under each treatment. In addition, shoot elongation was greatly affected by water depth. It is generally accepted that the submergence signal for enhanced shoot elongation is the gaseous phytohormone ethylene (Malone & Ridge, 1983). Ethylene is biosynthesized via an O₂ dependent pathway, and the endogenous concentration of this hormone is determined predominantly by the production rate and outward diffusion. Both aspects are affected by submergence (Bailey-Serres & Voosenek, 2008). On the other hand, shoot elongation has some costs. Increased cell division rates and the synthesis of new cell walls during fast cell elongation require a substantial amount of energy, and therefore of carbohydrates (Voosenek et al., 2006). In our study, the plants that were under high dissolved oxygen in the water column had a higher increase rate of stem height. The main reason for this phenomenon is presumably that the high oxygen concentration in water improved
the oxygen status in the plants, which thereby could produce more energy and use carbohydrates more efficiently, enabling them to elongate the stem better than plants under low oxygen concentration. However, the much higher RGR of both stem height and biomass at shallow submergence (with low water pressure) than at deep submergence (with high water pressure), even at similar oxygen and light regime, is extremely interesting and merits further investigation into the question whether the physical collapse of aerenchyma is to blame.

The formation of adventitious roots largely depends on the dissolved oxygen concentration

Another common response of plants to flooding is the formation of an adventitious root system, which usually forms on their stem or branches (Etherington, 1984; Naidoo & Naidoo, 1992; Rich et al., 2008; 2012). Aquatic adventitious roots are adapted to the flooded environment and support or replace the primary soil roots, which lose their water and nutrient uptake functions during prolonged flooding (Sauter, 2013). The production of adventitious roots usually depends on the surrounding environment (Gislerød, 1983). In our study, the production of adventitious roots was affected by water pressure, dissolved oxygen and light regimes, among which particularly the dissolved oxygen in the water column affected the production of adventitious roots. The plants under high dissolved oxygen produced more and longer adventitious roots than those under low dissolved oxygen, which confirms previous findings indicating that dissolved oxygen is essential to root formation and root growth (Soffer & Burger, 1988; Jeong et al., 2006). It is thought to influence the oxygen status in cells, which has an impact on cell growth and metabolite production (Han & Zhong, 2003). However, another interesting question arising is why the dissolved oxygen has more influence on adventitious growth than on RGR of stem length or RGR of total biomass. We assume that the growth of adventitious roots has more benefits for plant survival under limiting energy and resource conditions under water; in other words, there is a trade-off between the growth of adventitious roots and growth of stem for plants under limiting resource conditions.
The light regime has less influence on growth and survival of plants under complete submergence.

Generally, plants under a sufficient light regime have good growth or survival condition because photosynthesis depends on light capture. Some submerged plants improve their growth or survival because of their underwater photosynthesis (Voesenek et al., 2006). Improved survival of submerged plants in the presence of light was found to correlate with the carbohydrate status of the plants and internal oxygen from underwater photosynthesis (Mommer et al., 2005a). However, in our study, the light regime had less influence on growth and survival of plants under complete submergence compared to water pressure or dissolved oxygen; under low dissolved oxygen condition, there were no significant differences of RGR of stem height, number of adventitious roots and total length of adventitious roots between plants under light and shaded conditions. Some previous studies have shown that the underwater photosynthesis of submerged terrestrial plants is considerably lower than that in air, and the light saturation point of underwater photosynthesis is lower than that of atmospheric photosynthesis (Mommer et al., 2005a); and the net assimilation rate underwater is also lower than that in air (Pedersen & Sand-Jensen, 1992; Mommer et al., 2005a). All the above evidence points to light regime having less influence on growth and survival in our study, but the real reasons still need further investigation.

In summary, water pressure, dissolved oxygen and light regime all affected the growth of completely submerged plants, with important interactions between these environmental drivers too. Within these three factors, the water pressure has the largest influence on the plant's behavior, and this may be the main reason for the zonation of riparian plant species in the floodplain. Additionally, different plant components are differently affected by these factors, of which dissolved oxygen concentration largely affects the growth of adventitious roots, while the light regime has less influence on the growth and survival of completely submerged terrestrial plants. There is a need for both in-depth studies to further elucidate the mechanisms of water depth effects on terrestrial plant performance (see above), as well as broader studies on other terrestrial species prone to flooding.
High water pressure affects the growth and survival of plants

References:


High water pressure affects the growth and survival of plants


