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# Consecutive submergence and de-submergence both impede growth of a riparian plant during water level fluctuations with different frequencies

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## ABSTRACT

Repeated exposure to submergence and de-submergence may induce acclimation in plants growing in riparian areas. However, the effect of each consecutive submergence and de-submergence event has not been evaluated separately. We subjected a riparian species *Alternanthera philoxeroides* to two different fluctuation frequencies: low fluctuation frequency (LFF) and high fluctuation frequency (HFF). Consecutive submergence and de-submergence had comparable negative effects on growth of *A. philoxeroides*, while they respectively down- and up-regulated photosynthetic electron transport in both LFF and HFF. The submergence effects on growth were significantly smaller in the 2nd cycle than in the 1 st cycle of LFF, suggesting reduced tissue loss in the 2nd cycle as a result of acclimation. In HFF, the growth of *A. philoxeroides* was more strongly suppressed than in LFF. During de-submergence, biomass increased in both control and de-submerged plants in LFF, whereas growth recovery was not always seen in HFF. At the end of the experiment, the treatment plants in HFF had only ~50% biomass of the corresponding plants in LFF. Although HFF enhances tissue loss during submergence and thus impairs growth recovery more strongly during de-submergence than LFF, both LFF and HFF induced photosynthetic, photoprotective or growth acclimation in *A. philoxeroides*.

## 1. Introduction

Water level fluctuations are major events that influence riparian and littoral ecosystems along streams and lakes (McGowan et al., 2011; Hirabayashi et al., 2013; Garssen et al., 2015). During water level fluctuations, by which riparian plants are subjected to frequent submergence and de-submergence, light transmission and gas diffusion change greatly, leading to extreme variations in availability of light, $O_2$ and $CO_2$ for photosynthesis and respiration of these plants (Colmer et al., 2013; Voesenek et al., 2016; Sasidharan et al., 2018). Furthermore, submergence and de-submergence also strongly influence redox potential and concentrations of nutrients and toxic compounds in riparian soil (Leyer, 2005; Colmer et al., 2013; Baastrup-Spohr et al., 2016). The toxic compounds include potentially toxic ions such as $Mn^{2+}$ and $Fe^{2+}$, and some volatile organic acids such as propionic and butyric acids, which can accumulate in water-saturated soil and damage roots (Greenway et al., 2006). Therefore, water level fluctuations have profound effects on plant performance and community assembly (Garssen et al., 2015; Baastrup-Spohr et al., 2016).

Fluctuation frequency (i.e., the number of cycles of water level changes within a certain time period) is one of the most important factors of water level fluctuations (Nilsson and Svedmark, 2002; Gerard et al., 2008; De Jager, 2012). Global climate change is predicted to increase the frequency of intense precipitation events in most temperate regions (IPCC, 2014). Consequently, hydrological interaction between rivers and surrounding riparian regions may be altered significantly, resulting in more frequent water fluctuation events in the near future (Hirabayashi et al., 2013; Garssen et al., 2015).

Increasing fluctuation frequency can become very challenging due to frequent variations in $O_2$ and light (Bornette et al., 2008; Baastrup-Spohr et al., 2016). Frequent changes in $O_2$ level leads to production of harmful reactive oxygen species and acetaldehyde in plant tissues (Blokhina et al., 2003; Boamfa et al., 2005; Sasidharan et al., 2018), and frequent variations in light intensity may damage the photosynthetic apparatus (Luo et al., 2009; Voesenek et al., 2016). Water fluctuations with high frequency disturb seedling establishment, damage tissues and impair growth and reproduction of sensitive species (Casanova and Brock, 2000; De Jager, 2012; Baastrup-Spohr et al., 2016). However,

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low or intermediate frequency of water level fluctuations has little effect on, or even promote establishment and growth of some species (Casanova and Brock, 2000; Leyer, 2005; Cunha et al., 2006; Stokes et al., 2010).

In fact, riparian species differ in their responses to frequent water level fluctuations (Casanova and Brock, 2000; Gerard et al., 2008; Luo et al., 2016; Striker et al., 2017). Tolerant species can quickly resume photosynthetic capacities and/or establish gas diffusion between submerged and emerged tissues to alleviate energy and $O_2$ deficiency in roots and/or rhizomes, while sensitive species cannot. Such differences in their response may be related to their habitats along riparian regions to which they are adapted or acclimated (Nakai and Kisanuki, 2011; Baastrup-Spohr et al., 2016; Winkel et al., 2016). For example, plants at higher elevations may experience water level fluctuations less frequently than those at lower elevations (Gerard et al., 2008; McGowan et al., 2011; De Jager, 2012). In general, published reports are at variance concerning the effects of fluctuation frequency on plant growth (Casanova and Brock, 2000; Leyer, 2005; Stokes et al., 2010; McGowan et al., 2011; Baastrup-Spohr et al., 2016).

Acclimation to consecutive fluctuation cycles is of central importance for survival and growth of plants during water level fluctuations (Dylewski et al., 2012; Milroy and Bange, 2013). Many studies have investigated growth and photosynthetic responses of riparian plants to water level fluctuations, focusing on the overall performance at the end of fluctuations (Casanova and Brock, 2000; Nakai and Kisanuki, 2011; Dylewski et al., 2012; Milroy and Bange, 2013; Striker et al., 2017). In comparison, dynamic responses to consecutive fluctuation cycles have not been examined extensively (Nakai and Kisanuki, 2011; Milroy and Bange, 2013). Importantly, the effect of each submergence and de-submergence event, separated from the effect of the preceding cycle(s), has not been assessed (Baastrup-Spohr et al., 2016; Dolinar et al., 2016; Striker and Colmer, 2017).

Here we investigated the effects of fluctuation frequency in *Alternanthera philoxeroides* (alligator weed) which typically inhabits shallow water where it naturally experiences water level fluctuations (Zhang et al., 2015). Following a single submergence event, this species is able to quickly recover the photosynthetic capacity (Luo et al., 2009). We subjected the plants to water level fluctuations with different frequencies: low-frequency fluctuation (LFF), high-frequency fluctuation (HFF) and the corresponding control treatments to assess the impact of each submergence and de-submergence cycle. Specifically, we tested the following three hypotheses: (1) consecutive submergence or de-submergence events have negative effects on growth of *A. philoxeroides*, but (2) negative effects of later cycles may become smaller if acclimation helps the plant to better cope with the fluctuations, and (3) HFF may induce acclimation in *A. philoxeroides* more effectively than LFF as this species is adapted to shallow water conditions.

## 2. Material and methods

### 2.1. Plant species

*Alternanthera philoxeroides* (Mart.) Griseb. (Amaranthaceae) can survive in aquatic, semi-aquatic and terrestrial environments and is found frequently in riparian regions (Zhang et al., 2015). This species is native to South America but highly invasive in many countries including China. It can spread vegetatively and produces hollow, creeping stolons at the water surface. When completely submerged, it quickly elongates shoots to regain the contact with the atmosphere (Luo et al., 2009).

### 2.2. Material preparations

Plants of *A. philoxeroides* were collected from five clumps, at least 10 m apart from each other, of two wetlands in Taizhou, Zhejiang Province, China. The genetic variation of this species is very low in China and plants from different clumps are probably from the same genet (Xu et al., 2003). Therefore, the collected plants were mixed and propagated vegetatively for two months in a greenhouse of Beijing SFK Technology Co., Ltd. Stolon fragments, each 15 cm long with five nodes and an apex, were obtained from the stock population and planted in pots (17 cm in diameter × 14 cm in height) filled with 1:1 (v:v) mixture of peat and sand containing 0.65 ± 0.05 g $kg^{-1}$ total phosphorus, 0.48 ± 0.03 g $kg^{-1}$ total nitrogen and 7.83 ± 0.62 g $kg^{-1}$ total organic carbon (mean ± s.e., n = 4).

### 2.3. Experimental design

After two weeks from planting, 192 plants of similar size were selected for the experiment. Eight of them were harvested to measure initial plant height and biomass: 30.71 ± 1.16 cm and 1.04 ± 0.08 g (mean ± s.e.), respectively. The remaining 184 plants were randomly assigned to three treatments: (1) control, (2) LFF and (3) HFF. The control plants were kept in waterlogged conditions, as were the plants during de-submergence treatment. In LFF, the water level for the plants changed from 0 to 150 cm deep (submergence) and then back to 0 cm (de-submergence), which was repeated twice (two cycles of ten-day submergence followed by ten-day de-submergence) during a 40-day experiment from 5 July to 13 August 2014 (Fig. 1). Also in HFF the water level fluctuated between 0 and 150 cm, but each cycle lasted only ten days (i.e., five-day submergence followed by five-day de-submergence), resulting in four cycles during the same experimental period. Notably, the control plants of the 1 st submergence treatment in LFF and the control plants of the 1 st de-submergence treatment in HFF

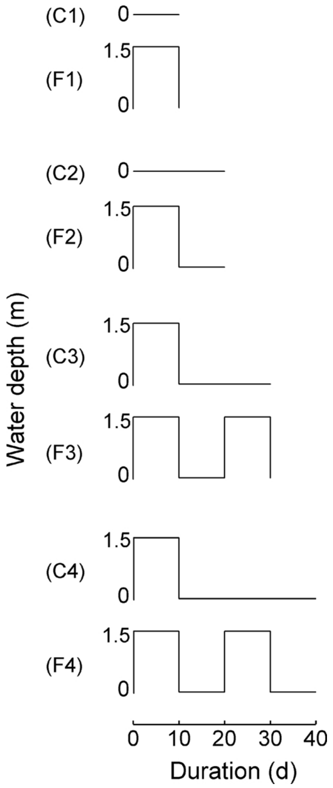

**Fig. 1.** Schematic representation of eight treatments of low-frequency water level fluctuations (LFF), consisting of four fluctuation treatments (F1–F4) and four corresponding control treatments (C1–C4). The four fluctuation treatments included two submergence (F1 and F3) and two de-submergence (F2 and F4) events, lasting ten days for each event. Similarly, high-frequency fluctuations (HFF) had eight fluctuation and eight corresponding control treatments during the same 40-day period. The eight fluctuation treatments included four submergence and four de-submergence events, lasting five days for each event.