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Flooding effects on rapid responses of the invasive plant *Alternanthera philoxeroides* to defoliation

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ABSTRACT

In experiments under controlled growth conditions it was examined how flooding affected the responses of the invasive plant *Alternanthera philoxeroides* to defoliation. In drained and flooded conditions, plants were subjected to five defoliation levels: 0, 10, 50, 90% removal of leaf tissue and apex removal (90% leaf tissue plus apical bud removal). Plants were harvested weekly for five weeks. In drained conditions, plant biomasses including total biomass, shoot biomass and root biomass after 50% defoliation rapidly recovered to the control plant level. They were significantly lower for the 90% defoliation and apex removal treatments compared to control plants throughout the experiment. In flooded conditions, total biomass and shoot biomass after 50% defoliation, 90% defoliation, and apex removal treatments could return to control plant levels before the end of the experiment. In 90% defoliation and apex removal treatments root to shoot biomass ratios of both drained and flooded plants were initially much higher than in control plants, but the difference disappeared rapidly. The final biomasses decreased with increased defoliation intensity in drained conditions, but no significant difference was generally found in any of the defoliation treatments in flooded conditions. The rapid re-growth of *A. philoxeroides* plants after defoliation may partly be responsible for its invasion success. However, defoliation capable of removing 90% of the leaf tissue may be desirable in restricting the growth of this invasive species in drained conditions.

Introduction

In certain types of wetlands, natural flooding is a major factor in the disturbance regime. Flooding has been reported to affect the composition, diversity (Nicol et al., 2003; Van der Valk et al., 1994; Van Geest et al., 2005), and distribution (Pennings et al., 2005; Vervuren et al., 2003) of macrophyte communities. Wetland plants suffer also from a diversity of herbivory effects (Lodge, 1991; Schmieder et al., 2006; Van den Wyngaert et al., 2003). Herbivory has been shown to influence plant photosynthesis (Retuerto et al., 2004), growth rates (Cebrián et al., 1998; Meyer, 1998; Schooler et al., 2007; Engloner, 2009), mortality of species (Reichman and Smith, 1991), inflorescence production (Canto et al., 2004; Mauricio, 1993) and physiological characters (Eklöf et al., 2008). Plant responses to herbivory depend on the type of tissue removed (i. e. root, leaf, stem, meristem, tuber) (Hjältén et al., 1993; Raghu et al., 2006), the frequency and intensity of herbivory (Hayball and Pearce, 2004), the timing of herbivory and the availability of resources in the environment (McNaughton, 1983; Rosenthal and Kotanen, 1994). Generally, high herbivory diminishes plant performance, and, therefore, may be used for the control of invasive species (Raghu et al., 2006).

Herbivory and flooding could interact to lead to differential susceptibility to herbivory along littoral inundation gradients. In such cases the effect of herbivory is influenced by the water regimes. Li et al. (2005) observed the interaction effect of herbivory and flooding on the biomass allocation of one woody plant, black willow (*Salix nigra*). Changes in biomass allocation in response to herbivory depended on whether the plants were continuously flooded or not. Middleton (1990) showed that individuals of three emergent species, *Ipomoea aquatica* Forssk., *Paspalidium punctatum* A. Camus, and *Paspalum distichum* L. usually died when clipped underwater, but lived when clipped every 2 weeks in damp conditions.

Alternanthera philoxeroides ((Martius) Grisebach (Amaranthaceae)) is a serious economic and environmental weed which originates from South America and now invades many countries all over the world (Julien, 1995). It is an amphibious plant because it grows in a range of habitats from dry terrestrial to aquatic, where it may be rooted or free-floating. Though *Agasicles hygrophila* Selman and Vogt, a flea-beetle, introduced to some countries as a biological control agent, has been successful in controlling *A. philoxeroides* in warm temperate aquatic habitats (Julien, 1981), the flea-beetle is an aquatic insect and rarely attacks the terrestrial form of *A. philoxeroides* (Sainty et al., 1998).

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Previous studies have reported the effects of herbivory on *A. philoxeroides* biomass, reproduction and nutrient allocation (Schooler et al., 2006, 2007; Wilson, 2007). However, little is known about difference in *A. philoxeroides* responses to defoliation between drained and flooded conditions. In this study, we simulated herbivory by manual removing leaf tissue and the main stem apex. A prior study found that *A. philoxeroides* biomass responds similarly to simulated herbivory by defoliation and real herbivory by *Agasicles hygrophila* (Schooler et al., 2006). We aimed to determine (i) how quickly the plant could recover from defoliation under both drained and flooded conditions; (ii) whether flooding affected the responses of *A. philoxeroides* to defoliation.

Materials and methods

Plant material

In early May 2007, 335 tip cuttings of *A. philoxeroides* were collected from Liangzi Lake in Hubei province of China (N 30°05′–30°18′, E 114°21′–114°39′), and then planted vertically into ten pots with soil from the lake side. The cuttings were approximately 8 cm long and contained three nodes. Ten days later, a homogeneous subset of 300 vigorously growing plants were selected.

Experimental design

The experiment was conducted in the National Field Station of Freshwater Ecosystem of Liangzi Lake, Wuhan University. The 300 selected plants were randomly transplanted to 30 aquaria ($100 \times 100 \times 100\ cm^3$) filled with fine-textured, homogeneous soil, among which half were randomly selected and filled with water and half were kept well-drained. Plants were grown for a further ten days before the defoliation treatments were applied. We used five defoliation levels within each aquarium, and plants were randomly selected for the applied treatments with two replicates per aquarium.

Artificial damage with scissors was applied in this study to control the magnitude of defoliation. We cut across the midrib to remove 10%, 50% or 90% of tissue from every leaf on each plant. Because some beetles tend to damage stem tissue and cause some of the stem tips to fall off during high defoliation (Schooler et al., 2006), 90% defoliation with apical bud removal was an additional treatment level. This is hereafter referred to as the apex removal treatment. The defoliation treatments were done over seven days and were undertaken by one person to minimize bias. The flooding treatment was applied by maintaining a water depth of 18 cm above the soil surface, while plants were kept well-drained in the drained treatment. Every aquarium was covered with a piece of white net to protect plants from natural herbivory. 93% full sunlight could penetrate the white net. Average temperature was 25 °C during the day. Natural light provided an average daily photon flux density of about 1200 $\mu mol\ m^{-2}\ s^{-1}$ at the top of the plant canopy on the cloudless days.

Data collection

Three drained aquaria and three flooded aquaria were randomly selected, within which all plants were harvested at the end of each week for the following five weeks after the defoliation treatment was completed. Plant was separated into shoot (leaf and stem) and root, dried to constant weight at 65 °C for three days, and weighed. Plant material removed during defoliation treatment was not included in plant biomass.

Data analysis

All data were log (x+1) transformed to meet assumptions of normality and homoscedasticity. Root:shoot biomass ratios were arcsine transformed. Two-way ANOVA was used to analyze factorial effects on final plant growth, with defoliation and flooding as main factors. One-way ANOVA was used to analyze defoliation effects on the plants harvested weekly. Post-hoc pairwise comparisons of means were made to examine difference between treatments using Studentized Tukey's HSD test. Statistical significance was $P < 0.05$. All data analyses were done using SPSS 13.0.

Results

The 10% defoliation treatment generally did not affect drained *A. philoxeroides* biomass during the experiment (Fig. 1). Though 50% defoliation reduced total biomass and shoot biomass in the second week, it quickly returned to the control level in the third week (Fig. 1a, b). *A. philoxeroides* responded to 50% defoliation later for root biomass than for total biomass and shoot biomass. Root biomass declined in the third week, and then returned to the control level by the end of the experiment (Fig. 1c). In 90% defoliation and apex removal treatments these three kinds of biomasses were significantly lower than for control plants throughout the experiment. In 90% defoliation and apex removal treatments root to shoot biomass ratios were much higher than in control plants, but the difference disappeared in the second week (Fig. 1d).

In flooded conditions, 10% defoliation treatment had no significant effect on *A. philoxeroides* biomasses throughout the experiment (Fig. 2). Total biomass and shoot biomass were negatively affected by 50% defoliation, 90% defoliation, and apex removal treatments in the second week, but these biomasses returned to control levels in the fourth or fifth week (Fig. 2a, b). 50% defoliation negatively affected root biomass only in the third week. 90% defoliation and apex removal negatively affected root biomass after the second week (Fig. 2c). In 90% defoliation and apex removal treatments root to shoot biomass ratios were much higher than in control plants, but the difference disappeared in the third week (Fig. 2d).

Flooding and defoliation had significant effects on final plant growth (total biomass, shoot biomass and root biomass). A significant interaction occurred between flooding and defoliation (Table 1). Flooding significantly reduced these biomasses in all defoliation intensities (Table 2). Biomasses decreased with increased defoliation intensity under drained conditions, but no significant difference was found among all the defoliations in flooded *A. philoxeroides* (Table 2). Flooding and defoliation did not affect root to shoot biomass ratio at the end of the experiment (Table 1).

Discussion

By repeated destructive sampling, we were able to determine how the plant re-grew after defoliation. Defoliation can affect plant growth by reducing photosynthetic area and, as a consequence, reduced above-ground net primary production (Crawley, 1983). In drained conditions, *A. philoxeroides* was tolerant of moderate defoliation (50%). Severe defoliation (90% and apex removal) had a great impact on plant total biomass in the first week after clipping. Massive loss of biomass due to treatments may be the main reason for the result. Total biomass as well as shoot and root biomass in the two severe defoliation treatments

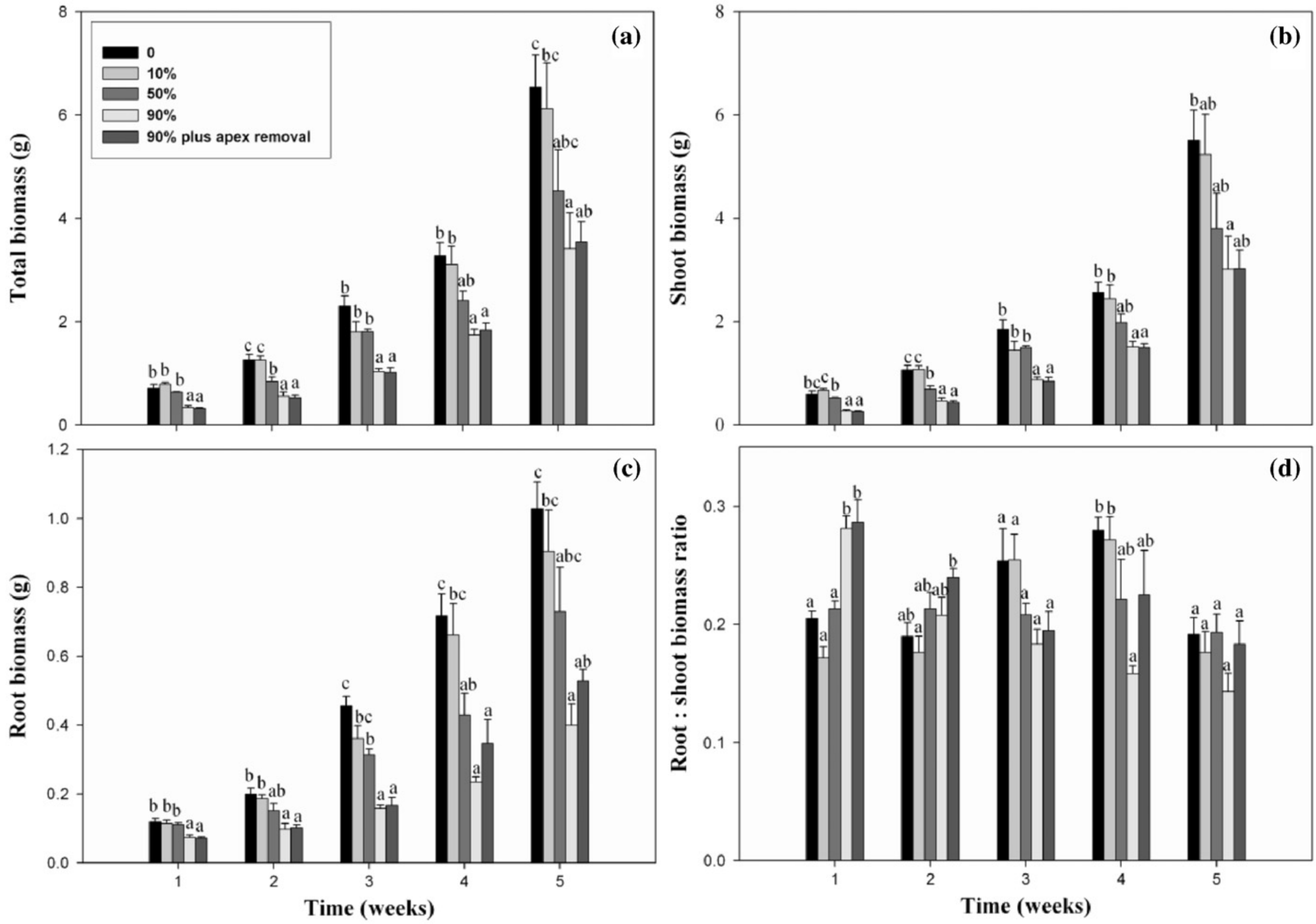

Fig. 1. Growth of drained *Alternanthera philoxeroides* after different defoliation intensity expressed as (a) total biomass, (b) shoot biomass, (c) root biomass, (d) root to shoot biomass ratio during the experiment. Significant differences of variables among treatments are indicated with different letters within each time period. All data are given as mean $\pm$ standard error.

remained lower than in control plants also after five weeks. This indicates that drained *A. philoxeroides*' ability to tolerate severe defoliations may be limited. In contrast, for some species was reported to be capable tolerating severe defoliations. For example, it has been found that the biennial scarlet gilia, *Ipomopsis aggregata* can benefit from the effects of herbivory even when herbivores remove 95% or more of its above-ground biomass (Paige and Whitham, 1987).

Shoot biomass of drained *A. philoxeroides* plants recovered faster from 50% defoliation than root biomass, even though the direct loss of biomass affected directly the shoots. Thus, *A. philoxeroides* may firstly ensure photosynthetic capability by compensatory growth of shoots, and then recovery of root biomass to ensure acquisition of water and nutrients from the soil.

Root to shoot biomass ratios of drained plants was higher with severe defoliation (90% and apex removal) than with control levels, possibly because of leaf tissue loss after the defoliation treatments. However, the ratios did return to the level of control plants already in the second week after defoliation. It has been reported that species tend to allocate resources between plant parts to an optimal level to increase plant fitness according to resource availability, and this is considered a strategy that can maximize total plant growth (Poorter and Nagel, 2000; Agren and Franklin, 2003; Aikio and Markkola, 2002). It can be extrapolated that *A. philoxeroides* quickly invests resources in stem and leaf material bringing back the root to shoot biomass ratio to the control level after damage.

In flooded conditions, *A. philoxeroides* total biomass recovered faster from moderate defoliation (50%) than from severe defoliation (90% and apex removal) – as expected. After all defoliation treatments total biomass returned to control levels, but at different times. This result demonstrated that flooding enhanced the ability of *A. philoxeroides* plants to recover from defoliation. However, root biomass did not return to control levels during the five week recovery period. This result further indicted the priority for compensatory growth of shoots as the strategy when plants were defoliated.

In the present study flooding significantly reduced growth of the plants. By contrast, it has been reported that growth of *A. philoxeroides* in flooded conditions always exceeded growth in drained conditions. This may have resulted from cold, moisture stress, limited nutrients and interspecific competition in drained habitats (Sainty et al., 1998). In our study, drained plants were not subjected to competition, nor were temperature, water or nutrients growth limiting in the greenhouse. However, flooded *A. philoxeroides* plants were almost submerged at the start of the experiment. Slow gas diffusion underwater dramatically reduces oxygen and carbon dioxide influxes into the plant tissues that have normal respiration and photosynthesis, retarding plant growth (Poorter et al., 1990).

Our study demonstrated a significant interaction between flooding and defoliation on growth responses, such as total biomass, shoot biomass and root biomass. Previous studies have shown that herbivory-intensity is an important factor influencing plant responses (McNaughton, 1983; Moser and Schütz, 2006; Vanderklein and Reich, 1999). In drained conditions, total biomass

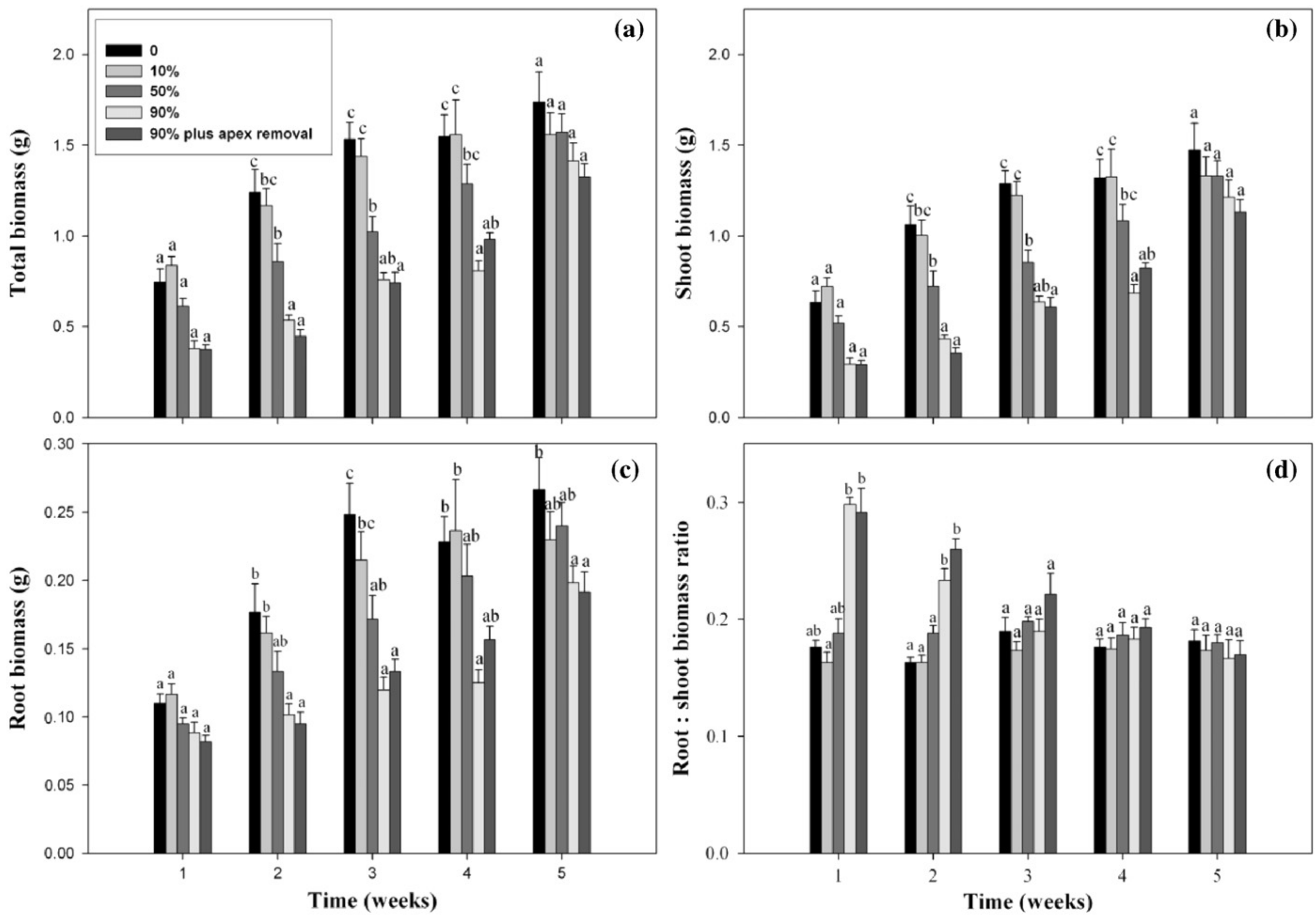

Fig. 2. Growth of flooded *Alternanthera philoxeroides* after different defoliation intensity expressed as (a) total biomass, (b) shoot biomass, (c) root biomass, (d) root to shoot biomass ratio during the experiment. Significant differences of variables among treatments are indicated with different letters within each time period. All data are given as mean ± standard error.

Table 1
Two-way ANOVAs testing the effects of flooding and defoliation on final growth parameters of *Alternanthera philoxeroides.*

Dependent variable	Flooding (*F*)	Defoliation (*D*)	*F* × *D*
Total biomass	$F_{1,50}$=187.363***	$F_{4,50}$=5.892**	$F_{4,50}$=2.608*
Shoot biomass	$F_{1,50}$=171.509***	$F_{4,50}$=5.122**	$F_{4,50}$=2.365*
Root biomass	$F_{1,50}$=170.858***	$F_{4,50}$=9.825***	$F_{4,50}$=5.456**
Root:shoot biomass ratio	$F_{1,50}$=0.074 ns	$F_{4,50}$=1.665 ns	$F_{4,50}$=0.566 ns

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, ns = no significant.

Table 2
Mean values (g) (± S.E.) for final growth parameters of *Alternanthera philoxeroides* subjected to defoliations under drained and flooded conditions. Different letters indicate significant differences among treatment-levels.

Factor		Total biomass	Shoot biomass	Root biomass	Root:shoot biomass ratio
Drained	0	6.54 ± 0.62c	5.52 ± 0.58c	1.03 ± 0.08d	0.19 ± 0.01a
	10%	6.13 ± 0.88c	5.23 ± 0.78c	0.90 ± 0.12d	0.18 ± 0.02a
	50%	4.53 ± 0.80bc	3.80 ± 0.68bc	0.73 ± 0.13cd	0.19 ± 0.02a
	90%	3.41 ± 0.70b	3.01 ± 0.64b	0.40 ± 0.06ab	0.14 ± 0.02a
	Apex removal	3.55 ± 0.39b	3.02 ± 0.36b	0.53 ± 0.03bc	0.18 ± 0.02a
Flooded	0	1.74 ± 0.17a	1.47 ± 0.15a	0.27 ± 0.02a	0.18 ± 0.01a
	10%	1.56 ± 0.12a	1.33 ± 0.11a	0.23 ± 0.02a	0.17 ± 0.01a
	50%	1.57 ± 0.10a	1.33 ± 0.08a	0.24 ± 0.02a	0.18 ± 0.007a
	90%	1.41 ± 0.10a	1.22 ± 0.10a	0.20 ± 0.01a	0.17 ± 0.02a
	Apex removal	1.33 ± 0.07a	1.14 ± 0.06a	0.19 ± 0.01a	0.17 ± 0.01a

of *A. philoxeroides* decreased with increasing defoliation. This finding is consistent with a previous study of responses of *A. philoxeroides* to different defoliation levels (Schooler et al., 2006). Severe defoliation significantly reduced plant biomass at the end of the experiment, again consistent with Schooler et al. (2007) who found that severe defoliation greatly reduced the cumulative biomass of *A. philoxeroides.* In their study, all leaves were repeatedly removed at weekly intervals for five weeks, while in our study, we removed 90% (by area) of leaves only once, which was enough to reduce total plant biomass. Biomasses after apex removal were higher than those with 90% defoliation treatment though this effect was not significant. The result suggested that apex removal weakened the effect of defoliation to some extent possibly due to the release of apical dominance. In flooded conditions, *A. philoxeroides* can tolerate defoliation without significant biomass decline even under severe defoliation (90% and apex removal). Therefore, flooded *A. philoxeroides* must have a greater compensatory growth than drained plants. However, *A. philoxeroides* has been successfully controlled by *A. hygrophila* in warm temperate aquatic habitats (Julien, 1981). This contradiction can be explained in that the flea-beetle, in the field, may eat *A. philoxeroides* frequently during the whole plant growing season. By contrast, defoliation treatments in our study were done only once during the experimental period. Frequent herbivory has been reported to reduce growth of the graminoids *Bolboschoenus caldwellii*, *Phragmites australis* and *Schoenoplectus validus* (Hayball and Pearce, 2004), and of Jarrah, *Eucalyptus marginata* (Abbott et al., 1993). Therefore, the effect of frequent defoliation of *A. philoxeroides* under flooded species may severely reduce the plant's vitality, but this still needs additional investigations.

In summary, flooded *A. philoxeroides* plants had high compensatory growth even when subjected to severe defoliation (90% and apex removal), whereas drained *A. philoxeroides* could rapidly recover only from moderate defoliation (50%). The remarkable ability of rapid re-growth may be one important trait favoring the high capacity of this species for invasion. However, drained *A. philoxeroides* was sensitive to severe defoliation. Our results suggest that, among the leaf-feeding guilds, defoliating agents capable of removing 90% of the leaf tissue may be desirable in restricting the growth of this invasive plant in drained conditions. It is important, that defoliating animals, which tend to damage plant apical bud should not be selected as biocontrol agents, because apical bud removal weakens the effect of defoliation to some extent, possibly due to the release of apical dominance.

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