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Influence of precipitation dynamics on plant invasions: response of alligator weed (*Alternanthera philoxeroides*) and co-occurring native species to varying water availability across plant communities

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Abstract Over the last few decades, rainfall has become more variable, with a worldwide increase in the frequency of extreme precipitation events. While increases in rainfall variability are expected to significantly affect plant species, the effects of precipitation dynamics on plant invasions remains understudied. We examined the growth response of *Alternanthera philoxeroides* to varying water availability at the community level when grown in a monoculture and mixed community with four commonly co-occurring native species. The native species were also grown together as a control to compare to the invasive species communities. Seven water treatments were applied to each community, including a 'normal' treatment (based on the average rainfall for the area), drought (water was one third of the normal treatment), flood (water was double the normal treatment), and other simulated extreme events (where water availability was more variable than the normal treatment). All plants were measured for growth (e.g., biomass and stolon length) and competitive traits (i.e., relative competitive dominance and relative interaction indices). Most growth traits in *A. philoxeroides* were enhanced with increased and/or more variable water availability in both the monoculture and mixed community. In contrast, differences in growth traits in the native plants were mostly non-significant across treatments in each plant community. Compared to the normal treatment, *A. philoxeroides* had higher relative competitive dominance (RDI) and interaction (RII) indices in response to flooding. Conversely, RII in the native species was not significantly different among treatments. Overall, our results suggest that *A. philoxeroides* is more responsive to flooding compared to the natives. Our study provides useful insights into growth response and competitiveness of *A. philoxeroides* to precipitation variability across different plant communities.

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Introduction

Climatic change has been identified as one of the major factors that facilitate the colonization of new areas by invasive species (Chown et al. 2015), and is primarily represented by changes in environmental variability (i.e., alterations in the mean state of climate-dependent environmental conditions, from seasonal changes to variations over a geological timescale, Keyl and Wolff 2008). Such environmental changes can be examined either through an analysis of long-term climatic records or by comparing unusual or extreme climate responses to the typical environmental conditions for a specific ecosystem (Smith 2011). For decades, the field of ecology has used mean values as indicators of climatic site conditions (Jentsch et al. 2007), with previous research often focusing on changes in static average values, and less attention being paid towards dynamic variables (Sisco et al. 2017; Wang et al. 2018). In recent years there has been a worldwide increase in the frequency and magnitude of extreme precipitation events (e.g., very high rainfall and severe droughts, Lehmann et al. 2015). Long-term changes in mean precipitation cause gradual changes in plant establishment and mortality, species composition, and population density (Jin and Goulden 2014); and may result in large-scale alterations in community structure, ecosystem function, and ecotone boundaries (Allen and Breshears 1998; White et al. 2000). In contrast, short-term changes in water availability associated with precipitation variability (including extreme events) can rapidly alter plant physiology, phenology, and leaf growth (Paruelo et al. 1999; Zhang et al. 2005). Precipitation variability may also result in the sudden mortality of populations and extinction of some species (Greenwood et al. 2017).

Changes in precipitation can alter competition for shared resources among native and non-native species (Radford 2013; Schooler et al. 2010). Although much research in invasion biology has focused on the links between environmental variation and invasive species (e.g., Bradley et al. 2010; Parepa et al. 2013), the impacts of precipitation variability (including extreme events) on plant invasions have received

less attention (Sardans et al. 2017). Previously it was found that invasive Commelinaceae species displayed higher average performance (e.g., biomass and relative growth rates) compared to native species in the same family for both high nutrients and across water availabilities (Burns 2004). Moreover, Chen et al. (2019) and Wang et al. (2016) found that invasive clonal plants in a native community benefited more from clonal integration under variable water availability compared to consistent watering. Based on these findings, invasive species may be expected to display greater growth and performance under more variable precipitation compared to native species. However, in secondary tropical forests in the Seychelles, only small differences in growth response of native and invasive species to different light and water treatments were found, with the native species performing better under low water availability (Schumacher et al. 2008). Another study revealed that biomass of invasive species did not differ significantly across water treatments (Han et al. 2012). Therefore, further research on how invasive plant species cope with hydrological fluctuations compared to native species is necessary for a more comprehensive understanding of the response of invasive species to varying water availability in native landscapes (Wang et al. 2018). Specifically, research focusing on the impacts of extreme precipitation events (which may result in high levels of disturbance) on invasive plants and co-occurring native species is likely to offer insights into how communities may alter under climate change.

Habitat disturbance is one of the most important variables involved in shaping life-history traits and influences the survival strategies of organisms in ecosystems with highly fluctuating environmental conditions (Gerisch et al. 2012). Disturbance can be defined as an event that disrupts any ecological level, environmental component, and/or organizational status of a biological cycle of organisms (and may include extreme precipitation events, such as floods and severe droughts, Pickett et al. 1989; Battisti et al. 2016). The strength and direction of feedback loops are influenced by external temporal factors, including changes in soil resource availability (e.g., soil moisture) following disturbance (Kardol et al. 2013). For example, increased disturbance is often associated with greater environmental variability (Parepa et al. 2013), and high levels of disturbance

have been found to promote biological invasions (Hobbs and Huenneke 1992). The invasibility of a habitat can be enhanced due to disturbance since new sites are cleared and opened up for other species to colonise (Davis et al. 2000; Reznick et al. 2020). Therefore, initial disturbance can promote invasions, which then further disturb the ecosystem. High levels of disturbance can lead to environments becoming increasingly less hospitable for native species (Davidson et al. 2011; Gaertner et al. 2017). Invasive species often display higher phenotypic plasticity than native plants (Liu et al. 2017; Parepa et al. 2013), and as such, disturbance resulting from fluctuating environmental conditions may provide an advantage for non-native species (Gaertner et al. 2017). Consequently, invasive species might be expected to show enhanced competitiveness in response to extreme events. In the current study, we define competition as occurring when individuals of the same or different species (e.g., neighbouring plants) utilize common resources (e.g., light, nutrients, water, space) (Birch 19,757; Milne 1961; Grime 1973). As such, interspecific competition often results in the negative effect of one species on another due to limited shared resources (Birch 1957; Craine 2005), and therefore a good competitor might be one that: (1) exerts a strong negative effect on other species, and (2) has limited response to the presence of other species.

Here, we examine the effects of precipitation variability on the growth response of alligator weed (*Alternanthera philoxeroides*) at the community level. To do this we grew *A. philoxeroides* in a monoculture and in a mixed community (with four commonly co-occurring species native to China) to compare differences in growth traits among seven water treatments, including drought, flooding, as well as simulated precipitation events (e.g., alternate drought and flood). Additionally, we grew the native species together (to simulate a native species community) and applied the same seven water treatments. As such, we tested the following hypotheses: (1) invasive *A. philoxeroides* will display enhanced growth in response to precipitation variability, (2) growth trait response of *A. philoxeroides* and the native species will vary among plant communities (i.e., invasive species only, native species only, and mixed community), and (3) competitiveness of *A. philoxeroides*

will increase in response to higher precipitation variability.

Materials and methods

Study species and plant propagation

Alternanthera philoxeroides is a creeping perennial, stoloniferous, and amphibious herb native to South America (Spencer and Coulson 1976), and has become an aggressive alien invader in 32 countries around the world (Tanveer et al. 2018). The species was introduced to Shanghai as a forage crop in the 1930s and is now widely distributed in over 20 provinces in China (Huang et al. 2017; Yan et al. 2020). *Alternanthera philoxeroides* disperses rapidly and occurs in aquatic, semi-aquatic, and terrestrial environments, mainly because each stolon consists of nodes that are capable of producing roots and new shoots, which can become new individual plants if disconnected (Xi et al. 2019).

To assess the response of *A. philoxeroides* to precipitation variability compared to native species from China, we selected four native species to simulate a local community, namely *Eleusine indica*, *Solanum nigrum*, *Cynodon dactylon*, and *Youngia japonica* (Fig. 1a). During our previous field surveys in Jiangsu Province, we found that these native species often co-exist in the same ecosystem with *A. philoxeroides*. Moreover, a recent species diversity study based on 59 plots across 10 provinces in China revealed that these four native species co-occur with *A. philoxeroides* (Wu et al. 2016). Communities where the native species co-occur with *A. philoxeroides* are primarily associated with aquatic habitats, but can spread into moist terrestrial environments (Schooler et al. 2010).

In early autumn (September 2016), healthy and uniform stems of the invasive species (i.e., cuttings) and seeds of the four native species were sampled from natural wetland habitat along the Yangtze River (119°32′E, 32°11′N) and transplanted to a greenhouse at Jiangsu University (119°27′E, 32°12′N, Zhenjiang, Jiangsu Province, China). To investigate differences in plant responses to fluctuations in water supply between the invasive and native plants, 70 similar-sized seedlings per species were selected and three plant communities
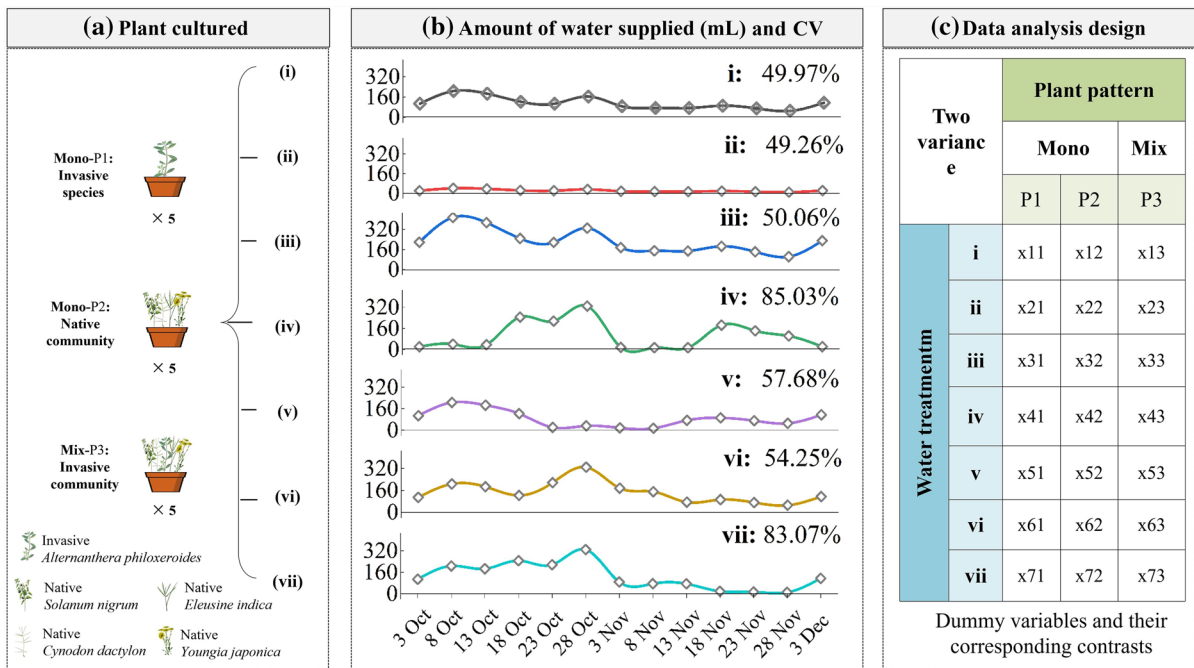
(a) Plant cultured

(i)
(ii)
(iii)
(iv)
(v)
(vi)
(vii)

Mono-P1: Invasive species ×5

Mono-P2: Native community ×5

Mix-P3: Invasive community ×5

Invasive *Alternanthera philoxeroides*

Native *Solanum nigrum*

Native *Cynodon dactylon*

Native *Eleusine indica*

Native *Youngia japonica*

(b) Amount of water supplied (mL) and CV

i: 49.97%
ii: 49.26%
iii: 50.06%
iv: 85.03%
v: 57.68%
vi: 54.25%
vii: 83.07%

3 Oct 8 Oct 13 Oct 18 Oct 23 Oct 28 Oct 3 Nov 8 Nov 13 Nov 18 Nov 23 Nov 28 Nov 3 Dec

(c) Data analysis design

Two variance		Plant pattern		
		Mono		Mix
		P1	P2	P3
Water treatment	i	x11	x12	x13
	ii	x21	x22	x23
	iii	x31	x32	x33
	iv	x41	x42	x43
	v	x51	x52	x53
	vi	x61	x62	x63
	vii	x71	x72	x73

Dummy variables and their corresponding contrasts

Fig. 1 Experimental design showing: **(a)** number of species per plant community, and number of replicates in each community and water treatment combination; **(b)** water treatments; and **(c)** data analysis design for the effects of water treatment and plant community (i.e., plant pattern). Plant communities in **(a)** include: P1 (invasive species only), P2 (native species only community), and P3 (mixed plant community comprising both native and invasive species). Water treatments in **(b)** include: (i) normal (N), (ii) drought (D), (iii) flood (F), (iv) flood-drought interaction (D→F→D→F), (v) drought pulse (N→D→N), (vi) flooded pulse (N→F→N), and (vii) multiple pulses (N→F→N→D→N). Each plot in **(b)** repre-sents the amount of water (mL) applied every five days during the 65 days of the experiment, with the total amount of water being based on the frequency and amount of rainfall at an interval of five days from 1st October to 5th December between 1950 and 2015 (sourced from the Nanjing weather station). The coefficient of variation (CV) of each treatment (%) is also shown in **(b)**. The data-analysis design in **(c)**, shows a factorial study with dummy variable coding (×11-×73) which represents the plant trait values and their corresponding contrasts (contrasts are only between water treatments within communities or between communities within water treatment)

were established: **P1** comprising a monoculture of the invasive species only (*A. philoxeroides*), **P2** which was a native species only community (with four species native to China), and **P3** which comprised a mixed community of invasive *A. philoxeroides* and the four native species (Fig. 1). We transplanted one seedling of each species into plastic pots (30 cm × 20 cm × 8 cm, length × width × height respectively) filled with straw, sand, vermiculite, peat, and fine vermiculite (at a ratio of 1:2:2:3:2). Plants were grown from autumn until early winter (1st October to 5th December) 2016. Due to limited availability of space in the greenhouse, our experiment had to be conducted over a shorter time-period than we

initially intended. However, during extreme events, plants are often exposed to higher or lower resource availability at a large magnitude and for short periods of time (Yang et al. 2008). A plant's fitness can depend on its ability to utilize resources during such events (e.g., flooding, drought) especially in low resource environments (Funk and Zachary 2010). In addition, many studies have demonstrated that invasive species display higher plasticity compared to natives in response to environmental variability on time scales of weeks to months (e.g., Burns and Winn 2006; Muth and Pigliucci 2007). In the case of our study, *A. philoxeroides* is a fast-growing clonal species, and individuals can become very large when grown under the right conditions. Therefore, given that a major focus of

our study is on extreme events and *A. philoxeroides* is a fast-growing invader, we consider two months an appropriate timeframe for exploring the early growth response of this species to precipitation variability and extreme events.

Precipitation variability and water treatments

One week after transplanting the seedlings, we applied the water treatments. We obtained daily precipitation data from the China Meteorological Administration database (http://data.cma.cn/, accessed September 25, 2016). From this dataset, we selected daily precipitation data from the Nanjing weather station for the growing period of the experiment (autumn to early winter 2016) from 1950 to 2015. Specifically, we focused on the frequency of precipitation at an interval of five days from 1st October to 5th December. We calculated the mean precipitation at five-day intervals based on the frequency of rainfall over the 65 years between 1950 to 2015 (i.e., 1468.92 mL in total, with the following precipitation values determined according to the amount of rainfall over five days: 108.95 mL, 207.55 mL, 186.73 mL, 123.63 mL, 108.41 mL, 164.96 mL, 88.19 mL, 75.33 mL, 74.30 mL, 92.79 mL, 71.22 mL, 51.76 mL, and 115.10 mL) and this was used as the basis for the 'normal' water treatment (N) in our study [see (i) in Fig. 1]. For the drought treatment (D), we applied one-fifth of the normal water treatment [see (ii) in Fig. 1]. Plants treated with this amount of water in the D treatment were water-stressed, although the amount of water was sufficient to maintain plant survival. For the flood treatment (F), we used twice the amount of water as the normal water treatment [see (iii) in Fig. 1]. In addition, we had four water treatments that simulated more than one precipitation event. These included a flood and drought interaction, where we applied water simulating alternating drought (D) and flood (F) events (i.e., D→F→D→F); drought pulse treatment, which alternated between normal and drought treatments (N→D→N); flooded pulse treatment, alternating between normal and flood treatments (N→F→N); and multiple pulses treatment (N→F→N→D→N) (iv, v, vi, and vii respectively from Fig. 1). As such, there were seven water treatments in our experiment (see Fig. 1b for specific details). Tap water was used and the water volume was measured out using a measuring cylinder. Water was supplied to the plants through an artificial spray, which was applied 13 times (once every 5-days) during the growing period

(on the 3, 8, 13, 18, 23, and 28 October; 3, 8, 13, 18, 23, and 28 November; and 3 Dec 2016). To categorize the degree of variability of the water treatments, we calculated the coefficient of variation (CV) for each treatment (these are given in Fig. 1b).

We used a two-factor study design with 5 replicates per community per treatment. There was a total of 105 pots (3 plant communities×7 water treatments×5 replicates) that were arranged in the greenhouse. Pots were spaced at least 20 cm apart from each other to avoid cross-contamination, and pot position was randomized every two weeks to counteract the effects of environmental patchiness within the greenhouse.

Growth trait measurements

All the plants were harvested after 65 days (on the 5th December 2016), which was after the plants had stabilised and displayed vigorous growth. We measured the main stolon length of each plant of *A. philoxeroides* using a ruler and counted the number of nodes. The diameter of each plant was measured at three points along the stolon (the apex, middle, and terminal points) using a digital Vernier caliper (MNT, Shanghai, China). The root fractions were carefully removed from the soil and thoroughly rinsed using tap water. All plant parts were oven-dried at 60 °C to constant mass and weighed to the nearest 0.01 g (Portela et al. 2019). The four native species were considered together when calculating the native species biomass (and this was measured using the same approach as for *A. philoxeroides*). Finally, the root to shoot (root/shoot) ratio of plants in each treatment for all species was calculated.

Competition and invasion efficacy in the mixed community

The proportion of invasive plant biomass to total plant biomass can be used as an indicator for invasion efficacy in the vegetation community (Parepa et al. 2013; Wang et al. 2021). We calculated the dominance of *A. philoxeroides* in only the mixed community using the relative dominance index (RDI) (Myers and Bazely 2003), calculated as follows:

$$RDI = \frac{\text{biomass of } A.philoxeroides}{(\text{biomass of } A.philoxeroides + \text{biomass of native species})}$$

In the case of *A. philoxeroides*, RDI is the proportion of community biomass represented by *A. philoxeroides*, and ranges between 0 and 1, with a high RDI (i.e., values closer to 1) indicating that the focal species is highly competitive. In our study, RDI values above 0.6 are considered relatively high (see Zhang et al. 2017). We used the relative interaction index (RII) (Armas et al. 2004; Uddin and Robinson 2018) to characterise interspecific competition (i.e., native versus invasive species in the mixed community) under different precipitation treatments, which was calculated as:

$$RII = \frac{(Bw - Bo)}{(Bw + Bo)}$$

For RII, Bw is the biomass of the focal plant growing with the neighbouring plants, and Bo is the biomass of the focal plant growing in the monoculture. So, when calculating RII for the invasive species, Bw represented the biomass of *A. philoxeroides* in the mixed community, while Bo was the biomass of *A. philoxeroides* in the monoculture. For the native species, the four native species were considered together when calculating RII. Therefore, Bw represented the biomass of the native species in the mixed community, while Bo was the biomass of native species in the monoculture. The RII is a metric of interaction intensity, and ranges between −1 and 1. A negative RII indicates that competition prevails, a positive value suggests the prevalence of facilitation, and a value of 0 represents when the net balance of the interaction is neutral (Cavieres et al. 2017). In our study, RII values above 0.1 were considered to be high (see Tirado and Pugnaire 2005; Anthelme et al. 2012; Schöb et al. 2013).

Data analysis

For all growth and competitive traits, differences across treatments were explored using multivariate analysis of variance (MANOVA). Since many of the response variables we measured are likely to be highly correlated, MANOVA was considered appropriate for investigating treatment level differences on all growth traits (as MANOVA enables all response variables to be considered simultaneously, Quinn and Keough 2002). A one-way MANOVA was performed to investigate differences in growth traits across water treatments for each plant community (i.e., *A. philoxeroides* only community, native species only community, and mixed community). A two-way analysis of variance (ANOVA) was used to examine the effects of water treatment, plant community and their interactions on plant growth traits. In our study, water treatment and plant community were independent variables, while plant growth traits were dependent variables. To further examine competitiveness in *A. philoxeroides*, we used a one-way MANOVA to investigate differences in RDI and RII across water treatments (N = 5 each for RDI and RII). Tukey's honest significant difference (HSD) test was applied for multiple comparisons at 0.05 level of significance among the treatments. To determine whether the data met the assumptions of ANOVA, we tested all data for normality using the Shapiro-Wilks test and QQ plots, and for equality of variance with Levene's test. We used Box's M test of equality of covariance to test whether the variance–covariance matrices assumptions of MANOVA were met. We found that all traits met the normality and variance assumptions of parametric tests. All statistical analyses were performed using SPSS (version 22.0; IBM, Armonk, NY, USA).

Results

To compare the level of variability across water treatments, we determined the coefficient of variation (CV) of each treatment (Fig. 1b). The drought treatment was the least variable of all the treatments (CV = 49.26%), followed by the normal and flood treatments (CV values were 49.97% and 50.06% respectively, Fig. 1b). The flood-drought interaction was the most variable of all the treatments (CV = 85.03%), followed by the multiple pulse (CV = 83.07%). Overall, our analyses revealed that for each plant community, growth traits were significantly different across water treatments ($p < 0.01$, see Table 1 for outputs from one-way MANOVA). We also found that competitive traits significantly varied across the water treatments ($p < 0.005$, one-way MANOVA, Table 2). For invasive *A. philoxeroides*, all growth traits were significantly affected by water treatment ($p < 0.01$, two-way ANOVA, Table 3). In contrast, only stolon length and root/shoot ratio in *A. philoxeroides* were significantly affected by plant

Table 1 One-way multivariate analysis of variance (MANOVA) results for differences in growth traits across water treatments for each plant community

(a) *A. philoxeroides* only

Effect	F	Hypothesis df	Error df	p
Water treatment	2.814	30	140	< 0.001
Intercept	2941.223b	5	24	< 0.001

(b) Native species only

Effect	F	Hypothesis df	Error df	p
Water treatment	2.678	12	56	0.006
Intercept	523.867b	2	27	< 0.001

(c) Mixed community

Effect	F	Hypothesis df	Error df	p
Water treatment	2.746	42	162	< 0.001
Intercept	1012.039b	7	22	< 0.001

(**a**) *Alternanthera philoxeroides* monoculture, (**b**) native species only community, and (**c**) mixed community. Lawley–Hotelling trace, Wilk's Lambda, and Pillai's trace all gave similar estimates of *F*. Outputs for Pillai's trace are shown. Significant differences ($p < 0.05$) are in bold. "b" denotes exact statistics

Table 2 One-way multivariate analysis of variance (MANOVA) results for difference in competitive traits (i.e., RDI and RII for invasive *Alternanthera philoxeroides*, and RII for the native species) across water treatments

Effect	F	Hypothesis df	Error df	p
Water treatment	2.562	18	84	**0.002**
Intercept	1715.392b	3	26	**< 0.001**

Lawley–Hotelling trace, Wilk's Lambda, and Pillai's trace all gave similar estimates of *F*. Outputs for Pillai's trace are shown

Significant differences ($p < 0.05$) are in bold. "b" denotes exact statistics

Table 3 Significance levels from a two-way analysis of variance (ANOVA) showing differences in growth traits measured from the invasive species (*Alternanthera philoxeroides*) and native species (*Eleusine indica, Solanum nigrum, Cynodon dactylon,* and *Youngia japonica*) across water treatments, plant community, and all interactions (N = 105)

Species	Traits	Water treatments (W)	Plant community (P)	W × P
A. philoxeroides	Stolon length	11.43**	27.11**	6.67**
	Stolon diameter	5.19**	0.29	1.17
	Node number	8.82**	3.48	1.60
	Total biomass	11.82**	0.24	1.88
	Root/shoot ratio	12.05**	4.08*	1.82
Native species	Total biomass	1.55	4.16*	1.70
	Root/shoot ratio	3.85**	0.18	3.04*

Values provided in the table are *F* values

* and ** indicate a significant difference at $p < 0.05$ and $p < 0.01$, respectively

community ($p < 0.01$, two-way ANOVA, Table 3). For the native species, total biomass was significantly affected by plant community, while root/shoot ratio was significantly affected by water treatment ($p < 0.05$, two-way ANOVA, Table 3). The interaction between water treatment and plant community had a significant effect on stolon length in *A. philoxeroides* and root/shoot ratio in the native species ($p < 0.05$, two-way ANOVA, Table 3).
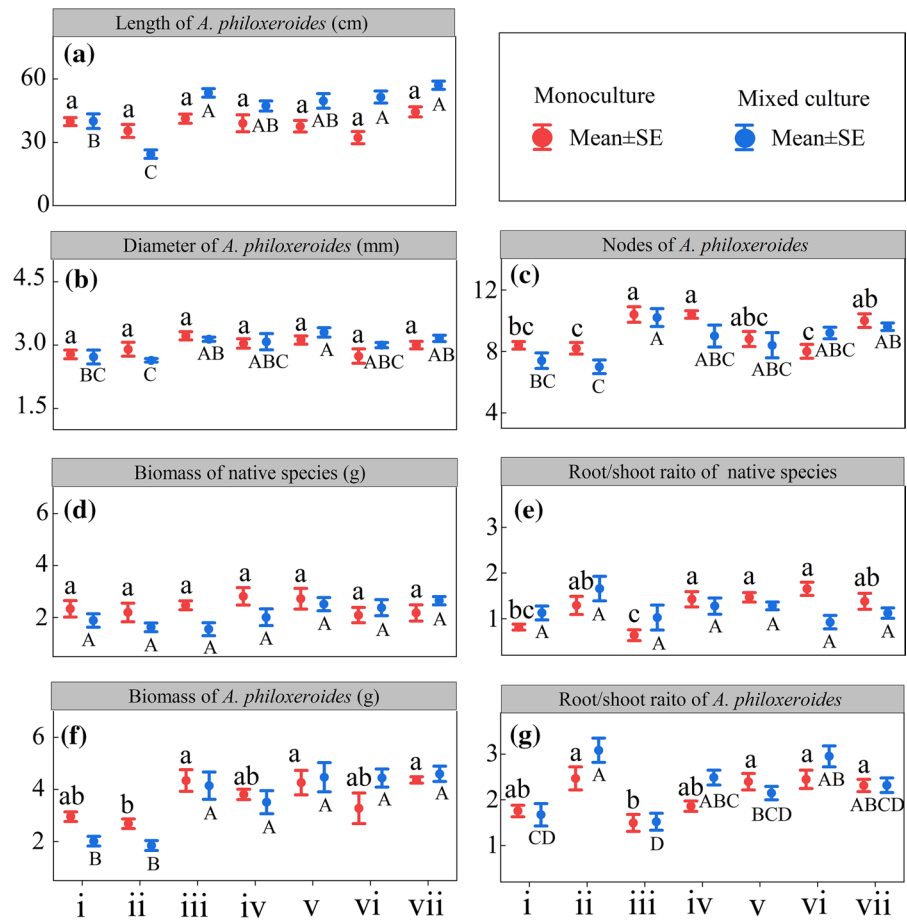
Fig. 2 Effects of water treatment on growth traits in *Alternanthera philoxeroides* and native species (*Eleusine indica*, *Solanum nigrum*, *Cynodon dactylon*, and *Youngia japonica*) across plant communities (N = 5). Significant differences (*p* < 0.05) among treatments are denoted by different letters above and below the data points (upper case letters are used for the mixed culture, while lower case letters are used for the monoculture). Codes for water treatments (i–vii) are given in Fig. 1

Effects of water treatments and plant community on growth response of invasive and native species

When grown in the monoculture, only biomass, node number and root/shoot ratio of *A. philoxeroides* significantly varied among water treatments (*p* < 0.05, Tukey's HSD test, Fig. 2c, f and g). Conversely, in the mixed community, all growth traits of *A. philoxeroides* differed significantly among water treatments (*p* < 0.05, Tukey's HSD test, Fig. 2). In the mixed community, compared to the normal treatment, stolon length of *A. philoxeroides* was 37% shorter in the drought treatment; and 32.5%, 27.5%, and 47.5% longer in the flood, flooded pulse and multiple pulse treatments respectively (Fig. 2a). Stolon diameter was significantly wider (*p* < 0.05, Tukey's HSD test) in the drought pulse treatment compared with the normal and drought treatments (21.3% and 25% wider respectively, Fig. 2b). Root/shoot ratio in *A. philoxeroides* was lowest in the flood treatment and highest

in the drought treatment irrespective of plant community (Fig. 2g).

We found that the total biomass of native species was not significantly different across treatments in either the native species only or mixed communities (*p* > 0.05, Tukey's HSD test, Fig. 2d). Similarly, root/shoot ratio of native species did not significantly vary among treatments in the mixed culture (Fig. 2e). In the monoculture, root/shoot ratio of native species in the flood-drought interaction, drought pulse and flooded pulse treatments were significantly higher than in the normal and flood treatments (*p* < 0.05, Tukey's HSD test, Fig. 2e).

Competition between *A. philoxeroides* and native species across water treatments

The highest RDI of *A. philoxeroides* was in the flood treatment, which was significantly greater than the normal and drought treatments (*p* < 0.05, Tukey's HSD
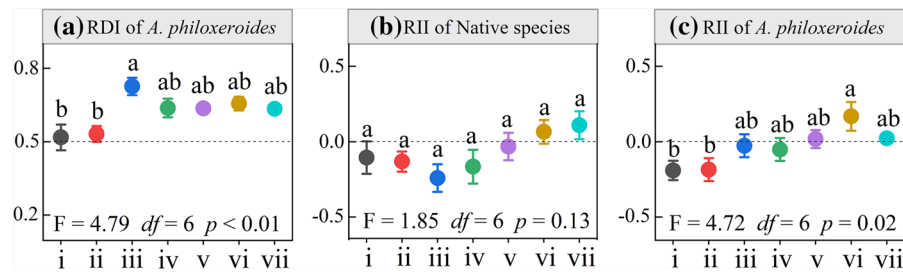
Fig. 3 Competitive traits in the mixed community (comprising both native and invasive species) showing **a** the relative dominance index (RDI) or proportion of community biomass of *Alternanthera philoxeroides*, **b** relative interaction index (RII) of the native species, and **c** RII of *A. philoxeroides*. Codes for water treatments (i–vii) are given in Fig. 1. Significant differences ($p < 0.05$) among treatments are denoted by different letters above the data points. Values represent the mean ± standard error (SE) (N = 5)

test, Fig. 3). RII of *A. philoxeroides* was highest in the flood pulse treatment, which was significantly greater than in the normal and drought treatments ($p < 0.05$, Tukey's HSD test, Fig. 3). In contrast, RII of the native species was not significantly different among treatments (Fig. 3). Thus, our findings suggest that while RII of the native species was not influenced by water availability, RII of *A. philoxeroides* was affected by changes in water level.

Discussion

Improving our understanding of plant invasions is critical not only because of its importance to invasion management, but also because it may offer insights into ecological patterns and processes (Guo et al. 2015). In the current study, our approach of subjecting different plant communities (invasive species only, native species only and mixed community) to a wide range of water treatments provided important information on growth, competitiveness and resource allocation strategy of *A. philoxeroides*. Our study offered insights into the effects of invasion from *A. philoxeroides* on biomass, competitiveness and resource allocation of the native species community. The findings from this study have implications for the response and impacts of invasive *A. philoxeroides* to precipitation variability under climate change, particularly extreme events, at the community level.

Growth of *A. philoxeroides* was enhanced in response to precipitation variability and extreme events

We found that precipitation variability and extreme events (e.g., flooding) significantly increased most growth traits of *A. philoxeroides* compared to the normal treatment, particularly in the mixed community (Fig. 2). Thus, our first hypothesis that this invasive species would display enhanced growth in response to precipitation variability was supported. Stolon length is positively associated with water fluctuations, and increases in this trait may enable plants to escape from canopy shading, thereby facilitating greater light resource acquisition (Chen et al. 2019). Increases in stolon length and node number can result in greater clonal propagation (Xi et al. 2019), which likely provides clonal species with a competitive advantage. Additionally, increases in stolon diameter can boost buoyancy in clonal plants, enhancing their ability to survive in aquatic environments (He et al. 1999), ensuring photosynthesis is maintained during flooding (Ayi et al. 2016). *Alternanthera philoxeroides* has been found to have higher tolerance and plasticity in response to water fluctuations than native *Ludwigia adscendens* (Chen et al. 2016). It is likely that under conditions where water availability is variable, the ability of *A. philoxeroides* to invade a new habitat may be enhanced as the species can increase stolon growth and clonal propagation in response to a range of precipitation events. This notion agrees with Chen et al. (2019), who found that the positive effect of clonal integration on biomass and ramets of *A. philoxeroides* was stronger under a variable watering regime compared to constant watering.

In contrast to *A. philoxeroides*, total biomass of the native species from the current study did not vary in response to precipitation variability or extreme events in either plant community (Fig. 2). Our findings for the native species agrees with Chen et al. (2019) who revealed that water variability had a limited effect on biomass in a native plant community. These findings have implications for restoration purposes with climate change impacts and provide a good avenue for future research. Differences in response across native species may account for the limited effects of water variability on total biomass of native plant communities. For the native species, root/shoot ratio was significantly affected by water treatment (Table 3, Fig. 2). Water availability is one of the major limiting factors for plant performance and strongly affects plant allocation strategy (and root/shoot ratio) (Viciedo et al. 2021). Our findings for the native species here are consistent with predications of resource-limitation whereby plants should allocate biomass to structures that help them acquire more of the most limiting resource (Qi et al. 2022).

Growth of invasive and native species and resource allocation under varying precipitation

Our study revealed that while all growth traits in *A. philoxeroides* were significantly affected by water treatment, fewer traits were significantly affected by plant community (Table 3). Similarly, although native species biomass was significantly different between the mixed- and monoculture, differences in root/shoot ratio of native species between plant communities was not significant (Table 3). Consequently, our second hypothesis that growth trait response of the invasive and native species will vary among plant communities was supported to a lesser extent. Unlike in the mixed community, stolon length and diameter of *A. philoxeroides* did not significantly vary among water treatments when the species was grown in a monoculture (Fig. 2). In addition, compared to the monoculture, both stolon length and diameter were often greater in the mixed community under the more variable water treatments. Thus, our results suggest that interspecific competition in combination with highly variable water availability affects growth response in *A. philoxeroides* in mixed communities. This finding agrees with previous research which suggest that the success of an invasive species is

dependent on its ability to persist in competition with other species (Bando 2006; Ullah et al. 2021; Wang et al. 2021). The role of interspecific competition with native co-occurring species on the growth performance of invasive *A. philoxeroides* in response to increasingly variable precipitation provides a promising avenue for future studies.

Plants tend to enhance root growth when soil nutrients and water are limited and allocate less to their root systems when aboveground resources are limiting, maximizing their acquisition of limiting resources (Gill and Finzi 2016; Qi et al. 2022). In our study, we found a significant increase in the root/shoot ratio in response to the drought and flooded pulse treatments compared to the normal treatment in *A. philoxeroides* in the mixed community (Fig. 2). The higher root/shoot ratios of *A. philoxeroides* in these treatments in the mixed community suggest that this invasive species is able to alter its biomass allocation to obtain moisture under limiting and variable water availability (Freschet et al. 2018). In contrast, although the species in the natives only community had a significantly higher root/shoot ratio in the flood-drought interaction, drought pulse and flooded pulse treatments than in the normal treatment, in the mixed community this trait did not significantly differ across water treatments (Fig. 2). Our findings are consistent with the results of Wang et al. (2018) which revealed that invasive *A. philoxeroides* displayed higher root allocation than co-occurring native species in disturbed habitats. It appears that some exotic plants have a superior resource allocation strategy under environmental stress compared to native species. The findings from our study indicate that precipitation variability may favour *A. philoxeroides* (through an enhanced root system in response to water stress), making it more competitive than the native species used in this study (Gill and Finzi 2016). Our results therefore support the hypothesis that resource allocation strategies can play a major role in the success of this invasive species in limited or disturbed resource environments (Portela et al. 2019; Ren et al. 2019).

Competitive traits and the role of facilitation

Our findings revealed that competitive traits in *A. philoxeroides* in the mixed community were influenced by variations in water level (Fig. 3). As

such, our third hypothesis that competitiveness of *A. philoxeroides* will increase in response to increased precipitation variability was met. Overall, our results suggest that water variability can improve competitiveness of *A. philoxeroides* which may mitigate the inhibitory effects from neighbouring species. In contrast, the RII of native species in the mixed community remained unchanged in response to water variation (Fig. 3). This finding could be interpreted in multiple ways. For example, it may indicate that species diversity is equivalent to trait diversity, leading to low overall community response. The result could also suggest that the native species were equally unaffected by the treatments. Growth response measurements collated from each species would offer further insights into the competitive ability of the natives. The mixed community was affected by the presence of invasive *A. philoxeroides* and previous studies suggest that there is a complex set of interactions between invasive species, native species, and the environment when resources are limiting or variable (Sardans et al. 2017).

Biotic interactions are important drivers of biological invasions (Simberloff and Von Holle 1999), with many studies demonstrating the biotic containment of invaders by native species and greater competitive ability of invasive species (e.g., Levine et al. 2004; Callaway and Aschehoug 2000). Yet, other studies have shown that there can be positive interactions between native and invasive species and these interactions may promote plant invasions (Mitchell et al. 2006; Bulleri et al. 2008). Such biotic interactions can be strongly influenced by changes in environmental conditions (Good et al. 2014). In our study, positive RII values were found for *A. philoxeroides* under increasing precipitation variability indicating facilitation. Specifically, the highest RII was found for *A. philoxeroides* in response to the flooded pulse treatment (RII = 0.17, Fig. 3). Positive RII values were also found for the native species in the flooded pulse and multiple pulse treatments (Fig. 3). Thus our findings suggest that the native species are facilitating the invader under variable precipitation. This result is consistent with a previous study where it was revealed that invasive *Acer negundo* in a floodplain was facilitated in a native *Salix* community (Saccone et al. 2010). As such, while competition may be important under favourable environmental conditions, facilitation may be more important in more stressful conditions with resident native species facilitating rather than competing with invasive species (Badano et al. 2007; Saccone et al. 2010). Facilitation can be an important driver of plant community structure (Brooker et al. 2008), and facilitative interactions among plants can result in increases in species abundance and diversity (Callaway 2007). In the case of stressful environments, facilitation may be a very important mechanism with established plants providing a beneficial microclimate underneath their foliage and protecting other plants from stressors (Callaway et al. 2002; Good et al. 2014). For example, facilitation in flooded environments may involve some plants ameliorating the anoxic rhizosphere for neighbouring plants via oxygen leakage (Luo et al. 2010). Therefore, facilitation among species may promote biological invasions through changes in environmental conditions (Flory and Bauer 2014), and positive interactions among species may result in an invasive species facilitating further invasions (Simberloff and Von Holle 1999).

Conclusion

We found that invasive *A. philoxeroides* displayed enhanced growth and competitiveness, and optimised biomass allocation in response to precipitation variability and extreme precipitation events (e.g., flooding). Consequently, *A. philoxeroides* can increase clonal growth and invest more resources into roots when water availability is variable or under extreme conditions, which likely confers a competitive advantage over native species in the wild. A limitation of our study was that only biomass was measured for the native species (and this measure was pooled for all species). Another limitation of this study is that it was conducted over a relatively short period of time. Future work should involve collating growth trait measurements of each individual native species to enable a species-level comparison, to provide further insights into the invasion of alligator weed in native communities. In addition, further work should apply treatments over a longer time period, include repeat trials, and involve altering water regimes for the extreme events in order to demonstrate clear effects of disturbance on these

species. Specifically, conducting an experiment over an entire growing season or over several years may provide information on the demographic impacts of competition and variable water availability. Overall, the findings from our study suggest that highly variable precipitation could facilitate the future spread of *A. philoxeroides* to new regions.

Data availability All data generated or analysed during this study are included in this article.

Declarations

Conflicts of interest The authors declare no conflict of interest.

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