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# Experience of inundation or drought alters the responses of plants to subsequent water conditions

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## Summary

**1.** The availability of water is often highly variable over the life of a plant in nature, and most plants experience episodic extremes in water scarcity and abundance. The importance of plant plasticity in coping with such experiences is widely recognized, but little is known about how plastic responses to current conditions are affected by prior environmental experiences.

**2.** Our objectives were to investigate the effects of early inundation or drought on the subsequent responses of plant species to the same, opposite or more favourable conditions.

**3.** To address these questions, we subjected four invasive and four native herbaceous perennial species from different habitats (xeric, mesic, hydric) to two rounds of hydrological treatments (drought, moderate water, inundation) and analysed the effects of the early treatments on survival and performance (total biomass and relative growth) of individuals in the later treatments.

**4.** In general, (i) early drought reduced the performance of more species than did early inundation, and decreased the final total mass of all species; (ii) early inundation and early drought did not lead to lower survival immediately or later, but improved the relative growth of survivors across all late conditions; (iii) late drought resulted in the highest mortality and lowest performance after any early treatment.

**5.** With respect to habitat of origin: (i) early inundation was more beneficial for species from wet habitats than for other species; (ii) species from xeric habitats had the strongest drought tolerance after early drought; (iii) mesic species were more likely to suffer reduced later growth after either inundation or drought experience. Invasive species benefitted more from early inundation than did native species, but native species grew better after experiencing early drought.

**6.** Results indicate that early exposure to inundation or drought conditions alters how plants respond to later conditions and suggest that exposure to extreme events can induce physiological or morphological changes that improve tolerance for either extreme conditions later. This increased tolerance can be at the cost of poorer performance under more benign conditions.

**7.** *Synthesis.* Early inundation or drought experience may be harmful immediately, but can be beneficial for the later growth of plants. The ability of species to utilize early hydrological experiences was associated with the water range of their habitats and whether the species is invasive or native. The ability to modulate future plastic responses may be as important as short-term plasticity in adapting to temporal environmental heterogeneity. Such 'metaplasticity' can optimize current performance, while avoiding the potential costs of maintaining a high degree of plasticity throughout life.

**Key-words:** drought, habitat range, inundation, invasiveness, metaplasticity, plasticity, priming effect, stress memory, stress tolerance, temporal heterogeneity

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## Introduction

In nature, plants experience large variation in environmental conditions over the course of their lives. Plants deal with such environmental heterogeneity via phenotypic plasticity: the ability to produce different phenotypes in different environments (Pigliucci 2005). The ability of a plant to generate plastic responses is not independent of its past experiences. Extreme events that occur at an early stage of growth not only affect the survival and performance of plants at the time they occur, but also can have profound influences on an individual's growth potential and responses to future environmental conditions (Huber *et al.* 2012; Niu *et al.* 2014). Experiencing biotic stress such as herbivory or abiotic stress such as drought, inundation, frost or heat can alter the response of an individual plant to subsequent stresses (Tahkokorpi *et al.* 2007; Onate, Blanc & Munne-Bosch 2011), a phenomenon referred to as the 'priming effect' (Tanou, Fotopoulos & Molassiotis 2012) or 'stress memory' (Walter *et al.* 2013). For example, *Urtica dioica* subjected to combined drought and nutrient deficiency in the juvenile phase showed improved drought tolerance in their mature leaves (Onate, Blanc & Munne-Bosch 2011). Similarly, pretreatment of wheat seedlings with submergence during vegetative growth improved tolerance to submergence after anthesis (Li *et al.* 2011). Such responses to previous conditions are thought to involve a series of mechanisms including epigenetic modifications (Robertson & Wolf 2012; Scholes & Paige 2015), as well as metabolic, physiological and morphological changes (Bruce *et al.* 2007; Walter *et al.* 2013).

Experiencing extreme conditions not only alters a plant's subsequent performance in a single environment but can also affect the ability of plants to respond to different environmental conditions in the future. This has been called 'plasticity in plasticity' (Schmid & Weiner 1993) or 'metaplasticity' (Novoplansky 2009). When a plant is exposed to different extreme environments at different stages of their growth, the effects of temporal heterogeneity may be similar to those of 'multiple stressors'. The cumulative effect of multiple stressors can be either greater (synergistic) or less (antagonistic) than the additive sum of effects of isolated stressors (Hay 1996; Piggott, Townsend & Matthaei 2015). The effects of individual stresses are relatively well studied, but few studies have focused on the effect of multiple stresses (Darling & Côté 2008), even fewer in the context of temporal heterogeneity.

Water availability is crucial for plants, and variation in water availability over time can have profound effects on plant survival and growth (Niu *et al.* 2014). In many environments, plants are exposed to alternating drought and inundation at different life stages (Parolin *et al.* 2010), and they are able to cope with such heterogeneity through rapid plastic responses (Lande 2009). Even though inundation and drought are at opposite ends of an environmental continuum, they may elicit similar physiological responses from plants, suggesting that exposure to one condition might prepare a plant for exposure to the other. To cope with re-oxygenation and subsequent water deficit, species that display quiescence during complete submergence may be better adapted to dehydration after submergence (Fukao, Yeung & Bailey-Serres 2011), and some drought-tolerant species may also be flood tolerant (Gomes & Kozlowski 1980). A transcription factor that increases during both submergence and drought (Fukao, Yeung & Bailey-Serres 2011) also suggests a common mechanism. On the other hand, some studies have reported a trade-off between tolerance to drought and to inundation in wetland species (Luo, Song & Xie 2008). Different sequences of inundation and drought can affect plant survival and growth differently (Miao, Zou & Breshears 2009). These imply that early inundation and early drought have different effects on later plant responses to either stress. Studies that investigated the combined effects of inundation and drought have produced inconsistent results, and we have no information on how early exposure to either of the extremes affects plant performance under favourable conditions later. Plant plasticity in response to water stress has been studied extensively (Williams & Black 1994; Pezeshki 2001; Casper, Forseth & Wait 2006; Baraloto *et al.* 2007), but little attention has been paid to how prior occurrence of water extremes affects responses to subsequent water conditions.

Species from different habitats may have evolved different abilities to adjust their plastic responses to the same environmental experience. For example, species from flooded forests have a greater ability to tolerate inundation, but lower tolerance for drought stress, than congeners from drier habitats (Baraloto *et al.* 2007). It is unknown whether species from hydric habitats have increased or decreased responses to inundation or drought later in their lives than do other species. Also, invasive species have been hypothesized to show greater phenotypic plasticity than native species (Richards *et al.* 2006), but this has not been supported in several studies (Funk 2008; Hulme 2008; Palacio-López & Gianoli 2011). This could be addressed by investigating plasticity to an environmental factor more closely linked to the context of the specific environmental habitats occupied by invasive and native species. For example, Williams & Black (1994) found that exotic species from arid regions were more plastic in traits related to drought tolerance than their native counterparts.

As far as we know, variation in plasticity in response to earlier hydrological experience has not been investigated. To address this, we performed an experiment with eight species, four native and four invasive, from three hydrological habitats (wet, mesic and xeric), asking the following questions: (i) Does early exposure to inundation or drought influence later performance under inundation, drought or moderate conditions? (ii) Are such effects on later responses different (a) for early inundation vs. early drought? (b) for different late conditions? (c) for species from different hydrological habitats? or (d) for native vs. invasive species?

## Materials and methods

### STUDY SPECIES

We chose eight species, including four invasive species: *Leucanthemum vulgare* Lam. (oxeye daisy), *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek (spotted knapweed; née *C. stoebe* L.), *Leonurus cardiaca* L. (common motherwort) and *Potentilla recta* L. (sulphur cinquefoil), and four native species: *Heterotheca villosa* (Pursh) Shinners (hairy false golden aster), *Gaillardia aristata* Pursh (common gaillardia), *Agastache urticifolia* (Benth.) Kuntze (nettleleaf giant hyssop) and *Potentilla arguta* Pursh (tall cinquefoil). All seeds were collected from natural grasslands in western Montana. The distributions of these species can overlap, but we selected pairs of target species that generally occur in habitats that differ in soil moisture: *C. stoebe* and *H. villosa* occur primarily in more xeric habitats, *L. vulgare*, *P. recta*, *G. aristata* and *P. arguta* primarily in mesic habitats, and *L. cardiaca* and *A. urticifolia* generally in very wet habitats (Table 1).

### EXPERIMENTAL DESIGN

The experiment was conducted in a glasshouse on the campus of the University of Montana, Missoula, Montana. Glasshouse temperatures were maintained at 15–30 °C, corresponding roughly to natural summer temperatures in the region. Natural light was supplemented by metal halide bulbs and maximum total photosynthetically active radiation during the day reached 1200 μmol · m$^{-2}$ s$^{-1}$. Seeds of all species were sown in plastic trays (54.2 × 27.3 cm in width and 6.5 cm in height) in January 2010. One week after seedling emergence, individual seedlings were transplanted into pots (7 × 7 cm in width and 20.6 cm in height) filled with a 1:1 mixture of top garden soil and sterile silica sand. Forty days after transplanting, before the first round of treatments were applied, the longest leaf of each plant was measured as an estimate of the initial size of each individual. A split plot design was implemented with the first round of treatments as a main factor, and the second round of treatments and species as subfactors. For both the first and second rounds, there were three treatments: inundation, moderate watering and drought. At the end of the first round, a subgroup of plants from each of the early treatments was harvested to obtain information on their initial responses to the three water treatments [early responses (ER)] and as a reference for calculating their relative growth after a subsequent treatment. The remaining plants from each of the three early-treatment groups [early inundation (EI), early moderate watering (EM) and early drought (ED)] were divided into three subgroups, each of which was later exposed to one of the same three treatments [late inundation (LI), late moderate watering (LM) and late drought (LD)] in the second round (Fig. 1). For each treatment combination, ten individuals of each species were used, with one individual per pot, giving 10 individuals × 8 species × 3 early treatments × 3 late treatments + 10 × 8 × 3 (individuals with early treatments only) = 960 pots in total.

Six identical tanks were used to create inundation, drought and moderate water conditions, with two tanks assigned to each treatment. Tanks were 161 × 91.3 cm in width and 8.5 cm in height, lined with heavy plastic and fit with drains to regulate the maximum water depth. For the inundation treatment, the water level was maintained at 7 cm depth above the bottom of the tank, and approximately 10 cm below the surface of the soil in the pots. These pots were watered to saturation from the top every day. There was no standing water in the moderate and drought treatment tanks. In the moderate treatment, pots

**Table 1.** Summary of the attributes of the eight species studied and abbreviations for their names

| Latin name | Abbrev. | English name | Family | Moisture range of habitats | Invasiveness |
|---|---|---|---|---|---|
| *Centaurea stoebe* L. ssp. *micranthos* (Gugler) Hayek | C | Spotted knapweed | *Compositae* | Mesic~xeric | Invasive |
| *Heterotheca villosa* (Pursh) Shinners | H | Hairy false golden aster | *Compositae* | Mesic~xeric | Native |
| *Leucanthemum vulgare* Lam. | Lv | Oxeye daisy | *Compositae* | Hydric~mesic | Invasive |
| *Potentilla recta* L. | Pr | Sulphur cinquefoil | *Rosaceae* | Hydric~mesic | Invasive |
| *Gaillardia aristata* Pursh | G | Common gaillardia | *Compositae* | Hydric~mesic | Native |
| *Potentilla arguta* Pursh | Pa | Tall cinquefoil | *Rosaceae* | Hydric~mesic | Native |
| *Leonurus cardiaca* L. | Lc | Common motherwort | *Lamiaceae* | Hydric | Invasive |
| *Agastache urticifolia* (Benth.) Kuntze | A | Nettleleaf giant hyssop | *Lamiaceae* | Hydric | Native |

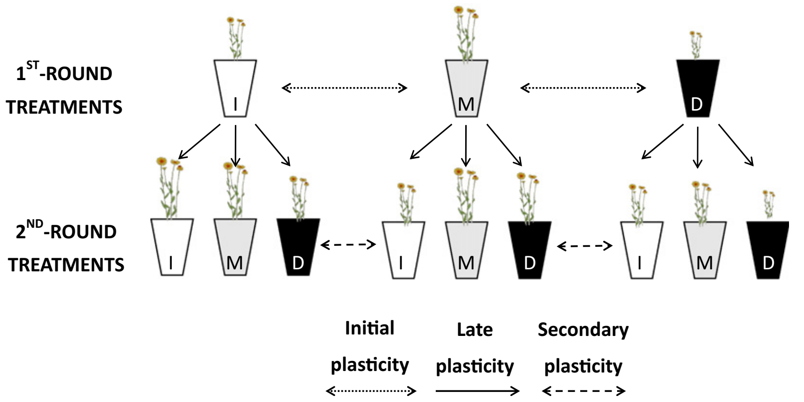

**Fig. 1.** Experimental design showing the two rounds of inundation (I), moderate (M) and drought (D) treatments used in this study. A subset of plants was harvested and measured after first-round treatments. [Colour figure can be viewed at wileyonlinelibrary.com]

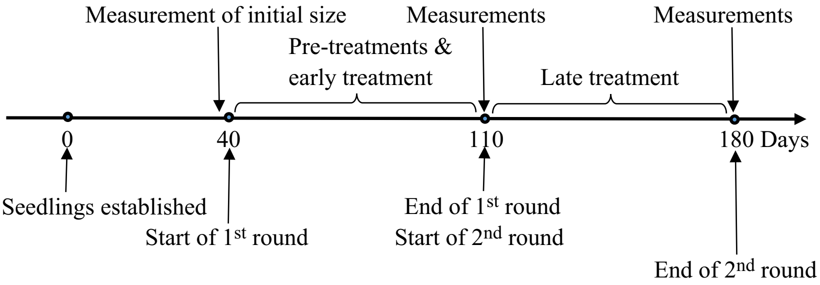

**Fig. 2.** The timing of the two rounds of treatments.

were watered to saturation every other day, while those in the drought treatment were watered to saturation once or twice per week in an effort to create very dry conditions, but prevent high mortality rates. The first round of treatments lasted for 70 days before plants in each treatment were divided and assigned to one of the three different conditions in the second round or harvested and measured to evaluate their early responses (Fig. 2). The duration of the second round of treatments was another 70 days, and glasshouse and hydrological conditions were as similar as possible to the first round. Thus, plants receiving both rounds of treatments were harvested and measured 140 days after the beginning of the first round. Height and leaf number were measured and then separated into roots and shoots at harvest, dried at 60 °C for 2 days and weighed.

### DATA COLLECTION AND STATISTICAL ANALYSES

We calculated mortality rates for all treatment combinations. A total of 728 individuals survived to the end of the experiment and these were used for further analyses. All five traits: total plant biomass (TM), height (HE), leaf number (LN), shoot mass (SM) and root mass (RM), were used to assess the performance of species in each treatment. For each of the five traits of each species, relative growth (RG) for all early–late treatment combinations was calculated according to the formula:

$$\mathrm{RG} = \frac{Y - X}{X},$$

where $X$ is the mean trait value of 10 individuals of the early response group, and $Y$ is the mean trait value in the late treatment of 10 individuals that had the same early treatment as the early response group. For example, to calculate the RG of total biomass in late drought for a species with early inundation treatment, $X$ is the mean total mass of individuals harvested after early inundation and $Y$ is the mean value of individuals in the late drought after early inundation. For each species in each treatment combination, RGs of the four traits: height, leaf number, shoot mass and root mass, were combined into a single composite measure of relative growth ($\mathrm{RG_C}$) by averaging the RGs of the four traits. Thus, we used four response variables in evaluating the performance of each species: mortality rate, total biomass, relative growth in biomass ($\mathrm{RG_M}$) and composite relative growth ($\mathrm{RG_C}$).

For any individual or group of species, early inundation and drought treatments can affect their subsequent responses in different ways and/or to different extents. To address this for a given trait, we defined ‘difference variables (‘Diff-’)’, as the difference in the mean trait value from the control (moderate early treatment) due to an early inundation or drought treatment:

$$\text{Diff-}Y = Y_2 - Y_1,$$

where Diff-$Y$ was the difference in late performance between individuals with early inundation or drought and those with early moderate treatment for a trait of a species, $Y_1$ was the mean value of the trait for the species in a late condition after early moderate treatment (control) and $Y_2$ was its mean trait value in the same late condition after early inundation or drought. For example, to calculate the Diff-TM due to early inundation (EI) for a species in late drought, $Y_1$ is the mean total biomass of individuals in late drought after the early moderate treatment, and $Y_2$ is the mean total biomass of individuals in late drought after early inundation.

Mean values of height, leaf number, shoot mass, root mass and total plant biomass were log-transformed to minimize variance heterogeneity. The $r^2$ from models for ANOVA or ANCOVA on mortality, the five measured traits, relative growth in biomass and composite relative growth were higher with species as a variable than models with habitat type and exotic status as variables. Therefore, the results of three-way ANOVA or ANCOVA for effects of the first round of treatments, the second round of treatments, species and their interactions for all traits were used for analyses of mean values. The five measured traits were analysed with three-way ANCOVA with the initial size of individuals nested within species as a covariate, and mortality and two measures of relative growth were analysed with three-way ANOVA. All dependent variables were then analysed with one-way ANOVA or ANCOVA to evaluate the effects of the early treatments for each species within each of three late treatments, and differences among the late treatments and among different species (for the two measures of relative growth) within each early treatment. Since there were not sufficient degrees of freedom to analyse the effects of individual species on these variables, we compared the degree of effects of early experiences, differences in mortality, total biomass, relative growth in biomass and composite relative growth (Diff-MR, Diff-TM, Diff-$\mathrm{RG_M}$ and Diff-$\mathrm{RG_C}$, respectively) due to early treatments with four-way ANOVA, with the first and second rounds, habitat type, exotic status and their interactions as effects. The LSD method was used for multiple comparisons on mean values for mortality, total biomass, relative growth in mass and composite relative growth and the four Diff- variables among first-round treatments, among second-round treatments and among species (or among different habitat types and between invasive and native species for differences of variables), across all and within each of the other treatments.

## Results

### MORTALITY

Across all species and treatments, mean mortality rate in the first round was 8.6%, significantly lower than 20.7%, which occurred in the second round ($P = 0.007$; Tables 2 and 3; Fig. 3). The overall mortality during late drought was 36.3%, nearly two times higher than in the late inundation and moderate treatments ($P < 0.001$; Fig. 3, Table 3). Two rounds of drought increased the overall mortality of all species to

47.5%, compared with 28.8% in late drought after early moderate conditions ($P = 0.029$), while no effects of early inundation on later mortality were found. Species from xeric habitats showed a decrease in mortality in late inundation ($P < 0.001$) and an increase in mortality in late moderate conditions after early drought ($P < 0.05$), compared with that after early moderate conditions (Fig. 3). Species from hydric habitats had higher mortality than other species under late moderate conditions after moderate experience ($P < 0.01$).

**Table 2.** Three-way ANOVA or ANCOVA for the effects of species (SP), the 1st and 2nd rounds of treatments (1st and 2nd) and their interactions on mortality rate (MR), $\log_{10}$ (Total mass (TM)), relative growth of TM ($RG_M$) and composite relative growth ($RG_C$, mean RG of four traits including height, leaf number, shoot mass and root mass), for plants that had been subjected to two rounds of treatments. $Log_{10}$ [Initial size (IS)] was used as a covariate in the ANCOVA on $\log_{10}$ (TM) and was nested in the species effect

| | | ANOVA on MR | | ANOVA on $RG_M$ | |
|---|---|---|---|---|---|
| Source | d.f. | *F* | *P* | *F* | *P* |
| SP | 7 | 2.58 | 0.022 | 10.33 | <0.001 |
| 1st | 2 | 0.63 | 0.537 | 1.75 | 0.184 |
| 2nd | 2 | 15.53 | <0.001 | 8.07 | <0.001 |
| 1st × 2nd | 4 | 1.61 | 0.185 | 1.10 | 0.366 |

| | | ANCOVA on $Log_{10}$ (TM) | | ANOVA on $RG_C$ | |
|---|---|---|---|---|---|
| Source | d.f. | *F* | *P* | *F* | *P* |
| $Log_{10}$ (IS) | 8 | 29.74 | <0.001 | | |
| SP | 7 | 50.07 | <0.001 | 17.80 | <0.001 |
| 1st | 2 | 51.52 | <0.001 | 4.49 | 0.012 |
| 2nd | 2 | 22.00 | <0.001 | 18.53 | <0.001 |
| SP × 1st | 14 | 2.18 | 0.008 | 3.48 | <0.001 |
| SP × 2nd | 14 | 2.72 | <0.001 | 1.54 | 0.098 |
| 1st × 2nd | 4 | 0.86 | 0.081 | 1.24 | 0.293 |
| SP × 1st × 2nd | 28 | 1.22 | 0.203 | 0.84 | 0.698 |

### TOTAL BIOMASS

For plants harvested after the first round, the mean total biomass of all species was significantly lower under drought than under moderate and inundation conditions ($P < 0.001$; Fig. 4). Compared with moderate conditions, drought reduced the biomass of five of the eight species (the exceptions were *G. aristata*, *P. arguta* and *L. cardiac*; $P < 0.05$), whereas inundation only reduced the biomass of *A. urticifolia* ($P = 0.02$), indicating the treatment of inundation was much less stressful than drought at the early stage.

For plants that received both rounds of treatments, there were highly significant effects of both the first- and second-round treatments on all measured variables, with strong interactions of species with the first- and second-round treatments (Table 2 and Table S1 in Supporting Information). However, there were few significant interactions between the first- and second-round treatments. Across all species and all late treatments, the mean biomass after early drought was 0.31 g, 43.5% lower than after early moderate conditions (0.54 g, $P < 0.001$), but there was no effect of early inundation ($P = 0.221$; Table 3 and Fig. 4). For individual species, early drought decreased final biomass in many more cases than did early inundation (Fig. 4).

The effects of late treatments on biomass were more species specific than those of early treatments, as indicated by greater significance of second-round × species interactions than first-round × species interactions (Table 2). Overall, the mean biomass after late drought was significantly lower than after late inundation and moderate conditions ($P < 0.05$, Table 3). Biomass was greatest under continuous (both rounds of) moderate conditions ($F = 6.20$; d.f. = 2, 172; $P = 0.003$; Table 3), especially for *P. recta* and *C. stoebe* (Fig. 4). After early inundation, negative responses of biomass to late drought were found for more species than after any other early treatment ($P < 0.05$), whereas early moderate or drought treatments resulted in a negative response to late inundation for only *C. stoebe* ($P < 0.01$ and $P = 0.01$ for early moderate and drought experience, respectively).

**Table 3.** Overall effects of the 1st and 2nd rounds of treatments on second-round mortality rate (MR), Log (total mass) [log (TM)], relative growth of total mass ($RG_M$) and composite relative growth ($RG_C$), for plants with both rounds of treatments

| Treatment | MR | $Log_{10}$ (TM) | $RG_M$ | $RG_C$ |
|---|---|---|---|---|
| The 1st round | | | | |
| Overall | | EI = EM > ED | | ED = EI > EM |
| LI | | EI = EM > ED | ED > EM | ED = EI > EM |
| LM | | EM = EI > ED | | |
| LD | EM < ED | EI = EM > ED | | |
| The 2nd round | | | | |
| Overall | LI = LM < LD | LI = LM > LD | LI = LM > LD | LI > LM > LD |
| EI | LI < LD | LI > LD | | LI > LM = LD |
| EM | LM < LD | LM = LI > LD | LM > LD | LI = LM > LD |
| ED | LI = LM < LD | LI > LD | LI = LM > LD | LI = LM > LD |

EI, early inundation; EM, early moderate condition; ED, early drought; LI, late inundation; LM, late moderate condition; LD, late drought.
Significance levels for '>'or '<'are at $P \leq 0.05$, and '=' indicates no differences between two treatments ($P > 0.05$).

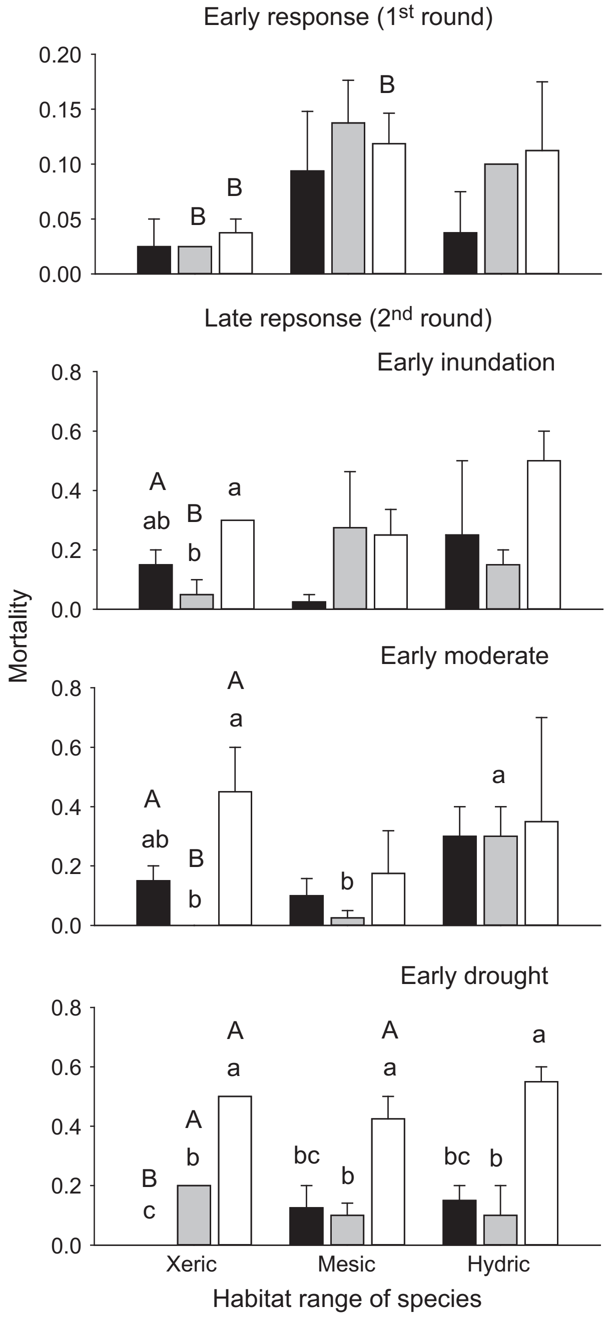

**Fig. 3.** Mean mortality rate in inundation (■), moderate (▨) and drought (□) treatments in the 1st round (early response, ER), and in the 2nd round (late response, LR) for early inundation (EI), moderate (EM) and drought (ED) treatments (1st round) for species grouped according to the hydrology of their habitats. Different lower-case letters signify differences among the 2nd round or among the groups of species, and different upper-case letters signify differences among first-round treatments and between those in early response and in late response ($P < 0.05$).

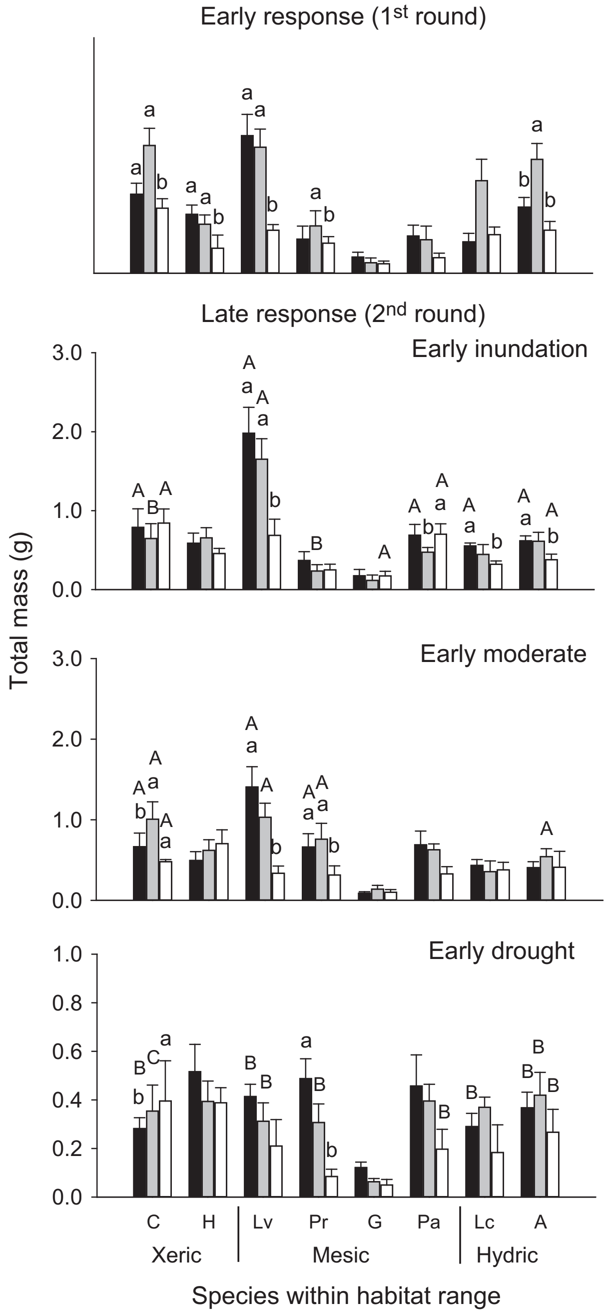

**Fig. 4.** Mean total mass of individual species in inundation (■), moderate (▨) and drought (□) treatments for early responses (1st round), and for late response (2nd round) after the early treatments (1st round). Species are grouped according to the hydrology of their habitats. Abbreviations for all species are in Table 1. For early responses, different lower-case letters signify differences among treatments; for late responses, different lower-case letters signify differences due to first-round treatments; different upper-case letters signify differences due to first-round treatments ($P < 0.05$).

### RELATIVE GROWTH

For both relative growth in biomass ($RG_M$) and the composite measure of relative growth ($RG_C$, mean relative growth of all the other four traits), and across all species, the effects of the second round of treatments were much stronger than the first round (Table 2). Both measures of relative growth, $RG_M$ and $RG_C$, were significantly lower under late drought than in more favourable late conditions ($P < 0.01$; Table 3 and Figs S2 and 5). For the effects of the first-round treatments, early drought improved relative biomass growth in late inundation only when compared to the early moderate treatment (+99.7% vs. +42.4%, $P = 0.037$; Table 3 and Fig. S2a). Across all late conditions, both early inundation and drought increased the mean composite measure of growth, $RG_C$, by 29.7% and 32.4%, respectively, relative to +11.3% of the control ($P = 0.017$ and $P = 0.006$; Table 3).

Significant differences in growth among species were found between the two fastest growing species (*P. arguta* and *H. villosa*) and the other species (Figs S2b and 5). There were also differences in growth between *L. vulgare* and *P. recta* versus the remaining species for composite relative growth (Fig. 5). For individual species, differences in relative growth among the first round treatments were found only for species from hydric and xeric habitats (Fig. S2c; $P < 0.05$), and there was little difference among the second-round treatments (Fig. S2d). For the composite measure of relative growth, interactions between species and treatment were much stronger for the first than for the second round (Table 2). Species from wet and xeric habitats were more likely to show improved $RG_C$ than species from mesic habitats (Fig. 5). After early inundation, *C. stoebe*'s $RG_C$ in late inundation and drought was +15.9% and +20.1%, higher than the control [−26.9% ($P = 0.065$) and −38.9% ($P = 0.006$), respectively]. $RG_C$s of *L. cardiaca* and *A. urticifolia* were +47.0% and −4.1%, respectively, across all late treatments, 217.5% and 91.8% higher than controls (−40.0% and −49.7%, $P < 0.05$). Early inundation reduced the composite relative growth of *P. recta* in the late moderate treatment ($P = 0.032$). Similarly, effects of early drought were positive for *A. urticifolia* in all late treatments, as it increased the average $RG_C$ from −49.7%

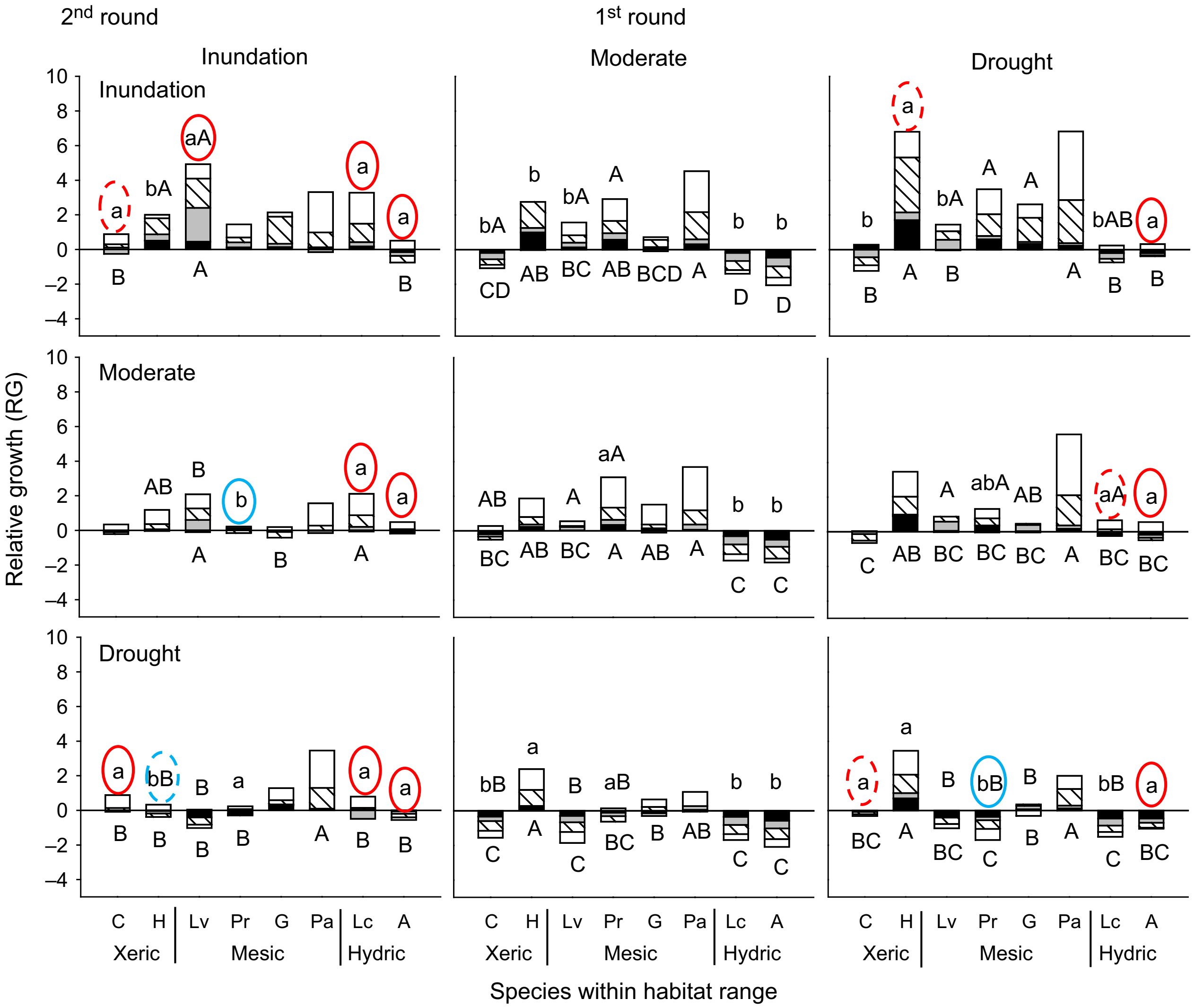

**Fig. 5.** Relative growth (RG) in the traits: height (■), leaf number (▣), shoot mass (▧) and root mass (☐) during the second-round treatments for eight species after the first-round treatments. Species are grouped according to the hydrology of their habitats. For a single species, different letters in lower case above the columns indicate significant differences in mean RG of the four traits or the composite relative growth ($RG_C$) among the fist-round treatments for each second-round treatment; different letters in upper case above the columns represent significant differences among the second-round treatments within the same first-round treatment ($P < 0.05$). Different letters in upper case below the columns denote a significant difference among species ($P < 0.05$). Red circles represent a significant increase and blue circles a significant decrease ($P \le 0.05$), due to first-round inundation or drought, compared with the control (after first-round moderate watering); red and blue dashed circles represent marginally significant increase or decrease ($0.05 < P < 0.10$). Abbreviations for all species are in Table 1. [Colour figure can be viewed at wileyonlinelibrary.com]

to −8.6% ($P < 0.05$). However, early drought also had some adverse effects: it decreased $\mathrm{RG_C}$ of *P. recta* in late drought by 257.8% (from −11.90% to −42.60%; $P = 0.043$).

### CHANGES DUE TO EARLY TREATMENTS

Significant effects of early, late treatments and habitat type were found for all Diff- values except mortality (Tables 4, S3 and Fig. S3). There were significant interactions between late treatments and invasiveness for both Diff-$\mathrm{RG_M}$ and Diff-$\mathrm{RG_C}$ (Tables 4 and S3). For composite relative growth, there were significant interactions between early treatment and habitat type, late treatments and habitat type, and early treatments and invasiveness. Among the early treatments, we found a significant difference between effects of inundation and drought only for Diff-TM. Early inundation resulted in an average increase in biomass (Diff-TM = 0.06) across all species and all late treatments, significantly higher than the average decrease in biomass due to early drought (Diff-TM =ucodep>−0.24, $P = 0.031$).

Comparing species from different habitats in the late treatments, hydric species showed an increase in relative growth after early inundation relative to the control, with a Diff-$\mathrm{RG_M}$ = 1.02 and Diff-$\mathrm{RG_C}$ = 0.66 for *L. cardiaca* and *A. urticifolia*, respectively, which was higher than those of xeric and mesic species [averaged Diff-$\mathrm{RG_M}$ = 0.06 ($P < 0.05$) and Diff-$\mathrm{RG_C}$ = −0.01 ($P < 0.001$); Table S3]. Xeric species demonstrated a greater increase in composite relative growth after the early drought treatment (average of 0.32) than after early inundation (average of 0.02) across all late treatments ($P = 0.030$). For species from mesic habitats, differences in composite growth due to early inundation were higher for late inundation and drought treatments than for late moderate conditions (0.13 and 0.29 vs. −0.35, $P < 0.001$ in both cases). For invasive versus native species across all late treatments, the beneficial effect of early inundation on composite growth was greater for invaders than for natives (0.44 vs. 0.04, $P < 0.001$), but the beneficial effect of early drought was greater for natives (0.41 vs. 0.10, $P = 0.003$).

**Table 4.** *F*-values from four-way ANOVA on the differences due to effects of early experience (Diff-, between after inundation or drought experience and after moderate experience) for mortality rate (MR), total mass (TM), relative growth in mass ($\mathrm{RG_M}$) and composite relative growth ($\mathrm{RG_C}$), for the effects of the 1st and 2nd rounds of treatments (1st and 2nd), habitat (HA), invasiveness (IN) and their interactions

| Source of variation | d.f. | Diff-MR | Diff-TM | Diff-$\mathrm{RG_M}$ | Diff-$\mathrm{RG_C}$ |
|---|---|---|---|---|---|
| 1st | 1 | 0.11 | **7.87*** | 0.01 | 0.16 |
| 2nd | 2 | 1.73 | 0.62 | 1.83 | **4.81**** |
| HA | 2 | 1.20 | 0.33 | **4.36*** | **14.19***** |
| IN | 1 | 0.58 | 0.74 | 0.01 | 0.00 |
| 1st × 2nd | 2 | 0.70 | 0.08 | 0.56 | 1.52 |
| 1st × HA | 2 | 0.11 | 0.29 | 0.87 | **5.37**** |
| 1st × IN | 1 | 0.19 | 1.47 | **4.62*** | **21.20***** |
| 2nd × HA | 4 | 1.09 | 0.46 | 0.83 | **2.78*** |
| 2nd × IN | 2 | 2.61 | 0.47 | 0.37 | 0.23 |
| 1st × HA × IN | 4 | 1.17 | 0.22 | 0.75 | 2.11 |
| 2nd × HA × IN | 4 | 1.48 | 0.51 | 0.60 | 2.10 |
| 1st × 2nd × HA | 4 | 0.43 | 0.01 | 0.46 | 1.10 |
| 1st × 2nd × IN | 2 | 0.00 | 0.17 | 0.44 | 2.14 |
| 1st × 2nd × HA × IN | 4 | 0.44 | 0.17 | 0.23 | 0.53 |

Significance levels: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.
Significant values are in bold font.

## Discussion

### EFFECTS OF EARLY TREATMENTS ON LATER PERFORMANCE

Improved tolerance for environmental stress after previous exposure to stress has been called the ‘priming effect’ (Tanou, Fotopoulos & Molassiotis 2012) or ‘stress memory’ (Walter *et al.* 2013) and has been documented for drought and inundation in previous studies (Li *et al.* 2011; Onate, Blanc & Munne-Bosch 2011). But there has been little discussion of how the occurrence of these two stresses at different points in time during plant growth might influence performance (Miao, Zou & Breshears 2009). Our results are the first experimental evidence that either kind of experience early in the life can improve a plant’s performance to both forms of stress at a later stage. This is consistent with the theoretical and empirical studies on synergetic effect of multiple stressors (Folt *et al.* 1999; Coors & Meester 2008; Crain, Kroeker & Halpern 2008; Piggott, Townsend & Matthaei 2015). Thus, as philosopher Fredrick Nietzsche said, ‘that which does not kill us, makes us stronger’ may apply to plants.

Part of the explanation for improved performance under second-round inundation or drought after either early inundation or drought may be that some of the mechanisms for tolerance to drought and inundation are similar (Lopez & Kursar 2003). For example, an ethylene-response-factor-like gene Sub1A that confers submergence tolerance to rice (Xu *et al.* 2006) also improves survival when rice is exposed to rapid dehydration (Fukao, Yeung & Bailey-Serres 2011). The submergence-inducible gene Sub1A may endow plants with the ability to overcome prolonged submergence, oxidative damage and rapid dehydration that often occur during recovering from submergence, as well as water deficit caused by drought (Fukao, Yeung & Bailey-Serres 2011). ABA, the effects of which can be augmented by Sub1A, is a key signalling molecule that coordinates water balance, expression of stress-inducible genes and metabolic adjustment under water-deficient conditions (Zhu 2002; Seki *et al.* 2007). Dehydration is also a component of a transient submergence event (Setter, Bhekasut & Greenway 2010), and exogenous ABA increases survival of oxygen deprivation in plants (Hwang & Vantoai 1991; Ellis, Dennis & Peacock 1999). Therefore, the levels of ABA may also act as a positive regulator for submergence tolerance as well as for drought tolerance. The shared mechanisms for tolerance to inundation and drought stress also observed in physiological and anatomical traits (Parolin *et al.* 2010). For example, both inundation and drought can induce stomatal closure (Parolin 2001; Elcan & Pezeshki 2002), reduce leaf gas exchange and decrease leaf transpiration and carbon assimilation (Parolin 2001; Baraloto *et al.* 2007). Adventitious roots, aerenchyma and leathery xeromorphic leaves of trees in Amazonian floodplains are commonly recognized as adaptation to inundation (Parolin 2001), but they may also alleviate the effects of drought.

Plants may have the ability to compensate for harsh conditions early in their lives through increased growth later, just as plants can compensate for herbivory, sometimes performing as well as or better than plants that were not grazed (McNaughton 1979; Paige & Whitham 1987; Agrawal 2000). Damage results in lower immediate growth, but sometimes promotes faster growth afterwards, enabling damaged plants to catch up. An increase in relative growth rate after damage or prior extreme experience can also be an allometric effect: the relative growth rate of a plant decreases as it grows. An event that makes or keeps plants smaller can therefore increase a plant's relative growth rates afterwards.

### METAPLASTICITY ASSOCIATED WITH SPECIES' HABITATS

Our species from hydric, mesic or xeric habitats responded to the experience of early inundation or drought in ways that were generally consistent with the hydrology of the habitats in which they occur. For example, gas exchange rates in flood-tolerant species usually recover rapidly following a inundation event (Kozlowski 1982; Elcan & Pezeshki 2002). Here, species from hydric habitats had the greatest increase in relative growth after early experience with inundation, although early drought was not worse for them than for other species. Similarly, species from xeric habitats showed greater tolerance for drought after exposure to early drought than did other species, consistent with other studies of drought priming (Onate, Blanc & Munne-Bosch 2011; Walter *et al.* 2011; Wang *et al.* 2014). Enhanced performance by species from both more extreme habitats later under the same or different stressful conditions, relative to species from more moderate habitats, suggests the hypothesis that plants may evolve a general tolerance for various forms of stress.

Repeated exposure can lead to the evolution of a more stress-tolerant genotype (Chapin, Autumn & Pugnaire 1993), which may show reduced performance under more favourable conditions. We did not find a significant decrease in relative growth under later moderate conditions for species from hydric or xeric habitats after early drought or inundation. Evidence for such a cost was only found in one species from a mesic environment (*P. recta*) after exposure to inundation. This could be because (i) a cost of acclimation to early stress may be more likely to occur in species without a history of adaptation to extreme environments; or (ii) that the cost of responses to early stress may be small and difficult to detect (Sultan & Spencer 2002; Weijschedé *et al.* 2006; Auld, Agrawal & Relyea 2010); or (iii) the decreased relative growth of *P. recta* in late drought after early drought may simply be due to damage from a longer period of continuous drought, which had more adverse effects than inundation.

Long-term adaptation to benign habitats may lead to the evolution of genotypes with reduced ability to tolerate extreme events. According to this hypothesis, species from mesic habitats, especially *P. recta*, are less able to cope with more extreme environmental events. The ability of a species to develop metaplasticity in response to prior extreme experience may be closely linked to its tolerance for such experience. It is to be expected that the habitat in which a species occurs plays an important role in determining metaplasticity in response to early experience. This could be a useful focus for future studies on variation in plasticity and metaplasticity.

The ways by which different species adjust their later plasticity in response to prior experience may play an important role in ecotypic differentiation (Bradshaw & Hardwick 1989; Palacio-López & Gianoli 2011). Metaplasticity may be as important as genetic differentiation for the expansion of a species (Williams & Black 1993; Parker, Rodriguez & Loik 2003) and allow species to respond to a wide range of environments and tolerate novel stresses during invasion. After expansion, the maintenance of a high degree of plasticity throughout a plant's lifetime may be very costly. Assuming that the costs of plasticity increase with the degree of plasticity (DeWitt, Sih & Wilson 1998; Givnish 2002; Auld, Agrawal & Relyea 2010), natural selection in response to environmental heterogeneity may favour greater variability in the plasticity of a specific trait (but see (Pigliucci, Murren & Schlichting 2006; Crispo 2007). The complexity and high operational costs of plasticity suggest the involvement of higher-order control and coordination (Novoplansky 2009). Such flexibility in plasticity may allow plants to produce adaptive plastic responses rapidly when needed, while minimizing costs of maintaining broad plasticity to the degree possible. Flexibility in plasticity may therefore be as important for species' acclimation to temporal heterogeneity in environmental conditions as the degree of plasticity at one point in time.

### METAPLASTICITY OF INVASIVE VERSUS NATIVE SPECIES

Our results show that plastic responses can be changed by previous environmental experiences, and suggest that the ability of species to regulate their plasticity is related to the habitats in which they occur, and whether they are invasive or native species. Invasive species have been hypothesized to be more plastic than natives, but we found little evidence for this. Contrary to some predictions (Marshall & Jain 1968; Daehler 2003) and some empirical results (Davidson *et al.* 2011), our four invasive species were not different than their four native counterparts in their responses to water conditions, as found in other studies (Brock, Weinig & Galen 2005; Funk 2008; Palacio-López & Gianoli 2011). Plasticity is highly trait dependent, and a high degree of plasticity in one trait may be associated with low plasticity in other traits (Valladares *et al.* 2000). This suggests that integrated measures of plant performance may be more important for understanding the role of plasticity in invasion than quantifying the degree of plasticity (or metaplasticity) in individual traits (Hulme 2008). Based on our composite measure of relative growth, the invasive species benefitted from early inundation more than native species did, whereas native species benefited more from early drought. Comparison of a larger number of native and invasive species is needed to draw stronger conclusions.

### ADAPTIVE METAPLASTICITY VERSUS CONSTRAINTS AND DAMAGE

Since A.D. Bradshaw's landmark paper over a half century ago (Bradshaw 1965), there have been extensive discussions and debates concerning the relevant traits, measurement, evolutionary and ecological significance of phenotypic plasticity, as well its costs and mechanisms. It may be premature to theorize about these same issues with respect to the higher-order phenomenon of metaplasticity (Novoplansky 2009). Still, the current study suggests some theoretical considerations:

1. It is important to distinguish between adaptive behaviours and those that are inevitable results of plant growth form, unavoidable constraints or damage. If a plant suffers from phosphorus deficiency, its leaves will be purple, and it may have difficulty dealing with additional stresses. It does not seem useful to interpret this as adaptive plasticity/metaplasticity. Similarly, plant growth is allometric, and a plant's relative growth rate decreases with size. Therefore, any treatment that reduces plant growth but has no other negative effects will result in a higher relative growth under better environmental conditions later when compared to plants that did not suffer from reduced growth earlier (Weiner 2004). This is better interpreted in terms of allometry than as metaplasticity.
2. When should plants evolve metaplasticity rather than simple plasticity? Assuming that there is a cost of plasticity and that this cost increases with the breadth of plastic responses of which the plant is capable, we would expect metaplasticity to evolve when specific environmental conditions are predictably associated with specific later environmental conditions. Under such a scenario, plants could reduce the cost of future broad plasticity by maintaining more limited plasticity for the predicted environment. The life span of the plant relative to the temporal variation in its environment becomes important here. We would expect metaplasticity to evolve when the lifespan of a plant is long enough for it to experience different environmental conditions during its life, but not if its lifespan covers many such changes in different directions (unless the metaplasticity is temporary). Thus, metaplasticity would be expected to evolve in short-lived plants, but not those with the very shortest lifespan, for example desert annuals.

## Conclusions

This study demonstrates that early experience of drought or inundation can modify responses to drought or inundation later in life. The ability to modulate subsequent plasticity in response to early experience is affected by the species' habitat, whether it is invasive or native, and the type of environmental experience. Adaptive metaplasticity may be associated with greater stress tolerance and reduced costs.

Species from different hydrological habitats not only showed different short-term responses to water conditions at both stages, but also showed differences in the variation in later plasticity in response to the early treatments, and these differences were usually interpretable in terms of their habitats. Species from hydric and xeric habitats benefitted most from early inundation and drought experiences, respectively, while evidence of later costs of such exposure was found in one species from mesic habitats. Invasive species did not show higher short-term plasticity than native species, but the effects of early inundation versus drought on later growth were different for these two groups. Flexibility in producing different degrees of plasticity may be as important for adaptation to environmental heterogeneity as plasticity at one point in time. Future research should focus on the development of a general theory for the evolution of plasticity and metaplasticity of traits, and on the mechanisms involved.

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## Data accessibility

All data are present in the paper and its supporting information.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Three-way ANCOVA for the effects of species (SP), the 1st and 2nd rounds of treatments (1st and 2nd) and their interactions on $\log_{10}$ (Height), $\log_{10}$ (Leaf number), $\log_{10}$ (Shoot mass) and $\log_{10}$ (Root mass), for plants with two rounds of treatments.

**Table S2.** Overall effects of the 1st and 2nd rounds of treatments respectively on $\log_{10}$ (Height), $\log_{10}$ (Leaf number), $\log_{10}$ (Shoot mass) and $\log_{10}$ (Root mass), as well as the corresponding relative growth (RG) of each variable, and their effects within each of the other factors, for two rounds of treatments.

**Table S3.** Comparisons of differences (Diff-), due to the effects of early experiences, for four variables (Diff-MR, Diff-TM, Diff-$\mathrm{RG}_{\mathrm{M}}$ and Diff-$\mathrm{RG}_{\mathrm{C}}$), for effects of early inundation vs. drought experience, late treatments, habitat of origin, and invasive vs. native species.

**Fig. S1.** Mean height, leaf number, shoot mass and root mass in inundation (■), moderate (▨) and drought (□) conditions of early response (ER), and of late response (2nd round) for eight species after the 1st-round treatments.

**Fig. S2.** Relative growth in total mass ($\mathrm{RG}_{\mathrm{M}}$; a–d): a) mean $\mathrm{RG}_{\mathrm{M}}$ of eight species in the 2nd-round inundation (■), moderate (▨) and drought (□) conditions after early inundation (EI), moderate (EM) and drought (ED) treatments (1st round); b) mean $\mathrm{RG}_{\mathrm{M}}$ across all 1st-round and 2nd-round treatments for each species; c) mean $\mathrm{RG}_{\mathrm{M}}$ of all 2nd-round conditions for each species after EI (■), EM (▨) and ED (□) treatments; and d) mean $\mathrm{RG}_{\mathrm{M}}$ of all 1st-round treatments for each species in the 2nd-round inundation (■), moderate (▨) and drought (□) conditions. Species are grouped according to the hydrology of their habitats.