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History of exposure to herbivores increases the compensatory ability of an invasive plant

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Abstract Release from natural enemies is frequently cited as an important factor contributing to plant invasions. But such effects are likely to be temporary—native herbivores can form new plant-herbivore associations and co-evolved insects might reach the new range. While the potential effects of the initial enemy release have been well studied, the consequences of any resumption of herbivory are poorly understood. *Alternanthera philoxeroides* is one of the most widespread invasive plants in China and is attacked both by a specialist herbivore introduced from the native range, *Agasicles hygrophila*, and a native beetle *Cassida piperata* Hope which has formed a new association. However, these insects are not found throughout the invaded range. To test the effect of the history of population exposure to herbivory on compensatory ability, plants were cultured from 14 populations around China that differed in whether *A. hygrophila* or *C. piperata* were present. Treatment plants were exposed to herbivory by *A. hygrophila* for a week until 50% of the leaf area was defoliated, then grown for 80 days. Plants from populations with prior exposure to herbivory (of any kind) accumulated more root mass than populations without prior exposure, indicating that prior exposure to insects can stimulate plant compensation to herbivory. We would recommend that potential changes in plant tolerance in response to prior exposure to herbivory are considered in invasive plant management plans that employ biocontrol agents.

Keywords Biological control · Biological invasion · Insect exposure history · *Alternanthera philoxeroides* · Compensation

Introduction

Most invasive plant species have been introduced to their new ranges without the full suite of natural enemies with which they co-evolved (e.g. natural enemy release) (Keane and Crawley 2002). In the absence of specialist herbivores, invasive species may reallocate resources from defence to growth, reproduction or both, as proposed by the Evolution of Increased Competitive Ability Hypothesis (EICA) (Blossey and Nötzold 1995). However, the enemy release, and the associated fitness gain, might be temporary as native herbivores tend to accumulate on non-native species over time (Siemann et al. 2006). Moreover, co-evolved natural enemies, such as herbivorous insects, might also eventually arrive either accidentally or deliberately (e.g. through classical biological control releases), although the character and

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intensity of the re-association between plant and herbivore can differ from the interaction in the native range (Garcia-Rossi et al. 2003).

In response to the re- or new-associated interactions with herbivores, invasive plants may undergo rapid evolutionary changes in defence, e.g. resistance and/or tolerance (Thompson 1998). For instance, in populations of invasive wild parsnips, *Pastinaca sativa*, there was an increase in toxic furanocoumarins content after re-association with Parsnip webworm, *Depressaria pastinacella* (Zangerl and Berenbaum 2005), leading to an increase in herbivore resistance. What has received less attention is the potential for invasive plants to evolve greater tolerance of herbivory after re- or new-association with herbivores.

Tolerance is the ability of a plant to re-grow and reproduce after herbivory (Strauss and Agrawal 1999). Plant compensatory ability, defined here as the difference in fitness between herbivory damaged and undamaged individuals of the same genotype, is known as an important measure of plant tolerance (Belsky 1986). Herbivory-induced compensatory growth for a single plant genotype can range from under-compensation if herbivory damage is not fully replaced, to equal-compensation if plants fully recover from herbivory, and overcompensation if plants have greater fitness when damaged (Maschinski and Whitham 1989). Proposed mechanisms for plant compensation include increases in photosynthetic ability, utilization of stored reserves, and changes in phenology and resource reallocation (Strauss and Agrawal 1999; Tiffin 2000). Empirical evidence indicates that herbivory may evolutionarily increase a plant's compensatory ability, especially when the risk of damage is predictable and high (Juenger and Bergelson 2000; Lennartsson et al. 1997). Therefore, the re- or new-associated herbivores would be expected to create a selection pressure on the compensatory ability of invasive plants, particular if herbivores occur at high densities.

The evolutionary responses of invasive plants to herbivore have been well studied (Müller-Schärer et al. 2004), providing insights into many aspects of plant evolutionary biology, especially evolution of plant defence (Müller-Schärer et al. 2004; Thompson 1998). However, almost all these studies focus on sexual plants, while little information is available on the evolutionary responses of clonally propagated invasive plants to herbivores. In fact, some of the globally important invasive plants reproduce mainly clonally, e.g. *Alternanthera philoxeroides* (Julien et al. 1992) and *Eichhornia crassipes* (Li et al. 2006), in their non-native ranges. There is increasing evidence indicating that somatic mutation and genomic modification in clonal plants are frequent and provide genetic and epigenetic variation that contributes to their adaptive evolution, especially for clonally propagated domesticated plants (Prentis et al. 2008; McKey et al. 2010). Moreover, intra-clonal variation in plant defence and selective impacts of herbivory on plant defence has been reported in clonal plants (Monro and Poore 2004; Whitham and Slobodchikoff 1981). Therefore, herbivory can impose selection on defence of clonal invasive plants; indeed such effects are likely to be promoted by the invasion process (Prentis et al. 2008).

Here, we report the results of an experiment designed to examine the consequences of prior exposure to insect herbivores on the compensatory ability of the clonal invasive plant alligator weed, *Alternanthera philoxeroides* (Mart.) Griseb (Amaranthaceae). Specifically, we hypothesized that plant populations from sites with herbivores would show a greater capacity for compensation than populations from sites without them. We also tested whether the source of herbivory encountered (native insects, introduced insects, or both) influenced the form of plant compensation.

Materials and methods

Study species

Alternanthera philoxeroides is a perennial herbaceous plant with horizontal to vertical stems that can grow in aquatic and terrestrial habitats. Each stem consists of nodes that are capable of producing individual plantlets. Roots develop at closely spaced nodes along stems (Julien et al. 1995). The species is native to South America and has become a widespread invader in the Asia–Pacific region and the United States (Julien et al. 1995). It was first introduced into China (Shanghai) as a forage plant in the 1930s, and since then it has been distributed to as many as 20 provinces in Central and Southern China (Ma 2001), with its range still expanding in Northern China (Geng et al. 2007). According to Julien et al. (1992) *A. philoxeroides*

produces seeds in its native South American range, but rarely sets seeds and propagates solely by vegetative means from stem and root buds in Australia, the United States and China.

Agasicles hygrophila, a host-specific leaf grazer of *A. philoxeroides*, has been widely distributed for biological control (Buckingham 2002). The beetle has curbed *A. philoxeroides* invasion in many infested rivers and ponds (Ma 2001; Sainty et al. 1998), but has failed to control the plant in semi-aquatic and terrestrial habitats despite occurring on *A. philoxeroides* in these habitats (Ma 2001). The beetle was first introduced to China in 1986, but has not spread to all areas affected by *A. philoxeroides* (Ma 2001), and so plant populations have different histories of re-association. In China *A. philoxeroides* is also defoliated by a native tortoise beetle, *Cassida piperata* Hope (Coleoptera: Cassididae) (Lin et al. 1990) in terrestrial habitats and occasionally in aquatic habitats (Lu and Ding, unpublished). Both *A. hygrophila* and *C. piperata* are aboveground herbivores. Adults and larvae of *A. hygrophila* feed on leaves and stems of *A. philoxeroides*, often producing feeding holes and "trenches" on leaves; adults and larvae of *C. piperata* only feed on leaves of *A. philoxeroides*, often producing tiny feeding holes. Previous studies have found that *A. philoxeroides* can compensate rapidly in terms of biomass production after damage by herbivory (natural and simulated) and mowing in terrestrial habitats, which may be related to its high root mass (Lu et al. 2010; Lu and Ding 2010; Sun et al. 2009; Wilson et al. 2007). Moreover, in common garden experiments we found that *A. philoxeroides* compensates for defoliation caused by *A. hygrophila* and *C. piperata* in a similar manner (Lu and Ding, unpublished).

In this study, we focused on herbivory by *A. hygrophila*. The *A. hygrophila* adult beetles used in our experiments were collected from *A. philoxeroides* in the suburbs of Wuhan, Hubei Province.

Plant sampling locations

In early spring 2007, we collected plants from 14 terrestrial populations (>10 km apart from each other) of *A. philoxeroides* in five Chinese provinces (Table 1); populations from the same province were assumed to be independent for purposes of this study. Based on biological control records (Ma 2001; Yang 2001), feeding records for *C. piperata* (Lin et al. 1990), and our 2006–2007 field surveys on insect feeding, these populations were categorized into four groups based on the presence (or absence) of *A. hygrophila* and *C. piperata* (Table 1). At each site we collected 10 plants from 4 locations (40 plants/population) >20 m apart in open fields near aquatic habitats (riverbank). We collected a stem (10–15 cm long) from each plant and immediately placed the stems in moist foam in coolers with dry ice for transport to the laboratory. In the laboratory we cut stems to 4–5 cm lengths; each cut stem contained a single node. Stem pieces were then planted vertically in plastic containers (50 × 40 × 30 cm deep) filled with a homogenized mixture of peat, topsoil and sand in a greenhouse under natural light at Wuhan Botanical Garden (Chinese Academy of Sciences). The containers were caged to exclude herbivores. To reduce the possible carryover impact of parental environment on plant compensation, we removed 4–5 cm stem pieces (each bearing one node) from the new shoots for our experiments after 10 weeks.

Herbivory treatments

The experiment was conducted in a greenhouse at Wuhan Botanical Institute/Wuhan Botanical Garden (Chinese Academy of Sciences) from April to early December, 2007. Mean daily air temperature in the greenhouse was 20–35°C from late April to September and 15–25°C from October to early December.

Three randomly selected stem pieces from the same population (stems from the same population were mixed together before planting) were planted vertically in a pot (16 cm in diameter, 14 cm in height) filled with a homogenized mixture of peat, topsoil and sand. Twenty days before herbivory treatment, we retained similar-sized plants and thinned the plants to one plant per pot to minimise plant size variation among pots. Depending on the availability of stem pieces, there were 34–46 plants per population.

Half the potted plants for each population received insects (herbivory treatment: 50% of the leaf area of each plant was removed by herbivores), and half served as controls (undamaged control) (giving 17–23 replicates for each treatment). Two days before herbivory treatment, half the shoots for each plant were caged. In the herbivory treatment, 6–8 *A. hygrophila* adults were released into each cage.

Table 1 Locations of source populations of *A. philoxeroides* and their insect exposure history

Provinces/populations	Longitude	Latitude	Exposure history	Defoliation level	Release time	Reference
Yunnan						
HG	24°58′46.0″	102°39′57.9″	I	20–30%	1987	Ma (2001)
KM	24°58′36.4″	102°39′58.8″	I	20–30%	1987	Ma (2001)
DC	24°57′38.4″	102°33′27.7″	–			
DL	25°43′17.2″	100°11′31.0″	–			
Shanghai						
CM	31°34′23.0″	121°30′21.7″	N	10–20%		
YSL	31°10′47.2″	121°23′22.6″	–			
HQ	31°10′29.7″	121°22′32.4″	–			
NH	31°10′04.4″	121°34′20.0″	I	10–20%	1995	Yang (2001)
LHL	31°07′45.6″	121°23′39.6″	N	20–30%		
Zhejiang						
LP	30°24′23.5″	120°18′06.0″	I + N	30–40%	1987	Ma (2001)
Henan						
XY	32°00′54.9″	114°05′13.6″	N	20–40%		
Hubei						
ZWY	30°32′44.5″	114°24′45.6″	I + N	20–40%	1987	Ma (2001)
YMC	30°32′32.3″	114°18′32.7″	–			
Shandong						
SD	36°41′40.3″	116°54′50.5″	–			

Exposure history is categorized as exposure to *A. hygrophila* (I), *C. piperata* (N), both (I + N) or neither (–), as judged from records of release of *A. hygrophila* (cited under Reference in the table) and from surveys in 2006–2007. Defoliation level is from these surveys. Release time is for intentional release of *A. hygrophila*

After 7 days, all the caged shoots in the herbivory treatment were completely defoliated and the insects and cages were removed. Plants were then grown for an additional 80 days. During this time, plants were watered every 2 days and pot positions in the greenhouse were randomised every month. At harvest the numbers of stem and root buds were counted, and above and below ground biomass were separated and dried (80°C for 48 h) before weighing.

Data analysis

Prior to analysis, total, root and shoot mass, and root to shoot biomass ratio (R/S) were $\log_{10}$-transformed to achieve normality and homoscedasticity.

We carried out analyses with the full data set, including data for all harvested plants, to test the potential impacts of herbivory, insect exposure history (previously exposed or un-exposed to herbivory), population and their interactions on plant performance. We also analysed the data for plants with insect exposure history only (previously exposed to *A. hygrophila*, *C. piperata*, or both), to compare the impacts of previous exposure to different insect species on plant response to subsequent herbivory.

All measured plant traits were analysed with three-way nested ANOVAs. With the full data set, the ANOVA model included insect exposure history (previously exposed or un-exposed to herbivory) and herbivory treatment as fixed factors, and plant population as a random factor nested within insect exposure history. For the data for plants with insect exposure history alone, the ANOVA model included insect species (*A. hygrophila*, *C. piperata*, or both) and herbivory treatment as fixed factors, and plant population as a random factor nested within insect species. The effects of insect exposure history and insect species were tested over the nested population term. Differences between individual means were tested with *t* tests.

Data analyses were carried out using Statistical analysis system (SAS Version 8.1, SAS Institute).

Results

Effect of herbivory and insect exposure history on plant biomass and vegetative bud formation

The interaction between herbivory and insect exposure history affected plant root mass, but did not affect plant shoot mass, R/S, or total biomass (Table 2, Fig. 1). In support of our prediction, herbivory significantly increased root mass ($P = 0.0007$, Fig. 1c) of plants with insect exposure history when compared to undamaged control plants, while herbivory did not affect root mass of plants without insect exposure history when compared to undamaged control plants ($P > 0.05$, Fig. 1c).

The interaction between herbivory and population had a significant effect on plant total and shoot mass, and marginally affected plant root mass (Table 2). Of the 14 plant populations, five overcompensated, eight equal-compensated and one under-compensated in terms of plant total biomass in response to herbivory (Fig. 2a). In support of our prediction, four of the five populations that overcompensated for herbivory (HG, XY, ZWY and LHL) were from locations with herbivores that removed 10–40% plant leaf area historically, while only one (YMC) was from a location with no herbivores and had no known history of herbivore interaction (Fig. 1a, Table 1), and the one (DL) that under-compensated for herbivory was from a location with no known insect exposure history (Fig. 2a). In three of the overcompensating populations (HG, ZWY and YMC), the shoot mass of damaged plants was significantly higher compared with that of the undamaged plants (Fig. 2b).

The total number of vegetative buds was only affected by herbivory and plant population (Table 2), which did not support our predictions. The total number of vegetative buds was greater (14.57%, $F_{1, 426} = 1.787$, $P = 0.008$) in damaged than in control plants.

The number of root buds was significantly affected by herbivory, plant population and their interaction, whereas the number of root buds was not affected by other factors or their interactions (Table 2), which also failed to support our prediction. The number of root buds of plants from HG, CM, HQ and ZWY populations increased under herbivory, while herbivory did not influence the number of root buds of plants from other populations (Fig. 2c). The number of stem buds

Table 2 A three-way nested ANOVA for the effects of insect exposure history (*Eh*), population (*P*), herbivory (*H*) and their interactions on plant total, root and shoot mass; root to shoot biomass ratio (*R/S*); total number of buds; and numbers of root and stem buds

Source of variation	df	Total biomass		Root mass		Shoot mass		R/S	
		F	P	F	P	F	P	F	P
Exposure history	1, 12	0.058	0.81	0.019	0.89	0.1207	0.73	0.217	0.65
Population [Eh]	12, 402	25.810	**<0.0001**	15.00	**<0.0001**	24.310	**<0.0001**	6.050	**<0.0001**
Herbivory	1, 402	5.060	**0.025**	9.470	**0.002**	1.260	0.26	3.000	0.084
Eh*H	1, 12	3.819	0.075	10.77	**0.006**	1.704	0.22	2.291	0.16
P[Eh]*H	12, 402	3.030	**0.0004**	1.720	0.061	2.880	**0.0008**	1.410	0.16
Error	402								

Source of variation	df	Total no. of buds		No. of root buds		No. of stem buds	
		F	P	F	P	F	P
Exposure history	1, 12	0.0001	0.99	0.072	0.79	0.621	0.45
Population [Eh]	12, 399	9.020	**<0.0001**	7.390	**<0.0001**	2.330	**0.007**
Herbivory	1, 399	6.530	**0.011**	9.640	**0.002**	1.330	0.25
Eh*H	1, 12	0.454	0.51	1.656	0.22	2.006	0.18
P[Eh]*H	12, 399	1.470	0.13	1.800	**0.047**	1.210	0.27
Error	399						

Square brackets indicate nesting of terms

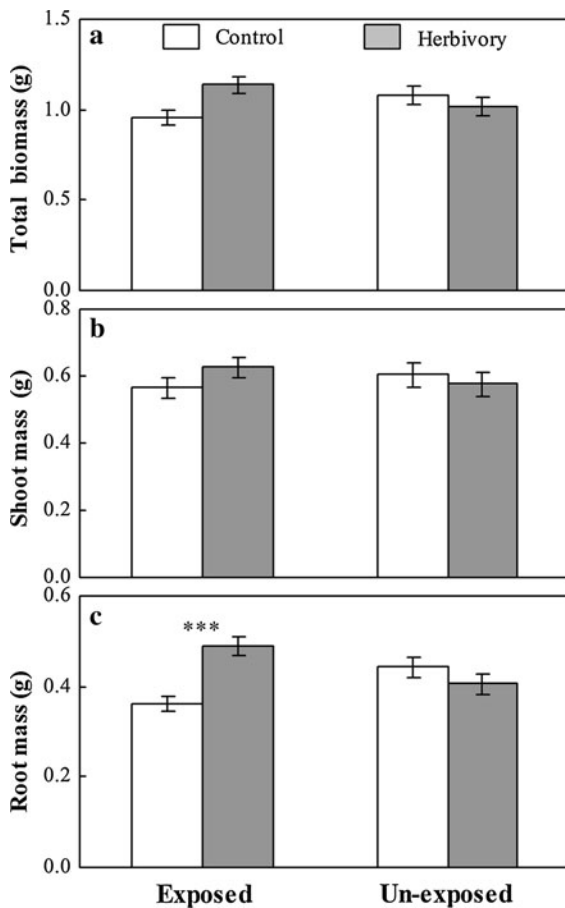Statistically significant values ($P < 0.05$) are in bold

Fig. 1 Effect of herbivory in the greenhouse experiment on **a** total, **b** shoot and **c** root mass of plants exposed or unexposed to herbivores in the field: means across populations. Values are means ±1 SE (back transformed for the total, shoot and root mass). Symbols above pairs of *bars* show probability (*t* test) that the two means did not differ: (no symbol) >0.05; *0.01–0.05; **0.001–0.01; ***<0.001

was affected by plant population and was not affected by other factors or their interactions (Table 2).

Differential effects of previous exposure to different insect species

For the plants with insect exposure history, insect species (previously damaged by native, introduced, or both insects) did not influence plant total biomass, total number of vegetative buds, or numbers of root and stem buds (Table 3). None of the traits were affected by the interaction between herbivory and insect species, while plant total biomass, shoot mass

and R/S were affected by the interaction between herbivory and plant population (Table 3).

Discussion

Compensatory growth can potentially facilitate a plant invasion (Schierenbeck et al. 1994; Wilsey and Polley 2006) and could be a factor that hampers the biological control of exotic plants (Garcia-Rossi et al. 2003). However, this has received little attention (Bossdorf et al. 2005; Müller-Schärer et al. 2004). We examined here the compensatory ability of *A. philoxeroides* populations across its large new range in China. As hypothesized, we found differences in compensatory ability between plants with and without insect exposure history. *A. philoxeroides* populations from locations with insect exposure history accumulated more root mass and showed greater compensatory ability in response to herbivory than populations from locations without insect exposure history. While there was a large inter-population variance, the type of herbivory (*A. hygrophila*, *C. piperata*, or both) was not found to affect the level of compensation.

Differences in compensatory ability between plant populations with different grazing histories have also been reported in *Artemisia ludoviciana* (Damhoureyeh and Hartnett 2002), *Sorghastrum nutans* (Damhoureyeh and Hartnett 2002), *Agropyron smithii* Rydb (Detling and Painter 1983; Polley and Detling 1988) and *Bouteloua curtipendula* var. *caespitosa* (Smith 1998). However, the differing intensities of compensatory response by populations of *A. philoxeroides* with varying herbivory exposure history, and the clonal nature of the plant, suggests that the effect seen here might be due to epigenetic inheritance (McKey et al. 2010; Prentis et al. 2008). Indeed, Gao et al. (2010) reported that genome-wide DNA methylation alternations enable *A. philoxeroides* to adapt to varying water availability rapidly.

In response to long-term herbivory, a plant may display evolutionary or plastic changes in physiology or morphology that may increase compensatory ability, e.g. forming more horizontally-oriented leaves, allocating fewer resources to new leaves or more resources to roots, or storing more reserves belowground (Carman and Briske 1985; Mack and Thompson 1982; McIntire and Hik 2002). For example, ramets of the clonal aquatic plant *Ranunculus lingua*

Fig. 2 Impacts of herbivory in the greenhouse experiment on **a** total and **b** shoot mass, and **c** number of root buds of plants exposed or unexposed to herbivores in the field: means for individual populations. Values are population means ±1 SE (back transformed for the total and shoot mass). Symbols above pairs of *bars* show probability (*t* test) that the two means did not differ: (no symbol) >0.05; *0.01–0.05; **0.001–0.01; ***<0.001
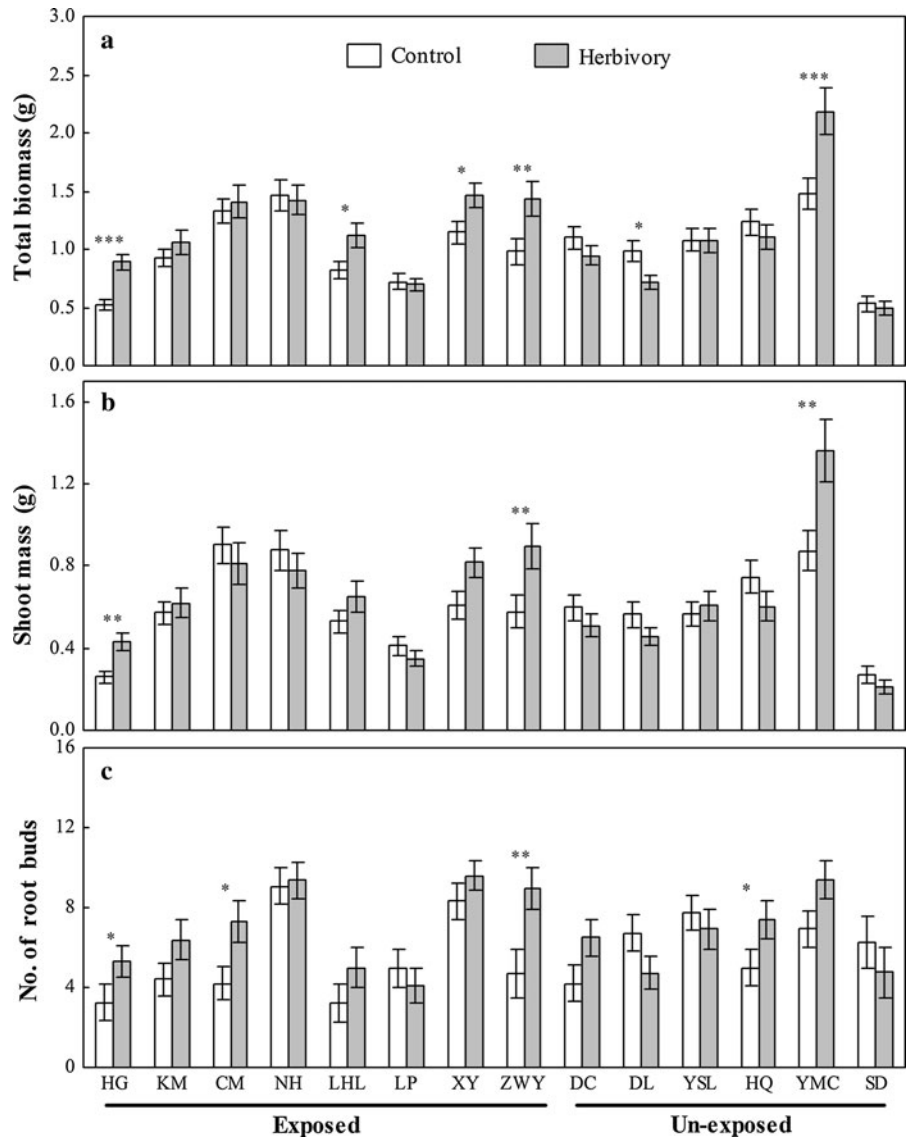
that had experienced substantial herbivory produced larger but fewer rhizomes and experienced less reduction in most growth parameters when exposed to extensive herbivory, in comparison with ramets that had experienced less herbivory (Johansson 1994). The greater compensatory ability of *A. philoxeroides* with insect exposure history compared to plants without insect exposure history may have resulted primarily from increase in root storage mass, which has been reported to be highly correlated with its compensatory ability (Wilson et al. 2007; Lu and Ding 2010).

Our finding that *A. philoxeroides* from five populations (four with and one without herbivory exposure history) over-compensated herbivory provides insights into the plant's physiological potential for compensation. However, whether the plant can overcompensate in response to herbivory under natural field conditions needs further clarification, since a plant's compensation intensity is also influenced by other environmental conditions, including resource availability, time, frequency and intensity of damage, neighbouring plants, and duration of the recovery period (Maschinski and Whitham 1989; Strauss and Agrawal 1999). Schooler et al. (2006, 2007) found that herbivory significantly suppressed the growth of *A. philoxeroides* when the recovery period was just 5 weeks or less.

Table 3 A three-way nested ANOVA for the effects of insect species (*Is*), population (*P*), herbivory (*H*) and their interactions on plant total, root and shoot mass; root to shoot biomass ratio (*R/S*); total number of buds; and numbers of root and stem buds

Source of variation	df	Total biomass		Root mass		Shoot mass		R/S	
		F	P	F	P	F	P	F	P
Insect species	2, 5	0.468	0.65	0.302	0.75	0.514	0.63	0.502	0.63
Population [Is]	5, 241	23.410	**<0.0001**	14.260	**<0.0001**	22.730	**<0.0001**	8.970	**<0.0001**
Herbivory	1, 241	17.390	**<0.0001**	32.820	**<0.0001**	6.170	**0.014**	7.980	**0.005**
Is*H	2, 5	0.013	0.99	0.2007	0.82	0.006	0.99	0.131	0.88
P[Is]*H	5, 241	3.440	**0.005**	1.560	0.17	3.840	**0.002**	2.500	**0.03**
Error	241								

Source of variation	df	Total no. of buds		No. of root buds		No. of stem buds	
		F	P	F	P	F	P
Insect species	2, 5	0.002	0.99	1.051	0.42	0.040	0.96
Population [Is]	5, 241	17.690	**<0.0001**	2.940	**0.013**	14.140	**<0.0001**
Herbivory	1, 241	6.900	**0.009**	3.700	0.056	13.430	**0.0003**
Is*H	2, 5	0.104	0.90	0.518	0.62	0.138	0.87
P[Is]*H	5, 241	2.010	0.078	1.150	0.33	1.670	0.14
Error	241						

Square brackets indicate nesting of terms

Statistically significant values (P < 0.05) are in bold

Our findings may hold broad implications for the biological control of invasive plants. Introducing and releasing natural enemies in some cases may favour, rather than suppress, the growth of target species through increased compensatory response to herbivory—an undesirable outcome. The ability of native herbivores to reduce plant performance and increase the mortality of invasive plants (Maron and Vilà 2001), has prompted the suggestion to use native herbivores as biological control agents (Cronin et al. 1999; Mitchell et al. 2006). However, the compensatory growth of *A. philoxeroides* in response to the native beetle in our study show that even the use of native species may not always result in control. Thus, to improve biocontrol efficacy and avoid potential negative effect of biocontrol agents on native plants, an explicit understanding of the target plant's defence strategy is crucial before approval and introduction of foreign natural enemies, as well as the use of native herbivores.

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