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ORIGINAL PAPER

Flooding compromises compensatory capacity of an invasive plant: implications for biological control

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Abstract Plant compensatory growth is proposed to be insidious to biological control and known to vary under different environmental conditions. However, the effects of microsite conditions on compensation capacity and its indirect impacts on biological control of plant invaders have received little attention. Alligator weed, *Alternanthera phioxeroides*, is an invasive plant worldwide, growing in both aquatic and terrestrial habitats that are often affected by flooding. Biological control insects have been successful in suppressing the plant in many aquatic habitats but have failed in terrestrial habitats. To evaluate the impact of flooding on compensation capacity, we conducted common garden and greenhouse experiments in which plants were grown under different moisture conditions (aquatic versus terrestrial). Our results show that plants were able to fully recover from continued herbivory in the terrestrial habitat, but failed in the aquatic habitat, indicating a flooding-regulated plant compensatory capacity. Also, the grazed plants increased below-ground growth and reproductive root bud formation in the terrestrial habitat, but there was no such difference in the aquatic habitat. Our findings suggest that the differing plant compensatory capacity, affected by flooding, may explain the different biological control efficacy of alligator weed in aquatic and terrestrial habitats. Understanding mechanisms in plant invader compensation in different microsite conditions is important for improving management efficiency.

Keywords Alligator weed · Biological control · Compensatory response · Flooding

Introduction

Invasive species cause economic loss in agriculture and alter native communities in natural ecosystems (Mack et al. 2000). Classical biological control, i.e., introduction and release of nature enemies from the home range of invasive species, is advocated as an economic and sustainable approach for management of invasive species and has been widely used in noxious species management (McFadyen 1998; Moran et al. 2005). However, in practice, the efficiency of biological control is low, only 33% of released agents successfully controlled targets in biological control of weeds (McFadyen 1998). Understanding the reasons for failure in biological control is crucial for improving its efficiency. Many abiotic and biotic factors have been suggested to contribute to the failure (Freckleton 2000; Mcevoy

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and Coombs 1999; Shea et al. 2005). However, the impacts of plant tolerance, which has been reported in many plant invaders (Bossdorf et al. 2005; Müller-Schärer et al. 2004), have received little attention (but see Callaway et al. 2001; Garcia-Ross et al. 2003).

Tolerance is the ability of a plant to relieve negative impacts of herbivory and disease on fitness by compensatory growth and reproduction (Strauss and Agrawal 1999). Mechanisms leading to tolerance include a series of physiological and morphological changes that occur in plants in response to herbivory, ranging from increased photosynthetic ability, activation of dormant meristems, and utilization of stored reserves, to phenological changes and resource reallocation (Stevens et al. 2008; Strauss and Agrawal 1999; Tiffin 2000). Plant tolerance varies from under-compensation, equal-compensation to over-compensation, depending on resource availability, timing and intensity of damage, existence and identity of neighbor plants, activity of below-ground organisms, and duration of recover period (Blouin et al. 2005; Eskelinen 2007; Lennartsson et al. 1998; Mascchinski and Whitham 1989; Paige 1992; Sadras 1996; Tiffin 2002; Wise and Abrahamson 2007).

It is widely acknowledged that tolerance is affected by water availability (Cox and McEvoy 1983; Zhao et al. 2008); however, flooding may compromise the compensatory capacity of a plant in response to herbivory, because flooding restricts the availability of oxygen to plants and adversely affects plant fitness (Lenssen et al. 2004; Pacheco 2001). Also, flooding may alter the composition of soil microbial communities (Graff and Conrad 2005) which then indirectly affect plant performance. Even some plants that are able to grow in both terrestrial and aquatic habitats may show phenotypic changes in morphology and physiology when flooded (Insausti et al. 2001; Julien et al. 1995). For example, the roots of alligator weed, *Alternanthera phioxeroides* Griseb, are relatively short and fine in aquatic habitat, while in terrestrial habitat they are thicker, woody, rhizome-like and longer (Julien et al. 1995). However, little is known about the impact of flooding on plant tolerance.

Native to South America, alligator weed has invaded North America, China, Australia, New Zealand, and even threaten Africa (Julien et al. 1995; Sainty et al. 1998). In its invasive range, it rarely sets seeds but propagates by vegetative means from stem and root buds (Julien et al. 1995). It is able to grow in both terrestrial and aquatic habitats, and the terrestrial form may switch to the aquatic form, and vice versa, depending on flooding level. A host-specific flea beetle, *Agasicles hygrophila*, was introduced to control this noxious weed in America, Australia, and China, but has only been successful in aquatic habitats and has no or limited control in terrestrial habitats, though it can reach high densities in terrestrial habitats (Ma and Wang 2004; Sainty et al. 1998) and significantly defoliate the plant (X. Lu and J. Ding, unpublished). The plant genetic diversity of ecotypes is not considered to be the reason for the different response to herbivory by the beetle (Li and Ye 2006), but Ma and Wang (2004) demonstrated that the beetle's pupation rate was lower in terrestrial habitats than that in aquatic habitats. A recent 5-week laboratory test showed that alligator weed was able to rapidly compensate for damage caused by herbivory and shoot removal (Schooler et al. 2006; Wilson et al. 2007).

Here, to test whether the compensatory capacity of alligator weed is affected by flooding, we set up common garden and greenhouse experiments. Specifically, we propose the following hypothesis: the plant tolerance to herbivory is higher in non-flooding treatments than that in flooding treatments, resulting in the decreased fitness of alligator weed in aquatic habitat, but not in terrestrial habitat, when grazed by *A. hygrophila*.

Methods

Experimental species

Alligator weed is an herbaceous perennial, with horizontal to ascending stems. Plants grow rooted in soil either on land or emerging from shallow water or as floating mats attached to banks. Each stem consists of nodes that are capable of producing roots and new shoots which may become new plants after disconnecting from the mother plant. Both *A. hygrophila* adults and larvae eat leaves, often producing feeding "holes" and "trenches".

Common garden experiment

To test whether compensatory response to herbivore differ between plants grown in terrestrial and aquatic habitats, we carried out a field experiment in both habitats at Wuhan Botanical Garden, Chinese Academy of Sciences in Wuhan, China, from June to October 2006. We collected alligator weed stems from four locations in Yunnan Province: KM (Kunming), AN (Anning), CX (Chuxiong), and DL (Dali) (Table 1). At each location, we collected plants from four sites ($\sim$20 m apart) and considered them as one population. Each population consisted of both terrestrial and aquatic forms. The cut stems were kept moist and cool and were brought to the laboratory within 1 week of collection.

We conducted our terrestrial habitat test with only terrestrial form of alligator weed. We mowed a portion of the field, and 40 plots, each 0.5 × 0.4 m separated by 0.5 m, were established. The plots were weeded of all plants. Similar cut stems were selected (biomass between populations: $F = 0.097$; $P = 0.961$). In late June 2006, ten individuals from the same population were planted vertically per plot and immediately caged to exclude herbivores. Each cut stem was 4–5 cm long with one node. Stems from each population were transplanted into ten plots. Plants were watered and plots were weeded every 2 days. After 20 days, we retained six similar-sized plants for each plot and manually removed the others. Half the plots were assigned to receive insects (herbivory treatment) and the other half as controls without insects.

We conducted our aquatic habitat test in two large cement and brick pools of 8 × 8 × 1 m with water depth of 0.5 m. Twenty plastic tubs, each 0.50 × 0.4 m × 0.30 m deep, were filled with soil and placed in each pool. As above, similar sized stems were chosen (biomass between population: $F = 0.181$; $P = 0.908$) and 100 individuals from each population (aquatic forms) were evenly transplanted into ten tubs and caged in late June 2006. The plants were thinned to six similar-sized plants 20 days later. Half the tubs were assigned to receive the insects and half to receive no insects. The water level in each pool was maintained so that all tubs sat under water.

One newly mating pair of *A. hygrophila* was released onto each herbivory treatment plot or tub in early August 2006. The insects were collected nearby the Wuhan Botanical Garden and cultured in a laboratory on alligator weed for one generation. Adults of the second generation were selected for this experiment. Six weeks later, we harvested each plant and measured stem and root lengths and counted the number of shoots for each plant. Plants were dried at 80°C for 48 h and then weighed. Numbers of adults, egg clusters, pupae, and larvae in each plot and tub were counted and then dried and weighed.

Greenhouse experiment

As the common garden experiment cannot exclude possible effects of plant resistance to herbivory, a

Table 1 Information on plant populations selected for this study

Provinces/populations	Longitude (N)	Latitude (E)	Exposure history[a]	Insect species[b]	Time of introduction[c]
Yunnan					
KM	24°58′36.4″	102°39′58.8″	+	I	1960s–1970s
DL	25°43′17.2″	100°11′31.0″	−		1960s–1970s
AN	24°56′54.7″	102°28′45.6″	−		1960s–1970s
CX	25°03′53.3″	101°30′50.9″	−	I + N	1960s–1970s
Shanghai					
CM	31°34′23.0″	121°30′21.7″	+	N	1930s–1940s
Henan					
XY	32°00′54.9″	114°05′13.6″	+	N	After 1980

Terrestrial and aquatic forms of plants from KM, DL, AN and CX populations were used in the common garden experiment, while only terrestrial form of plants from KM, DL, CM and XY were used in the greenhouse experiment

[a] + denotes signs of defoliation, while − means no detected feeding on plants during 2006–2007 field surveys

[b] *I* refers to the introduced biocontrol agent, *Agasicles hygrophila*; *N* indicates that feeding was by native insects, mostly the beetle, *Cassida piperata*; *I* + *N* denotes herbivory on the plant by both native and introduced insects

[c] The earliest time when the plant occurred, as determined from the literature and herbarium specimens

greenhouse experiment was performed in 2007 from April to early December to further test tolerance when flooded or not. Since there were no differences among DL, CX, and AN populations in their response to herbivory in the 2006 common garden experiment, only one (DL) of these populations was tested in the greenhouse experiment, together with the KM population. To better understand alligator weed tolerance, we included two more populations (XY and CM); thus, each of the four (KM, DL, XY, and CM) had distinct invasion and exposure histories to insects (more detailed information for each population see Table 1).

In early spring 2007, plants were sampled at four sites (~ 20 m apart) from each population. All plants were collected from terrestrial habitats such as river bank and farmland and kept cool and moist during transportation to the laboratory. The stems were cut to similar size (length of 4–5 cm) with one node for each and planted vertically in plastic containers filled with a mixture of peat, soil and sand (1:1:1) and caged immediately to exclude herbivores. These plants were grown in identical condition for two and a half months to remove maternal effects before selected stems were used in the experiment.

The experiment was performed in a greenhouse at the Wuhan Botanical Garden from April to early December 2007, where average temperatures were between 20 and 35°C from late April to September and 25–15°C from October to early December. Three stems selected randomly from the same population were planted vertically in a 16-cm-diameter pot, 2/3 filled with a mixture of peat, soil and sand, ratio 1:1:1. Half the pots for each population were randomly selected for the flooding treatment and were kept filled with water. During the entire period of the experiment, all plant roots and the lower portion of the stems were submerged in the flooding treatment group. The other pots (non-flooding treatment) had three 1-cm-diameter holes cut in their bottoms to allow drainage, thus plant stems and roots were never submerged. Plants were watered every 2 days. After 20 days, to minimize plant size variation, we selected and only kept one similar sized plant in each pot. Twenty days later, insects were added to the herbivory treatment plants.

For each population in each flooding treatment, half the plants received insects (herbivory treatment) and half were controls without insects. Two days before herbivory treatment, half the shoots for each plant were caged. In the insect treatment, six to eight *A. hygrophila* adults were released into each cage. After all the caged shoots were defoliated (in 7 days), the insects and cages were removed. The number (replicates) of grazed (with insect) or ungrazed plants (no insect) in each population varied from 17 to 23 due to availability. Plants were then allowed to grow for an additional 80 days after cessation of grazing. Each month, the pots were randomly rearranged. We counted the number of shoots and measured the primary stem length on 6 October and again on 5 December, when we harvested the plants. We counted the number of leaf and root buds and measured root length, then separated and dried the above and below ground parts at 85°C for 48 h before weighing.

Statistical analysis

To evaluate the effects of herbivory, habitat and their interaction on plant performance in the common garden experiment, a three-way mixed ANOVA was conducted, where the model included herbivore and habitat as fixed effects and plant population as random effect. When the interactive effects of habitat, herbivory and plant population were significant, two-way ANOVAs were conducted using the data of terrestrial or aquatic tests, where the model included herbivore and plant population as fixed effects. A two-way ANOVA was performed to test whether there were variations in the total number and biomass of insects between habitats and among plant populations. This model included plant population and habitat as fixed effects. When ANOVA indicated a significant effect, further tests for differences were made using Bonferroni post hoc multiple comparisons ANOVA.

To evaluate the effects of herbivory, flooding and their interaction on plant vegetative and reproductive characters in the greenhouse experiment, a three-way mixed ANOVA was conducted, where the model included herbivore and flooding as fixed effects and plant population as random effect. Since the interactions between plant population with other effects were non-significant, we removed the interactions including population from the model. The effects of time on the number of shoots and stem length were analyzed using repeated ANOVA. Root and shoot biomass ratio (R/S) was log-transformed to improve normality and reduce heterogeneity of variances. When ANOVA indicated a significant effect further tests for differences were made using Bonferroni post hoc multiple comparisons ANOVA.

Results

Common garden experiment

Effects of herbivory and habitats on plant performance

There were significantly interactive effects between herbivory and habitat on plant biomass and the lengths of the primary stems and roots (Table 2). In the terrestrial habitat, plant biomass, the number of shoots, and the lengths of primary stems and primary roots were not affected by insect feeding (Fig. 1). In the aquatic habitat herbivory significantly reduced plant biomass (Fig. 1a) and stem length (Fig. 1c), while the number of shoots and root length were not affected (Fig. 1).

Plant populations varied in response to herbivory between habitats, indicated by the significantly interactive effects of herbivory × plant population × habitats on the primary root length (Table 2). In the terrestrial habitat, the plant's primary root length was significantly affected by the interaction between plant population and herbivory (two-way ANOVA result: $F_{3,29} = 6.127, P = 0.002$). The primary root length of plants from KM population, which has been exposed to herbivore for 20 years, was significantly increased when grazed (grazed 19.739 ± 1.452 cm vs ungrazed 12.017 ± 1.298 cm. $F_{1,9} = 14.131$, $P = 0.007$), while those of plants from other populations were neutrally affected (for all $P > 0.05$) in terrestrial habitats. However, in aquatic habitats, the interaction between population and herbivory was not significant (two-way ANOVA result: $F_{3,31} = 0.336, P = 0.800$).

Insect population on plants in both habitats

The number and biomass of insects on plants per plot did not vary among population origins (KM, AN, CX, and DL) and habitats (terrestrial and aquatic) (Fig. 2). There were no significant interactive effects between plant population and habitat on insects' performance.

Table 2 Effects of herbivory, habitat and their interaction on plant performance in the common garden experiment (three-way mixed ANOVA results)

Source	*df*	MS	*F*	*P*
Biomass				
Habitat	1, 62	589.508	130.959	<0.001
Herbivory	1, 62	0.011	0.002	0.961
Population	3, 62	18.773	4.170	0.009
Ha × He	1, 62	20.600	4.576	0.036
Ha × P	3, 62	21.970	4.881	0.004
He × P	3, 62	5.461	1.213	0.312
Ha × P × He	3, 62	10.839	2.408	0.076
No. of shoots				
Habitat	1, 60	5,191.830	398.402	<0.001
Herbivory	1, 60	39.816	3.055	0.086
Population	3, 60	52.984	4.066	0.011
Ha × He	1, 60	27.759	2.130	0.150
Ha × P	3, 60	52.200	4.006	0.011
He × P	3, 60	14.345	1.101	0.356
Ha × P × He	3, 60	32.188	2.470	0.071
Stem length				
Habitat	1, 60	517.052	2.070	0.155
Herbivory	1, 60	4,229.314	16.931	<0.001
Population	3, 60	116.691	0.467	0.706
Ha × He	1, 60	1,731.807	6.933	0.011
Ha × P	3, 60	107.467	0.430	0.732
He × P	3, 60	99.448	0.398	0.755
Ha × P × He	3, 60	308.549	1.235	0.305
Root length				
Habitat	1, 60	645.106	134.698	<0.001
Herbivory	1, 60	8.365	1.747	0.191
Population	3, 60	4.575	0.955	0.420
Ha × He	1, 60	42.960	8.970	0.004
Ha × P	3, 60	10.188	2.127	0.106
He × P	3, 60	21.225	4.432	0.007
Ha × P × He	3, 60	13.531	2.825	0.046

Greenhouse experiment

Effects of flooding on plant fitness

Flooding greatly reduced plant biomass by 60.7% and decreased the proportion of resources invested in below-ground tissues compared to non-flooding treatment. The number of shoots, the lengths of primary stems and primary roots also decreased significantly ($P < 0.001$ for all) when flooded. Flooded plants only

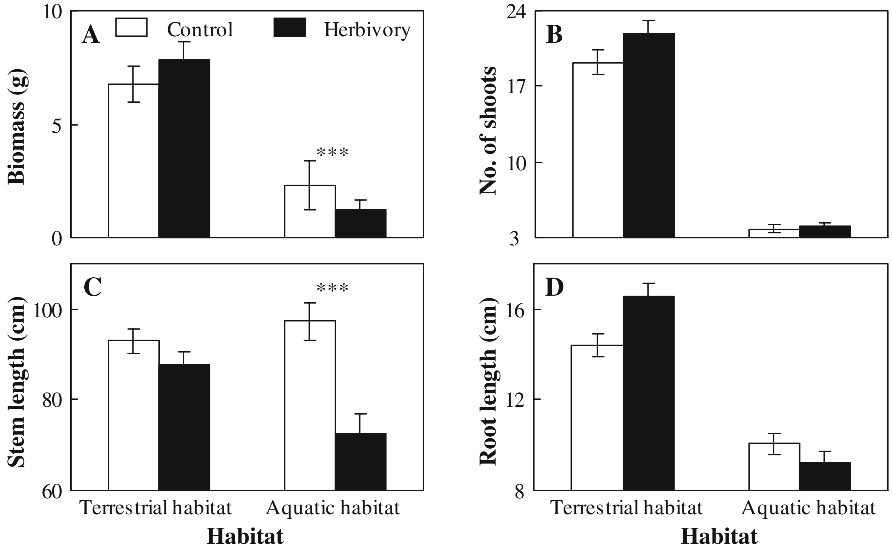

Fig. 1 Effects of herbivory on traits of alligator weed: biomass (**a**), number of branches (**b**), the primary stem and root length (**c** and **d**, respectively) in terrestrial and aquatic habitats in the common garden experiment. *Bars* indicate ±1SE. Significant differences in one-way ANOVA Bonferroni correction are indicated as follows: ***$P < 0.001$

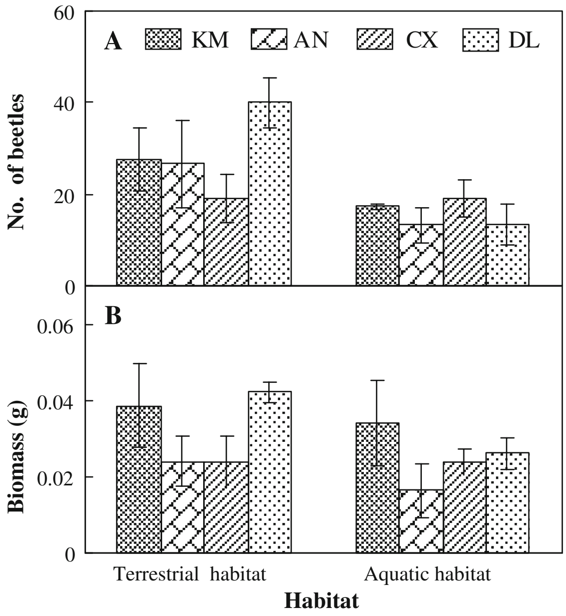

Fig. 2 Number (**a**) and biomass (**b**) of beetles per plot on plants from *KM*, *AN*, *CX* and *DL* populations in terrestrial (*left hand graphs*) and aquatic (*right hand graphs*) habitats. *Bars* indicate ±1SE

produced 33.3% vegetative buds and 8.08% root-buds of those of non-flooded plants.

Interactions between herbivory and flooding

Flooding impaired plant compensatory ability significantly in the greenhouse experiment. In the non-flooding treatment group, grazed plants produced 25.7% more biomass than ungrazed plants ($F_{1,123} = 10.833$, $P = 0.01$) suggesting an over-compensatory response to herbivory. However, no differences in biomass were found between grazed and ungrazed plants in the flooding treatment ($F_{1,134} = 1.284$, $P = 0.259$), indicating an equal-compensatory response (Fig. 3a).

Defoliation significantly decreased root length when flooded ($F_{1,105} = 7.389$, $P = 0.008$), but there was no change in the non-flooding treatment ($F_{1,138} = 0.115$, $P = 0.735$), as implicated by a significant herbivory × flooding interaction (Table 3; Fig. 3e). However, flooded plants did not suffer more than non-flooded plants in terms of the number of shoots and primary stem length, indicated by a non-significant herbivory × flooding interaction (Table 3; Fig. 3c, d).

Plant resource allocation pattern (indicated by R/S) was also affected by the interaction between herbivory and flooding (Table 3). Grazed plants invested 23.4% more biomass in below-ground growth than ungrazed plants in the non-flooding treatment group ($F_{1,134} = 10.223$, $P = 0.002$), but there was no such difference in the flooding treatment ($F_{1,129} = 0.036$, $P = 0.850$; Fig. 2b). The number of vegetative buds was not influenced by the interaction between herbivory and flooding (Table 3). However, in the non-flooding treatment grazed plants produced 51.4% more root buds following defoliation, compared to ungrazed plants, but there was no such difference in the flooding treatment group (Fig. 3g).

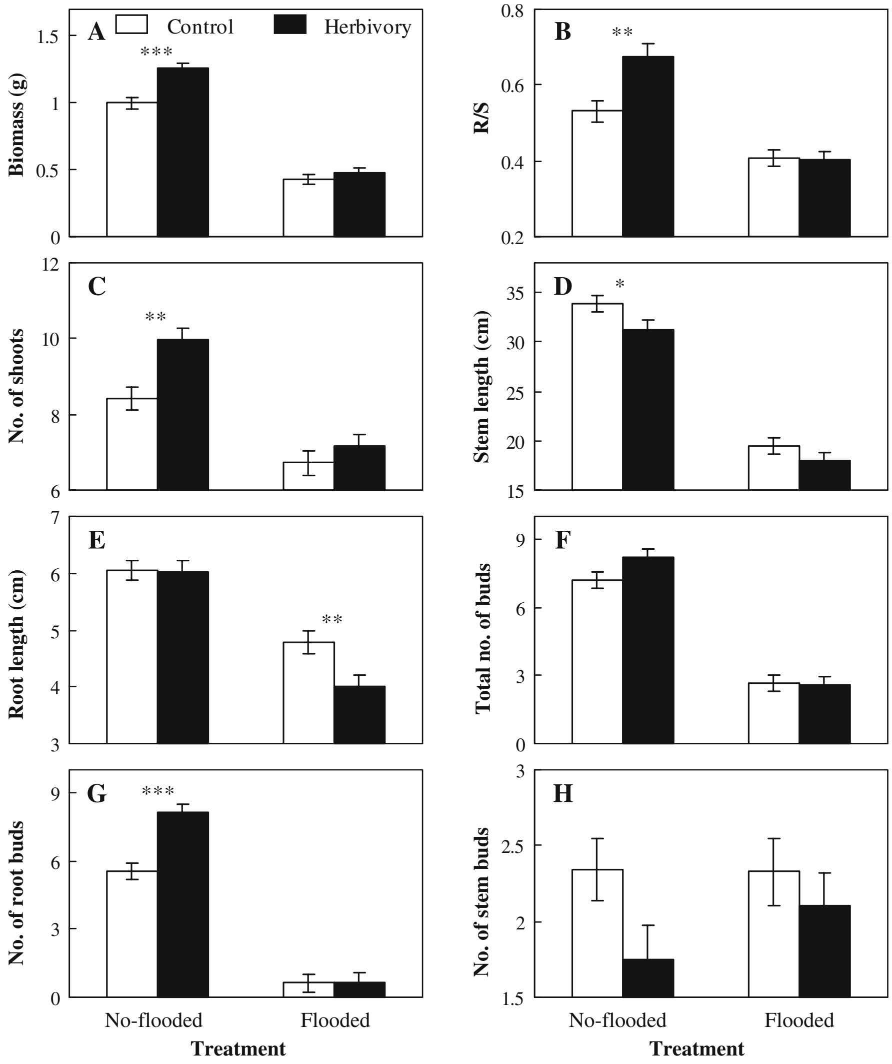

Fig. 3 Effects of herbivory on traits of alligator weed: biomass (**a**), root and shoot biomass ratio(R/S) (**b**), number of shoots (**c**), primary stem and root length (**d** and **e**, respectively), the total number of buds (**f**) and that formed below- and above-ground (**g** and **h**, respectively) when flooded and non-flooded in the greenhouse experiment. *Bars* indicate ±1SE. Significant differences in one-way ANOVA Bonferroni correction are indicated as follows: $^{**}P < 0.01$, $^{***}P < 0.001$

Discussion

As we expected for the common garden experiment, herbivory by *A. hygrophila* did not affect the fitness of alligator weed in the non-flooding treatments (terrestrial habitat), i.e., grazed plants accumulated similar biomass as un-grazed plants. In contrast, in the aquatic habitat, all variables of plant growth were significantly reduced by herbivory. In our greenhouse experiment, the non-flooded, grazed plants accumulated markedly more biomass than ungrazed plants, whereas grazed plants failed to recover from herbivory when flooded. Together, these results indicate that the impact of herbivory on alligator weed was magnified by flooding, which is consistent with the current distinct efficiency of biological control against alligator weed, i.e., it succeeds in aquatic habitats while it fails in terrestrial habitats. Schooler et al. (2006) and Wilson et al. (2007) also reported that alligator weed could accumulate similar biomass as undamaged plants when damaged by mowing and herbivory in terrestrial habitat in their laboratory test.

In response to herbivory, alligator weed expressed significantly different compensatory capacity between habitats, i.e., higher tolerance in terrestrial habitats than in aquatic habitats, as indicated clearly in our greenhouse experiment. Alligator weed even showed an over-compensatory response to herbivory when non-flooded, because the grazed plants produced more biomass than ungrazed plants. It is not surprising that non-flooded plants from all populations over-compensated in the greenhouse experiment, while plants did

Table 3 Effects of flooding, herbivory and their interaction on plant performance in the greenhouse experiment (three-way mixed ANOVA results, where the non-significant interactions including plant population were removed from the model)

Source	*df*	MS	*F*	*P*
Biomass				
Flooding	1, 254	29.610	296.452	<0.001
Herbivory	1, 254	1.543	15.450	<0.001
Population	3, 254	1.257	12.582	<0.001
$F \times H$	1, 254	0.697	6.977	0.009
R/S				
Flooding	1, 260	1.711	49.351	<0.001
Herbivory	1, 260	0.110	3.178	0.076
Population	3, 260	0.114	3.302	0.021
$F \times H$	1, 260	0.156	4.512	0.035
No. of shoots				
Flooding	1, 474	601.936	55.225	<0.001
Herbivory	1, 474	120.904	11.092	0.001
Population	3, 474	51.930	4.764	0.003
$F \times H$	1, 474	36.724	3.369	0.067
Survey time	1, 474	4.607E-02	0.004	0.948
Stem length				
Flooding	1, 480	23,328.743	298.806	<0.001
Herbivory	1, 480	539.237	6.907	0.009
Population	3, 480	717.532	9.191	<0.001
$F \times H$	1, 480	35.146	0.450	0.503
Survey time	1, 480	12.775	0.164	0.686
Root length				
Flooding	1, 240	161.868	71.475	<0.001
Herbivory	1, 240	9.758	4.309	0.039
Population	3, 240	17.173	7.583	<0.001
$F \times H$	1, 240	9.225	4.073	0.045
Total no. of buds				
Flooding	1, 256	1,657.470	192.876	<0.001
Herbivory	1, 256	14.057	1.636	0.202
Population	3, 256	30.532	3.553	0.015
$F \times H$	1, 256	15.630	1.819	0.179
No. of root buds				
Flooding	1, 276	2,632.384	236.363	<0.001
Herbivory	1, 276	119.832	10.760	0.001
Population	3, 276	47.869	4.298	0.006
$F \times H$	1, 276	112.854	10.133	0.002
No. of leaf buds				
Flooding	1, 276	1.998	0.609	0.436
Herbivory	1, 276	11.661	3.551	0.061
Population	3, 276	5.280	1.608	0.188
$F \times H$	1, 276	2.360	0.719	0.397

not over-compensate in the terrestrial habitat in the common garden experiment. Over-compensation has been known to be environmentally dependent. Upon competition or when the resource is limited, the compensation capacity may be decreased (Strauss and Agrawal 1999). There was no competition in our greenhouse experiments as only one plant grew in each pot. Also, an extended period of recovery and high resource availability may contribute to plants over-compensation as suggested by Mascchinski and Whitham (1989) and Sadras (1996).

Considering the result of the common garden experiment, we cannot rule out the possible effects of resistance by the plant in response to herbivory. However, the variations in plant performance between habitats most likely resulted from their different tolerance other than resistance. Plant resistance usually has negative effects on insect fitness while tolerance does not (Espinosa and Fornoni 2006). If there were variations in resistance, the biomass and number of insects in the two habitats should have been significantly different. However, at the end of the trial, we did not detect such differences. Fu et al. (2007) reported that there was no difference in the growth rate of insects when *A. hygrophila* fed on different ecotypes of alligator weed, and the insect accumulated similar amount of biomass when it consumed similar leaf areas of different ecotypes.

Several tolerance traits, for example, plant resource allocation between above- and below-ground growth, may lead to plant recovery from herbivory damage (Rosenthal and Kotanen 1994; Stevens et al. 2008). In our study, when grazed, alligator weed increased the proportion of resources allocated to below-ground growth in terrestrial habitat. Schooler et al. (2006) demonstrated that when shoots were removed, alligator weed quickly reallocated root resources to shoot growth to ensure photosynthetic capacity, and then increased root growth to ensure resource uptake. Alligator weed is known not to set seeds but to propagate by vegetative means from stem and root buds in the invasive ranges (Julien et al. 1995). In the greenhouse experiment, non-flooded, grazed plants formed more root buds, while the total number of buds remained unchanged. The strategy of allocating more resource to below-ground allows many weeds to overcome defoliation and benefits weeds by limiting further defoliation (Sadras 1996).

Why did alligator weed fail to compensate herbivory in aquatic habitat? Plants' compensatory capacity depends on the ability of plants to overcome physical constraints imposed by abiotic and biotic factors (Mascchinski and Whitham 1989; Paige 1992). Flooding in our study system may play a key role in the magnitude of tolerance. We found that herbivory induced increasingly vigorous root growth of alligator weed in terrestrial habitats compared to aquatic habitats. Unlike aquatic habitats, terrestrial habitats may provide more and faster nutrient paths to compensate herbivory in alligator weed. When the plant grows in water, it usually stands vertically. Thus, we assume that it gains nutrients mainly from its primary root. However, when the plant lives in terrestrial habitats, it grows horizontally and generates roots from each node, allowing the plant to absorb nutrients from more sources. Our assumption about how it grows is consistent with a previous report that, when alligator weed shoots were manually removed, resources were quickly allocated to root growth and shortly after above-ground biomass increased to the similar level with that of plants with no shoots removed (Schooler et al. 2006).

We only subjected the terrestrial form of alligator weed to terrestrial and flooded conditions in the greenhouse experiment. Further tests are warranted to investigate whether plants from flooded habitats show similar or different effects when they are subjected to terrestrial and flooded conditions. For example, if there is a carry-over effect of herbivory on compensation capacity in alligator weed, then the terrestrial forms will express a stronger compensatory capacity than their aquatic counterparts. Phenotypic carry-over effects, such as those caused by clipping, light exposure or nutrient levels, usually last for the lifetime of the offspring, or even into more than two seasons and generations (Bullock et al. 1993; Gratton and Denno 2003).

In our experiments, flooded plants performed less well than non-flooded plants. The result is in contrast to that of a previous experiment conducted by Geng et al. (2007). They compared growth characters of alligator weed in aquatic and terrestrial habitats and found plants from three out of four populations grew better in aquatic habitat. This difference may come from the different root morphology. In their study, young plants were flooded during the stage when storage roots were forming, but in our study 4–5 cm clones with one node were immediately flooded after planting and the plants only formed thin roots during this experiment. This may have led to limited resource storage and uptake ability and cause the poorer performance. Both these two situations may happen in the wild, depending on the plant conditions (young plants with shoots and roots vs single clones with only one node) and the time of flooding.

Our results suggest that differing plant compensatory capacity affected by flooding may explain the different biological control efficacy of alligator weed in aquatic and terrestrial habitats. Previous studies also indicated that flooding facilitated the management of the invader *Tamarix ramosissima* (Sher et al. 2000) and *Spartina alterniflora* (Wang et al. 2008). In China, alligator weed mainly distributes along middle and downstream of the Yangtze River. Because of increasing human activities, global climate change and decreasing water-level in many ponds, lakes and rivers in this area, more and more areas invaded by the weed have switched from aquatic habitats to semi-aquatic or terrestrial habitats in recent decades (Gemmer et al. 2008; Li et al. 2007). For example, in the past 150 years, the area of Dongting Lake, in the middle-stream of the Yangtze river, has decreased from 6,000 to 2,625 km^2 (Tao and Cai 2007). Accordingly, aquatic forms of alligator weed in these areas have switched into terrestrial forms that have higher tolerance to insect feeding. Thus, we anticipate that biological control against alligator weed will become less efficient in the future in this area in China.

With the expectation that top-down regulation impacts of herbivory would reduce fitness and competition ability of exotic weeds, natural enemies were widely introduced and released for invasive species management (McFadyen 1998). However, in practice, the failure rate is high (McFadyen 1998), and abiotic and biotic reasons were proposed to explain it (Freckleton 2000; Mcevoy and Coombs 1999; Shea et al. 2005). Recently, plant compensatory capacity has received increasing attention and a body of literature suggests that some plant invaders have efficient compensatory capacity to endure herbivory by biological control agents (Callaway et al. 2001; Garcia-Ross et al. 2003). In some cases, damage by released agents improved plant performance and competitive capacity, contrary to expectation (Callaway et al. 1999). However, all such studies were conducted in simple environmental conditions and ignored the complexity of natural conditions, where exotic plant species are distributed in environments that vary in light, nutrients, water, herbivory, and plant competition. Our results illustrated that flooding compromised the compensatory capacity of alligator weed and benefited biological control. Other environment stresses (i.e., drought, herbicide, low resource availability) can also compromise plant compensatory capacity and improve the efficiency of biological control. For example, the biological control agent *Ceutorhynchus litura* has no impact on fitness of the invader Canada thistle, due to its ability to re-grow from its extensive deep, creeping root system. However, when combined with herbicide or drought stress, the insect significantly suppressed its root growth (Collier et al. 2007). Julien et al. (1987) reported that the invader *Salvinia molesta* can compensate damage caused by herbivore *Cyrtobagous salviniae* only at high levels of nitrogen availability. Our findings, collaborated by others, suggest that understanding mechanisms leading to plant compensation, and the impacts of microsite conditions on compensation, are important for improving efficiency of biological control.

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