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ORIGINAL ARTICLE

Effects of generalist herbivory on resistance and resource allocation by the invasive plant, *Phytolacca americana*

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Abstract Successful invasions by exotic plants are often attributed to a loss of co-evolved specialists and a re-allocation of resources from defense to growth and reproduction. However, invasive plants are rarely completely released from insect herbivory because they are frequently attacked by generalists in their introduced ranges. The novel generalist community may also affect the invasive plant's defensive strategies and resource allocation. Here, we tested this hypothesis using American pokeweed (*Phytolacca americana* L.), a species that has become invasive in China, which is native to North America. We examined resistance, tolerance, growth and reproduction of plant populations from both China and the USA when plants were exposed to natural generalist herbivores in China. We found that leaf damage was greater for invasive populations than for native populations, indicating that plants from invasive ranges had lower resistance to herbivory than those from native ranges. A regression of the percentage of leaf damage against mass showed that there was no significant difference in tolerance between invasive and native populations, even though the shoot, root, fruit and total mass were larger for invasive populations than for native populations. These results suggest that generalist herbivores are important drivers mediating the defensive strategies and resource allocation of the invasive American pokeweed.

Key words evolution of increased competitive ability; generalist; *Phytolacca americana* L.; resistance; tolerance; resource allocation

Introduction

The successful invasion of some exotic plants is often attributed to release from their specialist natural enemies of home ranges (Enemy Release Hypothesis, ERH) (Maron & Vilà, 2001; Keane & Crawley, 2002). Under the selective pressure of novel herbivory, exotic plants may re-allocate resources from defense toward traits conferring increased competitive ability, such as growth and reproduction (Evolution of Increased Competitive Ability Hypothesis, EICA) (Blossey & Nötzold, 1995). Over the last two decades, these hypotheses have been extensively tested and many studies have demonstrated that the loss of specialists is the major cause of some plant invasions (Blair & Wolfe, 2004; Stastny *et al.*, 2005; Huang *et al.*, 2012a). In spite of the fact that some generalists also have profound effects on plant defense, growth and reproduction (Ali & Agrawal, 2012; Stam *et al.*, 2014), the impacts of generalists on plant invasions are largely neglected and little research has been conducted on the effects of an altered generalist community on the resource allocation of invasive plants (Müller-Schärer *et al.*, 2004; Callaway & Maron, 2006; Inderjit, 2012; Prior *et al.*, 2015).

Emerging evidences have shown that invasive plants are not completely released from insect herbivores, and that they may in fact encounter a new suite of generalists in the introduced range (Keane & Crawley, 2002; Colautti *et al.*, 2004; Verhoeven *et al.*, 2009; Bezemer *et al.*, 2014). Thus, the success of a plant invasion may be

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in part determined by the diversity and density of generalists in the introduced range. So far, while several studies have compared plant performance and generalist damage between invasive and native populations of a single invasive plant, these have only examined the effects of one or a few generalists (Leger & Forister, 2005; Caño *et al.*, 2009; Schaffner *et al.*, 2011; Huang *et al.*, 2012b; Liao *et al.*, 2014). In such cases, it is difficult to evaluate the impact of generalist herbivores on plant invasion since only one or a few generalists chosen haphazardly cannot represent the effect of the whole generalist community. Community-level studies of generalists in the introduced range will help us better understand the impact of diversity and density of generalists on plant invasion.

Plants generally defend against herbivores with two strategies, resistance and tolerance. Resistance is any plant trait that reduces the preference or performance of herbivores, while tolerance is the ability of the plant to withstand a given amount of damage without a corresponding reduction in fitness (Agrawal, 2007; Núñez-Farfán *et al.*, 2007; Turley *et al.*, 2013). Previous studies examining the impact of generalists on plant defensive strategies have mainly focused on resistance (Caño *et al.*, 2009; Schaffner *et al.*, 2011; Liao *et al.*, 2014). Emerging studies have found that the selective pressure imposed by generalists may be strong enough to also affect tolerance, and this tolerance may play a role in the plant invasion (Müller-Schärer *et al.*, 2004; Bossdorf *et al.*, 2005; Chun *et al.*, 2010). However, few studies to date have addressed both resistance and tolerance of invasive plants to generalist herbivores simultaneously (but see Huang *et al.*, 2010).

American pokeweed (*Phytolacca americana* L.) is a large herbaceous perennial plant in the family of Phytolaccaceae. Native to North America, it has been introduced into South America, Europe, Africa and Asia (Aweke, 2007). American pokeweed was introduced in China for medicinal and ornamental purposes over 80 years ago (Xu *et al.*, 2006). In recent years, it has become severely invasive in many regions of China (Fu *et al.*, 2012; Ma, 2014). The plant is extremely toxic to humans and livestock since all parts of plant contain saponins and oxalates (Lampe & McCann, 1985; Ma *et al.*, 2014; Zhang *et al.*, 2014). In North America, American pokeweed is attacked by many generalist herbivores such as eggplant flea beetle (*Epitrix fuscula* Crotch), tobacco flea beetle (*Epitrix hirtipennis* Melsheimer), potato flea beetles (*Epitrix subcrinata* Lec.) (Carter *et al.*, 1994; Brust, 2008), armyworms (*Spodoptera eridania* Stoll and *Persectania ewingii* Westwood) (Capinera, 1999; Eastman, 2003) as well as giant leopard moth (*Hypercompe scribonia* Stoll) (Hall, 2014). In China, little research has gone into identifying the species and abundance of insects on this plant. However, in a previous field survey we found that Americana pokeweeds are mainly attacked by foliar insects (e.g. caterpillars and beetles), which produce holes and scars on the leaves. In addition, generalists associated with the congener plant Indian pokeweed (*Phytolacca acinosa* Roxb.), which is native to China, also feed on American pokeweed (W. Huang, personal observation).

In this study, we examined the impact of generalist herbivores on American pokeweed invasion by comparing plant defense (resistance and tolerance) and performance (growth and reproduction) between invasive populations from China (hereafter CHN) and native populations from the United States of America (hereafter USA) under natural herbivory in the introduced range. Specifically, we sought to determine whether invasive and native populations exhibit different defensive strategies when exposed to natural generalist herbivory, and whether invasive populations exhibit greater growth and reproduction than native populations.

Materials and methods

Seeds and seedlings

In September 2011, seeds of American pokeweed were collected from nine populations across southern China (invasive populations) and nine populations across the eastern United States (native populations) (Table 1). For each population, seeds were collected from 10 to 15 randomly selected individuals, which were at least 10 m apart. Seeds were air-dried and stored at room temperature. In early April 2012, these seeds were sown separately into seed trays (50 cells/tray) and maintained in an unheated greenhouse at Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, China (30.53° N, 114.40° E). Four weeks later, seedlings were transplanted individually into pots (height 12 cm, diameter 9 cm) containing a mixture of field soil and sphagnum peat moss (1 : 1) and were randomly arranged in the same greenhouse. Seedlings were watered every 2 days and their positions re-arranged every week until the beginning of the experiment.

Common garden experiment

To examine the impacts of generalists on the resistance, tolerance, growth and reproduction of American pokeweed from invasive and native populations, a common garden experiment was conducted in a field at Wuhan Botanical Garden, which is surrounded by fields of various vegetable crops such as eggplant and potato. Such environmental conditions are the typical habitat that American pokeweed invades in China, and generalists from nearby vegetable fields can easily feed on American

Table 1 Geographical locations of the invasive (China) and native (United States) *Phytolacca americana* populations used in this study. For each population, the numbers of surviving plants at the end of the growing season in insecticide or non-insecticide treatment are given.

ID	Site of seed collection	Latitude	Longitude	Insecticide	Non-insecticide
Invasive	China				
GX-1	Guilin, Guangxi	25.3° N	110.3° E	6	5
GZ-1	Guiyang, Guizhou	26.7° N	106.5° E	6	6
JX-1	Pingxiang, Jiangxi	27.5° N	114.2° E	6	5
HN-1	Xiangtan, Hubei	27.8° N	112.9° E	6	6
HB-1	Xianning, Hubei	29.9° N	114.3° E	6	5
HB-2	Suizhou, Hubei	31.7° N	113.4° E	6	6
HB-3	Shiyan, Hubei	32.1° N	110.7° E	6	6
SC-1	Ermeishan, Sichuan	29.5° N	103.7° E	5	5
SC-2	Dujiangyan, Sichuan	31.0° N	103.6° E	6	6
Native	United States				
FL-1	Ona, Florida	27.4° N	81.9° W	6	5
FL-2	Citra, Florida	29.4° N	82.2° W	6	6
FL-3	Dairy, Florida	29.8° N	82.4° W	4	6
FL-4	Jacksonville, Florida	30.3° N	81.5° W	6	6
GA-1	Madison, Georgia	33.6° N	83.5° W	6	6
GA-2	Athens, Georgia	33.9° N	83.2° W	5	4
GA-3	Gainesville, Georgia	34.3° N	83.9° W	6	6
NJ-1	Flanders, New Jersey	40.8° N	74.8° W	5	5
NY-1	Richford, New York	42.4° N	76.2° W	4	5

pokeweed. These generalist herbivores mainly include caterpillars and beetles, which feed on the leaves and produce irregular holes (W. Huang, personal observation). The experiment was established as a 2 × 2 × 9 full factorial design incorporating two levels of generalist herbivory (insecticide-based insect exclusion *vs*. non-insecticide control), two plant origins (invasive *vs*. native ranges), and nine plant populations per range (Table 1). There were six replicates for each combination (for a total of 216 plants).

In early June, similar-sized plants were selected with an average plant height of 27.2 ± 0.8 cm for invasive populations and 28.2 ± 0.7 cm for native populations ($F_{1,16} = 0.18$, $P = 0.67$, nested analysis of variance [ANOVA]). Then, pots were removed and plants were transplanted to one of six plots (2.5 × 5 m), separated from adjacent plots by 2 m wide strips. Within each plot, 36 plants (two plants each per 18 plant populations) were randomly planted (nine rows of four plants), spaced 0.5 m from each other, with plants from invasive populations neighboring plants from native populations. After transplanting, three plots randomly assigned to the insecticide treatment were sprayed with a broad-spectrum insecticide (esfenvalerate, trade name: Asana XL, DuPont Agricultural Products, Wilmington, DE, USA) twice per month. A previous study has indicated that esfenvalerate is effective at reducing generalist herbivory while having little effect on plant growth (Siemann & Rogers, 2003a). The other three plots served as a control and were sprayed with an equal amount of water. During the experiment, the plants were watered every 1–3 days. In early September, the number of damaged leaves and the total number of leaves were recorded for each plant. Then, one damaged leaf was randomly selected from each plant in the non-insecticide treatment and leaf-damage area was measured using Digimizer software (MedCalc Software bvba; Mariakerke, Belgium). Fruits and shoots were harvested, and roots were carefully removed from the soil and washed with pressurized water. The fruits, shoots and roots of each plant were dried separately (60 °C for 96 h) and weighed (to the nearest 0.1 g).

Statistical analyses

To examine the difference in plant resistance to herbivory between invasive and native populations, two-way mixed ANOVAs were performed on absolute and relative leaf damage. The absolute leaf damage was estimated by the number of damaged leaves for each plant and the relative leaf damage was calculated as the number of damaged leaves / the number of total leaves × 100% for each plant. Higher leaf damage indicated lower resistance. Models included plant origin (invasive *vs.* native), herbivory level (insecticide *vs.* non-insecticide) and their interaction as fixed effects and plant populations (nine populations per range) nested within origin as the random effect. Where significant terms were present, least square means *post hoc* tests were conducted using the LSMEANS CONTRAST statement in Proc MIXED. The leaf-damaged area was analyzed using nested ANOVA with origin (invasive *vs.* native) as fixed effect and plant populations (nine populations per range) nested within origin as the random effect. To examine the difference in tolerance to herbivory between invasive and native populations, a series of regressions was performed. In these regressions, the origin and origin × damage terms were fitted, but intercept or damage terms were not included, so that a separate intercept and slope of mass versus damage was fitted for each origin. The populations were nested within origin as the random effect. Higher intercepts indicated greater mass under undamaged conditions and higher slopes indicated higher tolerance. Contrasts were then conducted to determine whether intercepts or slopes differed between origins. To examine the impact of plant origin and herbivory on plant growth and reproduction, the same two-way mixed ANOVAs were performed on shoot mass, root mass, fruit mass and total mass. Total mass was calculated as shoot mass + root mass + fruit mass. Since some plants died during the experiment, data obtained from the survivors (200 plants) were used in the final analyses (Table 1). All data was analyzed using SAS, version 9.1 (SAS Institute Inc., Cary, NC, USA).

Results

Resistance and tolerance

Plant origin, insecticide treatment and their interactions, all significantly affected plant resistance (Table 2). In the insecticide spray treatment, there was no significant difference in number of absolute ($t_{16} = 0.84$, $P = 0.414$) or relative ($t_{16} = -0.29$, $P = 0.777$) damaged leaves between invasive and native populations (Fig. 1). In the non-insecticide treatment, although the leaf-damaged area was not significantly different between invasive and native populations ($F_{1,16} = 0.29$, $P = 0.599$), the number of absolute ($t_{16} = 11.38$, $P < 0.0001$) and relative ($t_{16} = 4.68$, $P < 0.001$) damaged leaves were greater for the invasive populations than for native populations (Fig. 1). However, there was no significant difference in tolerance

Table 2 Two-way MIXED anaylese of variance for the effects of plant origin (invasive *vs.* native), insecticide treatment (insecticide *vs.* non-insecticide) and their interactions on the resistance, growth and reproduction of *Phytolacca americana* at the end of the growing season. Population nested in origin, and its interactions with insecticide sprays, were treated as random effects. Only the results for fixed effects are shown.

Effect	df	Absolute leaf damage		Relative leaf damage		Shoot mass		Root mass		Fruit mass		Total mass	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Origin (O)	1,16	75.19	< 0.0001	5.97	0.0265	19.26	0.0005	7.71	0.0135	7.87	0.0127	15.83	0.0011
Insecticide (I)	1,164	235.94	< 0.0001	594.58	< 0.0001	304.11	< 0.0001	142.41	< 0.0001	131.71	< 0.0001	299.19	< 0.0001
O × I	1,16	56.09	< 0.0001	33.12	< 0.0001	10.56	0.0050	5.38	0.0339	8.48	0.0102	13.39	0.0021

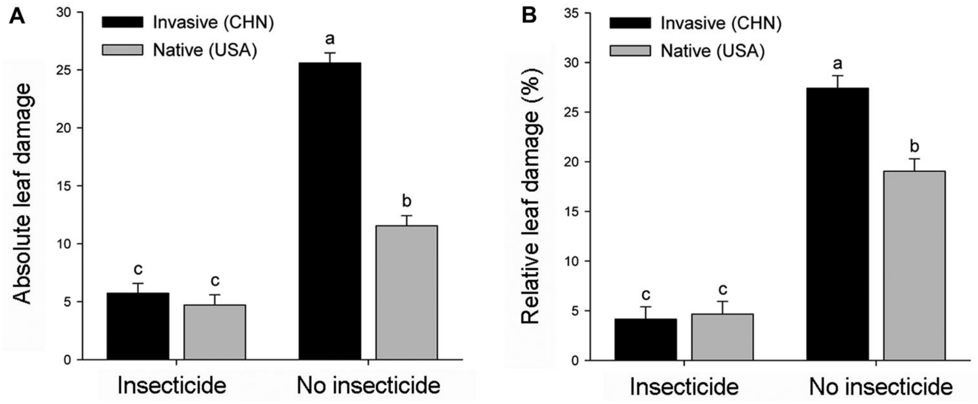

Fig. 1 Impact of insecticide treatments on absolute (A) and relative (B) leaf damage of *Phytolacca americana* from invasive populations (CHN, black bars) and native populations (USA, gray bars) at the end of the growing season. The absolute leaf damage was estimated as the number of damaged leaves for each plant, while the relative leaf damage was calculated as the number of damaged leaves / number of total leaves × 100% for each plant. Higher leaf damage indicates lower resistance. Values are means ± SE. Means with the same letter were not significantly different ($P < 0.05$) in *post hoc* multiple comparisons of adjusted means.

Table 3 Response to herbivory in regressions in Proc MIXED. Population nested in origin, and its interactions with insecticide treatment were treated as random effects. Only the results for fixed effects are shown. The response to herbivory was estimated by regressions with separate intercepts and separate slopes for amount of leaf damage (percentage of damaged leaves) for plants from invasive versus native populations. *T*-values (tests of parameter differences from zero), *F*-values (tests of differences in intercepts or slopes) and significance levels are shown. A significantly higher intercept indicates greater plant mass in the absence of that herbivore. A significantly steeper slope indicates lower tolerance to herbivory. Values in brackets are *P*-values. $^{**}P < 0.01$, $^{***}P < 0.001$, $^{****}P < 0.0001$.

Term	Shoot mass		Root mass		Fruit mass		Total mass	
	Estimate	t_{16}	Estimate	t_{16}	Estimate	t_{16}	Estimate	t_{16}
Intercept – Invasive	37.22	27.69****	9.12	23.84****	25.77	12.36****	71.65	27.02****
Intercept – Native	26.94	19.00****	6.94	17.26****	16.30	7.63****	49.64	17.89****
Intercept – Difference	$F_{1,16} = 27.69$****		$F_{1,16} = 15.42$**		$F_{1,16} = 10.04$**		$F_{1,16} = 32.89$****	
Slope – Invasive	−0.66	−10.56****	−0.15	−9.19****	−0.45	−5.86****	−1.21	−11.97****
Slope – Native	−0.57	−6.74****	−0.11	−5.02***	−0.39	−3.99**	−1.00	−6.87****
Slope – Difference	$F_{1,16} = 0.64[0.44]$		$F_{1,16} = 1.37[0.26]$		$F_{1,16} = 0.25[0.62]$		$F_{1,16} = 1.45[0.25]$	

between invasive and native populations as indicated by similar slopes for regressions of mass (shoot, root, fruit or total) versus relative leaf damage (Table 3, Fig. 2).

Growth and reproduction

Plant origin and insecticide treatment each significantly affected plant mass (Table 2). Invasive populations had more mass than native populations and insecticide spray significantly increased plant mass of both invasive and native populations (Fig. 3). Furthermore, plant origin and insecticide treatment had a significant interactive effect on plant growth and reproduction. For example, there was a bigger difference in shoot and total mass between invasive and native populations in the insecticide treatment (shoot mass: $t_{16} = 5.42$, $P < 0.0001$; total mass: $t_{16} = 5.11$, $P < 0.0001$) than in the non-insecticide treatment (shoot mass: $t_{16} = 2.26$, $P = 0.038$; total mass: $t_{16} = 2.19$, $P = 0.043$) (Fig. 3A, D). Similarly, root and fruit mass were larger for invasive populations than for native populations in the insecticide treatment (root mass: $t_{16} = 3.60$, $P = 0.002$; fruit mass: $t_{16} = 3.61$, $P = 0.002$), but were similar for invasive and native populations in the non-insecticide treatment (root mass: $t_{16} = 1.10$, $P = 0.289$; fruit mass: $t_{16} = 1.86$, $P = 0.112$) (Fig. 3B, C).

Discussion

Our study clearly demonstrates that American pokeweed plants from invasive populations have lower defenses

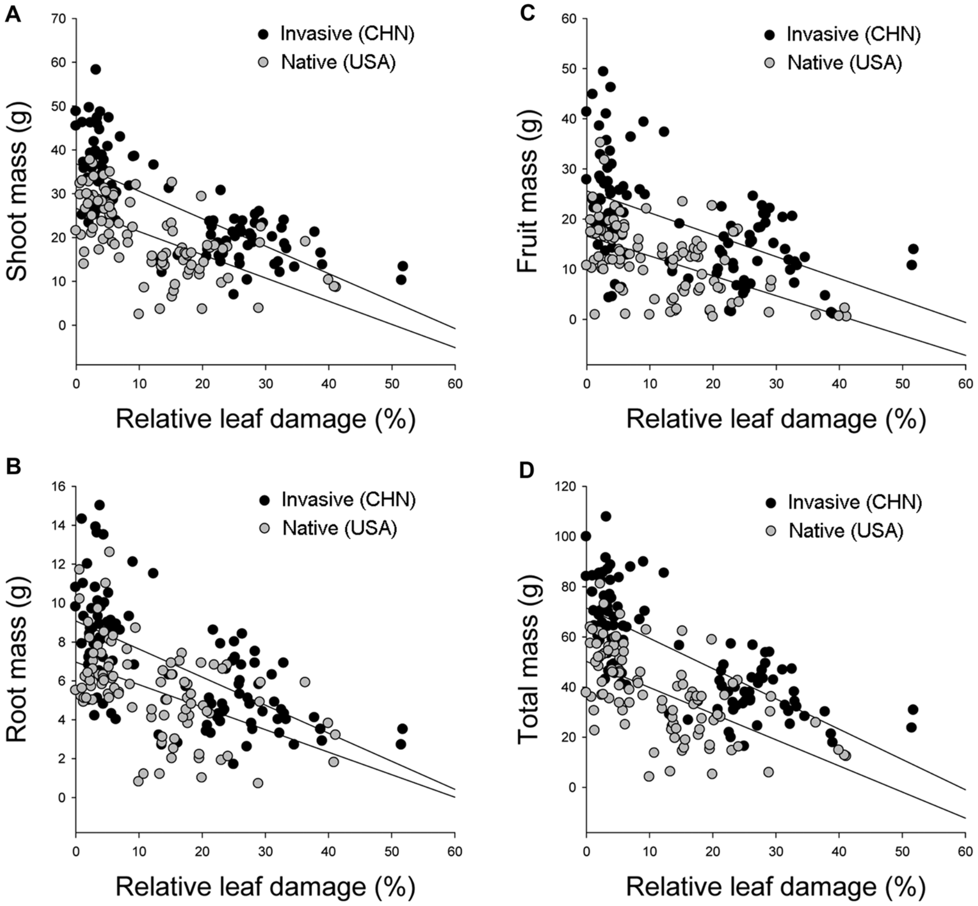

Fig. 2 Regression of shoot mass (A), root mass (B), fruit mass (C) and total mass (D) against relative leaf damage (percentage of damaged leaves) for *Phytolacca americana* from the invasive populations (CHN, black circle) and native populations (USA, gray circle) at the end of the growing season. The difference between slope and intercept can be seen in Table 3.

(e.g. lower resistance and comparable tolerance, Figs. 1, 2) and greater growth and reproduction (Fig. 3) than plants from native populations under natural generalist herbivory levels in the invasive range. These results are consistent with the prediction of the EICA hypothesis (Blossey & Nötzold, 1995) that invasive populations allocate fewer resources to defense and greater resources to growth and reproduction, and highlight the importance of generalists when examining the impacts of natural enemies on plant invasion (Müller-Schärer *et al.*, 2004; Chun *et al.*, 2010).

While many studies have examined the impact of generalist herbivory on plant resistance, they have produced inconsistent results. In some cases, invasive populations have higher resistance to generalists than native populations (Leger & Forister, 2005; Caño *et al.*, 2009; Liao *et al.*, 2014), while results from other studies have found the opposite pattern (Siemann & Rogers, 2003b; Hull-Sanders *et al.*, 2007; Fortuna *et al.*, 2014). Such observed differences may be caused by a species-specific response, especially when only a few generalists are examined. For example, Wang *et al.* (2012) found that Chinese tallow plants from invasive populations had higher resistance to the generalist *Grammodes geometrica* Fabricius than plants from native populations, while there was no significant difference in resistance to the generalist *Cnidocampa flavescens* Walker. Although recent studies have recognized the impact of generalists at the community level, these studies were mainly conducted in the native range (Zou *et al.*, 2008; Joshi & Tielbörger, 2012; Yang *et al.*, 2014). In fact, invasive plants are often attacked by new generalists in the introduced range (Stam *et al.*, 2014; Prior *et al.*, 2015). As a whole, studies focusing on only a few generalists or conducted only in the native range may give us limited insights into the impact of generalist herbivores. In this study, we examined the

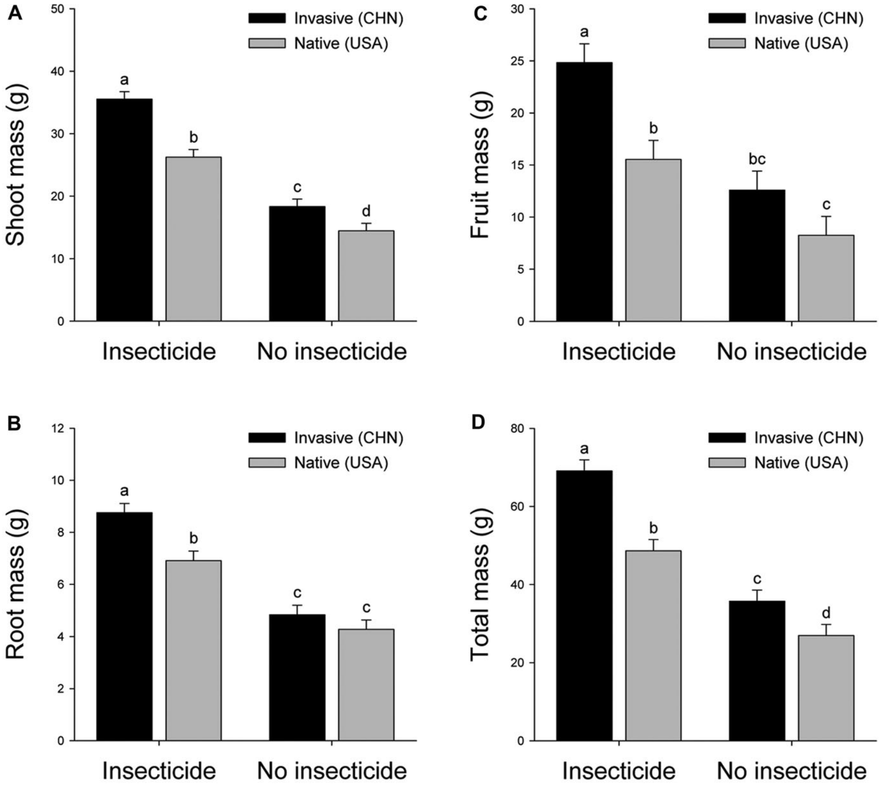

Fig. 3 Impact of insecticide sprays on shoot mass (A), root mass (B), fruit mass (C) and total mass (D) of *Phytolacca americana* from invasive populations (CHN, black bars) and native populations (USA, gray bars) at the end of the growing season. Values are means ± SE. Means with the same letter were not significantly different ($P < 0.05$) in *post hoc* multiple comparisons of adjusted means.

impact of generalists by exposing American pokeweed plants from both invasive and native ranges to the natural herbivore levels in the invasive range, and we found that both absolute and relative leaf damage were both significantly higher for plants from invasive populations (Fig. 1). These results provide direct evidence of a decreased resistance by American pokeweed to generalist herbivores during invasion. Further studies comparing invasive plants under natural herbivory levels in the invasive range could provide a more comprehensive understanding of the impacts of generalist herbivores on plant invasions.

In addition to resistance, the selective pressure imposed by generalists is often strong enough to affect tolerance (Ashton & Lerdau, 2008; Huang *et al.*, 2010; Oduor *et al.*, 2011; Carrillo *et al.*, 2014). However, we did not find a significant difference in tolerance between American pokeweed plants from invasive and native populations under natural herbivory levels (Fig. 2). Similar results have been found in other study systems, such as *Chromolaena odorata* L. (Li *et al.*, 2012) and *Alliaria petiolata* Bieb. (Gard *et al.*, 2013). It is likely that other stresses beside herbivory also affect tolerance. The maintained tolerance of invasive populations may provide efficient protection from a wide range of abiotic stresses (Müller-Schärer *et al.*, 2004).

According to the prediction of the EICA hypothesis, invasive populations should perform better than native populations under lower herbivory pressure (Blossey & Nötzold, 1995). In this study, we found that invasive populations had greater growth and reproduction than native populations under natural herbivory levels (no insecticide, Fig. 3), indicating that plants from invasive populations are more adaptive to a novel environment than plants from native populations. However, the magnitude of differences between invasive and native populations were even more pronounced in the no-herbivory treatment (insecticide, Fig. 3), suggesting that maintaining a higher resistance is costly. Together, these findings indicate that decreasing resistance and reallocating resources to growth and reproduction may be a major mechanism promoting the American pokeweed invasion in China.

In summary, we found that the invasive populations of American pokeweed had greater growth and reproduction and lower resistance than native populations under natural herbivory levels in the introduced range. These results clearly suggest generalist herbivory to be an important driver in mediating defensive strategies and resource allocation during the invasive process of American pokeweed. Considerating the role of generalists at the community level may help better understand ecological and evolutionary interactions in plant invasions.

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Disclosure

The authors declare that they have no conflicts of interest.

References

Agrawal, A.A. (2007) Macroevolution of plant defense strategies. *Trends in Ecology and Evolution*, 22, 103–109.

Ali, J.G. and Agrawal, A.A. (2012) Specialist versus generalist insect herbivores and plant defense. *Trends in Plant Science*, 17, 293–302.

Ashton, I.W. and Lerdau, M.T. (2008) Tolerance to herbivory, and not resistance, may explain differential success of invasive, naturalized, and native North American temperate vines. *Diversity and Distributions*, 14, 169–178.

Aweke, G. (2007) *Phytolacca americana* L. *Record from PROTA4U* (eds. G.H. Schmelzer & A. Gurib-Fakims), PROTA (Plant Resources of Tropical Africa), Wageningen , Netherlands.

Bezemer, T.M., Harvey, J.A. and Cronin, J.T. (2014) Response of native insect communities to invasive plants. *Annual Review of Entomology*, 59, 119–141.

Blair, A.C. and Wolfe, L.M. (2004) The evolution of an invasive plant: an experimental study with *Silene latifolia*. *Ecology*, 85, 3035–3042.

Blossey, B. and Nötzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, 83, 887–889.

Bossdorf, O., Auge, H., Lafuma, L., Rogers, W., Siemann, E. and Prati, D. (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, 144, 1–11.

Brust, G.E. (2008) *Insect Pests of Tomato*. Maryland Cooperative Extension. p. 9.

Caño, L., Escarré, J., Vrieling, K. and Sans, F.X. (2009) Palatability to a generalist herbivore, defence and growth of invasive and native *Senecio* species: testing the evolution of increased competitive ability hypothesis. *Oecologia*, 159, 95–106.

Callaway, R.M. and Maron, J.L. (2006) What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology and Evolution*, 21, 369–374.

Capinera, J.L. (1999) Southern armyworm, *Spodoptera eridania* (Cramer) (Insecta: Lepidoptera: Noctuidae). *Featured Creatures from the Entomology and Nematology Department, UF/IFAS Extension*. UF/IFAS Extension, Gainesville, FL.

Carrillo, J., Mcdermott, D. and Siemann, E. (2014) Loss of specificity: native but not invasive populations of *Triadica sebifera* vary in tolerance to different herbivores. *Oecologia*, 174, 863–871.

Carter, C.C., Stephan, D.L., Baker, J.R. and Sorenson, K.A. (1994) Top eight reported insect pests on Carolina organic produce farms. *Insects and Related Pest of Vegetables: Some Important, Common and Potential Pests in Southeastern United States* (eds. K.A. Sorenson & J.R. Bakers), pp. 6–7. North Carolina Cooperative Extension Service publication AG 295, Raleigh, NC, USA.

Chun, Y.J., van Kleunen, M. and Dawson, W. (2010) The role of enemy release, tolerance and resistance in plant invasions: linking damage to performance. *Ecology Letters*, 13, 937–946.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. and Macisaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, 7, 721–733.

Eastman, J. (2003) *Book of Field and Roadside: Open-country Weeds, Trees, and Wildflowers of Eastern North America*. Stackpole Books, Mechanicsburg, PA.

Fortuna, T.M., Eckert, S., Harvey, J.A., Vet, L.E.M., Müller, C. and Gols, R. (2014) Variation in plant defences among populations of a range-expanding plant: consequences for trophic interactions. *New Phytologist*, 204, 989–999.

Fu, J., Li, C. and Xu, J. (2012) Prevention and control of invaded plant *Phytolacca americana* in sandy coastal shelter forests. *Chinese Journal of Applied Ecology*, 23, 991–997.

Gard, B., Bretagnolle, F., Dessaint, F. and Laitung, B. (2013) Invasive and native populations of common ragweed exhibit strong tolerance to foliar damage. *Basic and Applied Ecology*, 14, 28–35.

Hall, D.W. (2014) Giant leopard moth, *Hypercompe scribonia* (Stoll 1790) (Lepidoptera: Erebidae: Arctiinae). *Featured Creatures from the Entomology and Nematology Department, UF/IFAS Extension*. UF/IFAS Extension, Gainesville, FL.

Huang, W., Carrillo, J., Ding, J.Q. and Siemann, E. (2012a) Invader partitions ecological and evolutionary responses to above- and belowground herbivory. *Ecology*, 93, 2343–2352.

Huang, W., Carrillo, J., Ding, J.Q. and Siemann, E. (2012b) Interactive effects of herbivory and competition intensity determine invasive plant performance. *Oecologia*, 170, 373–382.

Huang, W., Siemann, E., Wheeler, G.S., Zou, J., Carrillo, J. and Ding, J. (2010) Resource allocation to defence and growth are driven by different responses to generalist and specialist herbivory in an invasive plant. *Journal of Ecology*, 98, 1157–1167.

Hull-Sanders, H., Clare, R., Johnson, R. and Meyer, G. (2007) Evaluation of the evolution of increased competitive ability (EICA) hypothesis: loss of defense against generalist but not specialist herbivores. *Journal of Chemical Ecology*, 33, 781–799.

Inderjit (2012) Exotic plant invasion in the context of plant defense against herbivores. *Plant Physiology*, 158, 1107–1114.

Joshi, S. and Tielbörger, K. (2012) Response to enemies in the invasive plant *Lythrum salicaria* is genetically determined. *Annals of Botany*, 110, 1403–1410.

Keane, R.M. and Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, 17, 164–170.

Lampe, K.F. and Mccann, M.A. (1985) *AMA Handbook of Poisonous and Injurious Plants*, American Medical Association, Chicago, IL, USA.

Leger, E.A. and Forister, M.L. (2005) Increased resistance to generalist herbivores in invasive populations of the California poppy (*Eschscholzia californica*). *Diversity and Distributions*, 11, 311–317.

Li, Y.P., Feng, Y.L. and Barclay, G. (2012) No evidence for evolutionarily decreased tolerance and increased fitness in invasive *Chromolaena odorata*: implications for invasiveness and biological control. *Plant Ecology*, 213, 1157–1166.

Liao, Z.Y., Zheng, Y.L., Lei, Y.B. and Feng, Y.L. (2014) Evolutionary increases in defense during a biological invasion. *Oecologia*, 174, 1205–1214.

Müller-Schärer, H., Schaffner, U. and Steinger, T. (2004) Evolution in invasive plants: implications for biological control. *Trends in Ecology and Evolution*, 19, 417–422.

Ma, J. (2014) *The Survey Reports on Chinese Alien Invasive Plants*, China Higher Education Press.

Ma, X.C., Teng, R.M., Zhao, Y., Lu, H.Y., Yan, L., Sun, J.D. and Zheng, D.S. (2014) Epidemiological survey of a food poisoning event caused by *Phytolacca americana* leave. *Disease Sueveillance*, 29, 333–334.

Maron, J.L. and Vilà, M. (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, 95, 361–373.

Núñez-Farfán, J., Fornoni, J. and Valverde, P.L. (2007) The evolution of resistance and tolerance to herbivores. *Annual Review of Ecology, Evolution, and Systematics*, 38, 541–566.

Oduor, A.M.O., Lankau, R.A., Strauss, S.Y. and Gómez, J.M. (2011) Introduced *Brassica nigra* populations exhibit greater growth and herbivore resistance but less tolerance than native populations in the native range. *New Phytologist*, 191, 536–544.

Prior, K.M., Powell, T.H.Q., Joseph, A.L. and Hellmann, J.J. (2015) Insights from community ecology into the role of enemy release in causing invasion success: the importance of native enemy effects. *Biological Invasions*, 17, 1283–1297.

Schaffner, U., Ridenour, W.M., Wolf, V.C., Bassett, T., Muller, C., Müller-Schärer, H., Sutherland, S., Lortie, C.J. and Callaway, R.M. (2011) Plant invasions, generalist herbivores, and novel defense weapons. *Ecology*, 92, 829–835.

Siemann, E. and Rogers, W.E. (2003a) Herbivory, disease, recruitment limitation, and success of alien and native tree species. *Ecology*, 84, 1489–1505.

Siemann, E. and Rogers, W.E. (2003b) Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. *Oecologia*, 135, 451–457.

Stam, J.M., Kroes, A., Li, Y., Gols, R., van Loon, J.J.A., Poelman, E.H. and Dicke, M. (2014) Plant interactions with multiple insect herbivores: from community to genes. *Annual Review of Plant Biology*, 65, 689–713.

Stastny, M., Schaffner, U.R.S. and Elle, E. (2005) Do vigour of introduced populations and escape from specialist herbivores contribute to invasiveness? *Journal of Ecology*, 93, 27–37.

Turley, N.E., Godfrey, R.M. and Johnson, M.T.J. (2013) Evolution of mixed strategies of plant defense against herbivores. *New Phytologist*, 197, 359–361.

Verhoeven, K.J.F., Biere, A., Harvey, J.A. and van der Putten, W.H. (2009) Plant invaders and their novel natural enemies: who is naïve? *Ecology Letters*, 12, 107–117.

Wang, Y., Siemann, E., Wheeler, G.S., Zhu, L., Gu, X. and Ding, J.Q. (2012) Genetic variation in anti-herbivore chemical defences in an invasive plant. *Journal of Ecology*, 100, 894–904.

Xu, H.G., Qiang, S., Han, Z.M., Guo, J.Y., Huang, Z.G., Sun, H.Y., He, S.P., Ding, H., Wu, H.R. and Wan, F.H. (2006) The status and causes of alien species invasion in China. *Biodiversity and Conservation*, 15, 2893–2904.

Yang, X.F., Huang, W., Tian, B.L. and Ding, J.Q. (2014) Differences in growth and herbivory damage of native and invasive kudzu (*Peuraria montana* var. *lobata*) populations grown in the native range. *Plant Ecology*, 215, 339–346.

Zhang, P., Li, Y., You, Y.Z., Feng, Y., Teng, R.M., Ma, R., Gao, S., Ning, J.Y., Jing, H.M., Li, G.J., Tan, Z.S. and Ma, L. (2014) Using three methods to test and evaluate the fruit and leaf's toxicity of *Phytolacca Americana* L. *Chinese Journal of Food Hygiene*, 26, 332–336.

Zou, J.W., Siemann, E., Rogers, W.E. and Dewalt, S.J. (2008) Decreased resistance and increased tolerance to native herbivores of the invasive plant *Sapium sebiferum*. *Ecography*, 31, 663–671.

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