ORIGINAL ARTICLE

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

Wei Huang and Jian-Qing Ding

Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan, Hubei 430074, China
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; resistance; tolerance; resource allocation; *Phytolacca americana* L.
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 towards traits conferring increased competitive ability, such as growth and reproduction (Evolution of Increased Competitive Ability Hypothesis, EICA) (Blossey & Nötzel, 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., 2014).

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 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. In a previous field survey, however, 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 (Huang, personal observation).

In this study, we examined the impact of generalist herbivores on the 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 per 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 two days and their positions re-arranged every week
until 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 pokeweed. These generalist herbivores mainly include caterpillars and beetles, which feed on the leaves and produce irregular holes (Huang, personal observation). The experiment was established as a $2 \times 2 \times 9$ 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 $27.2 \pm 0.8 \text{ cm}$ for invasive populations and $28.2 \pm 0.7 \text{ cm}$ for native populations ($F_{1,16} = 0.18, P = 0.67$, nested ANOVA). Then, pots were removed and plants were transplanted to one of six plots ($2.5 \times 5 \text{ m}$), separated from adjacent plots by 2 m wide strips. Within each plot, 36 plants (two plants per each of 18 plant population) were randomly planted (nine rows of four plants), spaced 0.5 m from each other, with plants from invasive populations neighboring with 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, Delaware) twice per month. 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 non-insecticide treatment and leaf damaged 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,
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).

**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 significant 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 between invasive and native populations as indicated by similar slopes for regressions of mass (shoot, root, fruit, or total) vs. 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 (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 less resources to defense and more 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 of 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 (Prior et 
al., 2014; Stam et al., 2014). 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 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. More such 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. Consideration
the role of generalists in community level may help better understand ecological and evolutionary interactions in plant invasions.

Acknowledgments

We would like to thank Xue-Fang Yang and Shun-Liang Feng for plant harvest. We also thank English editing by Van Driesche Scientific Editing. This work was supported by the National Natural Science Foundation of China (31470447 and 31200286 to W. Huang, 31370404 to J.Q. Ding).

Disclosure

The authors declare that they have no conflicts of interest.

References


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


populations of common ragweed exhibit strong tolerance to foliar damage.


Accepted June 9, 2015
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.
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.
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.
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.

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

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>Absolute leaf damage</th>
<th>Relative leaf damage</th>
<th>Shoot mass</th>
<th>Root mass</th>
<th>Fruit mass</th>
<th>Total mass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
<td>P</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Origin (O)</td>
<td>1,16</td>
<td>75.19</td>
<td>&lt; 0.0001</td>
<td>5.97</td>
<td>0.0265</td>
<td>19.26</td>
<td>0.0005</td>
</tr>
<tr>
<td>Insecticide (I)</td>
<td>1,164</td>
<td>235.94</td>
<td>&lt; 0.0001</td>
<td>594.58</td>
<td>&lt; 0.0001</td>
<td>304.11</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>O × I</td>
<td>1,16</td>
<td>56.09</td>
<td>&lt; 0.0001</td>
<td>33.12</td>
<td>&lt; 0.0001</td>
<td>10.56</td>
<td>0.005</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Term</th>
<th>Shoot mass</th>
<th>Root mass</th>
<th>Fruit mass</th>
<th>Total mass</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>t_{16}</td>
<td>Estimate</td>
<td>t_{16}</td>
</tr>
<tr>
<td>Intercept – Invasive</td>
<td>37.22</td>
<td>27.69**</td>
<td>9.12</td>
<td>23.84**</td>
</tr>
<tr>
<td>Intercept – Native</td>
<td>26.94</td>
<td>19.00**</td>
<td>6.94</td>
<td>17.26**</td>
</tr>
<tr>
<td>Intercept – Difference</td>
<td>F_{1,16} =</td>
<td>15.42**</td>
<td>F_{1,16} =</td>
<td>10.04**</td>
</tr>
<tr>
<td>Difference</td>
<td>27.69****</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope – Invasive</td>
<td>-0.66</td>
<td>-10.56*</td>
<td>-0.45</td>
<td>-5.86**</td>
</tr>
<tr>
<td>Slope – Native</td>
<td>-0.57</td>
<td>-6.74**</td>
<td>-0.39</td>
<td>-3.99**</td>
</tr>
<tr>
<td>Slope – Difference</td>
<td>F_{1,16} =</td>
<td></td>
<td>F_{1,16} =</td>
<td></td>
</tr>
<tr>
<td>Difference</td>
<td>0.64[0.44]</td>
<td>1.37[0.26]</td>
<td>0.25[0.62]</td>
<td>1.45[0.25]</td>
</tr>
</tbody>
</table>