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Solidago gigantea plants from nonnative ranges compensate more in response to damage than plants from the native range

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Abstract. Resistance and tolerance are two ways that plants cope with herbivory. Tolerance, the ability of a plant to regrow or reproduce after being consumed, has been studied less than resistance, but this trait varies widely among species and has considerable potential to affect the ecology of plant species. One particular aspect of tolerance, compensatory responses, can evolve rapidly in plant species; providing insight into interactions between consumers and plants. However, compensation by invasive species has rarely been explored. We compared compensatory responses to the effects of simulated herbivory expressed by plants from seven *Solidago gigantea* populations from the native North American range to that expressed by plants from nine populations from the nonnative European range. Populations were also collected along elevational gradients to compare ecotypic variation within and between ranges. *Solidago* plants from the nonnative range of Europe were more tolerant to herbivory than plants from the native range of North America. Furthermore, plants from European populations increased in total biomass and growth rate with elevation, but decreased in compensatory response. There were no relationships between elevation and growth or compensation for North American populations. Our results suggest that *Solidago gigantea* may have evolved to better compensate for herbivory damage in Europe, perhaps in response to a shift to greater proportion of attack from generalists. Our results also suggest a possible trade-off between rapid growth and compensation to damage in European populations but not in North American populations.

Key words: biogeography; compensatory growth; ecotype; elevation; exotic invasion; genetic variation; herbivory; population variation; resistance; tolerance.

INTRODUCTION

Interactions with herbivores can greatly influence the abundance and distribution of plant species and alter community composition (Price et al. 1980, Huntly 1991, Olf and Ritchie 1998, Müller-Schärer et al. 2004, Maron and Crone 2006, Lau et al. 2008). These effects can be caused by disproportionate preferences of consumers for different plant species (Callaway et al. 1999, 2005, Chase et al. 2000, Fine et al. 2004, Gómez 2005) or variation in the resistance or tolerance of different plant species to consumers (Paige and Whitham 1987, Strauss and Agrawal 1999, Chase et al. 2000, Stowe et al. 2000). Despite being much less studied than resistance, tolerance may be of exceptional importance in natural systems (Maschinski and Whitham 1989, Lennartsson et al. 1997, Augustine and McNaughton 1998, Fornoni 2011). In the literature, tolerance and compensatory growth are often

used synonymously, or compensation is often referred to as a form of tolerance. Here we define tolerance as the ability of a plant to buffer the negative effects of natural enemies on fitness through regrowth or reproduction after damage (Strauss and Agrawal 1999, Stowe et al. 2000, Müller-Schärer et al. 2004), whereas compensation is defined as any kind of induced response to damage (Fornoni 2011). Compensation is an important mechanism to replace tissue loss due to herbivory (Cain et al. 1991, Maron and Vilà 2001), and compensation can vary from zero (no regrowth) to substantial overcompensation (greater increase in size or reproduction compared to undamaged controls) depending on the plant species, the kind of herbivory experienced, the degree of herbivory experienced, and the biotic and abiotic environment in which herbivory occurs (Paige and Whitham 1987, Maschinski and Whitham 1989, Lehtilä and Strauss 1999, Wise and Abrahamson 2005, Abhilasha and Joshi 2009, Fornoni 2011). For example, compensatory responses to clipping can be limited by nutrient supply (Hicks and Turkington 2000, Hawkes and Sullivan 2001, Leriche et al. 2003). Neighboring species can reduce the

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compensation of damaged individuals through resource competition (Maschinski and Whitham 1989) or affect compensation mediated by arbuscular mycorrhizal fungi (Bennett and Bever 2007, Garrido et al. 2010).

Invasive species can gain competitive advantages against natives by escaping specialist (Mack 1996, Stastny et al. 2005, Jongejans et al. 2006, Pan et al. 2013) and generalist enemies (Maron and Vilà 2001, Han et al. 2008, Kalisz et al. 2014). In some cases, these advantages appear to derive from evolutionary changes (Blossey and Nötzold 1995, Leger and Rice 2003, Ridenour et al. 2008), and these changes in growth patterns have the potential to also contribute to changes in compensation to herbivory. For example, Stastny et al. (2005) found that *Senecio jacobaea* populations from the nonnative range grew larger and showed greater compensatory responses to herbivores than populations from its native range. Zou et al. (2008) found weaker resistance but stronger compensation to herbivory damages in plants from invasive populations than plants from native populations of *Sapium sebiferum*. Others have reported that some invasive species are more tolerant to herbivory than the native species they interact with (Schierenbeck et al. 1994, Rogers and Siemann 2002). Compensation may be favored in nonnative ranges for several reasons. First, though enemy release may benefit invasion at early stages, the accumulation of natural enemies following invasion can be rapid (Hawkes 2007). Resistance mechanisms may not be effective against the new suite of natural enemies, but tolerance would remain effective in reducing herbivory (Fornoni 2011). Second, even though optimality theory assumes that resistance and tolerance may trade off with competitive ability (Uriarte et al. 2002), many traits, such as rapid growth rates, which might confer stronger compensation to herbivory, may also contribute to stronger competitive ability (Callaway et al. 2006, Zou et al. 2008). Thus, strong compensation may be a byproduct of evolution of increased competitive ability. Third, compensation can be a general response to tissue injuries, such as fire, frost, and desiccation-induced tissue loss, in addition to a response to herbivory. Invaders are often favored in disturbed habitats, and this could be facilitated by high tolerance to damage in general (Belsky et al. 1993, Müller-Schärer et al. 2004). However, we know little about tolerance to herbivory in the context of exotic plant invasion (but see Jogesh et al. 2014, Lin et al. 2015).

There is substantial ecotypic variation within species in tolerance to herbivory, thus there is reason to explore differences in ecotypic variation in tolerance within native and nonnative ranges. Dyer et al. (1991) compared compensatory responses between ecotypes of *Panicum coloratum* that had been collected from two locations in African grasslands that differed in grazing intensity. Pre-grazing photosynthetic fixation rates, translocation rates, and carbon storage pools were identical for the two ecotypes, but, after grazing, photosynthetic rates were 39% higher for “grazed” ecotypes than before, and

“grazed” ecotypes compensated completely for experimental defoliation. In contrast, the yield of the “non-grazed” ecotypes was reduced 21% by grazing. In exotic invasions, ecotypic variation may be constrained by low genetic diversity in small numbers of founding individuals (but see Maron et al. 2004, Monty and Mahy 2009). However, rapid ecotypic differentiation has been found in some invasive species (Hedge et al. 2006, Schierenbeck and Ellstrand 2009, Stohlgren et al. 2014). To our knowledge, there have been very few studies of ecotypic variation in the ability to tolerate or compensate for herbivory in populations from the native and nonnative ranges of an invasive species (but see Williams et al. 2014).

Solidago gigantea AITON (Asteraceae) is a perennial forb native to North America. It was introduced to Europe approximately 250 years ago and is now one of Europe’s most problematic invaders (Weber and Schmid 1998). In both ranges, *S. gigantea* occurs in relatively moist habitats across large geographic areas; however, European populations occupy a broader range of habitats (Weber and Jakobs 2000). *Solidago gigantea* is attacked by both specialist and generalist insects in North America, whereas, in Europe, only a few generalist insects have been reported to feed on it, and significant damage appears to be rare (Weber and Jakobs 2000, Jakobs et al. 2004). However, *S. gigantea* is grazed by cattle and sheep (Gilhaus et al. 2014, Pal et al. 2015), and thus, if a larger proportion of herbivory in Europe is from generalists, this may select for stronger tolerance and weaker resistance by *S. gigantea* (Abhilasha and Joshi 2009).

Despite the ability to exploit a broader range of soil moisture in its nonnative range, European *S. gigantea* populations are generally found below 1200 m in elevation (Weber and Jakobs 2000; R. W. Pal; *personal observation*). In contrast, North American populations of *S. gigantea* can be found at over 1,600 m (R. W. Pal, *personal observation*). Thus, *S. gigantea* populations in Europe may not possess the ecotypic variation to allow them to occupy high elevations or to respond to consumers along elevational gradients. Adaptation to elevational gradients, such as faster growth rate, is an important aspect of the range expansion of invasive plants (Williams et al. 1995, Monty and Mahy 2009, Trtikova et al. 2011), and high growth rates have been found to correspond to strong compensatory growth responses (Stastny et al. 2005, Zou et al. 2008, Hochwender et al. 2012). Therefore, we hypothesized that there would be ecotypic differences in growth and compensatory responses among *S. gigantea* populations in the nonnative range.

Thus, *S. gigantea* provides a good opportunity to test (1) if compensatory response to herbivory is stronger in the nonnative range than the native range, (2) if compensatory responses to herbivory vary among different ecotypes, and (3) whether ecotypic differences in compensatory responses correlate with the elevation at which populations occur or growth rate traits of ecotypes.

MATERIALS AND METHODS

Seed collection

We collected seeds from nine European and seven North American *S. gigantea* populations between January and December 2012. For both ranges, the populations were sampled across a wide range of latitude, longitude, and elevation (see detailed information for sites in Appendix S1: Table S1). From each population, we collected seeds from at least 10 maternal plants and pooled these seeds. Maternal plants were at least 10 m from each other, avoiding collecting from the same clone. Seeds were stored at room temperature in the laboratory prior to the greenhouse experiments (see the timing of seed collection in Appendix S1: Table S1).

Greenhouse experiment

The experiment was conducted in a greenhouse at the University of Montana, Missoula, Montana, USA. In February 2013, seeds from each *S. gigantea* population were sown in 0.25-L pots filled with 50% sand and 50% Osmocote potting soil (Scotts Australia Company, New South Wales, Australia). After emergence, 16 seedlings were randomly selected from each population and individuals were transplanted into 0.5-L pots with the same sand/soil mixture. The positions of the pots were randomly assigned on benches and, during the experimental period, plants were grown in a naturally lit greenhouse (22–26°C) and were watered once a day.

In August 2013, we paired individuals with similar sizes from each population ($n = 8$ pairs for each population). For each pair of plants, one individual was subjected to severe defoliation to simulate herbivory: all aboveground biomass was removed, leaving only one basal leaf. The dry mass of the clipped tissue was measured. The remaining eight plants per population served as undamaged controls. In mid-October, roughly the end of the growing season for natural *S. gigantea* populations, plants were harvested, dried at 60°C for three days, and their aboveground and belowground biomass were weighed separately.

Data analysis

All data analyses were conducted in SPSS (version 22.0; IBM SPSS Statistics, Armonk, New York, USA). Compensatory response to damage was calculated as the ratio of the total biomass of a clipped individual after regrowth to its paired unclipped control. The growth rates for the unclipped control from 6 February to 14 August (189 d, the growth period before clipping treatment was conducted) and from 15 August to 14 October (60 d, the growth period after clipping the treatment plants) were quantified as the increases in aboveground biomass per day. The growth rates of the unclipped controls from February to August were

assumed to be the same as that of clipped individuals since treatments were chosen randomly, whereas the growth rate for a control plant from August to October was the difference between the final aboveground biomass of the control and the aboveground biomass of the clipped individual of the same pair at the time of clipping (i.e., clipped biomass) divided by 60 d. Root-shoot ratios (RSR) were calculated as the belowground biomass divided by aboveground biomass.

We used mixed effect linear models to assess the effects of range (North America vs. Europe) and the elevation of population origin on the total biomass of the controls, growth rate of controls, and the compensatory response to damage. In the models for total biomass and compensatory response, range, elevation (designated as a covariate), and their interactions were fixed factors. Population was nested within range as a random factor. Biomass was square-root-transformed to fit a normal distribution and reduce variance heterogeneity when necessary. Because the clipping treatment was conducted more than six months after germination, after which the growth of *S. gigantea* might have slowed down and thus affected the ability to compensate for tissue loss, we also compared the difference between the growth rates of the unclipped controls before and after the clipping treatment. Thus, range, elevation, stage of the experiment (before clipping vs. after clipping) and all two-way interactions among these three factors were used as fixed factors in the statistical model for growth rate. Population nested within range was still selected as a random factor. Additionally, to explore whether there was a potential bias toward comparing some growth rates that were based on aboveground biomass, the effects of range, elevation, and stage of the experiment on RSR were also explored. The model for the analysis for RSR was the same as that for growth rate with the same fixed factors and random factors.

We also regressed total biomass produced by control plants at the time of harvest, growth rates of control plants, and compensatory responses to damage against the elevation at which the populations were collected. The potential trade-off between the vegetative growth of the controls and compensatory responses was tested by regressing total vegetative biomass against compensatory response. Finally, compensatory responses were also regressed against the growth rates of control plants before and after clipping. Population means were used in all the regressions.

RESULTS

Ecotypic variation in compensatory responses

For all compensatory responses by *S. gigantea*, there were significant differences between the native and non-native ranges (Table 1). Based on estimated marginal means, European populations demonstrated $19.5\% \pm 11.0\%$ greater total compensation than North American populations

TABLE 1. Results of mixed effect linear models testing the effects of range, elevation, range \times elevation interaction, and population on the compensatory growth and growth without damage of *Solidago gigantea*.

Source	Compensatory growth			Vegetative growth		
	df	<i>F</i> , <i>Z</i>	<i>P</i>	df	<i>F</i> , <i>Z</i>	<i>P</i>
Range	1.0	4.62	0.053	1.0	1.83	0.202
Elevation	1.0	6.45	0.026	1.0	5.07	0.044
Range \times Elevation	1.0	2.35	0.151	1.0	3.66	0.080
Population (Range)	12.0	1.97	0.049	12.0	0.96	0.337
Error	112.0			112.0		

Notes: Range, elevation, and their interactions were tested as fixed factors, and population was nested within range as a random factor. The column labeled *F*, *Z* shows the *F* value for fixed effects and *Z* value for random effects. Values shown in boldface type represent significant effects ($P \leq 0.05$).

(Table 1). Elevation was negatively correlated with compensatory response (Table 1). There was also a significant interaction between range and elevation for compensatory responses (Table 1), indicating that tolerance to damage decreased with elevation in Europe ($R^2 = 0.58$, $P = 0.017$; Fig. 1a), but not in North America ($R^2 = 0.08$, $P = 0.532$; Fig. 1a).

Ecotypic variation in vegetative growth

There was no difference in the total biomass of control (undamaged) *S. gigantea* plants from the native North American range vs. the nonnative European range (Table 1). However, there was a significant positive relationship between elevation and total biomass when both ranges were combined (Table 1). The interaction between range and elevation was not significant for total biomass (Table 1), but the trend suggested that the growth of undamaged plants from *S. gigantea* populations from North America and Europe might respond differently to gradients in elevation. For European populations, as elevation increased, the total biomass of undamaged control plants increased ($R^2 = 0.79$, $P = 0.001$; Fig. 1b), but no such correlation was found for North American populations ($R^2 = 0.04$, $P = 0.891$; Fig. 1b).

The aboveground growth rates of European populations did not differ from those of North American populations (Table 2). The growth rate of *S. gigantea* populations increased with increasing elevation (Table 2). The growth rate of control plants from August to October (i.e., the growth period after clipping) was greater than the growth rate from February to August (i.e., the growth period before clipping; Table 2), indicating that the growth of *S. gigantea* did not slow down after clipping. The significant interaction between range and elevation for the growth rate of *S. gigantea* indicated that the correlations between growth rate and the elevation of population origin differed for North American and European populations, whereas the significant interaction between stage and elevation indicated that the correlations between growth rate and the elevation of population origin differed before and after the clipping treatment

was conducted. Growth rates of the control plants from February to August for both European and North American populations did not correlate with elevation (European populations, $R^2 = 0.39$, $P = 0.071$; North American populations, $R^2 = 0.08$, $P = 0.538$; Fig. 1c). Growth rates from August to October of European populations decreased as elevation increased (European populations: $R^2 = 0.76$, $P = 0.002$), but North American populations did not show this relationship ($R^2 = 0.00$, $P = 0.961$; Fig. 1d). There were no effects of range, elevation, and experimental stage on RSR (Table 2), indicating that the biomass allocation patterns were similar for North American and European populations, and these remained relatively stable across elevations and treatments. There was variation in RSR among different populations within each range (Table 2).

Trade-off between vegetative growth and compensatory response

For *S. gigantea* plants from the nonnative European range, the biomass of the control plants and the compensatory response to damage were negatively correlated ($R^2 = 0.54$, $P = 0.023$; Fig. 2a). For plants from North American populations, however, there was no such relationship between biomass and compensatory responses ($R^2 = 0.30$, $P = 0.199$; Fig. 2a). There was no correlation between the growth rate of control plants from February to August and the compensatory response for either European or North American populations (European populations, $R^2 = 0.017$, $P = 0.734$; North American populations, $R^2 = 0.00$, $P = 0.972$; Fig. 2b). Finally, the growth rate of control plants from August to October was negatively correlated with the compensatory response for European populations ($R^2 = 0.59$, $P = 0.015$; Fig. 2c), whereas there was no correlation for North American populations ($R^2 = 0.35$, $P = 0.160$; Fig. 2c).

DISCUSSION

Plants from European populations exhibited stronger compensatory responses than plants from North

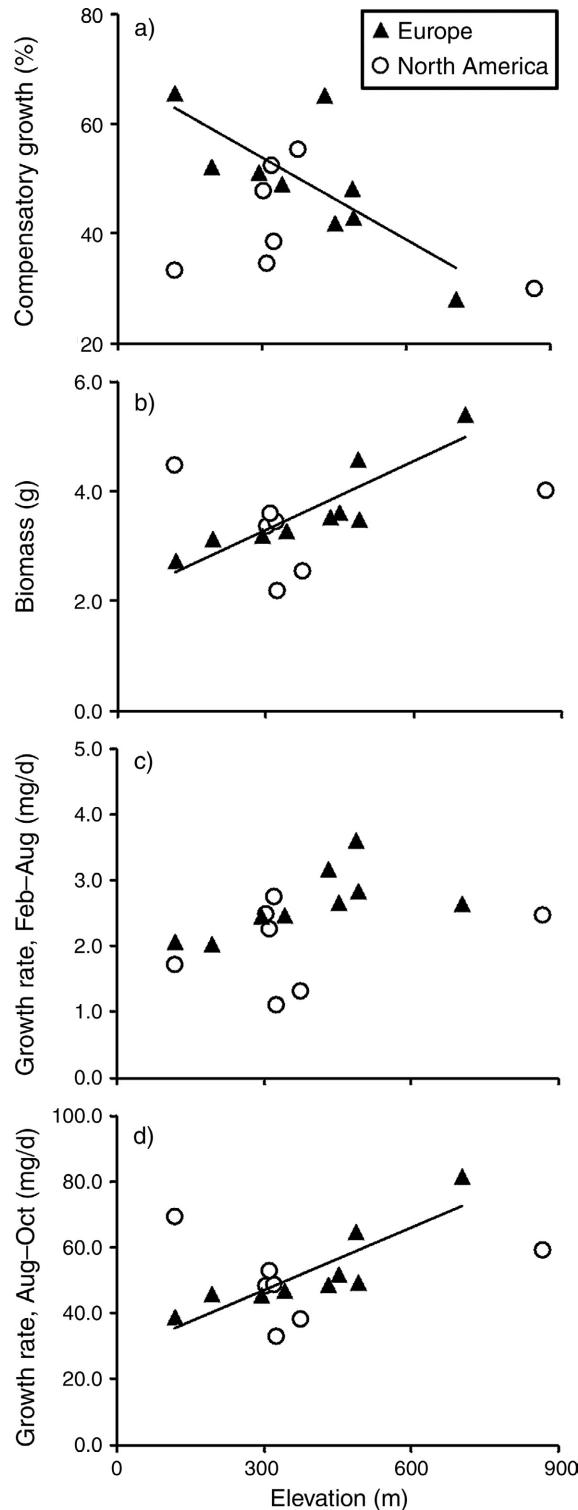


FIG. 1. Linear regressions between elevation and population means for (a) compensatory growth, (b) total biomass of controls, (c) growth rate of controls from February to August, and (d) growth rate of controls from August to October. Open circles represent North American populations and solid triangles represent European populations. Regressions for all traits, except for growth rate from February to August, for European populations are significant, whereas those for North American populations are not (refer to statistics in Tables 2; see R^2 and P values for the regressions in *Results*).

plants from the nonnative range have been found to show a concomitant decrease in resistance to herbivores and an increase in growth and fecundity, relative to plants from the native range (Meyer et al. 2005, Zou et al. 2008, Abhilasha and Joshi 2009). However, we found greater growth only in the context of response to damage. Our results suggest that the evolution of a stronger compensatory response might be a strategy to deal with consumers in nonnative ranges, where generalist herbivores and disturbance are not escaped.

Though evidence has shown that aboveground and belowground biomass allocation pattern can affect herbivory tolerance (Hochwender et al. 2012), we did not find this. Differences in compensatory growth between North American and European populations did not correspond with variation in root–shoot ratios.

We found an apparent trade-off between growth in the absence of herbivory and compensatory growth for nonnative European populations. In other words, as plant biomass and growth rate in the undamaged controls increased, compensatory growth decreased for European populations (Fig. 2a, c). This contrasts with other studies that have shown tolerance to herbivory, or compensatory growth, is often positively related to high growth rates (Stastny et al. 2005, Zou et al. 2008, Abhilasha and Joshi 2009). However, this result is consistent with modeled evolution of tolerance to herbivory indicating that highly herbivore-tolerant genotypes may not always grow vigorously (Stowe et al. 2000), and that being strongly tolerant to herbivory may incur fitness costs in an environment with low herbivore abundance (Strauss and Agrawal 1999). Compared to herbivory-intolerant genotypes with similar vegetative growth abilities, highly tolerant genotypes may be more adaptive to moderate damage (Stowe et al. 2000). In Europe, *S. gigantea* is almost certainly attacked less frequently by herbivores in general than conspecifics in North America, and there is little to no attack by specialists (Jakobs et al. 2004). Therefore, the increased compensatory responses observed for European populations may be adaptive to a scenario where disturbance and consumption by generalist herbivores are disproportionately more common causes of damage than specialist herbivores. Müller-Schärer et al. (2004) hypothesized that the absence of specialists is likely to favor an increase in low-cost qualitative chemical defense and a decrease in costly quantitative chemical defense, in which case, more energy could be reallocated to growth. For invaders that decrease in

American populations. However, plants from European populations were not larger in the absence of damage than plants from North American populations, which is consistent with other research (Meyer et al. 2005; R. W. Pal, unpublished data). For a number of invasive species,

TABLE 2. Results of mixed-effect linear models testing the effects of range, elevation, experimental stage, and population on the growth rates of unclipped controls and the final root:shoot ratios.

Source	Growth rate			Root-shoot ratio		
	df	<i>F</i> , <i>Z</i>	<i>P</i>	df	<i>F</i> , <i>Z</i>	<i>P</i>
Range	1.0	3.33	0.093	1.0	0.87	0.368
Stage	1.0	69.39	0.000	1.0	3.37	0.067
Elevation	1.0	6.07	0.030	1.0	0.33	0.574
Range × Stage	1.0	0.17	0.682	1.0	1.58	0.209
Range × Elevation	1.0	5.38	0.039	1.0	0.04	0.846
Stage × Elevation	1.0	6.14	0.014	1.0	0.03	0.856
Population (Range)	12.0	0.85	0.394	11.9	2.10	0.036
Error	237.0			235.0		

Notes: Range, elevation, experimental stage, and all two-way interactions among these three factors were tested as fixed factors, and population was nested within range as a random factor. Two outliers were excluded from the analysis of root-shoot ratio. The column labeled *F*, *Z* shows the *F* value for fixed effects and *Z* value for random effects. Values shown in boldface type represent significant effects ($P \leq 0.05$).

qualitative chemical defense in their nonnative ranges, increased growth may be manifest as a general trait with or without damage, or as increased compensation to damage. Therefore, in a subtle parallel to the prediction that invaders may reallocate energy from tolerance to growth in general (Blossey and Nötzold 1995, Müller-Schärer et al. 2004), our results indicate that some energy gained by escaping natural enemies might be allocated to compensatory response in invasive *S. gigantea* populations. Interestingly, such reallocation may also be important in highly disturbed habitats where many invasive species thrive.

When combined across the native and nonnative ranges, plants from high elevations, especially in the nonnative range, showed substantially weaker tolerance to damage than plants from low elevations. In addition, plants from European populations at high elevations were larger and grew faster than those from low elevations. This is consistent with Weber and Schmid (1998) who found *S. gigantea* populations from high elevation had higher relative growth rates in response to a shorter growing period than low elevation populations. Faster

growth should allow individuals to achieve maturity and reproduce in less time, which is thought to be adaptive to shorter growing seasons at high elevation (Kollmann and Bañuelos 2004, Alexander 2010). Our results show that either a range of elevation-adapted ecotypes has been introduced to Europe or that this ecotypic variation has evolved since introduction.

Environmental stress is thought to affect how plants cope with herbivory (Hawkes and Sullivan 2001, Wise and Abrahamson 2005). In general, plants show less tolerance to tissue injury under stressful conditions (e.g., low resources, high competition), than in favorable conditions (Maschinski and Whitham 1989). In the nonnative range, where there appears to be a lower elevational limit to the distribution of *S. gigantea* than in the native range, environmental conditions at high elevation may be stressful, selecting for decreased compensatory growth, perhaps because of limited genetic variation. Increased growth rate and decreased compensatory growth at high elevation suggests the possibility of a trade-off between developmental speed and the ability to compensate to herbivory. To calibrate elevations tested between North

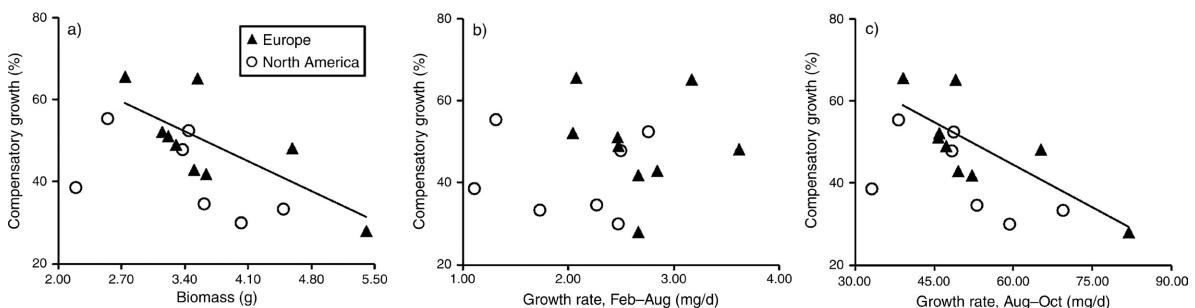


FIG. 2. Linear regressions for population means between compensatory growth and (a) total biomass of controls, (b) growth rate of controls from January to August, and (c) growth rate of controls from August to October. Open circles represent North American populations and solid triangles represent European populations. Regressions for European populations are significant, but those for North American populations are not (see R^2 and *P* values for the regressions in Results).

American and European populations of *Solidago gigantea*, we only compared populations from 100 to 900 m in each range, because the populations we sampled (i.e., east and central European populations) were below 900 m in elevation. *Solidago gigantea* has been reported at elevations up to 1,540 m in Europe (Becker et al. 2005), and if the species can form viable populations at these higher elevations, including them might provide greater insight into the evolution of elevational clines in herbivory tolerance, perhaps reversing our general findings.

Solidago gigantea is a clonal perennial, but we only tested the compensatory responses of seedlings. We do not know if adult rhizomatous *Solidago* plants would exhibit the same sort of compensation. It is also important to note that clipping, performed to keep damage level similar among individuals, often does not have the same effect on plants as natural herbivory (see Strauss and Agrawal 1999). Thus, actual herbivory may elicit responses that differ from ours. Also, we calculated compensation as the ratio between the biomass of the clipped individual and control in this study, creating a potential bias toward a negative correlation between biomass and compensation. However, we only found a significant correlation between biomass and compensation for European populations, indicating that our approach was not biased in a way that masked important biogeographic differences.

In summary, our results demonstrate greater compensatory response to damage by nonnative European *S. gigantea* populations than native North American populations. Furthermore, there was an apparent trade-off between compensation and growth rate in the nonnative range, which may result from rapid ecotypic evolution. These compensatory responses to damage by invasive plants might enable invaders to better withstand frequent disturbance and herbivory. However, at some point, the evolution of tolerance to herbivory is likely to be constrained by the adaptive evolution in response to environmental stress. For instance, faster growth at higher elevation may constrain the evolution of increased compensatory responses. Studying the evolution of compensatory growth, and the mechanisms that cause it, has the potential to shed light on subtle ways that escape from natural enemies might contribute to the spread and impact of exotic invasive plant species.

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