Evolutionary Ecology (2018) 32:547–559
https://doi.org/10.1007/s10682-018-9954-3

ORIGINAL PAPER

Evolutionary and environmental effects on the geographical adaptation of herbivory resistance in native and introduced *Solidago altissima* populations

Yuzu Sakata[1,2] · Timothy P. Craig[3] · Joanne K. Itami[3] · Mito Ikemoto[1,5] · Shunsuke Utsumi[4] · Takayuki Ohgushi[1]

Received: 3 March 2018 / Accepted: 10 September 2018 / Published online: 14 September 2018

Abstract

To understand rapid evolution in plant resistance to herbivory, it is critical to determine how the genetic correlation among resistances varies genetically and/or environmentally. We conducted a reciprocal transplant experiment of tall goldenrod, *Solidago altissima* with multiple replicates within the native range (USA) and the introduced range (Japan) to explore the differences in phenotypic traits of resistance to multiple herbivorous insects and their relationships between and within the countries. The Japanese plants were more resistant to the lace bug, *Corythucha marmorata*, which had recently invaded Japan, but were more susceptible to other herbivorous insects compared to the USA plants. An antagonistic relationship was found between plant resistances to lace bugs and other herbivorous insects in both USA and Japanese plants. In addition, this relationship was more obvious in gardens with a high level of foliage damage than in gardens with a low level of foliage damage by other herbivorous insects. An antagonistic relationship between resistances to aphids and lace bugs was also observed in USA gardens, but not in Japanese garden. These results suggest that the strength of constraints on the evolution of plant resistance due to genetic trade-offs may differ among biotic environments, including community structure of herbivorous insects. Therefore, differences in herbivorous insect communities between the native and introduced ranges can result in the rapid evolution of greater resistance in plants in the introduced range than in the native range.

Keywords Biological invasion · Plant-insect interaction · Plant defense · Reciprocal transplant experiment · *Solidago altissima*

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10682-018-9954-3) contains supplementary material, which is available to authorized users.

✉ Yuzu Sakata
sakatayuzu@gmail.com

Extended author information available on the last page of the article

Introduction

Plants with a wide geographic distribution, are subject to different selective pressures due to geographic variations in herbivory (e.g., Woods et al. 2012; Anstett et al. 2014; Bhattarai et al. 2016). Plant resistance is shaped by an evolutionary history shared with herbivores that interacts with an environment to form the genotype (G) x environment (E) interaction (Johnson and Agrawal 2005; Tack et al. 2010; Bhattarai et al. 2016). Since individual plants are usually attacked by multiple herbivore species, plants either evolve resistance to specific herbivores in a pairwise coevolutionary arms race, or respond simultaneously to multiple herbivores through diffuse coevolution (Agrawal 2005; Strauss et al. 2005; Berenbaum and Zangerl 2006). Therefore, plant resistance is an integrated system of different traits constrained by trade-offs in response to multiple herbivores.

Plant invasions provides an ideal opportunity to study how plant resistance evolves in response to changes in plant-herbivore interactions (Mitchell et al. 2006). For instance, exotic plants can escape from their natural enemies including specialized herbivorous insects in a new range (e.g., Elton 1958; Crawley 1987). The reduction in herbivory is hypothesized to lead to a shift in the resource investment from defense to growth and/or reproduction, resulting in the evolution of increased competitive ability (EICA) in the exotic populations (Blossey and Notzold 1995; Siemann and Rogers 2003; Colautti et al. 2004). The EICA hypothesis has been experimentally tested in numerous systems, however, there have been inconsistent results (Orians and Ward 2010). These conflicting outcomes could be due to an underlying G × E interaction that varies among the experimental sites. Large scale reciprocal transplant experiments (i.e., plant individuals from more than two populations are grown in their own environment and in the environments of the other populations) throughout the native and introduced ranges allow a clear separation of genetic and environmental effects on traits for plants that have wide geographic distributions (Nuismer and Gandon 2008; Kueffer et al. 2013). Plant traits are highly variable among sites (Maron et al. 2004; Moloney et al. 2009; Siemann et al. 2017), however, only a few of these studies compared herbivory between native and introduced ranges at multiple sites. Maron et al. (2004) found that the plant traits in different gardens were inconsistent within ranges due to an interaction effect between garden location and genetic provenance of the plants (a form of genotype by environment, (G × E) interaction). Here we conducted a reciprocal transplant experiment with multiple replicates within the native and introduced ranges of the tall goldenrod, *Solidago altissima*, to explore the differences in resistances against multiple herbivores between and within the native and introduced ranges.

S. altissima is an herbaceous perennial native to old-field habitats in North America. Several studies have found large genetic variability in goldenrod's resistance to insect herbivores (Maddox and Root 1987; Craig et al. 2007; Utsumi et al. 2011; Uesugi et al. 2013). In Japan *S. altissima* was introduced 100 years ago and it has extensively invaded abandoned fields across the country (Shimizu 2003). The lace bug, *Corythucha marmorata* (Hemiptera; Tingidae), is one of the major herbivorous insects feeding on *S. altissima* in the native range of North America (Cappuccino and Root 1992). It was introduced to Japan in 2000, and it is still expanding its distribution. Our previous study revealed that lace bug density increased as the annual temperature increased and as the other herbivorous insects decreased both in the USA and Japan. This indicates that the parallel abiotic and biotic factors drove the geographic variation in lace bug density, which in turn selected for variation in plant resistance (Sakata et al. 2017). In addition, while diverse taxa of herbivorous insects were observed in the USA, only a few of them were observed in Japan. Also, lace bug density was higher in Japan compared to the USA. These results suggest that the level of resistance to the herbivorous insects and the trade-offs among different resistances may differ between and within the USA and Japan due to differences in the insect community (Sakata et al. 2017). Thus, we hypothesized that there is a negative genetic correlation between resistances to lace bugs and other herbivorous insects, and that its degree differs across native and introduced ranges. In this study, we specifically asked whether the level of resistance to lace bugs and other herbivorous insects, and its relationships differed among (1) *S. altissima* origin populations between and within the native and introduced ranges, and (2) environments (garden location of the native and introduced ranges), and the interactions of these two factors.

Materials and methods

Multiple reciprocal transplant experiment

From June to August 2013, we collected *S. altissima* rhizome segments of 10 genotypes from plants at least 5 m apart from two populations in the USA (Minnesota and Kansas), and three populations in Japan (Saga, Shiga, and Yamagata). Sakata et al. (2016, 2017) showed that lace bugs were abundant on *S. altissima* populations in Kansas, Saga, and Shiga, while they were absent or at low densities on populations in Minnesota and Yamagata. The rhizome segments were planted in a greenhouse at the Center for Ecological Research, Kyoto University, and at the Research and Field Studies Center, University of Minnesota Duluth (Table 1), and cultivated for two growing seasons to remove historical effects. In April 2015, rhizomes were cut into 6 cm long segments with an average diameter of 5 mm; 25 ramets of each identical genotype were planted in pots and grown in the greenhouse. In the first week of June, five ramets per genotype of approximately the same size (250 plants in total) were planted in larger sized pots (30 cm in diameter) with culture soil and placed randomly in each of the five gardens (Table 1). The arrangement of the pots was identical in all the gardens. Because *S. altissima* ramets grow densely in natural populations, all of the pots were placed without space between them in all gardens. All plants were watered as needed for plant survival.

The number and species or families of herbivorous insects, levels of lace bug damage, and the number of leaves damaged by galls, mines, and chewing damage, excluding lace bug damage, which we term “foliage damage by other herbivorous insects” for each ramet were recorded once in the end of July. Lace bug herbivory can be distinguished from other insect herbivory by their yellow feeding scars. The level of lace bug damage (lace bug damage score) was assessed by classifying the damaged leaves into four levels: (1) no

Table 1 Locations of the five gardens used in the reciprocal transplant experiment

State (prefecture)	Country	Latitude	Longitude
Minnesota	USA	N 46.86	W 92.03
Kansas	USA	N 39.22	W 96.61
Yamagata	Japan	N 38.69	E 139.82
Shiga	Japan	N 34.97	E 135.96
Saga	Japan	N 33.24	E 130.28

damage, (2) < 33% damage, (3) 33–66% damage, and (4) > 66% damage of total leaf area. Subsequently, we counted the number of leaves in each damage level, and added the values for all four levels. We also counted the number of all leaves for all plants as a measure of the plant size. For further analyses, we used the number of lace bugs and aphids, *Uroleucon nigrotuberculatum* (Hemiptera; Aphididae), lace bug damage, and foliage damage by other herbivorous insects as resistance indices for herbivorous insects. We chose lace bugs and aphids because they were the widespread herbivores common in both countries.

Garden and population variations in number of herbivores and their damage

To test whether plant resistance is influenced by the evolutionary history with the biotic and abiotic factors and/or the environment (i.e., herbivorous insect community), we explored the effect of plant origin population and garden location on the number of lace bugs, aphids, lace bug damage score, and foliage damage by other herbivorous insects, using generalized linear mixed effects models (GLMMs) with a Poisson distribution. However, for aphids we did not include the effect of garden locations because they were absent in some gardens. Additionally, we conducted the GLMM analyses on the number of leaves to explore whether the plant growth is genetically and/or environmentally determined. The natural logarithm of the number of leaves was added into the model as an offset term to account for plant size except for the model predicting number of leaves. The origin of the plant population and garden location both have nested factors (i.e., states nested within a country). Because it is ecologically less informative to interpret the interactions between state-plant origins (the five locations that plants originated from) and state-garden location (the states where the gardens were located), we completed the two following analyses. First, we set state-plant origin, country-garden location (the USA garden or Japanese garden), and their interaction as explanatory variables. Second, we set country-plant origin (the USA plant or Japanese plant), state-garden location, and their interaction as explanatory variables. Country-garden location contrasted 50 USA and Japanese genotypes measured in USA gardens vs. Japanese gardens (pooling 2 USA populations and 3 Japanese populations) with 25 replicates (5 replicates for each five garden) per genotype. Country-plant origin contrasted 20 USA genotypes and 30 Japanese genotypes. We included genotypes nested within a garden and genotype nested within a population as a random effect in the first and second model, respectively. In the first analysis, we predicted that plant resistance would be influenced by differences in the environments (i.e., herbivorous insect community) between the USA and Japanese gardens, and the evolutionary history with the biotic and abiotic environments (i.e., genetic background) of the plant origin population among states, and their interactions. In the second analysis, we predicted that plant resistance would be influenced by differences in the environment of each garden and the evolutionary history with the biotic and abiotic environments of USA and Japan, and their interactions.

Next, we explored the relationships between the three resistance indices (aphids, lace bug damage score, and foliage damage by other herbivorous insects). We set the three resistance traits as response variables and set country-garden location, country-plant origin and their interaction as explanatory variables in the GLMM analyses. Note that for aphids we only included country-plant origin as an explanatory variable. We included genotypes as a random effect.

In all the GLMMs analyses described above, the significance of main effects and interactions was determined using a likelihood ratio test, compared to a Chi square distribution. All analyses were conducted using the "lme4" package (Bates et al. 2015) and "car" package (Fox and Weisberg 2011) of R 3.3.2 (R Development Core Team 2016). When the effect of a variable was significant, we tested for differences in resistance indices among gardens and plant origin populations using Tukey's honestly significant difference (HSD) test on least-squared means with the overall type I error rate at 5% using the "lsmeans" package (Lenth 2015) of R3.3.2.

Results

Garden and population variations in the number of herbivores and their damage

A wide range of herbivorous insects were found in the USA, whereas the dominant herbivores in Japan were the exotic lace bug and aphid (Table S1). The number of lace bugs, lace bug damage, and foliage damage by other herbivorous insects all differed significantly in terms of the country-garden location, the state-plant origin, and their interaction (Table 2a). The number of lace bugs and their damage were much higher in the Japanese gardens than in the USA gardens (Table 2a, Fig. 1a, b). Minnesota plants had the highest level of lace bug damage, Kansas and Yamagata plants had intermediate levels of lace bug damage, and Shiga and Saga plants had the lowest damage levels (Fig. 1b). The number of aphids differed among state-plant origin, and it was more than 50% lower on Minnesota and Shiga plants than on Kansas and Saga plants in the USA gardens (Table 2a, Fig. 1c). The foliage damage by other herbivorous insects was more than three times higher in the USA gardens than in the Japanese gardens, and it was lower on Kansas plants than on other plant origin populations in the gardens of both countries (Table 2a, Fig. 1d). For the number of leaves, the factors of country-garden location and state-plant origin were significant but their interaction was not significant (Table 2a). The number of leaves was 50% greater in the USA gardens than in the Japanese gardens (Fig. S1a).

The number of lace bugs did not differ between plants from the USA and Japan, but differed significantly among garden locations and the interaction of these factors (Table 2b). It was more than twice as high in the Shiga and Saga gardens as in the Minnesota and Kansas gardens (Fig. 1e). Lace bug damage differed significantly between USA and Japanese plants, among the five garden locations, and due to the interaction of these factors (Table 2b). It was more than twice as high as on USA plants than on Japanese plants (Fig. 1f). Both the number of lace bugs and their damage level were especially high in Shiga and Saga gardens for both country-plant origins (Fig. 1e, f). The number of aphids did not differ between USA and Japanese plants (Table 2b, Fig. 1g). Because the aphids were nearly absent in the Shiga and Saga gardens (only a few of them surviving per plant) during our survey, we were not able to analyze either the effect of the garden being located in the USA or Japan, or the effect of the five garden locations (Table 2, Fig. 1g). The foliage damage by other herbivorous insects differed between USA and Japanese plants, and among the five garden locations, and the interaction of these factors. It was 50% higher on Japanese plants than on USA plants in Minnesota, Yamagata and Saga gardens (Table 2b, Fig. 1h). For the number of leaves, the country-plant origin was not significant, but state-garden location and the interaction term were significant (Table 2b, Fig. S1b).

Table 2 GLMM that predicts the resistance indices and number of leaves per ramet of *S. altissima*

Explanatory variables	No. lace bugs		Lace bug damage		Other-herbivore damage		No. aphids		No. leaves	
	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
(a)										
Country-garden location	84.62	< 0.001	55.63	< 0.001	160.55	< 0.001	–	–	91.26	< 0.001
State-plant origin	40.62	< 0.001	96.18	< 0.001	49.78	< 0.001	490.23	< 0.001	19.21	< 0.001
Country-garden location × state-plant origin	113.90	< 0.001	55.60	< 0.001	27.25	< 0.001	–	–	9.06	0.06
(b)										
Country-plant origin	0.86	0.35	83.17	< 0.001	6.21	0.01	0.40	0.52	0.37	0.54
State-garden location	1459.08	< 0.001	1726.18	< 0.001	468.9	< 0.001	–	–	525.62	< 0.001
Country-plant origin × state-garden location	121.90	< 0.001	65.18	< 0.001	56.81	< 0.001	–	–	41.20	< 0.001
(c)										
Country-garden location			2063.16	< 0.001	591.1	< 0.001	–	–		
Country-plant origin			117.42	< 0.001	26.14	< 0.001	12.00	< 0.001		
Country-garden location × country-plant origin			0.01	0.92	9.56	0.002				

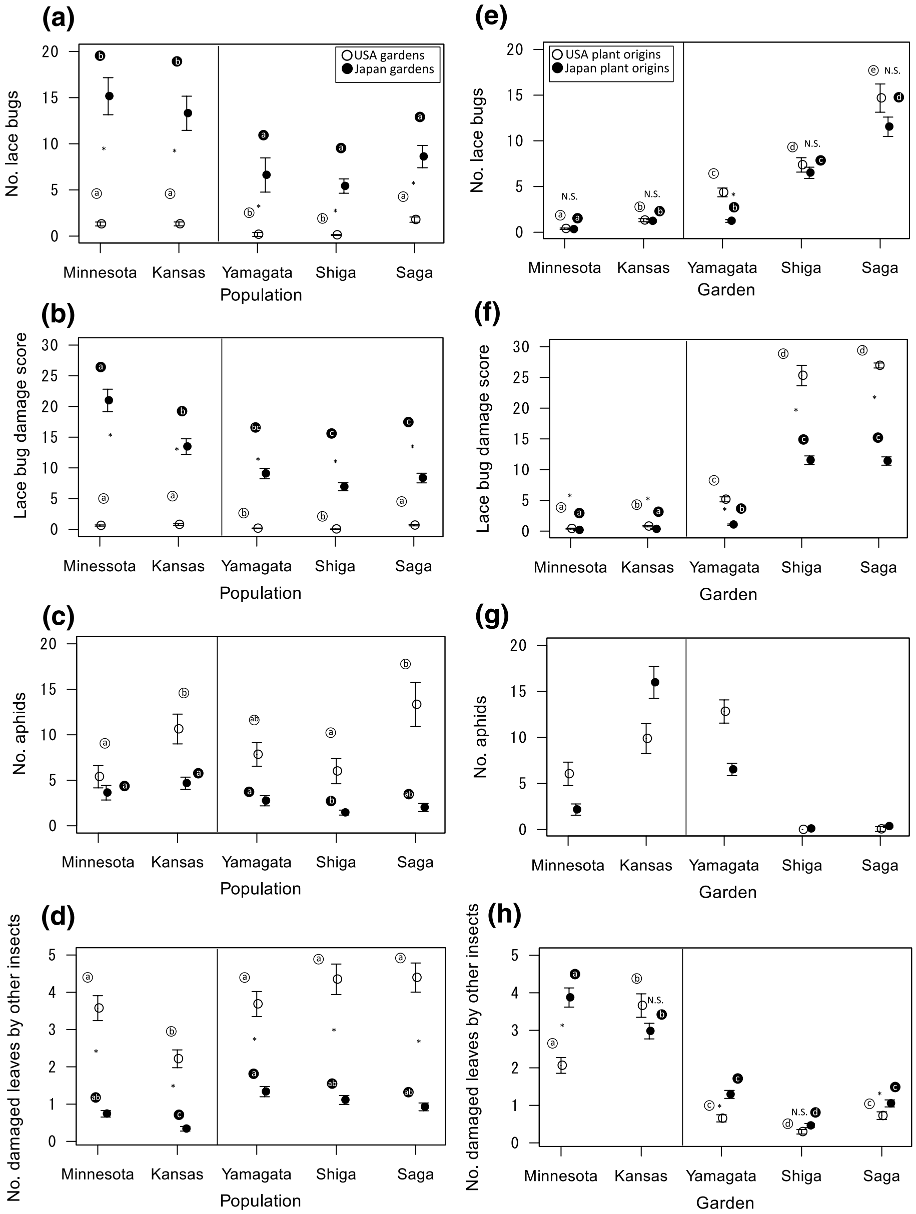

Fig. 1 Least square means (± SE) in the resistance indices of *S. altissima* in the multiple reciprocal transplant experiment among country-garden locations and state-plant origins (**a**–**d**), and among country-plant origins and state-garden locations (**e**–**h**). Different letters indicate significant pairwise difference after post hoc adjustment among state-plant origins in each country-garden locations (**a**–**d**) or state-garden locations in each country-plant origins (**e**–**h**). * or N.S. indicate significant ($P < 0.05$) or not significant difference between country-garden locations (**a**–**d**), or country-plant origins (**e**–**h**)

Relationships between plant resistances against different herbivores

USA plants had higher lace bug damage, but lower damage due to other herbivorous insects compared to Japanese plants in both USA and Japanese gardens (Fig. 2a, b). The effect of the country of the plant origin population on lace bug damage did not differ between USA and Japanese gardens, while it differed for the foliage damage by other herbivorous insects (Table 2c). USA plants had higher lace bug damage, but they had lower damage by aphids compared to Japanese plants in the USA garden (Fig. 2c). In other words, USA plants had higher resistance to both other herbivorous insects and aphids than Japanese plants (Fig. 2d). Minnesota, Kansas, and Yamagata plants, which had relatively higher lace bug damage than other plant origin populations, tended to have lower damage by other herbivorous insects (Fig. S2). The difference in lace bug damage among plant origin populations was greater in gardens with high lace bug damage. Conversely, the difference in the foliage damage by other herbivorous insects among plant origin populations was larger in Minnesota, Kansas, and Yamagata gardens, where the foliage damage by other herbivorous insects was high, than in Shiga and Saga gardens, where it was low. Plant origin populations with relatively higher damage by lace bugs tended to have lower damage by aphids in the USA gardens. However, in the Yamagata garden, plant origin populations that have relatively higher damage by lace bugs tended to have a higher damage by aphids as well. Kansas plants and Yamagata plants had relatively higher damage by aphids in the Minnesota garden, while Saga and Shiga plants had relatively higher damage by aphids in the Kansas garden. Yamagata plants tended to have relatively higher damage by both aphids and other herbivorous insects.

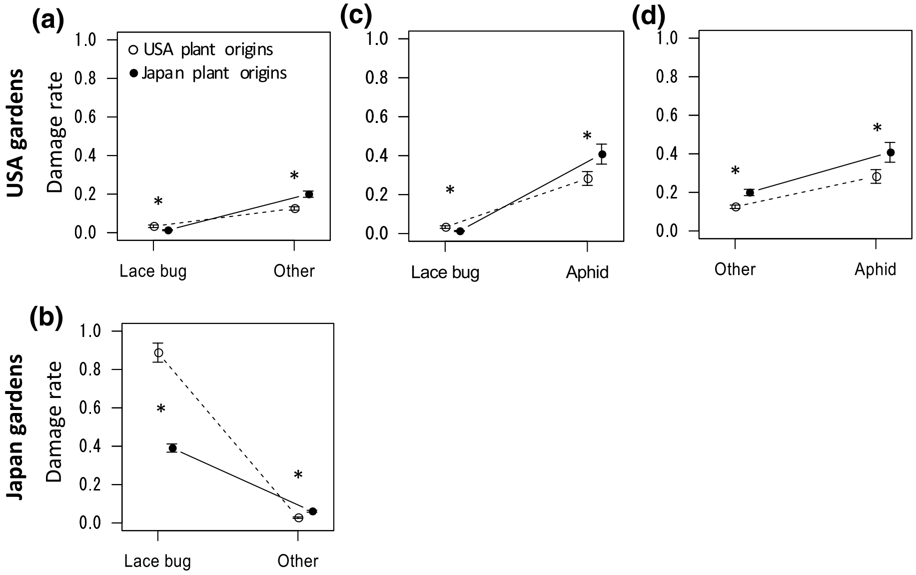

Fig. 2 Relationship between damage rate of lace bugs and other herbivorous insects (**a**,**b**), lace bugs and aphids (**c**), and other herbivorous insects and aphids (**d**) in Japan and USA plants in Japan and USA gardens, respectively. * indicates significant difference ($P < 0.05$) between Japan and USA plant populations. Damage rate is calculated by dividing the lace bug damage score, number of leaves damaged by other herbivorous insects, and number of aphids with the number of leaves, respectively

Discussion

Environmental and genetic differences in *S. altissima* resistance

The number of lace bugs and their damage to the plants were greater in the Japanese gardens than in the USA gardens (Fig. 1a, b), and foliage damage by other herbivorous insects was lower in the Japanese gardens than in the USA gardens (Fig. 1d). Although the number of leaves was greater in the USA gardens than in the Japanese gardens (Fig. S1a), this does not explain the differences in damage as the number of leaves was included as a factor in the analyses. Therefore, it is likely that mechanisms other than leaf availability influenced the difference in lace bug densities and their damage between the two countries. This result is consistent with Sakata et al. (2017), who found a higher density of lace bugs but a lower density of other herbivorous insects in natural populations of *S. altissima* in Japan compared to the USA. Other studies have also found highly diverse herbivore taxa on *S. altissima* in the USA (Root 1996), and few herbivores in Japan (Ando et al. 2010). While lace bug density did not differ significantly between USA and Japanese plants, lace bug damage was higher on USA plants, and foliage damage by other herbivorous insects was higher on Japanese plants (Fig. 1f, h). Herbivore damage may be a more accurate indicator of plant resistance than the number of insects because it measures the accumulation of herbivory throughout the growing season, in contrast to insect number which represents only a single point in time. Thus, our results suggest that the Japanese plants exhibited higher resistance to the lace bugs, but lower resistance to other herbivorous insects than USA plants due to the differences in selective pressure by the herbivorous insects between the two countries. Conversely, USA plants had higher resistance to other herbivorous insects, but lower resistance to lace bugs.

Resistance differences between plants from the two countries may be the result of differences in allocation of defense against lace bugs and other herbivorous insects. Rapid changes in resource allocation to defense have also been reported in other studies on invasive plants (Orians and Ward 2010). However, in the gardens of Kansas and Shiga, where foliage damage by other herbivorous insects was the highest and lowest respectively, no significant difference in resistance were found between USA and Japanese plants (Fig. 1h). This is likely due to the interaction of the abiotic or biotic environments of the gardens with the genetic differences in plant resistance between the two countries. Foliage damage by other herbivorous insects was especially low on Kansas plants compared to plants from the other populations (Fig. 1d). Although the foliage damage by other herbivorous insects was not as high as in the Minnesota garden, the damaged area per leaf was greater in the Kansas garden compared to other gardens (Sakata unpublished data). Thus, the higher damage level by other herbivorous insects in Kansas may have selected for the higher resistance to other herbivorous insects in Kansas plants compared to that in other plant origin populations.

It is exemplified that the aphids reduce their colony size when the maximum air temperature exceed 35 °C (Adachi et al. 2015). Because our survey was conducted during the summer, the low aphid density in Japanese gardens (especially in Saga and Shiga, see Fig. 1g) may have been due to the decrease in aphid colony size as a result of the hot climate. Although the number of aphids differed among the five plant origin populations, it did not differ overall between USA and Japanese plants indicating that the resistance to aphids differs locally within the country. We suggest that local evolutionary history (i.e., interaction with local climate or herbivorous insect community) rather than invasion history is responsible for the level of *S. altissima* resistance to the aphid. The significant effect of G by E (country-plant origin × state-garden location, and state-plant origin × country-garden location) in all resistance indices suggests that the phenotypic variation in the resistance to herbivores is due to the differences in selective pressure and/or gene expression among environments.

Relationships between plant resistances against different herbivores

The pattern of Japanese plants being more resistant to lace bugs, but more susceptible to other herbivorous insects compared to USA plants, can be explained by allocation differences based on the genetic correlations that produces a trade-off between the two types of resistances against different herbivores. Our results suggested that there was an antagonistic relationship between resistances to lace bugs and other herbivorous insects: plant origin populations that have relatively higher resistance to lace bugs were less resistant to other herbivorous insects. Moreover, the difference in resistance to other herbivorous insects between USA and Japanese plants was larger in the Minnesota, Kansas and Yamagata gardens, where lace bug density was low, than in the Shiga and Saga gardens, where lace bug density was high. This may be because, when lace bug densities are high, not only low-resistant plants against lace bugs but also high-resistant plants would receive severe lace bug damage, leading to decrease colonization rates of other herbivorous insects due to a decrease in foliage quality. In contrast, where lace bug densities are low, other herbivorous insects clearly respond to differences in genotypic variation in plant resistance.

Alternatively, the differences in evolutionary history of *S. altissima* and its herbivorous insects between the USA and Japan may affect the strength of antagonistic relationship among resistance traits. Because in the USA various herbivorous insects share a long evolutionary history with both *S. altissima* and lace bugs, specialized defensive traits may have evolved against these herbivorous insects, and a trade-off between specific resistance to lace bugs and other herbivorous insects may be solid as a result of coevolutionary processes. In contrast, in Japan other herbivorous insects share only a short evolutionary history with the introduced *S. altissima* and lace bugs. Thus, resistance to other herbivorous insects may be realized by generalized defensive traits against various herbivores so that the trade-off between resistances to other herbivorous insects and lace bugs might be weaker in the Japanese garden. These two explanations are not mutually exclusive. Therefore, in the environment with low foliage damage by other herbivorous insects, the genetic association between resistances to lace bugs and other herbivorous insects may not constrain the evolution of resistance to lace bugs due to weaker antagonistic relationship of the two resistances. This may be the underlying mechanism for driving rapid evolution of the enhanced defense against the lace bugs in approximately 10 years in Japan (Sakata et al. 2014). The latter explanation may also be responsible for the differences shown for the genetic trade-offs in resistances between lace bugs and aphids in the USA and Yamagata gardens. An antagonistic relationship between resistances to lace bugs and aphids in the USA gardens was suggested, however in the Yamagata garden, the only garden in Japan where aphids were present, a positive relationship was seen between resistances to lace bugs and aphids. In addition, although local adaptation in plant resistance to aphids from the their local population was not observed, the plant origin populations that had relatively higher resistance to aphids differed among gardens. These results suggest that the aphids in the USA and Japan may be genetically differentiated. The genetic trade-off exists between specific resistance to lace bugs and that to aphids due to long evolutionary history of the two insects and *S. altissima* in the USA. On the other hand, the lace bugs and aphids in Yamagata have jointly interacted with the plants for less than 5 years, and only a generalized resistance to both lace bugs and aphids may have evolved, resulting in a positive relationship between the two resistances.

Overall, these results suggest that the strength of constraints on the evolution of plant resistance due to genetic trade-offs differs among biotic environments, including community structure of herbivorous insects. Therefore, differences in herbivorous insect communities between the native and introduced ranges can result in the rapid evolution of greater resistance in plants in the introduced range than in the native range.

The antagonistic relationships in resistance to different herbivorous insects may be due to the two mechanisms. First, there may be negative genetic associations between genes encoding resistant traits, in other words, antagonistic relationships between signal transduction pathways (Paul et al. 2000; Leimu and Koricheva 2006). Second, there may be genetic variation in only one specific resistance trait that has antagonistic relationships with other traits. For example, there may be behavioral avoidance by an herbivorous insect of plant genotypes that have been colonized by a high density of the other herbivorous insects (Halitschke et al. 2011; Poelman and Kessler 2016; Ando et al. 2017). Although we cannot completely differentiate between the patterns produced by these two mechanisms, there is evidence supporting the first mechanism from previous studies showing labile genetic variation in *S. altissima* resistance to aphids and several leaf-chewing insects (Maddox and Root 1987; Utsumi et al. 2011). This suggests that genetic variation exists in several resistant traits that are genetically constrained. Future studies are needed to assess the response of each herbivore species independently in order to determine whether the negative relationship is truly based on a genetic trade-off between resistant traits.

Our multiple reciprocal transplant experiment revealed that the local environment has a critical impact on plant resistance, and so measuring plant traits in a single site in each range could mask the geographic variation within a range. This is especially true when populations are sampled from different localities or limited parts of their broad environmental gradients (Colautti et al. 2009; Moloney et al. 2009). In addition, plant resistance to herbivores differed among populations within each country. Comparing a species across multiple sites makes us recognize that populations (often representing different genotypes), but not species, become invasive (Parker et al. 2013). An evaluation based on populations is critical in understanding evolutionary ecology of invasive plants.

Acknowledgements We greatly appreciate T. Ida, K. Hashimoto, S. Hirano, S. Yamamura, M. Tokuda, S. Adachi, A. Yamasaki, and members of Laboratory of Systems Ecology in Saga University and Laboratory of Animal Ecology in Yamagata University for field work assistance. The present study was partly supported by the Japan Society for the Promotion of Science (JSPS) through Grant-Aid for Science Research (B-25291102) to T. O.

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Affiliations

Yuzu Sakata[1,2] · **Timothy P. Craig**[3] · **Joanne K. Itami**[3] · **Mito Ikemoto**[1,5] ·
Shunsuke Utsumi[4] · **Takayuki Ohgushi**[1]

[1] Center for Ecological Research, Kyoto University, Otsu 520-2113, Japan

[2] Department of Biological Environment, Akita Prefectural University, Akita 010-0195, Japan

[3] Department of Biology, University of Minnesota Duluth, Duluth, MN 55812, USA

[4] Uryu Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Horokanai, Hokkaido 074-0741, Japan

[5] Department of Life and Environmental Sciences, University of Tsukuba, Tsukuba 305-8572, Japan