Community structure of insect herbivores on introduced and native *Solidago* plants in Japan

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Abstract

We compared community composition, density, and species richness of herbivorous insects on the introduced plant *Solidago altissima* L. (Asteraceae) and the related native species *Solidago virgaurea* L. in Japan. We found large differences in community composition on the two *Solidago* species. Five hemipteran sap feeders were found only on *S. altissima*. Two of them, the aphid *Uroleucon nigrotuberculatum* Olive (Hemiptera: Aphididae) and the scale insect *Parasaissetia nigra* Nietner (Hemiptera: Coccidae), were exotic species, accounting for 62% of the total individuals on *S. altissima*. These exotic sap feeders mostly determined the difference of community composition on the two plant species. In contrast, the herbivore community on *S. virgaurea* consisted predominately of five native insects: two lepidopteran leaf chewers and three dipteran leaf miners. Overall species richness did not differ between the plants because the increased species richness of sap feeders was offset by the decreased richness of leaf chewers and leaf miners on *S. altissima*. The overall density of herbivorous insects was higher on *S. altissima* than on *S. virgaurea*, because of the high density of the two exotic sap feeding species on *S. altissima*. We discuss the importance of analyzing community composition in terms of feeding guilds of insect herbivores for understanding how communities of insect herbivores are organized on introduced plants in novel habitats.

Introduction

Introduced plants often have insect communities that differ in species richness, species composition, and density from those on native plants (Tallamy, 2004). As a result, the introduction of plants may have cascading effects on the ecological community that may reach as far as influencing the avian community (Burghardt et al., 2009). The first step for understanding the impacts of plant introduction on ecological communities is to know how herbivore communities are organized newly on introduced plants (Sax et al., 2007). This question has become increasingly important, because species ranges are rapidly shifting in response to global climate change and/or human transport (Cadotte et al., 2006; Parmesan, 2006). An important method for measuring the impact of plant introductions

on community structure is to compare the insect communities on introduced plants and closely related native plants that occupy similar niches and that have been displaced by the introduced species. Several studies have indicated that introduced plants have fewer species of herbivorous insects than native plants of the same genus (Goeden, 1974; Jobin et al., 1996; Wolfe, 2002; Frenzel & Brandl, 2003; Mitchell & Power, 2003), but perhaps more importantly there are differences between native and introduced plants in herbivore community composition in the relative abundance of species, species richness, and feeding guild composition. Introduced plant species often lack the specialized herbivores from their native range, and they are not attacked by specialists from their new habitat (Strong et al., 1984). Rather, introduced plants are more likely to be attacked by polyphagous native species (Connor et al., 1980; Strong et al., 1984; Jobin et al., 1996).

The association of insect herbivores with introduced plants largely depends on their feeding mode. Several studies have reported that the species richness of endophagous

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insects such as leaf miners and gallmakers is lower on introduced plants than on related native plants (Goeden & Ricker, 1986a; b; Jobin et al., 1996; Frenzel & Brandl, 2003), whereas chewers and sap feeders more readily colonize introduced species. The degree of specialization tends to be higher in endophagous than in ectophagous insects (Strong et al., 1984; Cornell & Kahn, 1989; Mopper, 1996), and specialized insects need more time to adapt to novel host plants (Strong et al., 1984; Cornell & Kahn, 1989; Gaston et al., 1992). The 'enemy release hypothesis' states that some introduced species owe their spectacular success to escape from attack by native herbivorous insects (Callaway & Maron, 2006), and this has generated interest in studying the community structure of herbivorous insects on introduced plants. To explain introduced plant success, most studies have focused mainly on overall species richness, although several studies have reported species richness of various taxa, feeding guilds, and feeding breadth (generalist vs. specialist) (e.g., Jobin et al., 1996). Furthermore, only a few studies have explored the abundance of herbivorous insects established on introduced plants (Yela & Lawton, 1997; Frenzel & Brandl, 2003; Agrawal et al., 2005).

It is essential to investigate not only species richness but also abundance-based characteristics of herbivore communities because relative abundance is one of the important components organizing community structure. In addition, to understand the nature of newly established interactions between introduced plants and a wide array of herbivores, we should accumulate evidence about how community structure is different in terms of species composition, species richness, feeding guild structure, and abundance of herbivores between native and introduced plants.

More than 100 years ago, *Solidago altissima* L. (Asteraceae) was introduced into Japan from North America as an ornamental plant (Shimizu, 2003). It has spread rapidly throughout Japan and has now become one of the most abundant weeds in urban areas. The aim of this study was to understand the organization of the herbivore communities on *S. altissima* by comparing its herbivore community and that of a related native species, *Solidago virgaurea* L., in the same habitat in Japan. We examined how the species composition, density, and species richness of the feeding guilds of insect herbivores differed between *S. altissima* and *S. virgaurea*. This study is intended not to unravel a general pattern of the difference in herbivore communities between native and introduced plants, but to examine how different responses of herbivorous insect species in terms of feeding modes to plants shift the community composition between an introduced and native *Solidago*.

Materials and methods

Plants

In Japan, the tall goldenrod, *S. altissima*, in the *Solidago* subsection Triplinervae, emerges from overwintering rhizomes as the ground warms in April, and its shoots grow continuously until September. Flowering occurs from late October to November. Although aboveground shoots disappear in winter, rhizome connections persist for up to 5–6 years (Cain, 1990). *Solidago altissima* is tolerant of a wide range of soil types, high fertility levels, and moisture regimes (Abrahamson et al., 1983). *Solidago virgaurea* is in the *Solidago* subsection Solidago, which is native to Japan. This native *Solidago* is widely distributed and a common herb in sunny forests, fields, and roadsides. Although *S. virgaurea* prefers dry soil, both species often occur in the same habitat, including river-floodplains and hills. The phenology of *S. virgaurea* is similar to that of *S. altissima*. *Solidago virgaurea* reproduces both vegetatively and sexually by producing seeds, and it emerges in April. Shoots grow continuously until September and flowering occurs from September to late October. Both *S. virgaurea* and *S. altissima* have short trichomes on the leaves, but only *S. altissima* has short trichomes on its stems. Leaves of *S. altissima* and *S. virgaurea* contain various polyphenol compounds such as flavonoids and caffeic acid derivatives (Björkman & Holmgren, 1960; Jin et al., 2008), but the similarity of the chemical compositions between the two species is unclear.

Census of insect herbivores

This study was performed in 2000 and 2001 in a 0.75-ha field of the Experimental Forest of the Field Science Education and Research Center of Kyoto University in Kyoto, central Japan (35°04′N, 135°46′E; altitude 109 m, annual mean temperature 14.6 °C, and mean precipitation 1 582 mm). In this study site, *S. virgaurea* and *S. altissima* grew intermixed. To compare the communities of herbivorous insects on *S. altissima* and *S. virgaurea*, we randomly selected 80 large, healthy plants of each species in early April in 2000 and 2001. On the plants selected in each year, we conducted censuses of insect herbivores three times a week from mid-May to late October in each year (67 times in 2000, 80 times in 2001). The abundance of each herbivorous insect species was recorded on each plant. By field observation and laboratory experiments, we confirmed whether each herbivore species feeds on either or both of the two *Solidago* species. Herbivorous insects were identified to species using field guides (Kawai, 1980; Moritsu, 1983; Nakane et al., 1984; Inoue et al., 1985; Asahina et al., 1986) and a published report (Sugimoto & Matsumoto, 2000), and they were classified into three feeding guilds:

leaf chewer, sap feeder, and leaf miner. We then performed a Mann–Whitney U-test to compare species richness and density of each feeding guild and of the overall herbivorous communities between the two plant species.

To illustrate how herbivore communities differed between the two plants, we used a non-metric multidimensional scaling analysis (NMDS) with a Bray–Curtis dissimilarity coefficient. This is a robust technique which represents samples as points in low-dimensional space (usually two dimensions) such that the relative distances apart, of all points, are in the same rank order as the relative dissimilarities of the samples (Minchin, 1987). Points that are close together represent samples that are very similar in species composition. The Bray–Curtis dissimilarity coefficient is widely used to analyze community structure, because it ignores absent data of species or groups, so that rare species or groups have little influence on the coefficient (Krebs, 1989). For this analysis, the numbers of each feeding guild in 2000 and 2001 were averaged. They were log(n + 1)-transformed and standardized by variance prior to calculating the coefficient.

An optimal NMDS solution was obtained by minimizing the stress value as described in Clarke & Gorley (2001). The stress value (goodness of fit of the NMDS plot) is an index to indicate how faithfully the high-dimensional relationships among samples are represented in a two-dimensional ordination plot. The stress value, which decreases as the rank-order agreement between distances and dissimilarities improves, was calculated as described by Kruskal (1964). When stress values are ≤0.1, the NMDS plot is considered to be an acceptable representation (Clarke, 1993). The relationships among samples were represented in a plot of the first two dimensions of the NMDS solution. Then, the difference in herbivorous insect communities between the two plants was determined by R value in an analysis of similarity (ANOSIM; Clarke, 1993). This analysis uses nonparametric permutation/randomization methods with a dissimilarity matrix (Clarke, 1993). In addition, we used similarity percentages (SIMPER) to identify which feeding guilds primarily accounted for the difference in herbivorous insect communities between the two plants. SIMPER is used to examine the contribution of each species or group to the average Bray–Curtis dissimilarity between samples (Clarke, 1993). We conducted NMDS, ANOSIM, and SIMPER analysis using the software program PRIMER-5 version 5.2.9 (Plymouth Marine Laboratory, Plymouth, UK).

Results

Community composition of insect herbivores

Non-metric multidimensional scaling analysis of the dissimilarity of the herbivore communities clearly showed that the community composition on *S. altissima* differed markedly from that on *S. virgaurea* (ANOSIM: n = 80, R = 0.01, P = 0.001; Figure 1). SIMPER analysis indicated that sap feeders, leaf miners, and leaf chewers accounted for 80, 11, and 9% of the dissimilarity of community compositions on the two plant species, respectively. Thus, the sap feeders contributed most strongly to the dissimilarity of community composition between the introduced and the native *Solidago*.

We recorded 20 herbivorous insect species in six orders including 11 families on *S. altissima*, and 19 herbivorous species in five orders including eight families on *S. virgaurea* (Appendices 1 and 2). There was a large difference in species composition of the communities on the two plants. Of the total 1 083 421 individuals found on *S. altissima* (Figure 2), 61.8% were two introduced sap feeders: an aphid (*Uroleucon nigrotuberculatum* Olive, species code 13), and a scale insect (*Parasaissetia nigra* Nietner, species code 17), both of which were observed only on *S. altissima*. Another sap feeder, *Nephotettix cincticeps* Uhler (species code 20), accounted for 10.2% of the total individuals, and it was also found exclusively on *S. altissima*. Other herbivorous insects comprised <10% of the total individuals, most of which also attacked *S. virgaurea*. The total 165 903 individual herbivores observed on *S. virgaurea* were predominately native insects. A dipteran leaf miner, *Phytomyza horticola* Goureau (species code 10), and two leaf chewers, the geometrid *Ascotis selenaria cretacea* Butler (species code 5) and Geometridae spec. 1 (species code 6), comprised 12.8, 12.3, and 10.6% of the total individuals, respectively (Figure 2). The most abundant leaf miner, *P. horticola*, was found only on *S. virgaurea*. Each of the remaining species constituted <10% of the total individuals.
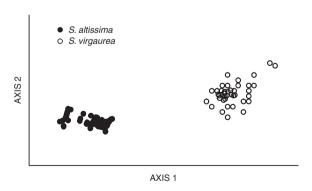

Figure 1 Non-metric multidimensional scaling analysis (NMDS) ordination of herbivore insect communities on *Solidago altissima* and *S. virgaurea* (NMDS stress = 0.01; ANOSIM: R = 0.01, P = 0.001).
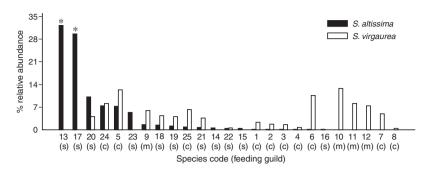
Figure 2 Relative abundance of herbivorous insect species on *Solidago altissima* and *S. virgaurea*. Total numbers of individuals were 1 083 421 and 165 903 on *S. altissima* and *S. virgaurea*, respectively. Each species is indicated by the species code and feeding guild (s: sap feeder, c: leaf chewer, m: leaf miner) in Appendices 1 and 2. Asterisk indicates exotic insect species.
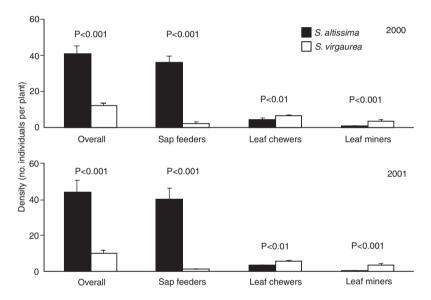

Figure 3 Mean (+ SE) overall and guild densities of herbivorous insects on *Solidago altissima* and *S. virgaurea* in 2000 (top) and 2001 (bottom).

Herbivore density

Solidago altissima had a significantly higher overall density of herbivorous insects than *S. virgaurea* in both years (Mann–Whitney U-test: U = 0, P<0.001 in 2000 and 2001; Figure 3). The difference was primarily due to the high densities of the two sap feeding exotic species, the aphid *U. nigrotuberculatum* and the scale insect *P. nigra*, on *S. altissima*. Sap feeders had a significantly higher density on *S. altissima* than on *S. virgaurea* in both years (U = 0, P<0.001 in 2000 and 2001). In contrast, leaf chewers and leaf miners had significantly lower densities on *S. altissima* than on *S. virgaurea* (U = 19 for leaf chewers, U = 0 for leaf miners in 2000; U = 0 for leaf chewers and leaf miners in 2001; P<0.001 in all four cases).

Herbivore species richness

There were no significant differences in the overall species richness of herbivorous insects on the two plant species in either year (U = 3 031, P = 0.56 in 2000; U = 3 006, P = 0.51 in 2001; Figure 4). However, *S. altissima* had significantly more species of sap feeders and fewer species of leaf chewers and leaf miners than *S. virgaurea* (U = 796 for leaf chewers, U = 1 218 for leaf miners, U = 1 067 for sap feeders in 2000; U = 124 for leaf chewers, U = 0 for leaf miners and sap feeders in 2001; P<0.001 in all six cases).

Discussion

We found large differences in the insect community composition on a native and an introduced *Solidago*, and these
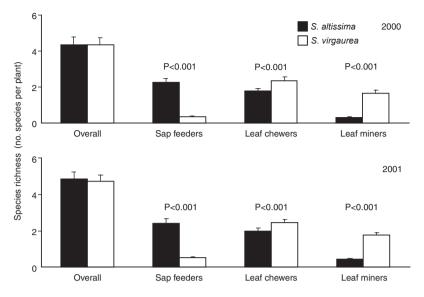
Figure 4 Mean (+ SE) overall and guild species richness of herbivorous insects on *Solidago altissima* and *S. virgaurea* in 2000 (top) and 2001 (bottom).

differences had important consequences for the understanding of the overall density and species richness of insect herbivores on introduced plants.

Overall and guild density of insect herbivores on introduced and native *Solidago*

We found a higher overall density of insect herbivores on the introduced *Solidago*. However, closer examination of the patterns underlying this simple measure showed important differences between the plants. The overall herbivore density on *S. altissima* was significantly higher than that on *S. virgaurea* due to high densities of the two introduced sap feeders, the aphid *U. nigrotuberculatum* and the scale insect *P. nigra*, found only on *S. altissima*, which comprised 61.8% of the total abundance. *Uroleucon nigrotuberculatum*, plays an important role in structuring the community of herbivores on *S. altissima* through ant- and plant-mediated indirect effects (Ando & Ohgushi, 2008). Thus, it has the potential to make a strong contribution to the large differences in community structures of herbivorous insects on introduced and native *Solidago*. In contrast, most native insects, including leaf chewers and leaf miners, had significantly lower densities on *S. altissima* than on *S. virgaurea*. This indicates that different feeding guilds respond to the two plants in a different manner. A similar pattern was found by Cripps et al. (2006) who showed that a greater abundance of herbivorous insects on Brassicaceae in novel habitats compared with those in original habitats was caused by an increase in polyphagous sap feeders in spite of a decrease in other herbivorous insects.

The two most abundant insect herbivores on *S. altissima* are exotic species: the aphid *U. nigrotuberculatum* came from North America in the 1990s, and the scale insect *P. nigra* came from Africa (CABI/EPPO, 2005). Why have these two exotic insects become dominant on the introduced *S. altissima* in this study area? Although little information is available on the scale insect, the aphid commonly occurs on *S. altissima* in North America, but at a lower density than we observed (Maddox & Root, 1990). The 'enemy release hypothesis' (ERH) states that the high abundances of exotic herbivorous insect species are often due to the absence of natural enemies that control their density in their original habitat (Settle & Wilson, 1990). In North America, there are at least seven predators and two parasitoids that attack the aphid (Moran, 1986). In contrast, we observed no parasitoids and only two predators, the ladybird *Coccinella septempunctata* (L.) and the crab spider *Misumenops tricuspidatus* (Fabricius), and predation was very low in our study area (Y Ando, pers. obs.). The low predation pressure may therefore have allowed these exotic insects to reach high densities on the introduced *S. altissima*.

An alternative hypothesis to ERH explaining the high aphid densities on *S. altissima* is that introduced plants lack defenses against specialists such as aphids. Joshi & Vrieling (2005) hypothesized that because introduced plants in their new habitat are primarily attacked by generalists and not specialists the plants have evolved to invest more in defenses against generalists and less in defenses against specialists. The aphid is a specialist mainly feeding on *S. altissima* in North America, and its recent introduction

into Japan may have allowed it to take advantage of the lack of specialized defenses against aphids that were lost during the 100 years in Japan when the aphids were absent. As a result aphid densities are much higher on *S. altissima* in this study area than in their native range in North America. These two hypotheses, however, are not mutually exclusive. Aphids would take greater advantage of the absence of natural enemies and/or the lack of specialized plant defense to utilize *S. altissima* than native, generalist herbivorous insects. Aphids on *S. altissima* fit the pattern that exotic specialist herbivorous insects often become dominant in their introduced range (Keane & Crawley, 2002; Strayer et al., 2006).

Species richness and relative abundance are both important aspects of community structure, but measures of relative abundance of insect herbivores on introduced plants are rare. Several studies have demonstrated that community structure can be altered through changes in the relative abundance of species even when species richness remains constant (Magurran, 1988; Stirling & Wilsey, 2001). Our study revealed that insect herbivore guilds responded differently to the native and introduced *Solidago* species. Sap feeders, especially exotic species, made a large contribution to the differences in community structure on the two plants. Our study demonstrates that abundance-based studies are necessary in order to understand the differences in community structure of herbivorous insects on native and introduced plants.

Overall and guild species richness on introduced and native *Solidago*

Overall species richness of herbivorous insects on introduced plants is often lower than that on native plants (Goeden, 1974; Jobin et al., 1996). In this context, escape from natural enemies has frequently been proposed to explain the success of introduced plants (Keane & Crawley, 2002; Shea & Chesson, 2002). However, not all feeding guilds show decreased species richness on introduced plants. For example, the species richness of sap feeders on introduced *S. altissima* in Switzerland was higher than that on native *S. virgaurea*, although total species richness was lower on *S. altissima* than on *S. virgaurea* (Jobin et al., 1996). We found that overall species richness did not differ between the two plant species, but the species richness of feeding guilds responded to *S. altissima* and *S. virgaurea* in different ways. The lack of difference in overall species richness between the two plants resulted because the increased species richness of sap feeders was offset by the decreased species richness of leaf chewers and leaf miners on *S. altissima*. As in Switzerland, we also found higher species richness of sap feeders on introduced *S. altissima*, compared with the native *S. virgaurea*. In contrast, species

richness of leaf chewers and leaf miners was significantly lower on *S. altissima* than on *S. virgaurea*.

Introduced plants are often highly colonized by polyphagous leaf chewers and sap feeders, resulting in a low ratio of monophagous to polyphagous species on introduced plants (Connor et al., 1980; Strong et al., 1984; Goeden & Ricker, 1986b; Frenzel & Brandl, 2003; Parker & Gilbert, 2004). Jobin et al. (1996) showed that 97% of 55 herbivorous insect species on introduced *S. altissima* in Switzerland were polyphagous. We also found that at least 85% of 20 herbivorous insect species on introduced *S. altissima* were polyphagous. In contrast, in North America most of the insect herbivores that utilize *S. altissima* attack only plants in the genus *Solidago* or only certain *Solidago* species within the genus. On the introduced *S. altissima* in this study area, there were no gallmakers, only one Agromyzidae leaf miner, and one monophagous exotic aphid, whereas in North America *S. altissima* is commonly attacked by 8–18 species of gallmakers and/or leaf miners (Maddox & Root, 1990; Abrahamson & Weis, 1997).

We documented large differences in the community structure of herbivorous insects on the introduced and native *Solidago* species. We also showed that overall measures of species richness and abundance are insufficient to understand the community structure because of the differential responses of different feeding guilds. Two species of sap feeders on the introduced *Solidago* were the main contributors to the differences in community structure. Although we cannot make generalizations based on a single comparison, this study suggests research directions that will improve the understanding of herbivorous insect communities on introduced plants. In particular, more research is needed on the interactions of plants and exotic specialized insects that have been introduced from the native range of the plants because they have a strong potential to structure the entire community. Also, because different feeding guilds respond differently to introduced plants, studies that measure the abundances of insect herbivores in different guilds will improve our understanding of the development of herbivore community structures on introduced plants.

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Appendix 1
Herbivorous insect species found on the introduced plant *Solidago altissima* in 2000 and 2001

Species and code	Stage	Feeding guild	Native or exotic[1]	Host plant
Coleoptera				
Chrysomelidae				
1. *Aulacophora femoralis*	Adult	Leaf chewer	Native[2]	a, v
2. *Chrysolina aurichalcea*	Adult	Leaf chewer	Native[2]	a, v
3. *Basilepta fulvipes*	Adult	Leaf chewer	Native[2]	a, v
4. *Aulacophora nigripennis*	Adult	Leaf chewer	Native[2]	a, v
Lepidoptera				
Geometridae				
5. *Ascotis selenaria*	Larva	Leaf chewer	Native[3]	a, v
6. Geometridae spec. 1	Larva	Leaf chewer	Unknown	a, v
Diptera				
Agromyzidae				
9. Agromyzidae spec. 1	Larva	Leaf miner	Unknown	a, v
Hemiptera				
Aphididae				
13. *Uroleucon nigrotuberculatum*	Nymph/adult	Sap feeder	Exotic	a
14. *Aphis gossypii*	Nymph/adult	Sap feeder	Native[3]	a
15. *Aulacorthum solani*	Nymph/adult	Sap feeder	Native[3]	a
16. *Macrosiphoniella yomogicola*	Nymph/adult	Sap feeder	Native[4]	a
Coccidae				
17. *Parasaissetia nigra*	Nymph/adult	Sap feeder	Exotic	a
Cercopidae				
18. *Aphrophora stictica*	Nymph/adult	Sap feeder	Native[4]	a, v
19. *Aphrophora maritima*	Nymph/adult	Sap feeder	Native[4]	a, v
Deltocephalidae				
20. *Nephotettix cincticeps*	Subadult	Sap feeder	Native[4]	a, v

Appendix 1 (*Continued*).

Species and code	Stage	Feeding guild	Native or exotic[1]	Host plant
Tettigellidae				
21. *Bothrogonia ferruginea*	Subadult	Sap feeder	Native[2]	a, v
22. *Cicadella viridis*	Subadult	Sap feeder	Native[3]	a, v
Hemiptera				
Plataspidae				
23. *Megacopta punctatissimum*	Adult	Sap feeder	Native[2]	a, v
Orthoptera				
Pyrgomorphidae				
24. *Atractomorpha lata*	Nymph/adult	Leaf chewer	Native[2]	a, v
Tettigoniidae				
25. *Phaneroptera falcata*	Nymph/adult	Leaf chewer	Native[3]	a, v

a, *S. alitissima*, v, *S. virgaurea*.
[1]Native or exotic species to Japan.
[2]Native to Asia including Japan.
[3]Native to Japan, but cosmopolitan.
[4]Native to Japan, but other distributions are unclear.

Appendix 2
Herbivorous insect species found on the native plant *Solidago virgaurea* in 2000 and 2001

Species and code	Stage	Feeding guild	Native or Exotic[1]	Host plant
Coleoptera				
Chrysomelidae				
1. *Aulacophora femoralis*	Adult	Leaf chewer	Native[2]	a, v
2. *Chrysolina aurichalcea*	Adult	Leaf chewer	Native[2]	a, v
3. *Basilepta fulvipes*	Adult	Leaf chewer	Native[2]	a, v
4. *Aulacophora nigripennis*	Adult	Leaf chewer	Native[2]	a, v
Lepidoptera				
Geometridae				
5. *Ascotis selenaria*	Larva	Leaf chewer	Native[3]	a, v
6. Geometridae spec. 1	Larva	Leaf chewer	Unknown	a, v
7. Geometridae spec. 2	Larva	Leaf chewer	Unknown	v
8. Geometridae spec. 3	Larva	Leaf chewer	Unknown	v
Diptera				
Agromyzidae				
9. Agromyzidae spec. 1	Larva	Leaf miner	Unknown	a, v
10. *Phytomyza horticola*	Larva	Leaf miner	Native[2]	v
11. *Liriomyza asterivora*	Larva	Leaf miner	Native[4]	v
12. *Ophiomyia maura*	Larva	Leaf miner	Native[4]	v
Hemiptera				
Cercopidae				
18. *Aphrophora stictica*	Adult	Sap feeder	Native[4]	a, v
19. *Aphrophora maritima*	Adult	Sap feeder	Native[4]	a, v
Deltocephalidae				
20. *Nephotettix cincticeps*	Subadult	Sap feeder	Native[4]	a, v
Tettigellidae				
21. *Bothrogonia ferruginea*	Subadult	Sap feeder	Native[2]	a, v

Appendix 2 (*Continued*).

Species and code	Stage	Feeding guild	Native or Exotic[1]	Host plant
22. *Cicadella viridis*	Subadult	Sap feeder	Native[3]	a, v
Orthoptera				
Pyrgomorphidae				
24. *Atractomorpha lata*	Nymph/adult	Leaf chewer	Native[2]	a, v
Tettigoniidae				
25. *Phaneroptera falcata*	Nymph/adult	Leaf chewer	Native[3]	a, v

a, *S. alitissima*; v, *S. virgaurea*.

[1]Native or exotic species to Japan.

[2]Native to Asia including Japan.

[3]Native to Japan, but cosmopolitan.

[4]Native to Japan, but other distributions are unclear.