

Community-wide impact of an exotic aphid on introduced tall goldenrod

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Abstract. 1. The aphid *Uroleucon nigrotuberculatum* Olive, which is specialised to the tall goldenrod, *Solidago altissima* L., in its native range, has become a dominant species on the introduced tall goldenrod in Japan. How this exotic aphid influenced arthropod communities on the introduced tall goldenrod in aphid-present (spring) and aphid-absent (autumn) seasons was examined, using an aphid removal experiment.

2. In spring, aphid presence increased ant abundance because aphid honeydew attracted foraging ant workers. A significant negative correlation was found between the numbers of ants and herbivorous insects other than aphids on the aphid-exposed plants, but no significant correlation was detected on the aphid-free plants. Thus, the aphid presence was likely to decrease the abundance of co-occurring herbivorous insects through removal behaviour of the aphid-tending ants. There were no significant differences in plant traits between the aphid-exposed and aphid-free plants.

3. In autumn, the numbers of lateral shoots and leaves, and the leaf nitrogen content were increased in response to the aphid infestation in spring. Because of the improvement of plant traits by aphid feeding, the abundance of leaf chewers increased on aphid-exposed plants. In contrast, the abundance of sap feeders decreased on the aphid-exposed plants. In particular, the dominant scale insect among sap feeders, *Parasaissetia nigra* Nietner, decreased, followed by a decrease in the abundance of ants attending *P. nigra*. Thus, aphid feeding may have attenuated the negative impacts of the tending ants on leaf chewers.

4. Aphid presence did not change herbivore species richness but changed the relative density of dominant herbivores, resulting in community-wide effects on co-occurring herbivores through ant-mediated indirect effects, and on temporally separated herbivores through plant- and ant-mediated indirect effects. The aphid also altered predator community composition by increasing and decreasing the relative abundance of aphid-tending ants in the spring and autumn, respectively.

Key words. Aphid–ant interaction, community-wide impact, exotic insect, introduced plant, invasion, plant-mediated indirect effect, *Solidago altissima*, tall goldenrod, *Uroleucon nigrotuberculatum*.

Introduction

It is well accepted that introduced plants lack interactions with herbivores, mutualists, and competitors associated with their original ranges, but can gain novel interactions with native species in new habitats (Schiffman, 1994; Mitchell *et al.*, 2006). Moreover, the establishment of an introduced

plant is often followed by invasion of exotic herbivorous insects that are specialised to the plant in its original region (Robinson, 1980; Memmott *et al.*, 2000; Hierro *et al.*, 2005; Ando & Ohgushi, 2008). These exotic insects may affect arthropod communities on introduced plants by adding new interactions or modifying existing interactions, such as inter-specific competition for shared resources (Moulton & Pimm, 1983; Louda *et al.*, 1997; Simberloff & Von Holle, 1999), ant-mediated indirect interactions (Thum *et al.*, 1997) or plant-mediated indirect interactions (Louda *et al.*, 1997; Louda & Arnett, 2000). Studying these relationships among introduced

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plants, and exotic and native insects is necessary to answer the questions of how direct and indirect insect–plant interactions are newly formed on novel plants (Sax *et al.*, 2007). Specifically, investigation of indirect effects induced by exotic herbivorous insects at the community level is required to understand the impacts of introduced species on the assemblage of native organisms (Howarth, 1991; Callaway *et al.*, 1999; Louda & Arnett, 2000). To our knowledge, no studies have examined how exotic herbivorous insects affect the organisation of the arthropod community in terms of overall density, species richness, and community composition on introduced plants. This is because most of the studies examining relationships between introduced plants and exotic herbivorous insects have focused on the colonisation success of such insects as biological control agents for introduced plants (Crawley, 1989; McClay, 1995; Wajnberg *et al.*, 2001).

Indirect interactions caused by herbivore-induced changes in plants occur frequently among temporally- and spatially-separated, and taxonomically-distinct species, resulting in community-wide impacts (Van Zandt & Agrawal, 2004; Ohgushi, 2005; Utsumi & Ohgushi, 2009; Utsumi *et al.*, 2009; Poelman *et al.*, 2010). In this context, aphid colonisation can alter host plant traits, such as plant growth, soluble nitrogen content, amino acid, and secondary compound concentrations, and resource allocation to roots, shoots, and seeds (Moran & Whitham, 1990; Waltz & Whitham, 1997; Petersen & Sandström, 2001; Wimp & Whitham, 2007). These changes in host plant traits caused by aphid attack can in turn alter arthropod communities. For example, Waltz and Whitham (1997) demonstrated that leaf-galling aphids increased the abundance and species richness of arthropods by improving the quality of juvenile cottonwood ramets. This implies that aphids can affect arthropod communities indirectly through changes in plant quality.

Interactions between ants and honeydew-producing aphids are common and widespread in arthropod food webs (Kaplan & Eubanks, 2005). Ant–aphid interactions potentially have community-wide impacts, because the presence of aphids can indirectly alter the density of other herbivorous insects and predators through the removal activities of tending ants (Wimp & Whitham, 2001, 2007). As honeydew is a renewable food resource, ants tending aphids not only protect aphids from predators and/or parasitoids (Way, 1963; Buckley, 1987), but also exclude potential competitors (Ando & Ohgushi, 2008). There is increasing evidence that an ant–aphid mutualism has strong indirect impacts on other herbivorous insects and/or their natural enemies through the removal behaviour of ants, leading to decreases in the species richness and relative abundance of herbivorous insects (Floate & Whitham, 1994; Wimp & Whitham, 2001, 2007). Herbivore species with a pervasive influence on the overall community composition are termed ‘keystone herbivores’ (Hunter, 1992), and their removal can produce a dramatic change in the associated community structure through altering an interaction web involving the host plant and other community members. Therefore, aphids have the potential to be a keystone herbivore that determines arthropod community structure through both plant- and ant-mediated indirect effects.

The tall goldenrod, *Solidago altissima* L., is an herbaceous plant which was introduced to Japan from North America approximately 100 years ago, and has since then spread widely over Japan. The aphid *Uroleucon nigrotuberculatum* Olive is one of the most dominant species on the tall goldenrod in Japan, and it also came from North America in the early 1990s. This exotic aphid–tall goldenrod system could provide profound insights into how an exotic aphid can affect the arthropod community on introduced plants through both ant-mediated and plant-mediated indirect effects.

In the present study, we examined how the exotic aphid affected community structures of co-occurring and temporally separated herbivorous insects and predators, using an aphid-removal experiment. Specifically, we focused on plant traits, species richness, and densities of insect herbivores belonging to different feeding guilds and predators of different taxa.

Materials and methods

Tall goldenrod and aphid

Tall goldenrod, *S. altissima*, is a rhizomatous perennial herb that was introduced to Japan from North America approximately 100 years ago (Shimizu, 2003). It has spread widely all over Japan, and become one of the most abundant weeds. It grows in open and disturbed areas, and frequently invades abandoned agricultural fields. In their original habitats, tall goldenrods are attacked by more than 100 herbivorous insect species, including a wide range of feeding guilds, such as leaf-chewers, suckers, miners, and gall-formers (Messina, 1978; Messina & Root, 1980).

Uroleucon nigrotuberculatum is a stem-feeding aphid that feeds exclusively on terminal shoots of *S. altissima*. It was also introduced from North America in the early 1990s (Ôtake, 1999), and more recently it has become very common in Japan. This aphid emerges from overwintered eggs in early March, and disappears by early August. It commonly occurs on *S. altissima* in North America, and at least seven predators and two parasitoids have been recorded to attack this species (Moran, 1986). In contrast, this aphid is almost free from natural enemies in Japan (Ôtake, 1999). Although we observed two ladybirds, *Coccinella septempunctata* Fabricius and *Harmonia axyridis* Pallas, and a crab spider, *Misumenops tricuspidatus brucki* Mulsant, preying on the aphid, the intensity of predation was negligible in the present study area (Y. Ando, pers. obs.).

Experimental design of aphid exclusion

The present study was conducted in a common garden of the Center for Ecological Research, Kyoto University, in Otsu, Shiga Prefecture, central Japan. To investigate the effects of the aphid colonisation on other herbivorous insects and predators, we performed an aphid exclusion experiment in 2001. Eighty seedlings of different clones of tall goldenrods were randomly taken from a 0.75-ha field of the Experimental Forest of Field Science Education and Research Center of Kyoto University

in Kyoto (35°04'N, 135°46'E; altitude 109 m, annual mean temperature 14.6 °C, and mean precipitation 1582 mm), and were individually planted in pots in early May 2001. Two weeks later, all of the potted plants were transplanted into an experimental plot in a 6 m × 16 m grid in the common garden by burying the bottom half of a pot in the ground, with individual plants being spaced 1.5 m apart without boundary fences. Aphid-exposed and aphid-free treatments were alternately arranged, and plants of the aphid-exposed treatment were allowed to undergo natural colonisation by aphids. All the plants were checked every day from mid-May to August, and aphids were removed from the aphid-free plants with forceps when they were found. To confirm whether aphid colonisation occurred in the aphid-exposed treatment, we counted aphids weekly throughout the season. We used 40 potted plants for an arthropod community census and the other 40 plants for an experiment to examine the effects of aphids on host-plant traits. In both experiments, 20 plants each were assigned to the aphid-free treatment, and the remaining 20 plants to the aphid-exposed treatment.

Effects of aphid colonisation on herbivore and predator communities

To examine how the aphid affected herbivore and predator communities in the common garden, we conducted a census three times a week from mid-May to late October 2001. The number of species and abundance of each arthropod species were recorded in the aphid-free and aphid-exposed plants. As the aphid colonisation occurs from mid-May to early August and none of the herbivorous insect species except one found in the aphid-present season appeared in the aphid-absent season (see Appendix I), we analysed the aphid effects separately in the 'early season' (aphid-present season, i.e. mid-May to August) and the 'late season' (aphid-absent season, i.e. September to late October). The census data for each arthropod species were averaged for the early and late season, respectively, and then we calculated the overall abundance and species richness of the herbivore and predator communities on each plant. Wilcoxon's signed rank test was used to compare these community properties between the aphid-free and aphid-exposed plants. Also, we compared the abundance of each feeding guild of herbivorous insects and predator taxa between the aphid-free and aphid-exposed plants. Herbivorous insects found on each plant were classified into two feeding guilds, namely, leaf chewers (caterpillars, grasshoppers, chrysomelid beetles, and scarab beetles) and sap feeders (aphids, leafhoppers, stinkbugs, scales, and spittlebugs). We excluded leaf miners from this analysis, because it was difficult to determine whether individual leaf miners were alive. Predators were categorised in terms of taxa: spiders, ants, and others (Appendix II). Wilcoxon's signed rank test was used to compare overall abundances of herbivore feeding guilds and predator taxa on the aphid-free and aphid-exposed plants. To examine the numerical relationships among aphids, ants, and co-occurring herbivores, we calculated Pearson's correlation coefficients between numbers of aphids and ants, between numbers of ants and leaf chewers, and between numbers of ants and sap feeders.

To examine whether arthropod communities differed between the treatments, we used non-metric multidimensional scaling analysis (NMDS) with the 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 community composition, based on the number of species and relative abundance of each species. For this analysis, the number of each herbivore and predator species used in the analysis was averaged for the early and late seasons. *Uroleucon nigrotuberculatum* on the aphid-exposed plants was excluded from the analysis. Individual numbers of each species were $\log(n + 1)$ -transformed and standardised by variance before calculating the coefficient.

An optimal NMDS solution was obtained by minimising the stress value as described in Clarke and 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, differences in community compositions of predators and herbivores between the aphid-exposed and aphid-free plants were determined using the *R*-value in an analysis of similarity (ANOSIM; Clarke, 1993). This analysis uses non-parametric permutation/randomisation methods with a dissimilarity matrix (Clarke, 1993). In addition, we used similarity percentages (SIMPER) to identify which arthropod species primarily accounted for the differences in herbivore and predator 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, U.K.).

Effects of aphid colonisation on plant traits

Because aphid infection induces subsequent branching, thereby enhancing new leaf production late in the season (Ando & Ohgushi, 2008), it has the potential to affect late-emerging arthropods on the tall goldenrod through the enhancement of plant regrowth.

To examine how plant traits differed between treatments in the common garden in the early and late seasons, we prepared aphid-exposed plants ($n = 20$) and aphid-free plants ($n = 20$) in the common garden, as described in the experimental design above. After the number of newly emerged lateral shoots and leaves were counted, 10 leaves were randomly taken from 10 each of aphid-exposed plants and aphid-free plants for measurement of foliar nitrogen and water contents in mid-July and

in early September 2001 just before the emergence of late season herbivores, the number of shoots and leaves of the remaining 10 each of aphid-exposed plants and aphid-free plants were counted, and then 10 leaves were randomly collected from each plant to measure foliar nitrogen and water contents. Individual leaves were weighed in the laboratory and oven-dried at 60 °C for 48 h to calculate the water content. After the dried leaves were powdered, nitrogen content was measured using an elemental analyser (Macro Corder JM1000CN, J-Science, Kyoto, Japan). Wilcoxon's signed rank test was used to compare these traits between the aphid-exposed and aphid-free plants.

Results

Effects of aphids on overall density and species richness

We recorded a total of 1701 individuals in 29 species as herbivores (Appendix I) and a total of 1379 individuals in 62 species as predators (Appendix II). All of the aphid-exposed plants were colonised by aphids throughout the early season (mean of aphid abundance \pm SE; 9.01 ± 0.39). We found no aphids on the aphid-free plants throughout the season. The aphid-exposed plants had significantly lower overall herbivore density, i.e. the number per plant, than the aphid-free plants in both the early and late seasons (Wilcoxon's signed rank test: $Z = 82.32$, $P < 0.001$ for early season; $Z = 20.02$, $P < 0.001$ for late season, Fig. 1). Although herbivore species richness in the early season showed a tendency to be lower on the aphid-exposed plants than on the aphid-free plants, the difference was not statistically significant ($Z = 3.12$, $P = 0.07$ for early season; $Z = 1.65$, $P = 0.13$ for late season). Out of 29 herbivorous insect species, 86% were found on both the aphid-exposed and aphid-free plants (Appendix I). Overall

predator density on the aphid-exposed plants was significantly higher in the early season ($Z = 52.36$, $P < 0.001$) but was lower in the late season ($Z = 47.78$, $P < 0.001$) than that on the aphid-free plants. Also, there were marginally significant differences in species richness in both seasons ($Z = 3.11$, $P = 0.06$ for early season; $Z = 3.28$, $P = 0.06$ for late season, Fig. 1). Predator species richness on the aphid-exposed plants in both seasons tended to be lower than that on the aphid-free plants. Out of 62 predator species, 90% were found on both the aphid-exposed and aphid-free plants (Appendix II).

Effects of aphids on community composition

NMDS analysis of the dissimilarity of arthropod community composition revealed that both herbivore and predator communities on the aphid-exposed plants were clearly distinct from those on the aphid-free plants in both seasons (ANOSIM: herbivore: $R = 0.60$, $P < 0.001$ for early season; $R = 0.82$, $P < 0.001$ for late season; predator: $R = 0.66$, $P < 0.001$ for early season; $n = 20$, $R = 0.22$, $P < 0.001$ for late season, Fig. 2). SIMPER analysis indicated that the leafhopper *Nephotettix cincticeps* Uhler and the moth caterpillar *Ascotis selenaria* Butler accounted for 46% and 35% of the dissimilarity of herbivore communities between the aphid treatments in the early season. The leafhopper constituted 66% and 89% of the overall sap feeder abundance on the aphid-exposed plants and aphid-free plants, respectively. Also, the moth caterpillar constituted 78% and 86% of the overall leaf chewer abundance, respectively. In the late season, the scale insect *Parasaissetia nigra* Nietner and the grasshopper *Atractomorpha lata* Motschulsky accounted for 62% and 29% of the dissimilarity of herbivore communities between treatments. The scale insect constituted 79% and 91% of the overall sap feeder abundance on the aphid-exposed plants and aphid-free plants,

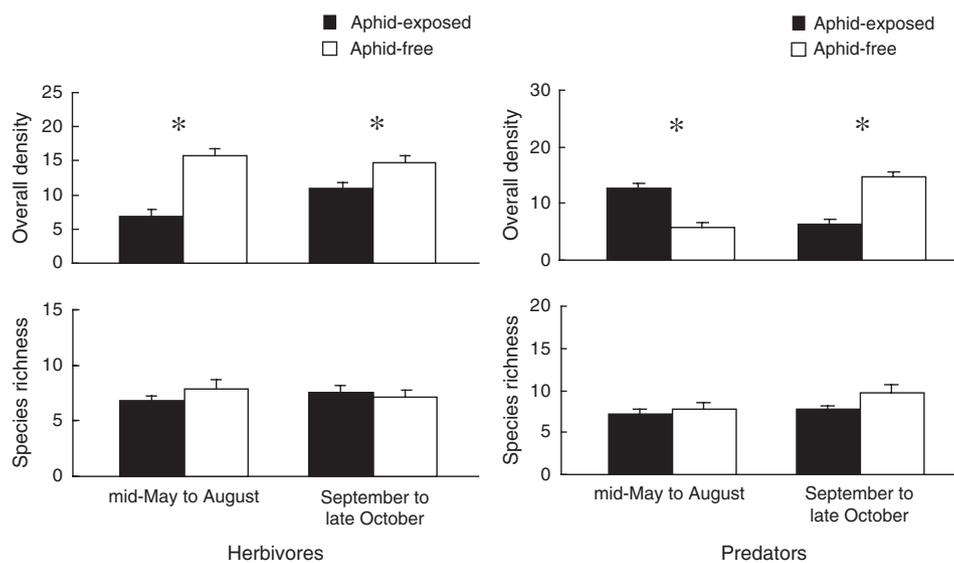


Fig. 1. Overall density (number per plant) and species richness of herbivores and predators on the aphid-exposed and aphid-free plants in the early season (mid-May to August) and late season (September to late October). Data from the aphid-exposed plants do not include *Uroleucon nigrotuberculatum*. Vertical bars indicate means with SE. * $P < 0.001$ (Wilcoxon's signed rank test).

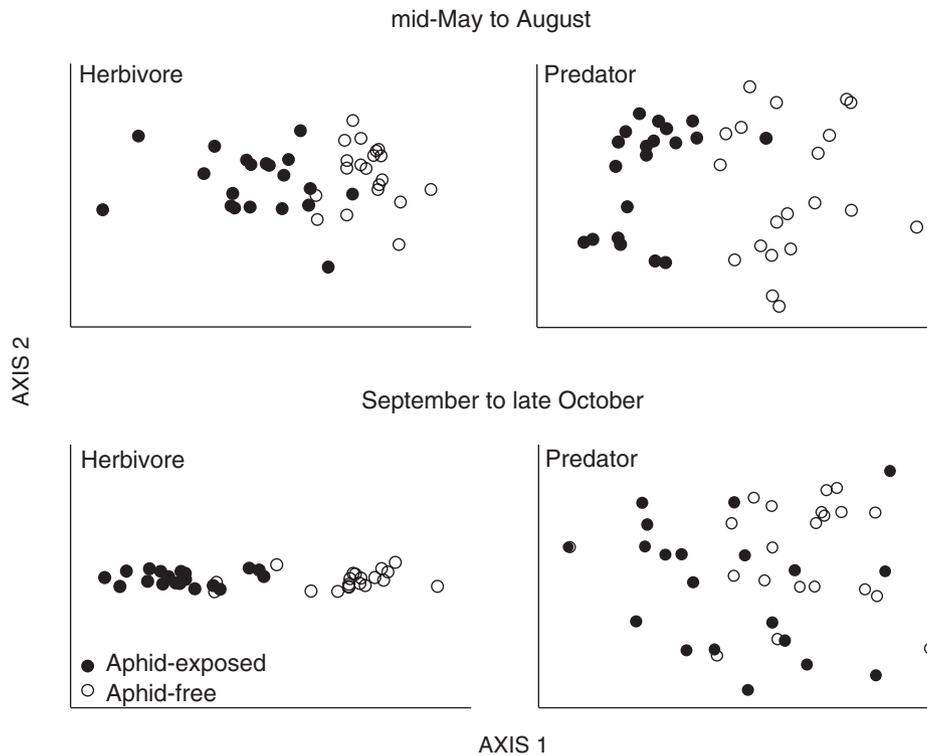


Fig. 2. Community compositions of herbivores and predators on the aphid-exposed plants (●) and aphid-free plants (○) in the early season (mid-May to August) and late season (September to late October) [herbivore; non-metric multidimensional scaling analysis (NMDS) stress = 0.12, ANOSIM: $R = 0.60$, $P < 0.001$ for early season, NMDS stress = 0.11, $R = 0.82$, $P < 0.001$ for late season; predator, NMDS stress = 0.20, ANOSIM: $R = 0.66$, $P < 0.001$ for early season, NMDS stress = 0.23, $R = 0.22$, $P < 0.001$ for late season). Data from the aphid-exposed plants do not include *Uroleucon nigrotuberculatum*.

respectively. Also, the grasshopper constituted 85% and 41% of the overall leaf chewer abundance on the aphid-exposed plants and aphid-free plants, respectively. The ant *Formica japonica* Matschinsky accounted for 95% and 92% of the dissimilarities of predator communities in the early season and the late season, respectively. Regarding the overall ant abundance on the aphid-exposed and aphid-free plants, the ant constituted 98% and 74% in the early season, and 91% and 93% in the late season, respectively. These results suggest that the differences between arthropod communities with and without aphids were as a result of the differences in relative abundances of the dominant herbivore species and ants.

Effects of aphids on densities of herbivore guilds and predator taxon

In the early season, the densities of leaf chewers and sap feeders were significantly lower on the aphid-exposed plants than on the aphid-free plants (Wilcoxon's signed rank test: $Z = 24.37$, $P < 0.001$ for leaf chewers; $Z = 38.66$, $P < 0.001$ for sap feeders, Fig. 3). In the late season, there was a significantly higher density of leaf chewers but a lower density of sap feeders on the aphid-exposed plants than on the aphid-free plants ($Z = 32.12$, $P < 0.001$ for leaf chewers; $Z = 39.65$, $P < 0.001$ for sap feeders).

Regarding arthropod predators, ant density was significantly higher in the early season but was lower in the late season on the aphid-exposed plants than on the aphid-free plants ($Z = 36.94$, $P < 0.001$ for early season; $Z = 62.34$, $P < 0.001$ for late season, Fig. 3). Neither spiders nor other predators differed significantly between the two treatments in either season (early season: $Z = 1.12$, $P = 0.07$ for spiders; $Z = 0.84$, $P = 0.13$ for others; late season: $Z = 0.58$, $P = 0.64$ for spiders; $Z = 0.21$, $P = 0.84$ for others).

The number of ants was positively correlated with the number of aphids on the aphid-exposed plants (Pearson's correlation coefficient: $r = 0.82$, $P < 0.001$, $n = 20$; two-tailed test). The numbers of leaf chewers and sap feeders were negatively correlated with the number of ants on the aphid-exposed plants (ants vs. leaf chewers: $n = 20$, $r = -0.75$, $P < 0.001$; ants vs. sap feeders: $n = 20$, $r = -0.77$, $P < 0.001$). In contrast, no significant correlations were found between the numbers of herbivorous insects and ants on the aphid-free plants (ants vs. leaf chewers: $n = 20$, $r = -0.41$, $P = 0.07$; ants vs. sap feeders: $n = 20$, $r = -0.53$, $P = 0.07$).

Effects of aphids on plant traits

Aphid infestation enhanced the production of newly emerged lateral shoots and leaves. The new leaf flush increased the

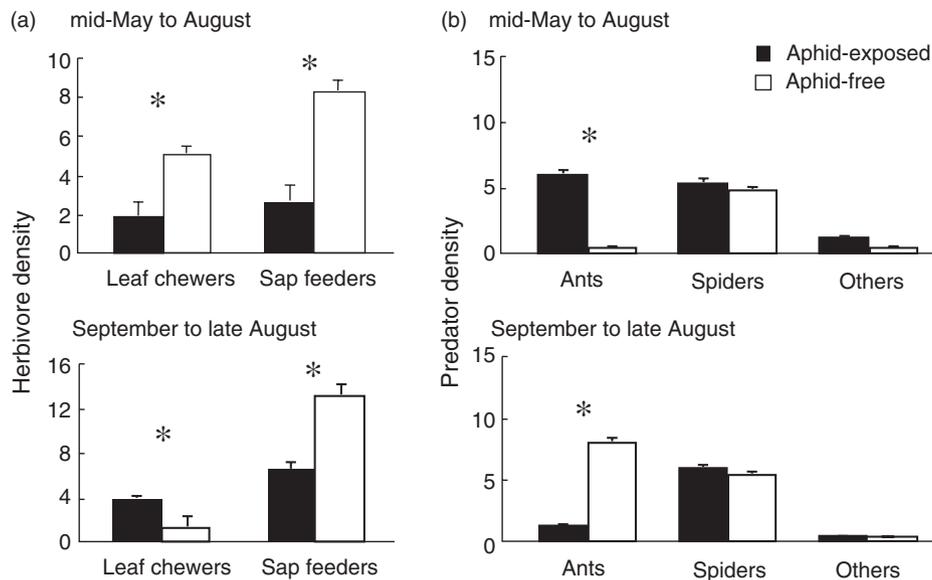


Fig. 3. Densities of (a) herbivore guilds and (b) predator taxa on the aphid-exposed and aphid-free plants in the early season (mid-May to August) and late season (September to late October). Data from the aphid-exposed plants do not include *Uroleucon nigrotuberculatum*. Vertical bars indicate means with SE. * $P < 0.001$ (Wilcoxon's signed rank test).

Table 1. Effects of aphid colonisation on traits of aphid-exposed plants and aphid-free plants.

Trait	Season	Mean \pm SE		Wilcoxon's signed rank test	
		Aphid-exposed	Aphid-free	Z	P
Number of lateral shoots	Mid-July	0	0	—	—
	Early September	2.02 \pm 0.63	0	-6.16	<0.001
Number of leaves	Mid-July	13.4 \pm 3.13	12.8 \pm 3.09	-1.18	0.24
	Early September	47.8 \pm 7.72	17.5 \pm 1.43	-6.24	<0.001
Nitrogen content (% DW)	Mid-July	1.36 \pm 0.14	1.32 \pm 0.18	-0.84	0.40
	Early September	2.64 \pm 0.27	1.80 \pm 0.23	-6.15	<0.001
Water content (% FW)	Mid-July	60.0 \pm 2.30	61.4 \pm 3.23	-0.51	0.61
	Early September	64.7 \pm 1.82	63.8 \pm 2.89	-0.12	0.23

DW, dry weight; FW, fresh weight.

foliar nitrogen content by 150% in the late season, but not in the early season (Table 1). There was no significant difference in the foliar water content between the aphid treatments. The aphid-exposed plants had about three times more leaves in the late season, compared with the aphid-free plants. Most of the increase of leaves in aphid-exposed plants was as a result of secondary growth in response to the early aphid colonisation. These results suggest that the aphid colonisation not only enhanced the production of lateral shoots and leaves, but also improved the quality of leaves that emerged in the late season.

Discussion

Effects of aphids on the co-occurring arthropod community

The present study clearly demonstrated the community consequences of the aphid-ant interaction as a driver structuring

arthropod communities. In the early season, the ant density was 12 times higher on the aphid-exposed plants than on the aphid-free plants, as a result of the provision of aphid honeydew to ant workers. Aphid-tending ants protect aphids from their natural enemies or competitors (Sloggett & Majerus, 2000; Stadler & Dixon, 2005). Although there are many studies on aphid-ant mutualistic interactions (Stadler & Dixon, 2005), to date the community consequences of their interactions have received little attention (but see Wimp & Whitham, 2001; Styrsky & Eubanks, 2007; Mooney & Agrawal, 2008; Sanders & van Veen, 2010). The present study showed that ants had a negative impact on other herbivores on the aphid-exposed plants, because the ants frequently removed herbivorous insects. In particular, the aphid presence decreased the dominant sap feeder, *N. cincticeps*, and the dominant leaf chewer *A. selenaria*, resulting in significant alterations in the herbivore community structure.

The aphid may have affected early-season insect herbivores through exploitative competition or induced plant responses

that changed plant quality. Co-occurring phloem feeders often compete for assimilates in the phloem vessels of host plants (Denno & Kaplan, 2007). Inbar *et al.* (1995) reported that aphids increased the mortality of co-occurring sap feeders via diversion of assimilates. In addition, aphids can change leaf nitrogen, plant growth, and resource allocation to roots, shoots, and seeds (Moran & Whitham, 1990; Petersen & Sandström, 2001), resulting in decreased food availability to leaf chewers or sap feeders. However, it is not likely that such effects on leaf chewers occurred in the present study, because aphid colonisation changed neither leaf nitrogen nor water content, nor production of lateral shoots or leaves of *S. altissima*.

The aphid presence also significantly increased predator abundance as a result of an increase in aphid-tending ants, although spiders and other predators were unaffected. On the other hand, predator species richness was marginally lower on the aphid-exposed plants, because three spider species found on aphid-free plants were lacking (see Appendix II). This negative impact of ants on other predators is in accord with the finding of an aphid removal experiment on cottonwood trees (Wimp & Whitham 2001), showing that species richness of generalist predators was two times greater when aphids and associated ants were absent than when they were present. Hence, the community composition of predators differed significantly depending on whether the aphids were present or absent.

Effects of aphids on the temporally separated arthropod community

The aphid colonisation in the early season impacted the herbivore community in the late season when the aphid was no longer present. Aphids influenced the late-season herbivore community composition by decreasing the sap feeder *P. nigra* and increasing the leaf chewer *A. lata*, both of which contributed robustly to the difference in the community composition of herbivorous insects.

The aphid colonisation in the early season influenced temporally separated herbivorous insects in the late season by alteration of food quality and quantity, depending on the feeding guild. Ando and Ohgushi (2008) showed that the aphid infestation in the early season did not affect plant traits in terms of secondary growth or foliar nitrogen, but rather increased the number of newly emerged lateral shoots and leaves and the foliar nitrogen in the late season. This trend was also supported by the present study. In late August, leaf flush continuously occurred in the aphid-exposed plants, although it rarely occurred in the aphid-free plants. This increase in newly flushed leaves in aphid-exposed plants resulted in an increase in the leaf nitrogen level, which improved food availability to the grasshopper *A. lata* (Ando & Ohgushi, 2008). Such a trait change in host plants owing to re-growth after early-season herbivory often has positive effects on late-emerging herbivorous insects because of increased resource quality and/or quantity (Mopper *et al.*, 1991; Masters *et al.*, 2001; Ohgushi, 2005).

In contrast, aphid infestation often decreases the abundance of subsequent sap feeders by reducing the nutritional quality of the sap of host plants, inducing amino acid alterations or increasing secondary compounds (Petersen & Sandström, 2001; Denno & Kaplan, 2007). Sap feeders would be strongly affected by qualitative changes in phloem sap but not by increased leaf production of the aphid-infested plants. Ando and Ohgushi (2008) showed that population growth and survival of *P. nigra* in autumn were decreased by spring aphid infestation. Moreover, aphids may have increased leaf chewers through a decrease in *P. nigra*. As honeydew of the scale insect attracts ants (Williams & Watson, 1990), a decrease of scale insects on the aphid-exposed plants may decrease the removal of other herbivores by tending ants. In the present study, ant density was decreased by 23% on aphid-exposed plants. Hence, the presence of aphids in the early season may attenuate the negative impact of the ants attending scale insects on leaf chewers in the late season.

The predator abundance significantly decreased on the plants with early-season aphid infestation because of the decreased number of ants tending scale insects. However, the early-season aphid infestation did not affect the abundance of spiders or other predators. Also, predator species richness was lower on the aphid-exposed plants with low density of ants attending scale insects relative to the aphid-free plants. As a result, the community composition of predators on the aphid-exposed plants with early-season aphid infestation differed significantly from that on the aphid-free plants.

Aphid as a keystone herbivore forming indirect interaction webs

The ant–aphid interactions would act as ‘keystone interactions’ in arthropod communities, and thus lead to community-wide impacts (Wimp & Whitham, 2001; Styrsky & Eubanks, 2007). On the other hand, aphid colonisation can also significantly affect the performance and/or preference of other herbivorous insects by altering the quality and quantity of host plants (Way & Cammell, 1970; Waltz & Whitham, 1997; Petersen & Sandström, 2001), which may alter the structure of herbivore communities. The present study highlighted that plant-mediated indirect effects of the aphid colonisation significantly influenced the community structure of temporally separated herbivorous insects via alteration of not only food quality and quantity, but also the strength of ant-mediated indirect effects. Note that indirect effects of aphids on temporally separated herbivorous insects depend on the feeding modes, resulting in a decrease in sap feeders but an increase in leaf chewers. This suggests that aphid infestation can have strong and different impacts on herbivorous insects through ant–aphid mutualism in the early season and can cause changes in host plants in the late season, extending to community-level consequences. Thus, aphids can act as a keystone herbivore in determining arthropod community structure through both ant-mediated and plant trait-mediated indirect effects. Future studies will be needed to obtain more information on the relative importance

of plant-mediated indirect effects, ant-mediated indirect effects, and their interactions in community organisation on plants, to achieve a better understanding of herbivore-induced indirect effects on ecological communities in nature.

Several previous studies on biological weed control argued that exotic herbivorous insects employed as control agents for introduced plants affected not only the target plants but also native organisms in a novel habitat through direct and/or indirect interactions (Howarth, 1991; Callaway *et al.*, 1999; Louda & Arnett, 2000). In this context, the present study revealed that the exotic aphid *U. nigrotuberculatum* played a key role in structuring the arthropod community on introduced tall goldenrods in both the early and late season. Investigating the relative importance of exotic herbivorous insects in interaction webs on introduced plants is a fruitful challenge for clarifying how exotic herbivorous insects that invade after the establishment of introduced plants have community-level consequences in invasion processes.

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Appendix I. Herbivorous insects found on *S. altissima*.

Species	Feeding guild*	Host-plant specificity†	Stage	Season‡	Aphid-exposed	Aphid-free
Coleoptera						
Cerambycidae						
Cerambycidae spec. 1	LC	Poly	Adult	Early	Y	Y
Chrysomelidae						
<i>Aulacophora femoralis</i>	LC	Poly	Adult	Early	Y	Y
<i>Chrysolina aurichalcea</i>	LC	Oligo	Adult	Early	Y	Y
Chrysomelidae spec. 1	LC	Poly	Adult	Early	Y	Y
Scarabaeidae						
Scarabaeidae spec. 1	LC	Poly	Adult	Both	Y	Y
Diptera						
Agromyzidae						
Agromyzidae spec. 1	LM	Unknown	Larva	Early	Y	Y
Hemiptera						
Acanthosomatidae						
Acanthosomatidae spec. 1	S	Poly	Adult	Late	Y	Y
Aphididae						
<i>Uroleucon nigrotuberculatum</i>	S	Mono	Nymph, adult	Early	Y	N
<i>Macrosiphoniella yomogicola</i>	S	Oligo	Nymph, adult	Late	Y	Y
Aphididae spec. 1	S	Poly	Nymph, adult	Late	Y	Y
Aphididae spec. 2	S	Poly	Nymph, adult	Late	Y	Y
Aphididae spec. 3	S	Poly	Nymph, adult	Late	Y	N
Aphididae spec. 4	S	Poly	Nymph, adult	Late	Y	Y
Aphididae spec. 5	S	Poly	Nymph, adult	Late	N	Y
Aphididae spec. 6	S	Poly	Nymph, adult	Late	Y	Y
Coccidae						
<i>Parasaissetia nigra</i>	S	Poly	Nymph, adult	Late	Y	Y
Coccidae spec. 1	S	Poly	Nymph, adult	Late	Y	Y
Cercopidae						
<i>Aphrophora maritima</i>	S	Poly	Adult	Late	Y	Y
Deltocephalidae						
<i>Nephotettix cincticeps</i>	S	Poly	Subadult	Early	Y	Y
Lygaeidae						
Lygaeidae spec. 1	S	Poly	Adult	Early	Y	Y
Plataspidae						
<i>Megacopta punctatissimum</i>	S	Poly	Adult	Early	Y	Y
Tettigellidae						
<i>Bothrogonia ferruginea</i>	S	Poly	Subadult	Early	Y	Y
<i>Cicadella viridis</i>	S	Poly	Subadult	Early	Y	Y
Lepidoptera						
Geometridae						
<i>Ascotis selenaria</i>	LC	Oligo	Larva	Early	Y	Y
Geometridae spec. 1	LC	Poly	Larva	Early	Y	Y
Geometridae spec. 2	LC	Unknown	Larva	Early	Y	N
Geometridae spec. 3	LC	Unknown	Larva	Early	Y	Y
Orthoptera						
Pyrgomorphidae						
<i>Atractomorpha lata</i>	LC	Poly	Nymph, adult	Late	Y	Y
Tettigoniidae						
<i>Phaneroptera falcata</i>	LC	Poly	Nymph, adult	Late	Y	Y

*LC, Leaf chewer; LM, Leaf miner; S, Sap feeder.

†Mono, Monophagous (feeds on the genus *Solidago*); oligo, oligophagous (feeds on Composites); poly, polyphagous (feeds on several families).

‡Both, early and late seasons.

N, absent; Y, present.

Appendix II. Predators found on *Solidago altissima*.

Species	Taxa	Stage	Season	Aphid-exposed	Aphid-free
Araneae					
Argiopidae					
<i>Oxyopes sertatus</i>	Spider	Nymph, adult	Early/late	Y	Y
Salticidae					
Salticidae spec. 1–25	Spider	Nymph, adult	Early/late	Y: spec. 1–22 N: spec. 23–25	Y: spec. 1–20, 22–25 N: spec. 21
Thomisidae					
<i>Misumenops tricuspidatus</i>	Spider	Nymph, adult	Early/late	Y	Y
Unidentified spider spec. 1–25	Spider	Adult	Early/late	Y	Y
Coleoptera					
Cantharidae					
<i>Athemellus adusticollis</i>	Other	Adult	Early	Y	Y
Coccinellidae					
<i>Coccinella septempunctata</i>	Other	Larva, adult	Early	Y	Y
<i>Harmonia axyridis</i>	Other	Larva, adult	Early	Y	Y
<i>Propylea japonica</i>	Other	Adult	Early	N	Y
Unidentified spec. 1	Other	Adult	Early	N	Y
Hemiptera					
Reduviidae					
<i>Ectrychotes andreae</i>	Other	Adult	Early/late	Y	Y
<i>Sphedanolestes impressicollis</i>	Other	Adult	Early/late	Y	Y
Hymenoptera					
Formicidae					
<i>Camponotus japonicus</i>	Ant	Adult	Early/late	Y	Y
<i>Formica japonica</i>	Ant	Adult	Early/late	Y	Y
<i>Pristomyrmex pungens</i>	Ant	Adult	Early/late	Y	Y

N, absent; Y, present.