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Herbivorous arthropod community of an alien weed *Solanum carolinense* L.

Osamu IMURA†

Division of Entomology, National Institute of Agro-Environmental Sciences; Tsukuba, Ibaraki 305–8604, Japan

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Abstract

Herbivorous arthropod fauna of the horse nettle *Solanum carolinense* L., an alien solanaceous herb of North American origin, was characterized by surveying arthropod communities in the fields and comparing them with the original community compiled from published data to infer the impact of herbivores on the weed in the introduced region. Field surveys were carried out in the central part of mainland Japan for five years including an intensive regular survey in 1992. Thirty-nine arthropod species were found feeding on the weed. The leaf, stem, flower and fruit of the weed were infested by the herbivores. The comparison of characteristics of the arthropod community with those of the community in the USA indicated that more sapsuckers and less chewers were on the weed in Japan than in the USA. The community in Japan was composed of high proportions of polyphages and exophages compared to that in the USA. Eighty-seven percent of the species are known to be pests of agricultural crops. Low species diversity of the community was also suggested. The depauperated herbivore community, in terms of feeding habit and niche on *S. carolinense*, suggested that the weed partly escaped from herbivory in its reproductive parts. The regular population census, however, indicated that a dominant coccinellid beetle, *Epilachna vigintioctopunctata*, caused a noticeable damage on the leaves of the weed.

Key words: Alien weed; *Solanum carolinense*; herbivorous arthropod community; community structure; feeding habits

INTRODUCTION

Many species of alien weeds have invaded Japan from overseas (Asai, 1993; Enomoto, 1999). These alien weeds often propagate abundantly and cause serious problems including yield loss of agricultural crops, threat to endemic plants, degradation of amenities and increased weed control costs.

Among the alien weeds, the horse nettle, *Solanum carolinense* L., is a perennial solanaceous herb of North American origin whose presence was initially recorded in 1906 in Japan (Asai, 1993). Recently, the weed has spread widely over agricultural fields, grasslands, roadsides, lawns, and abandoned areas, where *S. carolinense* forms dense populations. The weed is now present throughout almost all of Japan from the northern island, Hokkaido, to the southern island, Okinawa (Nishida, et al., 1999).

The proliferation of alien weeds can be accounted for by several factors, such as an absence of effective native herbivores or competitors, occupation of open niches, establishment in a more favorable environment than the native habitat, or greater fitness of aliens than endemics (Harper, 1965; Goeden, 1971a; Crawley, 1987; Cousens and Mortimer, 1995). However, these possible reasons are not mutually exclusive. The greater fitness or vigor of the aliens is often thought to be a result of the absence of effective native herbivores (enemy release hypothesis) (e.g. Blossey and Nötzold, 1995; Crawley, 1997; Tilman, 1999; Keane and Crawley, 2002).

Insect herbivore communities on alien plants have a different structure from those on the same plants in the native habitat (Strong et al., 1984). There is a possibility that such different structures of the herbivore communities on alien plants are related to the proliferation of alien weeds. In this paper, I characterize the herbivorous arthropod community associated with *S. carolinense* in Japan by surveying arthropod communities in the field and compare them with the native community to infer the impact of herbivores on the weed.

† Present address: Division of Grassland Ecology, National Institute of Livestock and Grassland Science; Senbonmatsu 768, Nishinasuno, Tochigi 329–2793, Japan. E-mail: imurao@affrc.go.jp

MATERIALS AND METHODS

Study sites. Arthropod herbivores of *S. carolinense* were surveyed at several sites in and around the National Institute of Agro-Environmental Sciences (NIAES), Tsukuba, Ibaraki Prefecture (lat. 36°N, long. 140°E). The survey was also carried out on *S. carolinense* populations along roadsides and in grasslands in the National Institute of Livestock and Grassland Science (NILGS), Nishinasuno, Tochigi Prefecture (lat. 37°N, long. 140°E). *S. carolinense* populations were naturally growing at these sites. The establishment of the weed populations in NIAES was quite possibly after 1980 when the institute moved there. *S. carolinense* in NILGS was first recorded in 1987. The two sites were located in the central part of the Japanese mainland.

Field survey. The ground area ($10\,\text{m}\times17\,\text{m}$) at the NIAES site (Tsukuba) was separated into 170 $1\,\text{m}\times1\,\text{m}$ square plots. The number of *S. carolinense* shoots (ramets) in each plot was counted once a week or every other week from May 27 to October 28 in 1992. Thirty shoots were randomly selected and the numbers of arthropod herbivores present on the shoots were counted (hereafter I refer the counting of the herbivores to the regular census). When feeding of the herbivores was not confirmed in the field, they were brought into the laboratory and reared on *S. carolinense* at 25°C to check their feeding trace, feces and/or molting. The herbivore fauna was also surveyed occasionally by visual inspections of *S. carolinense* populations in the area and the vicinities of NIAES and in NILGS from 1993 to 1996.

Literature survey. Information of herbivores on *S. carolinense* in the USA was collected by referring to the databases of CAB and BIOSIS, reference citations in related papers and correspondence with entomologists and plant scientists.

Data analyses. The *G*-test (Sokal and Rohlf, 1995) was performed to compare the frequencies of arthropod compositions in the communities. The species diversity index of the Shannon-Wiener function (H') was calculated using the regular census arthropod data; 95% C.L. (confidence limit) of H' was estimated by the bootstrap procedure with 500 runs (Krebs, 1999).

RESULTS

Arthropod community

Thirty-nine herbivorous arthropod species were found feeding on *S. carolinense* (Table 1). The most abundant was homopterous species (38% of the total number of species), followed by heteropterous species (20.0%), coleopterous species (12.8%), thysanopterous species (12.8%) and lepidopterous species (10.3%) (Fig. 1). Table 2 is a list of herbivorous arthropods of *S. carolinense* in the USA, the origin of the weed, which was compiled from miscellaneous literature. Although no studies have been conducted based on intensive faunal survey of the herbivorous arthropods feeding on *S. carolinense* in the USA, the list would represent a general character of the community in the place of origin. The ratio of homopterous species was larger (*G*-test, $p<0.01$) and that of coleopterous species was smaller (*G*-test, $p<0.01$) in the community of the introduced region than in that of the original site (Fig. 1). *Tetranychus urticae* was the only common species that was recorded in both Japan and the USA.

The majority of species (74%) were sapsuckers including species in Homoptera, Heteroptera, Thysanoptera, and Acarina in Japan (Fig. 2). Leaf chewers were lepidopterous and coleopterous species. The ratio of sapsuckers was larger (*G*-test, $p<0.01$) and that of chewers was smaller (*G*-test, $p<0.05$) in Japan than in the USA (Fig. 2). Among the lepidopterous species, there was one leaf roller. Those species were all exophages. The only endophagous species found was an agronomizid leaf miner, and neither stem borers nor gall formers were found on *S. carolinense* in Japan (Fig. 2). In the region of origin, however, endophagous species of two leaf miners and four stem and fruit borers were recorded (Table 2, Fig. 2). Additionally, the larvae of *Furumenta nundinella* bore into fruits to induce parthenocarpic development of the fruits in the manner of a gall former (Solomon, 1980). Thus, the endophagous species was relatively larger in the origin than in the introduced regional site (*G*-test, $p<0.05$).

Nineteen, 17, seven and one species infested leaves, stems, flowers and fruits, respectively (Table 1). A coccinellid beetle, *Epilachna vigintioctopunctata*, which was a voracious leaf feeder (Imura and Ninomiya, 1998), caused some damage

Table 1. Herbivorous arthropods associated with *S. carolinense* in Tsukuba and Nishinasuno, Japan

Order Family	Species	Feeding stages[a]	Feeding habit[b]	Associated plant parts[c]	Host range[d]/ pest status[e]
Acarina					
Tetranychidae	*Tetranychus urticae* Koch*	I, A	S	L	P/Sol
Tetranychidae	*Tetranychidae* sp.#	I, A	S	L	?
Thysanoptera					
Thripidae	*Thrips hawaiiensis* (Morgan)	I, A	S	Fl	P/Sol
Thripidae	*Thrips setosus* Moulton*	I, A	S	L	P/Sol
Thripidae	*Frankliniella intonsa* (Trybom)#	I, A	S	Fl	P/Sol
Thripidae	*Megalurothrips distalis* (Karny)#	I, A	S	Fl	P/Oth
Phlaeothripidae	*Haplothrips chinensis* Priesner	I, A	S	Fl	P/Sol
Heteroptera					
Plataspidae	*Megacopta punctatissimum* (Montandon)	A	S	St	P/Oth
Pentatomidae	*Eysarcoris ventralis* (Westwood)	A	S	St	P/Oth
Pentatomidae	*Plautia stali* Scott	A	S	St	P/Sol
Coreidae	*Acanthocoris sordidus* (Thunberg)*	I, A	S	St	O/Sol
Alydidae	*Riptortus clavatus* (Thunberg)	A	S	St	P/Oth
Lygaeidae	*Piocoris varius* (Uhler)*	A	S	St	P/Oth
Miridae	*Adelphocoris variabilis* (Uhler)	A	S	St, L	P/Oth
Homoptera					
Cercopidae	*Paracercopis assimilis* (Uhler)*	A	S	St	P/Oth
Aphrophodiae	*Aphrophora ishidae* Matsumura	A	S	St	P/Non
Tettigellidae	*Bothrogonia japonica* Ishihara#	A	S	St	P/Oth
Tettigellidae	*Cicadella viridis* (Linnaeus)*#	A	S	St	P/Oth
Tettigellidae	*Pagaronia* sp.*	I, A	S	St	?
Tettigellidae	*Kolla atramentaris* (Motschulsky)*	I, A	S	St	P/Oth
Cicadellidae	*Empoasca* sp.*	I, A	S	St, L	?
Cicadellidae	*Balchutha rubrinervis* (Matsumura)*	I, A	S	L	P/Oth
Ricaniidae	*Orosanga japonicus* (Melichar)*	I, A	S	St	P/Oth
Flatidae	*Geisha distinctissima* (Walker)*	A	S	St	P/Oth
Aleyrodidae	*Trialeurodes vaporariorum* (Westwood)*#	I, A	S	L	P/Sol
Aphididae	*Aphis gossypii* Glover*	I, A	S	L	P/Sol
Aphididae	*Aulacorthum magnoliae* (Essig et Kuwana)*	I, A	S	L	P/Sol
Aphididae	*Aulacorthum solani* (Kaltenbach)*#	I, A	S	L	P/Sol
Aphididae	*Macrosiphum euphorbiae* (Thomas)*	I, A	S	L	P/Sol
Lepidoptera					
Pyralidae	*Udea testacea* (Butler)	I	R	L	P/Oth
Geometridae	*Ectropis crepuscularia* (Deni et Schiff)	I	C	L	P/Oth
Arctiidae	*Arctia caja phaeosoma* (Butler)#	I	C	Fl	P/Oth
Noctuidae	*Agrotis segetum* (Denis et Schiffermuller)	I	C	L, St	S/Sol
Coleoptera					
Scarabaeidae	*Blitopertha orientalis* (Waterhouse)*	A	C	L	P/Oth
Scarabaeidae	*Popillia japonica* Newman#	A	C	Fl	P/Oth
Coccinellidae	*Epilachna vigintioctomaculata* Motschulsky*#	I, A	C	L	P/Sol
Coccinellidae	*Epilachna vigintioctopunctata* (Fabricius)*	I, A	C	L, Fl, Fr	O/Sol
Chrysomelidae	*Atrachya menetriesi* (Faldermann)	A	C	L	P/Sol
Diptera					
Agromyzidae	*Agromyzidae* sp.	I	MI	L	O?

* Species occurred in the regular census in 1992.

Species collected in NILGS, Nishinasuno.

[a] I: larva or nymph, A: adult.

[b] S: sapsucker, C: chewer, R: leaf roller, MI: leaf miner.

[c] L: leaf, St: stem, Fl: flower, Fr: fruit.

[d] O: specialist of solanaceous plants (oligophage); P: generalist which feeds on plants of Solanaceae and other plant families (polyphage), ?: host range not known.

[e] Sol: pests of solanaceous crops, *Solanum melongena*, *Solanum tuberosum*, *Lycopersicum esculentum*, *Capsicum annuum* and/or *Nicotiana tabacum*, Oth: pests of crops of other plant-families, Non: non pests. The host range and the pest status was based on Japanese Society of Applied Entomology and Zoology (1987).

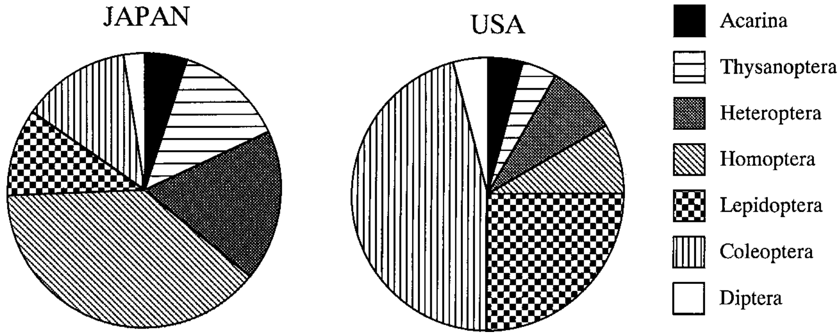

Fig. 1. Taxonomic composition of the herbivorous arthropod community on *S. carolinense* in the introduced region, Japan and in the region of origin, USA.

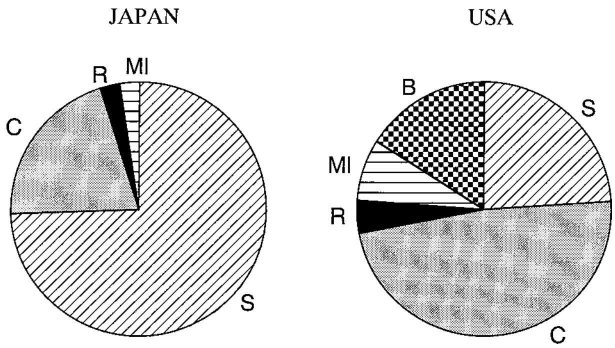

Fig. 2. Feeding habit of the herbivorous arthropod community on *S. carolinense* in the introduced region, Japan and in the region of origin, USA. S: sapsucker, C: chewer, R: leaf roller, MI: leaf miner, and B: stem borer.

on flowers by their infestation. Most of the thysanoptera species were flower feeders, and their damage on the flowers seemed to be slight. Three coleopterous species infest flowers in the original site (Table 2). Among the beetles, *Anthonomus nigrinus* was abundant on the plant growing in the flower buds (Burke, 1963). *E. vigintioctopunctata* also occasionally infested the surface of fruits (Table 1). In the USA, at least three species are described as fruit feeders (Table 2); sometimes a large proportion of the plant's fruits was infested by *F. nundinella* larvae, and the moth had a great impact on the fruit set (Solomon and McNaughton, 1979; Solomon, 1981). Two root feeders of flea beetles infested *S. carolinense* in the region of origin (Table 2), but no apparent root feeder was found in our fields, although the survey was mainly done for above ground fauna.

Hymenopterous species of *Lasionglossum japonicum* (Dalla Torre), *Apis mellifera* L., *Ceratina flavipes* Smith and *Xylocopa appendiculata circumvolans* Smith (pollen collectors) and a dipterous species of *Estrophe balteata* deGeer (pollen feeder) were recorded visiting flowers of *S. carolinense.* Since pollen collectors and feeders are not often noticed as herbivores, they were not included in Table 1.

In the region of origin, *F. nundinella* and *Leptinotarsa juncta* were monophagous feeders of *S. carolinense* (Table 2) and *Epitrix fuscula* fed almost exclusively on *S. carolinense* (Wise and Sacchi, 1996) (monophages). Further, most other herbivores listed in Table 2 were oligophagous species feeding only on plants of the solanaceous family (oligophages). In the introduced area, there was no monophagous species that fed exclusively on *S. carolinense* (Table 1). Only *E. vigintioctopunctata*, a coreid bug *Acanthocoris sordidus* and probably an agronomyzid fly were specialized on Solanaceae plants (oligophages). The Major hosts of *Epilachna vigintioctomaculata* were from Solanaceae. All others were polyphages feeding on Solanaceae and other plant families. Fifty percent of the herbivores were opportunists that did not breed on *S. carolinense*, since no immature stage of the species was found infesting the weed (Table 1).

The community on *S. carolinense* shared 41% of its species with those of solanaceous crops (oligophages) and 46% of its species with those of other crops (polyphages) (Table 1); thus, 87% of the species were pest species of agricultural crops.

Seasonal abundance and diversity of the arthropods in the regular census

Phenology of *S. carolinense* in 1992 in the NIAES field was as follows. Several shoots of *S. carolinense* began to emerge on May 22 and the

Table 2. Herbivorous arthropods recorded on *S. carolinense* in the USA, the origin of the weed, compiled from published references

Order Family	Species	Feeding habit[a]	Associated plant part[b]	Host range[c]	References[d]
Acarina					
Tetranichidae	*Tetranychus urticae* Koch	S	L	P	2
Thysanoptera					
Thripidae	*Thrips tabaci* Lind.	S	L	P	2
Heteroptera					
Lygaeidae	*Ischnodemus falicus* Say	S	L	P	1
Tingidae	*Gargaphia solani* Heid.	S	L	P	1
Homoptera					
Cicadellidae	*Scaphytopius acutus* (Say)	S	L	O	11
Psyllidae	*Paratrioza cockerelli* (Sulc.)	S	L	O	1
Lepidoptera					
Sesiidae	*Synanthedon rileyana* (Hy. Edward)	B	St	O	1
Gelechiidae	*Frumenta nundinella* Zeller	B, R	Fr, L	M	4, 5, 6, 7, 8, 9, 11
Gelechiidae	*Tildenia georgei* Hoges	MI	L	O	12
Gelechiidae	*Tildenia inconspicuella* (Murtfeldt)	MI	L	O	12
Sphingidae	*Manduca sexta* (L.)	C	L	O	1
Sphingidae	*Manduca quinquemaculata* Haw.	C	L	O	1
Coleoptera					
Mordellidae	*Mordella atrata* Melsheimer	C	Fl	P	3
Chrysomelidae	*Diabrotic undecimpunctata howardi* Barber	C	L	P	3
Chrysomelidae	*Epitrix cucumeris* Harr.	C	L, R	O	1
Chrysomelidae	*Epitrix fuscula* Crotch	C	L, R	O	1, 2, 3, 16, 19
Chrysomelidae	*Epitrix hirtipennis* (Melsheimer)	C	L	O	3, 11
Chrysomelidae	*Gratiana pallidula* (Boheman)	C	L	O	1, 3, 16
Chrysomelidae	*Leptinotarsa decemlineata* (Say)	C	L	O	2, 9, 10, 11, 15, 16, 17, 18
Chrysomelidae	*Leptinotarsa juncta* (Germar)	C	L	M	11, 15, 19
Curculionidae	*Anthonomus eugenii* Cano	C	L, Fr, Fl	O	14
Curculionidae	*Anthonomus nigrinus* Bohneman	C	Fl	O	3, 16, 20
Curculionidae	*Tricobaris trinotata* (Say)	B	St	O	1, 3, 13
Diptera					
Tephritidae	*Zonosemata electa* (Say)	B	Fr	O	11

[a] S: sapsucker, C: chewer, R: leaf roller, MI: leaf miner, and B: stem or fruit borer.
[b] L: leaf, St: stem, Fl: flower, Fr: fruit, R: root.
[c] M: specialist of *S. carolinense* (monophage); O: specialist of solanaceous plants (oligophage); P: generalist which feeds on plants of Solanaceae and other plant families (polyphage); ? not certain.
[d] 1. Somes (1916); 2. Ilnicki and Fertig (1962); 3. Burke (1963); 4. Solomon and McNaughton (1979); 5. Solomon (1980); 6. Solomon (1981); 7. Solomon (1983); 8. Solomon (1988); 9. Bailey and Kok (1982); 10. Hare and Kennedy (1986); 11. Bassett and Munro (1986); 12. Gross (1986); 13. Cuda and Burke (1986); 14. Patrock and Schuster (1992); 15. McCauley (1992); 16. Nichols et al. (1992); 17. Weber et al. (1995); 18. Mena-Covarrubias et al. (1996); 19. Wise and Sacchi (1996); 20. Clark and Burke (1996).

shoot density increased rapidly up to July, after which the increase was asymptotic. The maximum number of 7.16±5.16 (s.d.) shoots per m^2 was recorded on September 1. The shoot number decreased due to dying in late October when the temperature declined steeply.

Twenty arthropod species (species with * in Table 1), a total of 3,621 individuals, were recorded by the regular census in the NIAES field from May to October in 1992. The most abundant was *E. vigintioctopunctata* (34.0% of the total) followed by *Aulacorthum magnoliae* (24.6%), *Trialeurodes vaporariorum* (17.1%), *Thrips setosus* (5.2%), and *Aphis gossypii* (5.0%). The top three species occupied more than 75% of the total number of individuals leading the community to low species diversity ($H'=1.82\pm0.03$ (95% C.L.) nits).

The number of arthropods per shoot increased

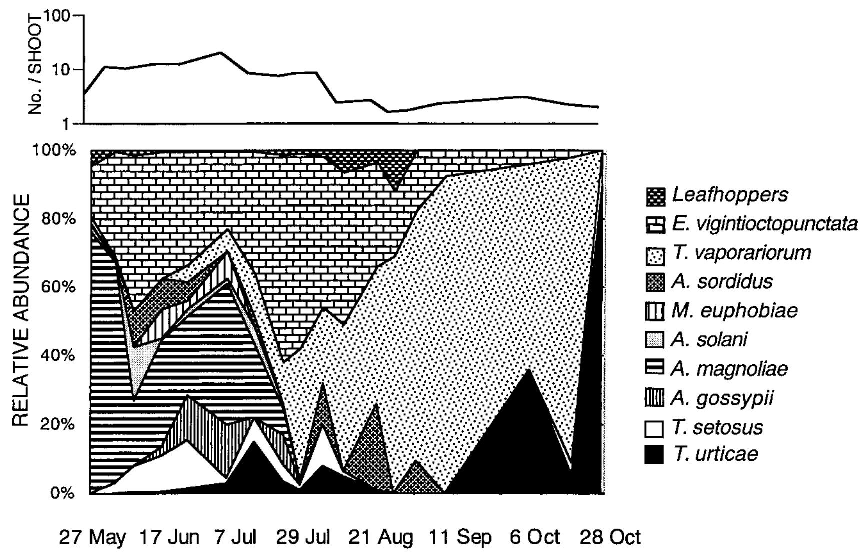

Fig. 3. Seasonal changes in total number of herbivorous arthropods per shoot (upper panel) and relative abundance of the top ten species (lower panel) in the regular census.

from May 27 and peaked at 20.5±23.5 (s.d.) on July 7, after which the number declined, while the number was small from September 11 to October 28 (Fig. 3, upper panel). Figure 3 also indicates the seasonal change in relative abundance of the arthropod species (lower panel). Two generations of *E. vigintioctopunctata* occurred on *S. carolinense* in a year and the beetle was abundant throughout the growing season of the weed. *A. magnoliae* was relatively abundant from May to early July, whereas *T. vaporariorum* was dominant in the latter part of the season when most of other species disappeared or deceased.

DISCUSSION

Since the faunal comparisons of herbivores on *S. carolinense* in Japan and the USA were based on data of a different nature, the results should be interpreted cautiously. It can be, however, valid to discuss the following points.

The herbivorous arthropod community feeding on *S. carolinense* was dominated by polyphagous exophages in Japan (Table 1 and Fig. 2). Neither stem borers nor gall formers were found on *S. carolinense* in Japan. Similarly, *Pueraria lobata*, which is an endemic vine of Japan, had no monophagous or oligophagous borers and gall formers in the USA where the plant was introduced about 100 years ago (Carstensen and Imura, unpublished). The results supported the fact that a high proportion of exophages and polyphages are characteristic for young herbivore communities that feed on alien plants (Goeden, 1971b, 1974; Goeden and Ricker, 1982; Zwölfer, 1988; Wilson and Flanagan, 1990).

Two root feeders of flea beetles infested *S. carolinense* in the region of origin. *Solanum nigrum* L., which is estimated to have been introduced into Japan in a prehistorical era (Osada, 1976), was growing in adjoining areas in NIAES. A flea beetle, *Psylliodes brettinghami* Baly, that is a root and leaf feeder of solanaceous plants like the flea beetles in the USA, was infesting the *S. nigrum* plants abundantly, but it was never observed on *S. carolinense*. Root feeders that are harmful for perennial plants may take a longer time to colonize on alien plants than other herbivores. This inference is supported by other evidence that newly introduced alien plants were often free from root feeders (Wilson and Flanagan, 1990; Jobin et al., 1996). Additionally, there were no destructive flower and fruit feeders in the introduced region, suggesting that the reproductive parts of *S. carolinense* may tend to be unexploited niches of the herbivores.

As demonstrated in this study, alien weeds are frequently colonized by arthropod herbivores from other crops (Goeden, 1968; Zwölfer, 1988; Wilson and Flanagan, 1993). Most agricultural crops are alien plants artificially introduced from overseas in the past (Hoshikawa, 1988). Pest arthropods which are often polyphagous and adapt to crops growing in disturbed areas, viz. agricultural fields, must be easy to move onto alien weeds growing in the same environments.

Although 39 herbivorous arthropod species feeding on *S. carolinense* were recorded in this study, no more than 20 arthropod species were found on the local *S. carolinense* population by the intensive one-year regular census. Additionally, the arthropod community was dominated by only three species, resulting in the low species diversity of the community. Although the phenomenon whereby the communities on alien plants are dominated by only a few species and thus the diversity is low cannot be generalized at the present, Southwood et al. (1982) reported that the diversity of the herbivorous arthropod community was lower on introduced trees than on native trees in Britain and South Africa. The fact that limited herbivore species move on to the alien plants during the early colonization process (Strong et al., 1984) may be partly responsible for the low diversity.

Goeden (1971a, b), Hilgendorf and Goeden (1983) and Jobin et al. (1996) reported that alien plants suffered relatively little insect damage. The present faunal studies of *S. carolinense* suggested that the weed appears to escape from the arthropod herbivores to a certain extent in its vegetative and sexual reproduction parts in the introduced region. The regular census of the herbivorous arthropods, however, demonstrated that the density of a few species was high on the local *S. carolinense* population. The life cycle of the most dominant species, *E. vigintioctopunctata*, seemed to conform well to the phenology of *S. carolinense*. This species caused marked damage to the leaves; about 68% of the leaf area of the plant was destroyed mainly by the beetle infestation in early September (Imura, unpublished). Thus, whether or not *S. carolinense* is actually released from the herbivory of these endemic herbivores in the introduced region is unclear at present. Further quantitative studies are needed to evaluate the impact of herbivory by the arthropod herbivores on the growth and reproduction of the alien weed, *S. carolinense*.

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