Effect of the key predatory ladybird, *Harmonia axyridis* (Coleoptera, Coccinellidae) on larval performance of aphidophagous insects

Yukie KAJITA[1,2], Hironori YASUDA[1], Edward W. EVANS[2]
[1] *Faculty of Agriculture, Yamagata University, Tsuruoka, Yamagata 997-8555, Japan*
[2] *Department of Biology and Ecology Center, Utah State University, Logan, UT 84322-5308, USA*

Introduction

Recent empirical studies of terrestrial arthropod communities have been focused on the widespread effects of generalist predators and higher-order predators, and have tended to support the idea of indistinct trophic levels in food-webs (e.g., Polis et al. 1989; Rosenheim and Corbett 2003). Previously, we have studied the aphidophagous - arthropod system on Hibiscus trees (*Hibiscus syriacus* L.) in Japan, and we have showed that *H. axyridis* has broad food habitats (generalist predator) and is a strong intraguild predator. We suggest that *H. axyridis* is a key predatory ladybird in this guild (Yasuda and Shinya 1997; Yasuda and Ohnuma 1999; Kajita et al. 2000; Yasuda et al. 2000; Yasuda et al. 2001; Sato et al. 2003). However, almost all of our studies have been based on laboratory experiments, and more studies under natural conditions are needed. Furthermore, it is still unclear how *H. axyridis* affects the survivorship of other aphidophagous predators (e.g., Scymnus sp., Syrphidae sp.). To understand and compare the effects of *H. axyridis*, and a second abundant ladybird, *Coccinella septempunctata*, on larval performance of co-occurring aphidophagous insects, factorial experiments involving the removal of one or both predators were carried out on hibiscus trees in the field. In addition, we investigated the interspecific and intraspecific interactions among the predatory ladybirds, *H. axyridis*, *C. septempunctata*, *Propylea japonica* and *Scymnus posticalis*, occurring over the course of larval development under greenhouse conditions wherein the larvae occurred together with resident aphid populations on host plants. Based on these results, we discuss the important role of the generalist *H. axyridis* as a top predator in this food-web.

Materials & Methods

1) Field experiment

Field experiments were conducted from May to July in 2000 and 2001 at a field plot in Yamagata University, Tsuruoka, Japan. There were 20 Hibiscus trees in the field plot, on which *Aphis gossypii* occurred from mid May to July. We manipulated the two predatory ladybirds to set up following treatments; 1) *H. axyridis* and *C. septempunctata* were present (no manipulation), 2) *H. axyridis* were excluded (*C. septempunctata* were present), 3) *C. septempunctata* were excluded (*H. axyridis* were present), 4) both *H. axyridis* and *C. septempunctata* were excluded. Eggs, larvae and adults of each of the two predatory ladybirds were removed. A life table was made for each of the three ladybirds, *H. axyridis*, *C. septempunctata*, and *P. japonica*, using the modified Kinitani-Nakasuji-Manly method (Yamamura 1998). The numbers of aphids, predatory ladybirds (*H. axyridis*, *C. septempunctata*, *P. japonica*, *S. posticalis* and *S. hoffmanni*), crab spiders (*Misumenops tricuspidatus*), and hover flies (Syrphidae sp.) were counted every other day in 2000, and every day without rain in 2001. Whittaker's Percentage Similarity (PS) (Whittaker 1952) was used to compare the temporal patterns of occurrence of third and forth instar of *H. axyridis*, *C. septempunctata* and those of other aphidophagous species (*P. japonica*, *S. posticalis*, *S. hoffmanni* and *Syrphid* sp.) on the Hibiscus trees.

2) Greenhouse experiments

The effects of *H. axyridis* and/or *C. septempunctata* on survivorship, development and emigration of larvae of *P. japonica* and *S. posticalis* were studied in a greenhouse at Yamagata University at Tsuruoka, Japan, during May and June in 2001. Young shrubs of *H. syriacus* L. (70cm in height) were planted in pots (20cm depth × 24cm diameter) and held upright with a 60cm steel stake. To water the shrubs and trap larvae that dropped from each shrub, a rectangular tray (10cm deep × 40cm wide × 70cm long) filled with water was placed under each flower pot. To catch the emigrating larvae, the inside of the rim of the flowerpots was sprayed with a sticky material. Seven hundred cotton aphids of mixed instar were placed on the Hibiscus trees and allowed to settle for 24 hours. Ladybird larvae were then added, according to seven treatments: 1) twelve second instar of *H. axyridis*, 2) twelve second instar of *C. septempunctata*, 3) twelve second instar of *P. japonica*, 4) twelve second instar of *S. posticalis*, 5) six second instar of *P. japonica* and *S. posticalis*, 6) four second instar of *H. axyridis*, *P. japonica* and *S. posticalis*, 7) four second instar of *C. septempunctata*, *P. japonica* and *S. posticalis*, 8) three second instar of *H. axyridis*, *C. septempunctata*, *P. japonica* and *S. posticalis*. Each treatment was replicated five times.

Systematic observations were carried out to determine rates of development, causes of death, emigration of ladybird larvae, and number of aphids present, until all larvae had pupated or emigrated. Mortality was attributed to (1) cannibalism, when we observed larvae being eaten by conspecifics, (2) IGP, when we observed larvae being eaten by heterospecifics, or (3) starvation, when a carcass remained (untouched by conspecifics or heterospecifics) or when individuals failed to moult to the next stage, (4) unknown, when we failed to find individuals from shrubs.

Results

1) Field experiments

The change in number of cotton aphids over time was significantly different in the absence versus the presence of either or both *H. axyridis* and *C. septempunctata* in 2000 and 2001. The number of aphids was significantly reduced following the occurrence of third and fourth instar larvae of *H. axyridis* and/or *C. septempunctata* on the hibiscus trees (Fig 1).

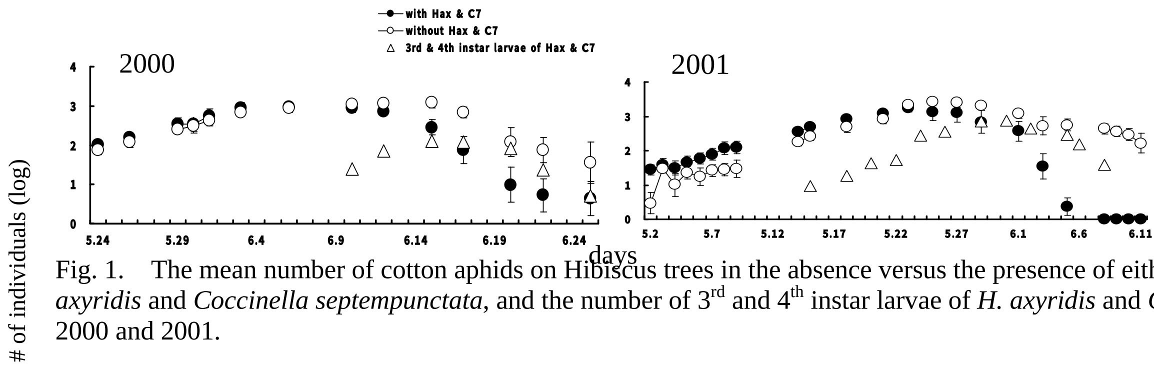

Fig. 1. The mean number of cotton aphids on Hibiscus trees in the absence versus the presence of either or both *Harmonia axyridis* and *Coccinella septempunctata*, and the number of 3rd and 4th instar larvae of *H. axyridis* and *C. septempunctata* in 2000 and 2001.

Correlations between the number of hatchlings and larval survival rate in both species of predator were determined by using data from the control treatment and each of the single-species treatments (Fig.2). There was a significant positive correlation between the number of hatchlings of *C. septempunctata* and the survival of *H. axyridis* when these two predators occurred together (r=0.91, P=0.009, n=6). In contrast, there was a negative correlation between the number of hatchlings of *H. axyridis* and the larval survival rate of *H. axyridis* (r=-0.51, P=0.06, n=14). There were no significant correlations between the larval survival rate of *C. septempunctata* and the number of hatchlings of *C. septempunctata* (r=0.14, P=0.65, n=14), or the number of hatchlings *H. axyridis*, although the latter correlation appears to have been negative (r=-0.64, P=0.19, n=6).

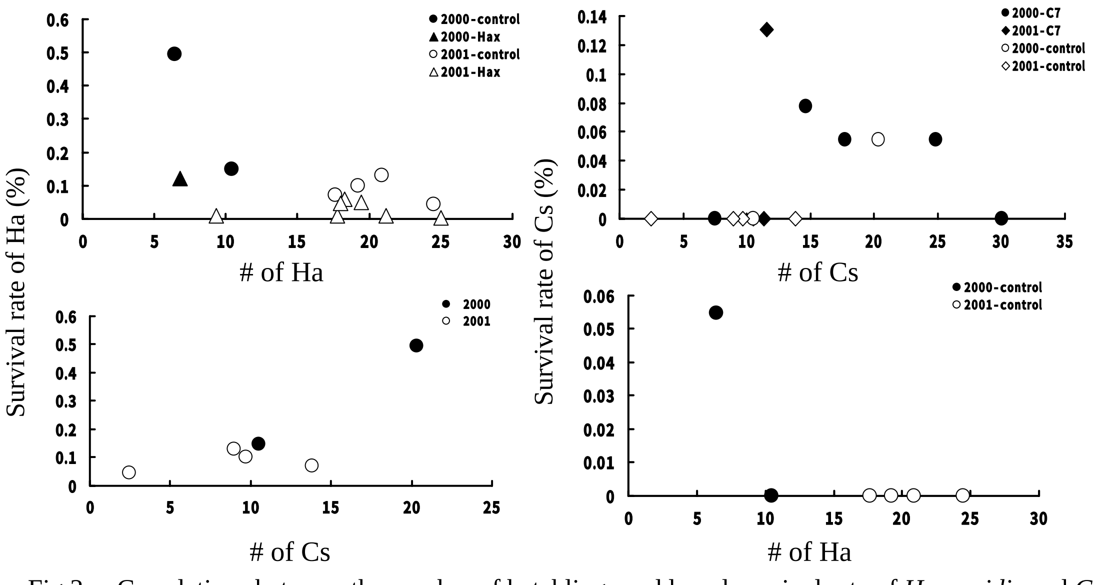

Fig 2. Correlations between the number of hatchlings and larval survival rate of *H. axyridis* and *C. septempunctata* by using data from the control treatment and each of the single-species treatments.

In both 2000 and 2001, the overlap in temporal patterns of *P. japonica* with *H. axyridis* and *C. septempunctata* was quite high (in 2000; ps=0.612, in 2001; ps=0.631). There was a significant difference in the survival rate of *P. japonica* among the treatments. Adults and larvae of *S. posticalis* occurred earlier on the trees than did adults and larvae of *H. axyridis* and *C. septempunctata*, leading to low percentage similarities (i.e., measures of temporal overlap) of *S. posticalis* with 3rd and 4th instar larvae of *H. axyridis* and *C. septempunctata* in both years (2000; ps=0.473, 2001; ps=0.429). Furthermore, late instar larvae of *S. posticalis* left the Hibiscus trees when they were ready to pupate (we found that they pupated off the host plants). Therefore, there were no significant differences in the number of surviving individuals of *S. posticalis* among the treatments. In both years, Syrphids overlapped extensively with *H. axyridis* and *C. septempunctata* in their occurrence on the trees (2000: *ps*=0.711, 2001; *ps*=0.752). There was a significant difference on the number of Syrphids larvae among the treatments; in particular, the number of larvae was significantly reduced in the presence of *H. axyridis*. Few crab spiders in either year, and there was no significant difference among the treatments.

2) Greenhouse experiments

The number of aphids was dramatically reduced in *H. axyridis* single-species treatments. In contrast, over 200 aphids remained on a potted tree in the *S. posticalis* single-species treatment even after ladybird larval development was completed. More aphids remained on the tree at the conclusion of the experiment when both *P. japonica* and *S. posticalis* were present than when only *P. japonica* was present.

The emigration rate of *H. axyridis* was not significantly different among treatments but larvae of *H. axyridis* emigrated at younger ages in the single species treatment of *H. axyridis* alone, compared with other treatments. Furthermore, there was a significant difference among treatments in the weight of 4^{th} instar larvae of *H. axyridis* that emigrated. Emigration rate, mortality rate and developmental time of larvae of *C. septempuctata* were not different among the treatments. Individuals of *C. septempunctata* tended to emigrate from the Hibiscus trees in all of the treatments. The emigration rate of *P. japonica* was significantly higher when *H. axyridis* was present than when it was absent. In addition, the survival to pupation in the presence of *H. axyridis* was significantly reduced, and intraguild predation of larvae of *P. japonica* by 4^{th} instar larvae of *H. axyridis* was observed. *C. septempunctata* did not have strong negative effects on *S. posticalis*. As observed in the field, older instars of *S. posticalis* emigrated from the Hibiscus trees. A few individuals of *S. posticalis* placed with *H. axyridis* and *C. septempunctata* died by starvation, and just one individual of *S. posticalis* was eaten by *H. axyridis*. The developmental time of 3^{rd} instars of *S. posticalis* was increased when *H. axyridis* was present. A negative effect of *P. japonica* and *C. septempunctata* on *S. posticalis* was not observed.

Discussion

Our field experiments show clearly the dynamic nature of interspecific interactions within the aphidophagous guild on the Hibiscus tree, even within a short single season. Our results suggest that the guild structure of aphidophagous insects on hibiscus trees was strongly influenced by *H. axyridis*, and that the strength of interactions among the predators varied both with development of the key species and with aphid abundance. We observed the occurrence of IGP by *H. axyridis* on other aphidophagous species in both the field and greenhouse experiments. Therefore, we suggest that IGP by *H. axyridis* is a key factor for determining the number of individuals of other aphidophagous species. However, the frequency of occurrence of IGP by *H. axyridis* in the field is still unclear.

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