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ScienceDirect
Biological Control 45 (2008) 368–379
Biological Control
www.elsevier.com/locate/ybcon

The role of natural enemy guilds in *Aphis glycines* suppression

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Received 30 August 2007; accepted 23 January 2008
Available online 31 January 2008

Abstract

Generalist natural enemy guilds are increasingly recognized as important sources of mortality for invasive agricultural pests. However, the net contribution of different species to pest suppression is conditioned by their biology and interspecific interactions. The soybean aphid, *Aphis glycines* (Hemiptera: Aphididae), is widely attacked by generalist predators, but the relative impacts of different natural enemy guilds remains poorly understood. Moreover, low levels of *A. glycines* parasitism suggest that resident parasitoids may be limited through intraguild predation. During 2004 and 2005, we conducted field experiments to test the impact of different guilds of natural enemies on *A. glycines*. We contrasted aphid abundance on field cages with ambient levels of small predators (primarily *Orius insidiosus*) and parasitoids (primarily Braconidae), sham cages and open controls exposed to large predators (primarily coccinellids), and cages excluding all natural enemies. We observed strong aphid suppression (86- to 36-fold reduction) in treatments exposed to coccinellids, but only minor reduction due to small predators and parasitoids, with aphids reaching rapidly economic injury levels when coccinellids were excluded. Three species of resident parasitoids were found attacking *A. glycines* at very low levels (<1% parasitism), with no evidence that intraguild predation by coccinellids attenuated parasitoid impacts. At the plant level, coccinellid impacts resulted in a trophic cascade that restored soybean biomass and yield, whereas small natural enemies provided only minor protection against yield loss. Our results indicate that within the assemblage of *A. glycines* natural enemies in Michigan, coccinellids are critical to maintain aphids below economic injury levels.

Keywords: *Harmonia axyridis*; *Orius insidiosus*; *Lysiphlebus testaceipes*; Intraguild predation; Generalist predators; Parasitoids; Trophic cascade

1. Introduction

There is increasing recognition that established generalist predators can provide pest suppression, due to their voracity and earlier presence in the field (Chang and Kareiva, 1999; Symondson et al., 2002; Stiling and Cornelissen, 2005). However, within these multiple enemy assemblages interactions among the natural enemy species may result in very different outcomes (Sih et al., 1998). Within-guild enemy interactions may result in either enhancement of pest suppression due to predator facilitation (Losey and Denno, 1998; Cardinale et al., 2003), or a reduction in pest control due to negative interactions such as predator interference, cannibalism, predator avoidance behavior, and intraguild predation (Snyder and Wise, 1999; Prasad and Snyder, 2006). Thus, it is important to identify the relative contribution of different natural enemy groups within multiple species assemblages to pest suppression, in order to focus management efforts on the most efficient species (Chang and Snyder, 2004).

Intraguild predation (IGP hereafter) involves trophic interactions among members of the same predator guild, i.e. predator species that share the same resource (Polis and McCormick, 1987; Polis et al., 1989; Polis and Holt, 1992; Rosenheim et al., 1995). IGP has been shown to be widespread among food webs, where it is postulated to confer stability in trophic relationships (Polis et al., 1989, 2000; Rosenheim et al., 1995; Rosenheim, 1998; Brodeur and Rosenheim, 2000; Müller and Brodeur, 2002). Since

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1049-9644/$ - see front matter
doi:10.1016/j.biocontrol.2008.01.018

generalist predators are prone to engage in IGP, they have the potential to provide pest suppression, but also to disrupt control by other natural enemies. In contrast, parasitoids that are specialized on herbivores typically do not have the potential to attack other members of the guild, with the exception of other parasitoid species sharing the same host (Brodeur and Rosenheim, 2000; Borer, 2002). Instead, parasitoids are themselves frequently susceptible to asymmetric IGP by predators in both immature and adult stages, and this has been suggested as a potential explanation for the failure of parasitoids to suppress their hosts (Rosenheim et al., 1995; Ferguson and Stiling, 1996; Heimpel et al., 1997; Rosenheim, 1998; Brodeur and Rosenheim, 2000; Müller and Brodeur, 2002).

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) is a pest of soybeans that is originally from Asia and has been found in North America since 2000 (Ragsdale et al., 2004; Venette and Ragsdale, 2004). Several studies have shown significant impacts of natural enemies on *A. glycines* in Asia (Van den Berg et al., 1997; Liu et al., 2004; Wu et al., 2004) and North America (Fox and Landis, 2003; Fox et al., 2004, 2005; Rutledge et al., 2004; Costamagna and Landis, 2006; Costamagna et al., 2007a). In Asia, the complex of natural enemies attacking *A. glycines* includes the predators *Propylaea japonica* (Thunberg), *Harmonia axyridis* (Pallas), and *H. arcuata* (Fabricius) (Coleoptera: Coccinellidae), and several species of syrphids and lacewings (Van den Berg et al., 1997; Wu et al., 2004). In addition, 10–53% parasitism by the parasitoid *Lysiphlebia japonica* (Ashmead) has been reported in China (Wu et al., 2004). In North America, the assemblage of *A. glycines* natural enemies is dominated by generalist predators, mainly the coccinellids *H. axyridis* and *Coccinella septempunctata* L., and the anthocorid *Orius insidiosus* (Say) (Fox et al., 2004, 2005; Rutledge and O'Neil, 2005; Costamagna and Landis, 2006, 2007; Mignault et al., 2006; Costamagna et al., 2007a). *Orius insidiosus* is typically present in the field before the arrival of soybean aphid, due to its ability to feed on alternative small prey, and on the soybean plant itself (Coll and Guershon, 2002; Rutledge and O'Neil, 2005). Therefore, it has been suggested that *O. insidiosus* can provide substantial suppression of soybean aphid (Rutledge et al., 2004; Rutledge and O'Neil, 2005; Desneux et al., 2006). In contrast, other studies suggest that coccinellids play a leading role in suppressing soybean aphid population increase (Fox et al., 2004; Costamagna and Landis, 2006, 2007; Costamagna et al., 2007a).

Reports of field parasitism of *A. glycines* in North America indicate generally null to very low levels, with only a handful of exceptions reporting parasitism levels above 10% (Landis and Brewer, 2003; Nielsen and Hajek, 2005; Costamagna and Landis, 2006; Baute, 2007; Noma and Brewer, 2008). Due to the lack of effective parasitoids, efforts are currently underway to introduce parasitoids from Asia (Heimpel et al., 2004). One potential explanation for the lack of parasitism of *A. glycines* in North America is the occurrence of asymmetric IGP on parasitoids. In a recent survey, Kaiser et al. (2007) detected 6 parasitoids species from sentinel *A. glycines* in Michigan, suggesting that North American parasitoid assemblages have the potential to attack soybean aphid. In addition, results of a 2003 field cage study revealed higher number of the native parasitoid *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae) in cages in which predators were excluded, supporting the hypothesis of IGP limitation of parasitism (Costamagna and Landis, 2006).

Here we report the results of field experiments using different types of exclusion cages to test the impact of ambient levels of different groups of *A. glycines* natural enemies. Specifically, we examined (1) the relative impact of the whole assemblage of natural enemies, versus small predators and parasitoids, and controls with all natural enemies excluded, on aphid abundance, (2) the impact of large predators as intraguild predators on resident parasitoids, and (3) the indirect impact of the different natural enemy groups on plant biomass and yield. Assessing the role of small versus large natural enemy suppression on *A. glycines* population dynamics has important management consequences, particularly to optimize sampling plans, since it involves considerably more effort for farmers and scouts to estimate field densities of the first group.

2. Material and methods

2.1. Field site

Field experiments were conducted in the Biodiversity Study of the Kellogg Biological Station-Long Term Ecological Research site (KBS-LTER, Hickory Corners, MI), during 2004 and 2005. The KBS-LTER station characterizes typical SW Michigan conditions, with crop yields representative of the US North Central Region (Robertson et al., 2000). The biodiversity study has a series of 21 different agronomic treatments that vary in plant species diversity in time and space, ranging from 0 to >15 species in 3-year rotation cycles (http://lter.kbs.msu.edu/). Treatments are replicated in 4 completely randomized blocks in 9.1 × 27.4 m plots, resulting in a large mixture of crops in a relatively small area. This diversity of habitats favors the presence of multiple natural enemy species that may potentially impact *A. glycines*, including several species of generalist parasitoids (Kaiser et al., 2007). Within this site, we utilized the 3 most similar treatments (all typical corn–soybean–wheat rotations) that varied only in the presence of cover crops in the non-soybean portions of the rotations. These included a system with a legume and a small grain cover crop in corn and wheat, a system with only a legume cover crop in corn, and finally a system with no cover crop. Our rationale in selecting these systems was primarily to increase replication (i.e. 4 blocks × 3 agronomic treatments = 12 plots), rather than explore the effects of cover crop systems *per se*, since our previous work had shown little impact of cover crop legacy in *A. glycines* population