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Impact of the parasitoid *Aphelinus certus* on soybean aphid populations

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ABSTRACT

Aphelinus certus Yasnosh (Hymenoptera: Aphelinidae) is an accidentally introduced parasitoid of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) in North America and it has become one of the most common natural enemies of soybean aphids in its adventive range. It is unclear, however, if increased prevalence of *A. certus* has resulted in increased biological control. We conducted an exclusion-cage experiment designed to isolate the impact of parasitoids from that of other resident natural enemies (mainly predators) of the soybean aphid. We found that *A. certus* greatly outnumbered all other soybean aphid parasitoids, and that it significantly reduced soybean aphid populations over a time span of less than two weeks compared to controls. Moreover, parasitoids alone resulted in aphid densities that were statistically equivalent to the combined effect of predators and parasitoids. Across all treatment cages, there was a significant negative association between parasitism rate and aphid population growth, with predicted zero aphid growth occurring at a parasitism rate of 42.2%.

1. Introduction

The soybean aphid was first reported in North America in 2000, and it is the most economically damaging insect pest in North American soybeans (Ragsdale et al., 2011). Yield loss due to soybean aphid infestation can reach 40%, increasing management costs by an average of $16–$33 per hectare (Ragsdale et al., 2007; Ragsdale et al., 2011). Foliar insecticide use in soybeans grown in the North Central United States increased 130-fold since the arrival of the soybean aphid, and most growers rely on foliar applied pyrethroids and organophosphates for soybean aphid management (Ragsdale et al., 2011; Heimpel et al., 2013) although use of insecticides in Canada is much more limited. Biological control is a critical component of effective soybean aphid integrated pest management (Ragsdale et al., 2007) and a suite of natural enemies is known to attack the soybean aphid in North America (Rutledge et al., 2004; Ragsdale et al., 2011; Rutledge et al., 2004; Mignault et al., 2006; Costamagna and Landis, 2006). Early studies of soybean aphid natural enemies in North America found several groups of parasitoids, both native and non-native, that attack the soybean aphid (Noma and Brewer, 2008); but as a functional group, parasitoids have been only minor players in North American soybean aphid biological control (Heimpel et al., 2010; Ragsdale et al., 2011). However, one potentially effective parasitoid species, *Aphelinus certus* Yasnosh (Hymenoptera: Aphelinidae), has been increasing in prevalence since 2005 when it was first recorded in North America (Heimpel et al., 2010; Frewin et al., 2010; Ragsdale et al., 2011; Brodeur, 2013).

Aphelinus certus is native to Asia (Heraty et al., 2007) and prior to its inadvertent introduction, it had been evaluated by researchers as a potential classical biological control agent to target the soybean aphid. However, quarantine host-specificity studies showed a broad host range within the aphid subfamily Aphidinae (Hopper et al., 2017). As a result, no petition for release of *A. certus* in North America was filed and we know of no intentional introduction. Nevertheless, *A. certus* was found in North America in 2005 – presumably as the result of an unintentional introduction – and it is now the dominant parasitoid attacking the soybean aphid throughout much of its adventive range (Heimpel et al., 2010; Frewin et al., 2010; Brodeur, 2013; Hallett et al., 2014; Leblanc and Brodeur, 2018).

While *A. certus* is continuing to increase in abundance in cultivated soybean fields (Kaser, 2016), and at times reaching relatively high parasitism rates (Frewin et al., 2010), it remains to be shown experimentally that *A. certus* field populations can effectively control the soybean aphid. Local population densities of any pest species are determined by the cumulative effects of birth, death, immigration, and emigration (Thomas and Kunin, 1999). These effects are influenced by a combination of top-down and bottom-up processes, and natural enemies are not always the driving force regulating populations (Hunter and Price, 1992). Indeed, neither high abundance of natural enemies nor high rates of parasitism necessarily result in decreased population density. For example, *Orius insidiosus* (Hemiptera: Anthocoridae) is thought to be an important predator of the soybean aphid (Rutledge and O'Neil, 2005), but this species has a preference for soybean thrips

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and may not consume soybean aphids when thrips densities are high (Desneux and O'Neil, 2008). Alternatively, if intraspecific competition of a pest species is high, increased consumption by natural enemies may simply be offset by reduced competition, without resulting in a net decrease in pest population size (May et al., 1981; Hamburg and Hassell, 1984; Ortega et al., 2012). Costamagna and Landis (2006) found that soybean aphid is largely regulated by top-down processes during the summer growth phase – before plant phenology (i.e. bottom-up factors) result in a declining population later in the season – but their study was done prior to the arrival of *A. certus* in the region.

To determine whether field populations of *A. certus* are causing increased control of the soybean aphid, we must differentiate between background aphid birth and death rates (or intrinsic growth rate) while controlling for migration. Exclusion cage experiments are designed for this task, and have been utilized successfully in the past with aphids to characterize the total effect of the community of natural enemies attacking a focal pest (Schmidt et al., 2003; Liu et al., 2004; Fox et al., 2004; Fox et al., 2005; Costamagna and Landis, 2006; Donaldson et al., 2007; Miao et al., 2007; Chacón et al., 2008; Gardiner et al., 2009; Rusch et al., 2016; Mohl et al., 2016). The objectives of the current study were to isolate the effects of parasitoids from that of other natural enemies and to determine if ambient densities of *A. certus* alone are capable of reducing field populations of the soybean aphid.

2. Materials & methods

2.1. Study site and experimental design

This study was conducted in a 0.7-hectare soybean field at the University of Minnesota Saint Paul Agricultural Experiment Station during July and August 2015. Peak aphid density typically occurs in late August at this area (Kaser, 2016), so the timing of this study was designed to occur during the exponential growth phase of the aphid population. Soybean aphid populations have been shown to be well described by an exponential growth equation with r decreasing linearly with time (Costamagna et al., 2007). The field was planted with 76 cm row spacing of a mixture of cultivars MN0303SP and MN0209SP, neither of which are known to exhibit soybean aphid resistance. Timing of the experiment was chosen based on aphid densities, so that aphid infestations were high enough to measure effects of treatments, but early enough in the season to avoid density-induced alate production and the summer alate migration phase (Hodgson et al., 2005; Costamagna et al., 2013). By conducting the experiment during this time window, we minimized the effects of immigration and emigration on soybean aphid density, so that treatments were largely a measure of birth and death factors. There were five treatment cages: 1) a fine mesh cage (240 μm × 240 μm gaps) that was intended to exclude all natural enemies (hereafter referred to as the "total exclusion" cage); 2) a broad mesh cage (1 mm × 1 mm gaps) that would only let in very small natural enemies, which are principally parasitoids (hereafter referred to as the "predator exclusion" cage); 3) an open cage with no mesh that would allow all natural enemies to enter; 4) a sham cage (hereafter referred to as "total exclusion sham") using the 240 μm mesh, with a 20 cm × 20 cm opening at the top, a 6 cm high opening around the base of the cage, and 4 cm × 15 cm slits on the north and south facing sides of the cage; and 5) a similarly designed sham cage using the 1 mm mesh (hereafter referred to as "predator exclusion sham"). The sham cages were intended to simulate the microclimate of the predator and total exclusion cages, but to allow natural enemies to enter in a manner similar to the open cages. By comparing the sham cages to the open cages, we are able to test for differences between treatments due to microclimate rather than the amount and types of natural enemies entering the cages. Entomophathogenic fungi are known to cause soybean aphid mortality – e.g. *Pandora neoaphidis* (Remaud. & Henn.) Humber (Nielsen and Hajek, 2005; Koch et al., 2010; Koch and Ragsdale, 2011) – however, we assume that pathogen pressure was low and relatively similar between treatments.

The experiment was established in 16 replicated blocks, with a single replicate of the five treatments present in each block. The cages in each block were placed ~1 m apart from each other, and treatment location was randomized within block. Each block was located in one of five different soybean rows, which were haphazardly selected with approximately 20-meter separation between each selected row so as to cover the length of the field. In each selected row, blocks were spaced along the row a minimum of 3 m apart and spanning the width of the field, resulting in 3–4 blocks per row. Each cage was constructed of a wire frame tomato cage that had the treatment mesh draped over it (except for the open treatment, which just had the wire frame). The frames were 85 cm tall and 35 cm × 35 cm square. At the base of each cage, the mesh was buried into the soil a minimum of 7 cm. As a further measure of possible microclimate effects, we placed temperature loggers within all cages of three randomly selected blocks to directly compare temperatures between treatments.

Eight blocks of the experiment were initiated on July 27, 2015, and the other eight began on July 30, 2015. Twenty-four hours prior to initiating the treatments, 10 soybean plants within five meters of each block were haphazardly selected, and all alate and apterous soybean aphids were counted, in addition to all soybean aphid natural enemies (Table 1). The median soybean aphid density from the 10 plants surrounding each block was used to determine the aphid inoculation level for each treatment cage within that block. This was done to avoid simulating an outbreak population or inducing aggregations of natural enemies (Schellhorn and Andow, 2005; Donaldson et al., 2007) that might differ from ambient densities in the surrounding field. For each treatment, a single soybean plant was selected and all plants within contact distance were removed so that aphids could not easily migrate by walking between plants. All insects were removed from the selected plants prior to inoculation with soybean aphids from a laboratory colony and were of mixed instar apterous aphids. Immediately after inoculation, all treatments were covered with an additional fine mesh (240 × 240 μm) for 48 h to allow aphids to settle without exposure to natural enemies. After 48 h, this fine mesh was removed from all cages, aphid densities were recounted to ensure successful transfer and record precise starting densities, and treatments were allowed to run for 12 days. This relatively short 12-day interval was chosen in order to avoid the development of alate aphids in cages reaching high aphid density.

Aphids that have developing parasitoid wasps inside them turn into easily recognizable leathery husks a few days after oviposition (approximately coinciding with parasitoid pupation), and this husk is termed a "mummy". Hymenopteran primary parasitoids of aphids belong to one of two groups – Aphidiinae (Ichneumonoidea: Braconidae), which form brown, globe-shaped mummies, and *Aphelinus* (Chalcidoidea: Aphelinidae), which form smaller black, spindle-shaped mummies (Powell, 1982; Müller et al., 1999). After the 12-day experimental period, all aphids and natural enemies were counted on each plant, and parasitoid mummies were placed in size zero gel capsules until adult emergence so that parasitoids and hyperparasitoids could be identified to species, or in a few cases when morphological characteristics were difficult to interpret, only to genus (as was the case for all hyperparasitoids). Each plant was then removed and placed in a sealed 30 cm × 18 cm × 43 cm paper bag and brought back to the laboratory. After approximately six days, the bags were opened, and all mummies that had formed were counted and placed into individual gel capsules for emergence and identification to genus or species. This was done to gain a more accurate estimate of parasitism rate, as *A. certus* require about 6 days to reach the mummy stage at 25 °C (Frewin et al., 2010), and not all parasitized aphids observed in the field would have yet mummified when plants were initially inspected. Parasitism rates were calculated as equal to $\frac{M_f + M_r}{M_f + M_r + A}$, where M_f is the total mummies counted in the field, M_r is the total mummies reared from samples