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Why two species of parasitoids showed promise in the laboratory but failed to control the soybean aphid under field conditions

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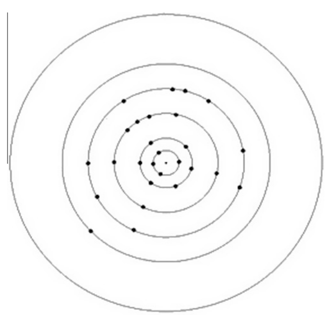
HIGHLIGHTS

- Two parasitoids were considered for biocontrol of the soybean aphid in America.
- Although promising in controlled environments, they failed in soybean fields.
- *Binodoxys communis* lost its ability to enter diapause during laboratory confinement.
- Field parasitism by *Aphidius colemani* was very low following inundative releases.

GRAPHICAL ABSTRACT



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ABSTRACT

Following the rapid spread of soybean aphid, *Aphis glycines* in North America in the early 2000's, biological control was identified as a cost-effective approach for management of this invasive pest. Two parasitoid species, *Binodoxys communis* and *Aphidius colemani*, were considered as potential candidates for classical and inundative biological control, respectively. The objectives of the present study were to determine the overwintering capacity of *B. communis* under climatic conditions prevailing in northeastern North America, and to measure parasitism and dispersal capacity of *A. colemani* when released in soybean fields. Field and laboratory assessments showed that the Chinese strain of *B. communis*, Harbin 2002, has a very poor capacity to enter into diapause (<0.8%), and thus to establish in North America. We suggest that this strain has gradually lost its ability to enter diapause during the extended periods of quarantine and laboratory confinement, during which it was continuously exposed to non-diapause rearing conditions. *A. colemani* did not show strong potential to control *A. glycines*. Following the release of approximately 8400 females in experimental plots, only 113 mummies were recovered within a radius of 60 m from the release point. Although both parasitoids were promising in controlled environments, the *B. communis* Harbin 2002 strain and the *A. colemani* commercial strain did not show strong potential to control *A. glycines* populations in soybean fields.

1. Introduction

A multitude of factors influence the establishment and effectiveness of biocontrol agents. Introduced natural enemies are expected to establish (classical biological control) or not (augmentative biological control), spread and reduce pest populations. Establishment rate of natural enemies is a significant concern in classical biological control. Although this parameter remains difficult to evaluate from large databases, only about 30% of introductions have resulted in the establishment of a biocontrol agent (Hall and Ehler, 1979; Greathead and Greathead, 1992). However, establishment rates are likely to have improved in recent decades,

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following on the development of more cautious and detailed evaluation of potential biocontrol agents prior to release (Cock et al., 2010). Introductions of natural enemies in a new habitat can be considered as a deliberate biological invasion, with characteristic biogeographic, demographic and genetic processes favouring or not the establishment of a given species (see Hopper and Roush, 1993; Simberloff, 2009; Fauvergue et al., 2012 and references therein). Similarly, a vast array of biotic and abiotic factors may determine the effectiveness of a biocontrol agent once it has been released in the environment. Of those, specificity likely establishes the intrinsic potential of a given species to become an efficient biocontrol agent (see Brodeur, 2012 and references therein). Specificity of a natural enemy can influence the probability it could find, attack, develop and reproduce on a target pest, and the likelihood of establishing self-perpetuating populations that could contribute to reduce pest populations.

Native to Asia, the soybean aphid, *Aphis glycines* Matsumura (Heteroptera: Aphididae), is a holocyclic and heteroecious species, alternating from primary (buckthorn; *Rhamnus* spp.) to secondary (soybean; *Glycine max*) hosts. This invasive species was first observed in North America in 2000 and has rapidly spread through all soybean growing areas in Canada and the United States (Venette and Ragsdale, 2004). *A. glycines* is now considered as the most important pest of soybeans (Ragsdale et al., 2011) as it can significantly reduce the yield of soybean through feeding (Macedo et al., 2003; Rhainds et al., 2007; Beckendorf et al., 2008).

Biological control was rapidly selected as a cost-effective approach for management of soybean aphid populations. In Asia, *A. glycines* is attacked by more than 55 taxa of predators, parasitoids and entomophagous pathogens (Wu et al., 2004; Miao et al., 2007). In North America, numerous studies showed that several species of predators attack *A. glycines* and play a major role in reducing aphid populations. For example, in Québec, Canada, field surveys and cage experiments showed that coccinellids, the most abundant predator group sampled (Mignault et al., 2006), together with other aphidophagous predators (Firlej et al., 2013), can suppress *A. glycines* populations and mitigate their impact on soybean plants (Rhainds et al., 2007). However, both in Canada and United States, indigenous and naturalized species of aphid parasitoids do not yet appear to play a major role in reducing populations of the invasive *A. glycines* (Kaiser et al., 2007; Noma and Brewer, 2008), although parasitism rates tend to increase over the course of the soybean invasion (Noma and Brewer, 2008; Heimpel et al., 2010; Frewin et al., 2010).

In this context, classical biological control using Asian parasitoids was considered a promising avenue to enhance the overall efficacy of *A. glycines* natural enemies in North America (Heimpel et al., 2004). Following foreign exploration in Asia (Heimpel et al., 2004) where parasitoids contribute to control *A. glycines* populations (Liu et al., 2004), host specificity studies (Wyckhuys et al., 2007; Desneux et al., 2009) and experiments to assess potential efficacy, *Binodoxys communis* (Gahan) (Hymenoptera: Braconidae) was identified as a promising candidate, and a permit from USDA-APHIS was granted for field release in the United States (Wyckhuys et al., 2007). However, *B. communis* has so far failed to establish in the field following multiple releases in the north-central United States (Ragsdale et al., 2011; G. Heimpel, personal communication). Several nonexclusive explanations may account for the perceived failure of establishment of this exotic parasitoid: inability to overwinter, low dispersal ability, intraguild predation, genetic bottlenecks and Allee effects in released parasitoid populations (Wyckhuys et al., 2008; Chacon et al., 2008; Heimpel et al., 2010; Heimpel and Asplen 2011).

Another potential biological control approach would be to inundate soybean fields early in the season with the parasitoid *Aphidius colemani* Viereck. Under laboratory conditions this species attacks, develops and reproduces successfully on *A. glycines* (Lin and Ives, 2003). Under greenhouse conditions *A. colemani* also showed the capacity to significantly reduce *A. glycines* populations (J. Doyon, unpublished data). Furthermore, this species is already available at low cost as a commercialized biological control agent of a number of aphid pest species, mainly for greenhouse crops.

The first objective of the present study was to obtain a better understanding of the seasonal biology of *B. communis* under climatic conditions prevailing in Québec, Canada. Parasitoid overwintering capacity was determined under insectary and laboratory conditions by measuring the capacity of *B. communis* to enter diapause as a prepupa within the mummified aphid. The second objective was to measure parasitism rate on *A. glycines* as well as dispersal capacity of *A. colemani* when released in soybean fields.

2. Material and methods

2.1. Diapause induction in *B. communis*

A soybean aphid colony was established at the Institut de recherche en biologie végétale (IRBV), Université de Montréal, from individuals collected near Saint-Mathieu-de-Beloeil, Québec (45°34′46″N, 73°14′24″W), in 2008. *A. glycines* was maintained on seedlings of soybean, *G. max*, *cv* Merrill, at 22 ± 1 °C, 50–70% RH, and 16L:8D photoperiod. A colony of *B. communis* was established at the IRBV from a Chinese strain of *B. communis* that was originally collected in 2002 by K. Hoelmer, K. Chen and W. Meikle in soybean fields near Harbin (45°41′ 27″N, 126°37′ 42″E) and in Suihua County (45°36′ 28″N, 126°57′ 49″E) in the province of Heilongjiang (Wyckhuys et al., 2008). This area of China provides a relatively good climate match to southern Québec, the minimum and maximum average temperatures in Harbin being similar to the ones in Montréal (Fig. 1). Specimens of the Harbin 2002 strain were identified by Dr. Petr Stary, Institute of Entomology, Biology Centre of the AS CR, Czech Republic. The *B. communis* culture was first maintained in quarantine at the USDA-ARS Beneficial Insect Introduction Research Laboratory in Newark, Delaware, USA. A stock culture was next moved to the University of Minnesota, St-Paul, USA (G. Heimpel's lab). In 2009, the Harbin 2002 strain was established at the Université de Montréal under the same rearing conditions as the aphid colony. This strain has never been restocked with other field-collected individuals. Voucher specimens are stored at the USDA-ARS Beneficial Insect Introduction Research Laboratory in Newark, Delaware, USA.

We tested the capacity of *B. communis* to enter diapause under laboratory conditions that induce diapause in aphid parasitoids from temperate regions (Brodeur and McNeil, 1989; Yu, 1992; Christiansen-Weniger and Hardie, 1999; Polgar and Hardie, 2000). Soybean plants infested with a few hundred soybean aphids in various instars were exposed to 150 2–3-d-old mated *B. communis* females for 24 h. Parasitoid females were then removed from the cage and parasitized aphids were reared in growth chambers under the following three conditions: 15 ± 1 °C and 12:12 (L:D), 13 ± 1 °C and 12:12 (L:D), 13 ± 1 °C and 10:14 (L:D); all at 60 ± 10% RH. Once aphid mummies had formed, from 116 to 155 mummies per treatment, they were collected, put in gelatine capsules and observed daily for emergence. Mummies that did not give rise to parasitoid adults were dissected 14 d following peak emergence, and their contents classified as either diapausing prepupae (yellow, fully developed larvae occupying the entire mummy) or dead parasitoids (dessicated individuals). Fisher's exact tests were conducted to compare parasitoid emergence, mortality and diapause among treatments.

The percentage of *B. communis* entering diapause under natural conditions was also determined at the end of the growing season