

# Ecology and Management of the Soybean Aphid in North America

David W. Ragsdale,<sup>1</sup> Douglas A. Landis,<sup>2</sup>  
Jacques Brodeur,<sup>3</sup> George E. Heimpel,<sup>1</sup>  
and Nicolas Desneux<sup>4</sup>

<sup>1</sup>Department of Entomology, University of Minnesota, St. Paul, Minnesota 55108; email: ragsd001@umn.edu, heimp001@umn.edu

<sup>2</sup>Department of Entomology, Michigan State University, East Lansing, Michigan 48824; email: landisd@msu.edu

<sup>3</sup>Institut de Recherche en Biologie Végétale, Département des Sciences Biologiques, Université de Montréal, Québec H1X 2B2, Canada; email: jacques.brodeur@umontreal.ca

<sup>4</sup>INRA (French National Institute for Agricultural Research), Sophia Antipolis 06903, France; email: nicolas.desneux@sophia.inra.fr

Annu. Rev. Entomol. 2011. 56:375–99

First published online as a Review in Advance on September 20, 2010

The *Annual Review of Entomology* is online at [ento.annualreviews.org](http://ento.annualreviews.org)

This article's doi:  
10.1146/annurev-ento-120709-144755

Copyright © 2011 by Annual Reviews.  
All rights reserved

0066-4170/11/0107-0375\$20.00

## Key Words

invasive species, biological control, economic threshold, IPM, *Aphis glycines*

## Abstract

The soybean aphid, *Aphis glycines* Matsumura, has become the single most important arthropod pest of soybeans in North America. Native to Asia, this invasive species was first discovered in North America in July 2000 and has rapidly spread throughout the northcentral United States, much of southeastern Canada, and the northeastern United States. In response, important elements of the ecology of the soybean aphid in North America have been elucidated, with economic thresholds, sampling plans, and chemical control recommendations widely adopted. Aphid-resistant soybean varieties were available to growers in 2010. The preexisting community of aphid natural enemies has been highly effective in suppressing aphid populations in many situations, and classical biological control efforts have focused on the addition of parasitoids of Asian origin. The keys to sustainable management of this pest include understanding linkages between the soybean aphid and other introduced and native species in a landscape context along with continued development of aphid-resistant varieties.

**Invasive species:** a nonindigenous species that has undergone substantial spread and population growth, often to the point of achieving pest or weed status

**Integrated pest management (IPM):** an ecosystem-based strategy that relies on a combination of techniques (e.g., biological control, cultural practices, pesticides) to prevent or control pest populations

**SBA:** soybean aphid

**USDA-APHIS:** U.S. Department of Agriculture - Animal and Plant Health Inspection Service

## INTRODUCTION

Invasive species represent a serious global threat to natural and managed systems (24, 119). In agriculture, invasive species can reduce yields, increase control costs, and result in increased reliance on pesticides (42, 54, 140), which can disrupt existing integrated pest management (IPM) systems (124, 142). Moreover, the establishment of an invasive exotic species has the potential to cause cascading ecological impacts that may extend into natural systems as well (153). The soybean aphid, *Aphis glycines* Matsumura, in North America has emerged as a classic case of an invasive, exotic species that has become a major source of economic loss in soybean production and whose presence has aided other invasive species (59). Here, we review the invasion history, ecology, economic impacts, and management of the soybean aphid (SBA) in North America. A review of these topics is timely considering that the rate of insect invasions is anticipated to increase in the future because of globalization and climate change (92, 151), and because major soybean-producing regions of the world, in particular South America (Brazil, Argentina, Paraguay, and Bolivia) and central India (United Nations, FAO data, <http://faostat.fao.org/default.aspx>), are at risk of being invaded by this pest.

## INVASION HISTORY

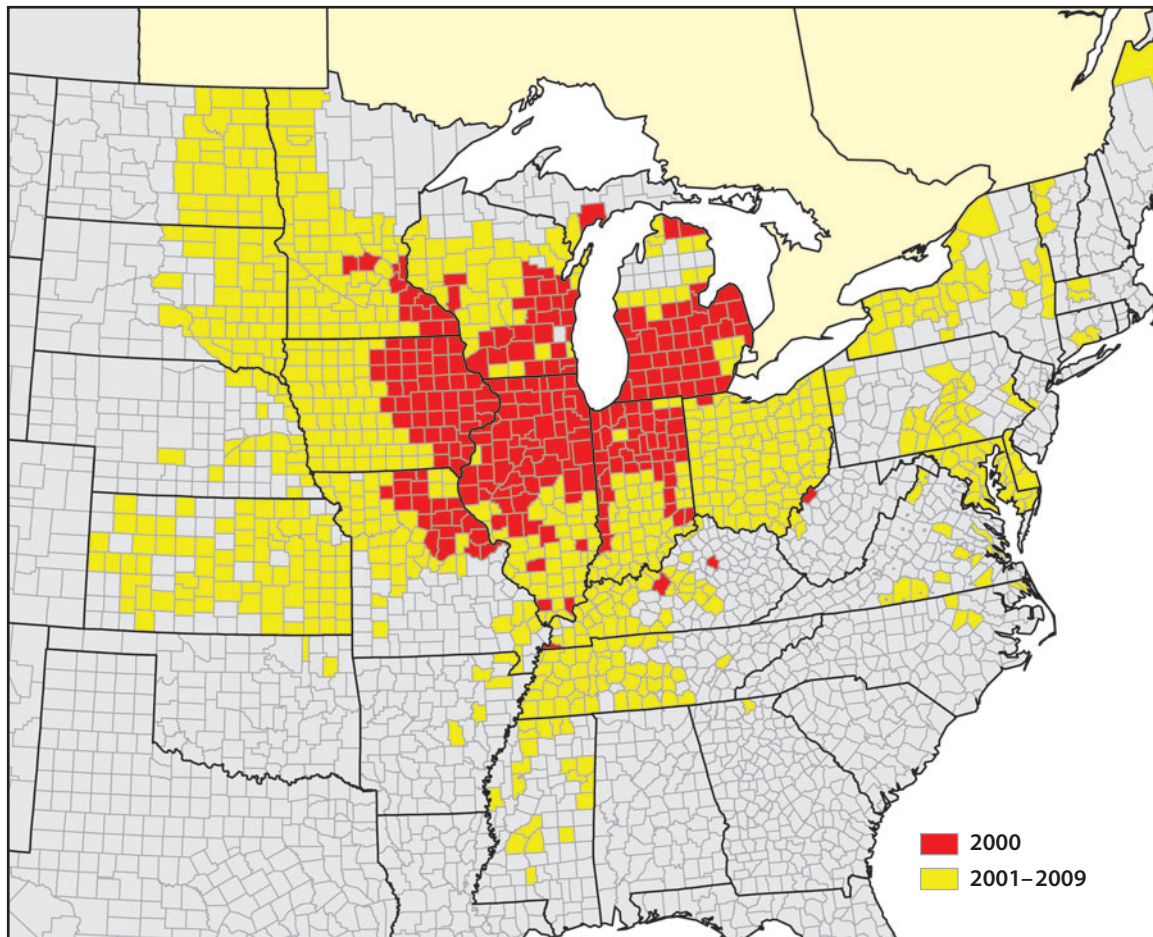
The invasion of SBA into the Americas from Asia was anticipated by Kogan & Turnipseed (84). This prediction was realized in July 2000 when SBA was first detected in Wisconsin, and by the end of summer 2000, SBA was found in 10 northcentral U.S. states (**Figure 1**). Although no prior records occur, SBA was likely present in the United States prior to its detection but went unnoticed until populations reached damaging levels (126). Alternatively, its capability for rapid expansion suggests that even recent infestations could become extensive. The aphid was first detected in late summer 2002 (111) in southwestern Québec, and by 2003, all soybean-growing regions throughout

the province were infested, with 51 of 54 sampled fields colonized by SBA. By 2009, the aphid had colonized 30 states and three Canadian provinces (**Figure 1**). Aphids can enter low-level jet streams and migrate long distances, for instance, between primary and secondary hosts or between geographic areas. SBA also has a great capacity to disperse within and between fields (127). Tethered alates engage in up to 11 h of active flight, covering an average estimated distance of 6.7 km during a single flight period (162). Interestingly, SBA was also discovered infesting soybean in Australia in 1999 (148) but has not become a major pest there, probably because of a lack of suitable primary hosts (<http://www.ars-grin.gov/>).

The origins of the U.S. infestation are not known. Analysis of USDA-APHIS (U.S. Department of Agriculture - Animal and Plant Health Inspection Service) aphid detections coupled with climate-matching of SBA spread in the United States suggested that Japan could have been the source of the infestation (148). More recently, the genetic diversity and differentiation among 2 South Korean and 10 North American populations have been compared (109, 110). These data indicate that South Korea was not the source of the North American invasion and suggest a pattern of a small colonizing population, followed by rapid clonal amplification and subsequent large-scale differentiation.

## SOYBEAN APHID ECOLOGY IN NORTH AMERICA

SBA is a heteroecious (host-alternating) aphid that utilizes a woody primary host for overwintering and an herbaceous secondary host in the growing season. In North America, neither of the known primary hosts in Asia, *Rbamnus davurica* or *R. japonica*, is present to any large extent outside botanical gardens. In contrast, an invasive buckthorn species from Europe, *R. cathartica* (common buckthorn), is widespread (149) and is used by SBA as its principal overwintering host (150). In one study, early-season SBA density in soybean



**Figure 1**

Distribution of the soybean aphid (SBA) in North America (125, 148). Red represents the initial 10 states (and counties within those states) that reported SBA by the end of summer 2000. Yellow represents the current known distribution (summer 2009) of SBA one decade after its initial discovery, with data recorded by county for the United States. For Canada, fine detail is not available, but pale yellow indicates provinces that reported SBA by 2009.

was best explained by the ratio of buckthorn density to field area (2). U.S. native *Rhamnus* spp., particularly *R. alnifolia* and *R. lanceolata*, are also potential primary hosts (150), and *Frangula alnus* (= *R. frangula*) is a less preferred but nonetheless acceptable primary host (65). *Glycine max* (soybean) is the principal secondary host of SBA in North America, although studies suggest reproduction is possible on Carolina horsenettle, *Solanum carolinense* (23), and red clover, *Trifolium pratense* (126). This exotic aphid from Asia survives in North

America by using a primary host (common buckthorn) introduced from northern Europe and a secondary host (soybean) from Asia.

Several studies have examined SBA growth rates in relation to temperature, and as a result, the optimal and upper lethal temperatures are well understood. SBA has an optimal development temperature of 28°C and exhibits a rapid decline in reproductive output as temperatures approach 35°C (102, 105). This constraint, along with reduced abundance of primary hosts, likely explains why SBA's

**Nonpersistent virus:** an insect-vectoring virus acquired by feeding on infected plants and immediately able to transmit virions to susceptible hosts via contaminated mouthparts without the need for a latent period between acquisition and transmission

**Economic threshold (ET):** the pest population level at which a control action must be taken to prevent economic damage to a crop

**Economic injury level (EIL):** the population level of a pest that will cause economic damage to a crop

range has not yet extended to the southern soybean-producing regions in North America (Figure 1). Temperature-dependent growth rates have also been incorporated into models of SBA population dynamics (29).

## ECONOMIC IMPORTANCE IN NORTH AMERICA

### Economic Impact on Soybean Production

In the United States, there are approximately 32 M ha of soybeans planted each year, with a production value in excess of US\$27 billion. Over 80% of the soybeans grown in the United States (26 M ha) are produced in just 12 north-central states (<http://www.nass.usda.gov/>). For producers in these states, SBA represents the first insect pest to consistently cause significant yield losses over wide areas (126), with yield decreases as high as 40% (125). As a result, pest management practices for soybean producers have changed dramatically. Prior to the arrival of SBA, less than 2% of the soybean acreage in the northcentral states was scouted for arthropod pests, and IPM programs centered almost exclusively on defoliating insects. Currently, 77% of the soybean acreage is routinely scouted for insects and mites, which represents a 40-fold increase in scouting activity since the arrival of SBA (138). In a survey of IPM practices adopted by soybean producers, 84%–94% considered scouting reports crucial for making management decisions for SBA (118). SBA has resulted in a tremendous economic impact on soybean production in the northcentral United States as producers must now budget for scouting and insecticidal control of aphids to remain profitable (138).

### Injury to Soybean

SBA-feeding injury manifests itself as a reduction in plant height, resulting in reduced pod set and fewer seeds within pods at maturity (5, 125, 128). At high aphid densities, seed size can also be reduced and protein content increases

with a concomitant decrease in oil content (5). Aphid injury consists of the removal of photosynthate as vast quantities of plant sap are removed (147). With SBA a unique form of feeding injury has been documented in which aphids interfere with the quenching process that restores chlorophyll to a low-energy state (99). Plant response to aphid-feeding injury can be highly variable and is dependent in large part on the overall physiological status of the crop. SBA populations that reach their peak density during the late reproductive soybean growth stages (R6–7; 63) are less likely to cause serious economic loss than populations that peak during mid-reproductive stages (R3–5) (125). Aphid injury could be exacerbated when plants are under intermittent drought stress (75, 130), but this specific injury has not yet been demonstrated with SBA.

### Transmission of Viruses

SBA is a competent vector of many plant viruses (22, 30, 31, 70, 76), and in this section we briefly review its ability to transmit plant-pathogenic viruses to crops other than soybean. SBA was, in part, responsible for widespread virus epidemics observed in snap bean (113) and has been implicated in a continuing problem with *Potato virus Y* in seed potato production (30, 31) and in squash production, demonstrating that the economic impact of this invasive aphid reaches well beyond soybean production. In soybean, outbreaks of *Soybean mosaic virus* have not occurred, although SBA is a competent vector and outbreaks were anticipated. Moreover, insecticide applications have not been effective in preventing spread of *Soybean mosaic virus* (122), so host plant resistance may be the most effective tool available to control spread of nonpersistent viruses in soybean.

## MANAGEMENT OF THE SOYBEAN APHID

### Development of Economic Thresholds

Economic thresholds (ETs) and economic injury levels (EILs) for SBA were developed

using whole-plant enumerative counts of aphids per plant. To count aphids on 30 plants per field is time-consuming and might lead to lower adoption rates for SBA IPM (125). A binomial sampling plan was developed that allows rapid assessment of aphid density and leads to a recommendation to either treat or resample (71). This binomial sampling protocol was validated in multiple states, and the correct management decision was attained 79% of the time. When the incorrect decision was reached, the binomial sampling plan was always more conservative, meaning a treatment decision was reached when aphid density was, in fact, below the ET (72). Other sampling plans based on aphid density at specific plant nodes (103) are available but have not yet been incorporated into any IPM decision tool.

The ET and EIL were developed using a common experimental protocol in six north-central states over a three-year period to produce a dataset of 19 location-years (125). The ET for SBA is 250 aphids per plant. This ET has proven applicable over a wide range of yield, price expectations, and control costs. The current ET is valid through growth stage R5 (full-size pods, immature seeds) and was developed on aphid-susceptible soybean varieties. This ET provides producers with a seven-day treatment window before aphid populations are projected to exceed the EIL of 674 aphids per plant. The current threshold is a balance between preventing catastrophic losses and conserving natural enemies with the goal of applying a single foliar spray per season to prevent aphid-induced yield loss. In a three-year comparison of the calculated ET versus treatment at a specified plant growth stage or use of seed treatments alone to control aphids, the best return on investment was the 250 aphid per plant ET (78). Valid ETs and EILs for aphid populations that reach peak density later in the growing season at plant growth stage R6 (full-size green seed in pods) are not yet available (125). The ET for SBA will need refinement as yield expectations, control costs, natural enemy abundance, aphid-resistant soybean plants, and

other factors affecting aphid population growth are better understood.

## Chemical Management

Prior to the discovery of SBA in North America, only 2 of the 12 northcentral U.S. states (Illinois and Ohio) reported any insecticide use in soybean, and the area treated in those 2 states was <1% of that state's soybean crop. Thus, in 2000, less than 0.1% of soybean acreage in the northcentral United States was treated for insect pests [United States Department of Agriculture–National Agricultural Statistical Service (USDA-NASS), <http://www.nass.usda.gov/>]. In contrast, by 2006, over 13% of the soybeans grown in the northcentral United States were treated with insecticides (USDA-NASS), suggesting that SBA has been responsible for a 130-fold increase in the use of insecticides on soybean fields. A similar situation has been observed in Canada, where, except for rare infestations of the fall armyworm, *Pseudaletia unipuncta*, insecticides were not used in soybean fields prior to the invasion of SBA. However, following a severe SBA infestation in 2007, 57% of the soybeans grown in Québec that were insured were treated with insecticides (Financière agricole du Québec; <http://www.fadq.qc.ca/>).

Most producers rely on foliar application of pyrethroids and organophosphate insecticides to control SBA, and during SBA outbreak years, up to 57% of a given state's soybean acreage had been treated with insecticides (USDA-NASS). Pyrethroids provide good efficacy at low use rates, and formulation allows for longer persistence than that typically found with organophosphate insecticides. Organophosphate insecticides continue to be used because they are less expensive and, unlike pyrethroids, most have some activity against the two-spotted spider mite, *Tetranychus urticae* (120), an occasional pest of soybean in dry years. Overall, insecticide use has increased production costs by US\$16–\$33 per ha (125). In addition, these insecticides can negatively affect

---

**Natural enemy:** an organism that kills or otherwise reduces the numbers of another organism

**USDA-NASS:** U.S. Department of Agriculture–National Agricultural Statistical Service

---

---

### Conservation

**biological control:** a general approach that refers to the provision of necessary requirements for biological control agents and the avoidance of practices that interfere with their beneficial activities

---

natural enemies because of lethal and multiple sublethal effects (34, 77). The use of neonicotinoid insecticides applied as seed treatments has become common (100). However, these compounds do not persist long enough within plants to provide economic control of SBA (78).

### Host Plant Resistance

Several soybean varieties and plant introductions (PIs) have been identified as resistant to SBA and present antibiosis, antixenosis, and tolerance as mechanisms of resistance (44, 64, 67, 94). The Germplasm Resources Information Network lists 16 plant introductions as resistant and 6 as mostly resistant (USDA-ARS, <http://www.ars.usda.gov/main/main.htm>).

All these accessions were initially identified in laboratory or greenhouse studies. Hill et al. (67) were the first to identify the varieties Jackson and Dowling as resistant to SBA via antibiosis and PI 71506 as having an antixenosis form of aphid resistance. Resistance in Dowling, a maturity group VIII soybean variety, has been further characterized as having a single dominant gene designated *Rag1* (Resistance to *Aphis glycines* gene 1) (69). Aphid resistance in the variety Jackson is also a single dominant gene and maps to the same linkage group (M) as Dowling and may simply be an allele of *Rag1* (65, 68, 69). Another gene showing antibiosis from PI 243540 is *Rag2* and is associated with linkage group F (107). Additional antibiosis was identified in PI 567541B and PI 567598B (106), and in these cases resistance appears to be controlled by two unnamed recessive genes. On aphid-resistant lines K1639, Pioneer 951397, Jackson, and Dowling, probing aphids required significantly longer time to reach the phloem and ingested from phloem tissues for only 2–7 min compared to >60 min on a susceptible control variety (43). In 2010, growers in the United States had SBA-resistant varieties (*Rag1*) available for the first time, and in field tests it appears that, although the primary mechanism of resistance is antibiosis, these resistant varieties also show some degree of tolerance to aphid feeding (21).

As aphid-resistant plants become available, aphids that perform equally well on resistant and susceptible varieties have been identified (81). The biotype that was found infesting lines bearing the *Rag1* gene was initially called the Ohio biotype because it was first recognized from a 2006 Ohio study. Subsequently, this biotype has been designated biotype2, with biotype1 referring to the aphid that commonly colonizes soybeans lacking any resistance genes (66). In 2007, SBA found colonizing *F. alnus* in Indiana were placed on soybean plants containing either *Rag1* or *Rag2* and readily colonized *Rag2* soybeans. These field-collected aphids have been designated biotype3 (65). Several aphid species have overcome single-gene resistance in many crops (147); however, the existence of aphid biotypes is often only the result of laboratory observations (143). Nonetheless, releases of single-gene resistance may be a poor way to deploy resistant soybean germplasm, and a combination of antibiosis and antixenosis may result in more stable resistance (146). At present, we know little about the geographic distribution of SBA biotypes or if this pattern could change over the course of a growing season as summer migrants colonize additional soybean fields.

### Natural and Conservation Biological Control

The arrival of SBA in North America prompted intense interest in the factors that may control it in its introduced range. Much of this work has focused on understanding the roles of existing natural enemies in North America and the potential to conserve them to achieve biological control of SBA.

**Natural enemies in Asia.** In China, SBA is attacked by over 55 taxa of natural enemies, including predators, parasitoids, and pathogens (154), and seminal works in Asia suggested that natural enemies play a major role in controlling this pest (18, 93). Working in Indonesia, Van den Berg et al. (145) reported that the coccinellid *Harmonia arcuata* was the

major predator reducing SBA infestations and recommended conservation of early-season natural enemies. Following the North American invasion of SBA, several studies were initiated in China to determine the relative impact of natural enemies on SBA population growth. Liu et al. (96) found that a combination of natural enemies dominated by the parasitoids (*Lysiphlebus* sp.), the coccinellid predators *Propylea japonica* and *Scymnus* (*Neopullus*) *babai*, and the dipteran predator *Paragus tibialis* reduced SBA populations by as much as 12-fold over uncaged plants. In a similar study, Miao et al. (108) found 16 species of natural enemies (3 parasitoids and 13 predators) that suppressed SBA below economic levels in a two-year study. These researchers explored the relative importance of natural enemy taxa by using cages with different mesh sizes. They concluded that, although parasitoids provided detectable aphid suppression, the combination of parasitoids and predators (dominated by *P. japonica*) was most effective in suppressing SBA.

**Natural enemies in North America.** Immediately after the discovery of SBA in North America, studies were initiated to determine the impact of natural enemies on SBA in the new invaded range. A diverse community of generalist natural enemies, both indigenous and naturalized, started to exploit SBA following invasion in North America (**Table 1**). Rutledge et al. (132) reported 43 predator taxa associated with SBA in soybean, including 30 species of Carabidae, 5 Coccinellidae, and 1 each of Anthororidae, Cantharidae, Chamaemyiidae, Chrysopidae, Forficulidae, Hemerobiidae, Lampyridae, Nabidae, and Syrphidae. In subsequent no-choice trials, 15 of these taxa fed on SBA, with *Forficula auricularia*, *Coccinella septempunctata*, *Harmonia axyridis*, *Hippodamia convergens*, *Nabis* spp., and *Chrysopa* spp. consuming the highest numbers of aphids. That seminal survey (conducted in Michigan and Indiana in 2001–2002) hinted that natural enemy communities can differ widely from state to state. In Québec, Coccinellidae, Anthororidae, Chrysopidae, Syrphidae, and Nabidae were

detected in SBA-infested soybean, with Coccinellidae the most abundant predator group observed (111). Among the seven coccinellid species found, *Propylea quatuordecimpunctata*, *H. axyridis*, *Coleomegilla maculata lengi*, and *C. septempunctata* were the most common. Nine species of predatory flies were found attacking SBA in Michigan, including seven Syrphidae and one each of Cecidomyiidae and Chamaemyiidae (79). In New York, among 59 species of carabids collected in soybean fields, the exotic *Agonum muelleri* was dominant and confirmed to eat SBA in no-choice tests (55). This species spent considerable time climbing on soybean, where it reduced the population of apterous adult SBA and indirectly the numbers of nymphs these adults produce (55, 56). Finally, both harvestmen (1) and the coccinellid *Scymnus louisianae* (10) consume SBA.

Parasitoid communities of SBA in North America have been documented. In New York, three species of braconid parasitoids (*Aphidius* and *Praon* spp.) were incidentally detected in studies focusing largely on pathogens (114). Subsequent targeted studies in Michigan revealed six hymenopteran parasitoids attacking SBA: *Lysiphlebus testaceipes*, *Aphidius colemani*, *Binodoxys kelloggensis* (123), a *Praon* sp. (braconids), *Aphelinus asychis*, and a member of the *Aphelinus varipes* complex (aphelinids) (79, 115). In addition, *Aphelinus certus*, a species presumed to have been introduced accidentally, has been found attacking SBA both in soybean fields and in buckthorn in the eastern United States and Canada (59). Despite the occurrence of multiple species, parasitoids have been so far only a minor component of SBA natural enemies in North America compared with Asia. However, parasitism rates, particularly by *A. certus* and the presumably native *L. testaceipes*, have increased over the course of the soybean invasion (59, 115).

Nielsen & Hajek (114) reported seven species of pathogenic fungi recovered from SBA in New York, including *Pandora neoaphidis*, *Conidiobolus thromboides*, *Entomophthora chromaphidis*, *Pandora* sp., *Zoophthora occidentalis*, *Neozygites fresenii*, and

**Table 1 Arthropod predators, parasitoids, and entomopathogenic fungi confirmed to attack soybean aphid in North America**

Order	Family	Scientific name	Reference(s)
<b>Predators</b>			
Arachnida	Opiliones	<i>Phalangium opilio</i> Linnaeus	1
Coleoptera	Carabidae	<i>Agonum muelleri</i> Herbst	55, 56
		<i>Anisodactylus sanctaecrusis</i> Fabricius	132
		<i>Bembidion quadrimaculatum</i> Say	46, 132
		<i>Clivina impressifrons</i> LeConte	46, 132
		<i>Elaphropus anceps</i> LeConte	46, 132
		<i>Harpalus herbivivus</i> Say	132
		<i>Poecilus chalcites</i> Say	132
		<i>Poecilus lucublandus</i> Say	132
		<i>Pterostichus melanarius</i> Illiger	132
		<i>Scymnus louisianae</i> J. Chapin	10
	Coccinellidae	<i>Coccinella septempunctata</i> Linnaeus	17, 26, 27, 47, 111, 116, 132, 159
		<i>Coleomegilla maculata</i> DeG.	17, 111, 116, 132
		<i>Coleomegilla maculata lengi</i> Timberlake	111
		<i>Cycloneda munda</i> Say	26, 116
		<i>Harmonia axyridis</i> Pallas	17, 26, 27, 47, 50, 111, 116, 132, 159
		<i>Hippodamia convergens</i> Guerin-Meneville	16, 26, 27, 116, 132
		<i>Hippodamia tredecimpunctata</i> Linnaeus	116
		<i>Hippodamia variegata</i> Goeze	52, 116
	Staphylinidae	<i>Philonthus thoracicus</i> Gravenhorst	132
Dermoptera	Forficulidae	<i>Forficula auricularia</i> Linnaeus	132
Diptera	Cecidomyiidae	<i>Aphidoletes aphidimyza</i> Rondani	79, 116
		<i>Leucopis glyphinivora</i> Tanasijtshuk	79
	Syrphidae	<i>Allograpta obliqua</i> Say	79, 116
		<i>Eupeodes americanus</i> Wiedemann	116
		<i>Eupeodes volucris</i> Osten Sacken	79, 116
		<i>Paragus bemorrhous</i> Meigen	79
		<i>Sphaerophoria contigua</i> Macquart	79, 116
		<i>Syrphus rectus</i> Osten Sacken	79
		<i>Toxomerus geminatus</i> Say	116
		<i>Toxomerus marginatus</i> Say	79, 116
Heteroptera	Anthocoridae	<i>Orius insidiosus</i> Say	17, 26, 27, 37, 47, 57, 58, 132
	Miridae	<i>Chlamydatus associatus</i> Uhler	26
		<i>Plagiognathus</i> sp. Fieber	26, 27
	Nabidae	<i>Nabis</i> sp.	25, 27, 132
Neuroptera	Chrysopidae	<i>Chrysopa</i> sp.	27, 132
		<i>Chrysoperla carnea</i> Stephens	17
<b>Parasitoids</b>			
Hymenoptera	Aphelinidae	<i>Aphelinus asychis</i> Walker	79, 116
		<i>Aphelinus certus</i> Yasnosh	59

(Continued)



Table 1 (Continued)

Order	Family	Scientific name	Reference(s)
		<i>Aphelinus varipes</i> complex	79, 116
	Braconidae	<i>Aphidius colemani</i> Viereck	17, 79, 116
		<i>Aphidius ervi</i> Haliday	116
		<i>Binodoxys communis</i> Gahan	16, 59
		<i>Binodoxys kelloggensis</i> Pike, Starý & Brewer	79, 123
		<i>Diaeretiella rapae</i> McIntosh	116
		<i>Ephedrus</i> sp.	116
		<i>Lysiphlebus testaceipes</i> Cresson	25, 79, 116
		<i>Praon</i> sp.	79, 114
<b>Entomopathogens</b>			
Entomophthorales	Ancylistaceae	<i>Conidiobolus thromboides</i> Drechsler	114
	Entomophthoraceae	<i>Entomophthora chromaphidis</i> Burger & Swain	114
		<i>Pandora neoaphidis</i> Humber	114
		<i>Pandora</i> sp.	114
		<i>Zoophtbora occidentalis</i> Batko	114
		<i>Zoophtbora radicans</i> Batko	82
Neozygitaceae	<i>Neozygites fresenii</i> Remaud et Keller	114	
Hypocreales		<i>Lecanicillium lecanii</i> Gams et Zare	114

*Lecanicillium lecanii*. Of these, *P. neoaphidis* was the most abundant species, responsible for an 84% infection rate and subsequent collapse of the SBA population in 2003. In Minnesota, the dominant entomopathogen was *P. neoaphidis* (90%) (82), with *C. thromboides* (9%) and *Zoophtbora radicans* (1%) comprising the remainder of the aphid infections in a two-year field study.

**Impact of North American endemic natural enemy communities.** Fox et al. (47) studied the potential impact of natural enemies on newly establishing SBA females in early-spring field trials in Michigan. They found that ground and foliar predators reduced aphids over a 24-h period in 50% of trials. The same authors demonstrated that, when protected from predation (predator communities dominated by *H. axyridis*, *Orius insidiosus*, and *Leucopis* spp.), SBA populations increased rapidly but declined when cages were subsequently opened (46). Using a similar exclusion cage design in Indiana, Desneux et al. (37) showed that a single generalist predator species, *O. insidiosus*, can decrease SBA population growth early in the

season. Predators exerted top-down control of SBA populations across a wide range of agronomic treatments, whereas bottom-up impacts through host plant quality were minimal (25), and the impact of natural enemy communities results in a trophic cascade; i.e., predator control of SBA results in increased soybean yields (28, 128).

**Biology of important natural enemies.**

Among natural enemies of SBA identified in the early years of the invasion into North America, coccinellids and the insidious flower bug, *O. insidiosus*, have emerged as particularly important (132).

The exotic lady beetles *H. axyridis* and *C. septempunctata* attack SBA in the majority of the northcentral U.S. field studies, and *C. septempunctata* is attracted to SBA-induced plant volatiles in the laboratory (163). Both coccinellids exhibit a type II functional response resulting in high rates of predation on SBA (159). When fed a diet of SBA, *H. axyridis* has a higher intrinsic rate of increase (0.238 per day) than either *P. quatuordecimpunctata* (0.215 per day) or *C. maculata lengi* (0.134 per day) (111).

Frequently associated with forested habitats (55), *H. axyridis* is commonly found preying on SBA both on soybean and on its overwintering host *Rhamnus cathartica* and is attracted to olfactory cues from naturally infested buckthorn leaves as well as visual cues from leaf silhouettes (3).

*O. insidiosus* can oviposit and feed on several host plants including soybean (97, 98) and can use alternative prey to build up populations in early soybean cropping season (160) prior to SBA arrival (132). Both immature and adult stages feed on SBA even when the aphids are present at low densities in the field (57, 58), and *O. insidiosus* can successfully survive, develop, and reproduce on a diet of SBA (11). SBA defensive behaviors reduce efficiency of *O. insidiosus* (13, 36); although 50% of attacks usually fail after initial probing by the predator (36), all aphids probed invariably die (13). *O. insidiosus* also feeds on soybean thrips, *Neohydatotrips variabilis*, a prey species on which it has higher fitness (12), and shows a preference for thrips over SBA (14, 36). The presence of soybean thrips may disrupt control of SBA by *O. insidiosus* in the short term through a dilution effect or preference for thrips (apparent commensalism; 36), but longer-term effects seem to favor increased suppression of SBA in the presence of thrips through apparent competition or amensalism because *O. insidiosus* reproduction is increased in the presence of soybean thrips (Figure 2) (12, 160).

### Relative effectiveness of natural enemies.

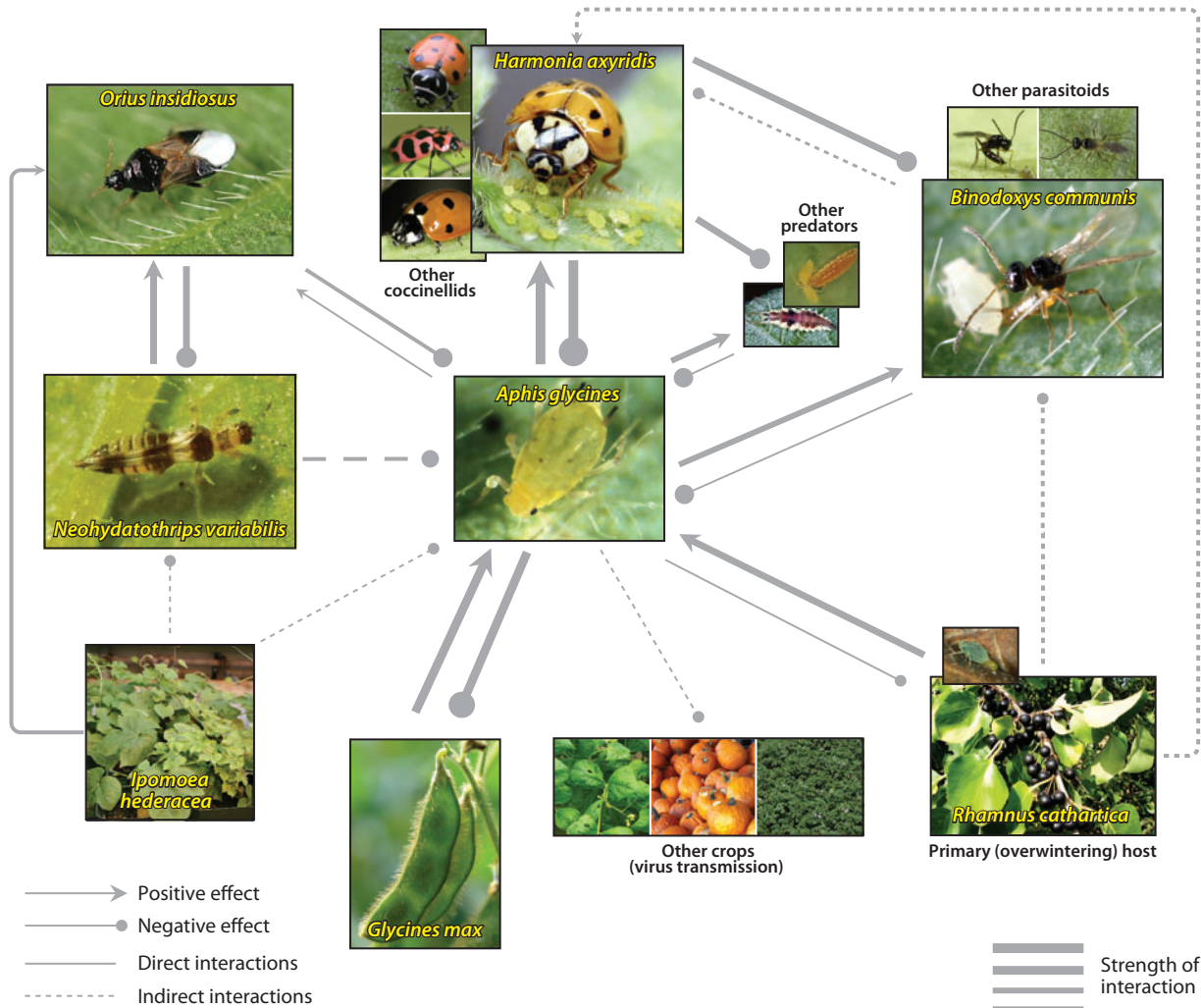
Several studies have attempted to characterize the relative effectiveness of SBA natural enemy species and guilds. A factorial field study in Michigan tested the separate and combined effects of SBA predators and parasitoids by releasing *L. testaceipes* into field cages with and without ambient levels of predators (28). Predators alone (primarily Coccinellidae) produced strong and season-long aphid suppression. However, the generalist parasitoid alone provided only minor aphid suppression, and only when predators were excluded. In a subsequent experiment, strong aphid suppression

(36- to 86-fold reduction) was observed in coccinellids exposed to treatments, but only minor reduction due to small predators (primarily *O. insidiosus*) and parasitoids was observed, with aphids rapidly reaching EILs when coccinellids were excluded (27). 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.

The importance of predation of SBA by coccinellids varies geographically in the northcentral United States, complicating their incorporation into IPM decision rules. Despite a relatively minor role of *O. insidiosus* on SBA population growth in Michigan (26), in states where coccinellids are sparse during the cropping season (or present only late in the season), as in Indiana (37, 160) and Nebraska (9), *O. insidiosus* appears to be important in SBA limitation. *O. insidiosus* suppressed SBA populations in laboratory trials (131) and was identified as a key predator of SBA in early cropping soybean fields in Indiana fields (37), but here aphid colonization dynamics are likely different because of the paucity of overwintering hosts (buckthorn) compared to that of northern states. Because *O. insidiosus* establishes in fields before SBA arrival, it can help to delay or prevent aphids from establishing in soybean fields (9, 37). However, once aphid density reaches a certain threshold (estimated in laboratory conditions at 32–64 aphids per plant depending on plant complexity; 36, 131); *O. insidiosus* is no longer able to significantly limit SBA population growth in the field (37).

### Conservation of SBA natural enemies.

Given the important role that existing natural enemy communities can play in regulating SBA populations, there has been considerable interest in conservation and enhancement of their populations and impacts. Several authors have examined the impacts of conventional (48) and reduced-risk insecticides (86, 117) on SBA and its natural enemies. Others have explored the impacts of alternative production systems including living-mulches (134), showing that an



**Figure 2**

Multitrophic interactions and potential linkages between the soybean aphid and other biotic components of North American ecosystems. Lines with arrows indicate a positive effect in the direction of the arrows, and lines with circles indicate negative effects in the direction of the circles. Solid lines indicate direct interactions, and dashed lines indicate indirect interactions (mediated by another component of the system). Thickness of lines is roughly proportional to the known or suspected strength of the interaction. Signs and magnitudes of arrows were derived from studies cited and discussed in the review. Photos from D. Cappaert: *Coccinella septempunctata*, *Coleomegilla maculata*, and *Hippodamia convergens* (i.e., other coccinellids), *Chrysoperla* sp. and hoverfly larvae (i.e., other predators), and *Aphidius colemani*; from C.D. Difonzo: snap beans and pumpkins; from D. Hansen: *Binodoxys communis*; from M. Kogan: *Neohydatothrips variabilis*; from J.G. Lundgren: *Ipomoea hederacea*; from J.C. Malausa: *Lysiphlebus testaceipes*; from R.J. O'Neil: *Glycines max*; from J. Samanek: *Rhamnus cathartica*; from Z.S. Wu: *Aphis glycines*; and from H.J.S. Yoo: *Orius insidiosus*.

alfalfa living-mulch treatment increased predator abundance and delayed SBA population increase. Vegetation diversity can also be used as a tool for conserving natural enemies in agricultural landscapes and enhancing their

potential as biological control agents (91). Lundgren et al. (98) demonstrated that *O. insidiosus* is more abundant in weedy than in weed-free soybean plots, that females prefer to oviposit onto weeds rather than into soybean,

## SOYBEAN APHID AND BIOFUEL PRODUCTION

Biofuel production systems are likely to change agricultural landscapes and affect SBA management systems. In the northcentral United States, biofuel production has focused on the use of corn grain to produce ethanol. In 2007, corn acreage reached its recent peak, reducing local landscape diversity and resulting in a loss of biocontrol services in soybean estimated at US\$58 million (89). Further expansion of biofuel production could negatively affect biocontrol of SBA if biofuel crops are unsuitable for natural enemies or replace habitats that are critical for their persistence (90). For example, wheat and alfalfa may provide an early-season source of aphids for reproduction of key SBA natural enemies such as coccinellids. If these crops are replaced by ones that do not support robust natural enemy communities, SBA outbreaks may become more frequent or intense. Alternatively, some biofuel crops may be more suitable for natural enemies than the crops they replace. Recent works suggest that floristically diverse biofuel crops such as mixed prairie or diverse switchgrass stands support higher abundance and diversity of beneficial insects than do monoculture crops (53). Future policy regarding the production of biofuel feedstocks should consider the ecosystem services they provide to agricultural landscapes.

and that nymphs live longest on these weeds (notably on morning glory, *Ipomoea hederacea*) (97, 98).

The influence of landscape structure on SBA–natural enemy interactions has been investigated in four midwestern U.S. states (Michigan, Iowa, Minnesota, and Wisconsin) (50). Predators, principally coccinellid beetles, dominated the natural enemy community of soybean and significantly reduced SBA populations. *H. axyridis* was the dominant exotic coccinellid in all states, comprising 45%–62% of the total coccinellid community, followed by *C. septempunctata* (13%–30%) (51). The level of biological control provided by natural enemies varied with landscape diversity. Landscapes dominated by corn and soybean fields provided less biological control to soybean than did landscapes with an abundance of crop and noncrop habitats. Landscape diversity and composition at a scale of 1.5 km surrounding the

focal field explained the greatest proportion of the variation in both coccinellid abundance and biocontrol service. Landscape structure also significantly influenced the composition of coccinellid communities, with native coccinellids more abundant in low-diversity landscapes with an abundance of grassland habitat while exotic coccinellids were associated with abundance of forested habitats (51). Biocontrol services to soybean are worth at least US\$239 million per year to the producers in these four states (89), and biofuel-driven growth in corn planting in 2007 resulted in lower landscape diversity, altering the supply of aphid natural enemies to soybean fields and reducing biological control by 24% (89).

### Contribution of natural enemies to SBA cycling.

Major outbreaks of SBA were observed in 2001, 2003, 2005, and 2007. This pattern of outbreaks in odd-number years was noted by many researchers (129) and led to investigations of its origin. In Indiana, an eight-year study suggests that a combination of intrinsic aphid dynamics amplified by late-season predation by coccinellids best explains the phenomenon, with *H. axyridis*, *C. maculata lengi*, and *H. convergens* the most abundant species. A long-term study of the population dynamics of coccinellids in Michigan suggests that *H. axyridis* is particularly responsive to SBA, with its abundance increasing sharply in years following SBA outbreaks, and its average abundance has more than doubled since 2000 (59). Increased *H. axyridis* survival may lead to increased SBA predation in the spring following outbreak years, thus resulting in the cycle (59, 129). Detailed modeling studies have suggested a similar relationship for wheat aphids and coccinellid predators in Europe (6).

### Classical Biological Control

Classical biological control of SBA is seen as a promising management option for a number of reasons. First, SBA rarely attains pest status in its native Asia (154) and a number of studies in Asia indicated that both insect predators and parasitoids were instrumental in keeping

#### Classical biological control:

pest-control strategy in which natural enemies are imported and released against an invasive pest from that pest's native range

densities below economically important levels (96, 108, 145, 154). Second, the natural enemy fauna of aphid parasitoids in North America apparently largely lacks effective species (8, 25, 37, 79, 95, 115, 116, 132). While parasitism levels of SBA in China often exceed 10%, they are typically far below 1% in North America (59, 96). These observations suggest that release from Asian parasitoids may be an important contributing factor to the pest status of SBA in North America, and consequently that classical biological control using Asian parasitoids has the potential to suppress SBA below economically important levels (60, 73).

### **Foreign exploration and taxa recovered.**

Exploration for parasitoids and other specialized natural enemies of SBA began in 2001 and has been conducted in China, South Korea, and Japan. Over 40 populations of parasitoids and one population of a chamaemyiid predator were collected during these explorations and brought into quarantine laboratories in the United States for further study. The parasitoids include *Aphelinus* spp. as well as members of the aphidiine Braconidae, and various populations of both of these groups are cryptic species, making a complete taxonomic characterization of the collections difficult (41, 61, 155). At a minimum, aphidiine braconids recovered in Asia include *Binodoxys communis*, *Binodoxys koreanus*, *Lipolexis gracilis*, *Lysipblebia japonica*, and *Lysipblebus orientalis*, as well as *Aphelinus* species belonging to three species complexes: *A. varipes*, *A. asychis*, and *A. mali*. Of these, four represent species new to science: *B. koreanus* (32, 41), *L. orientalis* (139), and two as yet unnamed *Aphelinus* species, *A. sp. nr. gossypii* and *A. sp. nr. engaeus*.

### ***Binodoxys communis* as a parasitoid of SBA.**

Of the species recovered in Asia, *B. communis* is the only one, as of this writing, for which a permit (from USDA-APHIS) allowing field release in North America has been granted (155). The permit was granted on the basis of laboratory studies demonstrating specificity of *B. communis*

to a subset of aphids in the genus *Aphis* and of field studies of native aphids suggesting the presence of strong ecological filters that would limit the exposure of native aphids to attack by *B. communis*.

Laboratory host specificity studies on *B. communis* were done on 20 aphid species within 11 genera and two tribes, all from the aphid subfamily Aphidinae (33). Reproduction in microcosm assays was highest on SBA (58% successful parasitism), and nil or <1% on 10 aphid species. For the remaining nine species, parasitism levels ranged between 3% and 50%, with *B. communis* host use appearing to be related to the phylogenetic proximity of aphid species to *A. glycines* (33). Three native species of *Aphis* exhibited some levels of suitability for *B. communis*, *A. monardae*, *A. oestlundii*, and *A. asclepiadis*, with *A. monardae* second only to SBA in suitability to *B. communis*. However, further laboratory and field studies provided evidence of two ecological filters that should greatly limit the ability of *B. communis* to exploit native aphids. Eighteen species of ants were found tending the three native aphids in surveys of various native prairie sites in Minnesota, with more than half of the colonies tended by ants (156, 157). The most commonly encountered ant species was *Lasius neoniger*, which strongly interferes with parasitism of the native nontarget aphid *A. monardae* by *B. communis* (156). The second ecological filter is a physical refuge for native aphids on their host plants. *A. monardae* is a specialist on the native North American prairie plant *Monarda fistulosa* and feeds mainly within internal spaces of the inflorescences, which are apparently difficult for *B. communis* to access (155, 156). These ecological filters are likely to restrict parasitism of native nontarget aphid species by *B. communis*.

**Release of *Binodoxys communis*.** Releases of *B. communis* into North America began in 2007, with permission to do laboratory studies in Canada following in 2009. As of this writing, there has been no documentation of successful overwintering despite the fact that this

parasitoid was collected in an area of China that provided a good climate match to the northcentral United States. Potential reasons for nonestablishment include absence of a suitable overwintering host and difficulty for *B. communis* to overwinter on SBA in *Rhamnus* stands (59). For example, while it is conceivable that *B. communis* could be transported to *Rhamnus* stands as eggs or larvae within alate aphids, alate aphids are parasitized at a lower rate than apterae in laboratory studies (59, 158). Another possibility is that strong predation of parasitized aphids by coccinellids and other intraguild predators severely depresses *B. communis* populations in soybean during the summer, reducing the numbers that survive to enter the overwintering season (17). Intraguild predation (IGP) has been evaluated in the field by using counts of *B. communis* mummies chewed by predators, and the fraction of chewed mummies tends to increase over the season (59) and as the SBA density increases and more predators are attracted to aphid aggregations (16). Other possible reasons for poor establishment include factors related to genetic bottlenecks in *B. communis*, and rapid emigration of *B. communis* from release sites coupled with Allee effects that increase with the distance from the release site (74). These hypotheses are under investigation.

**Exotic parasitoids other than *Binodoxys communis*.** A number of other Asian parasitoids merit discussion. A population of *Apbelinus atriplicis* (previously released against the Russian wheat aphid, *Diuraphis noxia*, in the early 1990s) was found to attack and develop on SBA in soybean fields (60, 154). This strain was released again in Minnesota and Wisconsin in 2002 (60), but establishment remains undocumented. *Apbelinus certus* has been found attacking SBA in eastern North America since 2005 (59). This species has not been intentionally introduced as far as we are aware and thus was likely cointroduced with SBA. If this is the case, it supports the hypothesis of at least two introductions of the SBA into North America: one

in or near Wisconsin and one in eastern North America. Beyond these species are a number of *Apbelinus* spp. and aphidiine braconids that have been alluded to above. Prominent among these are two unnamed *Apbelinus* species with a narrow host range and *Lysiphlebus orientalis*, which is thelytokous in addition to exhibiting a narrow host range (139).

### Intraguild Predation and Interactions with Ants

IGP may limit the effectiveness of natural enemies of SBA in North America (16, 17). In laboratory microcosms, when *H. axyridis* adults were present with *Aphidoletes aphidimyza* or *Chrysoperla carnea* larvae, the lady beetle acted as an intraguild predator (Figure 2) (49). However, intraguild feeding did not result in a release of aphid populations compared with microcosms containing only the intraguild and aphid prey. A similar result was found in a field cage experiment in which *H. axyridis* reduced numbers of *A. aphidimyza* and *C. carnea* larvae but also resulted in significantly fewer aphids. Thus, in both laboratory and field studies the direct impact of *H. axyridis* on SBA overcame its negative impact as an intraguild predator. Taken as a whole, the studies contrasting natural enemy impacts on SBA suggest that when present *H. axyridis* and *C. septempunctata* are keystone predators in the SBA system.

Herbert & Horn (62) recorded the ant species *Monomorium minimum*, *Formica subsericea*, and *Lasius neoniger* tending SBA populations in Ohio. In laboratory trials they demonstrated that *M. minimum* harassed or killed *O. insidiosus* and *H. axyridis* and reduced parasitism by *A. colemani*; however, in field trials exclusion of ants had no effect on SBA control (27). Tending by *L. neoniger* can strongly interfere with parasitism of nontarget aphids by *B. communis* and presumably for SBA as well. Whereas relatively high levels of tending were reported at low SBA densities in Ohio (62), virtually no tending was reported in Minnesota fields with relatively high SBA densities (157).

## IMPLICATIONS FOR BASIC ECOLOGY AND INVASION BIOLOGY

While the SBA has been studied primarily as an agricultural pest in North America, insights from its invasion are relevant to population biology, food web ecology, and invasion biology theory. Studies of SBA have contributed to our understanding of top-down versus bottom-up effects, IGP, trophic cascades in food webs, and landscape control on herbivore–natural enemy interactions (16, 25, 27, 28, 49–51). Population modelers have used the SBA system to elucidate a novel formulation of exponential growth based on cumulative density-dependent feedback (29, 101). Finally, the SBA system has been proposed as an example of invasional meltdown (*sensu* 135, 136). Researchers have documented interconnection of SBA with multiple Eurasian species (several represented in **Figure 2**) including the earthworm *Lumbricus terrestris*; *R. cathartica*; oat crown rust, *Puccinia coronata*; European starling, *Sturnus vulgaris*; an Asian predatory flatworm, *Bipalium adventitium*; *H. axyridis*; *C. septempunctata*; *Agonum muelleri*; and *Aphelinus certus* (59).

The presence of a new nonsaturated niche of soybean-related resources (i.e., SBA) has promoted the population-level enrichment of a number of coccinellid species, in particular the exotic *H. axyridis*. Since its first recorded establishment in 1988 in southeastern Louisiana (19), *H. axyridis* has gradually spread throughout much of the United States and southern Canada (83). This species was well established in the northcentral United States by the late 1990s (thus before the arrival of SBA), but the invasion of SBA has likely facilitated its population buildup within North America (59). A 15-year survey of predators in soybean fields in Michigan (1994–2008) showed that populations of *H. axyridis* generally remained low from 1994 to 2000 but doubled following the arrival of SBA (59). Although the beneficial impact of *H. axyridis* on top-down suppression of SBA populations in soybean and of other pest aphids in other crops is clear, the coccinellid

has multiple negative impacts as well (59, 83). For example, IGP by *H. axyridis* on other natural enemies may be problematic both for the establishment of new biological control agents against the SBA and the potential natural colonization of soybean fields by endemic aphid parasitoids (16, 17, 49).

The presence of the aphid has also induced a drastic change in arthropod community composition in soybean, in particular the relative proportions of aphidophagous species. Prior to SBA arrival, the coccinellids *Coleomegilla maculata*, *Coccinella septempunctata*, and *Hippodamia convergens* represented less than 5% of predators sampled in soybean fields in Iowa (4, 88). Following SBA arrival, populations of coccinellids increased and accounted for 39% (2004) and for 30% (2005) of the predator fauna (133). Conversely, *O. insidiosus* has decreased as a proportion of predators in soybean agroecosystems since the arrival of SBA in North America, more specifically in states where coccinellid populations have expanded. Schmidt et al. (133) reported that the percentage of predators that were *O. insidiosus* in Iowa soybean fields dropped from over 40% in 1977–1978 to less than 17% in 2004–2005.

## INTEGRATION OF MANAGEMENT STRATEGIES

Management tactics for SBA were developed soon after its arrival in North America. For example, the ET is widely adopted and is set high enough to allow for maximum response by natural enemies. In 2010, several seed companies released soybean varieties resistant to SBA, providing producers with another tactic for SBA management. Classical biological control programs are also being developed, and one parasitoid, *B. communis*, has been released with additional species under evaluation.

As thresholds were developed, a key consideration was to understand the effectiveness of resident natural enemies in keeping aphid populations below the EIL. Under ideal conditions, the laboratory SBA population doubling

time is as little as 1.5 days (105), whereas field population doubling times average 6.8 days (125). This difference in population dynamics can be attributed to density-independent and density-dependent mortality factors. ETs could conceivably be adjusted to explicitly incorporate natural enemy densities (161), but to date, effective sampling strategies for predators have not been developed. When aphid populations need to be controlled with insecticidal sprays, all registered chemical products are broad-spectrum materials that negatively affect natural enemies (34), and several authors have warned that the overuse of insecticides can result in resurgence of aphid populations (77, 85). One of the most commonly used insecticides against SBA is the pyrethroid lambda-cyhalothrin, which is lethal to natural enemies at field doses (39, 48) and can disrupt olfactory orientation toward host-infested plants and oviposition behavior in aphid parasitoids (38). Systemic insecticides such as the neonicotinoids, most commonly used at planting as a seed treatment, also have lethal and sublethal effects on aphid natural enemies (34). In laboratory studies, thiamethoxam reduced the emergence of the aphid parasitoid *Apbelinus gossypii* (144) and induced trembling, paralysis, and loss of coordination in exposed *H. axyridis* (112). The neonicotinoid imidacloprid negatively affected larval development, mobility, and adult fecundity in coccinellids (121, 137), and adverse effects on parasitoids have been documented as well (34, 87). Thus, if ETs are to be refined to incorporate natural enemy density, then negative effects of insecticides on natural enemies will need to be more thoroughly understood. This will require investigation of both lethal and sublethal (behavioral and physiological) effects of insecticides used against the soybean aphid (34, 35, 40).

The development of soybean varieties that are resistant to SBA also prompts questions about the interaction of host plant resistance and biological control. Interactions can be negative if resistant varieties interfere with biological control agents (7), or they can be positive if the two sources of mortality are complementary

or synergistic (e.g., 15, 45, 80). Experiments aimed at determining these relationships for the SBA are underway in North America.

As aphid-resistant soybean varieties become more widely used, it is clear that a modified ET will need to be developed. The current ET assumes a population doubling time of 6.8 days, yet population doubling times on aphid-resistant varieties are typically in the range of 10–14 days (20). Aphid-resistant soybean varieties are not immune to colonization by SBA. Indeed, SBA biotypes have been discovered that overcome known resistance genes, and these biotypes reproduce at the same rate as SBA on susceptible soybean varieties (65). It is unclear if these biotypes will present a problem to growers, and work needs to be done on the geographic distribution of these biotypes and their ability to overwinter.

To date, all aphid-resistant soybean varieties employ a single gene for resistance, which has led to the rapid development of resistant biotypes (143). In addition, aphid-resistant varieties are often sold with an insecticidal seed treatment, typically one of several neonicotinoids. Published results demonstrate that in most years there is no yield advantage of a seed treatment, and during SBA outbreaks, seed treatments lose efficacy within 35 days following planting, well before SBA populations typically reach the ET (104). Coupling seed treatments with aphid resistance is thus a serious misuse of available IPM strategies. Although it is unclear how much of the soybean crop is treated with seed treatments, one early estimate was that 20% of soybean and 71% of corn is seed treated with one or more active ingredients (152), and industry reports indicate that seed treatments are likely to increase across all commodities (141).

## CONCLUSIONS AND FUTURE OUTLOOK

The arrival of SBA in North America has linked a growing set of exotic organisms of Eurasian origin. Together, these invaders are having



major impacts on both agricultural and natural ecosystems. Much remains to be discovered regarding this remarkable insect, including such basic information as the country(ies) of origin for the North American invasion, patterns of movement of the insect at landscape and regional scales, and overwintering ecology. Development of resistant varieties and effective classical biological control are likely to reduce but not eliminate SBA as a pest of soybean. In addition, SBA has already adapted to resistant varieties in laboratory studies, which presents researchers with challenges such as discovering biotypes and determining whether biotypes persist in the field. Opportunities also exist to

explore the potential for regional or even continental control of the aphid via management of its primary hosts, and offer a unique opportunity to link the interests of agricultural producers and natural area land managers, both of whom have incentive to manage invasive buckthorn species. Active programs exploring classical biological control of buckthorn offer one alternative, as do physical and herbicidal control programs. Finally, molecular tools have just begun to be used to explore the biology and ecology of SBA. Use of these tools is likely to further enhance our understanding of this important pest and our ability to manage its multiple impacts.

### SUMMARY POINTS

1. SBA was first discovered in North America in 2000 in Wisconsin and has subsequently spread throughout the continent. It is a major constraint to profitable soybean production in North America. SBA feeding injury reduces yields, and SBA is an efficient vector of several viruses to soybean and other crops.
2. Reliable sampling methods and ETs have been developed and are widely adopted by producers, and control strategies rely on insecticides.
3. A large guild of existing aphidophagous enemies are capable of controlling SBA but are affected by landscape structure and within-field management practices. A classical biological control effort is underway with release of one parasitoid species from Asia, *Binodoxys communis*, but establishment has not been documented as of 2009.
4. SBA appears to be involved in a broad invasional meltdown that includes a web of interactions between a number of invasive species, including SBA's main overwintering host, the common buckthorn, which is facilitated by exotic earthworms and birds and in turn serves as the overwintering host for oat rust. SBA itself facilitates populations of the multicolored Asian lady beetle (*Harmonia axyridis*), which has negative impacts on native lady beetle communities.

### DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

### ACKNOWLEDGMENTS

One of the key laboratories studying the impact of natural enemies on SBA was that of Dr. Robert (Bob) J. O'Neil, who unfortunately passed away in February 2008. Bob challenged us to think broadly about biological and natural control, and this legacy lives on as we strive to unravel the complex relationships between invasive species and the response of native and introduced

natural enemies. We also wish to thank Rob Venette for developing the distribution map of SBA in North America. Funding from the North Central Soybean Research Program, USDA-RAMP, USDA-CAR, USDA-NRI, NSF, and the generous support of state-based soybean checkoff programs and our respective institutions is gratefully acknowledged.

## LITERATURE CITED

1. Allard CM, Yeargan KV. 2005. Effect of diet on development and reproduction of the harvestman *Phalangium opilio* (Opiliones: Phalangidae). *Environ. Entomol.* 34:6–13
2. Bahlai CA, Sikkema S, Hallett RH, Newman J, Schaafsma AW. 2010. Modelling distribution and abundance of soybean aphid in soybean fields using measurements from the surrounding landscape. *Environ. Entomol.* 39:50–56
3. Bahlai CA, Welsman JA, Macleod EC, Schaafsma AV, Hallett RH, Sears MK. 2008. Role of visual and olfactory cues from agricultural hedgerows in the orientation behavior of multicolored Asian lady beetle (Coleoptera: Coccinellidae). *Environ. Entomol.* 37:973–79
4. Bechinski EJ, Pedigo LP. 1981. Ecology of predaceous arthropods in Iowa soybean agroecosystems. *Environ. Entomol.* 10:771–78
5. Beckendorf EA, Catangui MA, Riedell WE. 2008. Soybean aphid feeding injury and soybean yield, yield components, and seed composition. *Agron. J.* 100:237–46
6. Bianchi FJJA, Van der Werf W. 2004. Model evaluation of the function of prey in noncrop habitats for biological control by ladybeetles in agricultural landscapes. *Ecol. Model.* 171:177–93
7. Birch ANE, Geoghegan IE, Majerus MEN, McNicol JW, Hackett CA, et al. 1999. Tri-trophic interactions involving pest aphids, predatory 2-spot ladybirds and transgenic potatoes expressing snowdrop lectin for aphid resistance. *Mol. Breed.* 5:75–83
8. Brewer MJ, Noma T. 2010. Habitat affinity of resident natural enemies of the invasive *Aphis glycines* (Hemiptera: Aphididae), on soybean, with comments on biological control. *J. Econ. Entomol.* 103:583–96
9. Brosius TR, Higley LG, Hunt TE. 2007. Population dynamics of soybean aphid and biotic mortality at the edge of its range. *J. Econ. Entomol.* 100:1268–75
10. Brown GC, Sharkey MJ, Johnson DW. 2003. Bionomics of *Scymnus (Pullus) louisianae* J. Chapin (Coleoptera: Coccinellidae) as a predator of the soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae). *J. Econ. Entomol.* 96:21–24
11. Butler CD, O'Neil RJ. 2007. Life history characteristics of *Orius insidiosus* (Say) fed *Aphis glycines* Matsumura. *Biol. Control* 40:333–38
12. Butler CD, O'Neil RJ. 2007. Life history characteristics of *Orius insidiosus* (Say) fed diets of soybean aphid, *Aphis glycines* Matsumura and soybean thrips, *Neobydatotrips variabilis* (Beach). *Biol. Control* 40:339–46
13. Butler CD, O'Neil RJ. 2006. Defensive response of soybean aphid (Hemiptera: Aphididae) to predation by insidious flower bug (Hemiptera: Anthocoridae). *Ann. Entomol. Soc. Am.* 99:317–20
14. Butler CD, O'Neil RJ. 2008. Voracity and prey preference of insidious flower bug (Hemiptera: Anthocoridae) for immature stages of soybean aphid (Hemiptera: Aphididae) and soybean thrips (Thysanoptera: Thripidae). *Environ. Entomol.* 37:964–72
15. Cai QN, Ma XM, Zhao X, Cao YZ, Yang XQ. 2009. Effects of host plant resistance on insect pests and its parasitoid: a case study of wheat-aphid-parasitoid system. *Biol. Control* 49:134–38
16. Chacón JM, Heimpel GE. 2010. Density-dependent intraguild predation of an aphid parasitoid. *Oecologia* 164:213–20
17. Chacón JM, Landis DA, Heimpel GE. 2008. Potential for biotic interference of a classical biological control agent of the soybean aphid. *Biol. Control* 46:216–25
18. Chang YD, Lee JY, Youn YN. 1994. Primary parasitoids and hyperparasitoids of the soybean aphid, *Aphis glycines* (Homoptera: Aphididae). *Korean J. Appl. Entomol.* 33:51–55
19. Chapin JB, Brou VA. 1991. *Harmonia Axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). *Proc. Entomol. Soc. Wash.* 93:630–35
20. Chiozza MV, O'Neal ME, MacIntosh GC. 2010. Constitutive and induced differential accumulation of amino acid in leaves of susceptible and resistant soybean plants in response to the soybean aphid (Hemiptera: Aphididae). *Environ. Entomol.* 39:856–64

21. Chiozza MV, O'Neal ME, MacIntosh GC, Chandrasena DI, Tinsley NA, et al. 2010. Host plant resistance for soybean aphid management: a multi-environment study. *Crop Sci.* In press
  22. Clark AJ, Perry KL. 2002. Transmissibility of field isolates of soybean viruses by *Aphis glycines*. *Plant Dis.* 86:1219–22
  23. Clark TL, Puttler B, Bailey WC. 2006. Is horsenettle, *Solanum carolinense* L. (Solanaceae), an alternate host for soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae)? *J. Kans. Entomol. Soc.* 79:380–83
  24. Clavero M, García-Berthou E. 2005. Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol.* 20:110
  25. Costamagna AC, Landis DA. 2006. **Predators exert top-down control of soybean aphid across a gradient of agricultural management systems.** *Ecol. Appl.* 16:1619–28
  26. Costamagna AC, Landis DA. 2007. Quantifying predation on soybean aphid through direct field observations. *Biol. Control* 42:16–24
  27. Costamagna AC, Landis DA, Brewer MJ. 2008. The role of natural enemy guilds in *Aphis glycines* suppression. *Biol. Control* 45:368–79
  28. Costamagna AC, Landis DA, Difonzo CD. 2007. Suppression of soybean aphid by generalist predators results in a trophic cascade in soybeans. *Ecol. Appl.* 17:441–51
  29. Costamagna AC, van der Werf W, Bianchi FJJA, Landis DA. 2007. An exponential growth model with decreasing *r* captures bottom-up effects on the population growth of *Aphis glycines* Matsumura (Hemiptera: Aphididae). *Agric. For. Entomol.* 9:297–305
  30. Davis JA, Radcliffe EB. 2008. The importance of an invasive aphid species in vectoring a persistently transmitted potato virus: *Aphis glycines* is a vector of potato leafroll virus. *Plant Dis.* 92:1515–23
  31. Davis JA, Radcliffe EB, Ragsdale DW. 2005. Soybean aphid, *Aphis glycines* Matsumura, a new vector of Potato virus Y in potato. *Am. J. Potato Res.* 82:197–201
  32. Desneux N, Barta RJ, Delebecque CJ, Heimpel GE. 2009. Transient host paralysis as a means of reducing self-superparasitism in koinobiont endoparasitoids. *J. Insect Physiol.* 55:321–27
  33. **Desneux N, Barta RJ, Hoelmer KA, Hopper KR, Heimpel GE. 2009. Multifaceted determinants of host specificity in an aphid parasitoid.** *Oecologia* 160:387–98
  34. Desneux N, Decourtye A, Delpuech JM. 2007. The sublethal effects of pesticides on beneficial arthropods. *Annu. Rev. Entomol.* 52:81–106
  35. Desneux N, Denoyelle R, Kaiser L. 2006. A multi-step bioassay to assess the effect of the deltamethrin on the parasitic wasp *Aphidius ervi*. *Chemosphere* 65:1697–706
  36. Desneux N, O'Neil RJ. 2008. Potential of an alternative prey to disrupt predation of the generalist predator, *Orius insidiosus*, on the pest aphid, *Aphis glycines*, via short-term indirect interactions. *Bull. Entomol. Res.* 98:631–39
  37. **Desneux N, O'Neil RJ, Yoo HJS. 2006. Suppression of population growth of the soybean aphid, *Aphis glycines* Matsumura, by predators: the identification of a key predator and the effects of prey dispersion, predator abundance, and temperature.** *Environ. Entomol.* 35:1342–49
  38. Desneux N, Pham-Delègue MH, Kaiser L. 2004. Effect of a sublethal and lethal dose of lambda-cyhalothrin on oviposition experience and host searching behaviour of a parasitic wasp, *Aphidius ervi*. *Pest Manag. Sci.* 60:381–89
  39. Desneux N, Rafalimanana H, Kaiser L. 2004. Dose-response relationship in lethal and behavioural effects of different insecticides on the parasitic wasp *Aphidius ervi*. *Chemosphere* 54:619–27
  40. Desneux N, Ramirez-Romero R, Kaiser L. 2006. Multi step bioassay to predict recolonization potential of emerging parasitoids after a pesticide treatment. *Environ. Toxicol. Chem.* 25:2675–82
  41. Desneux N, Starý P, Delebecque CJ, Garipey TD, Barta RJ, et al. 2009. Cryptic species of parasitoids attacking the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), in Asia: *Binodoxys communis* Gahan and *Binodoxys koreanus* Starý sp. n. (Hymenoptera: Braconidae: Aphidiinae). *Ann. Entomol. Soc. Am.* 102:925–36
  42. Desneux N, Wajnberg E, Wyckhuys KAG, Burgio G, Arpaia S, et al. 2010. Biological invasion of European tomato crops by *Tuta absoluta*: ecology, history of invasion and prospects for biological control. *J. Pest Sci.* 83:197–215
- 
25. Showed that in the early invasion period, soybean aphid was primarily controlled via top-down influences of generalist predators, and suggested complementary roles of different predator species.
- 
33. Assesses the host range of the exotic parasitoid *Binodoxys communis* and highlights the multifaceted nature of factors determining host specificity in parasitoids.
- 
37. Demonstrates that a single generalist predator species, *O. insidiosus*, can be responsible for decreasing soybean aphid population growth in soybean field early in the season.
-

---

50. Demonstrates that landscape structure within a 1.5-km radius of a focal soybean field is the key determinant of the level of soybean aphid biocontrol achieved by the natural enemy community.

---

43. Diaz-Montano J, Reese JC, Louis J, Campbell LR, Schapaugh WT. 2007. Feeding behavior by the soybean aphid (Hemiptera: Aphididae) on resistant and susceptible soybean genotypes. *J. Econ. Entomol.* 100:984–89
44. Diaz-Montano J, Reese JC, Schapaugh WT, Campbell LR. 2006. Characterization of antibiosis and antixenosis to the soybean aphid (Hemiptera: Aphididae) in several soybean genotypes. *J. Econ. Entomol.* 99:1884–89
45. Farid A, Johnson JB, Shafii B, Quisenberry SS. 1998. Tritrophic studies of Russian wheat aphid, a parasitoid, and resistant and susceptible wheat over three parasitoid generations. *Biol. Control* 12:1–6
46. Fox TB, Landis DA, Cardoso FF, Difonzo CD. 2004. Predators suppress *Aphis glycines* Matsumura population growth in soybean. *Environ. Entomol.* 33:608–18
47. Fox TB, Landis DA, Cardoso FF, Difonzo CD. 2005. Impact of predation on establishment of the soybean aphid, *Aphis glycines* in soybean, *Glycine max.* *Biocontrol* 50:545–63
48. Galvan TL, Koch RL, Hutchison WD. 2005. Toxicity of commonly used insecticides in sweet corn and soybean to multicolored Asian lady beetle (Coleoptera: Coccinellidae). *J. Econ. Entomol.* 98:780–89
49. Gardiner MM, Landis DA. 2007. Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Hemiptera: Aphididae) biological control in cage studies. *Biol. Control* 40:386–95
50. Gardiner MM, Landis DA, Gratton C, DiFonzo CD, O'Neal M, et al. 2009. Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecol. Appl.* 19:143–54
51. Gardiner MM, Landis DA, Gratton C, Schmidt NP, O'Neal M, et al. 2009. Landscape composition influences patterns of native and exotic lady beetle abundance. *Divers. Distrib.* 15:554–64
52. Gardiner MM, Parsons GL. 2005. *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae) detected in Michigan soybean fields. *Great Lakes Entomol.* 38:164–69
53. Gardiner MM, Tuell J, Isaacs R, Gibbs J, Ascher J, Landis DA. 2010. Implications of three model biofuel crops for beneficial arthropods in agricultural landscapes. *BioEnergy Res.* 3:6–19
54. Haack RA, Herard F, Sun JH, Turgeon JJ. 2010. Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: a worldwide perspective. *Annu. Rev. Entomol.* 55:521–46
55. Hajek AE, Hannam JJ, Nielsen C, Bell AJ, Liebherr JK. 2007. Distribution and abundance of Carabidae (Coleoptera) associated with soybean aphid (Hemiptera: Aphididae) populations in central New York. *Ann. Entomol. Soc. Am.* 100:876–86
56. Hannam JJ, Liebherr JK, Hajek AE. 2008. Climbing behaviour and aphid predation by *Agonum muelleri* (Coleoptera: Carabidae). *Can. Entomol.* 140:203–7
57. Harwood JD, Desneux N, Yoo HJS, Rowley DL, Greenstone MH, et al. 2007. Tracking the role of alternative prey in soybean aphid predation by *Orius insidiosus*: a molecular approach. *Mol. Ecol.* 16:4390–400
58. Harwood JD, Yoo HJS, Greenstone MH, Rowley DL, O'Neil RJ. 2009. Differential impact of adults and nymphs of a generalist predator on an exotic invasive pest demonstrated by molecular gut-content analysis. *Biol. Invasions* 11:895–903
59. Heimpel GE, Frelich LE, Landis DA, Hopper KR, Hoelmer KA, et al. 2010. European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America. *Biol. Invasions* 12:2913–31
60. Heimpel GE, Ragsdale DW, Venette R, Hopper KR, O'Neil RJ, Rutledge CE, Wu Z. 2004. Prospects for importation biological control of the soybean aphid: anticipating potential costs and benefits. *Ann. Entomol. Soc. Am.* 97:249–58
61. Heraty JM, Woolley JB, Hopper KR, Hawks DL, Kim JW, Buffington M. 2007. Molecular phylogenetics and reproductive incompatibility in a complex of cryptic species of aphid parasitoids. *Mol. Phylogenet. Evol.* 45:480–93
62. Herbert JJ, Horn DJ. 2008. Effect of ant attendance by *Monomorium minimum* (Buckley) (Hymenoptera: Formicidae) on predation and parasitism of the soybean aphid *Aphis glycines* Matsumura (Hemiptera: Aphididae). *Environ. Entomol.* 37:1258–63
63. Herman JC. 1988. How a soybean plant develops. *Spec. Rep. Iowa State Coop. Ext. No.* 53

64. Hesler LS, Dashiell KE, Lundgren JG. 2007. Characterization of resistance to *Aphis glycines* in soybean accessions. *Euphytica* 154:91–99
65. Hill CB, Crull L, Herman T, Voegtlin DJ, Hartman GL. 2010. A new soybean aphid (Hemiptera: Aphididae) biotype identified. *J. Econ. Entomol.* 103:509–15
66. Hill CB, Kim KS, Crull L, Diers BW, Hartman GL. 2009. Inheritance of resistance to the soybean aphid in soybean PI 200538. *Crop Sci.* 49:1193–200
67. Hill CB, Li Y, Hartman GL. 2004. Resistance to the soybean aphid in soybean germplasm. *Crop Sci.* 44:98–106
68. Hill CB, Li Y, Hartman GL. 2006. Soybean aphid resistance in soybean Jackson is controlled by a single dominant gene. *Crop Sci.* 46:1606–8
69. Hill CB, Li Y, Hartman GL. 2006. A single dominant gene for resistance to the soybean aphid in the soybean cultivar Dowling. *Crop Sci.* 46:1601–5
70. Hill JH, Alleman R, Hogg DB, Grau CR. 2001. First report of transmission of Soybean mosaic virus and Alfalfa mosaic virus by *Aphis glycines* in the New World. *Plant Dis.* 85:561
71. **Hodgson EW, Burkness EC, Hutchison WD, Ragsdale DW. 2004. Enumerative and binomial sequential sampling plans for soybean aphid (Homoptera: Aphididae) in soybean. *J. Econ. Entomol.* 97:2127–36**
72. Hodgson EW, McCornack BP, Koch KA, Ragsdale DW, Johnson KD, et al. 2007. Field validation of speed scouting for soybean aphid. *Crop Manag.* doi:10.1094/CM-2007-0511-01-RS
73. Hoelmer KA, Kirk AA. 2005. Selecting arthropod biological control agents against arthropod pests: Can the science be improved to decrease the risk of releasing ineffective agents? *Biol. Control* 34:255–64
74. Hopper KR, Roush RT. 1993. Mate finding, dispersal, number released, and the success of biological control introductions. *Ecol. Entomol.* 18:321–31
75. Huberty AF, Denno RF. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* 85:1383–98
76. Iwaki M, Roechan M, Hibino H, Tochihara H, Tantera DM. 1980. A persistent aphid borne virus of soybean, Indonesian soybean dwarf virus. *Plant Dis.* 64:1027–30
77. Johnson KD, O’Neal ME, Bradshaw JD, Rice ME. 2008. Is preventative, concurrent management of the soybean aphid (Hemiptera: Aphididae) and bean leaf beetle (Coleoptera: Chrysomelidae) possible? *J. Econ. Entomol.* 101:801–9
78. Johnson KD, O’Neal ME, Ragsdale DW, Difonzo CD, Swinton SM, et al. 2009. Probability of cost-effective management of soybean aphid (Hemiptera: Aphididae) in North America. *J. Econ. Entomol.* 102:2101–8
79. Kaiser ME, Noma T, Brewer MJ, Pike KS, Vockeroth JR, Gaimari SD. 2007. Hymenopteran parasitoids and dipteran predators found using soybean aphid after its midwestern United States invasion. *Ann. Entomol. Soc. Am.* 100:196–205
80. Kalule T, Wright DJ. 2002. Tritrophic interactions between cabbage cultivars with different resistance and fertilizer levels, cruciferous aphids and parasitoids under field conditions. *Bull. Entomol. Res.* 92:61–69
81. Kim KS, Hill CB, Hartman GL, Mian MAR, Diers BW. 2008. Discovery of soybean aphid biotypes. *Crop Sci.* 48:923–28
82. Koch KA, Potter BD, Ragsdale DW. 2010. Non-target impacts of soybean rust fungicides on the fungal entomopathogens of soybean aphid. *J. Invert. Pathol.* 103:156–64
83. Koch RL. 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control, and non-target impacts. *J. Insect Sci.* 3:1–16
84. Kogan M, Turnipseed SG. 1987. Ecology and management of soybean arthropods. *Annu. Rev. Entomol.* 32:507–38
85. Kraiss H, Cullen EM. 2008. Efficacy and nontarget effects of reduced-risk insecticides on *Aphis glycines* (Hemiptera: Aphididae) and its biological control agent *Harmonia axyridis* (Coleoptera: Coccinellidae). *J. Econ. Entomol.* 101:391–98
86. Kraiss H, Cullen EM. 2008. Insect growth regulator effects of azadirachtin and neem oil on survivorship, development and fecundity of *Aphis glycines* (Homoptera: Aphididae) and its predator, *Harmonia axyridis* (Coleoptera: Coccinellidae). *Pest Manag. Sci.* 64:660–68

---

71. The ET is based on a sample of 30 plants that takes 1 h to complete. The binomial sampling plan shortens sampling to 15 min and facilitates adoption of IPM by growers.

---

87. Krischik VA, Landmark AL, Heimpel GE. 2007. Soil-applied imidacloprid is translocated to nectar and kills nectar-feeding *Anagyrus pseudococci* (Girault) (Hymenoptera: Encyrtidae). *Environ. Entomol.* 36:1238–45
88. Lam WKF, Pedigo LP. 1998. Response of soybean insect communities to row width under crop-residue management systems. *Environ. Entomol.* 27:1069–79
89. Landis DA, Gardiner MM, van der Werf W, Swinton SM. 2008. Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proc. Natl. Acad. Sci. USA* 105:20552–57
90. Landis DA, Werling BP. 2010. Arthropods and biofuel production systems in North America. *Insect Sci.* 17:1–17
91. Landis DA, Wratten SD, Gurr GM. 2000. Habitat management to conserve natural enemies of arthropod pest in agriculture. *Annu. Rev. Entomol.* 45:173–201
92. Levine JM, D'Antonio CM. 2003. Forecasting biological invasions with increasing international trade. *Conserv. Biol.* 17:322–26
93. Li CS, Luo RW, Yang CL, Shang YF, Zhao JH, Xin XQ. 2000. Studies on the biology and control of *Aphis glycines*. *Soybean Sci.* 19:337–40
94. Li Y, Hill CB, Carlson SR, Diers BW, Hartman GL. 2007. Soybean aphid resistance genes in the soybean cultivars Dowling and Jackson map to linkage group M. *Mol. Breed.* 19:25–34
95. Lin LA, Ives AR. 2003. The effect of parasitoid host-size preference on host population growth rates: an example of *Aphidius colemani* and *Aphis glycines*. *Ecol. Entomol.* 28:542–50
96. Liu J, Wu KM, Hopper KR, Zhao KJ. 2004. Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and its natural enemies in soybean in northern China. *Ann. Entomol. Soc. Am.* 97:235–39
97. Lundgren JG, Fergen JK, Riedell WE. 2008. The influence of plant anatomy on oviposition and reproductive success of the omnivorous bug *Orius insidiosus*. *Anim. Behav.* 75:1495–502
98. Lundgren JG, Wyckhuys KAG, Desneux N. 2009. Population responses by *Orius insidiosus* to vegetational diversity. *Biocontrol* 54:135–42
99. Macedo TB, Bastos CS, Higley LG, Ostlie KR, Madhavan S. 2003. Photosynthetic responses of soybean to soybean aphid (Homoptera: Aphididae) injury. *J. Econ. Entomol.* 96:188–93
100. Magalhaes LC, Hunt TE, Siegfried BD. 2008. Development of methods to evaluate susceptibility of soybean aphid to imidacloprid and thiamethoxam at lethal and sublethal concentrations. *Entomol. Exp. Appl.* 128:330–36
101. Matis JH, Kiffe TR, van der Werf W, Costamagna AC, Matis TI, Grant WE. 2009. Population dynamics models based on cumulative density dependent feedback: a link to the logistic growth curve and a test for symmetry using aphid data. *Ecol. Model.* 220:1745–51
102. McCornack BP, Carrillo MA, Venette RC, Ragsdale DW. 2005. Physiological constraints on the overwintering potential of the soybean aphid (Homoptera: Aphididae). *Environ. Entomol.* 34:235–40
103. McCornack BP, Costamagna AC, Ragsdale DW. 2008. Within-plant distribution of soybean aphid (Homoptera: Aphididae) and development of node-based sample units for estimating whole-plant densities in soybean. *J. Econ. Entomol.* 101:1488–500
104. McCornack BP, Ragsdale DW. 2006. Efficacy of thiamethoxam to suppress soybean aphid populations in Minnesota soybean. *Crop Manag.* doi:10.1094/CM-2006-0915-01-RS
105. McCornack BP, Ragsdale DW, Venette RC. 2004. Demography of soybean aphid (Homoptera: Aphididae) at summer temperatures. *J. Econ. Entomol.* 97:854–61
106. Mensah C, DiFonzo C, Wang DC. 2008. Inheritance of soybean aphid resistance in PI567541B and PI567598B. *Crop Sci.* 48:1759–63
107. Mian MAR, Kang ST, Beil SE, Hammond RB. 2008. Genetic linkage mapping of the soybean aphid resistance gene in PI 243540. *Theor. Appl. Genet.* 117:955–62
108. Miao J, Wu KM, Hopper KR, Li GX. 2007. Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and impact of natural enemies in Northern China. *Environ. Entomol.* 36:840–48
109. Michel AP, Zhang W, Jung JK, Kang S, Mian MAR. 2009. Population genetic structure of the soybean aphid, *Aphis glycines*. *Environ. Entomol.* 38:1301–11
110. Michel AP, Zhang W, Jung JK, Kang S, Mian MAR. 2009. Cross-species amplification and polymorphism of microsatellite loci in the soybean aphid, *Aphis glycines*. *J. Econ. Entomol.* 102:1389–92

111. Mignault MP, Roy M, Brodeur J. 2006. Soybean aphid predators in Quebec and the suitability of *Aphis glycines* as prey for three Coccinellidae. *Biocontrol* 51:89–106
112. Moser SE, Obrycki JJ. 2009. Non-target effects of neonicotinoid seed treatments; mortality of coccinellid larvae related to zoophytophagy. *Biol. Control* 51:487–92
113. Nault BA, Shah DA, Straight KE, Bachmann AC, Sackett WM, et al. 2009. Modeling temporal trends in aphid vector dispersal and cucumber mosaic virus epidemics in snap bean. *Environ. Entomol.* 38:1347–59
114. Nielsen C, Hajek AE. 2005. Control of invasive soybean aphid, *Aphis glycines* (Hemiptera: Aphididae), populations by existing natural enemies in New York State, with emphasis on entomopathogenic fungi. *Environ. Entomol.* 34:1036–47
115. Noma T, Brewer MJ. 2008. Seasonal abundance of resident parasitoids and predatory flies and corresponding soybean aphid densities, with comments on classical biological control of soybean aphid in the Midwest. *J. Econ. Entomol.* 101:278–87
116. Noma T, Gratton C, Colunga-Garcia M, Brewer MJ, Mueller EE, et al. 2010. Relationship of soybean aphid (Hemiptera: Aphididae) to soybean plant nutrients, landscape structure, and natural enemies. *Environ. Entomol.* 39:31–41
117. Ohnesorg WJ, Johnson KD, O’Neal ME. 2009. Impact of reduced-risk insecticides on soybean aphid and associated natural enemies. *J. Econ. Entomol.* 102:1816–26
118. Olson KD, Badibanga T, DiFonzo CD. 2008. Farmers’ awareness and use of IPM for soybean aphid control: report of survey results for the 2004, 2005, 2006, and 2007 crop years. *Staff Pap. P08-12. Dep. Appl. Econ., Univ. Minn., St. Paul.* <http://ageconsearch.umn.edu/bitstream/45803/2/p08-12.pdf>
119. Olson LJ. 2006. The economics of terrestrial invasive species: a review of the literature. *Agric. Res. Econ. Rev.* 35:178–94
120. Ostlie K, Potter B. 2009. Managing two-spotted spider mites on soybeans in Minnesota. *Univ. Minn. Ext.* <http://www.soybeans.umn.edu/pdfs/2009/2009ManagingSpiderMitesinMinnesotaSoybean.pdf>
121. Papachristos DP, Milonas PG. 2008. Adverse effects of soil applied insecticides on the predatory coccinellid *Hippodamia undecimnotata* (Coleoptera: Coccinellidae). *Biol. Control* 47:77–81
122. Pedersen P, Gran C, Cullen E, Hill JH. 2007. Potential for integrated management of soybean virus disease. *Plant Dis.* 91:1255–59
123. Pike KS, Starj P, Brewer MJ, Noma T, Langley S, Kaiser M. 2007. A new species of *Binodoxys* (Hymenoptera: Braconidae: Aphidiinae), parasitoid of the soybean aphid, *Aphis glycines* Matsumura, with comments on biocontrol. *Proc. Entomol. Soc. Wash.* 109:359–65
124. Pimentel D, Lach L, Zuniga R, Morrison D. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50:53–65
125. Ragsdale DW, McCornack BP, Venette RC, Potter DB, Macrae IV, et al. 2007. Economic threshold for soybean aphid (Hemiptera: Aphididae). *J. Econ. Entomol.* 100:1258–67
126. Ragsdale DW, Voegtlin DJ, O’Neil RJ. 2004. Soybean aphid biology in North America. *Ann. Entomol. Soc. Am.* 97:204–8
127. Rhainds M, Brodeur J, Borcard D, Legendre P. 2008. Toward management guidelines for soybean aphid, *Aphis glycines*, in Quebec. II. Spatial distribution of aphid populations in commercial soybean fields. *Can. Entomol.* 140:219–34
128. Rhainds M, Roy M, Daigle G, Brodeur J. 2007. Toward management guidelines for the soybean aphid in Quebec. I. Feeding damage in relationship to seasonality of infestation and incidence of native predators. *Can. Entomol.* 139:728–41
129. Rhainds M, Yoo HJS, Kindlmann P, Voegtlin D, Castillo D, et al. 2010. Two-year oscillation cycle in abundance of soybean aphid in Indiana. *Agric. For. Entomol.* 12:251–57
130. Riedell WE. 1989. Effects of Russian wheat aphid infestation on barley plant response to drought stress. *Physiol. Plant.* 77:587–92
131. Rutledge CE, O’Neil RJ. 2005. *Orius insidiosus* (Say) as a predator of the soybean aphid, *Aphis glycines* Matsumura. *Biol. Control* 33:56–64
132. Rutledge CE, O’Neil RJ, Fox TB, Landis DA. 2004. Soybean aphid predators and their use in integrated pest management. *Ann. Entomol. Soc. Am.* 97:240–48
133. Schmidt NP, O’Neal ME, Dixon PM. 2008. Aphidophagous predators in Iowa soybean: a community comparison across multiple years and sampling methods. *Ann. Entomol. Soc. Am.* 101:341–50

---

111. Characterizes the predatory fauna associated with the soybean aphid in commercial fields in the northern range of the pest.

---

---

125. The first paper to describe the development of the EIL and the ET for soybean aphid in North America.

---

134. Schmidt NP, O'Neal ME, Singer JW. 2007. Alfalfa living mulch advances biological control of soybean aphid. *Environ. Entomol.* 36:416–24
135. Simberloff D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecol. Lett.* 9:912–19
136. Simberloff D, Von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* 1:21–32
137. Smith SF, Krischik VA. 1999. Effects of systemic imidacloprid on *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Environ. Entomol.* 28:1189–95
138. Song F, Swinton SM. 2009. Returns to integrated pest management research and outreach for soybean aphid. *J. Econ. Entomol.* 102:2116–25
139. Starý P, Rakhshani E, Tomanović Ž, Hoelmer K, Kavallieratos NG, et al. 2010. A new species of *Lysipblebus* Förster 1862 (Hymenoptera: Braconidae, Aphidiinae) attacking soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) from China. *J. Hymenoptera Res.* 19:184–91
140. Suckling DM, Brockerhoff EG. 2010. Invasion biology, ecology, and management of the light brown apple moth (Tortricidae). *Annu. Rev. Entomol.* 55:285–306
141. Taylor S. 2009. New and upcoming advancements in seed treatments. *Indiana CCA Conf. Notes.* 2 pp.
142. Thomas MB. 1999. Ecological approaches and the development of 'truly integrated' pest management. *Proc. Natl. Acad. Sci. USA* 96:5944–51
143. Tonet GL, DaSilva RFP. 1995. Resistance of wheat genotypes of C biotype of *Schizaphis graminum* (Rondani) (Homoptera, Aphididae). *Pesqui. Agropecu. Bras.* 30:1283–87
144. Torres JB, Silva-Torres CSA, de Oliveira JV. 2003. Toxicity of pymetrozine and thiamethoxam to *Aphelinus gossypii* and *Delphastus pusillus*. *Pesqui. Agropecu. Bras.* 38:459–66
145. Van den Berg H, Ankasah D, Muhammad A, Rusli R, Widayanto HA, et al. 1997. Evaluating the role of predation in population fluctuations of the soybean aphid *Aphis glycines* in farmers' fields in Indonesia. *J. Appl. Ecol.* 34:971–84
146. van Emden HF. 1997. Host-plant resistance to insect pests. In *Techniques for Reducing Pesticide Use*, ed. D Pimentel, pp. 129–152. Chichester, UK: Wiley
147. van Emden HF, Harrington R. 2007. *Aphids as Crop Pests*. Cambridge, MA: CABI North Am. Off. 800 pp.
148. Venette RC, Ragsdale DW. 2004. Assessing the invasion by soybean aphid (Homoptera: Aphididae): Where will it end? *Ann. Entomol. Soc. Am.* 97:219–26
149. Voegtlin DJ, O'Neil RJ, Graves WR. 2004. Tests of suitability of overwintering hosts of *Aphis glycines*: identification of a new host association with *Rhamnus alnifolia* L'Heritier. *Ann. Entomol. Soc. Am.* 97:233–34
150. Voegtlin DJ, O'Neil RJ, Graves WR, Lagos D, Yoo HJS. 2005. Potential winter hosts of soybean aphid. *Ann. Entomol. Soc. Am.* 98:690–93
151. Walther GR, Roques A, Hulme PE, Sykes MT, Pysek P, et al. 2009. Alien species in a warmer world: risks and opportunities. *Trends Ecol. Evol.* 24:686–93
152. White KE, Hoppin JA. 2004. Seed treatment and its implication for fungicide exposure assessment. *J. Expo. Anal. Environ. Epidemiol.* 14:195–203
153. Williamson M. 1996. *Biological Invasions*. London: Chapman & Hall. 256 pp.
154. Wu ZS, Schenk-Hamlin D, Zhan WY, Ragsdale DW, Heimpel GE. 2004. The soybean aphid in China: a historical review. *Ann. Entomol. Soc. Am.* 97:209–18
155. Wyckhuys KAG, Hopper KR, Wu KM, Straub C, Cratton C, Heimpel GE. 2007. Predicting potential ecological impact of soybean aphid biological control introductions. *Biocontrol. News Inf.* 28:N30–34
156. Wyckhuys KAG, Koch RL, Heimpel GE. 2007. Physical and ant-mediated refuges from parasitism: implications for non-target effects in biological control. *Biol. Control* 40:306–13
157. Wyckhuys KAG, Koch RL, Kula RR, Heimpel GE. 2009. Potential exposure of a classical biological control agent of the soybean aphid, *Aphis glycines*, on non-target aphids in North America. *Biol. Invasions* 11:857–71
158. Wyckhuys KAG, Stone L, Desneux N, Hoelmer KA, Hopper KR, Heimpel GE. 2008. Parasitism of the soybean aphid *Aphis glycines* by *Binodoxys communis*: the role of aphid defensive behavior and parasitoid reproductive performance. *Bull. Entomol. Res.* 98:361–70

157. A risk assessment of a classical biological control agent of soybean aphid that takes into account both exposure and effects of a biological control agent on nontarget species.



159. Xue Y, Bahlai CA, Frewin A, Sears MK, Schaafsma AV, Hallett RH. 2009. Predation by *Coccinella septempunctata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Homoptera: Aphididae). *Environ. Entomol.* 38:708–14
160. Yoo HJS, O'Neil RJ. 2009. Temporal relationships between the generalist predator, *Orius insidiosus*, and its two major prey in soybean. *Biol. Control* 48:168–80
161. Zhang W, Swinton SM. 2009. Incorporating natural enemies in an economic threshold for dynamically optimal pest management. *Ecol. Model.* 220:1315–24
162. Zhang Y, Wang L, Wu KM, Wyckhuys KAG, Heimpel GE. 2008. Flight performance of the soybean aphid, *Aphis glycines* (Hemiptera: Aphididae) under different temperature and humidity regimens. *Environ. Entomol.* 37:301–06
163. Zhu JW, Park KC. 2005. Methyl salicylate, a soybean aphid-induced plant volatile attractive to the predator *Coccinella septempunctata*. *J. Chem. Ecol.* 31:1733–46



# Contents

<i>Bemisia tabaci</i> : A Statement of Species Status <i>Paul J. De Barro, Shu-Sheng Liu, Laura M. Boykin, and Adam B. Dinsdale</i> .....	1
Insect Seminal Fluid Proteins: Identification and Function <i>Frank W. Avila, Laura K. Sirot, Brooke A. LaFlamme, C. Dustin Rubinstein, and Mariana F. Wolfner</i> .....	21
Using Geographic Information Systems and Decision Support Systems for the Prediction, Prevention, and Control of Vector-Borne Diseases <i>Lars Eisen and Rebecca J. Eisen</i> .....	41
Salivary Gland Hypertrophy Viruses: A Novel Group of Insect Pathogenic Viruses <i>Verena-Ulrike Lietze, Adly M.M. Abd-Alla, Marc J.B. Vreysen, Christopher J. Geden, and Drion G. Boucias</i> .....	63
Insect-Resistant Genetically Modified Rice in China: From Research to Commercialization <i>Mao Chen, Anthony Shelton, and Gong-yin Ye</i> .....	81
Energetics of Insect Diapause <i>Daniel A. Hahn and David L. Denlinger</i> .....	103
Arthropods of Medicoveterinary Importance in Zoos <i>Peter H. Adler, Holly C. Tuten, and Mark P. Nelder</i> .....	123
Climate Change and Evolutionary Adaptations at Species' Range Margins <i>Jane K. Hill, Hannah M. Griffiths, and Chris D. Thomas</i> .....	143
Ecological Role of Volatiles Produced by Plants in Response to Damage by Herbivorous Insects <i>J. Daniel Hare</i> .....	161
Native and Exotic Pests of <i>Eucalyptus</i> : A Worldwide Perspective <i>Timothy D. Paine, Martin J. Steinbauer, and Simon A. Lawson</i> .....	181

Urticating Hairs in Arthropods: Their Nature and Medical Significance <i>Andrea Battisti, Göran Holm, Bengt Fagrell, and Stig Larsson</i> .....	203
The Alfalfa Leafcutting Bee, <i>Megachile rotundata</i> : The World's Most Intensively Managed Solitary Bee <i>Theresa L. Pitts-Singer and James H. Cane</i> .....	221
Vision and Visual Navigation in Nocturnal Insects <i>Eric Warrant and Marie Dacke</i> .....	239
The Role of Phytopathogenicity in Bark Beetle–Fungal Symbioses: A Challenge to the Classic Paradigm <i>Diana L. Six and Michael J. Wingfield</i> .....	255
Robert F. Denno (1945–2008): Insect Ecologist Extraordinaire <i>Micky D. Eubanks, Michael J. Raupp, and Deborah L. Finke</i> .....	273
The Role of Resources and Risks in Regulating Wild Bee Populations <i>T'ai H. Roulston and Karen Goodell</i> .....	293
Venom Proteins from Endoparasitoid Wasps and Their Role in Host-Parasite Interactions <i>Sassan Asgari and David B. Rivers</i> .....	313
Recent Insights from Radar Studies of Insect Flight <i>Jason W. Chapman, V. Alistair Drake, and Don R. Reynolds</i> .....	337
Arthropod-Borne Diseases Associated with Political and Social Disorder <i>Philippe Brouqui</i> .....	357
Ecology and Management of the Soybean Aphid in North America <i>David W. Ragsdale, Douglas A. Landis, Jacques Brodeur, George E. Heimpel, and Nicolas Desneux</i> .....	375
A Roadmap for Bridging Basic and Applied Research in Forensic Entomology <i>J.K. Tomberlin, R. Mohr, M.E. Benbow, A.M. Tarone, and S. VanLaerhoven</i> .....	401
Visual Cognition in Social Insects <i>Aurore Avarguès-Weber, Nina Deisig, and Martin Giurfa</i> .....	423
Evolution of Sexual Dimorphism in the Lepidoptera <i>Cerisse E. Allen, Bas J. Zwaan, and Paul M. Brakefield</i> .....	445
Forest Habitat Conservation in Africa Using Commercially Important Insects <i>Suresh Kumar Raina, Esther Kioko, Ole Zethner, and Susie Wren</i> .....	465
Systematics and Evolution of Heteroptera: 25 Years of Progress <i>Christiane Weirauch and Randall T. Schuh</i> .....	487