



Biology of the Soybean Aphid, *Aphis glycines* (Hemiptera: Aphididae) in the United States

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ABSTRACT. The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is a significant insect pest of soybean in the north-central region of the United States and southern Canada, and if left untreated can reduce yield value by \$2.4 billion annually. The soybean aphid is native to eastern Asia, where soybean was first domesticated, and was first detected in the United States in 2000. It quickly spread within 4 years of its discovery across 22 states and three provinces of Canada. Heavy infestations can result in a covering of sooty mold, yellow and wrinkled leaves, stunted plants, and aborted pods leading to significant yield loss of 40% or more. It can also transmit plant viruses such as Soybean mosaic virus and Alfalfa mosaic virus. The soybean aphid has a complex life cycle that involves different physical forms, sexual stages, and two host plant species—soybean and buckthorn (the overwintering host). Plant nutrition, natural enemies, climate, and weather all affect population growth rate, but the typical population doubling time is ≈ 6 –7 days. Though at present management is primarily through broad-spectrum insecticides, biological control has a significant impact on soybean aphid population growth, and aphid-resistant soybean varieties are becoming increasingly available.

Key Words: *Aphis glycines*; soybean aphid; soybean aphid biology

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is a significant insect pest of soybean in the north-central region of the United States, and if left untreated can reduce yield by \$2.4 billion annually (Song et al. 2006). The soybean aphid is an invasive pest that was first detected in the United States in 2000 (Alleman et al. 2002), and quickly became the dominant insect pest in soybean throughout the Midwest, which had previously experienced relatively little regionwide pressure from other insect pests of this crop. Soybean aphid populations have the potential to increase rapidly, and heavy infestations can stunt plant growth and development, leading to significant yield loss.

This article reviews the invasion history and distribution of the soybean aphid, as well as its biology and the feeding damage it causes. Biological control, host plant resistance, and other factors affecting soybean aphid populations will also be discussed.

Invasion History and Distribution

The soybean aphid is native to eastern Asia, where soybean was first domesticated. Its Asian range includes China, Indonesia, Japan, Korea, Malaysia, the Philippines, Taiwan, and Thailand (Wang et al. 1994, Van den Berg et al. 1997, Blackman and Eastop 2000). Although soybean aphid was noted as an important pest of soybean in Asia by Kogan and Turnipseed (1987), and a sporadic pest in China (Wang et al. 1994), its impact in the United States has been markedly greater than that within its native range (Liu et al. 2004, Ragsdale et al. 2004, Wu et al. 2004). It is not surprising for invasive species, like soybean aphid, to have notably different population levels within their exotic ranges (Elton 2000). The first specimens in the United States were confirmed on soybean, *Glycine max* (L.), in Wisconsin in 2000 (Alleman et al. 2002), and quickly spread within 4 years of its discovery across 22 states and three provinces of Canada (Hunt et al. 2003, Venette and Ragsdale 2004). Its establishment across a large area of the soybean growing region of the United States was facilitated by the previous establishment and spread of its overwintering host, common buckthorn, *Rhamnus cathartica* L. (Ragsdale et al. 2004). Buckthorn was previously established in the United States before soybeans were widely cultivated and can be found throughout the north-central region, especially in the upper-Midwest (Ragsdale et al. 2004). The rapid population expansion of soybean aphid suggests high

mobility and few limits to migration and gene flow (Ragsdale et al. 2004, Venette and Ragsdale 2004).

The soybean aphid is a pest predominantly in middle to high latitudes in the Midwestern United States and the provinces of Manitoba, Ontario and Québec, Canada. It is seldom found south of Kansas, Missouri, Kentucky, or Virginia. In southern states it can sometimes be confused with cotton aphid (*Aphis gossypii* Glover), which can occur on soybean in that region.

Description

Soybean aphid was first described by Matsumura (1917), but more defined body characters were published by Voegtlin et al. (2004a). In soybean, wingless soybean aphids are pear-shaped, 1/16th inch (1.5 mm) long, and range from pale yellow to lime green in color (Fig. 1) (though on late-season soybeans, some aphids may be pale and smaller in appearance). Adults have dark-tipped cornicles (“tailpipes”) at the posterior end (Fig. 1). Winged soybean aphids have a dark thorax (central body segment) and cornicles, and transparent wings that extend well past the abdomen (Fig. 2).

Feeding and Injury

Soybean aphids have piercing-sucking mouthparts that are used to feed on phloem sap. Although soybean aphid will feed on leaves, stems, and pods, they are most often found on the undersides of leaves. The distribution of soybean aphids on the plant varies during the growing season (McCornack et al. 2008). Early in the season, aphids are more likely to be found on newly expanding trifoliate leaves (Fig. 3). As the season progresses and the plant matures, soybean aphids are more likely to be found lower in the canopy, on leaves that are attached to nodes further from the terminal bud. Soybean aphids may occur in low density of only a few aphids per plant, or may form large, persistent colonies of several hundred or even thousands per plant.

Soybean aphid colony size and infestation levels are influenced by ecological factors such as temperature and biological control (discussed below), but also by their nutritional feeding environment. Like most aphids, soybean aphid growth is limited by the nutritional quality of its host plant. The limiting component of the soybean aphids diet is often nitrogen, which has a relatively low concentration within the phloem. Studies have linked the population growth rate of the soybean aphid to nitrogen availability in soybeans. Population growth in-



Fig. 1. Soybean aphids range from yellow to pale green. Dark-tipped cornicles (“tailpipes”) are found on the abdomens of adults. Note the female in the upper left giving live birth to another female. Photo by Roy Scott.



Fig. 2. Winged soybean aphid (left) and an immature soybean aphid with developing wing buds (right) that will be a winged aphid upon maturation. Photo by Roy Scott.



Fig. 3. Soybean aphids infesting a young soybean trifoliolate. Photo by Roy Scott.

creases in plants with increased nitrogen concentration in phloem, such as plants growing in fields with potassium-deficient soils (Myers et al. 2005, Walter and DiFonzo 2007, Noma et al. 2010), or growth stages of the plant when nitrogen is more readily available.

The injury caused by phloem feeding insects like soybean aphids may go undetected without close visual inspection, and feeding damage may become readily apparent only after large, yield-reducing populations have developed. At moderate infestation levels (i.e., <50 aphids per leaflet), soybean aphid can significantly reduce gas exchange and negatively affect photosynthetic rates (Macedo et al.

2003). Heavily infested plants are stunted (Fig. 4) and may be covered with dark sooty mold growing on the sugary excretions or “honeydew” that aphids produce. Heavy infestations can result in yellow and wrinkled leaves, stunted plants and aborted pods (Lin et al. 1993) leading to significant yield loss of 40% or more (Ragsdale et al. 2007). Large infestations can negatively impact seed quality and size, pod number, plant height, and photosynthesis (Beckendorf et al. 2008).

Soybean aphid, like many aphids, can transmit plant viruses (Clark and Perry 2002). It has been shown to transmit both Soybean mosaic virus and Alfalfa mosaic virus to soybean (Hill et al. 2001). It may also vector plant pathogens, typically nonpersistent viruses, to other temporally visited crops, such as Alfalfa mosaic virus and Cucumber mosaic virus in snap bean, *Phaseolus vulgaris* L. (Gildow et al. 2008), and Potato virus Y in potato, *Solanum tuberosum* L. (Davis et al. 2005). Soybean aphid is able to transmit several other viruses (Wang et al. 2006), but its economic importance as a vector in North American soybean and other crops is still to be determined.

Biology and Life Cycle

The life cycle of the soybean aphid in the United States is similar to its native range (Wu et al. 2004). Like many aphid species, it has a complex life cycle that involves different physical forms (morphs) and two types of host plants. It is heteroecious (host-alternating) and holocyclic (generates sexual morphs with an egg that overwinters) (Ragsdale et al. 2004).

Through the spring and summer, soybean aphids reproduce asexually (without mating) on soybean, which is actually considered the secondary host; the aphids are all female and give live birth (Fig. 1) to all-female offspring. These features give soybean aphids the ability to increase very rapidly when conditions are favorable. The optimal developmental temperature is 82°F/27.8°C (McCornack et al. 2004). The upper developmental temperature is 94.8°F/34.9°C, and the lower developmental temperature is 47.5°F/8.6°C (McCornack et al. 2004). In general, aphid reproduction is affected by the growth stage of the host plant, with greater rates of reproduction during vegetative and late reproductive stages when senescence occurs (Dixon 1985), but these plant growth stage effects do not prove to be strong (Rutledge and O’Neil 2006, Rhains et al. 2010). Under favorable conditions (e.g., 77–86°F/25–30°C), soybean aphids are highly reproductive and can double in population size in as little as 1.5 to 2 days (McCornack et al. 2004). However, in the field where aphids experience multiple forms of mortality (weather, natural enemies, diseases) population doubling time is typically 6–7 days (Ragsdale et al. 2007). During the entire growing season, soybean aphid has ≈15 asexual generations on soybean and three or more generations on the primary host (buckthorn, see below), which is equivalent to the 18–20 generations that were recorded in China (Li et al. 2000).

During midsummer population increase, many wingless aphids will produce winged offspring that can colonize other areas within-



Fig. 4. A soybean plant (left) stunted by heavy aphid pressure (thousands per plant). The plant on the right contains the *Rag1* aphid resistance gene. Photo by Roy Scott.

field or can disperse great distances on the wind in mid- to late-summer (Hodgson et al. 2005, 2009), and later-season influx of aphids into fields may be an important contributing factor in outbreaks. Factors that typically contribute to aphids producing migrants in other systems include plant nutrition, crowding (Dixon 1985), temperature (Johnson and Birks 1960), plant phenology (Howard and Dixon 1992), and the presence of beneficial insects (Roitberg et al. 1979). Several of these factors are currently under investigation for soybean aphid.

At the end of the soybean growing season soybean aphids migrate in September and October back to their primary host plant, common buckthorn (*Rhamnus cathartica* L.) (Fig. 5), a deciduous shrub common in shelterbelts and woods in northern states. Buckthorn is a critical part of the soybean aphid life cycle; without this plant, they cannot spend the winter in a given area. *R. cathartica* is most widely infested, though it may also overwinter on *Rhamnus alnifolia* L'Héritier, among other *Rhamnus* species (Voegtlin et al. 2004b, 2005; Hill et al. 2010). Common buckthorn is itself an invasive species and is widespread across North America, particularly north of 41°N latitude where plant densities of >10,000/acre are known to occur (Ragsdale et al. 2004). It often appears as a shrub around 8 feet/2.4 m high but can also resemble a small tree up to 25 feet/7.6 m tall. It has gray bark, and glossy dark green leaves with curved veins and notched edges (Fig. 5).

The fall migration of soybean aphids to buckthorn is regulated by photoperiod and temperature. Winged females (gynoparae) leave soybean in search of buckthorn, where they feed and deposit a cohort of wingless, sexual females (oviparae). Winged males from soybean seek the oviparae on buckthorn, where mating occurs, followed by oviposition. Overwintering eggs are deposited along buckthorn buds (Fig. 6) (Ragsdale et al. 2004).

The overwintering egg is cold-hardy and can survive temperatures as low as -29°F/-34°C (McCornack et al. 2005). Eggs suffer significant mortality on buckthorn, likely because of a combination of abiotic and biotic factors including predators. Survivors hatch during spring and three or more generations develop on buckthorn (Welsman et al. 2007, Bahlai et al. 2008). During the time when soybeans germinate, colonies on buckthorn produce winged females, which colonize soybeans in the early vegetative growth stage (V1-V5) in late spring/early summer (Bahlai et al. 2008). Soybean fields in close



Fig. 6. A newly laid soybean aphid egg (green) and an older egg (black) at the base of a buckthorn bud. Photo by Robert O'Neil.

proximity to buckthorn may be at greater risk of early infestation (Bahlai et al. 2010); however, soybean fields distant from buckthorn are also at risk of secondary infestations occurring later in the growing season.

Biological Control

Field studies of soybean reveal a diverse community of natural enemies, which help suppress soybean aphid colonization and population growth. These natural enemies include ladybeetles, lacewings, pirate bugs, predatory flies, and entomopathogenic (insect disease-causing) fungi (Rutledge et al. 2004, Nielsen and Hajek 2005, Mignault et al. 2006, Brewer and Noma 2010) (Fig. 7). The community of insect predators within soybean has apparently been altered by the arrival of the soybean aphid, and now includes more species that focus on aphids (Schmidt et al. 2008). Included in this community is the multicolored Asian ladybeetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) (Fig. 7a, b), which contributes to biological control of soybean aphid in its native range (Van den Berg et al. 1997), and is one of the dominant soybean aphid predators in the United States (Gardiner et al. 2009a, 2009b).

Natural enemies cause significant mortality of soybean aphid. Several field studies have demonstrated the contributions of existing

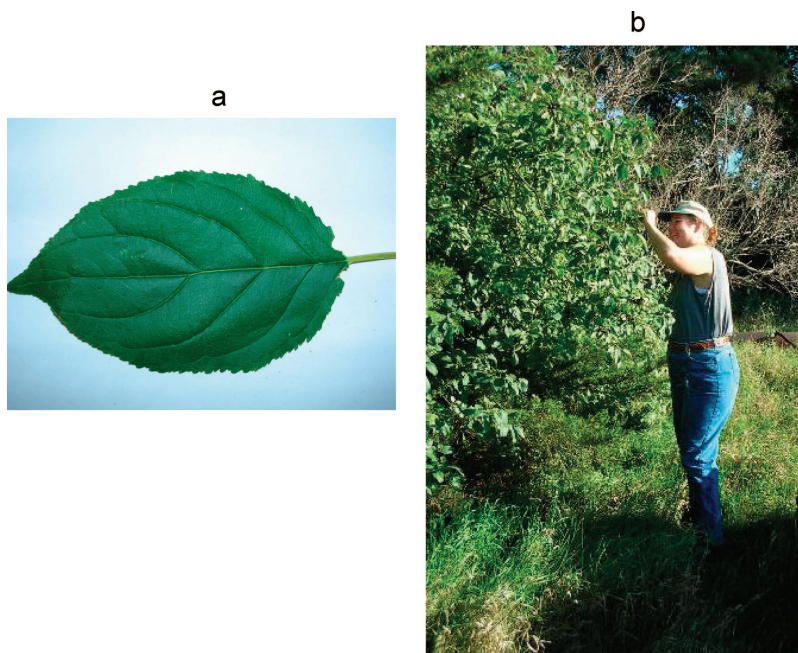


Fig. 5. Common buckthorn (*Rhamnus cathartica*). (a) Leaves have toothed edges and curved veins. (b) Plants are shrub-like and often occur in undergrowth. Photos by Kelley Tilmon.

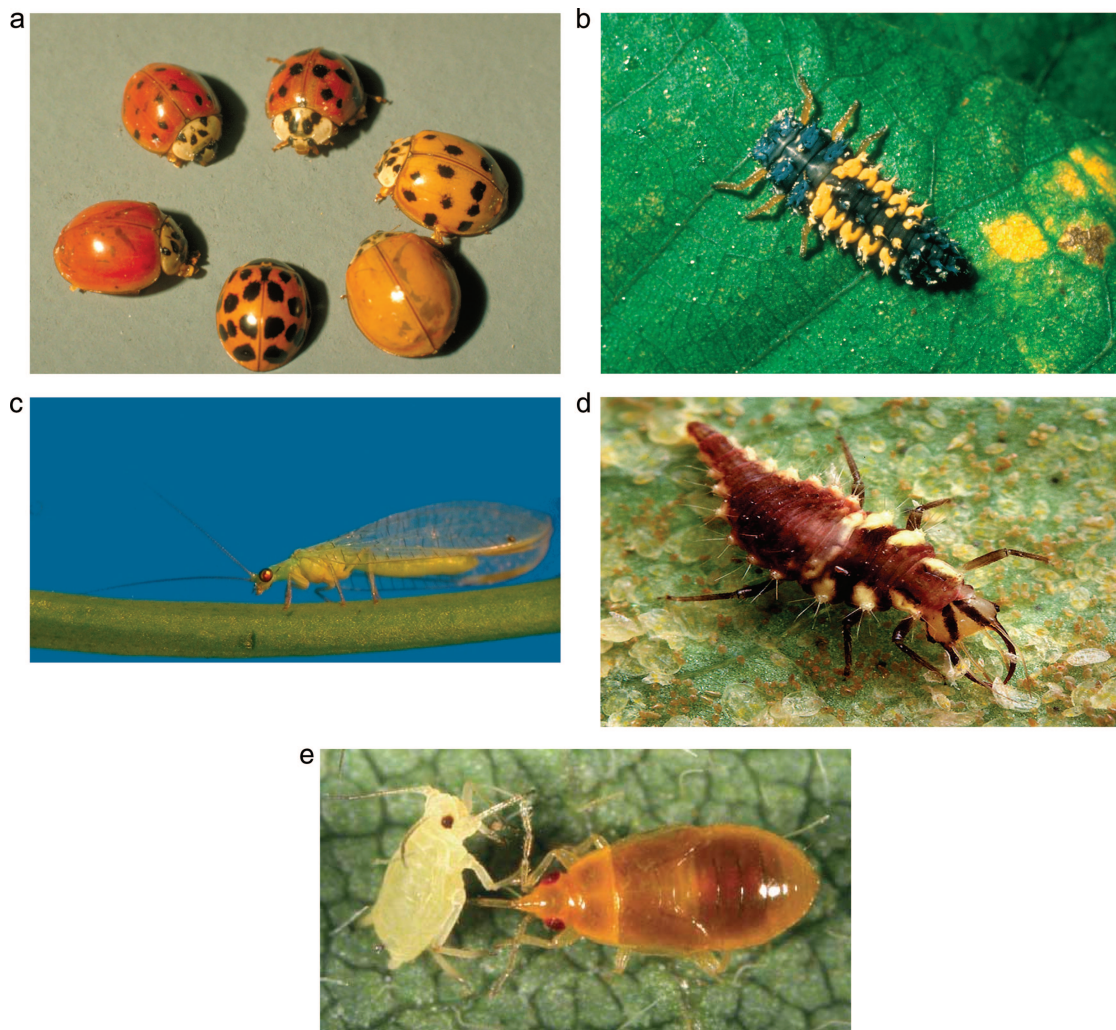


Fig. 7. Many predatory insects help provide background suppression of soybean aphids. (a) Asian ladybeetle adults range in color from pale orange-yellow to orange-red, and vary greatly in the number of spots. A pattern of black dots resembling the letter “M” behind the head is typical. Photo by Bill Ree, Bugwood.org (b) Asian ladybeetle larva. Photo by Allan Knutson, Bugwood.org (c) Green lacewing adult. Photo by Sonya Broughton, Bugwood.org (d) Green lacewing larva. Photo by USDA-ARS (e) immature *Orius* sp. bug feeding on a soybean aphid. Photo by Robert O’Neil.

communities of natural enemies to soybean aphid suppression (Fox et al. 2004; Rutledge and O’Neil 2005; Costamagna and Landis 2006, 2007). In the absence of predation, soybean aphid population growth is significantly faster (2–7 times) (Costamagna and Landis 2006). Prophylactic application of broad-spectrum insecticides (Ohnesorg et al. 2009) or fungicides (Koch et al. 2010) has the potential to ultimately exacerbate aphid pressure or cause secondary outbreak of other pests such as spider mites by removing the natural enemies that often keep pest populations in check. Conversely, management practices that encourage the recruitment and preservation of natural enemies in soybean have the potential to provide future conservation biological control strategies (Brewer and Noma 2010).

Landscape ecology can have a significant impact on biological control of soybean aphid. The soybean aphid is typically a pest of soybeans in areas where the crop is grown in large monocultures. This setting can influence the insect predators that provide biological control. In areas where the landscape is comprised mostly of corn and soybeans, the impact of insect predators will be lower than in regions where there is more landscape diversity (Gardiner et al. 2009a). Soybean fields located in landscapes that have a greater amount of perennial habitat are more likely to have a greater abundance of ladybeetles (Gardiner et al. 2009b). Such habitats include woodlots, where important predators like the multi-colored Asian ladybeetle

overwinter. Noma et al. (2010) found that landscapes with more diverse land cover tend to have lower aphid populations. Soybean fields in landscapes comprised of grassland habitats and annual crops are likely to have a lower density of natural enemies and, subsequently, less biological control. Landis et al. (2008) have suggested that as more land is used for corn production, the current level of soybean aphid biological control may decline, and Noma et al. (2010) found that habitats more dominated by corn and soybean were associated with greater soybean aphid populations.

Though soybean aphid can be heavily impacted by the natural enemies that already exist in the United States, as an invasive species it is also a candidate for classical (importation) biological control. Invasive species often have higher populations in their introduced ranges than in their native ranges; in part this is related to an escape from natural enemies, which are typically less abundant for a given pest across its introduced range than in its native range (Colautti et al. 2004). Though surveys of natural enemies in the United States reveal a rich community of natural enemies, parasitoids—a type of parasitic insect that is often nearly as large as its host and can specialize on particular prey species—have been notably lacking from this community (Rutledge et al. 2004, Kaiser et al. 2007, Noma and Brewer 2008, Schmidt et al. 2008.).

Parasitoids that attack soybean aphids are an important part of the community of predators that suppress soybean aphid in China (Liu et al. 2004); however, it is not uncommon for a newly introduced pest insect to arrive without its specialist natural enemies. A classical biological control program, whose goal is to introduce parasitoid species from the native range that specialize on soybean aphid, is underway. One particular species, *Binodoxys communis* (Gahan) (Hymenoptera: Braconidae) (Fig. 8) has undergone intense scrutiny for environmental impact, host specificity, and ecological interactions with soybean and other aphids (Wyckhus et al. 2007a, 2007b, 2008, 2009). Based on these studies, *B. communis* received federal approval for release in the United States in 2007. Releases of *B. communis* in the Midwest are on-going, though their impact on soybean aphid has not been measured, and depends in large part on the ability of populations of the parasitoid to establish and spread within the new range. Additional candidate species are in quarantine and may be released in the future (Heimpel et al. 2004).

Host Plant Resistance and Biotypes

Aphid-resistant varieties have the potential to augment natural enemies by reducing insecticide load, in addition to serving as important management tools in their own right. Host-plant resistance in the form of both antibiosis (reduced survival and number of offspring) and antixenosis (nonattractive or repellent plants) to the soybean aphid have been found (Hill et al. 2004a, 2004b; Mensah et al. 2005; Mian et al. 2008a; Zhang et al. 2009). Molecular mapping is ongoing (Li et al. 2007, Mian et al. 2008b, Zhang et al. 2009), but at least four genes have been identified: *Rag1* (Hill et al. 2006a, 2006b), *Rag2* (Mian et al. 2008b), and *rag3* and *rag4* (Zhang et al. 2009). [Capital letters

indicate a dominant trait and lower case letters indicate a recessive trait.] *Rag1* (an abbreviation for Resistance to *Aphis glycines* gene 1), is a single-gene source of antibiosis developed at the University of Illinois. It significantly reduces aphid populations compared with susceptible controls (Fig. 4) (Hill et al. 2004b, 2006a, 2006b). *Rag1* soybean lines first became commercially available in the United States on a limited basis in 2009; varieties containing additional resistance genes are likely to follow.

Despite the promise of aphid-resistant varieties, it should be noted that *Rag1*-containing soybeans are not aphid-free, and economically relevant populations sometimes occur. Biotypes have already been identified which can overcome *Rag1* and *Rag2* resistance (Kim et al. 2008, Hill et al. 2010) as well as a yet-unnamed source of resistance (Michel et al. 2010). How quickly and to what extent biotypes will arise that significantly limit the usefulness of host plant resistance is not yet known, and relates to the invasion history and genetic diversity of the soybean aphid. One consequence of the fact that soybean aphid is an invasive species is a possible reduction in its genetic variability because of a small founder-population. It is not clear how many times the soybean aphid has invaded the United States and how much genetic diversity was present in the invasion(s). Michel et al. (2009) observed a limited amount of genetic diversity in soybean aphids in North America in 2008, 8 years after the first observations of the soybean aphid. Nonetheless, the appearance of biotypes indicates that the genetic diversity to overcome resistant varieties is present to at least some extent.

Integrated Pest Management

Though natural enemies can have a significant impact on soybean aphid population growth (Costamagna and Landis 2006, Noma and Brewer 2008) and host plant resistance is an emerging tool, insecticides are currently the most-used control method for soybean aphid. Before the arrival of the soybean aphid, very little insecticide was used on soybean for insect pests in the north-central region (Fernandez-Cornejo and Jans 1999). In response to soybean aphid, growers have dramatically increased the use of insecticides for soybean production (USDA-NASS; www.nass.usda.gov), in some cases spraying up to three times in outbreak years, usually with broad-spectrum insecticides. Insecticides from multiple classes (organophosphates, pyrethroids, neonicotinoids) are effective for rapid soybean aphid control, but are most profitably used in an Integrated Pest Management (IPM) program based on scouting and the use of economic thresholds to guide application decisions. Significant field-based research has demonstrated that IPM strategies can limit yield loss while preventing unnecessary input-costs (Ragsdale et al. 2007, Johnson et al. 2009). A great deal of research has been conducted on the scouting and management of soybean aphid, which will be comprehensively reviewed in a separate article on consensus-based pest management recommendations, to appear at a later date in the Journal of Integrated Pest Management.

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References Cited

- Alleman, R. J., C. R. Grau, and D. B. Hogg. 2002. Soybean aphid host range and virus transmission efficiency. In Proceedings: Wisconsin Fertilizer Agline Pest Management Conference. (<http://www.soils.wisc.edu/extension/wcmc/2002proceedings/Alleman-conf-2002.pdf>)
- Bahlai, C. A., J. A. Welsman, A. W. Schaafsma, and M. K. Sears. 2008. Development of soybean aphid (Homoptera: Aphididae) on its primary

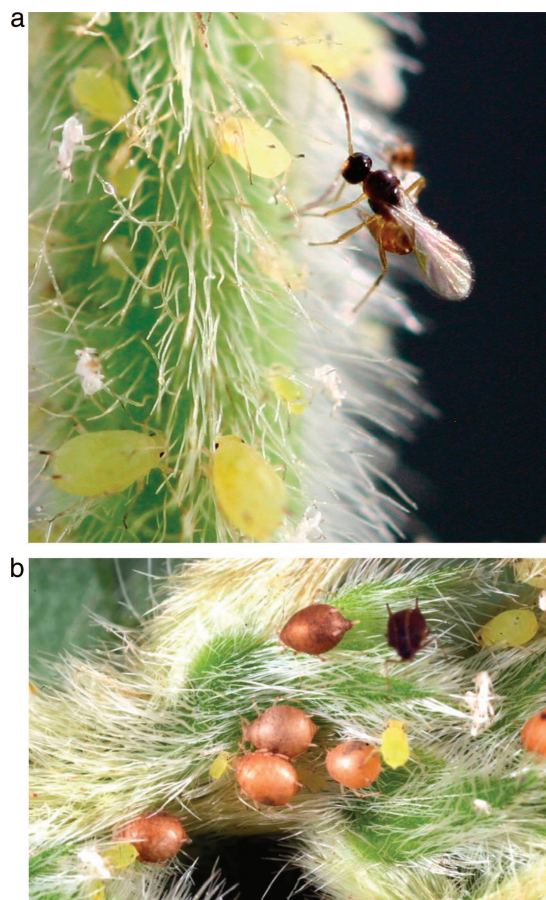


Fig. 8. *Binodoxys communis*, a specialist parasitoid imported from Asia for biological control of soybean aphid. (a) Adult parasitoid, (b) "mummies" the pupal form of the parasitoid inside the killed aphid's body. Photos by Roy Scott.

- overwintering host, *Rhamnus cathartica*. *Environmental Entomology* 36: 998–1006.
- Bahlai, C. A., S. Sikkema, R. H. Hallett, J. Newman, and A. W. Schaafsma. 2010. Modeling distribution and abundance of soybean aphid in soybean fields using measurements from the surrounding landscape. *Environmental Entomology* 39: 50–56.
- Beckendorf, E. A., M. A. Catangui, and W. E. Riedell. 2008. Soybean aphid feeding injury and soybean yield, yield components, and seed composition. *Agronomy Journal* 100: 237–246.
- Blackman, R. L., and V. F. Eastop. 2000. *Aphids on the world's crops: an identification and information guide*, 2nd ed. Wiley, New York.
- Brewer, M. J., and T. Noma. 2010. Habitat affinity of resident natural enemies of the invasive *Aphis glycines* (Hemiptera: Aphididae), on soybean, with comments on biological control. *Journal of Economic Entomology* 103: 583–596.
- Clark, A. J., and K. L. Perry. 2002. Transmissibility of field isolates of soybean viruses by *Aphis glycines*. *Plant Disease* 86: 1219–1222.
- Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7: 721–733.
- Costamagna, A. C., and D. A. Landis. 2006. Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. *Ecological Applications* 16: 1619–28.
- Costamagna, A. C., D. A. Landis, and C. D. DiFonzo. 2007. Suppression of soybean aphid by generalist predators results in a trophic cascade in soybeans. *Ecological Applications* 17: 441–451.
- Davis, J. A., E. B. Radcliffe, and D. W. Ragsdale. 2005. Soybean aphid, *Aphis glycines*, a new vector of Potato virus Y in potato. *American Journal of Potato Research* 82: 197–201.
- Dixon, A. F. G. 1985. *Aphid ecology*. Chapman and Hall, New York.
- Elton, C. S. 2000. *The ecology of invasions by animals and plants*. University of Chicago Press, Chicago, IL.
- Fernandez-Cornejo, J., and S. Jans. 1999. Pest management in U.S. agriculture. Resource Economics Division, U.S. Department of Agriculture Economic Research Service, Agriculture Handbook No. 717.
- Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. DiFonzo. 2004. Predators suppress *Aphis glycines* Matsumura population growth in soybean. *Environmental Entomology* 33: 608–618.
- Gardiner, M. M., D. A. Landis, C. Gratton, C. D. DiFonzo, M. E. O'Neal, J. Chacon, M. T. Wayo, N. P. Schmidt, E. E. Mueller, and G. E. Heimpel. 2009a. Landscape diversity impacts biocontrol services in north-central U.S. soybean. *Ecological Applications* 9: 143–154.
- Gardiner, M. M., D. A. Landis, C. Gratton, N. P. Schmidt, M. E. O'Neal, E. Mueller, J. Chacon, G. E. Heimpel, and C. D. DiFonzo. 2009b. Landscape composition mediates coccinellid community structure. *Diversity and Distributions* 15: 554–564.
- Gildow, F. E., D. A. Shah, W. M. Sackett, T. Butzler, B. A. Nault, and S. J. Fleischer. 2008. Transmission efficiency of *Cucumber mosaic virus* by aphids associated with virus epidemics in snap bean. *Phytopathology* 98: 1233–1241.
- Heimpel, G. E., D. W. Ragsdale, R. Venette, K. R. Hopper, R. J. O'Neil, C. E. Rutledge, and Z. S. Wu. 2004. Prospects for importation biological control of the soybean aphid: anticipating potential costs and benefits. *Annals of the Entomological Society of America* 97: 249–258.
- Hill, J. H., R. Alleman, D. B. Hogg, and C. R. Grau. 2001. First report of transmission of *Soybean mosaic virus* and *Alfalfa mosaic virus* by *Aphis glycines* in the New World. *Plant Disease* 85: 561.
- Hill, C. B., Y. Li, and G. L. Hartman. 2004a. Resistance to the soybean aphid in soybean germplasm. *Crop Science* 44: 98–106.
- Hill, C. B., Y. Li, and G. L. Hartman. 2004b. Resistance of *Glycine* species and various cultivated legumes to the soybean aphid (Homoptera: Aphididae). *Journal of Economic Entomology* 97: 1071–1077.
- Hill, C. B., Y. Li, and G. L. Hartman. 2006a. Soybean aphid resistance in soybean Jackson is controlled by a single dominant gene. *Crop Science* 46: 1606–1608.
- Hill, C. B., Y. Li, and G. L. Hartman. 2006b. A single dominant gene for resistance to the soybean aphid in the soybean cultivar Dowling. *Crop Science* 46: 1601–1605.
- Hill, C. B., L. Crull, T. Herman, D. J. Voegtlin, and G. L. Hartman. 2010. A new soybean aphid (Hemiptera: Aphididae) biotype identified. *Journal of Economic Entomology* 103: 509–515.
- Hodgson, E. W., R. C. Venette, M. Abrahamson, and D. W. Ragsdale. 2005. Alate production of soybean aphid (Homoptera: Aphididae) in Minnesota. *Environmental Entomology* 34: 1456–1463.
- Hodgson, E. W., N. P. Schmidt, and M. E. O'Neal. 2009. Landscape summary of aphid suction trapping network since 2005, pp. 111–115. *In Proceedings:* Iowa State University Integrated Crop Management Conference, Ames, IA, 2–3 December 2009.
- Howard, M. T., and A.F.G. Dixon. 1992. The effect of plant phenology on the induction of alatae and the development of populations of *Metopolophium dirhodum* (Walker), the rose-grain aphid, on winter wheat. *Annals of Applied Biology* 120: 203–213.
- Hunt, D., R. Footitt, D. Gagnier, and T. Baute. 2003. First Canadian records of *Aphis glycines* (Hemiptera: Aphididae). *Canadian Entomologist* 135: 879–881.
- Johnson, B., and P. R. Birks. 1960. Studies on wing production in aphids I: the developmental process involved in the production of the different forms. *Entomologia Experimentalis et Applicata* 3: 327–339.
- Johnson, K. D., M. E. O'Neal, D. W. Ragsdale, C. D. DiFonzo, S. M. Swinton, P. M. Dixon, B. D. Potter, E. W. Hodgson, and A. C. Costamagna. 2009. Probability of cost-effective management of soybean aphid (Hemiptera: Aphididae) in North America. *Journal of Economic Entomology* 102: 2101–2108.
- Kaiser, M. E., T. Noma, M. J. Brewer, K. S. Pike, J. R. Vockerth, and S. D. Gaimari. 2007. Hymenopteran parasitoids and dipteran predators found using soybean aphid after its Midwestern United States invasion. *Annals of the Entomological Society of America* 100: 196–205.
- Kim, S. K., C. B. Hill, G. L. Hartman, M. A. Rouf-Mian, and B. W. Diers. 2008. Discovery of soybean aphid biotypes. *Crop Science* 48: 923–928.
- Koch, K. A., B. D. Potter, and D. W. Ragsdale. 2010. Non-target impacts of soybean rust fungicides on the fungal entomopathogens of soybean aphid. *Journal of Invertebrate Pathology* 103: 156–164.
- Kogan, M., and S. G. Turnipseed. 1987. Ecology and management of soybean arthropods. *Annual Review of Entomology* 32: 507–538.
- Landis, D. A., M. M. Gardiner, W. van der Werf, and S. M. Swinton. 2008. Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proceedings of the National Academy of Sciences of the USA, Biology* 105: 20552–20557.
- Li, Y., C. B. Hill, S. R. Carlson, B. W. Diers, and G. L. Hartman. 2007. Soybean aphid resistance genes in the soybean cultivars Dowling and Jackson map to linkage group M. *Molecular Breeding* 19: 25–34.
- Li, C. S., R. W. Luo, C. L. Yang, Y. F. Shang, J. H. Zhao, and X. Q. Xin. 2000. Biology and control of *Aphis glycines*. *Soybean Science* 19: 337–340.
- Lin, C., L. Li, Y. Wang, Z. Xun, G. Zhang, and S. Li. 1993. Effects of aphid density on the major economic characters of soybean. *Soybean Science* 12: 252–254.
- Liu, J., K. M. Wu, K. R. Hopper, and K. J. Zhao. 2004. Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and its natural enemies in soybean in northern China. *Annals of the Entomological Society of America* 97: 235–239.
- Macedo, T. B., C. S. Bastos, L. G. Higley, K. R. Ostlie, and S. Madhavan. 2003. Photosynthetic response to soybean aphid (Homoptera: Aphididae) injury. *Journal of Economic Entomology* 96: 188–193.
- Matsumura, S. 1917. A list of the Aphididae of Japan, with description of new species and genera. *Journal of the College of Agriculture, Sapporo, Japan* 7: 387–388.
- McCormack, B. P., D. W. Ragsdale, and R. C. Venette. 2004. Demography of soybean aphid (Homoptera: Aphididae) at summer temperatures. *Journal of Economic Entomology* 97: 854–861.
- McCormack, B. P., M. A. Carrillo, R. C. Venette, and D. W. Ragsdale. 2005. Physiological constraints on the overwintering potential of the soybean aphid (Homoptera: Aphididae). *Environmental Entomology* 34: 235–240.
- McCormack, B. P., A. C. Costamagna, and D. W. Ragsdale. 2008. Within-plant distribution of soybean aphid (Hemiptera: Aphididae) and development of node-based sample units for estimating whole-plant densities in soybean. *Journal of Economic Entomology* 101: 1488–500.
- Mensah, C., C. D. DiFonzo, R. L. Nelson, and D. C. Wang. 2005. Resistance to soybean aphid in early maturing soybean germplasm. *Crop Science* 45: 2228–2233.
- Mian, M.A.R., R. B. Hammond, and S. K. St. Martin. 2008a. New plant introductions with resistance to the soybean aphid. *Crop Science* 48: 1055–1061.
- Mian, M.A.R., S. T. Kang, S. E. Beil, and R. B. Hammond. 2008b. Genetic linkage mapping of the soybean aphid resistance gene in PI243540. *Theoretical and Applied Genetics* 117: 955–962.
- Michel, A. P., W. Zhang, J. K. Jung, S. T. Kang, and M.A.R. Mian. 2009. Population genetic structure of *Aphis glycines*. *Environmental Entomology* 38: 1301–1311.
- Michel, A. P., M.A.R. Mian, N. H. Davila-Olivas, and L. A. Canas. 2010. Detached leaf and whole plant assays for soybean aphid resistance: differential responses among resistance sources and biotypes. *Journal of Economic Entomology* 103: 949–957.

- Mignault, M. P., M. Roy, and J. Brodeur. 2006. Soybean aphid predators in Quebec and the suitability of *Aphis glycines* as prey for three Coccinellidae. *Biological Control* 51: 89–106.
- Myers, S. W., C. Gratton, R. P. Wolkowski, D. B. Hogg, and J. L. Wedberg. 2005. Effect of soil potassium availability on soybean aphid (Hemiptera: Aphididae) population dynamics and soybean yield. *Journal of Economic Entomology* 98: 113–120.
- Nielsen, C., and A. E. Hajek. 2005. Control of invasive soybean aphid, *Aphis glycines* (Hemiptera: Aphididae), populations by existing natural enemies in New York State, with emphasis on entomopathogenic fungi. *Journal of Economic Entomology* 34: 1036–1047.
- Noma, T., and M. J. Brewer. 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 US Midwest. *Journal of Economic Entomology* 101: 278–287.
- Noma, T., C. Gratton, M. Colunga-Garcia, M. J. Brewer, E. E. Mueller, K.A.G. Wyckhuys, G. E. Heimpel, and M. E. O'Neil. 2010. Relationship of soybean aphid (Hemiptera: Aphididae) to soybean plant nutrients, landscape structure, and natural enemies. *Environmental Entomology* 39: 31–41.
- Ohnesorg, W. J., K. D. Johnson, and M. E. O'Neil. 2009. Impact of reduced-risk insecticides on soybean aphid and associated natural enemies. *Journal of Economic Entomology* 102: 1816–1826.
- Ragsdale, D. W., D. J. Voegtlin, and R. J. O'Neil. 2004. Soybean aphid biology in North America. *Annals of the Entomological Society of America* 97: 204–208.
- Ragsdale, D. W., B. P. McCornack, R. C. Venette, B. D. Potter, I. V. MacRae, E. W. Hodgson, M. E. O'Neil, K. D. Johnson, R. J. O'Neil, C. D. DiFonzo, et al. 2007. Economic threshold for soybean aphid (Hemiptera: Aphididae). *Journal of Economic Entomology* 100: 1258–1267.
- Rhainds, M., H.J.S. Yoo, L. Bledsoe, C. S. Sadof, S. Yaninek, and R. J. O'Neil. 2010. Impact of development maturity of soybean on the seasonal abundance of soybean aphid (Hemiptera: Aphididae). *Environmental Entomology* 39: 484–491.
- Roitberg, B. D., J. H. Myers, and B. D. Frazer. 1979. The influence of predators on the movement of apterous pea aphids between plants. *Journal of Animal Ecology* 48: 111–122.
- Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004. Soybean aphid predators and their use in integrated pest management. *Annals of the Entomological Society of America* 97: 240–248.
- Rutledge, C. E., and R. J. O'Neil. 2005. *Orius insidiosus* (Say) as a predator of the soybean aphid, *Aphis glycines* Matsumura. *Biological Control* 33: 56–64.
- Rutledge, C. E., and R. J. O'Neil. 2006. Soybean plant stage and population growth of soybean aphid. *Journal of Economic Entomology* 99: 60–66.
- Schmidt, N. P., M. E. O'Neil, and P. M. Dixon. 2008. Aphidophagous predators in Iowa soybean: a community comparison across multiple sampling methods. *Annals of the Entomological Society of America* 101: 341–350.
- Song, F., S. M. Swinton, C. DiFonzo, M. O'Neil, and D. W. Ragsdale. 2006. Profitability analysis of soybean aphid control treatments in three north-central states. Michigan State University Department of Agricultural Economics. Staff Paper 2006–24.
- Van den Berg, H., D. Ankasah, A. Muhammad, R. Rusli, H. A. Widayanto, H. B. Wirasto, and I. Yully. 1997. Evaluating the role of predation in population fluctuations of the soybean aphid, *Aphis glycines* in farmers' fields in Indonesia. *Journal of Applied Ecology* 34: 971–984.
- Venette, R. C., and D. W. Ragsdale. 2004. Assessing the invasion by soybean aphid (Homoptera: Aphididae): where will it end? *Annals of the Entomological Society of America* 97: 219–226.
- Voegtlin, D. J., S. E. Halbert, and G. Qiao. 2004a. A guide to separating *Aphis glycines* Matsumura and morphologically similar species that share its hosts. *Annals of the Entomological Society of America* 97: 227–232.
- Voegtlin, D. J., R. J. O'Neil, and W. R. Graves. 2004b. Tests of suitability of overwintering hosts of *Aphis glycines*: identification of a new host association with *Rhamnus alnifolia* L'Héritier. *Annals of the Entomological Society of America* 97: 233–234.
- Voegtlin, D. J., R. J. O'Neil, W. R. Graves, D. Lagos, and H.J.S. Yoo. 2005. Potential winter hosts of soybean aphid. *Annals of the Entomological Society of America* 98: 690–693.
- Walter, A. J., and C. D. DiFonzo. 2007. Soil potassium deficiency affects soybean phloem nitrogen and soybean aphid populations. *Environmental Entomology* 36: 26–33.
- Wang, X. B., Y. H. Fang, S. Z. Lin, L. R. Zhang, and H. D. Wang. 1994. A study on the damage and economic threshold of the soybean aphid at the seedling stage. *Plant Protection (China)* 20: 12–13.
- Wang, R. Y., A. Kritzman, D. E. Hershman, and S. A. Ghabrial. 2006. *Aphis glycines* as a vector of persistently and nonpersistently transmitted viruses and potential rises for soybean and other crops. *Plant Disease* 90: 920–926.
- Welsman, J. A., C. A. Bahlai, M. K. Sears, and A. W. Schaafsma. 2007. Decline of soybean aphid (Homoptera: Aphididae) egg populations from autumn to spring on the primary host, *Rhamnus cathartica*. *Environmental Entomology* 36: 541–548.
- Wu, Z., D. Schenk-Hamlin, W. Zhan, D. W. Ragsdale, and G. E. Heimpel. 2004. The soybean aphid in China: a historical review. *Annals of the Entomological Society of America* 97: 209–218.
- Wyckhuys, K.A.G., and G. E. Heimpel. 2007a. Response of the soybean aphid parasitoid *Binodoxys communis* to olfactory cues from target and non-target host-plant complexes. *Entomologia Experimentalis et Applicata* 123: 149–158.
- Wyckhuys, K.A.G., R. L. Koch, and G. E. Heimpel. 2007b. Physical and ant-mediated refuges from parasitism: Implications for non-target effects in biological control. *Biological Control* 40: 306–313.
- Wyckhuys, K.A.G., L. Stone, N. Desneux, K. A. Hoelmer, K. R. Hopper, and G. E. Heimpel. 2008. Parasitism of the soybean aphid *Aphis glycines* by *Binodoxys communis*: the role of aphid defensive behavior and parasitoid reproductive performance. *Bulletin of Entomological Research* 98: 361–370.
- Wyckhuys, K.A.G., R. L. Koch, R. R. Kula, and G. E. Heimpel. 2009. Potential exposure of a classical biological control agent of the soybean aphid, *Aphis glycines*, on non-target aphids in North America. *Biological Invasions* 11: 857–871.
- Zhang, G., C. Gu, and D. Wang. 2009. Molecular mapping of soybean aphid resistance in PI 567541B. *Theoretical and Applied Genetics* 118: 473–482.

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