

## Soybean Aphid Biology in North America

DAVID W. RAGSDALE,<sup>1</sup> DAVID J. VOEGTLIN,<sup>2</sup> AND ROBERT J. O'NEIL<sup>3</sup>

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**ABSTRACT** Soybean aphid, *Aphis glycines* Matsumura, a native of eastern Asia, was first discovered in North America in July 2000 in Wisconsin and subsequently in a total of 10 North Central U.S. states by September 2000. Currently, soybean aphid has spread to 20 U.S. states and three Canadian provinces, putting >60 million acres of soybean at risk to crop injury caused by this exotic insect. The life history of this species has been studied by a number of entomologists and crop protection specialists, and here we provide a summary of the observations made by ourselves and our colleagues. The soybean aphid has been observed at all stages of a heteroecious holocyclic life cycle and seems to be adapting to a large geographic area of the North Central United States. Soybean aphid uses native and exotic primary hosts found in North America, specifically *Rhamnus cathartica* L. and *Rhamnus alnifolia* L'Hér. The aphid's principal secondary host is soybean, *Glycine max* (L.) Merr., but there seems to be a lengthy gap in early spring between the production of alatae on buckthorn (*Rhamnus* spp.) and the occurrence of soybean. In the fall when soybean is senescing, a biological bottleneck is created as the aphid must develop sexual morphs on soybean that emigrate back to the primary host to complete the sexual phase of its life cycle. During the summer, *A. glycines* is prone to develop winged morphs during any generation on soybean, which puts much of the soybean crop at risk of invasion by this exotic species, even if the insect does not overwinter locally. The integrated pest management challenges presented by the aphid require a deeper understanding of its biology as it adapts to North America.

**KEY WORDS** soybean aphid, biology, primary host, *Rhamnus* spp.

THE SOYBEAN APHID, *Aphis glycines* Matsumura, is native to Asia where its principal summer host is cultivated soybean, *Glycine max* (L.) Merr. (Blackman and Eastop 2000). Soybean aphid is widely distributed in the soybean-growing regions of the Far East, spanning a wide climatic range. For example, *A. glycines* is a common pest of soybean in northern China (Wang et al. 1962), and it has been reported as an occasional pest in Korea (Chung et al. 1980), Japan (Takahashi et al. 1993), the Philippines (Quimio and Calilung 1993), Thailand (Paik 1963), Malaysia (Blackman and Eastop 2000), Indonesia (Iwaki 1979), and most recently in Australia (Fletcher and Desborough 2000). In addition to cultivated soybean, *A. glycines* has been collected from wild relatives of *G. max*, e.g., *Glycine soja* Sieb. & Zucc. (Wang et al. 1962).

In the United States, soybean aphid was first detected in soybean in July 2000 in Wisconsin (Alleman et al. 2002), and by the end of the summer, soybean aphids were found in 10 North Central U.S. states (Venette 2004). The consensus among soybean researchers is that *A. glycines* was present but remained

undetected for some years before 2000. Although there are reports that colonies of aphids were seen on soybean in southeastern Wisconsin before 2000, there are no insect samples available to confirm these observations. By the end of the 2003 growing season, 21 U.S. states and three Canadian provinces were infested with soybean aphid, showing this aphid is rapidly expanding its range (Venette 2004).

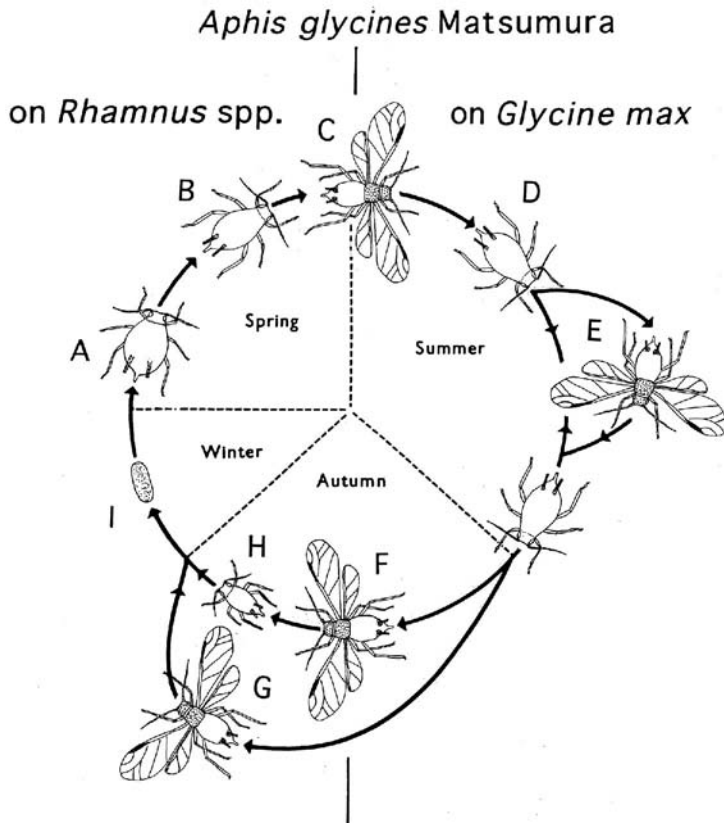
**Life History of Soybean Aphid in North America.** *A. glycines* is a typical heteroecious holocyclic species (host-alternating with sexual reproduction during part of its life cycle). The observed life history of soybean aphid in North America is similar to that observed in China and Japan, with the exception of the primary hosts, those plant species used as overwintering hosts (Fig. 1). In China and Japan, the most common overwintering hosts are *Rhamnus davurica* Pallus and *Rhamnus japonica* Maxim. (Takahashi et al. 1993). In North America, various buckthorn (*Rhamnus*) species are used as primary hosts (Voegtlin et al. 2004).

The life cycle begins each spring when nymphs hatch and develop into wingless fundatrices. Fundatrices produce a second generation that consists primarily of wingless females. The third and subsequent generations on *Rhamnus* consist primarily of winged morphs that emigrate in search of summer or secondary hosts, which for *A. glycines* is typically cultivated soybean. During the summer, many overlapping gen-

<sup>1</sup> Department of Entomology, University of Minnesota, St. Paul, MN 55108–6125.

<sup>2</sup> Center for Economic Entomology, Illinois Natural History Survey, Champaign, IL 61820–6970.

<sup>3</sup> Department of Entomology, Purdue University, West Lafayette, IN 47907–2089.



**Fig. 1.** Life cycle of the soybean aphid. (A) Fundatrix on *Rhamnus*. (B) Apterous viviparous female on *Rhamnus*. (C) Alate viviparous female, spring migrant from *Rhamnus* to soybean. (D) Apterous viviparous female on soybean. (E) Alate viviparous female, summer migrant from soybean to *Rhamnus*. (F) Gynopara, fall migrant from soybean to *Rhamnus*. (G) Male migrates from soybean to *Rhamnus*. (H) Ovipara, on *Rhamnus*. (I) Overwintering egg on *Rhamnus*.

erations can occur on soybean, and both wingless and winged morphs are produced throughout the growing season. In autumn, under the influence of reduced photoperiod and temperature, winged females called gynoparae are produced on soybean that emigrate in search of *Rhamnus*. Once on *Rhamnus*, they feed and produce nymphs that develop into oviparae. The gynoparae are followed by males, also produced on soybean, that emigrate in search of oviparae that are developing on *Rhamnus*. The males and oviparae mate, and overwintering eggs are deposited on *Rhamnus*.

**Observed Biology in North America on Primary Hosts.** There are two confirmed overwintering hosts in North America, *Rhamnus cathartica* L., common buckthorn, an invasive woody plant of European origin; and the native alderleaf buckthorn, *Rhamnus alnifolia* L'Hér (Voegtlin et al. 2004). In addition, gynoparae and oviparous nymphs have been observed on another exotic Rhamnaceae, glossy buckthorn, *Frangula alnus* P. Mill. (syn. *R. frangula*), although studies by Voegtlin et al. (2004) failed to confirm this species' primary host status. *R. cathartica* can be very abundant in the North Central United States, especially north of the 41st parallel, reaching densities as high as several thousand plants per acre in southern Minnesota. In comparison,

alderleaf buckthorn is relatively rare and associated with moister habitats than *R. cathartica*.

Even though *R. cathartica* can be abundant locally, colonies of *A. glycines* have been extremely difficult to find in the spring in spite of extensive surveys in the spring of 2001 and 2002 in Illinois, Indiana, Michigan, Minnesota, and Wisconsin. In fall 2002, *A. glycines* colonies were monitored on *R. cathartica* at multiple locations in Illinois, Indiana, Michigan, and Minnesota. Gynoparae were found on *R. cathartica* beginning in mid-September at all locations. Colonies of gynoparae and oviparae persisted some weeks. Males and eggs were observed in all locations, except for Minnesota where no eggs were observed through leaf drop in late November 2002. In all other locations, eggs were deposited beginning late October through mid-November when leaf drop occurred.

Eggs were deposited at various locations on the trees but most commonly at the interface between the bud and twig. Trees on which eggs were deposited were marked, and observations in spring 2003 showed hatching occurred the last week of March with colonies persisting on *R. cathartica* through the first part of May. Winged spring migrants on *R. cathartica* were first observed in late April in Illinois in 2003. No soy-

bean would be available at that time to support the emigrants.

To determine whether soybean aphids were overwintering locally and to determine whether spring migrants were flying before the soybean crop emerged, in early spring 2002 (April–mid-May) Minnesota researchers placed eight potted soybean plants near 42 separate woodlots scattered throughout the state that contained *R. cathartica*. These potted soybean plants were observed weekly until the soybean crop had emerged in the area. Soybean aphids were found on potted soybean in only four of 42 locations. This study illustrates the difficulty in demonstrating the link between *R. cathartica* and soybean. Spring surveys of *R. cathartica* have also not yielded *A. glycines* colonies. The difficulty in finding spring colonies of *A. glycines* on *R. cathartica* has generated some discussion regarding the possibility of there being another primary host (Voegtlin et al. 2004). *Rhamnus davurica* Pallas, one of the primary hosts of the soybean aphid in China, has been introduced into North America, but it seems to be a rare plant in much of the North Central United States. Whereas *R. davurica* would likely be a primary host for soybean aphid in North America, it is so uncommon that it is unlikely to be a significant source of spring migrants. The same is likely true for *R. alnifolia*. Although other primary host species cannot be eliminated, the abundance of *R. cathartica* in some areas of the North Central United States suggests that even if a fraction of a percentage of the *R. cathartica* plants have *A. glycines* colonies, they could generate sufficient number of spring migrants resulting in the observed spring infestation of soybean.

**Observations of Soybean Aphid in North America on Secondary Hosts.** The secondary host of *A. glycines* in North America is chiefly cultivated soybean, *G. max*. In the laboratory, soybean aphid can develop on red clover, *Trifolium pratense* L. (Alleman et al. 2002). Winged adult *A. glycines* have been collected from violet prairie clover, *Dalea purpurea* Vent. in southern Minnesota (K. Larsen, personal communication), but there was no indication of colony development. Neither of these legumes seems to be alternate hosts that play a significant role in early spring colonization of soybean.

Paik (1963) lists kudzu, *Pueraria thunbergiana* (Sieb. & Zucc.) Benth., and scarlet runner bean, *Phaseolus coccineus* L. (= *multiflorus*), as hosts in Korea. Attempts in Illinois to grow the aphid on kudzu commonly found in North America, *Pueraria lobata* (Willd.) Ohwi, have not succeeded. *P. lobata* is also common in Japan but is not known to be a host of *A. glycines* in Japan. Blackman and Eastop (2000) list tropical kudzu, *Pueraria phaseoloides* (Roxb.) Benth. and *Desmodium intortum* (P. Mill.) Urban, as secondary hosts. Although *A. glycines* seems to use other legumes as secondary hosts, observations suggest that these other hosts play only a minor role in the aphid's population biology in North America.

A common observation is that, when *A. glycines* initially colonizes a soybean field, its distribution is

highly patchy, with single scattered plants with small colonies consisting of early instars and no adults. A similar pattern has been seen in other aphid species, such as *Rhopalosiphum padi* (L.) and *Rhopalosiphum maidis* (Fitch) (D. Voegtlin, unpublished data). These small colonies are presumably produced by winged migrants that fed for a short time, deposited a few nymphs, and then moved on in search of another host plant. Colonization of an individual soybean field in early spring progresses rapidly resulting in no strong "edge effects" that would provide an opportunity to treat field borders to prevent colonization across the field. In contrast, colonization that occurs in midsummer can show distinct edge effects with areas closer to windbreaks more commonly colonized than other areas of a field. In many parts of the North Central United States, e.g., northern Minnesota, North Dakota, and Ontario, Canada, *A. glycines* has typically not been found before early July, suggesting that these fields are being colonized by winged individuals that have emigrated from other soybean fields rather than by individuals that have come directly from overwintering hosts.

When soybean is in vegetative growth, soybean aphid colonies are commonly found at the growing points, e.g., partially expanded young trifoliates, petioles, and stems. When plants begin to flower, set pods, and lateral branches begin to develop, soybean aphids tend to become more widely dispersed on the plant and can be found on the underside of mature leaves, on lower stems, lateral branches, petioles, and pods. Dense colonies are at times tended by ants, but in North America this behavior is the exception, whereas in China and Japan the authors observed that ant tended colonies were common.

In spring 2003, soybean aphids were found colonizing soybean on 3 and 11 June 2003 in Minnesota and Indiana, respectively, some 3 to 4 wk earlier than what had been observed in 2001 and 2002. In general, June temperatures in the North Central United States favors soybean aphid development, because maximum daily temperatures are often in the 22–25°C optimum range (Wang et al. 1962, 1996). Production of winged adults seems to be a part of every generation, but crowding can stimulate apterous adults to produce a higher proportion of alate offspring (Lu and Chen 1993). In China, Wang et al. (1962) recorded a total of 18 generations per year with 15 of those generations occurring on soybean. In their study, soybean aphid populations peaked at late vegetative to early reproductive stages with a second smaller peak as plants neared physiological maturity. To date, no one in North America has observed a late season population rebound Wang et al. (1962) observed in China. However, late-planted soybean or double-cropped soybean produces peak aphid populations relatively late in the season, aided presumably by a concomitant delay in crop maturity.

As the season progresses and plants switch from vegetative to reproductive growth, host quality for the aphids seems to change. Those soybean aphids found on lower mature leaves often look pale to almost white

and are smaller than the robust yellow aphids seen on the growing points in prereproductive plants. These small, pale aphids, when collected from the field and placed on young seedlings in the greenhouse, return to a normal yellow color after a few days of feeding (D.W.R., unpublished data). It seems that mature soybean leaves represent a lower quality host that results in a change in aphid color and a possible reduction in overall fecundity. Defining the nature of the relationships among temperature, plant maturity/quality, aphid reproduction, and population growth await further research.

Because its detection in 2000, the soybean aphid has displayed several patterns of population dynamics in North America. In 2001, aphid populations reached outbreak levels (e.g., thousands of aphids per plant) in many fields, particularly in Minnesota, Wisconsin, Michigan, Illinois, and Indiana, as well as parts of Ontario, Canada. In 2002, few fields anywhere in North America reached high densities, and many fields being sampled weekly had no aphids detected. In 2003, aphid densities again increased significantly, and outbreaks were observed for the first time in parts of Iowa, Ohio, and South Dakota. The mechanisms underlying these outbreaks are not well understood but are thought to include temperature and moisture regimes (cooler and wetter favoring aphid population growth), timing of invasion (earlier invasions into soybean reach higher densities), and impacts on population growth by natural enemies (particularly predators and entomopathogenic fungi). Further research is needed to better understand these mechanisms governing soybean aphid population dynamics.

**Phenological Disjunction.** The phenology of movement to and from summer and winter hosts seems to be a biological "bottleneck" that has the potential to limit the success of the soybean aphid to overwinter locally. The first observed colonies of *A. glycines* on *R. cathartica* in Illinois and Minnesota were in mid-May 2001 and 2002, respectively, and 2003 from April to early May in central Illinois and Indiana and to late May in Minnesota. These colonies were generating spring migrants several weeks before the occurrence of soybean. Searches in Illinois and Minnesota in early May 2002 and 2003 failed to find soybean aphids on any other host plants, including *T. pratense* on which it will live in the laboratory. In Illinois, as soybean begins to emerge soybean aphids began colonizing these fields, yet no local source was known to exist on *R. cathartica* by late May.

Fall migration can also be challenged by crop phenology. In some years, much of the soybean is harvested by the mid-September. These fields would have begun senescing and dropping leaves sometime before harvest, so only aphids colonizing stems and pods would survive until those parts of the plant are too desiccated to support further development. If soybean senescence precedes the development of gynoparae and males, there is little possibility of overwintering by the aphid in that area. Late-planted or double-cropped soybean may be the primary source of gynoparae and

males, at least in the southern part of the present distribution.

Together, data indicate that the soybean aphid seems to have adapted to the North Central United States. It has expanded its host range to use local *Rhamnus* species as overwintering hosts. The aphid has also overcome challenges to synchronize its life cycle with the senescence of soybean in the fall and the relative late emergence of the crop in the spring. Whether this species will expand its range into the southern soybean production area remains unknown. Sexual morphs collected by B. Putler (central Missouri) from *R. cathartica* in November 2001 were *A. glycines*. However, in recent studies *A. glycines* has failed to use Rhamnaceae of southern distribution as winter hosts (Voegtlin et al. 2004), which may slow or prevent colonization in this part of the United States. In the literature, soybean aphid is a pest of soybean in subtropical areas of Asia, which suggests it may be able to adapt to the warm humid conditions of the south central United States. Regardless of its final distribution in North America, the soybean aphid's establishment and current distribution already threatens a major portion of the soybean production area of North America and presents a challenge to soybean integrated pest management.

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