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Survivorship of soybean aphid biotypes (Hemiptera: Aphididae) on winter hosts, common and glossy buckthorn

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Survivorship of soybean aphid biotypes (Hemiptera: Aphididae) on winter hosts, common and glossy buckthorn

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Abstract. The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is a major pest of soybean, *Glycine max* (L.) Merr., both in Asia where it is native, and in the USA where it is adventive. The rapid spread and establishment of the soybean aphid in the USA since its discovery in 2000 was successful because of extensive soybean production in the Midwest and the wide distribution of common buckthorn, *Rhamnus cathartica* (L.), its preferred primary winter host. The survivorship of four soybean aphid biotypes on common and glossy buckthorn, *Frangula alnus* Mill., were compared. Our study showed that nymph oviparae of soybean aphid biotypes 1, 2, 3 and 4 reached adulthood and produced eggs on glossy buckthorn. When comparing morphs between the hosts, greater numbers were recorded on common than glossy buckthorn, with one exception where the number of eggs per bud for soybean aphid biotype 2 was not different between the hosts. We found for the first-time soybean aphid biotypes 2 and 3 apterous males produced on common and glossy buckthorn. Morphological descriptions of live and mounted alate and apterous males are presented.

Key words. Morphs, *Aphis glycines*, *Rhamnus cathartica*, *Frangula alnus*.

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Introduction

The soybean aphid, *Aphis glycines* (Matsumura), is an important pest of soybean [*Glycine max* (L.) Merr.] (Liu and Zhao 2007). Since its invasion into the USA in 2000 (Hartman et al. 2001), it has become a major pest of the North American soybean crop. By 2005, the soybean aphid had expanded throughout the Midwestern USA and Canada (Schmidt et al. 2012; Bahlai et al. 2014), causing up to 40% yield loss on those fields not engaged in effective pest management practices (Ragsdale et al. 2007; Kim et al. 2008a). The rapid spread and establishment of the soybean aphid in the USA was successful because of extensive production of soybean in the Midwest (Hatfield 2012) and the wide distribution of *Rhamnus cathartica* (L.), common buckthorn, which is the preferred primary winter host of soybean aphid (Voegtlin et al. 2005; Heimpel et al. 2010; USDA-NRSC 2021). *Rhamnus cathartica* is an invasive perennial shrub or small tree that has been in North America since early 1800s (Missouri Botanical Garden 2021).

An essential component of the life cycle of the soybean aphid is its overwintering survival. The life cycle of the soybean aphid is characterized as heteroecious and holocyclic (Wang et al. 1962), which means that this aphid is able to reproduce sexually to produce overwintering eggs, and that the winter sexual cycle and the summer parthenogenetic colonies occur on different host plants. In the summer, the soybean aphid reproduces by parthenogenesis on soybean (secondary host). In the fall season in the USA, when soybean senesces, and environmental conditions change to lower temperatures and fewer hours of daylight, the soybean aphid produces alate gynoparae, which are the females that migrate to the overwintering (primary) host. These winged females produce oviparae (egg-laying forms) on senescent leaves of the overwintering host. Winged males also develop on soybean. They migrate to winter host plants, mate with the oviparae, and the latter produce the overwintering, cold-hardy, eggs. Both gynoparae and males of soybean aphids migrate to their primary host plants, which

include various species of buckthorn. In the spring, aphids known as fundatrices hatch from eggs. After a few parthenogenetic generations on the primary host, a generation of alate individuals will migrate back to soybean (Ragsdale et al. 2004; Voegtlin et al. 2005). Although Sun et al. (2015) found in China that soybean aphid was able to reproduce by parthenogenesis on a transitional host plant, *Metaplexis japonica* (Thunb.) Makino, between buckthorn and soybean in the spring. This plant has been reported in the USA, in a cornfield near Ames, Iowa in 1958 (Missouri Botanical Garden 2021). Research conducted between 2002 and 2004 in the USA showed that the soybean aphid successfully overwintered on common buckthorn, and North American native relatives, *R. alnifolia* L'Héritier and *R. lanceolata* Pursh. A few gynoparae, males, and nymphs of oviparae were observed on glossy buckthorn, but never reached adulthood (Voegtlin et al. 2005). In the spring of 2007, fundatrices of the soybean aphid were found for the first time on glossy buckthorn, *Frangula alnus* Mill., in a natural setting located in Springfield Fen, Indiana. These aphids were identified as soybean aphid biotype 3 (Hill et al. 2010). This and other soybean aphid biotypes were determined based on their virulence to *Rag* (*Resistance to Aphis glycines*) genes. For example, Kim et al. (2008b) identified soybean aphid biotype 1 from avirulent populations to *Rag* genes collected on soybean in Urbana, Illinois. Biotype 2 is virulent only to *Rag1* gene and was collected on soybean in Ohio. Biotype 3 is virulent only to *Rag2* gene (Hill et al. 2010), and biotype 4 is virulent to *Rag1* and *Rag2* genes singularly or combined and was identified from populations collected on soybean in Wisconsin (Alt and Ryan-Mahmutagic 2013). To date, there is no information about the survivorship of soybean aphid biotypes 1, 2 and 4 on glossy buckthorn. Thus, the objective was to determine if the number of aphid morphs produced by each biotype were different on common buckthorn and glossy buckthorn.

Materials and Methods

A guide described by Voegtlin et al. (2004) was used to identify the different morphs (gynoparae, oviparae, and males) of the soybean aphid. Archival microscope slides were prepared using the technique described by Pike et al. (1991). Photographs of slide-mounted specimens were taken using a Leica DM 2000 digital camera and SPOT Software 4.6 (Diagnostic Instruments, Inc., Michigan, USA). Aphid morphs were identified and counted by using Leica stereo microscope (Leica Microsystems Inc., Illinois, USA). Colonies of the four known soybean aphid biotypes (maintained at the USDA-ARS Laboratory located in Urbana, Illinois) included biotype 1 from Illinois and biotype 2 from Ohio (Kim et al. 2008b), biotype 3 from Indiana (Hill et al. 2010), and biotype 4 from Wisconsin (Crossley and Hogg 2015). Each biotype was isolated from a single viviparous female and reared on soybean in BugDorm-44545 insect cages (47.5 cm³, MegaView Science Co., Taichung, Taiwan) in isolated plant growth chambers (Percival, TC-2) set at 23°C constant temperature, with a 16 h per day photoperiod. Each biotype clone was maintained on the following soybean genotypes to assure biotype purity: biotype 1 on Williams 82, biotype 2 on LD10-5903a (*Rag1*), biotype 3 on LD08-12435a (*Rag2*) and biotype 4 on LD12-12734a (*Rag1/Rag2*).

For each soybean genotype, three seeds were planted in 12.7 cm pots (Hummert International, Earth City, MO) in a soilless mix (Sunshine Mix, LC1, Sun Gro Horticulture Inc., Bellevue, WA). About 10 g of a slow-release fertilizer (17-5-11, NPK) Pellets (Osmocote® Blends, ICL Fertilizers, Dublin, OH) was spread over the soil surface at planting. Stems of common and glossy buckthorn were rooted in 20 cm pots in the same type of soilless mix using 30 g of slow-release fertilizer and were maintained in a walk-in growth chamber set to 25°C under a 16 h per day photoperiod.

Before infesting common and glossy buckthorn, populations of each of the aphid biotypes were increased on up to 24 plants of the soybean genotypes previously described by rearing them at 25°C under a 16 h per day photoperiod in a plant growth chamber (Percival, TC-2). After 14 days, the fully infested soybean plants were transferred to a growth chamber set at 16°C for 8 h per day with light and 12°C for 16 h per day without light. These conditions were tested in previous experiments (unpublished data) to induce the production of gynoparae and males. After 21 days at these conditions, a single plant of either glossy or common buckthorn was placed in the plant growth chamber without changing chamber conditions (Fig. 1A). After another 21 days of co-incubation of soybean and buckthorn plants, the soybean plants were discarded and morphs on the winter hosts were counted. Fifteen random leaves of similar size (Fig. 1B and 1C) from winter hosts were removed to count the number of gynoparae, males, nymphs and adult oviparae, and nymphs with wing pads on each leaf;

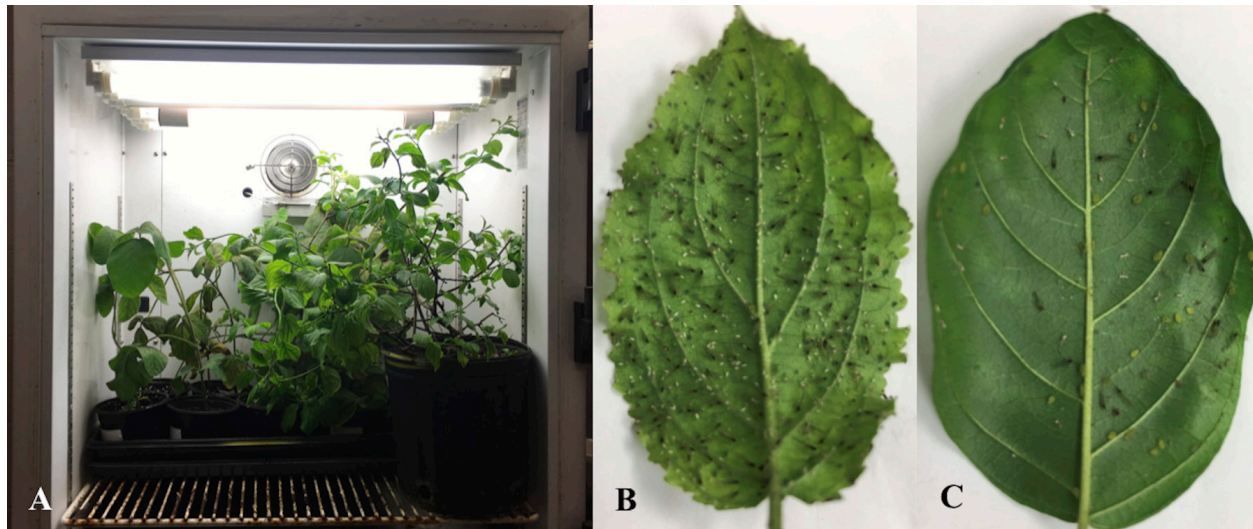


Figure 1. Plant tissue-culture growth chamber Percival. A) Soybean plants maintained in a plant growth chamber for 21 days before placed *Rhamnus cathartica*. B) Leaf of *R. cathartica* infested with soybean aphid biotype 1. C) Leaf of *Frangula alnus* with soybean aphid biotype 4.

these numbers were summed to represent a total count. A second evaluation was performed 21 days later by randomly sampling and removing 15 leaves and 15 buds to count the number of adult oviparae and eggs, respectively. A similar procedure was performed for each biotype on each host by using two identical plant growth chambers (Percival, TC-2) to house the two overwintering hosts, so that one biotype was tested during one time period. When one biotype of the experiment was complete (testing one biotype on both overwintering hosts), another biotype was completed with the same conditions as previously stated for the first biotype. In between testing biotypes, each growth chamber was turned off, cleaned up, and then turned on at a temperature set to 40°C for 2–3 days to kill any remaining aphids. All four biotypes of soybean aphids were tested sequentially in this manner. The entire process with the four biotypes was repeated and referred to as run 1 and run 2. Sampling protocol for each biotype against each host was the same for each run with one exception: for run one, the number of adult oviparae was not counted for biotype 4 on common buckthorn for the second evaluation. To determine if the number of aphid morphs produced by each biotype were different on common buckthorn and glossy buckthorn, a chi-square calculator was used to determine the goodness of fit at a significance of $P < 0.05$ (socscistatistics.com).



Figure 2. Adult morphs and eggs of soybean aphid, *Aphis glycines*, biotype 3 on *Rhamnus cathartica*. A) Gynopara. B) Ovipara. C) Dorsal view of apterous male. D) Ventral view of apterous male. E) Eggs on bud.

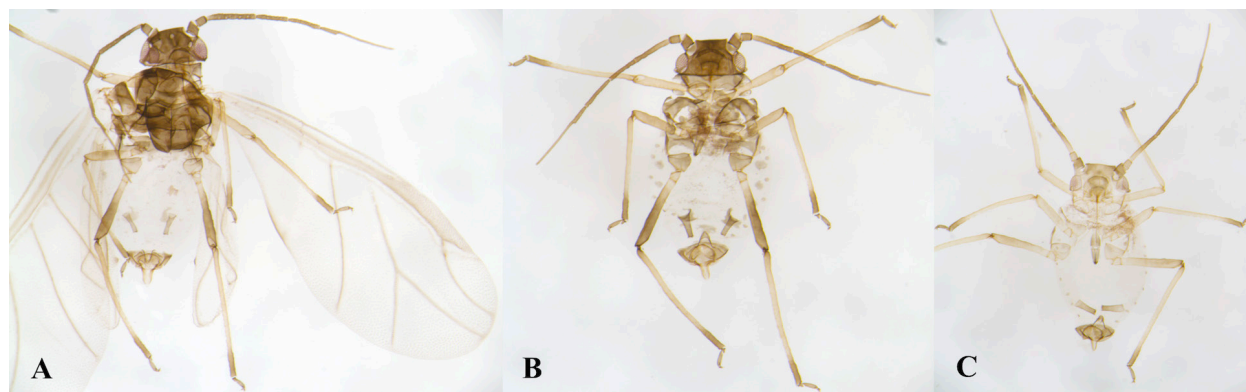


Figure 3. Males of soybean aphid, *Aphis glycines*, biotype 3. **A)** Alate male. **B)** Apterous male with sclerites on thorax. **C)** Apterous male without sclerites on thorax. The slides mounted images were magnified to 64.3x.

Results

Survival of soybean aphid biotypes on buckthorn. On common and glossy buckthorn, all the soybean aphid biotypes and their different morphs (gynoparae, nymph and adult oviparae, apterous males, eggs, and males) were found (Fig. 2–3). Based on chi-square analysis, there were significantly more total aphids on common buckthorn than glossy buckthorn for all biotypes (Table 1). The number of total aphids averaged over all four biotypes was 56.3 and 12.3 for common buckthorn and glossy buckthorn, respectively. In addition, there were significantly ($P < 0.05$) more adult oviparae on common buckthorn than glossy buckthorn for each biotype (Table 1). The numbers of adult oviparae averaged over all four biotypes were 53.5 and 3.5 for common buckthorn and glossy buckthorn, respectively. The numbers of eggs per bud differed ($P < 0.05$) for common buckthorn compared to glossy buckthorn for biotypes 1 and 4 but not for biotype 2 ($P > 0.05$) (Table 1). The number of eggs per bud averaged over biotypes was 18.3 and 5.8 for common buckthorn and glossy buckthorn, respectively.

Table 1. Number of soybean aphid biotypes morphs per leaf and bud on *Rhamnus cathartica* and *Frangula alnus* under controlled conditions. “All aphid morphotypes observed” data were recorded 21 days after infestation and are the mean number of individuals present on 30 leaves of each host after two complete runs of the experiment; this includes gynoparae, males, and adult oviparae. “Adult oviparae” and “Eggs per bud” data were recorded 42 days after infestation on 30 leaves or buds per host after two runs of the experiment, except for biotype 4 adult oviparae on common buckthorn where only data from one run of 15 leaves was recorded.

Trait	Biotype	<i>R. cathartica</i>	<i>F. alnus</i>	Chi Square	Probability
All aphid morphotypes observed	1	114	8	92.098	<0.00001
	2	46	20	10.242	0.00137
	3	23	4	13.37	0.00026
	4	42	17	10.593	0.00114
Adult oviparae	1	78	1	72.2	<0.00001
	2	13	4	4.765	0.02905
	3	39	7	22.261	<0.00001
	4	87	2	81.18	<0.00001
Eggs per bud	1	24	1	21.16	<0.00001
	2	15	11	0.615	0.43277
	3	21	9	4.8	0.02846
	4	13	2	8.967	0.00451

Soybean aphids alate and apterous males on buckthorn. Apterous males of soybean aphid biotypes 2 and 3 but not biotypes 1 and 4 were found on common and glossy buckthorn (Table 2). For biotype 2, out of the 36 males found on both winter hosts, one was apterous and that one was found only on glossy buckthorn. For biotype 3, out of the 63 males found on both hosts, 16 and 4 apterous males were found on common and glossy buckthorn, respectively. For biotype 1, 11 alate males were found only on common buckthorn and for aphid biotype 4, 39 and 18 alate males were found on common and glossy buckthorn, respectively.

Morphological characters for soybean aphids alate (n = 13) and apterous (n = 8) males (Table 3). Color in life: same color pattern as gynopara, which head and thorax are black. Abdomen light green, without wax (Fig. 2 A, C, D). Color and morphological characters on slide (Fig. 3): some apterous males had a sclerotic thorax suggesting that wings were stunted or failed to develop (Fig. 3B). Others do not show sclerites or other evidence of undeveloped wings on the thorax (Fig. 3C). Head: Dark without frontal setae. Antennal tubercles undeveloped. Antennae six-segmented, shorter than body. Antennae with secondary sensoria scattered on segments III, IV, and V. Antennal segments dark as head color. Rostrum reaches mesocoxae. Thorax: Coxae dusky for alate (Fig. 3 A) and apterous male (Fig. 3 C), and dark for a male with undeveloped wing pads (Fig. 3 B). Trochanters pale. Fore and mid femora dusky throughout, fore femora dark or dusky except at base. Tibia pale, darkening near distal tip. Tarsi dusky. Abdomen: Siphunculi cylindrical, dusky or dark. Cauda dusky, triangular. Marginal tubercles present on abdominal segments I and VII. Male genitalia dark with 2 short claspers anteriorly and aedeagus centrally.

Slide mounts of alate and apterous males as well as the other morphs (gynoparae and adult oviparae) were deposited at the Illinois Natural History Survey Insect Collection (biotype 1: 830,946 to 830,956; biotype 2: 830,916 to 930,933; biotype 3: 830,934 to 830,945; and biotype 4: 830,957 to 830,969).

Discussion

In our study, the suitability of common buckthorn as an overwintering host was confirmed as reported (Wang et al. 1962; Ragsdale et al. 2004; Voegtlin et al. 2004, 2005; Heimpel et al. 2010; Tilmon et al. 2011; Oka et al. 2018; Tian et al. 2018), and we showed for the first time, that nymphal oviparae of all the soybean aphid biotypes reached adulthood and laid eggs on glossy buckthorn. In the field, soybean aphid biotype 3 was described

Table 2. Total number of soybean aphid biotypes alate and apterous males on *Rhamnus cathartica* and *Frangula alnus* under controlled conditions based on counts from 30 leaves of each host.

Trait	Biotype	<i>R. cathartica</i>	<i>F. alnus</i>
Alate males	1	11	0
Alate males	2	27	7
Apterous male	2	0	1
Alate males	3	28	12
Apterous males	3	16	7
Alate males	4	39	18

Table 3. Measurements (means in mm \pm STDEV) of length of body, antenna (Ant) including processus terminalis (Pt) and siphunculi (Siph), and number of secondary sensoria on antennal segments III, IV and V of soybean aphid, *Aphis glycines*, biotype 3.

Morphs	Body length	Ant III	Ant IV	Ant V	Base VI	Pt	Sensoria III	Sensoria IV	Sensoria V	Siph
Alatae (n = 13)	1.27 \pm 0.12	0.23 \pm 0.03	0.17 \pm 0.03	0.17 \pm 0.02	0.10 \pm 0.01	0.27 \pm 0.03	17 \pm 2.4	14 \pm 4.0	8 \pm 2.78	0.11 \pm 0.01
Apterae (n = 8)	1.06 \pm 0.07	0.19 \pm 0.02	0.15 \pm 0.03	0.15 \pm 0.02	0.09 \pm 0.01	0.24 \pm 0.02	1 \pm 2.2	4 \pm 3.9	2 \pm 1.8	0.11 \pm 0.02

from a clone collected on glossy buckthorn in Springfield Fen, Indiana (Hill et al. 2010) but no other information had been reported about the suitability of glossy buckthorn for survivorship of the soybean aphid despite its wide invasive distribution in Canada and the United States (Gucker 2008; USDA-NRCS 2021). In the USA, three *Rhamnus* species, *R. alnifolia*, *R. cathartica*, and *R. lanceolata*, were reported as successful overwintering host plants (Voegtlin et al. 2005). Our study showed that common buckthorn provided better survivorship than glossy buckthorn regardless of the soybean aphid biotype, but we don't know if this is also true when comparing *R. alnifolia* or *R. lanceolata* since those two species were not part of our study. The information from counting adult oviparae and eggs 42 days after winter host infestation showed that nymphal oviparae were able to reach adulthood, and resulting adults produced eggs on glossy buckthorn for each of the four biotypes. According to our results, soybean aphid biotype 2 produced an equal number of eggs on both common and glossy buckthorn suggesting that this biotype has an equal chance of survival on both buckthorns, which differs from that of the other biotypes.

Another unique aspect of our study was that soybean aphid apterous males were produced under laboratory conditions. The majority of apterous males were produced by biotype 3, the only biotype described based on field collections from glossy buckthorn (Hill et al. 2010). Also, aphid polyphenism is unusual since in the field, alate males and gynoparae are usually produced on soybean so they can migrate to their winter host plant, buckthorn. In our study, soybean and buckthorn plants were clustered in the same plant growth chamber after soybean plants were exposed for 21 days to a short photoperiod and low temperatures to induce sexual morph production. Under these conditions apterous males were found. Aphid wing polyphenism has been observed in nature when soybean aphid apterous viviparous females produce more alate offspring because of environmental factors such as crowding, poor quality food and presence of predators (Müller et al. 2001). Vellichirammal et al. (2017) explained that the steroid hormone, ecdysone, plays an important role in wing polyphenism of *Acyrtosiphon pisum* (Harris), and that the ratio of apterous and alate embryos will be affected by the external clues that affect their apterous viviparous mothers. It also is possible that juvenile hormones play a role on reproductive polyphenism (Ogawa and Miura 2014). For example, the oleander aphid, *Aphis nerii* Boyer de Fonscolombe, is known to have asexual reproduction, but under short day conditions reproductive polyphenism (sexual morphs) was observed (Takada and Miyazaki 1993).

Both common buckthorn and glossy buckthorn are widely distributed in the USA and Canada (USDA-NRCS 2021). Distribution of the two species mostly overlaps with common buckthorn being reported from coast to coast and as far south as North Carolina in the USA and from Alberta to the east coast in Canada. Glossy buckthorn distribution is from Idaho east and as far south as North Carolina and from Saskatchewan to the east coast in Canada. Both species are referred to as threat species due to the invasion of natural habitats and replacement of native species (Gucker 2008). The overlap of these species with soybean is greatest in the Midwest where they are listed as restricted noxious weeds in Illinois, Iowa, Minnesota and Wisconsin (Illinois Department of Natural Resources 2021; Iowa Natural Resource Stewardship 2021; Minnesota Department of Natural Resources 2021; Wisconsin Department of Natural Resources 2021). The density of common buckthorn and glossy buckthorn may be important in these states and other Midwestern states for providing overwintering sites for the soybean aphid. Additional field surveys are warranted to understand more about how these buckthorn species play a role in comparative life tables for the soybean aphid biotypes especially when it comes to winter host preference, sexual reproduction, genetic recombination, and distribution of known and potential new biotypes (Cooper et al. 2015; Crossley and Hogg 2015; Alt et al. 2019; Lagos-Kutz et al. 2019; Tilmon et al. 2021).

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