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Host Plant Suitability of Rhamnaceae for Soybean Aphid (Homoptera: Aphididae)

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ABSTRACT We tested host plant suitability of 10 taxa in the Rhamnaceae for successful preoverwintering development of soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae). In the laboratory, we offered each gynopara and ovipara a single member of each putative host plant and measured survivorship and fecundity. *Rhamnus cathartica* L. and *Rhamnus alnifolia* L'Héritier were confirmed as suitable host plants, and eight other taxa were confirmed as unsuitable. This study supports results from a companion study in which soybean aphids were offered multiple members of the Rhamnaceae in field cages. Of the two suitable host plants, *R. cathartica* supported greater longevity and oviposition rates in oviparae. The importance of *R. cathartica* as an overwintering host to soybean aphid ecology and management is discussed.

KEY WORDS *Aphis glycines*, buckthorn, *Rhamnus cathartica*, *Rhamnus alnifolia*, primary host plant

THE SOYBEAN APHID, *Aphis glycines* Matsumura (Homoptera: Aphididae), is a pest of soybean, *Glycine max* (L.) Merrill, in Asia, and has recently invaded North America. The soybean aphid has a heteroecious holocyclic life cycle. It feeds and reproduces viviparously on soybean (the secondary host) during the summer and then develops winged morphs called gynoparae that disperse from soybean to a woody shrub, buckthorn (*Rhamnus* spp., the primary host), in the fall. Gynoparae produce wingless morphs called oviparae, which are subsequently mated by winged males migrating from soybean. Eggs are laid adjacent to twig buds or on bark crevices, where they overwinter. Wingless fundatrices hatch from eggs in the spring, and within a couple generations or so, produce winged morphs that disperse to soybean (Takahashi et al. 1993, Ragsdale et al. 2004).

Aphids are known for host alternation, or heteroecy, with different generations switching seasonally between two sets of unrelated host plants (Lambers 1966, Moran 1992, von Dohlen and Moran 2000). Like *A. glycines*, other species in the genus *Aphis* have similar biologies. In North America, a closely related species, *Aphis gossypii* Glover (the melon aphid or cotton aphid), alternates from primary hosts *Catalpa* or *Hibiscus* to a variety of herbaceous secondary hosts in the summer, and *Aphis helianthi* Monell uses *Cornus* spp. as primary hosts and *Helianthus* spp. as secondary hosts (Blackman and Eastop 1984).

In Asia, the primary hosts of *A. glycines* are identified as *Rhamnus davurica* Pallas (Wang et al. 1962) and *Rhamnus japonica* Maximowicz (Takahashi et al. 1993). These species are rare in North America (Voegtlin et al. 2004), but a few other species of the buckthorn family, Rhamnaceae, have been reported to be suitable hosts for the aphid in the Midwest. These species include *Rhamnus cathartica* L., *Rhamnus alnifolia* L'Héritier (Voegtlin et al. 2004), and *Rhamnus lanceolata* Pursh (Voegtlin et al. 2005). *R. cathartica* is widely distributed in midwestern soybean-growing regions, particularly Minnesota, Wisconsin, Michigan, Illinois, and Indiana (Ragsdale et al. 2004). Successful overwintering from the gynopara to spring migrant generation has been confirmed on *R. cathartica* in northern Indiana, but it has not been seen on *R. alnifolia* (Voegtlin et al. 2005). Only one survey of soybean aphid on *R. lanceolata* has been made (D.J.V. and R.J.O., unpublished data). No soybean aphids were found at the time of the fall collection.

We used laboratory studies to test putative overwintering (primary) hosts of the soybean aphid. Our study is a companion study to a multi-choice host plant test of soybean aphid in field cages (Voegtlin et al. 2005). In that study, soybean aphid cohorts were given a choice to settle and reproduce among 11 members of the Rhamnaceae. Three members, *R. cathartica*, *R. alnifolia*, and *R. lanceolata*, were found to be suitable overwintering hosts, as indicated by the presence of both eggs in the fall and fundatrices the following spring. In contrast to the multi-choice study, soybean aphids in this study were offered a choice of only one Rhamnaceae member. The objectives were to distinguish between plant preference by gynoparae in multi-choice experiments, and suitability of each Rhamnaceae member for development to the over-

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wintering egg stage in single-choice experiments. By offering each aphid only one Rhamnaceae member, we could determine, for the taxa rejected in the multi-choice case, whether the aphid failed to develop solely because it preferred other available taxa, or whether the plant was unsuitable as a primary host. To assess host plant quality, we compared life history characteristics of the preoverwintering aphid generations among the Rhamnaceae taxa. *R. lanceolata* was tested in the multi-choice experiment, but it was unavailable for the single-choice experiments.

Materials and Methods

Rearing Methods. We studied 10 taxa of the Rhamnaceae family, six *Rhamnus*: *R. alnifolia*, *Rhamnus caroliniana* Walter, *R. cathartica*, *Rhamnus frangula* L., *R. frangula* 'Asplenifolia', and *R. frangula* 'Columnaris'; and four species in different genera: *Berchemia scandens* (Hill) K. Koch, *Ceanothus americanus* L., *Hovenia dulcis* Thunberg, and *Rhamnella franguloides* (Maximowicz) Weberbauer. Plants were obtained from Iowa State University and The Illinois Natural History Survey and grown in pots of 16- to 29-cm diameter at Purdue University. The pots were maintained in a greenhouse at $22 \pm 4^\circ\text{C}$ and under ambient light conditions (no direct supplemental lighting) for the duration of the study, September 2003 through January 2004. Before the experiments, the Rhamnaceae were fertilized with Osmocote and treated with *Encarsia formosa* Gahan and predatory mites [*Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus californicus* (McGregor), and *Mesoseiulus longipes* (Evans)] to control whiteflies and twospotted spider mites.

Soybean aphids were obtained from a colony maintained on greenhouse-grown soybean. Gynopara and male production were induced by introducing viviparous apterae onto soybean cuttings in a controlled environment chamber at 16°C , 55% RH, and a photoperiod of 10:14 (L:D) h. Under these conditions, gynoparae and males will begin to be produced in the second generation, and the switch to the production of sexual morphs is not 100%. In the first generation to produce sexual morphs, a single viviparous female may produce viviparous females that will remain on or, if winged, settle on soybean, as well as gynoparae and males that will settle on an acceptable primary host. In subsequent generations, only gynoparae and males will be produced. Induction of gynopara development under laboratory conditions can therefore take over a week of exposure to the autumnal light regime (and for males, somewhat longer), and the alates produced initially in the colony contain a high proportion of viviparous summer alates, with gynopara production increasing over a several-week period. Gynoparae, in contrast to the summer alates, seek primary host plants on which to complete the sexual phase of their life cycles.

Gynoparae. A single-choice host suitability study in Fall 2003 measured survivorship and fecundity of gynoparae on putative host plants. Individual gynoparae

were offered twig cuttings from one of 10 taxa, and subsequent settling and reproduction were observed.

The experimental arena was a 14 by 7.8 by 2.9-cm plastic box with a 5-cm mesh-covered window on the lid. In each box, a stem cutting from a soybean seedling (only the two unifoliolate leaves fully opened) and a twig cutting from one of the 10 Rhamnaceae were placed in 8-cm water tubes. Each Rhamnaceae twig was cut to ≈ 10 cm with one to six leaves, depending on the taxon. Cuttings were rinsed with water before use.

In each box, a single gynopara was placed on the underside of a unifoliolate soybean leaf. The boxes were placed in a controlled environment chamber at $14 \pm 4^\circ\text{C}$, 60% RH, and a photoperiod of 10:14 (L:D) h. A complete randomized block design was used for statistical analysis with 16 blocks of 10 treatments (species or cultivars) each. In the experimental chamber, the boxes were arranged two blocks per tray and two trays per shelf on a total of four shelves.

The boxes were checked daily for aphid counts and location within the box. Individual replicates were restarted with a new individual if the alate died within the first 24 h ($n = 12$), was lost from the box within the first 7 d without reproducing ($n = 7$), or produced nymphs on the soybean, indicating that the selected alate was a viviparous summer alate rather than a gynopara. Of the 160 alates used to initiate the experiment, 37% ($n = 59$) were restarted due to reproduction on soybean. Of this second batch of replicates, 14% ($n = 8$) were restarted due to reproduction on soybean. All summer alates were evenly distributed among treatments (first batch, $\chi^2 = 3.46$, $df = 9$, $P = 0.9431$; second batch, one summer alate per taxon in six taxa, two summer alates in one taxon, and none in three taxa).

Soybean cuttings were removed from boxes starting on day 8 of each treatment, if transfer to and reproduction on the Rhamnaceae cuttings had already been observed, but they were left in boxes otherwise. Rhamnaceae cuttings were replaced as each began to senesce.

Oviparae. A second host suitability experiment was conducted, to measure survivorship and fecundity of oviparae on the potential host taxa of the Rhamnaceae. Oviparous nymphs were caged on potted plants and then transferred to cuttings as they matured, to allow for mating and oviposition. One-day-old nymphs were individually brushed onto the undersides of leaves of potted Rhamnaceae in the greenhouse on 19 November 2003 at $22 \pm 4^\circ\text{C}$ under ambient light conditions. Each nymph was enclosed within a clip cage 1.3 cm in diameter and 1.5 cm in height, constructed from a section of Nalgene tubing with foam rubber padding on one end and fine mesh screening on the other. There were 30 replicates each on *R. cathartica* and *R. alnifolia* and 15 replicates each on the remaining eight taxa. Within each host taxon, nymphs were distributed evenly over the available plant material.

The cages were checked daily for aphid survival. Nymphs were transferred up to three times to new foliage of the same plant, to maintain the quality of

available plant resource. As each ovipara matured, it was transferred to a 14 by 7.8 by 2.9-cm plastic box containing a cut stem of the same host taxon, in an 8-cm water tube. A male soybean aphid was immediately introduced, and the box was kept in a controlled environment chamber at $20 \pm 2^\circ\text{C}$, 60% RH, and a photoperiod of 10:14 (L:D) h. Aphids were counted daily from 20 November 2003 to 24 December 2003, and less frequently thereafter. All oviposition activity had ceased by 18 December 2003, although the last ovipara survived until 6 January 2004. Mating could not be confirmed for each pair, but for the duration of the ovipara's adult life, the male was always replaced immediately if found dead or missing. Dead females were dissected to obtain counts of ova within the ovaries. Egg load was defined as the sum of eggs laid by and ova dissected from each ovipara.

Analyses. Suitability of Rhamnaceae taxa for gynoparae was evaluated across treatments by comparing: proportion of individuals found on the Rhamnaceae twigs on day 3 of the treatment, mean longevity, proportion of reproductive individuals, and mean number of nymphs produced per individual. Gynopara location on (or off) the Rhamnaceae was examined on day 3 because the majority of reproductive individuals reproduced within 3 d. The effect of treatment was determined by contingency table analysis for the proportional data (PROC FREQ, SAS Institute 2001) and by two-way analysis of variance (ANOVA) for means. Subsets of contingency tables were compared using Fisher's exact test (Zar 1996). Means were compared using paired Tukey tests if the ANOVA was significant at the $\alpha = 0.05$ level (PROC MIXED, SAS Institute 2001).

Suitability of the host plants was further evaluated by examining life history traits of oviparae across the treatments. Aphids survived to maturity on only two of the host taxa tested. Proportions maturing and ovipositing on the two taxa were compared using Fisher's exact test. Mean longevity, time to first reproduction, egg load, and total number of eggs laid were compared using *t*-tests. In each of the *t*-tests, variances of trait measures were not significantly different between treatments; thus, the *t*-values were obtained by the pooled method.

Results

Host Plant Suitability for Gynoparae. In the single-choice arenas (soybean plus one member of Rhamnaceae), the proportion of gynoparae found on the Rhamnaceae twig on day 3 differed significantly among the treatments (Table 1; $\chi^2 = 73.66$, $df = 9$, $P < 0.0001$). When offered *R. cathartica*, *R. alnifolia*, *R. frangula* Columnaris, or *R. frangula*, at least half of the gynoparae were found on these taxa. In all other treatments, more gynoparae were observed on a surface other than the Rhamnaceae twig. Greater numbers of gynoparae were observed on the Rhamnaceae twig if they were offered *Rhamnus* species than if offered non-*Rhamnus* species (Fisher two-tailed $P < 0.0001$). Greater numbers of gynoparae were observed on the Rhamnaceae twig if offered *R. cathartica* or *R. alnifolia* than if offered other *Rhamnus* species (Fisher two-tailed $P < 0.0001$).

Treatment had a significant effect on longevity of gynoparae (Table 1; $F = 14.93$, $df = 9$, $P < 0.0001$), with greatest survival on *R. cathartica* and *R. alnifolia*. Longevity on *R. frangula* Columnaris was not statistically different from that on *R. alnifolia*. Longevities on the remaining taxa, however, were significantly lower than on *R. cathartica* and *R. alnifolia*.

A significantly greater proportion of gynoparae reproduced on *R. cathartica* and *R. alnifolia* than on other Rhamnaceae (Table 1; $\chi^2 = 88.52$, $df = 9$, $P < 0.0001$). There was no significant difference between the proportion reproducing on *R. cathartica* or *R. alnifolia* (Fisher two-tailed $P = 0.48$). Fewer gynoparae reproduced on the other *Rhamnus* species and *Rhamnella franguloides* (Fisher two-tailed $P < 0.0001$). No offspring were observed on *B. scandens*, *C. americanus*, or *H. dulcis*.

Treatment had a significant effect on number of nymphs produced per gynopara (Table 1; $F = 27.16$, $df = 9$, $P < 0.0001$). The greatest mean number of nymphs was produced on *R. cathartica* and *R. alnifolia*. Significantly lower fecundities were observed on *R. frangula* Columnaris, *R. frangula*, and *R. caroliniana*. A few nymphs were produced on *R. frangula* Asplenifolia and *Rhamnella franguloides*, but none survived longer than 5 d.

Table 1. Behavioral and life history parameter estimates of gynoparae on Rhamnaceae taxa in single-choice experiment

Taxon	Proportion of gynoparae on Rhamnaceae, day 3	Longevity ^a (d)	Proportion of gynoparae that reproduced	Nymphs produced per gynopara
<i>R. cathartica</i>	1.00	19.9 ± 2.2a	1.00	5.0 ± 0.4a
<i>R. alnifolia</i>	0.94	16.0 ± 2.2ab	0.88	3.9 ± 0.6a
<i>R. frangula</i> Columnaris	0.79	11.1 ± 2.3bc	0.69	2.0 ± 0.4b
<i>R. frangula</i>	0.50	6.3 ± 1.3cd	0.44	1.3 ± 0.4bc
<i>R. frangula</i> Asplenifolia	0.38	4.9 ± 0.6cd	0.19	0.4 ± 0.2c
<i>R. caroliniana</i>	0.31	9.6 ± 1.3cd	0.63	2.1 ± 0.5b
<i>B. scandens</i>	0.14	5.6 ± 0.6cd	0.00	0.0c
<i>C. americanus</i>	0.08	4.9 ± 0.7cd	0.00	0.0c
<i>H. dulcis</i>	0.07	4.8 ± 0.6cd	0.00	0.0c
<i>Rhamnella franguloides</i>	0.00	4.6 ± 0.6d	0.13	0.2 ± 0.1c

Mean ± SE; means followed by different letters are significantly different at $\alpha = 0.05$.

^a Soybeans were present in experimental arenas for at least 8 d and individuals may have fed upon both Rhamnaceae and soybean. Estimates of longevity in each treatment are thus based upon diets of possibly both plants.

Table 2. Life history parameter estimates of oviparae in single-choice experiment

Trait	<i>R. cathartica</i>			<i>R. alnifolia</i>		
	<i>n</i>	Mean \pm SE	Range	<i>n</i>	Mean \pm SE	Range
Longevity (d)	22	33.3 \pm 1.7	20–49	5	21.4 \pm 2.3	16–30
Time to first reproduction (d)	22	18.8 \pm 0.6	14–24	5	18.0 \pm 1.1	15–21
Total egg load ^a	10	4.9 \pm 0.6	2–8	12	4.3 \pm 0.3	3–6
Total eggs laid	22	4.2 \pm 0.5	1–8	12	0.8 \pm 0.4	0–4

Longevity and time to first reproduction are reported for ovipositing individuals only. Egg load and number of eggs laid are reported for all egg-bearing individuals, including those that did not oviposit.

^a Dissections were conducted until day 31 of the experiment, which includes the entire period of oviposition activity (days 14–29). Egg load calculations are based only on oviparae that were dissected.

Host Plant Suitability for Oviparae. Oviparous nymphs survived to maturity only on *R. cathartica* and *R. alnifolia*. There was no statistical difference between the 83% (25/30) and 73% (22/30) of nymphs maturing on *R. cathartica* and *R. alnifolia*, respectively (Fisher two-tailed $P = 0.5321$). The proportion of mature oviparae successfully ovipositing on *R. cathartica* was 88% (22/25), but fewer mature oviparae, 23% (5/22), oviposited on *R. alnifolia* (Fisher two-tailed $P < 0.0001$). Longevity of these individuals was greater on *R. cathartica* (Table 2; $t = 3.10$, $df = 25$, $P = 0.0048$), although number of days to first reproduction was statistically similar on both species ($t = 0.56$, $df = 25$, $P = 0.5804$). There was no difference between the treatments in egg load for egg-bearing oviparae (Table 2; $t = 0.88$, $df = 20$, $P = 0.3910$). However, seven of the 12 egg-bearing oviparae on *R. alnifolia* failed to oviposit, and the mean number of eggs laid per female was significantly greater on *R. cathartica* (Table 2; $t = 4.97$, $df = 32$, $P < 0.0001$).

Discussion

Among the 10 taxa tested, only *R. cathartica* and *R. alnifolia* were suitable hosts for soybean aphids to complete the sexual reproduction phase of their life cycle. Unsuitability of the eight other tested taxa was confirmed; soybean aphids were unable to develop on each of them when given no alternative plant choice. In particular, we showed that *R. cathartica* and *R. alnifolia* supported greater longevity of gynoparae and production of oviparous nymphs than did all other putative hosts and that only these two species supported maturation and oviposition by oviparae.

Our laboratory experiments largely confirm host plant suitability results from the field cage study of Voegtlin et al. (2005), in which aphids were offered a choice of potential primary rhamnaceous hosts. In that study, they identified *R. cathartica*, *R. alnifolia*, and *R. lanceolata* as primary host plants through evidence of successful oviposition by oviparae on each species. As in our study, they showed that the aphid rejected non-*Rhamnus* hosts, by largely failing to settle on plants as gynoparae. The main difference between studies was that when given no other choice of primary host plant in our study, gynoparae could produce oviparous nymphs on *R. franguloides* and the two cultivars of *R. frangula*, although the nymphs never matured. In the field cage study, however, gynoparae

did not produce nymphs on these three taxa when offered preferred hosts in a multi-choice setting.

Our laboratory study additionally showed that although *R. cathartica* and *R. alnifolia* supported similar longevity and reproductive effort by gynoparae and maturation and egg load of oviparae, oviposition on *R. alnifolia* was considerably lower than on *R. cathartica*. Oviposition on *R. alnifolia* may have been lower because the mean longevity of oviparae was nearly equivalent to the time to first reproduction, leaving a small window of time for oviposition on *R. alnifolia*. Both the low per capita rate of egg production on *R. alnifolia* and the limited distribution of the native *R. alnifolia* in midwestern soybean-growing regions (Rehder 1940; D.J.V. and R.J.O., unpublished data) suggest its importance as an overwintering host for soybean aphid is likely to be limited. In contrast, the introduced (from Eurasia) *R. cathartica* commonly occurs in high-density patches and is widely distributed across the Midwest (Ragsdale et al. 2004). Thus, *R. cathartica* is both more readily available and also provides a more suitable host for the soybean aphid.

The importance of *R. cathartica* to soybean aphid ecology and management is further reinforced from estimation of soybean aphid population growth on this host plant. Under laboratory conditions, gynoparae can produce an average of five nymphs and oviparae can produce five eggs on *R. cathartica* (Tables 1 and 2). In comparison, in a separate field study on *R. cathartica*, we have observed ratios of slightly greater than one ovipara per gynopara and three eggs per ovipara in the fall (R.J.O. and H.J.S.Y., unpublished data). Observations the following spring indicated that for every gynopara, more than four migratory alates were produced. Together, these data suggest a significant potential for aphid population increase at their overwintering sites. Considering both this growth potential and the extensive distribution and density of *R. cathartica* in the Midwest, effective soybean aphid management strategies will benefit greatly from field studies on the overwintering ecology of soybean aphid and the spatial relationships between *R. cathartica* and soybean.

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