Effect of Three Resistant Soybean Genotypes on the Fecundity, Mortality, and Maturation of Soybean Aphid (Homoptera: Aphididae)

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ABSTRACT The fecundity, longevity, mortality, and maturation of the soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae), were characterized using three resistant soybean, *Glycine max* (L.) Merrill, genotypes ('Dowling', 'Jackson', and PI200538 'Sugao Zarai') and two susceptible genotypes ('Pana' and 'Loda'). Antibiosis in the resistant genotypes was demonstrated by a significant decrease in fecundity and longevity and increased mortality of *A. glycines*. Aphid fecundity, measured as number of offspring produced in the first 10 d by each viviparous aptera, was higher on Pana than on the resistant genotypes. Aphid longevity, the mean number of days a 1-d-old adult lived, was 7 d longer on Pana than on Dowling and Jackson. The mortality of both viviparous apterae and nymphs on resistant genotypes was significantly higher than on susceptible genotypes. A greater number of first instars survived to maturation stage (date of first reproduction) on susceptible plants than on resistant plants. None of the first instars placed on Dowling and PI200538 leaves survived to maturation. Observations of aphid behavior on leaves indicated that aphids departed from the leaves of resistant plants 8–24 h after being placed on them, whereas they remained indefinitely on leaves of susceptible cultivars and developed colonies. Reduced feeding due to ingestion of potentially toxic compounds in soybean may explain the possible mechanism of resistance to the soybean aphid.

KEY WORDS *Aphis glycines*, aphid longevity, feeding preferences, host resistance, soybean aphid

THE SOYBEAN APHID, *Aphis glycines* Matsumura, was reported as a new pest of soybean in the Midwest in 2000 (Hartman et al. 2001). It rapidly spread throughout the region and into other parts of North America (Anonymous 2003). The damage caused by soybean aphid feeding includes stunting, leaf distortion, and reduced pod set (Sun et al. 1990). It can also transmit certain plant viruses to soybean and promotes a fungus called sooty mold that obtains nutrients from aphid honeydew. Yield losses caused by aphids in severely infested fields were >50% in Minnesota in 2001 (Anonymous 2003) and up to 52% in reports from China (Wang et al. 1994).

Many factors affect soybean aphid populations, such as climate, environment, planting time, predators, pathogenic fungi, insecticide, and host resistance (Onstad 2001). Host resistance is one way to control insects that is not detrimental to the environment and can reduce financial input of growers. Resistance to *A. glycines* was found in nine soybean germplasm accessions (Hill et al. 2004). Resistance in the germplasm accessions 'Dowling' and 'Jackson' was characterized in choice and nonchoice tests in greenhouse experiments and was proposed to be primarily antibiotic in action. In addition, Dowling resistance protected plants as well as the systemic insecticide imidacloprid in a field experiment (Hill et al. 2004). Aphid population development on some of the resistant genotypes was significantly curtailed compared with susceptible genotypes in nonchoice tests. The specific effects of the antibiosis on aphid biology were not determined.

The objective of this study was to determine specific antibiotic effects of resistance on the soybean aphid by comparing aphid fecundity, longevity, mortality, maturation, and feeding behavior on three resistant soybean genotypes, PI200538 ('Sugao Zarai'), Dowling, and Jackson, and two susceptible genotypes, 'Loda' and 'Pana'.

Materials and Methods

Plant and Aphid Culture. Seed of the resistant soybean genotypes Dowling (PI548663), Jackson (PI548657), and PI200538 was obtained from the USDA Soybean Germplasm Collection in Urbana, IL. Seed of Loda and Pana were obtained from Illinois Seed Foundation.

Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by the USDA implies no approval of the product to the exclusion of others that may also be suitable.

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Seeds were sown in 12-cm plastic pots filled with soil-less potting medium (Sunshine Mix, LC1, Sun Gro Horticulture Inc., Bellevue, WA). Plants were grown in a growth chamber at 22°C (night) and 26°C (day) under a photoperiod of 12:12 (L:D) h with 300 μmol m^{-2} s^{-1} PAR irradiation. Plants were infested with aphids 3–4 wk after planting when the plants reached growth stage R1 (Fehr and Caviness 1977).

The soybean aphid clone was established from a single first instar isolated from a collection in Urbana, IL, in 2000 and maintained on a continuous supply of seedlings of soybean 'Williams 82' grown in a plant growth chamber at 22°C under continuous 200 μmol m^{-2} s^{-1} PAR irradiation (Hill et al. 2004). Williams 82 was found to be ideal for raising soybean aphids because high aphid numbers develop on plants without killing them (Hill et al. 2004).

Age-synchronized 1-d-old viviparous apterae (wingless female adults with parthenogenetic reproduction) were used in all experiments. To synchronize the age of aphids, several viviparous apterae were put on detached leaves of Williams 82 within petri dishes containing moist filter paper for 24 h. All of the viviparous apterae were removed after 24 h, whereas the nymphs they produced were left on the detached leaves. The development of the nymphs was observed daily until the final molt.

Aphid Infestation. Clip cages, 10 mm in diameter and 12 mm in height with 1-mm-thick plastic walls, were used to isolate and restrict aphid movement on the leaves of test plants. One end of the cage was glued with fine mesh of 100-μm openings (Sterling Net Co., Montclair, NJ), and the opposite end was glued with a 10-mm-diameter foam ring (4 by 4 by 4 mm). A clip cage was set on the abaxial surface of the leaf (underside of the leaf facing away from the stem) and fastened by a clip, with a 25 by 16-mm piece of plastic label placed between the adaxial leaf surface (upper side of the leaf) and the clip to avoid damage to the leaf. A fine camel's-hair brush was used to pick up and transfer aphids to test plants.

Aphid Fecundity. Fecundity was calculated as the mean number of offspring produced by each viviparous aptera during the first 10 d. The net fertility rate (NFR), the number of nymphs (alive when counted) produced by each viviparous aptera during her lifetime, and total fertility rate (TFR), the reproduction in absence of mortality, were calculated (Carey 1993).

Aphid Mortality and Longevity. The viability, live or dead, of each viviparous aptera and each nymph was recorded at 48-h intervals. Dead aphids were identified as inactive and brown or deep yellow. The percentage of survival of viviparous apterae and nymphs on each cultivar was calculated, which is the complement of mortality. Longevity, the mean life span in days of each viviparous aptera, was also calculated. A complete life table (Carey 1993) was calculated including life expectation, e_x; the mean number of days of life remaining at age x; and period mortality or age-specific mortality, q_x.

Percentage of Maturation and Prereproductive Period. The development of first instars to viviparous apterae was observed every 48 h. The number of days to maturity (first reproduction) plus the number of the first instars that matured was determined. The percentage of maturation (percentage of first instars that survived to become viviparous apterae), and prereproductive period (mean number of days from birth to maturity) were calculated.

Experimental Design. Three experiments were conducted. Two experiments, 1 and 2, were arranged in a randomized complete block design. There were six blocks with one plant of each cultivar within each block, and four cultivars were used in each experiment. Experiment 3 was arranged in a completely randomized design with two plants of two cultivars. Three leaves on each plant were used for aphid observation.

Experiment 1. Two resistant genotypes, Dowling and Jackson, and two susceptible genotypes, Pana and Loda, were used in experiment 1. Three trifoliolate leaves on six different plants of each cultivar, starting from the second trifoliolate leaf (third node), were selected and numbered 1–3. The two side leaflets of each selected trifoliolate were used for the test. A single 1-d-old viviparous aptera was caged on the abaxial surface of one of the side leaflets. After 48 h, the number of offspring produced by each viviparous aptera was recorded and all of the first instars were removed except one. This first instar was retained in the cage and observed until it died or matured to an adult. The original viviparous apterae that produced the nymphs under observation were transferred to the opposite side leaflet of the trifoliolate leaf where they produced their first brood and were recaged.

The development of each first instar and 1-d-old adult that was originally put in each cage was recorded at 48-h intervals after aphid transfer. The date of death and the maturation date (date of first reproduction) of each first instar were recorded. The date of death and number of offspring (including live and dead nymphs) produced by each viviparous aptera were also recorded. The nymphs produced by the viviparous apterae were removed after recording the data to avoid overcrowding in the clip cages. Observations of the viviparous apterae were completed when the last one died. Aphid fecundity, mortality (the complement of percentage of survival), longevity, percentage of maturation, and prereproductive period were calculated as described previously. A life table was generated using the data.

Experiment 2. Three resistant genotypes, Dowling, Jackson, and PI200538, and one susceptible genotype, Pana, were used in experiment 2. Data were recorded as described in experiment 1, except that the observations were completed 10 d after aphid transfer. In addition, the position of each viviparous aptera 48 h after being placed on leaves was recorded as either being on or off of the leaf to which it had been transferred.

Experiment 3. Because viviparous apterae departed from resistant leaves within 48 h in experiment 2,

Table 1. Fecundity, longevity, and maturation of *A. glycines* on resistant (R) and susceptible (S) soybean genotypes in experiment 1

Cultivar	Fecundity[a] Mean ± SE	Longevity[b] Mean ± SE	Maturation (%)[c]
Pana (S)	17 ± 3.3a	12 ± 1.4a	72a
Loda (S)	4 ± 1.8b	7 ± 1.3b	50a
Jackson (R)	3 ± 1.1b	5 ± 0.7b	6b
Dowling (R)	1 ± 0.4b	5 ± 0.6b	0b

Within columns, means followed by the same letter are not significantly different by the least significant difference test ($P = 0.05$). The nymphs were removed after each count every 48 h.

[a] Number of nymphs produced by each viviparous aptera in 10 d.

[b] Days from first reproduction until the death of a viviparous aptera.

[c] Percentage of first instars that developed into viviparous apterae.

experiment 3 was conducted to determine whether the effect of the resistant plants was caused by starvation. A piece of filter paper was cut with a diameter just larger than the leaf cages and put between the leaf and the aphid separating the aphids from the leaf so they could not obtain sap from the leaves. Three leaves of each of two plants of both resistant Dowling and susceptible Pana in growth stage R3 (Fehr and Caviness 1977) were tested. Aphid positions (either on or off the surface of the leaf and the filter paper), and whether they were dead or alive, were recorded at 4, 8, 24, 48, and 72 h after aphid transfer.

Statistical Analysis. All statistical analyses were performed with the aid of JMP version 5 (SAS Institute 2002). Means were separated using the least significant difference (LSD) at $P = 0.05$ when treatment means were significantly different ($P < 0.05$) in the analysis of variance (ANOVA).

Results

Aphid Fecundity. Aphid fecundity (Tables 1 and 2) was significantly higher on Pana than on resistant genotypes in both experiments 1 and 2 ($F = 12.83$; df = 3, 63; $P < 0.0001$ in experiment 1 and $F = 18.62$; df = 3, 63; $P < 0.0001$ in experiment 2). NFR and TFR indicated significant differences ($F = 11.17$; df = 3, 63; $P < 0.0001$ for NFR and $F = 10.41$; df = 3, 63; $P < 0.0001$ for TFR) among genotypes (Table 3). TFR (total fertility rate) was 14 times greater on Pana than on

Table 2. Fecundity, maturation, and percentage remaining on leaf of *A. glycines* viviparous apterae 48 h after transferring on resistant (R) and susceptible (S) soybean genotypes in experiment 2

Genotype	Fecundity[a] Mean ± SE	Maturation (%)[b]	Viviparous apterae remaining on leaf (%)
Pana (S)	13 ± 1.9a	67a	89a
Jackson (R)	5 ± 0.5b	0b	28b
Dowling (R)	4 ± 0.6b	0b	0c
PI200538 (R)	3 ± 0.7b	0b	17bc

Within columns, means followed by the same letter are not significantly different by the least significant difference test ($P = 0.05$). The nymphs were removed after each count every 48 h.

[a] Number of nymphs produced by each viviparous aptera in 10 d.

[b] Percentage of first instars developed into viviparous apterae.

Table 3. Demographic analysis of 1-d-old viviparous apterae of *A. glycines* on resistant and susceptible soybean genotypes in experiment 1

	Susceptible		Resistant	
	Pana	Loda	Dowling	Jackson
Life expectancy[a]				
e_0	10.6	6.4	4.4	4.1
e_{10}	5.8	15.0	0	1.0
Mortality[b]				
$6q_0$	0.2	0.5	0.7	0.7
$10q_0$	0.6	0.9	1	0.9
Reproduction[c]				
NFR	19.4 ± 4.4	4.8 ± 2.5	0.3 ± 0.1	1.9 ± 1.0
TFR	19.9 ± 4.4	5.2 ± 2.5	1.3 ± 0.4	3.1 ± 1.1

[a] The average number of days of life remaining to an individual living at days 0 and 10 (Carey 1993). Day 10 was chosen because all of the aphids were dead on Dowling.

[b] Age-specific mortality qx; the probabilities of mortality by days 6 and day 10 (Carey 1993).

[c] NFR and TFR as defined by Carey (1993).

Dowling (Table 3). NFR on Pana was >50 times greater than on Dowling because of higher mortality of the nymphs on Dowling. Aphid fecundity was high-

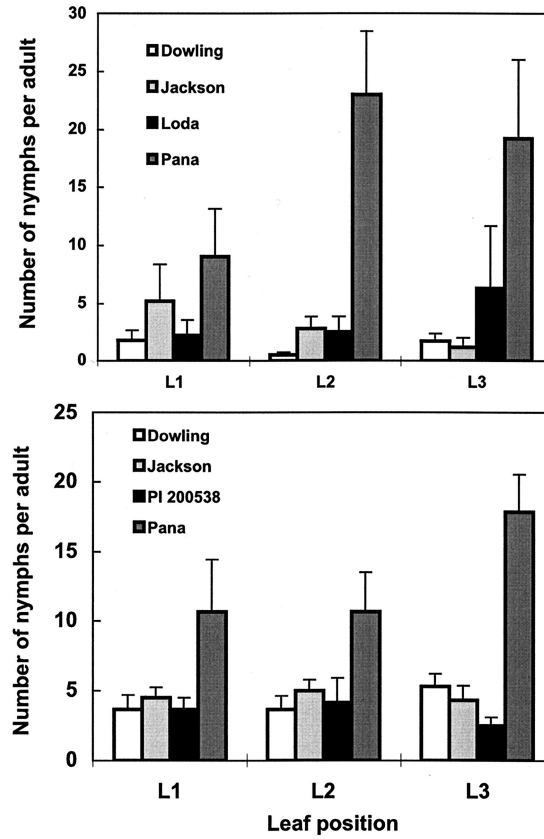

Fig. 1. *A. glycines* fecundity (number of nymphs produced by each 1-d-old aptera adult during 10 d) on soybean leaves in experiment 1 (top) and 2 (bottom). Leaf position refers to the position of the leaf on the plant starting with leaf number 1 (L1) being the second trifoliolate, L2 the third trifoliolate, and L3 the fourth trifoliolate up the plant. Vertical bars represent the standard error of the mean.

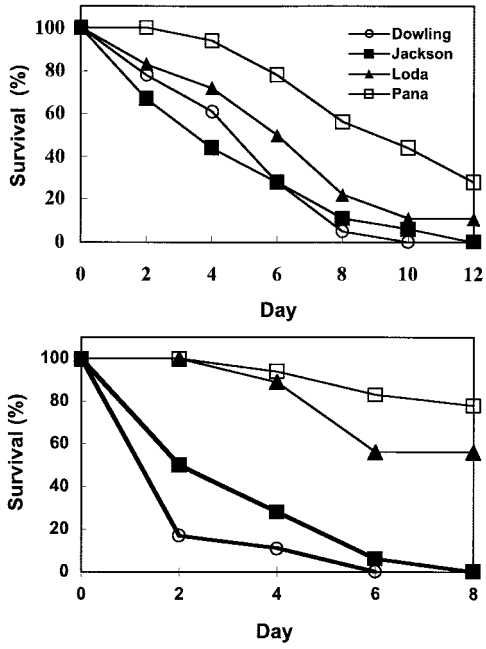

Fig. 2. Percentage of the total number of *A. glycines* viviparous apterae (top) and nymphs (bottom) that survived on four soybean genotypes 12 and 8 d, respectively, after transfer in experiment 1.

est on Pana, whereas fecundity on Loda was not significantly different from the resistant genotypes Jackson and Dowling (Table 1).

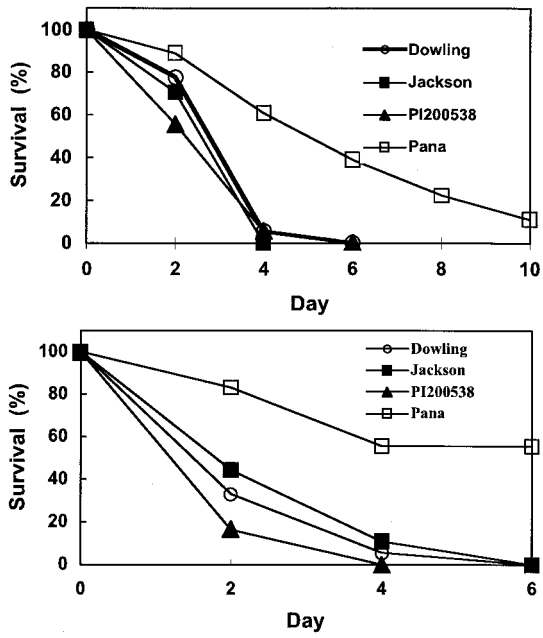

Fig. 3. Percentage of the total number of viviparous *A. glycines* apterae (top) and nymphs (bottom) that survived on four soybean genotypes 10 and 8 d, respectively, after transfer in experiment 2.

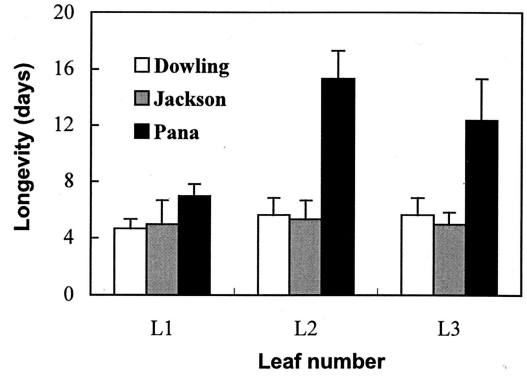

Fig. 4. Longevity of 1-d-old viviparous apterae of *A. glycines* on soybean genotypes in experiment 1. Leaf position refers to the position of the leaf on the plant starting with leaf number 1 (L1) being the second trifoliolate, L2 the third trifoliolate, and L3 the fourth trifoliolate up the plant. Vertical bars represent the standard error of the mean.

Reproduction on different leaves of Pana varied. It was higher on younger leaves than on older leaves ($P = 0.05$, LSD). Reproduction on different leaves of resistant genotypes did not vary (Fig. 1).

Aphid Mortality and Longevity. The percentage of aphid mortality, the complement of percentage of survival, was significantly higher on resistant genotypes Dowling, Jackson, and PI200538 than on Pana (Figs. 2 and 3). In experiment 1, 72% of viviparous apterae died on Dowling and Jackson compared with 22% on Pana 6 d after aphid transfer (Fig. 2). This trend was consistent after adjusting for age-specific mortality, $6q_0$ (Table 3). In addition, 100 and 94% of nymphs died on Dowling and Jackson, respectively, whereas 17% died on Pana (Fig. 2). In experiment 2, 100, 94, and 94%, of viviparous apterae died on the resistant genotypes Jackson, Dowling, and PI 200538, respectively, whereas 39% died on Pana 4 d after aphid transfer (Fig. 3). Similarly, high mortality of nymphs occurred on the three resistant genotypes with 100, 94, and 90% of the nymphs dead on PI200538, Dowling, and Jackson, respectively, compared with 50% on Pana 4 d after aphid transfer (Fig. 3).

Longevity of viviparous apterae on Pana was significantly ($F = 7.64$; df = 3, 63; $P = 0.0002$) higher than on resistant genotypes (Table 1). The life expectancy of 1-d-old viviparous apterae at days 0 and 10 on Pana was two and five times greater than on resistant Dowling and Jackson, respectively (Table 3). Longevity on Loda was not significantly different from Dowling and Jackson (Table 1). Longevity of 1-d-old viviparous apterae on different leaf positions on Pana differed significantly ($P = 0.05$, LSD) (Fig. 4) in correspondence with fecundity on Pana described above (Fig. 1).

Percentage of Maturation and Prereproductive Period. The percentage of maturation of first instars on susceptible soybean genotypes was higher than on resistant genotypes (Tables 1 and 2). More than 50% of the nymphs on the susceptible Loda and Pana ma-

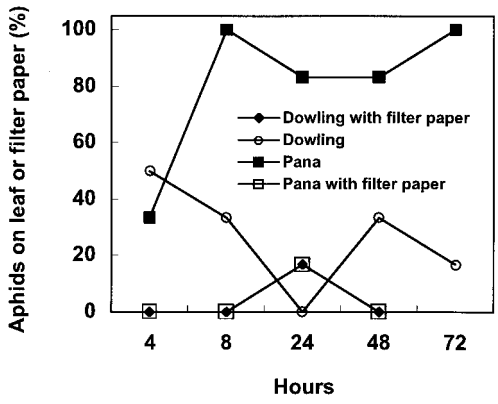

Fig. 5. Percentage of the total number of viviparous *A. glycines* apterae that were caged on four different surfaces (Dowling leaf, Pana leaf, Dowling leaf covered with filter paper, and Pana leaf covered with filter paper) that remained on either the leaf or filter paper surface over a 72-h period. Data are from experiment 3.

tured, whereas <6% on Jackson and 0% on Dowling and PI200538 matured. The prereproductive period (mean number of days from birth to maturity) of *A. glycines* was ≈6 d either on Pana, Loda, or Jackson.

Aphid Feeding Preference and Survival. In experiment 2, 89% of the viviparous apterae stayed on the leaves of Pana, whereas <20% stayed on leaves of Dowling and PI200538 48 h after aphid transfer (Table 2). In experiment 3, apterae departed Dowling leaves as early as 8 h after transfer, but remained on Pana leaves at much higher percentage from 8 to 72 h (Fig. 5). The apterae also did not stay on the filter paper to any great percentage regardless of the leaf under the filter paper (Fig. 5). Responses of aphids placed on filter paper that was covering leaves of Dowling or Pana were similar but differed significantly when placed on the uncovered leaves of either Dowling or Pana. After 48 h, 83% and after 72 h, 100% of the aptera died on filter paper (Fig. 6), compared with 17 and 83% on Dowling leaves after 48 and 72 h, respectively. There was no mortality of aphids on Pana leaves throughout the 72-h experiment.

Discussion

Fecundity and longevity of soybean aphids were dramatically reduced on the three resistant genotypes, Dowling, PI200538, and Jackson, compared with the susceptible genotype Pana. High percentage of mortality and no maturation of first instars were also observed on PI200538 and Dowling, which suggested that the effects of antibiosis on the soybean aphid were stronger on Dowling and PI200538 than on Jackson. Although aphid fecundity on Loda was not as high as on Pana, the higher percentage of maturation of first instars and lower percentage of mortality on Loda may explain its susceptibility to the soybean aphid.

Resistance expression was not affected by the physiological age of the soybean plants in accordance with our previous results (Hill et al. 2004). This situation contrasted with the developmentally regulated *Mi-1* [gene confers resistance to *Meloidogyne incognita* (Kofoid & White)]-mediated resistance to the potato aphid, *Macrosiphum euphorbiae* (Thomas), in tomato, where it was reported that the resistance was expressed only after plants were 6 wk old (Kaloshian et al. 1997).

A. glycines nymphs were more sensitive to the effects of soybean resistance than viviparous apterae in this study because there was a rapid decrease in survival within 48 h after aphid transfer onto resistant leaves. Nymphal sensitivity to some toxic compounds may be related to their higher rates of metabolism. It is interesting to note that when aphids were placed on filter paper covering leaves, ≈80% of the viviparous apterae died compared with 20% on uncovered Dowl-

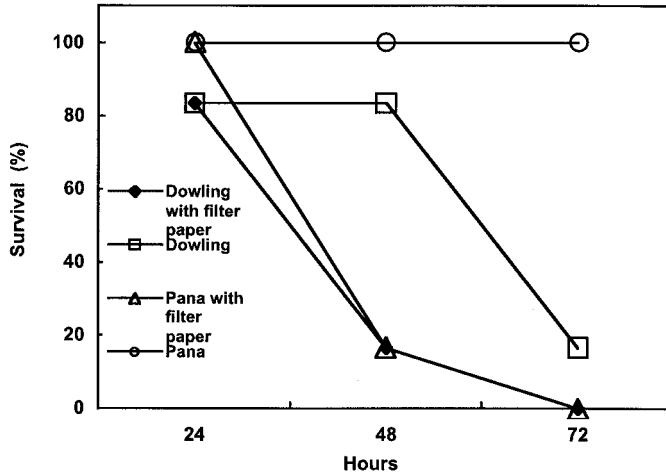

Fig. 6. Percentage of survival of the total number of *A. glycines* on leaves and on filter paper in experiment 3. Viviparous apterae were caged on four different surfaces (Dowling leaf, Pana leaf, Dowling leaf covered with filter paper, and Pana leaf covered with filter paper). The total number of dead aphids on each treatment was recorded at 24, 48, and 72 h after caging.

ing leaves after 48 h, whereas 80% of the viviparous apterae died on uncovered Dowling leaves compared with 0% on Pana leaves after 72 h. This difference strongly suggested that complete starvation was not the main reason behind the resistance and that less ingestion or ingestion of toxic compound(s) could be involved in increasing aphid mortality on resistant leaves. In addition, aphids departed between 8 and 24 h after they were transferred to resistant leaves, suggesting that antixenosis also played a role in resistance expression.

It was reported that the *Mi-1*-mediated resistance factors in tomato acting on the potato aphid (Kaloshian et al. 1995, Rossi et al. 1998) also affected aphid survival on resistant leaves comparable with survival on moist filter paper in a petri dish (Kaloshian et al. 1997). By using an electronic monitoring system, it was also shown that the mechanism of *Mi-1*-mediated resistance may be due to the limitation of ingestion of phloem fluids caused by shorter probing duration during the sieve element phase (Kaloshian et al. 2000). The structure and function of the *Mi* gene suggested that its polypeptide product might interact with other factors in a signal transduction pathway involved in resistance (Milligan et al. 1998, Kaloshian et al. 2000, de Ilarduya et al. 2001).

Studies of the molecular biology of resistance to the soybean aphid are just beginning. We have made crosses between resistant and susceptible genotypes with the goal to understand the mode of inheritance and to develop new resistant soybean cultivars.

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