

Flight Performance of the Soybean Aphid, *Aphis glycines* (Hemiptera: Aphididae) Under Different Temperature and Humidity Regimens

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ABSTRACT The soybean aphid, *Aphis glycines* (Matsumura), is native to eastern Asia and has recently invaded North America, where it is currently the most important insect pest of soybeans. The soybean aphid has spread rapidly within North America, presumably through a combination of active and passive (wind-aided) flight. Here, we studied the active flight potential of *A. glycines* under a range of environmental conditions using an aphid flight mill. Winged (alate) *A. glycines* were tested on a specially designed 32-channel, computer-monitored flight mill system. Aphids that were 12–24 h old exhibited the strongest flight behavior, with average flight durations of 3.3–4.1 h, which represented flight distances of 4.6–5.1 km. After the age of 72 h, *A. glycines* flight performance rapidly declined. The optimum temperature range for flight was 16–28°C, whereas optimum relative humidity was 75%. Our findings show that *A. glycines* possesses a fairly strong active flight aptitude (ability and inclination) and point to the possibility of flight initiation under a broad range of environmental conditions. These results have the potential to aid forecasting and management protocols for *A. glycines* at the landscape level.

KEY WORDS *Aphis glycines*, flight ability, flight mill, dispersal, environmental condition

The soybean aphid, *Aphis glycines* Matsumura, is a pest of soybean, *Glycine max* L. in many parts of the world. This aphid is native to Asia, where it is widely distributed in soybean-growing regions but only occasionally attains pest status (Van den Berg et al. 1997, Ragsdale et al. 2004, Wu et al. 2004). The soybean aphid was discovered in North America in 2000 and is currently found in 22 U.S. states and three Canadian provinces. Since its initial discovery, this insect has caused more than \$1 billion in crop losses and additional input costs in the United States, with a large share of the soybean acreage now requiring insecticide treatment (Ragsdale et al., 2004, 2007). The soybean aphid reduces soybean yield directly through plant feeding and indirectly through virus transmission and reduction in seed protein content (Wu et al. 2004). High soybean aphid densities generally affect soybean plants by reducing plant height, pod number, and total yield, with yield reductions reaching 50%. (Halbert et al. 1986, Wang et al. 1994, Van den Berg et al. 1997, Ragsdale et al., 2007). Aside from its effects on soybean, this aphid

also vectors various plant viruses and could thereby impact snap bean, seed potato, and melon production throughout the U.S. soybean belt (Donaldson and Gratton, 2007).

A number of conditions may have aided *A. glycines* establishment and subsequent spread through North America. Exotic species, such as *A. glycines*, are likely to establish when certain critical resources (e.g., host plants) are readily available. The presence of the overwintering host for the soybean aphid, the shrub *Rhamnus cathartica* L., in many parts of the United States has undoubtedly benefited the aphid's establishment (Voegtlin et al. 2005). Also, resident natural enemies in North America may have been unable to impede the establishment and spread of this aphid (Heimpel et al. 2004). However, considering the particularly rapid spread of *A. glycines* throughout the region, additional aspects of *A. glycines* ecology and biology could have facilitated this process. Geographical spread of *A. glycines*, within <2 yr, from its site of earliest discovery in Wisconsin to 20 U.S. states is rather exceptional for weak fliers such as aphids (Dixon and Howard 1986). Venette and Ragsdale (2004) attributed *A. glycines* impressive geographical spread to reliance on weather patterns for long-distance movements.

The large distances traveled by some aphids have drawn researchers' attention as early as the mid-1800s (Parry 1828, Elton 1925) when live aphids were re-

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Table 1. Flight aptitude, as determined with a flight mill, for *A. glycines* at different times after adult molt (i.e., alate age)

Ages (h)	Flight distance (km)		Flight duration (h)		Flight speed (km/h)		Percent of fliers
	Max	Mean ± SE	Max	Mean ± SE	Max	Mean ± SE	
6	2.98	1.23 ± 0.30c	3.22	1.35 ± 0.35c	2.13	1.10 ± 0.15b	100
12	15.26	5.11 ± 0.69a	8.18	3.31 ± 0.35ab	2.65	1.50 ± 0.07a	100
24	12.65	4.62 ± 0.55ab	8.14	4.17 ± 0.37a	2.06	1.12 ± 0.07b	100
48	11.50	3.56 ± 0.52ab	5.79	2.99 ± 0.34b	2.26	1.19 ± 0.08b	100
72	11.18	3.28 ± 0.55b	7.59	2.70 ± 0.43b	1.91	1.21 ± 0.05b	100
96	3.38	0.42 ± 0.21c	3.86	0.41 ± 0.21c	1.35	0.21 ± 0.09c	16.7

Aphid flight characteristics (distance, duration, speed) were recorded under standardized climatic conditions (30°C, 75% RH). Means in the same column followed by different letters are significantly different (Duncan's multiple range test, $P < 0.05$).

ported from the Spitsbergen snow plains in Norway, ≈1,500 km from the nearest thriving colony of live plants. Research has shown that aphids engage in (active) short-distance flight but also exploit weather patterns mainly for (passive) long-distance migration (Taylor et al. 1979, Robert 1987, Irwin and Thresh 1988, Isard and Gage 2001, Zhu et al. 2006). This two-pronged dispersal strategy aids aphids in successfully completing their often complex life cycle (Dixon 1987). Winged aphids (alates) engage in flight to colonize new plants, fields, or habitats, and at critical times, migrate between different host plants (Dixon 1998). Aphid flight is largely determined by the interplay between selected biological (e.g., age, nutritional status) and meteorological factors (e.g., wind speed, air temperature, relative humidity, barometric pressure, radiation) (Isard and Gage 2001).

The soybean aphid is heteroecious (use of primary and secondary host plants during winter and summer, respectively) and holocyclic (sexual morphs produce overwintering eggs on the primary host), with parthenogenetic reproduction during spring and summer (Dixon 1998). In spring, *A. glycines* maintain several generations on *Rhamnus* spp. before winged aphids depart and colonize soybean. Subsequently aphids develop winged morphs throughout the soybean growing season (i.e., summer migrants) and in early fall (i.e., fall migrants) (Ragsdale et al. 2004, Hodgson et al. 2005). Production of winged soybean aphids is likely triggered by photoperiod, although factors such as temperature, host plant quality, crowding, and presence of natural enemies could also play a role (Lu and Chen 1993, Hodgson et al. 2005). However, little is known about the biological and environmental factors that govern *A. glycines* flight. Such insights may prove crucial in explaining *A. glycines* rapid spread and pest status in North America but also help define forecasting and management protocols for soybean aphid at the landscape scale.

This paper describes the use of a computer-monitored flight mill to determine *A. glycines* flight performance under different temperature and humidity regimens (Cheng et al. 1997). Additionally, we assess the relationship between *A. glycines* flight aptitude and age.

Materials and Methods

Study Insects. A colony of soybean aphids was initiated with individuals collected from a soybean field

in Beijing, China, in early July 2006. The colony was maintained on soybean plants under controlled conditions (25°C, 75% RH, L:D 16:8 h). Soybeans were planted in potting soil in plastic containers and were transplanted individually as seedlings into 100-ml glass bottles filled with nutrient water (Wu et al. 1994). The aphids were cultured on these plants, which were renewed with aphids every 3 d to ensure appropriate aphid density and avoid crowding. Alatoid nymphs (i.e., older aphid instars with wing pads) were collected from these colonies, placed individually on a clean plant, and checked for molting into the adult stage every 8 h. The day of adult molt was considered as day 0 for the purposes of the experiment, and the time past this day was used to indicate alate age (Liquido and Irwin 1986).

Flight Mill. Flight of a great number of insect species has been successfully monitored in the laboratory using flight mills (Cheng et al. 1997, Wu et al. 2006). A computer-monitored flight mill was built for this purpose at the Institute of Plant Protection (Chinese Academy of Agriculture Sciences, Beijing, China). A total of 32 individual flight mills were connected to a computer and placed on glass shelves in a room where temperature, relative humidity, and photoperiod could be adjusted. Alate aphids were affixed to a copper thread cantilever with a droplet of 502 Glue (Yuyao Kexing Adhesive Co., Zhejiang, China), applied to the ventral side of their abdomen. The copper thread was subsequently placed between two miniature magnets on the flight mill, ensuring the aphid was placed horizontally as to not interfere with flight (Feng et al. 2004). Data recorded and catalogued by the software included the time of flight initiation and cessation and the number of mill revolutions that occurred in consecutive 5-s intervals. Flights interrupted by a 1-min or greater interval with zero counts were considered separate flights. The number of flight mill revolutions over a given period of time was recorded and flight distance, speed, and duration for each tested aphid were computed by a custom-made software package (Cheng et al. 1997).

Aphis glycines Tethered Flight. The term flight aptitude is used to define an organism's capacity and inclination for aerial movement (Isard and Gage 2001). We monitored flight of *A. glycines* alates of the ages of 6, 12, 24, 48, 72, and 96 h under standardized environmental conditions (30°C, 75% RH). We screened flight behavior of 12-h-old *A. glycines* alates under different temperature and humidity regimens.

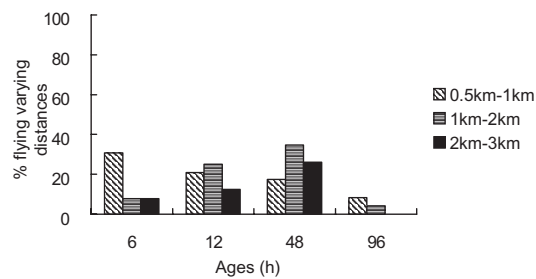


Fig. 1. Flight aptitude, as determined with flight mills under standardized environmental conditions, for *A. glycines* at different times after adult molt (alate age). A minimum of 15 alates was tested for each age category.

The temperature treatments were 12, 16, 20, 24, 28, and 32°C (at 75% RH), whereas relative humidity treatments were 30, 45, 60, 75, and 90% (at 24°C). A minimum of 15 individuals per treatment were tested either over a 24-h period or until flight was terminated. All experiments were carried out under a 24:0 (L:D) light regimen, because the soybean aphid has active flight ability under daylight. The barometric pressures in the test room under different temperature and humidity regimens were between 998 and 1,002 mbar.

Data Analysis. For each of the experiments, *A. glycines* flight distance, duration, and speed were compared using one-way analysis of variance (ANOVA) followed by a Duncan multiple range test. Before analysis, we ensured that data met the necessary assumptions of normality and homoscedasticity. Statistical analyses were executed using SAS (SAS Institute 1988).

Results

Effect of Age on Flight. Among the different *A. glycines* ages tested, 12- to 24-h-old alates possessed the strongest flight aptitude (Table 1). Flight distance ($F_{5,127} = 12.18$; $P < 0.05$), duration ($F_{5,127} = 15.05$; $P < 0.05$), and speed ($F_{5,127} = 32.21$; $P < 0.05$) significantly differed between the various ages. Between the age of 12–72 h old, >80% individuals sustained tethered flight over 0.5 km (Fig. 1). Flight performance gradually declined with age, with alates older than 72 h showing greatly reduced flight time, distance, and speed (Table 1).

Effect of Temperature on Flight. Alates exhibited normal flight throughout the range of tested temperatures, although great variability was noted in flight performance (Table 2). Flight distance ($F_{5,127} = 6.95$;

$P < 0.05$), duration ($F_{5,127} = 9.18$; $P < 0.05$), and speed ($F_{5,127} = 29.40$; $P < 0.05$) significantly differed between the various temperatures. Alates flew the longest distance at 24°C and at greatest speed at 32°C.

Effect of Relative Humidity on Flight. Alates exhibited normal flight throughout the range of tested humidity levels (Table 3). Flight distance ($F_{4,91} = 6.40$; $P < 0.05$), duration ($F_{4,91} = 11.16$; $P < 0.05$), and speed ($F_{4,91} = 4.10$; $P < 0.05$) showed significant differences between the range of 30–75% RH. The 75% RH seemed optimal for *A. glycines* flight, with humidity regimens of 60 and 90% being suboptimal.

Discussion

Our research confirms that biological factors such as alate age and environmental factors (e.g., temperature, humidity) affect *A. glycines* flight behavior. Flight distance and duration of soybean aphid alates peaked at ages of 12–24 h old. Also, flight distance and duration were highest for a temperature range of 16–28°C and a humidity range of 45–90%.

Flight mill studies have been used to characterize flight aptitude of a number of aphid species. The bird-cherry-oat aphid, *Rhopalosiphum padi*, could fly 6.6–8.2 km at 12–20°C (Cheng et al. 1997). The grain aphid, *Sitobion avenae* sustained flights over 2.7–4.8 km at 12–22°C (Cheng et al. 2002), whereas *Myzus persicae* alates flew 2.6 km in 1–5 h (Chen and Feng 2006). The flight distance of the cotton aphid, *Aphis gossypii* under characteristic environmental conditions of spring, summer, and autumn was 3.9, 1.4, and 6.1 km, respectively (Liu et al. 2003). Our data indicate similarity of *A. glycines* flight performance with that of *S. avenae*, which is known as a long-distance migrant. Duration and distance of tethered flight are indicative of an aphid’s capacity to engage in long-distance flight, despite differences in energy use and motivation to sustain tethered flight (Liquido and Irwin 1986). This could lead us to confirm the presumed status of *A. glycines* as a long-distance migrant. Despite the commonness of flight mill studies, we need to use caution when interpreting their results, because they do not necessarily explain flight action under natural conditions (Riley et al.1997).

However, because we only tested winged *A. glycines* produced on soybean, our findings exclusively explain the movement of migrants in summer. To understand flight of soybean aphids produced on *Rhamnus* spp.

Table 2. Effect of the temperature on the flight behavior of 12-h-old winged *A. glycines* adults (75% RH)

Temperature (°C)	Flight distance (km)		Flight duration (h)		Flight speed (km/h)		Percent of fliers
	Max	Mean ± SE	Max	Mean ± SE	Max	Mean ± SE	
12	4.08	1.33 ± 0.25c	3.55	1.13 ± 0.20d	1.71	1.18 ± 0.05d	100
16	18.54	5.12 ± 0.67ab	11.17	4.27 ± 0.49a	1.57	1.22 ± 0.04d	100
20	12.51	4.79 ± 0.83ab	6.80	3.1 ± 0.44ab	2.41	1.43 ± 0.09c	100
24	16.02	6.73 ± 0.78a	6.87	3.96 ± 0.38a	2.40	1.67 ± 0.06b	100
28	10.69	4.79 ± 0.55ab	5.26	2.4 ± 0.27bc	2.78	1.95 ± 0.08a	100
32	6.13	3.2 ± 0.37b	2.13	1.5 ± 0.13dc	3.07	2.08 ± 0.12a	100

Means in the same column followed by different letters are significantly different (Duncan’s multiple range test, $P < 0.05$).

Table 3. Effect of relative humidity on the flight behavior of 12-h-old winged *A. glycines* adults (24°C)

Relative humidity (%)	Flight distance (km)		Flight duration (h)		Flight speed (km/h)		Percent of fliers
	Max	Mean ± SE	Max	Mean ± SE	Max	Mean ± SE	
30	4.55	2.59 ± 0.16c*	2.11	1.39 ± 0.09c	2.81	1.92 ± 0.08a	100
45	11.87	4.19 ± 0.80bc	5.21	2.38 ± 0.34b	2.32	1.68 ± 0.10bc	100
60	8.20	4.70 ± 0.53b	4.44	2.61 ± 0.25b	2.43	1.79 ± 0.07ab	100
75	16.02	6.73 ± 0.78a	6.87	3.96 ± 0.38a	2.40	1.67 ± 0.06bc	100
90	11.44	4.85 ± 0.78b	5.89	3.07 ± 0.34b	2.28	1.49 ± 0.08c	100

Means in the same column followed by different letters are significantly different (Duncan’s multiple range test, *P* < 0.05).

(spring migrants) or fall migrants, additional experiments will need to be conducted. Very likely, flight of these phenological stages differs greatly from summer migrants, which are produced in environments with large abundances of host plants.

Although the time window of optimal flight for *A. glycines* (12–24 h) seems fairly narrow, similar results have been reported for *R. maidis* (Liquido and Irwin 1986). Isard and Gage (2001) suggested that aphids that engage in flight during this narrow temporal window are likely to enter a “long-distance flight mode.” Aphids, whose take-off from the natal plant is delayed, necessarily enter a “local dispersal flight mode.” However, outcomes of either scenario still largely depend on the stability of the atmosphere and more specifically the structure of the surface boundary layer.

The low flight aptitude of 72-h-old *A. glycines* alates in our study was not unexpected. Wind tunnel experiments with *R. padi* showed that 3- to 4-d-old alates were incapable of flight (Isard and Irwin 1996). Johnson (1954) relates this to gradual autolysis of aphid flight muscles 2–3 d after adult molt, which also explains the declining proportion of *A. glycines* initiating flight with increasing age (past 1 d). An alternate explanation is the commonly reported increased flight of insects during the prereproductive period. For example, flight aptitude of certain migratory moths (e.g., *Helicoverpa armigera*, *Mythimna separate*, *Spodoptera exemptata*) seems negatively correlated with reproductive performance (Gatehouse 1994, Wu and Guo 1996). Unpublished data indicated that *A. glycines* alates initiate (asexual) reproduction 24 h after molting. The stronger flight ability of 12- to 24-h-old alates implies that aphid movement mainly occurs before reproduction, which support partly the “oogenesis-flight syndrome” observed in some insects (Johnson 1969, Dingle 1996).

Data on *A. glycines* flight could readily be incorporated into spatially explicit simulation models that represent aphid population dynamics at broader spatial scales (Parry et al. 2006, Zhu et al. 2006). However, although considerable information is available on *A. glycines* biology (Ragsdale et al. 2004), demography (McCornack et al. 2004), and alate production (Hodgson et al. 2004), data are missing on the meteorological factors that influence *A. glycines* ascent (take-off) through the surface boundary layer above a crop. A myriad of novel techniques could help illuminate aphid ascent behavior (Isard and Irwin 1996, Isard and Gage 2001, Hardie and Powell 2002). Simulation mod-

els could yield insights in *A. glycines* spatial and temporal dynamics and constitute the cornerstone of forecasting and strategic pest management protocols.

Also, an appreciation of the underlying factors of *A. glycines* flight may provide baseline information to assess whether parasitoids take advantage of aphid flight for their dispersal (Feng et al. 2007). Research is being carried out to determine whether parasitism affects *A. glycines* flight aptitude (Y.Z., unpublished data). These studies may help predict the establishment potential and efficacy of parasitoids such as *Binodoxys communis*, an Asian braconid released to control the soybean aphid in North America (Wyckhuys and Heimpel 2007, Wyckhuys et al. 2007).

This paper provides insights into biological and environmental mediators of *A. glycines* flight. When supplemented with appropriate data on the meteorological conditions that influence *A. glycines* take-off and the weather patterns that guide long-distance migration, this work could lay the groundwork for management and forecasting protocols at the landscape scale.

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