Field and Laboratory Evaluation of Migration and Dispersal by the Sweet Potato Whitefly, *Bemisia tabaci* (Gennadius)

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Abstract

Although problems associated with the sweet potato whitefly, Bemisia tabaci (Gennadius), are not as dramatic as they were in 1992, they were still significant in 1993. Laboratory research in 1993 focused on defining the cues that result in migratory behavior, specifically host quality. In addition, field studies were conducted to learn more about timing, direction, and distance flown. Our goal is to develop a predictive model that can be used for forecasting whitefly movement. During our behavioral studies, B. tabaci was presented with two cues that lead to disparate behaviors. More than 70% of the whiteflies we tested ended their flights (within three presentations of the cue) when given a choice between settling on a 'host' (550 nm interference filter) and continued flight. Only 6% of the individuals we tested, demonstrated what would be considered to be true migration Both endogenoous and exogenous factors can play an important role in determining when insects will fly. Finally, although the oogenesis-flight syndrome is thought to be a strong component of insect migratory activity, whiteflies do not appear to postpone egg production until after they have engaged in flight. In the field marked whiteflies were also collected in the most distant of these traps. These field results support our hypothesis that most whitefly movement in the fall in the Yuma Valley is in a SW direction (prevailing winds are from the NE). Within a 3 hr time frame whiteflies can travel as far as 2.2 miles from the source field. We examined the effects of female flight distance and eggload. We found significant differences in the eggload of field collected whiteflies versus whiteflies collected in traps at all distances from the source field. There was no relationship between distance flown and eggload. These results may indicate that dispersing individuals are capable of delaying egg laying until a suitable host plant is located

Introduction

Bemisia tabaci (Gennadius), the sweet potato whitefly, is one of the principal pests of vegetables during the spring and fall in the Southwest. In 1992 the sweet potato whitefly was responsible for $56,000,000 in crop losses in Arizona. Crop losses were reduced in 1993, but were still significant. Pesticides do not always provide effective control of this pest, and alternative strategies are necessary. Dispersal and migration are aspects of the biology of the sweet potato whitefly requiring study because an understanding of flight behavior will provide growers with information that will lead to cultural control measures.

Laboratory research in 1993 focused on defining the cues that result in migratory behavior, specifically host quality. In addition, field studies were conducted to learn more about timing, direction, and distance flown. Our goal is to develop a predictive model that can be used for forecasting whitefly movement. This research was supported in part by the State of Arizona, the United States Department of Agriculture: Competitive Grants Program and the Imperial County Whitefly Management Committee.

Materials and Methods

Laboratory Studies

Experiments were conducted to examine the sweet potato whitefly's variability in response to host-plant cues during phototactic flight. A colored filter (that simulates a host plant) was positioned in the side wall of a vertical flight chamber (Blackmer & Phelan, 1991) and illuminated for 3 s during each minute of the whiteflies' flight. Previously we had identified two behaviorally distinct groups within whitefly populations; those that exhibited a station-keeping response (trivial flyers) and those that were migratory. We examined the response of these two groups of whiteflies in the vertical flight chamber and hypothesized that a larger percentage of the individuals that were removed directly from their host would exhibit a dramatic response to the visual target, whereas a larger percentage of the individuals engaging in pre-migratory behaviors would exhibit an inhibited response to the target (n=30 individuals for each group). The individuals engaging in pre-migratory behaviors were collected from the ceiling of the greenhouse shortly after they had left their host plant, so that the time away from the plants would be comparable for the two groups of whiteflies.

Another set of experiments addressed how age (from 1 to 6 days following pupal eclosion) might affect the whitefly's response to the visual target during its phototactic flight. Newly emerged individuals (< 4-h-old) were collected and placed in clip cages on whitefly-free poinsettia (n=20 individuals per clip cage) until they reached the appropriate age. We continued to test each age category until we had obtained 20 flights that were at least 3 min long or until 100 individuals had been given the opportunity to fly.

Males (n=38) and females (n=56) were flown for varying lengths of time, up to 2.5 h to determine if there was a relationship between flight duration and wing configuration. After each flight, the whitefly was collected and weighed and then both pairs of wings were removed at their base. A fore- and hindwing from each individual was photographed. Five characters were measured for each wing (characters previously shown to be polymorphic, Byrne & Houck, 1990) Wing-loading value was included in the analysis as a sixth parameter. Regression analysis was used to determine the relationship between flight duration and wing parameters.

To determine if *B. tabaci* exhibited the typical oogenesis-flight syndrome, females (n=38; collected from poinsettia) were flown for varying lengths of time (from 1 min to 2 h 30 min), weighed, placed in microcentrifuge tubes and stored at -80° C. These samples were later analyzed for levels of vitellogenin/vitellin using a newly developed egg-specific monoclonal antibody (MAB). The MAB was used in conjunction with an enzyme-linked immunosorbent assay (ELISA).

A second experiment examined whether flight activity enhanced egg protein production. Three categories of whiteflies were tested: (1) individuals exhibiting vegetative or station-keeping responses (2) individuals exhibiting pre-migratory behavior, but not given further opportunity to fly in a vertical flight chamber and (3) individuals exhibiting pre-migratory behavior that were flown for varying lengths of time (up to 75 min) in a vertical flight chamber. To obtain an estimate of how much egg protein was in the form of mature eggs versus that found in the haemolymph, fat body or ovaries, we collected an additional 35-45 female whiteflies from both the ceiling and poinsettia (>4 h old). These females were weighed, cleared in xylene for 10 min and mature eggs counted using a phase-contrast microscope.

Other studies were conducted in the greenhouse during the fall. Six heavily infested poinsettia plants were placed in an arena created by partitioning the house with black fabric. Temperature (^{0} C), relative humidity, solar radiance and the number of whiteflies ascending towards the ceiling were recorded. Regression analysis was used to determine relationships between whiteflies ascending and the measured environmental parameters. To determine differences between ascending individuals (putative migrators) and those remaining on the plants (putative trivial fliers), the sex ratio, egg-load and weight of individuals from the two groups were recorded. To determine if the same whiteflies were exhibiting phototactic orientation on consecutive days, individuals that were captured from the ceiling one day were marked with Day-Glo® and returned to the plants. The next day insects were collected from the ceiling. We made comparisons of sex ratio and egg load for dusted and undusted individuals from the ceiling. Finally, behavioral differences were compared for whiteflies remaining on the plants and those that ascended to the ceiling using the vertical flight chamber (Blackmer and Byrne, in press).

Field Studies

Field experiments were conducted at the Yuma Valley Agricultural Center on nine different dates in 1993: July 28, Aug. 3, Sept. 9, 10, 16, 21 and 30 and Oct. 7 to determine the effective migrational range of *B. tabaci*. A 1.8 acre melon, *Cucumis melo* L. "Crenshaw", field planted on June 8 and replanted on Aug. 10 was used as a whitefly source for the trapping studies.

In June the area west and southwest of the melon field was surveyed for placement of muffin fan traps that are capable of capturing insects alive (Figure 1). The traps were powered by 12-volt batteries. These trap locations were determined based on 1992 wind patterns, whereby prevailing winds in the early morning hours (06:00 to 09:00) were predominantly from the northeast. The number and placement of traps were determined using the geostatistical program Geo-EAS. Traps were placed at ground level along an existing network of roads, canals, ditches and fields.

At the beginning of each experiment (12 h before trapping the whiteflies), the melon field was sprayed with 40 lb of Day-Glo® pigment (AX-14 Fire Orange) using a tractor driven spray apparatus. Traps were turned on near daybreak on the day of the experiment. Three hours later whiteflies were collected from the traps using a battery-driven hand-held vacuum cleaner. Collected whiteflies were kept cool and brought directly into the laboratory for sorting. A Black-Ray® lamp was used to determine if fluorescent pigment was present on captured whiteflies. This insured that collected whiteflies originated from the marked field. Dispersal records were determined and a geographic information system (GIS), a computer database that organizes information in a spatial framework, was used for data analysis. On the morning of each experiment, temperature, humidity, wind direction and wind speed were determined at 5 minute intervals using a portable weather station (Weather Monitor II®, Davis Instruments, Hayward, CA).

Results and Discussion

Laboratory Studies

Byrne and Houck (1990), demonstrated that male and female *B. tabaci* are polymorphic in their wing configurations. They proposed that individuals captured outside the field were 'migrants,' whereas those whiteflies that remained within the source field were trivial fliers.

During our behavioral studies, *B. tabaci* was presented with two cues that lead to disparate behaviors. The mercury-vapor lamp represents sunlight and evokes take off, followed by extended flight. At the individual level, this response could lead to migration and at the population level to dispersal. The 550 nm narrow-band interference filter simulates the host plant and evokes a totally different set of behaviors, which invariably leads to cessation of flight. More than 70% of the whiteflies we tested ended their flights (within three presentations of the cue) when given a choice between settling on a 'host' (550 nm interference filter) and continued flight. We had hypothesized that a larger percentage of the 'pre-migratory' whiteflies would not respond to the host-plant cue until they had flown for a considerable period of time; however, their response to the target was not noticeably different from whiteflies that were engaging in 'station-keeping' behaviors prior to being tested in the vertical flight chamber. Only 6% of the individuals we tested, demonstrated what would be considered to be true migration It has been suggested that whiteflies are only capable of discerning colors, such as those associated with their host plants, from a few centimeters away (Coombe, 1982). In all of our experiments, the host-plant cue was less than 50 cm from the whitefly. In a field situation, whiteflies engaging in pre-migratory behaviors (takeoff followed by a phototactic response) would probably be between 10 and several 100 meters above their potential hosts. Under these circumstances, the lack of pertinent visual stimuli might lengthen the duration of the migratory phase.

When we examined the morphological characteristics of the wings of *B. tabaci* we found that there was an inverse relationship between wing dimensions and flight duration for males. These results agree with the findings of Byrne and Houck (1990), where trivial flying males had larger wing measurements than 'migratory' individuals. We found no relationship, however, between flight duration and wing characteristics for females. The different statistical techniques that were used may account for these inconsistencies. Byrne and Houck (1990) suggested that these slight differences in wing parameters could mean that populations of *B. tabaci* are in the process of developing dispersal dimorphism. However, it is possible that these differences merely represent inherent morphological variability and are not necessarily related to dispersal capabilities. For an insect that relies primarily on the wind for long-distance movement it is hard to imagine how the small differences in wing configuration that currently exist could assist them.

For a number of years (since Johnson, 1969), entomologists have believed that the development of ovaries and the development of flight apparatus are physiologically competing processes (Sappington & Showers, 1992). Interestingly, we found that *B. tabaci* does not appear to exhibit the typical migratory syndrome. We found that levels of egg proteins were actually higher in long-distance fliers and pre-migratory individuals than in short-duration fliers and settled individuals. Clearly, *B. tabaci* is capable of long-distance flight with high levels of egg protein.

Within the order Homoptera, migrants are often easily distinguished from the non-migrants on the basis of wing morphology. For example, aphids switch from the production of apterae to the production of alatae when host quality begins to deteriorate (Watt and Dixon, 1981), crowding occurs (Shaw, 1970; Watt and Dixon, 1981) or daylength changes (Matsuka and Mittler, 1978). The delphacid, *Prokelisia marginata* (Van Duzee) produces macropterous forms so that movement between the short and the tall, more nutrition, *Spartina alterniflora* Lois can occur (Denno, 1977, 1978, 1979). There are many other examples of delphacids and cicadellids that exhibit alary polymorphism (see Taylor, 1985). On the other hand, three major North American migrants, *Macrosteles fascifrons* (Stal), *Circulifer tenellus* (Baker) and *Empoasca fabae* (Harris) rarely exhibit such variability in wing length. In the absence of alary polymorphism, changes in the behavioral and/or physiological state must be responsible for the variation in flight capacity. In male *B. tabaci*, the differences we found in wing morphology were negligible and in the opposite direction of what would be expected for a migrant. The effect of reproductive maturity on flight duration also ran contrary to the current dogma (oogenesis-flight syndrome). Examination of other factors that can affect an insect's physiological state could prove more informative (i.e., JH titer and availability of flight fuels).

Several facts suggest that changes in the behavioral state of *B. tabaci* best explain its variability in flight duration. In the present experiments, we found that a small percentage of *B. tabaci* exhibited behaviors that are generally accepted as evidence for migration (Blackmer *et al.*, submitted). In a previous study, whiteflies in a greenhouse exhibited two distinctly different behaviors: the majority of whiteflies exhibited station-keeping responses that kept them in contact with their host plant, while a small percentage of the whiteflies exhibited what we termed 'pre-migratory behaviors' (Blackmer and Byrne, in press). When these two groups of whiteflies were tested in the vertical flight chamber the pre-migratory individuals flew for significantly longer periods than did the settled individuals. We also found that whiteflies would takeoff in flight at all hours of the photoperiod, but that their long-duration flights were confined primarily to the first 2 h after sunrise. Individuals that flew for long periods also had higher rates of climb than did short-duration fliers (Blackmer and Byrne, 1993). These two later characteristics would enable the long-distance fliers to escape the surface-boundary layer during the day when wind speeds are comparatively low. Once above the surface-boundary layer these insects probably drift passively in the atmosphere where meteorological conditions would have a profound effect on the distance flown. Nevertheless, it appears that a complex set of behaviors is essential for these insects to successfully leave their host plant, travel on the wind and then return to find a suitable host.

The number of whiteflies ascending to the ceiling was greatest from 0830 to 1000 h. Temperature was the best predictor. The addition of solar radiance, relative humidity and time of day only accounted for 6% more of the variance in ascent. The proportion of individuals exhibiting a positive response to the sky light never exceeded 5% of the population and the majority of these individuals were females. A higher portion of females on the ceiling contained eggs when compared to females on plants. Weights for the two groups of females did not differ statistically. The mark/recapture study showed that the phototactic response was short-lived; only 6.95 ± 2.39% returned to the ceiling the next day. Whiteflies exhibiting a phototatic response in the greenhouse were more likely to engage in long-duration flight in the flight chamber.

Both endogenoous and exogenous factors can play an important role in determining when insects will fly (Johnson 1969, Rankin and Rankin 1979, Denno 1985). Our results agree with these statements and temperature seems to be the largest determining factor. The other important finding that follows previous work (Blackmer and Byrne, 1993) is that there are important relationships between propensity to respond to phototactic cues and ability to engage in long-duration flights. Finally, although the oogenesis-flight syndrome is thought to be a strong component of insect migratory activity, whiteflies do not appear to postpone egg production until after they have engaged in flight.

Field Studies

Preliminary analysis of weather patterns in 1993 indicated that prevailing winds in the early morning in the Yuma Valley were from the Northeast and followed cold air drainages. In July and August marked whiteflies were collected in traps as far away as 2.5 miles from the source field. Postplots of the total trap counts for the Aug. 9 sampling date are shown in Figure 2. In September and October additional traps were placed as far as 3.5 miles from the source field. Marked whiteflies were also collected in the most distant of these traps. Postplots of the total trap counts for the September 9 sampling date are shown in Figure 1. These field results support our hypothesis that most whitefly movement in the fall in the Yuma Valley is in a SW direction (prevailing winds are from the NE). Within a 3 hr time frame whiteflies can travel as far as 2.2 miles from the source field (Figure 1, trap 127). However, only a few marked whiteflies were trapped at this distance. A better estimate of the effective migrational range of the sweet potato whitefly is 2.5 miles (Figure 1, trap 11).

Cost of Migration

We examined the effects of female flight distance and eggload (Table 1). We found significant differences in the eggload of field collected whiteflies versus whiteflies collected in traps at all distances from the source field. There was no relationship between distance flown and eggload. These results may indicate that dispersing individuals are capable of delaying egg laying until a suitable host plant is located.

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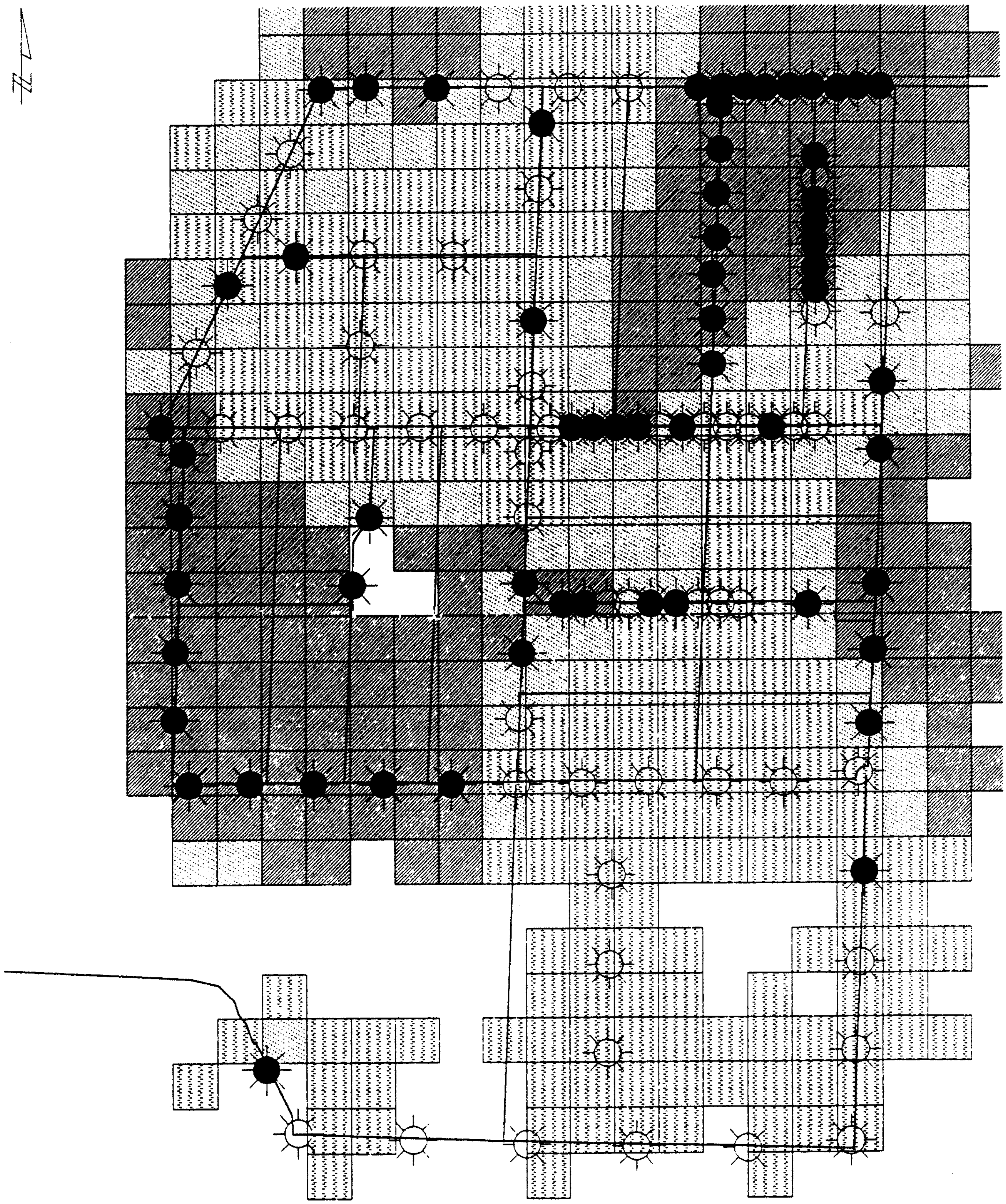
Table 1. Relationship between distance traveled and egg load for the sweet potato whitefly, *Bemisia tabaci*.

	September 9		
Distance (m)	N	Mean	SE
Field	50	2.5	0.18
500	106	3.6	0.23
1,000	114	3.3	0.23
1,500	116	4.2	0.21
2,000	89	3.9	0.26
2,500	53	3.8	0.36
	September 10		
500	97	4.0	0.25
1,000	130	4.4	0.20
1,500	98	4.0	0.24
2,000	116	3.8	0.23
2,500	55	3.9	0.40

September 9, 1993



1993 Grid Design