Ultraviolet-Deficient Greenhouse Environment Affects Whitefly Attraction and Flight-Behavior

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ABSTRACT The effect of a UV-deficient environment on the attraction and dispersal behavior of whiteflies, *Bemisia argentifolii* (Bellows & Perring), and on the transmission efficiency of the whitefly-borne tomato yellow leaf curl geminivirus, was tested under field conditions and through controlled experiments. We found that the rate of tomato yellow leaf curl virus-disease spread to tomato plants grown under walk-in tunnels covered with regular greenhouse plastic sheets increases sharply with time, whereas the virus infection-rate under UV-absorbing sheets proceeds at a very slow pace. Average number of whiteflies trapped under regular plastic sheet tunnels was significantly higher than numbers trapped in UV-absorbing plastic sheet tunnels. Similarly, the average number of whiteflies trapped on yellow-sticky traps placed on the outside walls of tunnels covered with regular plastic was higher than the number trapped on the outside walls of tunnels covered with UV-absorbing plastic sheets. No differences were found in the whitefly's ability to transmit tomato yellow leaf curl virus under the two types of plastic covers. Whitefly dispersal pattern under the two types of plastic covers was examined using a release-recapture experiment. In each type of walk-in tunnel we established a grid of yellow-sticky traps forming two concentric circles: an inner and an external. Under UV-absorbing tunnels, significantly higher numbers of whiteflies were captured on the internal circle of traps than the external circle. The fraction of whiteflies that were captured on the external circle was much higher under regular covers, when compared with UV-absorbing covers, suggesting that filtration of UV light hindered the ability of whiteflies to disperse inside these plastic tunnels. Our results indicate that the mechanisms by which UV-deficiency protects covered crops from insect infestation and spread of viruses are that the lack of UV interferes with insect flight orientation; and that the lack of UV radiation alters the normal behavior of the invading insects, resulting in reduced dispersal activity.

KEY WORDS whiteflies, flight behavior, tomato yellow leaf curl virus, pest management, ultraviolet light

During the past 20 yr, whiteflies, *Bemisia argentifolii* (Bellows & Perring), have become a major pest of crops throughout many tropical and subtropical zones of the world. The damage that whiteflies inflict on their plant hosts results from sap sucking, the heavy deposition of honeydew, and the induction of phytotoxic disorders such as silverleaf in cucurbits and uneven ripening in tomatoes. In addition to damage caused by direct feeding pressure, whiteflies transmit 50–60 different geminiviruses, including the notorious tomato yellow leaf curl virus, thus causing a large range of viral diseases (Markham et al. 1994, Brown et al. 1995).

Lacking an olfactory reaction (Mound 1962), whiteflies rely heavily on their vision for navigation and orientation. Visual sensitivity of insects to the UV component of the light spectrum was first described before the turn of the 20th century (Lubbock 1882). Since then, the spectral sensitivities of insects to both the UV and visible ranges of the spectrum have been extensively investigated (Bertholf 1931, 1932; Mound 1962; Vaishampayan et al. 1975a, 1975b; Coombe 1981, 1982; Goldsmith 1994). Previous studies on the visual sensitivity of whiteflies found that these insects are strongly attracted to the UV wavelength (Mound 1962). Therefore, interference with the UV-vision may lead to interruption of orientation and dispersal processes by whiteflies.

Recently, we have found that vegetable crops are efficiently protected from insect pests, and viral diseases transmitted by them, when grown in walk in tunnels or greenhouses covered either with UV-absorbing polyethylene films or with UV-absorbing 50-mesh nets (Antignus et al. 1996a, 1996b, 1998). These covers act as filters that eliminate the majority of the UV portion of the light spectrum between 280 and 380 nm. This light filtration has been shown to significantly reduce the infestation of crops by a wide range of insect pests, including whiteflies, aphids, thrips and leaf miners (Antignus et al. 1996a, 1996b, 1998). We also found that tomatoes and cucumbers grown under

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these UV-absorbing greenhouse covers were highly protected against whitefly-borne viruses such as tomato yellow leaf curl virus and cucumber yellowing stunting disorder virus (Antignus et al. 1996a, 1996b). These results lead us to suggest that the elimination of the UV portion of the light spectrum is interfering with the "UV vision" of insects, and as a consequence may affect their ability to orient themselves to the crop (Antignus et al. 1998, 2000).

In the current study we investigated the effect of UV-deficient environments on the rate of spread of the whitefly-borne tomato yellow leaf curl virus. We looked at behavioral aspects of natural populations of whiteflies invading a commercial crop covered by UV-absorbing plastic sheets. In particular, we investigated the effect of UV-absorption on the approach of whiteflies to structures covered with these plastics, on whiteflies penetration into these structures, and, once inside, on the flight activity of the invading whiteflies.

Materials and Methods

The polyethylene plastic sheets used throughout the experiments reported below are as follows: AB-IR-antivirus, a UV-absorbing sheet (IR-UV), and a regular non-UV-absorbing AB-IR-diffused (IR) (Ginegar Plastic Products, Ginegar, Israel). Both polyethylene-sheets were 0.15 mm thick. Light transmittance spectrum for both plastic sheets was previously characterized and is reported in Antignus et al. (1996).

Natural Whitefly Infestation and Tomato Yellow Leaf Curl Virus Dissemination in a UV-Deficient Environment. *Experient 1: Effect of Tunnel Cover on Whitefly Density and Tomato Yellow Leaf Curl Virus Infection Rate.* Field experiments were carried out in the Besor region, South Israel. Plants were grown in a complex of 12 walk-in tunnels (6 by 6 by 2.7 m) covered either with IR-UV or IR plastic sheets. The front and rear ends of each tunnel were covered with a 50-mesh screen. However, the entrances were not sealed to allow the infiltration of insects. Tunnels were 1.5 m apart from each other and the surrounding soil (in-between and around the experimental site) was kept bare. Each pair of contiguous tunnels was considered a block, forming a total of six contiguous blocks. Each block consisted of an IR and an IR-UV plastic sheet-covered tunnel, providing a total of six replicated tunnels per type of plastic sheet. In each block, the two different tunnel types were established at random.

Seventy tomato yellow leaf curl virus-susceptible tomato 'Hazera 144' (Cohen and Antignus 1994) were transplanted on September 1997 to each one of the tunnels. Plants were maintained by routine commercial procedures, except that insecticides were not applied to plants during the course of the experiment. The relative population size of infiltrating silverleaf whitefly known as the vector of tomato yellow leaf curl virus (Cohen and Antignus 1994) was estimated by monitoring the insect with two yellow sticky traps (14 by 19 cm) per tunnel. Traps were placed horizontally (sticky side facing up) inside the tunnels near the entrances. Traps were serviced at intervals of 7–10 d starting immediately after planting. The accumulation of tomato yellow leaf curl virus disease incidence in tomato plants was recorded visually at weekly intervals.

Experiment 2: Whitefly Trapping on the Outside Walls of Experimental Tunnels. To investigate the ability of whiteflies to reach the experimental tunnels, we established a grid of four yellow sticky traps on the outside walls of one IR-UV and one IR tunnel located a few meters apart from each other. The position and orientation of the traps on both IR-UV and IR tunnel walls was the same. The study was conducted on two independent dates: 23 and 29 July 1998. The experiments consisted of following trapping levels of whiteflies during a 4-h period. Traps were changed on an hourly basis, and the amount of trapped whiteflies per hour and trap was determined. Each trap-collection represented a replicate of the experiment (e.g., replication in time). In each experimental date, we started our observations at 0730 hours and ended at 1130 hours, when whitefly flight activity is at a peak (Cohen and Melamed-Madjar 1978).

Whitefly Behavior Under UV-Absorbing and Non-UV Absorbing Greenhouse Plastic Sheets. *Experiment 1: Effect of UV-Filtration on the Ability of Whiteflies to Transmit Tomato Yellow Leaf Curl Virus.* This experiment investigated the effect of plastic sheets on the ability of whiteflies to transmit the disease to healthy plants. That is, once the vector acquires the virus and reaches the host plant, will the elimination of UV light affect the transmission of the pathogen to the plant? This point was investigated as follows: after a 48-h acquisition period on tomato yellow leaf curl virus infected plants, whiteflies ($\approx$200) were released into cages (0.5 by 0.5 by 0.5 m) covered either with regular nonabsorbing or UV-absorbing plastic sheets. Each cage contained 10 tomato yellow leaf curl virus susceptible tomato plants. Each experiment consisted of two cages per type of cover-sheet. After a 48-h exposure period, plants were sprayed with imidacloprid (Confidor, Bayer, Leverkusen, Germany) to kill the whiteflies. Plants were placed in an insect-free greenhouse and monitored for 30 d to allow the development of disease symptoms. After 30 d, plants without disease symptoms were considered healthy, i.e., non-infected plants. The experiment was repeated on eight different occasions.

Experiment 2: Effect of UV on Whiteflies Dispersal Behavior. To follow the dispersal ability of whiteflies under the effect of UV-absorbing and non-UV absorbing sheets, we conducted a release-recapture experiment in the walk-in tunnels described at the beginning of this section. For each type of cover sheet we used six walk-in tunnels per experimental date. In each tunnel we established two concentric circles of yellow-sticky traps: an inner circle of traps with a total of eight sticky traps, and an outer circle of 12 traps (Fig. 1). The inner circle had a radius of 1 m (e.g., distance from the center), whereas the outer circle had a radius of 2 m. In each tunnel, and on each experimental date, we simultaneously released

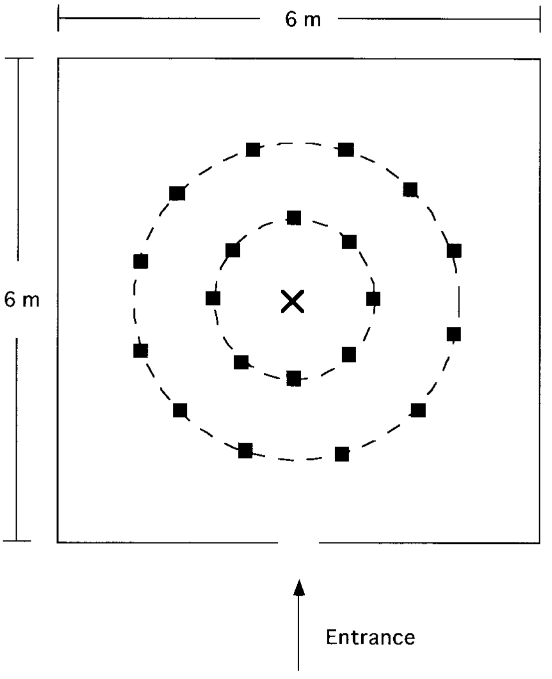

Fig. 1. Diagram of whiteflies release-capture experimental design. Black squares represent placement of yellow sticky traps. X, represents release site. The inner circle had a radius of 1 m, whereas the outer circle had a radius of 2 m from the center.

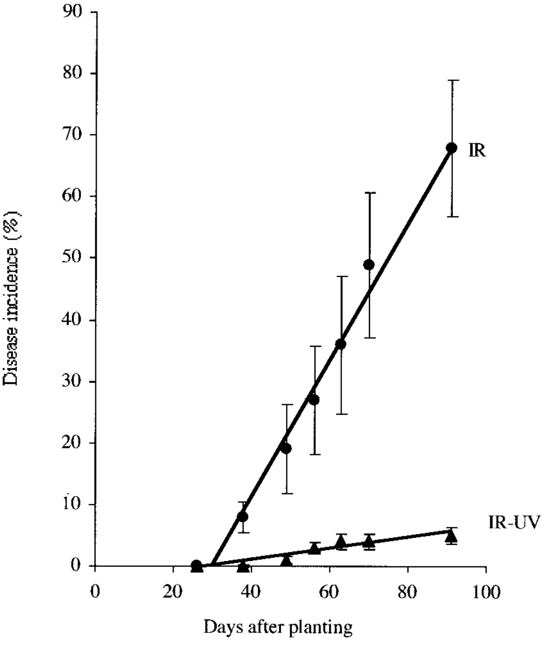

Fig. 2. Tomato yellow leaf curl virus disease advancement rate in tomato plants grown in tunnels covered either with regular (IR) or UV-absorbing (IR-UV) polyethylene sheets. Tomato yellow leaf curl virus disease incidence was scored visually, based on the appearance of symptoms and expressed as the percentage of the total number of plants that were infected. The infestation rate was described using linear regression. The regression lines were estimated from the average amount of infested plants per date. Estimated lines were calculated starting from the first date when plants started to express symptoms. The estimated slope for IR-UV was $b = 0.09$, whereas for IR $b = 1.06$.

≈9,000 whiteflies. Whiteflies colonies were reared on cotton plants grown in muslin-covered cages held in an insectary greenhouse. Early in the morning, cotton plants (containing whiteflies) were placed in light-tight plastic cages, positioned in the center of the circles in the walk-in tunnels, and the whiteflies were released. Immediately after the release the cotton plants were removed and 2 d later, traps were collected and whiteflies counted. The number of trapped whiteflies in each of the tunnels was expressed as the relationship between whiteflies per trap trapped in the inner circle versus whiteflies per trap trapped in the outer circle. The experiment was conducted twice: in August 1997 and in August 1998.

Statistical Analysis. Data on whitefly infestation rates under UV absorbing and non-UV absorbing sheets was described using linear regression. Regression lines for the increase in virus infection rates under each cover-sheet were estimated from the average amount of infected plants per date. Estimated lines were calculated starting from the first date when plants started to express symptoms. Data from previous dates were not included because they corresponded to the initial disease incubation period and, therefore, infected disease plants were invisible to our visual diagnostic method. For each regression line, slopes were estimated and a test of homogeneity of regression lines was applied to the data to uncover differences in infection rates (Sokal and Rohlf 1981). Differences in the number of whiteflies infiltrating UV and non-UV walk-in tunnels on each servicing date was tested with individual *t*-tests for each date (Sokal and Rohlf 1981). The average number of whiteflies per trap per tunnel-type was used as a replicate, thus, providing us with six replicates per treatment per sampling date.

Differences in the mean number of whiteflies trapped per hour on the outer walls of UV and non-UV tunnels were investigated with a Mann–Whitney nonparametric test (Sokal and Rohlf 1981). Similarly, differences in the amount of plants acquiring the virus from vectoring whiteflies under the two types of plastic sheets (physiological ability) were tested with a Mann–Whitney test. The relationship between whiteflies trapped in the inner circle versus the outer circle under the two plastic sheets was also tested using a Mann–Whitney test.

Results

Natural Whitefly Infestation and Tomato Yellow Leaf Curl Virus Dissemination in a UV-Deficient Environment. Fig. 2 shows the rate of disease spread under IR and IR-UV plastic sheets. Rate of disease incidence with time increased sharply ($b = 1.06$) in

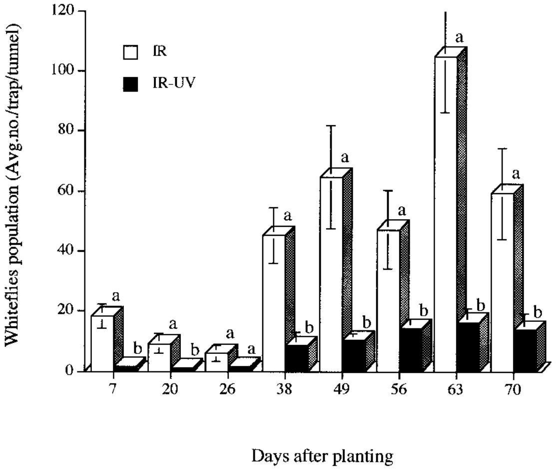

Fig. 3. Trapping of whiteflies in tunnels covered with either regular (IR) or UV-absorbing (IR-UV) polyethylene sheets. Tomato plants were grown in walk-in tunnels covered with the compared plastics. Two yellow sticky traps were placed in each tunnel, for whitefly monitoring. Means ± SEM with different letters differ significantly at $P < 0.05$ when analyzed by Student *t*-test.

walk-in tunnels covered with IR sheets. At the end of the experiment, 91 d after planting, 68% of the plants grown under regular (IR) plastic sheets were severely infected. In contrast, infection-rate under UV-absorbing (IR-UV) plastic sheets proceeded at a very slow pace ($b = 0.09$) (Fig. 2). At the end of the experimental period only 5% of the plants grown under the UV-absorbing IR-UV plastic sheets were infected. The differences in infection rate (e.g., differences between slopes) were highly significant ($F = 296$; df = 1, 10; $P < 0.01$). Under the UV-absorbing sheets, most of the tomato yellow leaf curl virus-infected plants were found next to the entrance of the tunnels, whereas under the regular covers, infected plants were dispersed all over the tunnel.

The average number of whiteflies per sampling date trapped on yellow sticky traps placed inside non-UV absorbing (IR) and UV-absorbing (IR-UV) walk-in tunnels is shown in Fig. 3. Average numbers of whiteflies trapped per sampling period under IR plastic sheet tunnels was significantly higher than numbers trapped in IR-UV plastic sheet tunnels in seven of eight times tested. Differences in trapped whiteflies between the two types of plastic sheet walk-in tunnels become greater 38 d after planting (Fig. 3). Similarly, the average number of whiteflies per trap per exposition-period trapped on the outside walls of IR and IR-UV covered tunnels was significantly different ($U_s = 6.0$, $n_1 = 7$, $n_2 = 7$, $P < 0.05$). Whiteflies were trapped in higher numbers outside IR tunnels (average of 80.1 ± 26 whiteflies per trap per hour) than on the outside wall of IR-UV walk-in tunnels (average of 32.5 ± 13 whiteflies per trap per hour).

Table 1. Effect of UV absorption on the dispersal of whiteflies inside tunnels covered with IR or IR-UV plastic sheets

Type of plastic covers	Avg no. of whiteflies per trap in inner vs outer circle		
	Ratio IC/OC	Avg no. of whiteflies per trap IC:OC	Avg total no. of whiteflies IC:OC
		Experiment I	
IR	0.78	128:208	1,027:2,492
IR-UV	4.28	469:146	3,755:1,750
U_s	1.5		
P	<0.01		
		Experiment II	
IR	2.73	299:114	2,390:1,396
IR-UV	6.88	657:93	5,258:1,116
U_s	0.5		
P	<0.01		

Each experiment was composed of six repetitions. Inner circle, 1 m; outer circle, 2 m from release site.

Whitefly Behavior Under UV-Absorbing and Non-UV Absorbing Sheets. Virus-susceptible tomato plants were placed in cages (0.5 by 0.5 by 0.5 m) covered with the two types, IR and IR-UV, plastic sheets. After being exposed for 48 h to viruliferous whiteflies, the proportion of plants expressing disease symptoms under the two types of plastic covers was similar (under IR sheets 51 ± 10% of plants while under IR-UV 59 ± 7%; $U_s = 94$, $n_1 = 14$, $n_2 = 14$, $P > 0.05$).

Results on the effect of plastic covers on the dispersal behavior of whiteflies are shown in Table 1. In both experiments, under UV-absorbing tunnels, significantly higher numbers of whiteflies were captured on the internal circle of traps than the outer circle. However, under regular covers, the fraction of whiteflies that were captured on the outer circle was much higher when compared with the UV-absorbing covers, suggesting that filtration of UV light affect the ability of whiteflies to disperse inside plastic tunnels.

Discussion

Crops grown under UV-absorbing greenhouse plastic sheets or screens are highly protected against insect pest infestation (Antignus et al. 1996, 1998). The current study confirms this fact by showing that penetration of whiteflies into walk-in tunnels covered with UV-absorbing polyethylene sheets is strongly inhibited (Fig. 3). Furthermore, our findings that fewer whiteflies were captured on traps placed on the outside walls of UV-absorbing plastic sheet tunnels than on traps placed on regular tunnels, suggests that lack of UV radiation not only affects whiteflies penetration into the covered tunnels but also the attraction of whiteflies to these structures.

Because of the physiological ability of whiteflies to transmit tomato yellow leaf curl virus is probably not affected by the type of plastic sheet, differences in infection-spread rate between the two types of plastic covers (Fig. 2) can be attributed to the reduced attraction and penetration of whiteflies to UV-absorbing tunnels. However, the relationship between whitefly penetration into regular tunnels and UV-absorbing tunnels was ≈5:1, which seems insufficient by itself to explain the sharp differences in the rate of spread of tomato yellow leaf curl virus infection between the two types of plastic (≈10:1). Similar results were recently obtained by Antignus (et al. 1999), in which they show that tomato yellow leaf curl virus disease level reached 15% in 250-m^2 greenhouses covered by UV-absorbing plastic, whereas under regular plastic disease level reached nearly 80%. However, in the study by Antignus (et al. 1999), the difference in the number of whiteflies trapped under the two covers was found to be small and statistically insignificant, suggesting that whitefly mobility inside greenhouses more than whitefly penetration to these big structures is responsible for the differences in infection level. This point is strengthened by our findings, which suggest that the decreased dissemination-rate of tomato yellow leaf curl virus under UV-absorbing tunnels seems to be the result of the reduced dispersion ability of whiteflies under these types of structures. Moreover, a further confirmation of this hypothesis is the fact that in our study tomato yellow leaf curl-infected plants under the UV-absorbing sheets were mainly located next to the entrance of the tunnels while under the regular covers infected plants were dispersed all over the tunnel. Thus, we can conclude that the modification in the dispersion, and flight, behavior of whiteflies under UV-absorbing plastic sheets is an important mechanism, which can explain the differences in whitefly infestation and tomato yellow leaf curl virus dissemination rates.

Nearly 40 yr ago, Mound (1962) found that two groups of light transmitted wavelengths, the blue/UV and the yellow sections of the spectrum, attract *B. tabaci.* Based on his results he postulated that *B. tabaci* is attracted either to yellow, or to UV, but not to both at the same time. He indicated that the sensitivity to short wavelength radiation would result in a strong stimulus for whiteflies individuals to fly toward the sky on a sunny day. He hypothesized that the reaction of whiteflies to UV light is related to migratory behavior, and suggested that yellow radiation induces vegetative behavior, and may be a component of the host selection mechanism of whiteflies. Our results agree and confirm Mound's postulations. Under the UV-absorbing plastic sheets, the signal for migratory behavior (UV light) is absent but the yellow signal for landing is present. Thus, in the release-recapture experiment most of the whiteflies trapped in the UV-absorbing plastic tunnels land, as expected, in the inner circle of traps rather than flying to the outer circle. In contrast, under regular plastic sheets both signals (UV and yellow) are present. Based on Mound's postulate we expected that the flight distance of the whiteflies would be the resultant of two "contrasting" signals: the flight toward the sky because of the existence of UV light and the drive to land caused by the signal of yellow wavelengths. Thus, we expected that whiteflies would tend to move in a centrifugal manner away from the center of release toward the walls of the UV-transmitting plastic tunnel, resulting, as observed, in a higher trapping level in the outer circle of traps.

Recently, Costa and Robb (1999) examined the effect of UV-absorbing plastic sheets on the flight behavior of thrips and whiteflies. They established a series of choice experiments where insects were released from a box at the center of two mini-tunnels covered with different plastic sheets. Their results clearly showed that most of the insects (>85% of the whiteflies and >90% of the thrips) move, and are trapped, inside tunnels covered with regular plastic. This indicates a distinct preference of both whiteflies and thrips to enter tunnels that transmit higher levels of UV light (Costa and Robb 1999), and are in agreement with our present and previous results (Antignus et al. 1996, 1998). However, when Costa and Robb (1999) released whiteflies at one extreme of a single tunnel covered either with regular or UV-absorbing plastic, they did not find any significant difference in the dispersal ability of whiteflies inside the two types of plastic tunnels. They interpreted their results as an indication that lack of UV light has no obvious negative effect on the flight behavior of whiteflies (Costa and Robb 1999). These results do not agree with our results and interpretations. The discrepancies between Costa and Robb's (1999) results and conclusions and ours may be related to two important differences in the experimental design of the two studies: (1) The UV-absorbing plastic used by Costa and Robb (1999) was different than the one used by us. Although IR-UV plastic used by us has no transmission of UV light between 300 and 350 nm (Antignus et al. 1996), the plastic used by Costa and Robb (1999) allows ≈15% transmittance of UV light in these wavelengths. Thus, it is possible that the differences in UV-blocking capacity of the plastics used in the two studies account for the observed differences in whiteflies flight behavior. (2) The space inside the tunnels available for whiteflies flight was vastly different between the two experiments. The size of tunnels used by Costa and Robb (1999) was 1.8 by 0.5 by 0.5 m (length, width, height), which results in a volume of 0.45 m^3. In contrast, the walk-in tunnels used in our study measured 6 by 6 by 2.7 m, giving a volume of 97.2 m^3. Thus, although we did not investigated this aspect, it is highly possible that the difference in the results of the two studies are linked to the effect of small volumes on the flying behavior of whiteflies, and not on the effect of UV on flight. Whiteflies being released from a box have a tendency to fly upward (Cohen 1990, van Lenteren and Noldus 1990). Thus, it is quite possible that in Costa and Robb's (1999) experiment, whiteflies first collide with the tunnel's ceiling, which is only at a height of 0.5 m from the release point, modifying their flying and dispersion behavior within these small space tunnels.

The results of the current study indicate that the blocking of UV light protects covered crops from infestation by insects and spread of viruses in at least two ways: (1) insects are not attracted to structures lacking UV, and fewer insects invade greenhouses covered with UV-absorbing cladding material. (2) Lack of UV radiation alters the normal behavior of the invading insects, resulting in reduced flight activity. Under these conditions the efficiency of virus transmission is reduced.

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