Characterization of Resistance, Evaluation of the Attractiveness of Plant Odors, and Effect of Leaf Color on Different Onion Cultivars to Onion Thrips (Thysanoptera: Thripidae)

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ABSTRACT Onion thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), is a worldwide pest of onion, *Allium cepa* L. In field studies on onion resistance conducted in 2007 and 2008 using 49 cultivars, 11 showed low leaf damage by *T. tabaci*. In laboratory studies, the 11 cultivars, along with two susceptible checks and four additional cultivars, were evaluated to characterize resistance to *T. tabaci* and to determine if color and/or light reflectance were associated with resistance to *T. tabaci*. No-choice tests were performed with adults and the numbers of eggs and larvae were counted on each cultivar after three and 10 d, respectively. In choice tests in which all cultivars were planted together in a circle in a single pot, 100 adults were released and the number of adults on each plant was evaluated 24 h later. The behavioral response of walking *T. tabaci* adults to plant odors was studied in a glass Y-tube olfactometer. The reflectance spectrum of leaves was measured using a UV-VIS spectrophotometer. Results indicate that resistant cultivars showed an intermediate-high antibiotic effect to *T. tabaci* and all of them showed a very strong antixenotic effect. There were no significant preferences in the response of walking *T. tabaci* adults to plant odors. The two susceptible cultivars had the highest values of leaf reflectance for the first (275–375 nm) and second (310–410 nm) theoretical photopigment-system of *T. tabaci*, and these values were significantly different from most resistant cultivars. These results suggest a strong response of *T. tabaci* to onion cultivars with higher reflectance in the ultraviolet range (270–400 nm). Overall, these results appear promising in helping to identify categories of resistance to *T. tabaci* in onions that can be used in breeding programs.

Resumen El trips de la cebolla, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), es una plaga cosmopolita de la cebolla, *Allium cepa* L. En estudios en campo entre 2007 y 2008, se evaluó la resistencia de 49 genotipos de cebolla, y 11 mostraron menor daño de la hoja por *T. tabaci* (Diaz-Montano et al. 2010). En estudios en laboratorio, los 11 genotipos, además de dos testigos susceptibles y otros cuatro genotipos fueron evaluados para caracterizar resistencia a *T. tabaci* y para determinar si el color y/o luz reflejada por las hojas estaba asociado con resistencia a *T. tabaci*. Experimentos de no-selección fueron llevados a cabo con adultos y el número de huevos y larvas fue contado en cada genotipo después de 3 y 10 días, respectivamente. En experimentos de libre selección, diferentes genotipos fueron sembrados en círculo en un mismo recipiente, 100 adultos fueron liberados y el número de adultos en cada planta fue contado 24 horas después. La respuesta de adultos de *T. tabaci* hacia olores de las plantas fue estudiada usando un olfactómetro de vidrio en forma de Y. La reflectancia del espectro de las hojas fue medida usando un espectrómetro Ultravioleta-Visible (UV-VIS). Los resultados indican que los genotipos resistentes mostraron un nivel intermedio-alto de antibiosis a *T. tabaci* y un nivel muy fuerte de antixenosis. No se presentaron diferencias significativas en la preferencia de adultos de *T. tabaci* hacia olores de plantas. Las variedades susceptibles tuvieron los valores mas altos de luz reflejada en el primer (275–375 nm) y segundo (310–410 nm) sistema teórico del fotopigmento de *T. tabaci* y estos valores fueron significativamente diferentes a valores en la mayoría de genotipos resistentes. Estos resultados sugieren una fuerte atracción de *T. tabaci* a variedades de cebolla con las mas altas reflectancias en el rango UV (270–400 nm). En general, estos resultados son promisorios y ayudan a identificar las categorías de resistencia de la cebolla a *T. tabaci* que pueden ser incluidas en programas de mejoramiento de cebolla.

KEY WORDS *Thrips tabaci*, *Allium cepa*, onion resistance, olfactometer, leaf color

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Onion thrips, *Thrips tabaci* Lindeman (Thysanoptera: Thripidae), is believed to be a native from the eastern Mediterranean region (Mound and Walker 1982, Mound 1997). *T. tabaci* is a polyphagous pest with a wide host range of >100 plant species in >40 families (Ghabn 1948, Morison 1957, Ananthakrishnan 1973). However, onion is a favorite host (Lewis 1973, 1997) and *T. tabaci* is a cosmopolitan pest of onions wherever they are grown (Lewis 1997), including New York state where a total of 4,330 ha were planted in 2010 (NASS 2011).

The rapid development time of *T. tabaci* from egg to adult in <15 d at temperatures between 23 and 30°C (Lall and Singh 1968, Gawaad and El-Shazli 1971, Edelson and Magaro 1988, Arrieche et al. 2006) and its high reproductive capacity frequently lead to population outbreaks of this thrips species, especially in hot, dry weather (Bailey 1934, Rueda et al. 2007). *T. tabaci* feeding on onion causes silvery leaf spots that turn into white blotches followed by the development silvery patches along the leaves (Bailey 1938), and this reduces the photosynthetic ability of the plant (Parrella and Lewis 1997). Its feeding can reduce onion bulb weight (Kendall and Capinera 1987, Fournier et al. 1995, Rueda et al. 2007, Diaz-Montano et al. 2010) and cause yield losses >50% (Fournier et al. 1995, Waiganjo et al. 2008). *T. tabaci* is also a vector of *Iris yellow spot virus* (IYSV) (family *Bunyaviridae*, genus *Tospovirus*) (Pozzer et al. 1999, Kritzman et al. 2001), which was confirmed in the United States in 1989 in Idaho and Oregon (Hall et al. 1993). IYSV has spread to several important onion producing states in the United States (Gent et al. 2006), including New York where it was confirmed in the summer of 2006 (Hoepting et al. 2007). This virus can reduce bulb size (Gent et al. 2004) and may cause crop losses up to 100% (Pozzer et al. 1999).

Use of foliar insecticides is the most common tactic to control *T. tabaci* on onion, but *T. tabaci* is difficult to control because insects are found mainly in the narrow spaces between the inner leaves (Shelton et al. 1987) where spray coverage may be deficient. This strategy has led to the development of populations resistant to pyrethroid and organophosphate insecticides in New York (Shelton et al. 2003, 2006), Canada (MacIntyre Allen et al. 2005), and other regions of the world (Martin et al. 2003, Herron et al. 2008, Morishita 2008). For a more comprehensive review of the history, biology, ecology, and management of *T. tabaci* see Diaz-Montano et al. (2011).

It is important to find alternative management strategies and host plant resistance is an important one that should be a foundation of an integrated pest management (IPM) program (Panda and Khush 1995, Kennedy 2008). Moreover, the use of resistant cultivars could reduce the application of insecticides. Since the 1930s, studies on onion resistance to *T. tabaci* have been conducted and resistance has been associated with bulb color (Verma 1966, Lall and Singh 1968, Brar et al. 1993) and leaf structure and color (Jones et al. 1934, 1935; Coudriet et al. 1979; Pawar et al. 1987; Patil et al. 1988; Loges et al. 2004a,b; Hudák and Pénzes 2004; Diaz-Montano et al. 2010). Despite these efforts on onion resistance to *T. tabaci*, we are not aware of any studies regarding the mechanisms or categories of resistance. There are three categories that characterize host plant resistance to insects: antibiosis, which adversely affects the biology of the insect; antixenosis or non preference, in which the plant is a poor host for the insect and the insect does not feed, lay eggs, or find shelter on it, and; tolerance, the ability of a plant to withstand or recover from insect feeding (Painter 1951, Smith 2005). Jones et al. (1935) compared *T. tabaci* populations on 44 onion cultivars and found that the resistant variety 'White Persian,' which has light green leaves, had significantly lower numbers of *T. tabaci* than all others. Diaz-Montano et al. (2010) screened 49 onion varieties and found 11 onion cultivars that were considered resistant to *T. tabaci* because they had very little leaf damage as well as lower populations of *T. tabaci* larvae compared with susceptible cultivars. These resistant varieties had yellow–green colored foliage compared with the susceptible ones that had blue–green color foliage. They suggested that such differences in onion leaf color are strongly associated with resistance to *T. tabaci*. While no direct measurements have been made to characterize visual sensitivity in *T. tabaci*, comparative studies have characterized the photopigment systems of two other thrips species. By measuring electroretinograms in response to flashes of monochromatic light between 365 and 630 nm, Matteson et al. (1992) determined two spectral regions in visual sensitivity in the western flower thrips, *Frankliniella occidentalis* (Pergande), one in the ultraviolet-A (UV-A) range (between 315–400 nm, sensitivity peak not determined) and one in the human visible range with a peak sensitivity around 545 nm. It has also been demonstrated that the thrips *Caliothrips phaseoli* (Hood) responds to solar UV-B (≤315 nm) radiation (Mazza et al. 1999, 2002). Mazza et al. (2010) studied behavioral responses (i.e., phototaxis) of *C. phaseoli* to monochromatic radiation (UV-B, UV-A, and visible wavelengths) from 250 to 590 nm and thrips seemed to have negative phototactic behavior to wavelengths between 290 and 400 nm. These studies suggest that visual cues, in particular in the UV spectrum, may be an important aspect in insect-plant interactions for thrips.

To elucidate the categories of resistance of onion cultivars to *T. tabaci* and to determine if there is a relationship between onion leaf color and onion resistance to *T. tabaci*, the present studies were conducted with the objectives of characterizing resistance of onion cultivars to *T. tabaci* by means of no-choice and choice tests and measuring the light reflectance of onion leaves of susceptible and resistant cultivars. In addition, the role of odor cues in host selections was examined via choice tests.

Materials and Methods

Insect Culture and Plant Material. *T. tabaci* populations used in these experiments were originally col-

Table 1. List of onion cultivars used in this study

Cultivar	Leaf color[c]	Response to *T. tabaci*	Days to maturity	Seed company
Yankee[a]	Blue–green	Susceptible[d]	108	Bejo
Nebula[a]	Blue–green	Susceptible[d]	100	Nunhems
OLYS05N5[a]	Yellow–green	Resistant[d]	120	Crookham
Tioga[a]	Yellow–green	Resistant[d]	118	Seminis
Peso[a]	Yellow–green	Resistant[d]	115	Bejo
Calibra[a]	Yellow–green	Resistant[d]	115	Bejo
Vaquero[a]	Yellow–green	Resistant[d]	118	Nunhems
Cometa[b]	Yellow–green	Resistant[d]	120	Nunhems
Medeo[a]	Yellow–green	Resistant[d]	106	Bejo
NMSU 03-52-1[a]	Yellow–green	Resistant[d]	120	[f]
Delgado[a]	Yellow–green	Resistant[d]	116	Bejo
T-433[a]	Yellow–green	Resistant[d]	117	Takii
Colorado 6[a]	Yellow–green	Resistant[d]	120	Crookham
Arcero[a]	Yellow–green	Resistant[e]	120	Nunhems
Mesquite[a]	Yellow–green	Resistant[e]	120	D. Palmer
White Wing[b]	Yellow–green	Resistant[e]	105	Bejo
Granero[a]	Yellow–green	Resistant[e]	118	Nunhems

Bulb color: [a] yellow, [b] white.
[c] Leaf color obtained by personal observation.
[d] According to Diaz-Montano et al. (2010).
[e] Onion cultivars confirmed as resistant in other studies (Diaz-Montano 2011).
[f] Onion line developed in the program of C.S. Cramer. Department of Plant and Environmental Science, New Mexico State University, Las Cruces, NM.

lected from onion fields in Yates Co., NY, in August 2008 and were maintained on onion plants under laboratory conditions at 25°C and 20–40% RH, with a photoperiod of 14:10 (L:D) h. Onions were grown in pots (10.0 cm in diameter × 10.0 cm in height) with four plants per pot.

In this study, a total of 17 onion cultivars (Table 1) were used. In previous field studies we identified 11 cultivars that we defined to be resistant to *T. tabaci* based on statistically lower numbers of larvae and lower leaf damage ratings than susceptible cultivars (Diaz-Montano et al. 2010). The cultivars 'Nebula' and 'Yankee' were used as the susceptible checks in all the experiments. The other four cultivars were confirmed as resistant in other studies (Diaz-Montano 2011). Information on days to maturity and bulb color was obtained from the respective companies or the breeder (Table 1). Plants were seeded into 200 cell 4.5 cm deep plug trays with one seed per cell filled with Cornell mix soil (Boodley and Sheldrake 1977), and then grown under greenhouse conditions at 20–30°C and 20–40% RH with supplemental lights set for a period of 14:10 (L:D) h.

No-Choice Oviposition Test. No-choice tests were performed with the onion cultivars mentioned above (Table 1). After 8 wk in the greenhouse, 10 onion plants per cultivar (between 10 and 15 cm in length and with four leaves) were transplanted individually into 3.8 cm diameter × 14.0 cm deep plastic Cone-tainers (Ray Leach Conetainer, Hummert International, Earth City, MO) filled with Cornell mix soil (Boodley and Sheldrake 1977) and each plant was infested with two similar-aged *T. tabaci* adults. Then a 3.5 cm diameter × 18.0 cm height plastic tube (Petro Packaging Company Inc., Cranford, NJ) was inserted into the soil of each plastic Cone-tainer and the upper side of the tube was covered with an organdy cloth (5 × 5 cm) attached by a rubber band. The Cone-tainers were placed in racks arranged in a completely randomized design and the racks were put in a climatic chamber (25–30°C and 40% RH, with supplemental lights set for a period of 14:10 [L:D] h).

To have similar-aged adults in all the Cone-tainers, before the experiments several *T. tabaci* adults were placed on the susceptible variety, 'Nebula,' and allowed to lay eggs. Adults were removed after 48 h. The development time of *T. tabaci* on onion from egg to adult is 13.9 d at 30.8°C (Lall and Singh 1968) and 14.2 d at 23°C (Arrieche et al. 2006). Therefore, thrips in this study were left for 15 d until they developed into adults before placing them inside the Cone-tainers.

The number of eggs laid by the two adults was counted after 3 d of confinement. To make the eggs more visible for recording after the period of confinement, the leaves of each onion plant were placed inside a beaker (100 ml) filled with water, put in a microwave for 40 s and then the eggs were counted using a stereomicroscope. Placing the leaves in the microwave makes the eggs expand so they become easier to locate and record.

No-Choice Progeny Test. In this experiment exactly the same set up was used as in the no-choice oviposition test: 10 plants per cultivar were transplanted individually into Cone-tainers and each plant was infested with two similar-aged *T. tabaci* adults confined by the cloth covered plastic tube. The *T. tabaci* progeny (larvae) in each Cone-tainer was counted after 10 d of confinement with the two *T. tabaci* adults. This test was repeated one more time with new plants and adult thrips.

Antixenosis (Choice Tests). Antixenosis was assessed on the same cultivars (Table 1) used in the no-choice tests but not the cultivar 'Mesquite' (lack of seed). After 10 wk in the greenhouse, one plant of each cultivar was transplanted and arranged in a circle

in a single pot (20 cm in diameter × 20 cm in height, with a distance of ≈3.0 cm between plants). Plants in the pots were randomized and the pots were arranged in a randomized complete block randomized design with six replications in a climatic chamber as in the no-choice tests. The test was replicated one more time. In total, 100 *T. tabaci* adults were released on a filter paper (15 cm diameter) placed at the center of the circle of potted plants. The number of adults on each plant was counted 24 h later.

Olfactometer Experiments. Orientation to or away from a host is one potential aspect of antixenosis. The behavioral response of *T. tabaci* adults to 17 different onion cultivars (Table 1) was studied using a glass Y-tube olfactometer (5 mm inner diameter, 8 cm in length for the base of the tube, and two 5 cm length arms of the tube with an angle of 45° between them) partially following the methods described by Koschier et al. (2000) and Davidson et al. (2008). The Y-tube was placed inside a box (26 × 18 × 18.5 cm) with its inner walls covered with white paper. The base of the Y-tube was connected to a pump that created suction and resulted in an airflow that was regulated to 10 cm/s (≈0.12 liter/min) in the base using an airflow meter (Cole Parmer, Vernon Hills, IL) connected to the silicone tubing between the base of the Y-tube and the pump. Each end of the two arms was connected to a glass jar (473 ml, wide mouth glass jar 7.5 cm in diameter × 12 cm in height with a metal screw cap) by means of two polypropylene bulkhead compression unions (06390–20, Cole Parmer) drilled into the metal screw cap. The air was first purified by passage through a charcoal filter (8131, Alltech, Activated Charcoal Trap, Alltech Associates, Inc., Deerfield, IL; 37 cm in length × 5.1 cm in diameter acrylic tube). All connections between the pump, the airflow meter, the Y-tube, the two glass jars and the charcoal filter were made with rigid silicone tubing (6.4 mm inner diameter, R-06406–72, Cole Parmer). Before using the olfactometer, the Y-tube and the two jars connected with the silicone tubing were placed into a bucket filled with water to ensure there was no air leakage through the connections. A smoke test showed that at the Y junction the air of the odor-laden arm did not mix with the air of the clean-air arm. After the set up was complete, the Y-tube was positioned at an incline of 25° in the box and the air was drawn through the Y-tube for 5 min before introducing the first *T. tabaci* adult. Experiments were carried out in a dark room at 20–24°C and 40–45% RH. Illumination was provided by two fluorescent tubes fixed ≈40 cm above the box.

After 10 wk in the greenhouse, onion plants from the 17 cultivars (Table 1) were placed individually in the odor-laden jar. Plants were gently removed from the potting medium and the soil from the roots was washed off before being placed into the jar. Before they were used, *T. tabaci* adults of unknown age were confined individually inside 0.6 ml Eppendorf polymerase chain reaction (PCR) microcentrifuge tubes (Laboratory Products Sales Inc., Rochester, NY). A single thrips of unknown age that had been starved for 2 h was released inside the Y-tube by placing the microcentrifuge tube at the base of the Y-olfactometer after disconnecting the silicone tubing at the base of the Y-tube. The recording time was started after the silicone tube was reconnected to the Y-tube and stopped when the *T. tabaci* adult reached the far end of one of the arms (clean-air or odor-laden). When a thrips made no choice within 5 min, it was removed and replaced by another thrips adult. There were 40 replications (*T. tabaci* adults) per each of the 17 onion cultivars evaluated resulting in a total of 680 thrips for the entire experiment. Four plants were used per each cultivar. After 10 thrips were tested, the onion plant was replaced with a new one and the Y-olfactometer set up was alternated 180° to avoid potential position effects. After each cultivar was evaluated, the entire set up was washed with acetone (10%).

Reflectance Spectrophotometry. The light reflectance of onion leaves was measured on the 17 cultivars in Table 1. After 8 wk in the greenhouse, four onion plants per cultivar were transplanted into plastic pots (15.0 cm in diameter × 15.0 cm in height, with four plants per pot) filled with Cornell mix soil (Boodley and Sheldrake 1977). Plants were kept in the greenhouse and after 4 wk they were moved to an onion field in Elba, NY. There were 10 pots per cultivar for a total of 40 plants per each cultivar. After, 3 wk onion leaves were collected from the field to measure their spectral reflectance. Four outer undamaged leaves per cultivar were carefully removed and placed inside labeled plastic bags. Leaves were collected in the morning and their spectral reflectance was assessed when the leaves were returned to the laboratory within 3 h. Until the measurements were completed, all leaves were kept in sealed plastic bags in a plastic cooler.

The reflectance spectrum of the leaves was recorded using an USB2000 spectrophotometer with an internal CCD and diffraction grating capable of UV detection and a PX-2 pulsed Xenon light source (Ocean Optics, Dunedin, FL). The spectrophotometer and the lamp were connected through a bifurcated fiber optic (Ocean Optics R200–7-UV/VIS), fitted at the common end with a copper cylinder to standardize measuring distance (≈5 mm) and spot size (≈7 mm) and to shield out ambient light. The probe was held perpendicular to the leaf surface. Four readings were taken on every leaf on intact upper surface areas, where the leaf cuticle was intact, resulting in a total of 16 readings per onion cultivar. Each individual 'reading' was the result of averaging 20, 10 ms duration flashes of the pulsed xenon lamp. Reflectance was corrected for 'dark noise' of the CCD detector and was calculated relative to a WS-2 white standard using Ocean Optics, Inc. Base32 operating software and the following equation:

$$\%\ \text{Reflectance}_\lambda = [(S_\lambda - D_\lambda)/(R_\lambda - D_\lambda)] \times 100\%$$

"... where S_λ is the intensity of the particular wavelength λ, D_λ is the dark intensity at wavelength λ, and R_λ is the reference intensity at wavelength λ" (Ocean Optics Inc. 2003). Although, spectral reflectance was determined every one-third of a nanometer from 170

Table 2. No-choice progeny test and no-choice oviposition test: number of *T. tabaci* larvae and eggs per plant produced by two confined adults on different onion cultivars, 10 and 3 d after infestation, respectively; free-choice antixenosis test: number of *T. tabaci* adults per plant found on cultivars after 24 h of releasing 100 adults per replicate

Cultivar	No-choice progeny test larvae (mean ± SD)[a]	No-choice oviposition test eggs (mean ± SD)[b]	Free-choice antixenosis test adults (mean ± SD)[c]
Yankee	23.3 ± 6.4a[d]	6.9 ± 2.0ab[e]	15.6 ± 3.0a[e]
Nebula	21.7 ± 7.1a	8.8 ± 1.6a	15.9 ± 2.2a
T-433	16.1 ± 8.6ab	3.3 ± 2.5cde	5.8 ± 2.8b
Peso	14.2 ± 4.9b	3.4 ± 1.6cde	5.5 ± 1.2b
Tioga	13.3 ± 5.7bc	3.1 ± 1.9cde	4.9 ± 1.8b
Calibra	12.2 ± 4.9bc	2.3 ± 1.3e	5.0 ± 1.6b
Granero	12.2 ± 7.2bc	3.2 ± 1.5cde	3.8 ± 2.2b
Mesquite	11.9 ± 4.5bc	2.9 ± 1.8de	
Arcero	11.7 ± 5.0bc	5.9 ± 1.8abc	4.5 ± 2.1b
OLYS05N5	11.7 ± 7.0bc	2.9 ± 1.8de	4.8 ± 1.7b
Vaquero	10.7 ± 4.5bc	2.3 ± 1.5e	4.8 ± 2.2b
Cometa	10.7 ± 6.9bc	3.5 ± 1.6cde	4.5 ± 1.9b
NMSU 03-52-1	10.4 ± 4.4bc	2.6 ± 2.0e	3.8 ± 1.5b
Medeo	10.2 ± 3.8bc	2.7 ± 1.7de	5.3 ± 1.8b
Colorado 6	9.6 ± 3.7bc	3.2 ± 2.2cde	4.2 ± 2.2b
White Wing	9.4 ± 4.9bc	5.6 ± 2.1bcd	4.0 ± 1.9b
Delgado	8.1 ± 3.7c	2.3 ± 1.6e	3.6 ± 1.4b

[a] Average of 20 replicates.
[b] Average of 10 replicates.
[c] Average of 12 replicates, 100 adults per replicate.
[d] Within a column, means followed by different letters are significantly different ($P < 0.05$; Games–Howell test).
[e] Within a column, means followed by different letters are significantly different ($P < 0.05$; Tukey's test).

nm to 880 nm a more limited spectral range was used in our analyses (see below).

Raw spectra were imported into a spreadsheet program, and then 'smoothed' by rounding down the wavelength values to an integer at which the reflectance was recorded and calculating the mean of the recorded values for every nm in the recording range. The following variables were computed from the smoothed spectra: 1) Brightness, which constitutes an estimate of the area under the spectral curve or total light reflected by the leaves, was calculated as the average reflectance (R_{av}), between 270 and 650 nm. 2) The relative amount of UV reflectance or "UV chroma" was calculated as reflectance in the UV range (270–400 nm) divided by total reflectance [$(R_{270-400}/R_{270-650}) \times 100$] and expressed as a percentage. Although the range of vision and the photopigments that *T. tabaci* possess remain unknown, based on electroretinogram recordings on *F. occidentalis* (Matteson et al. 1992) and observed behavioral response of *C. phaseoli* (Mazza et al. 2010), it was hypothesized that *T. tabaci* has four potential photopigment-systems with different (but partly overlapping) ranges of sensitivity. We use the term 'photopigment system' to describe 1) traditional photopigments that undergo chemical changes in response to different light wavelengths and 2) nontraditional mechanisms for detecting light, such as detection of florescence caused by UV radiation (e.g., Mazza et al. 2010). The average reflectance (brightness) was computed from the recorded reflectance spectra of onion leaves in the range of sensitivity of all four theoretical photopigment-systems of *T. tabaci.* Note, that this type of analysis is not modeling sensitivity based on photopigment data (such as what has been done with other organisms, e.g., Stoddard and Prum 2008), rather we are simply dividing up the spectrum to reflect where potential peaks of photosensitivity may be for *T. tabaci.* Accordingly, the average reflectance was computed in the range of sensitivity of the 3) first, 275–375 nm (R_{avps1}); 4) second, 310–410 nm (R_{avps2}); 5) third, 410–510 nm (R_{avps3}); and 6) fourth, 460–630 nm (R_{avps4}) theoretical photopigment-systems of *T. tabaci.*

Statistical Analyses. For the no-choice oviposition and Antixenosis tests, analysis of variance (ANOVA) for *T. tabaci* populations (eggs and adults, respectively) among onion cultivars was conducted by using PROC GLM (SAS Institute 2003). Multiple comparisons were computed by using Tukey's studentized (honestly significant difference) range test ($P < 0.05$) (SAS Institute 2003). The no-choice progeny (larvae) test data did not meet the assumption of homogeneity of variance; therefore, the Games–Howell test was used for pair-wise comparison of the cultivars (SPSS Inc. 2009). For the Olfactometer experiments, the response of *T. tabaci* adults to plant odor or the control for each onion cultivar was compared by the χ^2 test for goodness-of-fit ($\alpha = 0.05$) by using PROC FREQ (SAS Institute 2003). The reflectance spectrum of the leaves data were analyzed using Predictive Analytics SoftWare (PASW) Statistics (SPSS Inc. 2009). All six computed variables met the assumption of normality. In the case of all computed variables the untransformed data did not meet the assumption of homogeneity of variances; therefore, the Games–Howell test was used for pair wise comparisons of the cultivars. All data are reported as original means (±95% confidence limit). Pearson correlation coefficients were calculated between *T. tabaci* adults in the Free-Choice Antixenosis Experiment (Table 2), the intensity of reflectance in the sensitivity range of the four theoretical photopig-

Table 3. Reflectance (%) of: Brightness (R_{av}, 270–650 nm), relative amt of UV reflectance or UV Chroma [($R_{270-400}/R_{270-650}$) × 100], and the four theoretical photopigment-systems of *T. tabaci* [(R_{avps1}, 275–375 nm), (R_{avps2}, 310–410 nm), (R_{avps3}, 410–510 nm), and (R_{avps4}, 460–630 nm)] on 17 onion cultivars

Cultivars	R_{avps1}	R_{avps2}	R_{avps3}	R_{avps4}	UV Chroma	R_{av}
Yankee	9.7 ± 0.8a	8.8 ± 0.7a	9.1 ± 0.6a	12.4 ± 0.8a	29.9 ± 1.6a	10.7 ± 0.6a
Nebula	8.0 ± 0.6ab	7.4 ± 0.5ab	8.2 ± 0.4ab	10.8 ± 0.5a–c	29.2 ± 1.0a	9.2 ± 0.5b
Peso	7.7 ± 1.2a–c	7.4 ± 1.1a–c	8.8 ± 0.9a–c	12.2 ± 1.0ab	25.8 ± 1.8a–f	9.9 ± 1.0a–c
Tioga	6.6 ± 0.6bc	6.5 ± 0.6b–d	7.3 ± 0.6b–d	9.4 ± 0.6d–f	28.2 ± 0.7ab	8.0 ± 0.6b–e
Vaquero	6.6 ± 0.8b–d	6.3 ± 0.7b–e	7.7 ± 0.8a–d	10.3 ± 0.8b–e	26.6 ± 0.9bc	8.4 ± 0.8b–d
Medeo	6.3 ± 0.3c	5.8 ± 0.3c–e	6.7 ± 0.4de	9.3 ± 0.4ef	27.4 ± 0.7a–c	7.7 ± 0.4de
White Wing	6.0 ± 0.5cd	5.9 ± 0.5c–f	7.3 ± 0.6b–d	10.8 ± 0.8a–e	24.5 ± 0.6de	8.4 ± 0.6b–d
Granero	5.9 ± 0.6c–e	5.8 ± 0.6c–f	7.6 ± 0.7a–d	11.4 ± 0.7ab	23.2 ± 0.8e–g	8.7 ± 0.6b–d
Mesquite	5.7 ± 0.5c–e	5.4 ± 0.5c–f	6.7 ± 0.4d–f	9.2 ± 0.4ef	25.9 ± 0.8cd	7.4 ± 0.4d–f
Calibra	5.5 ± 0.4c–e	5.3 ± 0.4d–f	6.0 ± 0.4ef	8.2 ± 0.5f	27.6 ± 0.5a–c	6.8 ± 0.4ef
NMSU 03-52-1	5.4 ± 0.5c–e	5.3 ± 0.5c–g	7.2 ± 0.5b–d	10.9 ± 0.6 a–c	22.4 ± 0.9fg	8.2 ± 0.5b–d
T-433	5.1 ± 0.3de	5.1 ± 0.3e–g	7.2 ± 0.3cd	11.0 ± 0.4ab	21.5 ± 0.6gh	8.2 ± 0.3cd
Delgado	4.7 ± 0.4ef	4.8 ± 0.4f–h	7.7 ± 0.5a–d	11.0 ± 0.6a–c	20.1 ± 0.8 h	8.1 ± 0.5b–d
Colorado 6	4.7 ± 0.4ef	4.7 ± 0.4f–h	6.5 ± 0.5d–f	10.3 ± 0.6b–e	21.4 ± 0.7gh	7.6 ± 0.5d–f
OLYS05N5	4.0 ± 0.4fg	4.0 ± 0.4hi	5.7 ± 0.4f	9.3 ± 0.5d–f	20.1 ± 0.8 h	6.8 ± 0.4ef
Arcero	3.3 ± 0.6 g	4.0 ± 0.6 g-i	7.7 ± 0.7a–d	11.0 ± 0.8a–d	15.9 ± 1.5i	7.7 ± 0.7d–f
Cometa	3.0 ± 0.4 g	3.4 ± 0.4i	6.6 ± 0.4d–f	9.8 ± 0.4c–e	15.9 ± 1.5i	6.7 ± 0.4f

Average of 16 replicates.
Within a column, means followed by different letters are significantly different ($P < 0.05$; Games–Howell test).
All data are reported as original means (±95% confidence limit).

ment-systems and the UV chroma among the cultivars (Table 3).

Results

No-Choice Oviposition Test. This experiment was performed to observe the number of eggs laid by two *T. tabaci* confined adults to plants for 3 d. Differences in number of eggs per plant were ca four-fold between the most (Nebula, 8.8 eggs per plant) and least ('Calibra,' 'Vaquero,' and 'Delgado,' all with 2.3 eggs per plant) susceptible cultivars. Both susceptible checks ('Yankee' and Nebula) had significantly ($F = 9.98$; df = 16, 9; $P < 0.001$) higher numbers of *T. tabaci* eggs per plant than all other cultivars, except 'Arcero' and 'White Wing' (Table 2).

No-Choice Progeny Test. Two no-choice experiments were performed to observe the number of larvae produced by two *T. tabaci* adults confined for 10 d. Although the tests were run on separate dates, they were conducted using identical procedures and thus the two tests were combined and analyzed as a single set of data to increase the power of the test. There were significant differences ($F = 10.62$; df = 16, 19; $P < 0.001$) in numbers of *T. tabaci* larvae per plant among the onion cultivars (Table 2). The difference in numbers of larvae produced was ca three-fold between the most (Yankee, 23.3 larvae per plant) and least (Delgado, 8.1 larvae per plant) susceptible cultivars. Both susceptible checks (Yankee and Nebula) had significantly higher numbers of *T. tabaci* larvae per plant than all the cultivars except for 'T-433.' The number of larvae in the cultivar T-433 was not significantly different from any other resistant cultivar with the exception of Delgado, which supported the lowest larval population (Table 2).

Antixenosis (Choice Tests). Two choice tests were conducted to assess antixenosis or nonpreference of *T. tabaci* adults to the different onion cultivars after 24 h. As in the no-choice progeny test, two tests were run on separate dates but were conducted using identical procedures and therefore the two tests were combined and analyzed as a single set of data to increase the power of the test. The two susceptible checks (Yankee and Nebula) had significantly ($F = 41.65$; df = 15, 11; $P < 0.001$) more *T. tabaci* adults per plant than all the other cultivars (Table 2). Differences between the numbers of adults were ≈3- to 5-fold higher for the two susceptible checks compared with the other cultivars. The number of adults per plant on the resistant cultivars did not differ significantly.

Olfactometer. There were no significant differences ($P < 0.05$) in the response of walking *T. tabaci* adults to plant odors or to the control (Table 4). Of the 680 *T. tabaci* adults used in this experiment, 481 (71%) reached the far end of one the arms before 60 s and 611 (90%) before 120 s.

Reflectance Spectrophotometry. The spectrophotometer device measures a reflectance spectrum from 170 to 880 nm but for the purpose of this study only the spectral reflectance in the theoretical visual spectrum of *T. tabaci* was analyzed, that is, 270–650 nm. The brightness (R_{av}) or the total light reflected by the leaves on the different onion cultivars ranged between 6.7 and 10.7% (Table 3). The susceptible cultivar Yankee had the highest reflectance (10.7%) and was significantly ($P < 0.026$) different from all the other cultivars except from 'Peso' with a value of 9.9%. The other susceptible cultivar, Nebula, had a value of 9.2% and was significantly different from eight other cultivars ($P < 0.048$).

The results from the first theoretical photopigment-system of *T. tabaci* (R_{avps1}, from 275 to 375 nm) showed that the susceptible cultivars Yankee and Nebula, with the highest reflectance values, were significantly different from 14 ($P < 0.0002$) and 12 ($P < 0.0005$) other onion cultivars, respectively (Table 3). A similar outcome was observed in the second theo-

Table 4. Attractiveness assessment of different onion cultivars odors to *T. tabaci* adults in Y-tube olfactometer experiments

Cultivar	*T. tabaci* response (%)[a]		χ^2	*P*
	Control	Onion		
Nebula	45.0	55.0	0.40	0.5271
Yankee	52.5	47.5	0.10	0.7518
Medeo	52.5	47.5	0.10	0.7518
Peso	52.5	47.5	0.10	0.7518
Delgado	50.0	50.0	0.00	1.0000
OLYS05N5	52.5	47.5	0.10	0.7518
Colorado 6	55.0	45.0	0.40	0.5271
Tioga	57.5	42.5	0.90	0.3428
Cometa	57.5	42.5	0.90	0.3428
Calibra	52.5	47.5	0.10	0.7518
NMSU 03-52-1	45.0	55.0	0.40	0.5271
Vaquero	50.0	50.0	0.00	1.0000
T-433	52.5	47.5	0.10	0.7518
Granero	62.5	37.5	2.50	0.1138
Arcero	37.5	62.5	2.50	0.1138
Mesquite	57.5	42.5	0.90	0.3428
White Wing	57.5	42.5	0.90	0.3428

[a] There were 40 replications (*T. tabaci* adults) per cultivar (df = 1, 39). When a thrips made no choice within 5 min, it was replaced. However, 90% of the thrips reached the far end of one the arms before 2 min.

retical photopigment-system of *T. tabaci* (R_{avps2}, from 310 to 410 nm) where the susceptible cultivars Yankee and Nebula again had the highest values of reflectance and were significantly different from 14 ($P < 0.002$) and 12 ($P < 0.022$) cultivars, respectively (Table 3). In the third theoretical photopigment-system of *T. tabaci* (R_{avps3}, from 410 to 510 nm) the values of the two susceptible cultivars Yankee and Nebula were significantly different from 10 ($P < 0.004$) and seven ($P < 0.025$) out of the other 15 cultivars, respectively (Table 3). In the fourth theoretical photopigment-system of *T. tabaci* (R_{avps4}, from 460 to 630 nm) the values of the susceptible cultivars Yankee and Nebula were significantly different from eight ($P < 0.028$) and five ($P < 0.048$) cultivars, respectively (Table 3). The Pearson correlation coefficients between the number of *T. tabaci* adults in the Free-Choice Antixenosis Experiment (Table 2) and the intensity of reflectance values measured in the sensitivity range of the four theoretical photopigment-systems (Table 3) among the cultivars were 0.71 ($P < 0.0021$), 0.69 ($P < 0.0028$), 0.55 ($P < 0.0278$), and 0.35 ($P < 0.1862$), respectively.

The relative amount of UV reflectance (UV Chroma, $R_{270-400}/R_{270-650}$) was ca two-fold between the susceptible checks (Yankee, 29.9% and Nebula, 29.2%) and the cultivars with the lowest amount reflected ('Cometa' and Arcero, both with 15.9%) (Table 3). The amount of UV reflectance in the two susceptible cultivars was significantly ($P < 0.046$) different from 11 other cultivars that had values between 15.9 and 26.6%. The Pearson correlation coefficient between the number of *T. tabaci* adults in the Free-Choice Antixenosis Experiment (Table 2) and the UV Chroma (Table 3) among the cultivar was 0.55 ($P < 0.0258$).

Discussion

Results from the free-choice experiments (Table 2) suggest a very strong antixenotic effect present in all the resistant cultivars and this supports our previous research (Diaz-Montano et al. 2010) where *T. tabaci* were more attracted to susceptible cultivars with blue–green leaf color than to resistant cultivars that had yellow–green leaf color. However, to interpret the result of the no-choice oviposition test is not straightforward because sometimes it is not easy to differentiate the effect of antibiosis from antixenosis on reduced fecundity of the thrips adults (Panda and Khush 1995, Smith 2005). The strong antixenosis found in all the resistant cultivars in the free-choice tests may be caused by a plant trait that could have reduced the oviposition of *T. tabaci* even in the no-choice oviposition test. The observed reduced fecundity could have been because of an initial indirect feeding antixenotic effect, that is, reduced feeding, which is associated with reduced oviposition (Bell and Puterka 2004). However, it could also have been the result of the adverse effects on the biology of *T. tabaci* adults through feeding on the resistant cultivars for 3 d.

In the no-choice oviposition test, which lasted for 3 d, there were significantly more eggs laid on cultivars Arcero and White Wing than on cultivars Calibra, Delgado, 'NMSU 03–52-1' and Vaquero; however, there were no significant differences in the number of larvae on these cultivars, in the no-choice progeny test, which lasted for 10 d. This result could be either because of increased number of eggs laid by *T. tabaci* adults on the cultivars Calibra, Delgado, NMSU 03–52-1, and Vaquero after the fourth day of the no-choice progeny test, or more likely because of higher egg and/or larval mortality on the cultivars Arcero and White Wing. Based on this conclusion, it seems that the cultivars Arcero and White Wing have greater antibiotic resistance than the cultivars Calibra, Delgado, NMSU 03–52-1, and Vaquero.

However, the cultivars T-433, Peso, and Delgado had statistically equal numbers of eggs laid, but significantly fewer larvae were found on Delgado than on the other two cultivars. Therefore, it appears that Delgado has greater antibiotic resistance than T-433 and Peso. Similarly, statistically equal numbers of eggs were laid on the susceptible cultivars Nebula, Yankee, and Arcero, and significantly fewer larvae were found on Arcero than on the two susceptible onion cultivars. This also suggests an antibiotic effect present in the cultivar Arcero. The same phenomenon was observed in the cultivars White Wing and Yankee, suggesting a strong antibiotic effect in White Wing.

The cultivar T-433 had significantly fewer eggs laid in the no-choice oviposition test compared with the susceptible controls; however, the number of larvae found on this cultivar was statistically equal to the susceptible Nebula and Yankee in the no-choice progeny test. This suggests that the observed reduced fecundity of the thrips adults in the no-choice oviposition test was due more to an initial antixenotic effect rather than to antibiosis. Thus, further experiments are

needed to quantify the contribution of antibiotic resistance to the overall resistance of a given cultivar. However, comparing the results of our choice and no-choice tests, the above described conclusions regarding this category of resistance seem reasonable.

The free-choice experiments (Table 2) showed a strong antixenotic effect present in all the resistant cultivars. The results of the no-choice tests (Table 2) documented significant differences between the numbers of larvae and eggs found in some of the cultivars, suggesting an intermediate-high antibiotic effect to *T. tabaci* among the resistant cultivars. According to the results of the no-choice oviposition test (Table 2), it seems that Calibra, Delgado, NMSU 03–52-1, and Vaquero possess plant trait(s) that result in the strongest antixenotic resistance among the tested 17 cultivars and it is coupled with moderate antibiotic resistance only in Delgado. Arcero and White Wing seem to possess the strongest antibiotic resistance among the tested 17 cultivars but their antixenotic resistance is only evident in the free-choice test (Table 2). Calibra and T-433 seem to have the weakest antibiotic resistance, even weaker than the two susceptible cultivars, Nebula and Yankee. However, it is more than compensated by strong antixenotic resistance, suggesting a more important role of antixenosis in the overall resistance of these two cultivars.

Other studies using Y-tube devices have shown positive responses of *T. tabaci* (den Belder et al. 2001) and *Frankliniella occidentalis* Pergande (de Kogel et al. 1999, Koschier et al. 2000, Davidson et al. 2008) to different plant volatiles. A study using a straight-tube olfactometer showed responses of *Megalurothrips sjostedti* (Trybom) to flowers of different cowpea, *Vigna unguiculata* (L.) Walp., varieties (Ekesi et al. 1998). However, our study on behavioral responses of walking *T. tabaci* adults in the Y-tube olfactometer suggests that there is not an oriented movement toward the onion plant odors, regardless of their susceptibility to *T. tabaci.* According to this study, plant odor does not appear to be the central factor determining *T. tabaci* resistance in onion plants.

In our previous research (Diaz-Montano et al. 2010), we suggested that onion leaf color might be a key factor associated with resistance and/or susceptibility of onion cultivars to *T. tabaci* because all resistant onion cultivars had a visual yellow–green leaf color while all susceptible cultivars had blue–green leaf color. In this study, two susceptible cultivars Nebula and Yankee, with blue–green leaf color, were included, and they had the highest values of leaf reflectance in the sensitivity range of the first (275–375 nm) and second (310–410 nm) theoretical photopigment-system of *T. tabaci* and based on these values Yankee was significantly different from 14, and Nebula from 12 of the 15 resistant cultivars. Similarly, Nebula and Yankee had the highest UV Chroma values, and based on these values they were significantly different from 11 of the 15 resistant cultivars. Because the two susceptible cultivars Nebula and Yankee always had the highest number of thrips compared with other onion cultivars, both in our previous studies (Diaz-Montano et al. 2010) and in this study, these results suggest a positive response of *T. tabaci* to onion cultivars with higher reflectance in the UV range (270–400 nm).

The statistically significant correlation coefficients between *T. tabaci* adults in the Free-Choice Antixenosis Experiment and the measured reflectance values of the onion leaves in the sensitivity range of the first two theoretical photopigment-systems of onion thrips and the UV Chroma [0.71 ($P < 0.0021$), 0.69 ($P < 0.0028$), and 0.55 ($P < 0.0258$), respectively] might also indicate a preference of *T. tabaci* to onion cultivars with higher reflectance in the UV range (270–400 nm). However, there is no evidence supporting this and an observed correlation is never a proof of causal relationship. Furthermore, it is in contrast with the well-documented behavior of thrips, especially anthophilous species that seem to avoid surfaces with high reflection in the UV range of light (Kirk 1984).

Our present work corroborates our previous research findings from field studies (Diaz-Montano et al. 2010) where resistant cultivars had low numbers of *T. tabaci* and low thrips feeding leaf damage ratings. The results from our laboratory experiments help to identify antibiosis and antixenosis as categories of resistance to *T. tabaci* in onions, but additional work is needed to understand the actual mechanisms causing such differences in oviposition, larval development, and adult preference. The reflectance spectrophotometry study suggests a strong relationship between light spectra reflected by onion leaves and onion resistance to *T. tabaci.* Some studies have shown that some herbivores guard themselves from direct solar radiation by staying on lower leaf surfaces (Wahl 2008, Ohtsuka and Osakabe 2009). According to this study, *T. tabaci* prefer onion cultivars that reflect a higher amount of light; and it is possible that this characteristic may provide *T. tabaci* with shelter from heat and may make these onion cultivars a more preferable host.

This study indicates a strong response of *T. tabaci* to onion cultivars with higher reflectance in the UV range; however, the range of vision and the photopigment-systems of *T. tabaci* are unknown. Therefore, future work should focus on studies using electroretinogram recordings and/or observing behavioral responses on *T. tabaci* to different frequencies of light spectra to determine the photopigment-systems of *T. tabaci.* Additionally, the genetic basis of color in onions and its influence on the behavior of *T. tabaci* warrant further investigation.

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