Attractancy and Ovipositional Response of Adult *Bemisia argentifolii* (Homoptera: Aleyrodidae) to Type IV Trichome Density on Leaves of *Lycopersicon hirsutum* Grown in Three Day-Length Regimes[1]

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Abstract Clonal plants of six accessions of *Lycopersicon hirsutum* Humb. and Bonpl., a wild relative of tomato, were grown in three day-length regimes. Clones of an accession grown in different day-length regimes were genetically identical but differed in density of type IV and type VI trichomes on their leaves. Leaves on these plants were then evaluated for resistance to whiteflies (*Bemisia argentifolii* Bellows and Perring) in choice and non-choice bioassays. Plants grown under short days had elevated type IV density, reduced type VI trichome density, and were less attractive to whiteflies. Correlation and covariance analysis supported the hypothesis that high type IV trichome density resulted in reduced attractancy, especially on plants grown under short days.

Key Words Host plant resistance, *Lycopersicon hirsutum,* tomato, *Bemisia argentifolii, Bemisia tabaci* B strain, photophase, type IV trichome

Lycopersicon hirsutum Humb. & Bonpl. is highly resistant to insects and may serve as a source of insect resistance for genetic improvement of *L. esculentum* Mill., the common tomato (Rick 1982). On plants of *L. hirsutum,* trichome densities and their secretions have repeatedly been associated with resistance (Farrar and Kennedy 1992). Although other types of trichomes occur on leaves of *L. hirsutum* (Luckwill 1943), type IV and type VI trichomes have generally been associated with insect resistance (Farrar and Kennedy 1992, Carter and Snyder 1985, 1986, Good and Snyder 1988, Snyder and Carter 1984). However, little is known concerning the interaction of trichomes on *L. hirsutum* with *Bemisia argentifolii* Bellows & Perring (= strain B *Bemisia tabaci* [Gennadius], Bellows et al. 1994). Heinz and Zalom (1995) have reported that, for seven accessions of wild tomato including a single accession of *L. hirsutum,* there was no relationship between leaf trichome density and rate of oviposition by *B. argentifolii.*

Heinz and Zalom (1995), using an array of *L. esculentum* cultivars, investigated the interaction between trichome density and *B. argentifolii.* Higher density of trichomes was associated with greater susceptibility. In terms of density, the uniseriate

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type V trichome predominates on leaves on *L. esculentum* and the glanded type IV trichome predominates on leaves of *L. hirsutum* (Snyder and Carter 1985). Thus, the greater susceptibility of *L. esculentum* cultivars having elevated trichome density is probably associated with the presence of nonglandular type V trichomes.

Trichome density can be manipulated on *L. hirsutum* by modifying the day length (Snyder and Hyatt 1984, Good and Snyder 1988). When plants are grown under short days, type IV trichome density is usually elevated. Under long days, type IV densities are usually reduced. Type VI trichome density responds oppositely, generally being elevated on plants grown under long days compared with plants grown under short days. Although type IV density responds to day length, not all variation of type IV density is caused by environmental variation. Plant genotype also contributes to variation of type IV density (Good and Snyder 1988, Guo et al. 1993). Variation in type IV density, regardless of the cause of variation, is an excellent predictor of resistance to spider mites (Carter and Snyder 1985, 1986, Good and Snyder 1988).

Bemisia argentifolii has become an important insect pest of tomato, *L. esculentum,* and other vegetables because of injury from direct feeding and from disease and plant disorders (Byrne et al. 1990, Perring et al. 1991). Any environmentally friendly, practical method of reducing attack on tomato by this insect pest would be much welcomed by growers and the general public. Identification of plant features that mediate resistance to whitefly is one step in the development of such control methods. To evaluate the relative contribution of type IV and type VI trichomes to resistance to *B. argentifolii,* our objectives were threefold and involved the modification of trichome density phenotypes on *L. hirsutum* followed by bioassay of these altered plants. Our first objective was to document the variance of trichome densities among day length environments and among genotypes of *L. hirsutum.* Our second objective was to bioassay these genotypes grown in different day lengths with *B. argentifolii* and then partition any variation in resistance, as measured by attractancy and ovipostional response, into variation associated with genotype, photophase and their interaction. Our third objective was to evaluate the relative roles of type IV and type VI trichome densities in the resistance of *L. hirsutum* to *B. argentifolii.* Our hypothesis was that the greater type IV density resulting from growing plants under an 8-h photophase would be associated with greater resistance compared with plants grown under longer photophases.

Materials and Methods

Test plants. Individual plants were obtained from six accessions of *L. hirsutum.* The accessions (LA1298, LA1353, LA1777, LA1927, LA2144, and LA2329) were obtained from the Tomato Genetics Stock Center, University of California, Davis, CA. One of these accessions, LA2144, is classified as *L. hirsutum* f. *glabratum;* the remaining five are classified as *L. hirsutum* f. *typicum.* These accessions were selected because the composition of their trichome secretions differed (Guo et al. 1993). Plants were cloned by rooting cuttings from single plants of each accession. After the cuttings were rooted, two clones of each plant were placed in each of three growth chambers. Temperature regime was the same in each chamber (22 ± 2°C, 0800-1600 h; 18 ± 2°C, 1600-0800 h). Each chamber received 8 h of high light intensity (260-300 μEinsteins · m^{-2} · s^{-1}) from metal halide, incandescent, and fluorescent lamps. In one chamber, the length of the day was extended by 4 h of irradiation from incandescent lamps (30-40 μEinsteins · m^{-2} · s^{-1}) for 2 h in the morning (dawn) and 2 h in the

evening (dusk). In another chamber, the day length was extended by 4-h dusk and dawn periods to obtain a 16-h day; the third chamber received no extension of photophase. Thus, plants were either grown under an 8-, 12-, or 16-h photophase. This was done to alter the phenotypic expression of trichome densities on these plants. After 6 wks of growth in the chambers, the plants were about 1 m tall when the bioassays were performed. At this time the plants were removed from the growth chambers and bioassays were performed in environments described below. Tomato *L. esculentum* cultivar 'Ace' plants were included in the bioassays as a susceptible or positive control for the bioassay. Plants of 'Ace' were grown in a greenhouse under prevailing day length conditions of about 12 h and when bioassayed were at a stage of development similar to that of the *L. hirsutum* clones.

Trichome densities. Densities of type IV and type VI trichomes were determined on the abaxial surface of the leaf evaluated in the choice bioassay described later. Type IV and type VI trichomes were counted, with the aid of a microscope, in three 1-mm^2 areas (basal, medial, and terminal) on one of the leaflets adjacent to the terminal leaflet.

No-choice bioassay. A fully expanded leaf located six nodes below the apex was removed from each plant for use in the no-choice bioassay. For this bioassay whiteflies were confined in modified Petri dishes (illustrated in Simmons 1994); each was 15.2 cm diam by 2.2 cm depth, with four 2.54-cm diam openings evenly spaced on the dish bottom. Four leaflets from each leaf were placed on a moist filter paper in an inverted Petri dish lid. The dish's bottom was then placed inside the lid on top of the leaflets so that a 2.54-cm opening served as an exposure arena for the abaxial surface of a leaflet. This assembly was covered with an additional lid, and the whole apparatus was inverted. Thirty adult female *B. argentifolii* were placed into each dish. The dishes were then held at 27° C in complete darkness in an incubator. The number of adults on the exposed areas was determined after 6, 12, and 16 h. These observations were summed for each Petri dish. These sums were then divided by the leaf area exposed in the Petri dish (20.27 cm^2) to calculate adults/cm^2. The number of eggs per dish was determined after 16 h and was also divided by leaf area exposed in the dish to calculate eggs/cm^2.

Choice bioassay. After removing the leaf for the no-choice bioassay, the plants were then placed in a greenhouse heavily infested with *B. argentifolii* that were sustained on plants of assorted vegetables. Test plants were placed randomly on a single bench, and a fully expanded leaf (node five from the apex) was tagged for later observation and analysis. Because most (90 to 95%) of the eggs and nymphs reside on the abaxial surface of tomato (Simmons 1994), adult whiteflies were counted on the abaxial surface of the tagged leaf 24 h later. After an additional 14 h, the leaf was removed from the plant, and the number of eggs on the leaf and leaf area, measured using a leaf area meter (Model 3000, LI-COR, Lincoln, NE), were determined. The number of adult whiteflies was divided by leaf area to calculate adults/cm^2. Eggs/cm^2 were calculated likewise. The excised leaf also provided the leaflet sample for trichome density determination using procedures outlined above. Trichome density determinations were made after the conclusion of the bioassay.

Statistical analyses. The statistical treatment of the data was conducted in two phases. In the first phase, we ascertained whether or not the day length (photophase) under which the plant had been grown, the genotype of the plant, and their interaction made significant contributions to variation of trichome densities and to variation of adults/cm^2 and eggs/cm^2. Before these analyses, means, standard errors, and vari-

ances for each photophase and genotype were calculated for trichome densities and adults/cm^2 and eggs/cm^2 using the Univariate procedure of the Statistical Analysis System (SAS Institute 1989). Because means and variances were correlated, all data were transformed (log base 10 {X + 1}) before analysis of variance and analyses of regression and covariance discussed later. Means and standard errors of the untransformed data are listed in the accompanying tables. After transformation of the data, the analyses of variance were conducted using the General Linear Models procedure of the Statistical Analysis System (SAS Institute 1989). The experimental design was factorial with genotypes having 5 df, photophase having 2 df, their interaction having 10 df, and 18 df for error. In none of the analyses was the interaction between photophase and genotype significant, so only main effects were investigated further. To compare means among genotypes least significant difference (LSD) values were calculated using the error mean square from analyses of variance on the transformed data. The calculated LSD values were used to compare means, and then the comparisons were transferred to the untransformed means for presentation.

Correlation, multiple regression and covariance were used in the second phase of the analysis. This phase was conducted to evaluate the relationship between type IV and type VI trichome densities and between trichome densities and adults/cm^2 and egg/cm^2 in the choice and no-choice bioassays.

For correlation analysis, Spearman's rank correlation coefficients were calculated using the Correlation procedure of Statistical Analysis System (SAS Institute 1989). To evaluate whether a significant correlation coefficient between type VI density and adults/cm^2 in the choice bioassay was the result of collinearity of type VI density with the type IV density, multiple regression analysis was performed using the MaxR option of the Regression procedure (SAS Institute 1989). In this analysis, all data were transformed as outlined previously. Adults/cm^2 from the choice bioassay was the dependent variable. Type IV density and type VI density were the independent variables.

The relationship between type IV density and adults/cm^2 and eggs/cm^2 in the choice and no-choice bioassays were further investigated using covariance analysis. The covariance analyses were conducted using the General Linear Models procedure. In each analysis there was 1 df for the covariate (type IV density), 2 df for photophase, 5 df for genotype, 10 df for the interaction between genotype and photophase, and 17 df for experimental error. These analyses were conducted to determine to what degree including type IV density as a covariate would reduce the contribution of genotype, photophase and experimental error as sources of variance in the respective analyses of variance of the adults/cm^2 and eggs/cm^2 data obtained in the choice and no-choice bioassays.

Results

Trichome densities. Photophase was a significant source of variation in the analysis of variance (ANOVA) of type IV ($F = 26.77$, df = 2, $P = 0.0001$) and type VI ($F = 9.82$, df = 2, $P = 0.0013$) trichome densities. Type IV density was greatest under the 8-h photophase and least under the 16-h photophase (Table 1). Conversely, type VI density was greatest under the 16-h photophase, and least under the 8h photophase. Genotype was a significant source of variation for type IV ($F = 5.02$, df = 5, $P = 0.0047$) and type VI ($F = 6.9$ df = 5, $P = 0.0009$) trichome densities. Among genotypes, type IV trichome density ranged from 7/mm^2 on LA2144 to 25/mm^2 on

Table 1. Mean (± SEM) trichome densities for six genotypes of *L. hirsutum* grown in three photophases.

Photophase (hours)	Trichome Density	
	Type IV (no./mm^2)	Type VI (no./mm^2)
8	25 ± 3.2	1 ± 0.2
12	8 ± 2.4	3 ± 0.7
16	5 ± 2.4	4 ± 1.5

LA1353 and type VI density ranged from 1/mm^2 on three of the genotypes to 6/mm^2 on LA2329 (Table 2). There was no significant interaction between genotype and photophase for type IV trichome density ($F = 0.46$, df = 10, $P = 0.8932$) or for type VI trichome density ($F = 0.85$, df = 10, $P = 0.8932$).

No-choice bioassay. Photophase was a significant source of variation in the ANOVA of adults/cm^2 ($F = 4.03$, df = 2, $P = 0.0359$) but was not significant for eggs/cm^2 ($F = 2.16$, df = 2, $P = 0.1016$). Numbers of adults/cm^2 were least on the plants grown under the 8-h photophase (Table 3). Genotype was a significant source of variation for adults/cm^2 ($F = 5.73$, df = 5, $P = 0.0025$) and for eggs/cm^2 ($F = 5.08$, df = 5, $P = 0.0044$). Numbers of adults/cm^2 were least on LA1777 and LA1353, and greatest on LA2144 at a density nearly comparable to that on the susceptible *L. esculentum* cultivar 'Ace' (Table 4). Number of eggs/cm^2 was least on LA2329 and greatest on LA2144. The density of eggs on LA2144 was similar to that on 'Ace'. There was no

Table 2. Mean (± SEM) trichome densities for six genotypes of *L. hirsutum* grown in three photophases and the *L. esculentum* cultivar Ace.

Genotype	Trichome Density	
	Type IV (no./mm^2)*	Type VI (no./mm^2)*
LA1353	25 ± 4.3 a	1 ± 0.4 b
LA1298	21 ± 6.2 ab	1 ± 0.3 b
LA1927	19 ± 6.2 b	5 ± 0.4 a
LA1777	13 ± 4.9 bc	1 ± 0.3 b
LA2329	8 ± 4.9 c	6 ± 1.9 a
LA2144	7 ± 3.2 c	1 ± 0.2 b
ACE**	0	3 ± 0.8

* Means within a column followed by the same letter are not significantly different at $P = 0.05$ as determined by a LSD, SAS Institute 1989.

** 'Ace' is a *L. esculentum* cultivar that was not grown in the three photophases and consequently was not included in the analysis of variance.

Table 3. Mean (± SEM) numbers of whitefly adults and eggs per cm² of leaf for six genotypes of *L. hirsutum* grown under three photophases and tested in the no-choice bioassays with *B. argentifolii* in the laboratory.

Photophase (hours)	Adults (no./cm²)	Eggs (no./cm²)
8	0.35 ± 0.06	0.22 ± 0.08
12	0.79 ± 0.15	0.81 ± 0.33
16	0.59 ± 0.15	0.53 ± 0.24

Table 4. Mean (± SEM) numbers of whitefly adults and eggs per cm² of leaf surface for six genotypes of *L. hirsutum* grown in three photophases and tested in the no-choice bioassay with *B. argentifolii* in the laboratory.

Genotype	Adults (no./cm²)*	Eggs (no./cm²)*
LA1353	0.25 ± 0.07 b	0.15 ± 0.07 bc
LA1298	0.79 ± 0.14 ab	0.79 ± 0.39 a
LA1927	0.50 ± 0.20 b	0.10 ± 0.09 bc
LA1777	0.25 ± 0.07 b	0.64 ± 0.29 ab
LA2329	0.64 ± 0.12 a	0.05 ± 0.04 c
LA2144	1.08 ± 0.24 a	1.38 ± 0.57 a
ACE**	1.18 ± 0.18	2.37 ± 0.60

* Means within a column followed by the same letter are not significantly different at $P = 0.05$ as determined by a LSD, SAS Institute 1989.

** 'Ace' is a *L. esculentum* cultivar that was not grown in the three photophases and consequently was not included in the analysis of variance.

significant interaction between genotype and photophase for adults/cm² ($F = 1.43$, df = 10, $P = 0.2440$) or for eggs/cm² ($F = 1.10$, df = 10, $P = 0.4141$).

Choice bioassay. Photophase was a significant source of variation in the ANOVA of adults/cm² ($F = 5.68$, df = 2, $P = 0.0122$) and eggs/cm² ($F = 4.95$, df = 2, $P = 0.0203$). Numbers of adults/cm² and eggs/cm² were least on plants grown under the 8-h photophase (Table 5). Genotype was not a significant source of variation in the ANOVA of adults/cm² ($F = 1.85$, df = 5, $P = 0.1534$) or eggs/cm² ($F = 2.07$, df = 5, $P = 0.1192$). However, the LSD identified differences among these means. Number of adults/cm² was lowest on LA1927 and greatest on LA1777 (Table 6). Number of eggs/cm² was lowest on LA1353 and greatest on LA1777. There was no significant interaction between genotype and photophase for adults/cm² ($F = 0.51$, df = 10, $P = 0.8607$) or for eggs/cm² ($F = 0.87$, df = 10, $P = 0.8148$).

Table 5. Mean (± SEM) numbers of whitefly adults and eggs per cm^2 of leaf for six genotypes of *L. hirsutum* grown under three photophases and tested in the choice bioassay with *B. argentifolii* in the greenhouse.

Photophase (hours)	Adults (no./cm^2)	Eggs (no./cm^2)
8	0.02 ± 0.005	0.002 ± 0.001
12	0.11 ± 0.033	0.30 ± 0.121
16	0.08 ± 0.032	0.10 ± 0.630

Table 6. Mean (± SEM) numbers of whitefly adults and eggs per cm^2 of leaf surface for six genotypes of *L. hirsutum* grown in three photophases and tested in the choice bioassay with *B. argentifolii* in the greenhouse.

Genotype	Adults (no./cm^2)*	Eggs (no./cm^2)*
LA1353	0.016 ± 0.003 b	0.00 ± 0.001 b
LA1298	0.042 ± 0.018 ab	0.19 ± 0.109 ab
LA1927	0.015 ± 0.007 b	0.03 ± 0.023 b
LA1777	0.170 ± 0.075 a	0.41 ± 0.247 a
LA2329	0.073 ± 0.035 ab	0.09 ± 0.056 ab
LA2144	0.088 ± 0.032 ab	0.09 ± 0.048 ab
ACE**	0.180 ± 0.040	0.25 ± 0.093

* Means within a column followed by the same letter are not significantly different at $P = 0.05$ as determined by a LSD, SAS Institute 1989.

** 'Ace' is a *L. esculentum* cultivar that was not grown in the three photophases and consequently was not included in the analysis of variance.

Correlation and covariance analyses. Type IV trichome density was negatively correlated with type VI density ($r = -0.46$, $P = 0.0040$). Type IV density was significantly correlated with adults/cm^2 in the no-choice bioassay ($r = -0.4017$, $P = 0.0152$, $n = 36$) and choice bioassay ($r = -0.6006$, $P = 0.0001$, $n = 36$). Type IV density was not correlated with eggs/cm^2 in the no-choice bioassay ($r = -0.02297$, $P = 0.1776$, $n = 36$) but was correlated with eggs/cm^2 in the choice bioassay ($r = -0.3348$, $P = 0.0493$, $n = 36$).

Correlation coefficients between type VI density and adults/cm^2 and eggs/cm^2 in the bioassays were less prevailing than those for type IV density. Type VI trichome density was not correlated with adults/cm^2 in the no-choice bioassay ($r = +0.2181$, $P = 0.2014$, $n = 36$), but for the choice bioassay, type VI density was correlated with adults/cm^2 ($r = +0.4139$, $P = 0.0121$, $n = 36$). Type VI density was not correlated with eggs/cm^2 in the no-choice bioassay ($r = -0.0774$, $P = 0.6536$, $n = 36$) or choice bioassay ($r = 0.06992$, $P = 0.6898$, $n = 36$).

The significant positive correlation between type VI trichome density and adults/cm^2 in the choice bioassay could have two possible explanations. The effect may have been direct, that is, elevated type VI trichome density was the factor, or was positively related to some factor, that made the leaves more attractive to the whiteflies. Conversely, this positive correlation may have resulted from the collinearity or negative correlation between type IV trichome density and type VI trichome density. To clarify this matter, the relationships between adults/cm^2 in the choice bioassay (dependent variable) and type IV and type VI trichome densities (independent variables) were further investigated by regression analysis. The analysis estimated a significant negative slope for type IV density (slope = –0.104, df = 1, $P = 0.0034$) and a non-significant slope for type VI trichome density (slope = –0.003, df = 1, $P = 0.530$). The results of this regression analysis support the idea that the positive correlation between type VI density and adults/cm^2 in the choice bioassay was related to the collinearity of type IV and type VI trichome density, and was not the result of a direct effect of type VI density on attractancy.

To better understand the relationships between type IV trichome density and adults/cm^2 and eggs/cm^2, covariance analysis, using type IV density as the covariate, was conducted. Type IV density was chosen as the covariate because it was the variable most closely correlated with adults/cm^2 and eggs/cm^2 in the choice and no-choice bioassays (see discussion above).

Using type IV density as a covariate in the analyses of covariance had little effect on the estimates of experimental error. When sums of squares for experimental errors in analyses of variance for adults/cm^2 and eggs/cm^2 in the choice and no-choice bioassay were compared with those from the respective analyses of covariance, there was little reduction in the error sums of squares (Table 7). Consequently, inclusion of type IV density as a covariate did not improve or degrade estimates of experimental error.

For adults/cm^2 and eggs/cm^2 in the choice and no-choice bioassay, using type IV density as a covariate in the analyses of covariance caused a considerable reduction in the sums of squares for genotype and photophase as sources of variation (Table 7). For each bioassay, the reduction due to covariance with type IV density was

Table 7. Percent reduction in experimental error, genotype and photophase sums of squares for *B. argentifolii* adults/cm^2 and eggs/cm^2 in the choice and no-choice bioassays, after covariance analysis using type IV trichome density as the covariate.

		Source of variance and percent reduction in sums of squares		
Bioassay	Dependent variable	Experimental error	Genotype	Photophase
No-choice	Adults/cm^2	0.3	35.8	44.2
	Eggs/cm^2	0.3	19.9	26.1
Choice	Adults/cm^2	0.1	27.4	58.3
	Eggs/cm^2	5.0	2.9	36.4

greater for the photophase sum of squares than it was for the genotype sum of squares. Also, for each bioassay this reduction was greater for adults/cm^2 than it was for eggs/cm^2. In all covariance analyses using type IV density as a covariate, photophase was eliminated as a significant source of variation. For adults/cm^2 in the choice bioassay, the *F*-value for photophase was reduced to 2.13 (df = 2, $P = 0.1492$) and for the no-choice bioassay the *F*-value was reduced to 2.25 (df = 2, $P = 0.1354$). In the analyses of variance of eggs/cm^2, photophase was a significant source of variance only in the choice bioassay and use of type IV density as a covariate also reduced photophase as a source of variance to a non-significant level ($F = 3.30$, df = 2, $P = 0.0705$). For eggs/cm^2 in the no-choice bioassay, use of type IV density also reduced the *F*-value for photophase ($F = 1.85$, df = 5, $P = 0.1879$), but the interpretation of significance was unaltered because photophase was not a significant source of variation in the analysis of variance. In contrast to photophase as a source of variance, covariance analysis did not change the interpretation of genotype as a significant or non-significant source of variation. For adults/cm^2 and eggs/cm^2 in the choice bioassay, the *F*-values after covariance analysis remained non-significant ($F = 1.18$, df = 5, $P = 0.3613$; $F = 2.06$, df = 5, $P = 0.1242$, respectively). For the no-choice bioassay, the *F*-values for adults/cm^2 and eggs/cm^2, although reduced, remained significant ($F = 3.69$, df = 5, $P = 0.0192$, $F = 4.09$, df = 5, $P = 0.0127$, respectively) after covariance analysis.

Discussion

In answer to the first objective, results of statistical analyses indicate that type IV and type VI trichome densities differed among photophases and among genotypes of *L. hirsutum.* Partitioning variation in resistance among diverse genotypes, photophases and their interaction was performed to achieve our second objective. In the choice and no-choice bioassays photophase was a significant source of variation for attractancy (adults/cm^2). Photophase was significant for oviposition (eggs/cm^2) only in the no-choice bioassay. Genotype was a significant source of variation only in the no-choice bioassay and was significant for attractancy and for oviposition.

Lycopersicon hirsutum plants grown in an 8-h photophase had, on average, elevated type IV trichome densities and reduced type VI trichome densities compared with identical genotypes grown in longer photophases. Also, plants grown in the 8-h photophase were least attractive to adult whiteflies in both bioassays, and were poorer hosts for oviposition in the choice bioassay. These results indicate that the photophase or day length under which *L. hirsutum* is grown can affect its resistance, especially attractancy, to *B. argentifolii.* The elevation of type IV trichome density under the 8-h photophase suggests that type IV density was a cause of reduced attractancy and perhaps, oviposition observed on plants grown in the 8-h photophase.

To achieve our third objective, correlation and covariance analyses were conducted. Type IV density was negatively correlated with attractancy in both bioassays, and with oviposition in the choice bioassay. Type VI density was not correlated with oviposition in either bioassay; it was not correlated with attractancy in the no-choice bioassay, and was positively correlated with attractancy only in the choice bioassay. Multiple regression analysis indicates that the positive correlation between type VI density and oviposition in the choice bioassay was probably associated with collinearity between type IV and type VI density, which were negatively correlated with each other because their densities responded oppositely to photophase. Thus, based on

correlation analysis, type IV density rather than type VI density was associated with attractancy and oviposition of *B. argentifolii.*

If elevated type IV density was a cause of reduced attractancy or reduced oviposition, then including it as a covariate in analyses of variance for attractancy or oviposition should considerably reduce or eliminate the significant contribution of photophase and genotype as sources of variance. Inclusion of type IV density as a covariate in the analysis of variance for attractancy eliminated photophase as a significant source of variation in both bioassays and eliminated it as a significant source of variation for oviposition in the choice bioassay. Using type IV density as a covariate did not eliminate the significant contribution of genotype to attractancy or oviposition in the no-choice bioassay. The results of the covariance analysis further implicate type IV trichome density as a cause of the reduced attractancy, especially that associated with elevated type IV density resulting from growth under the 8-h photophase.

Based on our research with spider mite resistance in *L. hirsutum,* we were not surprised that elevated type IV trichome density was implicated as a cause of reduced attractancy (Carter and Snyder 1985, 1986, Good and Snyder 1988). Conversely, research on other plant species, including cotton and cultivated tomato, has shown a positive relationship between trichome density and whitefly abundance; namely, whitefly populations increased with increased trichome density (DePonti et al. 1990, Heinz and Zalom 1995). The negative relationship between whitefly attractancy and type IV trichome density in our study may be related to a combination of physical protection by the very high trichome density on these wild species of tomato, and chemical protection associated with the presence of the gland on type IV trichomes. Berlinger et al. (1983) reported that the resistance of several *Lycopersicon* accessions was the result of several mechanisms including pH, secondary plant substances, and sticky exudates.

Our results do not eliminate other factors as additional determinants of resistance status. In fact, intermediate to low, but significant, correlation coefficients between type IV trichome density and attractancy and oviposition are consistent with the concept that other factors play roles in plant resistance to arthropod pests. For spider mites, *L. hirsutum* plants with high type IV density are highly resistant. Plants having lower density may be resistant or susceptible, depending on the presence or absence of other resistance factors such as elevated type VI density, or trichome-borne chemicals such as the antibiotic 2-tridecanone or the antixenotic 2,3-dihydrofarnesoic acid (Carter and Snyder 1985, 1986, Snyder et al. 1993). The resistance of *L. hirsutum* to *B. argentifolii* may be similarly complex, that is, caused by multiple factors.

Plant resistance to an insect species is rarely explained by a single causal factor (Norris and Kogan 1980), and we do not suggest that the resistance of *L. hirsutum* to *B. argentifolii* is solely due to differences in type IV trichome density. Furthermore, because *L. hirsutum* is so highly defended against insects, it would not be surprising to uncover more than one mechanism of resistance, especially among an array of genetically diverse genotypes such as those chosen for this research. The covariance analysis for attractancy in the no-choice bioassay implies the presence of additional mechanisms. In this analysis, even after variation in type IV density was taken into account, significant differences among genotypes remained. Additional testing will be required to elucidate this observation. Genotypes used in this research were chosen because of the diversity of the compositions of their trichome secretions. Thus, in-

vestigation of how composition of secretion relates to attractancy and oviposition of *L. hirsutum* leaflets will provide useful information.

Clearly, the photophase in which a genotype of *L. hirsutum* is grown can dramatically alter its attractancy to whiteflies. This is an observation that should be considered in any future research designed to evaluate the resistance of *L. hirsutum* to *B. argentifolii.* Furthermore, because the data reported here provide substantial evidence that elevated type IV density can reduce attractancy, this relationship also should be considered in future research. Moreover, additional research is needed to assess the relative role of factors such as the composition of trichome secretion, type VI density, etc., in explaining the resistance of genotypes of *L. hirsutum* to *B. argentifolii.*

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