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Performance of the predator *Delphastus pusillus* on *Bemisia* resistant and susceptible tomato lines

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Abstract

Host plant resistance and biological control are often assumed to act additively to suppress populations of agricultural pests. Using tomato trichome based resistance to the whitefly *Bemisia argentifolii*, we tested this additivity assumption with *Delphastus pusillus*, a coccinelid predator of *Bemisia*. Various life history traits of *D. pusillus* were measured on the tomato cultivar 'Alta,' which possessed foliage with 3-fold greater trichome densities than the second cultivar 'VF145B7879.' Beetles housed on VF145B7879 exhibited significantly greater lifetime fecundities and walking speeds than beetles housed on Alta. No cultivar-specific differences were observed in *D. pusillus* longevities or handling times. Combining these observations with previously published reports of reduced *B. argentifolii* population growth rates on Alta compared to VF145B7879, we tested the hypothesis that increased levels of whitefly biological control could be obtained on VF145B7879 by comparison to Alta through releases of *D. pusillus*. Analyses of results obtained from replicated population trials detected significant reductions in whitefly populations due to *D. pusillus* releases, but they did not detect a significant influence of tomato cultivar on the ability of *D. pusillus* to suppress whitefly populations. Significantly longer beetle residence times on Alta than on VF145B7879 may have compensated for the significantly slower walking speeds and reduced lifetime fecundities observed on Alta and produced a neutral effect of foliar trichome densities on *B. argentifolii* biological control.

Introduction

A goal of integrated pest management is to combine optimally all available tactics to maintain pest populations below levels that will cause economic loss. Two strategies, host-plant resistance and biological control, are often assumed to be highly compatible and capable of acting additively when used simultaneously in time and space (Bergman & Tingey, 1979; Duffey & Bloem, 1986). However, plant traits such as allelochemistry, nutrition, morphology, and phenology that often confer resistance to plant pests may adversely affect beneficial insects. Many excellent reviews discuss various aspects of plant effects on natural enemies (Price, 1986; Fritz & Simms, 1992; Gauld & Gaston, 1994). The ability to quantify the compatibility between host-plant resistance together with biological control requires a knowledge of (1) the causal factor(s) of a plant's resistance, (2) the level of pest suppression obtained by the host plant resistance, and (3) how the resistance factor(s) affect the ability of the natural enemies to suppress the target pest population.

Previous work by Heinz & Zalom (1995) identified a positive correlation between densities of nonglandular leaf trichomes and ovipositions by whitefly (*Bemisia argentifolii* Bellows & Perring [Homoptera: Aleyrodidae]) across 20 commercial cultivars of tomato. Similarly, highly pubescent cotton cultivars support larger populations of *Bemisia tabaci* (Gennadius) than do glabrous cultivars (Mound, 1965; Butler & Henneberry, 1984; Ozgur & Sekeroglu, 1986). This phenomenon may be a result of the strong pref-

erence exhibited by *B. tabaci* for laying its eggs at the base of leaf trichomes (Berlinger, 1986), which may be an evolutionary response to selection exerted by predators and parasitoids. Whitefly natural enemy search efficiency is greatest on glabrous leaves and decreases with increasing trichome densities (Li et al., 1987; Hulspas-Jordan & van Lenteren, 1989). Whitefly offspring placed at the base of leaf trichomes may experience reduced levels of natural enemy-induced mortality and confer an increased fitness on females exhibiting this appropriate behavior (Heinz & Zalom, 1995).

Considering these observations, the trichome-based resistance mechanism in tomato should be compatible with biological whitefly control. Testing this prediction provides the framework for the studies we describe in the following text. The goals of our studies are, first, to examine the influence of tomato trichome resistance on several female fitness characters of the whitefly predator *Delphastus pusillus* LeConte (Coleoptera: Coccinellidae) that are likely to influence its ability to effectively suppress *B. argentifolii* infesting tomato. Second, we compare levels of whitefly suppression obtained through the use of this trichome-dependent host plant resistance to the levels of suppression obtained by inundative releases of *D. pusillus*. Third, we identify potential incompatibilities between these forms of host plant resistance and biological control.

Whiteflies in the genus *Bemisia* are serious pests of row crops grown in the tropical and subtropical regions of the world, and they have infested greenhouse grown crops worldwide with varying degrees of intensity. Management of *Bemisia* outbreaks in agricultural systems relies heavily on repeated applications of insecticides. Although these insecticides provide some suppression of whitefly populations, their toxicity to the environment and to nontarget species may cause increased outbreaks of whiteflies and other pests (DeBach & Rose, 1977). Moreover, resistance to insecticides in *Bemisia* populations has been well documented (Dittrich et al., 1985, 1990; Prabhaker et al., 1985, 1988; Cock, 1986). Although biological control is often espoused as an alternative to chemical control, it presently has only been effective in managing *B. argentifolii* infesting selected greenhouse crops (Breene et al., 1992; Heinz & Parrella, 1994a; McMahon et al., 1994). Biological control of *Bemisia* infesting field crops has been largely unsuccessful (Anonymous, 1981; Dittrich et al., 1985; Meyerdirk et al., 1986; Dowell, 1990), presumably due to episodes of mass migrations of whitefly that overwhelm the natural enemy complex (Heinz et al., 1994; Simmons & Minkenberg, 1994). Plant cultivars that may slow *Bemisia* population growth have been identified (Mound, 1965; Butler & Henneberry, 1984; Berlinger, 1986; Ozgur & Sekeroglu, 1986; Heinz & Zalom, 1995), but cultivars truly resistant to whitefly oviposition are not yet commercially available. Failure of each of these pest management strategies to control this severe agricultural pest when used alone will likely promote the use of several strategies in combination.

Materials and methods

Two commercial cultivars, representing opposite extremes in *B. argentifolii* oviposition rates and trichome densities (Heinz & Zalom, 1995), were selected as test plants to determine how tomato trichome densities influence several life history characters of female *D. pusillus*. Average whitefly oviposition rates and tomato leaf trichome densities were 6.4 (SEM = 0.73, $N = 50$ females) ovipositions per day and 388.5 (SEM = 33.94, $N = 115$ leaves) trichomes per 25 mm^2 of leaf tissue for the cultivar Alta, and 3.3 (SEM = 0.51, $N = 50$ females) ovipositions per day and 125.2 (SEM = 10.26, $N = 124$ leaves) trichomes for the cultivar VF145B7879) (Heinz & Zalom, 1995). *Delphastus pusillus* was selected as the test animal because it has previously been shown to significantly reduce *Bemisia* populations in laboratory (Hoelmer et al., 1993), greenhouse (Heinz & Parrella, 1994a), and field (Heinz et al., 1994) studies. Results from these life history studies were followed by population studies in greenhouses to test whether variation in trichome densities and *D. pusillus* life history characteristics yielded cultivar-specific differences in whitefly population growth and whitefly population suppression by *D. pusillus*. Results from the population studies prompted a final laboratory study with the purpose of measuring the potential influences of host plant characteristics and availability of whitefly prey on residence time, or the time beetles spend foraging on tomato plants. All beetles used in these studies were obtained from a laboratory culture of *D. pusillus* maintained on poinsettia (*Euphorbia pulcherrima* Wild. ex Koltz) infested with all developmental stages of *B. argentifolii*. The *D. pusillus* laboratory culture was initiated in 1991 from another laboratory culture maintained on a mix of *Bemisia tabaci* (Gennadius) and *Trialeurodes*

variabilis (Quaintance) (Heinz & Parrella, 1994b).

Cultivar mediated measures of D. pusillus *fitness.* Four measures of female *D. pusillus* fitness, presumed to be correlated with its ability to suppress *Bemisia* populations, were quantified using three laboratory experiments. Our studies concentrated on female beetles due to severe difficulties associated with measuring male reproductive success (see Visser, 1994 and Kazmer & Luck, 1995 for recent discussions). In the first study, 2 day-old, mated, female beetles were placed singly into 21.1 liter sleeve cages. Each cage contained a 1-month-old tomato plant infested with an excess of 1000 *B. argentifolii* eggs. Ten cages contained beetles on Alta tomato plants and ten cages contained beetles on VF145B7879 plants. Plants were replaced daily with *B. argentifolii* egg-infested plants for as long as each female beetle was alive. Immediately after removing plants from the sleeve cages, the number of eggs oviposited onto the tomato foliage by each female was censused with the aid of a dissecting microscope (30× power). After the death of all beetles, the right hind tibia of each was measured with the aid of a dissecting microscope (100× power) equipped with an ocular micrometer as an index of body size. The numbers of eggs oviposited by each female were pooled across her lifespan and whether lifetime fecundities differed significantly between cultivars were detected using a 1-way ANOVA. Similarly, whether adult longevities differed significantly between cultivars were detected using a 1-way ANOVA. In both analyses, hind tibia lengths were included as covariates to correct for inadvertent differences in beetle size associated with each treatment.

Two other measures, handling time of prey and walking speed, were obtained by direct observation. We define handling time as the total time a beetle spends in assessing and consuming prey when an encounter with a whitefly larva results in an attack. Individual beetles ($N = 20$ per tomato cultivar), obtained from the laboratory colony described previously, were placed into a 9-cm. diameter clear plastic petri dish together with a tomato leaf (either Alta or VF145B7879) infested with 4th instar *B. argentifolii*. Beetles were observed continuously under a dissecting microscope (30× power) for 30 min or until a beetle completed an attack, whichever occurred first. Whenever a whitefly larva was encountered, the times spent assessing the potential prey item and feeding on acceptable prey were recorded. All beetles were only used in a single observation period. Encounters not resulting in consumption of the whitefly larva were omitted from analysis. Between-cultivar differences in beetle handling time were detected using a 1-way ANOVA. Prior to conducting the ANOVA, homogeneity of variances among treatment groups was verified with a Scheffé-Box test (Sokal & Rohlf, 1981), and normality was confirmed using a G-test for goodness of fit (Sokal & Rohlf, 1981).

The speeds at which female beetles traverse the blades of uninfested tomato leaves were measured by placing individual beetles into a 9-cm diameter clear plastic petri dish together with a tomato leaflet. Once a beetle climbed onto the leaflet, its position on the blade of the leaflet was marked on the lid of the petri dish at 2 s intervals. Beetle positions were recorded for a period of 10 s after which the distance between each mark was measured and summed. All beetles ($N = 20$ per tomato cultivar) were only used in a single observation period, and the hind tibias of all beetles were measured at the conclusion of an observation period. Homogeneity of variances and normality were verified, and between-cultivar differences in beetle walking speeds were detected using a 1-way ANOVA with hind tibia length as a covariate.

Population study. Four whitefly enclosure cages measuring 1 m × 1.2 m × 2 m were positioned in a greenhouse maintained at an average temperature of 27 °C. Three 1000-W metal halide lamps within the greenhouse maintained a L16:D8 photoperiod. Twelve 1-month-old tomato transplants were planted into 4-liter pots within each cage; 2 cages were planted with the cultivar Alta and 2 cages were planted with the cultivar VF145B7879. Whitefly populations were established in the four cages by inoculating each cage with 100 adult *B. argentifolii* per week for 3 wk. After this inoculation, one cage of each cultivar received weekly releases of *D. pusillus* at the rate of 1 adult beetle per plant. For a period of ten weeks starting with the first *D. pusillus* release, one leaf was sampled indiscriminately from the top 1/3, the middle 1/3, and the bottom 1/3 of 6 randomly selected plants per cage to yield a total sample size of 18 leaves per cage per week.

Leaves were censused with the aid of a dissecting microscope (30 power) for whitefly and *D. pusillus* activity. The census included live or dead (due to natural causes or due to *D. pusillus* predation) whitefly eggs, 1st–2nd instar whitefly nymphs, 3rd–early 4th instar nymphs, and late 4th instar whitefly nymphs. Upon completing this microscopic examination, the adaxial surface area of each leaf was determined with

an area meter (Li-Cor LI–3100, Lincoln, NE, USA) so whitefly densities could be standardized to the number per cm^2 of leaf tissue per plant. The study was replicated 3 times, and tomato cultivars were assigned randomly to cages to control for position effects within the greenhouse. Homogeneity of variances and normality were verified, and significant among treatment differences in whitefly densities (numbers per square centimeter of leaf surface areas) among the 2 cultivar and 2 *D. pusillus* release treatments were detected with repeated measures ANOVA (StatSoft, 1994).

Host plant and prey influences on predator residence time. The amount of time female beetles resided on tomato plants was measured using a 2 × 2 factorial design that included the pubescent cultivar Alta and glabrous cultivar VF145B7879 either infested with an excess of 1000 *B. argentifolii* eggs or free of any whitefly. Single, 1-month-old tomato plants were placed in 21.1 liter sleeve cages for which the inner walls had been coated with a thin film of sticky material (Tanglefoot Pest Barrier, Grand Rapids, MI, USA). Groups of 10, 2-day-old female beetles were released onto tomato plants within 40 cages, 10 cages of every cultivar-whitefly infestation combination. The cages were housed in an environmentally controlled room with a mean daily temperature of 27.6 °C (range 25.8–30.1 °C) and a L14:D10 photoperiod. The numbers of beetles trapped on the sticky walls of the cages were censused every 2 h over a period of 8 h after the beetle inoculation. The initial number of beetles released minus the cumulative number of beetles trapped on the cage wall yields the number residing on each plant during a census period. Significant effects of whitefly density and tomato cultivar on beetle residence time were detected with a repeated measures ANOVA (StatSoft, 1994).

Results

Cultivar mediated measures of D. pusillus *fitness*

Tomato cultivar and presumably trichome density had a significant and negative influence on *D. pusillus* lifetime fecundity and walking speed (Table 1). Beetles residing on the glabrous tomato cultivar (VF145B7879) exhibited almost 5-fold greater lifetime fecundities than beetles residing on the pubescent cultivar (Alta). Beetle walking speeds were approximately 15% faster on VF145B7879 compared to the walking speeds measured on Alta. *D. pusillus* longevities and handling times did not differ significantly between the tomato cultivars (Table 1).

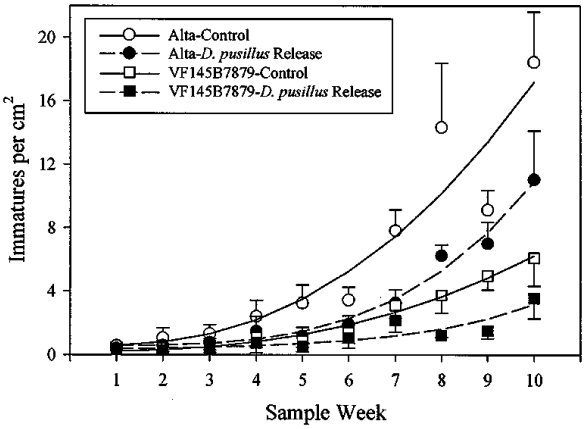

Figure 1. The influences of tomato cultivar and *D. pusillus* releases on *B. argentifolii* population dynamics. Means ± SEM for Alta and VF145B7879 were calculated for each sample week across 3 replicates. Best-fit lines were plotted for each tomato cultivar and *D. pusillus* release treatment with the aid of a computerized curve-fitting algorithm (Jandel, 1994). The equations of theses lines were: Alta – Control: $y^{0.5} = 0.783 + 0.025x^{1.5}$, $r^2 = 0.793$, $F = 95.515$, $P \ll 0.001$; Alta – *D. pusillus* Release: $y^{0.5} = 0.268 + 0.098x^{1.5}$, $r^2 = 0.766$, $F = 91.545$, $P \ll 0.001$; VF145B7878 – Control: $y^{0.5} = 0.541 + 0.025x^{1.5}$, $r^2 = 0.696$, $F = 64.234$, $P \ll 0.001$; VF145B7879 – *D. pusillus* Release: $y^{0.5} = 0.666 + 0.039x^{1.5}$, $r^2 = 0.290$, $F = 11.451$, $P < 0.005$.

Heinz & Zalom (1995) reported decreasing *B. argentifolii* population growth rates with decreasing leaf trichome densities. These trichome density dependent differences in the pest population together with the increasing *D. pusillus* lifetime fecundities and walking speeds with decreasing leaf trichome densities generated the hypothesis that biological control should be more effective on glabrous cultivars compared to pubescent cultivars. We tested this hypothesis in the following population level study.

Population study. We expected releases *of D. pusillus* onto whitefly infested VF145B7879 to suppress whitefly populations to a greater extent than beetle releases onto whitefly infested Alta. Results from our test of this expectation are presented in Figure 1 and Table 2.

Densities of immature *B. argentifolii* were significantly greater on Alta compared with VF145B7879, significantly greater in the no release compared with the *D. pusillus* release treatment, and increased significantly with sample date. The influence of tomato cultivar on whitefly density was independent of the

Table 1. Cultivar mediated measures of *D. pusillus* fitness

D. pusillus fitness character	cv. Alta[1]	cv. VF145B7879[1]	F	df	P
Lifetime fecundity (eggs)	7.9 ± 1.22	34.5 ± 3.69	120.339	1,17	<0.0001
Adult longevity (d)	21.2 ± 1.10	20.0 ± 0.75	0.858	1,17	0.3673
Handling time (min)	4.15 ± 0.433	3.02 ± 0.401	3.630	1,28	0.0671
Walking speed (mm/s)	2.09 ± 0.247	2.41 ± 0.298	9.098	1,37	0.0046

[1] Values represent the $\overline{x} \pm 1$ SEM per individual or observation.

Table 2. Results of repeated measures ANOVA conducted on numbers of immature *B. argentifolii* censused in population level studies

Effect	df	F	P
Cultivar	1,8	52.51	<0.001
Predatory release	1,8	21.09	0.002
Sample week	9,72	28.32	<0.001
Cultivar $\times$ predator release	1,8	4.30	0.072
Predator release $\times$ sample week	9,72	8.21	<0.001
Cultivar $\times$ sample week	9,72	2.65	0.010
Cultivar $\times$ predator release $\times$ sample week	9,72	0.88	0.545

presence or absence of *D. pusillus* ($P > 0.05$ for the cultivar $\times$ predator release interaction), indicating the lack of a significant difference in whitefly suppression from *D. pusillus* predation between the two tomato cultivars. Whitefly population growth rates varied significantly between cultivars (cultivar $\times$ sample week interaction) and between *D. pusillus* treatments (predator release $\times$ sample week interaction). The 3-way interaction among cultivar, *D. pusillus* treatment, and sample week was not significant. Due to the lack of a significant cultivar $\times$ predator release interaction, the hypothesis that biological control of *B. argentifolii* by *D. pusillus* should be more effective on a glabrous cultivar (VF145B7879) compared to a pubescent cultivar (Alta) was not supported by our population level experiment.

Host plant and prey influences on predator residence time. Tomato cultivar and presence of prey affected the amount of time beetles resided on plants (Figure 2). Residence times on Alta ($\overline{x} = 4.7$ h, SEM $= 0.32$, $N = 200$ beetles) were significantly greater than the residence times observed on VF145B7898 ($\overline{x} = 3.9$ h, SEM $= 0.30$, $N = 200$ beetles) at comparable sample times, and these differences were significant ($F = 29.93$, df $= 1, 36$, $P < 0.0001$). Residence times on plants with *B. argentifolii* eggs ($\overline{x} = 4.8$ h, SEM $= 0.32$, $N = 200$ beetles) were significantly longer than the residence times of beetles on plants without *B. argentifolii* eggs ($\overline{x} = 3.8$ h, SEM $= 0.31$, $N = 200$ beetles), and these differences were also statistically significant ($F = 46.36$, df $= 1, 36$, $P < 0.0001$). No significant 2-way or 3-way interactions were detected from the ANOVA.

Discussion

Plant trichomes form the basis of resistance against a number of arthropod pests (see Levin, 1973; Norris & Kogan, 1980; and Stipanovic, 1983 for reviews). However, whether whitefly oviposition rates increase or decrease with increasing densities of leaf trichomes varies greatly across host plants. Highly pubescent cultivars support larger populations of whitefly in the genus *Bemisia* than do glabrous cultivars of cotton (Mound, 1965; Butler & Henneberry, 1984; Ozgur & Sekeroglu, 1986) and tomato (Berlinger, 1986; Heinz & Zalom, 1995). However, in various species of cucurbits leaf pubescence is negatively correlated with densities of *Bemisia* sp. (McCreight & Kishaba, 1991; Kishaba et al., 1992). Densities of *B. tabaci* measured on 10 vegetable crops were not found to increase with increasing trichome densities (Simmons, 1994).

Responses to trichomes by natural enemies exhibit similar degrees of variability as that found in whiteflies. Obrycki et al. (1983) demonstrated that the combination of the sticky potato trichomes in hybrids of

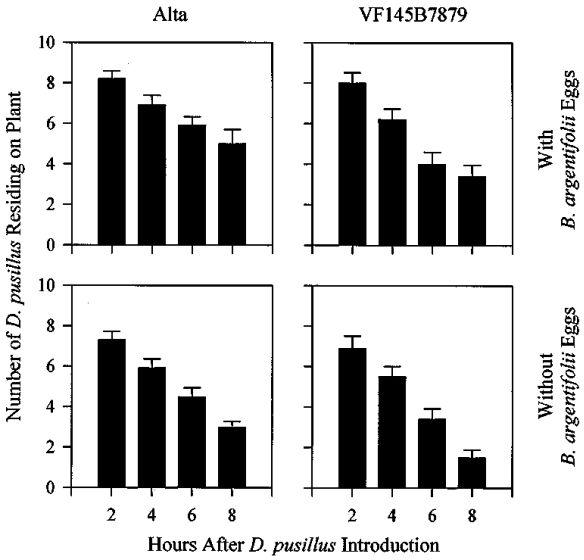

Figure 2. The influences of tomato cultivar and prey densities (*B. argentifolii* eggs) on the amount of time adult beetles reside (= residence time) on tomato plants before attempting to disperse. Mean numbers of beetles ± SEM obtained from 10 replications of each cultivar and prey density are graphed across the 8 h sampling periods.

Solanum tuberosum × *S. berthaultii* and the action of aphid predators and parasitoids (coccinellids, chrysopids, and aphidids) was more effective in reducing aphid populations than either enemies or trichomes alone. Heinz & Parrella (1994b) report that adult longevity of *D. pusillus* and four species of *Encarsia* (Hymenoptera: Aphelinidae) did not vary between poinsettia cultivars exhibiting different leaf trichome densities. Predator prey consumption, parasitoid host feeding, parasitism and the total number of *B. argentifolii* killed were significantly greater on the cultivar with less dense trichomes, but the numbers of wasps emerging from parasitised hosts were significantly fewer on this same comparatively glabrous cultivar (Heinz & Parrella, 1994b).

In several crops the simultaneous use of trichomes with parasitoids has proved to be an incompatible combination. In tobacco, the secretory hairs on foliage were found to interfere significantly with the ability of *Telenomus sphingis* (Ashmead) and *Trichogramma minutum* Riley to parasitize the eggs of the tobacco hornworm, *Manduca sexta* (L.) (Rabb & Bradley, 1968) because the sticky trichomal exudate restricted the movement of the parasitoids. Similar effects of tobacco trichomes on other parasitoid-host interactions have been reported (Elsey & Chaplin, 1978). In cucumber and tomato the efficacy of searching by the parasitoid *Encarsia formosa* Gahan for its host, the greenhouse whitefly *Trialeurodes vaporariorum* (Westwood), is greatly reduced by the presence of stiff foliar hairs that slow the parasitoid's walking, and also force the parasitoid to expend more time grooming if the hair's are coated with sticky honeydew (see Price et al., 1980; Li et al., 1987; Hulspas-Jordan & van Lenteren, 1989).

In the tomato–whitefly–coccinellid predator system we have described here, greater levels of *B. argentifolii* population suppression were obtained through the use of a glabrous tomato cultivar than were obtained through the release of *D. pusillus* (Figure 1). Although walking speeds and lifetime fecundity were reduced significantly in beetles housed on the pubescent compared to the glabrous cultivar, beetle residence times were significantly longer on the pubescent cultivar compared to the glabrous cultivar. Trichome-induced variation in these characteristics (and possibly other characters) produced a counterbalancing effect whereby the levels of whitefly suppression resulting from *D. pusillus* predation were not significantly different between cultivars differing in trichome density.

The reduced residence times on the glabrous cultivar may be a result of various 'decisions' made by foraging beetles. If beetles use the rate of encounter with suitable prey as means of measuring patch quality (as described by Stephens & Krebs, 1986), and if this encounter rate declines more quickly for beetles foraging on glabrous than on pubescent cultivars, then beetles may spend less total time foraging on glabrous cultivars. Encounter rates may decrease more quickly on glabrous cultivars due to the increased search efficiency (as indicated by faster walking speeds) of foraging beetles in comparison to beetles foraging on pubescent cultivars where their walking speeds are relatively slow. Furthermore, because beetles used in these studies were obtained from laboratory colonies where they were continually provided with a superabundance of prey, exit thresholds based upon encounter rates may be abnormally low. Because we did not explicitly test this hypothesis, it is also possible that the lack of a difference in whitefly suppression from *D. pusillus* predation may be due to plant characteristics other than trichome densities.

The patterns described here warrant further study due to the influence these counterbalancing properties may have on predator foraging behavior and due to their importance in developing effective control programs for *B. argentifolii*. Considering our current knowledge, agriculturists should obtain benefits

in terms of whitefly control by planting glabrous rather than pubescent tomato cultivars due to their negative effect on *B. argentifolii* population growth and neutral effect on *D. pusillus* efficacy. Further, the lack of evidence to suggest that biological control may the inhibited by a lack of foliar trichomes suggests that selection for glabrous foliage may lead to sustained or increased biological control for a wide range of arthropod pests of tomato.

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