

ARTHROPOD MANAGEMENT

Environmental and Host Plant Effects on Insecticide Susceptibility of the Cotton Aphid (Homoptera: Aphididae)

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INTERPRETIVE SUMMARY

The cotton aphid has become a serious insect pest of cotton in California and across the Cotton Belt during the past 10 to 15 y. In California, mid- and late-season infestations can significantly reduce cotton lint yields and threaten lint quality. In 1997, cotton aphids in California cotton caused an estimated \$34 million in crop loss and another \$38 million in control costs. Biological control from predatory and parasitic insects and from insect-infecting fungi is ineffective from June to October in California. Therefore, insecticides are a primary tool used by growers to protect cotton from this pest. Insecticide efficacy in controlling cotton aphids is often erratic and unpredictable. Upon exposure to insecticides, aphids have the ability to develop resistance rapidly, rendering subsequent treatments ineffective. However, aphids are also extremely dynamic organisms and may quickly adapt to the given set of conditions under which they are reared. This quick acclimation may involve developing different reproduction strategies (sexual vs. asexual), different color forms, or wings, or may involve more subtle (visually indistinguishable) changes. The cotton aphid's ability to develop tolerance to insecticides, when cotton aphids were grown under various environmental conditions and on different host plants, was investigated in this study. Field observations have shown that cotton aphids are less susceptible to some insecticides early in the growing season, for example in May, compared with later in the season, such as in July and August. If one infers that poor coverage and traditional insecticide resistance are the reasons for the poor control, these conditions should be more of a factor later in the growing season, and, therefore,

the control should be better during the early season. Thus, other factors may be influencing the resistance patterns. Results from this laboratory study showed that aphids reared under early-season environmental conditions (cooler temperatures and long days) were less susceptible to the insecticides (bifenthrin, chlorpyrifos, and triazamate) than were aphids reared under late-season conditions. The opposite trend in terms of differential insecticide susceptibility was seen with endosulfan. Also, aphids reared on melon plants were more susceptible to bifenthrin and chlorpyrifos than were genetically similar aphids reared on cotton.

ABSTRACT

Insecticidal control of the cotton aphid (*Aphis gossypii* Glover) in California is often erratic. Genetic, selection-induced resistance is certainly a factor in many cases. However, field observations indicate that other factors may be important in this phenomenon. Cotton aphids are more resistant to some insecticides before the period of significant use and exposure compared with after the period of use. Studies were conducted to examine the influence of environmental and host plant factors on insecticide susceptibility of cotton aphids under controlled laboratory conditions. Aphids were reared under selected conditions and evaluated in bioassay tests with insecticides from the organophosphate, carbamate, pyrethroid, and organochlorine classes. Genetically similar cotton aphids exhibited significantly different susceptibilities to the insecticides bifenthrin, chlorpyrifos, endosulfan, and triazamate when reared on cotton under temperature and photoperiod regimes reflective of the early and late cotton growing season in the southern San Joaquin Valley in California. Aphids reared under early-season conditions were less susceptible to bifenthrin, chlorpyrifos, and triazamate than were aphids reared under late-season conditions. The opposite trend in terms of differential insecticide susceptibility was seen with endosulfan. Also, aphids reared on melon plants were more susceptible to bifenthrin and chlorpyrifos than were genetically similar aphids reared on cotton. These results suggest

that a significant amount of phenotypic plasticity exists within insecticide susceptibility of cotton aphids. Cotton aphid management may be able to benefit from the knowledge of such environmental and host plant influences on insecticide susceptibility as seen in these experiments.

The cotton aphid (*Aphis gossypii* Glover) has developed into a significant pest of cotton in California. The importance of this pest to cotton production has changed significantly in the last 10 to 15 y. Before the mid-1980s, the cotton aphid was considered an occasional pest of cotton in the San Joaquin Valley. Beginning in ~1986, significant infestations of cotton aphids were seen on seedling and late-season cotton. Infestations on mid-season cotton (June to August) were minimal until 1992 when significant, damaging populations occurred. This trend has continued to varying degrees and was particularly severe in 1995 and 1997. In 1995, cotton yield losses from cotton aphids were estimated at 3.5% (Williams, 1996), in spite of management actions. This yield loss rivaled that from spider mites (*Tetranychus* spp.) and lygus bugs (*Lygus hesperus* Knight), the established cotton arthropod pests in California. Cotton aphid outbreaks were severe and widespread in 1997: an estimated 3.5% yield loss occurred and control costs of ~ \$40 per acre were incurred (Williams, 1998). In 1996, 1998, and 1999, years without widespread high cotton aphid densities, significant costs were incurred as preventative treatments were applied. In addition, the pest-management strategies used for other key cotton arthropod pests, that is, spider mites and lygus bugs, often are implemented only after considering the effect on and the potential for cotton aphid outbreaks. Reasons for this shift in cotton aphid population severity are unclear; however, the resulting yield losses and threat of contaminated lint from cotton aphid honeydew make aphid control a necessary production cost for California cotton growers.

Control of *A. gossypii* with insecticides, while frequently erratic and unpredictable, remains the most prevalent and important control measure in cotton aphid management in California. Biological control of the cotton aphid has a limited role in California cotton, given the extensive intraguild predation of natural enemies observed by Rosenheim et al. (1995a) and Cisneros and Rosenheim (1997) and the sparse occurrence in

California of the fungus *Neozygites fresenii* (Steinkraus and Rosenheim, 1995). *N. fresenii* is a very important natural control agent of *A. gossypii* in the southern, more humid states of the United States (Steinkraus et al., 1995). Host plant resistance in the form of cotton plants with lower trichome density (Harris et al., 1994; Weathersbee et al., 1994) and cultivars with lower petiole nitrate concentrations (Allen et al., 1992) affect aphid densities moderately, but these effects are often overshadowed by other biotic factors (Weathersbee and Hardee, 1995). Cotton plant N content may play a large role in determining cotton aphid population dynamics in the field (Slosser et al., 1992; McKenzie et al., 1995; Godfrey et al., 1999, 2000), but significantly reducing this input may be difficult, given the needs of the crop. Therefore, insecticides are the primary control tactic for *A. gossypii* in California cotton.

During the past 15 years, however, instances of cotton aphid resistance to insecticides have been documented throughout the world (Furk et al., 1980; Takada and Murakami, 1988; Grafton-Cardwell et al., 1992; Gubrun et al., 1992; Tang, 1992; Grafton-Cardwell et al., 1997). Also, individual cotton aphids may possess a significant level of inducible detoxification. Grafton-Cardwell (1991) reported that *A. gossypii* populations in the San Joaquin Valley of California exhibit a temporal and spatial variation in susceptibility to selected organophosphate and organochlorine insecticides. Whether this phenomenon results from changes in the genetic makeup of a population or from a phenotypically plastic characteristic of the aphids is not known. On a more anecdotal level, growers and researchers have noticed that changes in insecticidal control of cotton aphids may correspond to different times of the growing season (Allen et al., 1990; Fuson and Godfrey, 1994; Fuson et al., 1995) and different host plants (Xiwu and Bingzong, 1992). Temperature and host plants affect observable morphological features in *A. gossypii* such as color and size (Kring, 1959; Inaizumi, 1980; Wilhoit and Rosenheim, 1993), but studies on temperature and host plant effects on the practical and more cryptic characteristic of insecticide susceptibility are lacking. An understanding of the effects of seasonal environmental conditions and host plant changes on insecticide susceptibility would aid in the development of optimal cotton aphid management

strategies. In these studies, we examined changes in cotton aphid insecticide susceptibility to three currently used aphicides and one experimental aphicide in response to the temperature and photoperiod regime under which aphids were reared and in response to the host plant on which the aphids developed.

MATERIALS AND METHODS

The aphids used in this study were taken from a clonal colony of cotton aphids, initiated in September 1992 from a stem mother collected from cotton near Shafter, California. The colony had been reared on Acala cotton 'GC-510' under environmental conditions (23.9°C constant temperature and a photoperiod of 16:8 [light:dark] h) that did not promote sexual reproduction (Kring, 1959; Inaizumi, 1980). Population growth was, therefore, a result of asexual, viviparous reproduction. The colony was known to be susceptible to the insecticides studied in this experiment on the basis of results from a rapid petri dish bioassay technique (Fuson and Godfrey, 1994).

Seasonal Environmental Condition Effects

Seasonal environmental effects on cotton aphid insecticide susceptibility were examined by rearing aphids from the clonal, known-susceptible colony on Acala cotton GC-510 under temperature and photoperiod regimes reflective of the early and late cotton growing seasons in the southern San Joaquin Valley of California. Using data from California Irrigation Management Information System weather stations, the average day and night temperatures and photoperiods for late May and mid-August were estimated for the Kern County, California area. The early-season environmental condition consisted of a photoperiod of 16:8 (light:dark) h with an average day temperature of 23°C and an average night temperature of 15.0°C. The late-season condition consisted of a photoperiod of 14:10 (light:dark) h with an average day temperature of 29.4°C and an average night temperature of 24.4°C. Growth chambers (Percival, Boone, IA) were used to obtain the appropriate environmental conditions. Acala cotton GC-510 seeds, treated with fungicides (Apron Flowable and Nu-Flow M, Wilbur-Ellis, Fresno, CA) were first germinated in potting soil

(Supersoil, Rod McLellan, South San Francisco, CA) in 7.6-cm-square plastic pots under greenhouse conditions (26.7°C, 16:8 [light:dark] h). Fertilization of the plants occurred on a weekly schedule with a solution of Miracle-Gro 15-30-15 (N-P-K) (Stern's Products, Port Washington, NY). Plants were moved to the growth chambers after reaching a height of at least 7 cm. Light intensity, measured with a General Electric type 213 light meter (General Electric, New York, NY), was about 9.66 W m⁻² at plant canopy height within the growth chambers. Auclair (1967) indicated that this light intensity is suitable for cotton aphid growth. Aphids were initially taken from the clonal colony and placed, using a small camel-hair paintbrush, onto cotton plants in the growth chambers. Every 2 wk, new cotton plants were introduced into the growth chambers, and after 2 to 3 d, aphids were transferred from the older plants in the growth chambers to the newly introduced plants. Cotton plants harboring too large an aphid population were removed before high population densities induced the production of alate forms (Kring, 1959; Mousseau and Dingle, 1991).

Aphids were allowed to acclimate to the newly introduced cotton plants for at least three generations (about one month), after which adult aphids were removed from the plants and assayed for their susceptibility to the following chemicals: bifenthrin [2-methyl-1,1-biphenyl-3-yl)-methyl-3-(2-chloro-3,3,3-trifluoro-1-propenyl)-2,2-dimethyl cyclopropane carboxylate] (Capture 2E; FMC, Philadelphia, PA), chlorpyrifos [O,O-diethyl O-(3,5,6-trichloro-2-pyridinyl) phosphorothioate] (Lorsban 4E; DowElanco, Indianapolis, IN), endosulfan [6,7,8,10,10-hexachloro-1,5,5,6,9,9a-hexahydro-6,9-methano-2,4,3-benzodioxathiepin 3-oxide] (Phaser 50WP; Hoechst-Roussel Agri-Vet, Somerville, NJ), and triazamate [acetic acid, [[1-[(dimethylamino)carbonyl]-3-(1,1-dimethylethyl)-1H-1,2,4-triazol-5-yl] thio]-, ethyl ester] (Aphistar 25W-technical grade; Rohm & Haas, Philadelphia, PA). The modified petri dish bioassay technique (McKenzie et al., 1993) used 60-mm-diam. plastic petri dishes, the inner surfaces of which were each coated with a dilution of one of the four insecticides. Five serial dilutions with 95% ethyl alcohol were used for each chemical. Doses of 620 mL and 720 mL of the solutions were pipetted into the lid and bottom of the petri dishes, respectively.

The lids and bottoms were rotated gently to ensure even distribution and were allowed to air-dry. Aphids were placed into the dishes, and mortality was defined as the inability of an aphid to right itself or to move one body length forward in a directed manner after light prodding. Dishes were held at room temperature (25°C) and constant light during the 3-h exposure period. A minimum of 20 dishes were used per concentration, with a range of 10 to 20 aphids per dish.

Adult aphid weight was quantified using a Cahn 20 automatic electrobalance (Cahn, St. Louis, MO) to obtain the individual weights of 100 adult aphids reared under each environmental condition. Individual body size may affect bioassay results (Robertson and Preisler, 1992).

Host Plant Effects

Individuals from the aphid clonal colony were introduced to melon plants under the previously mentioned environmental conditions. Aphid populations from these plants then were used to determine insecticide susceptibility using the same procedure described earlier. Melon (*Cucumis melo* L. subsp. *melo* var. *cantalupensis* Naudin) seeds ('Hales Best Jumbo Cantaloupe', NK Lawn & Garden, Minneapolis, MN) were germinated in potting soil (SuperSoil) in 14-cm-diameter plastic pots under greenhouse conditions and grown until approximately the 4-true-leaf stage. Fertilization of these plants occurred at 1-wk intervals using Miracle-Gro. At the 4-true-leaf stage, the melon plants were moved to the growth chambers, which also housed aphid-infested cotton plants at the conditions described for the previous experiment. Aphids were placed onto the melon plants 2 to 3 d after the plants were introduced to the chambers, and at least three aphid generations passed before any bioassays were performed. Aphid movement between plants was prevented by covering the edges of the plastic pots with masking tape with the adhesive side exposed. New melon plants were introduced into the chambers at ~3-wk intervals, which helped prevent the production of alatae. The previously described petri dish bioassay was used to assess aphid susceptibility to bifenthrin and chlorpyrifos that developed on melon under the early- and late-season conditions.

Statistical Analyses

Probit analyses (Finney, 1971) were used to generate both an LC_{95} and a linear function describing aphid population response to the chemicals under both rearing conditions. The software package POLO-PC was used for the probit analyses (LeOra Software, 1994). The LC_{95} values were compared using a lethal concentration ratio (Robertson and Preisler, 1992) in which the LC_{95} of the aphids reared under experimental condition 1 (early-season or melon) was divided by the LC_{95} of the aphids reared under experimental condition 2 (late-season or cotton). An LC_{95} ratio in which the 95% confidence intervals did not include 1.0 indicated that the experimental condition significantly altered the mortality response to the insecticide. An LC_{95} ratio >1.0 suggested that aphids reared under condition 1 were less susceptible to the chemical than were the aphids reared under condition 2, and the inverse was true for resistance ratio values <1.0 . The slopes of the linear functions derived from probit analyses also were compared (LeOra Software, 1994). A steeper slope of the response function indicated that there was more response homogeneity in a population. A single-factor analysis of variance test (SAS Institute, 1985) was performed on the weight data to determine a relationship between adult aphid body weight and the condition under which the aphids were reared.

RESULTS

Aphid Weight

Aphids reared under early- and late-season conditions did not differ significantly for the body-weight variable (Table 1). Mean body weight of aphids reared on cotton under both early- and late-season environmental conditions was not significantly different from that of aphids reared on melon under the same conditions.

Seasonal Environmental Condition Effects

The efficacy of all four insecticides was significantly affected by the environmental conditions under which the aphids were reared.

Table 1. Mean body weight of aphids reared on cotton and melon under early-season and late-season environmental conditions.

Rearing condition	Mean aphid body weight	
	Cotton	Melon
	μg ± SEM	
Early season [†]	62.3 ± 4.9 (a, A) [§]	82.8 ± 8.1 (a, A)
Late season [‡]	57.2 ± 3.8 (a, A)	79.4 ± 9.9 (a, A)

[†] Late May conditions in San Joaquin Valley.

[‡] Mid-August conditions in San Joaquin Valley.

[§] Common lowercase letters between means within host plants indicate no significant difference ($P > 0.05$). (Cotton: $df = 1, 196, F = 4.16$; Melon: $df = 1, 196, F = 4.02$). Common uppercase letters between means within seasonal environmental conditions indicate no significant difference ($P > 0.05$). (Early season: $df = 1, 196, F = 1.45$; Late season: $df = 1, 196, F = 0.94$).

Cotton aphid response heterogeneity to bifenthrin, chlorpyrifos, and triazamate was significantly greater in aphids reared under early-season conditions, compared with aphids reared under late-season conditions (Table 2). This is illustrated by a significantly steeper slope of the probit lines for these insecticides from aphids reared under late-season conditions compared with the respective slopes from aphids reared under early-season conditions. There was not a significant effect of

environmental rearing condition on the response variability for the endosulfan probit lines. The LC_{95} ratios indicated that aphids reared under the early-season conditions were significantly less susceptible to bifenthrin, chlorpyrifos, and triazamate, compared with aphids reared under the late-season conditions. However, for endosulfan, the LC_{95} ratio indicated that aphids reared under the early-season conditions were significantly more susceptible than aphids reared under the late-season conditions.

Host Plant Effects

The effect of the host plant on cotton aphid insecticide susceptibility was significant only for bifenthrin efficacy in early-season environmental conditions. However, aphids reared under early-season environmental conditions had a more variable response to bifenthrin when reared on cotton than on melon, as evidenced by the significantly steeper probit line slope generated by aphids reared on melon (Table 3). Cotton aphid response heterogeneity to bifenthrin was not

Table 2. Probit analysis of insecticide bioassays with cotton aphids reared on cotton under early- and late-season conditions.

Chemical	Rearing condition	<i>n</i>	Slope (±SEM) [†]	LC ₉₅	LC ₉₅ ratio [‡]	95% CI limits of ratio
				mg kg ⁻¹		
bifenthrin	early season	761	1.18 ± 0.07 a	1.794	2.37	1.32–4.26
	late season	1039	1.46 ± 0.08 b	0.758		
chlorpyrifos	early season	597	0.99 ± 0.08 a	1151.6	9.25	7.68–10.82
	late season	944	1.36 ± 0.08 b	124.7		
endosulfan	early season	777	1.25 ± 0.08 a	102.5	0.20	0.12–0.32
	late season	690	1.04 ± 0.07 a	525.2		
triazamate	early season	837	1.14 ± 0.07 a	264.2	2.14	1.32–3.46
	late season	657	1.52 ± 0.10 b	123.8		

[†] Common letters between slope values derived from aphids reared under different environmental conditions within chemical treatments indicate no significant difference ($P > 0.05$).

[‡] Early-season/late-season comparison.

Table 3. Probit analysis of insecticide bioassays with cotton aphids reared on melon and cotton under early- and late-season conditions.

Chemical	Rearing condition	Host	<i>n</i>	Slope (±SEM) [†]	LC ₉₅	LC ₉₅ ratio [‡]	95% CI limits of ratio
					mg kg ⁻¹		
bifenthrin	early season	melon	625	1.50 ± 0.11 a	0.287	0.16	0.08–0.30
		cotton	761	1.18 ± 0.07 b	1.794		
	late season	melon	619	1.38 ± 0.10 a	0.367	0.48	0.28–0.82
		cotton	1039	1.46 ± 0.08 a	0.758		
chlorpyrifos	early season	melon	597	0.92 ± 0.07 a	191.9	0.17	0.06–0.47
		cotton	597	0.99 ± 0.08 a	1151.6		
	late season	melon	989	1.35 ± 0.08 a	56.3	0.45	0.27–0.75
		cotton	944	1.36 ± 0.08 a	124.7		

[†] Common letters between slope values derived from aphids reared on cotton and melon within chemical treatments and within environmental condition indicate no significant difference ($P > 0.05$).

[‡] Early-season/late-season comparison.

affected by the host plant when aphids were reared under late-season conditions, and response heterogeneity to chlorpyrifos was not significantly influenced by the host plant under late- or early-season conditions. Cotton aphids reared on melons were significantly more susceptible to bifenthrin and to chlorpyrifos compared with cotton aphids reared on cotton. Resistance ratio values ranged from 0.16 to 0.17 under early-season conditions and were 0.48 and 0.45 on bifenthrin and chlorpyrifos, respectively, under late-season conditions.

DISCUSSION

A significant phenotypic plasticity of insecticide susceptibility exists in genetically identical cotton aphids. This plasticity has important implications for both cotton aphid physiology and management. The lower susceptibility to bifenthrin, chlorpyrifos, and triazamate exhibited by aphids reared under early-season conditions raises questions regarding the physiology of *A. gossypii*. While classical cotton aphid insecticide resistance to carbamate (Furk et al., 1980; Furk and Hines, 1993), pyrethroid (Tang, 1992), and organophosphate (Grafton-Cardwell et al., 1992; O'Brien et al., 1992) insecticides has frequently been documented, the use of a clonal cotton aphid colony in this study minimized the chance that any observed differences were manifested through the presence of resistance genes. Also, while Robertson and Preisler (1992) noted that body size can significantly influence bioassay results, the weights of cotton aphids reared on cotton under different environmental conditions and on melons were not significantly different. This result suggests that *A. gossypii* undergoes significant, inducible insecticide susceptibility changes not related to body size or selection of resistance genes. The presence of inducible changes in insecticide susceptibility is further supported by the results of the host plant study. In this case, aphids reared on melons were more susceptible to bifenthrin and chlorpyrifos, compared with those reared on cotton. Again, genetic confounding effects were minimized, and body size was taken into account. There was more variation in aphid response to bifenthrin, chlorpyrifos, and triazamate when aphids were reared on cotton under early-season conditions than when aphids were reared on

cotton under late-season conditions. A similar situation holds for bifenthrin susceptibility in aphids reared on cotton compared with aphids reared on melon. Under early-season environmental conditions, the response homogeneity is significantly greater on melon, suggesting that variation in host plants can lead to variation in cotton aphid susceptibilities.

Questions now arise concerning the physiological mechanism behind these insecticide susceptibility changes in *A. gossypii*. Increased production of detoxicative enzymes (Sun et al., 1987; Takada and Murakami, 1988; O'Brien et al., 1992) and insensitive acetylcholine esterase (Furk and Hines, 1993) have been suggested as physiological mechanisms present in classic cases of cotton aphid insecticide resistance. It is necessary to examine the mechanistic reasons for the observed susceptibility changes due to temperature, light regime, and host plant. An understanding of the mechanisms behind susceptibility changes may allow proper measures to be taken to ensure acceptable cotton aphid control in the field.

The implications of these insecticide efficacy differences in the field are unknown. However, these data do support field observations of poorer insecticide performance from some products during the early season compared with the late season. The extent to which host plant effects on insecticide susceptibility will be retained after aphid movement among hosts is unknown. Commercial melon fields in California are generally a spring host for cotton aphids; the extent to which these aphids move into cotton is unknown. The data from Grafton-Cardwell (1991) suggest that both seasonal condition and host plant effects on susceptibility are discernible in the field, but genetic differences of aphids in that study were not controlled. This uncontrolled genetic factor was also prevalent throughout the field observations that prompted this study. Therefore, control of genetic variability allows the examination of whether phenotypic plasticity in insecticide susceptibility is important. With an increased prevalence of cotton aphid insecticide resistance in California (Rosenheim et al., 1995b) and throughout the U.S. Cotton Belt (King et al., 1987), it will be increasingly difficult to discern phenotypic plasticity from genetic-based cotton aphid insecticide susceptibility in the field.

However, it is clear that phenotypically plastic insecticide susceptibility in *A. gossypii* merits additional investigation and understanding.

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