The Impact of Cotton Plant Resistance on Spider Mites and Their Natural Enemies

Paul J. Trichilo and Thomas F. Leigh

ABSTRACT

A spider mite-resistant and a spider mite-susceptible variety of cotton were planted in the field in a replicated design. An acaricide (dicofol) and an insecticide (acephate) were used to manipulate numbers of spider mites and their natural enemies. In general, numbers of spider mites remained low until just before midseason when 650 °D air temperature had accumulated. At 650 °D, mite numbers began to increase more sharply and reached significantly (P<0.001) greater levels on susceptible plants than on resistant plants. Although natural enemies, such as *Geocoris pallens* Stål, *Orius tristicolor* (White), and *Frankliniella occidentalis* (Pergande), were slightly more apparent on susceptible plants than on resistant plants, these differences were not statistically significant, and cotton varietal resistance was compatible with biological control.

Acephate significantly (P<0.05) reduced predator densities for up to 2 weeks following each application, and after 550 °D mite populations had begun to explode on plants sprayed with acephate. Predators had a greater impact on mites on susceptible plants than on resistant plants, which was attributed to greater densities of spider mite prey on susceptible plants. After 900 °D, spider mites were out of control on susceptible plants treated with acephate, and the acaricide dicofol had no observable effect on mite numbers. Rapidly increasing mite populations appear to exhibit

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INTRODUCTION

A LARGE PORTION of California agriculture is devoted to the production of temporary crops which include cotton (Gutierrez et al. 1975). These temporary agroecosystems may be subject to severe outbreaks of rapidly colonizing pest species such as spider mites (Reynolds et al. 1982).

Role of Natural Enemies

Although omnivorous predators make up a large part of the spider mite natural enemy complex on cotton (Ehler 1977; Ehler and Miller 1978; Gonzalez and Wilson 1982; van den Bosch and Hagen 1966), there has been serious debate as to the ability of these general predators to control pests in temporary agroecosystems (Conway 1976; Hansberry 1968; Lloyd 1960; Newsom 1970; Price et al. 1980). Other evidence, however, indicates that such pests as spider mites that are well adapted to colonizing disturbed ecosystems are adequately controlled by a complex of omnivorous predators (i.e., generalists). For example, *Geocoris pallens* Stål and *Orius tristicolor* (White) are as equally well suited as are spider mites to colonizing these temporary habitats (Bisabri-Ershadi and Ehler 1981; Ehler 1977; Ehler and van den Bosch 1974; Force 1972).

Pest outbreaks in agroecosystems have often been attributed to the indiscriminate use of synthetic chemicals and widespread loss of beneficials (Debach 1974; Eveleens, van den Bosch, and Ehler 1973; Falcon et al. 1968; Pimentel 1961; Smith and Hagen 1959; Stern et al. 1959; Stoltz and Stern 1978b; van den Bosch et al. 1971; van Steenwyk et al. 1975). Integration of other pest management tactics, such as host-plant resistance (HPR), may reduce the need for chemicals and insure greater safeguards against the occasional loss of natural enemies when pesticides are used.

Potential for Host-Plant Resistance

An important feature of evolutionary success of colonizing species, such as spider mites, is the capacity for rapid population increase. Host-plant resistance can be effective in reducing the reproductive fitness (i.e., potential for increase) of spider mites on cotton (Schuster, Maxwell, and Jenkins 1972; Schuster et al. 1973; Trichilo and Leigh 1985). Plant resistance that induces chronic toxicity would slow herbivore population growth rates, increase exposure of phytophagous pests (i.e., spider mites) to natural enemies, and thereby augment the efficacy of both HPR and biological control (van Emden 1966; van Emden and Wearing 1965).

The subject of compatibility between HPR and biological control has received considerable attention (Adkisson and Dyck 1980; Bergman and Tingey 1979; Price et al. 1980; van Emden 1966). Investigators have demonstrated that plant resistance to herbivores may have a negative impact on predator and/or parasitoid populations (Bergman and Tingey 1979; Campbell and Duffey 1979; Landis 1937; Obrycki and Tauber 1984; Smith 1957; Strong 1984; Thurston and Fox 1972). Phytochemicals may also adversely affect omnivorous predators which occasionally feed on plant tissue, i.e., leaves, nectar, or pollen (Bergman and Tingey 1979). Consequently, HPR could have serious repercussions in a cotton agroecosystem, where most of the important natural enemies of spider mites are omnivorous.

On the other hand, there have also been examples where HPR was compatible with biological control (Adkisson and Dyck 1980; Bergman and Tingey 1979; Casagrande and Haynes 1976; Debach 1974; Fry 1980; Kartohardjono and Heinrichs 1984; Obrycki, Tauber, and Tingey 1983; Pimentel and Wheeler 1973; Schuster and Starks 1975; Starks, Muniappan, and Eikenbary 1972).

In our preliminary life table study of *Tetranychus urticae* on five varieties of cotton, 'Pima S-5,' a *Gossypium barbadense* from Arizona, was the most spider mite-resistant, and 'Acala SJ-2,' a *Gossypium hirsutum* from the San Joaquin Valley of California, was the most susceptible. Varietal resistance was expressed as lower mite fecundity (m_x) and survivorship (l_x), as well as a lower intrinsic rate of increase (r), for spider mites on Pima S-5, than on Acala SJ-2 (0.227 vs. 0.251, respectively) (Trichilo and Leigh 1985). Shortly thereafter, we documented the predation on spider mite eggs by the western flower thrips, *Frankliniella occidentalis* (Pergande), which had typically been considered a pest on cotton (Trichilo and Leigh, in press). The prospect of an herbivore which was also a predator, and thus an omnivore, was important with respect to our original interest in the compatibility of HPR and biological control. Because flower thrips are predators and herbivores, their predatory efficacy could be inhibited by phytochemicals in a spider mite-resistant variety of cotton. Our objective was to evaluate the impact of varietal resistance on spider mites and their natural enemies in a cotton agroecosystem, with a primary focus on the omnivorous predator complex of *G. pallens*, *O. tristicolor*, and *F. occidentalis*.

MATERIALS AND METHODS

Treatments and Agronomic Practices

On May 4, 1983, the spider mite-susceptible Acala SJ-2 and the spider mite-resistant Pima S-5 cotton cultivars were planted on sandy loam soil, in a replicated block design, at the USDA Cotton Research Station in Shafter, California. Each variety was subjected to four treatments which included: (1) insecticide (acephate), (2) acaricide (dicofol), (3) insecticide plus acaricide, and (4) untreated. Thus, the experiment consisted of eight treatments (4 × 2 varieties), replicated four times for a total of 32 plots. Each plot measured 404.2 m², for a total experimental area of 1.3 ha.

Plants were fertilized on June 4 with 90 kg N/ha, using 21-10-0 N P K fertilizer granules. Plots were treated with an herbicide (Treflan at 0.560 kg ai/ha) on July 7. Irrigation, which consisted of one preplant and seven postplant applications, corres-

ponded to local practices in the San Joaquin Valley. Acephate was first applied as a seed treatment at 5 mg ai/g seed, as 80 SP in methyl cellulose, and later as a spray at 0.224 kg ai/ha on June 12 and July 24. Dicofol was applied as a spray at 1.12 kg ai/ha on July 12 and July 29.

Sampling

Plots were sampled for spider mites and larval flower thrips 10 times during the season, usually on a weekly basis. A sample consisted of 25 mainstem, fifth-node (from the terminal) leaves, each removed from a different plant chosen at random (Mollet and Sevacherian 1984; Wilson et al. 1983). Samples from seedlings or young plants consisted of the first (lowest) primary leaf to emerge, until plants were old enough to have produced at least six mainstem leaves. Samples of 25 leaves were placed in 2-L cylindrical, cardboard cartons, chilled immediately, and transported to the laboratory where chilling (6.7°C) was continued until samples could be processed. Each leaf was classified as either infested or not infested with spider mites. All mite and flower thrips stages (except eggs) were counted directly from the leaf surface with the aid of a dissecting microscope. Although flower thrips usually remained on the leaves, adult and larval thrips were occasionally found at the bottom of the carton and were subsequently counted as part of the sample. Species identifications of spider mites, based on morphology of male aedeagi (Tuttle and Baker 1968), were conducted several times during the season. However, in the collection of data on treatment effects, species were not distinguished, and all mites were lumped into the category *Tetranychus* spp.

In addition to weekly leaf samples of larval flower thrips, all plots were sampled for general predators, with a vacuum sampling device, i.e., D-vac (Dietrick 1961) four times during midseason. Sampling for predators was initiated in the morning hours, after all dew had evaporated from the cotton plants (Byerly et al. 1978; Gonzalez et al. 1982). A sample consisted of vacuuming the top (30 to 40 cm) portion of 50 cotton plants (1 second/plant) chosen at random within a given plot. After each plot was sampled, the sealed bag containing the sample was immediately placed within a brown paper bag and again sealed with masking tape. Samples were chilled immediately. Sampling all plots with D-vac required 2 days (two replications per day).

Each day's samples were exposed to CO_2 gas for 1 minute and then immediately placed in Berlese funnels to separate the arthropods from plant debris. Each funnel was equipped with a heating element at the top, and a jar of 70 percent ethanol at the bottom, located 10 cm above a 40-watt incandescent light bulb, set for a 15-minute on/off cycle. After 24 hours, jars with samples in ethanol were removed, secured with lids, and set aside for later examination. Kinds and numbers of predators in each sample were determined with the aid of a dissecting microscope.

Yield

In late October, the center four rows of cotton in each plot were harvested with a traditional two-row harvester equipped to collect seed cotton, in 0.6-cm mesh bags,

separately from each row. Samples were subsequently weighed to determine the amount of seed cotton (lint plus seed) per unit row and later analyzed for fraction of lint.

Analysis

Analysis of variance (ANOVA) was used to compare the effects of treatments on populations of spider mites and their major predators within each sampling period. To facilitate plotting of the entire season's data, before analysis, spider mite numbers were modified through a log transformation. ANOVA was also used to compare the impact of these treatments (as they affected spider mites and their predators) on yield. Means were statistically compared at the 95 percent confidence level, using Tukey's multiple comparison test.

Percentage (%) effectiveness of the various treatments at peak mite densities (sample 9 on August 9) was calculated, using Abbott's formula (Abbott 1925) on the un-transformed data,

$$\%E = \frac{X - Y}{X} \times 100$$

where %E is percentage effectiveness, X is the number of mites occurring in the absence of a given key factor (i.e., predators, acaricide, or varietal resistance), and Y is the number of mites occurring in the presence of the key factor. This formula was used by Kartohardjono and Heinrichs (1984) to determine percentage mortality of the brown planthopper on different rice cultivars. In our study, Abbott's formula was a convenient way to assess the individual efficacy of predation, varietal resistance, and acaricide on spider mite populations. ANOVA was used to statistically evaluate per-centage effectiveness, while Tukey's multiple comparison of the means at the 95 percent confidence level was used to compare treatments.

To relate mite population growth rates to plant development, as well as to our original life table model, time was converted to degree-days. Degree-days (°D) were computed for the Shafter station, from the Integrated Pest Management Meteorological Data Center, University of California. A lower temperature threshold of 12°C was used, based on previous interpretation of spider mite developmental data (Carey and Bradley 1982; Trichilo and Leigh 1985).

RESULTS

Natural Enemies

Numbers of predators were usually lower in plots sprayed with acephate (figs. 1, 2, and 3). These differences were statistically ($P<0.05$) significant for 1 to 3 weeks following applications of the insecticide.

Densities of *Orius* nymphs were too low at the time of application to be visibly affected by the insecticide (fig. 1*a*), although numbers of adult *Orius* were significantly ($P<0.05$) reduced (fig. 2*a*). *Geocoris* were well established at the time of spraying and
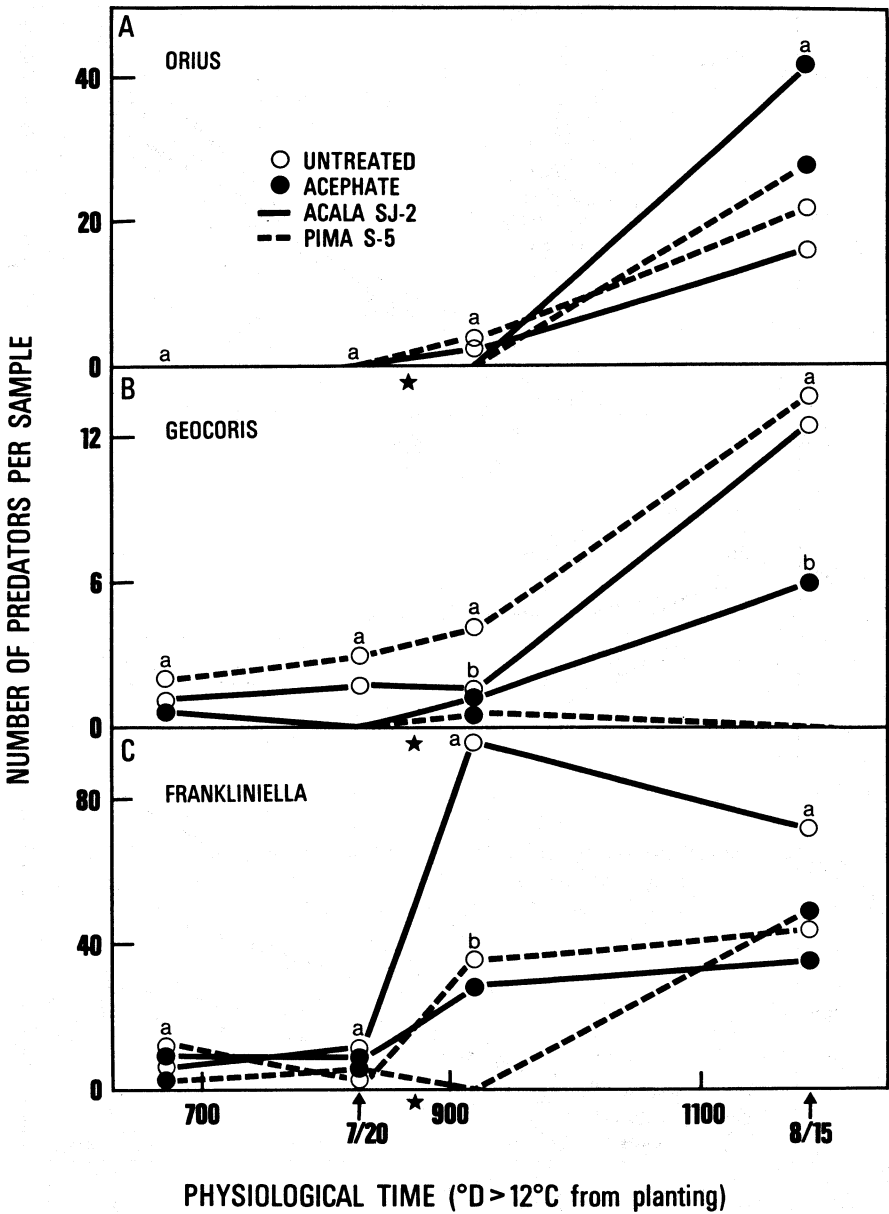
Fig. 1.   Influence of insecticide (acephate) and plant variety on the mean fluctuation of immature insectan predators on cotton, as determined by vacuum sampling (see text). Symbol (★) represents date of insecticide application. (*a*) *Orius tristicolor* (White). (*b*) *Geocoris pallens* Stål. (*c*) *Frankliniella occidentalis* (Pergande). Means preceded above by same letter are not significantly different at $\alpha = 0.05$ on a given sampling date (Tukey's multiple comparison test).
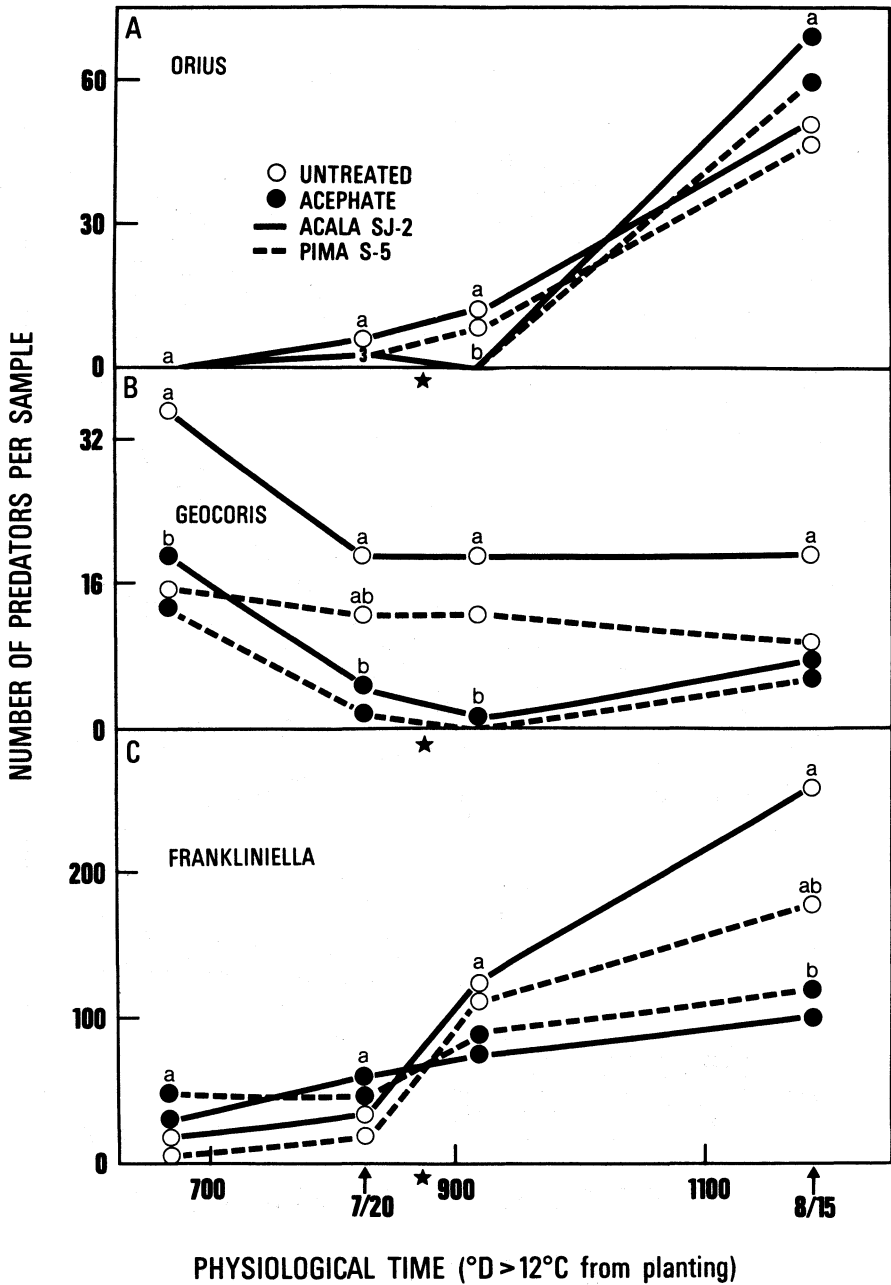
Fig. 2. Influence of insecticide (acephate) and plant variety on the mean fluctuation of adult insectan predators on cotton (see figure 1).
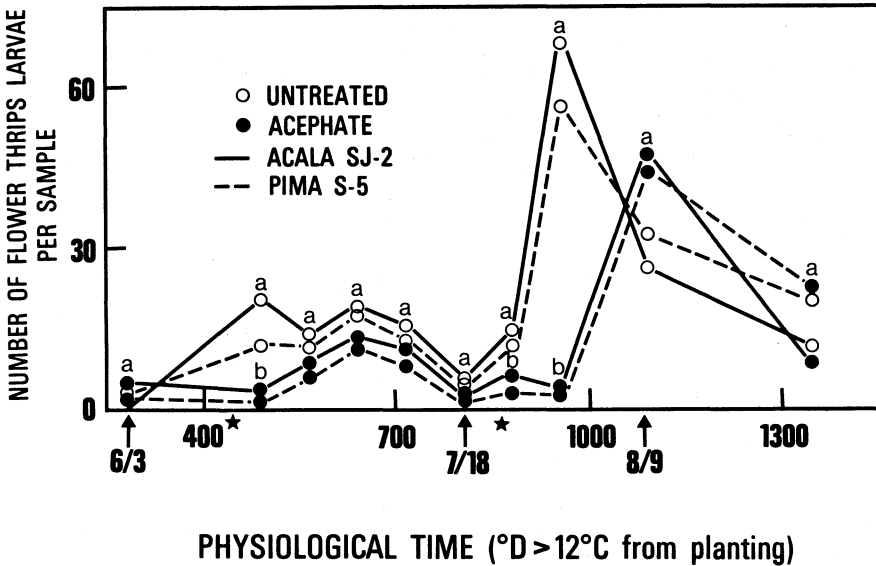
Fig. 3. Influence of insecticide (acephate) and plant variety on the mean fluctuation of larval *F. occidentalis* on cotton, as determined by leaf sampling (see text). Symbols (★) represent dates of insecticide application. Means preceded above by same letter are not significantly different at $a = 0.05$ on a given sampling date (Tukey's multiple comparison test).

their numbers were significantly (P<0.05) reduced by the application of acephate (figs. 1*b* and 2*b*). *Frankliniella* populations were difficult to manipulate and exhibited large fluctuations in numbers, although acephate sprays did reduce their population density as well (figs. 1*c* and 2*c*). Flower thrips reached the highest densities of all the predators sampled. Leaf samples indicated that numbers of larval thrips were significantly (P<0.05) reduced for 1 to 2 weeks after each spray application of acephate (fig. 3). Numbers of thrips larvae were slightly higher on susceptible plants than on resistant plants, although the difference was not statistically significant. About 2 weeks after the second spray application of acephate (August 9), numbers of larval thrips on acephate-treated plants peaked sharply, and numbers on untreated plants declined dramatically. This trend suggests that flower thrips resurged faster than other predators on plants previously treated with acephate, but were themselves subjected to heavy predation pressure (i.e., by *Geocoris* and *Orius*) on untreated plants.

The natural enemy component dramatically affected spider mite population growth rates and conferred a significant (P<0.001) reduction in numbers of spider mites on susceptible and resistant plants, from 550 °D until the end of the season (fig. 4*b*). By August 9 (1100 °D), predation was slightly more effective on the susceptible variety (83.5 percent) than on the resistant variety (72.6 percent) (table 1). Correspondingly, varietal resistance was slightly more effective at low predator densities (78.6 percent) than at normal predator densities (67.0 percent).

TABLE 1. RELATIVE EFFECTIVENESS OF DIFFERENT TACTICS
(VARIETAL RESISTANCE, ACARICIDE, AND PREDATION)
IN CONTROLLING SPIDER MITES ON COTTON WITHIN 1100 °D AFTER PLANTING

Accompanying treatments			Average % effectiveness[a] due to:		
Acaricide[b] (Dicofol)	Insecticide[b] (Acephate)	Variety[c]	Varietal resistance	Acaricide	Predation
+	+		94.6 a		
+	−		82.8 ab		
−	+		78.6 abc		
−	−		67.0 bc		
	+	S		46.9 c	
	+	R		87.7 ab	
	−	S		69.9 abc	
	−	R		87.3 ab	
+		S			91.3 ab
+		R			63.9 bc
−		S			83.5 ab
−		R			72.6 abc

[a]Based on Abbott's formula; means followed by same letter not significantly different at $\alpha = 0.05$ (Tukey's multiple comparison test).

[b]+ (present)
 − (absent)

[c]S (susceptible Acala SJ-2)
 R (resistant Pima S-5)

Varietal Resistance

In general, numbers of spider mites appeared to increase gradually until about 650 °D air temperature had accumulated (fig. 4). Spider mite numbers on susceptible Acala SJ-2 accelerated over those on resistant Pima S-5. Percentage infested leaves also increased rapidly at this time, indicating that mites were rapidly expanding their range to new uninfested plants. Beyond 650 °D, mite population growth accelerated on both susceptible and resistant plants, but increased more sharply on the susceptible variety. This trend continued until mite populations peaked on August 9 (fig. 4). Percentage effectiveness (Abbott's formula) of varietal resistance at this time was maximal (94.6 percent) in the presence of acaricide, at low predator densities (table 1).

Representatives of the three major species of spider mites (*Tetranychus urticae, T. pacificus,* and *T. turkestani*) were found on each variety. No observable difference in species ratio between the two varieties was observed, and although *T. pacificus* was dominant for most of the season, extreme spider mite damage on the susceptible SJ-2 near the end of the season (i.e., leaf reddening and defoliation) appeared to be caused by *T. turkestani.* Proportion of infested leaves was a good index of spider mite population growth rate and closely resembled data based on mite numbers (figs. 4, 5, and 6). By August 9 (1100 °D), spider mites had infested 100 percent of the leaves sampled and had reached peak densities on susceptible cotton plants treated with acephate. After this point, infestations remained at 100 percent, but numbers of mites began to decline on these plants.
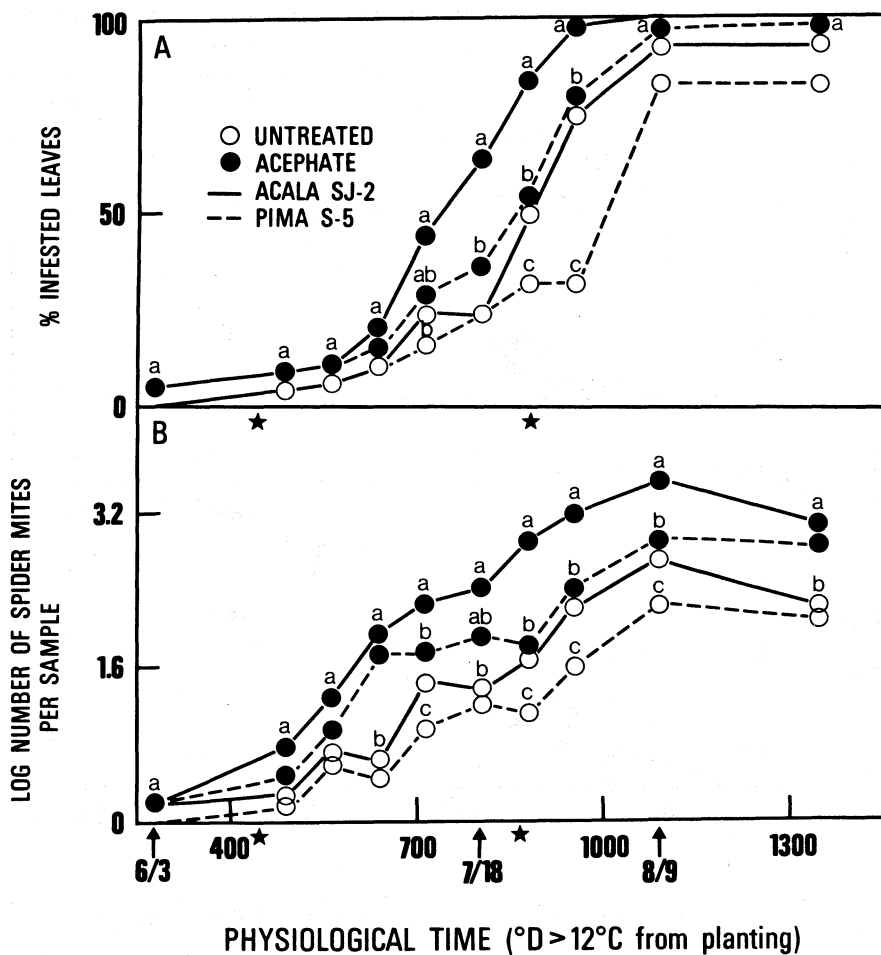
Fig. 4. Influence of insecticide (acephate) and varietal resistance on the mean fluctuation of spider mites on cotton, as determined by leaf sampling (see text). Symbols (★) represent dates of insecticide application. (*a*) Proportion mite-infested leaves. (*b*) Log numbers of male, female, and immature spider mites combined. Means preceded above by the same letter are not significantly different at $\alpha = 0.05$ on a given sampling date (Tukey's multiple comparison test).

Acaricide

Before midseason, at normal predator densities, the acaricide dicofol effectively reduced numbers of spider mites on both resistant and susceptible plants (fig. 5*b*). After 850 °D, dicofol did not visibly affect densities of spider mites on susceptible plants, but reduced mite numbers to significantly ($P < 0.001$) lower levels on resistant plants. This trend was substantiated by greater acaricide effectiveness on resistant plants (87.3 percent) than on susceptible plants (69.9 percent) on August 9 (table 1).
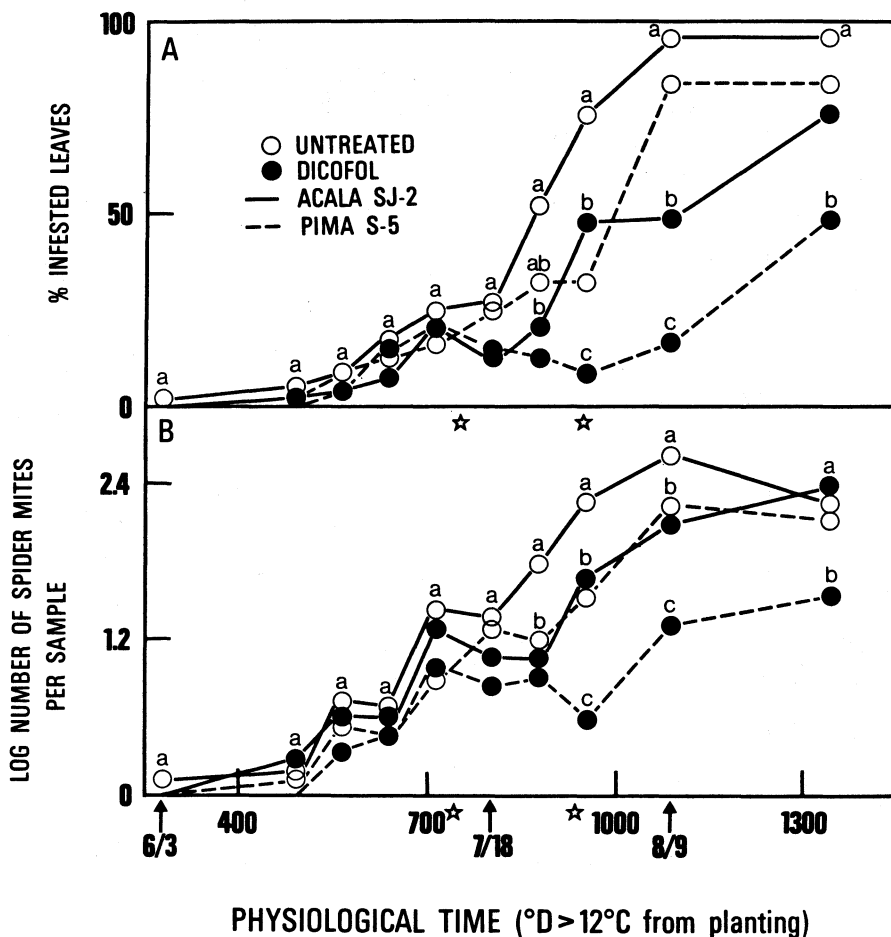
PHYSIOLOGICAL TIME (°D > 12°C from planting)

Fig. 5. Influence of acaricide (dicofol) and varietal resistance on the mean fluctuation of spider mites on cotton at normal predator densities. Symbols (☆) represent dates of acaricide applications (see figure 4).

In acephate-treated plots, the early application of dicofol (750 °D) lowered mite numbers on the resistant variety, but was not immediately effective on the susceptible variety, although a delayed effect was evident 2 weeks later (fig. 6b). This effect was immediately lost, however, by a second application of acephate, suggesting that a late resurgence of natural enemies had contributed to the acaricide effect. After 900 °D, mite populations accelerated too fast for the second application of dicofol to have an effect on either variety. However, mite densities were significantly (P<0.001) lower throughout midseason (650 ° to 1000 °D) on dicofol-treated plants, and the acaricide had a greater impact on resistant plants than on susceptible plants. By 1100 °D, acaricide efficacy on acephate-treated susceptible plants (46.9 percent) was significantly (P<0.05) lower than with any other treatment regime (table 1). Conversely, acaricide

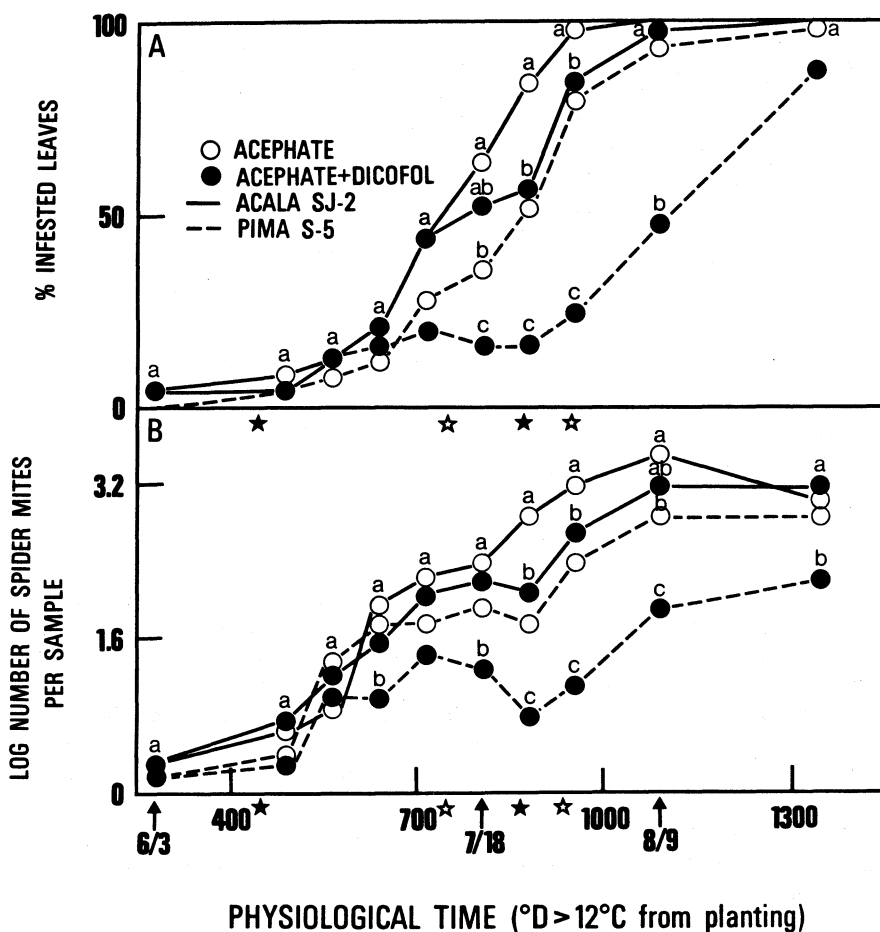PHYSIOLOGICAL TIME (°D > 12°C from planting)

Fig. 6.   Influence of acaricide (dicofol) and varietal resistance on the mean fluctuation of spider mites on cotton at low predator densities. Symbols represent dates of insecticide (★) and acaricide (☆) applications (see figure 4).

efficacy on resistant plants was high (87.7 percent), which suggests a synergistic interaction between varietal resistance and acaricide in the control of spider mites.

Yield

No significant differences in the fraction of lint between the two varieties under any of the four treatments were evident. Average lint fraction was 34 percent. In untreated plots, yield of the susceptible variety was significantly ($P<0.05$) greater than that of the resistant variety, with averages of 401.44 and 298.19 g/m row, respectively (table 2). However, this trend was reversed for plants treated with acephate. Susceptible SJ-2

TABLE 2.   IMPACT OF VARIOUS AGRONOMIC TREATMENTS
ON THE YIELD OF SPIDER MITE-SUSCEPTIBLE (ACALA SJ-2)
AND SPIDER MITE-RESISTANT (PIMA S-5) COTTON

Average yield of seed cotton (g/m row)			
Treatment[a]		Variety[b]	
Insecticide (Acephate)	Acaricide (Dicofol)	Acala SJ-2	Pima S-5
−	+	401.44 a	298.19 c
−	−	369.56 ab	305.75 c
+	+	318.31 bc	332.06 bc
+	−	244.13 d	332.13 bc

[a]+ (present)
  − (absent)

[b]Means followed by the same letter not significantly different at $\alpha = 0.05$ (Tukey's multiple comparison test).

plants treated with acephate experienced a significant (P<0.05) loss of yield (401.44 to 244.13 g/m row), which was also significantly (P<0.05) lower than similarly treated resistant plants. Yield in the resistant Pima S-5 was unaffected by acephate treatments (table 2). Although yield of resistant plants was slightly higher in acephate-treated plots than in untreated plots this difference was not statistically significant.

The synergistic interaction against spider mites, between dicofol and varietal resistance, did not translate into increased yield in the resistant variety (table 2). However, while the addition of dicofol had a small effect on spider mites on susceptible plants treated with acephate (fig. 6), yield from these plants was significantly (P<0.05) higher than from similar plants without dicofol, 318.31 vs. 244.13 g/m row, respectively (table 2).

DISCUSSION

Varietal Resistance

Spider mite population growth is a function of the intrinsic rate of increase (r), and external biotic and abiotic factors. Mite numbers initially increased gradually, but began to accelerate as the season progressed, as r has an exponential effect (i.e., finite rate of increase, $\lambda = e^r$). This acceleration became apparent by 650 °D, especially on susceptible plants treated with acephate, and continued until 1100 °D had elapsed on August 9. The decline in mite numbers after 1100 °D can be attributed to a combination of increased predation pressure (predator resurgence) and a decline in the availability of food, since most leaves at this time were heavily infested. The absence of a varietal effect on species ratio of spider mites suggests that the resistance inherent in Pima S-5 was equally effective against all three species of *Tetranychus.*

Based on a difference in r (Δr) of 0.024, in the original life table analysis, mite numbers were predicted to be 75 times higher on the susceptible Acala SJ-2 than on the resistant Pima S-5 after 10 mite generations (18 days per generation), in the absence of other environmental influences (Trichilo and Leigh 1985). Using these same criteria, we could predict that mite numbers should have been 8.7 times higher on SJ-2 than on S-5, after five mite generations that theoretically could have occurred between seedling emergence on May 11 and peak mite densities on August 9. At peak spider mite densities in acephate-treated (low predator) plots, mite numbers were only 4.6 times higher on susceptible plants than on resistant plants.

Superficially, it would seem that the original model overestimated the degree of resistance of Pima S-5. However, several external variables could have been responsible for the discrepancy between actual and predicted differences in mite numbers between the two varieties. After initial mite establishment on cotton, immigration of mites throughout the season, across plots and from other fields, would have diluted and somewhat obscured the effect of varietal resistance. A generation time of 18 days at a constant temperature of 24°C, produces a total of 216 °D, based on a minimum threshold temperature of 12°C (Trichilo and Leigh 1985). Carey and Bradley (1982) showed that generation time becomes longer with decreasing temperature. In the field, temperatures fluctuated greatly, and during June through August 216 °D usually accumulated after 19-20 days. Consequently, there would have been fewer than five generations of spider mites by August 9. With the original life table model (Δr = 0.024), we could predict a difference in mite numbers of 5.6 after four mite generations—still higher than the observed difference of 4.6.

Although at low densities for given periods of time, predators were always present at some level in acephate-treated plots and probably had a nullifying effect on the apparent impact of the resistant variety. This quenching by predators was accentuated because they had a more dramatic effect on susceptible plants than on resistant plants.

Finally, in the original investigation, varietal resistance was shown to increase with plant maturity (Trichilo and Leigh 1985). A Δr of 0.024 was recorded for relatively mature cotton plants. However, during the early part of the season (i.e., the first 45 days), Δr would have been somewhat less than 0.024, and hence mite populations would not have diverged as fast as originally predicted. The original life table model, under the circumstances, was relatively accurate. Our current study substantiates the usefulness and validity of life tables as a means to assess plant varietal resistance to arthropods.

Natural Enemies and Varietal Resistance

In several earlier studies, certain resistant plant genotypes had negative or variable effects on populations of natural enemies (Casagrande and Haynes 1976; Ellington et al. 1984; Katanyukul and Thurston 1973; Obrycki and Tauber 1984; Pimentel and Wheeler 1973). Our study indicated that predators were slightly, but not significantly less abundant on resistant plants. In agreement with Bergman and Tingey (1979), Casagrande and Haynes (1976), and Pimentel and Wheeler (1973), variation in predator densities on the two varieties in our study was most likely a numerical (migratory

and reproductive) response to greater numbers of spider mite prey on susceptible plants.

Frankliniella, often the first arthropod to become established on cotton after seedling emergence, may be present before either spider mites or such other predators as *Geocoris* or *Orius* have become established (Gonzalez et al. 1982). Trends of mite population increase are undoubtedly most critical early in the season before about 700 °D have elapsed. Furr and Pfrimmer (1968) and Mistric (1969) reported that early mite infestations caused greater reductions in yield than did late infestations. Once mite numbers begin to explode, it is extremely difficult for natural enemies to regain effective control. Our study showed that spider mite-resistant plants significantly inhibited the reproductive rate of mites in the field. Although resistance tends to increase with plant maturity (Trichilo and Leigh 1985), a resistant plant would lower the rate of initial establishment, and/or reduce the rate at which mite populations increase during the early part of the season. Coupled with such early-season natural enemies as flower thrips, HPR would be even more effective at inhibiting early spider mite establishment.

Numbers of *F. occidentalis* were the most variable of any of the predators sampled, possibly because flower thrips are also prey for other predators, including *G. pallens* and *O. tristicolor* (Gonzalez and Wilson 1982; Stoltz and Stern 1978b; Yokoyama 1978). Densities of flower thrips could be influenced by the presence of spider mite eggs, predation by other predators, and the availability of pollen.

Garcia, Gonzalez, and Leigh (1982) reported that *F. occidentalis* was the most abundant species present on cotton in the San Joaquin Valley. Flower thrips are critical elements in the interaction of natural enemies on cotton, as predators of mites, and as food to sustain an early colonization of *Geocoris,* before spider mites become established. Although present throughout the season, *F. occidentalis* would have the most crucial impact as a predator very early in the season, before plants have flowered and before *Geocoris* has become established (D. Gonzalez, personal communication).

Our study supports the findings of Adkisson and Dyck (1980), Obrycki, Tauber, and Tingey (1983), Starks, Muniappan, and Eikenbary (1972), and others, who reported that HPR and biological control were compatible. Varietal resistance may enable natural enemies to be more effective, because the predator/prey ratio is large enough for predators to adequately contain the prey. In our study, lowest mite densities were recorded for resistant plants with predators at normal densities. However, natural enemies had a greater impact on susceptible plants than on resistant plants, presumably because there were more spider mite prey available on susceptible plants and therefore the effect of natural enemies was more easily detected.

Omnivorous predators on cotton could have been susceptible to phytochemicals, which presumably conferred resistance of Pima S-5 cotton to spider mites. However, except for larval flower thrips, these predators seem to restrict their plant feeding to nectar and pollen (Askari and Stern 1972; de Lima and Leigh 1984; Stoltz and Stern 1978a; Stoner 1970, 1972) and probably do not successfully feed on leaves. Flower thrips may be more inclined to herbivory than other omnivorous predators. If allelochemicals that induce resistance are located in the leaves, flower thrips (especially larvae) would be potential targets, since they feed directly on leaf tissue.

Our unpublished observations indicate that flower thrips experience lower reproductive fitness on leaves of resistant plants than on leaves of susceptible plants. However, this negative effect due to plant genotype, was not apparent in the field, as numbers

of flower thrips were not significantly different between resistant and susceptible plants. We suspect that as with other omnivores, flower thrips can avoid feeding on the leaves, by switching to other sources of nutrition, including mite eggs, nectar, and pollen. These additional sources of nutrition, commonly used as alternative food by omnivorous predators, probably do not contain the phytochemicals that confer resistance against mites on the leaves. Larval thrips could theoretically be better predators on resistant plants than on susceptible plants, if chemicals in resistant leaves caused thrips to eat a greater proportion of mite eggs than would normally occur on susceptible leaves.

Impact of Insecticide

Insecticidal exclusion of natural enemies, as a means to assess predator/parasitoid efficacy, was suggested by Debach (1946). In other studies, as in ours, chemicals did not eradicate natural enemies from test plots, but they did reduce the numbers of predators sufficiently to cause a significant explosion of prey (pest) populations (Eveleens, van den Bosch, and Ehler 1973; Huffaker and Flaherty 1966; Smith and Hagen 1959; Stoltz and Stern 1978b; van Steenwyk et al. 1975).

The use of synthetic chemicals as an experimental control of natural enemies has been questioned (Bartlett 1968; Boykin and Campbell 1982; Boykin, Campbell, and Beute 1984; Huffaker, van de Vrie, and McMurtry 1970; White 1984). At least two theories have been proposed to explain the observed increase in pest densities following application of insecticides: (1) removal of natural enemies and (2) nutritional stimulation (hormoligosis) of the pest populations (Bartlett 1968; Huffaker, van de Vrie, and McMurtry 1970). Substantial evidence (Bartlett 1968; White 1984) suggests that hormoligosis may typically be associated with most synthetic insecticides.

Boykin, Campbell, and Beute (1984) reported that densities of spider mite predators on peanut were not reduced by insecticides and that predators were ineffective in curtailing spider mite numbers. However, acephate was not used, and *Geocoris* was not reported to be a predator of spider mites in their study. Powell (1981) found that resistance of alfalfa to the spotted alfalfa aphid was less effective in the presence of acephate than when plants were untreated.

In our study, resistant plants had a more dramatic effect in acephate-treated plots than in untreated plots, suggesting that if hormoligosis were present, it did not impair the level of resistance of Pima S-5. Insecticides significantly reduced predator densities, which suggests that predation pressure was a major factor restricting spider mite population increase. Undoubtedly, both theories have merit, and as Bartlett (1968) stated, neither theory alone offers a completely adequate explanation. We can speculate that even with chemical stimulation of mite growth rates, an increase in mite numbers would have been contained, if predators had been at normal densities.

Removal of biological control agents can alter the status of a once innocuous arthropod to an economic pest. Although spider mites are believed to be one of the most serious pests on cotton in the San Joaquin Valley, in agreement with Reynolds et al. (1982), our study suggests that the economic status of mites is largely insecticide induced. The spider mite problem can become so severe after midseason, following insecticidal applications, that acaricides will not change this trend.

Acaricide and Varietal Resistance

Acaricide efficacy was, in part, a function of spider mite density. A high reproductive rate, typical of spider mites, will allow a pest population to take advantage quickly of a temporary reduction in predation pressure (given sufficient food) and increase rapidly in numbers. When numbers of spider mites became very high (i.e., on susceptible plants treated with acephate), the mite population increased too rapidly for the acaricide to be effective. At this point, spider mites were essentially out of control, indicating that sheer numbers of mites may constitute a degree of acaricide resistance. In the absence of natural enemies, synthetic chemical control would require continuous applications of acaricide, and would inevitably lead to more rapid development of resistance to the chemical in the mite population. A stable complex of predators can provide a competent level of buffer to insure against pest outbreaks.

Dicofol remained effective longer on resistant plants because with a slower population growth rate, due to the varietal resistance, mites could not reach densities high enough to escape the acaricidal effect. Later in the season (1100 °D), acaricide plus varietal resistance compensated for the loss of natural enemies in the control of spider mites. The varietal resistance-acaricide combination produced an effect greater than additive, as predicted by Painter (1960), and it appeared to be a synergistic interaction. However, in our study, spider mite populations were well controlled by HPR alone. Although the acaricide-variety interaction is interesting, it may have little practical value. Adequate control of spider mites can be achieved with HPR in most cases without acaricide, although when a system is disrupted by insecticides, acaricide is very effective coupled with a resistant variety.

Yield

Many investigators have documented reduced yield resulting from spider mite damage to cotton (Canerday and Arant 1964; Furr and Pfrimmer 1968; Mistric 1969; Roussel et al. 1951). The degree of yield loss in the susceptible Acala SJ-2 was a function of mite density. Yield decreased inversely, relative to the numbers of spider mites throughout the season.

The significant effect of acaricide on the yield of susceptible plants treated with acephate is at first an anomaly, since acaricide minimally affected spider mites on these plants. Hence, one might expect an even greater increase in yield by resistant plants. However, this corresponding increase did not occur, which implies that resistant plants were already at maximum yield (for these environmental conditions) and were not visibly affected by spider mite stress. The absence of a yield response to spider mite pressure indicates a degree of tolerance (as well as resistance) associated with resistant plants. Susceptible plants, on the other hand, were severely stressed by spider mites, as exhibited by the dramatic drop in yield associated with high numbers of spider mites. In acephate-treated plots, susceptible plants were so stressed by spider mites that even the slight reduction in mite densities that occurred briefly (2 to 3 weeks) alleviated mite pressure and was eventually expressed as a significant improvement in yield.

Yield is the most important index of the success of a pest management program on cotton and is a relative value influenced by densities of spider mites as well as by plant genotype. Although highly desirable, the incorporation of varietal resistance and high yield is difficult to achieve. In environments where insecticides are commonly used (i.e., cotton) a spider mite-resistant plant may be the best alternative to combining high yield with resistance. A resistant variety is likely to be a poorer host to many arthropods, including such key pests as lygus bug, for which insecticides are often targeted. Hence, varietal resistance could reduce or even eliminate the need for synthetic chemicals, by essentially lowering the economic status of key pests as well as of spider mites. The capacity of resistant varieties in curbing pest populations, while remaining compatible with natural enemies, supports the potential of HPR as a viable tactic in the pest management of agroecosystems. Our study suggests that efforts to combine HPR with high-yielding varieties will result in even greater economic stability of crop systems. Ultimately, fewer chemical applications and greater yields in the presence of potentially damaging pests will lead to a more economically produced crop.

ACKNOWLEDGMENTS

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acaricide resistance, solely by attaining very high densities. Dicofol efficacy was relatively high on spider mite-resistant plants, because mite growth rates were slower, and thus mite populations could not "outgrow" the effect of the acaricide. Hence, there appeared to be a synergistic interaction between acaricide and varietal resistance.

In untreated plots, yield was significantly ($P < 0.05$) higher in the susceptible variety than in the resistant variety. However, this trend was reversed in plots treated with acephate, and yield from resistant plants was significantly ($P < 0.05$) greater than yield from susceptible plants. On crops heavily treated with insecticides, resistant varieties may offer the best alternative for pest management.