

# Effects of Operational and Environmental Factors on Evolution of Resistance to Pyriproxyfen in the Sweetpotato Whitefly (Hemiptera: Aleyrodidae)

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**ABSTRACT** Pyriproxyfen has been an important insecticide used as part of an integrated pest management (IPM) program for the sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (B biotype), in Arizona cotton. We used a simulation model to examine the effects of pyriproxyfen concentration, insecticide action thresholds, crop diversity, planting date, and pyriproxyfen decay on evolution of resistance to pyriproxyfen in *B. tabaci*. In the model, pyriproxyfen use was restricted to cotton with a limit of one application per season. Other model parameters were based on data from laboratory and field experiments. Whitefly population densities and the number of insecticide applications per year increased as resistance evolved. Resistance evolved slowest with a low pyriproxyfen concentration. Lower action thresholds for pyriproxyfen and higher action thresholds for insecticides other than pyriproxyfen also slowed the evolution of resistance. However, lower action thresholds for pyriproxyfen resulted in more insecticide sprays per year with a high pyriproxyfen concentration. Resistance to pyriproxyfen evolved fastest in cotton-intensive regions and slowest in multicrop regions. In regions with noncotton crops, increasing immigration to cotton slowed resistance. Resistance evolved faster with earlier planting dates, although fewer insecticide sprays were needed compared with fields planted later in the year. Faster rates of pyriproxyfen decay slowed resistance. In some cases, strategies that delayed resistance were effective from an IPM perspective. However, some strategies that delayed resistance resulted in higher population densities. Results suggest that modification of operational and environmental factors, which can be controlled by growers, could prolong the efficacy of pyriproxyfen.

**KEY WORDS** *Bemisia tabaci*, modeling, pyriproxyfen, insect resistance management, operational and environmental factors

Pyriproxyfen, an insect growth regulator (IGR), has been effectively used for over a decade in Arizona cotton (*Gossypium* spp.) as part of an integrated pest management (IPM) program for the sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (Dennehy and Williams 1997, Ellsworth and Martinez-Carillo 2001, Ellsworth et al. 2006). The selective use of pyriproxyfen in cotton fields, and neonicotinoids in vegetables and melon crops, has proven effective at controlling *B. tabaci* and reduced dependence on broad-spectrum insecticides (Ellsworth and Martinez-Carillo 2001, Palumbo et al. 2001, 2003, Ellsworth et al. 2006, 2007). However, bioassays show that resistance levels to pyriproxyfen are increasing in certain regions of Arizona (Li et al. 2003, Dennehy et al. 2004; unpublished results), representing a serious threat to the continued sustainability of the IPM program.

Crowder et al. (2006) used a simulation model to examine the effects of several factors on *B. tabaci* resistance to pyriproxyfen. Results showed that pyriproxyfen resistance evolved slower with a low initial resistance allele frequency, recessive resistance, and lower pyriproxyfen concentrations. To assess how the current *B. tabaci* IPM program could be modified to sustain use of pyriproxyfen in Arizona, we expanded the model of Crowder et al. (2006) to analyze the impact of operational and environmental factors on the evolution of resistance. We used sensitivity analyses to examine effects of variation in pyriproxyfen concentration, action thresholds, crop diversity, planting date, and pyriproxyfen decay on the evolution of resistance.

## Materials and Methods

**Model Structure.** We modified the temperature-dependent, deterministic model of Crowder et al. (2006). The updated model included new values for mortality caused by pyriproxyfen based on field and

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laboratory data (Crowder et al. 2007, 2008) and new functions for the distribution of adults and immatures. Except for the sensitivity analyses, all other functions in the model were unmodified from Crowder et al. (2006). The standard region had two dimensionless cotton fields: (1) treated—treated with pyriproxyfen and alternative insecticides and (2) external refuge—treated only with alternative insecticides (insecticides other than pyriproxyfen). Based on current patterns of pyriproxyfen use in Arizona, 20% of cotton fields were treated with pyriproxyfen (Crowder et al. 2006). In simulations with crop diversity (described later), the model considered crops other than cotton.

The model included three life stages: eggs, nymphs, and adults. All functions were simulated independently in each field with a daily time step. Accumulated degree-days (DDs) and temperature were based on the 30-yr average for each date in Maricopa, AZ (WRCC 2003), with degree-days accumulated using a base of 12.8°C and a maximum of 30°C (Silvertooth 2001a, b).

**Genetics of Resistance.** Resistance to pyriproxyfen was controlled by one gene with two alleles (Horowitz et al. 2003, Crowder et al. 2006) (S, susceptibility; R, resistance). Haploid males were S or R. Diploid females were SS, RS, or RR.

**Crop Phenology.** Cotton fields were planted on 20 April (225 DD) (Silvertooth and Brown 2001) at 98,800 plants/ha. The first leaves occurred on 1 May,  $\approx$ 95 DD after planting (UCDANR 1996). The number of leaves increased linearly to 200 per plant by 11 August,  $\approx$ 1,675 DD after planting (Silvertooth 2001b), and remained at 200 throughout the rest of the season. Increasing leaf age affected oviposition and movement after 11 August until 1 October,  $\approx$ 2,500 DD after planting, after which leaves were unsuitable for oviposition (Crowder et al. 2006).

**Development and Survival.** The time for immatures to complete development decreased exponentially with increased average daily temperature, which ranged from 14 to 32°C (Crowder et al. 2006). At 14°C, development times were 16 d for eggs and 39 d for nymphs. At 32°C, development times were 4 d for eggs and 14 d for nymphs. Survival from the egg to adult stage was 10% (63.5% of eggs hatched and 15.7% of nymphs became adults), which is similar to mortality observed for 14 *B. tabaci* cohorts on cotton in central Arizona from 1997 to 1999 (mean = 8.29%, 95% CI: 3.92–12.6%, Naranjo and Ellsworth 2005). Adult longevity declined linearly as average daily temperature increased (Crowder et al. 2006). At 14°C, longevity was 44 d for females and 36 d for males. At 32°C, longevity was 10 d for females and 9 d for males.

**Adult Movement.** Adults moved only once at 5-d-old (Crowder et al. 2006). Each day, 6% of 5-d-old adults went into a “movement pool” that was distributed between the two fields in proportion to their relative abundance (Crowder et al. 2006). Under standard conditions, 4.8% of 5-d-old adults moved from the treated field to the external refuge (6% in movement pool  $\times$  0.80 external refuge), and 1.2% of 5-d-old adults

moved from the external refuge to the treated field (6% in movement pool  $\times$  0.20 treated).

We also modeled immigration to and emigration from cotton fields (Crowder et al. 2006). From 1 wk after the first leaf appeared (8 May) until 7 June ( $\approx$ 560 DD after planting), 0.1 adults immigrated to cotton per plant per day. The number of immigrants to cotton per plant per day increased linearly from 0.1 to 50 from 7 to 23 June ( $\approx$ 830 DD after planting), was 50 from 23 June until 9 July (peak bloom), and was 0 for the rest of the year. The R allele frequency of immigrants in year 1 was 0.001. For all other years, the R allele frequency of immigrants was equal to the R allele frequency of adults that emigrated from cotton the previous year. The percentage of adults that emigrated from cotton was 0% before 11 August, increased linearly from 0 to 18% from 11 August until 1 October, and remained at 18% for the rest of the year.

**Mating and Oviposition.** One-d-old females mated randomly with males 2-d-old or older in the natal field (Li et al. 1989). Females began laying eggs when they were 2-d-old. Fecundity was affected by temperature and age (Crowder et al. 2006, equations 4 and 5). Oviposition was greatest for females 4–7-d-old and at temperatures from 21 to 25°C. Fecundity decreased linearly after 11 August until 1 October, corresponding with increasing leaf age (Gameel 1974). Forty percent of eggs were male (De Barro and Hart 2000).

**Distribution of Immatures and Adults.** *Bemisia tabaci* adults prefer to feed and oviposit on young leaves and are typically most abundant on the upper sections of cotton plants (Naranjo and Flint 1994, 1995). Each day, 50% of adults were located (and laid eggs) on the upper third of plants, 40% on the middle third, and 10% on the bottom third (Naranjo and Flint 1995).

**Pyriproxyfen.** In treated fields, pyriproxyfen was the first insecticide applied when adult densities exceeded a threshold of three adults per leaf (Ellsworth et al. 1996). Pyriproxyfen was limited to one use per year. External refuges were not treated with pyriproxyfen. Pyriproxyfen inhibits egg hatching and adult eclosion (Ishaaya and Horowitz 1992, Horowitz and Ishaaya 1994). Mortality caused by pyriproxyfen depended on the genotype of the insect and the concentration (high, medium, or low). The three concentrations are associated with an assumed range of variation that might be expected from variable rates used by growers and/or deposition of insecticide. *B. tabaci* on new growth after a pyriproxyfen spray were not affected because pyriproxyfen is not systemic (Ellsworth and Martinez-Carrillo 2001). Thus, as plants in treated fields grew after a pyriproxyfen spray, the new growth served as an internal refuge in the treated fields. The distribution of immatures and adults affected the proportion of individuals on the treated and nontreated portions of plants.

Although direct mortality caused by pyriproxyfen can decline significantly within 2 wk after a pyriproxyfen spray (Ellsworth and Martinez-Carrillo 2001, Crowder et al. 2007), *B. tabaci* populations can be suppressed for 4–8 wk (Ellsworth and Martinez-Car-

Table 1. Parameter values used in the model

Parameters	Values used <sup>a</sup>		
Percentage of cotton fields treated with pyriproxyfen	20		
Percentage of adults that move between cotton fields	6		
Percentage of adults on three cotton sections	Top	Middle	Bottom
	50	40	10
Initial R allele frequency	0.001		
Dominance of resistance in females ( <i>h</i> ) as a function of pyriproxyfen concn:			
High	0.1, 0.25*, 0.4		
Medium	0.25, 0.5*, 0.75		
Low	0.5, 0.7*, 0.9		
Mortality of susceptible (S males and SS females) eggs and nymphs as a function of pyriproxyfen concn	High	Medium	Low
	90%*	70%*	50%*
Mortality of resistant eggs and nymphs (R males and RR females) with any pyriproxyfen concn	0%		
Action threshold for pyriproxyfen (adults per leaf)	1, 3*, 5		
Action threshold for insecticides other than pyriproxyfen in pyriproxyfen treated field (adults per leaf)	5*		
Action threshold for insecticides in external refuges (fields not treated with pyriproxyfen) (adults per leaf)	3, 5*, 10		
Proportion of region planted to non-cotton crops	0*, 100% until 30 June and decreasing linearly to 0% for rest of year, 50% all year		
Ratio of adults immigrating to cotton from non-cotton crops relative to emigration from external cotton refuges	0.0*, 0.5, 1.0, 2.0, 3.0		
Planting Date	20 Mar., 20 April*, 20 May		
Percentage decrease in pyriproxyfen mortality per day for susceptible (S and SS) and heterozygous (RS) eggs and nymphs (pyriproxyfen decay rate)	0%*, 1% (slow), 3% (fast)		

<sup>a</sup> Standard values are indicated by an asterisk.

illo 2001). Population suppression after 2 wk may result from increased effectiveness of natural enemies at low *B. tabaci* densities or delayed population resurgence (Ellsworth and Martinez-Carillo 2001). In the standard simulations without insecticide decay, we assumed the direct effects of pyriproxyfen were constant over 28 d (Crowder et al. 2006). During the 28-d period, no alternative insecticide sprays were used. Pyriproxyfen did not affect resistant (R or RR) eggs and nymphs. Mortality of susceptible (S or SS) eggs and nymphs caused by pyriproxyfen was 90, 70, and 50% with a high, medium, and low concentration, respectively. Pyriproxyfen mortality for eggs and nymphs occurred at egg hatching and adult eclosion, respectively. The survival of RS female eggs and nymphs was affected by dominance (*h*) and insecticide concentration, where  $h = (\text{survival RS} - \text{survival SS}) / (\text{survival RR} - \text{survival SS})$  (Liu and Tabashnik 1997).

In laboratory bioassays, dominance decreased as pyriproxyfen concentration increased (Crowder et al. 2008). Based on these data and the levels of mortality described above, dominance was 0.25, 0.5, and 0.7 with a high, medium, and low concentration, respectively. We varied each value to determine the effects of dominance on resistance evolution (Table 1).

**Alternative Insecticides.** Insecticides other than pyriproxyfen (hereafter referred to as alternative insecticides) were applied to both field types depending on adult densities (Ellsworth et al. 1996, 2006, Naranjo et al. 1998). When densities first exceeded five adults per leaf in the external refuge, an alternative insecticide was applied that killed 90% of all immatures for 28 d. This control interval of 28 d was based on upper estimates for Spiromesifen and acetamiprid (Ells-

worth et al. 2006). In the treated field, an alternative insecticide was applied no less than 28 d after a pyriproxyfen spray if densities exceeded five adults per leaf. If densities in the external refuge or treated field again exceeded five adults per leaf >28 d after an alternative insecticide spray, another alternative insecticide was applied.

**Simulation Conditions.** For each set of conditions (Table 1), we ran the model for 100 yr. The time to resistance was the number of years for the R allele frequency to reach 0.5. For each year, the R allele frequency was calculated at the end of the cotton-growing season based on individuals that moved out of the region, because individuals remaining in the region died at harvest and thus did not influence future generations. In the standard simulations, each season ended on 20 November ( $\approx 3,000$  DD after planting). In simulations with early or late planting dates, the season ended 3,000 DD after the planting date. In the standard simulations of a cotton-intensive region, the R allele frequency was calculated based solely on individuals that emigrated from cotton. In simulations with crop diversity, the R allele frequency was calculated based on individuals that emigrated from cotton and noncotton crops.

**Sensitivity Analysis.** We analyzed the influence of four factors on the evolution of resistance: action thresholds, crop diversity, planting date, and pyriproxyfen decay (Table 1). For these analyses, all parameters except the one being varied were set to the standard values.

**Action Thresholds.** We simulated action thresholds of 1, 3, and 5 adults per leaf for pyriproxyfen and 3, 5, and 10 adults per leaf for alternative insecticides in external refuges (Table 1).

**Crop Diversity.** Three types of agricultural landscape were simulated, corresponding to typical regions in Arizona (Palumbo et al. 1999, 2003): cotton intensive (100% cotton all year); cotton/melon (100% cotton until 1 July, after which the amount of non-cotton crops [e.g., fall melons] increased linearly from 0 to 100% until the end of the year); and multicrop (50% cotton and 50% noncotton crops [e.g., leafy vegetables and melon] for the whole year). For simplicity, we assumed equal population growth in external cotton refuges and noncotton crops.

*B. tabaci* immigrated to cotton from noncotton crops and vice versa. We simulated four ratios for the number of emigrants from noncotton crops relative to the number of emigrants from external cotton refuges per unit area: 0.5, 1.0, 2.0, and 3.0 (Table 1). Emigration from cotton to noncotton crops, or immigration to cotton from noncotton crops, occurred based on these ratios and the relative abundance of the crop types. The four ratios reflect the impact of noncotton crops relative to external cotton refuges (i.e., ratios >1 indicate more emigrants disperse out of noncotton crops than external cotton refuges per unit area). For example, with a ratio of 2.0, 12% of 5-d-old individuals in noncotton crops (compared with 6% of individuals in external refuge cotton) entered into the "movement pool." Individuals in the "movement pool" were distributed between all crop types based on their relative abundance. The four ratios were also used to simulate the number of individuals that emigrated out of the region from noncotton crops compared with external cotton refuges. The R allele frequency in noncotton crops varied over time based on dispersal to and from cotton and population dynamics in the noncotton field.

**Planting Date.** We simulated three planting dates: 20 March, 20 April, and 20 May (Table 1). In each case, the growth of cotton, immigration of insects into the region, and emigration of insects out of the region was based on accumulated DD after the planting date based on the conditions of the standard model. Thus, the season length (in DD) was the same with any planting date.

**Pyriproxyfen Decay.** We simulated two rates of pyriproxyfen decay. Mortality caused by pyriproxyfen for susceptible and heterozygous insects decreased daily by 1% with slow decay and by 3% with fast decay. This mortality was applied only to eggs hatching and nymphs eclosing each day. For example, with a high concentration and slow decay, the mortality of susceptible eggs and nymphs completing development on day 1 after a pyriproxyfen spray was 90%, 89% on day 2, 88% on day 3, etc. Dominance was calculated each day as pyriproxyfen decayed based on the survival of susceptible, heterozygous, and resistant insects.

**Comparison of IPM and Insect Resistance Management (IRM).** For each factor that can be modified by farmers (pyriproxyfen concentration, action thresholds, crop diversity, planting date), we calculated the average seasonal maximum population density and the average number of insecticide sprays per year across

**Table 2.** Number of years for the frequency of the allele for resistance to pyriproxyfen, R, to reach 0.5 in simulations with three toxin concentrations and three values for dominance with each concentration

Dominance of resistance ( $h$ ) <sup>a</sup>	Concentration
	High
0.10	12
0.25*	12
0.40	10
	Medium
0.25	21
0.50*	17
0.75	14
	Low
0.50	29
0.70*	25
0.90	21

<sup>a</sup> The standard value is indicated by an asterisk.

the first 15 simulated yr. All results were averaged across the entire region. Thus, in simulations of the standard model, the seasonal maximum density (and the number of insecticide sprays) in the external cotton refuge was multiplied by 0.8 (80% of fields were external refuge), and the density in the treated cotton field was multiplied by 0.2 (20% of fields were treated with pyriproxyfen) to calculate the average density and insecticide sprays in the entire region. In simulations with crop diversity, the seasonal maximum population density and insecticide sprays in noncotton crops were included in the calculations. These values were used to compare strategies that were beneficial from an IPM perspective (i.e., low pest densities and fewer insecticide sprays) with those that were beneficial from an IRM perspective (i.e., low R allele frequency after 15 yr).

## Results

**Dominance.** With any pyriproxyfen concentration, varying dominance had little effect on resistance (Table 2). Thus, for all results to follow, we only simulated the standard values for dominance of 0.25, 0.5, and 0.7 with a high, medium, and low concentration, respectively.

**Population Density and Insecticide Use.** Population density reached a seasonal maximum of four to six adults per leaf in treated fields with a high concentration and R allele frequencies <0.4 (Fig. 1A). Population density reached a seasonal maximum of 8–12 adults per leaf in treated fields with a low concentration and R allele frequencies below 0.25 (Fig. 1B). As resistance evolved, the seasonal maximum population density in treated fields increased to 26 adults per leaf. With a high concentration, the total number of insecticide sprays in treated fields increased from one spray per year with  $R < 0.1$  to three sprays per year with  $R > 0.95$  (Fig. 1A). With a low concentration, the total number of insecticide sprays in treated fields increased from two sprays per year to three as resistance evolved (Fig. 1B). Results with a low and medium concentration were similar. With any concentration

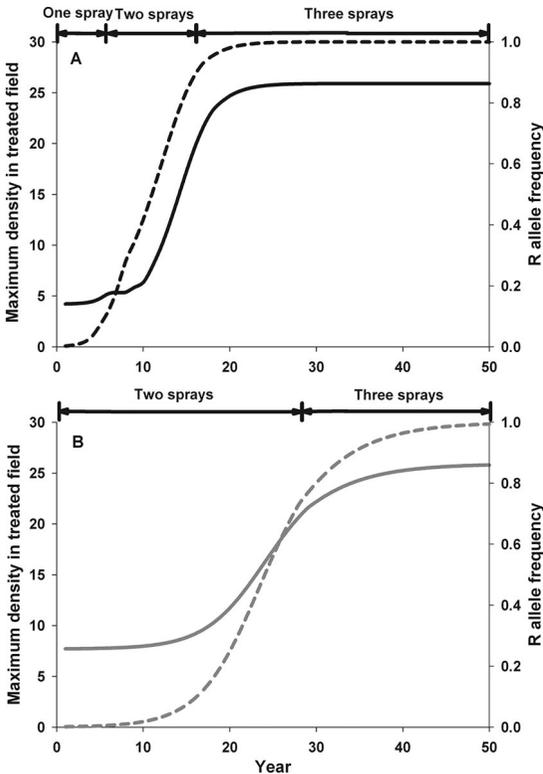


Fig. 1. Maximum population density (adults per leaf) in treated fields (solid lines) and frequency of the allele for resistance to pyriproxyfen, R (dashed lines), over 50 yr with a (A) high and (B) low pyriproxyfen concentration. The total number of insecticide sprays per year in the treated field is indicated with arrows.

or R allele frequency, the seasonal maximum population density in external refuges was six adults per leaf and two insecticide sprays were needed per year.

**Action Thresholds.** Resistance evolved slower as the action threshold for pyriproxyfen decreased (Fig. 2A). With a threshold of one adult per leaf, pyriproxyfen was applied on 25 June, nearly a month before pyriproxyfen was applied if the threshold was three adults per leaf (22 July) or five adults per leaf (26 July). Resistance evolved slower as the action threshold for alternative insecticides in external refuges increased (Fig. 2B). In several cases, lower action thresholds increased the total number of insecticide sprays per year (Fig. 2).

**Crop Diversity.** The effects of crop diversity on resistance evolution depended on immigration to and emigration from cotton (Table 3). Resistance evolved slower when more adults immigrated to cotton. Resistance evolved slower in simulations of a multicrop region compared with the cotton/melon region, especially as immigration to cotton increased (Table 3). The effects of crop diversity on resistance evolution were greatest with a medium or low pyriproxyfen concentration. With the highest levels of immigration to cotton and a medium or low concentration, resistance did not evolve in 100 yr in a multicrop region

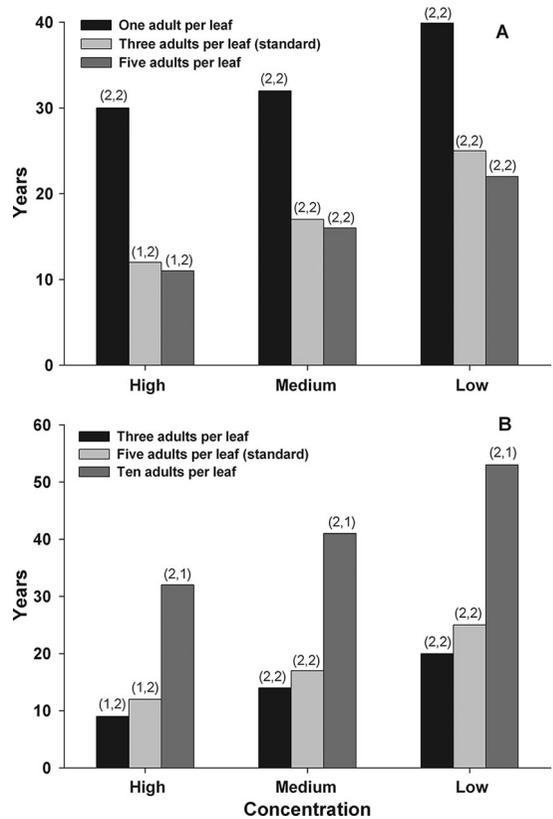


Fig. 2. Number of years for the frequency of the allele for resistance to pyriproxyfen, R, to reach 0.5 in simulations with (A) three action thresholds for using pyriproxyfen and (B) three action thresholds for insecticides in external refuges. The total number of insecticide sprays in treated and external refuge fields for the first simulated year is shown in parentheses.

(Table 3). The total number of insecticide sprays per year did not vary based on crop diversity.

**Planting Date.** Resistance evolved slower with later planting dates (Fig. 3). The impact of planting date on resistance evolution was consistent across all pyriproxyfen concentrations. Fewer insecticide sprays were used per year with earlier planting dates (Fig. 3).

**Pyriproxyfen Decay.** As pyriproxyfen decayed and survival of susceptible and heterozygous eggs and nymphs increased, dominance of resistance ( $h$ ) also increased, especially with a fast decay rate (Fig. 4). Resistance evolved slower as the pyriproxyfen decay rate increased (Fig. 5). The impact of pesticide decay was greater with a high or medium concentration compared with a low concentration, especially with a slow decay rate. Pyriproxyfen decay affected the number of total insecticide sprays in only one case (Fig. 5).

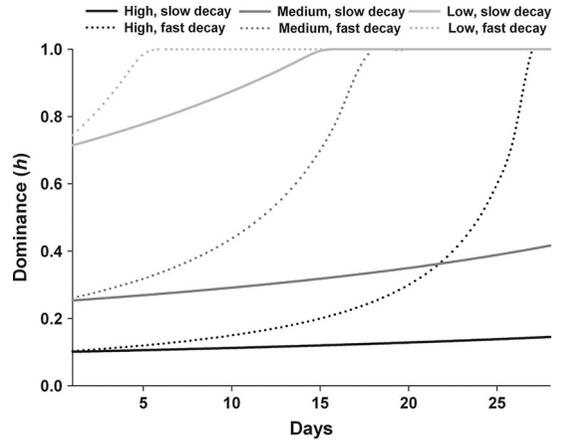
**Comparison of IPM and IRM.** Action thresholds in external refuges and to some extent planting date had the greatest impact on IPM (population density and number of insecticide sprays), whereas other factors had little effects (Fig. 6). In general, factors relating to insecticide use (pyriproxyfen concentration and ac-

**Table 3.** Number of years for the frequency of the allele for resistance to pyriproxyfen, R, to reach 0.5 in simulations with three simulated regions, varying levels of movement from noncotton crops, and three pyriproxyfen concentrations

Type of region	Ratio of adults emigrating from noncotton crops relative to emigration from external cotton refuges				
	0.0 (standard)	0.5	1.0	2.0	3.0
<b>High concentration</b>					
Cotton intensive	12	—	—	—	—
Cotton/melon	12	15	20	32	43
Multicrop	12	16	23	42	81
<b>Medium concentration</b>					
Cotton intensive	17	—	—	—	—
Cotton/melon	17	23	28	39	50
Multicrop	17	25	32	65	>100
<b>Low concentration</b>					
Cotton intensive	25	—	—	—	—
Cotton/melon	25	35	44	71	>100
Multicrop	25	37	51	>100	>100

Movement is expressed as the percentage of individuals moving out of noncotton refuges relative to the no. of individuals moving out of external cotton refuges (per unit area).

tion thresholds) had a greater impact on IRM (R allele frequency) than factors relating to crops (crop diversity and planting date). In some cases, strategies that were beneficial from an IRM perspective were also effective from an IPM perspective. For example, a low pyriproxyfen concentration delayed resistance evolution compared with a high concentration and resulted in similar population density and number of insecticide sprays (Fig. 6). Similarly, increased crop diversity delayed resistance without increased population density or number of insecticide sprays. However, some strategies that were effective from an IRM perspective did not improve IPM. An action threshold of 10 adults per leaf for alternative insecticides delayed resistance evolution, but population densities were over twice as high as in simulations with a threshold of three or five

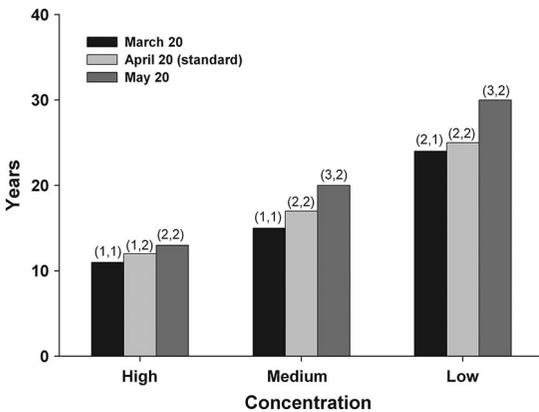


**Fig. 4.** Dominance of resistance in females (*h*) over 28 d after a pyriproxyfen spray with three pyriproxyfen concentrations and two decay rates.

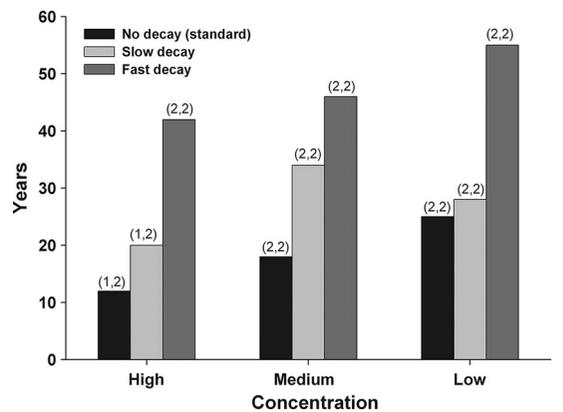
adults per leaf. Early planting dates reduced the number of insecticide sprays but the R allele frequency was somewhat higher than with a late planting date (0.08 versus 0.015; Fig. 6).

**Discussion**

The simulation results reported here show the potential impact of several operational and environmental factors on the evolution of pyriproxyfen resistance in *B. tabaci*. Variation in each of the five factors examined with the model could result in different rates of resistance evolution in Arizona and elsewhere. Over the range of values examined, pyriproxyfen concentration had the greatest impact on the evolution of resistance compared with the other factors. Crop diversity, action thresholds, and pesticide decay also had a large impact on the evolution of resistance (Table 3;



**Fig. 3.** Number of years for the frequency of the allele for resistance to pyriproxyfen, R, to reach 0.5 in simulations with three pyriproxyfen concentrations and three planting dates. The total number of insecticide sprays in treated and external refuge fields for the first simulated year is shown in parentheses.



**Fig. 5.** Number of years for the frequency of the allele for resistance to pyriproxyfen, R, to reach 0.5 in simulations with three pyriproxyfen concentrations and two decay rates. The total number of insecticide sprays in treated and external refuge fields for the first simulated year is shown in parentheses.

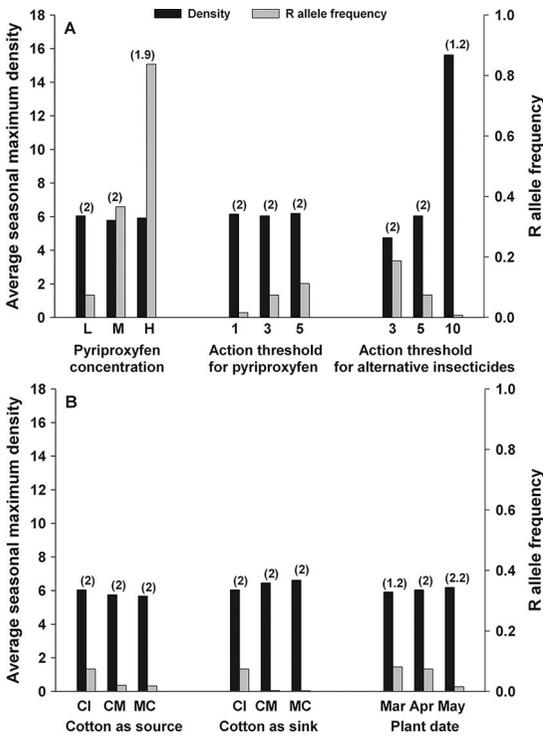


Fig. 6. The average seasonal maximum population density (adults per leaf) across the first 15 simulated years and the frequency of the allele for resistance to pyriproxyfen, R, after 15 yr in simulations with (A) variation in three factors associated with insecticide use and (B) variation in three factors associated with crops. The average number of insecticide sprays across the first 15 simulated yr is shown in parenthesis above each group of bars. All values shown represent the average for the entire region simulated. In simulations with cotton as a source or sink, the ratio of the number of emigrants from noncotton crops to emigrants from external cotton refuges was 0.5 or 2.0, respectively. L, low; M, medium; H, high; CI, cotton intensive; CM, cotton/melon; MC, multicrop; Mar, March; Apr, April.

Figs. 2 and 3). The impact of planting date on resistance evolution was relatively small compared with the other four factors examined. Over a shorter 15-yr time horizon, pyriproxyfen concentration had the greatest impact on the evolution of resistance, followed by action thresholds, crop diversity, and planting date. These results may be of practical significance for evaluating the effectiveness and economy of management strategies involving pyriproxyfen.

As simulated pyriproxyfen resistance evolved, population densities and the number of insecticide applications per year increased (Fig. 1). Simulation models have shown that insect densities, and/or yield loss, increase as insecticide resistance evolves (Onstad and Guse 1999, Onstad et al. 2003a, Crowder et al. 2005, 2006). Models also show that insecticide resistance can increase the number of insecticide applications needed for pest control (Gutierrez et al. 1979, Caprio 1998, Tang et al. 2005, Crowder et al. 2006). Population density and the number of insecticide applications are

often not reported in resistance models, despite the value of these metrics in evaluating the impacts of resistance. Our results suggest that farmers may not see appreciable reductions in pyriproxyfen performance until relatively high levels of resistance are reached (i.e.,  $R > 0.25$  with a low or medium concentration;  $R > 0.4$  with a high concentration), as population densities were relatively constant over time until these values were reached (Fig. 1).

Conducting both field efficacy tests and resistance bioassays are important components of IPM (Ellsworth et al. 2007). Simulation models can link results from these studies. For example, bioassays suggest that pyriproxyfen concentrations used in the field are low (Crowder et al. 2007). Under these conditions, the modeled seasonal maximum population densities increased from 8 to 12 adults per leaf (a 33% increase) over the first 20 yr of pyriproxyfen use despite a 250-fold increase in R allele frequency (0.001–0.25). Such a small increase in population density may be negligible to growers (and not significant in field efficacy studies), although bioassays would clearly show increasing levels of resistance. This may partially explain why bioassays have detected significant increases in resistance to pyriproxyfen in certain regions of Arizona (Li et al. 2003, Dennehy et al. 2004; unpublished results), but field efficacy studies have indicated that pyriproxyfen remains effective in the field (Ellsworth et al. 2007). Our results suggest that models can be used to reconcile differences between the bioassays and field efficacy studies. Models that relate the impact of resistance evolution to the field performance of an insecticide could improve the use of resistance bioassays as a predictive tool for IPM practitioners.

As pyriproxyfen resistance evolved to high levels, pyriproxyfen became less effective and more applications of other insecticides were needed to suppress *B. tabaci* populations (Fig. 1). The increased use of insecticides after pyriproxyfen resistance evolved could increase the risk of resistance to these other toxins. For pests such as *B. tabaci* that are controlled with multiple insecticides, resistance to any one insecticide can increase the potential risk of resistance to others. Preventing or delaying the evolution of pyriproxyfen resistance could prolong the efficacy of both pyriproxyfen and other insecticides.

Action thresholds for pyriproxyfen impacted resistance evolution by affecting both external and internal refuges. Resistance evolved slower when the action threshold for pyriproxyfen decreased (Fig. 2a) in part because population densities in the treated field decreased relative to populations in the external refuge field. As the action threshold for pyriproxyfen decreased, population densities in the treated field decreased, whereas population densities in the external refuge did not change. As the resistance allele frequency was lower in external refuges than treated fields, smaller populations in treated fields increased the effectiveness of external refuges and delayed resistance. Along these lines, raising action thresholds for insecticides in external refuges delayed resistance evolution (Fig. 2b).

Action thresholds for pyriproxyfen also impacted external refuges by affecting survival of whiteflies immigrating to treated fields. The immigration of whiteflies to cotton increased linearly from early June to early July. With a low threshold, pyriproxyfen sprays occurred before the maximum immigration period. Thus, fewer susceptible whiteflies immigrating to treated fields were exposed to pyriproxyfen than with a higher threshold. This allowed for greater survival of later arriving susceptible whiteflies, which delayed resistance. However, increased densities of susceptible whiteflies could increase a farmer's need to spray alternative insecticides later in a season, placing greater selection pressure for resistance to insecticides other than pyriproxyfen.

Action thresholds for pyriproxyfen influenced resistance evolution by affecting internal refuges, an important factor in delaying resistance evolution in *B. tabaci* (Crowder et al. 2006). Because pyriproxyfen is not systemic (Ellsworth and Martinez-Carrillo 2001), new growth in treated fields after a pyriproxyfen spray serves as an internal refuge. Decreased action thresholds for pyriproxyfen resulted in pyriproxyfen sprays earlier in the season when cotton was growing faster. Thus, as action thresholds decreased, internal refuges increased faster, which slowed resistance evolution.

A lower action threshold for pyriproxyfen delayed resistance, yet a threshold of one adult per leaf may not be advisable because of unpredictability in whitefly population dynamics. The action threshold of one adult per leaf was reached in late June in our simulations. Nevertheless, if left untreated, the population density decreased to 0.33 adults per leaf by mid-July before increasing again, after which time the thresholds of three and five adults per leaf were reached (Fig. 1a in Crowder et al. 2006). Monsoon-associated heavy rainfall and high winds are common beginning in July in Arizona and can delay initiation of the exponential population growth phase in the field (Naranjo and Ellsworth 2005, Ellsworth et al. 2007). Thus, field populations that reach a low threshold of one adult per leaf could sometimes fail to increase significantly later in the season. For example, up to 30% of fields in central Arizona were never sprayed for whiteflies in 2007, despite the presence of *B. tabaci* at low levels (unpublished data). In such cases, a pyriproxyfen spray would be unnecessary. Ideally, a better understanding of the interactions between whiteflies, their natural enemies, and the environment could be used to make more robust predictions about the growth of populations based on densities early in a season, which could be used to determine whether lower thresholds for pyriproxyfen would be warranted. However, until such information is obtained, our results do not warrant changing the current action threshold for pyriproxyfen. They do reinforce the idea that whitefly populations should be targeted as early as possible once populations begin to grow exponentially (Ellsworth and Martinez-Carrillo 2001) to increase the effectiveness of pyriproxyfen and the impact of refuges.

Action thresholds can affect the total number of insecticide sprays per year. In the field, an action threshold of five adults per leaf for pyriproxyfen resulted in fewer insecticide sprays than a threshold of one or three adults per leaf (Ellsworth and Diehl 1995). Similarly, our results show that fewer insecticide sprays were used with higher thresholds (Fig. 2). A potential trade-off of lowering the action threshold for pyriproxyfen is that more insecticide sprays may be needed, which could affect economic returns and resistance to insecticides besides pyriproxyfen.

The diversity and configuration of crops in a region can affect resistance evolution (Onstad et al. 2003a, b, Carrière et al. 2004a, b). Denholm et al. (1998) suggested that whitefly resistance to pyriproxyfen evolves fastest in cotton-intensive regions. Our model results reinforce this idea. Thus, cotton intensive regions may be the first place where resistance occurs in the field, whereas resistance evolution could take longer in multicrop regions. However, this result depends on the assumption that pyriproxyfen is used only in cotton and is sprayed at most once per season. In Arizona, pyriproxyfen was recently approved for use on leafy vegetables and cucurbits. As pyriproxyfen registrations change or expand, the potential impact of crop diversity on resistance evolution could differ from that reported here.

Movement between crops affected resistance evolution, especially in a multicrop region (Table 3). The number of insects that move between cotton and non-cotton crops could be influenced by several factors, including population densities, quality of host plants (e.g., decline of spring melons at harvest time), rate of harvest of noncotton crops (e.g., hay alfalfa harvested many times during the cotton season), and distance between crops. We assumed equal population growth in noncotton crops and external cotton refuges in simulations. However, faster population growth in noncotton crops compared with external cotton refuges would result in a lower resistant allele frequency in noncotton crops than was simulated here, whereas slower growth in noncotton crops than in external cotton refuges would have the opposite effect. We also assumed that the ratio of reciprocal movement between crops was constant. Naranjo and Ellsworth (2005) showed that the highest rates of immigration to cotton occur in mid-season (June–July), and the highest rates of emigration from cotton occur late in the season (September–October). If immigration is limited to June and July, fewer susceptible insects would move to cotton from noncotton crops, which could limit the impact of crop diversity in delaying resistance. In contrast, if emigration is limited to the late cotton season, more susceptible insects would remain in cotton and delay resistance. Thus, depending on the true difference in population dynamics between non-cotton crops and cotton, and the rates of movement between crops, our results could have underestimated or overestimated the role of crop diversity in delaying resistance. Nevertheless, results suggest that diverse regions with high levels of gene flow between crops

should represent a lower risk for evolution of pyriproxyfen resistance.

The timing of planting can affect the intensity of whitefly pressure during a season (Ellsworth and Martinez-Carillo 2001, Ellsworth et al. 2007). Planting earlier in the season has been suggested as a method to reduce whitefly pressure on crops into the summer and fall, when whitefly populations are typically at their peak. Our results suggest that early planting could result in faster evolution of resistance because plants were nearly fully grown before populations surpassed the action threshold for using pyriproxyfen, and internal refuges had little effect (Fig. 3). Cotton planted later was in an earlier stage of development when populations reached the action threshold, which increased the effectiveness of internal refuges once pyriproxyfen sprays were made. Planting earlier in the season did decrease the number of insecticide sprays per season, indicating that whitefly densities were lower in early planted fields. Thus, planting fields early could increase the likelihood that a farmer would not need to spray any insecticides for *B. tabaci*, which would be beneficial both economically and could actually delay the onset of resistance.

Pyriproxyfen residues decay rapidly in the field (Ellsworth and Martinez-Carillo 2001, Crowder et al. 2007). In our simulations, resistance evolved slower as pyriproxyfen decayed faster, consistent with other systems (Taylor et al. 1983, Luttrell et al. 1991, Baveco and De Roos 1996, Onstad and Gould 1998). Insecticide decay delays resistance because it allows for greater survival of susceptible and heterozygous insects. However, insecticide decay can also increase dominance of resistance. Field experiments showed that resistance became completely dominant 2 wk after a pyriproxyfen spray (Crowder et al. 2007). Despite the fact that resistance became more dominant as insecticides decayed in the model (Fig. 4), decreased mortality of susceptible and heterozygous individuals slowed resistance evolution.

Our results all depend on the simplifying assumption that resistance did not evolve to insecticides other than pyriproxyfen. Although resistance to some insecticides has generally declined in Arizona since the introduction of the whitefly IPM program (Dennehy and Williams 1997, Ellsworth and Martinez Carillo 2001, Dennehy et al. 2004), such resistance could evolve in the long run, thereby complicating the situation. The operational and environmental factors explored in this paper may affect the number of insecticide sprays, especially if pyriproxyfen field concentrations are high (Figs. 1–3). However, concentrations used in the field are unlikely to be high in most cases (Crowder et al. 2007). More sprays would increase the potential for resistance to insecticides other than pyriproxyfen. Ultimately, the durability of the scenarios explored here depends on management of resistance to all insecticides used against *B. tabaci* on cotton and other crops.

Our simulations indicate that the evolution of resistance to pyriproxyfen can vary greatly across regions based on operational and environmental factors.

Similar results have been documented over the past 11 yr in bioassays (Li et al. 2003, Dennehy et al. 2004; unpublished results). Lower action thresholds for using pyriproxyfen, later planting dates for cotton fields, and increased rates of pyriproxyfen decay could delay resistance, but with the potential cost of larger *B. tabaci* populations, more insecticide sprays, and increased selection pressure for resistance to other insecticides. One promising alternative would be to curtail the use of pyriproxyfen in cotton intensive regions and promote use of buprofezin, an IGR that has not been affected by increased *B. tabaci* resistance levels (Dennehy et al. 2004; unpublished results). When pyriproxyfen must be used in cotton-intensive regions, increasing the effectiveness of both internal and external refuges could delay resistance. Planting external refuges earlier than pyriproxyfen-treated fields could result in larger refuge populations at the time pyriproxyfen is sprayed and delay resistance. The same result could be achieved by increasing action thresholds for insecticides other than pyriproxyfen in external refuges. Application of lower pyriproxyfen concentrations could also delay resistance while providing effective control of populations. In regions with greater crop diversity, distributing noncotton refuges and cotton fields uniformly to reduce isolation of pyriproxyfen-treated fields, or synchronizing the harvest of spring noncotton crops with pyriproxyfen sprays in cotton fields could increase dispersal of susceptible individuals into cotton fields and delay resistance. Although these options seem promising for delaying pyriproxyfen resistance and sustaining the whitefly IPM program in Arizona, field testing will be needed to evaluate their feasibility and impact on cotton production.

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