Recovery of Cotton Crops after Early Season Damage by Thrips (Thysanoptera)

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ABSTRACT

The objective of this study was to assess the ability of cotton (*Gossypium hirsutum* L.) crops to recover after early-season damage by thrips (Thysanoptera). Such information may help clarify the actual need to control thrips. Ten experiments, resulting from the combination of two to four sites per season and three seasons, were carried out in commercial crops in the irrigation area of northwest New South Wales, Australia. Two treatments were compared: unprotected crops and crops protected with aldicarb[2-methyl-2-(methylthio)propanal *O*-[(methylamino)carbonyl]oxime] at sowing. Early season thrips communities were dominated by *Thrips tabaci* Lindeman, which accounted for 52 to 100% of the total phytophagous thrips present in the crops. Insecticide treatment consistently reduced the number of larval thrips compared with the unprotected crops. Number of larval thrips per plant ranged from 0 to 24. Thrips reduced crop leaf area in six experiments, dry matter production in four experiments, and yield in two experiments. Maximum differences in leaf area and dry weight between treatments were found about 40 d after sowing. In all cases, crops damaged by thrips recovered well and reached leaf areas and dry weights similar to protected crops after about 60 to 80 d after sowing. On average, protected crops reached maturity 3 d earlier than crops damaged by thrips, but differences were not statistically significant. Despite large reductions in early growth, yield reductions due to thrips were found in only two experiments. The magnitude of the reduction in yield in those experiments (11%) contrasts with the magnitude of the reduction in growth (about 40%) and highlights the ability of the cotton crop to recover after early season damage by thrips.

Young cotton crops host a range of insect pests, including thrips (Thysanoptera) (Hearn and Fitt, 1992). Common species of phytophagous thrips in high-input cotton cropping systems include *Thrips tabaci* and *Frankliniella* spp. (USA: Quisenberry and Rummel, 1979; Australia: Wilson and Bauer, 1993; Israel: Atakan et al., 1996).

Leaf distortion, reduced leaf area and plant height, and growth delay are often observed in thrips-damaged cotton and, in cases of severe infestation, loss of vegetative buds and branching after release of apical dominance have been reported (e.g., Watts, 1937; Quisenberry and Rummel, 1979; Attique and Ahmad, 1990). Because of these effects, thrips have the potential to reduce yield and delay the maturity of cotton crops (e.g., Watts, 1937; Attique and Ahmad, 1990). However, growth reduction and tissue destruction are "rarely, if ever, translated monotonically into a proportional reduction of final yield" (McNaughton, 1983). This is due to tolerance (sensu Belsky et al., 1993) mechanisms that allow plants to recover after damage has occurred. The mechanisms of plant tolerance to herbivory have recently been reviewed by Belsky et al. (1993), Trumble et al. (1993), and Rosenthal and Kotanen (1994).

Thrips control can be achieved either by using insecticide-treated seed, in-furrow treatment with systemic insecticides, or by foliar applications of broad spectrum systemic insecticides (Wilson and Bauer, 1993). However, many thrips species are opportunistic predators of mite (Acari: Tetranychidae) eggs (Wilson et al., 1996). Furthermore, experiments in the field showed that suppression of *T. tabaci* and *F. schultzei* with broad spectrum insecticides contributed to mite outbreaks in cotton (Wilson et al., 1996). Wilson et al. (1996) concluded that "preservation of thrips for the management of spider mites may be beneficial, yet they may also sometimes warrant control in their own right, which poses a pest management dilemma".

To assist in solving this pest management problem, we assessed to what extent early reduction in growth due to thrips translates into yield reduction and/or delay in maturity. Emphasis has been placed on analyzing the effects of thrips on plant growth and the subsequent recovery of plants after damage.

MATERIALS AND METHODS

Crops and Treatments

Ten experiments were carried out on commercial farms in northwest New South Wales, Australia (Table 1). Crops were fully irrigated and fertilized with nitrogen (100–150 kg N ha^{-1}) according to current practices in the area. Sowing dates were close to the recommended date (mid October) and plant densities ranged from 7 to 14 plants m^{-2}. Cultivar 'Siokra S324' was used in 1993-1994, and 'Siokra V-15' in 1994-1995 and 1995-1996.

Two treatments were compared: unprotected crops and crops protected with aldicarb applied in the soil at sowing (0.45 kg ha^{-1}). Each experiment used a randomized block design with three or four replicates; each plot was between 0.5 and 0.8 ha. No synthetic insecticides were used before 60 d after sowing (DAS). During this period *Heliothis* spp. were controlled, when necessary, with formulations of *Bacillus thuringiensis* var. *kurstaki* which are not toxic to non-lepidoptera. Thereafter, both treatments were managed identically for pest control by accepted commercial thresholds (Shaw, 1995).

Thrips: Species Composition and Abundance

We monitored thrips populations during the period of thrips occurrence as pests, viz., from seedling emergence to about 60 DAS (Wilson and Bauer, 1993). At weekly intervals, cotton shoots ($n \geq 5$) were collected from each plot and taken to the laboratory where insects were removed using a plant washing machine (Leigh et al., 1984). Numbers of adult and larval thrips, and all other insects present in the samples, were recorded. Estimates of the species composition of thrips were obtained by identifying subsamples of adults from each sample

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Published in Crop Sci. 38:399–409 (1998).

Abbreviations: DAS, days after sowing, LA:LDWT, slope of the regression between $\log_e$ leaf area and $\log_e$ leaf dry weight; LDWT:SDWT, slope of the regression between $\log_e$ leaf dry weight and $\log_e$ shoot dry weight; ULR, unit leaf rate.

Table 1. Season, site, and sowing date of field experiments. Time of maturity of protected and unprotected crops is also shown.

Season	Site†	Sowing date	Maturity (days after sowing)‡ Protected	Unprotected
1993–1994	Abbey Green (3)§	11 Oct	153	162
	Norwood (4)	02 Oct	162	168
	Oakville (4)	13 Oct	156	160
	Redmill (4)	08 Oct	151	151
1994–1995	Abbey Green (3)	11 Oct	–¶	–
	Norwood (4)	17 Oct	–	–
	Oakville (4)	10 Oct	–	–
	Redmill (4)	06 Oct	166	168
1995–1996	Kooiyong (4)	24 Oct	179	181
	Merrigal (4)	16 Oct	188	189

† Commercial farms in the Lower Namoi Valley (Abbey Green, Oakville), Upper Namoi Valley (Kooiyong, Merrigal), and in the Gwydir Valley (Norwood, Redmill) of New South Wales, Australia.
‡ 60% of open bolls. Differences between treatments were not significant ($P > 0.05$) in all experiments.
§ Number of replicates.
¶ Not measured.

late for each site. Wilson and Bauer (1993) found that for the main phytophagous species, the species composition of larval thrips closely followed that of adults. Adult thrips were slide mounted and identified by the keys of Mound (1967, 1972), Mound and Waker (1982, 1986), Mound et al. (1976), Pitkin (1973), Mound and Houston (1987), and Palmer et al. (1989).

Cotton Growth and Yield

Separate samples were collected for plant growth analysis. In 1993-1994, shoots were cut at ground level while plants were pulled and shoots and attached tap roots were collected in 1994-1995 and 1995-1996. Samples were taken at weekly intervals (sample size = 0.5 m^2 per replicate). Plant components were separated and oven-dried to constant weight. Green leaf area of at least two whole plants was measured with a leaf area meter (LI-3100, LI-COR, Inc., Lincoln, NE) to estimate specific leaf area, and this variable used to estimate plant leaf area from leaf dry matter values. Sequential hand harvests were done to determine time of maturity (i.e., 60% of open bolls, Snipes and Baskin, 1994) for all sites in 1993-1994, for Redmill only in 1994-1995 and for both sites in 1995-1996 (sample size = 2 m^2 per replicate). Cottou seed was machine harvested from a two or four row section through the complete length of each plot, and yield (seed + lint) determined with calibrated load cell scales.

Data Analyses

Response variables analyzed include (i) number of adult thrips, (ii) number of larval thrips, (iii) plant leaf area, (iv) shoot dry matter, (v) tap root dry matter, (vi) time of maturity, and (vii) yield. Effects of treatments were tested with analysis of variance (ANOVA) for each sampling date (variables i–v) and each experiment (all variables). Thrips numbers were $\log_e$ transformed before analyses.

Shoot relative growth rate and unit leaf rate (or "net assimilation rate") were calculated as in Evans (1972). Two allometric coefficients were calculated to explore relevant changes in partitioning due to thrips (i) LA:LDWT, the slope of the regression between $\log_e$ leaf area and $\log_e$ leaf dry weight, and (ii) LDWT:SDWT, the slope of the regression between $\log_e$ leaf dry weight and $\log_e$ shoot dry weight. Details and justification of this approach to analyze partitioning have been summarized by Coleman et al. (1994).

Table 2. Species composition of thrips on cotton crops.

Season	Site	n†	% Species *Thrips tabaci*	*Frankliniella schultzei*	*Thrips imaginis*	Other‡
1993–1994	Abbey Green	107	82.2	3.7	0	14.1
	Norwood	88	85.2	10.2	1.1	3.5
	Oakville	57	63.1	36.8	0	0
	Redmill	66	51.5	28.8	0	19.7
1994–1995	Abbey Green	25	68.0	12.0	0	20.0
	Norwood	4	75.0	25.0	0	0
	Oakville	26	84.6	15.4	0	0
	Redmill	8	100.0	0	0	0
1995–1996	Kooiyong	24	95.8	4.2	0	0
	Merrigal	19	94.7	0	0	5.3

† Variation in number of adult thrips identified reflects, in part, their actual abundance; in 1994–1995 some samples were lost after thrips counting and before species identification.
‡ Non-phytophagous thrips.

RESULTS

Thrips Species

Consistent with previous studies (Wilson and Bauer, 1993), we found early-season thrips communities to be dominated by *T. tabaci* (Table 2). Averaged over all the sites and seasons, *T. tabaci* accounted for 80% of the total thrips species and for 89% of the phytophagous species. Thus, no attempt was made to separate thrips species in the following analyses where we use the term "thrips" to refer to communities dominated by *T. tabaci*.

1993-1994 Experiments

Intensity and timing of thrips infestation varied among sites (Fig. 1). The insecticide treatment consistently reduced the number of larval thrips at all sites but was less effective at reducing numbers of adult thrips. In unprotected controls, the maximum number of larvae per plant varied between 2 (Oakville) and 24 (Norwood). The time of peak larval numbers ranged from 24 DAS (Redmill) to 44 DAS (Norwood).

Insecticide treatments affected crop leaf area and dry matter accumulation (Fig. 2). Effects on leaf area normally preceded effects on dry matter. Early in the season, unprotected crops usually had less leaf area and dry weight than protected crops, with significant reductions often observed in the period from 20 to 60 DAS. After about 50 to 60 DAS, leaf area and dry matter of unprotected crops usually recovered to the levels of protected crops.

Yield of protected crops ranged from 2 to 5 Mg ha^{-1}. Treatment effects on yield were only significant at one of the four sites, where the unprotected crop yielded 11% less than the protected one (Table 3). Unprotected crops normally reached maturity later than protected controls but differences were not significant (Table 1).

1994-1995 Experiments

As in the 1993-1994 season, the intensity and timing of thrips infestation varied among sites. Insecticide treatment consistently reduced the number of larvae at all sites and had a marginal effect on adult thrips (Fig. 3). Number of larvae were negligible at Norwood, great-

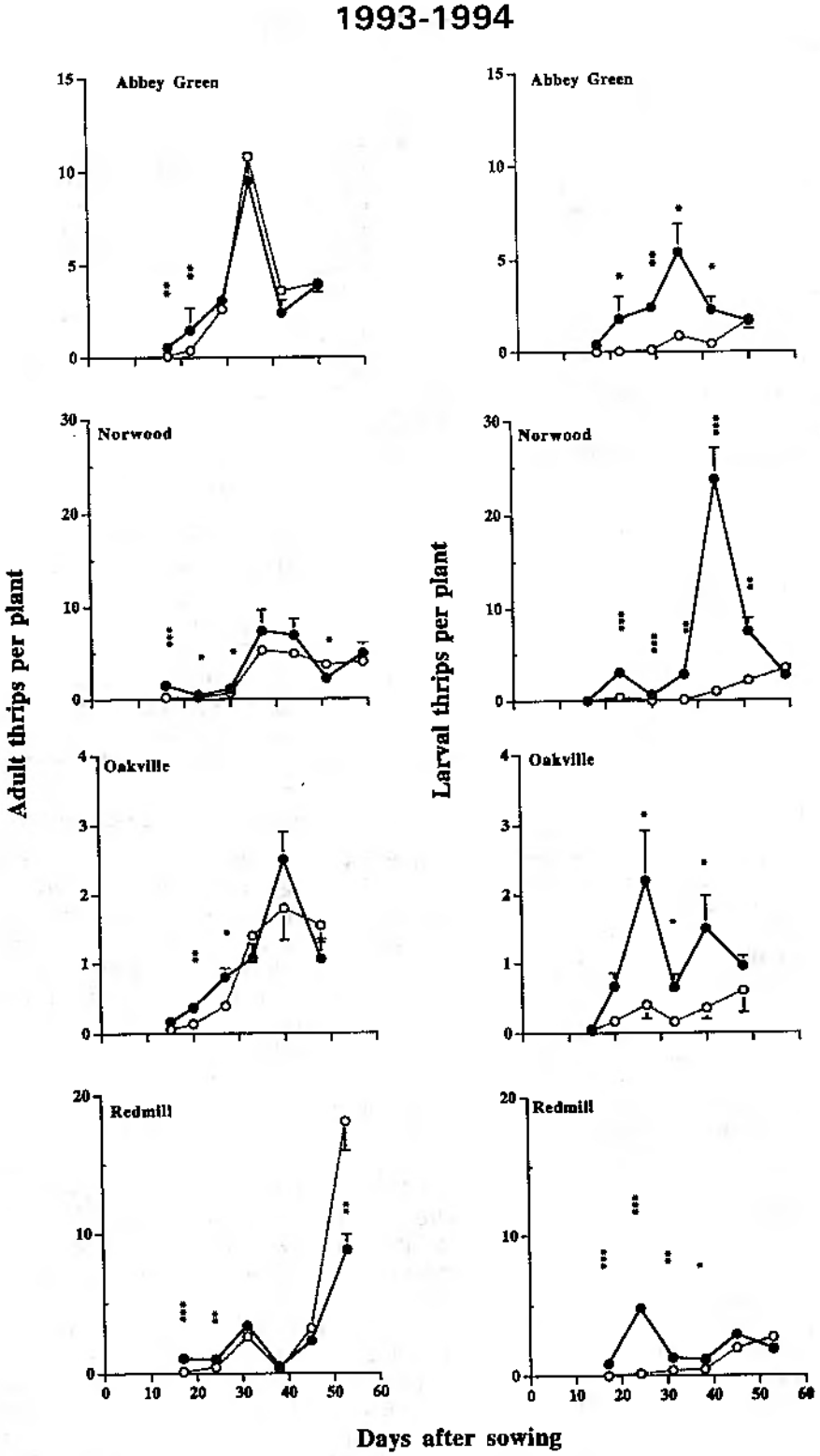

Fig. 1. Dynamics of thrips populations in four cotton crops during the 1993-1994 season. Closed symbols = unprotected crops, open symbols = protected crops. Levels of significance, from ANOVAs of log-transformed variables, are: $P < 0.0001$ (***), $P < 0.01$ (**), $P < 0.05$ (*). Bars are one standard error of the mean and are not shown when smaller than symbols.

est at Abbey Green and Redmill and intermediate at Oakville (Fig. 3). Redmill was the only site where a significant number of thrips developed early in the season.

Insecticide treatment did not affect crop growth at Oakville, Abbey Green, or Norwood (not shown). Comparison between unprotected and protected crops at Redmill (Fig. 4) showed early season reductions in: leaf

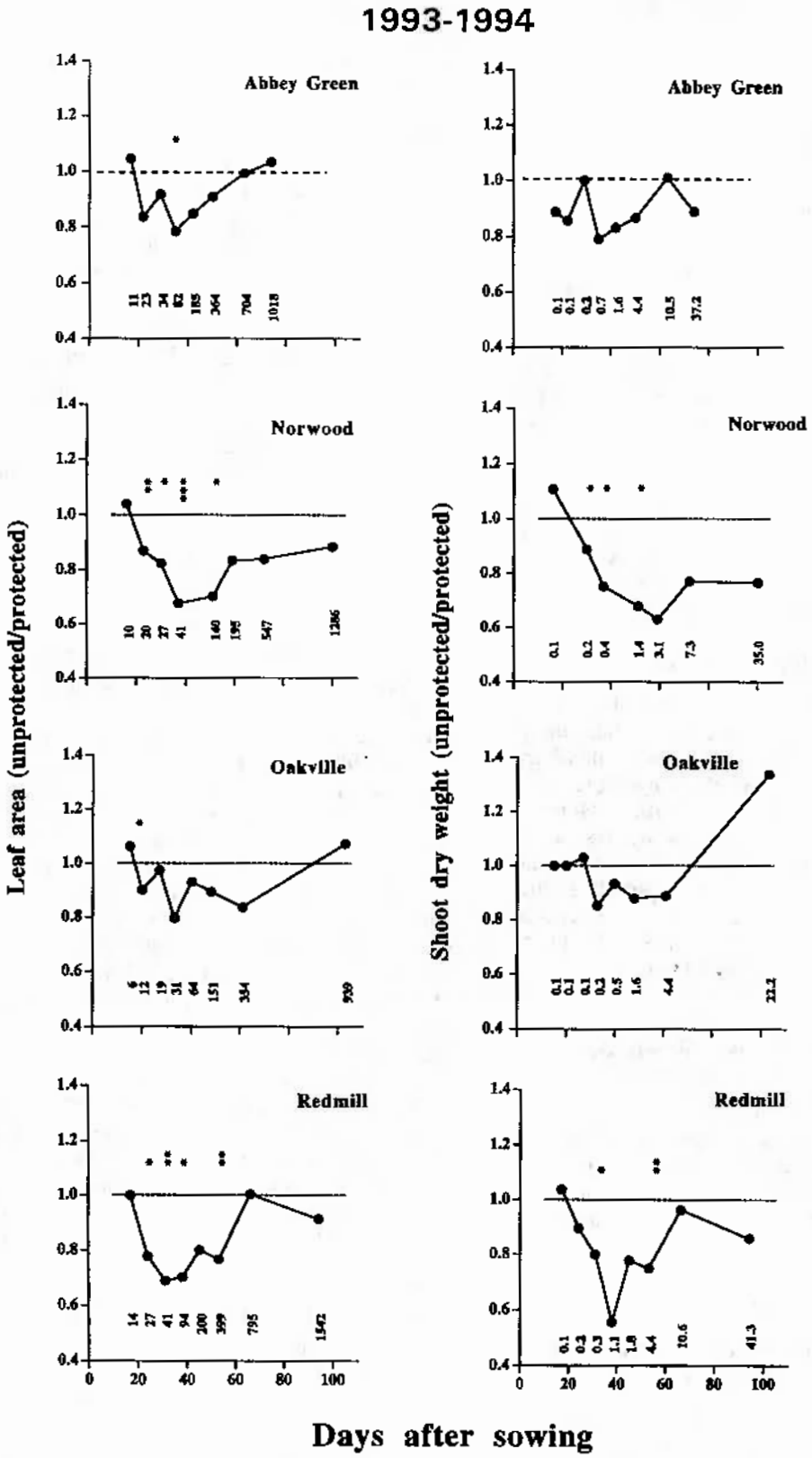

Fig. 2. Effect of insecticide treatment on leaf area and shoot growth of cotton at four sites in 1993-1994. The magnitude of treatment effect can be visualized as the divergence between the solid line and the $y = 1$ (dashed) line. Levels of significance, from ANOVAs comparing protected and unprotected treatments, are $P < 0.0001$ (***), $P < 0.01$ (**), $P < 0.05$ (*). Numbers below the plot are absolute values of protected crops in square centimeters per plant (leaf area) and grams per plant (shoot dry weight).

Table 3. Yield of cotton crops as affected by early-season thrips damage.

Experiment		Seed cotton (Mg ha^{-1})		P values from ANOVA
Season	Site	Protected	Unprotected	
1993–1994	Abbey Green	2.23	2.20	0.71
	Norwood	2.51	2.56	0.62
	Oakville	3.36	3.17	0.27
	Redmill	4.94	4.41	0.02
1994–1995	Abbey Green	5.15	4.95	0.30
	Norwood	6.25	6.22	0.82
	Oakville	4.89	4.57	0.21
	Redmill	5.46	4.88	0.05
1995–1996	Kooiyong	4.02	3.94	0.73
	Merrigal	3.87	3.89	0.90

area (up to 48% at 39 DAS), shoot dry weight (up to 43% at 48 DAS), and tap root dry weight (up to 59% at 53 DAS). At about 70 DAS, differences between protected and unprotected crops were no longer evident.

Yield of protected crops ranged from 5 to 6 Mg ha^{-1}. At Redmill, the unprotected crop yielded 11% less than the protected one; no effect of insecticide was found at any other site (Table 3). At Redmill, maturity was unaffected ($P > 0.6$) by insecticide treatment (Table 1).

1995-1996 Experiments

Again, insecticide treatment affected number of larvae markedly and number of adult thrips marginally. These effects were mostly evident at Merrigal, where thrips abundance was greater than at Kooiyong (Fig. 5). Insecticide treatments affected crop growth in Merrigal (Fig. 6) but not in Kooiyong (not shown). As in the previous seasons, treatments affected leaf area first, and then dry weight (Fig. 6). Despite severe growth reductions early in the season, unprotected crops recovered to the level of protected controls by about 80 DAS. Treatments did not affect maturity (Table 1, $P > 0.2$) nor yield (Table 3).

General Yield and Growth Responses to Insecticide Treatments

Fig. 7 shows the relationship between growth and yield, both expressed as the ratio between unprotected and protected treatments, for the 10 experiments in this study. No yield reductions were observed when shoot growth reductions early in the season were less than about 40%.

DISCUSSION

Effects of Insecticide Treatments on Thrips and Other Arthropods

Because of the high mobility of thrips, adults were found in both protected and unprotected crops in similar numbers (Fig. 1, 3, and 5). This probably reflects continuous influxes of adult thrips into the cotton crops as nearby spring hosts of thrips senesced (Wilson and Bauer, 1993). However, protected crops had consistently less larvae than unprotected crops (Fig. 1, 3, and 5), indicating that the insecticide treatment effectively reduced the colonization of crops by thrips. Despite the presence of adults in the protected treatment, there were no signs of damage to plants, indicating that the thrips probably died before causing visible injury to the crop.

Regular insect and mite counts in our study showed that aldicarb did not affect the abundance of beneficial arthropods or arthropod pests other than thrips (Wilson and Sadras, 1996, unpublished). Scott et al. (1985) in cotton cropping systems in the USA and Soares et al. (1996) in Brazil also found no effects of aldicarb on populations of beneficial arthropods.

Effects of Aldicarb on Crop Growth

Responses of crop growth (Fig. 2, 4, and 6), time of maturity (Table 1) and yield (Table 2) to insecticide treatment could be related to (i) effects of insecticide on arthropods other than thrips (see previous section), (ii) direct effects of insecticide on plant growth, and/or (iii) effects of insecticide on thrips.

In the absence of insects, mites and nematodes, aldicarb can increase, reduce or have no effect on plant growth (Womack and Schuster, 1986; Barker and Powell, 1988; Barker et al., 1988). In reviewing the effects of aldicarb on cotton growth, Terry (1992) highlighted the inconsistency of the responses; genotype, soil type, fertility, and soil moisture are among the factors that can influence plant responses to aldicarb (Barker and Powell, 1988; Barker et al., 1988). The inconsistent responses of plant growth to aldicarb are in sharp contrast to the consistent pattern of plant growth of unprotected and aldicarb-protected plants found in our study despite the environmental variation derived from a combination of locations and seasons (Fig. 2, 4, and 6). It is worth emphasizing the contrast between the cooler environment of the Upper Namoi Valley (Kooiyiong, Merrigal) where protected crops reached maturity at 179 to 188 DAS in comparison with the warmer Lower Namoi and Gwydir Valleys where crops reached maturity at 151 to 162 DAS (Table 1).

Thus, even though direct effects of aldicarb cannot be discarded, it is very unlikely that the pattern of plant growth in the present experiments could be due to direct effects of aldicarb. It is reasonable to assume, therefore, that the differences in growth and yield between protected and unprotected crops were mostly mediated by the effects of aldicarb on thrips. This premise is further supported by (i) the correspondence between thrips dynamics (Fig. 1, 3, and 5) and plant growth dynamics (Fig. 2, 4, and 6), and (ii) the known effects of thrips in reducing leaf area (see Introduction) and the sequence of responses whereby unprotected crops usually had reductions in leaf area preceding significant growth reductions (Fig. 2, 4, and 6).

Effects of Thrips on Crop Growth, Maturity and Yield

In six out of 10 experiments, thrips significantly affected cotton leaf area (Fig. 2, 4, and 6). Reductions in leaf area translated into growth reductions in four of

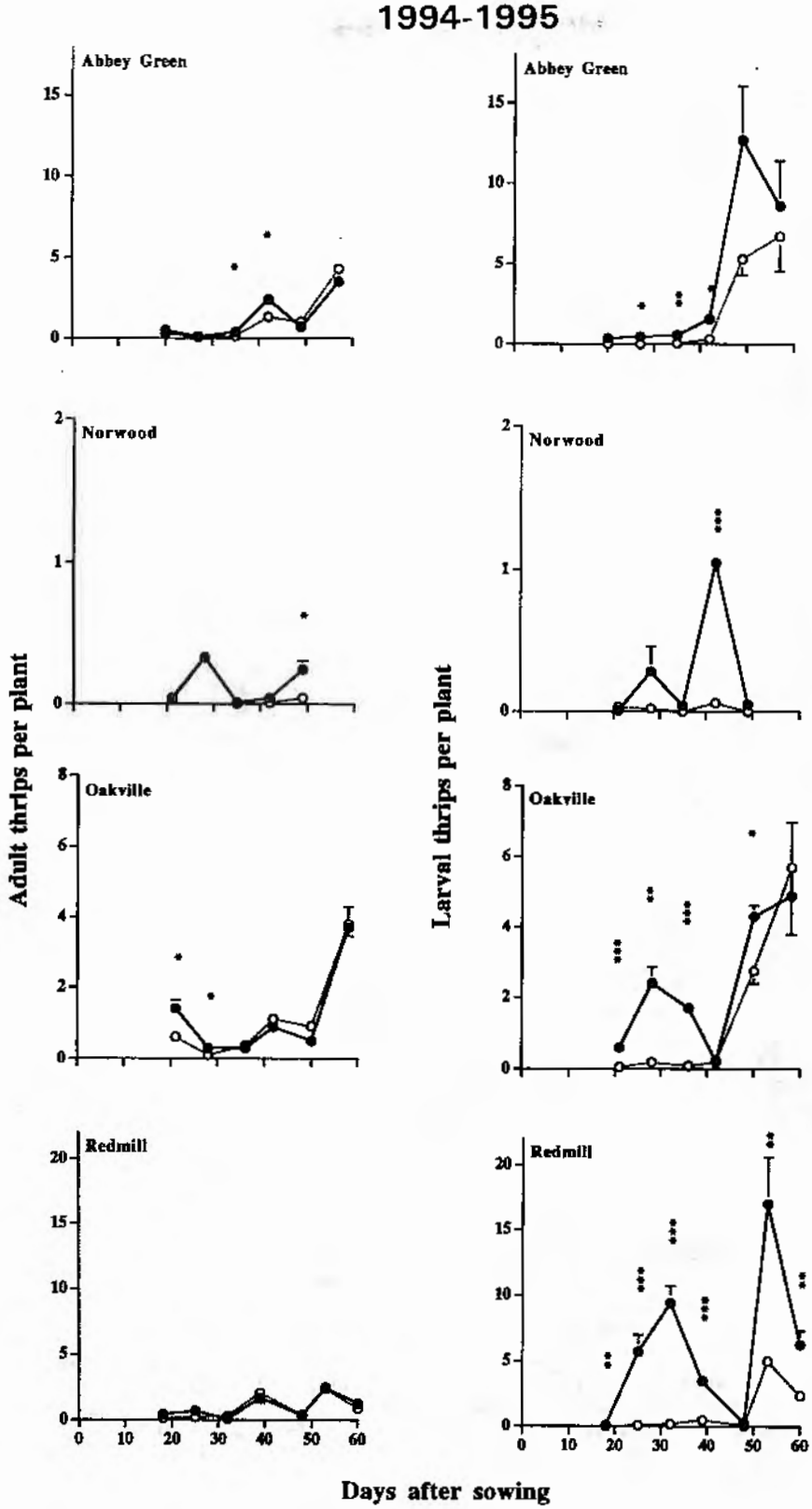

Fig. 3. Dynamics of thrips populations in four cotton crops during the 1994-1995 season. Closed symbols = unprotected crops, open symbols = protected crops. Levels of significance, from ANOVAs of log$_e$-transformed variables, are $P < 0.0001$ (***), $P < 0.01$ (**), $P < 0.05$ (*). Bars are one standard error of the mean and are not shown when smaller than symbols.

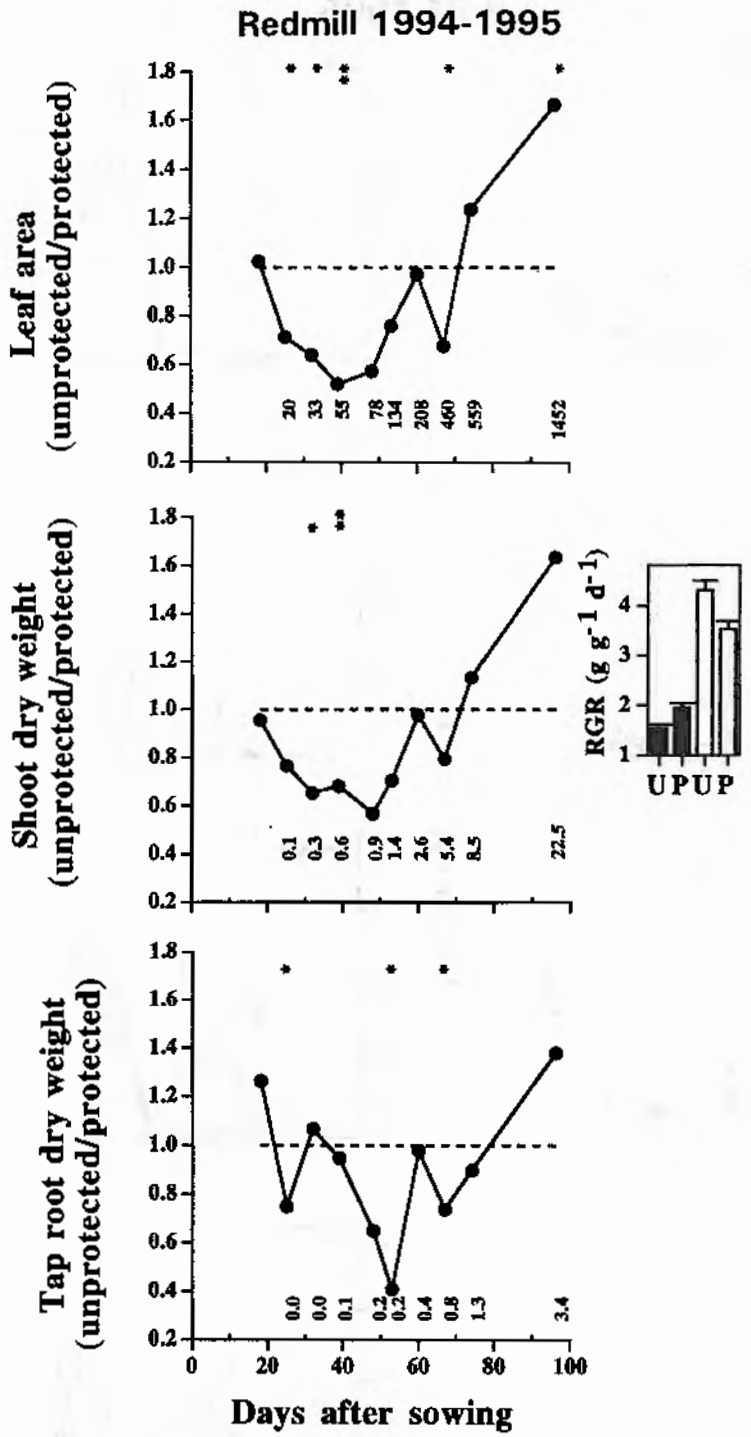

Fig. 4. Effects of insecticide treatment on leaf area, shoot and tap root growth of cotton at Redmill in 1993-1994. The magnitude of treatment effect can be visualized as the divergence between the solid line and the $y = 1$ (dashed) line. Levels of significance, from ANOVAs comparing protected and unprotected treatments, are $P < 0.01$ (**), $P < 0.05$ (*). Numbers below the plot are absolute values of protected crops in square centimeters per plant (leaf area) and grams per plant (shoot and root dry weight). Inset shows relative growth rates of unprotected (U) and protected (P) shoots during the period 18 to 48 DAS (closed bars) and 48 to 96 DAS (open bars). Bars are one standard error of the mean.

the 10 experiments (Fig. 2, Norwood and Redmill, Fig. 4 and 6). Reductions in growth translated into reductions in yield in only two cases (Fig. 7, Table 3). Thus, the general statement by McNaughton (1983), that tissue destruction is rarely translated into a proportional yield reduction, seems to be valid for the cotton-thrips system under study.

The dynamics of leaf area, expressed as the ratio between unprotected and protected treatments, showed a biphasic pattern (Fig. 2, 4, and 6). In the first phase, protected crops grew faster than unprotected crops, and the ratio declined consistently. A minimum value of the ratio, ranging from 0.8 to 0.5, was usually reached by 40 DAS. In the second phase, leaf area in crops damaged by thrips increased faster than in protected crops, and significant differences between treatments were not evi-

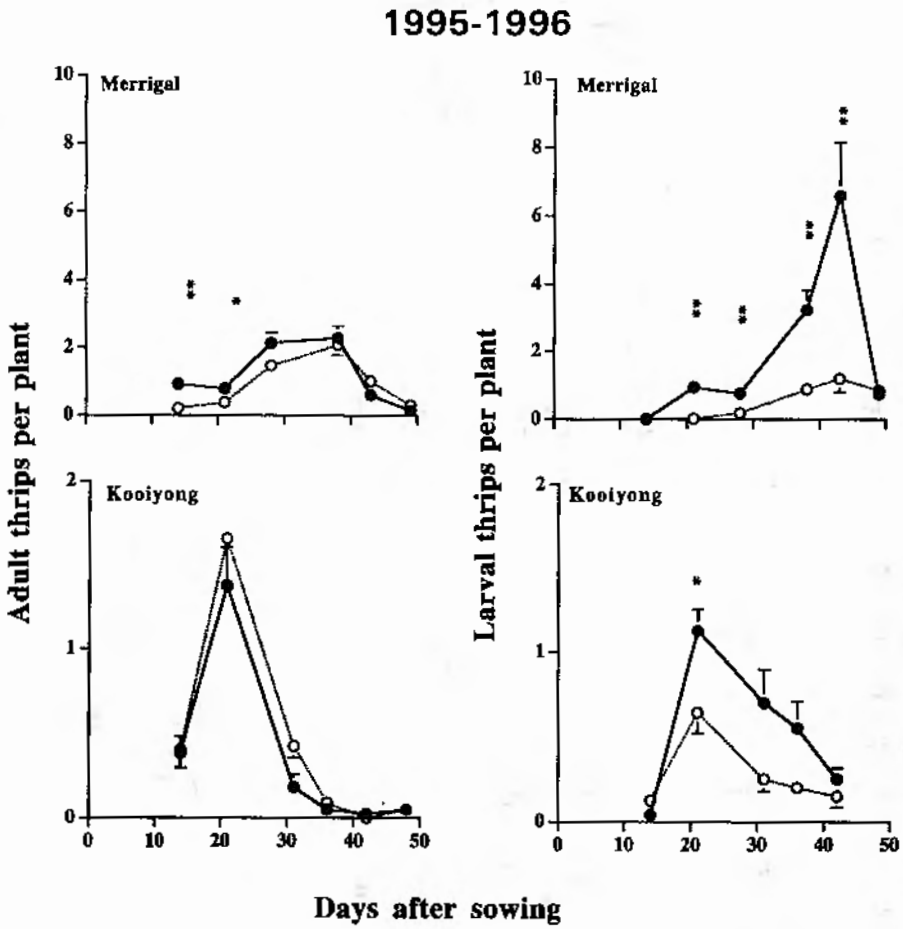

Fig. 5. Dynamics of thrips populations in two cotton crops during the 1995-1996 season. Closed symbols = unprotected crops, open symbols = protected crops. Levels of significance, from ANOVAs of $\log_e$-transformed variables, are $P < 0.01$ (**), $P < 0.05$ (*). Bars are one standard error of the mean and are not shown when smaller than symbols.

dent after about 60 to 80 DAS. A similar biphasic pattern, that was displaced in time by about 5 to 10 d, was observed for shoot and tap-root growth. This pattern is further illustrated by the insets of Fig. 4 and 6: a first phase, in which protected crops had higher relative growth rates than their unprotected counterparts was followed by a phase in which the opposite was true. The capacity of cotton plants to recover after substantial reductions in leaf area caused by thrips, found in this study (Fig. 2, 4, and 6), is consistent with other studies involving leaf area loss in this species (e.g., Lane, 1959; Gutierrez et al., 1975).

Four main mechanisms could be involved in plant recovery after reduction in leaf area. First, changes in partitioning, viz., increase in leaf area : leaf weight ratio and/or increase in leaf weight : shoot weight ratio could increase the relative growth rate of damaged plants. Second, new leaf addition can partially compensate for leaf loss due to insects (Lane, 1959; Bishop et al., 1978). Third, if leaves are involved in apical dominance (Töpperwein, 1993), then enhanced branching following leaf damage may also be a factor in the recovery of damaged crops. Fourth, there may be an increase in the photosynthetic rate of undamaged leaves in a damaged plant and/or in undamaged areas of damaged leaves, i.e., compensatory photosynthesis (Trumble et al., 1993). Our data allowed investigation of the first and, to some extent, the fourth mechanism.

Allometric analysis was used to explore relevant changes in partitioning during the first (i.e., growth reduction) and second (i.e., recovery) phases of cotton responses to thrips defined before. The consistent and substantial reduction in LA:LDWT caused by thrips in the first phase (Table 4) indicates that leaf expansion was more severely reduced than leaf dry matter accumulation. Reduction in export of carbohydrates from leaves damaged by thrips might also have contributed to reductions in LA:LDWT. Effects of thrips on LDWT:SDWT in this phase were small and inconsistent (Table 4). In the recovery phase, both LA:LDWT and LDWT:SDWT were consistently higher in crops damaged by thrips than in their protected counterparts (Table 4). Although differences between treatments were small (≤8%), small changes in dry matter partitioning may have a large impact on subsequent plant growth (Körner, 1991). Thus, an increased partitioning to photosynthetic tissue may have contributed to the recovery of damaged crops.

Unit leaf rate was reduced by thrips in the first phase (Table 4). Hence, thrips may have reduced dry matter accumulation of young cotton crops by reducing not only leaf area but also photosynthetic rate. Unit leaf

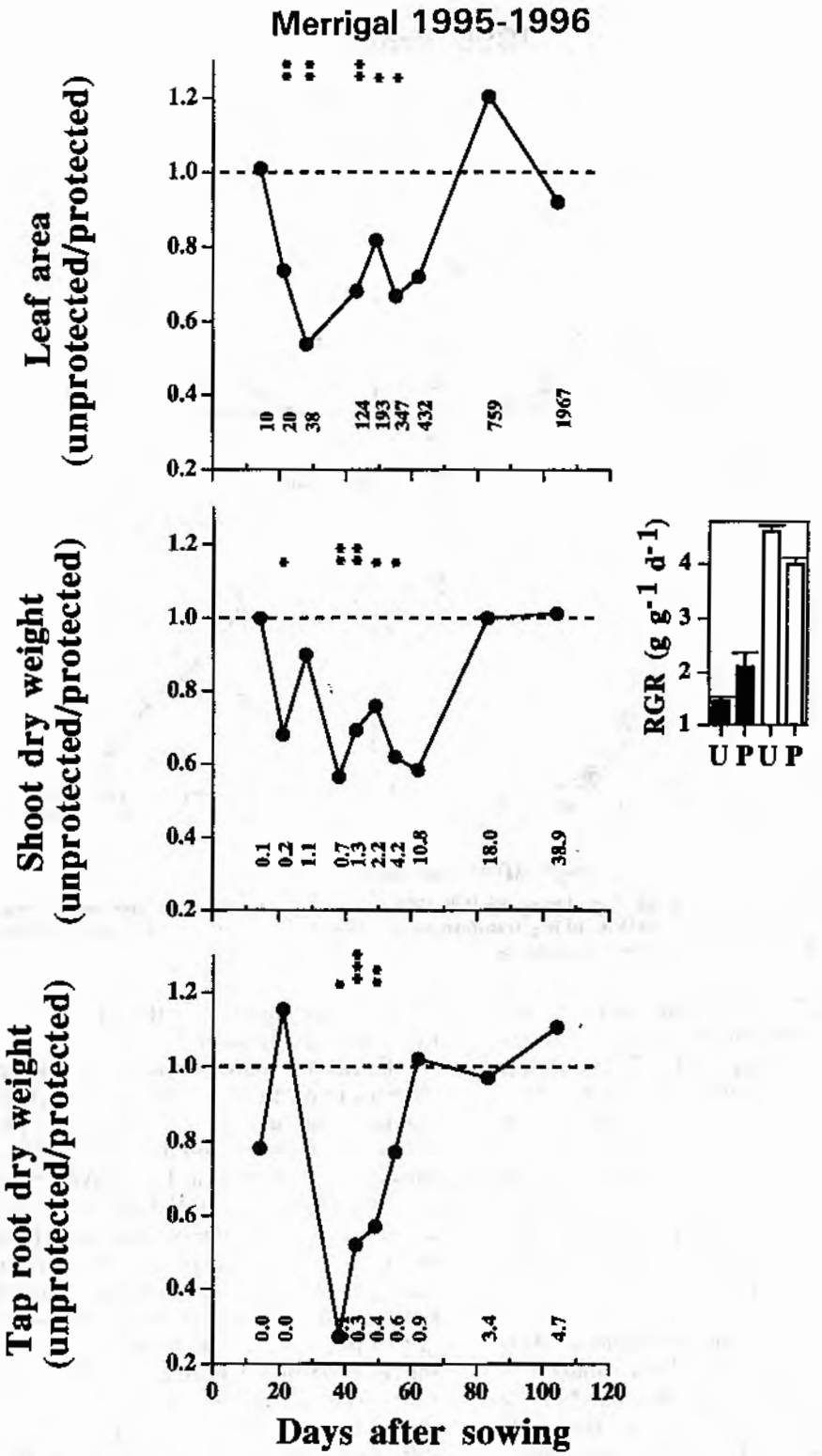

Fig. 6. Effects of insecticide treatment on leaf area, shoot and tap root growth of cotton at Merrigal in 1993-1994. The magnitude of treatment effect can be visualized as the divergence between the solid line and the $y = 1$ (dashed) line. Levels of significance, from ANOVAs comparing protected and unprotected treatments, are: $P < 0.0001$ (***), $P < 0.01$ (**), $P < 0.05$ (*). Numbers below the plot are absolute values of protected crops in square centimeters per plant (leaf area) and grams per plant (shoot and root dry weight). *Inset* shows relative growth rates of unprotected (U) and protected (P) shoots during the period 14 to 38 DAS (closed bars) and 38 to 104 DAS (open bars). Bars are one standard error of the mean.

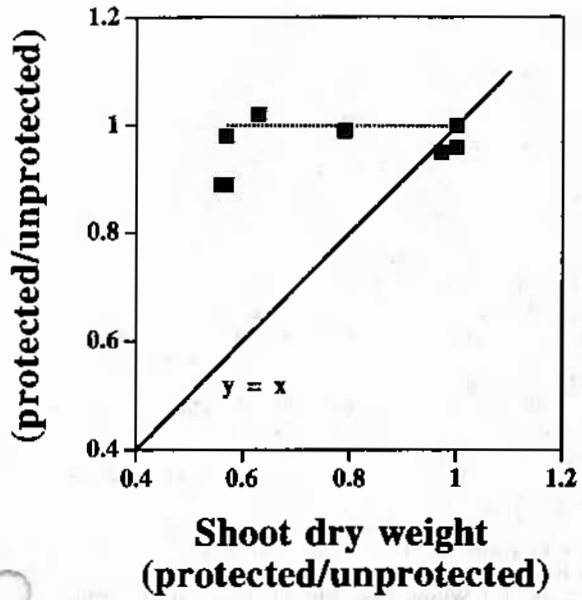

Fig. 7. Comparison of yield and shoot growth responses to thrips in 10 field experiments. Both variables are expressed as ratios between protected and unprotected crops. For shoot dry weight, the lowest ratio found in each experiment was used. The horizontal line joins data points from experiments where insecticide treatment did not affect yield (Table 3).

rate of crops damaged by thrips increased with respect to protected controls during the recovery phase in three out of four experiments (Table 4). Compensatory photosynthesis could therefore be a factor in the recovery of these crops. However, owing to limitations associated with the calculation of unit leaf rate (Evans, 1972; Monteith, 1994) our conclusions about putative effects of thrips on cotton photosynthesis should be considered with care. Direct measurements of leaf and/or crop photosynthesis are required to further assess these effects.

Implications for Pest Management

Key pests are those that are persistent, occur perennially and usually reach economically damaging levels (Kearn and Fitt, 1992). For cotton in Australia, thrips clearly meet the first two criteria as they are often found in significant numbers in young crops (Fig. 1,3, 5; Wilson et al., 1994). Similarly, early-season thrips infestations are common in cotton crops in the USA (e.g., Quisenberry and Rummel, 1979). The economic impact of thrips is less clear, however. We found yield reductions attributable to thrips in two out of 10 field experiments. Similarly, we found significant yield reductions in one out of seven experiments carried out in commercial farms in 1991-1992 and 1992-1993 (Wilson et al., 1994). The same picture arises for the peanut-thrips system in southeastern USA: *Frankliniella fusca* (Hinds) cause early-season foliar injury which often leads to stunting of peanut plants, but the economic justification for thrips suppression remains controversial and, in general, controlling thrips is not recommended (Brecke et al., 1996).

Although thrips had only minor effects on yield and maturity in the present study (Tables 1 and 2) and in previous experiments (Wilson et al., 1994), they reduced seedling growth dramatically (Fig. 2, 4, and 6). Given the contrasting visual aspect of healthy protected crops and typically stunted crops damaged by thrips, the perception of growers that thrips need to be controlled is understandable. The use of insecticides for "cosmetic" reasons has a number of side effects, however. First, it may reduce the number of beneficial arthropods early in the season, interfering with the implementation of integrated pest management programs. Second, it eliminates "phytophagous" thrips of cotton crops that are, in fact, facultative predators of twospotted spider mites (Wilson et al., 1996). Spider mites are an important secondary pest of cotton crops and have the potential to reduce severely lint yield, oil yield, and fiber quality (Wilson, 1993; Sadras and Wilson, 1996, 1997).

The quantification of thrips/yield relationships and development of thresholds for thrips management require experiments that cover a wider range of thrips densities. Our study has shown, however, the significant ability of cotton to recover after severe growth reduction caused by thrips. This observation, together with recognition of the negative side effects of using insecticides for thrips control, could assist in the rational assessment of the actual need to use insecticides for their control.

ACKNOWLEDGMENTS

We thank each of the co-operators, Steve, Andrew, and Elliot Benham, Jeremy Killen, Mike Logan, Steve Brown, John Mohr-Bell, Peter Glennie, Kylie May, Jeff Carolan, Phil Warmoll, and their staff for their interest in this research and

Table 4. ULR, LA:LDWT, and LDWT:SDWT in experiments where thrips reduced crop growth. ULR, unit leaf rate, was calculated using eq. 16.9.2 of Evans (1972), LA:LDWT is the slope of the regression between log, leaf area and log, leaf dry weight, and LDWT:SDWT is the slope of the regression between log, leaf dry weight and log, shoot dry weight.

		ULR ($g\ m^{-2}\ d^{-1}$)				LA:LDWT ($cm^2\ g^{-1}$)				LDWT:SDWT ($g\ g^{-1}$)			
Experiment	Treat.†	Phase 1‡	Δ%¶	Phase 2	Δ%	Phase 1	Δ%	Phase 2	Δ%	Phase 1	Δ%	Phase 2	Δ%
Redmill 1993–1994	P	9.2 ± 2.16§		10.5 ± 0.99		0.83 ± 0.030		0.92 ± 0.014		0.99 ± 0.013		0.79 ± 0.019	
	U	7.0 ± 0.90	−24	11.2 ± 1.16	+7	0.64 ± 0.054	−23	0.93 ± 0.035	+1	1.01 ± 0.022	+2	0.82 ± 0.017	+4
Norwood 1993–1994	P	8.5 ± 0.48		9.9 ± 1.07		0.79 ± 0.030		0.93 ± 0.014		0.89 ± 0.009		0.82 ± 0.017	
	U	8.1 ± 0.69	−5	9.1 ± 0.42	−8	0.45 ± 0.021	−43	1.00 ± 0.019	+8	0.89 ± 0.008	0	0.85 ± 0.014	+4
Redmill 1994–1995	P	6.1 ± 1.24		7.6 ± 1.52		1.00 ± 0.070		1.02 ± 0.022		0.98 ± 0.050		0.87 ± 0.013	
	U	5.5 ± 1.55	−10	10.3 ± 1.54	+35	0.75 ± 0.093	−25	1.06 ± 0.022	+4	0.94 ± 0.050	−4	0.89 ± 0.014	+2
Merrigal 1995–1996	P	5.7 ± 1.23		5.9 ± 0.33		0.43 ± 0.080		0.89 ± 0.020		1.01 ± 0.060		0.82 ± 0.018	
	U	3.1 ± 0.51	−46	6.8 ± 0.73	+15	0.23 ± 0.060	−47	0.93 ± 0.026	+4	0.94 ± 0.030	−7	0.83 ± 0.015	+1

† Treatments are protected with insecticide (P) and unprotected (U).
‡ Two phases were distinguished in the responses of cotton to thrips: Phase 1, growth reduction, and Phase 2, recovery. See text for details.
§ SE.
¶ $\Delta\% = 100(U - P)/P$.

their willingness to provide experimental sites and to assist with crop management. We also thank P. Walker and R. Mensah for comments on the manuscript; D. Lally, S. Warden, G. Nehrkon, M. Hickman, L. Bauer, T. Staines, M. Laird, and L. Gett for technical assistance; D. Lally for thrips identification; and the Cotton Research and Development Corporation for financial support (grants CSP46C, CSP39C, CSP68C).

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Bulletin of Entomological Research (1998) 88, 477–488

Effect of early season insecticide use on predators and outbreaks of spider mites (Acari: Tetranychidae) in cotton

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Abstract

The Australian cotton industry relies almost exclusively on synthetic insecticides for control of early season pests. These insecticides often disrupt predatory insect activity in the field. Potential predators of the twospotted spider mite, *Tetranychus urticae* Koch, in cotton, identified in field and confirmed in laboratory experiments, included a theridiid spider, a phytoseiid mite, a lacewing larva, predatory thrips, several Coccinellidae and several Hemiptera. These predators were mostly generalists, having previously been reported as predators of aphids or caterpillars of *Helicoverpa* spp. The effect of insecticides on *T. urticae* and its predators was evaluated in three field experiments. Cotton was artificially infested with *T. urticae* then sprayed five times at seven to ten day intervals with either dimethoate (140 g ai/ha), thiodicarb (750 g ai/ha and 187.5 g ai/ha), endosulfan (735 g ai/ha and 367.5 g ai/ha), methomyl (169 g ai/ha) or amitraz (400 g ai/ha). *Tetranychus urticae* populations reached higher densities in dimethoate, thiodicarb and methomyl treated cotton than in untreated cotton. Population densities of *T. urticae* in cotton treated with low rates of endosulfan or thiodicarb were similar to controls, while those in cotton treated with amitraz were lower. All insecticides caused significant reductions in at least one predator group. Significant negative relationships were found between early season abundance of predators and the mid-season abundance of *T. urticae* and positive relationships between predators and the lag-period for *T. urticae* outbreaks to develop. Predation is implicated as a key factor influencing the early season survival of *T. urticae*. The implications for developing integrated pest management strategies in cotton are discussed.

Introduction

The two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), is an important pest of cotton, *Gossypium hirsutum*, in Australia (Forrester & Wilson, 1988; Wilson, 1993). *Tetranychus urticae* colonize cotton shortly after seedling emergence (October) when they move off senesciug winter hosts nearby (Wilson & Morton, 1993; Wilson, 1995). Damaging outbreaks of *T. urticae* occurring later in the season (January/February) were shown to be positively correlated with this initial level of colonization and with the subsequent abundance of *T. urticae* populations prior to flowering (November and December). Identifying the factors which influence establishment and development of these early season populations is thus a high priority for the development of effective integrated pest management programmes in cotton.

Predation has been implicated as a key factor affecting the development of spider mite populations in many agricultural or horticultural systems and disruption of beneficial populations by insecticides has repeatedly been cited as a cause of outbreaks (Bartlett, 1968; McMurtry *et al.*, 1970; Readshaw, 1975; Leigh, 1985; Trichilo & Wilson, 1993; Gurr

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et al., 1996). Predation could have a significant influence on the development of early season *T. urticae* populations on Australian cotton but local evidence to support this is limited. Wilson *et al.* (1996) found that application of the organophosphate insecticide dimethoate to cotton early in the growing season resulted in severe outbreaks of *T. urticae* compared with unsprayed cotton. Suppression of predators, especially the facultatively predacious flower thrips, *Thrips tabaci* Lindeman and *Frankliniella schultzei* (Trybom) (Thysanoptera: Thripidae), by the insecticide was proposed as the cause of these outbreaks.

This study had two objectives: (i) to identify predators of *T. urticae* in Australian cottou; and (ii) to investigate the role of predators on *T. urticae* population dynamics and the interaction with insecticides. The predators of tetranychid mites have been reviewed by McMurtry *et al.* (1970), Chazeau (1985) and Sabelis (1985). While the predatory fauna of Australian cotton fields is well documented (Bishop & Blood, 1977; Room, 1979a,b), little is known about which predators feed on *T. urticae*.

The role of predators in the early season dynamics of spider mite populations and on the subsequent timing and severity of outbreaks was investigated in the field using the 'insecticidal check' technique (Dent, 1991; Kidd & Jervis, 1996). A range of insecticides is used to control early season pests such as thrips (*T. tabaci* and *F. schultzei*), mirids (*Creontiades dilutus* Stål and *Campylomma liebknechti* (Girault) (Hemiptera: Miridae) and *Helicoverpa* spp. (Lepidoptera: Noctuidae) on cotton. These include dimethoate, methomyl, amitraz, endosulfan, and thiodicarb. Use of these insecticides could suppress predator abundance. If predators effectively regulate incipient mite infestations then insecticide disruption should result in earlier outbreaks of spider mites. Clarifying the role of predation and also the relative impact of each early season insecticide on beneficial insects, is essential for developing integrated pest management systems.

Materials and methods

All experiments were conducted at the Australian Cotton Research Institute (ACRI) (30° 13'S, 149° 47'E), 25 km west of Narrabri in New South Wales.

Predators of T. urticae

Insects and mites, seen in association with colonies of *T. urticae* or seen consuming eggs or motile stages of *T. urticae* were collected from unsprayed cotton plots. Potential to consume motile stages or eggs of *T. urticae* was evaluated by placing potential predators on cotton leaf discs in perspex cells (1 cm diameter×6 mm high) as described in Wilson *et al.* (1996). Each cell contained either six spider mite eggs laid directly in the cell by a female *T. urticae*, or six motile *T. urticae* (protonymph or deutonymph). Twelve rearing cells were used for each species (or stage of that species) tested. A single specimeu of the test species was placed in each of six cells, while the other six served as controls for survival of spider mite eggs or immatures. The cells were held in a constant temperature room at 29 ± 1°C, 14:10 L:D and the number of *T. urticae* eggs or immatures still surviving after 24 h was recorded. Insects were initially identified using the illustrations of Room (1979a). Specimens were sent later to specialists (Taxonomy Section, New South Wales Agriculture, Rydalmere, Sydney) for confirmation of identification.

Effect of insecticides on spider mites and predators

Three experiments were carried out from 1993/94 to 1995/96 in otherwise unsprayed cotton fields of cultivar Deltapine 90. Experiments 1 and 2 were planted in early October (1993/94, 1994/95), while experiment 3 was planted on November 1, 1995. The planting seed used was treated with fungicides, but not insecticides. Four treatments were common to all experiments; an untreated control, or treatment with either dimethoate (Rogor, 140 g ai/ha), thiodicarb (Larvin, 750 g ai/ha) or endosulfan (Thiodan, 735 g ai/ha). In experiment 2, (1994/95) lower registered rates of thiodicarb (187.5 g ai/ha, referred to as thiodicarb/4) and endosulfan (367.5 g ai/ha, referred to as endosulfan/2) were included. In experiment 3, methomyl (Lannate 169 g ai/ha) and amitraz (Ovasyn, 400 g ai/ha) were included as they are used widely as early season ovicides for control of *Helicoverpa* spp.

A randomized block design with four replicates was used for all experiments. Plots were 24 rows (1 m spacing) by 20 m. The middle six rows of each plot were artificially infested shortly after planting (24, 27 and 34 days after planting for experiments 1, 2 and 3 respectively) with *T. urticae* which had been mass reared on cotton seedlings in a glasshouse. Infested cotton seedlings were placed onto cotton plants in the field at the rate of five to ten per metre. The central eight rows of the treated plots were sprayed with insecticide five times at seven to ten day intervals (depending on weather), beginning within a week of the infestation. We used five consecutive applications because the often low abundance of beneficial insects relative to pests means that statistically significant results may not be obtained by using single applications. Such repeated usage of a single product is unusual in commercial cotton, though it does occur with endosulfan, however the interval used between applications is typical. The 16 unsprayed rows in each plot helped to minimize insecticide drift between plots. All insecticide formulations were water miscible. They were applied using three hollow cone nozzles (TX6 Spraying Systems Co., Wheaton, Illinois, USA) per row at 300 kpa and 5 km/h giving a total spray volume of 142 l/ha.

Sampling to assess *T. urticae* and predator abundance was conducted 24 h before the first insecticide application and at least once and sometimes twice between consecutive applications. Sampling continued at approximately weekly intervals after the final insecticide had been applied until the experiment was terminated when *T. urticae* showed an increase over three or four successive checks in untreated plots (experiments 1 and 3) or until hail damaged the crop (experiment 2). Samples were collected on 13, nine or 12 dates in experiments 1 to 3 respectively. Sampling to assess abundance of spider mites or thrips involved either ten whole plants per plot, or 25 leaves per plot (from the third or fourth mainstem node below the plant terminal) (Wilson *et al.*, 1996). The samples were processed using a 'mite wash' machine (Leigh *et al.*, 1984). The change from sampling whole plants to leaves occurred at about 12 nodes as plants grew too large to fit into the mite wash machine. Numbers of adult and immature *T. urticae* and adult and immature

thrips (*T. imaginis* (Thysanoptera: Thripidae), *T. tabaci*, or *F. schultzei*) extracted from each sample were counted using a binocular microscope.

Predator abundance was assessed using suction samplers (De Barro, 1991), in conjunction with the sampling above. On each sample date a complete row was sampled in each plot. To avoid predator depletion in any particular row, sampling was alternated between the spider mite infested rows in each plot. When plants were small, a single pass of the suction sampler along the row, at a speed of about 0.5 m/s, was used. As plants grew taller, a zigzag sampling technique, where the suction device was passed along the lower, middle and top strata of the canopy, was adopted to ensure adequate coverage of the canopy. Insects collected were killed using chloroform and the abundance of spider mite predators (species listed in table 1) was scored.

Statistical analysis

Statistical analyses were run using SuperANOVA (Gagnon *et al.*, 1989). All insect or *T. urticae* counts were transformed (ln + 1) prior to analysis as required to stabilize the mean/variance relationship. The experiments were divided into two periods; before *T. urticae* populations began to increase termed 'early-season' and after populations began to increase consistently in at least one treatment, termed 'mid-season'. This separation allowed analysis of the effects of insecticides on the abundance of beneficial insects before and after *T. urticae* populations increased and overcame potential problems with analysis due to auto-correlation caused by repeated sampling of the same plots over time.

Differences between treatments in each experiment in final abundance of *T. urticae* and mean abundance of *T. urticae* during the early-season and mid-season periods were

Table 1. List of species tested as predators of *Tetranychus urticae* in the laboratory and the amount of predation observed (%).

Predator			% Prey eaten	
Species	Common name	Stage	Mite stage offered	
			motiles	eggs
Acarina: Phytoseiidae				
Amblyseius niasiaka Blommers & Chazeau	Predacious mite	Adult	100 +	100 +
Araneida: Theridiidae				
Achaearanea veruculata (Urquhart)[a]	Tangle web spider	Adult	93.3 ± 4.2 +	0
Coleoptera: Coccinellidae				
Coccinella transversalis (Fabricius)[a]	Transverse ladybird	Adult	30.5 ± 12.5	11.1 ± 8.2
		Larva	100	100
Coelophora inaequalis (Fabricius)	Variable ladybird	Adult	100	100
Adalia bipunctata (Linnaeus)[a]	Two-spotted ladybird	Adult	100 +	100 +
		Larva	100 +	100 +
Harmonia testudinaria (Fabricius)	Three banded ladybird	Adult	100	100
		Larva	100	100
Stethorus sp.	Mite-eating ladybird	Adult	100 +	100 +
		Larva	100 +	100 +
Harmonia conformis (Boisduval)[b]	Common spotted ladybird	Adult	66	–
Hemiptera: Anthocoridae				
Orius sp.	Plower bug	Adult	100 +	100 +
		Nymph	100 +	100 +
Hemiptera: Lygaeidae				
Geocoris sp. Kirkaldy	Big-eyed bug	Adult	100 +	100 +
		Nymph	100 +	100 +
Hemiptera: Miridae				
Campylomma liebknechti (Girault)[a]	Apple dimpling bug	Adult	100 +	100 +
		Nymph	100 +	100 +
Deraeocoris signatus (Distant)[a]	Brown smudge bug	Adult	100 +	100 +
		Nymph	100 +	100 +
Hemiptera: Nabidae				
Nabis sp.	Damsel bug	Nymph	100 +	100 +
Neuroptera: Hemerobiidae				
Micromus tasmaniae Walker[ab]	Brown lacewing	Larva	100 +	–
Thysanoptera: Thripidae				
Scolothrips sexmaculatus (Pergande)	Six-spotted thrips	Adult	100 +	100 +
		Larva	100 +	100 +

'+' indicates predation on mites was observed in the field.
Values are means ± SE where appropriate.
[a]These species identified as predators of *Helicoverpa* spp. on cotton in Australia (Room, 1979a,b).
[b]Only one individual tested.

tested using analysis of variance (ANOVA). Means were separated from the control using Fisher's Protected Least Significant Difference (LSD). Mean mid-season abundance of *T. urticae* was regressed against mean early-season abundance for data from all experiments combined.

Regressing ln (*T. urticae* + 1) against thermal time (accumulated day degrees above 12°C, DD12) from the time when *T. urticae* populations began to increase until the end of the experiment provided the rate of increase of *T. urticae* popnlations (slope) and population lag-period (intercept) (Wilson, 1993) for each treatment in each experiment. The population lag period is the interval (DD12) between the date of artificial infestation of the crop with *T. urticae* and the time at which they began to increase. The effect of insecticide treatments on these parameters was analysed as above, with the exception of experiment 2 where, due to the effects of hail, these parameters could only be calculated for the thiodicarb treatment.

Predators of *T. urticae* were grouped into several groups as the abundance of most species was too low for individual analysis. These groups were:

1. Thrips; adnlts and larvae of the facultatively predacious *F. schultzei*, *T. tabaci* and *T. imaginis* Bagnall (Thysanoptera: Thripidae) (Wilson *et al.*, 1996).
2. Coccinellids, five species (see table 1).
3. *Campylomma liebknechti*, omnivorous adults and larvae (Chinajariyawong *et al.*, 1988).
4. Other Hemiptera, consisting of adults and nymphs of four additional species (see table 1).
5. *Achaearanea veruculata* (Urquhart) (Araneae: Theridiidae), a spider commonly seen in association with *T. urticae*.

Other potential predators of *T. urticae* such as lacewings (*Micromus tasmaniae* Walker) (Neuroptera: Hemerobiidae), predatory mites (*Amblyseius masiaka* Blommers & Chazeau) (Acari: Phytoseiidae) and six-spotted thrips (*Scolothrips sexmaculatus* (Pergande) (Thysanoptera: Thripidae) were too few to analyse. The mean abundance of each of the predator groups was analysed as above for the early and mid-season phases for each experiment.

Regression analysis was used to test if there was a relationship between the mean early-season abundance of each beneficial insect group and the mean mid-season abundance of *T. urticae*. This was done for each experiment separately as the mid-season abundance of *T. urticae* depended partially on when the experiment was terminated.

A second analysis was done to test how much of the variability in the population lag-period of *T. urticae* across all experiments could be explained by variations in the abundance of predators between years and treatments. In this case, the dependent variable (population lag-period) was not affected by the termination date of the experiment. If predation was important in determining the length of the population lag-period then a consistent relationship across years (experiments) could be expected. The mean early-season abundance of each predator group (ln + 1 transformed) was added to a multiple regression against the population lag-period, using a stepwise procedure.

Endosulfan, endosulfan/2 and amitraz were excluded from these analyses as they are acaricidal (British Crop Protection Council & the Royal Society of Chemistry, 1994), however, dimethoate, also an acaricide, was included in the analysis because *T. urticae* in Australia are highly resistant to it (>1000 fold; Herron *et al.*, 1998).

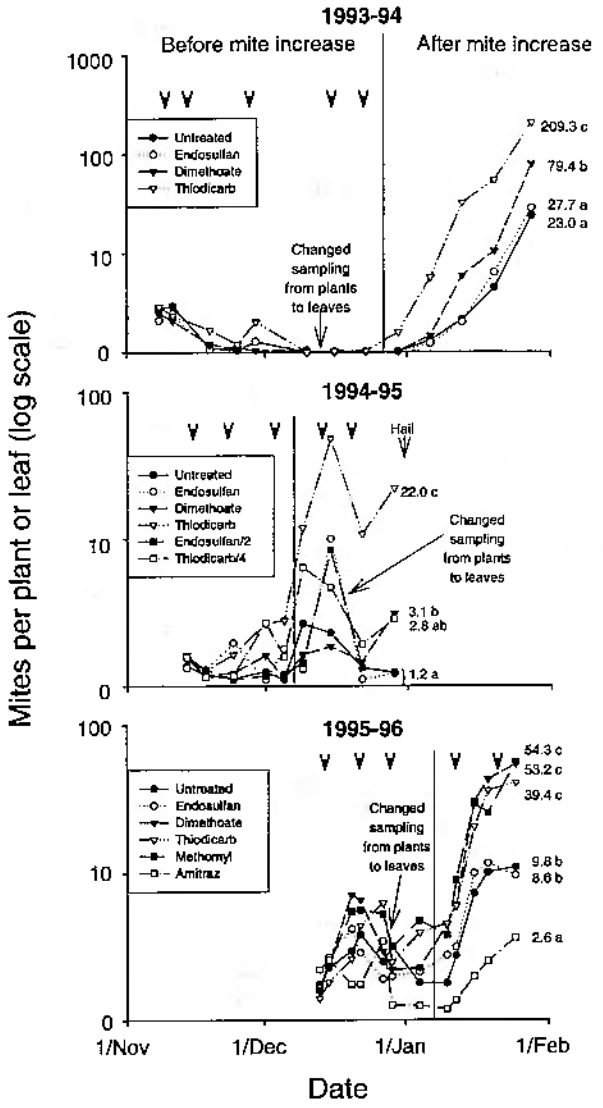

Fig. 1. Mean abundance of *Tetranychus urticae* in each treatment in experiments 1 to 3, 1993–94, 1994–95, 1995–96 respectively. For each experiment, final values followed by different letters are significantly different using ANOVA LSD at $P = 0.05$. Arrows indicate dates of insecticide application.

Results

Predators of T. urticae

Table 1 shows the putative predators investigated and the proportion and stage of *T. urticae* eaten. There was no mortality in control cells. All of the candidates tested consumed eggs and most also ate motile stages of *T. urticae*.

Effect of insecticides on T. urticae *and its predators*

There were highly significant differences in final abundance of *T. urticae* between treatments in all three

experiments (experiment 1, $F=64.2$; df=3, 15; $P=0.0001$, experiment 2, $F=14.2$; df=5, 15; $P=0.0001$, experiment 3; $F=18.2$; df=5, 23; $P=0.0001$) (fig. 1). Cotton treated with thiodicarb, dimethoate or methomyl developed significantly higher numbers of *T. urticae* than the control treatment (fig. 1). Cotton treated with endosulfan, endosulfan/2 or thiodicarb/4 (fig. 1) had final levels of *T. urticae* which were no different from the untreated controls. Cotton treated with amitraz had significantly lower final spider mite abundance than the control treatment (fig. 1).

There were no significant differences between treatments in early-season abundance of *T. urticae* (table 2). However, mean mid-season and mean-early season abundance of *T. urticae* were positively correlated ($F=26.69$; df=1, 60; $P=0.0001$, $R^2=0.51$) indicating that those treatments with higher mid-season abundance of *T. urticae* (table 2) also had numerically higher abundance in the early season, i.e. thiodicarb in experiments 1, 2 and 3 and methomyl and dimethoate in experiment 3.

Tetranychus urticae populations increased significantly earlier in cotton treated with thiodicarb (20–50%), dimethoate (7–42%) or methomyl (62%) than in the control treatments (table 2). In cotton treated with endosulfan, *T. urticae* increased later than the control in experiment 1 but earlier in experiment 3. Populations in cotton treated with amitraz increased at the same time, but more slowly than those in the controls (table 2 and fig. 1). Other insecticide treatments had no significant effect on the rate of increase of *T. urticae* poplations.

The coccinellid and hemipteran groups consisted mostly of generalist predators, with specific spider mite predators such as *Stethorus* sp. (Coleoptera: Coccinellidae) less common (table 3). All insecticide treatments except amitraz caused some significant reductions in the early season abundance of thrips including, but to a lesser extent, endosulfan/2 and thiodicarb/4 (fig. 2). All insecticide treatments except endosulfan/2 also caused some reductions in the abundance of coccinellids, while all insecticides except amitraz caused some reductions in the abundance of *C. liebknechti*. Hemipteran predators were relatively low in abundance so only dimethoate, endosulfan and methomyl caused significant reductions in their abundance (fig. 2). The abundance of the theridiid spider, *A. veruculata*, was significantly reduced in at least one experiment by all insecticides with the exception of amitraz, thiodicarb/4 and endosulfan/2.

There were no significant differences in the mid-season abundance of any predator group for experiment 1 (fig. 3). In experiment 2, mid-season abundance was significantly lower in all insecticide treated plots for thrips (fig. 3), and in endosulfan and endosulfan/2 treated plots for *C. liebknechti*. In contrast, predatory Hemiptera were significantly more abundant in thiodicarb treated cotton than in other treatments. In experiment 3, the abundance of thrips and *C. liebknechti* was significantly lower in all insecticide treatments than in controls, with the exception of amitraz (fig. 3).

Early season abundance of predators and outbreaks of T. urticae

The early-season abundance of several groups of predators showed significant negative relationships with the mid-season abundance of *T. urticae* (table 4) – the mid-season abundance of *T. urticae* was higher in cotton with fewer of these predators. Stepwise multiple regression of population lag-period against the abundance of each predator group

Table 2. Population lag-period and rate of increase of *Tetranychus urticae* populations in each treatment and mean numbers of *T. urticae* per plant or leaf before and after populations began to increase in experiments 1 to 3, 1993–94, 1994–95, 1995–96 respectively.

Treatment	Population lag-period (DD12 from planting)	Rate of increase ($DD12^{-1}$)	Mean no. of *T. urticae* per plant early-season	Mean no. of *T. urticae* per leaf mid-season
		Experiment 1 (1993–94)		
Untreated	742.3 ± 8.6 a	0.008 ± 0.001	0.34 ± 0.11	5.6 ± 1.9 a
Endosulfan	782.9 ± 11.5 b	0.009 ± 0.001	0.28 ± 0.04	6.9 ± 2.0 a
Dimethoate	691.1 ± 14.7 c	0.009 ± 0.0002	0.21 ± 0.05	18.8 ± 3.0 b
Thiodicarb	592.9 ± 4.6 d	0.011 ± 0.0002	0.47 ± 0.12	59.8 ± 6.0 c
		Experiment 2 (1994–95)		
Untreated	–	–	0.17 ± 0.005	0.9 ± 0.3 a
Endosulfan	–	–	0.53 ± 0.20	2.4 ± 1.9 a
Dimethoate	–	–	0.28 ± 0.14	1.0 ± 0.3 a
Thiodicarb	–	–	1.07 ± 0.55	22.1 ± 8.6 b
Endosulfan/2	–	–	0.19 ± 0.05	2.1 ± 1.5 a
Thiodicarb/4	–	–	0.64 ± 0.14	2.9 ± 1.2 a
		Experiment 3 (1995–96)		
Untreated	304.1 ± 7.7 a	0.013 ± 0.002 a	1.74 ± 0.64	5.5 ± 1.0 b
Endosulfan	253.8 ± 12.4 b	0.012 ± 0.002 a	1.61 ± 0.37	6.4 ± 1.9 b
Dimethoate	176.7 ± 16.5 c	0.010 ± 0.001 a	2.90 ± 1.21	26.5 ± 11.0 c
Thiodicarb	144.4 ± 23.0 c	0.009 ± 0.001 ab	2.56 ± 0.56	20.4 ± 5.2 c
Methomyl	131.3 ± 7.4 c	0.009 ± 0.001 ab	3.43 ± 0.51	23.6 ± 4.1 c
Amitraz	302.6 ± 23.3 a	0.005 ± 0.001 b	1.00 ± 0.17	1.1 ± 0.2 a

Values for treatments are mean ± SEM based on $n=4$ for each treatment. For each experiment means in each column followed by the same letter are not significantly different at $P=0.05$ using ANOVA (Gagnon *et al.*, 1989). Population lag-period and rate of increase could not be estimated for experiment 2 because hail interrupted the experiment, see text. DD12 is the accumulated day degrees above 12°C.

Table 3. Percentage of each predator species in the coccinellid and hemipteran predator groups for the control treatment in experiments 1–3, 1993–94, 1994–95, 1995–96 respectively.

Species	Experiment 1 1993–94		Experiment 2 1994–95		Experiment 3 1995–96	
	early-season	mid-season	early-season	mid-season	early-season	mid-season
			Hemiptera			
Geocoris sp.	7.2	9.1	83.3	80.0	90.9	0
Orius sp.	0	0	0	10.0	0	0
Nabis sp.	87.0	90.9	16.7	10.0	9.1	100.0
Deraeocoris signatus	5.8	0	0	0	0	0
			Coccinellids			
Coccinellidae (large)[a]	21.4	50.0	79.4	82.0	61.4	80.1
Stethorus sp.	1.3	50.0	20.0	0	6.4	0
Adalia bipunctata	77.3	0	0	18.0	32.2	19.9

[a]The larger Coccinellidae consisted of the following species; *Coccinella transversalis, Coelophora inaequalis, Harmonia testudinaria* and *H. conformis*.

showed highly significant effects of coccinellids ($F = 141.5$; df = 1, 28; $P = 0.0001$), thrips ($F = 53.9$; df = 1, 28; $P = 0.0001$) and *C. liebknechti* ($F = 6.59$; df = 1, 28; $P = 0.016$) with an overall coefficient of determination (r^2) of 0.88. The slopes for all predictors were positive (slope ± SE, coccinellids, 214.2 ± 0.45; thrips, 185 ± 0.01; *C. liebknechti*, 503.0 ± 0.016) indicating that populations of *T. urticae* increase earlier in cotton with fewer of these predators early-season.

Discussion

This study reveals, for the first time, the pivotal role of predators in the population dynamics of a key pest in Australian cotton. Furthermore, the selection of insecticides used early in the season to control other pests was found to have a significant effect on the survival of predator populations and hence, on the development of outbreaks of *T. urticae*.

Predators of T. urticae

All of the insect predators observed in association with colonies of *T. urticae* in the field were shown to eat eggs and/or nymphs of *T. urticae*. Most of these species, or related species elsewhere, have also been recorded previously as predators of spider mites (McMurtry *et al.*, 1970; Chazeau, 1985). The most abundant predators of *T. urticae* in the field were either generalists (i.e. coccinellids and Hemiptera) or omnivorous (i.e. thrips or *C. liebknechti*). Wilson *et al.* (1991) similarly found that the major predators of spider mites in Californian cotton systems were generalist predators such as omnivorous thrips and generalist predatory Hemiptera. Several predators regarded as specialists on spider mites were found, including *A. masiaka, Stethorus* sp., and *Scolothrips sexmaculatus* (McMurtry *et al.*, 1970 and references cited within), however, these were scarce during the early season in cotton crops. The low numbers of specialist spider mite predators may, at least in part, be explained by the low abundance of prey (*T. urticae*) in early-season cotton crops.

Effects of insecticides on predators

All insecticides caused significant reductions in at least two groups of predators with the exception of amitraz which only affected the Coccinellidae. Methomyl caused significant reductions in all beneficial groups, while thiodicarb (full rate), dimethoate and endosulfan caused a significant reduction in at least four of the five predator groups in at least one experiment. The lower rates of both endosulfan and thiodicarb still had a significant effect on several predator groups when compared with the unsprayed control, but were less detrimental to predators than the full rates. The magnitude of effects of insecticides on predators is probably underestimated in these experiments due to re-invasion of the treated portions of each plot (eight rows) by predators from the untreated portions (16 rows). Application of insecticides to larger areas (i.e. commercial cotton crops are often >100 ha) would be expected to have a more severe effect on beneficial populations which would take longer to recolonize the field (cf. Duffield & Aebischer, 1994).

Negative effects of the insecticides tested on beneficial species, especially coccinellids, have been reported previously (i.e. endosulfan, Botha *et al.*, 1986; Mizell & Schiffhauer, 1990; Van Den Berg *et al.*; 1990; dimethoate, Dinkins *et al.*, 1971; Scott *et al.*, 1986; Mizell & Schiffhaner, 1990; Duffield & Aebischer, 1994; methomyl, Hoy *et al.*, 1979; Broadley, 1983; Katayama *et al.*, 1987; Mizell & Schiffhauer, 1990; thiodicarb, Osman *et al.*, 1985; Bellows & Morse, 1993). Endosulfan is a contact poison, while dimethoate and methomyl have systemic action as well as contact activity. Thiodicarb, in contrast, needs to be ingested to be effective (Sousa *et al.*, 1977). It is possible that predators could ingest thiodicarb during self cleaning (cf. Roger *et al.*, 1994). The results with amitraz are consistent with reports of low toxicity to predatory bugs (Solomon *et al.*, 1989; Wynholds & Godfrey, 1995) but contradictory to Bellows & Morse (1993) who found low toxicity to coccinellids.

Relationship between predator abundance and mite abundance

Outbreaks of *T. urticae* developed earlier and reached higher peak densities in cotton which was treated with either

thiodicarb, dimethoate or methomyl and which consequently harboured lower densities of predators. In commercial cotton crops earlier, more severe outbreaks of *T. urticae* cause greater yield reductions than less severe infestations occurring later in the season (Wilson, 1993). Significant negative relationships were found between early-season abundance of one or more predator groups and mid-season abundance of *T. urticae* in all three experiments. Furthermore, a highly significant positive relationship was found between three predator groups and the population lag-period for *T. urticae* across all experiments. These relationships strongly implicate a key role of predators in delaying spider mite outbreaks. Furthermore, insecticides may also have sublethal effects on natural enemies not accounted for in this study, such as reduced foraging efficiency (Waage, 1989), which could mean that the significance of relationships between early season predator abundance and mid season abundance or population lag-period for *T. urticae* are underestimated.

Spider mites are highly 'r' selected (Sabelis, 1985; Brandenburg & Kennedy, 1987) and populations typically show exponential growth unless checked by some factor such as an acaricide or predation. Small declines in spider mite abundance while the population is low (in the 'flat' part of the exponeutial curve called the lag-phase) can substantially delay the timing of population growth (see Trichilo & Wilson, 1993). In our study, no significant differences in early-season abundance of *T. urticae* were found between treatments, although the low numbers may have prevented detection of such differences. Nevertheless, the abundance of *T. urticae* in the mid-season was positively correlated with that in the early-season, indicating that higher early-season abundance, due to lack of predation, may lead to earlier outbreaks.

In our study, predator populations varied in abundance between years. If predation has an important influence on population development of *T. urticae* then such between-year differences in predator abundance should also be reflected in between-year differences in the population lag-period, i.e. the population lag period should be longer in years with higher abundance of predators. Such patterns are indeed supported by the results – the population lag period for untreated cotton was significantly longer in experiment 1 where predator populations were higher than in experiment

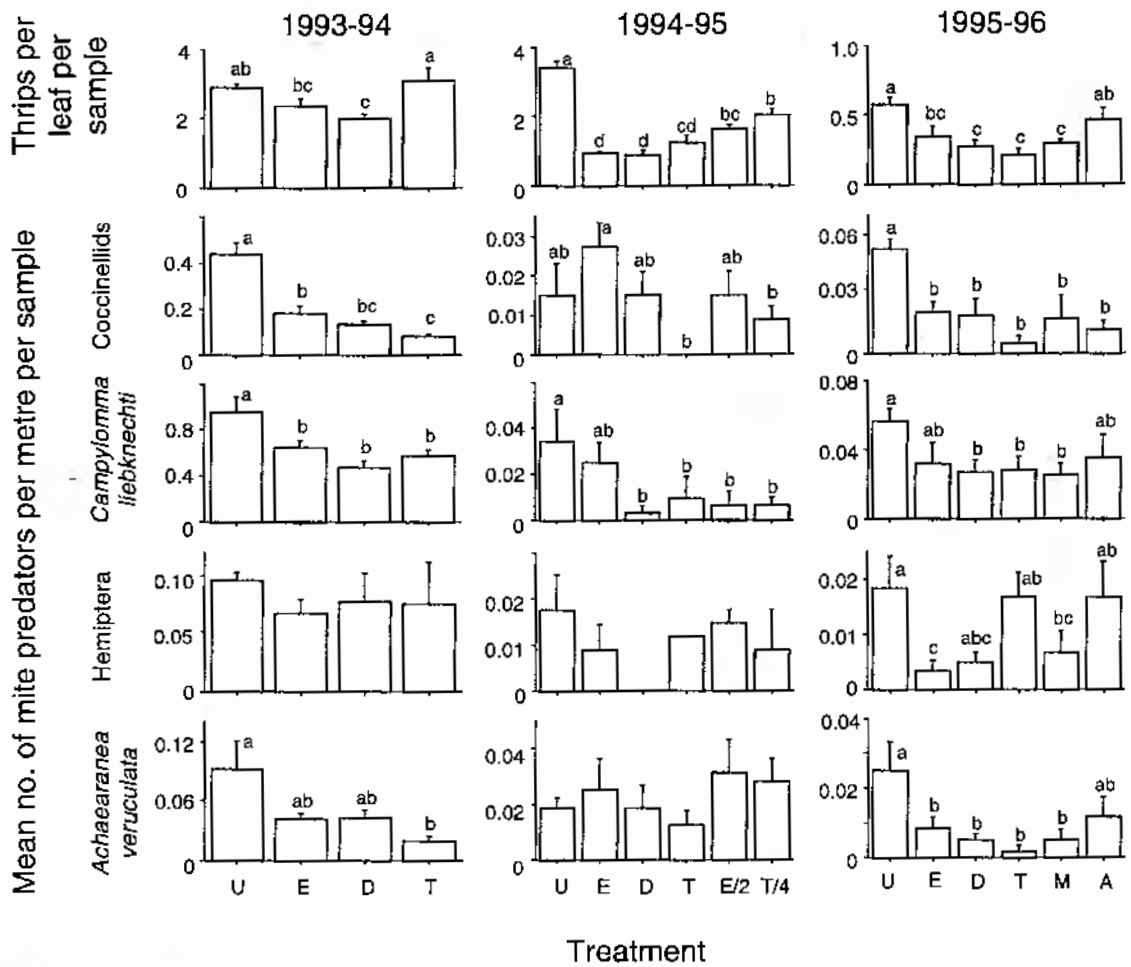

Fig. 2. Mean early-season abundance of predators in each treatment in experiments 1 to 3, 1993–94, 1994–95, 1995–96 respectively. Treatments: U, untreated; E, endosulfan; D, dimethoate; T, thiodicarb; E/2, half rate endosulfan; L/4, quarter rate thiodicarb; M, methomyl; A, amitraz, see text for rates. Data are means ± SEM. For each predator group within an experiment, bars with different letters are significantly different using ANOVA LSD at $P = 0.05$.

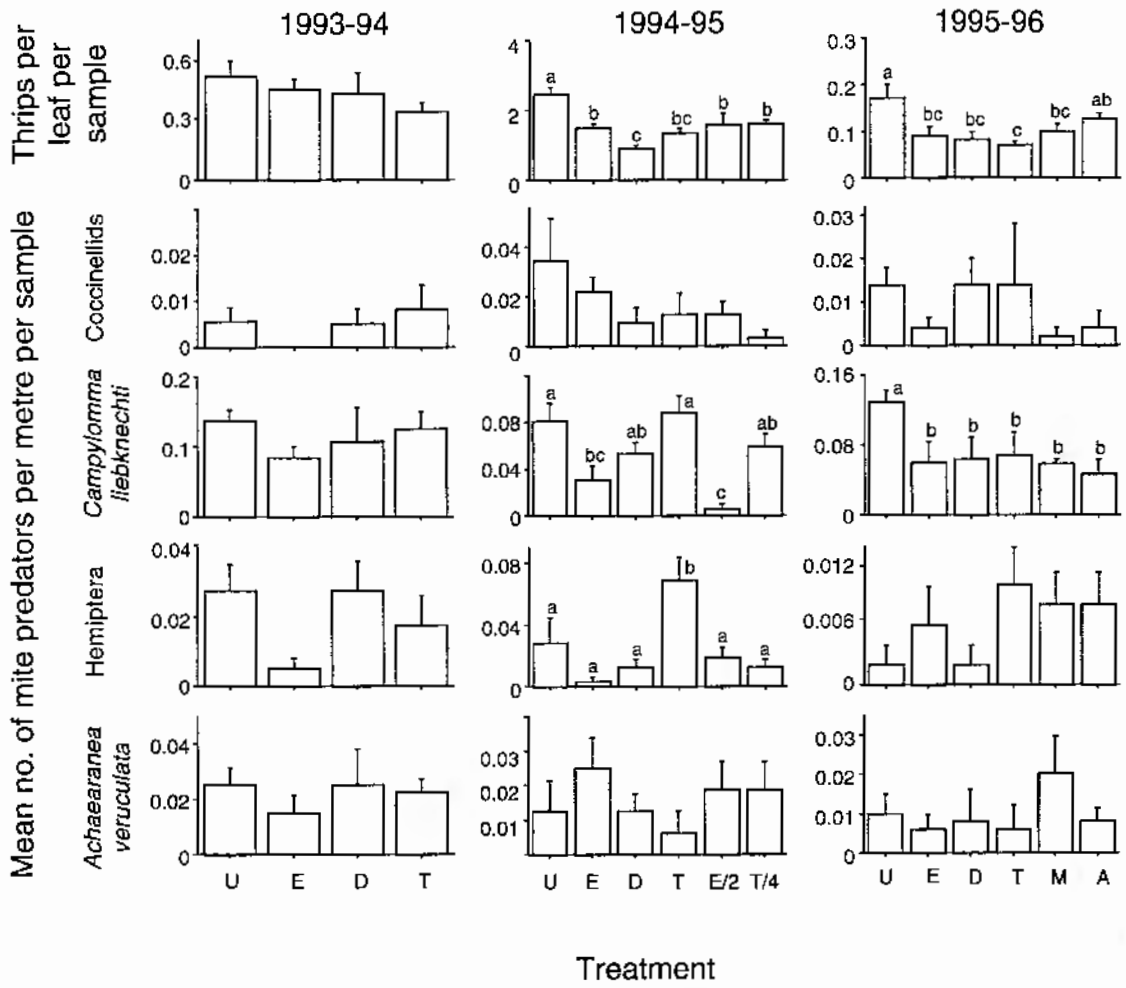

Fig. 3. Mean mid-season abundance of predators in each treatment in experiment 1 to 3, 1993–94, 1994–95, 1995–96 respectively. Treatments: U, untreated; E, endosulfan; D, dimethoate; T, thiodicarb; E/2, half rate endosulfan; L/4, quarter rate thiodicarb; M, methomyl; A, amitraz, see text for rates. Data are means ± SEM. For each predator group within an experiment, bars with different letters are significantly different using ANOVA LSD at $P = 0.05$.

3 where they were lower (fig. 4). A similar pattern occurs between years for thiodicarb treated cotton and comparisons between the untreated and thiodicarb treated plots further support this pattern (fig. 4). In our study therefore, between-year differences in the abundance of predators were reflected in between-year differences in the population

Table 4. Slopes (b) and coefficients of determination (r^2) for *Tetranychus urticae* mid-season abundance regressed on early season predator abundance.

	Experiment 1 1993–94		Experiment 2 1994–95		Experiment 3 1995–96	
	b[a]	r^2	b	r^2	b	r^2
Coccinellids	−6.7***[b]	0.70	−51.9*	0.27	−12.4	0.15
Achaearanea veruculata (Urquhart)	−18.5**	0.51	−3.7	0.01	−35.6*	0.38
Hemiptera	23.2	0.03	14.2	0.02	−25.6	0.08
Campylomma liebknechti (Girault)	−3.1	0.19	−17.7	0.09	−20.2*	0.24
Thrips	1.0	0.03	1.2	0.14	−4.1***	0.45

[a]Slopes were derived from the regression of ln (early season predators per m + 1) against ln (mid-late season *T. urticae* per leaf + 1). Treatments including either endosulfan or amitraz were excluded from the analysis.

[b]Significance of regression equation indicated as *, **, ***; $P < 0.05$, 0.001, 0.001 respectively, using ANOVA (Gagnon *et al.*, 1989).

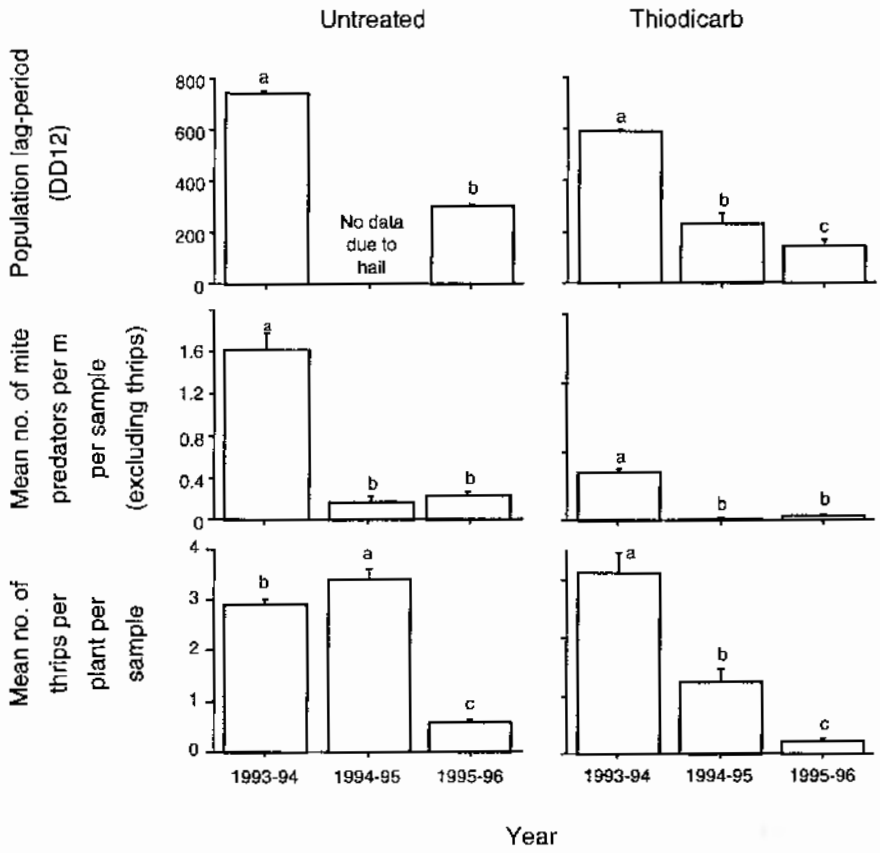

Fig. 4. Mean population lag-period (time from initial infestation to population increase) of *Tetranychus urticae* and mean abundance of predators, excluding thrips, and mean abundance of thrips for untreated control and thiodicarb treated cotton for experiments 1 to 3, 1993–94, 1994–95, 1995–96 respectively. Thrips and other predators are presented separately due to differences in sampling unit. Bars within each graph followed by different letters are significantly different using ANOVA LSD at $P = 0.05$. DD12 is the accumulated day degrees above 12°C.

lag-period for *T. urticae*, providing further evidence of the role of predation in influencing the timing of *T. urticae* population development.

Implications for integrated pest management in cotton

The selection of insecticides by cotton growers for control of early-season pests such as thrips. *Helicoverpa* spp. or mirids can dramatically affect the abundance of predators of *T. urticae* and other pests such as aphids and *Helicaverpa* spp. Application of pesticides, such as thiodicarb, methomyl and dimethoate, that have little acaricidal activity but which significantly reduce the abundance of predators, can lead to earlier more severe outbreaks of *T. urticae*. Application of pesticides with acaricidal activity, such as endosulfan or amitraz, may help to reduce or delay outbreaks of *T. urticae*, but will still significantly affect some predator groups which may have an impact on the abundance of other pest species.

The predator, *C. liebknechti*, is also regarded as an early season pest of cotton (Chinajariyawong *et al.*, 1988; Forrester & Wilson, 1988). Four other predators; three 'phytophagous' thrips (Wilson *et al.*, 1996) and a mirid (Miles *et al.*, 1992) are also pest species. This causes a pest management dilemma; when does the value of these species as predators outweigh their damage as pests (Wilson *et al.*, 1994, Sadras & Wilson, 1998). Incorporation of these species as predators into integrated pest management recommendations is not possible until their predatory behaviour and pest status are better understood. Nevertheless, when these insects are present at sub-economic levels, their beneficial activity will add to that of other predatory species.

The results reported here show that maintenance of predator populations through the early growth of the cotton crop is crucial in delaying outbreaks of *T. urticae*. Conservation of predator populations within cotton crops can be assisted by reducing the frequency of application of broad-spectrum insecticides through the use of economic thresholds for pests such as thrips, *Helicoverpa* and mirids (Shaw, 1996) and by selecting, when necessary, those control options that cause the least disruption to predator populations. The latter includes: (i) use of selective insecticides such as *Bacillus thuringiensis* var. *kurstaki*; (ii) use of reduced rates of insecticides, where appropriate, such as endosulfan/2 or thiodicarb/4, which are less detrimental to predator populations than full rates; and (iii) use of transgenic cotton (Ingard® cotton) containing the gene to produce Cry IAc protein derived from *B. thuringiensis* var. *kurstaki*, which is efficacious against lepidopteran pests, to reduce insecticide use and allow survival of predators (Fitt, 1997).

Our studies also show that seasonal variations in the early-season abundance of natural predator populations can affect the timing of *T. urticae* outbreaks, which may occur earlier in cotton seasons where the early abundance of predators is low. Use of lucerne interplantings in cotton to serve as a refuge for predators may help to reduce the significance of such seasonal variations in predator abundance by augmenting natural populations (Mensah & Harris, 1996; Mensah, 1998). This approach can be combined with use of food attractant sprays which attract predators from lucerne into cotton to increase the impact of predators on pests, especially *Helicoverpa* spp. and *T. urticae*, thereby also reducing reliance on synthetic insecticides early in the season (Mensah, 1997; Mensah & Khan, 1997). Lucerne also acts as a trap crop for mirids, reducing populations in adjacent cotton and reducing the frequency with which they exceed threshold and require control with broad-spectrum insecticides (Mensah & Khan, 1997).

However, often the only effective and reliable means available to control high populations of mirids or *Helicoverpa* spp. are broad-spectrum insecticides which are detrimental to predators (i.e. endosulfan, thiodicarb, methomyl, pyrethroids) (Forrester *et al.*, 1993; Simpson *et al.*, 1996). This is particularly relevant for *H. armigera* (Hübner) (Lepidoptera: Noctuidae), which has become increasingly resistant to pyrethroids, endosulfan and carbamates and for which organophosphates (such as profenofos) or insecticide mixtures are often required to achieve control in the field. Furthermore, the implementation of transgenic cotton in the field has required the development of strategies to delay the development of resistance in *Helicoverpa* spp. to the Cry IAc protein, such as restricting the area of transgenic cotton sown and growth of refuge crops to produce moths naive to the protein, of which sprayed conventional cotton is one option (Forrester & Bird, 1996). In such refuge crops and in conventional commercial cotton crops therefore, there remains an urgent need for more selective insecticides to allow control of primary pests without disruption of predator populations, thereby reducing the incidence of outbreaks of secondary pests such as *T. urticae* (Wilson, 1996).

Acknowledgements

We thank Lisa Bird (New South Wales Agriculture), James Farris (Commonwealth Scientific and Industrial Research Organization), Mark Laird (CSIRO), Trudy Staines (CSIRO) and Lyn Gett (CSIRO) for technical assistance with aspects of this study, the late Tom Leigh (University of California) for encouraging this work, Eberhard Schicha (NSW Agriculture) for taxonomic assistance, Andy Sheppard, Gary Fitt (CSIRO) and Robert Mensah (NSW Agriculture) for critical review of the manuscript and the Cotton Research and Development Corporation for funding (grant number CSP46C).

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(Accepted 4 April 1998)