

anism which obviated efforts to combat DDT resistance with resistance proof analogues and synergists (Metcalf, 1989). However, we should not be overly dismayed by this experience with *A. aegypti*. As mentioned previously in Section 8, blood feeding public health and livestock pests are probably predisposed to developing nerve insensitivity type pyrethroid resistance mechanisms while many phytophagous agricultural pests have predominantly oxidative metabolic resistance mechanisms. Furthermore, implementation of carefully designed IRM strategies may be able to select preferentially for the more amenable oxidative metabolic resistance mechanism. The oxidative resistance mechanisms developed by some of the world's most important pyrethroid resistant agricultural pests, e.g. *Plutella xylostella*, *Leptinotarsa decemlineata* and *Helicoverpa* spp. (discussed in Section 8) show remarkable parallels. This is probably not surprising as most of these resistance problems were selected with conventional phenoxybenzyl pyrethroid esters such as fenvalerate, deltamethrin, cypermethrin and permethrin which were used almost exclusively for phytophagous agricultural pests until the mid-1980s. For example, these four pyrethroids alone accounted for over 97% of world-wide pyrethroid use in the early

1980s (Hervé, 1985). Thus it is not unreasonable to assume that a resistance breaking pyrethroid designed to counter oxidative metabolic resistance in, say, pyrethroid resistant *Helicoverpa armigera* in Australia, may have more general utility in overcoming oxidative pyrethroid resistance in many other key phytophagous agricultural pests throughout the world. If this is so, and if IRM strategies can be successfully implemented, then resistance breaking pyrethroids are a potentially lucrative market and the price differential for resistance breaking and conventional compounds may not be so large as that documented in the *A. aegypti* example stated earlier.

We have come a long way in the understanding of resistance over the last three decades. We have also had some experience in successfully managing pyrethroid resistance (see earlier Sections). The incorporation of synergists and resistance breaking pyrethroids is a logical extension of this management programme. We are rapidly accumulating the knowledge required to develop a sustainable IRM strategy employing synergists and/or resistance breaking pyrethroids. Let us hope the agrochemical industry has the foresight and courage to complement these developments.

## Discussion

This study has shown that resistance is not necessarily a 'one-way street' (Keiding 1967) and that it can be managed to at least slow down the resistance treadmill, thereby extending the usefulness of available chemicals (Hammock & Soderlund, 1986; Sawicki & Denholm, 1987). The economic implications of successful insecticide resistance management (IRM) have been shown by Cox & Forrester (1992) who compared the impact of managed and unmanaged pyrethroid resistance in *Helicoverpa armigera* in the Australian and Thai cotton industries, respectively. They found that the Thai cotton industry declined dramatically despite a strong local demand for raw cotton for the booming textile industry, while the Australian cotton industry thrived and steadily expanded. Similar dramatic collapses due to uncontrolled resistance have been recorded previously (e.g. Hearn, 1975; Bottrell & Adkisson, 1977) and there is no doubt that those countries adopting successful IRM strategies, will enjoy significant economic advantage in highly competitive international markets. However, it must be stressed that successful IRM is not just a clever re-organization of chemical countermeasures into mixture and/or rotation schemes. IRM strategies must complement good integrated pest management (IPM) practices and only when IRM is properly incorporated into acceptable IPM programmes, will there be any hope of successful resistance management (Bull & Menn, 1990; Croft, 1990; Forrester, 1990a; Forrester & Fitt, 1992). As Riley (1990) suggests 'it is those states and countries that rely on these means of cotton production, that will manage the resistance problem'.

As mentioned in the Prologue, this study attempts to redress the imbalance between the large body of theoretical information on the genetics, physiology and biochemistry of resistance and the lack of application of these in practical IRM. It is hoped that this study has been successful in this regard. Many useful points for practical IRM have been highlighted throughout this study and some have already been incorporated into the 'Supplementary Guidelines' for the strategy (Forrester, 1990b; Shaw, 1991), for example:

- Grow early maturing crops to avoid dominant *H. armigera* late in the season, high resistance and expensive Stage III insecticides.
- Avoid growing certain alternative host crops (especially early maize and sunflowers) near cotton, as they serve as early season nursery crops for resistant *H. armigera*.
- Avoid consecutive sprays of pyrethroids where *H. armigera* are emerging from neighbouring early season alternative host crops, as resistance levels will be exacerbated by selection of moths before mating.
- Sample over-wintering pupae under cotton stubble and cultivate should they exceed threshold.
- If a pyrethroid is used to control sorghum midge, do not follow up with a pyrethroid for *Helicoverpa* control, as the midge spray will have already selected for pyrethroid resistant *H. armigera*.
- Add piperonyl butoxide (Pbo) to one only of the three recommended pyrethroid sprays (either the second or the third), preferably at night or late evening, to maximize its activity against moths.

The monitoring technique employed in this study (discriminating dose screening of larvae reared from field collected eggs) proved extremely successful and had a number of advantages over the conventional resistance monitoring technique (full bioassay of lab reared F1 progeny) or the alternative discriminating dose testing of pheromone trapped male moths of uncertain age or previous pesticide exposure. The development and refinement of this sensitive and cost-effective technique proved invaluable in maintaining user confidence in the strategy, combating complacency and allowing the fine tuning of strategy recommendations as and when necessary (Riley, 1990) (e.g. the reduction of the pyrethroid window from 42 to 35 days and the decision to commercialize Pbo).

However, as in most research, just as many questions seem to have been raised as resolved. Perhaps the most important is what has been the reason for the preferential selection of the oxidative metabolic

pyrethroid resistance mechanism in the Australian IRM strategy. If this can be determined, then the principle could be employed in designing IRM strategies for similar resistance situations throughout the world. This would then give the necessary commercial incentive for agrochemical industry to develop light stable oxidative synergists and/or resistance breaking pyrethroids. Other areas for further research will be the possible development of synergists such as propargite and phosmet and their potential impact on other pests (e.g. will the increased use of propargite as a pyrethroid synergist, in addition to its use as a miticide, necessitate the development of a miticide resistance management strategy?) There will also be increasing reliance on mixtures of biological insecticides (especially *Bacillus thuringiensis*) with conventional insecticides for both environmental and IRM reasons and there will be a need to develop new strains, formulations and delivery systems (Gelernter, 1990).

Cultivation of over-wintering pupae under cotton stubble has been strongly recommended as an IRM tool but its adoption in practice has not achieved the desired level. This can probably be traced back to the inability of growers and consultants to assess easily which fields require cultivation, without laborious pupal sampling. Perhaps the development of a predictive model to estimate pupal diapause from late summer/early autumn egg lays, would assist in overcoming the necessity for pupal sampling.

It is currently not possible to determine the species of mixed populations of *H. armigera* or *H. punctigera* eggs or small larvae in the field. Because of this inability, growers and consultants often have difficulty in deciding the optimum time to apply the one recommended Pbo spray or when to avoid pyrethroids and endosulfan in high *H. armigera* pressure situations. The development of a quick field oriented diagnostic kit to separate *H. armigera* and *H. punctigera* would prove very useful for insecticide management choices in the field. It would also be useful for determining the species of survivors in order to help determine the reason for the spray failures (e.g. resistance in *H. armigera*, or poor application, etc.) and in choosing a suitable 'clean up' spray. This research has already been initiated and will be reported elsewhere. The lack of significant adulticidal activity of endosulfan can also be a problem during periods of high pest pressure in the Stage I period. This can lead to the need for repetitive spraying to control larvae hatching from continuous egg lays. Obviously, this increased selection pressure is undesirable from an IRM point of view, especially in the more northerly cotton growing areas where *H. armigera* is usually more abundant in the early part of the season. The only recourse available to growers and consultants at present for control of moths in Stage I is to add an adulticidal organophosphate (e.g. parathion) to endosulfan. However, this is potentially disruptive to the current IPM programme in cotton which is designed to use 'soft chemicals' early so as not to 'flare' mites. A possible solution is the development of baits (e.g. thiadicarb/molasses) to attract and kill moths without affecting mite predators such as thrips. A similar approach has been adopted in Stage II with the recommendation to use Pbo as a pyrethroid synergist to control resistant moths. The search for pro-insecticides requiring preferential bioactivation in the resistant strain was only mildly successful in this study (pyrazophos identified as a possible synergist for further study). However, the potential rewards for discovering compounds expressing negative cross resistance are great and this area should be pursued further. It also introduces an element of ambiguous selection pressure which can be exploited to further temper the development of resistance (Brattsten, 1990).

The study presented here deals with reactive (= curative) management of pyrethroid and endosulfan resistance in *H. armigera* in Australia. There is no doubt that IRM strategies should preferably be implemented preventatively to ensure a greater chance of success (Forrester, 1990a). Moberg (1990) suggests that resistance potential 'is a fact of nature that must be integrated into the discovery and development of new products and the use of existing ones'. Preventative (and curative) IRM strategies will be increasingly adopted but they will need to be tailored to suit the idiosyncrasies of each particular resistance situation (National Research Council, 1986; Tabashnik, 1986; Roush & McKenzie, 1987; Sawicki, 1989; Forrester, 1990a) and the findings in this study should not be blindly extrapolated to other ecosystems, etc.

This study deals with the science behind the Australian IRM strategy. Equally important to the success of this strategy, have been the efforts of growers, consultants, resellers, aerial operators, agrochemical industry and extension personnel in supporting the strategy (Forrester, 1990a). Indeed, Knight & Norton (1989) also recognized the need for this multi-pronged approach to IRM and stated that 'unless a simultaneous assault is undertaken at the farm, agrochemical company and public policy levels, agriculture and the environment (and hence people) will suffer the consequences of a sharply escalating resistance problem in the immediate future'.

Finally, as an applied biologist, I would like to think that we could learn from our past mistakes and that we, one day, may begin to heed Brattsten's (1990) advice that valuable, new, resistance-naive, chemical groups 'should not be used according to present day economic marketing ideas but rather in accordance with biological and evolutionary processes'.



Picking irrigated cotton, Moree (northern New South Wales, Australia).  
*New South Wales Agriculture.*



Mechanised harvesting of irrigated cotton, Narrabri (northern New South  
Wales, Australia). *New South Wales Agriculture.*



Picking cotton in late afternoon, Narrabri (northern New South Wales,  
Australia). Nandewar Range in background. *New South Wales Agriculture.*



## Epilogue

In their report to the Council for Agricultural Science and Technology, Day *et al.* (1983) stated that 'the development of resistance is part of the endless process of evolutionary adaptation to a changing environment'. Clearly, the development of resistance will be a continuing phenomenon and that of resistance management, a continuing necessity. With the possible arrival of pyrethroid alternatives in the not too distant future, it is perhaps opportune to reflect on Hervé's (1985) parting comments in his 76 page review of the early commercial use of pyrethroids. He concluded, 'Finally, I would say that pyrethroids have in most situations replaced organochlorine compounds with all the advantages of these products but without any of their disadvantages; this is the greatest compliment one can pay to this family of compounds. It only remains to endeavour to use pyrethroids rationally so as to ensure that they will continue to be used for as long as possible. Thus I conclude with a final wish: may pyrethroids be the first example of concerted action with a view to drawing up a utilisation strategy for a new chemical family so that, at least, the development of resistance to an insecticide group can be successfully held in check'. Perhaps, next time.

## Appendix 1

# Rearing methods for *Helicoverpa* spp.

### *Moths*

On emergence, moths are placed into 27 litre ventilated perspex mating cages. Up to 20-30 pairs are placed in each cage. The moths are fed a 10% honey solution which is changed three times a week. Honey feeders are of two types, 4.5 ml drop dispensers hung from the top of the cage (four per cage), and 28 ml containers stuffed with cotton wool, soaked in honey solution and placed on the cage floor (three per cage). 0.1% oxytetracycline hydrochloride is added to the honey solution to control possible bacterial contamination. Paper towel is used to line the bottom of the cage whilst fine white muslin is used on the sides. Moths lay mostly on the muslin liners. Eggs are harvested three times a week, washed off in 0.1% sodium hypochlorite solution and collected by filtering the suspension through a Buchner funnel. The concentrated eggs are then rinsed by flushing with water and left to dry until the filter paper is just moist to the touch. The filter paper is then clipped to a sheet of paper towelling which is placed inside a 250 x 305 mm plastic bag and sealed with masking tape. The bag is hung vertically in a constant temperature room ( $25 \pm 1^\circ \text{C}$ ) with the tape seal to the bottom. As the neonates are negatively geotropic, this minimizes larval losses due to escapes or entrapment on the tape. The moth rearing room is maintained at  $25 \pm 2^\circ \text{C}$  and L:D 14:10. Humidity is maintained at 70-80% for the last 2 h of the day cycle and the entire 10 h night cycle, using a steam humidifier.

### *Small larvae*

Neonates are transferred with a very soft, fine hair paintbrush onto artificial diet (table 36) in 11 cm diam. (300 ml) round plastic tubs. A 7 cm diam. hole in the lids of these containers is covered with a semi-permeable plastic wrap (Rapfast, Kent Paper Co., Spit Junction, NSW) to allow adequate aeration without loss of larvae. About 30 neonates are placed in each container (stacked with the lids down to minimize escapes) and when they reach the second instar are separated to prevent cannibalism. Larvae are transferred with soft blunt nosed forceps to individual wells of 12 well larval rearing trays. These trays are Limbro tissue culture trays (Flow Laboratories, North Ryde, NSW) modified for entomological use by removal of the small aeration lugs to allow better sealing. The use of these trays has resulted in substantial savings in labour and operating costs as the trays allow handling of 12 larvae with the one lid on/off operation. They are also stackable and therefore space saving, sturdy enough to be recycled, and transparent to allow efficient viewing of larval development without lid removal. They also save on diet as only 2-3

ml of diet is poured into each of the 7.5 ml (2.4 cm diam.) wells.

The diet is poured into the trays from modified soft plastic squeeze bottles (outlet tube cut short and internal tube removed). Generally, 100 trays can be poured from one batch of diet, kept warm and pourable by immersing the blender jug containing the diet, into a hot water bath. Diet is poured inside a laminar flow cabinet and allowed to cool there. This procedure has virtually eliminated the incidence of fungal contamination of diet by *Aspergillus* spp. etc. Once cool, trays of diet are kept in the refrigerator (not frozen) until required.

### *Large larvae*

Larvae for bioassay are sorted and tested daily in fresh trays. Larvae being reared to the adult stage are left in the 12 well trays until the last instar when they are placed on 8-10 cc of artificial diet in 28 ml Rheem plastic pots (Durapak, Lidcombe, NSW). This diet is slightly modified from the early instar/testing diet in that the amount of agar is increased by 50% and 2.2g of oxytetracycline hydrochloride is added to control bacterial infections. The extra agar is added to reduce the moisture content of the final instar diet/prepupal burrowing medium which was found necessary to improve larval to pupal viability. Contaminant yeasts/bacteria can cause fermentation of the diet at this stage, particularly on diet older than seven days. This problem can be overcome by adding 1.2 g of sodium metabisulphite or 50 mg chloramphenicol to the diet.

The pots housing the last instar larvae are kept in place by perspex frames and lids, primarily to prevent escape of large larvae from chewing through the soft plastic lids supplied with the pots. These frames are stackable, reusable and hold 48 larvae under one lid. The size and number of holes in the lid above each pot

Table 36. Artificial diet for larval *Helicoverpa* spp., based on a modification of Teakle & Jensen (1985).

Artificial diet recipe	
Blend up	— 1 litre hot water — 60 gms wheat germ — 53 gms brewer's yeast — 130 gms soybean flour — 3.3 gms nipagin — 1.7 gms sorbic acid — 13.5 mls of 10% formaldehyde — 7 mls pure sunflower oil (no antioxidants)
Combine with	— 16 gms agar — 300 mls boiling water
Blend, allow to cool and add 5.3 gms of ascorbic acid when diet reaches less than $60^\circ \text{C}$	

is critical to allow a fine balance between the need to dry the diet for optimum pupation conditions and the need for the diet to remain moist enough to be palatable (four 2 mm dia holes/pot have been found to be ideal). The base frame and lid are held together by five 30 mm long, 4 mm diam. bolts with wing nuts for easy removal.

#### *Pupae*

Larvae pupate in the residual diet medium and when the pupal case has hardened, pupae are removed with soft, blunt nosed forceps and surface sterilized in 0.1% sodium hypochlorite for 8 min. Pupae are then dried, sexed and placed in dry vermiculite in 1.2 l ventilated plastic emergence jars. Up to 30 pupae are placed in each jar and paper towelling is placed around one side of the emergence jars to enable a suitable vertical

surface for newly emerged moths to expand their wings.

#### *Tray recycling*

Larval rearing trays are cleaned with a high pressure water blaster. Trays are held in place by a specially designed metal frame and old diet, frass and dead larvae are removed quickly and efficiently by the sprayer. Any remaining residues are removed by hand washing. Trays are sterilized before reuse by soaking in 0.2% sodium hypochlorite for at least 6 h. They are then rinsed in fresh water and dried in direct sunlight.

#### *Species suitability*

The rearing methods described have been found to be equally effective for both *Helicoverpa armigera* and *H. punctigera*.

## Appendix 2

# Base line susceptibility data for *Helicoverpa* spp. and calibration of discriminating doses

### Introduction

The basis for any resistance monitoring programme requires an accurate knowledge of the susceptible phenotypic response. Consequently, it is important to isolate and establish susceptible colonies to measure the organism's base line response level. Ideally this should be done before any resistance development (Tabashnik, 1986), otherwise it can become quite difficult to find and establish susceptible strains. In this study, a number of susceptible strains were collected off a range of hosts from a wide geographical area and their bioassay response checked against a standard laboratory susceptible strain.

Historically, resistance has been most popularly measured by changes in log dose probit (ldp) responses but discriminating doses had been used also (e.g. Georghiou & Taylor, 1976). However, even as far back as 1960, Davidson had recognized the importance of using discriminating dose testing when measuring resistance in heterogeneous populations (Davidson, 1960). The decision to use discriminating doses from the beginning of this study (1983/84 season) was subsequently vindicated by Roush & Miller's (1986) illuminating analysis indicating that 'a discriminating dose test is more efficient than a dose/response regression in monitoring for resistance'. However, ldp lines are also very useful for certain toxicological studies (especially cross resistance studies), so both base line bioassays and discriminating doses were calibrated on various susceptible strains, for the insecticides of interest in this study.

### Methods and materials

#### *Insecticides*

Various pyrethroid and cyclodiene insecticides were made up as solutions of technical material dissolved in analytical grade acetone. Sources of insecticides were fenvalerate 94.3% a.i. from Shell, Melbourne; deltamethrin 99.4% a.i. from Hoechst, Melbourne; cypermethrin 93.7% a.i. from FMC, Brisbane; endosulfan 98.1% a.i. from Hoechst, Melbourne; dieldrin 99.0% a.i. from Shell, Melbourne; endrin 96.0% a.i. from Velsicol, Sydney, and Series Two (see Section 10 for structure) 86.0% a.i. from ICI, UK.

#### *Source of colonies*

Various strains of susceptible *Helicoverpa armigera* and *H. punctigera* were collected as eggs or larvae on a range of host crops from 1983 to 1985 and tested in the first to third laboratory generation. Long-term suscep-

ble laboratory cultures of both species, obtained from Dr R. Teakle, Department of Primary Industries, Brisbane, Qld, were used as checks for susceptibility of the field collected strains. The long-term laboratory culture of pyrethroid and endosulfan susceptible *H. armigera*, collected originally off sorghum at Gatton, Qld, in 1979, was also tested on a number of occasions after the 34th generation to determine the repeatability of bioassay results on a standard colony, and the effect of long-term laboratory culture on phenotypic expression of susceptibility.

#### *Larval testing*

Larvae were reared on artificial diet (see Appendix 1), checked twice daily and third or fourth instars weighing 30-40 mg were placed on fresh diet and tested with various pyrethroid and cyclodiene insecticides. Each larva was dosed dorsally on the thorax with 1 µl of insecticide/acetone solution with a Hamilton 50 µl microsyringe in a repeating dispenser (Alltech Associates, Homebush, NSW). A calibration test was also carried out for fenvalerate on 40-60 mg *H. armigera* larvae. Larval mortality was assessed at three days post treatment (held at 25 ± 2°C). Larvae were considered dead if they were unable to move in a co-ordinated manner, when prodded from behind.

#### *Moths: topical eye test*

Male and female moths were kept separate on emergence and fed for one day on 10% honey solution. They were then weighed, anaesthetised briefly with carbon dioxide and dosed on the left eye with 1 µl of insecticide/acetone solution. Moths were held individually in 28 ml containers for 24 h after treatment, to assess the initial response. Moths showing any signs of activity were then held in 300 ml plastic tubs (in groups of 2-5) with access to 10% honey, for a further 48 hours, to allow for any recovery. Final moth mortality was assessed at three days post treatment (held at 25 ± 2°C). Moths were considered dead if they were unable to move (walk or fly) in a co-ordinated manner, when prodded from behind. Because of variation in moth weights (both within and between sexes) LD50s were adjusted to a standard 200 mg moth.

#### *Moths: tarsal plate test*

Male and female moths were treated as above for the first day. After being weighed, they were quickly placed in groups of two to five on a treated glass petri dish bottom (9 cm diameter, 1 cm deep). The petri dish bottoms had been treated with 1 ml of insecticide/acetone solu-

Table 37. Calibration of fenvalerate bioassays and discriminating doses (for two larval weight ranges) on various strains of susceptible *Helicoverpa armigera* collected as eggs or larvae on a range of hosts from 1983 to 1984 and tested in the F1-3.

Strain data		LD <sub>50</sub>	95% Conf. interval		Slope	% Mortality at µg/larva		
Collection site	Host	(µg/larva)	Lower	Upper		0.1	0.2	0.5
30-40 mg larvae								
Narrabri, NSW	cotton	0.02	0.021	0.029	3.3	100	100	
Kerang, VIC	maize	0.02	0.018	0.026	2.8	100	100	
Melbourne, VIC	maize	0.02	0.019	0.029	2.1	93	98	
Narrabri, NSW	light trap	0.02	0.014	0.028	2.9	89	100	
Narrabri, NSW	cotton	0.02	0.018	0.024	4.9	100	100	
Wee Waa, NSW	cotton	0.02	0.018	0.029	3.2	96	100	
Moree, NSW	cotton	0.02	0.015	0.023	2.9	94	100	
Wee Waa, NSW	cotton	0.02	0.018	0.026	3.3	100	100	
Narrabri, NSW	cotton	0.02	0.020	0.028	2.7	89	98	
Moree, NSW	sorghum	0.02	0.018	0.032	2.5	95	98	
Moree, NSW	sorghum	0.02	0.013	0.021	2.5		98	
Emerald, Q	cotton	0.02	0.019	0.029	3.1	97	100	
Emerald, Q	cotton	0.02	0.017	0.030	2.6		96	
Moree, NSW	cotton	0.02	0.010	0.025	2.8	95	100	
Moree, NSW	cotton	0.03	0.022	0.033	3.4	100	100	
Wee Waa, NSW	cotton	0.03	0.026	0.035	3.1	95	100	
Darwin, NT	pumpkin	0.03	0.022	0.034	2.9	95	100	
Emerald, Q	cotton	0.03	0.024	0.035	4.0	100	100	
Dalby, Q	cotton	0.03	0.020	0.034	2.9	97	100	
Dalby, Q	cotton	0.03	0.025	0.045	2.4	86	100	
Wee Waa, NSW	cotton	0.03	0.022	0.041	3.2	91	100	
Narrabri, NSW	cotton	0.03	0.026	0.040	3.0	97	100	
Laboratory susceptible colony	colony	0.03	0.026	0.041	3.0	92	100	
Wee Waa, NSW	sunflowers	0.03	0.026	0.038	3.5	97	100	
Gatton, Q	sorghum	0.03	0.028	0.038	3.5	96		
Emerald, Q	maize	0.04	0.029	0.043	2.4	78	96	
Wee Waa, NSW	sunflowers	0.04	0.033	0.048	2.9	88	95	
Wee Waa, NSW	maize	0.04	0.030	0.048	2.3	80	100	
Wee Waa, NSW	maize	0.04	0.034	0.048	3.0	89	100	
Wee Waa, NSW	maize	0.04	0.036	0.050	2.5	65	98	
Mareeba, Q	tobacco	0.04	0.033	0.051	3.7	86	100	
Narrabri, NSW	light trap	0.04	0.034	0.052	2.5	87		
Narrabri, NSW	light trap	0.04	0.032	0.053	3.0	91		
Dalby, Q	cotton	0.04	0.029	0.053	2.4	75	100	
Emerald, Q	cotton	0.04	0.027	0.046	2.8	85	97	
Wee Waa, NSW	maize	0.05	0.039	0.052	2.8	85	97	
Moree, NSW	cotton	0.05	0.044	0.067	2.9	83	97	
Average		0.030			3.0	91.0	99.1	
± standard error		± 0.015			± 0.09	± 1.4	± 0.3	
40-60 mg larvae								
Narrabri, NSW	cotton	0.03	0.026	0.038	3.5		100	100
Moree, NSW	sorghum	0.04	0.034	0.055	2.9		97	100
Darwin, NT	pumpkin	0.05	0.042	0.061	3.2		100	100
Narrabri, NSW	cotton	0.06	0.045	0.073	2.2		100	100
Dalby, Q	cotton	0.07	0.051	0.089	2.2		80	100
Laboratory susceptible colony	colony	0.08	0.065	0.100	2.1		80	
Emerald, Q	cotton						87	98
Average		0.055			2.7		92.0	99.7
± standard error		± 0.076			± 0.24		± 3.6	± 0.3

tion which was just enough to cover the surface of the plate with a thin film. The acetone was allowed to evaporate off and the insecticide dose was expressed in µg of toxicant/cm<sup>2</sup> of glass surface. After the moths had been placed on the treated plates, an untreated lid was placed on top in order to confine the moths to walking on the treated surface. Moths were held on the plates for 24 h and then those showing any signs of activity were held

as above, for a further 48 h. Mortality was assessed at three days post treatment as above and LC<sub>50</sub>s were also adjusted to a standard 200 mg moth.

#### Statistical analysis

At least 48 larvae and 36 moths were tested at each dose within a 0-100% mortality range. Any control mor-

Table 38. Calibration of deltamethrin bioassays on various strains of susceptible *Helicoverpa armigera* collected as eggs or larvae on a range of hosts from 1983 to 1984 and tested in the F<sub>1-3</sub>.

Strain data		LD <sub>50</sub> (µg/30-40 mg larva)	95% Conf. interval		Slope
Collection site	Host		Lower	Upper	
Moree, NSW	cotton	0.004	0.0020	0.0057	1.6
Narrabri, NSW	cotton	0.005	0.0034	0.0066	1.5
Kerang, VIC	maize	0.005	0.0038	0.0069	1.5
Galton, Q	sorghum	0.005	0.0038	0.0061	1.8
Darwin, NT	pumpkin	0.005	0.0033	0.0066	1.5
Wee Waa, NSW	cotton	0.006	0.0050	0.0080	1.4
Narrabri, NSW	cotton	0.006	0.0047	0.0075	1.7
Laboratory susceptible colony		0.006	0.0048	0.0080	2.0
Moree, NSW	sorghum	0.007	0.0042	0.0112	1.2
Melbourne, VIC	maize	0.008	0.0064	0.0108	1.7
Wee Waa, NSW	cotton	0.009	0.0057	0.0177	0.9
Emerald, Q	cotton	0.009	0.0061	0.0124	1.5
Narrabri, NSW	cotton	0.009	0.0066	0.0177	1.7
Moree, NSW	sunflowers	0.011	0.0086	0.0145	1.3
Narrabri, NSW	cotton	0.011	0.0089	0.0144	2.3
Moree, NSW	sorghum	0.012	0.0088	0.0157	2.1
Moree, NSW	sunflowers	0.012	0.0089	0.0157	1.8
Wee Waa, NSW	cotton	0.013	0.0098	0.0173	2.4
Wee Waa, NSW	cotton	0.013	0.0096	0.0180	2.0
Mareeba, Q	tobacco	0.014	0.0080	0.0199	1.7
Narrabri, NSW	cotton	0.016	0.0120	0.0200	2.1
Average		0.009			1.7
± standard error		± 0.0008			± 0.08

Table 39. Calibration of cyclodiene (endosulfan, dieldrin and endrin) bioassays and endosulfan discriminating doses on various strains of susceptible *Helicoverpa armigera* collected as eggs or larvae on a range of hosts from 1983 to 1984 and tested in the F<sub>1-3</sub>.

Strain data		LD <sub>50</sub> (µg/30-40 mg larva)	95% Conf. interval		Slope	% Mortality at µg/larva	
Collection site	Host		Lower	Upper		5.0	10.0
Endosulfan							
Laboratory susceptible colony		0.49	0.33	0.65	2.4	100	100
Narrabri, NSW	cotton	0.59	0.48	0.73	3.0	100	100
Wee Waa, NSW	cotton	0.68	0.52	0.84	2.7	100	100
Laboratory susceptible colony		0.70	0.56	0.92	2.2	98	100
Dalby, Q	cotton	0.73	0.27	1.29	1.0	79	90
Narrabri, NSW	cotton	0.79	0.35	1.19	1.8	90	95
Moree, NSW	sorghum	0.84	0.76	1.16	3.6	95	100
Darwin, NT	pumpkin	0.96	0.77	1.20	3.1	100	100
Moree, NSW	sunflowers	0.98	0.81	1.19	3.7	98	100
Average		0.75			2.6	95.6	98.3
± standard error		± 0.054			± 0.29	± 2.4	± 1.2
Dieldrin							
Laboratory susceptible colony		2.86	2.17	3.81	1.8		
Endrin							
Laboratory susceptible colony		0.60	0.456	0.761	2.0		

tality was corrected with Abbott's formula. Log dose probit lines were analysed using the Genstat statistical package.

### Results

#### *Larval Helicoverpa armigera: pyrethroids / cyclodienes*

Fenvalerate was tested on 37 susceptible strains for 30-40 mg larvae (table 37). Considering the wide variation in collection sites and hosts (Melbourne in the south to Darwin in the north), there was remarkably little vari-

ation (2.5-fold) in the LD<sub>50</sub> response (0.02-0.05 µg/larva). Slopes were generally quite high (average 3.0) which resulted in a confident determination of a discriminating dose (0.2 µg fenvalerate averaged out at 99.1 ± 0.3% mortality for 30-40 mg larvae). However, this dose was shown to be too low on the larger 40-60 mg larvae and 0.5 µg fenvalerate proved to be a better discriminating dose (99.7 ± 0.3% mortality).

Deltamethrin was assessed on 21 susceptible strains over a similar range of collection sites and hosts as for fenvalerate (table 38). There was more variability (4.0-fold) in the response to deltamethrin (LD<sub>50</sub> range 0.004-

Table 40. Consistency of bioassay results on a long term laboratory culture of pyrethroid and endosulfan susceptible *Helicoverpa armigera*, collected originally off sorghum at Gatton, Qld in 1979 and reared subsequently on artificial diet without any further infusion of field material. (Colony maintained by Dr. R. Teakle, Department of Primary Industries, Brisbane, Qld.). Colony bioassayed at irregular intervals after the 34th generation (approx. eight generations per year in the laboratory).

Chemical	Generation tested	LD <sub>50</sub> ( $\mu\text{g}/30\text{-}40\text{ mg larva}$ )	95% Conf. interval		Slope
			Lower	Upper	
fenvalerate	34	0.03	0.028	0.038	3.5
	42	0.03	0.026	0.041	3.0
	58	0.03	0.024	0.034	3.2
	59	0.03	0.026	0.037	3.4
	60	0.04	0.036	0.048	3.3
	61	0.02	0.017	0.025	3.5
	75	0.03	0.025	0.039	2.4
	76	0.03	0.025	0.033	3.1
	79	0.03	0.028	0.040	3.0
	83	0.03	0.021	0.029	3.4
	88	0.04	0.035	0.046	3.5
94	0.03	0.023	0.031	3.6	
deltamethrin	34	0.006	0.0047	0.0075	1.7
	35	0.006	0.0048	0.0080	2.0
	43	0.005	0.0038	0.0061	1.8
	59	0.004	0.0033	0.0053	2.1
	60	0.004	0.0032	0.0046	2.9
	81	0.013	0.0110	0.0149	2.3
	94	0.009	0.0075	0.0108	2.3
endosulfan	34	0.70	0.56	0.92	2.2
	43	0.49	0.33	0.65	2.4
	59	0.46	0.39	0.54	3.8
	76	0.50	0.41	0.61	2.7
	95	0.69	0.60	0.79	3.7

Table 41. Calibration of Series Two bioassays and discriminating doses on four generations of the laboratory susceptible *Helicoverpa armigera* colony. n = total number of larvae tested at each candidate discriminating dose.

Date tested	LD <sub>50</sub> ( $\mu\text{g}/30\text{-}40\text{ mg larva}$ )	95% Conf. interval		Slope	% Mortality at $\mu\text{g}/\text{larva}$		
		Lower	Upper		0.07	0.1	0.2
Aug 1989	0.015	0.0129	0.0174	3.4	92.6 n = 759	96.7 n = 1,212	99.9 n = 1,000
Jan 1990	0.031	0.0277	0.0349	2.8			
Feb 1990	0.029	0.0259	0.0312	2.7			
May 1990	0.019	0.0170	0.0215	3.3			
Average	0.024			3.1			
$\pm$ standard error	$\pm 0.0039$			$\pm 0.18$			

0.016  $\mu\text{g}/\text{larva}$ ) and much lower slopes (average 1.7). Because of these low slopes and greater variability, no attempt was made to calibrate a discriminating dose.

Endosulfan was assessed on eight susceptible strains (table 39). There was little variability (2.0-fold) in response to endosulfan (LD<sub>50</sub> range 0.49-0.98  $\mu\text{g}/\text{larva}$ ) and reasonably high slopes (average 2.6) which resulted in a confident determination of a discriminating dose (10  $\mu\text{g}$  endosulfan averaged out at  $98.3 \pm 1.2\%$  mortality for 30-40 mg larvae. As endrin and dieldrin were only being used in cross resistance studies, they were tested only on the laboratory susceptible colony and no discriminating doses were evaluated.

The repeated bioassays on the laboratory susceptible colony indicated excellent consistency of results for all three of the compounds tested, over a seven year testing period (table 40).

The Series Two compound was not available for testing until late 1989, so it was only able to be calibrated on the laboratory susceptible colony (table 41). Repeated bioassays on this strain indicated little variability (2.0-fold) in response to Series Two (LD<sub>50</sub> range 0.015-0.031  $\mu\text{g}/\text{larva}$ ) and generally high slopes (average 3.1). A large number of larvae were screened at a number of candidate doses, with 0.1  $\mu\text{g}/30\text{-}40\text{ mg larva}$  being chosen as the most suitable discriminating dose (96.7% mortality).

*Larval Helicoverpa punctigera: fenvalerate / endosulfan*

Fenvalerate and endosulfan were assessed on 10 and 11 susceptible strains, respectively, from a wide range of collection sites and hosts (table 42). There was little variation (2- to 2.5-fold) in the LD<sub>50</sub> response for either

Table 42. Calibration of fenvalerate and endosulfan bioassays and discriminating doses on various strains of susceptible *Helicoverpa punctigera* collected as eggs or larvae on a range of hosts from 1983-85 and tested in the F<sub>1-2</sub>.

Strain data		LD <sub>50</sub> (µg/30-40 mg larva)	95% Conf. interval		Slope	% Mortality at µg/larva	
Collection site	Host		Lower	Upper		0.025	0.05
<b>Fenvalerate</b>							
Narrabri, NSW	cotton	0.008	0.0064	0.0088	4.3	97.4	100
Narrabri, NSW	cotton	0.009	0.0076	0.0117	3.3	92.0	100
Emerald, Q	cotton	0.009	0.0076	0.0106	3.5	92.5	100
Moree, NSW	cotton	0.010	0.0083	0.0114	4.3	94.9	100
Emerald, Q	cotton	0.011	0.0091	0.0124	3.2	86.3	98.3
Mareeba, Q	tobacco	0.011	0.0078	0.0138	3.2	85.0	100
Bourke, NSW	cotton	0.013	0.0108	0.0156	2.7	74.0	97.6
Narrabri, NSW	geraniums	0.014	0.0120	0.0164	4.3	88.2	97.1
Long term laboratory colony		0.014	0.0121	0.0170	3.0	76.0	98.0
Emerald, Q	cotton	0.015	0.0126	0.0177	3.7	72.7	100
Average		0.011			3.6	85.9	99.1
± standard error		± 0.0008			± 0.18	± 2.8	± 0.4
<b>Endosulfan</b>							
Narrabri, NSW	cotton	0.37	0.310	0.430	3.9	% Mortality at 2.5 µg/larva	
Narrabri, NSW	cotton	0.42	0.356	0.496	3.4	100	
Long term laboratory colony		0.47	0.398	0.553	3.5	100	
Emerald, Q	cotton	0.53	0.458	0.619	3.4	97.9	
Moree, NSW	sunflowers	0.68	0.542	0.839	3.3	96.2	
Moree, NSW	cotton	0.73	0.642	0.840	4.0	100	
Emerald, Q	cotton	0.81	0.708	0.927	3.5	97.9	
Bourke, NSW	cotton	0.82	0.689	1.009	3.5	90	
Moree, NSW	sunflowers	0.83	0.684	1.014	2.8	90	
Mareeba, Q	tobacco	0.92	0.706	1.230	3.1	88.9	
Narrabri, NSW	geraniums	0.97	0.822	1.149	3.7	94.7	
Average		0.69			3.5	96.0	
± standard error		± 0.063			± 0.10	± 1.3	

Table 43. Calibration of fenvalerate bioassays and discriminating doses (for two testing techniques) on adults of the laboratory susceptible *Helicoverpa armigera* colony, tested between 1985 and 1988. Moths dosed either directly on the eye (topical eye test) or indirectly, by enforced contact with treated glass plates (tarsal plate test). LD & LC<sub>50</sub>s adjusted to standard 200 mg moth. n = total number of moths tested at each candidate discriminating dose.

Date tested	Sex	Av. weight of 1 day old, fed, unmated moths (mg) ± s.e.	LD <sub>50</sub> (µg/moth)	95% Conf. interval		Slope	% Mortality at µg/moth			
				Lower	Upper		1.0	2.0		
<b>Topical eye test</b>										
Nov 1985	♀	211 ± 2.8	0.29	0.22	0.36	2.5	} 82.8	} 100		
	♂	193 ± 2.1	0.35	0.25	0.49	1.5				
Nov 1986	♀	247 ± 2.4	0.31	0.24	0.43	2.3			} n = 99	} n = 91
	♂	218 ± 2.2	0.45	0.34	0.63	2.6				
Average ± standard error		♀	0.30 ± 0.010			2.4 ± 0.10				
		♂	0.40 ± 0.050			2.1 ± 0.55				
Date tested	Sex	Av. weight of 1 day old, fed, unmated moths (mg) ± s.e.	LC <sub>50</sub> (µg/cm <sup>2</sup> )	95% Conf. interval		Slope	% Mortality at µg/cm <sup>2</sup>			
				Lower	Upper		0.79	1.57		
<b>Tarsal plate test</b>										
Nov 1985	♀	240 ± 2.8	0.21	0.17	0.25	2.8	} 93.5	} 98.3		
	♂	216 ± 2.1	0.28	0.23	0.32	3.0				
Nov 1986	♀	247 ± 2.4	0.27	0.17	0.45	2.1			} n = 170	} n = 120
	♂	218 ± 2.2	0.25	0.20	0.31	3.2				
Nov 1988	♀	244 ± 2.3	0.14	0.11	0.18	2.5				
	♂	231 ± 2.8	0.24	0.19	0.31	2.3				
Average ± standard error		♀	0.21 ± 0.038			2.5 ± 0.20				
		♂	0.26 ± 0.012			2.8 ± 0.27				

Table 44. Topical eye test bioassays and discriminating dose calibrations (Series Two only) for two cyclodienes (endosulfan and dieldrin) and two pyrethroids (cypermethrin and Series Two) on adults of the laboratory susceptible *Helicoverpa armigera* colony. LD<sub>50</sub>s adjusted to standard 200 mg moth. n = total number of moths tested at each candidate discriminating dose.

Chemical	Sex	Av. weight of 1 day old, fed, unmated moths (mg) ± s.e.	LD <sub>50</sub> (µg/moth)	95% Conf. interval		Slope	% Mortality at µg/moth	
				Lower	Upper		0.1	0.2
endosulfan	♀	237 ± 3.1	0.52	0.44	0.63	4.2		
	♂	205 ± 1.8	1.24	1.05	1.47	4.5		
dieldrin	♀	237 ± 3.1	5.62	4.62	6.79	4.5		
	♂	205 ± 1.8	8.61	7.26	10.25	4.4		
cypermethrin	♀	215 ± 1.9	0.10	0.08	0.12	2.2		
	♂	195 ± 1.7	0.19	0.16	0.23	2.4		
Series Two	♀	215 ± 1.9	0.04	0.033	0.042	4.7	} 98.2	100
	♂	195 ± 1.7	0.04	0.038	0.048	4.3		

chemical and slopes for both were high (3.6 and 3.5 average, respectively) which resulted in a confident determination of discriminating doses (99.1 ± 0.4% and 96.0 ± 1.3% mortality on 30-40 mg larvae for 0.05 µg fenvalerate and 2.5 µg endosulfan, respectively).

#### Adult *Helicoverpa armigera*: pyrethroids / cyclodienes

Fenvalerate was assessed using both testing techniques on repeated bioassays of the laboratory susceptible colony (two and three assays for the topical eye and tarsal plate tests, respectively) (table 43). With both testing techniques, there was no significant difference in bioassay responses between the sexes and there was excellent consistency of assay results over time (weights adjusted to standard 200 mg moth). Candidate doses were evaluated for both techniques and 2.0 µg/moth (topical eye test) and 1.57 µg/cm<sup>2</sup> (tarsal plate test) were chosen as the most suitable discriminating doses, giving 100% and 98.3% mortality, respectively.

The simple benzyl alcohol pyrethroid Series Two was more toxic to moths (topical eye test, table 44) than the conventional phenoxybenzyl alcohol pyrethroids fenvalerate (up to 10x) or cypermethrin (up to 5x). The discriminating dose chosen for Series Two for the topical eye test was 0.2 µg/moth. Consistent with previous comments on the greater toxicity of Series Two to moths, this discriminating dose is 10x lower than the equivalent fenvalerate discriminating dose.

As expected, the cyclodienes were less toxic to moths, particularly dieldrin.

#### Discussion

The fenvalerate and deltamethrin LD<sub>50</sub>s (µg/larvae) and slopes for *H. armigera* obtained in this study (0.03/3.0 and 0.009/1.7, respectively) agree well with previously published data (0.03/3.0 and 0.010/2.6, respectively) from Gunning *et al.* (1984). Except for deltamethrin, there was relatively little variation in the LD<sub>50</sub>s (less than 2.5- and 2.0-fold, for fenvalerate and endosulfan, respectively). This variation is slightly lower than the 3- to 7-fold variation found for similar data for aphids and diamondback moth (Stribley *et al.*, 1983;

Furk & Roberts, 1985; Zoebelin, 1986). It is also very much lower than the 12-fold variation found for susceptible laboratory cultures of *Heliothis virescens* in the USA (Staetz, 1985). It was suggested that this variation was due to long-term cultures becoming inbred, less vigorous and usually more susceptible than the original population from which they were taken (Staetz, 1985). If this problem was universal, then it would be risky to rely on long-term susceptible laboratory cultures which could overestimate the degree of resistance. However, in this study, no evidence of increasing susceptibility could be found in the long-term laboratory 'Teakle' strain of susceptible *Helicoverpa armigera* for any of the compounds tested. So this strain, at least during the course of this study, remained a suitable benchmark for susceptibility.

The greater variability and lower slopes for deltamethrin bioassays in comparison to other pyrethroids, has also been noted previously. Gunning *et al.* (1984) noted this for deltamethrin versus fenvalerate in susceptible *H. armigera* and Leonard *et al.* (1988a) for deltamethrin versus fenvalerate and cypermethrin in susceptible *Heliothis virescens* and *Helicoverpa zea*. Thus, deltamethrin was not considered suitable for confident determination of a discriminating dose with narrow error estimates (Sawicki *et al.*, 1989; Halliday & Burnham, 1990), despite its being the most popular pyrethroid in commercial use at the time (see Appendix 3). Because of its higher slope, fenvalerate (also used commercially at the time), was considered better for this purpose.

Both adult testing techniques gave consistent results and high slopes. Topical testing of adult Lepidoptera has always been a problem in the past due to the need to remove scales to allow accurate dosing. In order to avoid this problem, dosing on the eye was evaluated as this was the most accessible scale-free cuticle available. Welling & Paterson (1985) suggested that the compound eye cuticle, even though without pore canals, could still manifest substantial absorption of insecticides. The technique proved very simple and effective, giving results as good as the more commonly used residue on glass technique. This latter self dosing technique needs careful design to minimize problems of avoidance behaviour (Brown & Brogdon, 1987), particularly with the strongly repellent pyrethroids.

## Appendix 3

# Insecticide use surveys

One of the most important factors affecting resistance frequency is selection pressure. Thus it is important to determine the intensity and pattern of insecticide use within each study area. Such a survey also serves as an indicator of the compliance rate with the voluntary strategy.

### Methods

Each season, growers or consultants were surveyed as to the insecticide use on their properties falling within the Namoi/Gwydir and Emerald study areas. Each grower or consultant was asked to document the area sprayed, the insecticide/s and rates used and the total area of cotton sown. The survey was not just confined to sprays put on for *Helicoverpa* spp. but also included sprays put on for other pests (such as cotton tipworm (*Crocidosema plebejana* Zeller (Lepidoptera: Tortricidae), rough bollworm (*Earias huegeli* Rogenhofer (Lepidoptera: Noctuidae) and mites) which could also impact on any *Helicoverpa* spp. present. However, it did not include organophosphate sprays for thrips, mirids or aphids (e.g. dimethoate, omethoate) which are ineffective against *Helicoverpa* spp. Most properties (90-100%) in each study area participated in the surveys. Selection pressure was expressed as the number of sprays per hectare (total hectares sprayed ÷ total cotton area), not as sprays per farm, as this would have biased the figures towards the smaller properties. Also, early season ground rig band applications were included on a sown area basis and not just as the area of the treated band.

### Results and discussion

#### Total insecticide use (fig. 52)

The total number of *Helicoverpa* sprays per season varied from 7 to 11, depending on the infestation level. Generally higher pest pressure in the northern Emerald irrigation area required one half to two sprays more than the Namoi/Gwydir.

#### Insecticide use by stage (fig. 53)

Most insecticide use was in Stage I (47% in the Namoi/Gwydir averaged over the last six seasons and 43% in the Emerald irrigation area averaged over the last three seasons). The 1985/86 season at Emerald was excluded from this analysis as the Stage II pyrethroid window for that season was positioned one month later

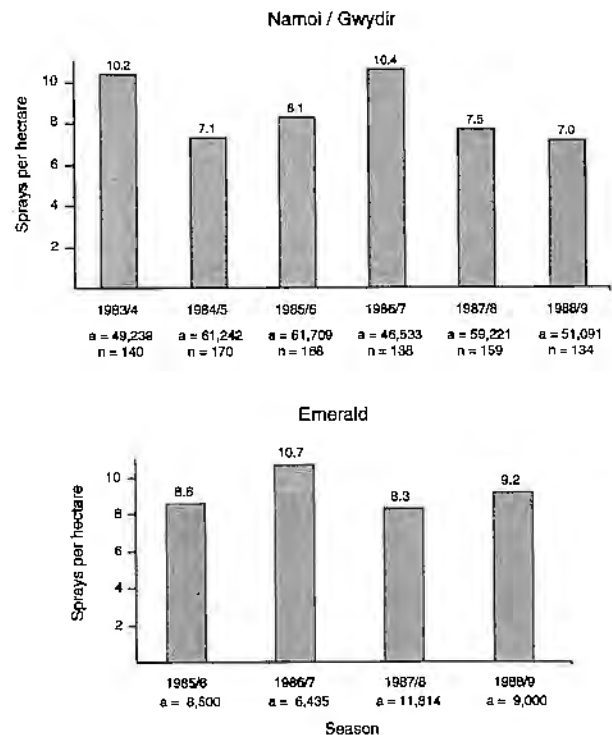
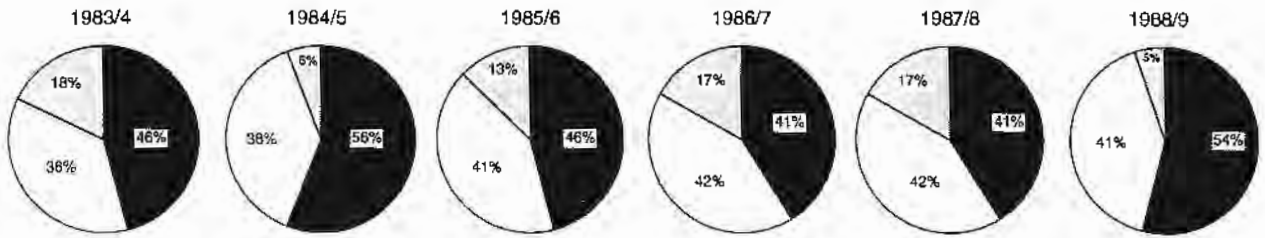


Fig. 52. Total season usage (Stages I, II, and III combined) of insecticides against *Helicoverpa* spp. in cotton in the Namoi and Gwydir river valleys of northern New South Wales and the Emerald irrigation area of central Queensland. a, n = the total number of hectares and properties surveyed, respectively.

Insecticide use by Stage

Namoi / Gwydir



Emerald

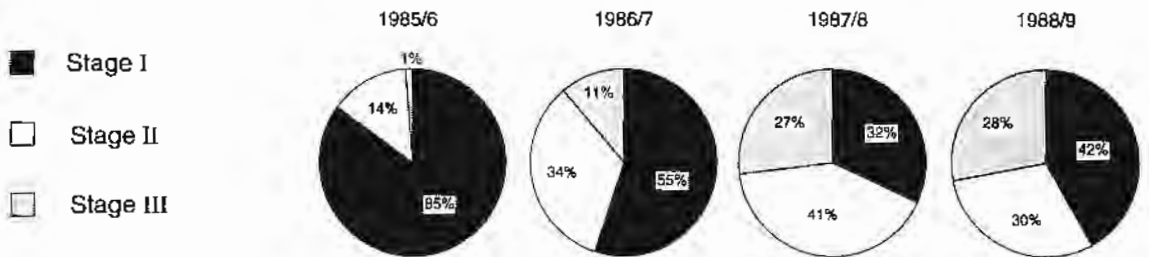


Fig. 53. Breakdown of insecticide use against *Helicoverpa* spp. in cotton in the Namoi and Gwydir river valleys of northern New South Wales and the Emerald irrigation area of central Queensland, for each of the Stages (I, II and III) of the Resistance Management Strategy. NB 1985/86 Stage II period at Emerald was 1st Feb–14th Mar, all subsequent years 1st Jan–10th Feb.

Table 45. Average cost of insecticides for the most commonly used rates for control of *Helicoverpa* spp. larvae in cotton (1984/85 to 1988/89 seasons). Costs are reported in Australian \$ per hectare for the average sized cotton farm (200–400 ha). Larger growers and corporate farms would obviously have access to lower prices.

Chemical grouping	Insecticide	Commonest application rate (grams a.i./hectare)	Cost (\$)/hectare				
			84/85	85/86	86/87	87/88	88/89
organochlorines	endosulfan	720	9.60	11.91	14.07	14.70	13.50
organophosphates	profenofos	750	29.70	32.43	26.79	29.76	31.71
	chlorpyrifos	750		22.50	25.05	26.25	28.35
	sulprofos	1,008	26.60	27.94	35.38	35.48	35.48
	parathion	1,250	10.50	10.50	14.40	16.65	15.80
carbamates	methomyl	450	17.00	23.80	29.00	29.84	29.90
	thiodicarb	750	25.04	25.04	24.50	50.00	50.00
pyrethroids	deltamethrin	15	16.65	15.81	13.68	15.00	11.49
	lambdacyhalothrin	18			13.68	15.00	11.49
	esfenvalerate	25					11.50
	alphacypermethrin	40			13.68	15.00	11.50
	cypermethrin	84	16.38	15.54	14.18	14.99	
	fenvalerate	90	16.65	15.30	13.68	14.99	
	fluvalinate	105					25.34
Average pyrethroid cost/ha, excluding fluvalinate			16.69	15.72	13.77	15.00	11.50

than in subsequent years. This was done intentionally to allow the gradual phasing in of pyrethroids after their withdrawal following the widespread field resistance problems in the 1982/83 Emerald season.

Insecticide use in Stage II was slightly lower than in Stage I (40 and 35% overall average in the

Namoi/Gwydir and Emerald, respectively). Because of the high cost of Stage III insecticides (table 45), there is a strong incentive for growers to avoid using Stage III insecticides. Consequently, Stage III insecticide use was the lowest (13 and 22% overall average in the Namoi/Gwydir and Emerald, respectively).

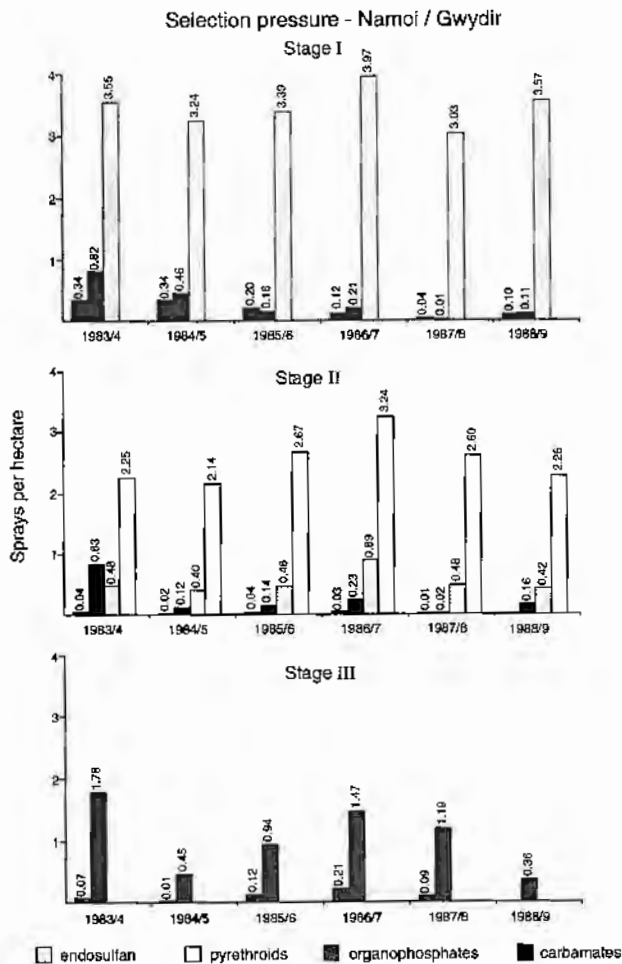


Fig. 54. Spray intensity of various insecticide groups used with-in each Stage (I, II and III) against *Helicoverpa* spp. in cotton in the Namoi and Gwydir river valleys of northern New South Wales for the six seasons since the introduction of the Resistance Management Strategy.

#### Endosulfan - Namoi/Gwydir (figs 54 & 55)

Three to four endosulfan sprays were used in Stage I, with a smaller amount (about half a spray) being used in the Stage II pyrethroid window. Consistent with the strategy recommendations, no endosulfan was used on cotton in Stage III. Growers and consultants were at first very tentative in accepting endosulfan as an effective insecticide against *Helicoverpa* spp. (only 75% and 81% use in Stage I in the first two years of the strategy). However, endosulfan proved to be a reliable, cost-effective insecticide for *Helicoverpa* spp. control and the industry accepted it so well, that it is now virtually the sole insecticide used against *Helicoverpa* spp. in Stage I. It also retains a small but consistent use in Stage II at about 15% of Stage II sprays. It is used mainly to break up the pyrethroid sprays and was the main product chosen to replace pyrethroids when they performed poorly

due to resistance problems in the 1986/87 late Stage II period. The Stage II data also indicate that growers and consultants were tentative in accepting endosulfan in the first year of the strategy, preferring organophosphates to relieve their anxiety about the performance of the pyrethroids. However, as their confidence in endosulfan grew, the use of the expensive organophosphates declined and endosulfan came to be regarded as the preferred break chemical in Stage II. In fact, endosulfan would now account for approximately half of all the sprays used against *Helicoverpa* spp. in cotton.

#### Endosulfan - Emerald (figs 56 & 57)

As in the Namoi/Gwydir area, endosulfan is by far the most commonly used insecticide in cotton. Stage I use was similar to the Namoi/Gwydir but somewhat more variable (two to five sprays). The higher use in 1985/86 season was no doubt due to the later timing of the Stage II pyrethroid window in that season. Data for Stage II clearly indicate an increasing reliance on endosulfan concomitant with decreasing use of pyrethroids and organophosphates. This is probably due to the reduced reliability of the pyrethroids under the higher *H. armigera* pressure at Emerald along with the greater cost-effectiveness of endosulfan over the organophosphates. The increase in confidence in the efficacy of endosulfan noted in the Namoi/Gwydir, was also clearly evident at Emerald, in both Stages I and II. There was also no endosulfan use in the Stage III closed period, indicating excellent compliance with the voluntary strategy.

#### Pyrethroids - Namoi/Gwydir (figs 54, 55 & 58)

Two to three pyrethroid sprays were applied in Stage II. As recommended in the voluntary strategy, no pyrethroids were applied outside of the pyrethroid window. In the first year of the strategy (1983/84 season) growers and consultants were somewhat reluctant to use the pyrethroids (63% of Stage II sprays). However, by the next season, their new found confidence in the strategy's ability to contain pyrethroid resistance saw pyrethroid use rise quickly to 81% of Stage II sprays and except for the 1986/87 season, pyrethroid use has stabilized at around this level. The lower acceptance of pyrethroids in the high pressure 1986/87 season was due to the occurrence of several pyrethroid resistance spray failures in the late Stage II period, with a consequent swing to alternatives, principally endosulfan.

For the first three seasons of the strategy, deltamethrin and cypermethrin were the most commonly used pyrethroids. However, after the introduction of lambda-cyhalothrin in the 1986/87 season, cypermethrin use plummeted and it has now been replaced by its resolved isomer alphacypermethrin. Deltamethrin use also continued to decline but at a much slower rate. Fenvalerate use has increased slightly (10-20%) and it has just been replaced by its resolved isomer esfenvalerate. Lambda-cyhalothrin use has gradually increased since its introduction and it is now the most popular pyrethroid used on Namoi/Gwydir cotton, accounting for just over half of all pyrethroids used.

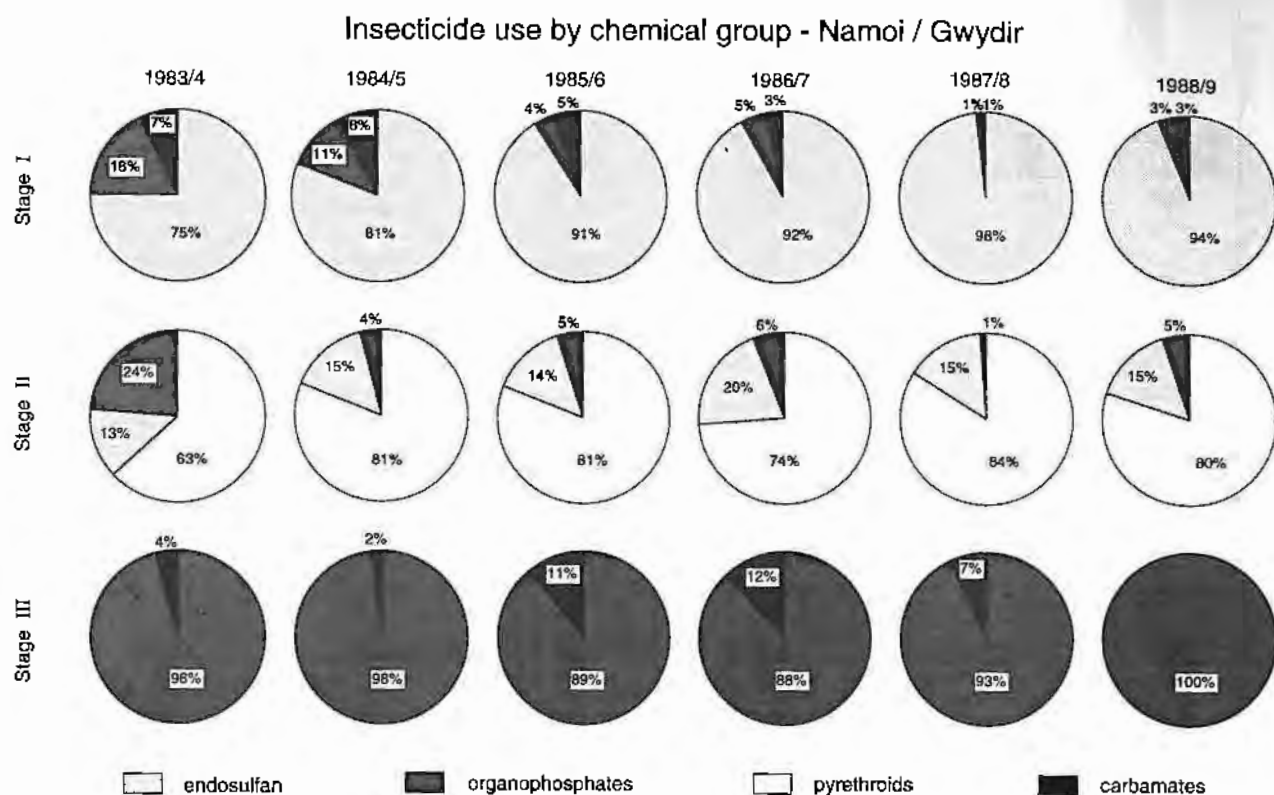


Fig. 55. Percentage use of various insecticide groups within each Stage (I, II and III) against *Helicoverpa* spp. in cotton in the Namoi and Gwydir river valleys of northern New South Wales, for the six seasons since the introduction of the Resistance Management Strategy.

#### Pyrethroids - Emerald (figs 56, 57 & 58)

After the 1982/83 field failures at Emerald, pyrethroids were withdrawn for one season (1983/84) and then phased in gradually over the following two seasons (1984/85 and 1985/86) by intentionally positioning the pyrethroid window towards the end of the season. Consequently, pyrethroid use at Emerald was nil to low (maximum half a spray in 1985/86 season) for the three seasons following the 1982/83 field failures. However, after the repositioning of the Stage II pyrethroid window to the preferred opening date of 1 January at Emerald, pyrethroid use quickly resurged to levels similar to the Namoi/Gwydir levels, mainly to relieve the intense selection pressure on endosulfan which had occurred over the previous three seasons. However, because of the greater *H. armigera* pressure at Emerald, pyrethroid use has decreased slightly since

and has stabilized at a lower level than the Namoi/Gwydir level (about 50% of Stage II sprays).

Patterns in pyrethroid selection were similar to those in the Namoi/Gwydir except that the market seemed much more volatile and responsive to local supply and pricing policies, etc. No single pyrethroid clearly dominated the market for more than one season.

#### Organophosphates/carbamates - Namoi/Gwydir and Emerald (figs 54, 55, 56 & 57)

Organophosphates and carbamates were used in all three stages but their main use period was in Stage III when both endosulfan and pyrethroids are not recommended. In this Stage, organophosphates predominated in the Namoi/Gwydir area (90-100% of sprays) but greater reliance on carbamates (principally thiodicarb) at

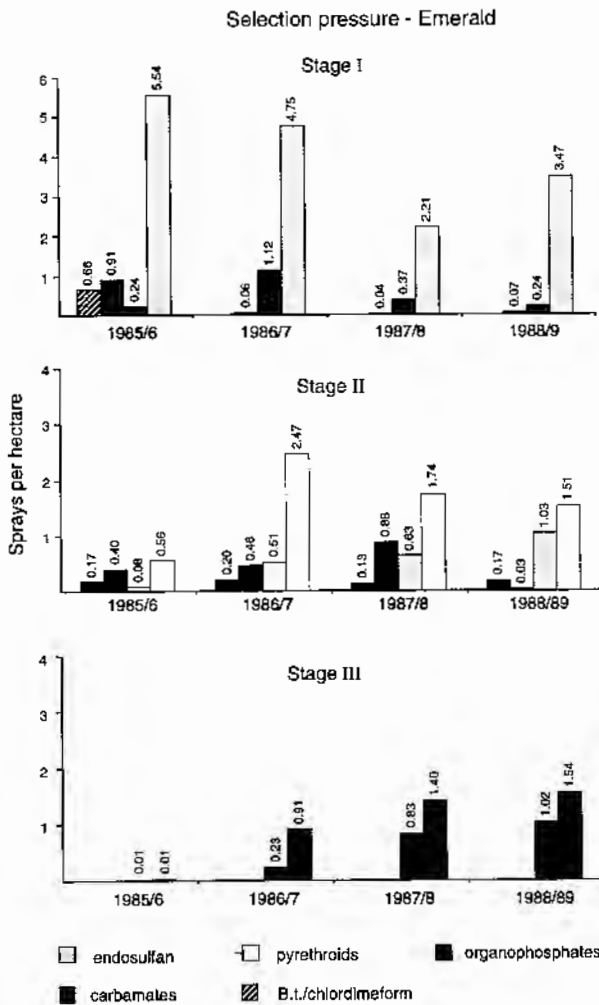


Fig. 56. Spray intensity of various insecticide groups used within each Stage (I, II and III) against *Helicoverpa* spp. in cotton in the Emerald irrigation area of central Queensland for the past four seasons of the Resistance Management Strategy. NB 1985/86 Stage II period was 1st Feb–14th Mar, all subsequent years 1st Jan–10th Feb.

Emerald reduced this to 60–80% of Stage III sprays there.

Stage III insecticide use is normally quite variable due to unpredictable late season pest pressure. This varied from 0.5 to 2.0 sprays in the Namoi/Gwydir area and 1.0 to 2.5 at Emerald. Because of the high cost of organophosphates and carbamates relative to pyrethroids and endosulfan, growers attempt to minimize use of these Stage III insecticides, wherever possible. The most commonly used organophosphate was profenofos (55% and 45% of organophosphate sprays in the Namoi/Gwydir area and Emerald, respectively) followed by parathion (15% and 34%, also respectively). Minor use organophosphates were sulprofos (12% and 12%), monocrotophos (15% and 4%) and chlorpyrifos

(3% and 5%), all respectively as above. The main carbamate used was thiodicarb (over two-thirds of all carbamate sprays in both the Namoi/Gwydir and Emerald areas), with the balance being ovicidal rates of methomyl.

#### Use of mixtures - Namoi/Gwydir (fig. 59)

The use of ovicide/larvicide mixtures has been strongly advocated as a component of the Australian resistance management strategy (see Section 1). When the strategy was first introduced, the use of mixtures with both endosulfan and pyrethroids was quite high but this has declined with time. This was particularly apparent with endosulfan where use of mixtures dropped steadily from 74% in 1983/84 to 3% in 1988/89. A similar but less pronounced trend occurred with the pyrethroids. The reverse trend to increasing use of mixtures with pyrethroids in 1986/87 was due to the pyrethroid resistance problems which occurred in the latter half of the Stage II window in that season. The main mixtures used were larvicide/ovicide mixtures (with methomyl or chlordimeform) or larvicide/miticide mixtures (with chlorpyrifos, monocrotophos or profenofos). Some mixtures of larvicides were also used (eg. endosulfan/parathion). The decline in reliance on mixtures over time was probably due to a combination of the following factors:

- Increasing confidence in the ability of the strategy to contain pyrethroid resistance.
- Increasing confidence in the efficacy of endosulfan used alone.
- The ever present need to reduce costs.
- Lower insect pressure in the last two seasons.
- Increased awareness of the capacity of organophosphate/endosulfan mixtures to flare mites.
- Withdrawal of the very effective ovicide chlordimeform after the 1985/86 season.

#### Use of mixtures - Emerald (fig. 59)

The trend to declining reliance on mixtures was also evident for endosulfan at Emerald. However, the trend for pyrethroids was completely the reverse and most likely reflects the greater *H. armigera* pressure and hence resistance problems, at Emerald.

#### Comparison with pre-strategy use patterns

Few data are available on insecticide use in the formerly unregulated system prior to the introduction of the resistance management strategy. However, a number of publications on pest management in Emerald before 1983/84 indicate the dramatic change that has occurred since the strategy's implementation. For the five seasons prior to the introduction of the strategy in 1983/84, pyrethroids at Emerald accounted for 60–90% of the total sprays applied (currently about 20%), ranging from 5–10 sprays/season (currently 1.5–2.5), spread

Insecticide use by chemical group - Emerald

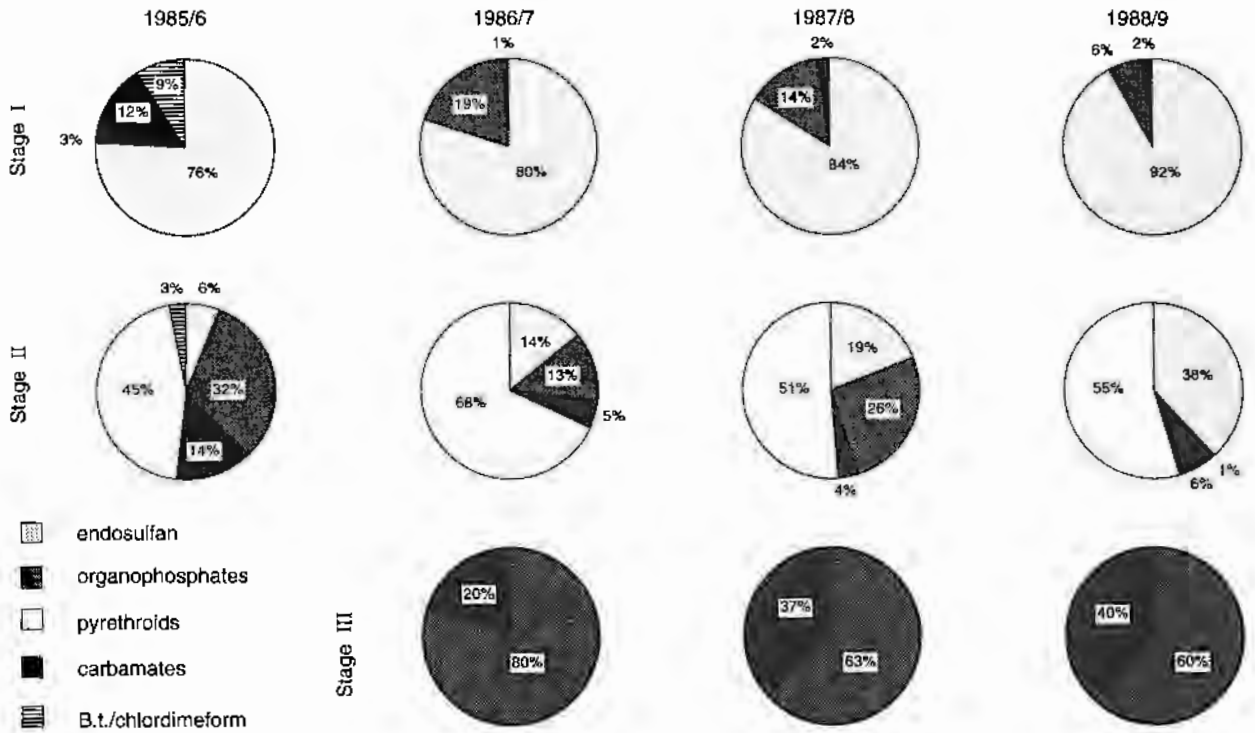
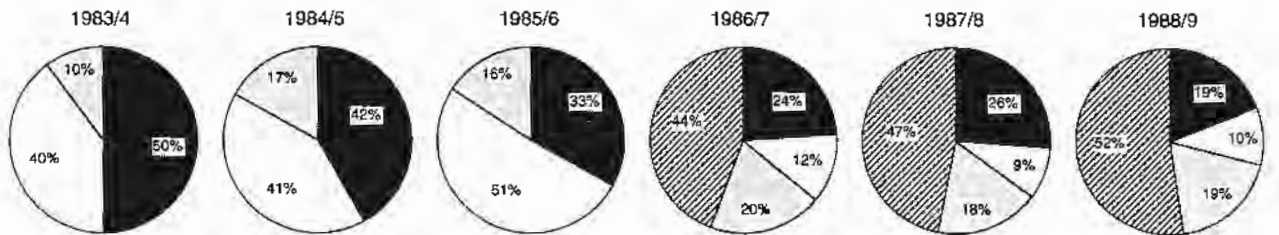


Fig. 57. Percentage use of various insecticide groups within each Stage (I, II and III) against *Helicoverpa* spp. in cotton in the Emerald irrigation area of central Queensland, for the past four seasons of the Resistance Management Strategy. NB 1985/86 Stage II period was 1st Feb-14th Mar, all subsequent years 1st Jan-10th Feb.

Pyrethroid use  
Nanoi / Gwydir



Emerald

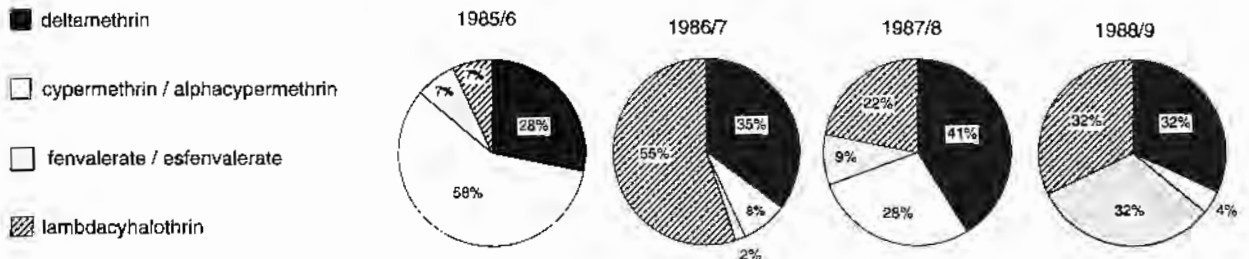


Fig. 58. Breakdown of pyrethroid use against *Helicoverpa* spp. in cotton in the Nanoi and Gwydir river valleys of northern New South Wales and the Emerald irrigation area of central Queensland.

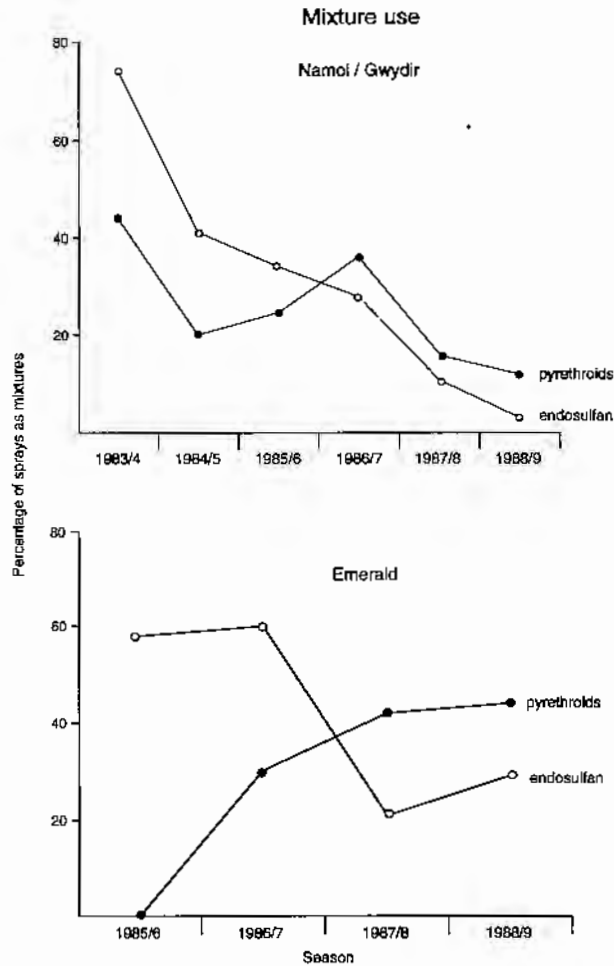


Fig. 59. Use of mixtures with pyrethroids and endosulfan against *Helicoverpa* spp. in cotton in the Namoi and Gwydir river valleys of northern New South Wales and the Emerald irrigation area of central Queensland. Results expressed as the percentage of the total pyrethroid or endosulfan sprays applied as mixtures with either ovicides (e.g. methomyl, chlordimeform) or with other larvicides or miticides (e.g. parathion, monocrotophos, profenofos, chlorpyrifos), as opposed to those applied alone.

more or less equally over the entire 160 day growing period (currently a 35 day window) (Waite & Murray, 1981; Adams & Pyke, 1983; Waite, 1983). Riley (1990) documented a very similar pre-strategy use pattern for pyrethroids in USA cotton (70% of the total treatments applied for *Helicoverpa* spp. and up to 8.4 sprays per season). Although no hard confirmatory data are available, it is generally agreed that most of the pre-strategy Australian cotton industry had a broadly similar pattern

to that at Emerald. Current pyrethroid use patterns in the Namoi/Gwydir are also similar to Emerald but at a slightly higher level (30-35% of total *Helicoverpa* spp. sprays and up to two to three sprays per season), probably because of the lower *H. armigera* pressure in the south. Thus, it is quite clear that the implementation of the Australian resistance management strategy has had a profound and lasting impact on insecticide use in Australian cotton.

## Appendix 4

# Pyrethroid and endosulfan resistance in *Helicoverpa punctigera*: field and laboratory studies

### Introduction

One of the most intriguing problems in Australian entomology has been the differential response of *Helicoverpa armigera* and *H. punctigera* to insecticide selection pressure. Whereas *H. armigera* has developed resistance to virtually every insecticide used against it in any quantity (see fig. 1), there has not been any recorded resistance to any insecticide in the sibling *H. punctigera*. This is quite extraordinary as the two species are co-incident on many crop hosts which are subjected to intense insecticidal protection especially cotton, tobacco and many broadleaf vegetable crops. In addition, whenever studied, the two species have consistently shown similar potential for metabolic detoxification of xenobiotics, e.g. monooxygenases (Collins & Hooper, 1984a) and DDT dehydrochlorinase (Sucksoong, 1979). Thus it would seem that biochemically at least, both species are capable of developing resistance and that some other factor/s must be operating.

The most common explanation put forward for this differential response has been that the pool of unsprayed *H. punctigera* is so vast, that the treated proportion of the total population is only trivial. This would mean that any resistance genes would be swamped by the susceptibles in the refugia and that *H. punctigera* would effectively manage its own resistance. This of course, is an ideal natural insecticide resistance management (IRM) strategy, even though it may mean that the IRM benefits may be offset by higher pest pressure. If this ecological explanation is correct, then theoretically, it should be possible to detect resistance genes, albeit at low frequencies, in the intensively sprayed crop areas. Furthermore, it should be possible to breed from these survivors and intensify the resistance levels by further selection in a closed laboratory colony.

The monitoring programme for evaluating insecticide resistance in *H. armigera* has already been described in Section 2. The sampling technique used in that study resulted in a large number of the 'contaminant' *H. punctigera* in addition to the 'desired' *H. armigera*. As these superfluous *H. punctigera* were normally discarded after identification, it was decided to exploit this ready supply of field collected *H. punctigera* to investigate the above ecological explanation for the differential

response of the two closely related species to insecticide selection pressure.

### Methods and materials

#### Field screens

The sampling procedure, areas and processing were as described in Section 2. However, in order to maximize the chance of detecting resistance, only the intensively sprayed cotton growing sites were sampled (that is, Emerald and the Namoi/Gwydir area). *Helicoverpa punctigera* larvae were reared to 30-40 mg and screened as either third or fourth instars with the fenvalerate (0.05 µg/larva) or endosulfan (2.5 µg/larva) discriminating dose, as indicated in Appendix 2. The screening results were pooled for each Stage of the resistance management strategy and expressed as the percentage of larvae surviving the discriminating dose plus the upper 95% confidence limit based on the pooled binomial standard error (see table 1). The number of larvae tested in each Stage varied according to the abundance of *H. punctigera* (less abundant later in the season) and the work load associated with the higher priority *H. armigera* component of the programme. When *H. punctigera* were abundant (mainly Stage I), only a random subsample was screened. No attempt was made to calibrate a 'twin' discriminating dose technique as mentioned for *H. armigera* in Section 2, so larvae greater than 40 mg were discarded. The actual numbers tested in each Stage (up to 1300/Stage) are given in figure 60. The fenvalerate screens were initiated in mid and late 1986/87 in the Namoi/Gwydir and Emerald areas, respectively, and in early 1987/88 for both areas for endosulfan. The *H. punctigera* screening was terminated at the end of the 1988/89 season in both sampling areas.

#### Laboratory studies

The survivors of the pyrethroid discriminating dose were pooled for both areas from the 1987/88 season onwards. This colony was further selected in the laboratory, initially at 0.05 µg but increasing gradually to 0.5 µg/30-40 mg fourth instar larva. Third instar larvae were excluded from these screens and subsequent bias-

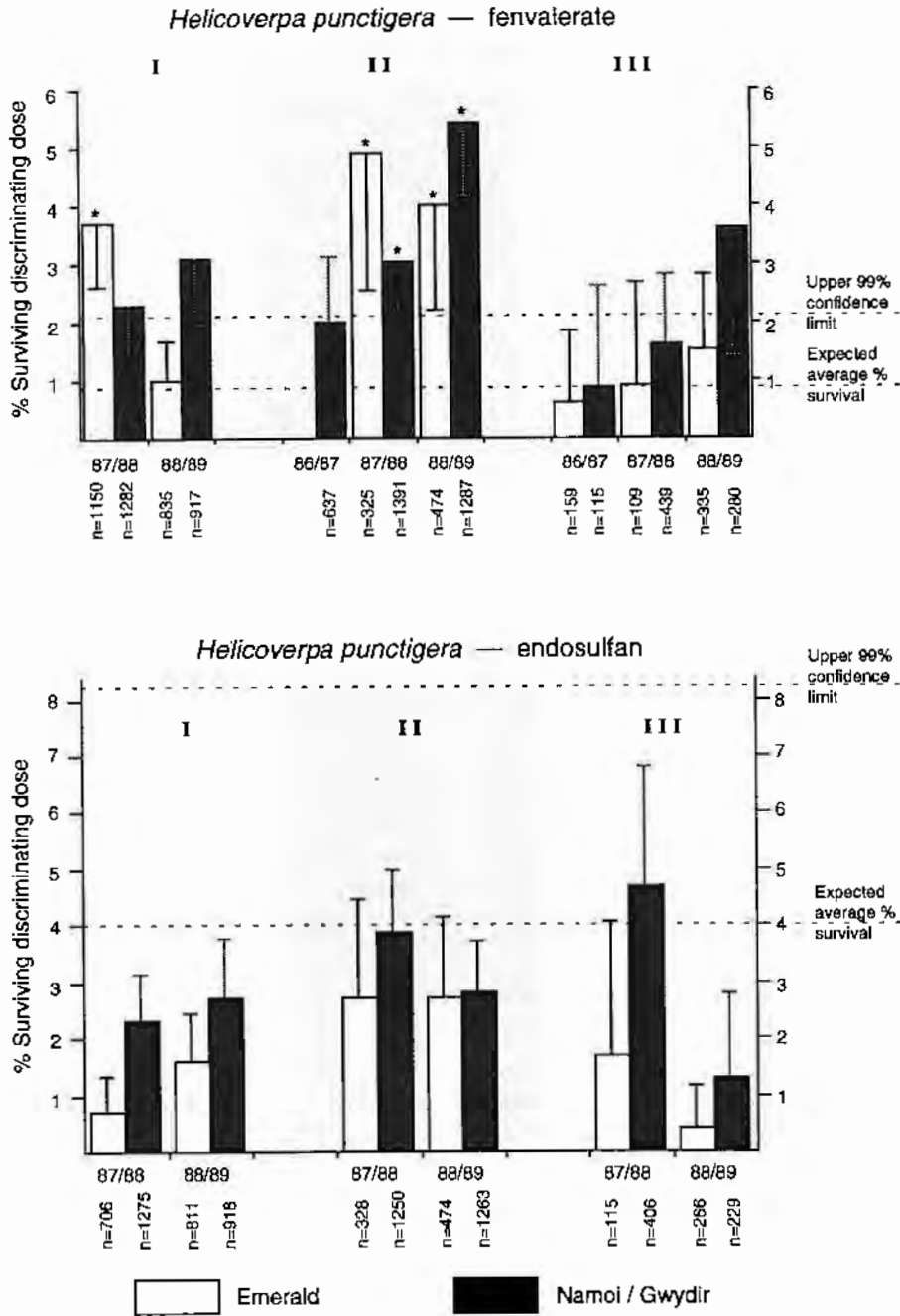


Fig. 60. Survival of *Helicoverpa punctigera* at the fenvalerate and endosulfan discriminating doses (0.05 and 2.5 µg per 30–40 mg larva respectively) at two sites (the Namoi and Gwydir river valleys of northern NSW and the Emerald irrigation area of central Queensland) for Stages I, II and III of the Resistance Management Strategy. Horizontal lines represent the average and upper 99% confidence limit for the expected survival at the discriminating doses of fenvalerate (0.9% and 2.1%, respectively, calibrated on 10 susceptible strains) and endosulfan (4.0% and 8.2%, respectively, calibrated on 11 susceptible strains) (data taken from table 42). Vertical bars indicate the upper 95% confidence limit (based on the pooled binomial standard error). \* indicates % survival at the discriminating dose significantly greater ( $P < 0.05$ ) than the expected upper 99% confidence limit. n = the number of larvae tested in each Stage.

says to minimize the possible variability due to fluctuating metabolic detoxification capacity during the moulting cycle (Wilkinson & Brattsten, 1972; Wilkinson, 1983; Collins & Hooper, 1984b; Hodgson, 1985). This screening process continued for approximately two and a half years (20 generations) with fresh field material (fenvalerate discriminating dose survivors) being added to the colony as and when available, until the end of 1988/89 season. A comparable colony of endosulfan discriminating dose survivors was also maintained but was abandoned in late 1988 after no response to 12 months of selection at the 2.5 µg discriminating dose.

Once pyrethroid resistance levels stabilized, bioassays were performed against a range of pyrethroid structures including phenoxybenzyl alcohols with phenylacetic or cyclopropanecarboxylic acids and the resistance breaking simple benzyl alcohol pyrethroid, Series Two (see Section 10 for structures, sources, etc). The synergists piperonyl butoxide (Pbo) and (S,S,S, -tributylphosphoro-trithorate (Def) were used in set amounts (50 and 20 µg/30-40 mg fourth instar larva, respectively), to determine the contribution of polysubstrate monooxygenase (PSMO) or esterase mediated resistance mechanisms, respectively. The maximum sublethal dose of each synergist was applied as indicated in Appendix 2, 5-15 min prior to the insecticide dose. The various pyrethroid structures ( $\pm$  synergists) were bioassayed against both the selected pyrethroid resistant colony and a pyrethroid susceptible field strain. Resistance factors were calculated (LD<sub>50</sub> resistant strain  $\div$  LD<sub>50</sub> susceptible strain) and were considered to be significant if there was no overlap of the 95% confidence intervals. The pyrethroid resistant strain was also tested with DDT and compared to two susceptible field strains. At least 48 larvae were tested at each dose within a 0-100%

mortality range. Log dose probit lines were analysed using the Genstat statistical package.

## Results

### Pyrethroid resistance

The pooled Stage survival at the discriminating dose varied from less than 1% to just over 5%. The expected average survival was 0.9% with an upper 99% confidence limit of 2.1% (from table 42). There were five occasions when the actual survival at the discriminating dose was significantly greater than the expected upper 99% confidence limit (fig. 60). Four of these occurred in the Stage II pyrethroid window in both of the study areas in consecutive seasons.

Resistance levels to the phenoxybenzyl alcohol pyrethroids varied from 17.4x (deltamethrin) to 2.5x (cycloprothrin). There was no clear trend to higher resistance to the aromatic acid phenoxybenzyls (fenvalerate, fluvalinate, flucythrinate, cycloprothrin) compared to the aliphatic acid phenoxybenzyls (deltamethrin, cypermethrin, cyhalothrin) as was shown for pyrethroid resistant *H. armigera* (see Section 10). However, the simple benzyl alcohol pyrethroid (Series Two) was able to fully overcome pyrethroid resistance in *H. punctigera*, as it does in *H. armigera* (see Section 10). The synergists Def and Pbo gave partial and full suppression of pyrethroid resistance, respectively (table 46). However, early on in the colony's life, Pbo did not give full suppression (data not shown) so it is quite possible that an additional Pbo insensitive resistance mechanism/s may have been lost during culturing.

The pyrethroid resistant strain (LD<sub>50</sub> 1.07 µg/30-40 mg larva, 95% confidence interval 0.90 - 1.26, slope 2.8) was only 1.6x resistant to DDT (susceptible strain LD<sub>50</sub>s

Table 46. Pyrethroid resistance in a strain of *Helicoverpa punctigera* obtained initially from pooled survivors of the Emerald and Namoi/Gwydir 1987/88 and 1988/89 fenvalerate discriminating dose survivors (see fig. 60) and selected further in the laboratory with increasing fenvalerate doses (0.05-0.5 µg/30-40 mg fourth instar larva) until resistance levels stabilised (approx. F20). Synergists (Def and Piperonyl butoxide [Pbo], 20 and 50 µg/30-40 mg fourth instar larva, respectively) were applied 5-15 minutes before the insecticide dose. LD<sub>50</sub> expressed in µg/30-40 mg fourth instar larva. Resistance factors (RF) expressed as LD<sub>50</sub> resistant strain  $\div$  LD<sub>50</sub> susceptible strain. \*, ns indicate non-overlap and overlap of susceptible and resistant 95% confidence intervals, respectively.

Pyrethroid alone or + synergist	Resistant strain			Susceptible strain		
	LD <sub>50</sub> (95% Confidence limits)	Slope	RF	LD <sub>50</sub> (95% Confidence limits)	Slope	
deltamethrin	0.087 (0.074, 0.104)	2.7	17.4*	0.005 (0.004, 0.006)	2.8	
fenvalerate	0.116 (0.096, 0.141)	2.4	10.5*	0.011 (0.009, 0.012)	3.2	
fluvalinate	0.258 (0.214, 0.312)	2.3	8.0*	0.032 (0.028, 0.038)	3.3	
flucythrinate	0.111 (0.092, 0.133)	2.4	6.5*	0.017 (0.014, 0.020)	2.9	
cypermethrin	0.118 (0.095, 0.149)	1.6	6.3*	0.019 (0.016, 0.022)	3.4	
cyhalothrin	0.025 (0.019, 0.031)	1.6	6.0*	0.004 (0.003, 0.005)	3.0	
cycloprothrin	0.254 (0.213, 0.305)	2.7	2.5*	0.101 (0.083, 0.129)	2.2	
Series Two	0.032 (0.026, 0.039)	1.7	1.0 <sup>ns</sup>	0.032 (0.028, 0.037)	3.8	
Def20 + fenvalerate	0.043 (0.034, 0.054)	2.1	2.2*	0.019 (0.016, 0.023)	2.3	
Pbo50 + fenvalerate	0.014 (0.012, 0.016)	2.9	1.1 <sup>ns</sup>	0.013 (0.011, 0.016)	3.2	
Pbo50 + cycloprothrin	0.077 (0.067, 0.090)	3.5	1.2 <sup>ns</sup>	0.065 (0.055, 0.077)	3.0	
Pbo50 + fluvalinate	0.039 (0.033, 0.047)	2.6	1.3 <sup>ns</sup>	0.029 (0.025, 0.033)	3.4	

0.60 and 0.67 µg/larva, 95% confidence intervals 0.53 - 0.69 and 0.57 - 0.78, slopes 3.8 and 3.3, for DDT susceptible Emerald and Narrabri strains, respectively).

#### Endosulfan resistance

The pooled Stage survival at the discriminating dose varied from less than 1% to just over 4%. The expected average survival was 4.0% with an upper 99% confidence limit of 8.2% (from table 42). However, on no occasion did the actual survival at the discriminating dose exceed the expected upper 99% confidence limit.

The endosulfan selected laboratory colony LD<sub>50</sub> started at 0.52 µg/30-40 mg larva (95% confidence interval 0.45 - 0.61, slope 3.1), peaked at 1.41 (95% confidence interval 1.19 - 1.68, slope 2.5) and dropped to 0.77 (95% confidence interval 0.66 - 0.90, slope 3.1) by the end of the 12 month selection period. Working from an average *H. punctigera* susceptible LD<sub>50</sub> of 0.69 µg/larva (range 0.37 up to 0.97) (data from table 42), it is clear that continued laboratory selection (at 2.5 µg/30-40 mg larva) could not increase endosulfan resistance above a 2.0x vigour tolerance level.

#### Discussion

Pyrethroid resistance was detected in field populations of *H. punctigera* at low frequencies (usually <5%). It is significant that the majority of these occasions occurred within the Stage II window. It was shown in Section 2 that the immediate increase in pyrethroid resistance in *H. armigera* during this period was due to the selection of resistant adults. The eggs laid by these surviving resistant moths are then sampled and the selection pressure is immediately manifested as a sharp jump in resistance frequency. Although not specifically documented in this study, it is not unreasonable to assume that *H. punctigera* adults can also be selected for pyrethroid resistance. This would mean that pyrethroid resistance detected in *H. punctigera* within the Stage II window, would be due to selection of a local adult population. This would be the only time in the season when the impact of selection pressure would be manifested locally. Pyrethroid selection of larvae would be manifested in the following generation in Stage III and therefore subject to the confounding influence of dilution from susceptibles immigrating from the unsprayed refugia. This is particularly so for the obligate migrant *H. punctigera* which is much more mobile than the facultative migrant *H. armigera* (Zalucki *et al.*, 1986). In fact, because of its greater mobility, wider host range and complex diapause strategy, Fitt *et al.* (1989) suggest that the composition of *H. punctigera* populations may include elements of recent local origin, locally produced individuals which had entered diapause some time before and long distance migrants whose numbers are affected by seasonal climatic patterns far from the cropping areas. Thus it is no surprise that this complex mixing pattern and dilution from numerically superior susceptibles would mask any detectable resistance in Stages I and III. However, no such problem should occur in Stage II where selection pressure on adults can be immediately detected. Indeed, this was the case in this study, where low but significant levels of pyrethroid resistance

were found within the Stage II window in both intensively sprayed cotton areas in consecutive years.

Closed laboratory selection of these survivors indicated clearly that *H. punctigera* can express its resistance to the range of currently commercial available pyrethroid structures. It would seem that the dominant resistance mechanism is metabolic detoxification mediated by monooxygenases. The partial synergism indicated by Def could indicate some esterase activity as well mentioned in Section 9, Def is not a specific inhibitor and can inhibit oxidases as well. Thus the synergism by Def could simply indicate inhibition of the monooxygenase resistance mechanism without necessarily any esterase role. Early in the culture, Pbo did not give full suppression could have been due to a low level residual nerve sensitivity mechanism or a reduced penetration factor both, as was found in pyrethroid resistant *H. armigera*. However, this Pbo insensitive resistance seemed to be lost during culturing and oxidative metabolic detoxification mechanisms dominated as indicated by the partial suppression by Pbo, the full efficacy of the oxidative metabolic resistance breaking pyrethroid and the cross resistance to DDT.

No detectable endosulfan resistance was found in any Stage. This could be due to either there was no resistance to be found, or that the resistance frequency was too low to be detected. The total number of *H. punctigera* screened with endosulfan was 8041 which should be able to detect resistance frequencies down to 3.7% with 5% error (calculated from Roush & Miller's rearranged formula given in Rosenheim & Hoy, 1983). This is within the normally quoted range (10<sup>-3</sup> to 10<sup>-1</sup>) of the frequency of resistance genes in unselected populations (Wood, 1981; Georghiou, 1983). However, it cannot be concluded from this study that *H. punctigera* did not develop resistance to endosulfan, as the resistant phenotypes could well occur at lower frequencies.

The difference in detectability of pyrethroid and endosulfan resistance can probably be attributed to the greater importance of adult selection for pyrethroids. This, coupled fortuitously with a sampling procedure which can immediately detect this selection, avoids the confounding influence of population mixing and migration in a highly migratory, polyphagous species.

Many authors have long recognized that highly migratory pest species exploit a wide variety of non-economic hosts and are unlikely to be subject to extreme selection pressure encountered by other pests subject to efficient centralized control (Wood, 1981).

Table 47. Ecology of *Helicoverpa punctigera* and *Helicoverpa armigera* host plants (data derived from Zalucki *et al.*, 1986)

	No. of host plants (% of total in brackets)		
	<i>Helicoverpa punctigera</i>	<i>Helicoverpa armigera</i>	
Unsprayed	Native	30 (24%)	8 (11%)
	Naturalised weed/garden	36	21
	Crops	41	24
Sprayed	Crops	20 (16%)	22 (29%)
Total		127	75

Bishop, 1981; Tabashnik & Croft, 1982). *Helicoverpa punctigera* would seem to fit well into this category. This polyphagous species has a wide range of predominantly (84%) unsprayed hosts (table 47) and is highly migratory, being well adapted to the erratic distribution of rainfall and suitable hosts in inland Australia (Farrow & Daly, 1987). On the other hand, the relatively oligophagous and facultatively migratory *H. armigera*, seems less well adapted to the Australian scene. It has relatively few native hosts and a high proportion (29%) of sprayed host crops (table 47). Bull & Menn (1990) suggest a similar scenario for the American *Heliothis/Helicoverpa* complex (*Heliothis virescens* and *Helicoverpa zea* being ecologically equivalent to *H. armigera* and *H. punctigera*, respectively). Resistance would also be expected to evolve faster in the less mobile, oligophagous *H. armigera* due to significant pre-mating selection pressure, particularly in the mixed cropping areas (see Sections 2 & 7). On the other hand, resistance would be expected to evolve much slower in *H. punctigera* due to predominant post-mating selection pressure (immigrating females generally pre-mated) (Georghiou & Taylor, 1976, 1986; Wood & Bishop, 1981; Wood & Mani, 1981; Mani & Wood, 1984; Rosenheim & Hoy, 1988).

The preceding information can help to explain the recidivist resistance nature of *H. armigera*. Australia has always figured prominently at the forefront of insecticide resistance problems in *Helicoverpa/Heliothis* spp. (e.g. DDT resistance in the Ord, pyrethroid resistance at Emerald). Some people suggest that this reflects poorly

on the pest management practices of Australian summer crop growers. However, an unfortunate combination of a poorly adapted, possibly relatively recent immigrant in an ecosystem dominated by recurring droughts, has probably had a far greater impact on resistance development than putative poor pest management. The already relatively narrow range of hosts for *H. armigera* would be even further restricted to irrigated crop hosts during periods of drought. *Helicoverpa armigera* populations would be then concentrated on these high value irrigated crops such as cotton and would be subject to intense selection pressure with little opportunity for dilution. Thus, it is not surprising, in a land where frequent droughts are the rule rather than the exception, that resistance in *H. armigera* has been an all too familiar problem.

The above situation with *H. armigera* contrasts sharply with that in *H. punctigera*. This difference clearly illustrates the value of maintaining an effectively large susceptible gene pool. One of the first workers to recognize this was Benson who in his remarkably avant-garde 1971 treatise on IRM (Benson, 1971), went so far as to suggest the large scale release of susceptible insects into the pest population even if it meant 'sacrificing some of our food to the right insects, those with susceptible genotypes'. He suggested that this 'genetic infusion' technique would be the only ultimate long-term solution to IRM as it 'controlled the evolution of pest species'. Perhaps the case of self regulated resistance management in *H. punctigera* described in this paper, is a living example of Benson's 'ultimate IRM solution'.

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