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A survey of insecticide resistance in *Helicoverpa armigera* in the Indian subcontinent

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Abstract

Helicoverpa armigera (Hübner) larvae were collected from field crops and wild hosts in India, Nepal and Pakistan from 1991 to 1995, and ninety eight laboratory cultures established. Cypermethrin, fenvalerate, endosulfan, quinalphos, monocrotophos and methomyl insecticides were topically applied to 30–40 mg, first laboratory generation larvae and resistance determined from log dose probit bioassays. Significant levels of cypermethrin and fenvalerate resistance were found in all field strains, demonstrating that resistance to at least some pyrethroids is now ubiquitous in *H. armigera* populations in the Indian subcontinent; cypermethrin and fenvalerate resistance levels ranged from 5- to 6500-fold and 16- to 3200-fold respectively. Pyrethroid resistance levels were highest in the intensive cotton and pulse growing regions of central and southern India where excessive application of insecticide is common. In all field strains assayed, pre-treatment with the metabolic synergist piperonyl butoxide (pbo), resulted in significant suppression of pyrethroid resistance. However, in nearly all cases, full suppression of resistance was not achieved. This residual non-pbo-suppressible resistance was most likely due to a nerve-insensitivity resistance mechanism. Pbo-insensitive resistance was highest in regions of India where insecticides were frequently applied to cotton and legume crops. In some regions where insecticides were heavily overused, a second high order nerve-insensitivity mechanism (possibly a *Super-Kdr* type mechanism), may have been present. Incipient endosulfan resistance (1–28-fold), was present throughout India, Nepal and Pakistan. Low to moderate levels of resistance (2–59-fold), were reported to the phosphorothionate group organophosphate, quinalphos, in India and Pakistan, but there was no evidence of significant resistance (0.4–3-fold), to the phosphate group organophosphate, monocrotophos, under our bioassay conditions between 1993 and 1994. *H. armigera* strains collected in Nepal in 1993 and 1994 were susceptible to quinalphos, but by 1995, 4–5-fold resistance was detected. It is probable that much of the resistance to pyrethroid, organophosphate and carbamate insecticides in the Indian subcontinent can be attributed to an inherited or inducible mixed function oxidase complex. Non-pbo-suppressible resistance becomes significant in regions and periods in the season when insecticide selection pressure on resistant *H. armigera* larvae on cotton and legume crops is very high.

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Introduction

The cotton bollworm, *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae), is the major pest of cotton and legumes in most regions of the Indian subcontinent. Annual yield losses attributable to this pest in India alone are estimated to be of the order of US$ 290–350 million per annum (Indian Council of Agricultural Research, unpublished data). In recent years, insecticide control of *H. armigera* has become increasingly difficult, particularly as its pest status on cotton has increased dramatically in the past twelve years and over the last nine years it has developed resistance to most chemical classes of insecticides commonly used by cotton and legume growers in the subcontinent. Insecticide resistance was first implicated in failures to control *H. armigera* on cotton in 1987, when high levels of resistance to those pyrethroids in commercial use at the time were reported in bollworm populations in south-east India (Dhingra *et al.*, 1988; McCaffery *et al.*, 1989). Cotton yield losses in this region, resulting from field control failures during the 1987–88 season, were estimated at US$ 150 million (N.M. Kishor, unpublished report). Prior to 1989, it was believed that insecticide resistance was restricted to populations in the south-east India coastal cotton growing area (Dhingra *et al.*, 1988). However, bioassays conducted between 1989 and 1991 showed that cypermethrin-resistant populations were common throughout southern India and tolerance to endosulfan, some organophosphates and methomyl had increased significantly (Armes *et al.*, 1992). By 1991, resistance to cypermethrin had been reported in *H. armigera* from cotton crops in the northern Indian state of Punjab (Mehrotra & Phokela, 1992), where its pest status had changed from minor to major since 1988 and had, in some seasons displaced the 'traditional' cotton bollworm pests, *Pectinophora gossypiella* Saunders and *Earias* spp., (Lepidoptera: Noctuidae). Similarly, in Bangladesh, the pest status of *H. armigera* has increased markedly since the late 1980s and in 1993 it was reported that control with pyrethroid insecticides was becoming less effective; resistance was implicated, but this has yet to be confirmed by laboratory tests (Ibrahim Ali, 1994).

A basic tenet of resistance management is that refugia of unsprayed susceptible (or at least less resistant) insects exist to decrease resistance frequencies by immigration and subsequent breeding with populations in heavily insecticide treated crops (Tabashnik & Croft, 1982; Forrester *et al.*, 1993). With increasing reports of poor field control of *H. armigera* with insecticides over large areas of India and the likelihood that gene flow through migration had been sufficiently high to introduce resistance alleles into *H. armigera* populations in regions where insecticides were little used (Armes *et al.*, 1994), it was important to confirm the status of resistance to the major chemical classes of insecticides used by farmers for *H. armigera* control. This paper reports the results of a resistance survey on *H. armigera* collected from a wide range of host plants subject to differing insecticide selection pressures from 1991 to 1995 in India, Nepal and Pakistan. The aims were to determine if refugia of susceptible *H. armigera* existed in the major cotton and pulse growing regions of India and to identify where resistance problems were most acute.

Materials and methods

Sample collection and bioassay

Third to sixth instar *H. armigera* larvae were collected from a range of host plants at various times over four cropping seasons between 1991 and 1995. Most collections comprised 100–400 larvae sampled from usually one or occasionally two to three nearby fields planted to the same crop. In the laboratory, larvae were reared on a chickpea flour based artificial diet. Laboratory cultures of each strain were established from 50–300 moths. Bioassays were conducted on 30–40 mg F1 larvae using a topical application procedure detailed previously (Armes *et al.*, 1992), based on the standard *Heliothis* susceptibility test recommended by the Entomological Society of America (Anon., 1970).

In general, at least 48 larvae were treated at each of five or more concentrations of technical grade insecticide in analytical grade acetone. Using a microapplicator, 1.0 µl of solution was applied to the dorsal thorax. Control larvae were treated with acetone alone. In pyrethroid assays including the oxidative synergist piperonyl butoxide (pbo), this was applied to the thorax of larvae at a set rate of 50 µg/larva, 20–30 min prior to application of either cypermethrin or fenvalerate.

Treated larvae were held individually in 7.5-ml cells of 12-well, tissue culture plates (Linbro, ICN Flow Ltd.), and provided with excess chickpea-based artificial diet. End point mortality was assessed at 144 h after treatment; larvae were considered dead if they were unable to move in a co-ordinated manner when prodded. Control mortality was uncommon and never exceeded 2%; where necessary, correction was made with Abbott's formula (Abbott, 1925).

Log dose probit (ldp) mortality regressions were computed using MLP 3.08 software (Ross, 1987). Significance of differences between treatments with and without pbo were determined from Position χ^2 (test to determine whether relative potencies differ from unity), and Parallelism χ^2 (test to determine whether a common slope is adequate). Heterogeneity χ^2 tests were performed on all probit lines to determine whether or not residual variation was consistent with binomial sampling (Ross, 1987).

Rearing and bioassays were conducted at 25 ± 2°C, either under natural photoperiod (*c.* 13:11 h light:dark), at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), India, or constant 14:10 h light:dark at the Natural Resources Institute (NRI), UK.

Wherever possible, farmers were interviewed to determine the number of insecticide sprays applied to their crop up to the time of sampling. The data given in table 1 does not include early season sprays (up to 40 days after sowing), on cotton and legumes for control of aphids and jassids (e.g. dimethoate, metasystox, monocrotophos), as these were applied before *H. armigera* infestation occurred on the crop.

Insecticide susceptible strains

In view of the fact that no insecticide-susceptible *H. armigera* strains of Indian origin were found during the course of the study, three laboratory maintained susceptible strains derived from Africa and China were used for ldp comparisons with the field collected strains. The Reading strain was obtained from Reading University, UK, and had

been maintained in a number of laboratories for at least 15 years, and was believed to have originated from southern Africa. The NRI strain was originally collected from the Gedaref region of Sudan where insecticides were little used for *H. armigera* control, and had been in culture at NRI for over three years. The Nanjing strain was from Nanjing Agricultural University, Jiangsu Province, China, where it had been maintained in culture for approximately two years. This strain was tolerant to pyrethroid insecticides (by enhanced metabolic detoxification), and was therefore used only for endosulfan comparisons. Endosulfan was released for commercial use in China after the Nanjing laboratory strain had been established. Bioassays showed this strain to be fully susceptible to endosulfan.

Sampling regions

Sampling locations were categorized into agro-climatic regions corresponding to the India Planning Commission's Resource Development Regions (see table 1 and fig. 1), described by Geddes & Iles (1991). They ranked major pests and diseases in India in terms of economic importance and identified *H. armigera* as 'very important' in regions 8, 9 and 13; 'important' in 5, 6, 10, 11 and 14; 'significant' in region 7. Nepal is divided into three cropping system zones (Geddes & Iles, 1991). *H. armigera* strains were collected from two zones; the Tarai and Siwaliks zone which is the main cropping region of the country on the low plains, and from the Middle Mountains zone where it is a major pest on vegetables. Pakistan has six major cropping zones

Table 1. Sources of *Helicoverpa armigera* strains collected as larvae from host plants between 1991 and 1995 and bioassayed in the F1 (excluding strains from the IAC farm).

Region, State	Map ref.*	Collect date	Parental host	No. of sprays	Region, State	Map ref.*	Collect date	Parental host	No. of sprays
Region 4					Malkapur, A.P.	6	Nov. 91	Pigeonpea	3
Varanasi, U.P.	45	Oct. 91	Pigeonpea	0	Ibrahimpatan, A.P.	7	Dec. 91	Pigeonpea	0
Varanasi, U.P.	45	Mar. 92	Chickpea	0	Homnabad, K.	11	Jan. 92	Chickpea	0
Varanasi, U.P.	45	Apr. 92	Pigeonpea	0	Abilabad, A.P.	13	Jan. 92	Chickpea	0
Varanasi, U.P.	45	Oct. 93	Pigeonpea	0	Vikarabad, A.P.	8	Feb. 92	Chickpea	0
Region 6					Narayankher, A.P.	2	Feb. 92	Chickpea	0
New Delhi, Delhi	46	Nov. 91	Pigeonpea	0	Zahirabad, A.P.	3	Feb. 92	Chickpea	1
Region 7					Coimbatore, T.N.	15	Feb. 92	Chickpea	2
Dhenkanal, O.	44	Feb. 93	C'pea+Saff	0	Neredikonda, A.P.	12	Oct. 92	Cot+P'pea	0
Raipur, M.P.	43	Feb. 93	C'pea+Saff	0	Coimbatore, T.N.	15	Oct. 92	Cotton	3
Durg, M.P.	42	Feb. 93	C'pea+Must	0	Coimbatore, T.N.	15	Feb. 93	Chickpea	0
Rajnandgaon, M.P.	41	Feb. 93	Pigeonpea	0	Narsapur, A.P.	9	Apr. 93	Tomato	3
Deori, M.	40	Feb. 93	C'pea+Lin	0	Coimbatore, T.N.	15	Nov. 93	Okra	2
Region 8					**Region 11**				
Sodalpur, M.P.	39	Jan. 92	Chickpea	3–5	Pulladigunta, A.P.	16	Aug. 91	Cotton	3
Region 9					Jujuru, A.P.	20	Aug. 91	Cotton	8
Tuljapur, M.	35	Oct. 91	Pigeonpea	1	Pulladigunta, P.A.	16	Sep. 91	Cotton	8
Nandur, M.	33	Oct. 91	Pigeonpea	0	Guntur, A.P.	17	Sep. 91	Cotton	10
Badnapur, M.	27	Oct. 91	Pigeonpea	1	Guntur, A.P.	17	Sep. 91	Cotton	8
Akola, M.	29	Oct. 91	Cotton	1	Nandigama, A.P.	19	Sep. 91	Cotton	4
Akola, M.	29	Oct. 91	Pigeonpea	1	Guntur, A.P.	17	Sep. 91	Cotton	3
Yavatmal, M.	31	Oct. 91	P'pea+Cot	5	Guntur, A.P.	17	Oct. 91	Cotton	7
Rahuri, M.	26	Jan. 92	Chickpea	1	Guntur, A.P.	17	Dec. 91	Pigeonpea	4
Nashik, M.	25	Jan. 92	Chickpea	0	Pulladigunta, A.P.	16	Dec. 91	Chickpea	0
Jhabua, M.P.	23	Jan. 92	Chickpea	0	Srikakulum, A.P.	22	Jan. 92	Tomato	0
Kannod, M.P.	24	Jan. 92	Chickpea	0	Guntur, A.P.	17	Oct. 92	Cotton	6
Hinghanghat, M.	30	Jan. 92	Chickpea,	0	Guntur, A.P.	17	Nov. 92	Cotton	14
Indapur, M.	36	Aug. 92	Mung bean	0	Guntur, A.P.	17	Oct. 93	Cotton	11
Umri, M.	34	Sep. 92	Cotton	3	Bapatla, A.P.	18	Mar. 94	Groundnut	5–6
Barsi Takli, M.	28	Sep. 92	Sorg+Cot	5	Rajahmundry	21	Jul. 94	Cleome	0
Akola, M.	29	Sep. 92	Sorg+Cot	4	**Region 13**				
Parbhani, M.	32	Oct. 92	P'pea+Cot	6	Vansada, G.	37	Jan. 92	Chickpea	0
Region 10					Dahod, G.	38	Jan. 92	Chickpea	1
Morangpalli, A.P.	4	Jul. 91	Cotton	2	Dahod, G.	38	Feb. 94	Chickpea	2
Morangpalli, A.P.	4	Aug. 91	Cotton	6	**Nepal**				
Morangpalli, A.P.	4	Sep. 91	Cotton	10	Pokhara, Gandaki	47	Apr. 93	Tomato	Spr?
Shankarpalli, A.P.	5	Sep. 91	Cotton	8	Pokhara, Gandaki	47	May 94	Tomato	Spr?
Adilabad, A.P.	13	Oct. 91	P'pea+Cot	9	Nepalganj, Bheri	48	Apr. 95	Chickpea	Spr?
Dichpalli, A.P.	10	Oct. 91	Pigeonpea	0	Pokhara, Gandaki	47	Apr. 95	Tomato	Spr?
Dharwad, K.	14	Oct. 91	Cotton	3	**Pakistan**				
Shankarpalli, A.P.	5	Nov. 91	C'pea+Sun.	0	Bahawalnagar	49	Nov. 91	Cotton	5

States: A.P., Andhra Pradesh; G., Gujarat; K. Karnataka; M., Maharashtra; M.P., Madhya Pradesh; O., Orissa; T.N., Tamil Nadu; U.P., Uttar Pradesh.

*Map reference refers to fig. 1.

Host plants: Cot, cotton; C'pea, chickpea; Lin, linseed; Must, mustard; P'pea, pigeonpea; Saff, safflower; Sorg, sorghum; Sun, sunflower.

Insecticides: Spr?, sprayed but no. of applications not known.

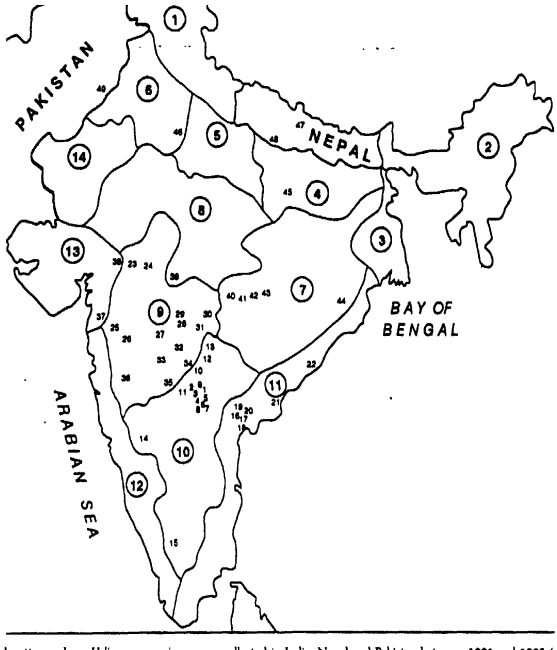

Fig. 1. Sampling locations where *Helicoverpa armigera* were collected in India, Nepal and Pakistan between 1991 and 1995 (refer to table 1 for key to locations).

(Geddes & Iles, 1991). Only one strain was collected during the course of this study, from the Northern irrigated plains, where *H. armigera* is considered 'very important' on cotton.

Insecticides

The following technical grade insecticides were used for bioassays: *c.* 50:50 *cis*:*trans* cypermethrin (900 g/kg; Zeneca Agrochemicals, UK); endosulfan (940 g/kg; Excel Industries, India); fenvalerate (976 g/kg; Sumitomo Corp., Japan; methomyl (980 g/kg; DuPont, France); monocrotophos (680 g/kg, Khatau Junker, India); quinalphos (720 g/kg; Sandoz, India). The synergist, piperonyl butoxide (2-(2-butoxyether)-ethyl-6-propyl piperonyl ether) (900 g/kg), was obtained from Gooddeed Chemical Co. Ltd., UK.

Results

Ninety eight strains were collected and bioassayed from 51 locations between July 1991 and April 1995 (table 1, fig. 1). For logistical reasons, by far the largest number of samples were from regions 9 and 10. By virtue of the crops grown, and principally because of the absence of cotton and pulses in the cropping systems, *H. armigera* is of minor significance in regions 1 (primarily wheat, maize and rice), 2 and 3 (rice, tea, jute, potato), 12 (rice, coffee, coconut, cassava) and 15 (Andaman, Nicobar and Lakshadweep Islands growing primarily coconut and rice). Therefore the only major *H. armigera* source areas in India not covered by this survey were regions: 5 (western Uttar Pradesh growing wheat, sugarcane, rice, chickpea), and 14 (western Rajasthan growing chickpea, millet, wheat, mustard). Four strains were obtained from two of the three cropping system zones recognized in Nepal (Geddes & Iles, 1991), one from the Tarai region where *H. armigera* is an important pest of pulses and three from the middle mountains region where *H. armigera* was not ranked as a pest. A single strain was obtained from Pakistan from cotton in the northern irrigated plains where *H. armigera* was ranked as very important.

Insecticide susceptible strains

Cypermethrin was assayed against two susceptible strains and variation in the LD_{50} response was less than

3-fold between these (table 2). Slopes were quite high (average 2.4), and heterogeneity was not significant (Heterogeneity χ^2, $P > 0.1$). Fenvalerate was only tested on the Reading strain on two occasions, approximately one year apart. LD_{50}'s and slopes (average 2.1), did not change between years. Similarly, quinalphos was tested against the same strain as was fenvalerate and on the same occasions; no significant difference between LD_{50}s were recorded and slopes were high in both tests (average 2.4). Endosulfan was assayed on two occasions for each of two strains; there was little variability in LD_{50}s (1.5-fold) and slopes, which were high (average 3.0). A 4.6-fold variation in monocrotophos LD50's was observed between the Reading and Nanjing susceptible strains. The steepest slope (4.3) was recorded for the Nanjing strain. Methomyl was only tested against one strain on one occasion; the slope was reasonably high (2.0) and heterogeneity was not significant (Heterogeneity χ^2, $P > 0.1$).

Pyrethroid resistance

Cypermethrin LD_{50}'s ranged from 0.05–65 µg/larva (table 3). All 98 field strains recorded significant tolerance or resistance compared to the laboratory susceptible strains, with resistance factors (RFs), ranging from 5- to 6500-fold. Slope values for field strains ranged from 0.6–2.6, compared to 1.8–3.0 for the laboratory susceptible strains. Seventy-five percent of field strains recorded ldp slope values lower than the lowest slope for a susceptible strain (1.8), suggesting phenotypic segregation. Only two of the field strains recorded RFs of less than 10. These were from Badnapur, Maharashtra (RF=5), from insecticide sprayed pigeonpea in 1991 and from Nepal (RF=8), collected from insecticide sprayed tomatoes in 1993. The ldp line of the Nepal strain showed systematic curvilinearity and significant heterogeneity (Heterogeneity χ^2, $P < 0.01$), indicating that, despite its low RF, the test population comprised a mix of susceptible and resistant phenotypes.

Looking at the data overall, it was not possible to identify obvious associations between cypermethrin resistance levels and geographic regions. In part this may be because, for regions other than 9, 10 and 11, the number of samples collected was small and collections were generally made only once. Within India, the northern regions 4 and 6 where larvae were collected from unsprayed pigeonpea and chickpea, recorded the lowest cypermethrin resistance levels (RFs 20–37), but the number of strains assayed was small. All the high resistance levels (RFs > 100), were from the central area of India comprising regions 7, 8, 9, 10 and 11 (plus one collection from Coimbatore in the south peninsular). Region 11 consistently recorded very high resistance levels (RFs > 1000). The Guntur district cotton growing belt was prominent in this regard. Risk-averse farmers in this district regularly make 20–30 applications to cotton crops in a season. Interestingly however, resistance levels varied markedly over relatively short distances. For example, in September 1991 five samples were collected in region 11, each separated by a maximum of 58 km and RFs ranged from 23–1700. Such large variations in resistance are most likely a reflection of within-field selection in the larval samples collected, as the highest resistance levels (RFs of 670 and 1700), were recorded from fields with the most intensive insecticide inputs (8–10 sprays on the crop prior to the time of sampling). The single sample collected in January 1992 from unsprayed tomatoes in Srikakulum, recorded much lower resistance (RF=49), at a time in the season when pyrethroid resistance in region 11 was expected to be at its peak because of intensive spraying on cotton crops from September to November (see Discussion). Although in region 11, Srikakulum is approximately 370 km north-east of the main cotton belt, and the strain was collected in a tribal region where subsistence farmers rarely use pesticides. The highest pyrethroid resistance level recorded since monitoring commenced in India in 1986, was the Bapatla sample collected from heavily sprayed groundnut in March 1994 (RF=6500).

Table 2. Toxicity of topically applied insecticides to 30–40 mg *Helicoverpa armigera* larvae derived from susceptible laboratory strains.

Insecticide/Strain	*n*	LD_{50} (95% C.I.) (µg/larva)		LD_{90}	Slope ±S.E.
Cypermethrin					
Reading susceptible	240	0.0062	(0.005–0.007)	0.017	3.0±0.3
Reading susceptible	288	0.0073	(0.006–0.009)	0.025	2.4±0.2
NRI susceptible	240	0.017	(0.01–0.02)	0.13	1.8±0.2
Fenvalerate					
Reading susceptible	240	0.019	(0.01–0.02)	0.083	2.0±0.2
Reading susceptible	240	0.018	(0.01–0.02)	0.070	2.2±0.3
Endosulfan					
Reading susceptible	210	0.65	(0.55–0.78)	1.8	3.0±0.4
Reading susceptible	212	0.63	(0.53–0.75)	1.7	3.0±0.4
Nanjing susceptible	239	0.44	(0.36–0.53)	1.5	2.5±0.3
Nanjing susceptible	240	0.67	(0.57–0.79)	1.5	3.6±0.5
Quinalphos					
Reading susceptible	240	0.052	(0.04–0.07)	0.21	2.1±0.3
Reading susceptible	240	0.056	(0.05–0.07)	0.17	2.6±0.3
Monocrotophos					
Reading susceptible	240	0.87	(0.71–1.1)	3.6	2.1±0.2
Reading susceptible	288	0.65	(0.50–0.85)	5.2	1.4±0.2
Nanjing susceptible	240	0.19	(0.16–0.21)	0.37	4.3±0.5
Methomyl					
Reading susceptible	248	0.13	(0.11–0.17)	0.61	2.0±0.3

Table 3. Toxicity of topically applied cypermethrin to 30–40 mg larvae of field strains of *Helicoverpa armigera*.

Strain	Map ref.	Collect date	*n*	LD_{50} (95% C.I.) (μg/larva)		LD_{90}	Slope ±S.E.	RF[a]
Region 4								
Varanasi	45	Oct. 91	522	0.20	(0.16–0.26)	1.3	1.6±0.1	20
Varanasi	45	Mar. 92	261	0.31	(0.23–0.41)	2.1	1.6±0.2	31
Varanasi	45	Apr. 92	236	0.30	(0.23–0.39)	1.6	1.7±0.2	30
Varanasi	45	Oct. 93	180	0.24	(0.19–0.31)	1.0	2.1±0.3	24
Region 6								
New Delhi	46	Nov. 91	237	0.37	(0.27–0.50)	2.4	1.6±0.2	37
Region 7								
Dhenkanal	44	Feb. 93	288	0.78**	(0.63–0.95)	2.9	2.2±0.2	78
Raipur	43	Feb. 93	288	0.71	(0.59–0.86)	2.5	2.3±0.2	71
Durg	42	Feb. 93	432	0.83*	(0.66–1.2)	5.4	1.6±0.1	83
Rajnandgaon	41	Feb. 93	384	1.4**	(1.1–1.8)	9.7	1.5±0.1	140
Deori	40	Feb. 93	528	0.81	(0.62–1.1)	10	1.2±0.1	81
Region 8								
Sodalpur	39	Jan. 92	157	2.5	(2.0–3.2)	8.0	2.6±0.4	250
Region 9								
Tuljapur	35	Oct. 91	226	0.19	(0.14–0.28)	1.5	1.5±0.2	19
Nandur	33	Oct. 91	223	0.17	(0.11–0.26)	2.2	1.2±0.2	17
Badnapur	27	Oct. 91	234	0.054	(0.04–0.07)	0.27	1.8±0.2	5
Akola	29	Oct. 91	234	0.27	(0.17–0.40)	4.3	1.1±0.2	27
Akola	29	Oct. 91	285	0.12	(0.08–0.15)	0.80	1.5±0.2	12
Yavatmal	31	Oct. 91	334	0.17	(0.12–0.24)	2.6	1.1±0.1	17
Rahuri	26	Jan. 92	280	4.8	(3.7–6.3)	31	1.6±0.2	480
Nashik	25	Jan. 92	202	0.72	(0.51–0.98)	4.9	1.5±0.2	72
Jhabua	23	Jan. 92	195	0.72	(0.53–1.0)	5.0	1.5±0.2	72
Kannod	24	Jan. 92	298	0.31	(0.22–0.44)	4.4	1.1±0.2	31
Hinganghat	30	Jan. 92	200	0.27	(0.21–0.34)	1.2	2.0±0.3	27
Indapur	36	Aug. 92	243	0.89	(0.61–1.2)	6.9	1.4±0.2	89
Umri	34	Sep. 92	411	3.0	(2.2–4.2)	67	1.0±0.1	300
Barsi Takli	28	Sep. 92	243	0.66	(0.53–0.83)	3.4	1.8±0.2	66
Akola	29	Sep. 92	241	0.97	(0.76–1.3)	5.5	1.7±0.2	97
Parbhani	32	Oct. 92	250	0.64	(0.48–0.85)	4.5	1.5±0.2	64
Region 10								
Morangpalli	4	Jul. 91	221	0.33	(0.26–0.42)	1.3	2.2±0.3	33
Morangpalli	4	Aug. 91	197	1.3	(1.2–2.7)	20	1.2±0.2	130
Morangpalli	4	Sep. 91	303	8.4	(6.1–12)	82	1.3±0.1	840
Shankarpalli	5	Sep. 91	245	0.44	(0.32–0.65)	3.5	1.4±0.2	44
Adilabad	13	Oct. 91	198	1.0	(0.72–1.4)	8.5	1.4±0.2	100
Dichpalli	10	Oct. 91	265	0.46	(0.36–0.58)	2.5	1.8±0.2	46
Dharwad	14	Oct. 91	270	0.53	(0.42–0.67)	2.6	1.9±0.2	53
Shankarpalli	5	Nov. 91	230	0.43	(0.32–0.58)	2.8	1.6±0.2	43
Malkapur	6	Nov. 91	261	0.38	(0.23–0.60)	10	0.9±0.1	38
Ibrahimpatan	7	Dec. 91	220	0.20	(0.13–0.31)	2.5	1.2±0.1	20
Hornabad	11	Jan. 92	260	1.1	(0.87–1.5)	5.6	1.9±0.2	110
Adilabad	13	Jan. 92	173	1.2	(0.83–1.8)	13	1.3±0.2	120
Vikarabad	8	Feb. 92	275	0.84	(0.60–1.2)	10	1.2±0.2	84
Narayankher	2	Feb. 92	310	0.50	(0.29–0.78)	22	0.8±0.1	50
Zahirabad	3	Feb. 92	181	0.90	(0.59–1.3)	11	1.2±0.2	90
Coimbatore	15	Feb. 92	221	0.62*	(0.47–0.81)	3.3	1.8±0.2	62
Neredikonda	12	Oct. 92	239	2.1	(1.5–3.1)	24	1.2±0.1	210
Coimbatore	15	Oct. 92	227	0.83	(0.59–1.2)	7.5	1.3±0.2	83
Coimbatore	15	Feb. 93	432	1.4*	(1.1–1.8)	9.3	1.6±0.1	140
Narsapur	9	Apr. 93	336	0.58	(0.44–0.74)	4.1	1.5±0.1	58
Coimbatore	15	Nov. 93	235	0.25	(0.19–0.33)	1.7	1.5±0.2	25
Region 11								
Pulladigunta	16	Aug. 91	380	0.27	(0.19–0.43)	7.3	0.9±0.1	27
Jujjuru	20	Aug. 91	204	1.4	(0.95–2.1)	14	1.3±0.2	140
Pulladigunta	16	Sep. 91	304	6.7	(4.7–9.9)	133	1.0±0.1	670
Guntur	17	Sep. 91	343	17	(13–25)	216	1.2±0.1	1700
Guntur	17	Sep. 91	230	0.46	(0.35–0.61)	2.8	1.6±0.2	46
Nandigama	19	Sep. 91	237	0.53	(0.41–0.69)	3.2	1.6±0.2	53
Guntur	17	Sep. 91	200	0.23	(0.15–0.36)	2.6	1.2±0.1	23
Guntur	17	Oct. 91	254	1.4	(0.90–2.1)	25	1.0±0.1	140
Guntur	17	Dec. 91	280	12	(8.3–19)	286	0.9±0.1	1200
Pulladigunta	16	Dec. 91	268	0.93	(0.65–1.3)	12	1.2±0.2	93

Table 3—*continued opposite*

Table 3—*continued from previous page*

Strain	Map ref.	Collect date	*n*	LD_{50} (μg/larva)	(95% C.I.)	LD_{90}	Slope ±S.E.	RF*
Srikakulum	22	Jan. 92	215	0.49	(0.37–0.64)	2.5	1.8±0.2	49
Guntur	17	Oct. 92	245	0.37	(0.28–0.48)	2.5	1.5±0.2	37
Guntur	17	Nov. 92	280	14	(7.6–28)	1627	0.6±0.1	1400
Guntur	17	Oct. 93	276	3.4	(2.1–5.2)	102	0.9±0.2	340
Bapatla	18	Mar. 94	213	65**	(28–6689)	–	0.6±0.2	6500
Rajahmundry	21	Jul. 94	198	0.73	(0.49–1.0)	8.5	1.2±0.2	73
Region 13								
Vandada	37	Jan. 92	218	1.2	(0.97–1.6)	5.9	1.9±0.2	120
Dahod	38	Jan. 92	255	0.20	(0.13–0.32)	5.4	0.9±0.1	20
Dahod	38	Feb. 94	237	0.33	(0.26–0.43)	1.6	1.9±0.2	33
Nepal								
Pokhara	47	Apr. 93	410	0.082**	(0.06–0.11)	0.86	1.3±0.1	8
Pokhara	47	May 94	240	0.39	(0.31–0.48)	1.4	2.3±0.3	39
Nepalganj	48	Apr. 95	369	0.72	(0.60–0.87)	4.0	1.7±0.2	72
Pokhara	47	Apr. 95	240	0.19	(0.15–0.26)	1.5	1.4±0.2	19
Pakistan								
Bahawalnagar	49	Nov. 91	200	4.6	(3.3–6.1)	24	1.8±0.2	460

*RF (resistance factor)=LD_{50} field strain/LD_{50} susceptible strain (from table 2).
Heterogeneity χ^2: *, significant at $P < 0.05$; **, $P < 0.01$.

Characteristically, for such highly resistant strains, the ldp line slope was shallow (0.58), and showed obvious segregation of phenotypes (Heterogeneity χ^2, $P < 0.01$).

Resistance levels in regions 9 and 10 were similar (RFs ranging from 5- to 840-fold), reflecting the similar insecticide use patterns for *H. armigera* control on cotton and legumes in south central India (typically 6–15 applications to cotton and 2–5 to legumes). The highest resistance levels were recorded either in strains collected from sprayed cotton or from late season samples from legumes from January onwards. High tolerance levels had developed even on unsprayed crops, because of cumulative selection for resistance over the earlier part of the season; firstly on cotton and later on legumes, with most insecticide being applied to field crops between September and December.

The three samples collected from chickpea in the west Indian state of Gujarat (region 13), recorded moderate to high cypermethrin resistance (RF=20–120).

In the middle mountains region of Nepal, cypermethrin resistance was highest in 1994 (RF=39), when *H. armigera* populations on tomato crops were high, necessitating 2–6 insecticide sprays to contain bollworm damage. In 1995, populations on tomato were lower, hence less frequent insecticide applications were made, most probably accounting for the lower resistance levels (RF=19) at that time. The highest cypermethrin resistance (RF=72), in Nepal was recorded in the single strain collected from chickpea in the Terai region. This is the most intensively cultivated region in the country and insecticides are widely used.

The single *H. armigera* strain collected from sprayed cotton in the Bahawalnagar region of the Pakistan Punjab in 1991 was highly resistant to cypermethrin (RF=460).

At the ICRISAT Asia Center (IAC) farm, it was possible to collect *H. armigera* larvae at fairly regular intervals over three cropping seasons. LD_{50} values are plotted in fig. 2 and clear seasonal resistance patterns were apparent. Resistance increased steadily over each season reaching a peak in samples collected from chickpea in March. This correlated with increased insecticide usage with progression of the cropping season from September to March. April collections in 1992 from chickpea and in 1993 from the wild host *Lagascea mollis* (Compositae) exhibited lower resistance (particularly in 1992). In 1994, residual soil moisture was lower than previous years and rapid drying up of host plants with the progression of the dry summer season precluded finding significant *H. armigera* populations beyond March, so no end of season decrease in resistance could be determined in that year. Cypermethrin resistance levels were highest over the 1991/92 season (maximum LD_{50}=8.1 μg/larva) and lowest over 1993/94 (maximum LD_{50}=1.7 μg/ larva).

Twenty strains from nine regions were assayed with fenvalerate (table 4) and all were significantly resistant, with RFs ranging from 16- to >3000-fold. In general, resistance levels were similar to those reported for cypermethrin tested on the same strains, but on average, RFs were marginally higher for fenvalerate.

Pbo suppression of pyrethroid resistance

The effect of pre-treatment with pbo on cypermethrin and fenvalerate resistance was assayed on 34 and 13 strains

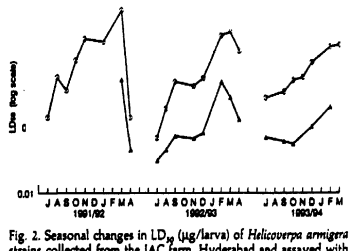

Fig. 2. Seasonal changes in LD_{50} (μg/larva) of *Helicoverpa armigera* strains collected from the IAC farm, Hyderabad and assayed with cypermethrin alone (open circles) and cypermethrin in combination with piperonyl butoxide (closed triangles) over three consecutive cropping seasons from 1991 to 1994.

Table 4. Toxicity of topically applied fenvalerate and effect of piperonyl butoxide in suppressing fenvalerate resistance in 30–40 mg larvae derived from field strains of *Helicoverpa armigera*.

Strain	Map ref.	Collect date	Fenvalerate alone			Fenval.+Pbo pretreatment			
			LD_{50} (µg/larva)	Slope	RF[a]	LD_{50} (µg/larva)	Slope	RF[b]	SR[c]
Reading susceptible	–	–	0.019	2.0	–	0.018	2.2	–	1
Region 4									
Varanasi	45	Oct. 91	1.3	1.9	70	0.078	2.1	4	17
Region 6									
New Delhi	46	Nov. 91	1.5	1.6	81	0.022	1.7	1	68
Region 7									
Dhenkanal	44	Feb. 93	1.5***	1.6	81	0.080	2.6	4	19
Raipur	43	Feb. 93	1.3**	1.1	70	0.093	2.7	5	14
Durg	42	Feb. 93	1.7*	1.0	92	0.11*	2.8	6	15
Rajnandgaon	41	Feb. 93	0.99	0.9	54	0.082	2.5	5	12
Deori	40	Feb. 93	1.6	1.4	86	0.075	1.8	4	21
Region 9									
Kannod	24	Jan. 92	0.83	1.6	45				
Region 10									
IAC	1	Mar. 92	60	1.2	3243				
Coimbatore	15	Feb. 93	2.5	1.7	135	0.090	2.5	5	28
IAC	1	Apr. 93	1.4**	1.2	16	0.090	2.9	5	16
IAC	1	Jun. 93	0.93	1.2	50				
IAC	1	Jul. 93	0.74	2.2	40	0.028	1.7	2	26
Coimbatore	15	Nov. 93	0.58	0.8	31				
Region 11									
Guntur	17	Nov. 92	22	1.6	1189	2.3	1.7	128	10
Region 13									
Dahod	38	Jan. 92	1.1	1.3	59				
Dahod	38	Feb. 94	1.3	1.6	70				
Nepal									
Pokhara	47	Apr. 93	0.43	1.7	23				
Pokhara	47	May 94	1.0	1.1	54	0.032	1.5	2	31
Nepalganj	48	Apr. 95	2.4	1.2	126	0.064*	2.4	4	38

[a]RF (resistance factor)=LD_{50} field strain/LD_{50} Reading susceptible.
[b]RF (resistance factor)=LD_{50} field strain/LD_{50} Reading susceptible (both pretreated with pbo).
[c]SR (synergist ratio)=LD_{50} without pbo/LD_{50} with pbo pretreatment.
Heterogeneity χ^2: *, significant at $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

respectively (tables 4 and 5). Pbo pre-treatment had no significant effect on toxicity of cypermethrin and fenvalerate to the Reading susceptible strain (Parallelism and Position, χ^2s $P > 0.05$). All field strains recorded significant suppression of pyrethroid resistance by pbo, with synergist ratios ranging from 2–82 for cypermethrin and 12–68 for fenvalerate. However, with the exception of the New Delhi strain, full suppression of pyrethroid resistance by pbo pre-treatment was not achieved in any of the strains tested. Typically, RFs for strains assayed with pyrethroid plus pbo averaged 27-fold for cypermethrin and 15-fold for fenvalerate, indicating that residual non-pbo-suppressible resistance was greater in the cypermethrin treatment compared to fenvalerate. Pbo-insensitive resistance was generally more significant in the central Indian regions (7, 9, 10 and 11), and highest in region 11 in strains collected from heavily sprayed cotton, pigeonpea and groundnut. The Varanasi and Nepal strains recorded increasing levels of pbo-insensitive resistance in three successive years from 1991–93 for the Varanasi strains and 1993–95 for the Nepal strains.

The IAC data provides evidence that pbo insensitive resistance tended to increase during the cropping season from July to February. Resistance factors increased from 5- to 73-fold and 11- to 30-fold in the 1992/93 and 1993/94 seasons respectively (fig. 2). There was some recovery of pbo suppression after March in 1991/92 and 1992/93. In 1993/94 no strains were collected after February.

Endosulfan resistance

Overall, resistance levels to endosulfan were quite low with RFs ranging from 1–28 (table 6). On the basis of LD_{50} RFs, two strains out of the 46 assayed would be considered susceptible. However, only the Srikakulum strain from region 11 was probably truly susceptible on the basis of high slope (2.4) and no significant heterogeneity (χ^2, $P > 0.05$). In all other field strains, segregation of resistant and susceptible phenotypes was likely, particularly in region 7 where significant ldp line heterogeneity (χ^2, $P < 0.05$), was recorded in three out of five strains assayed. The sample from IAC collected from the wild host *Lagascea mollis*, in July 1991, although recording a low LD_{50} of 0.50 µg/larva, the ldp line showed systematic curvilinearity and significant heterogeneity (χ^2, $P < 0.01$), indicating that the strain comprised a mixture of resistant and susceptible phenotypes. RFs greater than 10 were recorded in regions 10 and 11. In all cases with the exception of a single end of season

collection at IAC from the wild host *Datura metel* (Solanaceae), in April 1993, these were all from sprayed hosts. Strains from the middle mountains zone of Nepal recorded low resistance (2–4-fold). The single strain from the Tarai and Siwaliks zone (where insecticide use was more intensive), had 9-fold resistance.

Organophosphate resistance

Thirty seven strains were assayed with the nitrogen heterocycle phosphorothionate group organophosphate (OP), quinalphos (table 7). Low to moderate levels of resistance were recorded relative to the Reading susceptible strain. Interestingly, the two Nepal strains collected in 1993 and 1994 from Pokhara were fully susceptible to quinalphos, recording LD_{50}'s in the range 0.047–0.063 µg/larva and very steep ldp line slopes (3.3–4.4). However, in 1995, the Pokhara strain was significantly resistant to quinalphos (RF=6), and the slope had decreased appreciably (2.1). Similarly, the 1995 Nepalganj strain from the Tarai region was also resistant (RF=4). Moderate levels of resistance (RFs > 10) were recorded in strains from regions 9, 10 and 11 and the single strain from Pakistan.

Only two of the 11 strains assayed with monocrotophos (phosphate group OP), were more tolerant (RF=2–3) than the Reading susceptible strain, indicating no or only low

Table 5. Effect of piperonyl butoxide in suppressing cypermethrin resistance in 30–40 mg larvae derived from field strains of *Helicoverpa armigera*.

Strain	Map ref.	Collect date	Cypermethrin alone		Cypermethrin+Pbo Pretreatment			
			LD_{50} (µg/larva)	Slope	LD_{50} (µg/larva)	Slope	RF[a]	SR[b]
Reading susceptible	–	–	0.0073	2.4	0.0066	2.3	–	1
Region 4								
Varanasi	45	Oct. 91	0.20	1.6	0.013	1.5	2	15
Varanasi	45	Apr. 92	0.30	1.7	0.020	2.0	3	15
Varanasi	45	Oct. 93	0.24	2.1	0.099	1.8	15	2
Region 6								
New Delhi	46	Nov. 91	0.37	1.6	0.012	1.5	2	31
Region 7								
Dhenkanal	44	Feb. 93	0.78	2.2	0.066	2.4	10	12
Raipur	43	Feb. 93	0.71	2.3	0.070*	2.3	11	10
Durg	42	Feb. 93	0.83	1.6	0.18	1.8	27	5
Rajnandgaon	41	Feb. 93	1.4	1.5	0.14	1.7	21	10
Deori	40	Feb. 93	0.81	1.2	0.080*	1.7	12	10
Region 9								
Hinganghat	30	Jan. 92	0.27	2.0	0.025	1.5	4	11
Indapur	36	Aug. 92	0.89	1.4	0.14	2.4	21	6
Umri	34	Sep. 92	3.0	1.0	0.080	1.6	12	38
Akola	29	Sep. 92	0.97	1.7	0.095	1.8	14	10
Parbhani	32	Oct. 92	0.64	1.5	0.088	1.7	13	7
Region 10								
Abilabad	13	Jan. 92	1.2	1.3	0.10	0.9	15	12
Vikarabad	8	Feb. 92	0.84	1.2	0.095	1.8	14	9
Coimbatore	15	Feb. 92	0.62	1.8	0.11	1.6	17	6
Neredikonda	12	Oct. 92	2.1	1.2	0.21	1.4	32	10
Coimbatore	15	Oct. 92	0.83	1.3	0.10	1.7	15	8
Coimbatore	15	Feb. 93	1.4	1.6	0.11*	1.2	17	13
Narsapur	9	Apr. 93	0.58	1.5	0.064	1.3	10	9
Coimbatore	15	Nov. 93	0.25	1.5	0.080	2.0	12	3
Region 11								
Guntur	17	Dec. 91	12	0.9	1.3	1.7	197	9
Pulladigunta	16	Dec. 91	0.93	1.7	0.11	1.2	17	9
Srikakulum	22	Jan. 92	0.49	1.8	0.015	1.3	2	33
Guntur	17	Oct. 92	0.37	1.5	0.042	2.0	6	9
Guntur	17	Nov. 92	14	0.6	1.0	2.5	151	14
Guntur	17	Oct. 93	3.4	0.9	0.40	2.3	61	9
Bapatla	18	Mar. 94	65	0.6	0.80	1.6	121	82
Region 13								
Dahod	38	Jan. 92	0.20	0.9	0.024	2.1	4	8
Dahod	38	Feb. 94	0.33	1.9	0.050*	2.4	8	7
Nepal								
Pokhara	47	Apr. 93	0.082	1.3	0.013	1.9	2	6
Pokhara	47	May 94	0.39	2.3	0.073**	2.0	11	5
Nepalganj	48	Apr. 95	0.72	1.7	0.077*	1.8	12	9

[a]RF (resistance factor)=LD_{50} field strain/LD_{50} Reading susceptible (both pretreated with pbo).
[b]SR (synergist ratio)=LD_{50} without pbo/LD_{50} with pbo pretreatment.
Heterogeneity χ^2, * significant at $P < 0.05$; ** $P < 0.01$.

Table 6. Toxicity of topically applied endosulfan to 30–40 mg larvae of field strains of *Helicoverpa armigera*.

Strain	Map ref.	Collect date	*n*	LD_{50} (95% C.I.) (μg/larva)	LD_{90}	Slope ±S.E.	RF[a]
Region 4							
Varansi	45	Oct. 91	256	1.7 (1.3–2.1)	7.7	1.9±0.2	3
Varansi	45	Oct. 93	187	3.4 (2.6–5.0)	22	1.6±0.3	5
Region 6							
New Delhi	46	Nov. 91	336	2.2 (1.7–2.8)	16	1.5±0.2	4
Region 7							
Dhenkanal	44	Feb. 93	288	2.1 (1.7–2.6)	10	1.9±0.2	4
Raipur	43	Feb. 93	240	3.1*** (2.4–4.1)	21	1.5±0.2	5
Durg	42	Feb. 93	336	1.7*** (1.3–2.1)	11	1.6±0.2	3
Rajnandgaon	41	Feb. 93	288	3.1 (2.3–4.3)	32	1.3±0.2	5
Deori	40	Feb. 93	288	1.7* (1.2–2.3)	23	1.1±0.2	3
Region 9							
Tuljapur	35	Oct. 91	245	1.0 (1.4–2.7)	17	1.4±0.2	3
Akola	29	Oct. 91	270	2.5 (1.5–3.7)	37	1.1±0.2	4
Yavatmal	31	Oct. 91	249	2.9* (2.0–4.3)	27	1.3±0.1	5
Rahuri	26	Jan. 92	235	4.4 (3.0–7.0)	70	1.1±0.2	7
Jhabua	23	Jan. 92	278	2.5 (1.8–3.6)	23	1.3±0.2	4
Kannod	24	Jan. 92	170	2.9 (2.3–3.7)	10	2.5±0.3	5
Hinganghat	30	Jan. 92	260	2.6 (1.7–3.9)	57	1.0±0.2	4
Umri	34	Sep. 92	246	4.8 (3.8–6.4)	22	1.9±0.3	8
Barsi Takli	28	Sep. 92	304	2.7 (2.1–3.6)	20	1.5±0.2	4
Akola	29	Sep. 92	252	2.6 (2.1–3.2)	12	2.0±0.2	4
Parbhani	32	Oct. 92	208	4.5 (3.4–6.6)	29	1.6±0.3	7
Region 10							
IAC	1	Jul. 91	220	0.50** (0.39–0.65)	2.3	2.0±0.2	1
IAC	1	Aug. 91	275	9.0 (7.6–11)	23	3.1±0.3	14
IAC	1	Sep. 91	208	1.0 (0.75–1.4)	6.3	1.6±0.2	2
IAC	1	Nov. 91	267	3.5 (2.8–4.5)	17	1.9±0.2	5
Malkapur	6	Nov. 91	192	1.4 (1.1–1.9)	6.0	2.0±0.3	2
Ibrahimpatan	7	Dec. 91	247	1.4 (1.0–2.1)	16	1.2±0.2	2
Adilabad	13	Jan. 92	213	5.7 (4.4–7.4)	27	2.0±0.3	9
Vikarabad	8	Feb. 92	227	2.8 (2.0–4.0)	23	1.4±0.2	4
Narayankher	2	Feb. 92	186	6.7 (5.1–9.3)	34	1.8±0.3	10
IAC	1	Feb. 92	259	16 (12–22)	172	1.2±0.2	25
Neredikonda	12	Oct. 92	224	1.7** (1.3–2.2)	8.8	1.8±0.3	3
Coimbatore	15	Oct. 92	289	3.9 (3.2–4.9)	18	1.9±0.2	6
IAC	1	Apr. 93	336	10 (7.3–10)	135	1.1±0.1	16
Narsapur	9	Apr. 93	384	6.8 (5.3–8.7)	49	1.5±0.1	11
IAC	1	Jul. 93	279	3.0 (2.4–3.8)	15	1.9±0.2	5
Coimbatore	15	Nov. 93	289	2.4 (1.9–3.2)	13	1.8±0.2	4
Region 11							
Gudjuru	20	Aug. 91	242	0.88 (0.69–1.1)	4.3	1.9±0.2	1
Pulladigunta	16	Sep. 91	429	3.9* (3.0–5.2)	44	1.2±0.1	6
Guntur	17	Oct. 91	286	1.6 (1.3–2.0)	8.1	1.8±0.2	3
Guntur	17	Dec. 91	206	18 (14–22)	66	2.3±0.3	28
Srikakulum	22	Jan. 92	240	0.49 (0.40–0.59)	1.7	2.4±0.3	1
Guntur	17	Nov. 92	282	9.0 (7.4–11)	40	2.0±0.2	14
Bapatla	18	Mar. 94	308	4.9* (3.8–6.4)	36	1.5±0.2	8
Region 13							
Vansada	37	Jan. 92	183	6.7 (5.1–8.9)	33	1.9±0.3	10
Dahod	38	Jan. 92	241	3.3 (2.6–4.3)	16	1.8±0.2	5
Dahod	38	Feb. 94	240	3.4 (2.6–4.4)	21	1.6±0.2	5
Nepal							
Pokhara	47	Apr. 93	245	1.0* (0.78–1.2)	4.4	2.0±0.2	2
Pokhara	47	May 94	288	1.8 (1.5–2.2)	8.5	1.9±0.2	3
Nepalganj	48	Apr. 95	240	5.2 (4.2–6.3)	21	2.1±0.2	9
Pokhara	47	Apr. 95	240	2.2 (1.7–3.0)	12	1.8±0.3	4

[a]RF (resistance factor)=LD_{50} field strain/LD_{50} susceptible strain (from table 2).
Heterogeneity χ^2: *, significant at $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

istance to this insecticide (table 8). In nearly all cases ldp line slopes were shallow (< 1.5). Four of the five strains from region 7 recorded significant heterogeneity (χ^2, $P < 0.05$), and segregation of an allele for monocrotophos resistance was likely.

Carbamate resistance

Twelve strains were assayed with the oxime carbamate, methomyl (table 9). High RFs (> 30-fold) were recorded in one strain each from regions 9, 10 and 11. All three of these

strains were collected from crops treated at least once with insecticide. Low levels of incipient resistance (RF=2–5) were found in the strains from Nepal, Pakistan and all other locations in India.

Discussion

Pyrethroid resistance

This is the first study to examine insecticide resistance in *H. armigera* over a broad geographic area in India and the results indicate that resistance to cypermethrin and fenvalerate was widespread between 1991 and 1995, with moderate to very high levels of resistance being recorded in all the strains tested. The most highly resistant populations were generally found in the central and southern regions of India. It was from here that reports of inadequate control of *H. armigera* were most frequent and concomitant numbers of insecticide applications very high.

Earlier resistance reports using standardized bioassay techniques are only available for the southern Indian states of Andhra Pradesh (McCaffery *et al.*, 1989; Armes *et al.*, 1992), Tamil Nadu (Armes *et al.*, 1992; Pasupathy & Regupathy, 1994) and the northern states of Delhi, Punjab and Haryana (Mehrotra & Phokela, 1992). For Andhra Pradesh, where regular resistance monitoring has been conducted since 1987, cypermethrin resistance levels have continued to increase; RFs ranged from 40- to 750-fold between 1987 and 1988 (McCaffery *et al.*, 1989), 7- to 2100-fold between 1989 and 1990 (Armes *et al.*, 1992), and

Table 7. Toxicity of topically applied quinalphos to 30–40 mg larvae of field strains of *Helicoverpa armigera*.

Strain	Map ref.	Collect date	*n*	LD_{50} (95% C.I.) (μg/larva)		LD_{90}	Slope ±S.E.	RF*
Region 4								
Varanasi	45	Oct. 91	269	0.12	(0.10–0.15)	0.34	2.8±0.2	2
Varanasi	45	Oct. 93	240	0.37	(0.27–0.51)	4.0	1.2±0.2	7
Region 6								
New Delhi	46	Nov. 91	288	0.28	(0.22–0.36)	1.9	1.6±0.2	5
Region 7								
Dhenkanal	44	Feb. 93	288	0.11*	(0.07–0.14)	0.90	1.4±0.2	2
Raipur	43	Feb. 93	336	0.25*	(0.19–0.33)	2.5	1.3±0.1	5
Durg	42	Feb. 93	280	0.37	(0.28–0.48)	12	1.5±0.2	7
Rajnandgaon	41	Feb. 93	336	0.26*	(0.22–0.33)	1.4	1.8±0.2	5
Deori	40	Feb. 93	288	0.26*	(0.22–0.32)	1.0	2.2±0.3	5
Region 9								
Tuljapur	35	Oct. 91	249	0.088	(0.06–0.12)	0.68	1.4±0.2	2
Yavatmal	31	Oct. 91	240	0.24	(0.19–0.30)	1.1	2.0±0.2	4
Rahuri	26	Jan. 92	240	1.3	(0.85–2.0)	24	1.0±0.2	24
Jhabua	23	Jan. 92	172	1.0	(0.75–1.5)	7.5	1.5±0.2	19
Kannod	24	Jan. 92	240	2.6	(1.7–3.8)	36	1.1±0.2	48
Hinganghat	30	Jan. 92	275	0.31	(0.26–0.38)	0.97	2.6±0.3	6
Region 10								
IAC	1	Jun. 91	240	0.17	(0.14–0.21)	0.66	2.2±0.2	3
IAC	1	Aug. 91	216	0.11	(0.09–0.14)	0.41	2.3±0.3	2
IAC	1	Nov. 91	314	1.0	(0.85–1.3)	4.2	2.1±0.2	19
Homnabad	11	Jun. 92	240	2.0	(1.5–2.5)	8.8	2.0±0.2	37
IAC	1	Feb. 92	288	1.5	(1.2–2.0)	11	1.5±0.2	28
IAC	1	Apr. 92	280	0.47	(0.38–0.57)	2.1	2.0±0.2	9
IAC	1	Nov. 92	294	0.43	(0.33–0.57)	18	1.4±0.2	8
IAC	1	Nov. 92	240	0.21	(0.14–0.29)	9.1	1.4±0.2	4
IAC	1	Apr. 93	288	0.66*	(0.51–0.82)	3.5	1.8±0.2	12
Narsapur	9	Apr. 93	384	0.95	(0.75–1.2)	5.4	1.7±0.2	18
IAC	1	Jul. 93	312	0.29	(0.24–0.37)	1.7	1.7±0.2	5
Coimbatore	15	Nov. 93	238	0.22	(0.18–0.27)	0.91	2.1±0.2	4
Region 11								
Pulladigunta	16	Sep. 91	144	0.34	(0.23–0.51)	2.0	1.7±0.3	6
Guntur	17	Sep. 91	240	3.2	(2.4–4.0)	18	1.7±0.2	59
Guntur	17	Dec. 91	200	0.70	(0.53–0.95)	4.6	1.6±0.3	13
Guntur	17	Nov. 92	288	1.2	(0.93–1.5)	7.7	1.6±0.2	22
Region 13								
Dahod	38	Jan. 92	256	0.37	(0.28–0.52)	3.1	1.4±0.2	7
Dahod	38	Feb. 94	242	0.15*	(0.12–0.18)	0.57	2.2±0.3	3
Nepal								
Pokhara	47	Apr. 93	257	0.063	(0.056–0.070)	0.12	4.4±0.4	1
Pokhara	47	May 94	192	0.047	(0.040–0.055)	0.11	3.3±0.5	1
Nepalganj	48	Apr. 95	288	0.21	(0.18–0.25)	0.73	2.4±0.2	4
Pokhara	47	Apr. 95	240	0.30	(0.20–0.40)	1.2	2.1±0.3	5
Pakistan								
Bahawalnagar	49	Nov. 91	271	0.86	(0.69–1.1)	5.0	1.7±0.2	16

*RF (resistance factor)=LD_{50} field strain/ LD_{50} susceptible strain (from table 2).
Heterogeneity χ^2: *, significant at $P < 0.05$.

Table 8. Toxicity of topically applied monocrotophos to 30–40 mg larvae of field strains of *Helicoverpa armigera*.

Strain	Map ref.	Collect date	*n*	LD_{50} (μg/larva)	(95% C.I.)	LD_{90}	Slope ±S.E.	RF[a]
Region 7								
Dhenkanal	44	Feb. 93	432	0.81**	(0.54–1.1)	15	1.0±0.1	1
Raipur	43	Feb. 93	384	0.48***	(0.29–0.69)	9.0	1.0±0.1	0.6
Durg	42	Feb. 93	288	0.46	(0.35–0.59)	3.2	1.5±0.2	0.6
Rajnandgaon	41	Feb. 93	432	0.64*	(0.46–0.85)	9.5	1.1±0.1	0.8
Deori	40	Feb. 93	432	0.34***	(0.23–0.46)	4.7	1.1±0.1	0.4
Region 10								
IAC	1	Apr. 93	432	1.81	(1.2–2.6)	46	0.9±0.1	2
IAC	1	Jul. 93	372	0.66	(0.49–0.84)	6.2	1.3±0.2	0.9
Region 11								
Guntur	17	Oct. 93	336	2.6	(2.0–3.3)	20	1.5±0.2	3
Region 13								
Dahod	38	Feb. 94	285	0.96	(0.72–1.3)	8.9	1.3±0.2	1
Nepal								
Pokhara	47	Apr. 93	336	0.71	(0.55–0.92)	6.1	1.4±0.1	1
Pokhara	47	May 94	288	0.37	(0.29–0.46)	2.0	1.8±0.2	0.5

[a]RF (resistance factor)=LD_{50} field strain/LD_{50} susceptible strain (from table 2).
Heterogeneity χ^2: *, significant at $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

20- to 6500-fold between 1991 and 1994 (this study). Two strains were collected in Tamil Nadu between 1989 and 1991 and these were highly resistant to cypermethrin (RFs >140-fold) (Armes *et al.*, 1992); four strains were assayed between 1992 and 1993 and a slight reduction in cypermethrin resistance levels was indicated (25- to 140-fold resistance). This may be partly due to a real reduction in pyrethroid use on cotton in the Coimbatore region where the strains were collected. Regional Departments of Agriculture in Tamil Nadu were discouraging pyrethroid use to reduce sucking pest resurgence. There was also a realization that field control of bollworms with the available pyrethroids had become less effective in recent years (A. Regupathy, personal communication).

In northern India, cypermethrin RFs of 4-fold and 3- to 4-fold were reported in 1987 (Dhingra *et al.*, 1988), and 1988–1989 (Mehrotra, 1990), respectively. Our data, which records RFs of 20- to 37-fold in the Varanasi and New Delhi strains collected between 1991 and 1993, suggest that cypermethrin resistance has increased in importance in *H. armigera* populations in northern India. In a parallel study, discriminating dose monitoring showed that, by 1993, cypermethrin resistance frequencies in northern India were similar to those in central and southern India (Armes *et al.*, 1994). Cotton farmers in northern India experienced severe *H. armigera* control problems during the 1993/94 and 1994/95 seasons because populations were exceptionally high and spray failures common. Prior to 1993, farmers in the Indian Punjab typically applied 5–9 insecticide sprays to cotton, but poor control from 1993 onwards necessitated frequent repeat applications and 10–25 sprays were not uncommon. During the 1994/95 season, it was estimated that approximately 30% of the expected cotton yield in the northern Indian states of Punjab and Haryana were lost due to a combination of uncontrollable infestations of *H. armigera* and leaf curl virus transmitted by whiteflies (Anon.,

Table 9. Toxicity of topically applied methomyl to 30–40 mg larvae of field strains of *Helicoverpa armigera*.

Strain	Map ref.	Collect date	*n*	LD_{50} (μg/larva)	(95% C.I.)	LD_{90}	Slope ±S.E.	RF[a]
Region 7								
Durg	42	Feb. 93	320	0.67	(0.50–0.91)	58	1.2±0.1	5
Region 9								
Rahuri	26	Jan. 92	240	4.7	(3.5–7.1)	41	1.4±0.2	36
Kannod	24	Jan. 92	360	0.38	(0.29–0.47)	2.7	1.5±0.2	3
Region 10								
IAC	1	Nov. 91	240	5.0	(3.3–8.4)	129	0.9±0.2	38
IAC	1	Dec. 91	249	0.28	(0.20–0.36)	1.5	1.7±0.2	2
Hoshangabad	11	Jan. 92	280	0.29	(0.19–0.41)	3.9	1.1±0.1	2
IAC	1	Apr. 92	240	0.25	(0.19–0.34)	1.8	1.5±0.2	2
Region 11								
Guntur	17	Dec. 91	280	21	(16–27)	154	1.5±0.2	162
Region 13								
Dahod	38	Feb. 94	289	0.45	(0.31–0.63)	7.0	1.1±0.2	3
Nepal								
Pokhara	47	May 94	240	0.28	(0.22–0.38)	1.9	1.5±0.2	2
Nepalganj	48	Apr. 95	288	1.4	(1.1–1.9)	11	1.4±0.2	11
Pakistan								
Bahawalnagar	49	Nov. 91	240	0.45	(0.33–0.86)	12	1.0±0.1	4

[a]RF (resistance factor)=LD_{50} field strain/LD_{50} susceptible strain (from table 2).

1995). From the evidence presented, it is likely that increasing pyrethroid resistance levels in northern India in recent years contributed significantly to these problems.

The single strain collected from cotton in Bahawalnagar, Pakistan, in November 1991 was highly resistant to cypermethrin (RF=460-fold). During the 1991–92 season, *H. armigera* populations on cotton were very high and even 10–13 insecticide applications compared to the usual 6–8 in previous years, did not achieve satisfactory control on many farms (D. Chamberlain, personal communication). The situation in the Indian Punjab was similar. It was also in 1991 that significant levels of cypermethrin resistance in *H. armigera* were confirmed there (Mehrotra & Phokela, 1992). As Bahawalnagar is only about 60 km west of the border with the Indian Punjab, it is likely that the *H. armigera* populations are contiguous. In 1991, Ahmad *et al.* (1995) also reported high levels of cypermethrin resistance (RFs 29–168), for the first time from widely spaced locations across the Pakistan Punjab.

The discovery of high levels of cypermethrin and fenvalerate resistance in the strain collected from the Tarai zone of Nepal was not a surprise in view of its proximity to the Indian state of Uttar Pradesh (zone 4). However, appreciable levels of pyrethroid resistance in the Pokhara strains are more noteworthy as the area is located in a valley surrounded by mountains, where the lowest elevations are of the order 3000 m above sea level. Independent local selection of resistance is possible, but seems unlikely in view of the fact that *H. armigera* is only a pest on tomatoes and *Capsicum* spp. in this region and insecticide use on these crops was not excessive. Dispersal of resistant moths from India seems the most likely cause (although unproven), for the introduction of resistance alleles into populations in this region, highlighting the extensive gene flow that can occur in *H. armigera*, as has been observed in Australia (Daly & Gregg, 1985).

The fact that all the strains collected during this survey, including those from remote areas, were resistant to cypermethrin and fenvalerate, is significant. This provides further evidence that pyrethroid resistance is widespread in *H. armigera* populations across the Indian subcontinent. The implication is that the susceptible allele is probably now rare (Armes *et al.*, 1992). Further work is needed to establish the extent of cross-resistance to other pyrethroid compounds, although some degree of resistance to all molecules is likely.

Clearly, resistance levels recorded for all localities were highly dependent upon the time in the cropping season when the strains were collected. Both from the IAC data (fig. 2), where regular collections were made over three seasons and from data for areas such as Guntur, where 3–5 collections were made during each of the 1991/92 and 1992/93 seasons, it can be seen that steep increases in resistance occurred between August and March, coinciding with the period of *H. armigera* infestation on a succession of insecticide treated crops (typically cotton–pigeonpea–chickpea). At IAC for example, pyrethroid resistance typically increased 5- to 14-fold over the season and in the Guntur region where insecticide use was much greater, 19- to 44-fold. In nearly all cases, late season (April–May), resistance levels were much reduced and this was most likely a feature of low *H. armigera* populations and little insecticide use during the summer period. Such conditions would result in significantly reduced resistance selection pressure, allowing reversion to lower resistance levels at that time. An exception to this was the very high cypermethrin resistance (6500-fold), reported from the strain collected from an unprecedented *H. armigera* outbreak on groundnut over large areas in the Bapatla region in March 1994, when farmers applied 5–6 sprays between February and March in an attempt to contain the outbreak.

A similar seasonal patterning of cypermethrin resistance frequencies was reported in discriminating dose monitoring studies conducted at IAC and Guntur between 1990 and 1995 (Armes *et al.*, 1994; Armes unpublished data). At present, it is not known whether end of season resistance dilution is a result of immigration of less resistant populations or a competitive disadvantage of resistant genotypes in the absence of insecticide selection.

Pyrethroid resistance mechanisms

In all the strains tested, pbo was a synergist for cypermethrin and fenvalerate, indicating that metabolic detoxification was an important pyrethroid resistance mechanism in larval *H. armigera*. The fact that full suppression of resistance was never achieved in any strain suggests that metabolic detoxification was probably only one of two or more mechanisms conferring pyrethroid resistance.

On the basis of mechanisms studies on *H. armigera* in Australia, it is likely that the non-pbo-synergizable component was a result of the presence of nerve-insensitivity or penetration resistance mechanisms, or a combination of both (Gunning *et al.*, 1991, 1995). Both mechanisms have been shown to exist in *H. armigera* populations in India: West & McCaffery (1992) demonstrated that nerve-insensitivity was present to varying degrees in *H. armigera* strains collected from Maharashtra and Andhra Pradesh in 1992, and the frequency of resistant individuals in a population carrying the nerve-insensitivity allele was greater in strains collected from insecticide treated cotton crops. Padma Kumari *et al.* (1995) have shown that reduced cuticle permeability confers resistance to deltamethrin in some northern Indian *H. armigera* populations.

As penetration resistance usually confers only a low order resistance (Gunning *et al.*, 1991, 1995), it is most likely that nerve-insensitivity is the major contributor to the non-pbo-suppressible resistance. The high order pbo-insensitive resistance recorded in this study in strains collected from intensively sprayed cotton and legume crops, particularly from coastal Andhra Pradesh, may be indicative of a second high order nerve-insensitivity allele, but this is only speculative at this stage. *Super-Kdr* was reported in *H. armigera* strains in Australia in the early 1980s when pbo-insensitive resistance levels were of the order of 100-fold (Gunning *et al.*, 1991); in this study we have recorded levels of up to 197-fold. In both countries, such high order resistance was associated with excessive use of insecticides against pyrethroid-resistant *H. armigera* over multiple generations in a season.

For the Hyderabad region, our data indicate that pbo-insensitive resistance increases during the season, most probably as a result of the cumulative selection effect of frequent insecticide applications on the three to five *H. armigera* generations found on cotton and legume crops between August and January. Pbo-suppressible resistance appears to increase again at the end of the post-rainy season (from March onwards), when little insecticide is used on field

crops in central India. It is probable, therefore, that reduced pyrethroid resistance at this time may result from the decreasing importance of nerve-insensitivity resistance once insecticide selection pressure is removed. In support of this there is preliminary evidence for a fitness deficit associated with nerve-insensitivity (A.J. West & A.R. McCaffery, unpublished data). Similarly, in Australia, it is believed that the significant reduction in pyrethroid resistance selection pressure, brought about by the introduction of a management strategy, was responsible for the shift in pyrethroid resistance mechanisms from nerve-insensitivity to oxidative metabolism (Forrester *et al.*, 1993).

Endosulfan resistance

Our bioassay data show that low level (2- to 28-fold), endosulfan resistance is a feature of *H. armigera* throughout the sampling range. In general, strains from northern India and Nepal were less tolerant than those collected in central and southern India. Resistance levels have not changed markedly in India since 1987 when the peak RF recorded in the coastal Andhra Pradesh cotton region was 13 (McCaffery *et al.*, 1989). The highest recorded RF in this study was 28 from the same region. However, even low levels of endosulfan resistance appear to be associated with unreliable control of *H. armigera*. On the IAC farm for example, endosulfan has given very poor control of *H. armigera* even when tolerance was only 5- to 10-fold. In coastal Andhra Pradesh, 13-fold resistance was sufficient to render this chemical ineffective for *H. armigera* control (McCaffery *et al.*, 1989). Similarly in Australia, 20- to 30-fold resistance caused control problems on cotton crops in the mid 1970s (Kay, 1977; Gunning & Easton, 1994).

Organophosphate resistance

In southern India, resistance to quinalphos has increased appreciably since 1989–91, when levels were 2- to 9-fold (Armes *et al.*, 1992). In part, this is likely to be due to the increasing popularity of quinalphos for cotton pest control in recent years, particularly in Andhra Pradesh where it is considered superior to the available pyrethroids. In the low rainfall dryland cotton tracts where water availability for spraying is sometimes a problem, quinalphos dust is popular. This may be the reason for the high quinalphos resistance levels reported in region 9. Conversely, we found no significant change in the status of resistance to monocrotophos to that reported in 1986–87 (McCaffery *et al.*, 1989), and *H. armigera* remained susceptible or only slightly tolerant in all regions.

OP cross resistance is likely to be related to chemical structure of the insecticides concerned. The significant difference in resistance between the two test OPs, quinalphos and monocrotophos, may well be due to the fact that the phosphorothionate insecticides (e.g. quinalphos) largely act as AChE inhibitors through an oxidative transformation catalysed by mixed function oxidases (mfo) (Eto, 1990), and/or by hydrolytic action of phosphotriester hydrolases (Price, 1991). Classically, resistance to the phosphate type OPs is attributed to insensitive AChE mechanisms (Oppenoorth, 1985), and it has been demonstrated that monocrotophos susceptibility in *H. armigera* is unaffected by oxidative inhibitors (Forrester *et al.*, 1993).

It has been shown in OP oxidative resistant housefly strains that degradation of the P=O bond and concomitant activation of P=S into P=O are increased over susceptible strains (Oppenoörth, 1985). The latter bioactivation should in theory result in greater sensitivity to the toxicant but is largely overruled by detoxication. This is further complicated by strong inhibition of detoxication of the resultant P=O compound by its P=S precursor (Welling *et al.*, 1974).

We believe that a similar scenario occurs in phosphorothionate resistant *H. armigera* in India. The apparent lack of, or very low levels of, resistance to monocrotophos indicates that insensitive AChE mechanisms and glutathione *s*-transferases are probably of minor importance in OP resistant *H. armigera* in India at the present time. Enhanced metabolic detoxification, by mfos, possibly as a result of pyrethroid cross resistance, seems to be (although untested to date), the most likely mechanism responsible for phosphorothionate OP resistance. Certainly it is clear from our survey, that quinalphos resistance was highest in regions 9–11 where the pyrethroid resistance problem was most acute.

Carbamate resistance

The number of strains assayed with methomyl were quite small, but the data indicate that low level resistance was widespread. Interestingly, in all three strains where RFs were greater than 30-fold, high levels (RFs >150), of pyrethroid resistance were also recorded. It is considered that even low level methomyl resistance is sufficient to cause field control failures, as methomyl is not very toxic to *H. armigera* larvae (Gunning *et al.*, 1992).

Methomyl has only been used widely in India over the past four seasons, so it is difficult to account for such rapid independent resistance development. Even earlier data indicated that pyrethroid resistant *H. armigera* populations in intensive insecticide use areas of south India were resistant to methomyl as early as 1990 (Armes *et al.*, 1992). Prior to this, methomyl had only been imported into India as a one-off emergency measure in an attempt to control the very high populations of pyrethroid resistant *H. armigera* on cotton crops in coastal Andhra Pradesh in 1988.

Carbamate resistance is considered to result from mechanisms conferring enhanced mfo detoxification or insensitive AChE (Oppenorth & Welling, 1976; Eto, 1990; Sun, 1992). It is feasible therefore that methomyl resistance has resulted from pyrethroid cross resistance to specific microsomal oxidases, but this needs clarification by synergist and *in vitro* investigation. In Australia however, it is believed that methomyl resistance developed independently and cross resistance has not been inferred, but in this case methomyl had been widely used on crops such as sweet corn and tobacco for many years (Gunning *et al.*, 1992).

Conclusions

It seems probable that a large proportion of the resistance to certain pyrethroids, methomyl and quinalphos in *H. armigera* in India can be attributed to an efficient inherited or inducible mfo complex similar to the situation which exists in *Plutella xylostella* Linnaeus (Lepidoptera: Plutellidae) (Cheng *et al.*, 1992), and *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) (Yu, 1991). Unfortunately, prior to field failures resulting from pyrethroid resistance, no

H. armigera resistance monitoring had been conducted in India, so the status of resistance to endosulfan, OPs and carbamates before the detection of pyrethroid resistance is not known. It does however seem likely that, in view of the fact that the first widespread field failures in cotton were attributable to pyrethroid resistance, overuse of these chemicals was the main cause of the cross resistance patterns evident today.

The fact that resistance to cypermethrin and fenvalerate is now so widespread in *H. armigera* populations in the Indian subcontinent, even in regions where insecticides are little used, suggests that it is too late to consider implementation of strategies to contain the further spread of resistance to these molecules. Clearly a stable level of metabolic mediated pyrethroid resistance is present throughout the Indian subcontinent and refugia of susceptibles probably no longer exist. The high mobility and genetic mixing of *H. armigera* populations is most likely responsible for this. Even a low immigration rate can facilitate the rapid spread of resistance alleles between isolated populations (Caprio & Tabashnik, 1992). It appears probable that nerve-insensitivity and possibly also high order nerve-insensitivity (*Super-Kdr*) genes contributed to the very high resistance levels reported for some *H. armigera* populations. It is likely that *Kdr* confers a fitness cost as very high levels of pyrethroid resistance only feature in areas where insecticides are over-used. It is likely, therefore, that with careful area-wide control over the use of insecticides, we could see a marked reduction in the magnitude of pyrethroid resistance through loss of the nerve-insensitivity alleles and reversion to more stable lower level metabolic mediated pyrethroid resistance. It is reasonable to assume that resistance levels could be reduced from the current 100- to over 1000-fold levels commonly recorded in cotton growing regions, to 20- to 60-fold simply by moderating insecticide use on cotton and legume crops.

In the short term, insecticide resistance management should aim to significantly reduce selection for nerve-insensitivity resistance. This suggestion follows experiences in Australia, demonstrating that good control of mfo mediated resistant *H. armigera* can still be achieved with pyrethroids through careful targeting of applications and use of metabolic synergists (Forrester *et al.*, 1993).

Currently, insecticides are grossly over-applied in most cotton growing regions. In many cases the number of applications could be significantly reduced without any detrimental effect on cotton yields (Armes, unpublished data). Clear benefits would result from reduced conventional insecticide inputs, not only from a reduction in the intensity of resistance, but also from a concomitant increase in the success of biological control for secondary pests. Incorporation of pest-specific biorational pesticides into spray schedules would further augment these benefits.

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