TO: KS
From: PRK
FOR 2PRINT
Database.
Thanks.

1157

JA 1735

PLANT RESISTANCE

Ide ...iotic and Antixenotic Resistance to *Helic ...erpa armigera* (Lepidoptera: Noctuidae) in Chickpea

SUSAN E. COWGILL AND S. S. LATEEF

International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh, India

J. Econ. Entomol. 89(1): 224–229 (1996)

ABSTRACT Five short-medium duration desi (small seeded) and 5 medium-long duration kabuli (large seeded) chickpea, *Cicer arietinum* L., genotypes were screened in the laboratory for antibiosis to *Helicoverpa armigera* Hübner. Larvae were reared on either chickpea leaves or on pods containing green seeds. Significant variation among the desi genotypes was found for pupal weight and larval survival. Pupae resulting from larvae reared on either pods or leaves of 'ICCV 7' weighed substantially less than those for larvae reared on the susceptible controls, 'Annigeri' and ICC 3137. Pupae of larvae reared on leaves of ICC 506 weighed substantially less than those reared on ICC 3137. There was no variation in the measured parameters for larvae reared on the kabuli chickpea genotypes. In general, pupae of larvae reared on chickpea pods were heavier and developed more quickly than those reared on chickpea leaves. Seven (3 short-medium desi, 2 long duration desi, and 2 long duration kabuli) genotypes were screened in the field for ovipositional antixenosis to *H. armigera*. Fewer eggs were recorded on ICC 506 than the susceptible controls in both years of the study. These observations were corroborated in laboratory studies of *H. armigera* oviposition behavior. There was no evidence for resistance to *H. armigera* in any of the long duration genotypes and it is concluded that long duration genotypes do not express the same level of resistance to *H. armigera* outside the agroecological zone in which they are normally cultivated.

KEY WORDS *Helicoverpa armigera*, *Cicer arietinum*, host plant resistance, antibiosis, antixenosis

Helicoverpa armigera HÜBNER is a major crop pest in Asia. In India it is the dominant pest of several legume crops including chickpea *Cicer arietinum* L. (Reed et al. 1987), and pigeonpea *Cajanus cajan* (L.) Millspaugh (Bhatnagar et al. 1982), and can cause serious losses to sorghum, *Sorghum bicolor* L. (Mote and Murthy 1990), and cotton, *Gossypium* spp. (Kishor 1992). Its high pest status arises from the preference of foraging larvae for plant structures rich in nitrogen (Fitt 1989) such as flowers, pods, and panicles.

Estimates of the avoidable losses caused by *H. armigera* in chickpea, the major grain legume crop in India, range from 14 to 20% (Srivastava and Srivastava 1990a). Options for the management of *H. armigera* include manipulation of sowing and harvesting time, intercropping, and pesticides. As a result of extensive use of pyrethroids, cyclodienes, and organophosphates, insecticide resistance is ubiquitous in *H. armigera* populations in the Indian subcontinent, resulting in field failures and economic losses (Armes et al. 1995). Consequently, there is increased impetus for the development of integrated pest management strategies for chickpea. Resistant host plants have an important role in such strategies.

Screening of chickpea germplasm accessions has shown that chickpea genotypes vary in their susceptibility to *H. armigera* (Singh and Sharma 1970, Dias et al. 1983, Lateef 1985). Rembold (1981) examined the biochemical basis of this variation and found a correlation between the malic acid content of chickpea leaf exudate and reduced pod borer damage. However, the mechanisms responsible for the reduced susceptibility to attack have not been elucidated. Srivastava and Srivastava (1989) suggested oviposition nonpreference as the cause of observed differences in pod damage among 8 chickpea genotypes. Studies of the relative performance of *H. armigera* larvae reared on different chickpea genotypes indicate that antibiosis also has a role in *Helicoverpa* resistance in some genotypes. Srivastava and Srivastava (1990b) fed larvae on a combination of chickpea leaves, flowers, and pods, and they recorded significant differences in larval survival, larval weight, pupal weight, and pupal period among genotypes. Larvae reared on less susceptible genotypes were lighter and took longer to develop than those reared on more susceptible genotypes.

In the current study a range of chickpea genotypes, for which the mechanisms of resistance to *H. armigera* had not previously been elucidated, were examined for antibiotic and antixenotic resistance to this pest. Larval growth and survival and adult ovipositional preference were used as criteria

0022-0493/96/0224–0229$02.00/0

to determine the presence of resistance. The relationship between the intensity of *H. armigera* attack and pod damage was also examined.

Materials and Methods

All experiments were carried out at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Asia Center (IAC), Patancheru, AP, India. *H. armigera* adults and larvae used in the laboratory experiments were from a culture maintained at IAC that was established from and regularly supplemented with eggs collected at IAC.

Antibiosis. Neonate *H. armigera* larvae were reared in individual glass tubes with cotton stoppers. The tubes were stored in an incubator maintained at 26 ± 1°C, 65 ± 5% RH, and a photoperiod of 12:12 (L:D) h. Larvae were provided with an excess of chickpea material until pupation. The plant material comprised either leaves or pods containing green seeds. It was replaced daily with freshly collected material from field plots at IAC. The experimental design was a randomized complete block design with 3 replicates of each treatment (genotype). In the 1985 postrainy season, each replicate was composed of 7 larvae; in the 1987 postrainy season, each replicate was composed of 10 larvae. Larval weight was recorded 10 d after hatching, and pupal weight was recorded 1 d after pupation.

Ten genotypes were evaluated for antibiotic effects. The genotypes varied according to their developmental duration and seed size: ICC 506, 'Annigeri', 'ICCV 7', ICC 3137 (desi short to medium duration); ICC 4935-E-2793 (desi long duration), ICC 8835, ICC 10870 (kabuli medium duration); ICC 5264-E10, ICCX 73024417-2-2H and L550 (kabuli long duration). 'Annigeri', ICC 3137 and L550 were used as *Helicoverpa* susceptible controls. The remaining genotypes had been identified as having reduced levels of susceptibility to *Helicoverpa* damage in screening trials at Patancheru (short-medium duration genotypes) or at All India Coordinated Pulse Improvement Program (AICPIP) Centers in northern India (long duration genotypes) (Lateef and Sachan 1990).

Because of the time required to replace the chickpea material it was not possible to run antibiosis experiments on all 10 genotypes concurrently. Therefore, the genotypes were divided into 2 groups according to their seed size. Experiments with kabuli material began 15 d after the start of experiments with desi material.

In the 1985 postrainy season, antibiosis experiments began on 12 December using leaves collected from field plots sown on 8 October. A 2nd experiment using green pods containing seeds began on 21 January 1986. In the 1987 postrainy season, experiments began on 11 November using leaves collected from field plots sown on 24 October. An experiment using pods collected from the same plots began on 17 January 1988.

Data for the 2 seasons were pooled for analysis. Data for the 2 groups were analyzed separately with SYSTAT nested ANOVA (Wilkinson 1990) with chickpea genotype nested within plant part. Means were separated at the 5% level using the Tukey honestly significant difference (HSD) test (Wilkinson 1990). Because of poor plant growth, data on larval growth on chickpea leaves in 2 seasons are not available for ICC 4935-E-2793. Data for this genotype were therefore not included in the analysis.

Oviposition Antixenosis: Laboratory Studies. Three-day-old female and 1-d-old male *H. armigera* were kept in pairs at 26 ± 1°C in cylindrical, transparent plastic cages, and supplied with 10% sucrose solution. Adults were paired together for 48 h before the start of the experiment. During the experiment, each pair was supplied with 2 chickpea plants having leaves and pods. The plants, 1 resistant and 1 susceptible genotype, were paired in the following combinations: ICC 506 and Annigeri; ICC 506 and ICCX 730266-3-4-1P; ICCV 7 and Annigeri; ICCV 7 and ICCX 730266-3-4-1P. It was not possible to compare all 4 combinations concurrently. Oviposition in each combination was observed on a minimum of 4 occasions during the period November 1985 to February 1986. There were 5 cages (pairs) of 1 susceptible-resistant combination on each occasion. The number of eggs laid on each genotype after 24 h was recorded in each cage. Analyses were performed on the mean number of eggs per plant for each date. The observed number of eggs on susceptible and resistant genotypes was compared with an expected ratio (50:50) using a replicated *G* test (Sokal and Rohlf 1981).

Oviposition Antixenosis: Field Studies. The density of *H. armigera* eggs and larvae on 7 chickpea genotypes in field plots was studied in the 1981 and 1982 postrainy seasons. The genotypes were sown in a randomized complete block design with 3 replications of each genotype. The genotypes were composed of 3 short-medium duration desi genotypes (ICC 506, Annigeri and ICC 3137), 2 long duration desi genotypes (ICCX 730200-11-1-1H-B and G130) and 2 kabuli long duration genotypes (ICC 5264-E10 and L550). Each replicate was composed of 2 rows each 9 m in length, with 60 cm of spacing between rows and between plants within rows. Five randomly selected plants were tagged in each replicate. The tagged plants were visually examined at weekly intervals and the number of *H. armigera* eggs and larvae per plant was recorded. In 1981 sampling began on 26 November 1981 and finished on 7 January 1982. In 1982 sampling began on 24 November and finished on 6 January 1983. In both years the sampling period covered the period from flowering to pod maturity.

The $\log_{10}(n + 1)$ transformed mean number of eggs per plant and the mean number of larvae per plant were analyzed using SYSTAT repeated measures ANOVA (Wilkinson 1990). Data for the 2 yr

Table 1. Mean weight (milligrams) ± SEM of 1-d-old pupae and mean pupal developmental duration for *H. armigera* larvae reared on chickpea leaves or pods containing seeds

Genotype	Pupal wt, mg		Pupal period, d	
	Leaves	Pods	Leaves	Pods
		Desi chickpea		
ICC 506	146.3 ± 4.1b	314.7 ± 6.6a	9.9 ± 0.3a	13.0 ± 0.1a
Annigeri	167.4 ± 9.3ab	305.4 ± 6.3a	9.3 ± 0.4a	12.6 ± 1.1a
ICCV 7	117.4 ± 6.3c	229.3 ± 6.0c	9.4 ± 0.3a	
ICC 3137	209.1 ± 22.7a	275.6 ± 6.7b	8.4 ± 0.1a	12.4 ± 1.1a
ICC 4935-E-2793	— —	255.6 ± 6.0+	— —	7.8 ± 0.3+
		Kabuli chickpea		
ICC 10870	169.7 ± 6.5a	279.4 ± 15.5a	10.6 ± 0.1a	12.4 ± 0.6a
ICC 8835	178.9 ± 10.0a	264.9 ± 15.1a	10.8 ± 0.2a	11.2 ± 1.3a
ICC 5264-E10	220.4 ± 33.0a	270.3 ± 10.7a	9.9 ± 0.4a	12.0 ± 0.5a
ICCX 730244-17-2-2H	222.3 ± 17.8a	295.9 ± 9.4a	10.8 ± 0.4a	10.9 ± 1.0a
L 550	221.0 ± 17.1a	266.6 ± 12.6a	11.2 ± 0.4a	11.1 ± 1.1a

Means calculated from data for 6 replicates. Means within a column followed by the same letter are not significantly different at the 5% level (Tukey test). Desi and kabuli genotypes were analyzed separately. +, Not included in analysis.

were analyzed separately. Because of the low number of eggs during the latter sampling periods in both 1981 and 1982 data for the 6th and 7th sampling dates were excluded from the analysis.

Pod Damage Assessment. At harvest all the pods were removed from the tagged plants in each replicate and placed individually into labeled paper bags. The pods were subsequently examined and the number of undamaged, damaged (*H. armigera* damage), and undeveloped pods was recorded. Data for the weekly counts of *H. armigera* larvae were used to calculate the mean cumulative number of larval days per genotype. Angular transformed percentage of pod damage was regressed on the mean cumulative number of larval days. The slope and elevation of the regression lines were compared using *t*-tests (Zar 1984).

Results

Antibiosis. There was no significant variation in the weight of 10-d-old *H. armigera* larvae, larval developmental duration, or pupal developmental duration among larvae reared on the desi genotypes (ICC 506, Annigeri, ICCV 7, and ICC 3137). However, pupae of larvae reared on leaves or pods of the desi genotype ICCV 7 were significantly lighter than those reared on the 2 susceptible controls, ICC 3137 and Annigeri (Table 1; $F = 15.83$ df = 6, 28; $P < 0.001$). Pupae of larvae reared on leaves of ICC 506 were significantly lighter than larvae reared on leaves of ICC 3137.

Table 2. Mean percentage ± SEM of larval survival of *H. armigera* larvae reared on chickpea pods containing seeds or leaves

Genotype	Larval survival, %	
	Leaves	Pods
	Desi chickpea	
ICC 506	26.67 ± 8.4bc	73.71 ± 9.8a
Annigeri	48.33 ± 12.8ab	73.81 ± 7.9a
ICCV 7	13.65 ± 4.6c	19.05 ± 10.2c
ICC 3137	73.33 ± 6.7a	57.38 ± 11.9ab
ICC 4935-E-2793		44.13 ± 6.9+
	Kabuli chickpea	
ICCX 732244-17-2-2H	44.52 ± 9.9a	78.10 ± 5.1a
ICC 8835	36.43 ± 5.3a	76.43 ± 6.4a
ICC 5264-E10	40.48 ± 11.1a	75.00 ± 7.2a
ICC 10870	36.67 ± 6.7a	70.00 ± 9.7a
L 550	58.33 ± 11.2a	77.14 ± 6.2a

Means calculated from data for 6 replicates; untransformed data. Means within a column followed by the same letter are not significantly different at the 5% level (Tukey test).

The survival of larvae reared on leaves or pods of ICCV 7 was significantly reduced compared with that of larvae reared on leaves or pods of ICC 3137 or Annigeri (Table 2; $F = 5.49$; df = 1, 40 $P < 0.001$). The survival of larvae reared on leaves of ICC 506 was significantly reduced compared to larvae reared on leaves of ICC 3137.

There was significant variation in the weight of 1-d-old pupae and pupal developmental duration among larvae raised on leaves versus pods of the desi genotypes. Pupae of larvae reared on leaves were significantly lighter (Table 1; $F = 378.14$; df = 1, 28; $P < 0.001$) and had shorter pupal development times (Table 1; $F = 11.21$; df = 1, 19; $P < 0.005$) than larvae reared on pods.

There was no evidence for significant genotypic variation in the suitability for *H. armigera* growth or larval survival among the kabuli genotypes studied. There was significant variation in the measured parameters, except pupal development time, among larvae reared on pods versus leaves of kabuli genotypes. Larvae reared on pods were heavier ($F = 4.54$; df = 1, 47; $P < 0.05$), had shorter larval development times ($F = 7.04$; df = 8, 46; $P < 0.001$) and heavier pupae (Table 1; $F = 46.33$; df = 1, 45; $P < 0.001$) than larvae reared on leaves. Survival of larvae reared on leaves was significantly reduced compared to larvae reared on kabuli pods (Table 2; $F = 23.27$; df = 1, 47; $P < 0.001$).

Ovipositional Antixenosis: Laboratory Studies. The distribution of *H. armigera* eggs between resistant and susceptible genotypes deviated sig-

Table 3. *G* statistics for the distribution of *H. armigera* eggs in laboratory choice tests

Genotypes	*G* statistic	df	*G* value
ICC 506[r] and Annigeri[s]	Pooled	1	51.91***
	Heterogeneity	12	150.16***
	Total	13	202.07***
ICC 506[r] and ICCX 730266 3 4 1P[s]	Pooled	1	40.04***
	Heterogeneity	5	57.48***
	Total	6	77.50***
ICCV 7[r] and ICCX 730266 3 4 1P[s]	Pooled	1	0.99NS
	Heterogeneity	3	81.59***
	Total	4	82.58***
ICCV 7[r] and Annigeri[s]	Pooled	1	2.65NS
	Heterogeneity	3	6.08NS
	Total	4	8.73NS

Expected distribution based on a 50:50 ratio of eggs between susceptible ([s]) and resistant ([r]) genotypes. NS, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

nificantly from the expected 50:50 ratio in the tests comparing ICC 506 and Annigeri, ICC 506 and ICCX 730266-3-4-1P, ICCV 7 and ICCX 730266-3-4-1P (Table 3). The significant pooled G for the comparison of the distribution of eggs between ICC 506 and Annigeri and ICC 506 and ICCX 730266-3-4-1P indicates that a consistently greater number of eggs were laid on the susceptible genotype than on the resistant genotype. The significant heterogeneity *G* indicates that the deviations were not uniform in magnitude. In the test comparing oviposition on ICCV 7 and ICCX 730266-3-4-1P there was significant deviation from the expected 50:50 ratio, but the deviation was not uniform in direction indicating that females did not consistently select one genotype in preference to the other. There was no significant deviation from the expected 50:50 ratio in the tests comparing oviposition on ICCV 7 and Annigeri.

Ovipositional Antixenosis: Field Studies. There was significant variation in egg density among the short-medium duration desi genotypes (ICC 506, Annigeri and ICC 3137) in the 1981 postrainy season. Significantly fewer eggs were recorded on ICC 506 (Table 4; $F = 5.69$; df = 2, 40; $P < 0.01$) than on ICC 3137 and Annigeri. In the 1982 post-rainy season there was no significant variation in egg density among the seven genotypes, nor among the desi genotypes when these were analyzed separately.

Larval Density and Pod Damage. In both seasons there was significant variation in larval density among chickpea genotypes (1981: $F = 10.86$; df = 6, 14; $P < 0.001$. 1982: $F = 30.46$; df = 6, 84; $P < 0.001$), and a significant effect of sampling date (1981: $F = 74.76$; df = 6, 84; $P < 0.001$. 1982: $F = 6.933$; df = 6, 14; $P < 0.005$) but no sampling date × genotype interaction. In 1981 significantly fewer larvae were recorded on ICC 506 than on ICC 3137. In 1982 there were significantly fewer larvae recorded on ICC 506 than on G130, ICC 3137 and the long duration kabuli genotypes, ICC 5264-E10 and L550.

Figure 1 shows the relationship between mean cumulative larval days and percentage of pod damage for 4 susceptible controls and 3 resistant genotypes, paired according to seed size and developmental duration. There was no significant difference in the regression coefficients for ICC 5264-E10 and the susceptible check L550. However, there was a significant difference in the elevation of the 2 lines (Fig. 1A; $t = 6.50$, df = 7, $P < 0.05$) indicating that, after taking into account differences in the intensity of insect attack the transformed pod damage was not the same in the 2 genotypes.

The regression coefficient for ICC 506 was significantly greater than that for Annigeri (Fig. 1B; $t = 2.37$, df = 7, $P < 0.001$). There was no significant difference in the regression coefficient or the elevation of the lines for the susceptible ICC 3137 and ICC 506. The regression coefficient for ICCX 730020-11-1H-B was significantly greater than that for G130, the long duration desi, susceptible control ($t = 2.82$, df = 7, $P < 0.05$); at >200 cumulative larval days, ICCX 7300020-11-1H-B suffered more pod damage than G130.

Discussion

Pupal weight and larval survival were both reduced in larvae reared on leaves and pods of ICCV 7 indicating appreciable levels of antibiosis in this

Table 4. Mean number ± SEM of *H. armigera* eggs and larvae recorded on 5 plants of each genotype during the 1981 and 1982 post rainy season

Genotype	1981		1982	
	Eggs	Larvae	Eggs	Larvae
ICC 506	1.26 ± 0.3b	5.96 ± 1.0b	1.09 ± 0.3a	1.41 ± 0.2c
Annigeri	2.29 ± 0.4a	8.01 ± 1.0ab	1.83 ± 0.5a	2.57 ± 0.4bc
ICC 3137	3.76 ± 0.9a	10.56 ± 1.3a	2.19 ± 0.5a	5.22 ± 0.6a
ICCX 730020-11-1H-B	1.55 ± 0.3ab	6.86 ± 0.8ab	1.00 ± 0.2a	2.82 ± 0.4bc
G130	2.09 ± 0.5ab	7.85 ± 1.1ab	1.19 ± 0.2a	3.17 ± 0.5bc
ICC 5264-E10	2.22 ± 0.6ab	10.08 ± 1.2a	1.43 ± 0.3a	3.41 ± 0.4ab
L 550	2.32 ± 0.5ab	9.87 ± 1.2ab	1.78 ± 0.4a	3.82 ± 0.6ab

Means calculated from data for 3 replicates on 5 (eggs) or 7 (larvae) sampling dates. Means within a column followed by the same letter are not significantly different at the 5% level (Tukey test).

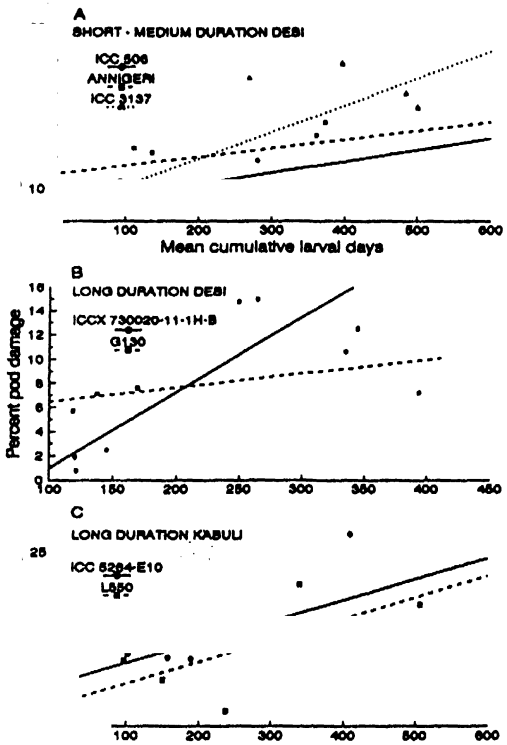

Fig. 1. Relationship between angular transformed percentage of pod damage and mean cumulative larval days.

genotype. The results for larvae reared on ICC 506 suggest that an antibiotic factor is present in the leaves of this genotype. Pupal weight has been shown to be correlated with fecundity in Lepidoptera (Bessin and Reagan 1990). Therefore, our results suggest that larvae reared on leaves or pods of ICCV 7 or leaves of ICC 506, would have reduced survival and result in females that produce fewer eggs than larvae reared on susceptible genotypes. Field and laboratory studies indicated that ovipositional antixenosis was also present in ICC 506.

Chickpea secretes an acidic exudate on its leaf surface, stem and pod wall (Khanna-Chopra and Sinha 1987). Differences in the biochemical constituents of the exudate among the genotypes may have had a role in determining the suitability of chickpea tissue for *H. armigera* in the current study. Analyses of the acid components of chickpea leaf exudate have suggested that differences in the relative concentration of malic acid (Rembold 1981) or oxalic acid (Yoshida et al. 1995) are important in resistance to *H. armigera*.

The current study has shown significant variation in growth and survival of *H. armigera* reared on chickpea leaves and pods. This observation is consistent with that of Sison and Shanower (1994) who showed that *H. armigera* larvae reared on leaves and flowers of pigeonpea had lower larval weights and longer development times than those reared on pods. Differences in the availability of nutrients among plant parts may effect the differences in the growth and survival of *H. armigera* on chickpea. However, differences in the amount of acidic exudate consumed by 1st to 3rd instars may also be important. In the current study, small larvae reared on chickpea pods containing seed were observed to penetrate the pod wall and commence feeding on the green seed, which does not secrete exudate. Larger larvae would consume the whole pod and seeds. In comparison, the larvae that were reared on leaves ingested plant material with surface exudate throughout their development. Further experiments are required to quantify the contribution of the 2 factors to the observed differences in growth among larvae reared on the 2 plant parts.

The regression of pod damage on mean cumulative larval days provides an indication that differences in tolerance to *H. armigera* occur among chickpea genotypes. Further experiments are also required to evaluate genotypes for this resistance mechanism.

The current study has identified antibiosis and ovipositional antixenosis as resistance mechanisms in the short-medium duration desi chickpea genotypes. However, none of the longer duration genotypes (desi and kabuli) which had previously been shown to have reduced susceptibility to *H. armigera* in screening trials in northern India showed any evidence of antibiotic or antixenotic resistance to *H. armigera*. One explanation for the poor performance of these genotypes is that environmental conditions prevailing at Patancheru (south India) altered their susceptibility to the pest. *H. armigera* population pressure in the south is also typically much higher than that in north India (Lal et al. 1986).

Comparison of data from 10 years multilocational testing of selected chickpea genotypes (Lateef and Sachan 1990), including ICC 5264-E10 and ICCX 730244-17-2-2H, shows that the relative resistance rating of chickpea genotypes frequently varies according to location. This may in part be caused by different perceptions of damage by researchers in the different locations; it may also reflect real difference in the susceptibility to *H. armigera* between locations. These observations highlight the need to screen genotypes in the environments in which they are intended to be grown, to avoid overlooking important sources of resistance to *H. armigera*.

Acknowledgments

We thank N. J. Armes, T. G. Shanower, and M. Yoshida for comments on an earlier draft of the paper. Approved as Journal Article No. JA1795 by ICRISAT. The data presented here were collected by staff of the Legumes Entomology staff, ICRISAT, under the supervision of S.S.L. and subsequently analyzed by S.E.C.

References Cited

Armes, N. J., D. R. Jadhav, and P. A. Lonergan. 1995. Insecticide resistance in *Helicoverpa armigera:* status and prospects for its management in India. *In* Proceedings, World Cotton Research Conference-1, 13–17 February 1994. Brisbane, Australia.

Bessin, R. T., and T. E. Reagan. 1990. Fecundity of sugar cane borer (Lepidoptera: Pyralidae) as affected by larval development on gramineous host plants. Environ. Entomol. 19: 635–639.

Bhatnagar, V. S., S. S. Lateef, S. Sithanantham, C. S. Pawar, and W. Reed. 1982. *Heliothis* research at ICRISAT, pp. 385–396. *In* Proceedings, International Workshop on *Heliothis* Management, 15–20 November 1981, International Crops Research Institute for the Semi-Arid Tropics, Patancheru India.

Dias, C.A.R., S. S. Lal, and C. P. Yadava. 1983. Differences in susceptibility of certain chickpea cultivars and local collections to *Heliothis armigera.* Indian J. Agric. Sci. 53: 842–845.

Fitt, G. P. 1989. The ecology of *Heliothis* in relation to agroecosystems. Annu. Rev. Entomol. 34: 17–52.

Khanna-Copra, R., and S. K. Sinha. 1987. Chickpea: physiological aspects of growth and yield, pp. 163–189. *In* M. C. Saxena, and Singh K. B. [eds.], The chickpea. CAB, Wallingford, UK.

Kishor, N. M. 1992. Impact of pesticide externalities on production and trade in agricultural commodities: the case of cotton cultivation in Andhra Pradesh. Unpublished report. Trade Policy Division, The World Bank, Washington, DC.

Lal, S. S., C. P. Yadava, and J. N. Sachan. 1986. Strategies for the development of an integrated approach to control gram pod borer, *H. armigera* infesting chickpea. Pesticides 20(5): 39–51.

Lateef, S. S. 1985. Gram pod borer *Heliothis armigera* (Hüb.) resistance in chickpeas. Agric. Ecosys. Environ. 14: 95–102.

Lateef, S. S., and J. N. Sachan. 1990. Host-resistance to *Helicoverpa armigera* in different agroecological contexts, pp. 181–190. *In* Chickpea in the nineties: Proceedings, 2nd International Workshop on Chickpea Improvement, 4–8 December 1989, International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Mote, U. N., and D. K. Murthy. 1990. Studies of loss estimation and relative susceptibility of genotypes of sorghum to *H. armigera.* Trop. Pest Manage. 36: 108–113.

Reed, W., C. Cardona, S. Sithanantham, and S. S. Lateef. 1987. Chickpea pests and their control, pp. 283–318. *In* M. C. Saxena, and K. B. Singh [eds.], The chickpea. CAB, Wallingford, UK.

Rembold, H. 1981. Malic acid in chickpea exudate—a marker for *Heliothis* resistance. Int. Chickpea Newsl. 4: 18–19.

Singh, H., and S. S. Sharma. 1970. Relative susceptibility of some important varieties of gram to *Heliothis armigera* Hübner.Indian J. Entomol. 32: 170–171.

Sison, M.L.J., and T. G. Shanower. 1994. Development and survival of *Helicoverpa armigera* (Lepidpotera: Noctuidae) on short-duration pigeonpea. J. Econ. Entomol. 87: 1749–1753.

Sokhal, R. R., and F. J. Rohlf. 1980. Biometry, 2nd ed. Freeman, New York.

Srivastava, C. P., and R. P. Srivastava. 1989. Screening for resistance to the gram pod borer, *H.armigera,* in chickpea: genotypesand observations on its mechanism of resistance in India. Insect Sci. Applic. 10: 255–258.

1990a. Estimation of avoidable loss in chickpea (*Cicer arietinum*) due to gram-pod borer (*Heliothis armigera*) in Rajasthan. Indian J. Agric. Sci. 60: 494–496.

1990b. Antibiosis in chickpea *Cicer arietinum* L. to gram pod borer, *Heliothisarmigera* (Hübner) in India. Entomol 15: 89–93.

Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT, Evanston, IL.

Yoshida, M., S. E. Cowgill, and J. A. Wightman. 1995. Mechanism of resistance to *Helicoverpa armigera* in chickpea: antibiosis of oxalic acid in leaf exudate. J. Econ. Entomol. (In Press)

Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.

Received for publication 19 October 1994; accepted 20 June 1995.