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Natural Occurrence and Salient Characters of Nonnodulating Chickpea Plants

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ABSTRACT

Nonnodulating (Nod⁻) lines are a valuable reference for assessing the amount of biologically fixed N₂ in a legume. Chance observation of a Nod⁻ plant in chickpea (*Cicer arietinum* L.) accession ICC 435 encouraged us to study the frequency of natural occurrence of this trait. Six hundred forty to 36260 plants of each of 11 chickpea accessions, field-grown under conditions favoring good nodulation, were uprooted for nodulation observations at 22 and 112 days after sowing (DAS). Plants identified as Nod⁻ at 22 DAS were potted to produce seeds and those at 112 DAS had physiologically mature seeds. Progenies of apparent Nod⁻ plants were inoculated with chickpea *Rhizobium* strain IC 59 and grown in pots for 28 d for confirmation. The frequency of Nod⁻ plants in four accessions (ICC 435, 4918, 5003 and 4993) ranged from 129 to 490 per million. One Nod⁻ plant from each of the four accessions was used for reconfirmation studies in the poststray season 1987-1988 and for agronomic evaluation in subsequent studies under field conditions. The Nod⁻ selections were indistinguishable from their respective parent accessions for plant growth except for nodulation, and most yielded similarly to their Nod⁺ accessions when supplied with 50 to 100 kg N ha⁻¹. On a low-N field without fertilizer N, the Nod⁻ plants were light green, grew poorly, had a short internodal distance with small leaves and leaflets, and had reddish-brown pigment on margins of leaflets, rachis, and sometimes branches.

CEREALS or other nonlegume crops are generally used as references in studies assessing amounts of biological N₂ fixation in legumes. These, however, may not be satisfactory reference crops in most such studies because of differences in plant growth rates and rooting patterns between the reference and the test crops (14). Also, cereals may fix some N₂. Therefore, nonnodulating lines of legumes are preferred as references. The possibility of their use in developing host

plants with restricted *Rhizobium* specificity, which would circumvent the problem of competition from native rhizobia, has also been indicated (4). The search for Nod⁻ chickpea plants began at IC-RISAT Center (18° N lat) in 1975 with initiation of research work on biological N₂ fixation. Nonnodulating plants were occasionally observed during 1976 to 1980 in segregating F₂ and F₃ populations, but could not be saved due to lack of sufficient knowledge and expertise in salvaging the uprooted chickpea plants. Methods developed in the early 1980s (2,9) were used to recover a Nod⁻ plant from a germplasm accession ICC 435, a landrace from Bihar, India. Progenies of this plant were confirmed to be Nod⁻ and were otherwise similar to the parent type (10). Unlike the Nod⁻ groundnut (*Arachis hypogaea* L.) mutant (5), this Nod⁻ line (named ICC 435M) did not show apparent N-deficiency symptoms when grown on traditional chickpea fields, suggesting good soil-N scavenging ability of its root system. This prompted us to see if Nod⁻ plants could be recovered from other genotypes. Procedures to identify Nod⁻ plants under field conditions at an early plant growth stage and at physiological maturity were proposed based on earlier nodulation studies and are described here. Frequency of occurrence of Nod⁻ plants and their characteristics are also discussed.

MATERIALS AND METHODS

Large populations of 11 chickpea accessions (Table 1) were grown on a Vertisol (Kasbeddipali soil series, Typic Pellustert) field with available-N concentration of =19 mg kg⁻¹ soil in the top 15 cm of the profile, and chickpea *Rhizobium* count of 4700 g⁻¹ dry soil as measured by the most probable number plant infection technique (13). Screening for Nod⁻ plants was conducted on four germplasm accessions at early plant growth stage, 22 DAS, and on 10 accessions (including three studied at 22 DAS) at physiological maturity at 112 DAS (Table 1). Four of the total 11 accessions were Desi type, characterized by light to dark-brown angular seeds; the other seven were Medi-

Abbreviations: DAS, days after sowing; Nod⁺, nodulating; Nod⁻, nonnodulating.

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Table 1. Description of chickpea accessions used in the search for nonnodulating (Nod⁻) plants at early plant growth stage and at physiological maturity.

Accession	Synonyms	Age at screening d after sowing	Seed type	Origin	Maturity [§]	Remarks
ICC 435	P 319-1	22:112	Desi†	India	L	Landrace
ICC 4918	Annigeri	22:112	Desi	India	L	Selection from a landrace
ICC 4948	C 30	22:112	Desi	India	L	Landrace
ICC 4973	L 550	112	Kabuli‡	India	L	Bred variety
ICC 4993	R 20	112	Kabuli	Morocco	L	Landrace
ICC 5003	K 850, 850-3/27	22:112	Desi	India	M	Bred variety
ICC 12328	Cyprus local	112	Kabuli	Cyprus	L	Landrace
ICC 12329	Iranian local	112	Kabuli	Iran	L	Landrace
ICC 12330	Jordanian local	112	Kabuli	Jordan	L	Landrace
ICC 12331	Syrian local	112	Kabuli	Syria	L	Landrace
ICC 12332	Turkish local	112	Kabuli	Turkey	L	Landrace

† Desi = light to dark brown color and angular head seeds.

‡ Kabuli = Mediterranean type, beige or ivory color, owl's-head-shape seeds.

§ L = long duration, M = medium duration, S = short duration.

teranean type, with beige or ivory-colored, owl's-head-shape seeds generally called kabuli. Conditions of high natural humidity and good soil moisture, considered necessary for good nodulation of chickpea, were ensured.

Plants were counted and uprooted with a crowbar to a depth of ≈ 20 cm to recover roots and nodules. Plants identified as apparently nod at 22 DAS were potted, inoculated with chickpea *Rhizobium* Strain IC 59 and grown to maturity, following the methods described by Rupela and Dart (9). Six hundred forty to 2200 plants of each of the 10 accessions were examined for nodulation at 112 DAS. Previous unpublished observations suggested that most chickpea nodules remain attached to roots when carefully dug at maturity. Irrigation a few days before observation facilitated uprooting of plants. Plants identified as apparently nod at 112 DAS were brought to the laboratory, and the roots were soaked in water for ≈ 1 h and observed again for nodules. Plants with tiny nodules were discarded, and seeds of the remaining plants were preserved for future use.

Seeds were produced from at least one Nod⁻ potted plant of each of ICC 435, -4918, and -5003, identified at 22 DAS, and sufficient seeds were available of Nod⁻ plants of ICC 4993 and -5003, identified at 112 DAS. Five to 10 seeds from each of these apparently Nod⁻ plants were sown in 10-cm diam. plastic pots filled with coarse river sand. Inoculation was done at sowing by applying 10 mL of a suspension of peat inoculant (*Rhizobium* Strain IC 59) in water that had at least 10^8 rhizobia mL⁻¹. Plants were irrigated with quarter-strength N-free nutrient solution following Arnon (1), as required. Pots were placed in a glasshouse, with temperatures ranging from 16 °C at night to 32 °C during day and relative humidity of $\approx 70\%$ in February-March 1987. Twenty-eight old plants were washed and examined for nodulation by spreading the root system in enamel trays filled with water.

Progenies of one confirmed Nod⁻ plant of each of the four accessions ICC-435, -4918, -4993 and -5003 were grown in the potstray season of 1987-1988 (November 1987-April 1988) on an Inceptisol (Singapura soil series, fine loamy mixed hyperthermic Typic Ustochrept) field at ICRISAT Subcenter, Gwalior, India, (26° N lat) for further confirmation against rhizobia of eight different environments. Plants were uprooted at 60 DAS for nodulation observations. The Nod⁻ lines retained their original accession number, but were suffixed by 'M'.

In the potstray season 1988-1989 (November 1988-April 1989) the Nod⁻ lines of the four chickpea accessions described above, PM233, and their Nod⁺ parents were grown on a low-N field at Gwalior for agronomic evaluations in

three replicates. The experimental design was a randomized complete block using a split-plot treatment arrangement with six fertilizer treatments (0, 20, 50, 100, 150, and 200 kg N ha⁻¹) as main plots and chickpea accessions as sub-plots of 4 by 1.2 m. The chickpea accessions were sown in 4-m long rows with interrow spacing of 30 cm and intrarow spacing of 10 cm. The soil pH (1:2.5 soil/water), electrical conductivity, available N, and Olsen P in the top 30-cm soil profile ranged 8.1 to 8.3, 0.02 to 0.04 S m⁻¹, 17 to 27 mg kg⁻¹ soil, and 5 to 12 mg kg⁻¹ soil, respectively. Chickpea *Rhizobium* count was 4300 g⁻¹ soil. Detailed results of this study will be reported separately. However, nodule dry (70 °C) mass on a sample of plants from 0.3 m² per plot at 58 DAS, apparent N-deficiency symptoms based on weekly visual records, and grain yield of 0 N and 50 N treatments for the chickpea accessions are reported.

A study of root hair morphology was conducted on the Nod⁻ plants from the four lines reported here and on the mutant PM233 of Davis et al. (3). The relevant Nod⁺ parents of these lines were included as checks. Fifty water-soaked seeds of each of these lines were germinated in 9-cm Petri dishes lined with water-soaked blotting paper. Plates were placed in a 8-L covered plastic container having a 2-cm water layer at the bottom. Temperature inside the container was 20 to 25 °C. Radicles on 5- to 8-d-old germinated seeds were observed for presence of root hairs under a stereomicroscope at 20 to 60 \times .

RESULTS AND DISCUSSION

The frequency of occurrence of the Nod⁻ character ranged from 120 to 490 plants per million (Table 2). Fourteen of the 21 transplanted plants died due to fusarium wilt (*Fusarium oxysporum* f. sp. *ciceri*) before producing seeds. All plants, however, survived for at least 3 wk and had formed new roots when examined. One plant of ICC 4948 produced nodules before dying. None of the progenies of the seven surviving Nod⁻ plants from three accessions ICC 435, -4918, and -5003 formed nodules when grown in pots inoculated with chickpea *Rhizobium* Strain IC 59. It was therefore assumed that the plants that died would have displayed the same frequency of Nod⁻ in the confirmation studies as those that lived. Progeny of Nod⁺ plants of these accessions nodulated normally under the same conditions. The chance of correct identification of Nod⁻ plants from a field-grown population at early plant growth stages was thus very good,

Table 2. Frequency of naturally occurring nonnodulating (Nod⁻) plants in chickpea accessions.

Accession	Observed in field	Apparently Nod ⁻	Survived trans- planting		Confirmed as Nod ⁻	Frequency† of Nod ⁻ × 10 ⁻⁴
			no. of plants	no. of plants		
			At 22 DAS			
ICC 435	14812	7	4	4	4	472
ICC 4918	26190	4	2	2	2	153
ICC 4948	36260	7‡	0	0	1	120
ICC 5003	25056	3	1	1	1	120
			At 112 DAS			
ICC 4918	1551	1	m§	0	0	0
ICC 4948	640	0	m	0	0	0
ICC 4973	1873	1	m	0	0	0
ICC 4993	2179	1	m	4	459	459
ICC 5003	2039	1	m	1	490	490
ICC 12328	2069	0	m	0	0	0
ICC 12329	2060	0	m	0	0	0
ICC 12330	2113	0	m	0	0	0
ICC 12331	1976	0	m	0	0	0
ICC 12332	1895	1	m	0	0	0

† It was assumed that the plants that died would have displayed the same frequency of Nod⁻ in the confirmation studies as those that lived. Multiply value shown by 10⁻⁴ to get actual value (= no. per million).

‡ One of the seven plants produced nodules before dying.

§ These plants had physiologically mature seeds, transplanting was not required.

but was associated with the substantial effort of salvaging these plants and risk of plant death due to adverse factors such as disease. It also required glass-house facilities. Only two (one each of ICC 4993 and ICC 5003) of the five apparent Nod⁻ plants selected at physiological maturity were actually Nod⁻. The latter method of identifying natural Nod⁻ plants seemed more convenient and may be applied to legumes where most nodules remain attached to roots even at physiological maturity (e.g., peanut and chickpea).

Progenies of the confirmed Nod⁻ plants in subsequent studies at Gwalior in the poststray season of 1987-1988 did not produce any nodules with native rhizobia. This further confirmed that the identified Nod⁻ plants were resistant not only to Strain IC 59 (used in confirmation studies in pots) but also to the mixture of *Rhizobium* strains that probably occurred in field soils. These plants grew similarly to their Nod⁺ accessions in this field up to 65 d when they were uprooted for nodulation observations, indicating their ability to grow well on the native soil fertility.

On a low-N field without fertilizer in the poststray season 1988-1989, the Nod⁻ lines at 60 DAS grew poorly, had small leaves and leaflets, short internodal distance and light green foliage compared with respective Nod⁺ accessions. Desi lines had reddish-brown margins on leaflets, rachis, and sometimes stems, most conspicuously in ICC 4918M and PM233. These symptoms matched well with the N-deficiency symptoms described by Smith and Pieters (12) for a chickpea line "Tyson". It seems that desi chickpea lines display reddish-brown pigment under several stresses, such as salinity or disease (8). It should, however, be possible to separate N deficiency from other stresses by examining symptoms other than the pigment. Kabuli line ICC 4993 did not show the characteristics reddish-brown pigment of the kind seen on

Table 3. Characteristics of nonnodulating (Nod⁻) lines compared with respective nodulating (Nod⁺) accession at 0 kg (0 N) and 50 kg N ha⁻¹ (50 N), at Gwalior, poststray season 1988-1989.

Chickpea line†	Nodule mass at 58 d after sowing		Apparent N-deficiency symptoms‡		Grain yield	
	0 N	50 N	0 N	50 N	0 N	50 N
	mg plant ⁻¹				t ha ⁻¹	
ICC 435	32	283	-	-	3.57	2.58
ICC 435M	0	0	+	-	2.24	3.02
ICC 4918M	211	139	+	-	2.91	3.25
ICC 4918	0	0	+	-	1.56	2.36
ICC 4993	163	120	+	-	2.55	2.40
ICC 4993M	0	0	+	-	2.06	2.33
ICC 5003	370	191	-	-	2.70	2.69
ICC 5003M	0	0	+	-	2.69	3.32
ICC 640	222	188	+	-	2.98	3.53
PM233	0	0	+	-	1.87	2.36
LSD (0.05)	65				0.47	

† Accession no. suffixed with 'M' are the Nod⁻ lines of the respective accession. PM233 is Nod⁻ mutant of ICC 640(3).

‡ Observation at 60 days after sowing: -, + = absence and presence of N-deficiency symptoms.

the desi types. In N-fertilized plots, these symptoms were absent. With moderate application of urea (50 kg N ha⁻¹), most lines yielded similarly to their respective Nod⁺ accessions, except PM233 and ICC 4918M (Table 3). These two lines seemed to require more N to produce as much yield as their Nod⁺ counterparts. All the Nod⁻ lines failed to nodulate. Occasional Nod⁺ plants observed in ICC 5003M were considered contaminants and discarded. The accession ICC 5003 had maximum nodule mass, followed by ICC 435. Nodule mass was greatly reduced (ranging from 13% in ICC 435 to 48% in ICC 5003), due to the application of 50 kg N ha⁻¹ (Table 3).

Very dense root hairs were generally observed 5 to 7 mm above root tips. All the radicles of Nod⁻ plants, including those of the irradiation mutant PM233 (3), and their Nod⁺ parents had apparently normal root hairs. This suggests that, unlike peanut (6), the Nod⁻ trait of chickpea is due to factor(s) other than absence of root hairs. Presence of root hairs perhaps allowed the Nod⁻ plants to scavenge the soil-N pool efficiently and made their visual identification difficult in the traditional chickpea fields. Leaves of Nod⁻ groundnut that lacked root hairs were generally pale green, and the plants did not grow as well as nodulated groundnut even when fertilized with 400 kg N ha⁻¹ (7). Chickpea Nod⁻ lines thus appeared to be suitable reference plants for studies of biological N₂ fixation.

Davis et al. (3) screened 10 000 M₂ seedlings to identify plants stable to chickpea line searching for natural Nod⁻ plants would be much faster and easier than developing induced Nod⁻ mutants. After screening a similar population size, we could identify Nod⁻ plants without the efforts of mutagenesis. Also, in natural Nod⁻ plants the chances of occurrence of undesirable changes on the genetic composition of identified plants are less than with mutagenized plants. Thus, further studies to establish suitable and desirable Nod⁻ plants would not be required.

It could be argued that all the Nod⁻ plants within a genotype are genetically the same and are progenies

of a natural mutation that occurred in the past. The Nod⁻ plants across different accessions, however, may be due to mutations at different loci, as established in the case of ICC 435M and PM233 (11). Seeds of Nod⁻ lines have already been given to interested researchers and will soon be a part of the gene bank at ICRISAT Center for general distribution.

In the screening procedure we looked for Nod⁻ plants only. It seems that some accessions may have natural variants of traits that may not be very apparent unless screened under the appropriate conditions. For example, some researchers have noticed occasional plants with resistance to fusarium wilt within a susceptible line in a disease screening nursery and found that the progeny of such plants were similar to the parent type but wilt resistant (M.P. Haware, 1990, personal communication). Screening for naturally occurring desirable traits thus offers a good opportunity of identifying genetic variability.

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1982. A potentially important source of bias in our between year comparisons was thus reduced by rejecting pre-1982 larval count data.

b) Light traps

Comparisons of numbers of *H. armigera* moths caught in a light trap at ICRISAT Center has provided circumstantial evidence for windborne migration of *H. armigera* from remote areas (Pedgley *et al.*, 1987). The evidence available suggests that such long distance migration does not play a significant role in the population dynamics of *H. armigera* at ICRISAT Center (Pedgley *et al.*, 1987). However, because moths can, from time to time, massively immigrate from afar and do regularly undertake short-range flights (5–40 km) we have also used the light trap data to interpret changes in pest abundance on ICRISAT farm over the last seven years. The light trap used was a modified Robinson type (Bhatnagar & Davies, 1979).

c) Natural enemy abundance

Light traps were used to monitor changes in the abundance of natural enemies of *H. armigera* during three dry and wet years on ICRISAT farm. This information was used along with the corresponding data on parasitism and predation levels to examine the influence of drought on the natural enemy complex of *H. armigera*.

d) Statistical analysis

The following parametric and non-parametric statistics were used to analyse the data:

1. Correlation and regression techniques (see Alder and Roessler, 1972) to explore the relationship between rainfall and pest abundance in different years and the cumulative effects of drought on the abundance of *H. armigera*.
2. The Kruskal-Wallis one way analysis of variance by ranks to compare pest abundance in normal *versus* rainfall deficient years. For details of the test see Seigel & Castellan (1988).

RESULTS

Larval counts

A summary of the larval count data obtained for the years 1983–88 is given in Table 1. Figures within $\pm 10\%$ of the long-term average rainfall can be counted as normal rainfall years. The number of *H. armigera* larvae per hectare were significantly lower during years of high rainfall (June–May 1983–84 and 1988–89) than during the four successive rainfall deficient years of 1984–87. Moreover, the abundance of the pest's population was compounded from one year to the next during this four year period of water deficit. Thus, on ICRISAT's cropped area, the larval population climbed from $218.1 \times 10^3 \text{ ha}^{-1}$ in 1984 to $638.9 \times 10^3 \text{ ha}^{-1}$ in 1987. A similar trend can be seen on the pest's two preferred host-plants (pigeonpea and chickpea) indicating that the relationship between increasing dryness and larval counts is not masked through excessive pooling of data (Table 2).

Regression and correlation analysis showed significant negative relationships between pest density and rainfall for the June–October period (Table 3). The lower the rainfall the higher the pest's abundance. Moreover, cumulative years of drought had a highly significant effect on *H. armigera* densities in pigeonpea ($r = -0.8$, $p < 0.01\%$). However, correlations between larval density and rainfall for the June–May data sets were not significant (Table 3). This was largely due to an apparently contradictory trend in 1987/88: high pest abundance associated with excess rainfall in 1987 (Tables 1, 2 and 3).

Light trap catches

In 1987, the direct and indirect effects of rainfall deficits on the pest's population dynamics were indeed confounded by the moth's long-range migratory activity. The light traps on ICRISAT farm recorded high moth catches in November–December 1987 (Figure 1). Our data show that in Nov–Dec 1987, the weeks with the highest catches (weeks 47, 48 and 51, 52) were preceded by periods when strong south-easterly winds blew across ICRISAT farm (weeks 46 and 50) (Figure 2). Previous work (Pedgley *et al.*, 1987) has shown that rises in light trap catches in October to December tend to be associated with winds veering from north-east to east to south-east, sometimes in response to tropical cyclones. Figure 3a. shows the streamlines of dominant surface wind directions for October–December based on direction frequencies at many observatories (India Meteorological Department, 1967). Deviations from long-term average rainfall in 1983–88 for the main cotton growing districts of coastal Andhra Pradesh (Prakasam, Guntur,

TABLE I

The relationship between rainfall and the abundance of *Helicoverpa armigera* at CRISAT, Patancheru, Andhra Pradesh, India.

Year	June-October			June-May		
	Rainfall (mm) (\pm long term average)	Area surveyed for larval population (ha)	Larval population 10^4 10^3 ha ⁻¹	Rainfall (mm) (\pm long term annual average)	Area surveyed for larval population (ha)	Larval population in 10^4 10^3 ha ⁻¹
1983-84	1021.2 (+52.4%)	327.4	14.94	1096.6 (+40.2%)	546.48	72.54
1984-85	591.3 (-11.7%)	333.1	24.90	670.3 (-14.3%)	532.77	116.21
1985-86	477.0 (-28.8%)	320.7	35.06	617.0 (-21.1%)	491.70	145.54
1986-87	538.0 (-19.7%)	255.7	57.65	633.3 (-20.3%)	406.50	154.10
1987-88	595.8 (-11.1%)	319.8	49.68	955.7 (+22.2%)	531.35	359.47
1988-89	900.2 (+34.6%)	420.3	35.58	1019.2 (+30.3%)	648.58	140.65

¹ Deviations from normal rainfall were computed from the long term average for Jun-Oct (670mm). More than 80% of the average annual rainfall occurs during these months at CRISAT. Long term average rainfall (1974-87): Jun-Oct 670mm; Jun-May 782mm.

² Larval population densities were significantly lower in excess rainfall years than in water deficient years ($P < 0.01$, Kruskal-Wallis one way analysis of variance by ranks).

TABLE 2

The relationship between rainfall and the abundance of *Helicoverpa armigera* on pigeonpea and chickpea at ICRISAT, Patancheru, Andhra Pradesh, India.

Year	June–October			June–May				
	Rainfall (mm) (± long term average) ¹	Pigeonpea		Rainfall (mm) (± long term annual average) ¹	Pigeonpea		Chickpea	
		Area surveyed for larval population (ha)	Larval population ² in 10 ³ ha ⁻¹		Area surveyed for larval population (ha)	Larval population in 10 ³ ha ⁻¹	Area surveyed for larval population (ha)	Larval population ² in 10 ³ ha ⁻¹
1983–84	1021.2 (+52.4%)	34.9	57.1	1096.6 (+40.2)	106.7	173.2	43.5	652.9
1984–85	591.3 (-11.7%)	57.9	86.4	670.3 (-14.3%)	124.5	210.2	56.6	1137.1
1985–86	477.0 (-28.8%)	55.4	140.1	617.0 (-21.1%)	110.7	190.1	57.0	1624.0
1986–87	538.0 (-19.7%)	39.6	151.4	623.3 (-20.3%)	65.5	303.1	49.8	1059.4
1987–88	595.8 (-11.1%)	32.8	455.9	955.7 (+22.2%)	121.9	1079.9	64.1	2492.4
1988–89	900.2 (+34.4%)	81.4	167.2	1019.2 (+30.3%)	177.8	252.6	76.9	910.3

¹Deviations from normal rainfall were computed from the long term average for Jun–Oct (670mm). More than 80% of the average annual rainfall occurs during these months at ICRISAT. Long term average rainfall (1974–87): June–Oct 670 mm; Jun–May 782 mm.

²Larval population densities were significantly lower in excess rainfall years than in water deficient years ($P < 0.01$, Kruskal-Wallis one way analysis of variance by ranks).

TABLE 3
Summary of regression and correlation analysis.

Relationship	Regression equation	r	Significance
<i>June–October</i> Rainfall (x) and larval density (y) on all crops at ICRISAT (Table 1)	$Y = 254.8 - 0.2 X$	-0.6	Significant at $P < 0.025\%$
Cumulative rainfall deficit and larval density on pigeonpea (Table 2)	$Y = 241.3 - 0.62 X$	-0.8	Significant at $P < 0.01\%$
<i>June–May</i> Rainfall and larval density on all crops at ICRISAT (Table 1)	$Y = 384 - 0.09 X$	-0.1	Not Significant
Cumulative rainfall deficit and larval density on pigeonpea (Table 2)	$Y = 448.5 - 0.62 X$	-0.3	Not Significant
Cumulative rainfall deficit and larval density on chickpea (Table 2)	$Y = 154.4 - 1.8 X$	-0.46	Not Significant

Note: In all cases, $n = 6$ pairs of observations.

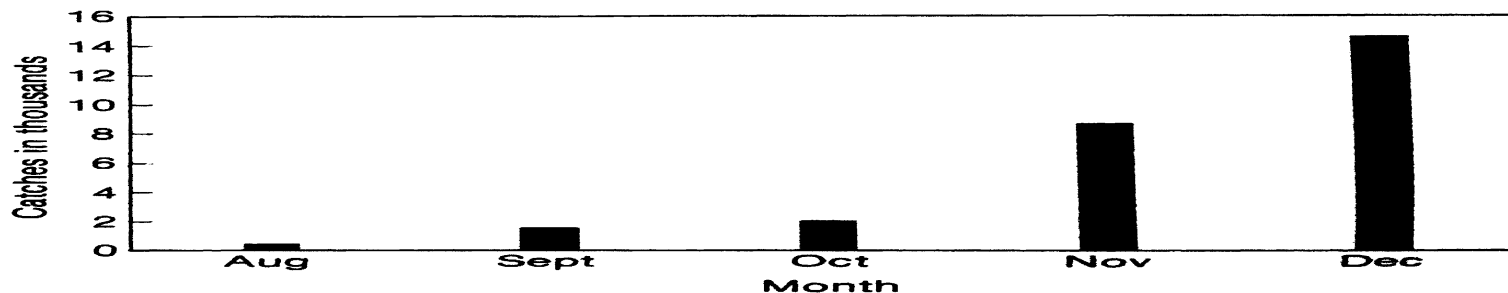


FIGURE 1. Monthly light trap catches for August to December 1987 at ICRISAT Centre, Patancheru, India.

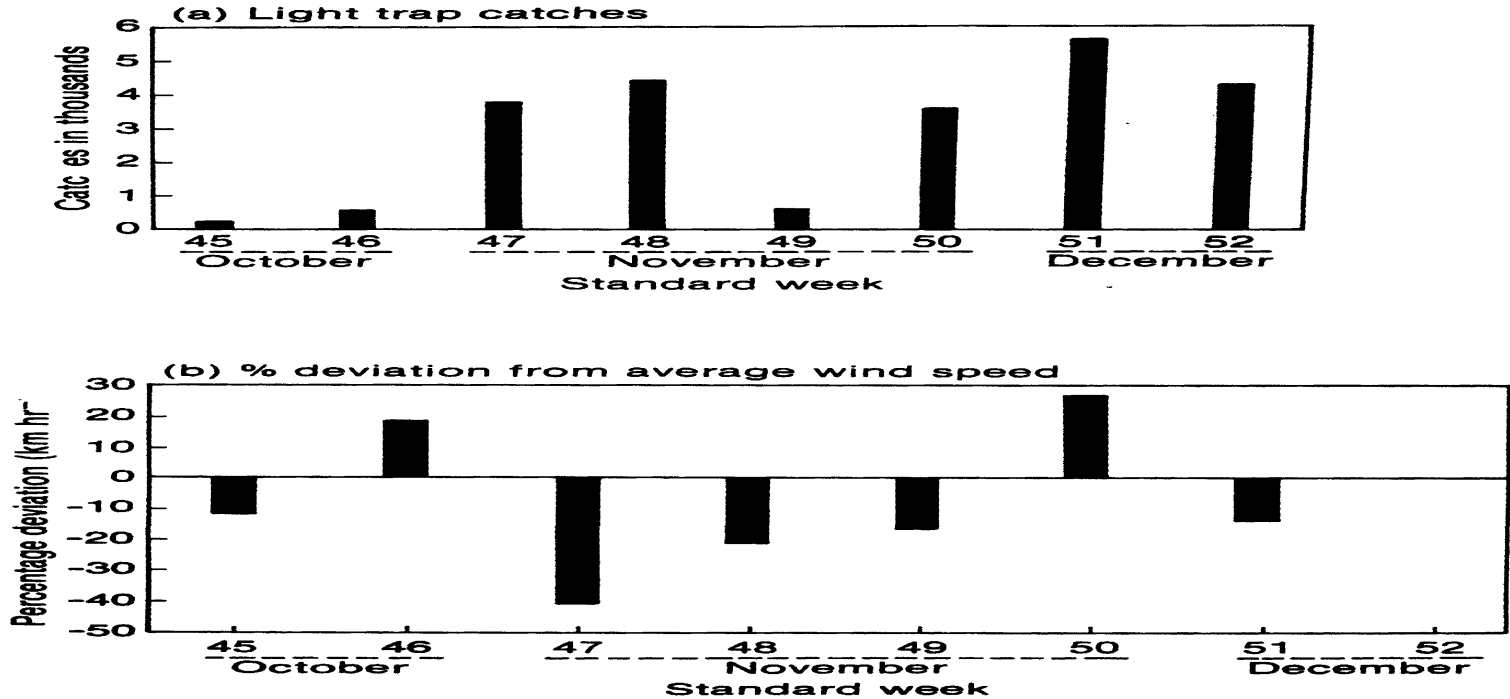


FIGURE 2. Light trap catches (a) and percentage deviation from long term average wind speed (b) during November and December 1987 at ICRISAT Centre, Patancheru, India.

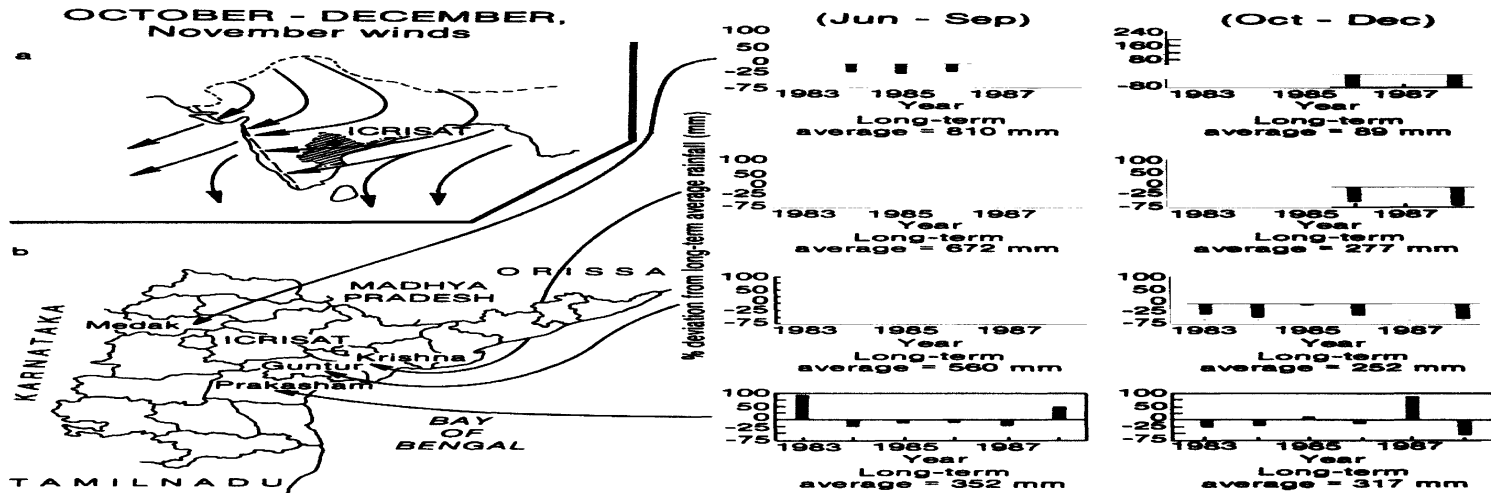


FIGURE 3. a) Streamlines of dominant wind directions at ICRISAT Centre, Patancheru, Andhra Pradesh, India. b) Percentage deviation from long-term average rainfall during the south-west (June-September) and north-east (October-December) monsoons from 1983-88 in Medak, Krishna, Guntur and Prakasam districts, Andhra Pradesh, India.

and Krishna) are also shown in Figure 3b. Rainfall values for Medak, Krishna, Guntur and Prakasam districts are means of 52, 75, 61 and 58 rain gauges respectively. The succession of drought years in the coastal area was associated with high pest abundance that led to the nearly complete destruction of the cotton crop and all other cultivated hosts grown under rainfed conditions in 1987 (King & Sawicki 1990; Thirumala Rao, personal communication, 1989). In the latter part of 1987, the moths thus moved with the prevailing winds from the drought stricken areas of coastal Andhra Pradesh (Figure 3b) to the inlands of the Deccan plateau where ICRISAT is based.

This interpretation is further supported by recent studies on the spread of

insecticide resistance in populations of *Helicoverpa armigera* across Andhra Pradesh (McCaffery *et al.*, 1989). *H. armigera* collected in October 1987 in the cotton growing districts of coastal Andhra Pradesh (Krishna, Prakasam and Guntur) were highly resistant to synthetic pyrethroids and endosulfan. Prior to 1986, *H. armigera* collected in pigeonpea and chickpea fields at ICRISAT Center were not resistant to endosulfan and pyrethroids, the latter being seldom used on ICRISAT farm. But by November–December 1987, *H. armigera* were found to be mildly resistant to endosulfan and highly resistant to pyrethroids at ICRISAT. The level of pyrethroid resistance steadily rose till March 1988. The insecticide resistant moths from the coastal areas of Andhra Pradesh migrated downwind to ICRISAT in a north westerly direction with the prevailing winds that occurred in the later part of 1987 (McCaffery *et al.*, 1989).

This incoming migration contributed to the increase in size of the *Helicoverpa* larval population in 1987–88 (Table 1). The cyclonic winds that carried the migrating moths from coastal Andhra Pradesh to ICRISAT farm were followed by heavy rains in November–December 1987 (Figures 3 and 4), thus explaining the apparent discrepancy in our June–May 1987–88 data, i.e., high *Helicoverpa* abundance associated with excess rainfall rather than with rainfall shortage as the previous years' trend suggests (Table 1).

We further analysed the ICRISAT light trap data to identify years when similar influxes of moths from coastal Andhra Pradesh occurred. Catches were low for all but the 1984/85 and 1987/88 years. The catches for June–May

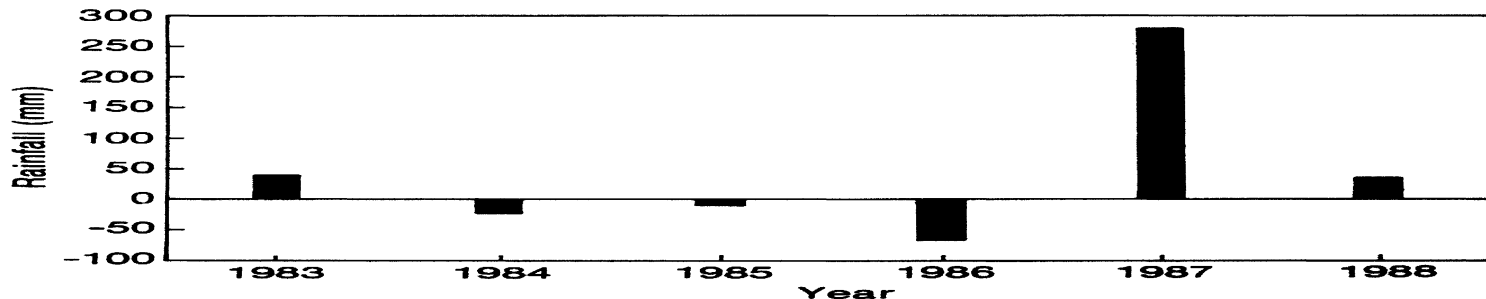


FIGURE 4. Deviation from normal rainfall for the period October to December 1983–88 at ICRISAT Centre, Patancheru, India.

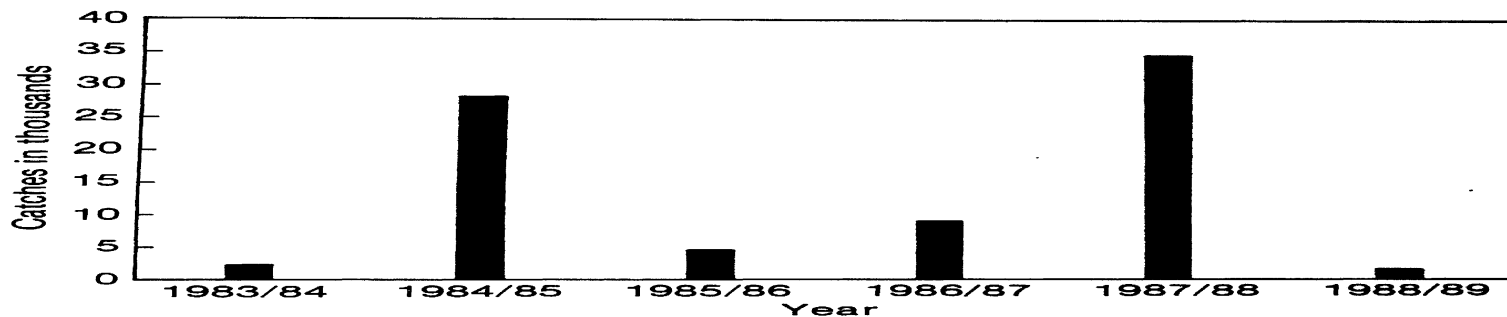


FIGURE 5. Yearly light trap catches (June to May) at ICRISAT Centre, Patancheru, India.

1984/85 were similar to those from 1987/88 (Figure 5). And, as in 1987, most of the 1984 windborne migration from the coastal cotton growing region occurred in the later part of the year when winds veer from NE to SE. As can be seen in Figure 6, the November 1984 catches were significantly higher than those of all other months.

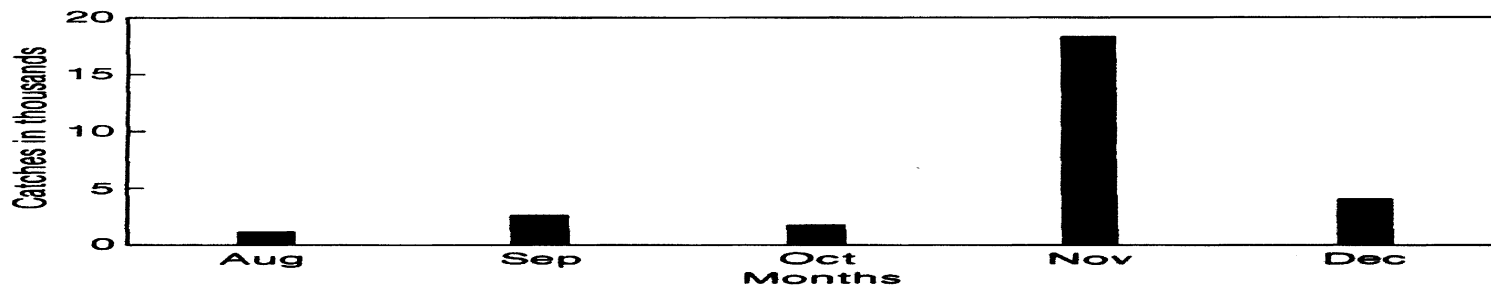


FIGURE 6. Light trap catches for August–December 1984 at ICRISAT Centre, Patancheru, India.

The effect of drought on the pest's population dynamics

The similarity in moth catches in Oct–Dec 1984 and Oct–Dec 1987 (24061 and 25153 respectively), and the timing of these two events in relation to the drought period, highlight the relative importance of climatic factors *versus* long distance migration in determining the abundance of *H. armigera* at ICRISAT Centre. The influxes of migrating moths were similar at the beginning (1984/85) and at the end (1987/88) of the four year drought. Through subsequent breeding the migrant moths presumably contributed equally to the build up of the local population, first in 1984 and then in 1987. However, the data show that the pest load on ICRISAT's mandate crops was significantly lower at the onset of drought than at the end of the four years of water deficiency: 218.1×10^3 larvae ha⁻¹ in 1984/85 and 638.9×10^3 larvae ha⁻¹ in 1987/88 (Table 1). The evidence thus suggests that the long-range migration which occurred did not play a major role in the population dynamics of *H. armigera* in 1987/88. It therefore follows that the direct and indirect effects of drought on the insect's life system promoted high population growth. This drought mediated process steadily built up across several dry years and eventually culminated in severe outbreaks of *H. armigera* at ICRISAT Center and in other parts of Andhra Pradesh in 1987/88. Moth dispersal and short-range flights (5–40 km) effectively ensured that the situation on ICRISAT farm partly mirrored the insect-host plant-environment interactions occurring in the surrounding countryside affected by drought.

The effect of drought on natural enemies of *H. armigera*

Altogether 77 parasitoids and 33 predators have been recorded on *H. armigera* in India (Manjunath *et al.*, 1989). It may be argued that the increased temperatures and decreased humidity associated with drought might reduce the numbers and efficiency of the pest's natural enemies and thus allow the pest to multiply unchecked. What little data we have on natural enemy abundance in dry and wet years are shown in Tables 4 and 5. Light trap records show that *Temelucha* sp. was the only parasitoid wasp whose abundance was greater in wet years than in abnormally dry seasons. However, ten year ICRISAT records obtained by the Cropping Systems Entomology group show that levels of larval parasitism by *Temelucha* sp. do not exceed 1% per season on each of ICRISAT's mandate crop (C.S. Pawar—unpublished data). This natural enemy therefore plays a minor role in regulating *H. armigera* populations,—even under optimal environmental conditions. As can be seen from the figures given in Table 5 *Campoletis chlorideae*, which feeds on 1–3 instar larvae, is a much more important biocontrol agent of *H. armigera*. ICRISAT's endemic, local pest population is at least partially regulated by

TABLE 4

The relationship between rainfall and the abundance of parasites of *Helicoverpa armigera* at ICRISAT Center, Patancheru, Andhra Pradesh, India, 1981-1986.

Year	June-October			June-May				
	Rainfall (mm) June-October (± long-term average)	<i>Temelucha</i> spp.	<i>Barichneumon</i> spp.	<i>Enicopsilus</i> spp.	Rainfall (mm) June-May (± long-term average)	<i>Temelucha</i> spp.	<i>Barichneumon</i> spp.	<i>Enicopsilus</i> spp.
1983-84	1021.2 (+52.4%)	3758	18	111	1096.2 (+40.2%)	5259	66	358
1984-85	591.3 (-11.7%)	466	59	1038	670.3 (-14.3%)	1142	96	1422
1985-86	477.0 (-28.8%)	185	67	252	617 (-21.1%)	286	71	398

Note: The natural enemies of *H. armigera* are all larval parasites (Hymenoptera: Ichneumonidae) and were captured in the light traps on ICRISAT farm.

TABLE 5

Annual percentage larval parasitism of *Helicoverpa armigera* by *Campoletis chlorideae* (Hymenoptera: Ichneumonidae) in crops grown on ICRISAT farm (June–May).

	1983–84 (excess rainfall)	1984–85 (deficient rainfall)	1985–86 (deficient rainfall)
Pigeonpea	6.6 (212)	2.6 (548)	—
Pearl millet	25.8 (97)	10.3 (29)	84.5 (209)
Sorghum	84.5 (187)	57.0 (121)	56.0 (325)
Chickpea	46.5 (155)	30.0 (2051)	22.9 (1605)

Notes: Values in parentheses indicate the total number of larvae (1–3 instars) examined.
— indicates data not available.

this parasitoid wasp. However, trends in percentage parasitism across crop backgrounds and dry versus wet years are not uniform (Table 5). Whilst levels of larval parasitism are lower in dry years on sorghum and chickpea backgrounds, the trend on millet is the exact opposite i.e. higher larval parasitism in abnormally dry years. There is thus no clear-cut evidence for the debilitating effects of drought on key natural enemies of *H. armigera* in this context. In the absence of a longer run of years we therefore assume that there are no significant differences attributable to parasitoid activity between the two sets of seasons (dry versus wet).

No data on changes in predator abundance in dry and wet years are available for ICRISAT farm. Ecophysiological studies suggest that hot and dry weather does increase the mortality of generalist predators like *Geocoris punctipes* (Say) (Hemiptera: Lygaeidae), *Reduviolus roseipennis* (Reuter) (Hemiptera: Nabidae) and workers of *Solenopsis invicta* Buren (Hymenoptera: Formicidae) (Cohen 1982; Mack *et al.*, 1988). None of these predators feed on *H. armigera* in India (Manjunath *et al.*, 1989) but their thermal and hygric adaptations may be similar to those of closely related species that do prey on this pest in India. However, the results of these ecophysiological studies on the water and temperature relations of these predators may exaggerate the importance of insect mortality in hot and dry conditions because they are not complemented by *in situ* studies of predator behaviour in desiccating conditions. Many predators of *H. armigera* in India are furtive insects that spend much of their time near the soil surface in plant litter e.g. *Geocoris* spp. Although the temperature is high near the ground, the humidity is also high—especially in soil fissures or in the plant litter which many generalist predators actively seek as part of their water balancing adaptations.

Moreover, there is generally little evidence that predators and parasitoids do regulate *H. armigera* populations on an area wide basis (Fitt, 1989). The mobility and high rate of increase of *H. armigera* permit rapid colonization and population growth in new habitats. Under these conditions, the capacity of natural enemies to respond functionally and numerically to changes in the pest's abundance is overwhelmed (Price, 1981; Fitt, 1989).

DISCUSSION

The exact reasons why drought favours high pest population growth are not known. Several case studies indicate that drought stressed plants are more susceptible to damage by some insect pests (Mattson & Haack, 1987, and references therein). The physical and physiological changes induced by water deficits can make wild and cultivated host plants more vulnerable and acceptable to *H. armigera*. Thus, when subjected to drought stress many of the cultivated and wild host plants on which *H. armigera* reproduces in and around ICRISAT Center accumulate high concentrations of proline, reducing sugars and other metabolites involved in osmotic adjustment. Selected examples are given in Table 6. Due to lack of information, Table 6 includes data for only one of the pest's wild host plants, *Rhynchosia minima*. However, the biochemical response of wild host plants to drought is probably similar to that of the cultivated host plants of *H. armigera* (Kramer, 1983).

Electrophysiological and behavioural studies on *H. armigera* have shown that some of these osmolytes (e.g., proline, fructose, sucrose, glucose) stimulate the feeding activity of adults and larvae as well as the mating success, fecundity and longevity of female moths (Blaney & Simmonds, 1988). When the concentrations of these osmolytes increase in host plants as water deficits intensify (ICRISAT, 1990; Pimbert, unpublished data), the insect's feeding behaviour is correspondingly stimulated. The first instar larvae probably benefit most from the drought-induced improvements in food quality and in the chemical cues involved in host selection behaviour. Young caterpillars normally have a very low chance of obtaining sufficient nitrogenous food when they first try to feed. This is partly why the first instars experience high mortality, as shown by life table studies of *H. armigera* (Fitt, 1989). Feeding on drought stressed plants scattered over large areas would thus improve early instar survival and enhance the growth, developmental rate and fecundity of *H. armigera*. In many areas of south India, *H. armigera* does not threaten cultivated crops until the second, third or even fourth generation. Intermittent or prolonged droughts that favour the build up of *H. armigera* populations through improved nutrition early in the season on wild host plants will be partly responsible for the high pest damage inflicted on crops later in the season.

TABLE 6

Changes in the nitrogen and carbohydrate fractions of host-plants of *Helicoverpa armigera* in response to water deficits.

Species	Nitrogen fraction		Carbohydrate fraction		References
	Organ or tissue	Fraction and trend	Organ and tissue	Fraction and trend	
Cultivated host-plants:					
Chickpea (<i>Cicer arietinum</i>)	Leaves	Pro +	Leaves	Fructose + Sucrose + Inositol +	Ford (1984)
Pigeonpea (<i>Cajanus cajan</i>)	Leaves	Pro +	Leaves	Inositol +	Ford (1984)
Groundnut (<i>Arachis hypogaea</i>)	Leaves	Pro +			Nageswara Rao <i>et al.</i> (1981)
Sorghum (<i>Sorghum bicolor</i>)	Leaves	Pro +	Leaves	Fructose + Glucose + Sucrose +	Sivaramakrishnan <i>et al.</i> (1988); Jones <i>et al.</i> (1980)
Pearl millet (<i>Pennisetum glaucum</i>)	Leaves	Pro +			Lal <i>et al.</i> (1988)

Cotton (<i>Gossypium hirsutum</i>)	Leaves	Pro +	Leaves	Glucose + Fructose + Sucrose +	McMichael & Elmore (1977); Cutler <i>et al.</i> (1977)
Tomato (<i>Lycopersicum esculentum</i>)	Leaves	Pro +	—	—	Aloni & Rosenshtein (1984)
Sunflower (<i>Helianthus annus</i>)	All parts	Pro +	Leaves	Starch – sugars +	Jones <i>et al</i> (1980)
Soyabean (<i>Glycine max</i>)	Leaves	Pro + Asp +	Leaves	Sucrose +	Ford (1984)
Mung bean <i>Vigna radiata</i>	Leaves	Pro =	Leaves	Inositol +	Ford (1984)
Cowpea (<i>Vigna unguiculata</i>)	Leaves	Pro =	Leaves	Inositol + Sucrose +	Ford (1984)
Maize (<i>Zea mays</i>)	Leaves	Pro +	Leaves	Sugars +	Pahlich & Grieb (1983); Barlow <i>et al.</i> (1976)
Wild host-plants:					
<i>Rhynchosia minima</i>	Leaves	Pro +	Leaves	Fructose + Glucose + Sucrose + Inositol +	Ford (1984)

Notes: Pro: Proline; Asp: Asparagine; +: increase; -: decrease; =: no change.

This interpretation blends into a more general theory of plant insect interactions that identifies plant nutritional quality as a major factor in the population dynamics of herbivorous insects (Chaboussou, 1967; House, 1967; Mattson, 1980; Slansky & Rodriguez, 1987). It has been suggested (Chaboussou, 1967, 1985; White, 1976, 1978, 1984) that insect populations remain at low abundance because of high early mortality resulting from starvation while feeding on nutritionally inadequate plant material. White (1984), in particular, argued that insect outbreaks are caused by weather induced plant water stress that improves the nutritional quality of plants and hence insect survival and population growth.

The higher air and host plant temperatures associated with drought may also have provided a more favourable thermal environment for the growth and reproduction of *H. armigera*. The insect's ability to find its host plants may have been improved as a result of drought induced changes. Vegetative growth slows or ceases along with protein and leaf chlorophyll synthesis in drought stressed plants (Kramer, 1983). This causes changes both in the visual part of the spectrum and the infra-red wavelengths. Nocturnal insects like *H. armigera* which may rely on far infra-red perception to locate their host plants would be favoured by the higher infra-red radiation associated with leaf temperature changes under conditions of water deficit. It is interesting to note that the closely related *H. zea* does rely on far infra-red electromagnetic cues in host finding (Callahan, 1965 a,b). However, further research is needed to determine the role of infra-red perception in the host selection behaviour of *H. armigera* and examine how these visual cues are modulated by drought.

Drought may also have improved the detoxification systems of *H. armigera*. With the sudden influx of insecticide resistant moths at ICRISAT in 1987, plant protection measures were unable to cope with the rapid multiplication of *H. armigera* (ICRISAT, 1988). It is therefore difficult to dissociate the relative influences of drought and ineffective insecticide control on the pest's abundance in the 1987 outbreak year. However, it is interesting to note that the more virulent insecticide resistant insects proliferated during the recent drought years in Andhra Pradesh (A.B.S. King, personal communication 1988; McCaffery *et al.*, 1989). The extent and severity of insecticide resistance declined dramatically one year later during the "wetter" 1988-90 season—despite the farmers' continued reliance on pyrethroids and endosulfan to control this pest in Andhra Pradesh (ICRISAT, 1989; King & Sawicki, 1990). Both the elevated temperatures associated with drought and the improved nutritional properties of drought stressed plants can enhance insect detoxification systems, at least with respect to some toxicants (Mattson & Haack, 1987). Increasing temperatures have thus been reported to reduce the susceptibility of the grasshopper *Melanoplus sanguinipes* to pyrethroid insecticides (Hinks, 1985). Moreover, nutrition may also influence pesticide

penetration and target site sensitivity in ways that are little understood (Campbell & Hayes, 1974). Further research should clarify the role of drought mediated processes in facilitating the spread of insecticide resistance in *H. armigera* populations in the semi-arid tropics.

Implications

Drought appears to have a profound influence on the regional abundance of *H. armigera* in the semi-arid parts of India. However, from a methodological point of view, climatic factors cannot be meaningfully considered in isolation from the water cycle and the way water is managed in semi-arid India. The impacts of monsoon failure and erratic rainfall on the dynamics of *H. armigera* reciprocally interact with various forms of man-induced drought in India. Many of the ecological processes that maintain the stability of the water cycle in these dryland environments are indeed being rapidly degraded through inappropriate land and water management policies; the promotion and preferential irrigation of water intensive cash crops, pumping of ground water beyond limits of recharge, diversion of organic manure from large areas of land to feed cash crop soils, deforestation . . . (Bandyopadhyaya, 1989; Gupta, 1986; Postel, 1989; Shiva 1988). Rainfall shortages may therefore have merely revealed the latent crisis in water management in the drylands of India and exacerbated already existing effects of water deficits on the plant-insect relationship described here. Rainwater, surface water, soil water and ground-water are, after all, inseparable and are linked to each other through processes of infiltration, percolation, evapotranspiration etc. The essential unity of the water cycle is such that water scarcity exists wherever and whenever the links in the cycle are broken or destabilised.

Thus, although our analysis has focussed on fluctuations in rainfall, we do recognize that a more holistic analysis may reveal that rainfall shortages play a role as an aggravating factor in outbreaks of *H. armigera*, the root causes of which are to be found elsewhere (i.e., in policies and development choices that lead to man-induced drought through destabilisation of the water cycle). In this connection, the structural approach developed by the "Drought and Man" project of the International Federation of Institutes for Advanced Study offers much scope for furthering our understanding of the processes described here (Garcia & Spitz 1986).

In terms of pest management, the main implication of our findings is that water conservation measures may need to be integrated in an overall plan of insect control in dryland India.

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