The Influence of Rainfall Deficits on the Abundance of *Helicoverpa (=Heliothis) armigera* in Andhra Pradesh, India*

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ABSTRACT

Analysis of larval counts, light-trap data and weather patterns over a six year period shows that prolonged rainfall deficits promote the growth of *Helicoverpa armigera* populations in Andhra Pradesh, India. Drought stress resulting from rainfall shortages enhances the chemical cues involved in larval host selection behaviour and improves the nutritional quality of many wild and cultivated host plants on which this polyphagous pest reproduces. A more holistic analysis of the causes of *H. armigera* outbreaks should also include the effects of man induced drought that stem from the destabilisation of the water cycle in the drylands of India. Water conservation measures may need to be integrated in an overall plan of insect control on an area-wide basis.

INTRODUCTION

Helicoverpa (=Heliothis) armigera (Hübner) (Lepidoptera: Noctuidae) is a major pest of several crops in the Old World semi-arid tropics (Reed & Pawar, 1982). Its caterpillars feed on cereals, pulses, cotton and tomatoes as well as many other crops and wild hosts. In India alone this polyphagous insect feeds on at least 180 plant species spread across 45 botanical families—the Amaranthaceae, Asteraceae, Brassicaceae, Euphorbiaceae, Fabaceae, Malvaceae, Poaceae and Solanaceae being the predominant host families (Manjunath *et al.*, 1989). Along with polyphagy the following ecological and physiological features contribute to boosting the pest status of *H. armigera*: high fecundity, multivoltinism, ability to migrate long distances and diapause

when environmental conditions become unfavourable (Fitt, 1989; Zalucki *et al.*, 1986).

The population densities of this pan-tropical pest vary greatly across seasons and among years but the reasons for these area-wide fluctuations in abundance are unknown. By virtue of its biological make-up this noctuid moth is particularly well adapted to dealing with ephemeral environments. *H. armigera* shares many traits found in r-selected species and we might therefore expect its regional abundance to be determined mainly by abiotic (e.g. climatic) rather than by biotic factors (Southwood, 1977a, b).

Prolonged or intermittent drought are characteristic and recurring features in the semi-arid parts of India where this insect has become a very serious pest over the last twenty years. The higher temperatures and reduced availability of water associated with drought may influence the insect's survival either directly or indirectly through their effects on host-plant abundance and quality. Both the direct and indirect effects of drought in semi-arid environments may therefore play a key role in determining the population dynamics of *H. armigera* on a regional scale. In this paper drought is broadly defined as a water deficit at any point in the water cycle. We present evidence for a positive relationship between rainfall deficits and high abundance of *H. armigera* on and around the 1400 ha farm of the International Crops Research Institute of the Semi-Arid Tropics (ICRISAT) in Andhra Pradesh, India. The possible reasons why drought favours high abundance of *H. armigera* on an area wide basis are discussed and the implications for pest management are mentioned.

BACKGROUND INFORMATION

The agroclimatic environment

Andhra Pradesh lies between 12°–37′ and 19°–54′N latitudes and 76°–46′ and 84°–46′E longitudes. This state of India is divided into three broad regions: Telangana, Rayalaseema, and Coastal Andhra Pradesh. Telangana receives over 75% of its mean annual rainfall during the southwest monsoon (June–September). In Rayalaseema (the driest part of Andhra Pradesh) and in northern coastal Andhra, 50 to 75% of the mean annual rainfall is received during this season. Dependence on the southwest monsoon decreases in southern coastal Andhra Pradesh where only 25 to 50% of the mean annual rainfall is received during this period. The retreating monsoon season (October–November) marks the transition between the rainy southwest monsoon and the winter northeast monsoon. During this season, the coastal area of southern Andhra Pradesh receives a larger share of its total rain.

Cyclones are very active at that time of the year and it is on account of them that the rainfall is widely distributed over the entire coastal belt. The northeast monsoon (December–February) is a dry season with practically no rain anywhere. Red sandy soils cover the largest area in the State (almost 70% of the total area). These zonal soils lose their pre-eminence to azonal alluvial soils in the coastal belt and to intrazonal black soils (Vertisols) in the river valleys.

ICRISAT is located at 18°N, 78°E near Patancheru village, 26 Km northwest of Hyderabad, in the Telangana region of Andhra Pradesh. The Institute's 1400 ha experimental farm includes two major soil types found in the semi-arid tropics: Alfisols (red soils), which are light and drought prone, with an available water holding capacity (AWHC) of 60–100 mm, and Vertisols (black soils) with high AWHCs (180–230 mm). The rainy season (monsoon) usually begins in June and extends into early October. More than 80% of the average annual rainfall (782 mm) is received in those months, during which the rainfed crops are grown. The post rainy or post monsoon winter season (mid-October to January) is dry and relatively cool. During this short day period crops can be grown on vertisols on stored soil moisture. The hot, dry summer season lasts from March until rains begin again in June. Any crop grown during this season requires irrigation.

The pest's population dynamics at ICRISAT Center

H. armigera reproduces throughout the year in southern India. On and around the Institute's farm, larvae have been observed to feed on 98 plant species, including ICRISAT's mandate crops; sorghum, millet, groundnut, pigeonpea and chickpea (Bhatnagar & Davies, 1978).

At ICRISAT Center, catches of *H. armigera* in light traps have been recorded daily since 1974 (ICRISAT, 1986). Each year, moths are captured almost every night from about mid-July to mid-May, with more than 1000 caught on some nights. Very few moths are caught from about mid-May to mid-July. Catches reach maximum values in about November–December, before the peak in local harvesting of pigeonpea and chickpea (ICRISAT, 1986). This maximum follows another, smaller, peak in August–September before the harvesting of sorghum, pearl millet and groundnuts.

The insect can reproduce throughout the year on a large number of wild hosts that grow on the Institute's farm. The pattern of infestation on ICRISAT's mandate crops is consistent over the years. Most larvae feed on groundnuts in July, on sorghum and millet in August and September, on pigeonpea and chickpea from October till February and on post rainy season groundnut, sorghum and millet from February until April (Bhatnagar *et al.*, 1982). During May, ICRISAT farm observes a closed season when cultivated

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plants that can act as hosts for *H. armigera* are all destroyed. However, the larvae of this polyphagous insect can survive this hot dry period on several weeds growing on the Institute's farm and on weeds and irrigated tomatoes grown outside ICRISAT boundaries on predominantly small farms. The *H. armigera* population on ICRISAT farm is connected with the surrounding countryside by movements of the flying moths over the research station's boundary fence (immigration and emigration due to dispersal, short- and long-range migration). The situation on ICRISAT farm thus partly reflects the dynamics of the insect/host-plant/environment interactions taking place in the surrounding countryside where rainfed crops are grown by predominantly small farmers. There is little evidence for summer diapause in *H. armigera* at ICRISAT Center and in Andhra Pradesh.

DATA AND METHODS

a) Larval counts

The Plant Protection Surveillance team at ICRISAT records every week the number of *H. armigera* caterpillars on the five mandate crops in all the fields in the pesticide protected areas. This represents 90% of the total cultivated area of ICRISAT farm. Larval counts are based on 30 to 50 randomly-picked plants per hectare. The mean number of larvae per plant is multiplied by the total plant stand in the cropped area to obtain a weekly estimate of the total number of larvae in that cropped area.

The standardised larval counts provide approximate estimates of the pest's abundance on a wide area basis for each week of the year. We have used such counts to compare the abundance of *H. armigera* populations across a series of abnormally dry and wet years—seven years' data altogether. Larval counts are available for a longer run of years (from 1978 onwards). However, we have rejected data collected prior to 1982 to minimise sources of error. Two important changes in farm management profoundly modified the ecology of *H. armigera* in 1982:

1. the farm-wide adoption of a closed season (Mid-April to June 1st week) during which none of ICRISAT's mandate crops are grown.
2. the introduction of stringent farm hygiene practices to ensure that the pest's wild hosts are kept in check. Prior to 1982–83 *H. armigera* populations could reproduce and build up on large acreages of wild hosts e.g. *Gomphrena cellosioides* (Mart); *Datura metel* L.; *Lagascea mollis* (Cav.). Although these hosts remained important features of the landscape during the run of years studied here, weed management on ICRISAT farm was more uniform within and between seasons from

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 ±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 218.1×10^3 ha^{-1} in 1984 to 638.9×10^3 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 preceeded 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 1

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

Year	June–October				June–May			
	Rainfall (mm) (± long term average)[1]	Area surveyed for larval population (ha)	Larval population 10^6	Larval population[2] in 10^3 ha^{-1}	Rainfall (mm) (± long term annual average)	Area surveyed for larval population (ha)	Larval population in 10^6	Larval population[2] in 10^3 ha^{-1}
1983–84	1021.2 (+52.4%)	327.4	14.94	45.6	1096.6 (+40.2%)	546.48	72.54	132.7
1984–85	591.3 (−11.7%)	333.1	24.90	74.4	670.3 (−14.3%)	532.77	116.21	218.1
1985–86	477.0 (−28.8%)	320.7	35.06	109.3	617.0 (−21.1%)	491.70	145.54	296.0
1986–87	538.0 (−19.7%)	235.7	57.65	244.6	623.3 (−20.3%)	406.50	154.10	379.1
1987–88	595.8 (−11.1%)	319.8	49.68	155.3	955.7 (+22.2%)	531.35	339.47	638.9
1988–89	900.2 (+34.4%)	420.3	35.58	84.7	1019.2 (+30.3%)	648.58	140.65	216.9

[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 ICRISAT. Long term average rainfall (1974–87): Jun–Oct 670 mm; Jun–May 782 mm.
[2]Larval population densities were significantly lower in excess rainfall years than in water deficient years (P<0.01, Kruskall-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 | | | |
| | Pigeonpea | | | | Pigeonpea | | Chickpea | |
	Rainfall (mm) (± long term average)[1]	Area surveyed for larval population (ha)	Larval population[2] in 10^3 ha^{-1}	Rainfall (mm) (± long term annual average)[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

[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 ICRISAT. Long term average rainfall (1974–87): June–Oct 670 mm; Jun–May 782 mm.
[2]Larval population densities were significantly lower in excess rainfall years than in water deficient years (P<0.01, Kruskall-Wallis one way analysis of variance by ranks).

TABLE 3

Summary of regression and correlation analysis.

| Relationship	Regression equation	r	Significance
June–October			
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 $P < 0.01\%$
June–May			
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.
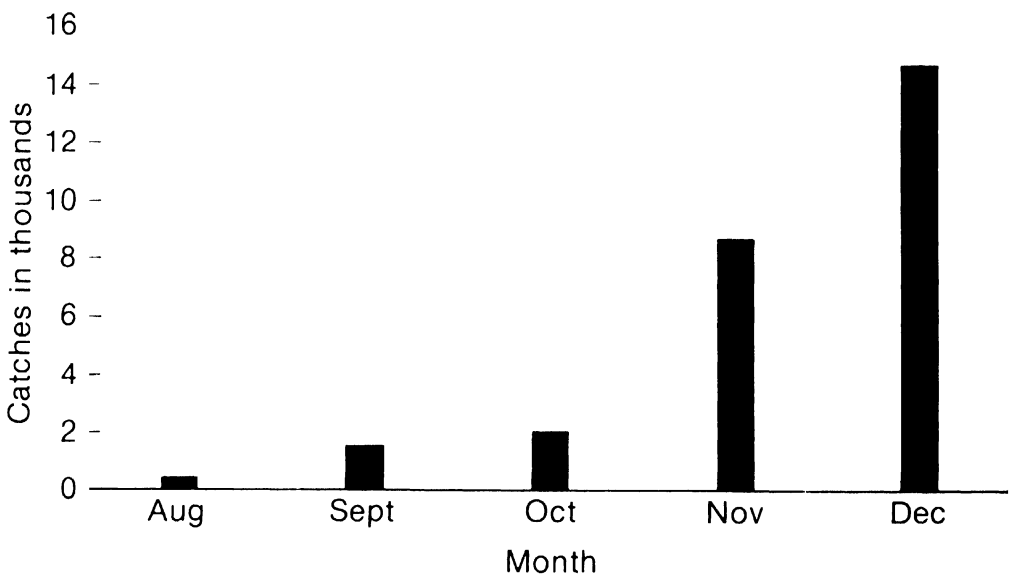
FIGURE 1.   Monthly light trap catches for August to December 1987 at ICRISAT Centre, Patancheru, India.
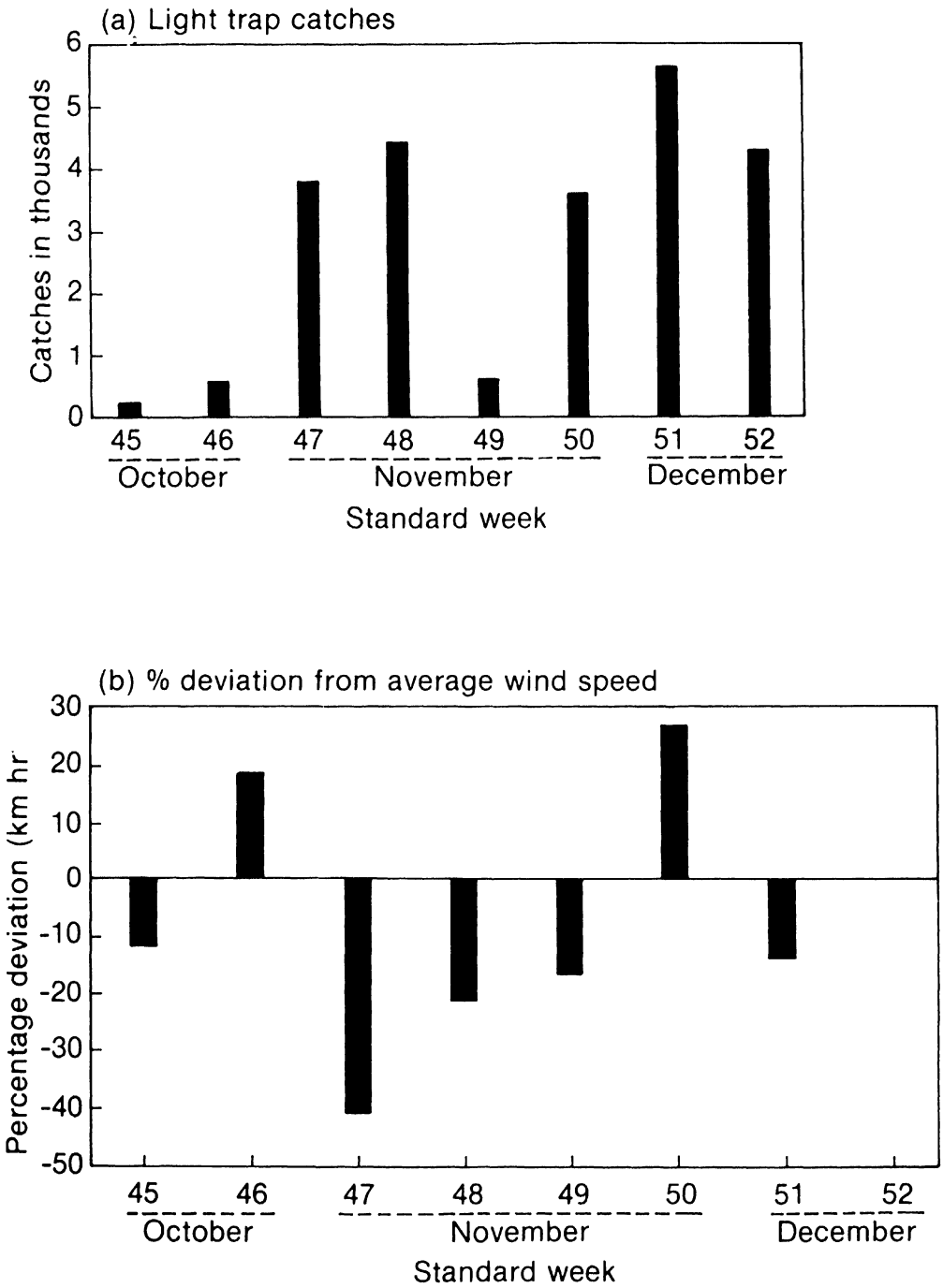
FIGURE 2.   Light trap catches (a) and percentage deviation from long term average wind speed (b) during November and December 1987 at ICRISAT Centre, Patancheru, India.
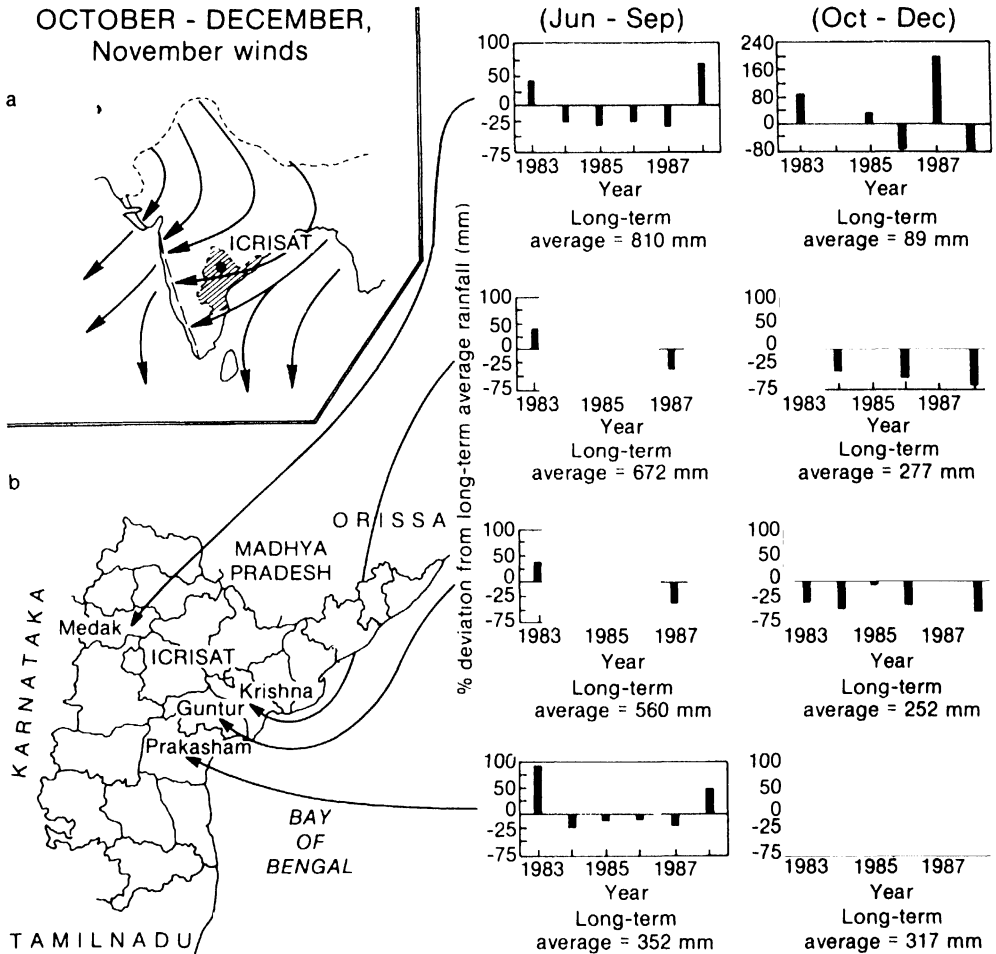
FIGURE 3.   a) Streamlines of dominant wind directions at ICRISAT Centre, Patancheru, Andhra Pradesh, India. b). Percentage deviation from long-term average rainfall during the south-west (June–September) and north-east (October–December) monsoons from 1983–88 in Medak, Krishna, Guntur and Prakasam districts, 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. arimgera* 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
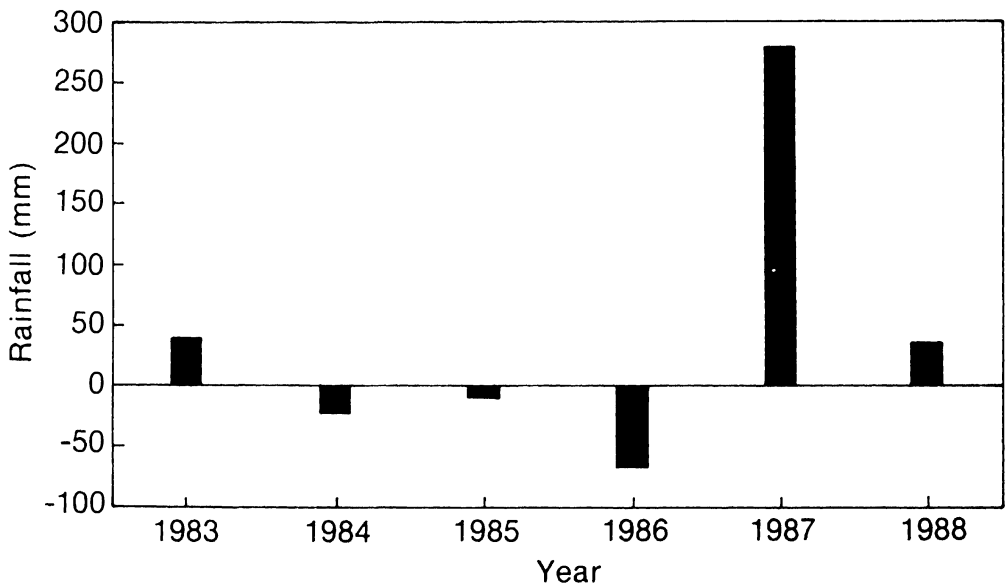

FIGURE 4.   Deviation from normal rainfall for the period October to December 1983–88 at ICRISAT Centre, Patancheru, India.
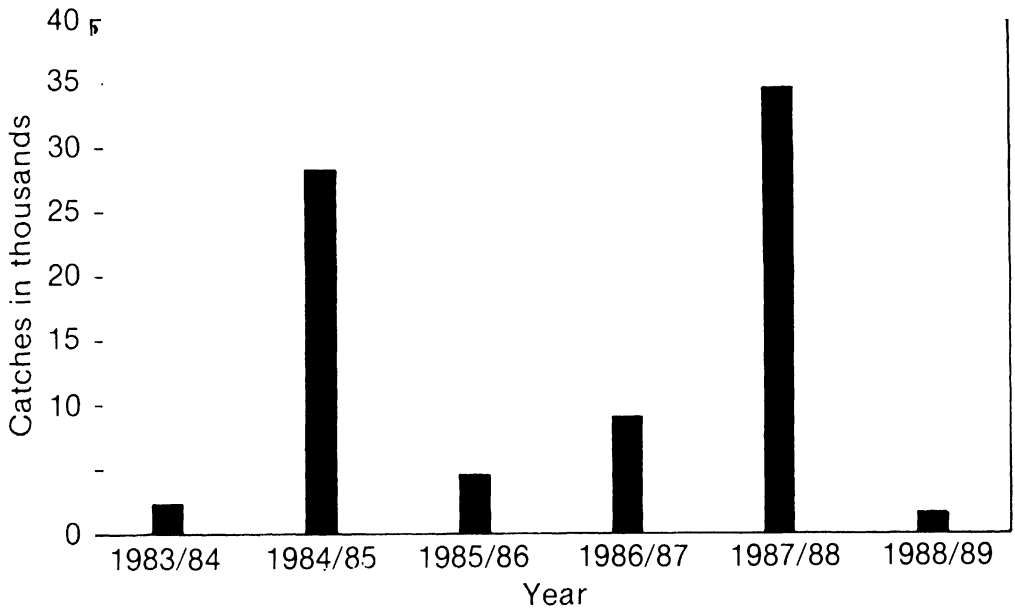
FIGURE 5.   Yearly light trap catches (June to May) at ICRISAT Centre, Patancheru, India.

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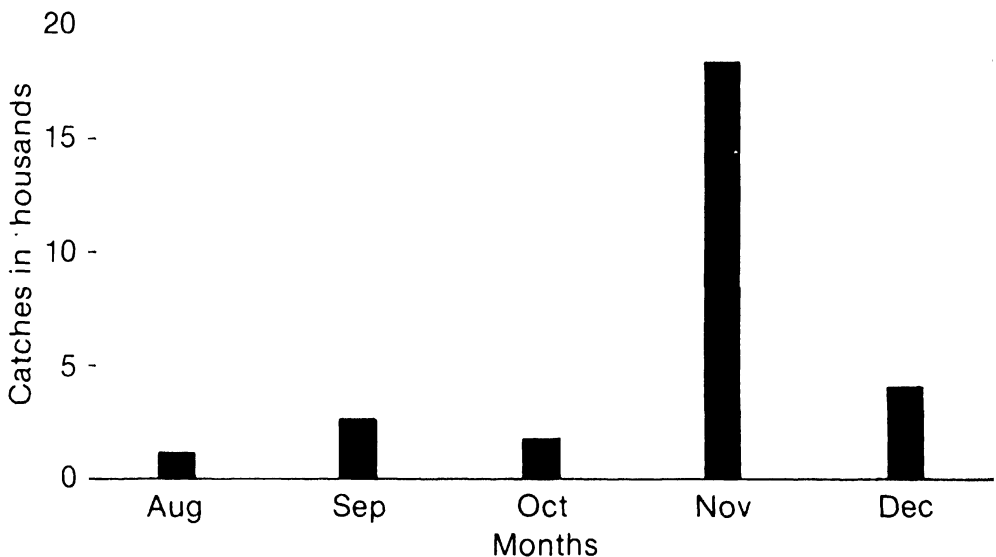
FIGURE 6.   Light trap catches for August–December 1984 at ICRISAT Centre, Patancheru, India.

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)	*Temelucha* spp.	*Barichneumon* spp.	*Enicopsilus* spp.	Rainfall (mm) June–May (± long-term average)	*Temelucha* spp.	*Barichneumon* spp.	*Enicopsilus* 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 (*Cicer arietinum*)	Leaves	Pro +	Leaves	Fructose + Sucrose + Inositol +	Ford (1984)
Pigeonpea (*Cajanus cajan*)	Leaves	Pro +	Leaves	Inositol +	Ford (1984)
Groundnut (*Arachis hypogaea*)	Leaves	Pro +			Nageswara Rao *et al.* (1981)
Sorghum (*Sorghum bicolor*)	Leaves	Pro +	Leaves	Fructose + Glucose + Sucrose +	Sivaramakrishnan *et al.* (1988); Jones *et al.* (1980)
Pearl millet (*Pennisetum glaucum*)	Leaves	Pro +			Lal *et al.* (1988)

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