Analysis of the Biology, Population Dynamics, Natural Enemies and Impact of the Groundnut Leaf Miner, *Aproaerema modicella* (Deventer) (Lepidoptera:Gelechiidae), on Groundnut in India

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ABSTRACT

The groundnut leaf miner (GLM), Aproaerema modicella (Deventer) (Lepidoptera: Gelechiidae) is a serious pest of groundnut and soybean throughout South Asia. Laboratory and field experiments were conducted over a two year period at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in peninsular India to collect biological and ecological data necessary for developing a systems model for groundnut.

Laboratory studies showed that temperature strongly influenced development and fecundity rates, egg and larval survivorship and adult longevity. A function describing the effect of temperature and female age on per capita GLM fecundity was fitted to laboratory data. GLM has five instars in India, and the larvae require ca. 180 mm^2 of leaf area to complete development.

Larval populations fluctuated dramatically in field studies over four seasons, and no correlation was found to climatic factors. Simulated rainfall did not increase egg or larval mortality. Outbreak populations appear to be triggered by large scale adult immigration. Lower populations were found in resistant

variety and insecticide plots. The late season, rapid decline in GLM density was likely a result of natural enemies .

Observed high GLM population in the 1987 rainy season reduced groundnut growth and yield in plants not protected with insecticides. Leaf mass was 33% lower, and stem and pod mass 30% lower in unsprayed plants relative to sprayed plants. In addition, flower and peg production was lower in plants defoliated by GLM.

A large number of natural enemies attack GLM in the ICRISAT area, and among them are nine primary parasitoids. In addition, a fungal and viral pathogen were found. Less than 10% of GLM larvae sampled in the field survived to the adult stage.

The plant and GLM data collected in field and laboratory experiments were summarized in a pre-existing, generalized metabolic pool model. This model was used to simulate growth and development of the groundnut plant as well as the population dynamics of GLM .

DEDICATION

To my parents, Pat and Don Shanower

and

To my wife, 'Ana Shanower

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In the five and a half years it took to complete this dissertation, three and a half in Berkeley and two in India, I received help, encouragement, support and friendship of many people. I would like to express my sincere appreciation and thanks to my major professor, Dr. A. P. Gutierrez, for his help throughout my tenure at the Division of Biological Control. Andy was always available, and his advice and suggestions helped me to achieve more than I thought I could. Much of what I learned from Andy, about hard work, dedication and setting a high standard, I learned by the example he set.

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Chapter 1. Introduction

Groundnuts in the Indian agroecosystem and the project objectives

- Groundnuts
  - Acreage, yield and production
  - Uses and importance
  - Origin and classification
  - Growth and general physiology
- The Indian agroecosystem
  - Agroecosystem
  - Yield constraints
- Project description
  - Purpose and objectives
  - Methodology
  - Location
- Literature Cited

GROUNDNUTS

Acreage, yield and production

Worldwide, groundnut (i.e., peanut), Arachis hypogaea L., is cultivated on approximately 19 million hectares annually. This figure includes multiple cropping systems, where 2 or more crops are grown on the same plot within one calender year. The bulk of the world's production is centered in Asia and Africa which respectively account for 66% and 28% of the total area planted. Less developed countries plant 95% of the world's groundnut acreage, but yields are much lower than in developed nations. India, for example, cultivates 38% of the worldwide groundnut acreage, but produces only 26% of the world's crop. Africa produces 19% of the world's groundnuts from 28% of the acreage. Developed countries plant 5% of the total area but produce 10% of the groundnuts. Average yields in developed countries (2405 kg/ha) are more than twice those obtained in less developed countries (1056 kg/ha) (FAO, 1986).

Uses and importance

Groundnuts are a multi-use crop in the traditional farming systems of Africa and South Asia. A substantial benefit of growing groundnut is the increased level of soil nitrogen available to subsequent crops (Norman et al., 1984). The main products derived from groundnut are shells, haulms and kernels, all of which are fully utilized by small farmers in the tropics.

Groundnut shells are used as fuel to produce electricity for shelling, crushing, milling and other groundnut processing equipment. Other agricultural uses include fillers for fertilizers, mulches, roughage in livestock feed, and litter for poultry houses. In addition, the shells are used as abrasives for polishing metal, as insulation, fuel, filler for particle board, and for making charcoal (Woodruff, 1973), and for the extraction of organic chemicals, as a resin extender and as a cork substitute Gibbons (1980).

Haulms are the above ground portion of the plant remaining at harvest and are important yield component for small farmers. The quality and yield of groundnut hay depends on the variety, incidence of pests and diseases (e.g. foliar diseases), and plant population. Fraps (1917, as reported in Woodruff, 1973) showed that though haulms are lower quality hay than alfalfa, they are good maintenance feed for cattle, sheep or horses. In Nigeria, haulms are an important dry season feed for domestic animals, and near urban areas may be as valuable as the nuts (Johnson et al., 1981).

The most valuable product of groundnut plants are the seed kernels which are utilized in many ways. Whole kernels are enjoyed around the world raw, roasted and boiled. In the West African savanna, kernels are consumed in stews and in roasted meat preparations (Kassam, 1976). In South America the kernels, sometimes in combination with maize meal, are used to prepare alcoholic drinks (Gibbons, 1980). Whole kernels are also widely used for confectionery purposes, principally in candies, bakery sweets and in dessert items.

Groundnuts are an excellent food, combining high energy value with good quality protein (Mottern, 1973). Because of its high oil content, groundnut has more food energy per unit weight than most crops, including other seed legumes. Groundnuts yield 22.9 megajoules (MJ) kg^{-1}, soybean 18.0 MJ kg^{-1}, and cereals 15.0 MJ kg^{-1} (Norman, et al., 1984). Groundnut kernels contain approximately 25% protein, but are insufficient in four essential amino acids. If consumed in high quantities, only methionine deficiency may result (Mottern, 1973). In contrast, soybean protein is more balanced and only a single amino acid falls below recommended levels. Legume seeds compensate for low levels of sulfur amino acids (e.g. methionine) by having relatively high lysine content (Norman et al., 1984). A balanced diet can be maintained when groundnuts are combined with cereals, which are relatively high in methionine and low in lysine. Groundnut proteins used for human consumption may be in the form of flour, protein concentrates, and isolates. In India, large scale utilization of groundnut flour and protein isolates occurs in high protein supplement foods that may contain 40% protein, bulk foods with 12-14% protein, and fortified flour, weaning foods and specialty foods with 15-20% protein (Natarajan, 1980). The United States is unique among groundnut producers in processing more than half of the crop into peanut butter (Mottern, 1973).

More than 60% of the world's groundnuts are crushed for vegetable oil production, but this accounts for only 20% of the total vegetable oil production (Woodruff, 1973). Groundnut kernels contain up to 50% oil, making groundnut the most efficient crop for oil production. Its production rate is well ahead of safflower and sunflower, and nearly three times greater than soybean (Pryde, 1983). The oil is used for cooking, salad dressings, margarine and soap production. The ratio of polyunsaturated to saturated oils is not particularly high in groundnut oil, but its high smoke point is a desirable feature for cooking oil. The residues (meal and cake) of oil production are used primarily as animal feed. Depending on variety, the amounts of shells and trash, and method of extraction, the meal may have a protein content of more than 35% (Gibbons, 1980).

Origin and classification

Groundnuts are native to South America. When Europeans began exploring and colonizing the New World, they found _A_. _hypogaea_ widely cultivated throughout the tropical and subtropical regions of the western hemisphere. Early explorers took groundnuts back to Europe and later to Africa, Asia and the Pacific Islands where it quickly became a staple crop (Hammons, 1973).

The geographic origins of the genus _Arachis_ are thought to be Paraguay and southern Brazil (Gregory _et al_., 1980) though earlier authors (Leppick, 1971) found evidence for Eurasian ancestors. Gregory _et al_. (1980) described the ecological distribution of different sections of the genus based on drainage patterns in Paraguay and southern Brazil. The development of _geocarpy_, which is the growth and maturation of fertilized ovules beneath the soil surface, had a very profound effect on the distribution and subsequent evolution of the genus. Within-season dispersal was limited to the distance lateral branches could extend (1 m or less), hence erosion and downstream seed movement within watersheds became significant, and probably determined the distributions of species within the genus (Gregory *et al*., 1980). Gibbons *et al*. (1972) suggest that new and distinct patterns of variation arose in Africa after groundnut's introduction (early 16th century) and hence this area should be considered a secondary center of variation.

There are 22 species described in the genus *Arachis* but there may be 40 or more undescribed species (Gregory *et al*., 1980). Domestic groundnut, *A*. *hypogaea*, is one of two annual tetraploid species within the genus *Arachis*. The other, *A*. *monticola*, is found only in the wild (Ashley, 1984). The subspecific classification of *A*. *hypogaea* is based primarily on branching and main-axis floral patterns. There are two subspecies and two varieties in each subspecies. The following classification is widely accepted:

Arachis hypogaea
- subspecies *hypogaea*
  - variety *hypogaea*
  - variety *hirsuta*
- subspecies *fastigiata*
  - variety *fastigiata*
  - variety *vulgaris*

Subspecies *hypogaea* is distinguished from *fastigiata* by an alternate branching pattern and the lack of inflorescences on the main stem axis. In contrast, *fastigiata* exhibits sequential branching and always produces flowers on the main stem axis (Gibbons et al., 1972). The two subspecies also differ in several other agronomic characteristics. Subspecies fastigiata matures faster (90-100 days), has an upright bunch growth form, compact fruiting pattern and lacks seed dormancy. Subspecies hypogaea has alternate branching, requires 120-150 days to mature, has a runner or spreading growth form, a scattered fruiting pattern and usually exhibits seed dormancy (Feakin, 1973).

Growth and general physiology

Groundnuts are cultivated under a wide range of environmental conditions between 40° N and S, and require a minimum of 90 frost free days and 450 mm water per growing season. A complete review of groundnut physiology has recently been published (Ashley, 1984) and the following discussion is drawn largely from that work.

Flowering generally begins 30 to 40 days after sowing and may continue throughout the season. Flowers open at night and are almost entirely self-pollinated. The development of subterranean fruit occurs via a structure called the peg which is formed from rapidly dividing cells beneath the ovary. The peg, carrying the developing ovary at its tip grows downward (geocarpy) until it penetrates the soil. The tip turns horizontally in the soil and the ovary and seeds begin to grow rapidly. Fruiting efficiency in groundnuts is thought to be low with only 10-15% of the flowers producing mature pods (Norman et al., 1984). Crop yield is thought to come predominantly from the first flowers suggesting that as photosynthate demand increases in the older fruits, further fruit formation is inhibited (Bunting and Elston, 1980).

The most important climatic variable for groundnut growth and development is temperature. Groundnuts are largely unaffected by photoperiod though changes in daylength can influence the relative amount of vegetative and reproductive growth and may affect pod number (Ashley, 1984). The rates of all aspects of growth and development from seedling emergence and canopy development to flower production and fruit maturation are regulated by temperature. Optimum growth occurs between 25° and 35°C though groundnuts tolerate a wider range of temperatures. The lower developmental threshold is 10°C (Leong and Ong, 1983), and high temperatures in the range of 45° and 50°C are often experienced in places such as India and Iraq during the growing season.

THE INDIAN AGROECOSYSTEM

Agroecosystem

Despite low yields, India is the largest single producer of groundnuts in the world. In 1986-87 groundnuts were cultivated on 7.15 million hectares (mha) in India (Anon., 1988). Production is concentrated in the states of Tamil Nadu, Andhra Pradesh, Karnataka, Maharashtra and Gujarat (see Fig. 1). These five states cultivate 77% of the Indian groundnut acreage (George et al., 1978).

Groundnuts may be found in the field at all times of the year in some part of India, but there are two main seasons: the rainy season and the post-rainy season. Rainy season planting begins in June in south India and follows the northward path of the northeast monsoon, ending in July. The rainy season crop is harvested in October or November. More than 85% of the 7.15 mha are cultivated during the rainy season (Anon., 1988) and most of these without irrigation.

The post-rainy season lasts from December to April, a longer season due to low ambient temperatures early in the season. Rainfall is crucial in the first two months after which irrigation is required for a successful crop. Because irrigation is necessary, the area cultivated in the post-rainy season is much smaller than in the rainy season. In 1986-87 for example, only 0.92 mha of the total 7.15 mha were planted in the post-rainy season (Anon., 1988), but this was a two-fold increase over the area planted in the 1974-75 post-rainy season (Rao, 1987). The post-rainy season supplies approximately 27% of the average 5.12 million tons of groundnuts annually harvested (Anon., 1988). Yields are much higher in the post-rainy season than in the rainy season, 1.49 versus 0.75 t ha^{-1} respectively.

Diverse cropping and farming systems are employed in different regions of India (Fig. 1). In the southeastern part of the country, two peak rainfall periods, corresponding to the northeast and southwest monsoons, provide a total annual rainfall of between 500 and 700 mm. Two crops are cultivated though not sequentially in the same field. The first is grown from June to October and the second from October to January or February (Huda, 1986). In this system, groundnuts are planted after rice is harvested and the rice stubble plowed under. The soils in this zone are generally light red soils.

The other major groundnut growing region is Gujarat, in western India where the growing season is about 45 days shorter than in the south, rainfall is from one monsoon, and moisture stress usually occurs by October (Huda, 1986). The black soils common in this area become hard and dry as a result of low rainfall late in the season, and the pods are held tightly by the soil making harvest difficult in most years.

Virmani (1988) recognized two additional groundnut growing zones in India: north-central and northeastern zones. The north-central zone has a 120-150 day growing season and an annual rainfall of between 700 and 1000 mm. The soils are sandy or shallow black soils. The same type of soils are also found in the northeastern zone. The northeastern zone has the highest rainfall (1000-1200 mm) and the longest growing season (150-180 days). The area under groundnut cultivation in the north-central and northeastern zones is much smaller than in the south and western zones.

In India, rice is commonly rotated with groundnut in areas where sufficient water is available. Other cereal crops, principally sorghum, millet and maize, are often intercropped with groundnut. Other crops interplanted with groundnut include pigeonpea, soybean, sugarcane, greengram, blackgram, sunflower, sesamum and sunnhemp.

Yield constraints

Constraints on groundnut production in India include agronomic, abiotic and biotic factors. Agronomic factors such as inadequate plant density, poor quality seeds, low yielding varieties and inefficient water and fertilizer management are major causes of low yields (Rao, 1987). Abiotic constraints such as poor soil fertility or structure, and drought and heat stress are the key abiotic factors which adversely influence yields but they are difficult to change. Among the biological constraints are diseases, weeds and insect pests. In general, these biological constraints are strongly influenced by climatic variables and farm management decisions, often resulting in decreased yields. Diseases such as leaf spots, rust, stem rot, root and pod rots, viruses and nematodes may have a significant impact on yields in groundnut (Gibbons, 1986). The impact of weeds on groundnut production has been inadequately studied, but Saini and Dhillon (1981) showed that uncontrolled, weeds may reduce pod yield 32%. Insect pests, including foliage feeders, aphids, thrips, jassids and termites, may cause yield losses in some seasons, but their impact is poorly understood. A list of the key insect herbivores attacking groundnut in India is given in Table 1. The groundnut leaf miner (GLM), Aproaerema modicella (Deventer), was the focus of the project described below. The biology and ecology of GLM are reviewed in Chapter 2.

THE RESEARCH PROJECT

Objectives

Previous research on arthropod pests in groundnut focused on their effects on yield or the efficacy of chemical control measures. A prerequisite to the development of a sound pest management program is a methodology for examining interactions between the crop, pests and natural enemies as modified by agronomic inputs and weather. Simulation modeling and other elements of systems analysis provide such a framework. These models are important both as tools for ecological research in the study of predator-prey interactions (used in the broadest sense these include plant-herbivore and herbivore-natural enemy interactions), and also in practical studies to evaluate the impact of herbivores on groundnut yields and the role of biological control in regulating the herbivores.

In this study, models of groundnut and the groundnut leaf miner were developed and used to examine the effects of GLM on plant growth and development. The effect of natural enemies on GLM population dynamics was also included. The impact of weather (e.g. rainy versus post-rainy season) and agronomic inputs (e.g. application of insecticide) on the plant-herbivore interactions was also examined.

Methodology

The analysis of a subsystem of a biological community has been termed the "life-system approach" (Clark *et al*., 1967). The use of this methodology has been reviewed by Hughes *et al*. (1984). The methodology used in this study is related, but has its origins in the study of ecological relationships (Gilbert, *et al*. 1976), and was recently reviewed by Baumgaertner *et al*. (1988).

The groundnut systems model consists of linked plant subunit -GLM population dynamic models. These models are time varying life tables that incorporate the important aspects of physiology, biology and behavior of each species and the interactions between species. Temperature drives the dynamics of each trophic level and is one of the important abiotic factors included in the models. Solar radiation, rainfall and/or irrigation are important abiotic factors included in the plant model.

Plant Model -- The first step in this approach was to gather the field data required to develop and parameterize a plant growth model for groundnut. A generalized plant model used previously to simulate the growth of several crops including alfalfa, apple, beans, cassava, cotton, cucumber, grape, rice and tomato (e.g. Baumgaertner et al., 1986; Graf et al., 1989; Gutierrez et al., 1976;, 1977; 1984; 1985; 1987; 1988a,b,c; M. Tamo in prep.; Gutierrez pers. comm) was used to simulate groundnut growth and development. The model simulates in considerable detail the patterns of dry matter growth and fruiting in these crops. The model uses temperature dependent growth rates to estimate maximum growth demands during a specific time period. Photosynthesis used to meet those demands depends on the estimated demand as well as solar radiation, soil nutrients and water availability. Carbohydrates are partitioned into leaves, stems, roots and fruits in a dynamic fashion based on the interplay between photosynthate supply and demand. The mathematical structure of the model is outlined in Gutierrez et al. (1988a) and briefly in Chapter 6.

The groundnut leaf miner -- The groundnut leaf miner is one of the most abundant pests of groundnut in peninsular India. To understand its impact on groundnut yields, field and laboratory data were collected on GLM biology and ecology. Important life history parameters measured under laboratory conditions included age-specific fecundity and survivorship, developmental rates, and per capita consumption rates, as well as field estimates of mortality. These elements of biology are incorporated in a time varying life table model for GLM.

In the systems model, trophic levels are linked via the flow of energy from one level to another. The plants derive energy from photosynthesis and GLM derives energy by mining leaves. GLM feeding reduces photosynthetic leaf area which decreases plant growth rates, increases plant stress and reduces yield. The mortality due to natural enemies and supply-demand constraints lower GLM survivorship. All of these interactions are influenced by environmental factors and farmer inputs such as fertilizer, water and pesticide applications.

One of the goals of this work is to use the model to evaluate the effects of alternative pest management strategies at each trophic level. Integrating three trophic levels and the relevant environmental factors into one model allows a more realistic assessment of system component interactions.

Description of the study site

The field work for this project was conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru (26 km northwest of Hyderabad), Andhra Pradesh, India. ICRISAT is one of 13 international centers of the Consultative Group on International Agricultural Research (CGIAR). Support for these institutions comes from the governments of 16 countries as well as private and international organizations. ICRISAT's mandate is to improve the yield, stability and quality of five crops important in the semi-arid tropics: groundnut, chickpea, pigeonpea, sorghum and millet (ICRISAT, 1988).

The semi-arid tropics (SAT) are characterized by mean monthly temperatures above 18° C and rainfall exceeding potential evaporation for two to seven months. The SAT cover 20 million square kilometers including all or part of 50 countries on five continents (ICRISAT, 1987). With the exception of Australia, all of these countries are considered less developed nations. More than 700 million people live in the SAT, including half of the population of India.

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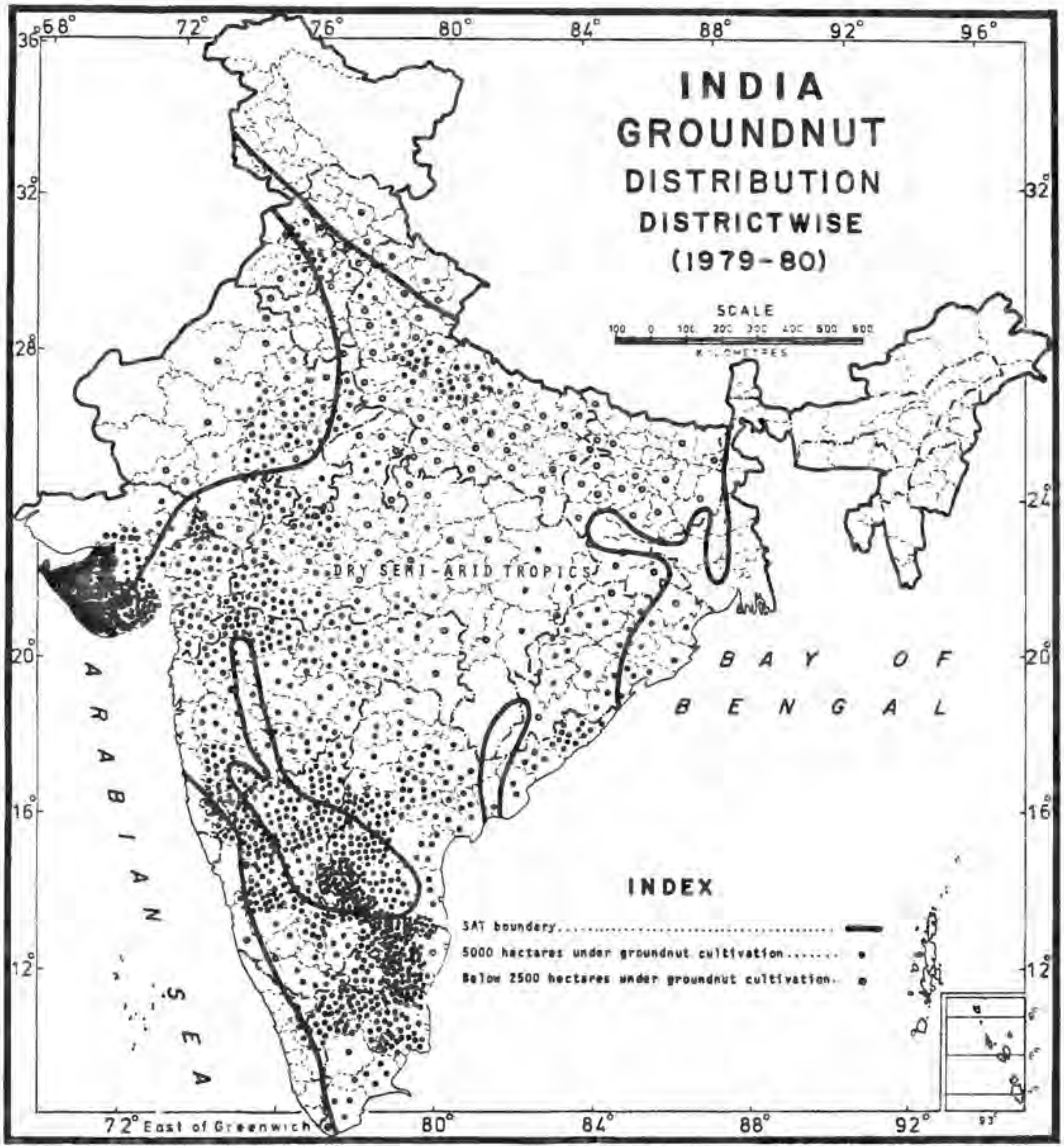
Table 1. Major arthropod pests of groundnut in India.[1]

Below-ground pests	
Termites	(Termitidae)
White grubs	(Scarabaeidae)
Pod borers	(includes millipedes, Dermaptera, Tenebrionidae, Elateridae, Formicidae and Lepidoptera)
Above-ground pests	
Aproaerema modicella (Deventer)	(Gelechiidae)
Spodoptera litura Fab.	(Noctuidae)
Heliothis armigera (Hub.)	(Noctuidae)
Mylabris spp. & *Epicanta* spp.	(Meloidae)
Aphis craccivora Koch	(Aphididae)
Thrips	(Thripidae)
Jassids (leaf hoppers)	(Jassidae = Cicadellidae)
Disease vectors	
Aphis craccivora Koch	(Aphididae)
Frankliniella schultzei (Trybom)	(Thripidae)

[1] Source: Wightman and Amin, 1988.

Figure 1. Groundnut production in India 1979-80.


INDIA
GROUNDNUT
DISTRIBUTION
DISTRICTWISE
(1979-80)
SCALE
100 0 100 200 300 400 500 600
KILOMETRES
DRY SEMI-ARID TROPICS
BAY OF BENGAL
ARABIAN SEA
INDEX
SAT boundary
5000 hectares under groundnut cultivation ●
Below 2500 hectares under groundnut cultivation ●
68°
72°
76°
80°
84°
88°
92°
96°
36°
32°
28°
24°
20°
16°
12°
72° East of Greenwich
93°

Conical Equal Area Projection with two Standard Parallels.
Base map from Survey of India.

PREPARED BY: M.N.S. Bose, ICRISAT, Patancheru P.O., A.P. India.
SOURCES: AGRICULTURAL SITUATION IN INDIA September 1981.
PROGRESS REPORT-5 OF AGROCLIMATOLOGY ICRISAT 1980-81.

Figure 1.

Chapter 2.

A review of the biology and control of the groundnut leaf miner, *Aproaerema modicella* (Deventer) (Lepidoptera: Gelechiidae).

Introduction

Taxonomy

Distribution

Host plants

Lifecycle

Damage and yield loss

Population dynamics

Cultural control

Host plant resistance

Biological control

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Conclusion

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INTRODUCTION

The groundnut leaf miner (GLM), *Aproaerema modicella* (Deventer) (Lepidoptera: Gelechiidae), is a serious pest of groundnut and soybean in South and Southeast Asia. It is present every season though often it does not reach damaging levels. When present in high numbers, it has the potential to severely limit groundnut yields. Amin (1983) has called it the most important groundnut pest in India. Mohammad (1981) previously reviewed the GLM literature, but since then much has been learned about this pest, and considerable progress made to control it. This review emphasizes studies published after 1981.

TAXONOMY

A variety of common names have been applied to the groundnut leaf miner, including the 'surul puchi' (Ramakrishna Ayyer, 1940), 'surul' moth (Cherian and Basheer, 1942), groundnut leaf webber (Srinivasan and Siva Rao, 1986), leaf folder (Lewin *et al*., 1971), *Arachis* leafminer (Van Der Laan and Ankersmit, 1951, in Mohammad, 1981), stem borer (Prasad *et al*., 1971), soybean leafminer (Shetgar and Thombre, 1984), and the peanut leaf folder (Abdul Kareem and Subramaniam, 1976). The establishment of its scientific nomenclature has also been confusing. It was originally described as *Anacampsis nerteria* Meyr. from specimens collected in India (Meyrick, 1906). Five other scientific names have been given to this insect: *Biloba subsecivella* Zeller, *Stomopteryx nerteria* Meyr., *Stomopteryx nertaria* Meyr., *Stomopteryx subsecivella* Zeller, and *Aproaerema nerteria* Meyr.

The confusion is due to the existence of two, non-congeneric leaf miners: one from South Africa, now called Stomopteryx subsecivella (Zeller), and the second, the Indian-Indonesian groundnut leaf miner, Aproaerema modicella (Deventer) (J.D. Bradley of the British Museum (Natural History) pers. comm. in Mohammad, 1981). Deventer (1904, in Mohammad, 1981) originally described A. modicella from a moth collected in Java, Indonesia.

GEOGRAPHIC DISTRIBUTION

The geographical range of A. modicella is restricted to South and Southeast Asia, from Pakistan to China and as far south as the Philippines and Sri Lanka. It has been reported from Pakistan, India, Sri Lanka, Bangladesh, Burma, Thailand, Laos, Kampuchea, Vietnam, China, the Philippines, Indonesia and Malaysia (references in Mohammad, 1981; Crowe, 1985; Campbell, 1982; 1983; 1985; and Islam et al., 1983). In India, where GLM has been studied most extensively, the leaf miner is known from the following states: Tamil Nadu (Lewin et al., 1971; 1979; Logiswaran et al., 1982), Andhra Pradesh (Srinivasan and Siva Rao, 1984; 1986), Karnataka (Jai Rao and Sindagi, 1973; 1974), Maharashtra (Khan and Raodeo, 1978; Mundhe, 1980; Jagtap et al., 1984), Madhya Pradesh (Kapoor et al., 1975, Singh and Rawat, 1981; Singh and Singh, 1983), Gujarat (Das and Misra, 1984; Bhalani et al., 1985; Yadav et al., 1987), Punjab (Sandhu, 1977; 1978), New Delhi (Prasad et al., 1971), Orissa (Samalo and Parida, 1983) and West Bengal (Singh, 1978).

HOST PLANTS

With the exception of *Boreria hispida* (Rubiaceae), the host plants of GLM are all legumes (Table 1). Several crop plants are among those attacked by *A. modicella*, the four most important being: groundnut (*Arachis hypogaea* L.), soybean (*Glycine max* (L.) Merr.), pigeonpea (*Cajanus cajan* (L.) Millsp.) and alfalfa (*Medicago sativa* L.). Phisitkul (1985) attempted to rear GLM on a variety of other plants, sunnhemp (*Crotalaria juncea* L.), winged bean (*Psophocarpus tetragonolobus* (L.) D.C.), yard long bean (*Vigna sinensis* (L.) Saviex Hask subsp. *sesquipedalis* Fruwirth), siratro (*Macroptilium atropurpureum* L.), hamata (*Stylosanthes hamata* L.), cowpea (*Vigna sinensis* (L.) Saviex Hask), showy crotolaria (*Crotalaria pallida* Ait.), and sword bean (*Canavalia gladiata* D.C.). Female GLM oviposited on these plants at a much lower rate than on groundnut or soybean, and larvae did not survive beyond the first instar.

LIFECYCLE

Maxwell-Lefroy and Howlett (1909) and Bainbridge-Fletcher (1914; 1920) were among the first to describe and document the lifecycle of GLM. Cherian and Basheer (1942), Kapadia *et al*. (1982) and Phisitkul (1985) also gave detailed accounts of GLM biology. The small (<1.0 mm), oval eggs are deposited by the female moth on the undersides of groundnut leaflets and on the stems and petioles. The number of eggs per female averages between 86.6 (Gujrati *et al*., 1973) and 185.8 with a maximum of 473 recorded (Cherian and Basheer, 1942). When freshly laid the eggs are white; older eggs are yellowish-brown and the head capsule of the first instar larva is clearly visible through the egg just before hatching. The surface of the egg is covered with longitudinal pits which reminded one author of the pits on groundnut pods (reference in Bainbridge-Fletcher, 1920). Under field conditions, eggs generally hatch in 3 to 4 days but may require 6 to 8 days at lower temperatures (Kapadia et al., 1982).

Newly hatched, first instar larvae generally begin chewing through the epidermis and into the leaf mesophyll close to the egg, but some larvae wander before beginning to feed. Larvae are pale white or yellow with a black or brown head capsule, though the body may become greenish or light brown in later instars. Different number of instars have been reported in the literature. Kapadia et al. (1982) reported three, Gujrati et al. (1973) four, Amin (1987a) five, and Islam et al. (1983) six larval instars.

Early instars feed entirely on leaf mesophyll creating short serpentine mines which widen as the larvae grow. Blotch-like mines are often formed which cause leaflets to pucker. Later instars exit the mine and web together two or more leaflets. Final instar larvae are approximately 6.0 mm long and very active. The total larval period at ambient temperature lasts between 9 and 28 days (Cherian and Basheer, 1942; Kapadia et al., 1982; Sandhu, 1978). Male caterpillars can be distinguished by the distinctive pink or brown gonads visible through the cuticle.

Pupation occurs within the webbed leaflets. Pupae are yellow when first formed and later turn dark brown. The pupal period is completed in 3 to 10 days (Cherian and Basheer, 1942; Sandhu, 1978). A development threshold temperature has not been established for GLM nor has development time been estimated in terms of physiological development (e.g. degree-days) for any GLM life stage. The development times reported for egg, larva and pupa are based on ambient temperatures. Under field conditions in south India, the egg to adult lifecycle is completed in 15 to 28 days (Cherian and Basheer, 1942). In northern India, where mean temperatures range between 14 to 22°C, the lifecycle may be require 37 to 45 days (Sandhu, 1978).

DAMAGE AND YIELD LOSS

Feeding by leaf miner larvae reduces leaf area and photosynthesis. If the reduction in leaf area is significant, lower pod yields will result. In terms of leaf area, a single larva will reportedly consume 34.8 cm^2 of leaf tissue (Islam _et al_., 1983). One method used to estimate potential damage by GLM is to calculate the proportion of infested leaves or plants. Sadakthulla _et al_. (1976) found 66.7% to 100% of the unsprayed (check) plants were infested in three trials carried out in Tamil Nadu. GLM larvae infested 38.5% of plants in selected plots in Bangladesh (Islam _et al_., 1983). In Karnataka, Sangappa and Mustak Ali (1977) reported 19.4% and 18.2% of the leaves attacked by GLM larvae, while in Maharashtra, Khan and Raodeo (1978) found 50% of the leaves infested. However, estimating the incidence of GLM does not give an indication of its impact on groundnut yields.

Based on three years of data, Jagtap _et al_. (1984) found that insect pests, principally GLM and _Aphis craccivora_ Koch, accounted for a 16% reduction in pod dry weight in variety JL 24 (equivalent to 303 kg ha^{-1}). Yield increases of up to 65% have been obtained in sprayed plots compared to unsprayed (check) plots (Sivasubramanian and Palaniswamy, 1983; Rajput et al., 1984; Rajput, et al., 1985). However, it is difficult to separate the losses attributable to GLM from other insects using this technique.

Tej Kumar and Devaraj Urs (1983) used screen cages and artificially infested groundnut plants with different levels of GLM. A regression of yield loss versus infestation revealed that each one percent infestation of GLM resulted in 1.2% yield loss. Data from screen cages can be misleading because the cages reduce sunlight which may confound the results.

Leaf miner populations vary from year to year, season to season, and between generations. The effect of an infestation on groundnut growth, development and yield is in part determined by the growth stage of the groundnut crop. An infestation of only 4 or 5 larvae per plant 10 days after emergence (DAE) has a much greater impact than 20 larvae per plant at 75 DAE. Ghule et al. (1987) found that groundnuts need protection from GLM between 45 and 75 DAE. But this would be true only if GLM populations are low, early in the season. A recommended action threshold in India is 61-70 larvae per 100 leaflets (Ghewande et al., 1987). The economic injury level determined by Tej Kumar and Devaraj Urs was 7.3 and 9.9 larvae per plant at 40 and 60 DAE (Tej Kumar and Devaraj Urs, 1983).

The impact of GLM on its other host plants is less certain.

Infestation rates in pigeonpea cultivars ranged from 27.5% to 44.2% of the plants in one study (Bhalani et al., 1985). Sandhu (1977) found 5% to 10% of alfalfa leaves damaged by GLM, and Gujrati et al. (1973) found 100% infestation of soybean plants in an outbreak year. In the two previous years, only 1% and 15% of the soybean plants had been attacked (Gujrati et al., 1973). When feeding on mung bean, Phaseolus aureus, GLM can reduce yields by more than 80% (Prasad et al., 1971).

POPULATION DYNAMICS

Over the last twenty years A. modicella has become an increasingly important pest of groundnut in India. Its growing importance is due in part to expanding acreage of groundnut and the increase in irrigation which allows cultivation in the post-rainy and summer seasons (Amin, 1987b). Associated with this is the potential for increased pesticide application and the well-known problems of inappropriate pesticide use. Continuous cultivation of groundnut, or a groundnut/soybean rotation, allow GLM populations to build up. In the absence of groundnut or soybean, GLM populations may persist on one of the wild host plants listed in Table 1. More than 3000 GLM larvae have been found on a single P. corylifolia shrub, indicating the potential of this plant as an alternate host (Manoharan and Chandramohan, 1986). Alternatively, GLM may survive the extremely hot, dry Indian summer in pupal diapause or aestivation, (Jagtap et al., 1985).

In Thailand, peak leaf miner populations occurred in July and August in groundnut planted at 15 day intervals over an entire year (Campbell, 1983). Mohammad (1981) reported that other researchers in Thailand found severe GLM infestations during November and December, with only negligible numbers from March to July. Groundnut in Bangladesh supports the largest populations of GLM in March and April (Islam et al., 1983) while in India, the peak season includes March, April and the first half of May (Amin and Mohammad, 1980). This is the end of the post-rainy season, when groundnuts are grown under irrigation. GLM can also be a problem towards the end of the rainy season (September and October), especially in drought or low rainfall years (Amin, 1983). Population levels fluctuate widely, so that seasons with low GLM incidence can be followed by outbreak populations. Khan and Raodeo (1987) recorded low GLM densities in the first half of 1971, followed by extremely high populations in August, September and October. In that study, high GLM populations continued through four generations but, by March, declined to a low level. These authors claimed that rainfall was the key factor regulating GLM populations, but their data do not support that conclusion. The high populations in August/September occurred during a high rainfall period, and the high population in January/February occurred when no rain was recorded (Khan and Raodeo, 1987). As this study pointed out, the effect of abiotic factors on GLM population dynamics is uncertain.

Amin (1987a) suggested that heavy rainfall reduces leaf miner populations though Wheatley et al. (1989) found that water from an overhead irrigation system did not lower GLM density. Lewin et al. (1979) found a significant negative correlation between

GLM incidence and rainfall; lower rainfall was correlated with higher GLM incidence, but temperature was also positively correlated with GLM incidence and accounted for more of the variation than did rainfall (Lewin _et al_., 1979). Another study at the same location revealed a significant negative correlation between infestation and temperature (Logiswaran _et al_., 1982). Temperature, rainfall, and other weather factors also affect leaf miner adults, which may influence mating and oviposition. A negative correlation between wind velocity and light trap catches of GLM moths was found in one study, but no significant correlation was found for five other variables: minimum and maximum temperature, rainfall and morning and evening humidity (Logiswaran and Mohanasundaram, 1986).

The number of GLM generations per season depends on several factors. At lower temperatures development takes longer and fewer generations are possible. Short-season cultivars also limit the number of generations by reducing the time host plants are available. Two GLM generations per crop are normal for Thailand (Campbell, 1983) while in China, seven generations have been reported on a single soybean crop (Yang and Liu, 1966). Three to four generations per season are common on groundnuts in India, though five generations have been reported for the rainy season in south India (Logiswaran and Mohanasundaram, 1986).

CULTURAL CONTROL

Several cultural control methods have been recommended for control of GLM, but evidence for a reduction in GLM populations has not been demonstrated. Cherian and Basheer (1942) first suggested using light traps to capture adults as a method of suppressing GLM populations. Nair (1975), Aswasthi et al. (1987), and Parasuraman and Prasad (1987) have also recommended light traps. Another technique frequently suggested is crop rotation with a non-host plant. Parasuraman and Prasad (1987) recommend rotation with millets to check multiplication of GLM populations.

Two studies, at the same location, came to different conclusions regarding the effect of sowing date on GLM infestations. The first study (Lewin et al., 1979) showed that early sowing led to higher infestations of GLM while the second study (Logiswaran et al., 1982) concluded that later plantings were more heavily attacked. One reason for the discrepancy may be that different varieties were used in these trials.

Logiswaran and Mohanasundaram (1985) found lower GLM larval densities when groundnut was intercropped with sorghum, millet or cowpea compared to monoculture groundnut at 30 x 10 cm spacing. However, the lowest GLM larval densities in this trial were recorded in monoculture groundnut at close spacing (15 x 10 cm). Mulching with rice straw had no effect on GLM levels but did have a positive effect on parasitism levels. Monoculture groundnut at 30 x 10 cm had the lowest percent parasitism while monoculture groundnut at 15 x 10 had the highest. Intercrop treatments all had intermediate levels of parasitization (Logiswaran and Mohanasundaram, 1985).

HOST PLANT RESISTANCE

The potential for developing GLM resistant/tolerant cultivars appears good. Lewin et al. (1971) found that bunch varieties had lower GLM infestation rates than spreading or semi-spreading varieties. Sathiamoorthy et al. (1978) evaluated 220 bunch varieties and classified them on the basis of GLM infestation rates. Seventeen of the varieties they compared were considered tolerant (1-5% GLM incidence) and 150 varieties less susceptible (5-10% incidence). Jai Rao and Sindagi (1973; 1974) screened a large number of varieties and infestation rates varied from 16-55%. Clear evidence of GLM resistance has been demonstrated in a wide range of genotypes, including spreading, Spanish bunch, and Valencia growth habits (ICRSAT, 1986). Five groundnut varieties: ICG 156, ICG 2248, ICG 2245, ICG 2271 and ICG 9883 were labelled resistant to GLM and recommended for use in breeding by the All India Co-Ordinated Research Project on Oilseeds in 1986 (Anon., 1987). Two of these varieties (ICG 156 and ICG 2271) also performed well in advanced screening against leaf miner the following year as well. In addition, 39 varieties in the first or second stage screening appeared promising. Amin (1987b) listed 16 cultivars as sources of resistance to leaf miner and 5 genotypes with multiple pest resistance which included protection against leaf miner.

Though bunch varieties are generally considered less susceptible to GLM, Motka et al. (1985) have shown enhanced growth and development of leaf miner on bunch varieties. They compared the growth rate, weight and percentage survival of larvae and pupae, and the weight and longevity of adults reared on five bunch and five spreading varieties of groundnut. The bunch variety JL-24 was significantly more conducive to GLM growth and development than other varieties. Larval, pupal and adult weights were significantly higher than on other varieties. In addition, larval survival was higher and adults lived significantly longer when larvae were reared on this variety (Motka et al., 1985).

Resistance to GLM in soybeans has not been observed. Mundhe (1980) compared 20 varieties and found no differences in GLM populations at 30, 45 and 60 days after sowing (DAS). Significant differences were noted at 75 DAS but this was too late in the crop cycle for GLM damage to affect yields. In another trial 18 varieties were compared (Shetgar and Thombre, 1984), but no differences in leaf miner populations were observed at 30, 45 or 75 DAS. At 60 DAS, however, two varieties had significantly lower GLM populations compared to the check variety. More recently, 40 soybean varieties were evaluated during two rainy seasons (Shrivastava et al., 1988) and all were attacked by GLM, though three varieties, JS 75-46, JS 73-22 and JS 78-41, had significantly lower larval populations.

BIOLOGICAL CONTROL

Natural control, by diseases, predators and parasitoids, plays a large role in suppressing GLM population growth. At least three disease agents infect GLM larvae in India: nematodes, viruses and fungi. A mermithid nematode was found infecting larvae (Kothai, 1974 in Mohammad, 1981; Srinivasan and Siva Rao, 1986), as was a new nuclear polyhedrosis virus (Godse and Patil, 1981). The fungus Aspergillus flavus has also been recovered from GLM larvae (Oblasami et al., 1969). Infected GLM larvae frequently are found in the field though the impact of these disease organisms on the population dynamics of GLM is unknown.

The role of predators has not been adequately studied. Maxwell-Lefroy and Howlett (1909) reported that Odynerus punctum Fabr. (Hymenoptera: Eumenidae) would attack GLM larvae and carry them away. Predation by spiders and robber flies (Diptera: Asilidae) also has been reported (Srinivasan and Siva Rao, 1986).

The most important and abundant natural control agents of GLM are hymenopterous parasitoids. Table 2 lists the parasitic hymenoptera reared from GLM eggs, larvae and pupae. Included are five species which Subba Rao et al. (1965) list as hyperparasites (Eurytoma sp., Tetrastichus sp., Pediobius sp., Ceraphron sp., and an unidentified pteromalid).

The geographical range and seasonal abundance of the parasitoids is not, however, well known. Nor is the relative contribution each parasitoid makes to the overall parasitism rate of GLM. In Maharashtra, Khan and Raodeo (1978) reported that six larval parasites were most abundant in August and September, but this could not be correlated with temperature, humidity or rainfall. At ICRISAT, four larval parasitoids listed by Bhatnagar and Davies (1979) were abundant in February and March. Nine parasitoids were active in both rainy and post-rainy seasons in southern Andhra Pradesh. Parasitism was highest in the September-November and February-March periods (Srinivasan and Siva Rao, 1986). Of eight parasitoid species recorded in Gujarat, six were present in the rainy season (July-October) and four were active at the end of the post-rainy season (March-May). Two species, *Goniozus* sp. and *Stenomesius japonicus* Ashm., were active in both seasons (Yadav *et al*., 1987).

When parasitoids attack GLM in soybeans, parasitism rates up to 84% occur in August and early September during the rainy season (Shetgar and Thombre, 1984). During the post-rainy season, parasitism peaks in February at a lower level (44%) than in the rainy season (Gujrati *et al*., 1973). The number of parasitoid species may be lower in soybeans or soybean may simply be less well studied. Gujrati *et al*. (1973) recorded only 2 species, *Bracon gelechiae* Ashm. and *Elasmus brevicornis* Gahan, while other authors recorded five species in soybean, *Chelonus* (*Microchelonus*) sp., *Apanteles* sp., *A. litae* Nixon, *Stenomesioideus ashmeadi* Subba Rao & Sharma and *Goniozus* sp. (Shetgar and Thombre, 1984).

When present, parasitoids attack a considerable portion of the available GLM. Three reports, from three different states in India, give peak parasitism rates of 83% in Maharashtra in 1972, 25% in Andhra Pradesh in 1983 and 90% in Gujarat in 1983 (Khan and Raodeo, 1978; Srinivasan and Siva Rao, 1986; Yadav *et al*., 1987). The impact of these parasitoids on groundnut leaf miner population dynamics is poorly understood.

CHEMICAL CONTROL

A wide variety of chemical insecticides have been screened for activity against the groundnut leaf miner (Table 3): botanicals, organophosphates, carbamates, organochlorines and synthetic pyrethroids. Notably absent from the list are commercial microbial insecticides. Most of the chemicals listed in Table 3 are applied to groundnut foliage either as a liquid spray or as a dust. Systemic insecticides have also been tested both as seed dressing or incorporated into the soil at the time of planting.

The history of chemical control against the groundnut leaf miner follows the paradigm described by Metcalf (1980), who traced the history of insecticide use on several different crops. In the early 1940s DDT was being recommended for the control of GLM (Ramakrishna Ayyer, 1940). DDT remained effective into the 1960s at which time BHC, dieldrin, endrin and parathion were also being recommended (Anon., 1950; Krishnamurthy Rao _et al_., 1962; Vittal _et al_., 1964; Vittal and Saroja, 1965). By 1965 carbaryl had been added to the list (Krishnananda & Kaiwar, 1965). Apparently GLM has not developed resistance to any chemical, or at least there are no reports of resistance, so there has not been a crisis of insecticide failure. Carbaryl, BHC and parathion have been used for more than 20 years and all three still provide effective control (Rajput _et al_., 1984; Ghule _et al_., 1987). As new insecticides have been developed, they have been evaluated for control of GLM and recommended. All of the synthetic chemicals listed in Table 3 were effective either in reducing GLM populations or in increasing yields relative to unsprayed check plots.

Through the 1970s, organochlorine compounds continued to be used even as the newer organophosphates and carbamates were recommended (Lewin et al., 1973; Kapoor et al., 1975; Devaraj Urs & Krishna Kothai, 1976). The only botanical insecticide tested for GLM activity was an extract from neem seed (Azadirachta indica A. Juss.) (Sadakathulla et al., 1976). In a single trial, 4 sprays of 1% extract failed to reduce the incidence of GLM relative to the unsprayed check. Synthetic pyrethroid insecticides were evaluated in the mid 1980s (Sivasubramanian & Palaniswmy, 1983; Rajput et al., 1985) and found to be highly effective, but they are more expensive than the older insecticides. Srinivasan and Siva Rao (1985) compared the cost and efficacy of 7 insecticidal dusts for control of GLM. A single application of lindane cost one third the price of an application of carbaryl or malathion and was just as effective.

Systemic insecticides are one way to reduce the negative impact chemical pesticides have on natural enemies. Application of systemic insecticides to the soil has effectively controlled a different lepidopterous leaf miner on citrus (Sohi and Varma, 1969). Khan and Raodeo (1979a) tested 4 granular insecticides, including carbofuran and phorate, for control of GLM in a potted plant experiment. All four chemicals reduced larval GLM populations by more than 85%. Logiswaran and Madhava Rao (1982) screened 5 systemic insecticides applied as foliar sprays at 30 and 45 DAS, and found that all 5 compounds reduced GLM larval populations. However, with foliar sprays it is likely that natural enemies would be negatively affected. Carbofuran applied as a seed treatment was evaluated by Lal et al. (1974). They found significantly lower numbers in both larval population and percentage of infested leaves without noticeable phytotoxic effects. Radhakrishnan et al. (1983) studied the use of isofenphos as a seed treatment, using 0.1% gum arabic as a seed sticker. All three dosages tested were found to have a lower GLM incidence than untreated plants. Insecticides applied as seed dressings or at the time of planting can be combined with fungicides to fully protect the crop as early as possible. Vembar and Thobbi (1967) and Thobbi et al. (1974) investigated the use of combined systemic insecticide and fungicide treatment on groundnut. They reported higher yields and reduced leaf miner damage though some phytotoxicity was noted early in the season. Using a package of crop protection measures including fertilizer and 2 sprays of a fungicide-insecticide mix, pod yields in Orissa (India) were increaseed 30-50% (Samola and Parida, 1983).

There are many problems with a pest management program relying solely on chemical pesticides (van den Bosch, 1978). These problems include the development of resistance to insecticides, creation of secondary pests and resurgence of the primary pest, not to mention environmental and human health hazards. Cotton production in the Rio Grande Valley in Texas provided an example of how this situation can develop (Adkisson et al., 1982). A recent survey of groundnut production areas in Andhra Pradesh indicated that pesticide applications for the control of GLM may be upsetting the natural biological control for *Heliothis armigera* and *Spodoptera exigua* (Ranga Rao and Shanower, 1988).

CONCLUSION

The groundnut leaf miner is a widespread and frequently serious pest of groundnut and soybean throughout South and Southeast Asia. Most of the published research deals with management and generally emphasizes chemical control. Given the negative aspects of reliance on insecticides and the limited resources available to farmers in the semi-arid tropics, a more integrated approach to leaf miner control is needed.

One of the goals of integrated pest management is to minimize the use of pesticides and thereby preserve the naturally occurring biological control agents (van den Bosch, 1978; Bottrell, 1979). From this perspective, it is unclear why more research has not been carried out on the use of microbial and soil incorporated systemic insecticides, and most important, the conservation of natural enemies.

In developing an integrated control program, it is important that the biology and ecology of the pest are well understood. The results published to date do not provide sufficient information on key aspects of the groundnut leaf miner biology. Reliable information on the effect of abiotic (e.g. temperature and rainfall) and biotic (e.g. natural enemies) factors on GLM population dynamics is incomplete. In addition, the impact of leaf miner damage on crop yields and the economics of yield loss have not been adequately quantified. One of the most difficult and important questions to understand is the cause(s) of the large GLM population fluctuations frequently observed. The development of an ecologically sound management program will be difficult as long as this information is lacking.

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Table 1. Host plants of *Aproaerema modicella*

Scientific name	Reference
Arachis hypogaea L.	Maxwell-Lefroy, 1906
Glycine max (L.) Merr.	Ramakrishna Ayyar, 1940
Vigna radiata (L.) Wilzcek (=*Phaseolus aureus*)	Prasad, *et al*., 1971
Cajanus cajan (L.) Millsp.	Bainbridge-Fletcher, 1914
Medicago sativa L.	Sandhu, 1977;1978
Psoralea corylifolia L.	Maxwell-Lefroy & Howlett, 1909
Inigofera hirsuta L.	Jai Rao & Thirumalachar, 1977
Vigna umbellata (Thunb.) Ohwi & Ohashi (=*Phaseolus calacaratus*)	Jai Rao & Thirumalachar, 1977
Glycine soja Sieb. & Zucc.	Vanhall, 1922 (in Mohammad, 1981)
Trifolium alexandrium L.	Thontadarya, *et al*., 1979
Teramnus labiolis (L.) Spreng	Das & Misra, 1984
Lablab purpureus L.	Das & Misra, 1984
Rhychosia minima Dc.	Srinivasan & Siva Rao, 1984
Boreria hispida K. Sch.	Srinivasan & Siva Rao, 1984

Table 2. Primary and secondary parasitoids of *Aproaerema modicella*[1/]

Family	Parasitoid	Host	Stage Attacked
Braconidae			
	Apanteles sp.	Gnut/Soybean	L
	A. javensis Rohwer	Gnut	L
	A. singaporensis Szep.	Gnut	L
	A. litae Nixon	Soybean	L
	Avga nixoni Subba Rao & Sharma	Gnut	L
	Bracon sp.	Gnut	L
	B. brevicornis Wesm.	Gnut	L
	B. gelechiae Ashm.	Gnut	L
	B. (*Microbracon*) *hebetor* Say	Gnut/Soybean	L
	Chelonus (*Microchelonus*) sp.	Gnut	L
	C. blackburni Cam.	Gnut	L
	C. curvimaculatus Cam.	Gnut	L
	Phanerotoma sp.	Gnut	L
Bethylidae			
	Goniozus sp.	Gnut	L
	G. stomopterycis Ram & Subba Rao	Gnut	L
	Perisierola sp.	Gnut	L
Ceraphronidae			
	Ceraphron sp.	Gnut	L

Chalcididae		
Brachymeria sp.	Gnut	L & P
B. plutellophaga Gir.	Gnut	L & P
B. minuta (L.)	Gnut	P
B. lasus (Walker)	Gnut	P
Eucepsis sp.	Gnut	P
Elasmidae		
Elasmus brevicornis Gahan	Soybean	L
Encyrtidae		
Capidosoma sp.	Gnut	L
Eulophidae		
Sympiesis (*Asympiesiella*) sp.	Gnut	L
S. india Gir.	Gnut	L
Euryscotolynx coimbatorensis Rohw.	Gnut	L
Pediobius sp.	Gnut	L
Stenomesioideus ashmeadi Subba Rao & Sharma	Gnut	L
Stenomesius japonicus (Ashmead)	Gnut	L
Tetrastichus sp.	Gnut	L
Eupelmidae		
Eupelmus sp.	Gnut	L & P
E. sp. near *anpingensis*	Gnut	L & P

Eurytomidae		
Eurytoma sp.	Gnut	L
Plutarchia giraulti Subba Rao	Gnut	L
Pteromalidae		
Habrocytus sp.	Gnut	L
Dibrachys sp.	Gnut	L
Trichogrammatidae		
Trichgramma sp.	Gnut	E

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[1] Source: Krishnamurthi and Usman, 1954; Subba Rao *et al*., 1965; Subba Rao and Sharma, 1966; Phisitkul, 1985; Srinivasan and Siva Rao, 1986;

Table 3. Pesticides evaluated for control of *Aproaerema modicella*

acephate	Rajput *et al*., 1984; Rajput *et al*., 1985
aldrin	Vittal & Saroja, 1965
ambithion	Sadakathulla *et al*., 1976
BHC	Vittal *et al*., 1964; Krishnananda & Kaiwar, 1965; Vittal & Saroja, 1965; Lewin *et al*., 1973; Kapoor *et al*., 1975; Rajput *et al*., 1984; Rajput *et al*., 1985;
BPMC	Singh & Singh, 1983
bromophosethyl	Rajput *et al*., 1985
bromophosmethyl	Rajput *et al*., 1985
carbaryl	Krishnananda & Kaiwar, 1965; Lewin *et al*., 1973; Kapoor *et al*., 1975; Devaraj Urs & Krishna Kothai, 1976; Sangappa & Mustak Ali, 1977; Khan & Raodeo, 1979b; Singh & Rawat, 1981; Singh & Singh, 1983; Sivasubramanian & Palaniswamy, 1983; Rajput *et al*., 1984; Rajput *et al*., 1985; Ghewande *et al*., 1987; Ghule *et al*., 1987
carbofuran	Lal *et al*., 1974; Devaraj Urs & Krishna Kothai, 1976; Sangappa & Mustak Ali, 1977; Singh, 1978; Khan & Raodeo, 1979a
carbophenothion	Palaniswamy & Ramachandran, 1978
chlorfenvinphos	Abdul Kareem & Subramaniam, 1976; Khan & Raodeo, 1979b; Sangappa, 1979

chlorphenamidine	Sadakathulla _et al_., 1976
chlorpyriphos	Sadakathulla _et al_., 1976; Sangappa, 1979
cyfloxylate	Rajput _et al_., 1985
cypermethrin	Sivasubramanian & Palaniswamy, 1983; Rajput _et al_., 1985
DDT	Vittal _et al_., 1964; Krishnananda & Kaiwar, 1965; Vittal & Saroja, 1965; Abdul Kareem & Subramaniam, 1976
DDVP	Sadakathulla _et al_., 1976
decamethrin	Sivasubramanian & Palaniswamy, 1983; Rajput _et al_., 1985
dibrom	Sangappa & Mustak Ali, 1977
dichlorvos	Lewin _et al_., 1973; Radhakrishnan _et al_., 1976; Sangappa & Mustak Ali, 1977; Palaniswamy & Ramachandran, 1978; Khan & Raodeo, 1979b
dicrotophos	Abdul Kareem & Subramaniam, 1976; Palaniswamy & Ramachandran, 1978
dieldrin	Vittal & Saroja, 1965; Kapoor _et al_., 1975
dimethoate	Lewin 1975
dimethoate	Lewin _et al_., 1973; Kapoor _et al_., 1975; Abdul Kareem & Subramaniam, 1976; Devaraj Urs & Krishna Kothai, 1976; Sangappa & Mustak Ali, 1977; Palaniswamy & Ramachandran, 1978; Khan & Raodeo, & Ramachandran, 1978; Khan & Raodeo, 1979a; Singh & Rawat, 1981; Logiswaran & Madhava Rao, 1982

disulfoton	Devaraj Urs & Krishna Kothai, 1976; Khan & Raodeo, 1979a
endosulfan	Lewin *et al*., 1973; Kapoor *et al*., 1975; Abdul Kareem & Subramaniam, 1976; Devaraj Urs & Krishna Kothai, 1976; Radhakrishnan *et al*., 1976; Palaniswamy & Ramachandran, 1978; Khan & Raodeo, 1979b; Singh & Rawat, 1981; Singh & Singh, 1983; Sivasubramanian & Palaniswamy, 1983;
endrin	Vittal *et al*., 1964; Krishnananda & Kaiwar, 1965; Vittal & Saroja, 1965; Lewin *et al*., 1973; Kapoor *et al*., 1975; Radhakrishnan *et al*., 1976; Palaniswamy & Ramachandran, 1978; Khan & Raodeo, 1979b
ethyl parathion	Kapoor *et al*., 1975; Devaraj Urs & Krishna Kothai, 1976; Sangappa & Mustak Ali, 1977
fenitrothion	Lewin *et al*., 1973; Kapoor *et al*., 1975; Abdul Kareem & Subramaniam, 1976; Sadakthulla *et al*., 1976; Palaniswamy & Ramachandran, 1978; Singh, 1978; Sangappa, 1979; Rajput, *et al*., 1984; Ghewande *et al*., 1987
fenthion	Singh & Rawat, 1981
fenvalerate	Singh & Singh, 1983; Sivasubramanian & Palaniswmay, 1983; Rajput *et al*., 1985
formothion	Devaraj Urs & Krishna Kothai, 1976; Palaniswamy & Ramachandran, 1978; Logiswaran & Madhava Rao, 1982

heptachlor	Lewin et al., 1973
imidan	Lewin et al., 1973
isofenphos	Radhakrishnan et al., 1983
leptophos	Sangappa & Mustak Ali, 1977
lindane	Kapoor et al., 1975
malathion	Devaraj Urs & Krishna Kothai, 1976; Sadakthulla et al., 1976; Palaniswamy & Ramachandran, 1978; Singh, 1978; Khan & Raodeo, 1979b; Sangappa, 1979
menazon	Krishnananda & Kaiwar, 1965; Sangappa & Mustak Ali, 1977
methamidophos	Singh & Singh, 1983; Sivasubramanian & Palaniswamy, 1983
methomyl	Rajput et al., 1984; Rajput et al., 1985
methyl dimeton	Kapoor et al., 1975; Palaniswamy & Ramachandran, 1978; Logiswaran & Madhava Rao, 1982
methyl parathion	Singh & Singh, 1983; Ghule et al., 1987
monocrotophos	Abdul Kareem and Subramanian, 1976; Sadakathulla et al., 1976; Sangappa & Mustak Ali, 1977; Khan & Raodeo, 1979b; Sangappa, 1979; Singh & Rawat, 1981; Logiswaran & Madhava Rao, 1982; Singh & Singh, 1983; Rajput et al., 1984; Rajput et al., 1985; Ghule et al., 1987
neem extract	Sadakathulla et al., 1976
parathion	Vittal et al., 1964; Krishnananda & Kaiwar, 1965; Vittal & Saroja, 1965; Lewin et al.,

	1973; Radhakrishnan *et al*., 1976
permethrin	Sivasubramanian & Palaniswamy, 1983; Rajput *et al*., 1985
phenthoate	Sadakathulla *et al*., 1976; Sangappa, 1979
phorate	Devaraj Urs & Krishna Kothai, 1976; Khan & Raodeo, 1979a
phosalone	Sadakathulla *et al*., 1976; Sangappa, 1979; Sivasubramanian & Palaniswamy, 1983; Ghule *et al*., 1987
phosphamidon	Lewin *et al*., 1973; Kapoor *et al*., 1975; Sangappa & Mustak Ali, 1977; Palaniswamy & Ramachandran, 1978; Singh, 1978; Khan & Raodeo, 1979b; Logiswaran & Madhava Rao, 1982; Singh & Singh, 1983; Rajput *et al*., 1984; Ghule *et al*., 1987
quinalphos	Abdul Kareem & Subramanian, 1976; Devaraj Urs & Krishna Kothai, 1976; Radhakrishnan *et al*., 1976; Sadakathulla *et al*., 1976; Singh, 1978; Khan & Raodeo, 1979b; Singh & Rawat, 1981; Singh & Singh, 1983; Sivasubramanian & Palaniswamy, 1983; Rajput *et al*., 1984; Ghule *et al*., 1987
sevimol	Singh & Singh, 1983; Ghule *et al*., 1987;
toxaphene	Abdul Kareem & Subramaniam, 1976; Sangappa & Mustak Ali, 1977; Khan & Raodeo, 1979b
TPTA	Abdul Kareem & Subramaniam, 1976
TPTH	Abdul Kareem & Subramaniam, 1976

trichlorphon	Sadakathulla *et al*., 1976
TTA	Sadakathulla *et al*., 1976
TTH	Sadakathulla *et al*, 1976
Zolone	Singh, 1978

Chapter 3.

The biology and population dynamics of the groundnut leaf miner, Aproaerema modicella (Deventer) (Lepidoptera: Gelechiidae), in peninsular India: I. Development, fecundity and leaf consumption.

Introduction

Materials and Methods

Results

Discussion

Literature Cited

INTRODUCTION

The groundnut leaf miner (GLM), Aproaerema modicella (Deventer) (Lepidoptera: Gelechiidae), is a key pest of groundnut and soybean throughout Asia. GLM was first recorded as a pest of groundnut more than 80 years ago, but many aspects of its biology remain poorly understood. Reported development times for A. modicella immature stages and adult longevity differ as much as two-fold (Gujrati et al., 1973; Kapadia et al., 1982; see Table 1). Published values for GLM fecundity vary by the same order of magnitude (Cherian and Basheer, 1942; Gujrati et al., 1973; Kapadia et al., 1982). The effect of temperature on development and fecundity has not been previously investigated, and may offer an explanation for the conflicting results of these earlier studies.

Reports in the literature also disagree concerning the number of A. modicella larval instars. Kapadia et al. (1982) reported three instars for A. modicella, Gujrati et al. (1973) and Phisitkul (1985) described four, and other authors recorded five (Amin, 1987) and some as many as six (Islam et al., 1983).

Only one observation has been reported on the per capita consumption of leaves by GLM larvae. Islam et al. (1983) estimated that, in terms of leaf area, GLM larvae consume 3480 mm^2 of leaf tissue, or the equivalent of 6 to 10 leaflets. By comparison, a mature Spodoptera frugiperda (J.E. Smith) which is approximately 20 times larger than GLM consumes only 3 times as much leaf tissue (Garner and Lynch, 1981) as reported by Islam et al. for GLM.

To develop an effective pest management program for A. modicella, its biology must be understood well. In this paper, experiments were designed to relate the rate of development, fecundity and longevity to temperature. In addition, the number of larval instars and per capita leaf consumption were determined. The results presented here resolve some of the confusion concerning the biology of this important pest of legumes.

MATERIALS AND METHODS

All experiments were carried out at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), located near Hyderabad (17° N), Andhra Pradesh, in peninsular India.

Rearing methods

Experimental insects were taken from laboratory colonies started in March 1988, and maintained under greenhouse conditions. GLM larvae were reared and tested on groundnut variety Kadiri 3 (ICG 799). The colony was maintained by collecting several hundred newly emerged moths and introducing them into cages with fresh plants. Deposited eggs were allowed to complete their lifecycle on the same plants. Cotton wool soaked in sucrose solution was provided for the adult moths.

Cohorts of insects were reared at 15°, 20°, 25°, 30° and 35°C in temperature cabinets programmed for 12:12 photophase and relative humidity in the range of 62 to 85%. These data were used to estimate temperature dependent growth and fecundity rates. The studies were conducted as described below.

Developmental time

Immature development times were studied using cohorts of newly laid eggs. Leaflets containing eggs were collected and all but one egg removed. The leaflets were placed on moistened filter paper in 12.0 cm diameter x 1 cm deep plastic petri dishes, and reared in temperature controlled incubators. Cohorts of eighty eggs held at each temperature were used to calculate the egg developmental rate.

To determine larval and pupal development times, cohorts of eggs were held at ambient temperature until hatching, and then put into incubators. Data from four larval and pupal replicates held at the same temperature were combined for analysis. The number of larvae completing development was not the same at all temperatures, and in one of the four 25°C replicates, ant predation reduced the initial number of larvae from 80 to 35. Daily observations were made to record hatching times, larval survival, pupation and adult emergence times.

Linear regression of the rate of development (i.e. the reciprocal of development time) on temperature was used to calculate the development threshold for each immature stage. The threshold was estimated by solving the regression line for the rate equal to zero (Gilbert et al., 1976). The degree-days (DD) required by each stage, as well as the fraction of time spent in each stage, were computed based on these thresholds.

Fecundity

The sex of pupae is easier to determine than that of the adults, hence for the fecundity and adult longevity studies, pairs of pupae (male and female) were put into 10 dram plastic screw-top vials containing a sucrose-soaked cotton ball. The opening of each vial was closed with cheese cloth held in place by a rubberband. Each pair was provided with a fresh groundnut leaflet for oviposition. Leaflets were replace daily, and the old one examined for eggs. Three fecundity parameters were analyzed: eggs per female, maximum one-day egg production and maximum total egg production. Eighty one pairs were tested at 20°, 25°, 30° and 35° C, but only 43 pairs were used at 15° C.

Age-specific life table parameters

The following age-specific life table parameters were calculated for each temperature on a day and a day-degree basis using a computer program to estimate the parameters exactly (Southwood, 1978; A.P. Gutierrez, unpublished).

r_m = the intrinsic rate of increase.

R_o = the number of females per female per generation.

G = generation time.

Instar number

Measurements of head capsule widths were used to determine the number of larval instars. Several hundred groundnut leaflets containing one day old eggs were taken from the colony and held at room temperature on moistened filter paper in petri dishes. An ocular micrometer was used to measure the head capsule width and body length of 10 larvae each day during the larval period.

Per capita consumption

Total consumption by GLM larvae was estimated from the area eaten per larva based on the relationship between leaf area and leaf wet weight. This latter relationship (mg/mm^2) was estimated using field collected leaflets of variety Kadiri 3. Leaflet area was calculated by tracing the outline on 1 mm graph paper and counting the squares, and wet weight was taken using a Mettler electronic balance. Fifty larvae were reared singly on leaflets in petri dishes on moistened filter paper, and the amount of leaf area eaten (mm^2) during the entire larval stage was measured. Only larvae which successfully pupated (43 of 50) and were included in the analysis. The leaf area eaten per larva was converted to wet weight (mg leaf tissue) using the leaf area/leaf wet weight ratio. The efficiency of conversion for ingested food (ECI) was calculated on a wet weight basis using the formula: (increase in larval weight (mg)/ food ingested (mg)) x 100 (Waldbauer, 1968).

Statistical analysis

Analysis of variance (ANOVA) was used to test differences in egg, larval and pupal survivorship and fecundity across temperatures (Zar, 1974). Regression analysis was used to estimate growth and development rates for immature stages, and to estimate development thresholds (Gilbert et al., 1976). The formula of Bieri et al. (1983) was generalized and used to describe daily egg production as a function of temperature and female age. This function was fitted to the oviposition data using multiple regression.

RESULTS

Stage developmental times and adult longevity

Total immature (egg to adult emergence from the pupa) developmental times (y) at various temperatures (x) ranged from 18.9 days to 58.1 days (Table 2). The threshold temperature for development of the egg stage based on the regression line $y = -0.2111 + 0.0171x$ was 12.3°C (Fig. 1). Eggs required an average of 60 DD to complete development, but at 25° and 30°C eggs hatched in 53 and 52 DD respectively. Approximately 13% of the total immature development time was spent in the egg stage. Temperature adversely influenced egg survivorship only at 15° C where only 79% of the eggs hatched. In contrast, the hatching rates at 20°, 25°, 30° and 35° C were close to 100%. The percentage of eggs hatching at 15° was significantly lower (ANOVA; $F_{4,28}=7.23$; $p<0.001$; $n=40$).

The longest period required for larval development was 34 days at 20° and the shortest was 12.4 days at 35° (Table 2). No larvae survived at 15°C, but despite this, the estimated developmental threshold for larvae was 8.9°C based the linear equation $y = -0.0308 + 0.0032x$ fitted to data on survivors (Fig. 1). Larval development was completed in the fewest DD at 25° (266 DD) with the next fewest at 30° (309 DD). Larval development averaged 327 DD or 71% of the total immature development time (Table 2). Larval development rates varied less than egg and pupal development rates (Fig. 1).

Temperature had a significant effect on larval survivorship (ANOVA; $F_{3,6}$=16.15; p<0.003; n=16). Mortality of early instar larvae was high at all temperatures (from 21 to 100%) and 100% in all replicates at 15°C.

Pupal development times ranged from 3.9 days at 30° to 15.1 at 20° C (Table 2). The threshold temperature for pupal development was calculated from the linear regression equation $y = -0.1379 + 0.0114x$, was 14.7°C (Fig. 1). Pupae averaged 72 DD to complete development, but required only 59 DD at 30°. Pupal development took 16% of total immature development time (Table 2). Pupal survivorship was unaffected by temperature (ANOVA; $F_{3,6}$=1.72; p<0.26; n=16) being uniformly high (87 to 100%) at all temperatures.

Adult longevity ranged from 17.7 days at 15° to 5.5 days at 35°C (Table 2) with a threshold of 5.7°C, based on the regression $y = -0.0297 + 0.0052x$ (Fig. 1). Adults at 30° lived for 258 DD and 247 DD at 25°. Average adult longevity was 202 DD or about 45% as long as the immature development time. The total life cycle, egg through adult, required 660 DD using different thresholds for each stage.

Fecundity

Egg production was also influenced by temperature (Fig. 2). The number of females producing at least 1 egg was different across temperatures. At 15° only 15 of the original 43 pairs produced eggs, while 69 of the original 81 pairs produced eggs at

25^{o} (Table 3). The average number of eggs per female, and the maximum total production from one female was at least 30% higher at 30^{o} C compared to other temperatures. Maximum one day egg production was, however, similar across temperatures (Table 3). The function describing fecundity on temperature and age of female is summarized below.

Gelechiid females do not feed to enhance egg production, hence the observed patterns of oviposition at different temperatures are the result of larval feeding. This simplifies the problem, because once adult size is determined, fecundity is determined. The age-specific patterns of daily egg production at different temperatures (Fig. 2) have similar shapes. The pattern of oviposition at one temperature (τ) may be described by equation [1] (Bieri et al., 1983):

$$R = R'/\Delta a = \alpha a/\beta^{a}, \qquad [1]$$

where a is age of the adult from emergence in degree-days, R is per DD oviposition rate and α and β are constants. The function can be linearized to obtain:

$$\log R = \log\alpha + \log a - a \log\beta \qquad [2]$$

Transforming the equation, the coefficients may be estimated by multiple regression yielding the following equation:

$$\log R = C_{o} + b_{1}\log a - a \log\beta \qquad [3]$$

with variable x_1 = log a and x_2 = a. Note an additional coefficient, b_1, results, giving a modification of eqn.[1]:

$$R = C_o a^{b1} / \beta^a \qquad [4]$$

The coefficients and regression statistics of the multiple regression analysis at the five temperatures are given in Table 4. The two best fits were at 25° and 30°. Combining the 25° and 30° C data, and assuming a mean of 27.5° gave a very close fit ($r^2 = 0.90$). Analysis of variance on this regression was highly significant (ANOVA; $F_{2,35}$=161.92, $p<0.001$, $n=40$), indicating that the model gives a satisfactory description of the data. However, the equation needs to be fit across all temperatures. Gutierrez and Baumgaertner (1984) showed that the observed patterns of fecundity across all temperatures could be modeled using the ratio of resource acquisition at temperature (τ) to the acquisition at the optimum temperature (τ_{opt}) (i.e. eqn. [4]).

$$S_{(\tau)} = \frac{M^*(\tau) - Q_{10}}{M^*_{max} - Q_{10}} \qquad [5]$$

The shape of this function is depicted in Figure 3 and has a value between 0 and 1. At less than 5.9° C the supply is insufficient to produce eggs, but at the optimum (τ) nearly all demands will be met and egg production maximized.

Combining equations [4] and [5] into one expression [6] gives the per capita egg production rate for individuals of age a under the conditions $S_{(\tau)}$ experienced at time t.

$$R_{(\tau)} = S_{(\tau)} C a^{b1} / \beta^{a} \qquad [6]$$

Though Q_{10} and consumption rate $M^{*}_{max}(t)$ in [5] may not be known, Gutierrez and Baumgaertner (1984) have shown that R_o is a good indicator of the adult assimilation rate. The data suggests that maximum assimilation occurred near 27° C (see above). Hence, $S_{(\tau)}$ may be approximated by the function [7] describing a concave function between 5.9° and 27° and a monotonically decreasing function between 27° and 40° C. At temperature (τ), $S_{(\tau)}$ is described as follows:

$$S(\tau) = \begin{cases} 1-10^{-\lambda(\tau-5.9^{o}C)} & \text{for } 5.9^{o} \leq \tau \leq 27.5^{o}C \\ 10^{-\lambda(\tau-27.5^{o}C)} & \text{for } 27.5^{o} < \tau \leq 40^{o}C \end{cases} \qquad [7]$$

where $\lambda = 0.17647$ is a fitted constant.

This expression describes per capita _A_. _modicella_ egg production as affected by temperature and the age of the female moth.

Age-specific life table parameters

The intrinsic rates of increase (r_m) were much lower than expected at all temperatures (Fig. 4) and were negative at 35° C. The net reproductive rates (R_o) were similarly low, and ranged from 0.30 at 35° to 3.32 at 30° (Table 5). Calculated generation times ranged from 69 days at 15° to 17 days at 35° C, and were close to average generation times given in Table 2, especially at the two highest temperatures.

Instar number and body size

The relationship between body length and larval head capsule width indicates that five larval instars are typical for GLM at ICRISAT (Fig. 5). The data cluster into five relatively distinct groups that are interpreted to indicate stages or instars. The first three clusters show minimal variation in head capsule widths and were easily differentiated (Table 6). The body length/head capsule width relationship was more variable in the fourth and fifth groups and the decision to separate them into 4th and 5th instars is based on their clustered distributions (Fig. 5).

Head capsule widths ranged from 0.12 to 0.68 mm and body lengths ranged from 0.56 to 6.4 mm. The correlation between head capsule width and body length was very strong ($r = 0.96$). The regression of body length on head capsule width is described by $y = -0.432 + 9.977x$, $n = 158$. Average wet weight of 19 first instar larvae was 0.09 (± 0.005) mg. Live weight of 43 final instar larvae averaged 2.77 (±0.012) mg and 2.38 (±0.073) mg for pupae.

Per capita consumption

A strong correlation was found between leaf area and wet weight per unit area for Kadiri 3 leaflets ($y = -0.037 + 0.0026 \times 10^{-4}$mg mm^{-2}; $r = 0.98$). Based on this relationship, the average leaf area consumed through 5 larval instars was 179.3 (± 7.15) mm^2 per larva using only the 43 larvae which completed development. This is equivalent to 33.29 (± 1.347) mg leaf tissue (wet weight). The efficiency of conversion of ingested food (ECI) for groundnut leaf miner larvae was 8%.

DISCUSSION

Effects of temperature on development

Studies on the effects of temperature on poikilothermic organisms are common in the literature (e.g. de Candolle, 1855; Andrewartha and Birch, 1954, Gilbert et al., 1976). Such studies assume that there is a continuous relationship between development times, longevity and fecundity across temperatures (Hughes, 1963; Gilbert et al., 1976; Curry and Feldman, 1987). The linear or degree-day method is the most common method of calculating development rate because data seldom are available across the full range of temperatures (Stinner et al., 1974, Gilbert et al., 1976). The linear method was used here.

Temperatures in peninsular India range from 9° to 42°C, though cropping season temperatures are more moderate and range from 18° to 32°C (ICRISAT, 1988). At low temperatures the groundnut leaf miner completed its life cycle in 80 days while at higher temperatures only 23 days were needed. A physiological time scale (degree-days above a threshold temperature) accounts for differences in development rate due to temperature. When development in physiological times are compared across temperatures, the differences are not large. The total GLM life cycle required 660 DD with only a 60 DD difference between the fastest and slowest development times.

Previously reported development times for GLM eggs, larvae and pupae vary widely (Table 1) and the reported ranges do not overlap. Temperatures in these earlier studies were not controlled so it is impossible to calculate temperature dependent development rates. The data reported in the literature fall within the range reported here (Table 2) and it seems likely that discrepancies in reported development times are due to differences in temperature. The development times of a related species, *Stomopteryx palpilineella*, were similar to the temperature dependent growth rates calculated for *A. modicella* (Valley and Wheeler, 1976).

Survivorship

Temperature influenced survivorship in GLM immature stages, especially the larval stage. Egg hatch was lower at 15° than at higher temperatures. Larval mortality was high at all temperatures and 100% at 15°C. This may have been due to the use of excised leaves instead of whole plants to rear larvae. At mid-range temperatures (25° and 30°C) survivorship was generally between 40 and 70% in the 4 experiments, but was as low as 8% in one experiment at 35°.

At 15°C dead larvae were frequently found on the leaf surface. To determine if first instar GLM were more vulnerable than older instars, several older instar larvae were kept at 15° for observation. These older instars survived and successfully pupated. These results suggest that a failure to establish is the cause of high mortality at 15°, however, once established, larvae can survive and grow at 15° C.

The only immature stage in which survivorship was apparently unaffected by temperature was the pupal stage. No significant differences in the percentage of pupae successfully emerging were found across temperatures. Emergence from the pupal stage was uniformly high (82-100%) at all temperatures.

Adult longevity

Temperature also affected adult longevity. In physiological time units, adults at 25° and 30°C lived approximately 50% longer than at the other three temperatures. These differences are important because they indicate that females at these temperatures have longer ovipositional periods than females at other temperatures (see below).

Fecundity

Adults at 15° and 35°C lived equivalent physiological time periods and produced the same number of eggs. But because females oviposit at night, females at 15° had three times as many nights for oviposition (Table 2), as females at 35°C. However, daily per capita egg production was much lower at 15°C. Daily per capita egg production was nearly the same at 25°, 30° and 35° (Fig. 2), but because adults lived fewer days at 35°, average egg production was lower. All three indicators of fecundity show that egg production was highest at 30° followed by 25° and fell significantly at both lower and higher temperatures. This result would be predicted from the model proposed by Gutierrez and Baumgaertner (1984).

The oviposition data suggest a relationship between oviposition and temperature. At high temperatures egg production is high but adult life span is short, while at low temperatures, adults live considerably longer but egg production is severely reduced. Under mid-range conditions (25° and 30°C), the optimum is reached; adults live relatively long and egg production is maximum.

Ambient temperatures were not recorded in three earlier studies measuring GLM fecundity (Cherian and Basheer, 1942; Gujrati et al., 1973; Kapadia et al., 1982), and it is likely that the large differences reported in fecundity, are due to temperature and possibly the experimental methods employed.

Age-specific life table analysis

Life table statistics incorporate aspects of developmental time, age-specific survivorship and fecundity (Southwood, 1978). The results are biased by the excessive larval mortality that occurred at all temperatures. The calculated intrinsic rates of increase (r_m) were quite low (< 0.076) in all five temperature treatments, and less than zero at 15° and 35°. The low r_m values were due to the low larval survivorship. Both r_m (Fig. 4) and R_o were highest at 30°, followed by 25° C (Table 5).

As indicated previously, the choice of experimental design may have adversely affected these life table statistics. The high larval mortality produced low l_x values which biased the calculation of r_m and R_o. The life table parameters need further confirmation and in future experiments, larvae should be reared on whole plants.

Number of instars

Larval age is frequently determined by measuring head capsule widths (Southwood, 1978), and the technique has also been used for species identification (Nemjo and Slaff, 1984). Dyar (1890) was the first to note that head capsule width between successive instars increases by a constant factor for a given species. Gujrati *et al*. (1973) reported the following GLM larval head capsule widths: 1st instar 0.07 mm, 2nd instar 0.14 mm, 3rd instar 0.21 mm and 4th instar 0.28 mm. Head capsule widths of the first two instars were smaller and larger than the width of the first instar reported here. The ratio of head capsule widths between successive instars (width of older instar/width of younger instar) is usually about 1.4 (Wigglesworth, 1972). The ratio of head capsule widths between first and second instars reported by Gujrati *et al*. (1973) was 2, which is too high. Head capsule width ratios in this study were between 1.39 and 1.67 (Table 6).

A second discrepancy in the Gujrati *et al*. (1973) study is that head capsule widths for the fourth and fifth instars are not reported. The largest head capsule size (0.28 mm) was the width of the third instar head capsule in this study (Table 6). Valley and Wheeler (1976) measured head capsule widths for the slightly smaller, related species, *S*. *palpilineella*. This species has only 4 larval instars, but the ranges reported are very close to the values reported here for A. modicella.

Per capita consumption

The amount of leaf tissue GLM consumed (179.3 mm^2) in this study is 1/20th the value (3480 mm^2) reported by Islam et al. (1983). Unfortunately Islam et al. did not mention the method used to calculate consumption. One way to evaluate estimates of GLM consumption is to compare leaf consumption rates to that of armyworm, S. frugiperda (Garner and Lynch, 1981), which consumes 9456 mm^2 and has a pupal mass of 142.8-189.7 mg. A ratio of the pupal mass of A. modicella/S. frugiperda should be roughly equivalent to the ratio of leaf tissue consumed by the two insects respectively. The pupal mass ratio is 0.01255 to 0.01667 depending on which sex pupae are used for S. frugiperda. In this study, the consumption ratio is 0.01896, closely approximating the pupal mass ratio. However, using Islam et al.'s data, the leaf area-consumption ratio is 19 times larger (0.36802) than the pupal mass ratio found in this study.

Groundnut leaf miner larvae gain approximately 2.68 mg (from 0.09 to 2.77 mg) during the larval period and consume 33.29 mg leaf tissue. The efficiency of conversion of ingested food (ECI) was calculated on a wet weight basis in this study because of the difficulty in obtaining accurate dry weight measurements of small larvae. Wet weight measurements can be biased because water content in leaves and larvae may be different. The estimated ECI for GLM was 8%, a figure well within the range reported for other leaf-eating lepidoptera larvae (Slansky and Scriber, 1982). The accuracy of this figure could be improved by calculating the ECI on a dry weight basis.

The results of the experiments described above have resolved much of the confusion over GLM development times, fecundity, instar number and consumption rates. Only the results of the age-specific life table analysis need further confirmation. Accurate information on the biology of GLM is a prerequisite for developing an effective pest management program against this important and widespread legume pest.

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Table 1. Previously published development and longevity times (days) for *Aproaerema modicella* (mean and range).

Stage		Gujrati *et al*. (1973)			Kapadia *et al*. (1982)	
Egg		3.0	(2-4)		7.45	(6-8)
Larva		9.3	(8-12)		18.48	(14-23)
Pupa		5.0	(4-6)		9.93	(6-13)
Adult	(both)	11.0	(5-20)	(males)	5.47	(2-7)
				(females)	7.27	(2-17)

Table 2. Duration of each life stages at five temperatures, degree-day requirements and development threshold for *Aproaerema modicella*.

Temp.	Days (mean ± SE)[1]			
(°C)	Egg	Larva	Pupa	Adult
15	22.96 ± 0.32 (63)	--	--	17.70 ± 8.24 (56)
20	9.13 ± 0.35 (76)	33.87 ± 5.01 (67)	15.11 ± 2.67 (64)	11.41 ± 6.25 (147)
25	4.19 ± 0.19 (79)	16.54 ± 2.89 (35)	7.50 ± 2.45 (34)	12.78 ± 5.09 (143)
30	2.97 ± 0.29 (78)	14.66 ± 2.63 (62)	3.85 ± 1.47 (54)	10.62 ± 5.48 (129)
35	2.79 ± 0.21 (78)	12.33 ± 1.87 (9)	3.89 ± 1.69 (9)	5.47 ± 3.01 (131)
Threshold	12.3°C	8.9°C	14.7°C	5.7°C
Mean developmental period (degree-days)	60.1	327.1	72.3	202.4

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[1] Numbers in parentheses refer to number (n) of experimental animals.

Table 3. Effect of temperature on _Aproaerema modicella_ fecundity.

Temp. (°C)	Pairs Producing[1]	Eggs/Female (mean±SE)[2]		Max. 1 Day Egg Production	Max. Total Egg Production
15	15	37.8c	(±6.91)	36b	88b
20	47	42.66bc	(±7.11)	52ab	160b
25	69	57.04b	(±6.71)	81a	170b
30	44	87.59a	(±9.85)	70a	248a
35	22	27.09c	(±6.29)	70a	105b

[1] Pairs producing at least one egg.

[2] Values within a column followed by the same letter are not significantly (p=0.05) Duncan's Multiple Range Test.

Table 4. Results of multiple regression analyses on the effect of female age on Aproaerema modicella fecundity at five temperatures.

Temperature	n	C	x_1	x_2	r^2
15^{o}	26	-4.335	-0.405	4.023	0.51
20^{o}	27	-0.260	-0.244	1.447	0.69
25^{o}	22	-0.052	-0.499	2.781	0.92
30^{o}	18	0.851	-0.592	2.882	0.94
35^{o}	7	3.229	-2.447	5.648	0.86
combined 25^{o} + 30^{o} (27.5^{o})	39	0.432	-0.519	2.704	0.9 0

Table 5. Intrinsic rate of increase (r_m), female per female per generation (R_o) and generation time (G) for lab-reared *Aproaerema modicella* at five temperatures.

Temperature (°C)	r_m	R_o	Generation time (days)
15°	-0.001	0.96	69.0
20°	0.005	1.30	49.9
25°	0.027	2.02	25.9
30°	0.048	3.32	24.8
35°	-0.074	0.30	16.4

Table 6. Head capsule widths (mm) and ratios between successive instars of lab-reared Aproaerema modicella larvae.

Instar	N	Range	Mean ± SE	Ratio between instars (n/n-1)
First	40	0.12	0.12	
Second	26	0.2	0.2	1.67
Third	22	0.24-0.28	0.277 ± 0.0103	1.39
Fourth	35	0.36-0.48	0.395 ± 0.0425	1.43
Fifth	35	0.52-0.68	0.578 ± 0.0349	1.46

Figure 1. Development rates (mean ± SE) for *Aproaerema modicella* egg, larval and pupal stage and adult longevity.

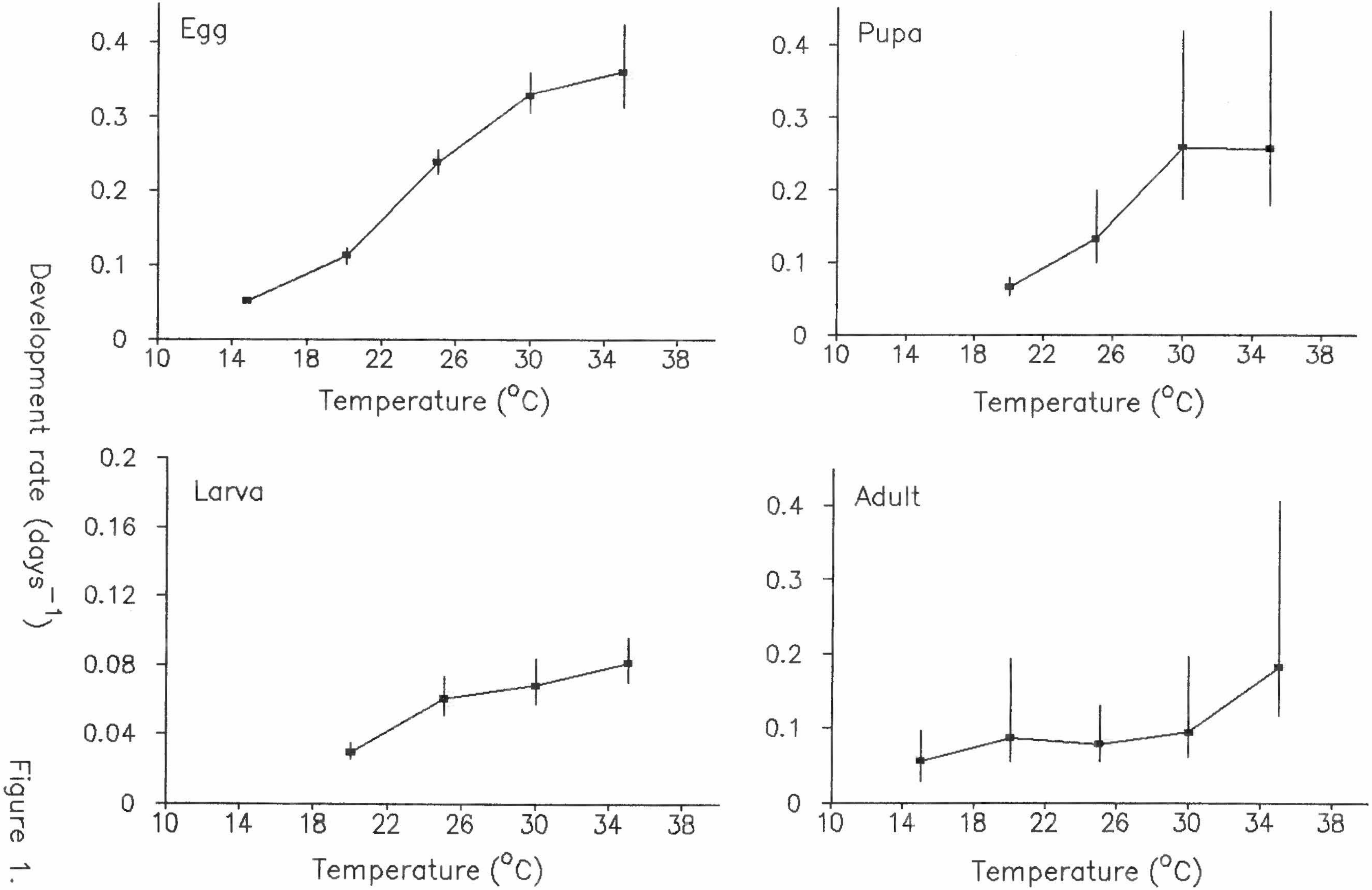
Egg
Pupa
Larva
Adult
Development rate (days^{-1})
Temperature (°C)
Temperature (°C)
Temperature (°C)
Temperature (°C)
0
0.1
0.2
0.3
0.4
0
0.04
0.08
0.12
0.16
0.2
10
14
18
22
26
30
34
38

Figure 1.

Figure 2. Aproaerema modicella daily per-capita egg production at five temperatures.

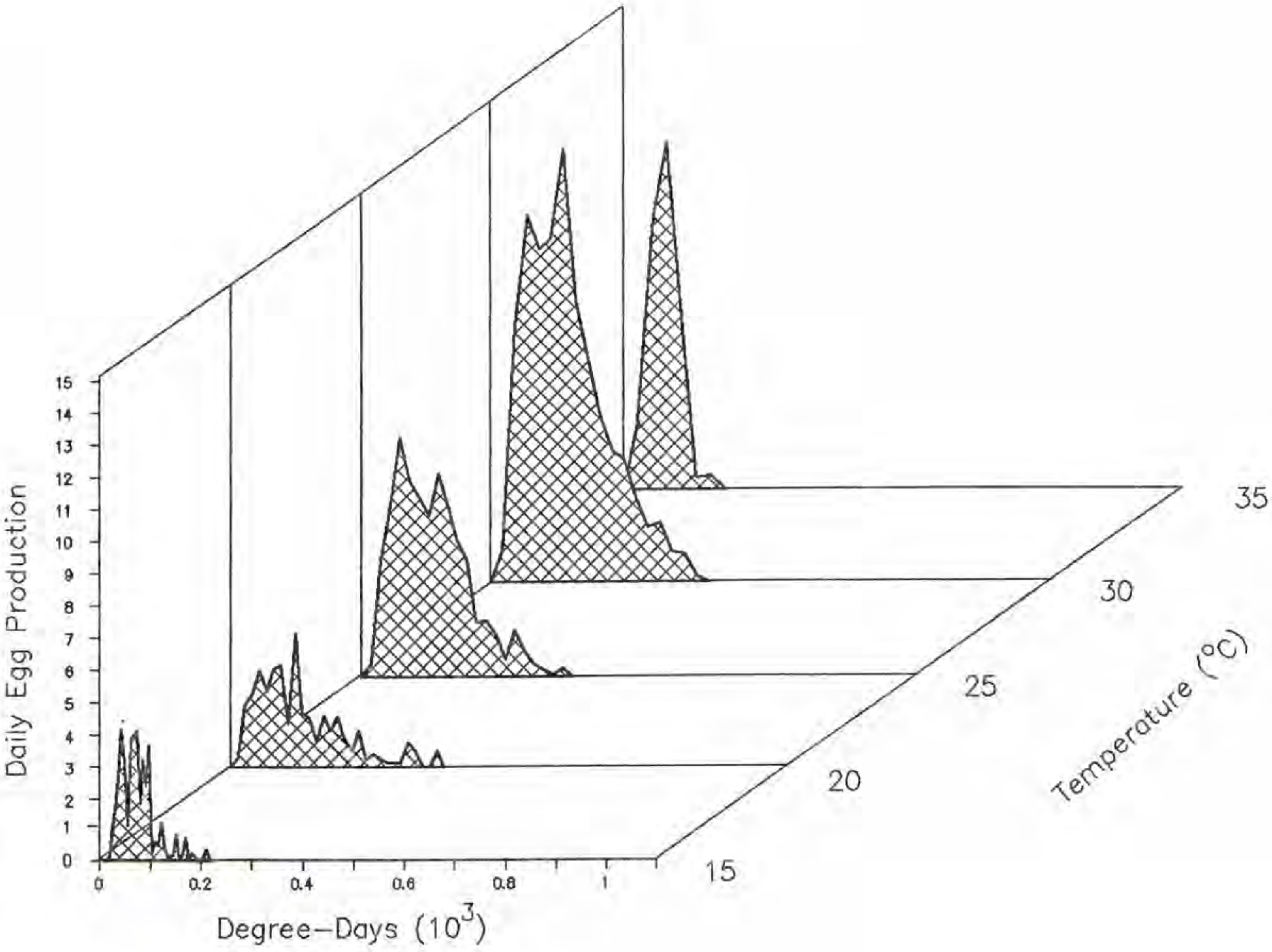
Daily Egg Production
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Degree-Days (10^3)
0
0.2
0.4
0.6
0.8
1
Temperature (°C)
15
20
25
30
35

Figure 2.

Figure 3. The relationship between *Aproaerema* *modicella* fecundity and temperature.

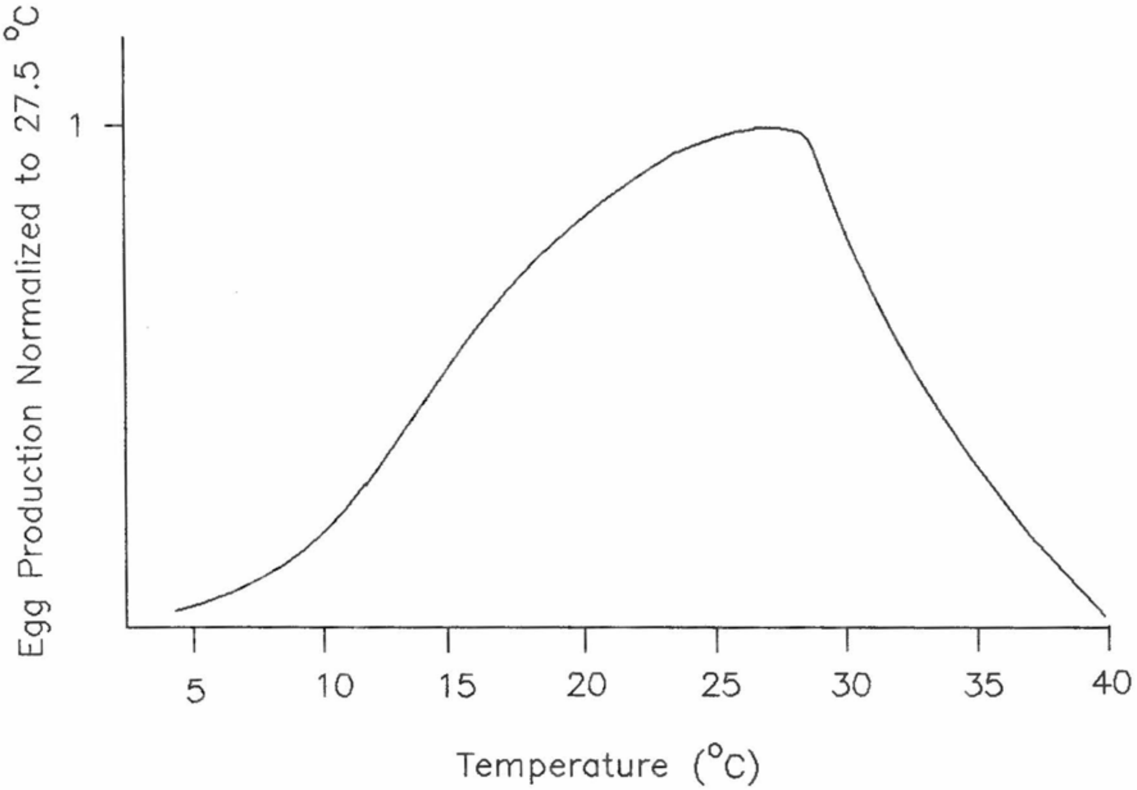
Egg Production Normalized to 27.5 °C
1
5
10
15
20
25
30
35
40
Temperature (°C)

Figure 3.

Figure 4. Intrinsic rate of increase (r_m) for lab-reared *Aproaerema modicella* at five temperatures.

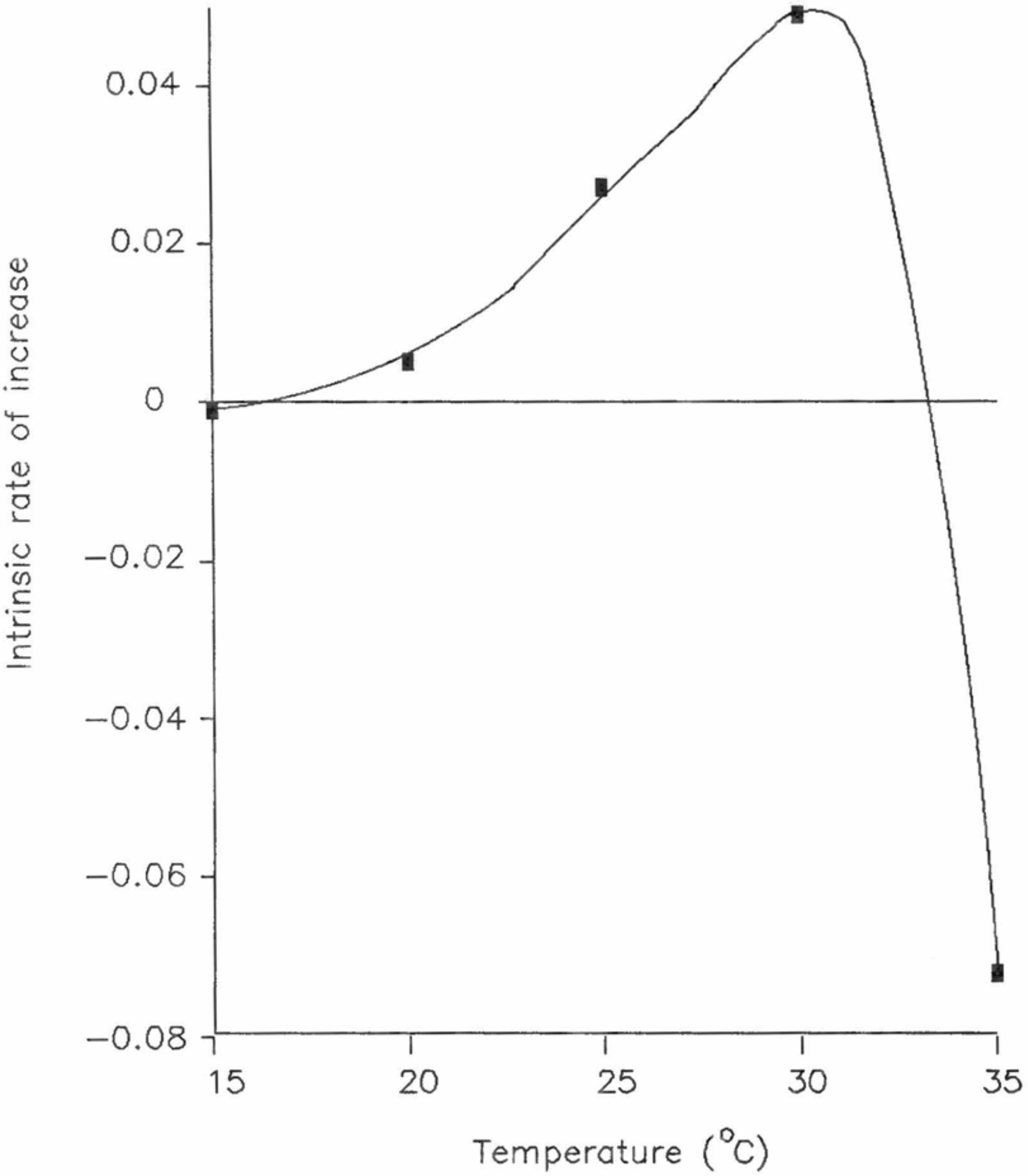
0.04
0.02
0
−0.02
−0.04
−0.06
−0.08
Intrinsic rate of increase
15
20
25
30
35
Temperature (°C)

Figure 4.

Figure 5. The relationship between head capsule width and body length for *Aproaerema modicella* larvae.

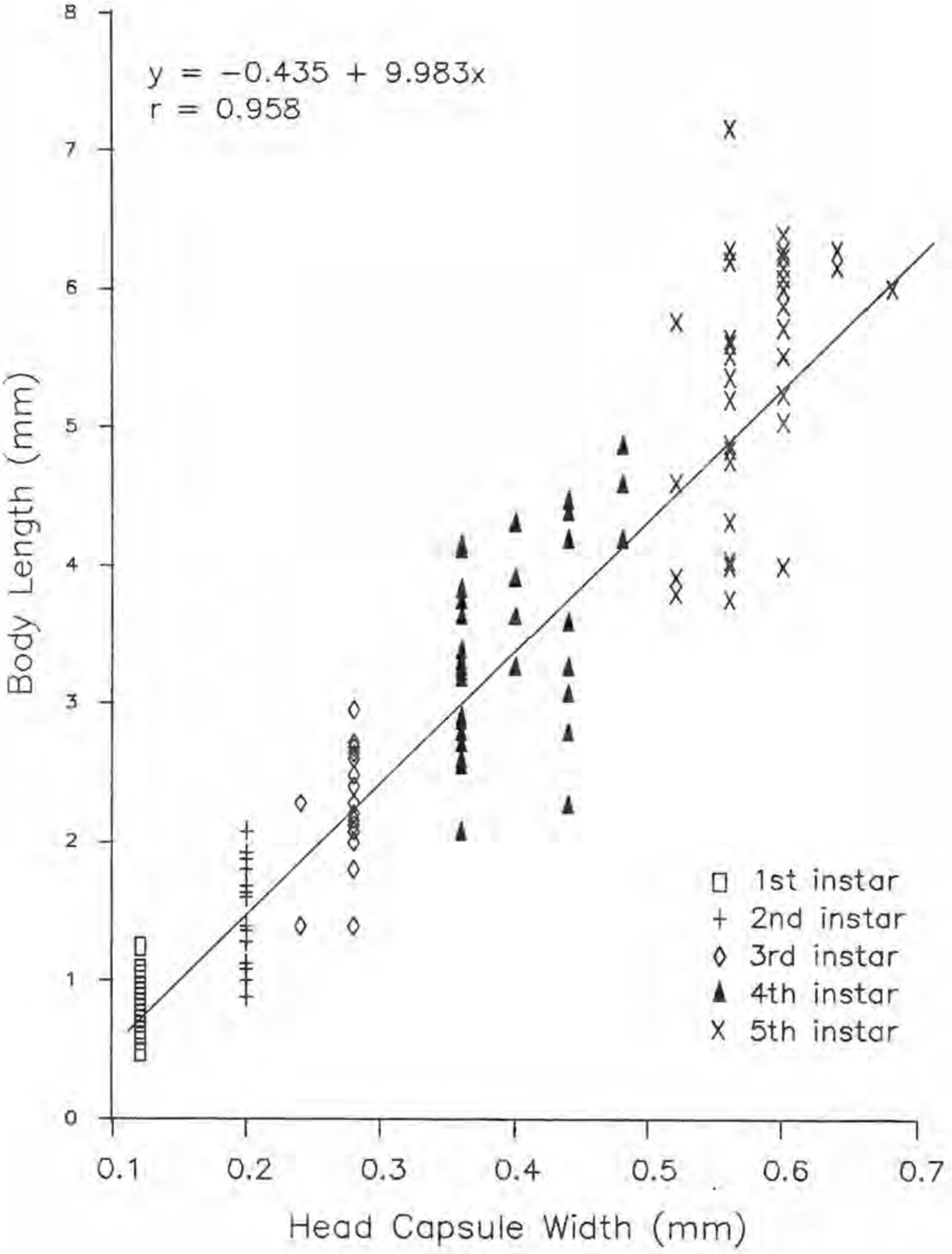
y = −0.435 + 9.983x
r = 0.958
Body Length (mm)
0
1
2
3
4
5
6
7
8
Head Capsule Width (mm)
0.1
0.2
0.3
0.4
0.5
0.6
0.7
□ 1st instar
+ 2nd instar
◊ 3rd instar
▲ 4th instar
X 5th instar

Figure 5.

Chapter 3.

The biology and population dynamics of the groundnut leaf miner, Aproaerema modicella (Deventer) (Lepidoptera: Gelechiidae), in peninsular India: II. Field population dynamics at ICRISAT Center, 1987-89

Introduction

Materials and methods

Results

Discussion

Literature cited

INTRODUCTION

Groundnut (Arachis hypogaea L.) in peninsular India is commonly grown in both the rainy (June to October) and the post-rainy seasons (December to April). One of its major pests is the groundnut leaf miner (GLM), Aproaerema modicella (Deventer) (Lepidoptera: Gelechiidae), which completes as many as 4 generations per season (Wightman and Amin, 1988). Population levels fluctuate dramatically between years, seasons and even between generations at the same location. Reports concerning the population dynamics of GLM are common in the literature (Amin and Mohammad, 1980; Logiswaran and Mohanasundaram, 1986; ICRISAT, 1986; 1987; 1988), though the causes of population fluctuations are uncertain.

Studies by Lewin et al. (1979) and Logiswaran et al. (1982) conducted at Tindivanum, Tamil Nadu (India) came to different conclusions concerning the effect of temperature and rainfall on GLM population dynamics. Lewin et al. (1979) used correlation and partial regression to test the effect of sowing time, temperature and rainfall on leaf miner populations. Temperature was positively and rainfall negatively correlated with leaf miner incidence (Lewin et al., 1979). Yield was affected more by sowing time than by GLM incidence. Logiswaran et al. (1982) reported a significant negative correlation between both maximum and minimum temperature and GLM infestation levels, but no correlation was found with rainfall.

In another study, Khan and Raodeo (1987) compared changes in several weather factors to GLM incidence over two years. None of the four weather variables measured, rainfall, maximum and minimum temperature, and relative humidity, offered a reasonable explanation for the fluctuations.

MATERIALS AND METHODS

The population dynamics of GLM larvae and adults were studied at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) located near Hyderabad, Andhra Pradesh, (17°N) in peninsular India. Weather data used in this study came from the ICRISAT meteorological station.

Agronomic procedures

Two groundnut crops are grown annually in this region, one during the rainy season and one during the dry, post-rainy season. In this study, four crops were studied during the period 1987-89. Rainy season crops were planted the first week of July and harvested in mid-October, and post-rainy season crops were planted in mid-December and harvested in mid-April. The ICRISAT recommendation of growing 4 rows of groundnut on raised beds was followed. Beds were 1 m wide and separated by a 0.5 m furrow. Seeds were planted 15 cm apart. Plot size for experiments described below was 396 m^2 in the first two seasons, 360 m^2 in the third and 288 m^2 in the fourth. Irrigation was supplied as needed and approximately 500 kg ha^{-1} gypsum (67% $CaSO_4$) was applied about 60 days after sowing (DAS) to assure sufficient calcium supply for plant growth.

Experimental design

Larval populations were sampled weekly beginning one week after plant emergence and continuing until harvest. The treatments used in each trial are presented in Table 1. Each of the four studies (2 rainy and 2 post-rainy season) was planted in a randomized block design of treatments (2 varieties x insecticide (sprayed vs. unsprayed control)) with four replicates per treatment. Field trials were blocked against the flow of water in irrigation furrows. Larval density is presented both as larvae plant^{-1} and as larval-days, which is the product of larval counts and sampling interval summed through the season.

The susceptible variety, Kadiri 3 (ICG 799) was planted in all studies, and one of two tolerant cultivars (NCAc 17090 or NCAc 343) was planted in all but the final season. An untreated (control) plot and one treated with at least one foliar spray of monocrotophos (40% EC) applied at a rate 181 mg a.i./ha in 331 l/ha water when GLM larvae were first observed were common across varieties. In the first study, three insecticide sprays were applied, two were applied in the second and third seasons and one spray was applied in the final season.

Two other insecticide treatments were included during some seasons. In the second, third and fourth studies, Kadiri 3 plants were sprayed with monocrotophos when adult moths were first observed visually in the field. And in the two rainy seasons (the first and third studies), an additional treatment consisting of Kadiri 3 plants treated at planting with a systemic insecticide (isofenphos 5G) incorporated in the soil at a rate of

2 kg a.i./ha.

The effect of variety, insecticide treatment, season, rainfall, and temperature on the population dynamics of GLM was tested using multiple regression (Zar, 1974). The log of total larval-days was used as the independent variable (y) because leaf miner densities were highly variable in the four seasons. The dependent variables (x) included variety, insecticide treatment and season, entered as dummy variables (Zar, 1974), total rainfall during the season and the mean temperature during the season. Variables and interactions which had significant regression coefficients (Student's t-test; t=2.145 for n=14) were included in the multiple regression equation.

Monitoring adult activity

The flight activity of adult GLM was monitored from July 1987 to April 1989 using daily light trap samples. The light trap was never closer than 500 m from fields where larval GLM counts were taken. Large trap catches were subsampled using half or less of the total. Counts were corrected for subsampling. Light trap data are summarized as total moths captured each week.

Simulation of rain induced mortality

Simulated rainfall was used to test the effects of rainfall on GLM egg and larval mortality. Potted plants infested with eggs and larvae were exposed to 50 mm of rainfall in a mechanical rain simulator. The rain simulator produced drops roughly equivalent in size and velocity to natural rainfall in the area (G.

Smith, ICRISAT, pers. comm.).

The effect of rain on eggs was tested using 10 pots with 5 plants each. Eight to 10 eggs were marked in each pot using a knotted string (1 knot for each egg) attached to the petiole. Egg numbers before and immediately after the simulated rainfall were compared to determine the direct effect of rain on egg survivorship. The eggs were observed daily to compare hatch rates between the two groups.

The effects of rain on larval survival was tested using 10 pots with 10 plants per pot and infested with third, fourth and fifth instar GLM larvae. Five pots were put into the rain simulator and five kept as control pots. The number of live larvae before and one week after treatment was recorded in each treatment.

Analysis of variance (ANOVA) was used to test differences in egg and larval survival between treated and control plants (Zar, 1974).

RESULTS

1987 Rainy season

GLM populations were very high in the 1987 rainy season (Fig. 1). Unsprayed plots of Kadiri 3 had up to 130 larvae per plant in the first generation. The numbers in the second and third generations were much smaller (<30 larvae per plant). The two unsprayed treatments reached the highest cumulative leaf miner populations, with the susceptible cultivar, Kadiri 3, having 50% more larval-days than NCAc 17090 (Fig. 2). The Kadiri 3

+ isofenphos treatment had the smallest, cumulative larval-days, being 1/10th that of the unsprayed Kadiri 3 treatment.

Two large peaks and several smaller peaks of moths were observed in light trap catches (Fig. 3). The low and scattered rainfall that occurred in the 1987 rainy season did not appear to adversely affect larval populations or disrupt adult oviposition (Fig. 3).

1987-88 Post-rainy season

Leaf miner populations were the lowest of the four seasons in the 1987-88 post-rainy season (Fig. 1). The four peaks in larval numbers correspond to the four generations of GLM. The population built up slowly through the season but reached only 0.35 larvae per plant by the end of the season. This population was at least three orders of magnitude smaller than the 1987 rainy season (Fig. 2).

GLM larval-days were less than 1 per plant across all treatments. Low rainfall and increasing temperatures, typical of the post-rainy season, were experienced (Fig. 3).

Light trap catches of adult moths were lower than during the rainy season (Fig. 3), but increased slightly towards the end of the season.

1988 Rainy season

The 1988 rainy season was wetter and cooler than the 1987 rainy season (Fig. 4), and leaf miner populations were much lower (Fig. 1). In unsprayed treatments of both varieties, a large, 450 degree-days (DD) broad peak of larval numbers may have resulted from 2 flights of immigrating moths (Fig. 1). GLM larval-days followed a pattern similar to the larval-days in the 1987 rainy season, but was 1/50th that of the 1987 rainy season.

Unsprayed plots had more larval-days than treated plots, and variety NCAc 343 had slightly more than Kadiri 3 (Fig. 2). Within Kadiri 3, the insecticide was less effective if applied when moths were present than applied when larvae were present.

Few moths were recorded in light traps (Fig. 4), thus most of the within-plot population came from within plots.

1988-89 Post-rainy season

During the 1988-89 post-rainy season, GLM populations were very low and of the same order of magnitude as the previous post-rainy season (Fig. 1). Populations "peaked" during the last week of February at densities less than 0.4 larvae per plant. These low densities were similar to the 1987-88 post rainy season, but the peak was reached earlier in 1988-89 (Fig. 2). Agroclimatic conditions were similar between the two post-rainy seasons except for a brief but intense thunderstorm that occurred in mid-March 1989 (Fig. 4).

Light trap catches of adults were low until the end of the season, when two small peaks of moths were recorded (Fig. 4).

Simulated rainfall experiment

Of 48 eggs exposed to simulated rain, 2 washed off and two failed to hatch. In the control group, 3 of the 51 eggs failed to hatch. The hatch rate under simulated rainfall (92%) and in the control group (94%) were statistically equivalent.

Larvae were also unaffected by the direct effects of simulated rainfall. Under conditions of simulated rain, 72.0 ± 6.0 larvae were observed before treatment and 64.4 ± 10.37 larvae were found one week after treatment, which was 89% of the original number. In the control pots, 63.0 ± 6.50 larvae were present before treatment and 59.8 ± 14.43 larvae one week later, or 95% of the original number. Differences between treatments were not significant (ANOVA; $F_{3,16}=2.79$; $p>0.1$; $n=10$).

DISCUSSION

Groundnut leaf miner populations in peninsular India vary dramatically between seasons and generations. During the two years of this study, larval GLM populations ranged from 3200 larval-days per plant in the 1987 rainy season to less than 1 larval-day per plant in the 1987-88 post-rainy season (Fig. 2). Fluctuations of this magnitude do not appear to be unusual (Amin and Mohammad, 1980; Logiswaran and Mohanasundarum, 1986; ICRISAT Legumes Entomology Unit, unpubl. data).

The effects of variety, insecticide versus no insecticide (control), rainfall and the role of adult immigration in the population dynamics of this pest are discussed here.

Varieties

The resistant NCAc varieties supported lower GLM densities than did the susceptible variety Kadiri 3 in all but the 1988 rainy season when populations were extremely low. Lower GLM population were found on unsprayed NCAc plants compared to unsprayed Kadiri 3 when populations were high (1987 rainy season), but yields were significantly lower. This suggests that NCAc may be resistant to GLM, and that agronomic characters were largely responsible for the significant yield difference. GLM populations were so low in the other seasons that comparisons are not meaningful.

Insecticides

Insecticides reduced GLM larval populations, especially when populations were high in the 1987 rainy season. Compared to the check, cumulative larval-days in this season were reduced 60% with three foliar sprays (Fig. 2), and reduced 85% with a systemic insecticide (not shown). Insecticides effectively reduced GLM larval populations, but one application of soil-incorporated systemic insecticide was as effective as three applications of a foliar insecticide. In addition, systemic insecticides have less impact on non-target organisms such as natural enemies.

Variety x insecticide interaction

The lowest leaf miner densities in both the 1987 and 1987-88 seasons were recorded in the plots combining insecticides and less-susceptible varieties. Aside from the 1987 rainy season, differences in GLM density across treatments were not important because GLM populations were far below economic injury levels and had no effect on yields.

Rainfall effects

Several authors have suggested that rainfall may reduce GLM larval populations in some seasons and have tried to correlate high GLM numbers with low rainfall seasons. Extremely low rainfall is typical of the post-rainy season in peninsular India (Figs. 3 and 4) and if rainfall were an important larval mortality factor, then GLM populations should be higher in the post-rainy season. Both post-rainy seasons had low rainfall and low GLM populations. The 1987 rainy season had the highest GLM population and had below average rainfall (58% less than the 1988 rainy season). These conflicting patterns of rainfall and GLM abundance point out the difficulty of using single factors to explain biological phenomena.

Historical data from 1980-86 (unpubl. data, ICRISAT Legumes Entomology Unit), indicate that groundnut leaf miner populations ranged from a high of 320 larvae per plant in the 1980-81 post-rainy season to less than 1 larva per plant in the 1985-86 post-rainy season. Very high (+50 larvae plant^{-1}) GLM populations were recorded in two post-rainy seasons and one rainy season. Moderate GLM populations, 20-50 larvae plant^{-1}, were observed in two rainy seasons and three post-rainy seasons. These data provide an historical background for GLM population dynamics at ICRISAT but give no indication of cause and effect.

Using artificial rain, no significant differences between treatment and control were found in egg or larval survivorship. Leaf miner abundance may be influenced by climatic variables, and rainfall in particular, in more subtle ways. For example, heavy and persistent rainfall may interfere with oviposition, or fungal and other pathogens may be favored by rainfall patterns different from the conditions in this experiment. This aspect of GLM ecology requires further investigation and is crucial to understanding the large, erratic fluctuations of GLM populations.

Adult immigration

Light trap data (Fig. 3) indicated a large influx of moths preceded the establishment of the large larval population in the 1987 rainy season. Larvae appeared more than 200 DD earlier than populations in other seasons (Fig. 1). The extremely high number of moths produced a large larval population which caused significant defoliation and up to 40% yield loss in unsprayed groundnuts (Chap.4). Moths migrating into the field may have emerged from a summer diapause or aestivation perhaps triggered by the onset of the monsoon, or may have migrated from some unknown source. Immigration is an important component in the population dynamics of most insect species. It may be especially important with an insect such as GLM which undergoes large population fluctuations routinely. The degree of trivial movement and directional or long range migration will need to be studied if GLM population dynamics are to be fully understood.

Summary

Summarizing the results using multiple regression analysis produced the following equation:

$$y = 4.598 + 0.437x_1 - 0.0043x_2 - 0.0444x_3x_2 \quad [1]$$

$$R^2 = 0.95 \quad n = 14$$

where y is log GLM larval-days, x_1 is insecticide treatment [0 = sprayed, 1 = unsprayed], x_2 is total rainfall (mm) and x_3 is season [0 = rainy, 1 = post-rainy]. x_1 and x_3 are dummy variables in this analysis (Zar, 1974). Other variables (e.g. season and variety) and interactions (e.g. rainfall x variety) did not contribute significantly to the regression equation and were not included.

Equation [1] indicates that during the four seasons of this study, unsprayed plants had the highest larval density but rainfall and season x rainfall interaction had the effect of decreasing larval density. This regression line is highly significant (ANOVA; $F_{3,10}=64.27$; $p<0.001$) but this does not imply a causal relationship between rainfall and GLM density. The multiple regression equation may indicate a more subtle connection between rainfall and GLM larval density.

Other results demonstrated that variety may affect GLM population size; that systemic insecticide is more effective than foliar applications; that rainfall by itself is not an important mortality factor for larvae and eggs; and that immigration of adults from unknown sources may trigger outbreaks.

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Table 1. Treatments used in groundnut experiments to monitor *Aproaerema modicella* population dynamics during rainy and post-rainy seasons at ICRISAT, India.

	1987-88		1988-89	
Treatment	Rainy	Post-rainy	Rainy	Post-rainy
Kadiri 3 sprayed[1/]	•	•	•	•
Kadiri 3 unsprayed	•	•	•	•
NCAc 17090 sprayed	•	•		
NCAc 17090 unsprayed	•	•		
Kadiri 3 systemic	•		•	
Kadiri 3 sprayed[2/]		•	•	•
NCAc 343 sprayed			•	
NCAc 343 unsprayed			•	
soybean				•
Total	5	5	6	4

[1/] Insecticide applied when larvae first observed.

[2/] Insecticide applied when adults first observed.

Figure 1. Population fluctuations of *Aproaerema modicella* larvae on two groundnut varieties, with and without insecticide, during four seasons at ICRISAT, India.

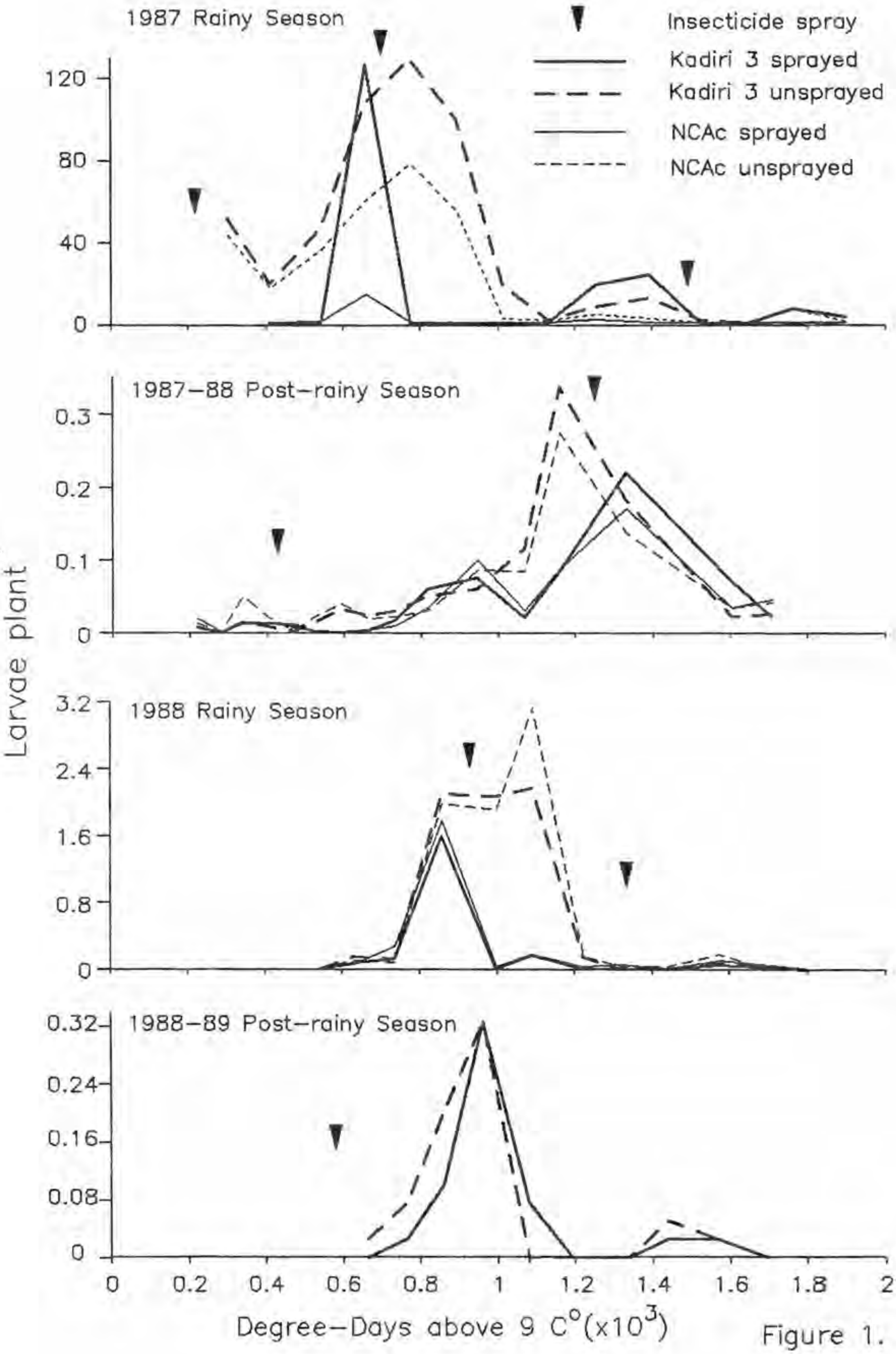
1987 Rainy Season
Insecticide spray
Kadiri 3 sprayed
Kadiri 3 unsprayed
NCAc sprayed
NCAc unsprayed
120
80
40
0
1987–88 Post-rainy Season
0.3
0.2
0.1
0
1988 Rainy Season
3.2
2.4
1.6
0.8
0
1988–89 Post-rainy Season
0.32
0.24
0.16
0.08
0
Larvae plant⁻¹
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
Degree–Days above 9 C°(x10³)

Figure 1.

Figure 2. Cumulative population of *Aproaerema modicella* on two groundnut varieties, with and without insecticide, during four seasons at ICRISAT, India.

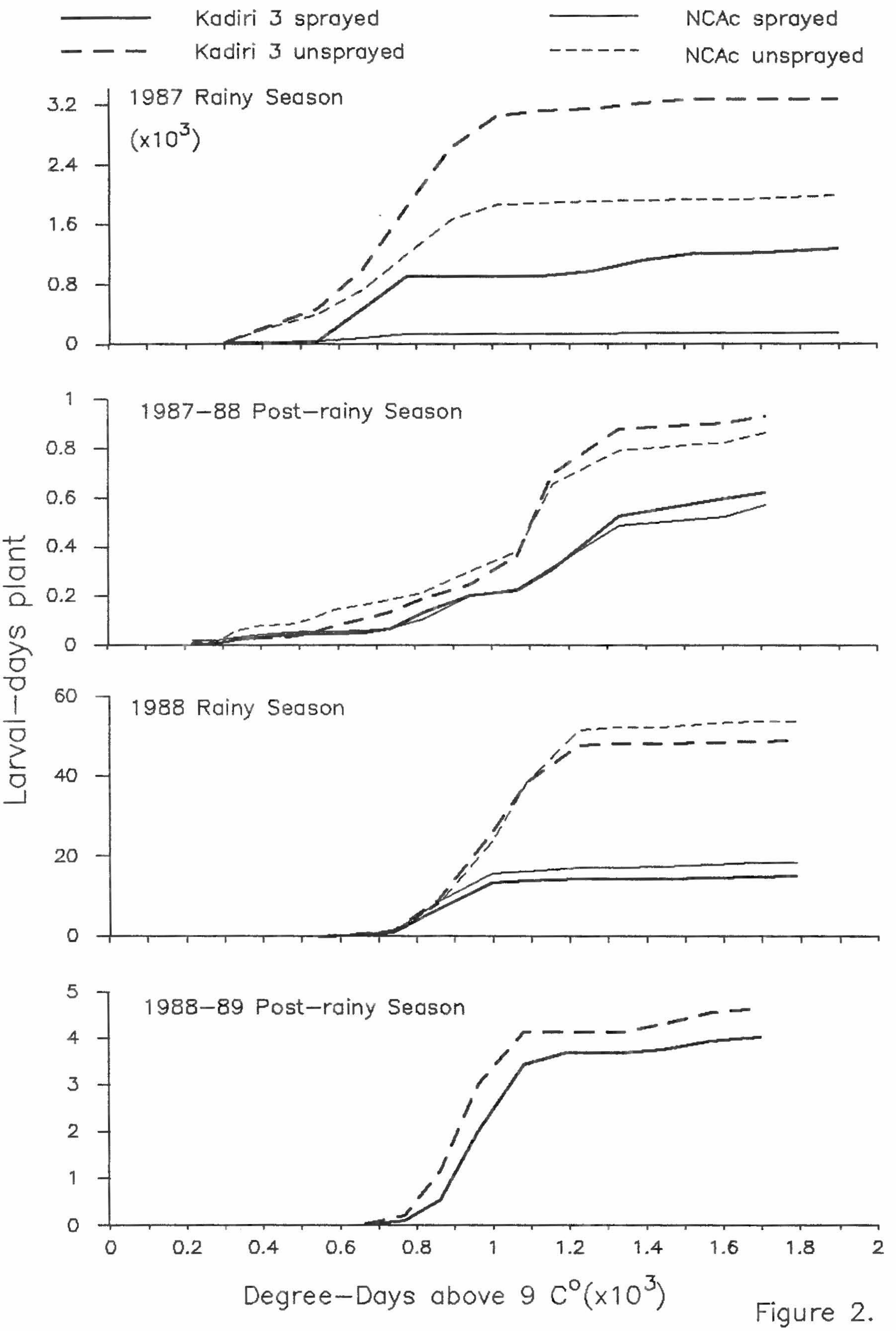
Kadiri 3 sprayed
Kadiri 3 unsprayed
NCAc sprayed
NCAc unsprayed
1987 Rainy Season
(x10³)
3.2
2.4
1.6
0.8
0
1987–88 Post–rainy Season
1
0.8
0.6
0.4
0.2
0
1988 Rainy Season
60
40
20
0
1988–89 Post–rainy Season
5
4
3
2
1
0
Larval–days plant⁻¹
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
Degree–Days above 9 C°(x10³)

Figure 2.

Figure 3. Daily maximum and minimum temperature, rainfall, weekly light trap catches and cumulative *Aproaerema modicella* larval population during the 1987 rainy and 1987-88 post-rainy seasons.

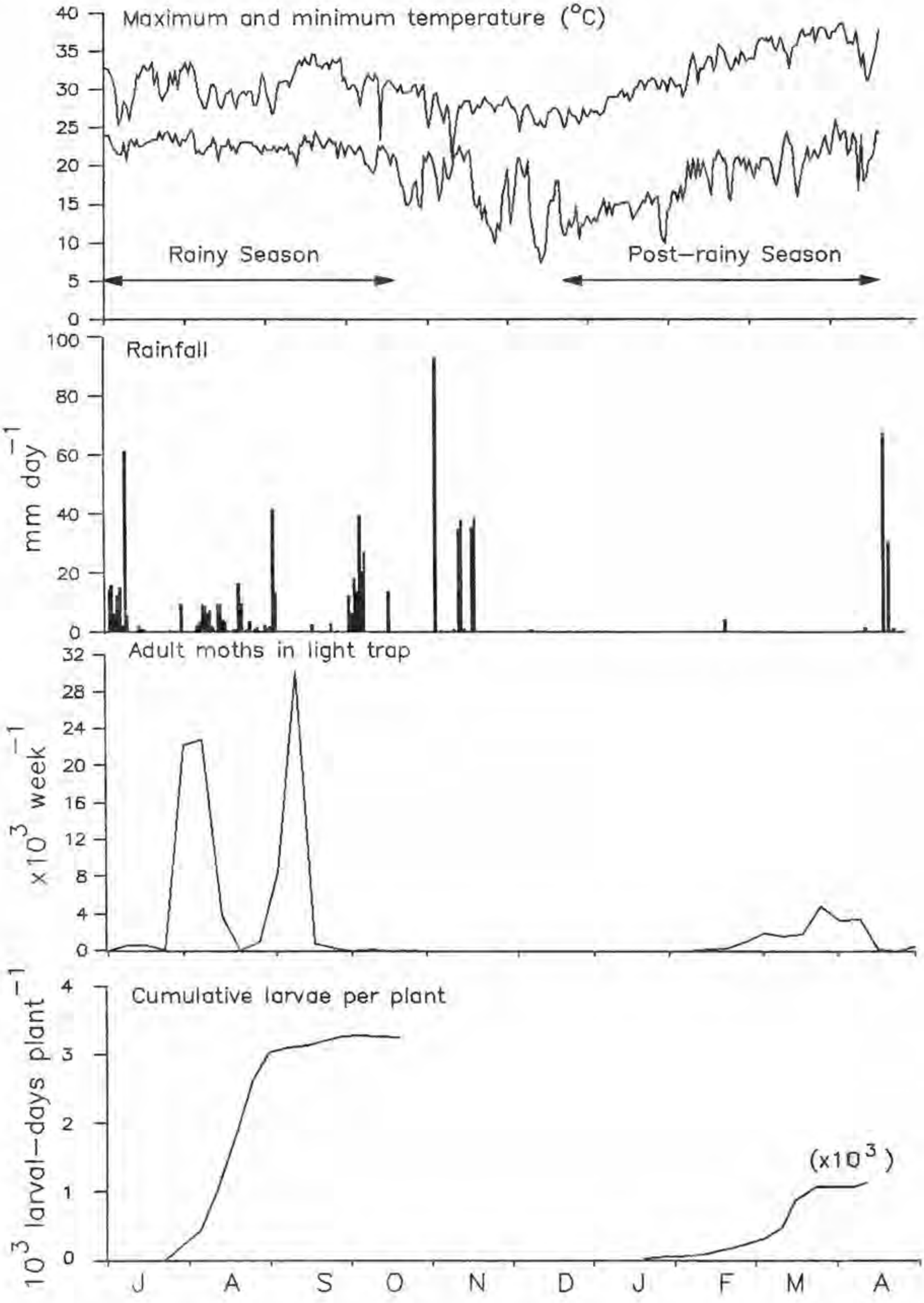
Maximum and minimum temperature (°C)
40
35
30
25
20
15
10
5
0
Rainy Season
Post–rainy Season
Rainfall
mm day^{-1}
100
80
60
40
20
0
Adult moths in light trap
x10^3 week^{-1}
32
28
24
20
16
12
8
4
0
Cumulative larvae per plant
10^3 larval–days plant^{-1}
4
3
2
1
0
(x10^3)
J
A
S
O
N
D
J
F
M
A

Figure 3.

Figure 4. Daily maximum and minimum temperature, rainfall, weekly light trap catches and cumulative Aproaerema modicella larval population during the 1988 rainy and 1988-89 post-rainy seasons.

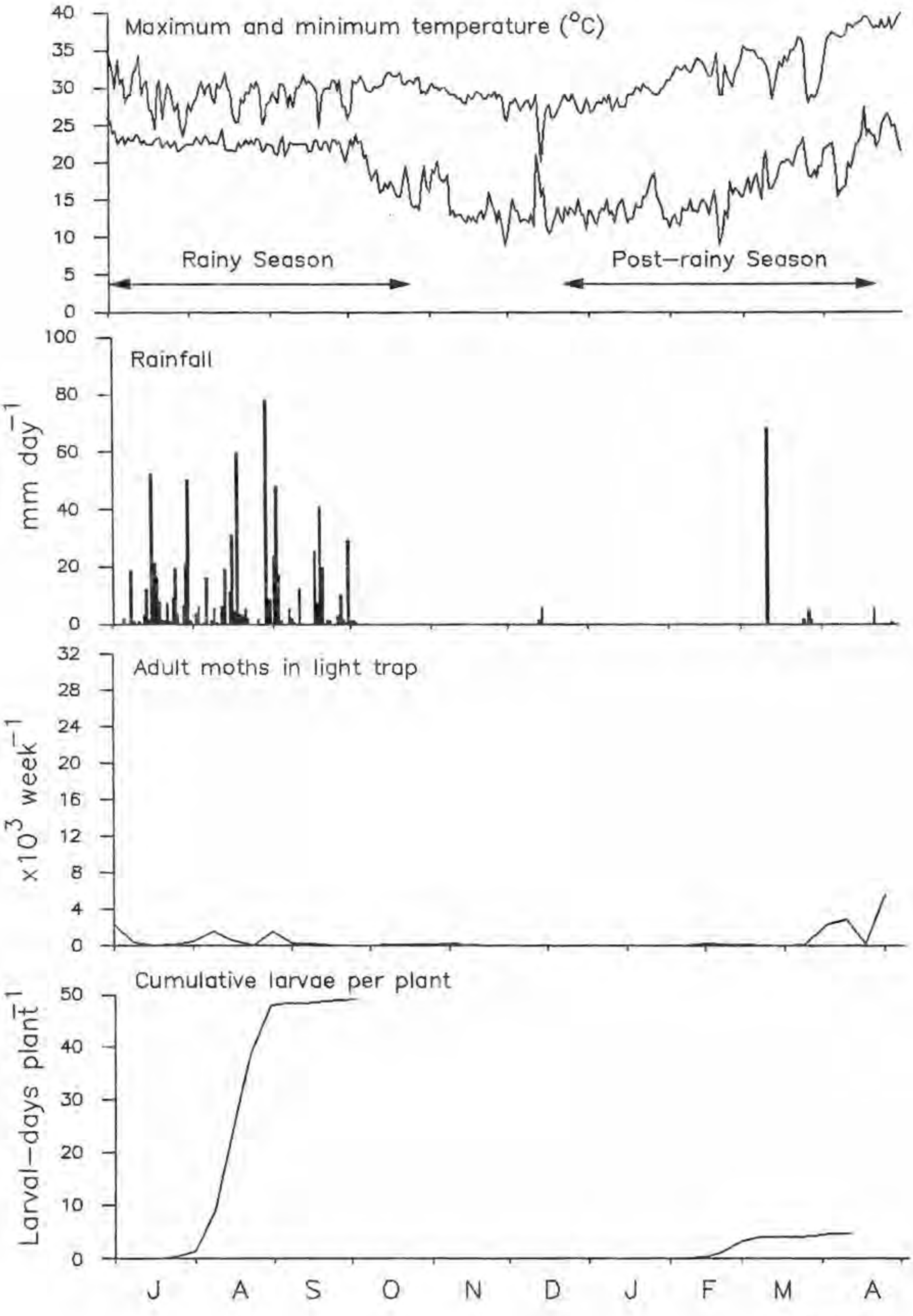
40
35
30
25
20
15
10
5
0
Maximum and minimum temperature (°C)
Rainy Season
Post–rainy Season
100
80
60
40
20
0
Rainfall
mm day^{-1}
32
28
24
20
16
12
8
4
0
Adult moths in light trap
x10^3 week^{-1}
50
40
30
20
10
0
Cumulative larvae per plant
Larval–days plant^{-1}
J
A
S
O
N
D
J
F
M
A

Figure 4.

Chapter 4.

Changes in the growth, development and yield of two groundnut (*Arachis* *hypogaea* L.) cultivars due to climate and insect attack in peninsular India.

Introduction
Materials and Methods
Results
Discussion
Conclusion
Literature Cited
Appendix

INTRODUCTION

Crop growth rates for groundnut (Arachis hypogaea L.) are thought to depend primarily on the amount and intensity of intercepted solar radiation, and the photosynthetic efficiency of leaves (Williams and Nageswara Rao, 1983). Other important factors affecting groundnut yields are temperature, water stress, photoperiod, genetic differences between varieties and biotic constraints, principally insects and diseases (Williams and Nageswara Rao, 1983).

Bolhuis and De Groot (1959) documented phenological changes in groundnut in response to temperature. Lower temperatures delayed germination and flowering, but the numbers of flowers and mature fruit had a more complicated relationship with temperature. Flower and mature fruit numbers were greatest at 27° C, but declined at lower and higher temperatures. More recent studies have shown that temperature influences all aspects of vegetative and reproductive growth in groundnut (e.g. Cox, 1979; Cox and Martin, 1974; Leong and Ong, 1983; Ong, 1984).

Lack of water is potentially the most important limiting factor for groundnut production (Ketring, 1986) but the timing of water stress determines its impact (Williams and Nageswara Rao, 1983). Early season water stress may suspend development, but lack of water during the reproductive phase may either hasten or delay fruit maturation (Williams and Nageswara Rao, 1983). Reports cited in Ashley (1984) indicate that groundnut is more susceptible to drought at flowering than at any other time. Drought stress is thought to promote extensive rooting, allowing the plant to explore a larger soil volume and increasing the root:shoot ratio (Ketring, 1986).

Photoperiod can affect both vegetative and reproductive phenology. Short-day conditions are thought to increase peg and pod numbers, and reduce the size and dry weight of plants (Ashley, 1984). Higher fruit numbers may result from higher fertilization rate, since no increase in flower production was observed (Wynne *et al*., 1973). Depending on the cultivar, pod yield may either increase or decrease in response to short-day conditions (Witzenberger *et al*., 1985).

Groundnut genotype also contributes to crop phenology. The two subspecies of *A*. *hypogaea*, subsp. *hypogaea* and subsp. *fastigiata*, have very different growth patterns. Subspecies *hypogaea* has a spreading or runner type growth form and takes 120-150 days to mature, but subspecies *fastigiata* has an upright, bunch growth form and matures in 90 to 100 days (Feakin, 1973).

Biotic constraints (insects, pathogens and weeds) may alter groundnut growth, development and yield (Gibbons, 1986). Rust (*Puccinia arachidis*) and leaf spot fungi (*Cercospora arachidicola* and *Cercosporidium personatum*) can cause rapid defoliation and yield reductions of more than 50% (Bell, 1986). Leaf diseases reduce photosynthetically active leaf area and reduce the photosynthetic rate of individual leaves (Boote *et al*., 1980), altering leaf production rates and the initiation and development of reproductive tissue (Bell, 1986).

Insects such as the defoliator, *Spodoptera* spp. (Lepidoptera: Noctuidae), and the leaf miner, *Aproaerema modicella* (Lepidoptera: Gelechiidae), affect groundnut phenology primarily by eating leaves and reducing photosynthetic area. Artificial defoliation studies have shown that yield losses are greatest when defoliation of 50% or more occurs during pod formation (Enyi, 1975; Panchabhavi et al., 1986). Groundnut appears to compensate for lower levels of defoliation, or when defoliation occurs early in the season (Turner, 1982). Stem weight has been shown to be particularly sensitive to defoliation (Enyi, 1975; Williams, 1979; Wilkerson et al., 1984) and lower stem weight has been associated with lower pod yields.

Application of additional nitrogen does not increase groundnut yield but may promote vegetative growth (Ashley, 1984). Nitrogen-fixing bacteria such as Rhizobium provide sufficient nitrogen for maximum yield (Norman, Pearson and Searle, 1984).

The experiments described below compare growth, development and yield of two groundnut cultivars during the rainy and postrainy seasons under different levels of insect herbivore pressure. Cultivars of the Virginia bunch variety (subsp. hypogaea), Kadiri 3, which has a semi-spreading habit, and the Valencia variety (subsp. fastigiata), NCAc 17090, with an upright growth form, were used in these studies. In the past, the effect of herbivores on growth, development and yield of groundnut has been studied using artificial defoliation, but this treatment may not reflect the true impact of herbivores.

MATERIALS AND METHODS

All field experiments were conducted at the International

Crops Research Institute for the Semi-Arid Tropics (ICRISAT), located near Hyderabad (17° N), Andhra Pradesh, India.

Experimental design

Two experiments were conducted, one in the rainy season (June-October) and one in the post-rainy season (December-April). Both utilized a randomized block design with four replicates per treatment. Each trial included four treatments: Kadiri 3 with insecticide, Kadiri 3 without insecticide, NCAc 17090 with insecticide, and NCAc 17090 without insecticide. Treatments without insecticide will be referred to as checks and NCAc 17090 will be abbreviated as NCAc throughout the text. The insecticide, monocrotophos (40% EC), was applied at a rate 181 mg a.i./ha in 331 l/ha water when early instar A. modicella larvae were visible on the plants. Three applications were made in the rainy season and two in the post-rainy season.

The rainy season crop was planted the first week of July 1987 and harvested in mid-October. The post-rainy season crop was planted in mid-December 1987 and harvested in mid-April 1988. Both crops were planted in four rows on raised, 1.5 m wide beds, in medium deep alfisol soil which was planted to pearl millet the previous season. Seeds were planted 15 cm apart at a density of ca. 210,000 ha^{-1}. Plots were 396 m^2 (11 beds, 24 m long). Beds were separated by an irrigation furrow and irrigation was supplied ad lib. Gypsum (67.2% $CaSO_4$) was applied at a rate of 500 kg ha^{-1} about 60 days after sowing (DAS) in both seasons to ensure an adequate calcium supply during pod enlargement. Fungicide was applied in the rainy season to protect against fungal leaf spot diseases.

Sampling and data collection

The initial sample size of fifteen plants per plot was reduced to 10 plants per plot seven weeks after sowing. During the first three weeks, samples were taken twice weekly, but thereafter samples were taken weekly. The number of leaves, flowers, pegs, branches, main stem nodes, mature and immature pods were recorded on a per plant basis. Dry weights of plant subunits were recorded after 48 hours storage at 60° C. Leaf areas were measured using a LI-COR (model LI-3100) photoelectric leaf area meter. Leaf area index (LAI), defined as the total leaf area divided by the area occupied per plant, was calculated each week using the average leaf area per plant and the per unit area plant density. Because the plant density at harvest was used in calculating LAI, early season estimates of LAI may have been underestimated.

Plant densities after germination and before harvest were recorded. At harvest, the number and dry weight of mature and immature pods per plant and per unit area were recorded. Haulm or hay yields also were recorded per plant and per unit area. Shelling percentage (the proportion of pod yield which is kernel), was measured by recording the kernel weight from 1 kilogram of pods from each replicate.

Weather data were obtained from the ICRISAT meteorological station, and are illustrated in Figure 1 and 2.

Statistical analyses

Analysis of variance (ANOVA) (Gomez and Gomez, 1984) was used to compare plant growth and yield variables across seasons (rainy vs. post-rainy), across cultivars (Kadiri 3 vs. NCAc), and across insecticide treatments (sprayed vs. unsprayed). Among the variables compared were leaf and stem biomass, and leaf area index (LAI). Reproductive growth was similarly evaluated by comparing the numbers of flowers and pegs, as well as the number and mass of pods produced, and fruit growth rates. ANOVA was used to compare the following yield data at harvest: pod and haulm yield per plant and per unit area, shelling percentage, and the numbers of mature, immature and total pods per plant.

Two-way analysis of variance (ANOVA) was used to compare the effects of season, cultivar, and insecticide treatment on measures of vegetative and reproductive growth. Within season, 1-way ANOVA was used to compare cultivar/insecticide treatment effects on plant growth variables, yield variables and plant populations at germination and harvest. Analysis of covariance was used to compare the linear portion of growth curves (g or number plant^{-1} day^{-1}) (Zar, 1974). The analyses of covariance are summarized in the Appendix.

Multiple regression was used to estimate the effects of insecticide treatment, cultivar and season on yield. Dummy variables (Zar, 1974) were used for season, variety and treatment. The t-values of the regression coefficients were used to determine whether a variable or an interaction was included in the regression equation, and partial derivatives of yield with respect to each variable were used to estimate the average contribution of each factor and interaction to yield.

RESULTS

Plant density

Rainy season - Plant densities in Kadiri 3 plots were significantly higher ($p<0.0005$) at germination and harvest compared to NCAc plots (Table 1). Lower germination rates in NCAc plots resulted in plant stands of about 15 plants m^{-2} compared to more than 20 plants m^{-2} in Kadiri 3 plots. Differences in initial and harvest plant population were not significant across insecticide treatments for either variety. Mean plant populations in the four cultivar/insecticide treatments were reduced 23.5% to 43.3% during the rainy season. NCAc plants protected with insecticide suffered the largest reduction in plant population.

Post-rainy season - No significant differences were observed in initial plant populations across cultivar/insecticide treatments in the post-rainy season (Table 2). In contrast to the rainy season results, the initial plant population was marginally higher in NCAc treatments, 17.9 to 18.27 plants meter^{-2}, than in Kadiri 3 plots. The seasonal decline in plant populations were smaller in the post-rainy season than in the rainy season for all treatments. Within the post-rainy season, the decline in plant density in Kadiri 3 treatments was significantly greater than in NCAc treatments ($0.01>p>0.005$).

Vegetative growth - leaves

Rainy season - Leaf production was significantly different across cultivar/insecticide treatments within the rainy season ($F_{3,9}$=24.7; p<0.001). Kadiri 3 plants produced significantly less leaf tissue than did NCAc plants (Fig. 3A). The rate of biomass accumulation was also lower in Kadiri 3 plants (see Appendix). Across insecticide treatments, sprayed plants produced more leaf tissue than check plants in both cultivars, but Kadiri 3 plants lost a larger proportion of leaf biomass (40%) when not sprayed than did NCAc plants (15%). The rate of leaf biomass production was also higher for insecticide protected plants (see Appendix).

In NCAc plots leaf biomass was added rapidly until the end of the season, whereas Kadiri 3 leaf growth rate slowed midway through the season (Fig. 3A). Unsprayed Kadiri 3 plots had the lowest rate of leaf production (see Appendix) but produced leaves longer than sprayed Kadiri 3 plants.

LAI increased at similar rates across all treatments within the rainy season (see Appendix). Maximum LAI in all treatments was below 2.2 (Fig. 4A), and differences across cultivar/insecticide were not significant ($F_{3,9}$=0.3). Across cultivar/insecticide treatments, leaf area per gram leaf tissue varied from 151.2 cm^2 to 172.1 cm^2, but the differences were not significant.

Post-rainy season - Cultivar and insecticide treatment differences in leaf growth observed in the rainy season disappeared in the post-rainy season (Fig. 3B). Marginally higher leaf growth rates were observed in Kadiri 3 plots compared to NCAc plots (see Appendix). Leaf biomass was statistically equivalent across cultivars because of higher production in Kadiri 3 and lower production in NCAc compared to the rainy season. No significant differences in leaf production rates were observed across insecticide treatments in either variety during the post-rainy season (see Appendix). Though rates were similar across cultivars, NCAc treatments produced leaf mass at a high rate until the end of the season, but Kadiri 3 leaf production rate began to slow approximately 30 days before the end of the season (Figs. 3B). Across seasons leaf production was statistically equivalent within cultivar/insecticide treatments (2-way ANOVA; $F_{1,9}=1.08$; $p>0.25$) .

The rates of increase in LAI were significantly different across cultivars and insecticide treatments within the post-rainy season (see Appendix). Kadiri 3 reached maximum LAI several weeks before the season ended, while LAI in NCAc continued to increase up to the end of the season. Within season, maximum LAI was significantly higher ($F_{3,9}=20.5$; $p<0.001$) in NCAc than in Kadiri 3 (Fig. 4B) but differences across insecticide treatments were not important. Differences in maximum LAI were significant between seasons (2-way ANOVA; $F_{3,9}=27.41$; $p<0.001$). Across cultivar/insecticide treatments, leaf area per gram leaf tissue varied from 158.8 cm^2 to 175.5 cm^2 and differences were not significant. These values were also very close to the leaf area per gram leaf tissue values in the rainy season.

Vegetative growth - stems

Rainy season - Stem (plus petiole) production was significantly higher in NCAc than in Kadiri 3 (Fig. 3C), and sprayed treatments produced more stem tissue than unsprayed treatments ($F_{3,9}=42.9$; $p<0.001$). Stem biomass was 30 to 60% higher in NCAc treatments than in Kadiri 3 treatments. When not protected with insecticides, stem biomass was only 70% as high in Kadiri 3 and 80% as high in NCAc relative to the sprayed treatments.

Stem production rates were significantly lower in Kadiri 3 than in NCAc, and unsprayed plants produced significantly less stem than sprayed plants (see Appendix). In addition, the period of rapid stem growth was longer in unsprayed treatments compared to sprayed treatments.

Post-rainy season - Within the post-rainy season no significant differences in the rate of stem production were observed across cultivar/insecticide treatments (see Appendix). Kadiri 3 stem production rates slowed before the end of the season, but NCAc continued to add stem at a high rate (Figs. 3D). Across cultivars, NCAc produced significantly more stem biomass than Kadiri 3 ($F_{3,9}=18.1$; $p<0.001$). Within cultivar, no significant differences in stem biomass were found between insecticide treatments. Stem growth rates and maximum production levels were higher across all treatments in the post-rainy season compared to the rainy season (Fig. 3C & D).

Reproductive growth - flower and peg production

Rainy season - Within season, more flowers were produced in insecticide treatments than in checks of the same variety ($F_{3,9}$=5.9; $p<0.05$). Cumulative flower production was 30-40% lower in Kadiri 3 and 15-20% lower in NCAc, in check plots compared to insecticide plots (Fig. 5A). However, flower production rates were not significantly different across the four rainy season treatments (see Appendix).

The number of flowers producing pegs was low in all rainy season treatments (Figs. 5C). NCAc produced pegs earlier than Kadiri 3, but produced only 70% as many. Unsprayed NCAc plants produced the same number of pegs as unsprayed Kadiri 3 plants, but on insecticide protected NCAc plants, there were fewer pegs than on sprayed Kadiri 3 plants. Kadiri 3 had significantly higher ($p<0.025$) rates of peg production than NCAc and sprayed plants had higher peg production rates than check plants (see Appendix).

Post-rainy season - Compared to the rainy season, post-rainy season flower production was higher in Kadiri 3 and lower in NCAc (Fig. 5B). NCAc produced 30% fewer flowers than Kadiri 3 in the post-rainy season, but produced them up to the end of the season. Across cultivar, NCAc produced flowers earlier and longer but at a lower rate ($p<0.10$) than did Kadiri 3 (see Appendix). Differences across insecticide treatments were not significant for either cultivar.

Peg production in the post-rainy season increased 50% in Kadiri 3 but only slightly in NCAc compared to the rainy season (see Appendix). Across season differences in peg production were highly significant (2-way ANOVA; $F_{1,9}$=150.96; $p<0.001$). Kadiri 3 produced pegs for a shorter period of time but at a significantly higher rate than NCAc (Fig. 5D). No differences in peg production were observed across insecticide treatments within cultivar.

Reproductive growth - pod production and fruit growth rate

Rainy season - In contrast to leaf and stem production, pod biomass production (g plant^{-1}) was similar across cultivars and treatments in the rainy season (Figs. 6A). Differences in pod mass across cultivars and insecticide treatments were not significant ($F_{3,9}$=2.2; 0.25>p>0.1).

Across cultivars, NCAc produced pods earlier than Kadiri 3 (Fig. 6C), though Kadiri 3 produced significantly more pods ($F_{3,9}$=44.3; p<0.001). Within cultivar, insecticide protected plants produced more pods than check plants, though differences across cultivar were greater than differences across insecticide treatments. Across cultivars, pod production rates (# plant^{-1} day^{-1}) were significantly different (p<0.025) but biomass production rates were similar. The much larger pod size of NCAc resulted in similar pod biomass despite the fact that fewer pods were produced.

No significant differences were observed in fruit growth rate (g pod^{-1} day^{-1}) across cultivar/insecticide treatments (Figs. 7A-D) during the rainy season. There was also remarkable similarity in the timing of rapid pod growth across treatments.

Post-rainy season - Pod mass was 2-fold greater in the post-rainy season compared to the rainy season (2-way ANOVA; $F_{1,9}$ = 278.90; p<0.001). Pod growth rate in the post-rainy season increased rapidly up to the end of the season, whereas in the rainy season, pod growth rate began to decline several weeks before harvest. Within the post-rainy season, differences across cultivar/insecticide treatments were not significant. The rate of pod growth and the period of maximum growth were also similar across cultivar/insecticide treatments (Fig. 6A & B).

Across season, the number of pods per plant increased in Kadiri 3 and remained the same for NCAc in the post-rainy season. The number of pods per plant was significantly different across cultivar/insecticide treatments ($F_{3,9}$=15.3; $p<0.001$), but cultivar differences were larger than differences across insecticide treatments (Fig. 6D). Across cultivar, NCAc produced pods longer but at a lower rate than Kadiri 3. Differences in the rate of production were significant across cultivars ($p<0.05$) but not across insecticide treatments within cultivar (see Appendix).

Growth rates of individual fruits were much higher in the post-rainy season compared to the rainy season (2-way ANOVA; $F_{1,9}$ =525.46; $p<0.001$). Within the post-rainy season, differences in fruit growth rate across cultivar/insecticide treatments were not significant (see Appendix). In contrast to the rainy season, fruit growth rates continued to increase up to the end of the season (Figs 8A-D).

Components of yield

Rainy season - Differences in per plant pod and haulm yields across cultivar/insecticide treatments were highly significant ($p<0.0005$) in the rainy season (Table 3). Across cultivars, NCAc pod yields were much lower than Kadiri 3. On a per plant basis haulm yields were significantly higher in NCAc, but on an area basis the two cultivars had equivalent haulm yields (Table 3). Within cultivar and across insecticide treatment, yields of both pods and haulms were not as large in unsprayed treatments. Kadiri 3 pod yields were reduced 35% and haulm yields 25%, and NCAc had 40% lower pod yield and 20% lower haulm yield in check plots.

Differences in shelling percentage (the fraction of kernel in 1 kg of pods) were due to cultivar (Table 3). Kadiri 3 treatments were significantly higher than NCAc treatments ($p<0.0025$). Within cultivar, the differences between insecticide and check treatments were not significant (Table 3). Kernel weight in NCAc treatments was 48-55% of the total pod mass, but Kadiri 3 pod mass was 65-70% kernel (Table 3).

Within cultivar, the total number of pods produced (Table 4) was higher in sprayed treatments than in unsprayed treatments for both cultivars ($p<0.0005$). Unsprayed treatments had fewer total pods and mature pods per plant, relative to sprayed treatments, but the percentage of mature pods was nearly the same across insecticide treatments and within cultivar (Fig. 9A).

Post-rainy season - Pod and haulm yields for both varieties were much higher in the post-rainy season compared to the rainy season (Table 5). Within cultivar, Kadiri 3 pod yield increased from 7.4 to 25.2 g plant^{-1} in the insecticide plots and from 4.8 to 22.2 g plant^{-1} in the check plots.

NCAc pod yields were 4 to 5 times greater than in the rainy season and haulm yields were 20% higher on a per plant basis (Table 5). NCAc haulm yield per unit area doubled over rainy season levels.

Within the post-rainy season, yields differed across cultivar. Pod yields were higher in Kadiri 3 on a per plant basis but statistically equivalent on an area basis between the two varieties. Haulm yields were higher in NCAc than in Kadiri 3 on both a per plant and per unit area. Within cultivar, only minor differences existed between sprayed and unsprayed treatments.

Shelling percentage increased in the post-rainy season over rainy season levels for all cultivars and treatments (Table 5). Within season, Kadiri 3 had significantly higher fractions of pod mass in kernel than NCAc. Within cultivar, only marginal differences between sprayed and unsprayed plots were observed.

Total pods per plant increased 2-fold over rainy season levels for all cultivars and treatments. Within the post-rainy season, differences in total, mature and immature pod number were significant only between cultivars (Table 6). A larger fraction of pods reached maturity in the post-rainy season, and the increase was most striking in NCAc which increased to 80% from about 50% in the rainy season (Fig. 9B). Within cultivar, differences between insecticide treatments were not significant.

DISCUSSION

Large and significant differences were observed in the growth, development and yield of the two groundnut cultivars used in these trials. Phenological differences between cultivars are genetically based and are not discussed here. Environmental factors further influenced growth and yield as did the use of insecticides (sprayed and unsprayed treatments) to protect against the groundnut leaf miner, *A. modicella*.

Seasonal effects

The effect of season can be examined by comparing the sprayed treatments across season. Low temperatures have been shown to retard groundnut germination (Bolhuis and De Groot, 1959; Leong and Ong, 1983) and probably account for the lower germination of Kadiri 3 in the post-rainy season. It is unclear why NCAc would show improved germination in the cooler, post-rainy season though differences in seed quality may have been responsible.

Vegetative growth was generally higher in the post-rainy season than in the rainy season for both varieties, except for the observed moderate decline in NCAc leaf biomass in the post-rainy season. Kadiri 3 had higher stem and leaf biomass as well as higher growth rates for those tissues in the post-rainy season. NCAc had lower rates of growth for both tissues in the post-rainy season, though final stem mass was higher. Leaf area index was also higher in the post-rainy season for both varieties. Cox (1979) and Ong (1984) report lower leaf and stem growth at temperatures above 30° C, and high temperatures typical in the rainy season may be responsible for less vegetative growth compared to the post-rainy season. Physiological time units (i.e. degree-days) accumulate more slowly in the early part of the post-rainy season because of lower temperatures compared to the same period in the rainy season.

The proportion of flowers which formed pegs and pods was higher for both varieties in the post-rainy season. Short-day conditions, typical of the post-rainy season, are known to produce higher peg and pod numbers (Wynne et al., 1973; Witzenberger, et al., 1985). Also contributing to the lower rainy season production of pegs and pods was the smaller amount of solar radiation reaching plants because of heavy monsoon clouds. Reports (Gautreau, 1973; Cox, 1978; Ketring, 1979) cited in Ashley (1984) have shown that lower irradiance levels result in fewer flowers, pegs and pods.

Pod mass was significantly higher in the post-rainy season for both varieties. Enyi (1975) and Williams (1979) have noted the association between higher stem mass and higher pod mass. It has been suggested that assimilates stored in stems are utilized by fruits when demand is greater than supply (Williams, 1979). The higher pod mass is due to the several-fold higher fruit growth rates observed in the post-rainy season compared to the rainy season. Temperatures above 30^{o}C have been shown to markedly reduce dry matter accumulation in pods (Cox, 1979; Ong, 1984).

In the rainy season, solar radiation is frequently reduced by extensive cloud cover, though temperatures remain high, with minimum temperatures frequently exceeding 22^{o}C. The data suggest that periods of reduced solar radiation in the middle of the season, coupled with high temperatures, resulted in less vegetative and reproductive growth relative to the post-rainy season. Less vegetative growth reduced the supply of assimilates which lowered the production rate of flowers, pegs and pods. Less solar radiation and high temperatures, in addition to the long-day conditions, reduced peg initiation and fruit growth rates in the rainy season.

Conversely, low early season temperatures, higher solar radiation and short-days led to significantly improved yields of both varieties in the post-rainy season. Pod yields increased 3-10 fold on a per plant basis and haulm yields were 20-100% higher. Shelling percentage increased from 64.4 to 72.9% for Kadiri 3 and from 55.6 to 68.9% for NCAc.

Herbivore effects

The groundnut leaf miner, _A_. _modicella_, was present in high numbers during the first half of the rainy season, and caused extensive defoliation in check plots. The effect of this herbivore was determined by comparing insecticide plots with check plots. In the post-rainy season, low populations of the leaf miner were present but no significant differences were observed between insecticide and check plots.

Damage from _A_. _modicella_ was extensive but did not increase plant mortality in check plots of either cultivar. Leaf consumption by leaf miner larvae had a greater impact on growth and development of Kadiri 3 than on NCAc. Leaf biomass was reduced by 33% with Kadiri 3 but only 10% with NCAc when compared with the check plots. The rate of leaf production was lower in check plots relative to insecticide plots for both cultivars. Leaf area index was not as strongly affected by GLM defoliation. LAI was lower in check plots but the difference was not significant.

Compared to sprayed plants, stem biomass was 30% and 20% lower in check plots of Kadiri 3 and NCAc respectively. The rate of stem biomass production was also lower in check plots. These results confirm findings from artificial defoliation studies. Enyi (1975) observed a reduction in stem mass of up to 40%, depending on the time of defoliation, when half of the leaflets were removed from the plants. Stem mass was 20-30% lower in another study when 50% of the leaves were removed artificially (Wilkerson _et al_., 1984).

Damage from leaf miner significantly reduced flower and peg production in check plots of both varieties relative to the insecticide plots. Unsprayed check plots had 15 and 30% fewer flowers (NCAc and Kadiri 3 respectively) and 20 and 40% lower peg production in NCAc and Kadiri 3 plots. Santos and Sutton (1983) reported lower flower and peg production when plants were defoliated by hand at 12 and 14 weeks, though the magnitude of the reduction was not reported.

Pod mass and number were lower in plots defoliated by _A. modicella_ compared to sprayed plots. The 33% reduction in leaf biomass in Kadiri 3 lead to 30% fewer pods and 30% less pod mass. The loss of 10% of leaf biomass in NCAc resulted in 25% fewer pods and a reduction in pod mass of 20%. Insecticide plots had more fruit and fruit mass per plant, but the growth rate of individual fruits was lower. Fewer pods were initiated in check plots due to heavy defoliation, but those pods grew faster.

Per plant pod yields were 35% lower in Kadiri 3 and 45% lower in NCAc plots defoliated by A. modicella compared to sprayed plots. Per plant haulm yields were 25% lower for Kadiri 3 and 20% lower for NCAc. Shelling percentages were statistically equivalent across cultivar/insecticide treatments, though the unsprayed (defoliated) Kadiri 3 treatment had a slightly higher (nonsignificant) shelling percentage compared to the sprayed Kadiri 3 treatment. Enyi(1975) found higher shelling percentage in defoliated plants.

The naturally occurring infestation of A. modicella and the extensive defoliation it caused suggest several important results. Defoliation and lower leaf mass resulted in lower stem mass. A reduction in stem biomass was clearly associated with lower pod number and mass. However, if fewer pods are initiated, the plant may compensate with a higher fruit growth rate. These findings support results from artificial defoliation studies (Enyi, 1975; Santos and Sutton, 1983; Wilkerson et al., 1984). The effects of heavy defoliation are not limited to pod yield reductions. The phenology of both vegetative and reproductive growth may be affected.

CONCLUSION

The per plant data presented here can be summarized using multiple regression analysis to compare the effect of season, cultivar and insect control on pod yield. Equation [1] summarizes the relationships:

$$y = 7.394 + 17.573x_3 - 2.389x_2 - 2.565x_1 - 3.22x_2x_3 + 2.958x_1x_2x_3 \qquad [1]$$

$$R^2 = 0.99; n = 32$$

where y is yield in g $plant^{-1}$ and x_1, x_2 and x_3 are dummy variables representing insect control [0 = sprayed, 1 = unsprayed], cultivar [0 = Kadiri, 1 = NCAc] and season [0 = rainy season, 1 = post-rainy season] respectively. Only variables and interaction terms which were significant ($t > 2.037$, $n = 32$; Student's t-test) were included. The regression was highly significant (ANOVA; $F_{5,26}=533.07$; $p < 0.005$).

The effect of each variable may be obtained by computing the partial derivatives of yield with respect to each variable and all interactions. The results suggest that under the conditions of these trials, yield was influenced more by season than by cultivar or insect attack. Across cultivars and insect control, yield was 17.21 g $plant^{-1}$ greater in the post-rainy season compared to the rainy season. The choice of cultivar and insect control had similar impacts on yield formation, but on average, yield was 2.4 g $plant^{-1}$ lower with NCAc and 2.6 g $plant^{-1}$ lower when insecticides were not used.

The results can be summarized as follows: 1) Environmental conditions during the post-rainy season led to superior vegetative growth, reproductive growth and yield for both varieties. These conditions included, lower early season temperatures, short-days, and higher incident solar radiation. 2) High populations of the groundnut leaf miner caused significant defoliation in unsprayed plots in the rainy season and the mass and number of vegetative and reproductive structures, and yield was lower than in sprayed plots. Pod yield was lower in defoliated plots of both cultivars compared to sprayed plots. Haulm yield in Kadiri 3 check plots was also much lower than in sprayed plots.

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Table 1. The effect of insecticide[1] and cultivar on groundnut plant population[2] meter^{-2} at 10 and 114 days after sowing (DAS) in the 1987 rainy season, ICRISAT, India.

Treatment	10 DAS[3]	114 DAS	% decrease
Kadiri 3 sprayed	21.68a	16.57a	23.6
Kadiri 3 unsprayed	21.28a	16.08a	24.4
NC Ac 17090 sprayed	15.26b	8.65b	43.3
NC Ac 17090 unsprayed	14.32b	10.12b	29.4
SE =	0.886	0.935	
CV%	1.39	2.3 0	
$F_{3,9}$ =	59.73	47.37	
p	<0.0005	<0.0005	

[1] Monocrotophos (40%) applied 3 times against *Aproaerema modicella* larvae

[2] Mean of four replicates.

[3] Means in column followed by the same letter are not significantly different (p=0.05) Duncan's multiple range test.

Table 2. The effect of insecticide[1] and cultivar on groundnut plant populations[2] meter^{-2} at 37 and 135 days after sowing (DAS) in the 1987-88 post-rainy season, ICRISAT, India.

Treatment	37 DAS[3]	135 DAS	% decrease
Kadiri 3 sprayed	16.36a	12.95a	20.4
Kadiri 3 unsprayed	16.37a	13.20a	19.4
NC Ac 17090 sprayed	18.27b	15.50b	15.2
NC Ac 17090 unsprayed	17.89b	15.17b	15.2
SE =	0.378	0.371	
CV%	2.10	1.74	
$F_{3,9}$ =	1.87	7.13	
	$0.25>p>0.1$	$0.01>p>0.005$	

[1] Monocrotophos (40%) applied 2 times against Aproaerema modicella larvae

[2] Mean of four replicates.

[3] Means in column followed by the same letter are not significantly different ($p=0.05$) Duncan's multiple range test.

Table 3. The effect of insecticide[1] and cultivar on groundnut pod and haulm yields, and shelling percentage[2] (g) in the 1987 rainy season, ICRISAT, India,

Treatment	Per plant Pod[3]	 Haulm	Per meter-2 Pod	 Haulm	Kernel mass[4]
Kadiri 3 sprayed	7.40a	13.24c	122.82a	219.49a	644.4a
Kadiri 3 unsprayed	4.82b	9.87d	77.92b	143.19b	687.5a
NC Ac 17090 sprayed	4.76b	23.83a	41.79c	205.81a	555.8b
NC Ac 17090 unsprayed	2.69c	19.14b	27.09c	192.29a	485.9b
SE =	0.454	0.448	9.883	9.177	24.643
CV%	12.3	14.0	15.8	13.3	9.0
$F_{3,9}$ =	40.70	28.69	64.62	6.90	11.4
p	<0.0005	<0.0005	<0.0005	<0.025	<0.0025

---

[1] Monocrotophos (40%) applied 3 times against Aproaerema modicella larvae

[2] Mean of four replicates.

[3] Means in column followed by the same letter are not significantly different (p=0.05) Duncan's multiple range test.

[4] Kernel mass from 1 kg groundnut pods.

Table 4. The effect of insecticide[1] and cultivar on groundnut pod number[2] per plant at harvest, 1987 rainy season, ICRISAT, India.

Treatment	Mature Pods[3]	Immature Pods	Total Pods	Percent Mature
Kadiri 3 sprayed	12.68a	7.71ab	20.39a	62.19
Kadiri 3 unsprayed	9.34b	4.91bc	14.25c	65.54
NC Ac 17090 sprayed	8.44b	8.33a	16.76b	50.36
NC Ac 17090 unsprayed	5.88c	6.26abc	12.14c	48.44
SE =	0.698	0.493	0.858	
CV%	17.34	24.9	9.62	
$F_{3,9}$ =	12.72	3.25	21.56	
p	<0.0025	<0.1	<0.0005	

---

[1] Monocrotophos (40%) applied 3 times against *Aproaerema modicella* larvae

[2] Mean of four replicates.

[3] Means in column followed by the same letter are not significantly different (p=0.05) Duncan's multiple range test.

Table 5. The effect of insecticide[1] and cultivar on groundnut pod and haulm yield, and shelling percentage[2] (g), 1987-88 post-rainy season, ICRISAT, India.

Treatment	Per plant Pod[3]	Per plant Haulm	Per meter-2 Pod	Per meter-2 Haulm	Kernel mass[4]
Kadiri 3 sprayed	25.20a	21.42ab	326.2a	280.2a	729.0a
Kadiri 3 unsprayed	22.17b	18.58a	291.7a	246.7a	738.2a
NC Ac 17090 sprayed	19.36c	27.87bc	299.9a	431.1b	689.4b
NC Ac 17090 unsprayed	19.75c	28.33c	294.2a	420.8b	682.1b
SE =	0.659	1.400	6.389	25.557	6.974
CV%	5.1	17.3	7.5	19.5	1.87
$F_{3,9}$ =	24.07	5.40	1.96	7.99	17.89
p	<0.0005	<0.025	NS	<0.01	<0.0005

---

[1] Monocrotophos (40%) applied 2 times against *Aproaerema modicella* larvae

[2] Mean of four replicates.

[3] Means in column followed by the same letter are not significantly different (p=0.05) Duncan's multiple range test.

[4] Kernel mass from 1 kg groundnut pods.

Table 6. The effect of insecticide[1] and cultivar on groundnut pod number[2] per plant at harvest, 1987-88 post-rainy season, ICRISAT, India.

Treatment	Mature Pods[3]	Immature Pods	Total Pods	Percent Mature
Kadiri 3 sprayed	35.61a	9.43a	45.04a	79.06
Kadiri 3 unsprayed	30.69a	7.04a	37.73a	81.34
NC Ac 17090 sprayed	19.05b	4.06b	23.11b	82.43
NC Ac 17090 unsprayed	18.76b	3.81b	22.58b	83.12
SE =	2.114	0.679	2.753	
CV%	18.2	27.1	18.9	
$F_{3,9}$ =	12.81	10.45	13.46	
p	<0.0025	<0.005	<0.0025	

---

[1] Monocrotophos (40%) applied 2 times against *Aproaerema modicella* larvae

[2] Mean of four replicates.

[3] Means in column followed by the same letter are not significantly different (p=0.05) Duncan's multiple range test.

Figure 1. Daily solar radiation, rainfall, maximum and minimum temperature during the 1987 rainy season, ICRISAT, India.

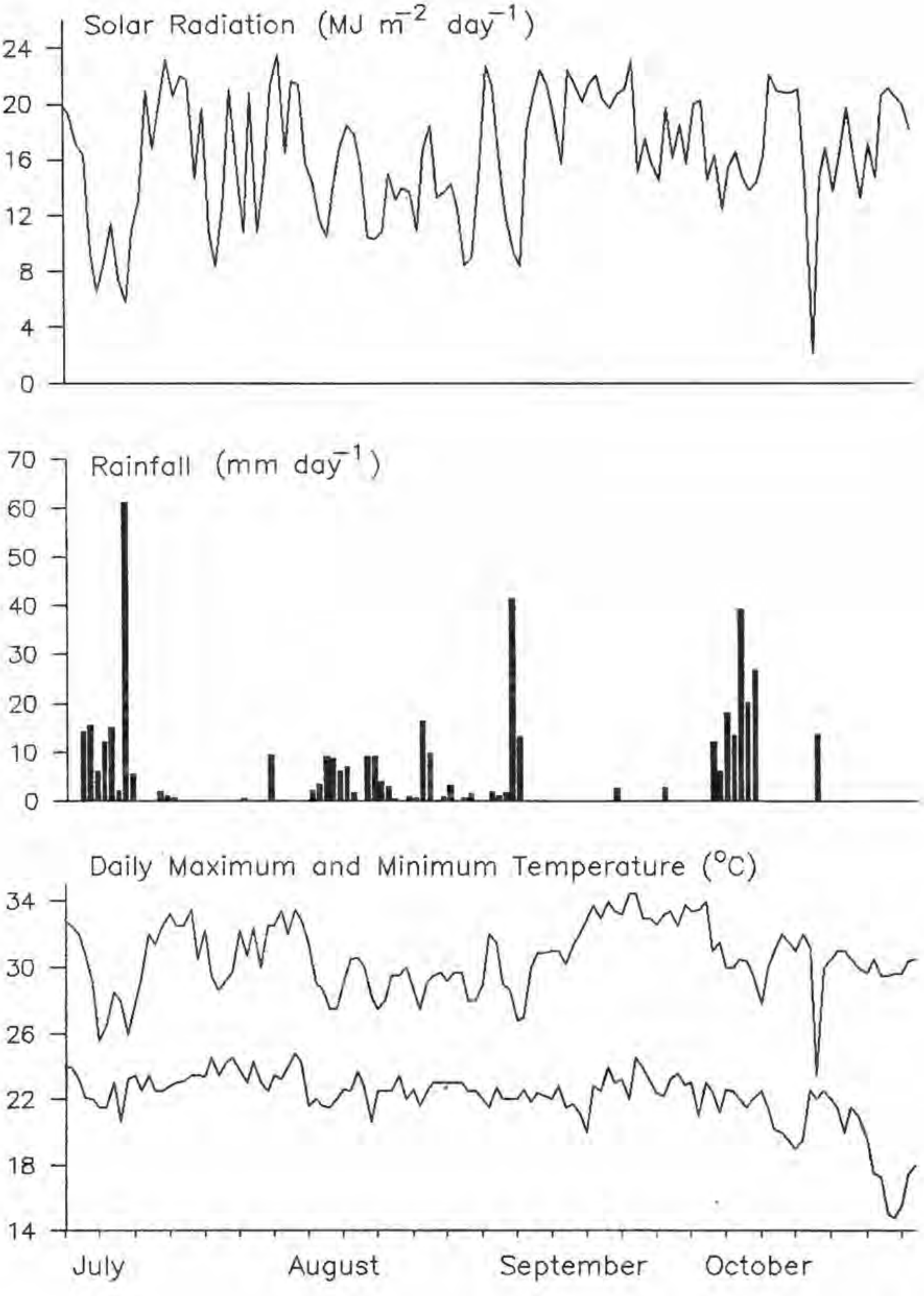

Solar Radiation (MJ m^{-2} day^{-1})
24
20
16
12
8
4
0
Rainfall (mm day^{-1})
70
60
50
40
30
20
10
0
Daily Maximum and Minimum Temperature (°C)
34
30
26
22
18
14
July
August
September
October

Figure 1.

Figure 2. Daily solar radiation, rainfall, minimum and maximum temperature during the 1987-88 post-rainy season, ICRISAT, India.

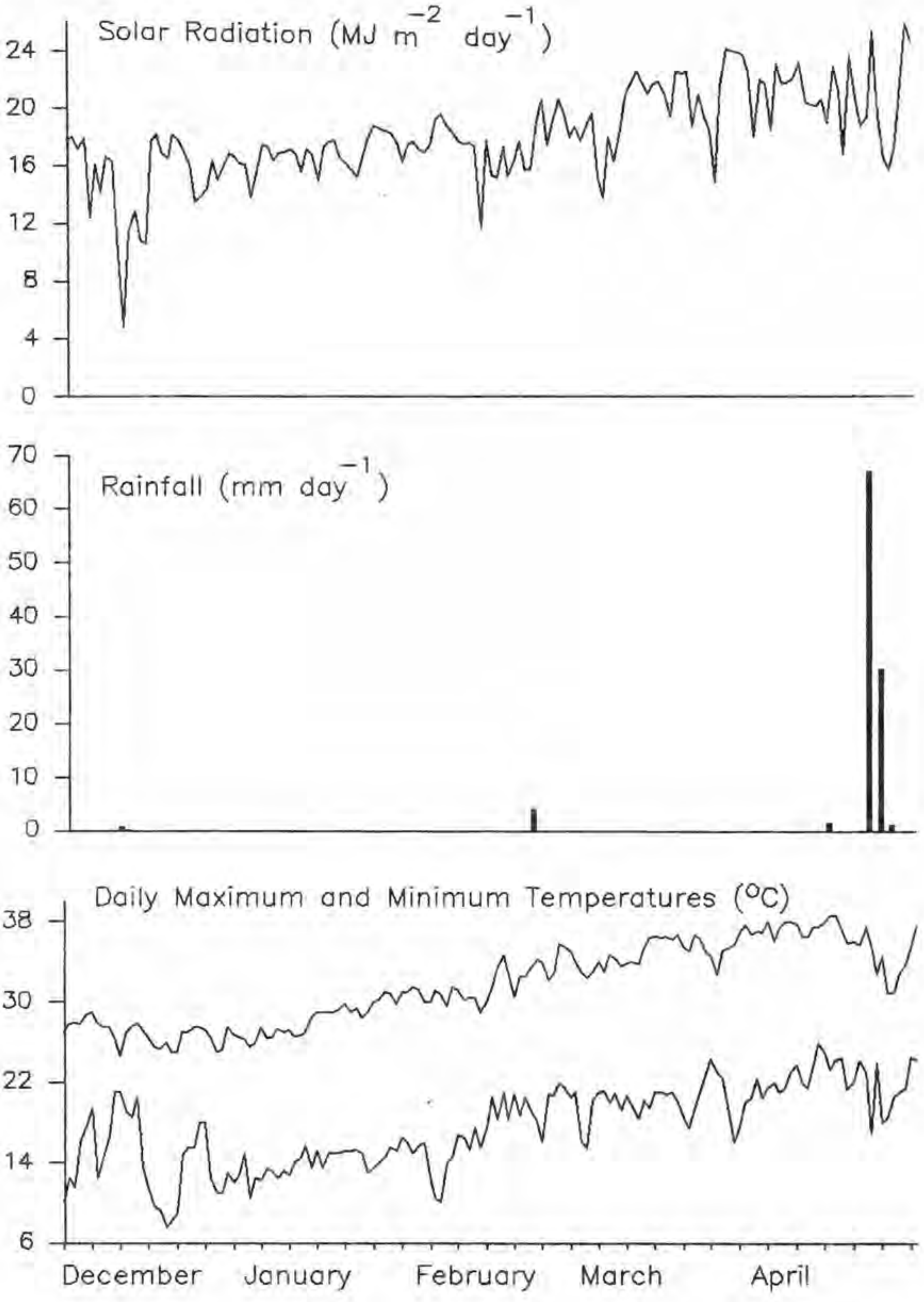
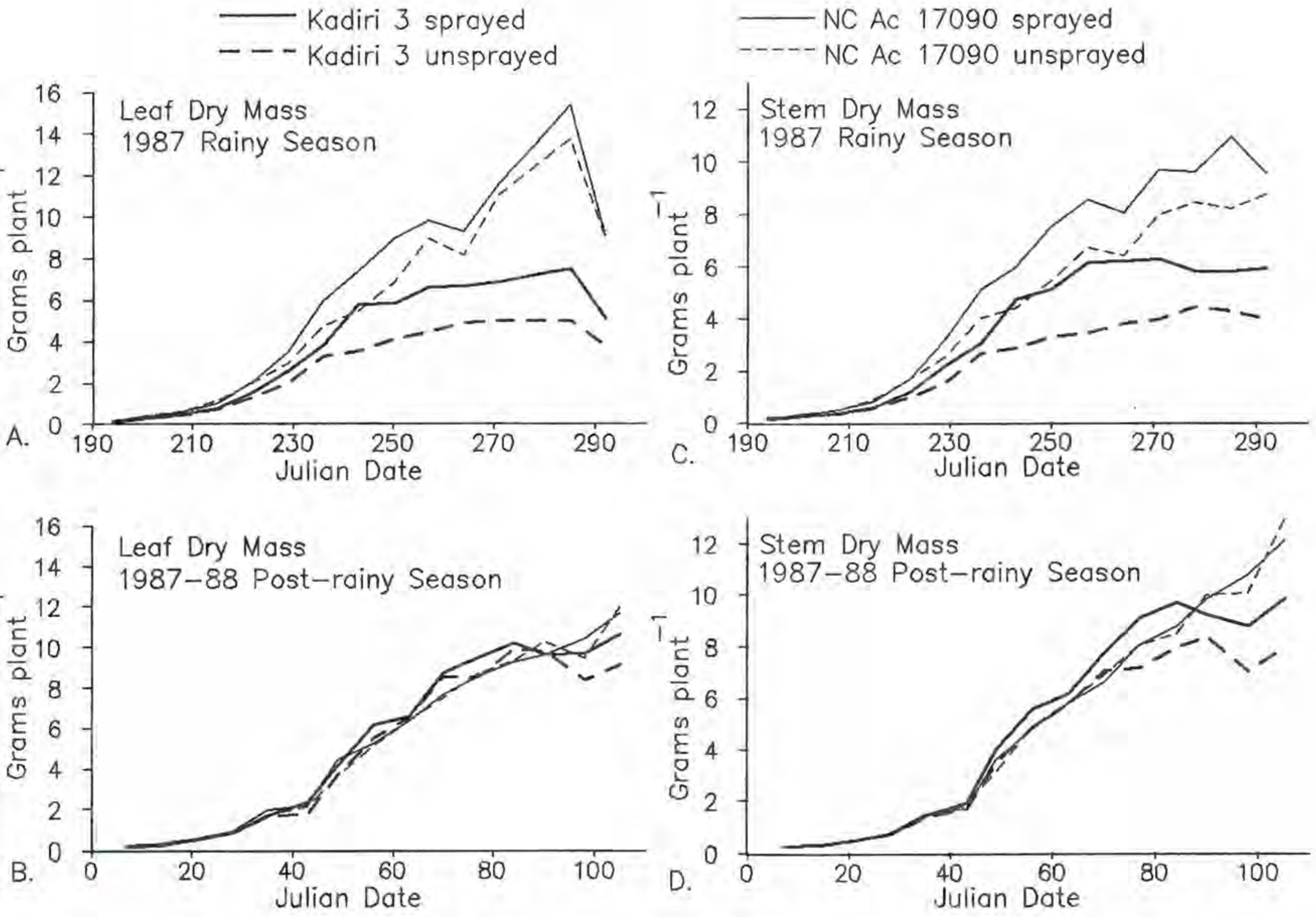

Solar Radiation (MJ m^{-2} day^{-1})
24
20
16
12
8
4
0
Rainfall (mm day^{-1})
70
60
50
40
30
20
10
0
Daily Maximum and Minimum Temperatures (°C)
38
30
22
14
6
December
January
February
March
April

Figure 2.

Figure 3. The effect of insecticide and cultivar on leaf and stem dry weight (g plant-1) during the 1987 rainy and 1987-88 post-rainy season, ICRISAT, India.



Kadiri 3 sprayed
Kadiri 3 unsprayed
NC Ac 17090 sprayed
NC Ac 17090 unsprayed
A.
Leaf Dry Mass
1987 Rainy Season
Grams plant^{-1}
0
2
4
6
8
10
12
14
16
190
210
230
250
270
290
Julian Date
C.
Stem Dry Mass
1987 Rainy Season
Grams plant^{-1}
0
2
4
6
8
10
12
190
210
230
250
270
290
Julian Date
B.
Leaf Dry Mass
1987–88 Post-rainy Season
Grams plant^{-1}
0
2
4
6
8
10
12
14
16
0
20
40
60
80
100
Julian Date
D.
Stem Dry Mass
1987–88 Post-rainy Season
Grams plant^{-1}
0
2
4
6
8
10
12
0
20
40
60
80
100
Julian Date

Figure 3.

Figure 4. The effect of insecticide and cultivar on the change in leaf area index during the 1987 rainy and 1987-88 post-rainy seasons, ICRISAT, India.

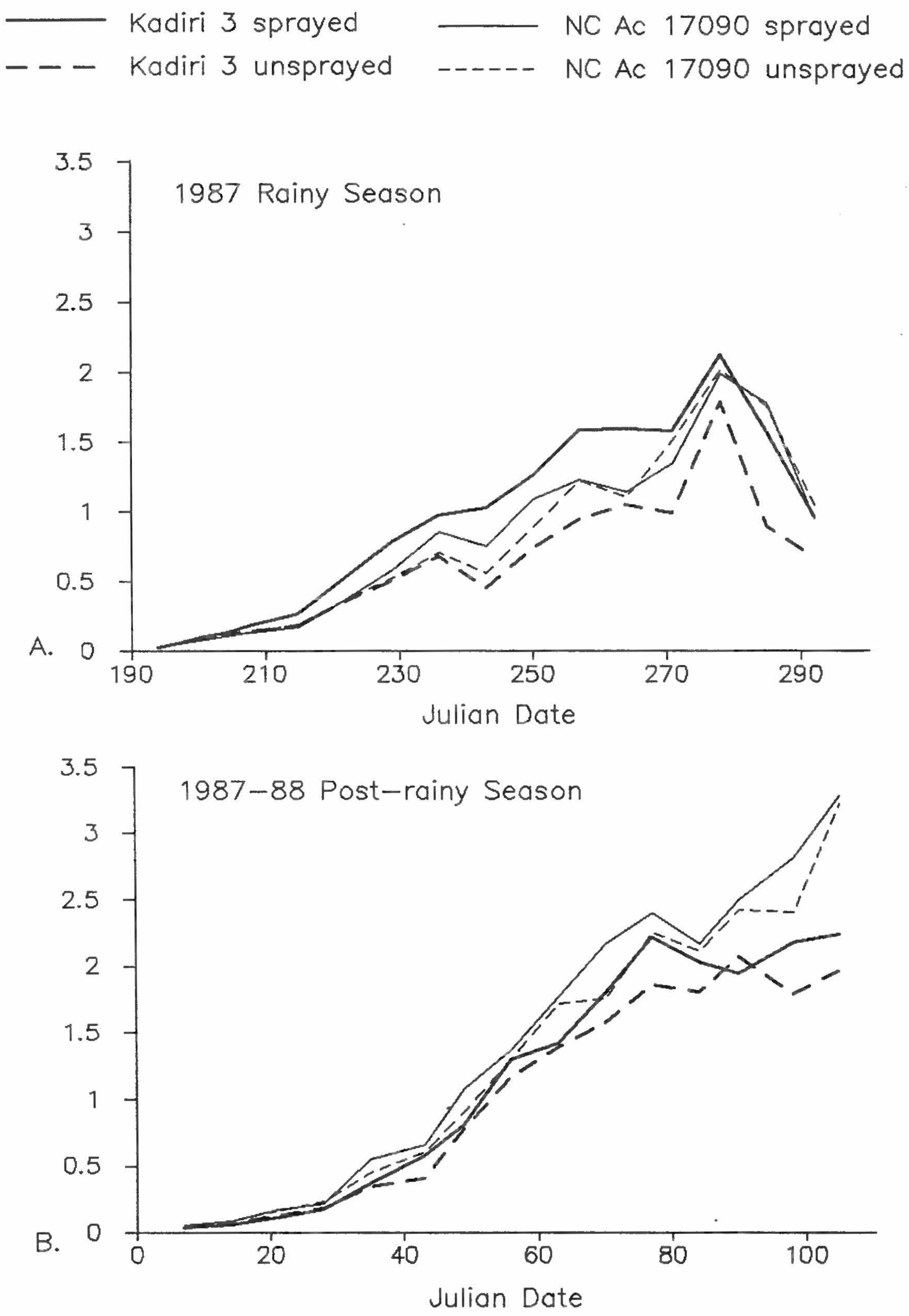

Kadiri 3 sprayed
Kadiri 3 unsprayed
NC Ac 17090 sprayed
NC Ac 17090 unsprayed
3.5
3
2.5
2
1.5
1
0.5
0
1987 Rainy Season
A.
190
210
230
250
270
290
Julian Date
3.5
3
2.5
2
1.5
1
0.5
0
1987–88 Post–rainy Season
B.
0
20
40
60
80
100
Julian Date

Figure 4.

Figure 5. The effect of insecticide and cultivar on flower and peg production during the 1987 rainy and 1987-88 post-rainy seasons, ICRISAT, India.

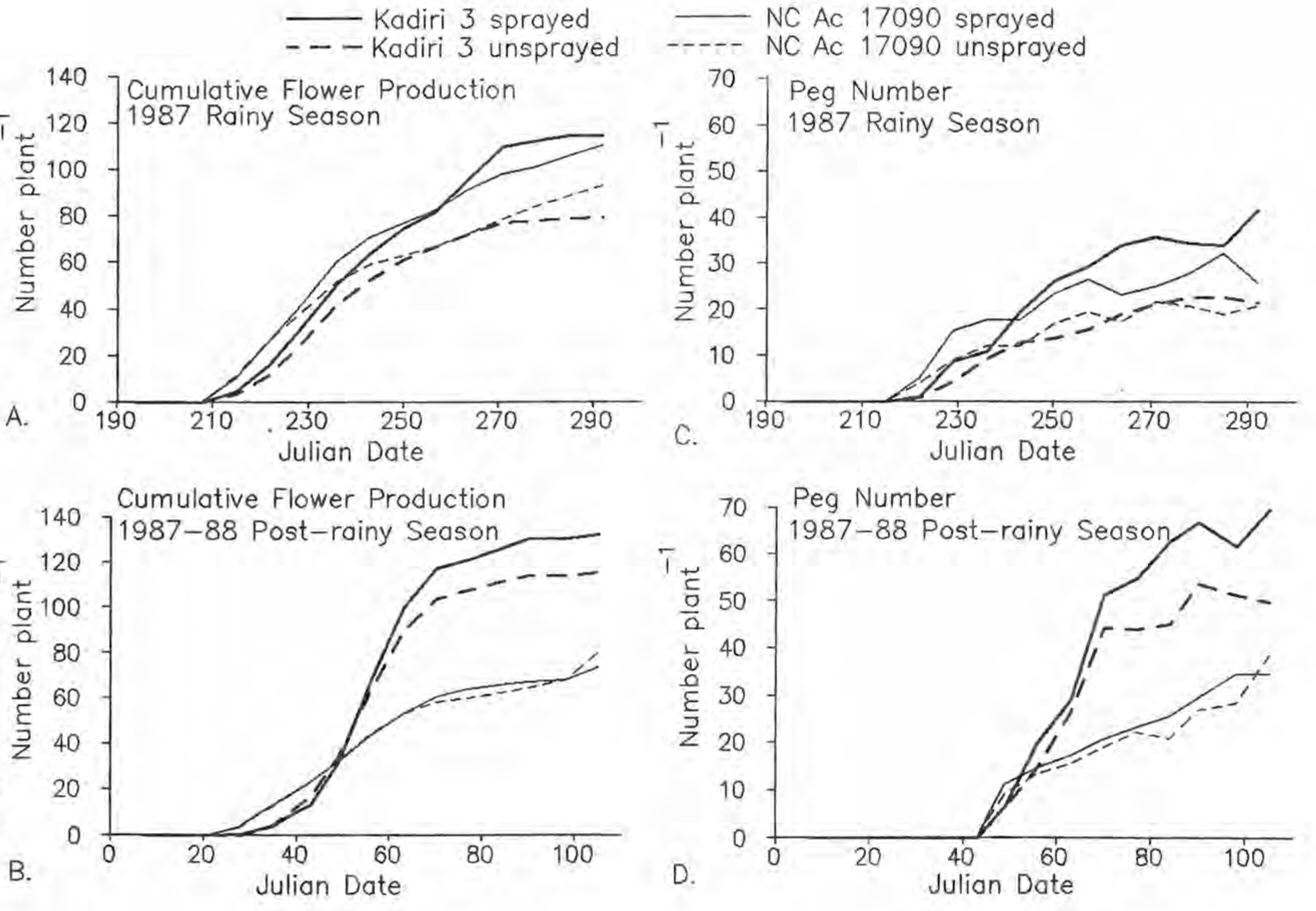

Kadiri 3 sprayed
Kadiri 3 unsprayed
NC Ac 17090 sprayed
NC Ac 17090 unsprayed
A.
Cumulative Flower Production
1987 Rainy Season
Number plant^{-1}
0
20
40
60
80
100
120
140
190
210
230
250
270
290
Julian Date
C.
Peg Number
1987 Rainy Season
Number plant^{-1}
0
10
20
30
40
50
60
70
190
210
230
250
270
290
Julian Date
B.
Cumulative Flower Production
1987–88 Post-rainy Season
Number plant^{-1}
0
20
40
60
80
100
120
140
0
20
40
60
80
100
Julian Date
D.
Peg Number
1987–88 Post-rainy Season
Number plant^{-1}
0
10
20
30
40
50
60
70
0
20
40
60
80
100
Julian Date

Figure 5.

Figure 6. The effect of insecticide and cultivar on the change in pod mass and number during the 1987 rainy and 1987-88 post-rainy season, ICRISAT, India.

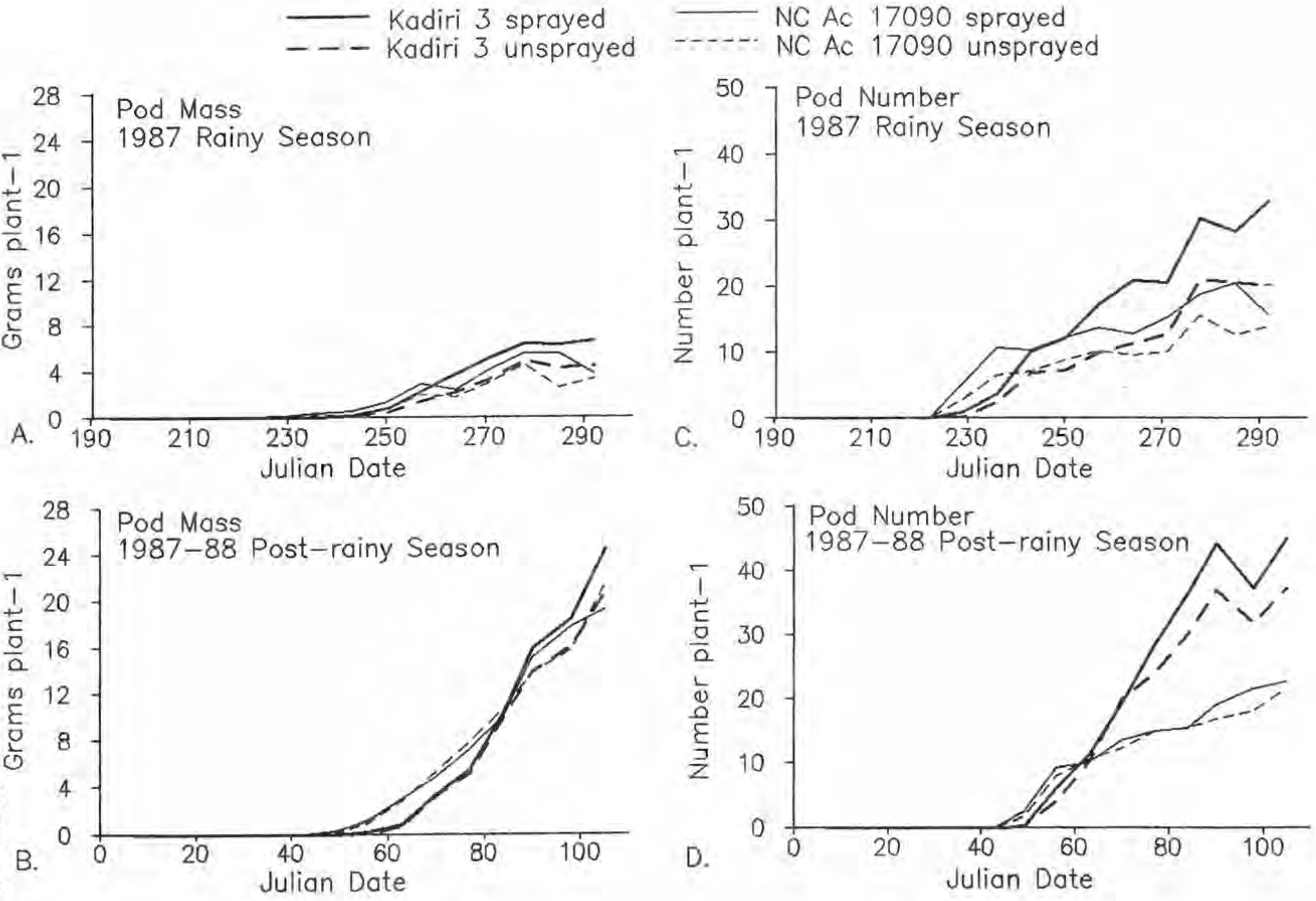

Kadiri 3 sprayed
Kadiri 3 unsprayed
NC Ac 17090 sprayed
NC Ac 17090 unsprayed
A.
Pod Mass
1987 Rainy Season
Grams plant−1
0
4
8
12
16
20
24
28
190
210
230
250
270
290
Julian Date
C.
Pod Number
1987 Rainy Season
Number plant−1
0
10
20
30
40
50
190
210
230
250
270
290
Julian Date
B.
Pod Mass
1987−88 Post−rainy Season
Grams plant−1
0
4
8
12
16
20
24
28
0
20
40
60
80
100
Julian Date
D.
Pod Number
1987−88 Post−rainy Season
Number plant−1
0
10
20
30
40
50
0
20
40
60
80
100
Julian Date

Figure 6.

Figure 7. The effect of insecticide and cultivar on fruit growth rate during the 1987 rainy season, ICRISAT, India.

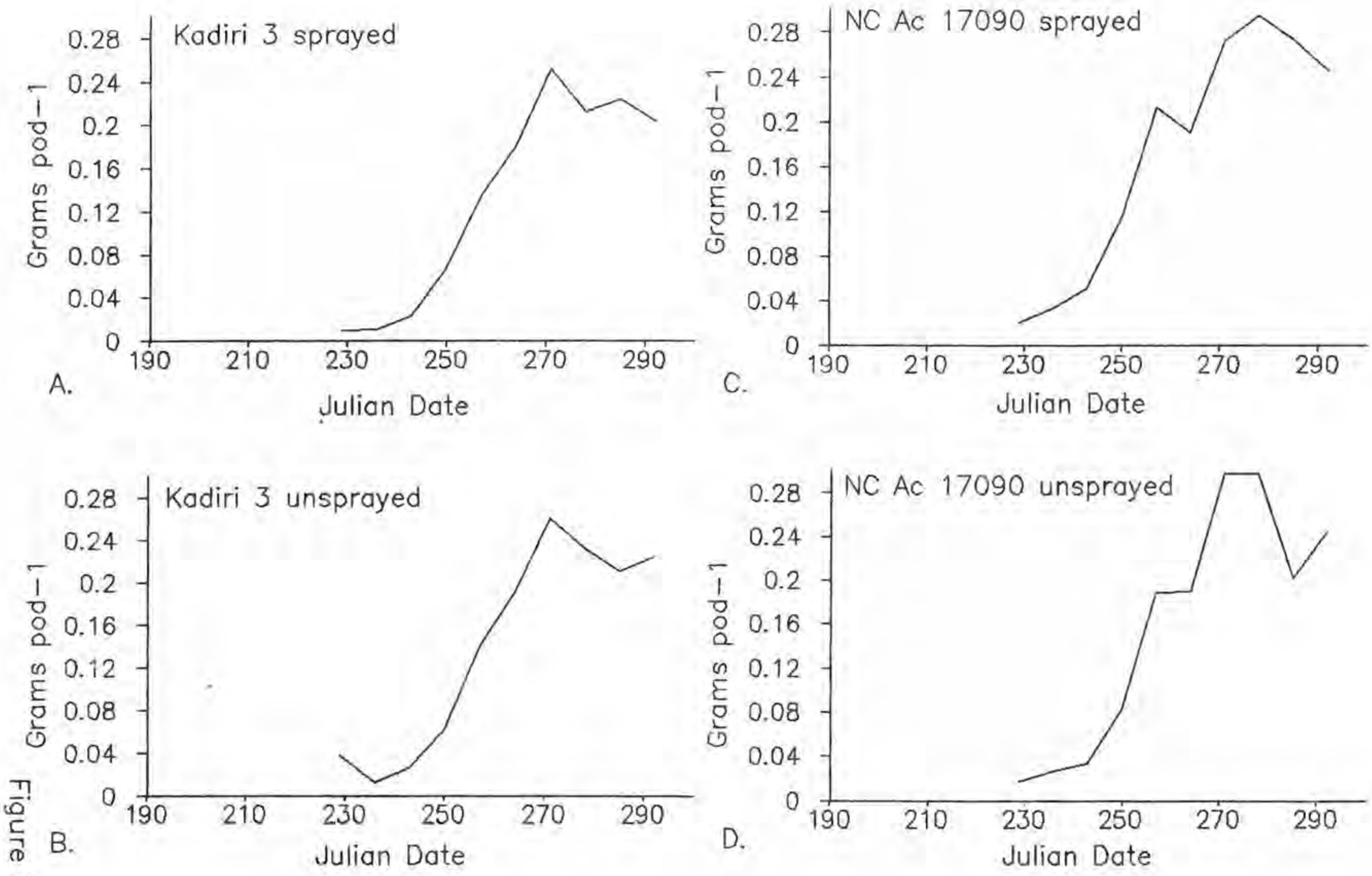

Kadiri 3 sprayed
Grams pod−1
0
0.04
0.08
0.12
0.16
0.2
0.24
0.28
190
210
230
250
270
290
Julian Date
A.
NC Ac 17090 sprayed
Grams pod−1
0
0.04
0.08
0.12
0.16
0.2
0.24
0.28
190
210
230
250
270
290
Julian Date
C.
Kadiri 3 unsprayed
Grams pod−1
0
0.04
0.08
0.12
0.16
0.2
0.24
0.28
190
210
230
250
270
290
Julian Date
B.
NC Ac 17090 unsprayed
Grams pod−1
0
0.04
0.08
0.12
0.16
0.2
0.24
0.28
190
210
230
250
270
290
Julian Date
D.

Figure 7.

Figure 8. The effect of insecticide and cultivar on fruit growth rate during the 1987-88 post-rainy season, ICRISAT, India.

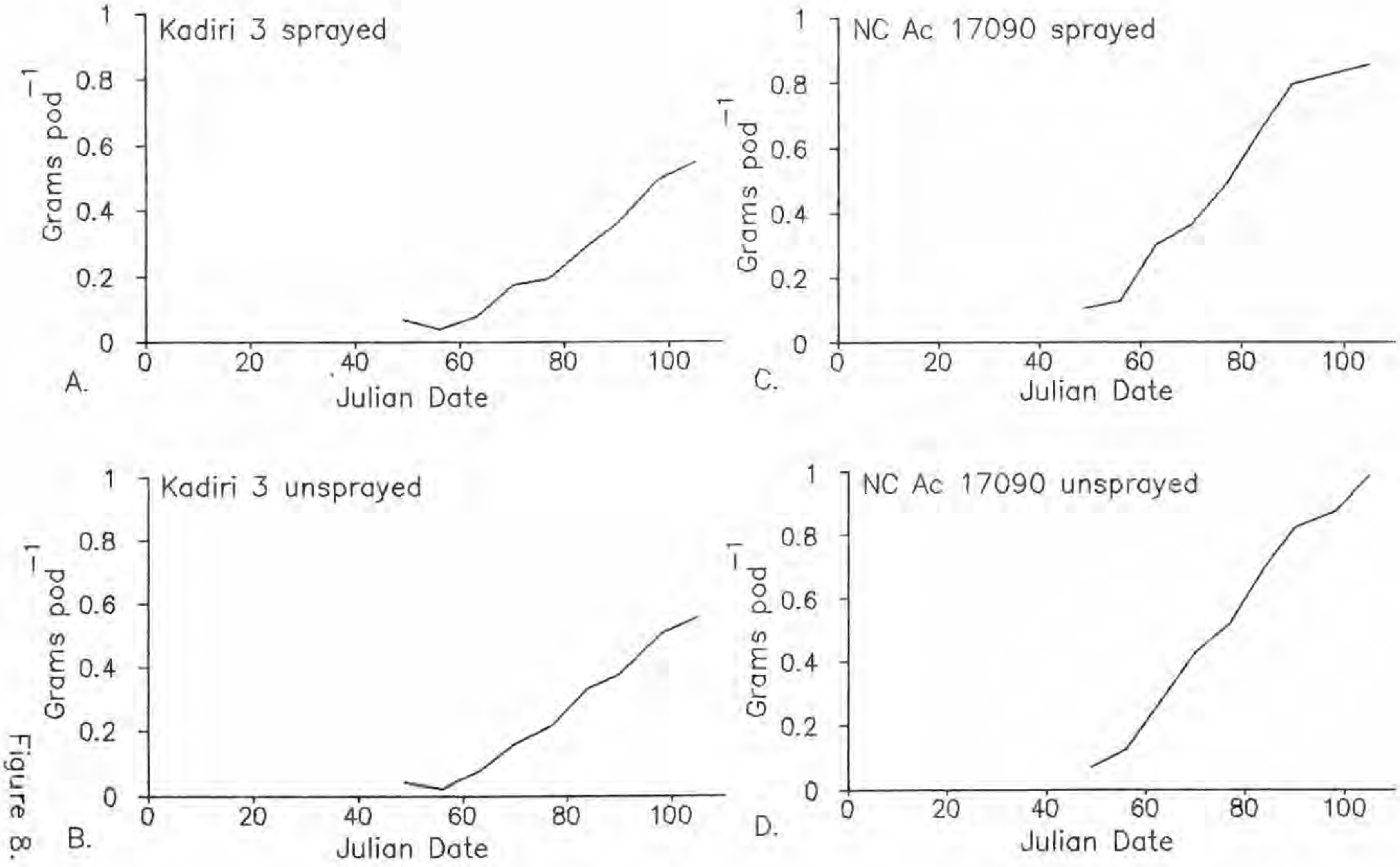

Kadiri 3 sprayed
Kadiri 3 unsprayed
NC Ac 17090 sprayed
NC Ac 17090 unsprayed
Grams pod^{-1}
0
0.2
0.4
0.6
0.8
1
0
20
40
60
80
100
Julian Date
A.
B.
C.
D.

Figure 8.

Figure 9. The effect of insecticide and cultivar on pod number per plant at harvest in the 1987 rainy and 1987-88 post-rainy seasons, ICRISAT, India.

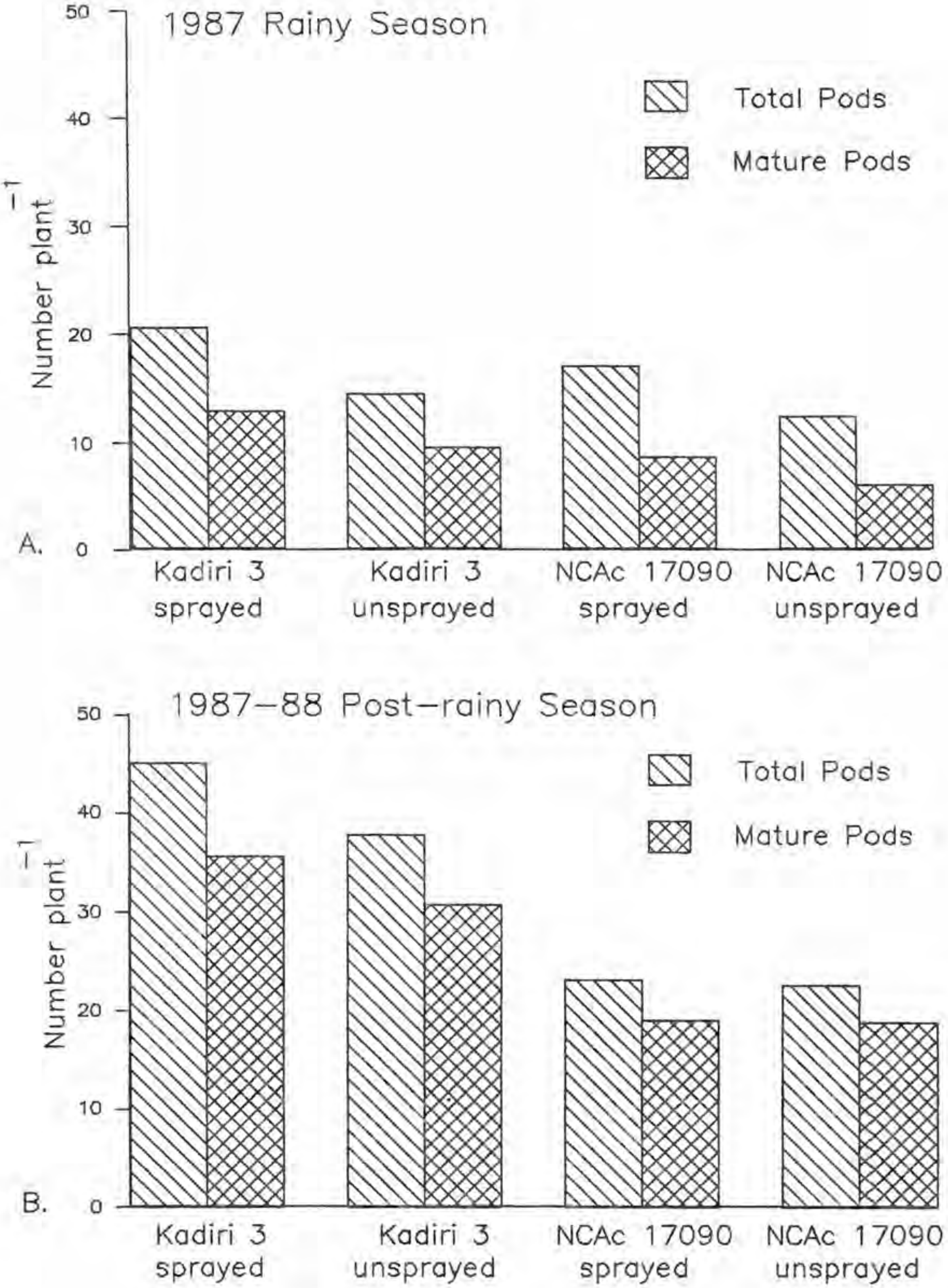

1987 Rainy Season
▧ Total Pods
▦ Mature Pods
Number plant^{-1}
50
40
30
20
10
0
A.
Kadiri 3 sprayed
Kadiri 3 unsprayed
NCAc 17090 sprayed
NCAc 17090 unsprayed
1987–88 Post-rainy Season
▧ Total Pods
▦ Mature Pods
Number plant^{-1}
50
40
30
20
10
0
B.
Kadiri 3 sprayed
Kadiri 3 unsprayed
NCAc 17090 sprayed
NCAc 17090 unsprayed

Figure 9.

APPENDIX

Analysis of covariance (ANCOVA) results.

Table 1. The effect of insecticide[1/] and cultivar on leaf growth rates (g plant-1 day-1) in the 1987 rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value ($\pm$SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -31.116 + 0.149x$	0.935	7.52 ± 1.077	208	236
Kadiri 3 unsprayed	$y = -17.447 + 0.086x$	0.974	5.03 ± 0.203	208	264
NC Ac 17090 sprayed	$y = -39.690 + 0.191x$	0.978	15.35 ± 1.756	208	285
NC Ac 17090 unsprayed	$y = -36.396 + 0.174x$	0.982	13.75 ± 2.235	208	285
	$F_{3,31} = 4.67$		$F_{3,9} = 24.71$		
	$p < 0.01$		$p < 0.0005$		

[1/] Monocrotophos (40%) applied 3 times against Aproaerema modicella larvae.

Table 2. The effect of insecticide[1/] and cultivar on leaf growth rates (g plant-1 day-1) in the 1987-88 post-rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value (±SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -4.564 + 0.181x$	0.981	10.65 ± 0.414	28	84
Kadiri 3 unsprayed	$y = -4.516 + 0.174x$	0.970	9.91 ± 0.884	28	84
NC Ac 17090 sprayed	$y = -2.897 + 0.142x$	0.982	11.65 ± 0.163	28	105
NC Ac 17090 unsprayed	$y = -3.215 + 0.145x$	0.969	11.95 ± 0.684	28	105
	$F_{3,34} = 0.1198$		$F_{3,9} = 2.86$		
	$p > 0.25$		$0.05 > p > 0.1$		

[1/] Monocrotophos (40%) applied 2 times against *Aproaerema modicella* larvae.

Table 3. The effect of insecticide[1/] and cultivar on stem growth rates (g plant-1 day-1) in the 1987 rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value (±SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -26.474 + 0.127x$	0.974	6.19 ± 0.307	208	257
Kadiri 3 unsprayed	$y = -12.216 + 0.061x$	0.960	4.43 ± 0.123	208	278
NC Ac 17090 sprayed	$y = -29.113 + 0.142x$	0.964	10.90 ± 0.728	208	285
NC Ac 17090 unsprayed	$y = -21.585 + 0.107x$	0.968	8.72 ± 0.221	208	292
	$F_{3,36} = 5.05$		$F_{3,9} = 42.87$		
	$p < 0.01$		$p < 0.0005$		

[1/] Monocrotophos (40%) applied 3 times against Aproaerema modicella larvae.

Table 4. The effect of insecticide[1/] and cultivar on stem growth rate (g plant-1 day-1) in the 1987-88 post-rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value (±SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -3.709 + 0.140x$	0.982	9.87 ± 0.447	28	84
Kadiri 3 unsprayed	$y = -2.798 + 0.114x$	0.966	7.97 ± 0.361	28	84
NC Ac 17090 sprayed	$y = -3.481 + 0.130x$	0.992	12.12 ± 0.173	28	105
NC Ac 17090 unsprayed	$y = -3.622 + 0.132x$	0.983	12.91 ± 0.655	28	105
	$F_{3,34} = 1.048$		$F_{3,9} = 18.12$		
	$p > 0.25$		$p < 0.0005$		

[1/] Monocrotophos (40%) applied 2 times against Aproaerema modicella larvae.

Table 5. The effect of insecticide[1/] and cultivar on the change in leaf area index (LAI) in the 1987 rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max Value (± SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 sprayed	$y = -5.260 + 0.026x$	0.962	2.12 ± 0.651	215	278
Kadiri 3 unsprayed	$y = -4.064 + 0.020x$	0.826	1.77 ± 0.679	215	278
NC Ac 17090 sprayed	$y = -4.891 + 0.024x$	0.915	1.99 ± 0.308	215	278
NC Ac 17090 unsprayed	$y = -5.319 + 0.025x$	0.909	2.04 ± 0.569	215	278
	$F_{3,32} = 1.28$ $p > 0.25$		$F_{3,9} = 0.30$ $p > 0.25$		

[1/] Monocrotophos (40%) applied 3 times against Aproaerema modicella larvae.

Table 6. The effect of insecticide[1] and cultivar on the change in leaf area index (LAI) in the 1987-88 post-rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max Value (± SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 sprayed	$y = -0.907 + 0.038x$	0.968	2.22 ± 0.237	21	77
Kadiri 3 unsprayed	$y = -0.759 + 0.033x$	0.963	2.06 ± 0.121	21	77
NC Ac 17090 sprayed	$y = -0.788 + 0.038x$	0.969	3.29 ± 0.157	28	105
NC Ac 17090 unsprayed	$y = -0.791 + 0.036x$	0.964	3.26 ± 0.381	28	105
	$F_{3,34} = 3.69$		$F_{3,9} = 20.5$		
	$p < 0.025$		$p < 0.0005$		

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[1] Monocrotophos (40%) applied 2 times against *Aproaerema modicella* larvae.

Table 7. The effect of insecticide[1/] and cultivar on cumulative flower production (# plant-1 day-1) in the 1987 rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value (±SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	y = -380.732 + 1.811x	0.992	114.50 ± 8.994	208	271
Kadiri 3 unsprayed	y = -283.593 + 1.357x	0.972	79.29 ± 3.425	208	271
NC Ac 17090 sprayed	y = -252.461 + 1.296x	0.906	110.16 ± 3.912	208	292
NC Ac 17090 unsprayed	y = -206.350 + 1.051x	0.945	92.51 ± 10.027	208	292
	$F_{3,38}$ = 1.82		$F_{3,9}$ = 5.92		
	$0.1 < p < 0.25$		$0.025 < p < 0.01$		

[1/] Monocrotophos (40%) applied 3 times against Aproaerema modicella larvae.

Table 8. The effect of insecticide[1/] and cultivar on cumulative flower production (# plant-1 day-1) in the 1987-88 post-rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value (±SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -162.460 + 4.062x$	0.988	132.29 ± 9.222	43	70
Kadiri 3 unsprayed	$y = -127.158 + 3.360x$	0.990	115.19 ± 7.231	43	70
NC Ac 17090 sprayed	$y = -35.591 + 1.391x$	0.998	73.72 ± 2.787	28	70
NC Ac 17090 unsprayed	$y = -34.257 + 1.355x$	0.994	92.83 ± 15.653	28	70
	$F_{3,16} = 3.034$		$F_{3,9} = 9.22$		
	$0.05 < p < 0.10$		$0.0025 < p < 0.005$		

[1/] Monocrotophos (40%) applied 2 times against Aproaerema modicella larvae.

Table 9. The effect insecticide[1/] and cultivar on peg production (# plant-1 day-1) in the 1987 rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value (±SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -113.064 + 0.538x$	0.903	41.68 ± 3.104	222	292
Kadiri 3 unsprayed	$y = -82.686 + 0.384x$	0.970	22.83 ± 0.988	222	278
NC Ac 17090 sprayed	$y = -78.129 + 0.390x$	0.863	25.85 ± 1.658	215	285
NC Ac 17090 unsprayed	$y = -75.887 + 0.364x$	0.931	20.80 ± 2.188	215	271
	$F_{3,32} = 4.22$		$F_{3,9} = 21.20$		
	$p < 0.025$		$p < 0.0005$		

[1/] Monocrotophos (40%) applied 3 times against *Aproaerema modicella* larvae.

Table 10. The effect of insecticide[1/] and cultivar on peg production (# plant-1 day-1) in the 1987-88 post-rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value ($\pm$SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -65.123 + 1.527x$	0.970	69.78 ± 7.508	43	90
Kadiri 3 unsprayed	$y = -49.075 + 1.180x$	0.941	53.85 ± 3.622	43	90
NC Ac 17090 sprayed	$y = -10.020 + 0.436x$	0.989	34.58 ± 1.781	49	105
NC Ac 17090 unsprayed	$y = -12.944 + 0.449x$	0.935	38.50 ± 3.780	49	105
	$F_{3,26} = 7.494$		$F_{3,9} = 12.11$		
	$0.0005 < p < 0.001$		$0.001 < p < 0.0025$		

[1/] Monocrotophos (40%) applied 2 times against Aproaerema modicella larvae.

Table 11. The effect of insecticide[1/] and cultivar on pod growth rate (g plant-1 day-1) in the 1987 rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value (±SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -45.181 + 0.186x$	0.990	6.69 ± 0.475	243	278
Kadiri 3 unsprayed	$y = -33.117 + 0.135x$	0.958	4.91 ± 0.371	243	278
NC Ac 17090 sprayed	$y = -30.068 + 0.126x$	0.943	5.54 ± 0.784	243	285
NC Ac 17090 unsprayed	$y = -28.314 + 0.117x$	0.924	4.63 ± 0.761	243	278
	$F_{3,17} = 0.635$		$F_{3,9} = 2.19$		
	$p > 0.25$		$0.1 < p < 0.25$		

[1/] Monocrotophos (40%) applied 3 times against Aproaerema modicella larvae.

Table 12. The effect of insecticide[1/] and cultivar on pod growth rate (g plant-1 day-1) in the 1987-88 post-rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value ($\pm$SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -36.632 + 0.572x$	0.978	24.53 ± 2.307	63	105
Kadiri 3 unsprayed	$y = -30.661 + 0.485x$	0.986	20.80 ± 2.248	63	105
NC Ac 17090 sprayed	$y = -22.311 + 0.400x$	0.977	19.31 ± 0.683	56	105
NC Ac 17090 unsprayed	$y = -22.625 + 0.404x$	0.983	21.39 ± 0.898	56	105
	$F_{3,22} = 0.087$ $p > 0.25$		$F_{3,9} = 1.45$ $p > 0.25$		

[1/] Monocrotophos (40%) applied 2 times against Aproaerema modicella larvae.

Table 13. The effect of insecticide[1/] and cultivar on pod production (# plant-1 day-1) in the 1987 rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value ($\pm$SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -114.847 + 0.509x$	0.970	32.93 ± 1.423	229	292
Kadiri 3 unsprayed	$y = -83.155 + 0.364x$	0.924	21.15 ± 0.913	229	278
NC Ac 17090 sprayed	$y = -56.308 + 0.269x$	0.899	15.65 ± 0.712	222	285
NC Ac 17090 unsprayed	$y = -47.405 + 0.221x$	0.886	13.93 ± 1.549	222	278
	$F_{3,29} = 3.83$		$F_{3,9} = 44.32$		
	$p < 0.025$		$p < 0.0005$		

[1/] Monocrotophos (40%) applied 3 times against Aproaerema modicella larvae.

Table 14. The effect of insecticide[1/] and cultivar on pod production (# plant-1 day-1) in the 1987-88 post-rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Max. Value (±SE)	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -55.157 + 1.088x$	0.991	45.10 ± 4.623	49	90
Kadiri 3 unsprayed	$y = -45.774 + 0.912x$	0.991	37.35 ± 2.622	49	90
NC Ac 17090 sprayed	$y = -11.008 + 0.329x$	0.951	22.68 ± 1.455	49	105
NC Ac 17090 unsprayed	$y = -10.038 + 0.302x$	0.929	21.63 ± 0.859	49	105
	$F_{3,24} = 3.506$		$F_{3,9} = 15.3$		
	$0.025 < p < 0.05$		$0.0005 < p < 0.001$		

[1/] Monocrotophos (40%) applied 2 times against *Aproaerema modicella* larvae.

Table 15. The effect of insecticide[1/] and cultivar on fruit growth rate (g pod-1 day-1) in the 1987 rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -1.954 + 0.0081x$	0.994	243	271
Kadiri 3 unsprayed	$y = -2.066 + 0.0086x$	0.990	243	271
NC Ac 17090 sprayed	$y = -1.584 + 0.0068x$	0.920	243	278
NC Ac 17090 unsprayed	$y = -2.173 + 0.0091x$	0.946	243	271

$F_{3,13} = 0.363$

$p > 0.25$

[1/] Monocrotophos (40%) applied 3 times against Aproaerema modicella larvae.

Table 16. The effect of insecticide[1] and cultivar on fruit growth rate (g pod-1 day-1) in the 1987-88 post-rainy season, ICRISAT, India.

Treatment	Linear Equation	r^2	Time Rate Inc	Time Rate Dec
Kadiri 3 spray	$y = -0.591 + 0.011x$	0.980	56	105
Kadiri 3 unsprayed	$y = -0.634 + 0.011x$	0.992	56	105
NC Ac 17090 sprayed	$y = -0.707 + 0.016x$	0.958	56	105
NC Ac 17090 unsprayed	$y = -0.838 + 0.018x$	0.985	56	105

$F_{3,24} = 1.325$

$p > 0.25$

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[1] Monocrotophos (40%) applied 2 times against Aproaerema modicella larvae.

Chapter 5.

Natural enemies of the groundnut leaf miner, _Aproaerema modicella_ (Deventer) (Lepidoptera: Gelechiidae), at ICRISAT Center, with special reference to the parasitoid fauna.

Introduction

Materials and Methods

Results

Discussion

Literature Cited

INTRODUCTION

Natural enemies are a component of natural control, the force "that keeps all living creatures in a state of balance with their environment" (van den Bosch et al., 1982), and keeps potentially damaging pests below economic levels. The importance of natural enemies has been demonstrated by the development of secondary pests and the resurgence of key pests following insecticide applications (DeBach et al., 1976; Luck et al., 1977). Changes in the natural enemy community due to pesticide use or other disturbances may cause some insects to exhibit dramatic increases in population.

The groundnut leaf miner (GLM), *Aproaerema modicella* (Deventer) (Lepidoptera: Gelechiidae), is an endemic pest of groundnut and soybean in South and Southeast Asia, and its population dynamics are characterized by dramatic fluctuations (see Chapter 3.2). Several diseases and generalist predators have been identified attacking GLM (Godse and Patil, 1981; Oblasami et al., 1969; Maxwell-Lefroy and Howlett, 1909; Srinivasan and Siva Rao, 1986; Shanower and Ranga Rao, 1989), but their impact has not been quantified. The most important GLM larval mortality agents are parasitic Hymenoptera. A large number of primary and secondary parasitoids have been reported in the literature (see Table 2 in Chapter 2) but little is known of their biology or impact.

Reports from India have shown that larval parasitoids are most abundant, and often parasitize up to 80% of GLM larvae, late in the rainy season (August and September) (Shetgar and Thombre, 1984; Khan and Raodeo, 1978). Yadav et al. (1987) found that the relative abundance and rank of primary parasitoids varied between sample dates. In the post-rainy season (December to April) Goniozus sp. was the most abundant, while Stenomesius japonicus (Ashmead) and Apanteles sp. were more prominent in the rainy season. Total parasitization reached 75% in the post-rainy season and 89% in the rainy season (Yadav et al., 1987).

The purpose of this study was to identify the important biotic mortality factors affecting GLM larvae and estimate the impact of each on GLM populations. Observations were also made of the relative abundance and trophic relationships between different parasitoid species.

MATERIALS AND METHODS

Sampling method

This work was carried out at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), located near Hyderabad, Andhra Pradesh, India. GLM larvae were collected at weekly intervals. Four GLM generations were sampled in the 1987-88 post-rainy season, but only one generation was sampled in the 1988 rainy season because GLM populations were very low. Leaf miner larvae were collected from field trials described in Chapters 3.2 and 4. Those studies were designed to evaluate the effect of resistant varieties and the efficacy of chemical control strategies on GLM populations. Leaves containing larvae were sampled from all replicates (four) in each variety x insect control treatment. After determining that only a single GLM larva was present per leaf, the leaf was placed on moistened filter paper in small (30 x 70 mm) plastic petri dishes and observed daily for the emergence of the moth or parasitoid(s) and/or the development of disease. A fresh leaf and/or additional water were added as needed to provide food for and prevent dissecation of the GLM larva. Larvae which died were examined for cause of death. Black, mushy bodied GLM larvae, characteristic of virus infection were common, and GLM larvae with fungal hyphae growing out of the bodies also were observed. The incidence of these diseases was recorded, but the diseases were not identified.

Parasitoids were identified by Z. Boucek, A. Polaszek and A.K. Walker at the CAB International Institute of Entomology, British Museum (Natural History). The relative abundance of each parasitoid was calculated for each of five GLM generations. The emergence of secondary parasitoids from pupae of primary parasitoids also was recorded.

Statistical analysis

Data on the proportions of each GLM generation killed by parasitoids and pathogens were transformed using an arc-sine transformation. Two-way analysis of variance (ANOVA) was used to test differences in mortality across variety x insect control treatments and generations (Zar 1974; Gomez and Gomez, 1984).

RESULTS

The number of larvae collected ranged from 22 to 65 per treatment in the first generation of the 1987-88 post-rainy season. In the second generation 8 to 54 larvae were collected, and in the third and fourth generations 68 to 116 and 98 to 122 larvae respectively were found. Between 62 and 114 larvae were sampled in the single GLM generation of the 1988 rainy season.

Mortality factors

The proportions of GLM larvae killed by parasitoids and pathogens were not significantly different across variety x insect control treatments (Tables 1 and 2), but there were significant differences in the proportion of diseased larvae in different generations. In all variety x insect control treatments, parasitization and disease infection increased through successive leaf miner generations (Fig. 1, only Kadiri 3 treatment shown). By the fourth generation, 25% of the larvae sampled were diseased, more than 50% were parasitized in the unsprayed Kadiri 3 treatment and only 10% reached the adult stage. In the 1988 rainy season, 10% died of disease and 45% due to parasitism.

The three insecticide treatments had slightly lower (not significant) parasitization rates compared to the two unsprayed treatments (Table 1 and Fig. 1). GLM populations densities were very low in all treatments during both seasons (<4 larvae plant^{-1}) and even unsprayed plots did not suffer yield loss (Fig. 6 B&D in Chap. 4). Parasitization rates were not significantly different across variety x insecticide treatments and hence data were lumped into sprayed and unsprayed treatments across varieties. The Kadiri 3 treatment with systemic insecticide was not included because there was no equivalent treatment in the NCAc 17090 variety.

Two-way analysis of variance on the lumped data indicated that parasitization rates were significantly lower in sprayed plots (Table 3) than in unsprayed plots. There was, however, no significant difference in disease incidence between sprayed and unsprayed treatments in the lumped data.

Parasitoid community

The relative abundance of the dominant primary parasitoid changed during the 5 GLM generations studied (Table 4). The trophic relationships between primary and secondary parasitoids were determined by direct observation of secondary parasitoids emerging from the pupae of primary parasitoids. The structure of the community is shown in Figure 2 with the arrows indicating the associations between trophic levels.

The primary parasitoids reared from GLM (Table 5) include several new records and indicate that this community is more complex than previously thought. New records of parasitoids in the GLM community include one primary, _Temelucha_ sp., and 4 secondary parasitoids, _Pteromalus_ sp., _Oomyzus_ sp., _Elasmus_ _anticles_ Walker and _Aphanogmus_ _fijiensis_ (Ferriere). What was initially considered to be a single braconid species was in fact three species in different genera: _Apanteles_ sp., _Avga_ _choaspes_ Nixon and _Bracon_ sp. All three are larval ectoparasitoids which paralyze the host before ovipositing. In analyzing this community the effect of these three primary parasitoids was combined.

In the first generation, _Sympiesis_ _dolichogaster_ Ashmead was the dominant species, emerging from more than 25% of the parasitized GLM larvae. The three braconids lumped as a single species combined to kill 28% of the first generation GLM larvae. The category "other" was composed of several unidentified species which may have included both primary and secondary parasitoids, and emerged from 26% of the first generation GLM larvae.

In subsequent generations, the proportion attacked by *S. dolichogaster* declined while the fraction killed by *Stenomesius japonicus* increased (Table 4). Parasitism by the three braconids (*Apanteles* sp., *Avga choaspes*, *Bracon* sp.) also declined. Two species, *Chelonus* sp. and *Goniozus* sp., never accounted for more than 15% of the parasitized larvae in any generation. Secondary parasitoids emerged from between 19% and 40% of the hosts in each generation.

DISCUSSION

This paper provides the first evidence of the importance of disease organisms on the population dynamics of groundnut leaf miner. As many as 30% of the GLM larvae were infected by viral and fungal pathogens. The proportion of larvae killed by pathogens was higher in the third and fourth generations of the post-rainy season indicating that pathogen levels built up through the season. Though disease producing organisms have been identified from GLM larvae in the past (Oblasami *et al*., 1969; Godse and Patil, 1981), the effect of these pathogens was not quantified.

The other major cause of GLM larval mortality are parasitic Hymenoptera. Parasitoids emerged from up to 53% of the larval population. Parasitoid populations increased during the season and later GLM generations, which were slightly larger, had marginally higher parasitization rates. The effectiveness of parasitoids was constrained by the use of insecticides which lowered parasitization rates in plots receiving insecticides. GLM populations were slightly lower on sprayed plots because the insecticide killed both the GLM larvae and the parasitoids. GLM populations were low in both seasons and no yield differences were observed between sprayed and unsprayed plots. Parasitism rates were reduced less in the systemic insecticide treatment than in the foliar spray treatment but the difference was not significant (Table 1).

The deleterious effect of insecticides on natural enemies is widely known and is the cause of secondary pest outbreaks and resurgence in primary pest species (Reynolds, 1971; DeBach et al., 1976; Luck et al., 1977; van den Bosch 1978;). It is not surprising that treatments receiving foliar insecticides had lower parasitization rates. However, it is interesting that the treatment using systemic insecticide had a slightly higher parasitization rate than the treatments with foliar insecticide.

The results reported here support the finding of Yadav et al. (1987) in Gujarat, India, who found that up to 89% of the GLM larvae were parasitized. Four species, Apanteles sp., Bracon gelechiae Ashmead, Goniozus sp. and S. japonicus were the key primary parasitoids, but their relative abundance varied markedly during the year (Yadav et al., 1987). The parasitoid community found at ICRISAT was also very dynamic with the composition and dominant species changing frequently. The dominant primary parasitoids were S. japonicus, S. dolichogaster and the group of three braconids, Apanteles sp., Avga choaspes and Bracon sp.

Four new secondary parasitoids were discovered in this community (Fig. 2). The only other report of secondary parasitoids in the GLM community listed 5 species, Pediobius sp. (Eulophidae), Ceraphron sp. (Ceraphronidae), Tetrastichus sp., Eurytoma sp. and an unidentified pteromalid (Subba Rao et al., 1965). Two of these secondary parasitoids, Tetrastichus sp. and Eurytoma sp. were found in the present study. Relationships between primary and secondary parasitoids are very complicated in this community. At least one secondary parasitoid (Oomyzus sp.) attacks two different primary parasitoids and other secondary parasitoids may also attack more than one primary. Unfortunately, because three braconid species were not differentiated it is unclear which secondary parasite was associated with which primary parasite. These secondary parasites may attack more than one primary or they may act as facultative secondary parasites.

The dashed line connecting E. anticles to GLM indicates the confusion concerning its role in the community. Yadav et al. (1987) and Phisitkul (1985) list Elasmus sp. as a primary parasitoid, though in the present study E. anticles clearly emerged from Goniozus sp. pupa. It is possible that the Elasmus sp. in the other two studies and E. anticles found at ICRISAT, are different species with different feeding habits, or E. anticles may be a facultative secondary parasitoid. Another interesting feature of the parasitoid community is the possibility that Stenomesius sp. is parasitic on a member of its own genus, S.

japonicus.

The groundnut leaf miner and its natural enemies are a complex component of the groundnut and soybean agroecosystems of South and Southeast Asia. At least three trophic levels function above the level of the plant. Parasitoids and disease organisms may kill 90% of the GLM larvae, and primary parasitoids are in turn attacked by a complex of secondary parasitoids. The results presented here begin to define and quantify the relationships that exist between and within the trophic levels in this system. However, more work on the biology of secondary parasitoids is needed to resolve the nature of their relationships with primary parasitoids.

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Table 1. Proportion (mean ±SE)[1] of each *Aproaerema modicella* generation killed by parasitoids at ICRISAT, India, 1987-88.

	Post-rainy Season (December - April)				Rainy Season (July - October)
Treatment	Gen. 1	Gen. 2	Gen. 3	Gen. 4	Gen. 1
Kadiri 3 sprayed	35.4 (9.67)	35.2 (15.99)	37.1 (2.42)	37.1 (12.10)	37.3 (6.39)
Kadiri 3 unsprayed	37.5 (9.96)	45.2 (6.05)	45.6 (9.16)	46.4 (4.06)	33.7 (5.34)
NCAc sprayed	45.3 (11.80)	31.8 (11.78)	36.9 (1.71)	36.2 (5.38)	32.0 (6.69)
NCAc unsprayed	39.6 (2.96)	37.8 (8.31)	36.1 (14.73)	45.7 (3.10)	41.9 (10.68)
Kadiri 3 systemic	31.6 (20.69)	43.4 (14.72)	35.4 (9.14)	43.7 (6.56)	27.4 (19.50)

Treatment	$F_{4,12} = 2.50$	$0.10 < p < 0.25$
Generation	$F_{4,12} = 1.37$	$p > 0.25$
Interaction	$F_{16,12} = 1.02$	$p > 0.25$

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[1] Mean of four replicates; arc-sine transformed values.

Table 2. Proportion (mean ±SE)[1/] of each *Aproaerema modicella* generation killed by disease at ICRISAT, India, 1987-88.

	Post-rainy Season (December - April)				Rainy Season (July - October)
Treatment	Gen. 1	Gen. 2	Gen. 3	Gen. 4	Gen. 1
Kadiri 3 sprayed	27.8 (14.42)	19.1 (7.49)	29.7 (5.39)	31.1 (7.66)	28.4 (9.99)
Kadiri 3 unsprayed	14.5 (9.14)	25.0 (19.46)	31.0 (7.60)	32.5 (6.76)	43.8 (4.06)
NCAc sprayed	18.1 (8.80)	27.1 (13.46)	36.4 (4.01)	38.2 (5.36)	39.2 (4.38)
NCAc unsprayed	24.2 (5.69)	24.1 (7.80)	34.8 (7.29)	34.5 (4.14)	35.6 (8.86)
Kadiri 3 systemic	23.9 (24.14)	29.9 (17.49)	34.3 (6.08)	34.8 (2.46)	32.8 (22.16)

Treatment	$F_{4,12} = 0.50$	$p > 0.25$
Generation	$F_{4,12} = 47.70$	$p < 0.0005$
Interaction	$F_{16,12} = 4.54$	$p < 0.01$

[1/] Mean of four replicates; arc-sine transformed values.

Table 3. Proportion (mean ± SE)[1/] of each *Aproaerema modicella* generation killed by parasites at ICRISAT, India, 1987-88; data lumped into 2 treatments (sprayed and unsprayed).

	Post-rainy Season (December - April)				Rainy Season (July - October)
Treatment	Gen. 1	Gen. 2	Gen. 3	Gen. 4	Gen. 1
sprayed	39.0 (3.22)	27.7 (17.33)	36.0 (1.37)	38.7 (3.27)	33.6 (3.47)
unsprayed	39.0 (3.36)	41.1 (6.54)	41.7 (7.78)	46.2 (1.92)	40.0 (3.16)

Treatment	$F_{1,12} = 15.68$	$p < 0.01$
Generation	$F_{4,12} = 0.73$	$p > 0.25$
Interaction	$F_{4,12} = 0.48$	$p > 0.25$

[1/] Mean of four replicates; arc-sine transformed values.

Table 4. Relative abundance of parasitoid species emerging from *Aproaerema modicella* larvae, by generation, 1987-88, ICRISAT, India.

	Season and GLM Generation				
	1987-88 Post-rainy				1988 Rainy
Parasitoid species	1	2	3	4	1
Sympiesis dolichogaster	0.26	0.29	0.12	0.16	0.01
Stenomesius japonicus	0.06	0.08	0.25	0.22	0.51
Goniozus sp.	0.00	0.12	0.11	0.07	0.04
Chelonus sp.	0.13	0.00	0.01	0.02	0.07
braconids[1/]	0.29	0.32	0.19	0.13	0.05
other	0.26	0.19	0.32	0.40	0.32

[1/] Includes three species: *Apanteles* sp., *Avga choaspes* and *Bracon* sp.

Table 5. Parasitoids[1] reared from *Aproaerema modicella* larvae at ICRISAT Center from 1987-89.

Family	Species	Relationship
Pteromalidae	*Pteromalus* sp.	Secondary
Eurytomidae	*Eurytoma* sp.	Secondary
Eupelmidae	*Eupelmus* sp.	Secondary
Eulophidae	*Stenomesius japonicus* (Ashmead)	Primary
	Stenomesius sp.	Secondary?
	Sympiesis dolichogaster Ashmead	Primary
	Tetrastichus sp.	Secondary
	Oomyzus sp.	Secondary
Elasmus	*Elasmus* sp. nr *luteus* Crawford	Secondary
	Elasmus anticles Walker	Secondary
Bethylidae	*Goniozus* sp.	Primary
Ceraphronidae	*Aphanogmus fijiensis* (Ferriere)	Secondary
Braconidae	*Chelonus* sp.	Primary
	Apanteles sp.	Primary
	Avga choaspes Nixon	Primary
	Bracon sp.	Primary
Ichneumonidae	*Temelucha* sp.	Primary

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[1] Identifications made by CAB International Institute of Entomology, Department of Entomology, British Museum (Natural History).

Figure 1. Larval mortality in five *Aproaerema modicella* generations at ICRISAT, India, 1987-88.

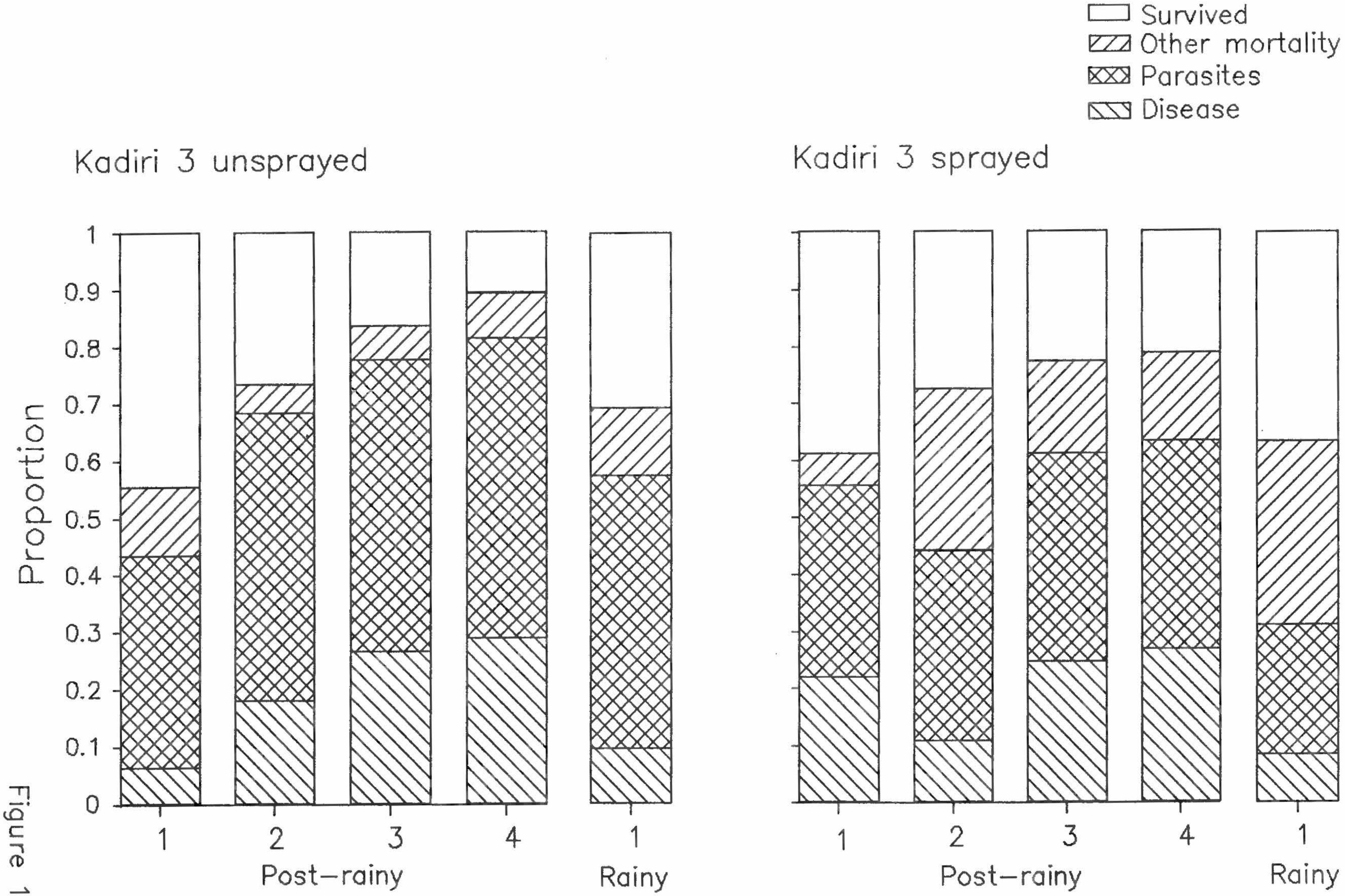
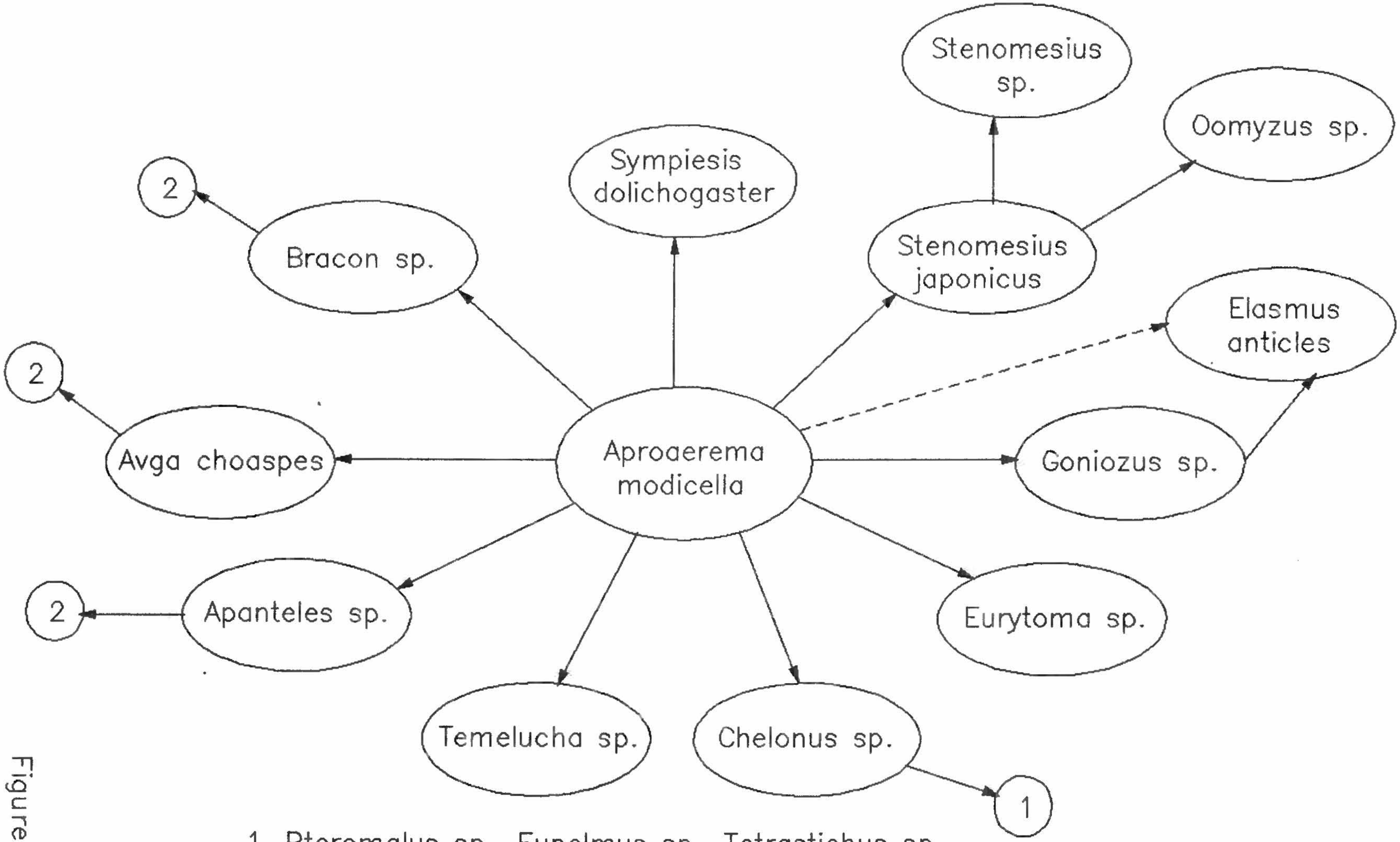

Survived
Other mortality
Parasites
Disease
Kadiri 3 unsprayed
Kadiri 3 sprayed
Proportion
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1
2
3
4
1
Post–rainy
Rainy
1
2
3
4
1
Post–rainy
Rainy

Figure 1.

Figure 2. Trophic relationships between Apraoerema modicella and its parasitoids at ICRISAT Center.


Stenomesius sp.
Oomyzus sp.
Sympiesis dolichogaster
2
Bracon sp.
Stenomesius japonicus
Elasmus anticles
2
Avga choaspes
Aproaerema modicella
Goniozus sp.
2
Apanteles sp.
Eurytoma sp.
Temelucha sp.
Chelonus sp.
1

1. Pteromalus sp., Eupelmus sp., Tetrastichus sp.
2. Oomyzus sp., Aphanagmus fijiensis

Figure 2.

Chapter 6.

A simulation model for groundnut (*Arachis hypogaea* L.) and one of its key herbivores, the groundnut leaf miner, *Aproaerema modicella* (Deventer).

Introduction

Conceptual framework

Field data and parameter estimation

Simulation results

Discussion

Literature Cited

Appendix

INTRODUCTION

Groundnut (Arachis hypogaea L.) is a New World crop grown extensively in the semi-arid tropics of Africa and Asia. These two regions cultivate 28% and 66% respectively, of the 19 million hectares sown annually worldwide (FAO, 1986). Groundnuts are a multi-use subsistence crop providing food, fuel, fodder and some cash to small farmers in traditional farming systems (Wightman and Amin, 1988; Chap. 1). Yields in developing countries are less than half those in developed countries (FAO 1986). Agronomic, biotic and abiotic factors adversely affect yields, and may interact in complex ways. Important agronomic factors which lower yields include low plant density, poor quality seeds, poor varieties and inefficient water and fertilizer management. Abiotic constraints which reduce yields significantly include poor soil structure, heat and drought stress. Among the biotic agents are diseases, insects and weeds. Of these pests, the groundnut leaf miner (GLM), Aproaerema modicella (Deventer) (Lepidoptera: Gelechiidae) is the key insect pest of groundnut throughout South Asia, and is the focus of this study. GLM may be present in extremely high numbers and has been shown to reduce yields by as much as 30% (Chap.4; Rajput et al., 1984). A large number of natural enemies, especially parasitoids, attack GLM. The biology, ecology and natural enemies of GLM have been reviewed in Chapter 2.

Crop and pest models have been successful in capturing the essential features of crop growth and development in several agroecosystems. Such models have enabled researchers to examine complex interactions between crop, pest, natural enemy, weather and farmer inputs. To investigate these interactions, a groundnut system model was developed by adapting the multi-trophic population dynamics model developed by Gutierrez et al. (1984a; 1987).

Four other groundnut models have been developed that simulate crop growth, development and yield. Duncan et al. (1978) used an unpublished model to compare physiological processes across several groundnut cultivars. Grosz et al. (1988) compared a physiologically detailed model developed by Young et al. (1979) to a simplified educational model developed by Ingram et al. (1981). Both adequately simulated pod yield but the Young et al. model also simulated top growth (leaves plus stems). The fourth simulation model was developed by adapting an existing soybean plant growth model (Boote et al., 1986). The groundnut model in this study is different from the other models because it is based on population dynamics principles (Gutierrez and Wang 1976).

CONCEPTUAL FRAMEWORK

The dynamics model

The dynamics models for both the plant and GLM are based on the Gutierrez et al. (1984) modification of the age-structured distributed-delay model (Manetsch 1976), with attrition included (Vansickle 1977). This model has been used it to simulate the dynamics of energy acquisition and allocation for several crops and insects (Gutierrez and Baumgaertner, 1984a; Gutierrez et al., 1985; Gutierrez et al., 1987; Gutierrez et al., 1988a; Gutierrez and Curry, 1989). Multiple trophic levels have been linked to incorporate the effects of disease and herbivores in several agroecosystems (Gutierrez and Baumgaertner, 1984a,b; Gutierrez et al., 1988b,c). The detail and mathematical structure of the model have been covered in depth in these papers, hence only a brief summary of the mathematics of the model and its components are presented here. The modifications to the general model necessary to simulate groundnut growth and development also are described.

The dynamics model [1] keeps track of changing birth and death rates, as well as net immigration and mass growth for each cohort $\rho_{i,j}$ where age i = 1...k in population (j).

$$\begin{aligned} d\rho_{1,j}/dt &= x_j(t) - r_{1,j}(t) - \mu_{1,j}(t,\bullet)\rho_{1,j} \qquad [1] \\ d\rho_{2,j}/dt &= r_{1,j}(t) - r_{2,j}(t) - \mu_{2,j}(t,\bullet)\rho_{2,j} \\ &\vdots \\ d\rho_{k,j}/dt &= r_{k-1,j}(t) - y_{j(t)} - \mu_{k,j}(t,\bullet)\rho_{k,j} \end{aligned}$$

As applied to plants, the model considers populations of plant subunits (leaves, stems, roots and fruits) linked via a metabolic pool (see Fig. 1, adapted from Gutierrez and Baumgaertner, 1984a). Birth rates enter the population via $x_j(t)$ in [1] and net mortality rates, including immigration and emigration, are included via $-\infty < \mu_{i,j} \leq 1$. The model is deterministic but simulates stochastic development. Age-specific mortality greatly affects the pattern of emergence from each stage and adds realism to the model. Individuals of a cohort move through the k substages at different rates depending on the number of age categories (Vansickle, 1977). When k is large, and in the absence of mortality, the emergence of the first individual is delayed, but the variation in development times is small (i.e. $k = x^2/S^2$). Time and age are measured in physiological time units (degree-days) above 10^oC.

Incorporating biology into the model

Subunit population attributes include numbers for flowers, pegs and pods, and mass for all components. For subunits in which number dynamics are followed, age specific growth may occur (e.g. fruit) via μ_i. For the other subunits, without the number attribute, mass accrues via x_k which enters the youngest age class.

The interplay between carbohydrate supply (resource acquisition) and demand (demand for assimilate) determines subunit population growth rates. The supply is daily photosynthesis which depends on LAI, solar radiation, soil water and nitrogen. For nitrogen fixing plants such as groundnut, nitrogen may not be limiting.

Photosynthesis in the model is estimated using the Frazer and Gilbert (1976) functional response model from animal ecology (Gutierrez and Baumgaertner, 1984a). This model is demand driven, which for plants is equal to the total vegetative and respiration demands for carbon. Fruit growth is also a part of the overall demand, but is not used to compute photosynthesis.

The order of priority for carbohydrate allocation at each time step (Δt) is (i) demand for respiration (and egestion in animals), (ii) reproduction (post-flower fruits), (iii) vegetative growth to all subunits except post-flower fruits. The maximum possible assimilation rate for growth and respiration is the "genetically determined" demand rate, measured for each organism under non-limiting conditions. Photosynthesis or consumption, and not the quantity of available resource, is the realized supply rate used in the production of new subunit numbers and growth of existing ones. In the model the maximum rates are constrained by shortfalls in the supply relative to the demand.

The demand rate may be computed as follows. The maximum demand rate (g plant^{-1}day^{-1}) for leaf (b_l), stem(b_s) and root(b_r) growth and reserves (b_θ) are assumed to be a fraction ($0 \leq \gamma \leq 1$ per dd) of the existing mass ($M_j(t)$, j= l,s,r) at time t.

$$0 \leq b_l(t) = \gamma_l(t)M_l(t)\Delta t \leq \lambda_{l,max} \qquad [2]$$

$$0 \leq b_s(t) = \gamma_s(t)M_s(t)\Delta t \leq \lambda_{s,max} \qquad [3]$$

$$0 < b_r(t) = c_o b_s(t) \qquad [4]$$

where $\gamma_j(t)$ and $\lambda_{j,max}$ are estimated from the field data, Δt is degree-days at day t and the constants c_i, i=1,..,4 were estimated empirically. The demand rates b_j reach a maximum $\lambda_{j,max}$ g plant^{-1}day^{-1} after maximum LAI. The $\gamma_j(t)$ are described as follows:

$$\gamma_j(t) = \begin{cases} \gamma_l & \text{if } b_l(t) < \lambda_{l,max} \\ \gamma_s & \text{if } b_s(t) < \lambda_{s,max} \end{cases} \qquad [5]$$

and $\lambda_{j,max}$ are constants. Normally the $\lambda_{j,max}$ are functions of plant density, but plant density was not included in this model. Reserve demands are a fraction of leaf demands.

$$b_\theta(t) = c_4 b_1(t) \qquad [6]$$

The total vegetative demand ($b_v(t)$) for growth is the sum of leaf, stem, root and reserve demand, scaled by nitrogen ($0 \leq \eta \leq 1$) and water ($0 \leq \omega \leq 1$) stresses at time t.

$$b_v(t) = \{b_1(t) + b_s(t) + b_r(t) + b_\theta(t)\}\ \eta(t)\omega(t) \qquad [7]$$

Reproductive structures also place a demand (b_f) on the supply of assimilate but this is not part of b_v used to compute photosynthesis. Field data from various crops (Gutierrez et al., 1987) have shown that maximum fruit and vegetative growth cannot occur simultaneously. Fruits have a higher priority than b_v, hence b_f is a major factor determining the allocation rates of assimilates to other subunits. Maximum age-specific per-capita fruit growth rates ($g_F(a)$) were estimated from field data:

$$g_F(a) = \begin{cases} c_1 \text{ for } 0 < a \leq a_f & \text{buds} \\ c_2 \text{ for } a_f < a \leq a_m & \text{post flower} \\ 0 \text{ for } a > a_m\ . & \text{fruit maturation} \end{cases} \qquad [8]$$

where $c_1 = 0.1/a_f$, c_2 are given in the Appendix, and a_m is the age when fruit growth ceases.

Metabolic pool model

Dry matter or energy is the medium for interactions between trophic levels. The distribution rates of assimilate in plants (photosynthate) are described by balance equation [9], but the process applies across trophic levels (Gutierrez and Wang, 1976). Energy is acquired from a lower trophic level and utilized by the higher trophic level. Here the emphasis is on plant biology, but the analogies to animals will be noted and incorporated into this general model (Gutierrez *et al*., 1987).

$$\begin{aligned} dA/dt &= \Theta_V\{dG/dt + d\theta/dt\} + \Theta_F dR/dt \\ &= \psi f(\psi,\Delta t,b(\eta,\omega,\bullet),s(\bullet)) - z(\Delta t,\bullet)M_T\,(t) + \theta^*(t) \\ &= M^*(t) - z(\Delta t,\bullet,t)M_T(t) + \theta^*(t) \qquad [9] \end{aligned}$$

For plants at time t: dA/dt = assimilate rate, dG/dt = maximum vegetative growth rate (leaves + stems + roots + reserves), dR/dt = maximum reproductive growth rate, $d\theta/dt$ = maximum reserve growth rate, Θ_F = supply/demand ratio ($0 < \Theta_V \leq 1$) for fruit growth at priority level 1 (see Gutierrez and Wang, 1976), Θ_V = supply/demand ratio ($0 < \Theta_V \leq 1$) for vegetative growth at priority level 2, $f(\bullet)$ is acquisition (i.e., Frazer and Gilbert (1976) functional response model) where $(\bullet)$ implies all relevant factors, $z(\Delta t,\bullet)$ is the Q_{10} rule for estimating metabolic cost rate ($\alpha 2^{0.1(T-20)}$) per unit mass of active plant mass (M_T) at temperature T and base rate α, $dt=\Delta t$ is the change in physiological time, $s(\bullet)$ is the light interception function in plants based on leaf mass and the search rate in animals based on animal mass, M_T is the total dry biomass of respiring tissues, and ν is the fraction of reserves (θ) available ($\theta^{*}=\nu\theta_{(t)}$), M^{*} is the photosynthetic rate (i.e. supply).

In the model [10], metabolic costs $z(\Delta t,\cdot)$ are first subtracted from M^{*} and the remaining photosynthate is used to meet growth demands at rates modified by θ_F and θ_V respectively. The age-specific demands of fruit are met first, after which the remaining photosynthate is allocated to vegetative growth and reserves. Similar food supply and demand relationships regulate resource allocation in other trophic levels.

GLM model

The above modeling paradigm was also used for the groundnut leaf miner, _A_. _modicella_. The herbivore model is a distributed delay model similar to eqn. [1] which accounts for changing rates of birth, death, net immigration and mass growth in cohorts of different age. Energy acquisition and allocation in the herbivore trophic level is analogous to the process described above for the plant. The groundnut leaf miner is a single population linked to the leaf population via the GLM functional response model which computes GLM leaf consumption rates. Mortality rates for GLM were not available from field data, hence a value of 0.975 per day for adults after 600 degree-days was used to produce the results reported here. This is a major deficiency in the model, and it must be corrected by further research.

FIELD DATA AND PARAMETER ESTIMATION

The plant

Field data on the growth and development of groundnut variety Kadiri 3 were used to parameterize the plant model. The data were collected at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), near Hyderabad (17° N), India. Weekly samples were collected during the post-rainy season which lasted from January to mid-April 1988. A second data set was collected at weekly intervals during the rainy season (July to October 1987) was used to compare groundnut phenology across seasons. A detailed description of the collection and analysis of plant growth data can be found in Chapter 4. Parameters used in the model and initial starting conditions are given in the Appendix.

GLM data

Population dynamics of the groundnut leaf miner (GLM) were recorded in the field during the same 2 seasons. The collection and analysis of this data are described in Chapter 3.2.

GLM temperature dependent growth and fecundity rates, adult longevity and per capita consumption rates were studied in the laboratory. The details of these investigations are given in Chapter 3.1. The parameters and initial conditions for the herbivore model are listed in the Appendix.

Weather data from 1987 to 1988 collected by the ICRISAT meteorological station were used to run the model.

SIMULATION RESULTS

1987-88 Post-rainy Season

Leaf and stem mass accumulation and the change in LAI were simulated quite closely for the first half of the post-rainy season (Fig. 2). During the second half of the season the model underestimated leaf and stem biomass as well as LAI.

Flower, peg and pod production were simulated accurately (Fig. 3). Flowers last a day and their numbers are plotted on a per degree-day basis. Pegs and pods remain on the plant, hence are plotted as per plant totals. The model accurately simulated the accumulation of dry matter in pods in the post-rainy season.

GLM populations were very low during this season (see Chap. 3.2), hence they are not reported.

1987 Rainy Season

The model accurately simulated leaf and stem biomass accumulation and the change in LAI up to the end of the season (Fig. 2). The rapid drop off in leaf and stem biomass, and LAI observed in the field at the end of the season were not predicted by the model and the reasons for this are discussed below.

With the exception of pegs, the model simulated the production of reproductive structures closely in the rainy season (Fig. 3). The model over-estimated the number of pegs produced. Despite the discrepancy in peg number, pod production was predicted accurately. The timing of pod mass accumulation was captured very closely by the model though the final mass was slightly over-estimated (Fig. 3).

GLM populations in the rainy season

GLM larval populations were several-fold higher in the rainy season compared to the post-rainy season. The model's fit to the data were very good (Fig. 4). Because GLM mortality was not modeled *per se*, the good results must be considered a fit of the simulation model to the data. Despite this deficiency, the model simulated the two generations of GLM seen in the field data. The model also predicted, but at a lower level of resolution, the initial rapid increase in larval population and the ensuing slight leveling off at ca. 300 DD.

DISCUSSION

The plant

In the post-rainy season, the model simulated less leaf and stem biomass, and LAI than were observed, but the model captured peg and pod number, and fruit mass very closely. Plant density declined approximately 20% during the season and this was not incorporated into the model. At low plant densities, individual plants are larger, but it is difficult to say what effect this had in these studies.

In the rainy season, initial simulation runs over-predicted dry matter accumulation. However, by reducing the photosynthetic rate by 10%, the model simulated both vegetative and reproductive growth very closely until the end of the season. Boote *et al*. (1980) have shown that fungal leaf diseases may reduce single leaf photosynthetic rates in groundnut by as much as 80% compared to uninfected leaves. Fungal leaf diseases may also cause defoliation, further reducing total plant productivity (Boote et al., 1980; Cole, 1982; Bell, 1986).

In this study, the incidence of fungal leaf diseases was high in the rainy season in both fungicide treated and check plots (see Chapter 4) and some defoliation was observed. Leaf and stem biomass, and LAI were lower in the field than predicted by the model at the end of the season, and it seems likely that this discrepancy was due to pathogen induced defoliation. This defoliation also may have reduced peg numbers and fruit mass in the field below the levels predicted by the model.

Other differences in groundnut growth across the two seasons were also apparent. For example, in the rainy season, plants had less leaf and stem biomass, lower LAI, fewer flowers, pegs and pods and a much lower pod mass compared to plants grown in the post-rainy season. These differences were captured by the model. However, because plant density effects were not incorporated, the observed vegetative growth rates from each season were used in the model (see Appendix). The importance of density effects on groundnut growth and development are well know. For example, Ishag (1970) recorded higher yields (kg ha^{-1}) but fewer flowers per plant at higher plant densities. More recently, Kvien and Bergmark (1987) found that higher plant densities increased partitioning of dry matter into stems and increased plant height but that yield differences were dependent on planting date and location. Incorporation of density effects in the model would enable one to examine these conclusions.

Groundnut leaf miner

The high GLM population observed in the rainy season was simulated very accurately by the model, given the constraints described above. Larval populations were very high early in the season, indicating a high adult immigration rate. The rapid decline in GLM numbers after the first generation was simulated using a high level of adult GLM mortality. This mortality was probably caused by the many natural enemies which attack GLM immatures and not the adults. While the specifics may not be correct, the model does predict that a high mortality rate probably occurred in the field.

The effect of GLM on leaf, stem and pod mass, and LAI can be seen by comparing sprayed and unsprayed plots in the rainy season (Fig. 5). Leaf, stem and pod mass were reduced approximately 30% in unsprayed plots, indicating the significant impact that GLM can have. The model did not accurately capture this effect of GLM on groundnut growth and development, and this is an aspect which requires additional work.

Summary

The groundnut/GLM simulation model highlighted the several areas needing additional research. Questions which need to be resolved include, are differences in photosynthetic rates between seasons accurate, what are the cause(s) of the differences (e.g. fungal diseases or climatic effects), what are the effects of plant density on groundnut growth and development, including both within-season changes in plant density and differences in initial planting density, why was the predicted impact of GLM on growth and yield so small, and why did GLM populations declined so dramatically after the first generation?

The purpose of models is not to predict or model every aspect of nature, but to gain insights into the patterns and processes of nature. Model building is an interactive process between experiments and field trials, and model refinement. As the model is developed, weaknesses and deficiencies in the model and the data become apparent, and further experiments can be designed to determine where the error(s) lies. The groundnut/GLM models and simulation results presented in this paper are the first steps in this process and have indicated where future research should be directed.

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Figure 1. Major components of the groundnut system model.

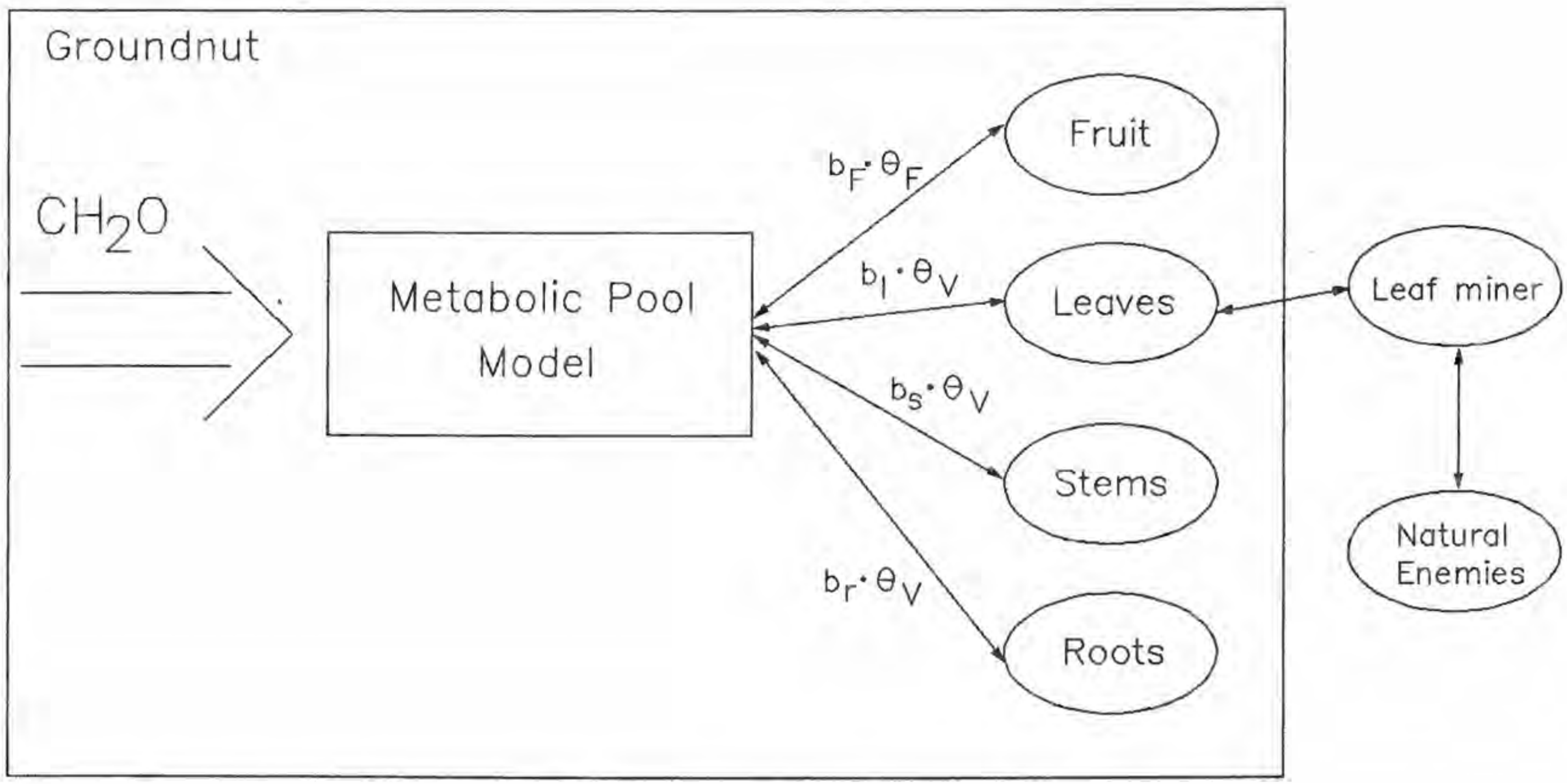
Groundnut
CH_2O
Metabolic Pool Model
$b_F \cdot \theta_F$
$b_l \cdot \theta_V$
$b_s \cdot \theta_V$
$b_r \cdot \theta_V$
Fruit
Leaves
Stems
Roots
Leaf miner
Natural Enemies

Figure 1.

Figure 2. Leaf and stem mass (plant^{-1}) in post-rainy (A) and rainy (B) seasons. Leaf area index (LAI) in post-rainy (C) and rainy (D) seasons.

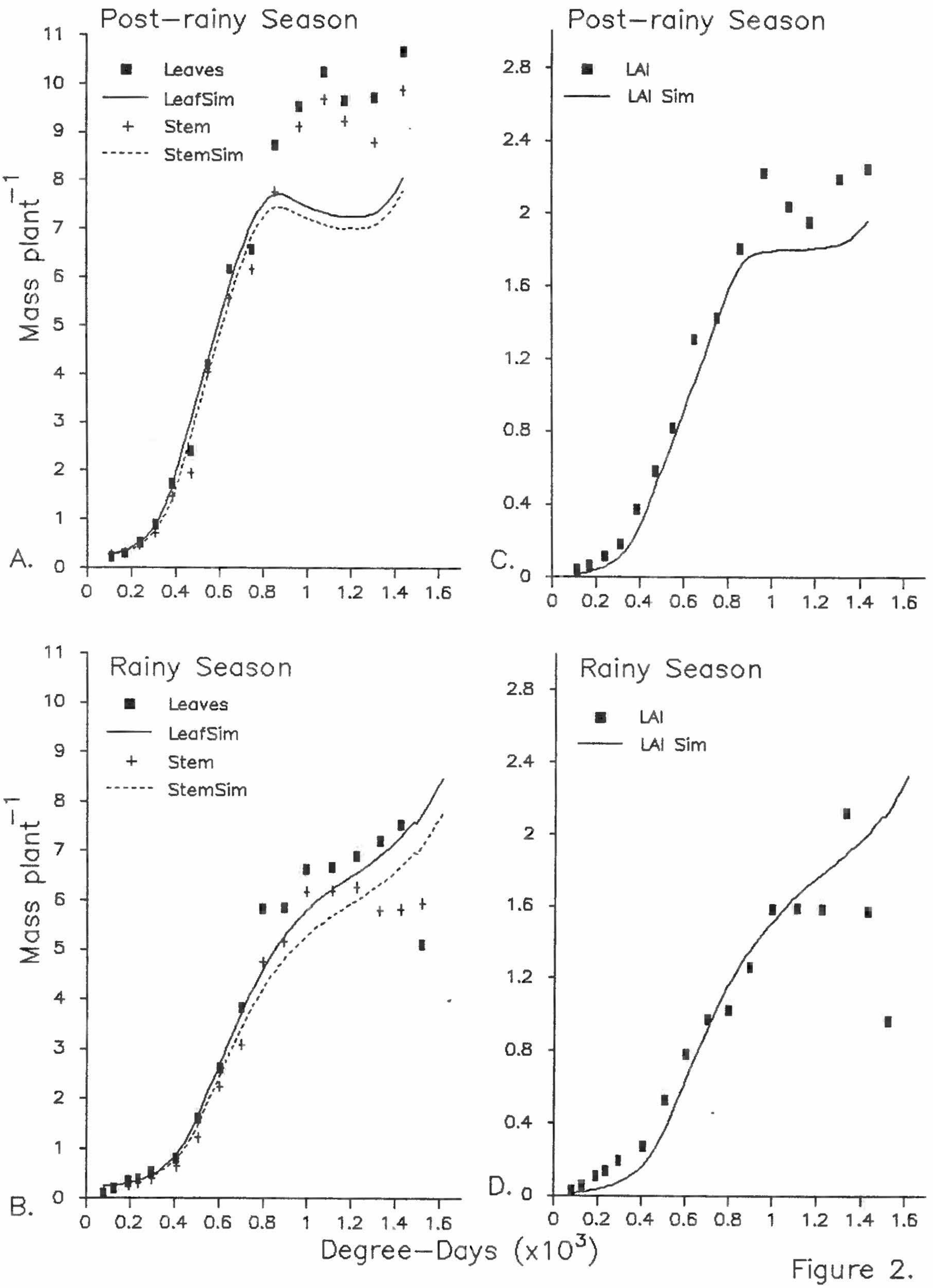
Post-rainy Season
Leaves
LeafSim
Stem
StemSim
Mass plant^{-1}
A.
0
1
2
3
4
5
6
7
8
9
10
11
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
Post-rainy Season
LAI
LAI Sim
C.
0
0.4
0.8
1.2
1.6
2
2.4
2.8
Rainy Season
Leaves
LeafSim
Stem
StemSim
Mass plant^{-1}
B.
Rainy Season
LAI
LAI Sim
D.
Degree-Days (x10^3)

Figure 2.

Figure 3. Flower, peg and pod number (plant^{-1}) in post-rainy (A) and rainy (B) seasons. Fruit mass (plant^{-1}) in post-rainy (C) and rainy (D) seasons.

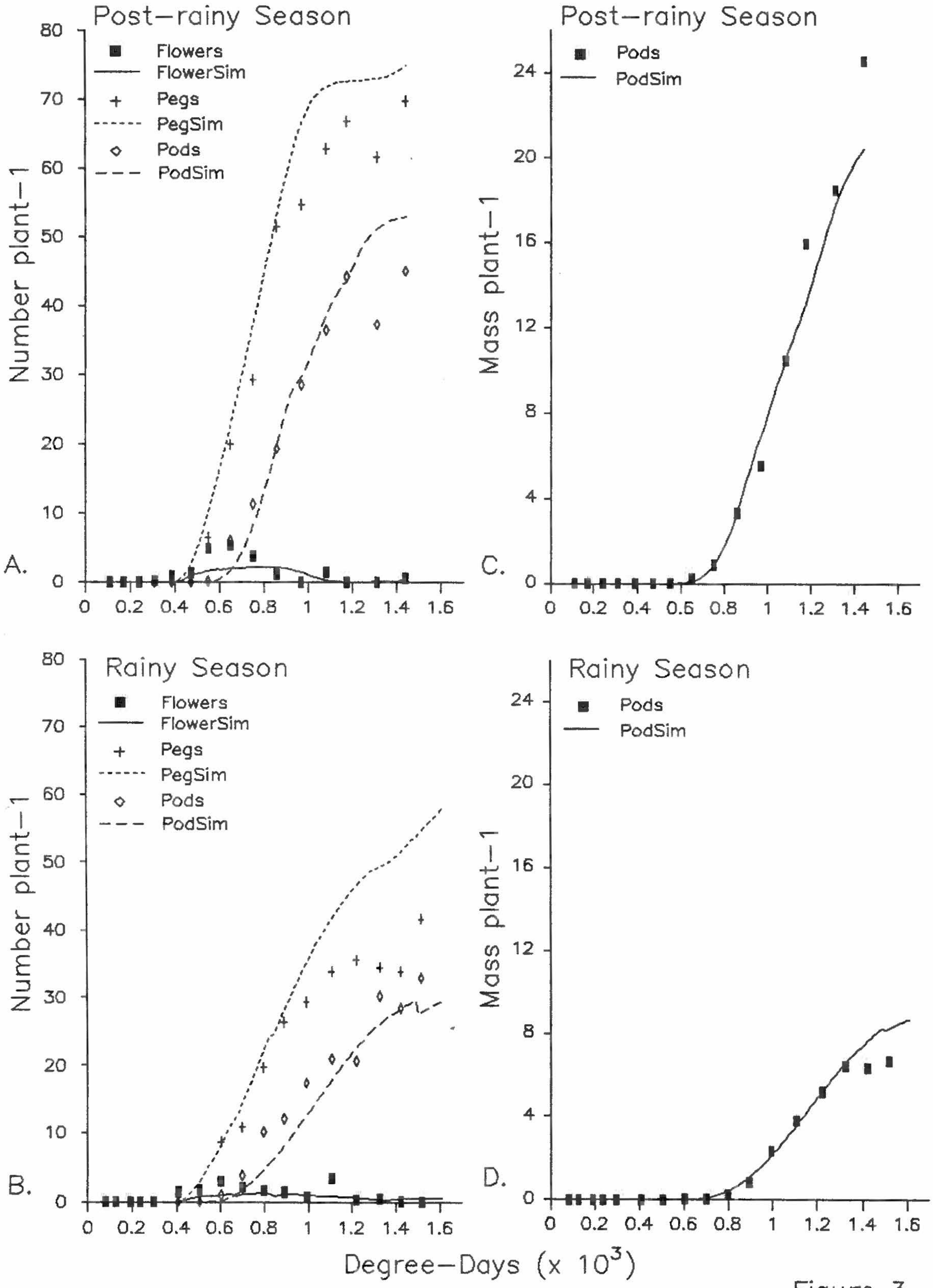
Post−rainy Season
Flowers
FlowerSim
Pegs
PegSim
Pods
PodSim
Number plant−1
0
10
20
30
40
50
60
70
80
A.
Post−rainy Season
Pods
PodSim
Mass plant−1
0
4
8
12
16
20
24
C.
Rainy Season
Flowers
FlowerSim
Pegs
PegSim
Pods
PodSim
Number plant−1
B.
Rainy Season
Pods
PodSim
Mass plant−1
D.
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
Degree−Days (x 10^3)

Figure 3.

Figure 4. Simulated and observed Aproaerema modicella population dynamics (larvae plant^{-1}) in the 1987 rainy season.

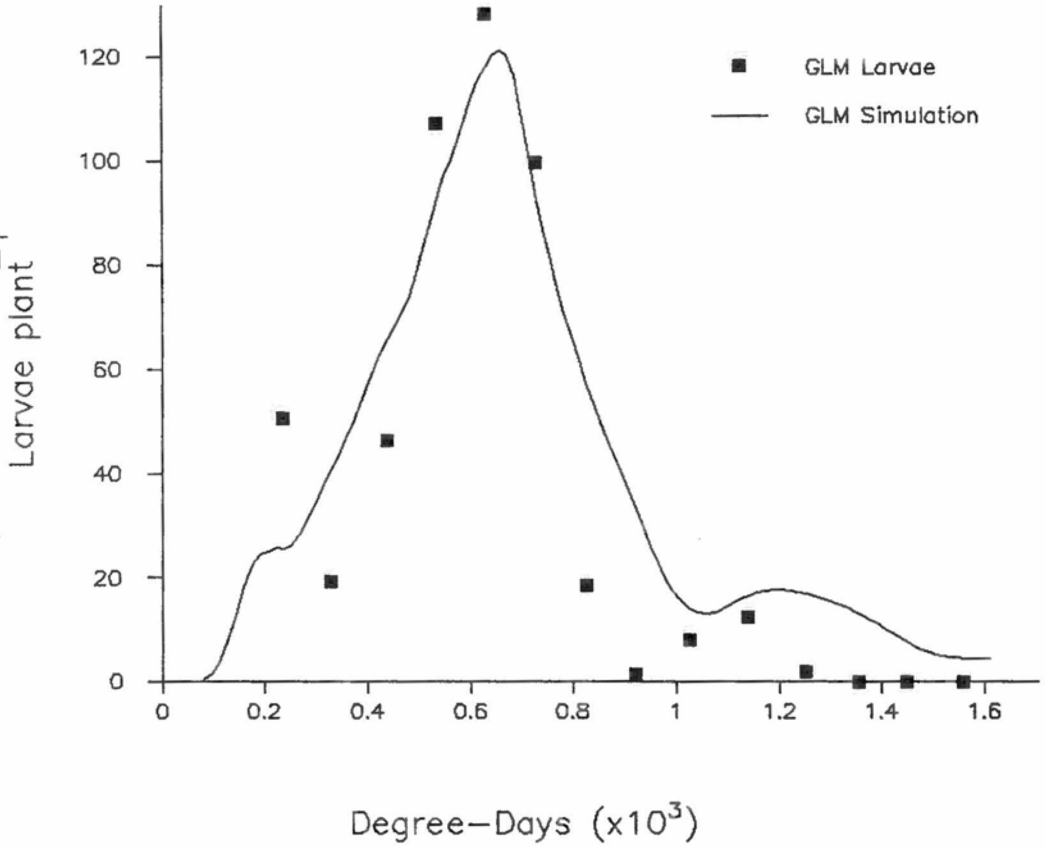
Larvae plant^{-1}
0
20
40
60
80
100
120
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
Degree—Days (x10^3)
GLM Larvae
GLM Simulation

Figure 4.

Figure 5. The effect of defoliation by Aproaerema modicella on leaf mass, stem mass, leaf area index and pod mass under field conditions in the 1987 rainy season.

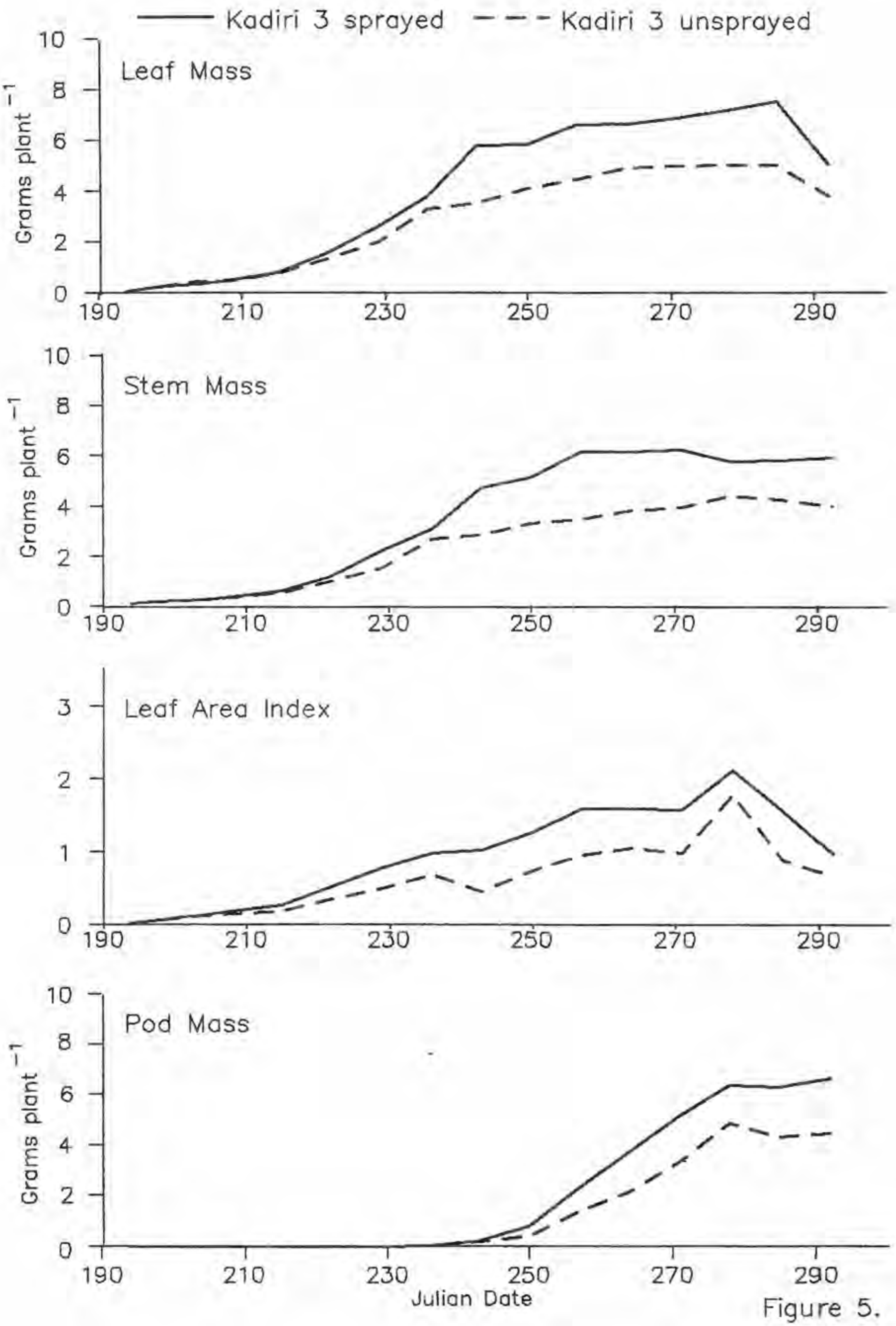
Kadiri 3 sprayed
Kadiri 3 unsprayed
Leaf Mass
Grams plant $^{-1}$
10
8
6
4
2
0
190
210
230
250
270
290
Stem Mass
Grams plant $^{-1}$
10
8
6
4
2
0
190
210
230
250
270
290
Leaf Area Index
3
2
1
0
190
210
230
250
270
290
Pod Mass
Grams plant $^{-1}$
10
8
6
4
2
0
190
210
230
250
270
290
Julian Date

Figure 5.

APPENDIX

Groundnut parameters

	Post-rainy season	Rainy season
Plants m^{-2}	13	16.5
Emergence	25 December 1987	8 July 1987
Harvest	22 April 1988	26 October 1987
Plant age (dd) to first fruit	350	350
Fruit age (dd) flower (a_{fl})	475	475
Delay in pod growth (a_{fl} +)	140	140
To max growth	375	375
Shed windows		
Bud	0-50	0-50
Maturing fruit (a_{fl} +)	100	100
Fruit growth rate (g dd^{-1} day^{-1})		
Pre-peg =	$0.1/a_{fl}$	$0.1/a_{fl}$
Young fruit (c_6)	0.00185	0.0015
Fruit point production rate (FP dd^{-1} $plant^{-1}$)	0.15	0 .12
Leaves (L), stem (S) and root (R)		
development time (dd)		
leaves	1500	1500
stem	2500	2500
root	2500	2500
leaf mass dm^2g^{-1}	1.95	1.95

Growth paramters

$L(0)$ (g)	0.025	0.025
γ_1 (g/g/dd)	0.0105	0.0085
$\lambda_{1,max}$ (g/day)	0.0125	0.01
$S(0)$ (g)	0.025	0.025
γ_s (g/g/dd)	0.0105	0.0085
$\lambda_{s,max}$ (g/day)	0.0125	0.01
$\gamma_r = c_o \cdot \gamma_s$ (g/dd)	0.17	0.17
$\gamma_{res} = c_4 \cdot \gamma_1$ (g/dd)	0.300	0.300

Constants for plant growth rate functions in eqns. [5 - 8].

c_o fraction	0.17	0.17
c_1 "	0.001	0.001
c_2 "	0.078	0.078
c_3 "	0.144	0.144
c_4 "	0.300	0.300

Aproaerema modicella parameters and initial values

Adult immigration rate (# plant^{-1} DD^{-1})	0.0325
Development threshold (^{o}C)	12.0
Development time (DD)	
Eggs	60.1
Larvae	327.1
Pupae	72.3
Adult longevity (DD)	202.4
Oviposition rate (eggs DD^{-1})	1.54