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Natural enemies of the groundnut leaf miner, Aproaerema modicella (Deventer), were studied at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) located near Hyderabad in peninsular India. Hymenopterous parasitoids attacking leaf miner larvae were the most important group of natural enemies. Nine primary and eight secondary parasitoids emerged from host larvae, and killed up to 50 % of the leaf miner larvae sampled. The trophic relationships between primary and secondary parasitoids are incompletely understood. The influence of pathogens of this species is reported for the first time. These pathogens killed up to 30 % of the leaf miner larvae. The combined effects of all mortality agents killed up to 95 % of the leaf miner larvae per sample period. However, use of insecticides in sprayed plots reduced the efficacy of parasitoids. The impact of predators on larval populations was not studied and may explain underestimates of leaf miner mortality rates.

KEY-WORDS: Aproaerema modicella, parasitoid, pathogen, groundnut, India.

The groundnut leaf miner (GLM), Aproaerema modicella (Deventer) (Lepidoptera: Gelechiidae) is a key pest of groundnut and soybean in South and Southeast Asia (Wightman & Amin, 1988). On groundnut in India, leaf miner populations typically complete four generations per season. Population densities fluctuate widely between generations and seasons, and pod yield losses of > 30 % have been associated with high density GLM populations (ICRISAT, 1986; Shanower, 1989). A number of GLM predators and pathogens have been identified (Godse & Patil, 1981; Oblasami et al., 1969; Maxwell-Lefroy & Howlett, 1909; Srinivasan & Siva Rao, 1986; Shanower & Ranga Rao, 1990), but their impact has not been quantified. The most important natural enemies are parasitic Hymenoptera, which primarily attack the larval stage (table 1).

In India, GLM larval parasitoids often parasitize > 90 % of the available hosts late in the rainy season (August and September) (Shetgar & Thombre, 1984; Khan & Raodeo, 1978; Wightman, unpublished). Yadav et al. (1987) found that the relative abundance of primary parasitoids changed markedly during the year. Goniozus sp. was the most abundant species in the post-rainy season (December to April), and Stenomesius japonicus (Ashmead) and Apanteles sp. were most abundant in the rainy season. Total parasitization reached 75 % in the post-rainy season and 89 % in the rainy season (Yadav et al., 1987).

TABLE 1

Parasitoids reported from Aproaerema modicella (1) on groundnut and soybean, host stage attacked, and host-parasitoid relationship

Family	Parasitoid	Host Stage Attacked	Host-Parasitoid Relationship (if known)
Bethylidae			
	ozus sp.	Larva	Primary
G. st	omopterycis Ram & Subba Rao	Larva	
Peris	ierola sp.	Larva	
Braconidae			
•	nteles sp.	Larva	Primary
	vensis Rohwer	Larva	
	ngaporensis Szepligeti	Larva	
	tae Nixon	Larva	
	ga choaspes Nixon	Larva	Primary
	ixoni Subba Rao & Sharma	Larva	
	on sp.	Larva	Primary
	revicornis Wesmael	Larva	
	elechiae Ashmead	Larva	
	Microbracon) hebetor Say	Larva	
	onus (Microchelonus) sp.	Egg/Larva	Primary
	lackhurni Cameron	Egg/Larva	
	urvimaculatus Cameron	Egg/Larva	
Phan	perotoma sp.	Egg/Larva	
Ceraphroni			
	hanogmus fijiensis (Ferriere)	Larva	Secondary
Cera	phron sp.	Larva	Secondary
Chalcididae	:		
Brac	hymeria sp.	Larva/Pupa	
	utellophaga Girault	Larva/Pupa	
	inuta (Linnaeus)	Pupa	
	sus (Walker)	Pupa	
Euce	psis sp.	Pupa	
Elasmidae			
	mus sp. nr. luteus Crawford	Larva	Secondary
	smus anticles Walker	?	Secondary
Elasi	mus brevicornis Gahan	?	
Encyrtidae			
Capi	dosoma sp.	Larva	
Eulophidae			
	scotolynx coimbatorensis Rohwer	Larva	
* 00	myzus sp.	?	Secondary
Pedi	obius sp.	Larva	Secondary
	omesioideus ashmeadi Subba Rao & Sharma	Larva	
	omesius japonicus (Ashmead)	Larva	Primary
Sten	omesius sp.	?	Secondary?
	piesis (Asympiesis) sp.	Larva	
	mpiesis dolichogaster Ashmead	Larva	Primary
	dica Girault	Larva	
Tetr	astichus sp.	Larva	Secondary

Family	Parasitoid	Host Stage Attacked	Host-Parasitoid Relationship (if known)	
Eupelmidae	;			
Eupelmus sp. (urozonus-group)		Larva/Pupa Secondary		
E. sp	o. nr anpingensis	Larva/Pupa		
Eurytomida	ne.			
Eurytoma sp. (braconidis-group)		?	Primary?	
Plute	archia giraulti Subba Rao	Larva	·	
Ichneumon	idae			
* Temelucha sp.		Larva Primary		
Pteromalida	ae			
Dibr	achys sp.	Larva		
	rocytus sp.	Larva		
	eromalus sp.	?	Secondary	
Trichogram	nmatidae			
Trichogramma sp.		Egg Primary		

⁽¹⁾ From: Krishnamurthi & Usman, 1954; Subba Rao et al., 1965; Subba Rao & Sharma, 1966; Mohammad, 1981; Phisitkul, 1985; Srinivasan & Siva Rao, 1986; Shanower, 1989.

* New record.

The purpose of the research reported here was to identify the important natural enemies of GLM larvae and indicate their impact on GLM population dynamics. The relative abundance and trophic relationships among parasitoid species were also studied.

MATERIALS AND METHODS

This research was carried out on the 1,300 ha farm of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), located near Hyderabad (17°N), Andhra Pradesh, in peninsular India. In this region, groundnuts are mostly grown in the rainy (July to October) and the post-rainy (December to April) seasons. GLM larvae were collected at weekly intervals in both seasons. The population dynamics of GLM show very distinct peaks in the number of larvae per plant (Shanower, 1989) and it seems likely that these indicate distinct generations. However, immigration and overlap between generations are possible so, to avoid using the term "generation", samples collected during the 2 seasons were grouped into sampling periods. Each period included 3 or 4 weekly samples. Samples were grouped into 4 periods in the 1987-88 post-rainy season, and one period in the 1988 rainy season.

GLM larvae were collected from field experiments designed to evaluate the effect of 2 varieties (NC Ac 17090, partly resistant and Kadiri 3, susceptible) and the efficacy of chemical control strategies on GLM populations. Each field experiment had 5 variety \times insecticide treatments with 4 replicates per treatment in a randomized block design. The treatments included a control (unsprayed) and sprayed treatment for both varieties. A foliar spray of dimethoate (at 240 g ha⁻¹ in 350 L water) was applied twice per season. The 5th treatment was oftanal applied only to Kadiri 3 as granules at 2 kg ai ha⁻¹.

Leaves containing GLM larvae were randomly sampled from all replicates in each treatment. After determining that only a single GLM larva was present per leaf, it was

placed on moistened filter paper in 30×70 mm plastic Petri dishes and observed daily until the potential host died or eclosed. The number of larvae sampled ranged from 22 to 65 per treatment in the 1st period of the 1987-88 rainy season. In the 2nd period 8 to 54 larvae were collected, and in the 3rd and 4th periods 68 to 116 and 98 to 122 larvae respectively were found. Between 62 and 114 larvae per treatment were sampled in the single sampling period of the 1988 rainy season. The cause of each host death was recorded.

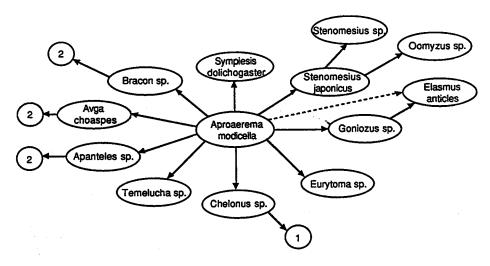
Parasitoids were identified by Z. Boucek, A. Polaszek and A. K. Walker at the CAB International Institute of Entomology, British Museum (Natural History). The relative abundance of each parasitoid was calculated for each of five sampling periods. The emergence of secondary parasitoids from pupae of primary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

Data on the proportions of GLM larvae killed by parasitoids and pathogens in each sampling period were transformed using an arc-sine transformation. Two-way analysis of variance (ANOVA) was used to test differences in mortality across treatments and sampling periods (Zar, 1974; Gomez & Gomez, 1984).

RESULTS

PARASITOID COMMUNITY

Parasitoids reared from GLM larvae at ICRISAT (fig. 1) include new records for 3 primary parasitoids, *Temelucha* sp., *Avga choapes* Nixon, and *Sympiesis dolichogaster* Ashmead, and 4 secondary parasitoids, *Pteromalus* sp., *Oomyzus* sp., *Elasmus anticles* Walker and *Aphanogmus fijiensis* (Ferriere). The food web which includes GLM and its primary and secondary parasitoids (fig. 1) is much more complex than previously thought (Mohammad, 1981).



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

Fig. 1. Trophic relationships between Aproaerema modicella and its parasitoids at ICRISAT, India.

What was initially considered to be a single braconid species was later determined to be three species in different genera: Apanteles sp., Avga choapes and Bracon sp. All 3 are larval ectoparasitoids which paralyze the host before oviposition. The effect of these 3 primary parasitoids was combined in the analysis of the community.

The relative abundance of the dominant primary parasitoids changed during the five GLM generations studied (table 2). In the first sampling period, *Sympiesis dolichogaster* was dominant, emerging from more than 25 % of the parasitized GLM larvae. The 3 braconids mistakenly considered a single species, combined to kill 28 % of the GLM larvae collected in the first sampling period. Secondary parasitoids, including several unidentified species, emerged from 26 % of the GLM larvae in the first sampling period.

In subsequent sampling periods, the proportion attacked by S. dolichogaster declined while the fraction killed by Stenomesius japonicus increased (table 2). Parasitism by the 3 braconids (Apanteles sp., Avga choaspes, Bracon sp.) also decreased. Two species, Chelonus sp. and Goniozus sp., never emerged from more than 15% of the parasitized larvae in any sampling period. Secondary parasitoids emerged from between 19% and 40% of the hosts collected within any sampling period.

TABLE 2

Relative abundance of primary parasitoids emerging from different generations of Aproaerema modicella larvae, 1987-1988, ICRISAT, India

	Season and Sampling period					
Prasitoid species	1987-88 Post-rainy				1988 Rainy	
	1	2	3	4	1	
Sympiesis dolichogaster	0.26	0.29	0.12	0.16	0.01	
Stenomesius japonicus	0.06 0.00	0.08 0.12	0.25 0.11	0.22 0.07	0.51 0.04	
Goniozus sp.						
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 (2)	0.26	0.19	0.32	0.40	0.32	

⁽¹⁾ Includes three species: Apanteles sp., Avga choaspes and Bracon sp.

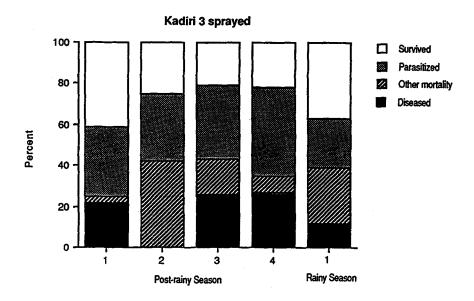
MORTALITY FACTORS

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.

Parasitization rates did not differ significantly across either treatments (ANOVA; $F_{4,75}=1.77$; p=0.14) or sampling periods (ANOVA; $F_{4,75}=1.30$; p=0.28). The proportion of diseased larvae did not differ across treatments (ANOVA; $F_{4,75}=0.35$; p=0.84) but showed significant differences across sampling periods (ANOVA; $F_{4,75}=13.99$; p<0.0001)). In all treatments, parasitization and disease infection increased through the season (fig. 2, only data for cv. Kadiri 3 shown). By the 4th sampling period, 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 % were parasitized.

A separate analysis consisting of only the 2 unsprayed control treatments showed that parasitization rates were not significantly different (ANOVA; $F_{1.30} = 5.88$; p = 0.06). A

⁽²⁾ Includes all remaining parasitoids which emerged from A. modicella larvae.



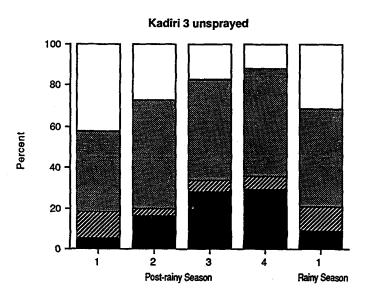


Fig. 2. Larval mortality in Aproaerema modicella through five sampling periods at ICRISAT, India, 1987-88.

similar analysis showed that parasitization rates in the 2 insecticide spray treatments also were not significantly different (ANOVA; $F_{1,30}=0.61$; p=0.44). The 2 control treatments and the 2 insecticide spray treatments were then pooled into overall control and insecticide treatments and compared. The Kadiri 3 treatment with oftanal was not included in this analysis because there was no equivalent treatment in the NC Ac 17090 variety.

Two-way analysis of variance on the pooled data set indicated that parasitization rates were significantly lower in the sprayed treatment than in control treatment (ANOVA; $F_{1,70} = 5.56$; p = 0.02). There was, however, no significant difference in disease incidence between sprayed and unsprayed treatments in the pooled data (ANOVA; $F_{1,70} = 1.19$; p = 0.28).

DISCUSSION

In Gujarat, India, 4 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, in peninsular India, was equally dynamic, with the composition and dominant species changing through the year. The dominant primary parasitoids were S. japonicus, S. dolichogaster and the group of three braconids, Apanteles sp., Avga choaspes and Bracon sp.

Four previously unreported secondary parasitoids were discovered in this community (see table 1). The only other report of secondary parasitoids in the GLM community included 5 species, *Pediobius* sp., *Ceraphron* sp., *Tetrastichus* sp., *Eurytoma* sp. and an unidentified pteromalid (Subba Rao et al., 1965). Relationships between primary and secondary parasitoids are complicated and are incompletely understood. At least one secondary parasitoid (*Oomyzus* sp.) attacks 2 different primary parasitoids and other secondary parasitoids may also attack more than one primary host. Because 3 species of braconid were not differentiated it is unclear which secondary parasitoid is associated with which primary parasitoid.

The dashed line connecting E. anticles to GLM (fig. 1) indicates the confusion concerning the role of this species 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 a Goniozus sp. pupa. It is possible that the Elasmus sp. in the two earlier studies and E. anticles found at ICRISAT are different species with different feeding habits. Alternatively, 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.

This paper provides the first evidence of the importance of disease organisms on the population dynamics of A. modicella. Up to 30 % of the larvae in a sample were infected by viral and fungal pathogens. The proportion of GLM larvae killed by pathogens was higher in the latter two sampling periods of the post-rainy season indicating that pathogen levels built up through the season. Fungal and viral pathogens have been identified from GLM larvae (Oblasami et al., 1969; Godse & Patil, 1981), but the effect on GLM populations had not been 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 sampling periods, which had higher GLM densities, had marginally higher parasitization rates.

The effectiveness of parasitoids was constrained by the use of insecticides, resulting in lower parasitization rates in insecticide treatments. GLM populations were slightly lower on sprayed plots because the insecticide killed both GLM larvae and the parasitoids. But because GLM populations were low in both seasons 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 differences between treatments were not significant.

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). The potential negative impact of insecticides on GLM natural enemies in groundnut agroecosystems of India has been demonstrated in this study. Ranga Rao & Shanower (1988) noted the increased incidence of Spodoptera litura (Fab.) in groundnut fields treated for GLM. These results should serve as a warning against the excessive use of chemical insecticides for groundnut pest management.

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 3 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 of this system. Additional work on the biology of the secondary parasitoids is needed to resolve the nature of their relationships with primary parasitoids. The impact of predators on leaf miner larvae is another area where additional work is required. Generalist predators (beetles, birds and spiders) may account for the higher mortality rates reported in field studies.

ACKNOWLEDGEMENTS

We thank the field staff of the Legumes Entomology Unit at ICRISAT for help in sampling and rearing Aproaerema modicella; Z. Boucek., A. Polaszek and A. K. Walker at the CAB International Institute of Entomology, British Museum (Natural History) for identifying the parasitoids; and The Rockefeller Foundation for providing fellowship support to the senior author.

RÉSUMÉ

Pathogènes et parasitoïdes larvaires d'Aproaerema modicella (Lep. : Gelechiidae) en Inde

La mineuse des feuilles d'arachide, Aproaerema modicella (Deventer) (Lepidoptera: Gelechiidae) est un ravageur important des cultures d'arachide et de soja en Asie du sud. Un grand nombre d'ennemis naturels des larves de la mineuse, notamment des parasitoïdes hyménoptères, ont été signalés. Au cours de cette étude, neuf espèces de parasitoïdes primaires et huit espèces de parasitoïdes secondaires ont été obtenues par émergence à partir de larves prélevées sur le terrain. Les taux de mortalité dûs à ces parasitoïdes peuvent atteindre 50 % des larves de chaque génération de la mineuse. L'efficacité de ces ennemis naturels est diminuée par l'emploi d'insecticides.

Les interactions trophiques entre parasitoides primaires et secondaires au sein de cette biocoenose

sont complexes et ne sont pas entièrement élucidées.

Deux pathogènes non-identifiés ont aussi été notés sur les larves de la mineuse. Les taux de mortalité des larves de la mineuse dûs à ces deux pathogènes en combinaison ont atteint 30 % dans le cas d'une des générations étudiées. Au total, les ennemis naturels en Inde péninsulaire provoquent une mortalité de 95 % des larves de la mineuse.

MOTS CLÉS: Aproaerema modicella, parasitoïde, pathogène, arachide, Inde.

Received: 15 March 1991; Accepted: 25 October 1991.

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