The influence of drought stress on the distribution of insects on four groundnut genotypes grown near Hyderabad, India

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Abstract

Four groundnut genotypes were grown in a randomized block design across a drought-stress gradient to determine the influence of this factor on insect distribution in the 1985–86 post-rainy season near Hyderabad, in peninsular India. The leaf-miner *Aproaerema modicella* (Deventer) was most abundant on the most stressed plants. The cicadellid *Empoasca kerri* Pruthi had the reverse distribution. The thrips *Frankliniella schultzei* (Trybom) and *Scirtothrips dorsalis* Hood were at first densest where drought stress was least. Their distribution subsequently became reversed and, as the condition of their hosts worsened, they again became most abundant at the wetter end of the gradient. Bud necrosis disease caused most mortality where drought stress was highest. A subsidiary experiment indicated that the intensity of overhead irrigation did not influence the density of *A. modicella*. There were marked genotype effects: JL 24 carried the highest density of insects and was most susceptible to bud necrosis disease; NC Ac 343 had the lowest leaf-miner and cicadellid populations. M 13 and ICGS 11 had intermediate characteristics.

Introduction

Groundnuts are the major source of edible oil in India and are an important component of the diet of many subsistence farmers in Africa, South-East Asia and China. The constraints to production include pests, diseases and a multiplicity of agronomic factors including drought. The last is particularly relevant to farmers in the semi-arid tropics, the climatic zone where annual rainfall is concentrated in a period of a few months (the 'monsoons') and has an uneven distribution.

In this paper, research is reported that was carried out to determine the effect of drought stress on the incidence of four pest taxa and one virus disease that occur regularly on groundnut crops on the research farm at International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Center, near Hyderabad, Andhra Pradesh, India. Four genotypes with a range of resistance to insects were compared.

The groundnut leaf-miner *Aproaerema modicella* (Deventer) (Lepidoptera: Gelechiidae) is a major pest of groundnuts in India and is also found throughout South-East Asia. It was the main focus of this experiment. Newly hatched larvae mine the leaflets. When

they are too large to occupy the mine, they vacate it and form a refuge by joining together with silk webbing two halves of a leaflet or two or more individual leaflets. They continue to eat mesophyll tissue. They have three or four, more or less discrete generations per groundnut-growing season. In the absence of natural mortality factors, their number can increase by up to a factor of 20 per generation so that, by the pod-filling stage, they have the potential to be present in high densities.

Other foliar pests of groundnut are thrips, including *Frankliniella schultzei* (Trybom), *Thrips palmi* Karny and *Scirtothrips dorsalis* Hood. They can be vectors of tomato spotted wilt virus, which causes bud necrosis disease (BND), a major constraint to yield in India and other parts of the world.

Cicadellids are very common on groundnut crops wherever they are grown, but their pest status, other than as vectors of mycoplasma-like organisms in South-East Asia, is not fully established. *Empoasca kerri* Pruthi is the species most often encountered on groundnut plants in India, and the insect studied in these experiments.

Termites of a wide range of species reduce yields by killing plants and damaging pods. They are a particular problem throughout Africa and are also pests in Asia (Verma & Kashyap, 1980). As insects living in the soil can be sensitive to soil moisture levels (Wightman, 1973), the soil moisture gradient established in the present study was used to determine whether this factor influenced the distribution of termites.

A line source irrigation system (Hanks *et al.*, 1976) made it possible to produce a drought-stress gradient across the field. As water was applied from sprinklers, it was possible to examine the possibility that water falling on the leaves had an effect on *A. modicella* density. This was done by surface-irrigating an area adjacent to the main experiment. Plants in half of this area received scaled amounts of water from an overhead irrigation system; those in the other half received none. Thus, no plants were drought-stressed, but half received varying amounts of water from an overhead irrigation system.

Materials and methods

Genotypes

The genotypes compared were:

ICGS 11: a high yielding variety bred at ICRISAT and released for distribution in parts of peninsular India as a post-rainy season crop. It is a Spanish bunch selection from Robut 33-1 (renamed Kadiri 3) which is stated to have resistance to *F. schultzei* (Amin, 1985).

JL 24: an early maturing Spanish type. A high yielding cultivar known to have little or no resistance to pests; grown throughout India.

M 13: a late maturing Virginia runner cultivar with some resistance to some pests including *A. modicella*.

NC Ac 343: a parent of cultivar NC 6 released in North Carolina in the late 1970s (Campbell *et al.*, 1977); it has multiple pest resistance and other satisfactory agronomic characteristics.

None of these genotypes has drought resistance *per se*, although JL 24 may escape late season drought by virtue of its short growing period.

The experimental area was sown on 18 December 1985 on an Alfisol to which superphosphate (60 kg P_2O_5/ha) had been added before sowing. It was surface-irrigated immediately after sowing to ensure germination. Three hand weedings were required during the growing season.

The main experimental area was 40 m long and consisted of nine 1·25-m-wide beds separated by a 30-cm-wide furrow. There were four rows of seeds per bed. The rows were 25 cm apart. NC Ac 343 was sown with 10 cm between seeds. The other cultivars had a 15-cm seed spacing. The cultivars were randomly distributed along the beds. There were five replicates, each occupying an 8-m length of the total area. There were four 1·5-m-long rows within each replicate, each row being separated by 0·5 m of unsown bed. The plots (i.e. the drought stress 'treatments') consisted of two adjacent beds for Treatments 1–4 (T1 to T4) or one bed only (T5). T1 was closest to the line source and, therefore, received most water. T5 received virtually no water.

The subsidiary experiment was sown with ICGS 11 as a 60-m continuation of the main experiment. It was divided into two equal blocks, both of which received surface (furrow) irrigation to saturation at approximately six-day intervals. One block was irrigated with the line source system at the same time as the main experiment.

Environmental factors

Rainfall and maximum and minimum air temperatures were recorded at the main ICRISAT agrometeorological station, some 500 m from the experimental area. Leaf-surface temperatures were measured with an infrared thermometer between 11.00 and 14.00 h from 82 days after 50% emergence (DAE) until harvest. The amount of water applied by the line-source system was monitored by placing plastic buckets in each plot before irrigation and measuring the amount applied. Soil moisture in the top 10 cm of soil was determined gravimetrically by taking cores 5 cm in diameter from each treatment in each replication at the start and end of each irrigation cycle. The field capacity and wilting point of the soil were measured with a pressure membrane apparatus.

Insect and plant sampling and plant mortality caused by bud necrosis disease

In the main experiment, 5–10 plants per plot were searched for *A. modicella* mines and webs at about ten-day intervals. The number of leaves on these plants was recorded at the same time.

E. kerri density was assessed five times during the season by counting the number of adults and nymphs on five plants per plot. The number of thrips per terminal and the total number of terminals per plant were recorded on the same day.

In the subsidiary experiment, 30 plants from the plots to which line-source irrigation was applied were sampled for *A. modicella* on the days the samples were taken from the main experimental area. As the block which received surface irrigation alone was small enough to be considered uniform, 30 plants were sampled at random from the whole area in the same way. The number of plants dying because of bud necrosis disease was also recorded towards the end of the experiment.

Five plants were removed at random every 10–15 days from each plot in the subsidiary area and were examined in the laboratory. The numbers of leaves, and *A. modicella* mines and webs were recorded.

Each plot in the main experimental area was delimited by bamboo pegs driven 10 cm into the ground. At the end of the experiment, those pegs that had not been disturbed were examined for the presence of termites.

Results

The environment

Air temperatures increased markedly during the study period. There was measurable rainfall on five occasions (Fig. 1) which only temporarily relieved the drought stress experienced by the plants in T4 and T5. A marked drop in the weekly mean maximum temperature followed rainfall 18 and 117 days after emergence. The amount of water applied to each set of plots fluctuated from occasion to occasion, but the ratio between treatments was fairly constant (Fig. 2). The time between water applications was decreased as the season progressed to compensate for the increase in evapotranspiration rate caused by the rising temperature. The mean soil moisture content ranged from field capacity immediately after irrigation in T1 to 6·0% field capacity in T5 at the end of an irrigation (Table I). Wilting point was 12·0%. This indicates the degree of drought stress that the plants experienced in the unirrigated plots.

The temperatures of the upper leaves in the canopy followed the air temperatures and were influenced by irrigation and rainfall (Fig. 3). There was a consistent gradient from T1 to T5 across genotypes. The highest leaf temperature recorded was 47°C.
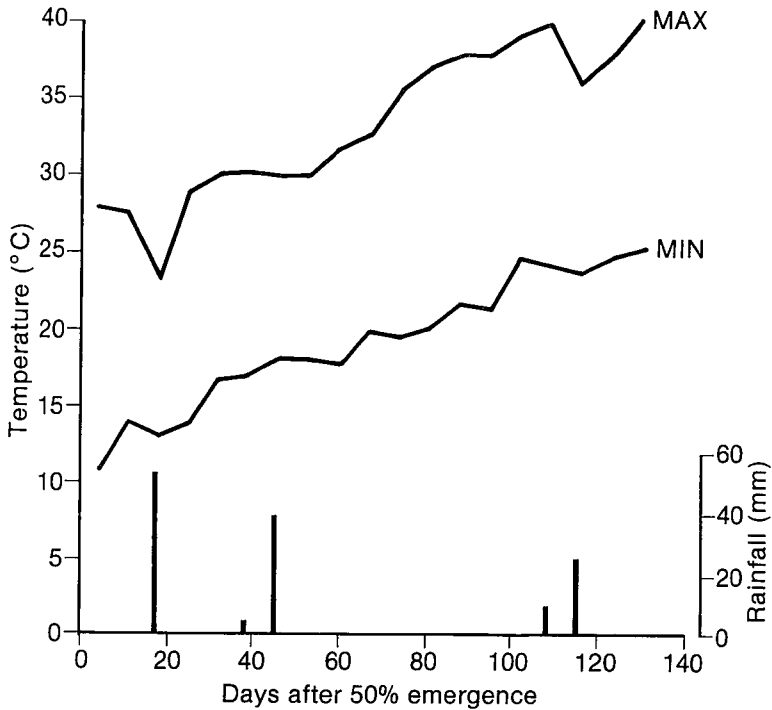
Fig. 1.—Mean and maximum weekly temperatures and daily mean rainfall during the study period.

The plants

Fifty per cent. of the seedlings had emerged by 31 December 1985 (DAE = 0). There was little effect of the drought gradient on leaf production or genotype until 80 DAE (Table II). The plants in the unirrigated sectors were presumably exploiting residual soil moisture up to this time. Thereafter, there was a continued response in NC Ac 343 and M 13, where the plots receiving most water continued to increase their leaf number (Table II). ICGS 11 and JL 24 produced about the same number of leaves as NC Ac 343 and M 13 in the drought-stressed plots but did not respond as strongly to irrigation in the plots receiving most water. The final haulm weight is a good indication of the effect of the irrigation regime on the four genotypes (Table III).

TABLE I.   *Soil moisture at the beginning (114 days after 50% emergence) and end (120) of one irrigation cycle*

| | Days after 50% emergence | |
Treatment	114	120
1	18·6*	14·6*
2	14·1	12·7
3	12·3	11·4
4	9·4	9·0
5	6·6	6·0

*Soil moisture (%).
    Field capacity (−0·33 bar) = 18·3% (±0·24), $n = 5$.
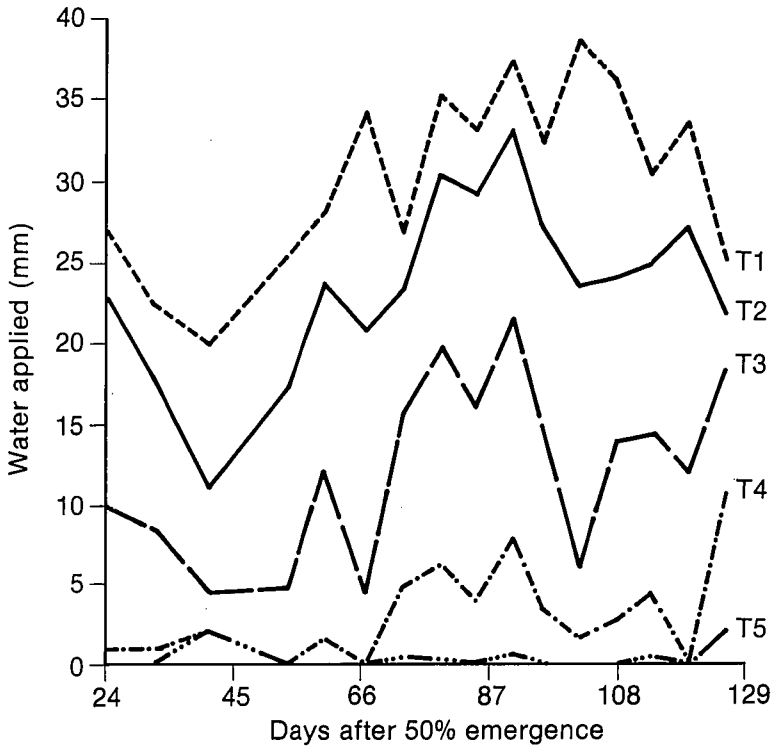   Wilting point (−15·0 bar) = 12% (±0·14), $n = 5$.

Fig. 2.—Amount of water applied to each plot (T1–T5) by the line source
irrigation system.

TABLE II. *Mean numbers of leaves per plant in four groundnut genotypes at five
positions (T1–T5) along a drought-stress gradient on three dates during
the growing season*

Drought-stress gradient	Genotypes			
	ICGS 11	NC Ac 343	JL 24	M 13
80 days after 50% emergence				
T1 wettest	46·1*	54·4	40·7	49·8
T2	49·8	55·8	40·3	52·8
T3	42·2	42·2	36·5	45·3
T4	42·9	42·1	34·9	47·7
T5 driest	45·3	49·3	35·7	30·1
SEs: levels of drought stress ± 2·0; genotypes ± 1·3.				
102 days after 50% emergence				
T1 wettest	67·2	113·9	63·5	107·6
T2	69·4	121·1	58·8	119·4
T3	59·3	81·4	51·0	84·7
T4	50·1	66·3	42·4	68·9
T5 driest	55·7	58·1	43·4	67·0
SEs: levels of drought stress ± 3·2; genotypes ± 3·1.				
130 days after 50% emergence				
T1 wettest	83·2	167·3	70·0	155·8
T2	70·2	170·1	61·6	135·8
T3	58·2	103·6	50·0	115·9
T4	46·6	71·8	41·6	68·6
T5 driest	54·4	58·8	40·4	63·2
SEs: levels of drought stress ± 5·4; genotypes ± 4·5.				

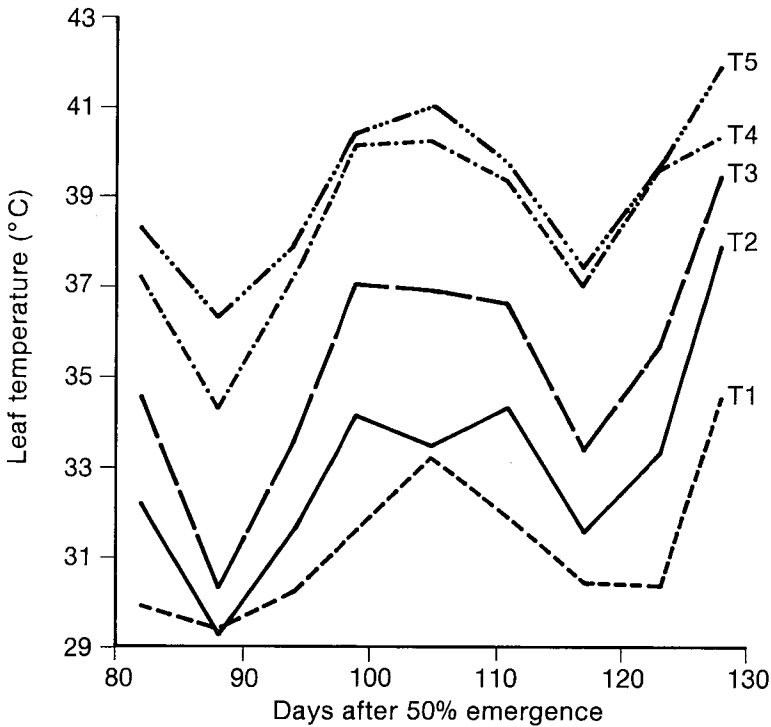*Mean (of five replicates) numbers of leaves per plant.

Fig. 3.—Weekly mean leaf surface temperature measured 3–4 times per week with an infrared thermometer between 11.00 and 14.00 h each day.

TABLE III.   *Mean haulm harvest weights of four genotypes grown along a drought-stress gradient*

Drought-stress gradient	Genotypes			
	ICGS 11	NC Ac 343	JL 24	M 13
T1 wettest	742*	3366	1268	2816
T2	822	3072	1057	2603
T3	629	1942	827	1404
T4	551	1116	638	653
T5 driest	306	314	348	351

SEs: levels of drought stress ± 99; genotypes ± 4·5.
*Mean (of five replicates) haulm weight (g/plot).

There were differences in response to drought among the genotypes. NC Ac 343 and M 13 are long duration runner types, whereas JL 24 and ICGS 11 are Spanish bunch types. The former were more affected by drought stress than the latter. Clearly, JL 24 and ICGS 11 would tend to avoid drought stress by maturing earlier because they are more determinate.

Aproaerema modicella

There were three complete *A. modicella* generations and a partial fourth during the study period. The density was low, especially in the first generation, but there was a consistent and significant trend for there to be higher populations in T4 and T5 (Table IV).

The ratio between *A. modicella* density at the wet and dry ends of the gradient indicates that the gradient effect in ICGS 11 was not great (1·45 in the second generation and

TABLE IV. *Mean number of larvae of* Aproaerema modicella *per 100 plants at the peak density of the second and third generations on four groundnut genotypes growing along a drought-stress gradient*

Drought-stress gradient	Genotypes			
	ICGS 11	NC Ac 343	JL 24	M 13
Peak population of 2nd generation, 62 days after 50% emergence				
T1 wettest	13·5*	9·9	10·9	13·8
T2	13·4	11·0	16·1	13·8
T3	14·8	16·3	16·0	16·8
T4	19·3	19·6	23·4	23·6
T5 driest	19·6	17·2	24·2	23·2
SEs: levels of drought stress ± 0·7; genotypes ± 1·0.				
Peak population of 3rd gneration, 96 days after 50% emergence				
T1 wettest	6·9*	2·3	5·2	3·7
T2	5·8	2·7	7·0	3·8
T3	8·2	3·8	6·7	6·5
T4	7·5	7·0	9·3	8·0
T5 driest	7·7	7·5	8·5	6·7
SEs: levels of drought stress ± 0·3; genotypes ± 0·2.				

*Mean (of five replicates) numbers of *A. modicella* larvae per 100 plants.

indeterminate in the third generation). In the other three genotypes, the densities in T4 and T5 were about twice those in T1 in the second generation. However, in the third generation, when the plants were really stressed, the ratio between the wettest and driest plots of NC Ac 343 was markedly higher than for the other three genotypes.

Water falling on the leaves from the overhead irrigation system apparently did not

TABLE V. *Mean number of larvae of* Aproaerema modicella *per 100 plants on groundnuts (ICGS 11) receiving surface irrigation, with and without overhead irrigation*[a]

Treatment[b]	Days after 50% emergence	
	105	127
Surface irrigation[c] only[d]	4·58 ± 0·28[e]	3·9 ± 0·34
Surface irrigation plus line source T1	7·50 ± 0·65	3·1 ± 0·58
T2	5·80 ± 0·39	4·7 ± 0·60
T3	5·10 ± 0·38	4·5 ± 0·34
T4	6·40 ± 0·46	3·8 ± 0·30

[a]Amount of water applied by the line source to treatments T1–T4 is indicated in Fig. 2.
[b]Thirty plants per treatment.
[c]Furrow irrigation applied every 7–10 days during the season.
[d]Mean insect population for whole of plot.
[e]Mean number per 100 plants ± SE.

reduce the leaf-miner density (Table V). In fact, the reverse trend was apparent at 105 DAE, when there were significantly more immature leaf-miners in the plot that received overhead irrigation. 'Artificial rain' was not apparently among the notional mortality factors of this species in this experiment. There was no reason to suspect that egg density was reduced by overhead irrigation as the distribution of newly formed mines followed the same pattern as that of larvae that were close to pupation.

Thrips and bud necrosis disease

The total thrips population (>90% were *S. dorsalis*, the balance being *T. palmi* and *F. schultzei*) peaked at 85–97 DAE. Their numbers were highest on JL 24 (Table VI).

Although there were some irregularities within genotypes, the pattern was of higher densities at the wettest end of the gradient at 80 DAE and a reversal of the trend by 97 DAE. This pattern changed again as the intensity of drought stress increased (and as the populations declined) between 97 and 115 DAE. This was least evident in ICGS 11 at

TABLE VI. *Mean number of thrips† per 100 terminals on four groundnut genotypes along a drought-stress gradient on three dates during the growing season*

Drought-stress gradient	Genotypes				Mean
	ICGS 11	NC Ac 343	JL 24	M 13	
80 days after 50% emergence					
T1 wettest	50·0*	31·5	53·2	38·6	43·3
T2	30·6	28·9	30·8	29·3	29·9
T3	35·2	20·2	26·4	31·0	28·2
T4	26·0	22·2	34·9	20·2	25·8
T5 driest	—	—	—	—	—
SEs: levels of drought stress ± 3·6; genotypes ± 3·25.					
97 days after 50% emergence					
T1 wettest	41·2	32·8	38·1	17·9	32·5
T2	39·6	15·4	41·0	32·3	32·1
T3	35·5	34·1	39·2	31·1	45·0
T4	42·9	47·9	66·4	33·4	47·7
T5 driest	36·0	54·3	74·0	44·8	52·3
SEs: levels of drought stress ± 1·7; genotypes ± 2·5.					
115 days after 50% emergence.					
T1 wettest	16·3	13·2	36·4	19·4	21·4
T2	8·9	13·6	36·0	14·9	18·8
T3	12·3	11·7	24·9	14·5	15·8
T4	10·1	16·7	21·6	11·3	14·9
T5 driest	8·8	9·4	22·2	12·1	13·1
SEs: levels of drought stress ± 2·6; genotypes ± 3·0.					

†Mainly *Scirtothrips dorsalis* (>90%) but also *Thrips palmi* and *Frankliniella schultzei.*
*Mean (of five replicates) numbers of thrips per 100 terminals.

97 DAE when all plots had about the same thrips density and at 115 DAE, when, with NC Ac 343, no pattern was evident. In the case of ICGS 11, this reflects the comparative lack of response of this genotype to drought (Tables II & III).

Plant mortality attributable to bud necrosis disease clearly increased with level of drought

TABLE VII. *Mean percentage plant mortality attributable to bud necrosis disease (BND) at 97 DAE*

Drought-stress gradient	Genotypes			
	ICGS 11	NC Ac 343	JL 24	M 13
T1 wettest	1·4*	0	8·9	1·4
T2	1·4	1·2	14·4	0
T3	1·4	2·7	12·0	4·8
T4	9·5	7·1	17·4	4·2
T5 driest	9·8	7·8	19·8	2·2

Approximate number of plants per plot = 80 in T1–T4, 40 in T5.
*Percentage of dead plants per plot; arcsine transformed data, refer only to death caused by BND.
SEs: levels of drought stress ± 2·6; genotypes ± 3·0.

stress although, again, the pattern within cultivars was not consistent (Table VII). JL 24 was clearly the most susceptible to this disease just as it was most attractive to the vector.

Empoasca kerri

E. kerri densities were low at the beginning and end of the experiment. Therefore, only data for the peak population at 75 DAE are shown (Table VIII). Numbers were significantly higher in the plots that received most water. ICGS 11 and JL 24 carried significantly higher populations than NC Ac 343 and M 13.

Termites

The termites colonizing the plot pegs towards the end of the experimental period

TABLE VIII.   *Mean number of* Empoasca kerri *per 100 leaves (at their peak population density)*

Drought-stress gradient	Genotypes			
	ICGS 11	NC Ac 343	JL 24	M 13
75 days after 50% emergence				
T1 wettest	8·9*	6·7	8·2	6·3
T2	4·6	4·0	4·6	4·9
T3	4·2	3·6	2·3	5·2
T4 driest	4·2	3·6	3·8	3·0

*Mean (of five replicates) number per 100 leaves.
SEs: levels of drought stress ± 0·4; genotypes ± 3·0.

belonged to the genera *Odontotermes* (probably *O. obesus* (Rambur)) and *Microtermes* (probably *M. obesi* Holmgren). Of the 313 undisturbed pegs (which were distributed evenly throughout the experimental area) 63 were colonized by termites, eight by *Odontotermes* and 55 by *Microtermes*. The pegs with no termites are not considered because it is not known whether the absence of the termites was due to environmental or distributional factors. Seventy-six per cent. of the pegs with *Microtermes* were in the treatments where
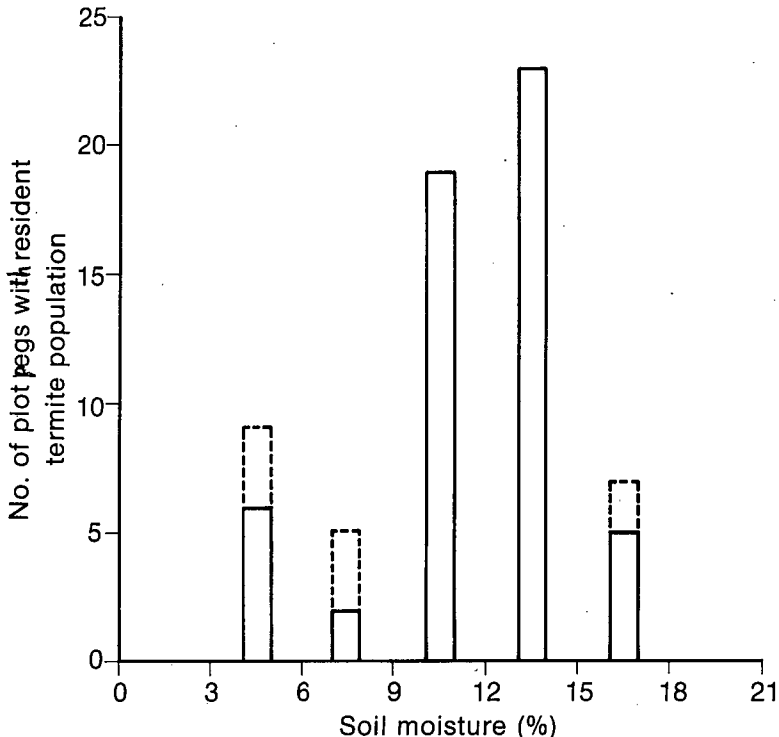

Fig. 4.—The distribution pattern of termites (solid line, *Microtermes* sp.; broken, line, *Odontotermes* sp.) with respect to percentage soil moisture (field capacity = 18·3%, wilting point = 12·0%).

the mean soil moisture was between 9·0 and 15% (Fig. 4). The number of pegs with *Odontotermes* was too small to draw any firm conclusions about their distribution, but it was noted that they were only on pegs in soil with a water content that was outside the 8–16% range apparently preferred by *Microtermes*.

Discussion

The distribution of the foliar feeding taxa shows three distinct patterns. *A. modicella* was most dense on the most stressed plants and where the leaf surface temperatures were highest through genotypic variation. *E. kerri* concentrated where there was no drought stress and leaf temperatures were lowest. Thrips were, initially, more abundant on the plants that were least stressed, but as the condition of the plants worsened, their distribution across the gradient became reversed and, later, reversed again. As would be expected, plant mortality due to bud necrosis disease followed the distribution pattern of its thrips vectors. This was certainly greatest in the treatments receiving least water, indicating that drought stress should be avoided to reduce plant death caused by this disease. JL 24 carried the highest thrips densities and was most susceptible to bud necrosis disease.

Biochemical changes occur in plants when they become drought-stressed, including increases in levels of soluble carbohydrate and amino acids in the leaf (Miles *et al.*, 1982). A food medium such as this is a more favourable diet for insects, especially phloem-feeders, than is provided by non-stressed plants. Hence the often observed phenomenon that insects feeding on drought-stressed plants have higher reproductive and development rates. The results of the present experiment show that the responses of different insect taxa differ both between each other and also with time or degree of stress.

However, food quality is not the only factor that regulates the success of an insect population. In the tropics, temperature can also be important. Many studies show that insects undergo fatal heat stress at about 35°C. At this temperature, their growth rate is slower than at lower temperatures and they usually die before completing their development. This temperature corresponds with that at which insect protein begins to denature (Wigglesworth, 1965). This makes the observation that *A. modicella* densities were highest where leaf surface temperatures exceeded 35°C noteworthy, but it is not unique. El Rayah (1970) reported that some desert-dwelling beetles survive at sand substrate temperatures of up to 45°C. As far as *A. modicella* is concerned, it is necessary to know the daily temperature cycle inside the larval refuge (mine or webbed leaflets) rather than on the upper leaf surface, together with the response of the larvae to temperatures in the 35–45°C range. That this species lives in such conditions suggests that it has a physiological adaptation to permit it to survive in such high temperatures. However, further experimentation will be required to determine whether its refuge within the mine and the webbed leaflets protects it from these high temperatures.

A consideration underlying the initiation of this experiment was the question of which cultivar to recommend that farmers should grow, given the risk of outbreaks of a range of pests on land with or without irrigation. The results indicate that, overall, NC Ac 343 was the 'best bet' and that JL 24 should be avoided if there was any risk of bud necrosis disease. In the latter situation, M 13 appeared to be better in dry conditions. ICGS 11 appeared to stand up to thrips attack under drought. The results gave no clear indication that any of the four genotypes would have a clear advantage under high *E. kerri* population densities.

This study demonstrated that certain phenomena exist, but it was not designed to explain them. There is clearly scope for research in this direction. We are also aware that *A. modicella* has a number of parasites that would also be influenced by heat stress. This adds a further level of complexity that the relatively low population density did not allow us to explore. Perhaps the most important factor to emerge is the conclusion that, when considering the host relationships of field populations of insects in tropical climates, heat stress and its avoidance have to be included together with the more obvious biochemical and behavioural factors and the interactions of natural enemies.

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