Studies on the ecology and disease transmission of the psyllid vectors of the citrus greening disease, with special reference to the South African vector, *Trioza erytreae* (Del Guercio) (Homoptera : Psyllidae)

by

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ABSTRACT

A comparatively new virus-like disease called greening has become a very serious threat in many citrus producing countries of the world. The disease is transmitted by two insect vectors belonging to the Psyllidae (Homoptera) namely, *Trioza erytreae* (Del Guercio), the African vector, and *Diaphorina citri* Kuw., the Oriental vector.

Field studies were made on the ecology, biology and control of *T. erytreae* in the northern Transvaal and in Swaziland during 1965 - 1970. This vector is extremely fecund but has weak powers of dispersal. The main ecological factors found to regulate populations of this insect were the flushing rhythm and flush quality of citrus, extremes of weather, and natural enemies. Other factors involved included interspecific competition with citrus aphids, and in some seasons intraspecific competition for breeding sites. Fundamentally flushing rhythm determines the potential population density of the vector, while the occurrence and sequence of lethal weather extremes mainly regulate the population size during citrus growth periods. A weather index was found to explain the pest status of the vector in southern Africa and partly accounts for previous outbreaks of vector and disease. A population model is given which explains the seasonal abundance of the insect. Studies were also made on the general biology including sex ratio, egg laying, mating behaviour, and the influence of temperature on the duration of the immature stages.

The greening disease represents a severe limiting factor to citrus production in the higher-lying regions of the eastern Transvaal and Swaziland. The hotter lowveld areas are virtually free of disease symptoms and vector populations though present are usually low. Transmission studies showed that *T. erytreae* is the principal vector, several other psyllid species feeding on citrus were not found to be transmitters. It appears that a fairly small proportion of field adults are infective and that there is a seasonal fluctuation in transmission efficiency. Single males and females were able to transmit the disease. Unsuccessful attempts were made to screen adults for infectivity using a chromatographic method, and to isolate the causal organism from excised salivary glands.

The control of *T. erytreae* depends on the use of insecticides. Experiments to select a suitable material and to determine its correct time of application are described. A spray programme for the control of citrus psylla has been used with apparent success by farmers in the Malkerns district of Swaziland.

Comparative field observations and surveys for both Asian greening disease and the Oriental vector are described, and the world distribution of greening and of the two psyllid vectors are given.

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C O N T E N T S

INTRODUCTION

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INTRODUCTION

1. GENERAL

Studies on the ecology of *Trioza erytreae* (Del Guercio) were begun in 1965 in the Letaba district of the northern Transvaal and continued until February, 1967, in this district. Part of this work formed the basis of a master's thesis entitled "Studies on the ecology of the South African citrus psylla, *Trioza erytreae* (Del Guercio) (Homoptera : Psyllidae)". This study was continued in greater depth and extended to include investigations into vector transmission and epidemiology of the citrus greening disease from February, 1967, to January, 1970, in Swaziland.

For three months during 1968 the author was employed by the Food and Agricultural Organization of the United Nations to assist the Philippine Bureau of Plant Industry in initiating research on the Oriental vector of the greening disease. Surveys for the distribution of this vector, *Diaphorina citri* Kuw., and comparative observations on symptoms of declining citrus groves, were made in the Philippines and several other countries in Asia and the Far East. During November, 1969, the author attended the 5th Conference of the International Organization of Citrus Virologists held in Japan and participated in a Post-Conference tour of several citrus-producing countries of South-East Asia.

Ecological studies on the two psyllid vectors are of vital importance in gaining an understanding of the nature of this serious and widespread citrus disease. Until the start of the Transvaal study this aspect had been largely neglected in southern Africa, while work on the Oriental vector was started in the Philippines in 1968. Likewise, little attention has been paid to the vector transmission of the disease. From an academic point of view the study on *T. erytreae* may contribute to our knowledge of the ecology of the Psyllidae. Waloff (1968) recognizes the work of Clark (1962, 1963a, b etc.) on *Cardiaspina albitextura*, and Watmough (1968a) on two *Arytaina* spp. as the only basic studies on the ecology of this superfamily. To these may be added the work of Moran (1967) on the psyllid, *Paurocephala calodendri* Moran.

2. PEST STATUS OF *T. ERYTREAE*

Until it was shown to be a vector of the greening disease, *T. erytreae* was regarded as a minor pest of citrus in southern Africa. Closely-related groups of the Homoptera, such as aphids, leaf-hoppers and white flies, have been known as vectors of virus-like diseases of plants for many years. But apart from the "psyllid yellows" condition, which is a localized chlorosis caused by toxins secreted during feeding (Carter, 1962), it is only comparatively recently that psyllids have been shown to be involved in disease transmission. In 1964 Jensen *et al.*, clearly demonstrated that *Psylla pyricola* Foerster was the vector of the pear decline disease in California. Following this discovery, first *T. erytreae* then *D. citri* were shown to be vectors of the greening disease of citrus. Both of these diseases are graft transmissible but are spread more effectively by the insect vector.

3. THE GREENING DISEASE OF CITRUS

In the last three decades a number of closely related virus-like diseases have appeared in most regions of the world where citrus is grown. Many workers now believe that the greening disease of South Africa, leaf mottling of the Philippines, and a major component in the citrus die-back of India, are caused by the same pathogen or pathogen complex. It is also becoming increasing clear that the stubborn disease of America, vein-phloem degeneration of Indonesia, yellow-shoot of mainland China, and likubin of Taiwan, are very similar to greening. Recently greening has also been reported from Brazil (Rossetti, 1969). In November, 1969, it was the considered opinion of delegates to the 5th Conference of the International Organization of Citrus Virologists that this comparatively new virus-like disease constitutes the most serious disease problem facing citriculture at the present time.

Several workers now believe that the greening pathogen, which has always been a somewhat 'atypical virus', may be a mycoplasm and not a true virus at all. This would account for many of the anomalies associated with the disease complex. In the case of the pear decline disease, which closely parallels citrus greening, recent electron microscopy studies have revealed the presence of mycoplasms in the salivary glands of infected insects and in the sieve tubes of pear trees (Schneider, H. 1969, personal communication). Since mycoplasms are susceptible to tetracyclines, there is some hope of a curative treatment being developed in the future.

4. LITERATURE REVIEW

(i) *T. erytreae*. Citrus psylla was first reported in southern Africa by Lounsbury in 1897. Van der Merwe (1941) published a general account of the insect discussing such aspects as taxonomy, pest status, biology, distribution, and control measures. Additional biological notes were contributed from laboratory studies by Annecke & Cilliers (1963). The latter authors also discussed the parasitic species attacking *T. erytreae*.

Field studies by Schwarz (1964) suggested that either *T. erytreae* or the black citrus aphid, *Toxoptera citricidus* (Kirk.), was a vector of greening, while field observations by Oberholzer *et al.*, (1965) implicated the former. Shortly afterwards McClean & Oberholzer (1965b) were finally able to demonstrate that *T. erytreae* is in fact an important vector of the disease.

Immature stages of the psylla and T. citricidus did not transmit the disease in their experiments. Subsequently, a large number of transmission tests have confirmed these results (McClean A.P.D. & Catling H.D. - unpublished results).

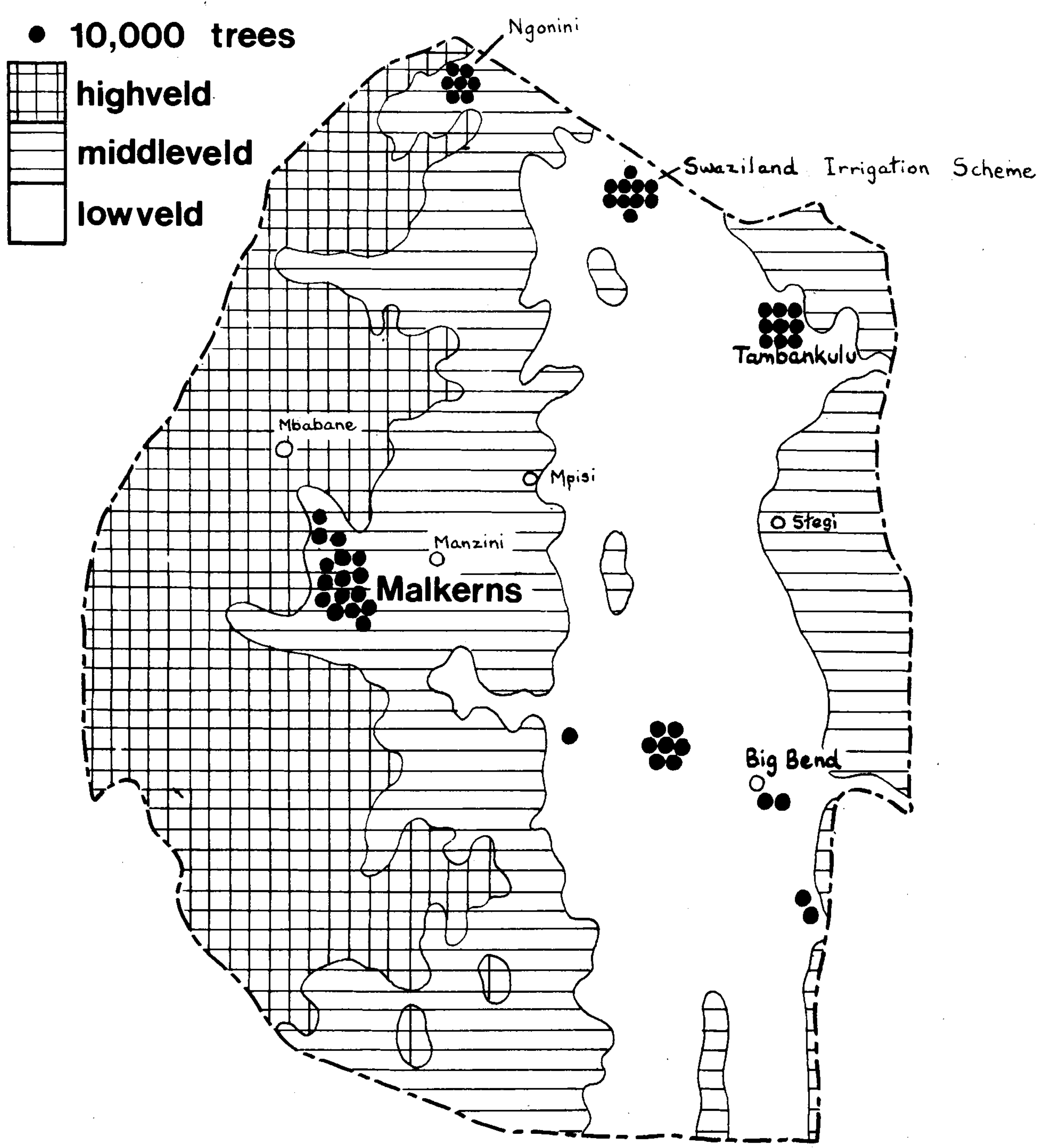
The elevation of T. erytreae to major pest status encouraged several workers to begin basic studies on this citrus pest. Moran & Blowers (1967) described the egg and nymphal stages, and under controlled, fluctuating conditions in the laboratory studied the life history and noted the effects of three temperature regimes on development and survival. In the same year these authors described the structure and development of the female reproductive system (Blowers & Moran, 1967). From field studies in the northern Transvaal, Catling (1967) gave a general account of the biology and bionomics of the insect and enumerated the main ecological factors. A brief account of this study was published the following year (Catling & Annecke, 1968). Moran (1968a) compared the development of T. erytreae on five different host plants, and in a companion paper (Moran, 1968b) described preliminary studies on the choice of host plants by the adult. The work of that author was brought together in a Ph.D. thesis (Moran, 1967) which included additional biological notes and a discussion on the distribution of both vector and greening disease.

Catling (1969a, b, c) published three papers on the bionomics of T. erytreae and described studies on the chemical control of the insect (1969d). The influence of weather-induced mortality on the distribution of the vector, and an explanation for past outbreaks of both vector and disease were given by Green & Catling (in press). All of the above five papers are included in this thesis.

The ecology of the psyllid vectors of citrus greening was reviewed by Catling (1969 f and g).

(ii) South African greening. Oberholzer et al., (1965) described the history of greening outbreaks in South Africa. The latter authors' and McClean & Oberholzer (1965a) gave accounts of the host range and symptoms of the disease, and led evidence to show that greening is a transmissible virus. Studies on the anatomical aspect of the disease were made by Schneider (1968). A close correlation between the incidence of T. erytreae and the spread of greening in southern Africa has been clearly established (Catling, 1967; Schwarz, 1967; Schwarz et al., in press).

Schwarz (1965b; 1968a; 1968b) discovered a fluorescent marker substance in the albedo of fruit and the bark of twigs of infected branches. He then developed a reliable chromatographic method for detecting the disease in many species and varieties of citrus. Schwarz (1968c) also succeeded in the



10,000 trees
highveld
middleveld
lowveld
Ngonini
Swaziland Irrigation Scheme
Tambankulu
Mbabane
Mpisi
Stegi
Manzini
Malkerns
Big Bend

mechanical transmission of greening to cucumber. Definite strains of greening were reported in South Africa by the same author (1969). Schwarz & Green (1969) found the degree of symptom expression in the eastern Transvaal to be governed by a heat index correlated with altitude, and reported the successful heat inactivation of infected budwood.

5. THE CITRUS INDUSTRY IN SWAZILAND

Citrus is a young industry in Swaziland and the first signigicant exports of fruit began in 1965. The oldest commercial groves were planted in Malkerns in 1954 and 1955. Fig. 1 shows the distribution of citrus in relation to the main ecological regions. As at March, 1969, there were 554,000 trees in Swaziland, 58% situated in the arid Lowveld region and 42% in the Middleveld. Sweet oranges, mainly Valencias, form 60% of the plantings, 35% are Marsh Seedless grapefruit planted mainly in the Lowveld, and the remaining 5% is made up of several other types including lemons.

6. OTHER PSYLLID SPECIES ON CITRUS

T. erytreae and D. citri are the only two psyllid species known to breed on citrus. However, a number of other species are occasional feeders and some may exist on citrus for extended periods when their normal host is unattractive or dormant. In Japan, for instance, Psylla coccinea (Kuw.) has been collected on citrus but does not feed on this host (Eastop V.F., 1967, personal communication). The following psyllid species were found on citrus during the present study:-

1. Diaphorina punctulata Pettey, widely in Transvaal and Swaziland
2. Diaphorina zebrana (Capener MS*), widely in Transvaal and Swaziland
3. nr Desmiostigma sp., Swaziland, April, 1968, rare
4. Arytaina nr mopani Pettey, Letaba and Agatha, December, 1965
5. Agonoscena sp., Swaziland Lowveld, January and March, 1969
6. nr Pauropsylla sp., Malkerns, December, 1968
7. Arytaina sp., Malkerns, 1968

Six more species were found on other host plants adjacent to citrus groves:- two undescribed Trioza spp.; Ciriacremum sp.; Pauropsylla nr trichaeta Pettey; nr Allceneura sp.; Psylla sp.

The above two Diaphorina species feed on citrus in large numbers in the Transvaal and have been observed on citrus in Swaziland. Transmission tests with these two psyllids are described in Section B. It is possible that undetected psyllids feeding intermittently on citrus may be responsible for

* to be published shortly

EXPLANATION OF FIGURE

Fig. 1 Map of Swaziland showing the main ecological regions and distribution of citrus the slow spread of the stubborn disease in California and Arizona (Calavan, E.C., Carpenter, J.B., and Allen, R.M. 1969, personal oommunication).

(i) D. punctulata. This species is widely distributed in South Africa and has been recorded on over 30 different indigenous shrubs and trees (Capener, L., 1967, personal communioation). Its main breeding plant is the marula, Sclerooarya oaffra Sond. In the Letaba distriot it was colleoted by the author on marula at Ofoolaco and New Agatha, and was partioularly abundant in October of 1966 at Letaba Estates when 57.2% of 110 buds removed from 22 widely-separated marula trees were found to be infested. It was oollected on marula at Mpaka and Sipofaneni, northern Swaziland Lowveld, and on citrus at Malkerns and Ezulwini.

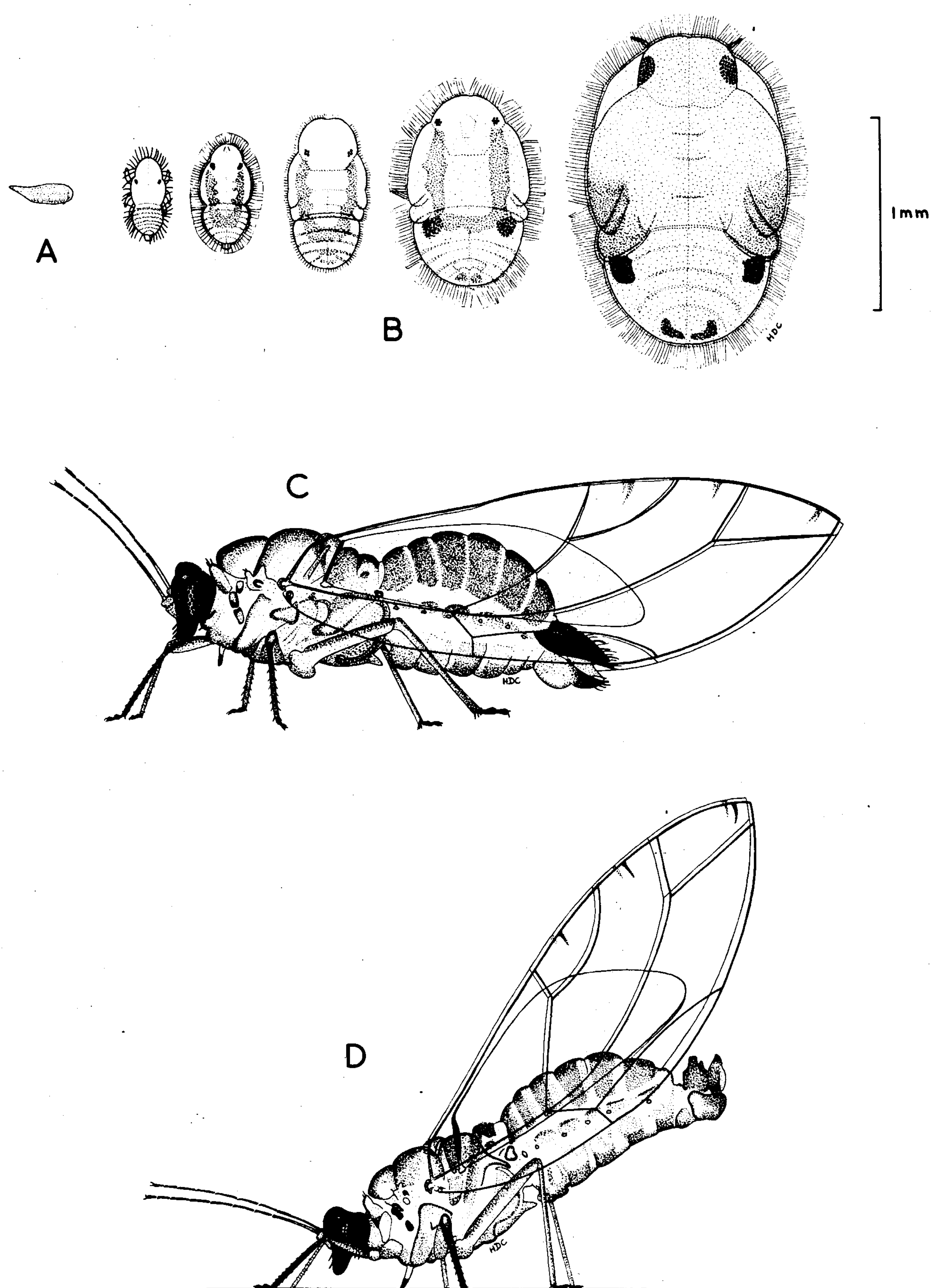
D. punctulata was present on citrus in the Letaba district throughout the year. During July, 1966, when marulas were dormant large numbers of adults were found feeding on citrus at Letaba Estates. Collections with the insect sampling machine showed that the psyllid was present in citrus at all times of the day and night, and that their numbers steadily declined at the end of August when their breeding host came into flower. Adults survived for 45 days in the laboratory on citrus seedlings. In one marula tree studied at Letaba, overwintering adults were noticed on the petioles of old leaves in early September. Shortly afterwards, eggs of the first spring generation were laid in expanding buds giving rise to colonies of nymphs between the braots of young flowers or in developing shoots. With further shoot growth some of the darkish nymphs were noticeable on unfurling leaves but later the nymphs became enolosed between the upper halves of the leaf which fold inwards. Distinctive coils of white, spaghetti-like excreta appear on infested flowers and shoots. By the middle of October many teneral adults were observed, indicating a 5-6 week period for the first spring generation. The main peak of adults was seen in November and the psyllid was again fairly abundant on the January growth cycle.

Buds examined in October, 1966, indicated that severe weather extremes had caused a high mortality rate in first and second instar nymphs.

(ii) D. zebrana. Both in life history and general biology this species is remarkably similar to D. punctulata. The clearly striped wings, however, distinguish it from punotulata. Both species breed on the young growth of the marula tree and are frequently found together on the same leaf or shoot. During the early summer of 1966 D. zebrana was found to be the predominant species on some trees at Letaba.

This species was collected at New Agatha and Letaba in 1966, and at Malkerns and Sipofaneni in Swaziland in 1967. Like punctulata it appears to overwinter in the adult stage on several evergreen trees, including citrus.

When confined on citrus in the laboratory, however, this species survived for a comparatively short period.


A
B
1mm
C
D

SECTION A

Ecological Studies on *Trioza erytreae* (Del Guercio)

1. NOTES ON *T. ERYTREAE*

The taxonomy of *T. erytreae* has been discussed by Catling (1967) and Moran (1967). The eggs are laid on young growth, usually along the margin of young leaves (Pl. I.). There are five nymphal instars (Fig. 2B). The first instar settles on the underside of the leaf and a characteristic open gall begins to form (Pl. II). The adult is winged and sexes are separate (Fig. 2 C,D). The leaves and shoots of heavily populated plants may become sprinkled with white granules of excreta (Pl. II). The feeding of large numbers was not observed to cause any serious toxic effect to plant tissue, leaf chlorosis being slight and extremely rare.

T. erytreae has been reported in all the main citrus areas of southern Africa and was observed or collected by the author in Rhodesia, northern and eastern Transvaal, Swaziland, Zululand, and at Cape Town and Tulbagh in the western Cape Province. Specimens were also received from the arid Citrusdal area of the western Cape.

The world distribution of *T. erytreae*, and of the Oriental vector, *Diaphorina citri* Kuw., is discussed in Section C. In Appendix 1 salient differences in the biology and appearance of the two vectors are tabulated.

2. FIELD METHODS

This chapter describes the experimental sites and the main field methods used in the study of *T. erytreae*. Other methods used in small-scale field studies or laboratory experiments are described in the appropriate chapter. The main method of sampling for *T. erytreae*, the *in situ* counts, and the method of parasitism assessments were described by Catling (1967) but are included here for the sake of completeness and because of additional data obtained in the field on the validity of these methods. Similarly, brief descriptions of experimental sites in the Letaba district are included.

EXPLANATION OF FIGURE

Fig. 2 *Trioza erytreae* (Del Guercio). A - egg; B - five nymphal instars, third instar shown as newly-moulted; C - gravid female; D - male in feeding position. All stages to same scale. del. H.D. Catling

Plate I. Eggs of *T. erytreae* on the margin of young citrus leaves

Plate II. Citrus seedlings heavily populated with *T. erytreae* showing leaf galls and white deposits of excreta

(i) Experimental sites (Fig. 3)

Letaba District, Transvaal. The Letaba district is flanked on the west by the Drakensberg escarpment and extends eastwards into the Lowveld Sour Bushveld of Acocks (1953). For the three main experimental sites in this area, blocks of 50 citrus trees of comparable age, size, aspect and distance from natural bush were selected at three different altitudes. None of the trees had received a regular spray programme for at least three years. Table 1 shows further details of the sites. A thermohygrograph was operated at each site according to specifications suggested by the South African Weather Bureau.

Two minor sites, each with a small weather station, were established in commercial groves at Letswalo and Riverside. Regular surveys were made in the 400,000 trees planted along the northern side of the Letaba River belonging to Letaba Estates.

Table 1. Details of main experimental sites in the Letaba district

	Letaba	Fairview	Forest Hill
Altitude..................	1960 ft	2800 ft	4200 ft
Mean canopy area of trees .	279 sq. ft	225 sq. ft	292 sq. ft
Variety	mid-seasons	24 Navels 26 Valencias	Valencias
Water supply	irrigation	rain only	rain only
Nutrition	good	fair	poor

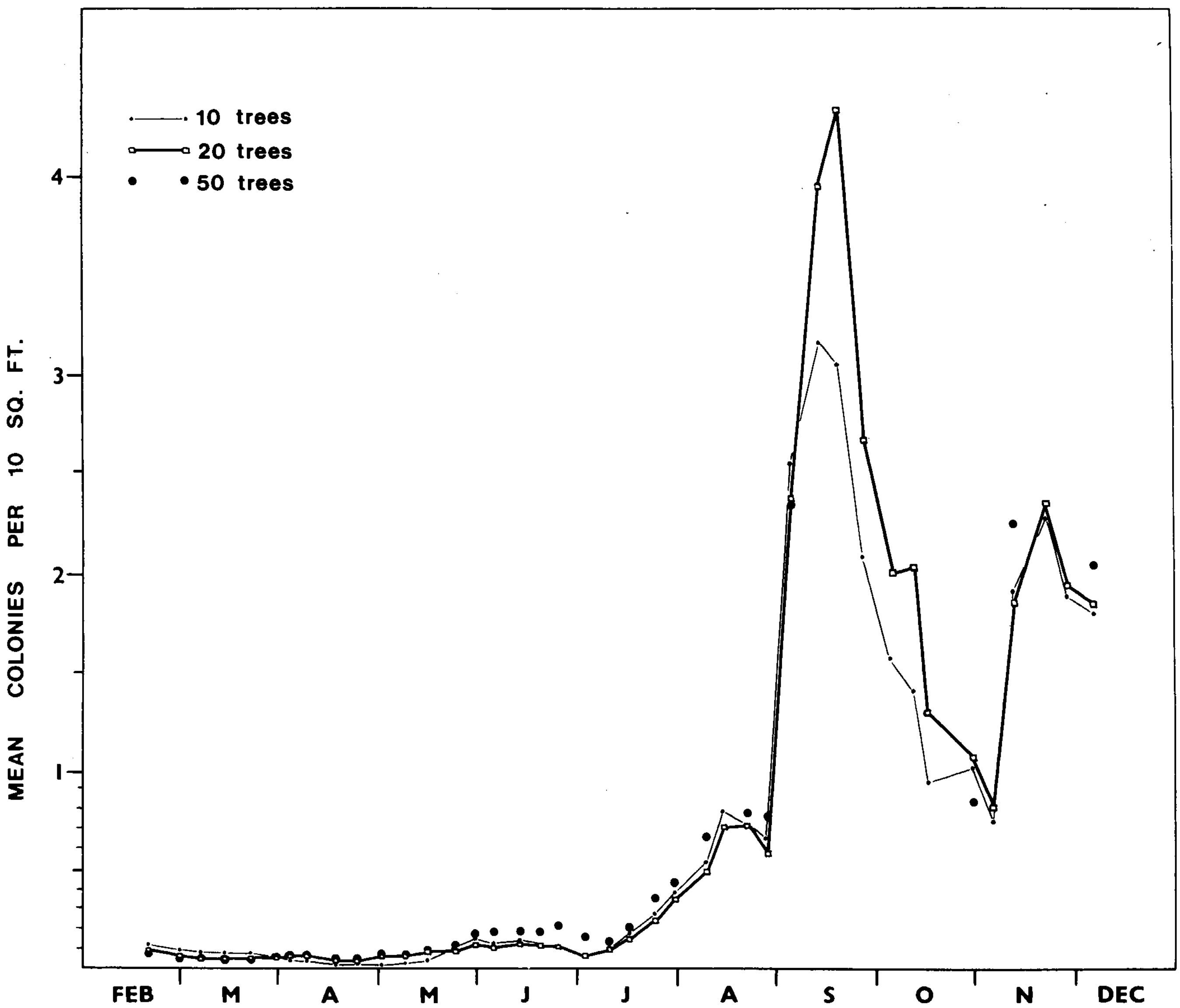
Malkerns District, Swaziland. Malkerns is situated in the Swaziland middleveld at an average altitude of 2,500 feet and falls within the same veld type as the Letaba district. The experimental sites comprised three, fifty-tree blocks and a single hundred-tree block (Ross Citrus), all at similar altitudes. Further details of the sites appear in Table 2. No insecticides were applied during the study period. Meteorological data was available from a class 2 weather station at Malkerns Research Station and a thermohygrograph was operated at Kelly's Hope from March, 1967, to March, 1968.

Table 2. Details of experimental sites in the Malkerns District

	Malkerns Research Station	Kelly's Hope	Usutu Orchards	Ross Citrus Estates
Mean canopy area of trees .	261 sq. ft	337 sq. ft	256 sq. ft	250 sq. ft
Variety	Valencias	Valencias	Navels	Navels
Water supply	irrigation	irrigation	rain only	irrigation
Nutrition	good	good	very poor	good

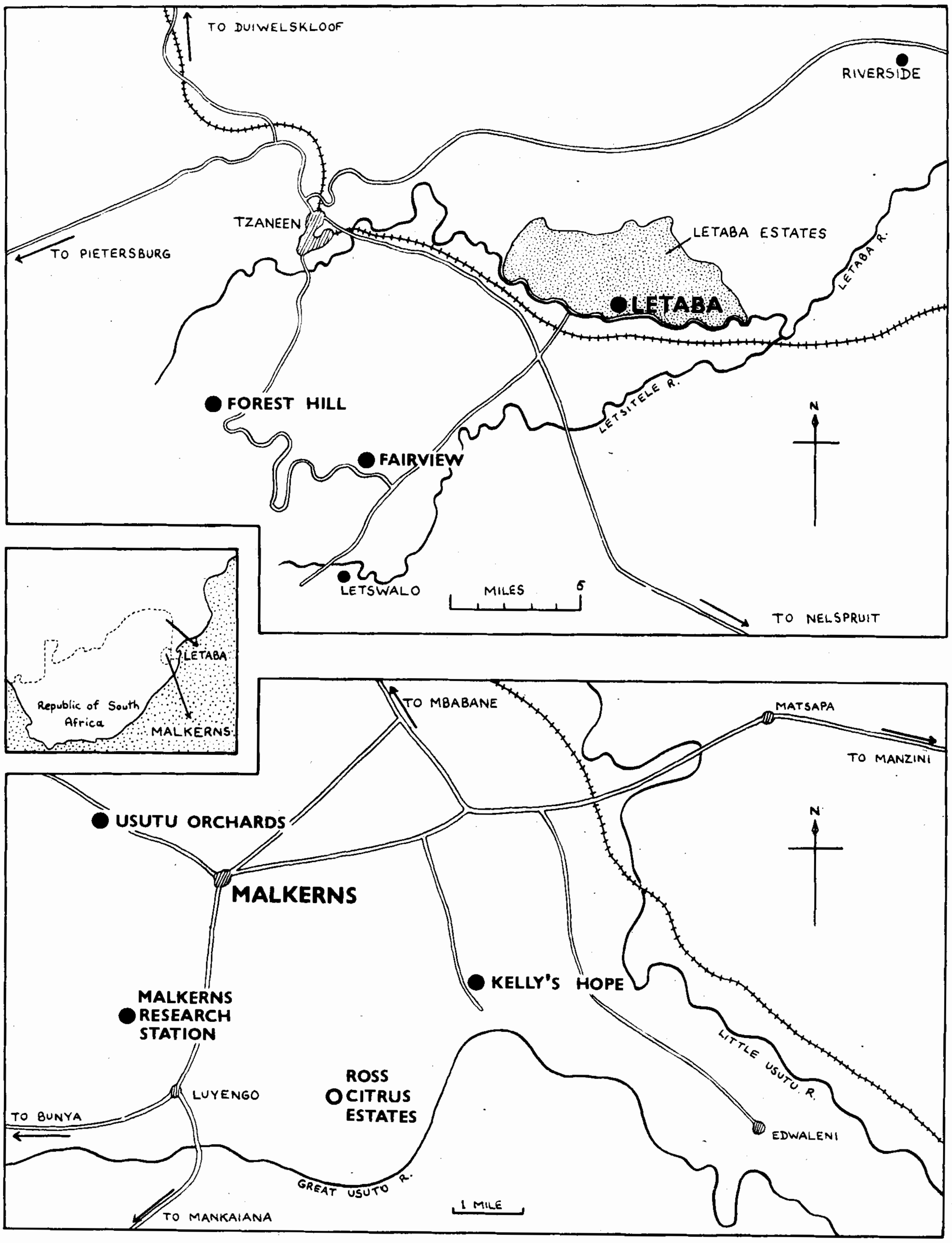
Swaziland Lowveld. At a mean altitude of approximately 700 feet a.s.l. and average annual rainfall of 20-25 inches, the climate of the Swaziland Lowveld is slightly more arid than that of Letaba Estates. Small-scale studies and observations were made at Tambankulu Estates, Swaziland Irrigation Scheme and Big Bend. (Fig. 1).

Fig. 4



10 trees
20 trees
50 trees
MEAN COLONIES PER 10 SQ. FT.
4
3
2
1
FEB
M
A
M
J
J
A
S
O
N
DEC

Fig. 3



TO DUIWELSKLOOF
RIVERSIDE
TZANEEN
TO PIETERSBURG
LETABA ESTATES
LETABA R.
LETABA
FOREST HILL
LETSITELE R.
N
FAIRVIEW
LETSWALO
MILES 6
TO NELSPRUIT
LETABA
Republic of South Africa
MALKERNS
TO MBABANE
MATSAPA
TO MANZINI
USUTU ORCHARDS
N
MALKERNS
KELLY'S HOPE
MALKERNS RESEARCH STATION
LITTLE USUTU R.
ROSS CITRUS ESTATES
LUYENGO
TO BUNYA
EDWALENI
GREAT USUTO R.
1 MILE
TO MANKAIANA

(ii) Population assessments of T. erytreae. Several methods have been used to sample the immature, relatively sessile stages of psyllids. Georgala (1957) sampled leaf clusters and made observations on tagged pear spurs in a study of Psylla pyricola Foerster; Clark (1962) made field ratings of the level of abundance on selected parts of the eucalypt host of Cardiaspina albitextura Taylor; while Moran (1967) removed leaves and Watmough (1968a) green twigs, for laboratory examination. The latter author used a carbon dioxide sampler for assessing the numbers of adults.

T. erytreae fluctuates violently in numbers. Since the insect is at very low densities on dormant citrus trees, where possible destructive sampling was carefully avoided.

(a) Direct field count of colonies. Because females lay exclusively on young flush points and the nymphs are relatively sessile, the developmental stages of T. erytreae are aggregated into distinct, easily-spotted colonies. In this method, population assessments were made by a direct count of colonies on the lower four feet of canopy of each data tree using a constant team of 3-4 field scouts. The area searched comprised 40-50% of the total canopy area of the tree. Each colony was recorded separately according to its predominant age class, i.e. eggs, instars I-III, instars IV-V. Assessments were usually made at weekly intervals. At Malkerns the 10 randomly-chosen data trees used for flush studies were searched for T. erytreae, plus one consecutive tree giving a total of 20 trees. This means that 16-20% of the total tree canopy at the site was searched on each occasion.

Fig. 4 shows that at Malkerns Research Station the searching of 10, 20 or 50 trees usually made little difference to the mean population density recorded. From calculations of the 95% fiducial limits of a series of sample sizes at various population densities, the size of the ratio of confidence interval/mean x 100 was unacceptable when 10 trees were sampled, but was below 20% for moderate and high populations and from 20-30% for low populations of T. erytreae. At low populations there was little improvement by taking a 50 tree sample. The population was expressed as total colonies per 10 square feet of canopy.

EXPLANATION OF FIGURES

Fig. 3. Experimental sites in the Letaba and Malkerns districts

Fig. 4. Mean population densities of T. erytreae at Malkerns Research Station as indicated by the sampling of 10, 20, and 50 trees

The number of individuals per colony was studied from *in situ* counts and from a number of haphazardly selected colonies in the field. Colony size was extremely variable (from 2-5 to several hundred individuals) and in the egg stage was related to the number of leaves per flush point and the rate of egg-laying. At Malkerns Research Station, 178 counts made during January and from May to November, 1968, showed the mean egg colony size to be the lowest in mid-winter (June 20.4; July 60.5) and the highest in September (176.7 eggs per colony). The mean for all counts was 86.7 eggs per colony.

Simple tests for the reliability of searching by this method were carried out in the Letaba district at various densities of the insect (Catling, 1967). After a normal search, trees were searched for a second time for twice the original period, sometimes switching the scouts. The double search increased the number of colonies found by a mean of 21% at moderate to high densities of *T. erytreae*, while at low densities the population was increased by 157%.

The direct count of colonies was found to be a rapid and reliable field method for assessing population densities of the immature stages and was extensively employed at the main study sites. Destructive sampling was avoided and the method facilitated regular field observations on aspects of biology and the activity of natural enemies. Estimates of age distribution, an important aspect in population ecology, enabled the calculation of field generations.

At four other sites of mature trees in the Malkerns district, namely Amaswazi Estates, Lenhaven Estates, and Ross Citrus Estates (2 sites), populations were assessed at monthly intervals by examining the lower four feet of canopy of 20 trees along two diagonals.

(b) Direct field count of all stages. At Forest Hill from January, 1966, to January, 1967, total counts were made of all individuals occurring on infested flush points enclosed by the frame when making flush counts. Populations of eggs, instars I-III, and instars IV-V on the 10 data trees were expressed as the mean number per 10 square feet of canopy. It is estimated that approximately 3% of the total site canopy area was searched. This method indicated similar population trends and field generations to that obtained by the previous method, but due partly to the small area sampled, mean densities for successive counts were extremely variable during some periods. Also the counting of each individual was excessively tedious and frequently inaccurate since many of the young stages in populous colonies may be obscured by leaf-curling.

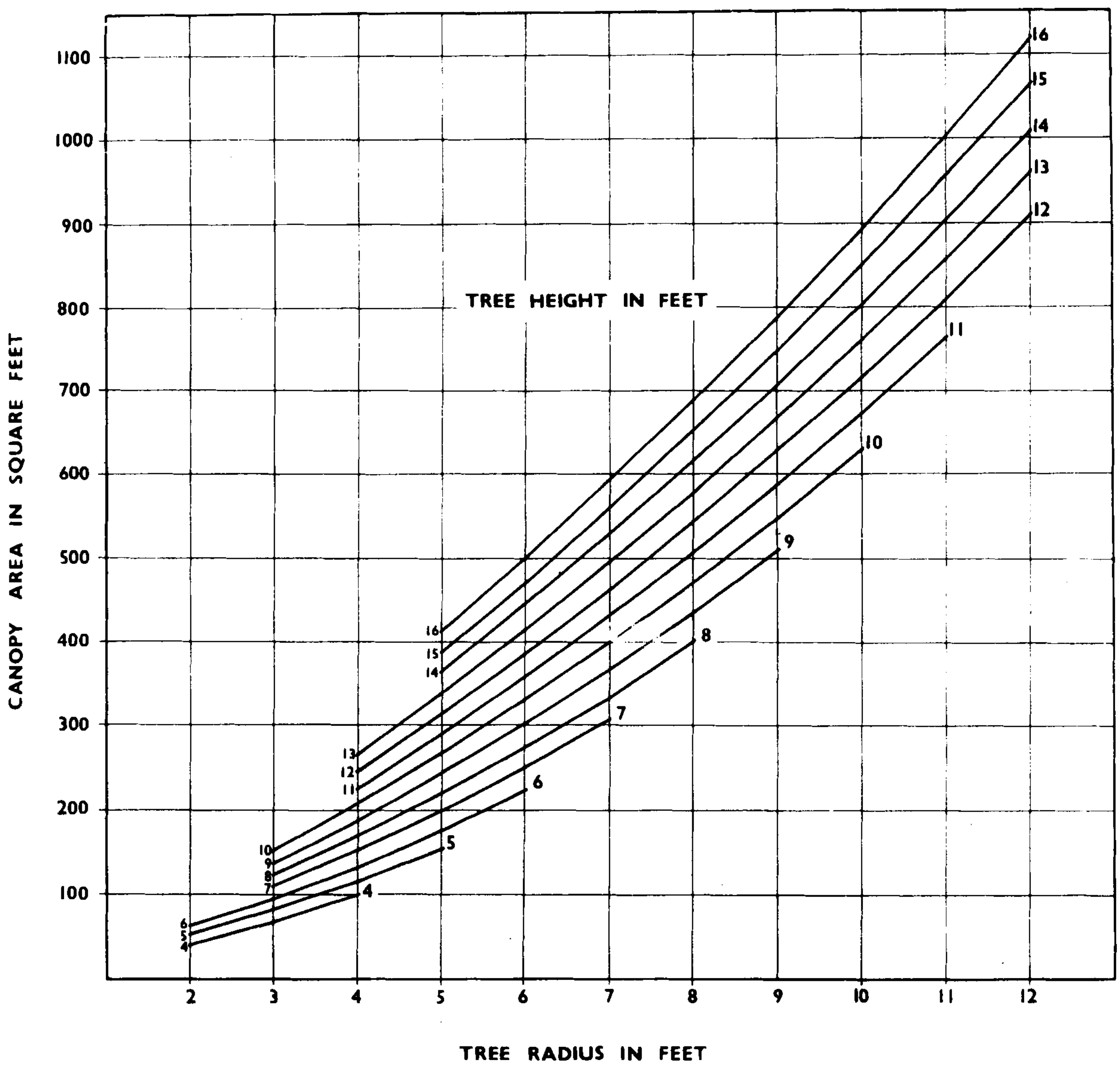
(c) Insect sampling machine. The adults of *T. erytreae* and the active stages of the associated complex of natural enemies were sampled with a Model 1 D-Vac Vacuum Insect Sampling Machine at fortnightly intervals from August, 1967, to December, 1970, at Malkerns Research Station, and during the 1967/68 season at Ross Citrus Estates. An eight inch band around the canopy of each of five haphazardly-selected trees were sampled for one minute, the mean canopy area of the trees at each site being within 2% of each other. Usually trees bordering the experimental site were selected but at high population densities two or three of the experimental trees were included. Samples were mostly taken between 10.00 a.m. and 3.00 p.m.

Adults collected by the insect sampling machine augmented the data from population assessments of the sessile stages. Fig. 8 shows that at moderate to high densities, peaks of adults corresponded closely with field generations indicated by a count of colonies. At low population densities, however, very few or no adults were collected. Larger samples were not considered due to the destructive nature of this sampling method. Catches from the machine also proved to be valuable in plotting parasite population fluctuations and, to a lesser extent, in the study of predator activity. No attempt was made to test the reliability of this method.

(d) Sticky traps. Yellow sticky traps have been used to sample the adults of several psyllid species (Eastop, 1961; Wilde, 1962; Moran, 1967) and were shown to indicate the activity of *T. erytreae* in preliminary trials in Malkerns. Sticky traps were used mainly to study flight activity in and around the Malkerns Research Station experimental grove and were similar to those used by Moran (1967). They consisted of a 12 inch square of hardboard painted a bright lemon yellow colour and covered with transparent plastic sheeting smeared with "Ostico", a sticky tree-banding compound. The yellow colour was clearly visible through the plastic and sticky coating. Further details on the operation of these traps is given in the chapter on dispersal.

(e) Jarring of adults onto sticky plates. A 12 inch square glass plate coated with "Ostico" and placed in a wooden frame was used to sample adults from flush points in two groves at Malkerns Research Station between October, 1968, and September, 1969. This method was initially used to sample the citrus thrips, *Scirtothrips aurantii* Faure (Stassen & Catling, 1969). Five flush points on 10 haphazardly-selected trees were jarred against the edge of the frame, dislodging and trapping the adults on the sticky layer. This method gave a fair reflection of the adult activity during this period.

(iii) Assessments of flushing rhythm. In order to assess flush densities in the field it was necessary to make measurements of the canopy area (surface area) of the data trees. Accordingly, a suitable formula was derived


CANOPY AREA IN SQUARE FEET
TREE RADIUS IN FEET
TREE HEIGHT IN FEET
100
200
300
400
500
600
700
800
900
1000
1100
2
3
4
5
6
7
8
9
10
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12
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15
16

by Serfontein & Catling (1968). Previously it has been commonly assumed that the shape of a citrus tree approximates a hemisphere. However, further observations showed that because tree height and diameter frequently vary independently of one another, one or other conic section will represent a more realistic shape for most trees.

The required form was found to be an ellipse the half of which, standing on its minor axis, represents a tree in cross-section. The minor axis then becomes the tree diameter and the semi-major axis its height. It can be shown that the canopy area (S) is given by the following formula:-

$$S = 2\pi b^2 + \frac{\pi ab}{e} \text{ arc sin } e$$

where a = tree height
b = skirt radius
e = eccentricity of ellipse

From measurements of tree diameter (at skirt level) and height (from bottom of skirt to apex), Fig. 5 gives the canopy area of any tree likely to be encountered in the field.

Flush counts. The canopy areas of all experimental trees were calculated by the above method. A four foot square metal frame was held against the canopy of the tree at random height in each quadrant. The area sampled per quadrant was in direct proportion to the size of the tree and ranged from four square feet for small trees, to 16 square feet for large trees. All flush points enclosed by the frame and regarded as being suitable for the development of *T. erytreae* were counted and recorded per unit area. The frame was fitted with a grid to reduce counting when dense, evenly-distributed flush points were present.

Young flush points were classed into two categories:

Class A points (Pl. III A,B) on which eggs of *T. erytreae* are usually laid; from the first unfurling of the bud to a stage when the majority of the leaves are longer than about $1\frac{1}{2}$ inches; weight usually 0.05-0.50 gm (maximum 1.00gm).

Class B points (Pl. III C,D) are more advanced and support nymphs of *T. erytreae*; for normal nymphal development leaves must remain soft and succulent for at least 2-3 weeks - the moment the tissue hardens and is no longer "tacky" to the touch the leaves are unsuitable; weight usually 0.50 gm (maximum 3.00 gm).

EXPLANATION OF FIGURE

Fig. 5 The canopy area of a citrus tree from measurements of tree radius and height

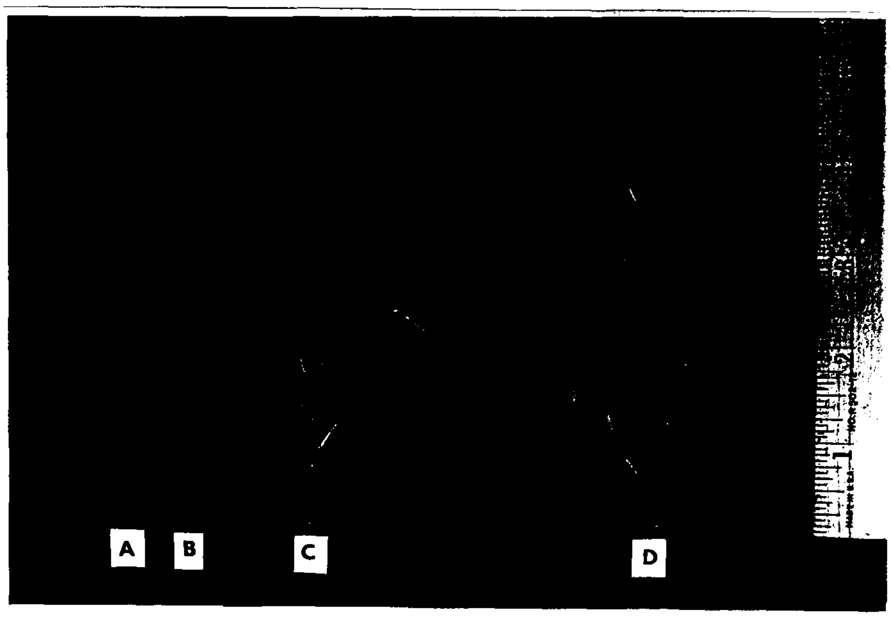


Plate III. Breeding sites of *T. erytreae*. A and B - class A flush points; C and D - class B flush points. Scale in inches

Though water shoots, blossom flushes and prematurely-hardening flush points were sometimes difficult to classify, the above flush categories proved adequate for the study. Experimental sites were sampled mostly at weekly intervals. In the Letaba district ten different trees were selected randomly at each sampling date; at Malkerns, in order to gain a stronger correlation between flushing and fluctuations of T. erytreae, the same ten trees were sampled on each occasion. Except for very low flush densities, the 95% fiducial limits of the sample size were always below 20% of the confidence interval/mean x 100.

Flush surveys. Extensive flush surveys were made on Letaba Estates between August, 1966, and February, 1967. Basically the surveys were designed to chart the annual flushing rhythm and to assist in the spotting of T. erytreae outbreaks, but they were also found to yield data on flushing differences due to tree age and variety. Sixty plots were chosen in proportion to the number of trees of each variety grown on the Estate. A "starter" tree, representative of the plot, was selected by a method of Serfontein, C.M.A., (personal communication, 1966) who found that the probability of a tree being representative of the population in any plot varies with its position in the plot. This variation, when plotted as a function of the tree's position (with reference to any baseline, i.e. plot edge) generates a function very closely resembling the probability distribution function resulting from the totals obtained from the simultaneous throwing of three dice. On each successive survey another tree was taken with reference to the "starter" tree. Flush was counted at fortnightly intervals using a simplified version of the frame method described previously.

At four groves in the Malkerns district flush volume was rated at monthly intervals on a scale from 0-6.

(iv) Assessment of parasite activity. Parasitism. The assessment of parasitism was based on a microscopic examination of the nymphs. At regular intervals single leaves were removed from a number of haphazardly-selected T. erytreae colonies in the field and examined almost immediately before the nymphs vacated their leaf galls. Where the population allowed, sufficient leaves were picked to provide a minimum of 500 susceptible nymphs. With the exception of the Ross Citrus site some colonies were usually selected from trees bordering the experimental trees in order to limit destructive sampling. At higher host densities, however, and on each occasion at Ross Citrus, all the leaves were removed from the experimental trees. At times of very low host density, as in midwinter, unsprayed trees further afield were searched for suitable material.

Nymphs were examined under a dissecting microscope at 16-25x. The ventrum and leaf gall of instars III-V, which are the susceptible stages for T. radiatus, were examined externally for parasite eggs, larvae and pupae. The instar of each nymph and, where parasitized, the species and stage of the parasite, were recorded. Dried exoskeletons of parasitized hosts which remain after the emergence of the parasite were included as these structures invariably remain firmly attached to the leaf, but final moults indicating the emergence of adults were ignored as they are fragile and soon lost. Nymphs attacked by *P. pulvinatus* become recognizable by the formation of a distinctive mummy.

Population fluctuations of parasites. Adult parasites were sampled with the insect sampling machine as described previously.

The affect of parasites on single colonies was studied *in situ* either on experimental trees or on potted citrus seedlings infested from a laboratory culture of *T. erytreae* and placed at an experimental site.

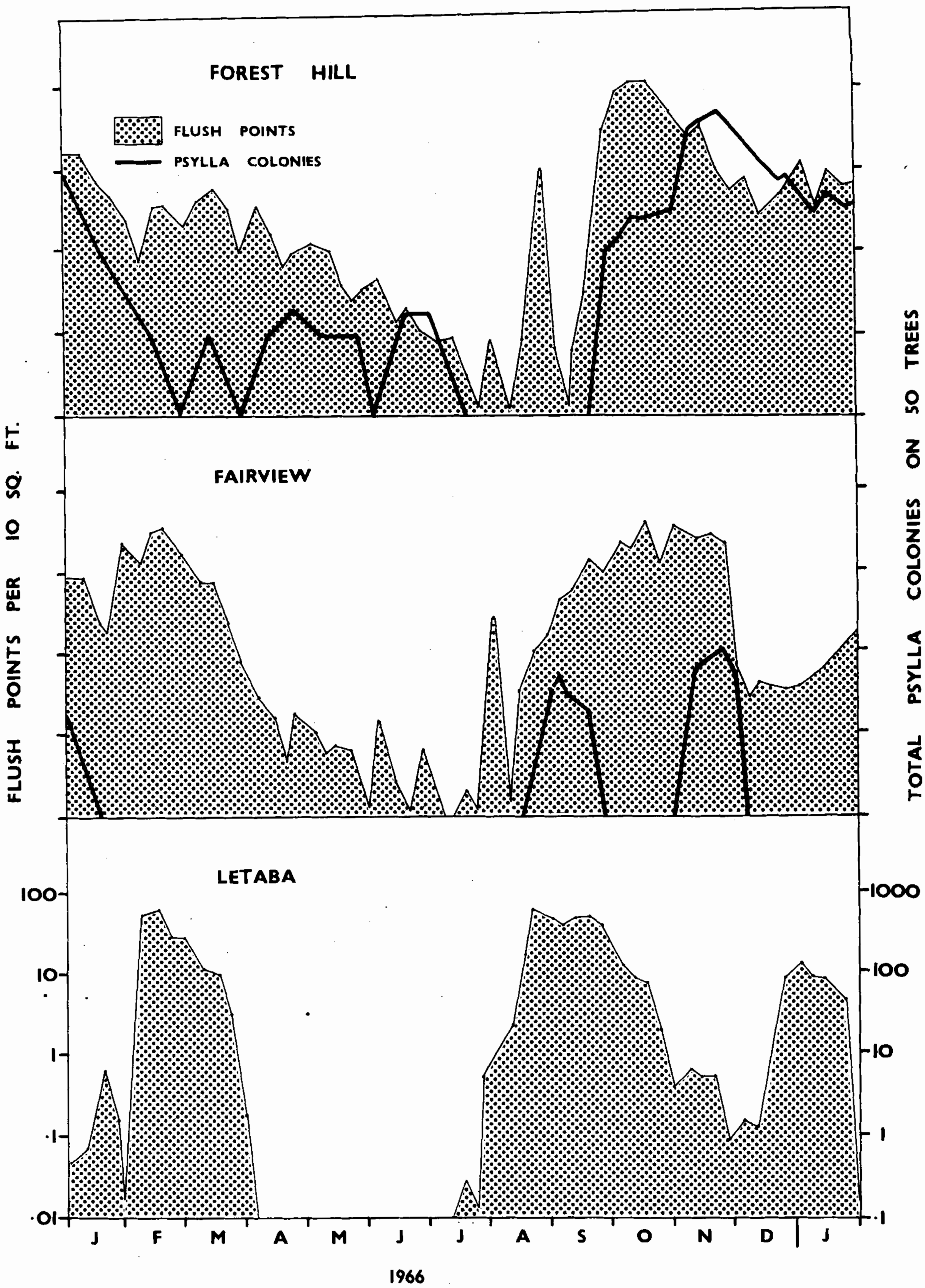
Adult parasites were reared from material used for parasitism counts and from other leaves collected specially for this purpose.

(v) *In situ counts.* The eggs and nymphal stages of *T. erytreae* situated on young flush points are clearly visible *in situ*. By marking colonies in the egg stage on experimental trees near a weather station and following up with detailed counts at regular intervals until the emergence of adults, complete life tables were constructed showing the influence of various ecological factors. Counts were done daily or on alternate days at Letaba and usually at 2-3 day intervals at the other sites. Using a hand lens and a small strip of paper marked with the mean lengths of instars III-V it was possible to recognize each of the five nymphal instars with reasonable accuracy. The random selection of colonies on all parts of tree canopy tended to compensate for differences due to microclimate and foliage condition. When suitable colonies were not available in the field, adults from a laboratory culture of *T. erytreae* were confined on a vigorous citrus seedling, allowed to lay eggs for 24 hours, and the seedling placed in the crotch of a tree near a weather station.

(vi) *Greening assessments.* The incidence of greening was determined by searching the foliage of trees for vein-yellowing and greening-induced deficiency symptoms in the winter months, by examinations of the fruit at picking with the help of the "albedo-fluorescence test" of Schwarz (1968a), and by the screening of twigs for the marker substance indicative of greening by the same method.

3. INFLUENCE OF FLUSHING RHYTHM

Like most psyllids, *T. erytreae* breeds on the young leaves of its plant host and thus population fluctuations are strongly correlated with the flushing rhythm of citrus. Alternate host plants were extremely rare in both study areas and were never found to be infested. There was thus no evidence of any large indigenous reservoir of *T. erytreae* capable of rapidly re-infesting sprayed groves. Unlike the eucalypt psyllid, *Cardiaspina albitextura* (Clark, 1963a) individual citrus trees or flush points rarely differed in their attractiveness for oviposition or feeding.



FOREST HILL
FLUSH POINTS
PSYLLA COLONIES
FAIRVIEW
LETABA
FLUSH POINTS PER 10 SQ. FT.
TOTAL PSYLLA COLONIES ON 50 TREES
100
10
1
·1
·01
1000
100
10
1
·1
J
F
M
A
M
J
J
A
S
O
N
D
J
1966

There is little doubt that populations of other important citrus pests are regulated by the flushing rhythm of citrus, e.g. Panonychus citri (McGr.) and Papilio spp. Oscillations of Toxoptera citricidus (Kirk.), the black citrus aphid, are closely correlated with the presence of new citrus flush (Schwarz, 1965a). Bodenheimer & Swirsky (1957) contend that the physiological status of host plants (new growth) is more important to Toxoptera aurantii than the influence of climate and natural enemies. Bedford (1943) states that the citrus thrips, Scirtothrips aurantii Faure, feeds and breeds on tender foliage only. Studies by Stassen & Catling (1969) revealed that a close correlation exists between flushing rhythm and population fluctuations of this pest.

It is therefore surprising to find that the study of the flushing rhythm of citrus has been so neglected. Webber (1948) and Cameron et al., (1952) discuss briefly the main growth cycles in California but there is no such data for South African citrus.

(i) Flushing rhythm and population fluctuations of T. erytreae Letaba District, Transvaal - January, 1966 to February, 1967

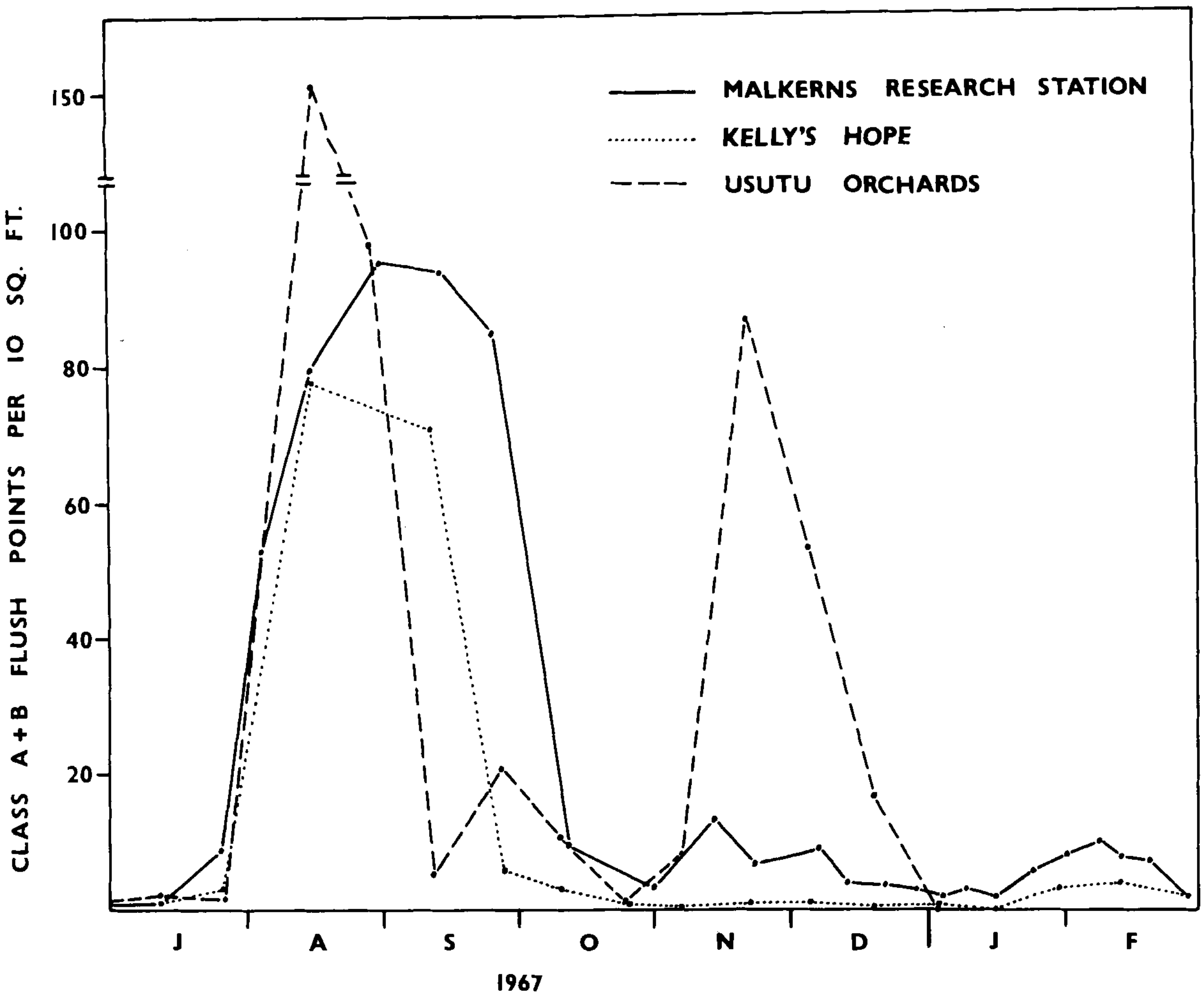
Fig. 6 indicates flush incidence and populations of T. erytreae at the three main experimental sites for 1966. Three main cycles were produced during the study period, these being the most distinct at Letaba where well-defined peaks occurred during August/September, December/January, and February/March. The flushing pattern was the least discernible at Forest Hill. The main spring cycle began in early August at Letaba but at Forest Hill was a month later and more profuse than at the two lower sites. Whereas small amounts of flush were recorded during the winter months at Forest Hill, the Letaba trees were completely dormant for a $3\frac{1}{2}$ month period.

Not only were the highest populations of T. erytreae recorded at Forest Hill, but this was the only site to support breeding populations during the winter. T. erytreae was not found at the Letaba experimental site at any time during the study period. An examination of mature leaves at each site for the distinctive pits made by the insect showed that there was an almost linear relationship between altitude and previous indidence. In all respects flushing rhythm and populations of T. erytreae were intermediate at Fairview.

EXPLANATION OF FIGURE

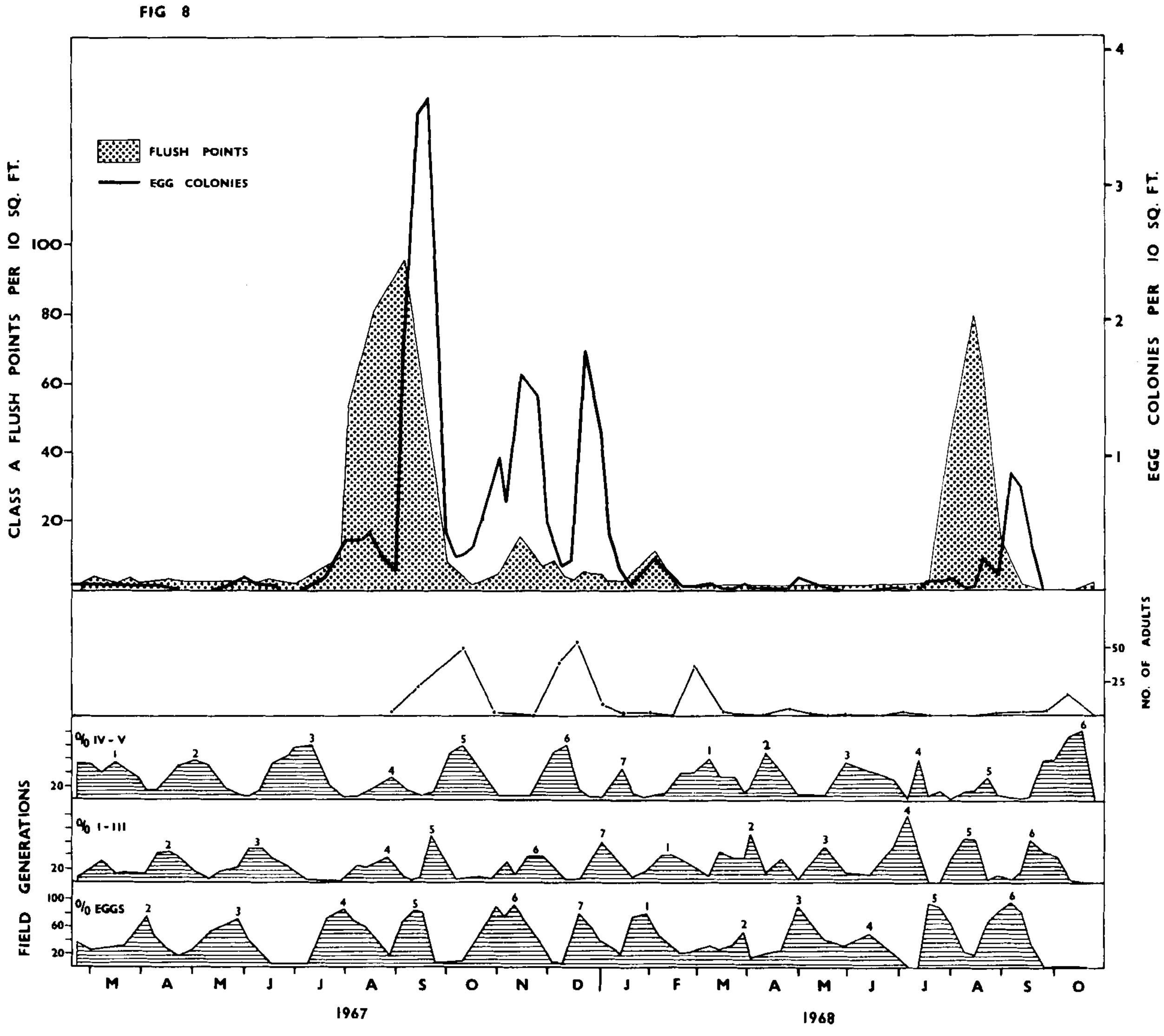
Fig. 6 Incidence of flush points and populations of T. erytreae at the three main experimental sites in the Letaba district from January, 1966, to January, 1967. Class A and B flush points summed; semi-logarithmic scale; vertical scales identical

FIG. 7



MALKERNS RESEARCH STATION
KELLY'S HOPE
USUTU ORCHARDS
CLASS A+B FLUSH POINTS PER 10 SQ. FT.
150
100
80
60
40
20
J
A
S
O
N
D
J
F
1967

FIG 8



FLUSH POINTS
EGG COLONIES
CLASS A FLUSH POINTS PER 10 SQ. FT.
EGG COLONIES PER 10 SQ. FT.
NO. OF ADULTS
FIELD GENERATIONS
% IV - V
% I - III
% EGGS
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
1967
1968

Malkerns District, Swaziland. February, 1967 to February, 1969

In the 1966-67 season the trees at each site bore small amounts of flush during the winter and produced fairly well-defined growth cycles in August/September, November and January/February. Fig. 7 shows that the spring cycle began simultaneously in the last week of July at all sites. Usutu Orchards produced more flush in winter and flushed more heavily in August and November than the other sites. The trees were virtually devoid of flush in January and February at Usutu Orchards. Flush density was consistently the lowest at Kelly's Hope, the November and January/February flushes being very light and separated by periods of virtual dormancy. At the Research Station, however, flush was present throughout the study period and at all times these trees supported higher populations of *T. erytreae* than the other two sites.

Fig. 8 indicates how peaks of egg colonies invariably succeeded peaks of young flush points at Malkerns Research Station. The correlation between flush and populations of *T. erytreae* was shown further by a comparison of their coefficients of variation, these following one another closely, being the highest for the sparse, scattered winter flush and the lowest for the major growth cycle in spring.

Though there was little difference in the winter flush densities of 1967 and 1968 at Malkerns Research Station, *T. erytreae* populations in June and July, 1968, were approximately one-third of those for the previous year. The timing and volume of the spring flush cycle was very similar in both seasons (Fig. 8). Beginning in mid-July, the production of new growth reached a maximum in August and was followed by a peak of *T. erytreae* eggs in the first two weeks of September. But insect populations were considerably lower in the spring of 1968 and became negligible in October. The trees were almost completely devoid of flush at this time. The second flush of the season, which reached a peak in December and was 3-4 weeks later than in the previous year, and the February flush, were both smaller than those recorded in the 1967-68 season. *T. erytreae* populations increased strongly on the December flush to reach their highest densities for the season, but by mid January had declined sharply and extremely low numbers were recorded during late summer and into the following winter.

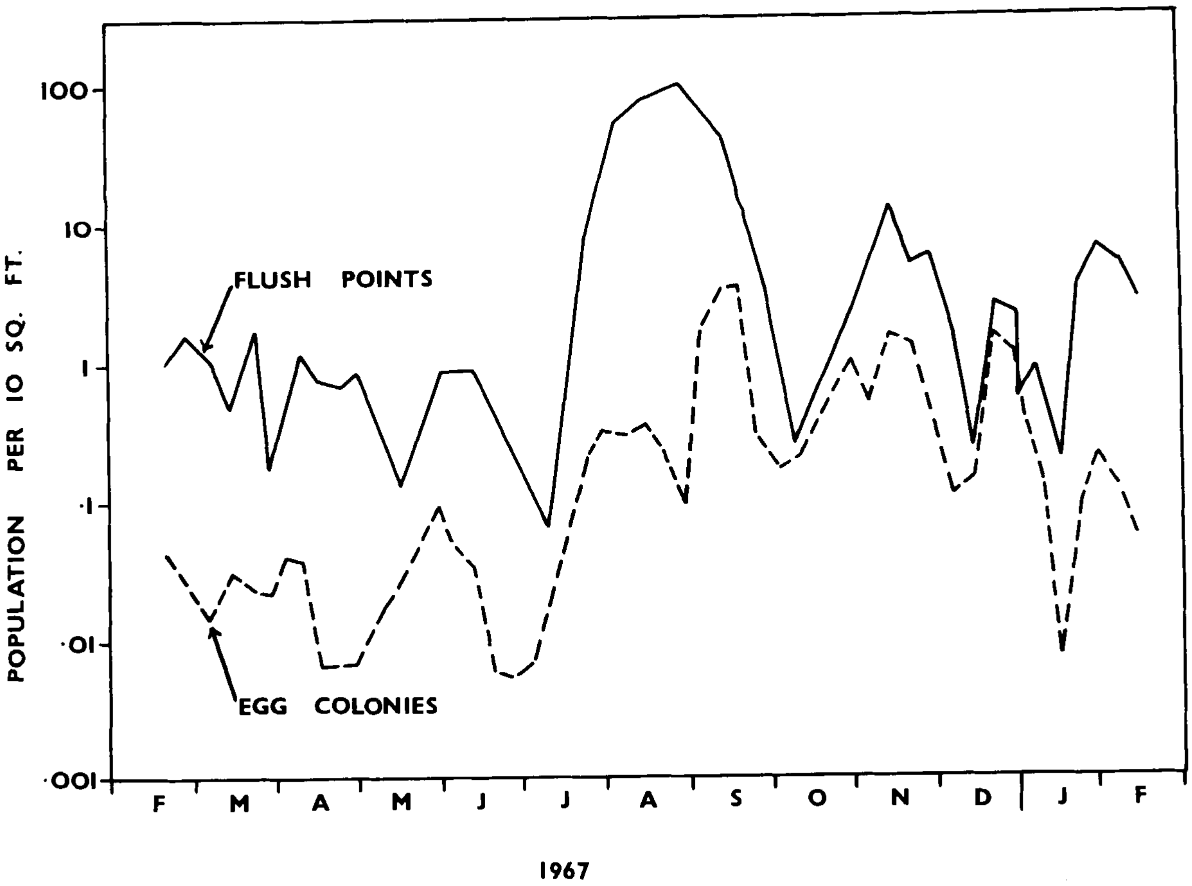
By plotting the proportion of egg, instar I-III, and instar IV-V colonies as a percentage of the total population, Fig. 8 shows that there were 7-8 distinct broods or field generations per annum. A similar pattern of field generations was plotted for Usutu Orchards and Kelly's Hope during 1967 and early 1968.

EXPLANATION OF FIGURES

Fig. 7 Flushing rhythm of the three experimental sites in the Malkerns district from July, 1967, to February, 1968. Class A and B flush points summed

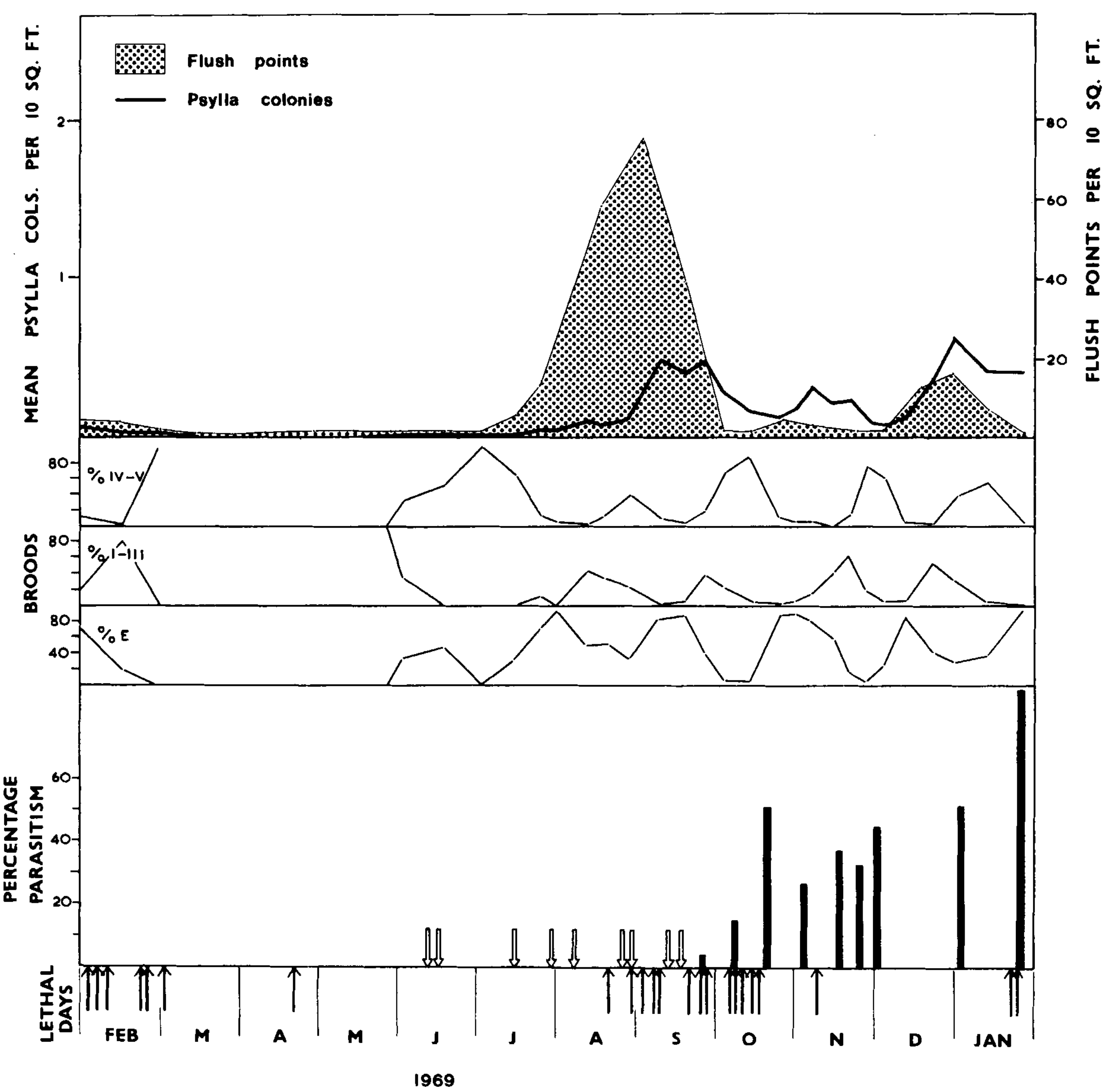
Fig. 8 Populations of class A flush points and egg colonies; and field generations of *T. erytreae* at Malkerns Research Station from February, 1967, to October, 1968

FIG. 9



100
10
1
·1
·01
·001
POPULATION PER 10 SQ. FT.
FLUSH POINTS
EGG COLONIES
F
M
A
M
J
J
A
S
O
N
D
J
F
1967

FIG 10



Flush points
Psylla colonies
MEAN PSYLLA COLS. PER 10 SQ. FT.
FLUSH POINTS PER 10 SQ. FT.
2
1
80
60
40
20
BROODS
% IV–V
% I–III
% E
PERCENTAGE PARASITISM
LETHAL DAYS
FEB
M
A
M
J
J
A
S
O
N
D
JAN
1969

Fig. 8 indicates that immediately after peaks of instars IV-V there usually followed waves of adults. Because females require class A flush points for egg-laying within several days of their emergence, it is of obvious importance to the population that the adults of each field generation be well synchronized with flush cycles - particularly in July and August at the time of the main population upsurge. At Malkerns Research Station there was excellent synchrony during the study period but at the other sites it was less favourable since in 1967 there was a two-week interval at Usutu Orchards and a 3-4 week interval at Kelly's Hope between adult emergence and the onset of the spring flush cycle. At both these sites populations of T. erytreae rose little during August. In the 1968 season there was a very sparse spring cycle at Usutu Orchards on which no T. erytreae was found, while at Kelly's Hope on a heavy spring flush with slightly better synchrony there was a higher population than the previous year.

Fig. 9, which compares populations of class A flush points and colonies of T. erytreae at Malkerns Research Station for the 1967-68 season on the same log scale, indicates the progressive increase in the proportion of flush points which served as breeding sites. By the end of December, just prior to the population crash in January, all flush points were grossly overcrowded.

March, 1968 to January, 1970. Flushing rhythm, and population fluctuations and broods of T. erytreae for this period are shown in Fig. 10. Due mainly to the exceptionally severe weather which prevailed from December to February, mean population densities of T. erytreae from May to the end of July were one fifth of those recorded in the previous season, and thus only a small winter nucleus existed at the start of the 1969/70 season. Flush densities between April and July were very similar to previous years.

Starting about one week earlier than in 1968, the main spring flush cycle began in the second week of July. The emergence of adults from the June/July brood was well synchronized with the growth cycle and there was a gradual population rise in late July and August. However, the density of this first flush was lower and more irregular than usual giving rise to a greater variation in the population density of T. erytreae from tree to tree. This tendency was also observed in other groves in the district. Hailstorms in September and November and outbreaks of aphids reduced the volume and quality of young foliage and populations of T. erytreae were comparatively low in the first part of the season. The storm on November 21 was particularly severe and badly defoliated the southern and western quadrants of the trees. This stimulated a strong growth flush in December, 85.0% of the total

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EXPLANATION OF FIGURES

Fig. 9 Class A flush points and egg colonies of T. erytreae at Malkerns Research Station from February, 1967, to February, 1968. Semi-logarithmic scale

Fig. 10 Population fluctuations and broods of T. erytreae at Malkerns Research Station from February, 1968, to January, 1970, in relation to flushing rhythm, percentage parasitism, and "lethal days" (shown by arrows). On a "lethal day" the saturation deficit exceeded 25.9mm Hg (34.6 mbars)

FIG. 11

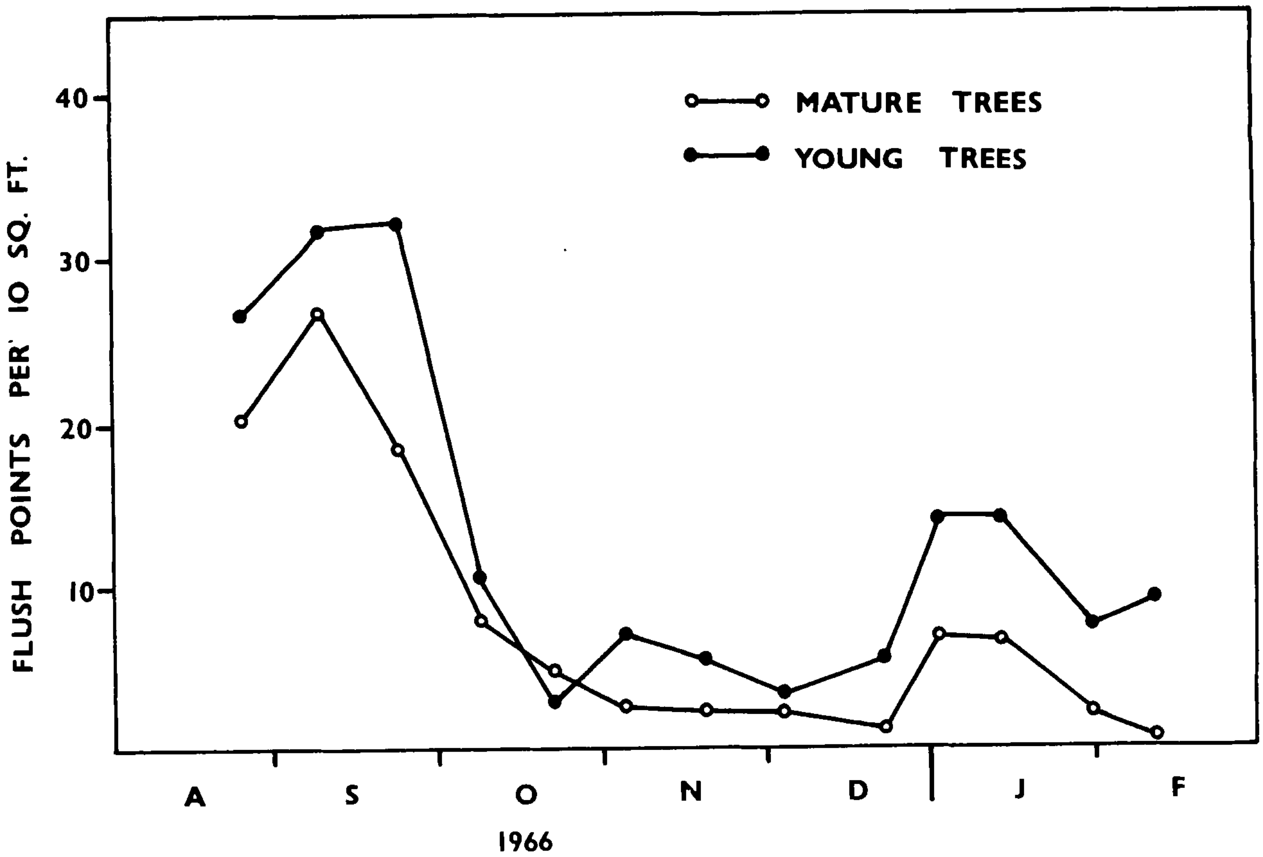
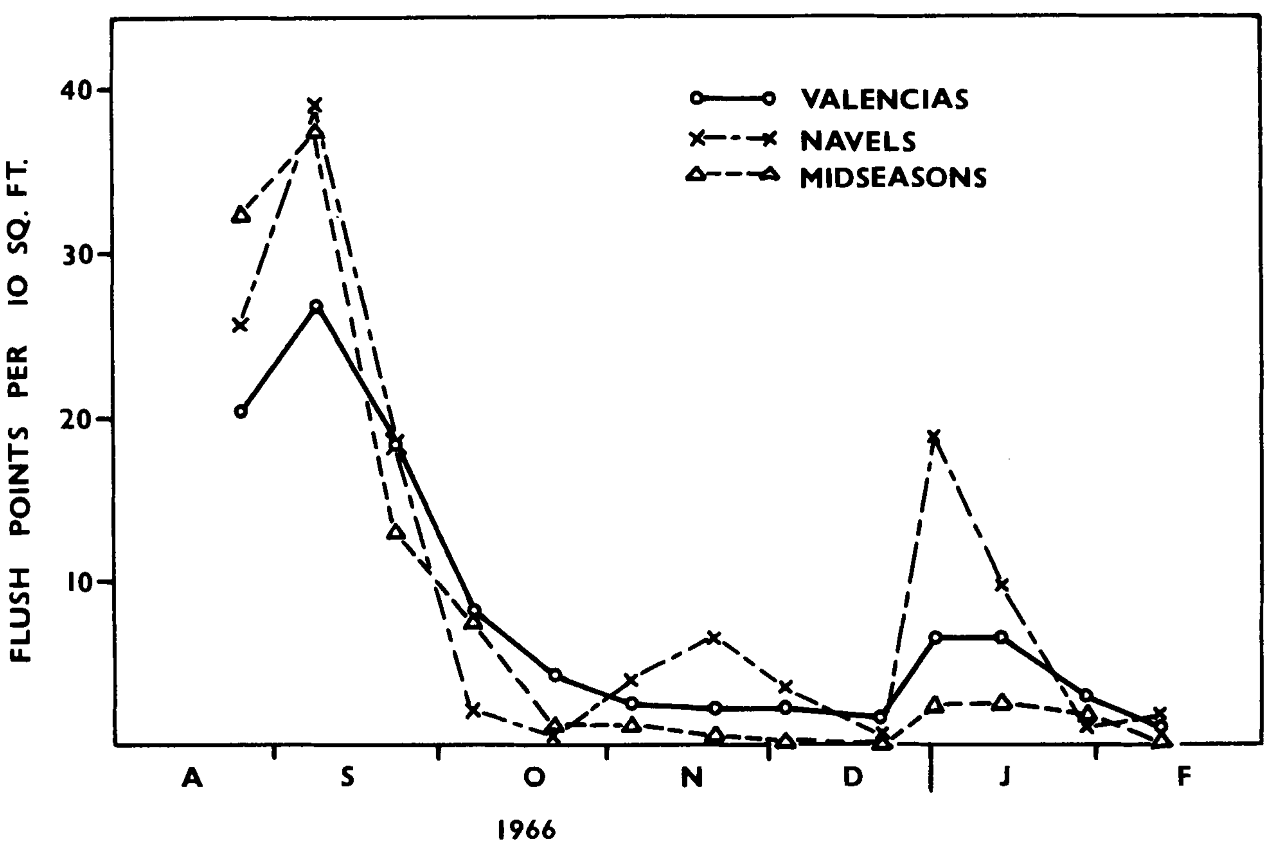

MATURE TREES
YOUNG TREES
40
30
20
10
FLUSH POINTS PER 10 SQ. FT.
A
S
O
N
D
J
F
1966

FIG. 12


VALENCIAS
NAVELS
MIDSEASONS
40
30
20
10
FLUSH POINTS PER 10 SQ. FT.
A
S
O
N
D
J
F
1966

flush at this time appearing on the damaged half of the tree. With favourable weather in November and December there was another surge of *T. erytreae* in December. During January, however, the normal midsummer population crash took place and some egg colonies were observed on advanced class A flushes indicating a relative shortage of breeding sites.

(ii) Influence of flushing on oviposition. As suspected earlier (Catling, 1967), young flush stimulates egg-laying and the pre-oviposition period of the adult is considerably extended in the absence of young growth. In May, 1967, 40 newly-emerged adults were collected in the field and caged in the insectary on citrus seedlings having mature leaves only. Flushing was discouraged on these plants and where young growth appeared it was immediately removed. Under these conditions the mean longevity for males was 62.3 days (44-73) and for females 52.2 days (16-82). Almost without exception the females died without laying eggs. On one plant where a flush was allowed after 64 days, a single female laid 297 eggs before her death at 82 days.

(iii) Influence of tree age and variety on flushing rhythm. Populations of class A plus B flush points from 39 Valencia survey plots on Letaba Estates were grouped into those from mature trees (15 years and above) and those from young trees (six years and below). Fig. 11 shows that there were two main flushing cycles in the 1966-67 season, August/September and January. Apart from the survey on October 20 the young trees flushed more profusely, and produced an additional cycle during early November. A similar trend was evident in the few mid-season plots studied.

Flush surveys also demonstrated inherent differences in the flushing rhythm of mature Valencias, Navels and mid-seasons (mainly Letaba Earlies, Rubies and Tomangoes). It is seen from Fig. 12 that each variety produced a growth cycle in August/September and again in December/January. When comparing Navels and mid-seasons with Valencias, the Navels bore heavier flushes in November and December/January. On the other hand once the spring cycle was over the mid-seasons produced very little growth for the rest of the study period, their January flush being very light.

EXPLANATION OF FIGURES

Fig. 11 Flushing rhythm of young and mature Valencias from August, 1966, to February, 1967, at Letaba Estates. Class A and B flush points summed. A log (x + 1) transformation and t-test showed the more profuse flushing of young trees to be significant at the 1% probability level on Dec. 20 and Feb. 28, and at the 5% probability level on Nov. 18 and Jan. 27

Fig. 12 Flushing rhythm of mature Valencias, Navels and mid-seasons from August, 1966, to Februay, 1967, at Letaba Estates. Class A and B flush points summed. A log (x + 1) transformation and t-test showed the following: Valencias vs Navels - Nov 18**, Dec 29**; Valencias vs mid-seasons - Dec 2*; Navels vs mid-seasons - Nov 18*, * significant at the 5%, ** at the 1% probability level

FIG. 13

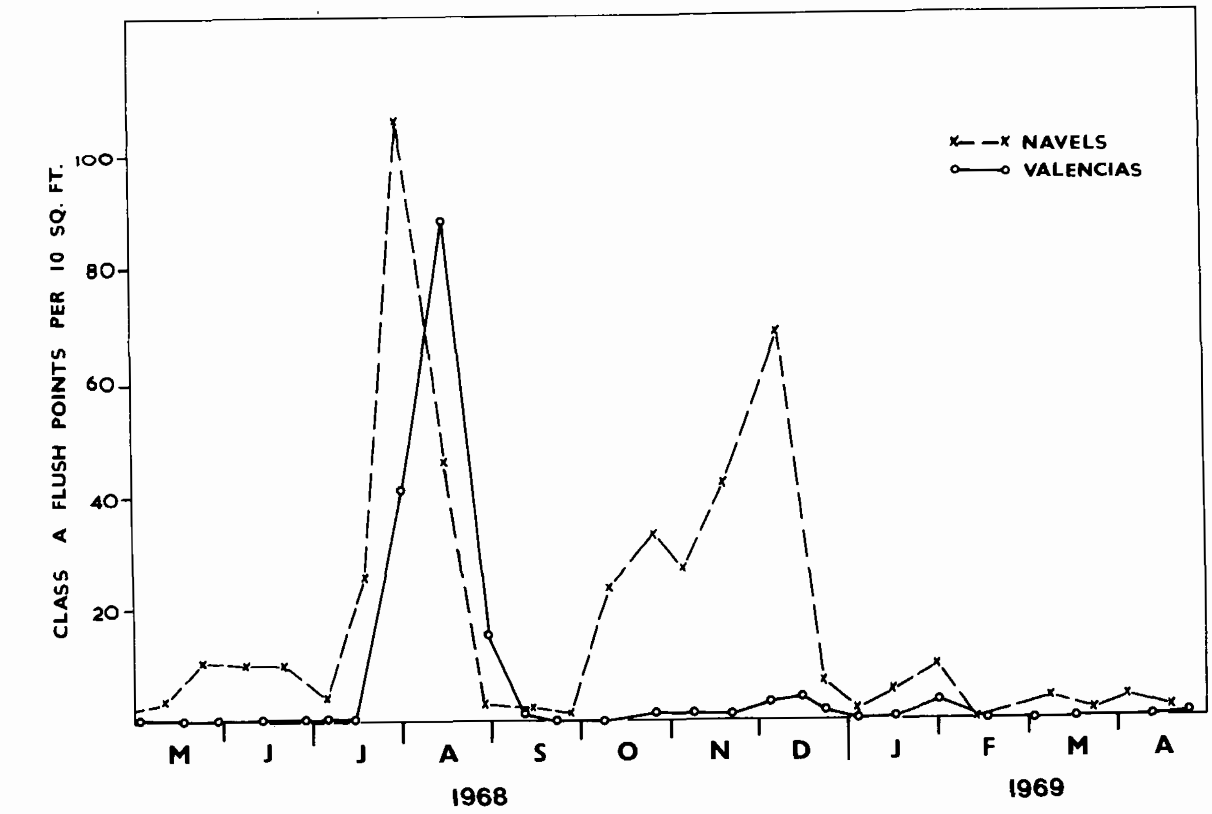

CLASS A FLUSH POINTS PER 10 SQ. FT.
20
40
60
80
100
NAVELS
VALENCIAS
M J J A S O N D J F M A
1968
1969

FIG. 14

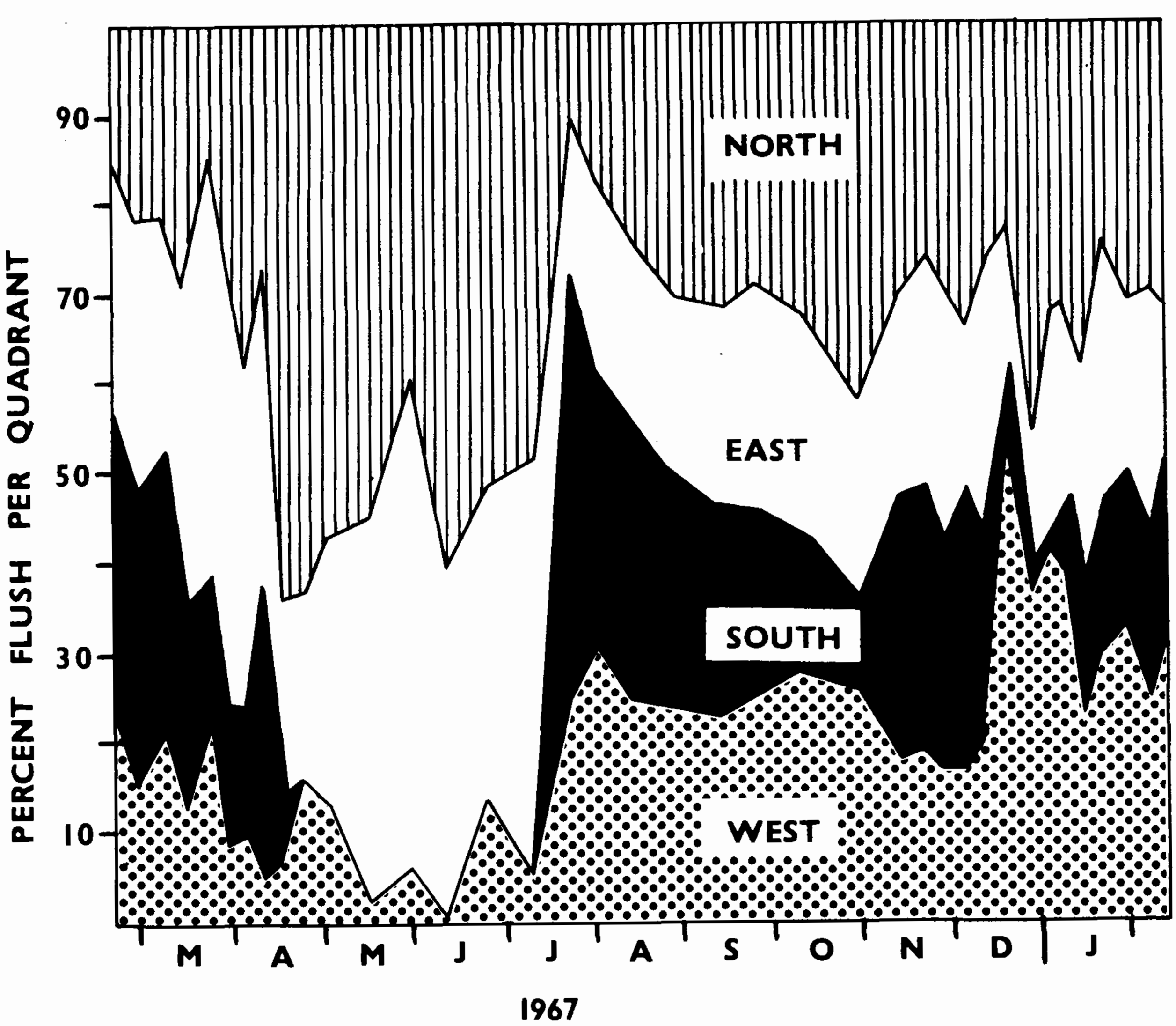

PERCENT FLUSH PER QUADRANT
10
30
50
70
90
NORTH
EAST
SOUTH
WEST
M A M J J A S O N D J
1967

Table 3. Flush indidence in two Navel and two Valencia groves in the Malkerns area for 1967/68. Flush volume rated on scale 0-6.

Date	NAVELS			VALENCIAS		
	Amaswazi	Ross Citrus	Mean	Ross Citrus	Lensvelt	Mean
1967 Mar 30	3	2	2.5	2	2	2.0
May 5	4	6	5.0	3	1	2.0
Jun 5	4	2	3.0	4	2	3.0
Jul 6	2	2	2.0	2	1	1.5
Aug 8	6	6	6.0	6	6	6.0
Sept 14	5	6	5.5	6	6	6.0
Oct 12	2	2	2.0	2	2	2.0
Nov 9	3	4	3.5	2	2	2.0
Dec 14	3	1	2.0	1	2	1.5
1968 Jan 18	2	2	2.0	0	0	0.0
Feb 23	4	4	4.0	2	2	2.0
Mar 21	2	2	2.0	2	1	1.5

Table 3 shows the results of a monthly rating of flush volume in two Navel and two Valencia groves in the Malkerns area. Though both varieties had a similar spring cycle, the Navels flushed more heavily during May and in the November/December and February/March cycles. During 1967 high populations of T. erytreae developed at Ross Citrus in April/May, and in a nearby grove in July, on flushing Navels. Again, the trend for heavier flushing by Navels was demonstrated in studies made in two similarly-managed groves on Malkerns Research Station (Fig. 13).

(iv) Influence of the greening disease on flushing rhythm. The scattered winter flushes and overlapping growth cycles at Forest Hill were mainly due to a severe leaf drop caused by severe water stress and the high incidence of greening.

There was a high incidence of greened fruit at Forest Hill. Greening surveys based on leaf symptoms showed 41 trees at Forest Hill and 32 trees at Fairview to have definite symptoms, while at Letaba only six trees showed greening symptoms. A similar trend was evident from the screening of twigs.

It was shown previously that there were marked differences in the flushing rhythm and populations of T. erytreae at Malkerns Research Station and Kelly's Hope. Observations indicated that T. erytreae populations have been lower in the trees at Kelly's Hope in previous years. Yet the Valencias at both sites have been similarly managed since they were taken from the same nursery and planted out on similar soil types in the 1957-58 season.

EXPLANATION OF FIGURES

Fig. 13 Flushing rhythm of mature Navels and Valencias from May, 1968, to April, 1969, at Malkerns Research Station

Fig. 14 Flush populations according to tree aspect from February, 1967, to February, 1968, at Malkerns Research Station

Table 4. Incidence of greening and fruit yield at Malkerns Research Station and Kelly's Hope

Site	Mean symptoms per 32 sq. ft of tree canopy		Percent greened fruit at picking		Fruit yield mean lugs per tree	
	Vein-yellowing	Greening-induced deficiency symptoms	1967	1968	1967	1968
Kelly's Hope	1.7	1.9	2.6	1.5	7.7	6.7
Malkerns R.S.	5.4	13.3	19.5	23.5	5.3	4.1

There were, however, slight climatic differences which may have induced a greater winter dormancy at Kelly's Hope.

Table 4 shows that there were notable differences in the incidence of greening at the two sites. From Tables 2 and 4 it is evident that the trees at Kelly's Hope were 30% larger in canopy area, had one fifth of the greening symptoms and produced nearly twice as much healthy fruit as the trees at the Research Station. At Kelly's Hope T. erytreae populations were lower and the flushing rhythm less favourable for the vector.

(v) Distribution of flush according to tree aspect. Studies at Forest Hill, Malkerns and in a small plot on Letaba Estates, revealed that the bulk of winter flush is borne on the northern and thus warmest aspect of the tree. This is shown graphically in Fig. 14 where at the Malkerns Research Station site negligible amounts of flush were recorded on the southern quadrant of the trees from the last week of April to the second week of July. At other times of the year flush was fairly evenly distributed in all quadrants of the tree. These trends were also evident in the Swaziland Lowveld in June, 1968.

(vi) Discussion. There are three, sometimes four, annual flush cycles in the citrus areas of the eastern Transvaal and Swaziland Middleveld. The main flushes occur typically in August/September, November, and January/February. With the exception of Forest Hill, the heavy spring cycle, which bears the blossom and supports the spring build-up of T. erytreae, began towards the end of July at all study sites.

Biotic Factors Regulating Flushing Rhythm

Variety. Limes, Citrus aurantifolia (Christm.), and lemons, C. limon (Linn.), are known to flush more freely than the sweet orange, C. sinensis (Linn.). Within the sweet orange group this study indicated that Navels flush more profusely, and midseasons less profusely than Valencias. Hall (1930) showed that at Mazoe, Rhodesia, Navels blossom about three weeks before Valencias but on Letaba Estates the present author observed that there was little difference in the timing of the spring growth cycle where both varieties were similarly irrigated. Because T. erytreae breeds exclusively on young flush, it seems possible that the more profusely-flushing varieties are more susceptible, and the quieter varieties less susceptible to attack. This fact may partly account for the lower incidence of greening observed in many mid-season groves.

Age. The more prolonged and profuse flushing of young trees and the decline in flushing vigour with age is supported by Schwarz (1965a). In the higher-lying citrus areas vigorously-flushing young trees are extremely attractive to *T. erytreae* at all times. In the hotter areas young trees may become infested in the cooler months. Immature trees frequently support quite large populations when mature trees are semi-dormant. Infestations on young trees at Malkerns Research Station reached sprayable proportions in February and March, 1968, at a time when populations were very low in mature trees.

Greening and tree condition. Any factor which causes stress or brings about the premature dropping of mature leaves may result in a compensatory, out-of-season growth flush. Strong flushes were observed to follow severe hailstorms in both study areas. Hall (1930) states that the time of fruit picking influences the flushing and blossoming of citrus.

The greening disease was shown to have a profound effect on the flushing rhythm of citrus, the flushing of severely greened trees being commonly out of phase with that of healthy trees. Like the closely related stubborn disease, greening causes dieback, leaf drop, and out-of-season growth and blossoming (McClean & Oberholzer, 1965a). Holtzhausen, L.C. (personal communication, 1968) has found that greened trees shed leaves continuously whereas leaf drop from healthy trees is mainly confined to spring and summer.

Evidence presented previously suggests that high populations of *T. erytreae* have caused a high incidence of greening at Malkerns Research Station and Forest Hill. The disease has in turn modified the natural flushing rhythm by inducing heavier winter flushes and overlapping growth cycles during the growing season. There is thus a vicious cycle as this new pattern of growth is more favourable for the vector.

Abiotic factors regulating flushing rhythm

Of the abiotic factors which influence the growth of citrus, Webber (1948) states that photoperiod is relatively unimportant and is always dominated by temperature and moisture.

Temperature. Based on Californian work this author gives the mean threshold temperature for citrus growth as 12.8°C and shows that in Mediterranean regions with a winter rainfall, the mean daily and soil temperatures do not rise sufficiently above this temperature to permit growth during the three winter months. He shows that comparisons of heat indices for the growing season of the year explain differences in the growth of citrus in various areas; that the mean temperature for the two months preceding the spring growth cycle (June and July in the Transvaal and Swaziland) largely determines the timing of this cycle; and that midsummer temperatures slow down and inhibit growth.

Because of the equal importance of moisture in regulating growth, it appears that in the subtropical regions of South Africa with a dry winter, moisture and temperature work together to regulate flushing. The conversion of mean monthly temperatures to monthly heat indices above 12.8°C indicated that heat units at most of the study sites were sufficient to permit small winter flushes. At Letaba Estates and in the Swaziland Lowveld citrus areas which have still higher winter temperatures, the potential for winter growth is greater.

The regulating affect of temperature is shown by the fact that the bulk of normal winter flush is borne on the northern aspects of the tree. This is of practical importance in that insecticides for the control of pests developing on winter flushes, such as _T. erytreae_ and citrys aphids, will best be concentrated on the northern sides of the trees. Local flush points developing in winter at the sites of leaf drop caused by greening were on occasions observed to develop on the cool aspects of the tree.

Moisture. Under conditions of favourable temperature citrus may be forced to flush at almost any time by manipulating the water supply (Webber (1948). The present author has observed that a drought period during the rainy season may delay or indefinitely postpone a recognized growth cycle. This occurred at Letaba Estates during the 1966/67 season (Fig. 6) where the usual November cycle was delayed for approximately three weeks due to a dry November-early December and a critical shortage of irrigation water.

In the summer rainfall areas of South Africa the spring growth cycle is strongly influenced by water supply, heavy irrigations in July being a common practice to stimulate vigorous shoot growth and regular blossoming. Hall (1930) states that dates of irrigation (and picking)..."may induce a different date of blossoming in two groves of the same variety and that unless trees are kept fairly dormant during winter their natural flushing rhythm is lost".

In the warmer areas especially during mild winters, heavy rains or irrigations may stimulate significant flushes and precipitate outbreaks of _T. erytreae_. Catling (1967) was of the opinion that the naturally high water table and excessive use of sprinkler irrigation was the main reason for the history of midwinter outbreaks on some farms in the upper Letsitele Valley of the Letaba District.

Aggravated by the greening disease, the prolonged wilting of trees at Forest Hill and Usutu Orchards caused considerable leaf drop during the winter. This stimulated exceptionally heavy growth cycles which at Usutu Orchards supplied virtually a complete new leaf canopy.

Effect of flushing rhythm on populations of _T. erytreae_

The hot dry climate and well-defined flush cycles of Letaba Estates and the Swaziland Lowveld work against the development of high populations of _T. erytreae_; whereas the cool, moist upland areas such as Forest Hill and Malkerns which tend to flush more regularly, are extremely favourable.

In areas with a favourable climate population fluctuations of *T. erytreae* follow closely on peaks of flush production. Flushing imposes a rhythm both on the numbers and developmental stage of the insect. Field generations are more distinct on fairly well-defined flush cycles (as at Malkerns in 1967) than on flushes which tend to overlap (as at Forest Hill in the 1966-67 season).

The synchrony between the emergence of adults at the end of a field generation and the production of young flush appears to be of significance, particularly to the rising spring population.

Under exceptionally favourable conditions populations of *T. erytreae* may exceed the supply of breeding sites, become grossly overcrowded and suffer intraspecific strife. Overcrowding was observed at Ross Citrus Estates in September, 1967, and again in December at the Malkerns Research Station experimental site. Counts showed that in December virtually every flush point was infested, a large proportion being densely overcrowded with eggs and young instars and supporting 9-10 adults or more. Between July and September, 1968, however, a maximum of 3 adults per colony was found, the mean for 733 colonies examined being 0.42 adults per colony. There is little doubt that the overcrowding of breeding sites and consequent mortality contributed to the midsummer population crash.

The size of the winter nucleus of *T. erytreae*, which is responsible for the spring population upsurge, is largely determined by winter flushing activity. Small but significant winter flushes in groves along the Transvaal escarpment and Malkerns district frequently bring about severe spring outbreaks. The three-month near cessation of growth at Letaba Estates during winter, and the relatively flush free periods between summer growth cycles tend to break up the continuity of breeding populations. During such periods when the trees are semi-dormant the pre-oviposition period is considerably prolonged. Any factor or practice which tends to promote dormancy will assist in limiting populations of *T. erytreae*.

Competition with citrus aphids

In most seasons at Malkerns there was a certain amount of interspecific competition between *T. erytreae* and citrus aphids. Aphids are quick to colonize young flush and produce copious honeydew which renders many leaves unattractive to *T. erytreae*. In a small, replicated laboratory trial on citrus seedlings, 30-40 adults of *T. erytreae* were given a choice between seven flushes heavily infested with citrus aphids, and seven healthy uninfested flushes. In the first trial, 87.5% and in the second, 68.8% of the adults selected aphid free flushes for feeding or breeding sites. The adults constantly avoided foliage covered with honeydew. A small laboratory trial and field observations indicated that the nymphs are not severely affected by aphids or by moderate amounts of honeydew.

Large populations of aphids developed on the September and midsummer flushes and were particularly severe in the 1967-68 and 1969-70 seasons. In September, 1969, 300 randomly-selected flushes revealed that 90.8% were infested with aphids.

4. INFLUENCE OF FLUSH QUALITY

Catling (1967) cited preliminary field evidence that the condition of the host plant is important in the development of the immature stages of *T. erytreae*. Nymphs developing on young growth of poor condition were reduced in size, showed prolonged instar duration, and suffered high mortality. Moran (1968a) showed that the immature stages reacted similarly when developing on less-favoured host species. It was suggested by Catling (1967) that this was mainly due to inadequate amounts of available food in the leaves, particularly deficiencies of protein.

(i) Effect of nutrition on nymphal development. Between July and October, 1967, small-scale experiments were carried out in the insectary to investigate the influence of leaf composition on the survival and development of *T. erytreae* nymphs. Fourteen Valencia seedlings were grown in washed river sand in one gallon tins fitted with a gauze bottom to ensure efficient drainage. After planting and cutting back to stimulate new growth, two applications of the Long Ashton Standard Nutrient Solution (Hewitt, 1966) were applied to all plants after which they were matched for size and divided into two sets. Seven plants were given a weekly application of the nutrient solution and routine watering. No further nutrients were applied to the second set of plants and in addition, these plants were watered heavily thrice daily for the first five weeks of the experiment to leach out all dissolved nutrients. Two successive generations of *T. erytreae* were reared on both sets of plants, adults being allowed to oviposit for 2-3 days and the developing insects examined and counted at regular intervals until reaching the fifth instar or adult stage. Separate records were kept for each plant. On completion of the first generation the plants were cut back and the experimental process repeated on four plants of each treatment. After the final count the infested leaves were analysed for nitrogen content. During the first generation several plants became heavily infested with the citrus red mite, *Panonychus citri* (McGregor).

No deficiency symptoms developed in the leached plants during generation one, the nitrogen content of both sets of plants remaining in the region of 4.3 percent nitrogen of dry weight. During the second generation the leached plants showed a slight leaf yellowing when compared with fertilized plants, the nitrogen content being 2.41 and 2.72% nitrogen respectively. In Table 5 is shown the survivals for leached and fertilized plants in both generations. In both generations the mean survivals on the leached plants were slightly higher but an analysis of variance found this difference to be non-significant.

Table 5 Nymphal survivals of T. erytreae on normally fertilized and leached Valencia seedlings

		No. of plants	Initial no. of eggs	No. of insects to reach fifth instar or emerge as adults	Percentage survival
Generation one	leached plants	7	1612	1276	79.2
	fertilized plants	7	1736	1270	73.2
Generation two	leached plants	4	1450	903	62.3
	fertilized plants	4	1044	587	56.2

In the first generation there was an unaccountable trend for nymphal instars II and III to develop faster on the leached plants. However, this difference in growth rate was not continued in the later instars for both populations completed their nymphal development at about the same time. In the second generation, though considerable variation was observed, the rate of development in instars I-III was very similar in both treatments. By the time the fifth instar was reached, however, development was clearly more rapid on the fertilized plants, the first adults emerging a full five days before those on the leached plants.

No obvious differences were noticed in nymphal size between nymphs developing on leached plants and fertilized plants. In generation one, however, P. citri caused considerable mesophyll-collapse in some of the leaves supporting nymphs. Table 6 shows that individuals developing on leaves with mesophyll-collapse tended to be smaller in size. Yet the nitrogen content of these affected leaves (3.8%) was apparently sufficient for basic nitrogen requirements.

Table 6 Length measurements of T. erytreae nymphs developing on healthy and mesophyll-collapsed leaves. Measurements in mm, not including nymphal marginal fringe. Number of measurements in brackets. IV-V- fourth and fifth instars

	Healthy leaves		Leaves with mesophyll-collapse	
	IV	V	IV	V
Aug 23	0.99 (40)	1.37 (24)	0.93 (29)	-
Aug 28	-	1.42 (20)	-	1.33 (20)

(ii) Fluctuations in nitrogen content of young flush in the field. Between March, 1967, and August, 1968, seventy-seven class A and class B flush points were removed from well-fertilized citrus trees in the Malkerns district for the determination of nitrogen content. Each sample consisted of 20-30 flushes selected haphazardly from all parts of the data tree. Flush was sampled at all times of the year, and from trees of different age and variety or species. In young flushes the succulent stem, which is frequently used for oviposition and

FIG. 15

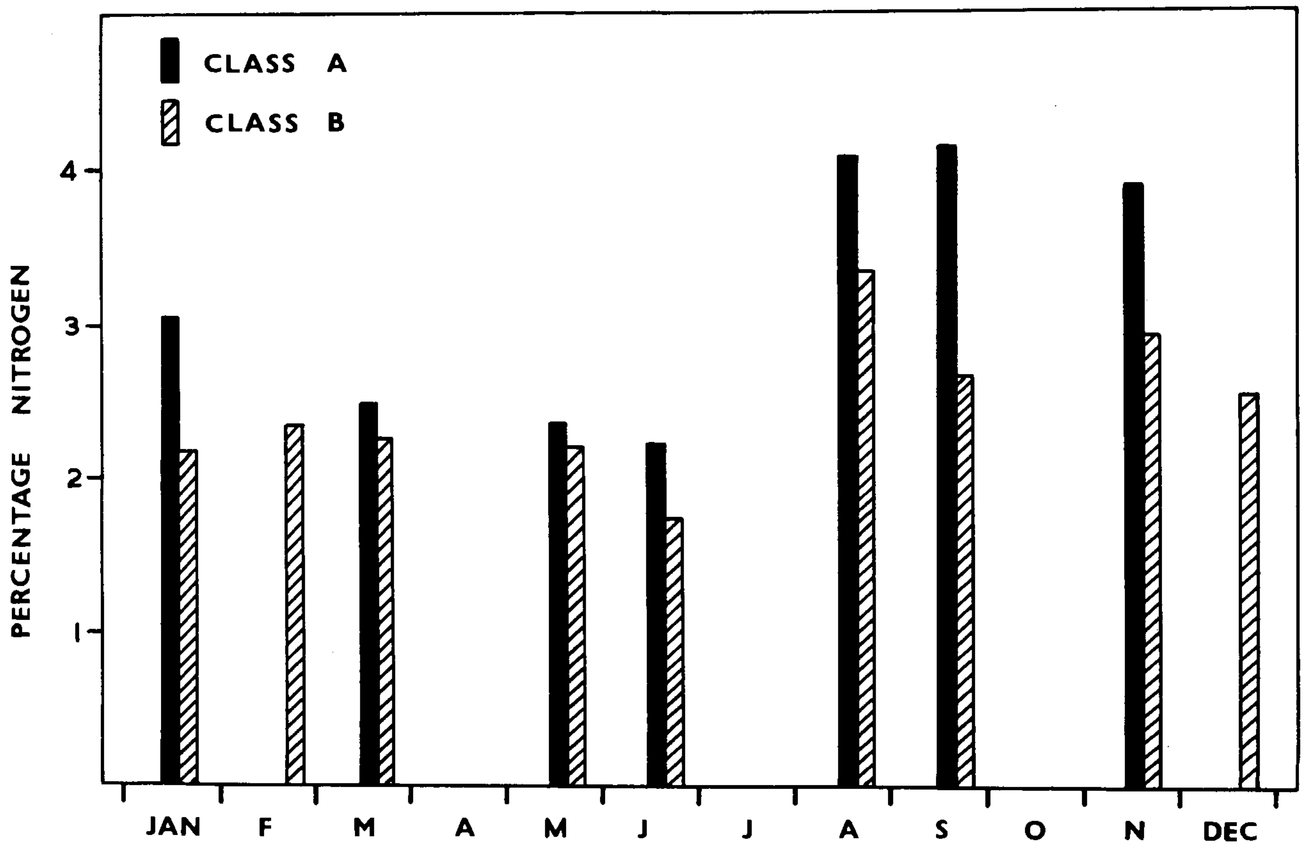
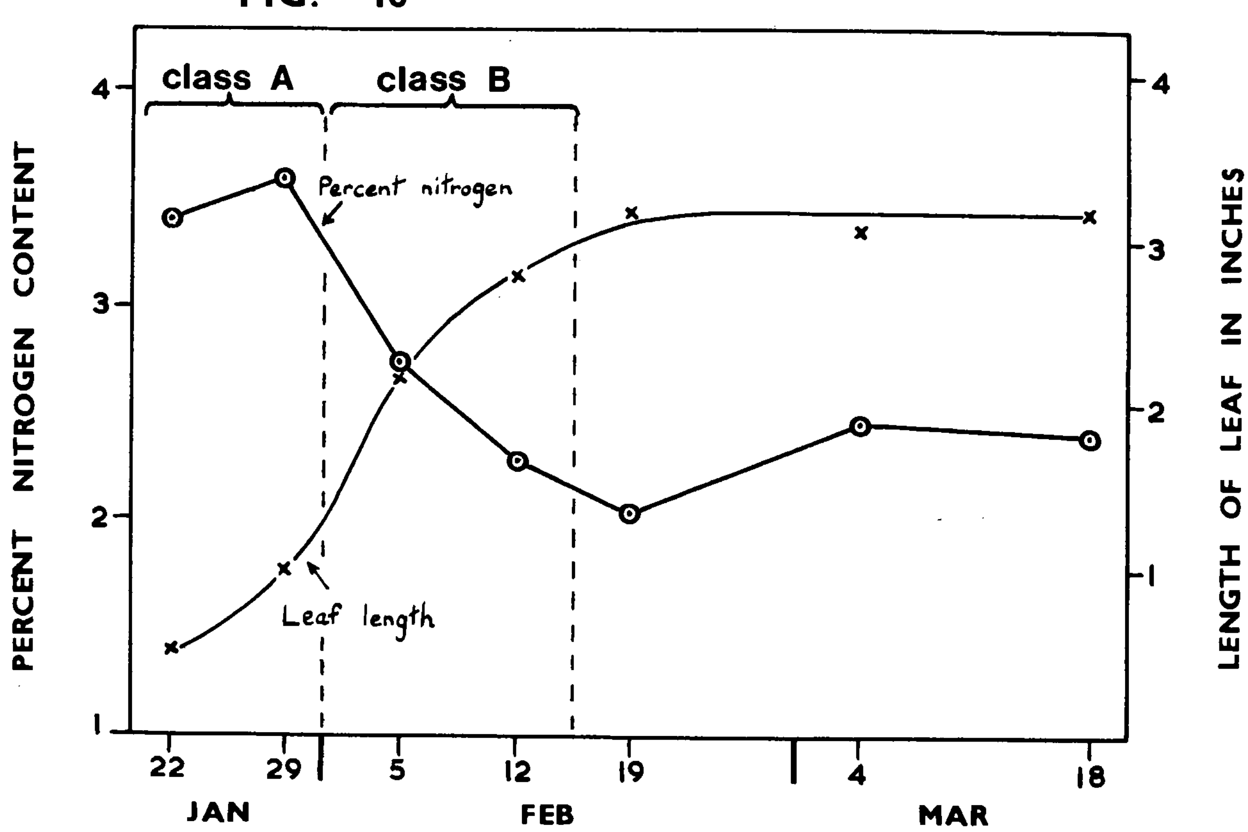

CLASS A
CLASS B
PERCENTAGE NITROGEN
4
3
2
1
JAN
F
M
A
M
J
J
A
S
O
N
DEC

FIG. 16


class A
class B
Percent nitrogen
Leaf length
PERCENT NITROGEN CONTENT
LENGTH OF LEAF IN INCHES
4
3
2
1
22
29
5
12
19
4
18
JAN
FEB
MAR

adult feeding, was included in the sample, while the tougher stem of more advanced flushes was rejected. Plant tissue was dried in an oven for 1-2 days, ground into a powder, and then analysed by the micro-Kjeldahl method using a Markham still. Nitrogen content was expressed as the percentage nitrogen of dry weight. By this method only organic or proteinaceous nitrogen is determined. Several determinations of total nitrogen in young foliage revealed the presence of negligible amounts of inorganic nitrogen in winter and only small amounts in August following the late winter application of fertilizer (0.3% inorganic and 3.9% organic nitrogen).

There were only small differences in nitrogen content from tree to tree, and in the flush from Navels, Valencias and grapefruit. However, nitrogen content was found to vary with the age of the tree. Table 7 shows the results of four comparisons between flush from young trees and flush of the same stage from mature trees. Each sample consisted of 20-30 flushes of the same stage taken

Table 7 Comparisons of nitrogen content (percent dry weight) of flush from young and mature trees

	Class A		Class B	
Young trees	2.91	2.96	3.25	2.19
Mature trees	2.52	2.37	2.27	1.99

from sweet orange trees in May, 1967. The flush from young trees appears to be higher in nitrogen and thus more nutritious. Similarly, there were indications that the young growth of seedlings is higher in nitrogen than the flush of mature trees. The mean nitrogen content of class B flushes from six seedlings was 3.46% nitrogen, while the mean for the two composite samples of the same stage from mature trees shown in Table 7 was 2.47% nitrogen.

It was shown conclusively by the series of sequential samples that the nitrogen content of young flush declines with age. Firstly, the averaging of 66 nitrogen determinations distributed over nine months of the year (Fig. 15) showed that at all times the younger flush points were highest in nitrogen.

EXPLANATION OF FIGURES

Fig. 15 Monthly means for nitrogen content, as percent dry weight, of class A and class B flush points on citrus in the Malkerns district. Means based on the following numbers of composite samples: Jan - 11, Feb - 3, Mar - 9, May - 12, Jun - 4, Aug - 6, Sept - 12, Nov - 7, Dec - 2

Fig. 16 Decline in nitrogen content, as percent dry weight, with age and length of leaf in midsummer flush of mature Navels

The nitrogen content of class A flushes varied from 2.22 - 4.14% with a mean of 3.18% nitrogen, and class B flushes varied from 1.73 - 3.34% with a mean of 2.47% nitrogen. Secondly, by tagging flush points in a mature Navel grove at the start of a midsummer flush for nitrogen determinations at regular intervals (Fig. 16), it was shown that a maximum nitrogen content of 3.6% was attained while growth was in the class A stage with leaves below 1.3 inches in length. With an increase in length of leaf to 3.0 inches during the class B stage, nitrogen content declined to 2.2%. After maturing beyond the B stage nitrogen dropped to 2.0% before a modest climb to 2.4 - 2.5% nitrogen. Thirdly, the grouping of 38 samples into four catagories according to length of leaf revealed a similar trend for a decrease in nitrogen content with age. Lastly, separate analyses of the five terminal leaves of class A flushes showed a decrease in nitrogen content from 4.5% for the terminal leaf, to 3.8% for leaf 5. This trend was not shown by class B flushes.

Probably of far greater ecological significance was the marked seasonal fluctuation in the nitrogen content of young flush. It is seen from Fig. 15 that the highest levels of nitrogen, > 4.0%, were present during the main flush cycles of August/September and in November, while the lowest levels, < 2.5%, were recorded in the small autumn and winter flushes from March to June. Nitrogen contents recorded from December to February were intermediate. The averages shown for the months of August and September include samples taken in 1967 and 1963, class A nitrogen contents exceeding 4.0% in both seasons.

(iii) Discussion.

The role of protein in the diet of *T. erytreae*. Amino acids are the most important source of protein for insects, many species requiring proteinaceous food to promote ovulation and egg production (House, 1965). So, for example, during reproduction when protein demands are high, the aphid, *Tuberolachnus salignus* (Gmelin), contributes some stored nitrogen from her own body (Craig, 1960).

The precise protein requirements of insects is not well known and has not been studied in the Psyllidae. Homopterans such as aphids and scale insects are known to excrete large quantities of amino acids in their honeydew (Wigglesworth, 1965; Doutt, 1964). This was also found in the case of *T. erytreae*. Table 8 shows the results of an analysis of several grams of excreta collected over several weeks from a laboratory culture. It is seen that apart from a small amount of ammonia, 15 amino acids were present. Eight of these are known to be present in the honeydew of coccids and all have been detected in the honeydew of aphids (Auclair, 1963). Typically, amino acids present in the honeydew of aphids are found in the phloem of the host plants (Craig, 1960) and in *T. erytreae*, 14 of the 15 amino acids shown have been isolated from citrus leaves in Florida (Erickson, 1968). Particularly large amounts of proline are present in the excreta and in Florida citrus leaves. It would thus appear that most of the amino acids are not synthesized by

Table 8 Amino acids present in the excreta of T. erytreae. Ammonia was also present at 0.195 gm/100 gm excreta

Amino acid	Grams amino acid per 100 grams excreta
Proline	2.260
Aspartic acid	1.738
Glutamic acid	1.257
Valine	0.973
Alanine	0.279
Histidine	0.126
Glycine	0.107
Threonine	0.092
Leucine	0.083
Tyrosine	0.080
Arginine	0.058
Lysine	0.057
Phenylalanine	0.049
Isoleucine	0.040
Serine	0.029

T. erytreae but are merely ingested in excess and promptly excreted. The shunting of large amounts of sugar (Catling, 1967) and free amino acids in the excreta is thought to be necessary for the procurement of some other essential compound or compounds such as vitamins (Auclair, 1963), or even certain minor elements which Erickson (1968) has found to influence the supply of free amino acids in citrus leaves.

The effect of low nitrogen levels. The pot experiment, which was designed to investigate the influence of low levels of nutrition, gave disappointing results. Prolonged leaching of the sand culture did not seriously reduce the nitrogen content or noticeably affect the general leaf composition, In most respects both sets of plants remained favourable for nymphal development and survival was not affected. The persistence of nitrogen in the leaves of the leached plants may be explained by the work of Gates et al., (1961) who showed that in citrus cuttings nutrients shifted preferentially to developing parts of the plant and that reserves in the stem are mobilized for growth. However, nymphal development was prolonged on the leached plants, partly confirming earlier field observations by Catling (1967), and a size reduction was indicated in nymphs developing on mesophyll-collapsed leaves.

According to Chapman (1968) nitrogen shortage and disorders may be expected in mature leaves when the nitrogen content drops below 2.0%. Catling (1967) reported on apparent protein starvation in the nymphs of T. erytreae which developed on young leaves in the Letaba district during midsummer with a nitrogen content of between 1.25 and 1.34% nitrogen - normal nymphal development proceeding in another grove over the same period on flush of the same stage with a nitrogen content of 2.4%. It would thus appear that the critical level below shich protein starvation can be expected is in the region of 1.5 - 2.0% nitrogen.

Catling (1967; 1969a) referred to the effect of high midsummer temperatures and intense sunlight in slowing down and inhibiting citrus growth.

Odum (1964) showed that these conditions may reduce protein synthesis and photosynthesis in the leaves, thereby decreasing the nutritive value at a time when the demand for nutrients is at its highest (Bursell, 1964). It was shown that nitrogen levels in midsummer flushes are lower than in spring and early summer growth cycles. Thus it is concluded that the lower nutrient levels in midsummer flushes are detrimental to nymphal development and that in poorly-nourished citrus trees the nitrogen content may decline to reach levels which cause nymphal mortality. Similar conditions are believed to affect the nymphal stages of the psyllid, Paurocephala calodendri Moran (Moran, 1967).

Besides the direct effect on development, nutrient levels in the plant host are known to influence the fecundity of many phytophagous insects and mites. The aphid, Acyrthosiphon pisum (Harris), develops more slowly and is less fecund on resistant plant varieties with low levels of amino acids, while treatments causing the accumulation of amino acids result in improved growth and reproduction (Beck, 1965). A better growth rate was reported by Auclair (1963) in aphids feeding on susceptible pea varieties with higher levels of three key amino acids and precursors. However, according to Branson & Simpson (1966) work on the influence of plant nutrition on aphid populations has led to inconsistent results. These authors found that a decrease in the fecundity of Rhopalosiphum fitchii (Sanderson) on nitrogen deficient sorghum was due to crowding on poorly-growing plants rather than a direct effect of low nitrogen levels. The mite, Tetranychus telarius (Linn.), was found by Henneberry (1962) to be more fecund on young bean leaves and on plants fed at higher rates of nitrogen. The lowering of fecundity with increase in leaf age was most pronounced on plants fed at low nitrogen rates. Unfortunately no work has been done to determine the influence of nutrition on the general fecundity of T. erytreae. In oviposition studies described elsewhere young, freely-flushing citrus seedlings were used at all times. As will be discussed later, this is an important factor to be investigated in the ecology of T. erytreae.

Differences in the nitrogen content of young flush. Figures quoted for the nitrogen content of mature citrus leaves are similar for the U.S.A., Australia and South Africa and usually vary between 2.0 - 2.8% nitrogen (Chapman, 1968; Williams & Gates, 1956; Stanton, D.A. 1969, personal communication). No published data is available on the nitrogen of young flush in southern Africa. Results from the series of sequential samples in the Malkerns district were in general agreement with a more detailed study of the composition of Valencia leaves by Cameron et al., (1952) in southern California. In both regions there were three annual growth cycles and the nitrogen content of young flush declined steadily with age - from 4.0% nitrogen in tender class A flushes to 2.0 - 2.5% for advanced class B flushes in Malkerns. The age factor was the dominating influence on flush composition. Similarly, when compared with the two later flushes, highest levels of nitrogen were found in young leaves of the spring cycles - 4.4% in California, 4.1% in Malkerns.

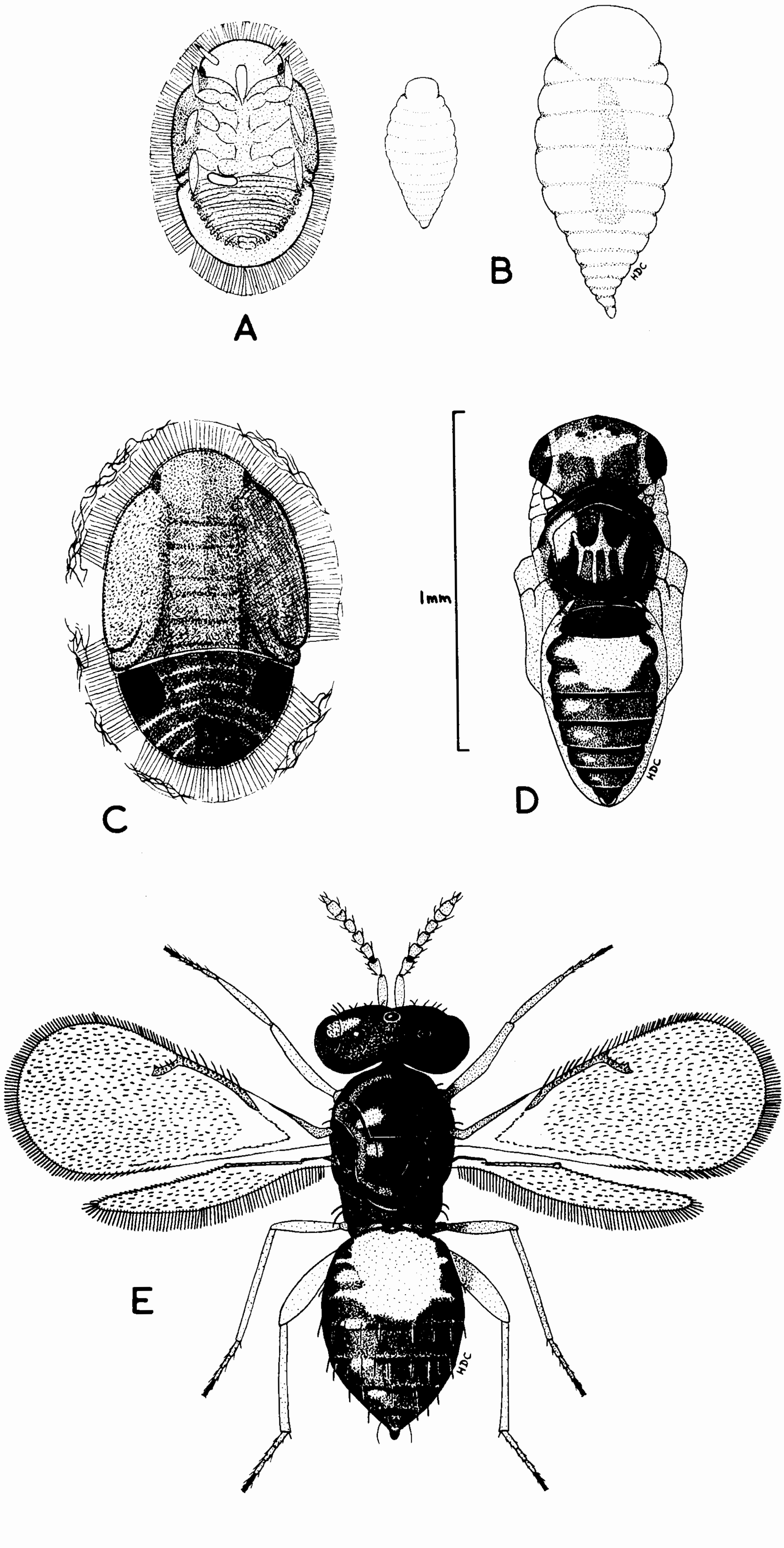
The Malkerns study also revealed little variation in the nitrogen content between trees of the same variety, and between Navels, Valencias and grapefruit. The flush from young trees, and seedlings, was higher in nitrogen than flush borne by mature trees. This agrees with the work of Gates et al., (1961) on citrus cuttings where the youngest leaves started with a nitrogen content of 4.0 - 5.0%, declined slightly with age, and then remained fairly constant at levels of 3.0 - 4.0% nitrogen for some months. Thus young trees, besides flushing more profusely (Catling, 1969a), also appear to bear young growth higher in nitrogen which makes them more attractive to T. erytreae than mature trees. The same reason is advanced for the fact that populations of the red scale, Aonidiella aurantii (Mask.), develop faster on young citrus trees than on mature ones (Bedford, E.G.C. 1969, personal communication).

The very definite seasonal fluctuation in the nitrogen content of young flush is of especial interest though at this stage it is only possible to speculate on its ecological significance. It is perhaps meaningful that the highest nitrogen levels are present in the spring and early summer flushes when the main population upsurges of T. erytreae take place. This means that the host plant is likely to be at its most nutritious to the young stages and, perhaps of greater significance, to ovipositing females. Nitrogen levels decline towards late summer and are at their lowest during winter. Leaves are the major reservoir for nitrogen in citrus trees and it is possible that in late summer the fruit tend to draw on this reserve (Chapman, 1968). But it must be remembered that young growing tissues are preferentially supplied with nutrients so that it would seem that only under exceptional conditions of nitrogen shortage would young flush become deficient in nitrogen - as at Forest Hill in 1966-67 (Catling, 1967). The influence of midsummer weather conditions was mentioned earlier.

Cameron et al., (1952) in California, discovered that the levels of nitrogen, calcium, magnesium, iron and manganese in citrus leaves varied from season to season. Wellington (1957) considers that annual variations in food quality, a factor which is frequently overlooked or neglected by ecologists, are extremely important in the population fluctuations of some insects.

5. INFLUENCE OF PARASITES

Parasites are a limiting factor to populations of T. erytreae (Van der Merwe, 1941; Catling & Annecke, 1968). Only the nymphal stages are attacked, there being no records in South Africa of adults or eggs being parasitized. The main primary parasite, whose identity was confirmed by Dr. B.D. Burks of the U.S. National Museum, Washington D.C., on specimens from the Letaba district, was Tetrastichus radiatus Waterston. Tetrastichus sicarius Silvestri


A
B
HDC
C
1mm
D
HDC
E
HDC

and Tetrastichus dryi Waterston recorded from T. erytreae in Kenya (Jensen, 1957) are not known to occur in South Africa (Annecke & Cilliers, 1963).

The biology and interrelationships of the parasite complex of T. erytreae were provisionally determined from field studies and small scale laboratory studies. A detailed biological study was made by Blowers (in preparation) in the Salisbury district of Rhodesia where a similar parasite complex exists. Studies on parasite activity were started in 1965 in the Letaba district and were continued in Swaziland at Malkerns Research Station until January, 1970. At less frequent intervals, similar observations were made at Ross Citrus Estate in the 1967-68 season. None of these trees received insecticidal sprays during the study period. Occasional parasitism counts were made in other groves in the Malkerns district.

(i) Parasites of T. erytreae.

Tetrastichus radiatus Waterston (Eulophidae)

T. radiatus was originally described from Diaphorina citri Kuw. (Euphalerus citri Kuw.), the Indian citrus psylla, by Husain & Nath (1924) in the Punjab. Annecke & Cilliers (1963) were the first to record T. radiatus in Africa, regarding this to be the species mentioned by Van der Merwe (1941) as attacking citrus psylla nymphs in South Africa. T. radiatus has since been collected widely in the Transvaal, Swaziland and Rhodesia. According to Moran (1967) there are slight morphological differences between specimens from various parts of southern Africa. The biology of T. radiatus, which was found to correspond closely with that mentioned briefly by Husain & Nath (1924), was described by Catling (1967, 1969b) and drawings of all stages are shown in Fig. 17. A few additional notes from observations in Malkerns are given here. Table 9 shows that the fourth instar is preferred for egg-laying, followed by the fifth instar. Many fifth instars with parasite eggs appear to survive the attack.

Table 9 Host instar preference for egg-laying by T. radiatus

Site	Number of nymphs with eggs	Percentage of each instar preferred for egg-laying		
		III	IV	V
Forest Hill	459	10.2	73.0	16.8
Malkerns Research Station 1967-68	2118	18.4	42.4	39.2
Ross Citrus 1967-68	1010	22.2	47.2	30.6

EXPLANATION OF FIGURE

Fig. 17 Tetrastichus radiatus Waterston. A-egg on venter of nymph; B-larvae; C-dead nymph with parasite in pupal stage; D-pupa; E-adult female. All stages to same scale. del. H.D. Catling

A certain amount of super-parasitism was always found at high levels of parasitism. In the two seasons of study at Forest Hill, 6.8% of 617 nymphs had more than one *T. radiatus* egg; in the 1967/68 season at Malkerns Research Station superparasitism was 3.0% of 2118 nymphs and at Ross Citrus 3.5% of 1010 nymphs. There was no sign of host feeding or host mutilation, adults readily feeding on the sugary faecal pellets of their host. Females were more abundant at all times of the year, the sex ratio of 2127 adults reared from emergence boxes or caught in the insect sampling machine was 41.1% males.

Psyllaephagus pulvinatus (Waterston) (Encyrtidae)

This species was briefly described by Catling (1967; 1969b). In Malkerns the sex ratio of 294 adults reared from emergence boxes or caught in the insect sampling machine was 31.0% males.

Aphidencyrtus cassatus Annecke (Encyrtidae)

A. cassatus, a hyperparasite which attacks *T. radiatus* and *P. pulvinatus*, is a new species described by Annecke (1969). The pupal stage is external and readily distinguishable from *T. radiatus* and *Tetrastichus* sp., the adult usually emerging through the abdomen of the nymph. Sixty-two percent of 1340 specemens examined in the Malkerns district were males, this tendency being consistent throughout the year. In one *in situ* count at Malkerns, *A. cassatus* successfully attacked every larva of *T. radiatus* present in the colony.

Tetrastichus sp. (Eulophidae)

This species was placed in the genus *Tetrastichus* by Dr B.D. Burks. Known by the present author as a hyperparasite of *T. erytreae*, Blowers, J.R. (personal communication, 1967) found it to be a tertiary parasite attacking the larval and pupal stages of *A. cassatus*. Unlike *T. radiatus*, the head, thorax and abdomen are all black and the legs have darkish coxae and femora. The adult emerges through the dorsum of its host. Females are predominant, 29.8% of 299 adults examined being males.

Species of minor importance

Several other parasites were reared in small numbers from *T. erytreae* nymphs but all are regarded as hyperparasites. *Coccophagus pulvinariae* Compere, (Aphelinidae) males were reared on several occasions in the Letaba and Malkerns district.

Pachyneuron sp. (Pteromalidae) was reared in the Letaba district only. *Euxanthellus* sp. (Aphelinidae) males were recorded in the Malkerns district. A few specimens of *Marietta exitiosa* Compere (Aphelinidae) were reared in the Malkerns district.

According to Catling (1967, 1969b) the two primary parasites, *T. radiatus* and *P. pulvinatus*, and the hyperparasites, *A. cassatus* and *Tetrastichus* sp., were reared from another psyllid, Trioza sp. on two creepers which grow alongside citrus groves at some places in the study areas.

(ii) Field studies at Malkerns Research Station (Figs. 18 and 10)

Parasitism. In the 1967-68 season the percentage parasitism of susceptible stages was constantly between 30-50% with a mean of 45.2% from March to early August on low densities of T. erytreae.

On the spring upsurge of the host, however, parasitism declined sharply to levels of 1.2% on September 5 and 7. After a rapid recovery in mid September, parasitism remained fairly constant (usually from 50-70%) until early December when there was another drop, followed by a quick return to high levels on rapidly diminishing populations of the host. With a mean of 42.1%, parasitism was similarly maintained at fairly high levels during the winter of the following season. There was no serious decline in parasitism on the spring upsurge in 1968, the percentage parasitism never dropping below 38% during the critical months of August to October.

Since T. radiatus attacks only instars III, IV and V, parasitism is most accurately assessed when the bulk of the host population is in these susceptible stages. Well-defined field generations or broods were shown for T. erytreae during the study period and are included in Fig. 18. Parasitism during this susceptible period is referred to as "effective parasitism" and is shown for each field generation at Malkerns Research Station for 1967 and 1968 in Table 10.

Table 10 Parasitism by T. radiatus and P. pulvinatus during the susceptible period of each field generation of citrus psylla at Malkerns Research Station

Field generation	Period	No. parasitism counts within this period	Mean percentage parasitism
2	1967 Apr. 9-30	1	31.8
3	Jun. 6-July 9	2	44.7
4	Aug. 17-31	2	10.3
5	Sept. 21-Oct. 12	4	42.2
6	Nov. 22-Dec. 14	3	9.3
7	1968 Jan. 2-19	2	33.5
1	Feb. 6-Mar. 7	1	35.2
2	Apr. 1-18	1	10.8
3	Mar. 9-28	1	48.1
4	Jun. 22-Jul. 9	1	30.1
5	Aug. 1-25	1	51.1
6	Sept. 15-Oct. 18	5	47.7

From November, 1968 to January, 1969, 40-50% of the susceptible stages were parasitized until the population crash of T. erytreae in mid January. Due to exceptionally low host populations, no further material was available for parasite counts until the midwinter of 1969. Between June and mid September no sign of parasitism was recorded in 9 counts (1,789 susceptible stages examined),

FIG. 18

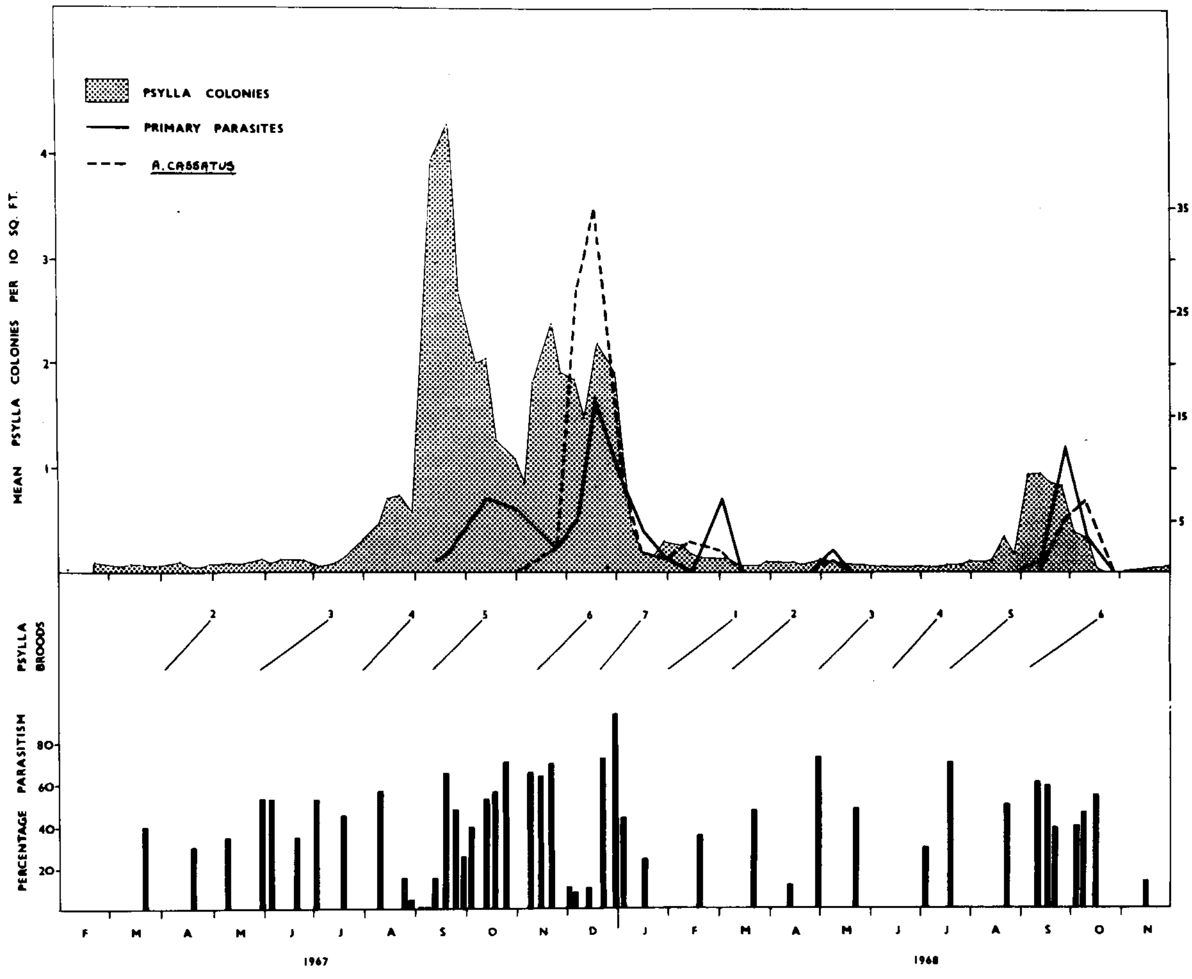
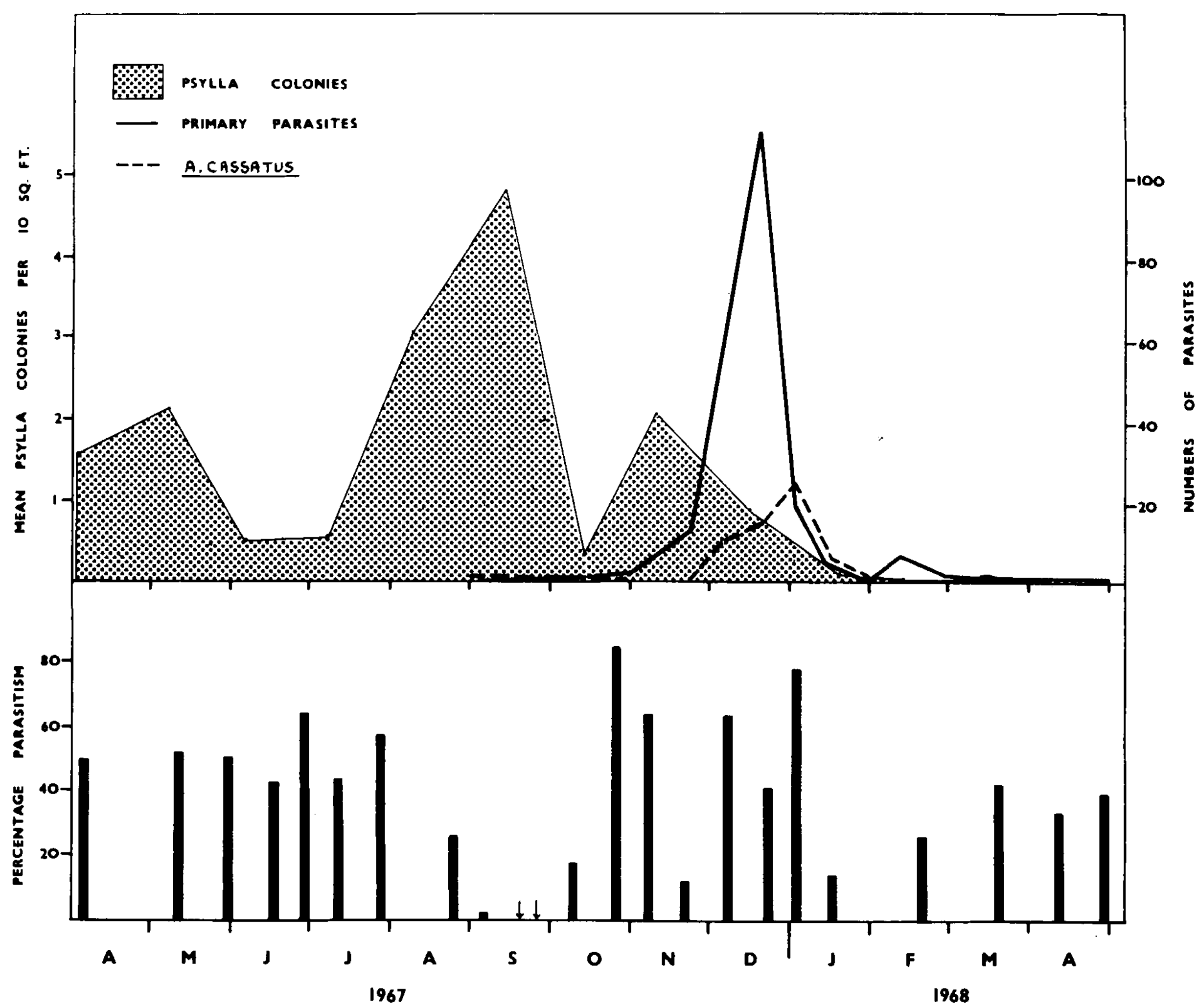

PSYLLA COLONIES
PRIMARY PARASITES
A. CASSATUS
MEAN PSYLLA COLONIES PER 10 SQ. FT.
NUMBERS OF PARASITES
PSYLLA BROODS
PERCENTAGE PARASITISM
F M A M J J A S O N D J F M A M J J A S O N
1967
1968

FIG. 19


PSYLLA COLONIES
PRIMARY PARASITES
A. CASSATUS
MEAN PSYLLA COLONIES PER 10 SQ. FT.
NUMBERS OF PARASITES
PERCENTAGE PARASITISM
A M J J A S O N D J F M A
1967
1968

whereas in both of the previous seasons, parasitism was above 40% for the winter months. Similarly, no parasites were evident in counts made in three other groves during August and early September. Parasites first made their appearance in nymphs examined on September 24 and Fig. 10 shows a steady rise in activity in October to reach normal summer levels which persisted to January, 1970. Mean "effective parasitism" rose progressively in the four broods of the season as follows: 0.0% July/August; 9.6%, 37.6%; and 50.5% December/January.

Parasite population fluctuations. Fluctuations of parasites and the relative importance of the four main species were assessed by (a) an examination of parasitism counts and the rearing of adult parasites from this material, and (b) by a consideration of the catch from the insect sampling machine.

T. radiatus was the predominant primary parasite at all times but was challenged by *P. pulvinatus* at low host densities in May/June, August/September in 1967, and in May, 1968. *P. pulvinatus* was also active from December to February in rapidly declining populations of *T. erytreae*. The primary parasites were consistently attacked by *A. cassatus*, this species heavily outnumbering primaries in the latter half of December, 1967, and again to a lesser extent in February, 1968. In the following season the secondary parasite became slightly more numerous than its host in October, again on a declining psylla population. Small numbers of *Tetrastichus* sp. were present during the study period.

All species were at low levels during winter and early spring, the seasonal increase in numbers beginning in September. In the 1967-68 season the primaries had increased in numbers by October but declined in November only to build up once more to reach their highest peak in mid December. There were small spikes of primaries in February and May. In the following season primaries were very active in September on a considerably smaller outbreak of *T. erytreae*. Fig. 18 shows that high levels of parasitism coincided with peaks of activity of primary parasites.

In 1969 no parasites were collected in the insect sampling machine between April 11 and the end of July, nor were parasites observed in the field during this period. Small numbers first appeared in September and small peaks were recorded at the end of October and again in December. *T. radiatus* was

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EXPLANATION OF FIGURES

Fig. 18 Population fluctuations and broods of *T. erytreae*, percentage parasitism and numbers of parasites at Malkerns Research Station from February, 1967, to November, 1968

Fig. 19 Population fluctuations of *T. erytreae*, percentage parasitism and numbers of parasites at Ross Citrus Estate from April, 1967, to April, 1968. Arrows indicate nil parasitism predominant until January when P. pulvinatus accounted for a greater share of parasitism. A. cassatus was very quiet during the 1969-70 season.

(iii) Field studies at Ross Citrus Estate (Fig. 19). Parasite activity was studied at this site from April, 1967, to May, 1968. Apart from higher densities in the winter, population fluctuations of T. erytreae were very similar to those at Malkerns Research Station.

Parasitism. From March to August parasitism was fairly constant with a mean of 51.1% of susceptible stages attacked. There was a sharp decline in September, parasites being totally absent from two counts made at the end of this month. Parasitism recovered in October to remain at moderate, though irregular, levels for the remainder of the study period.

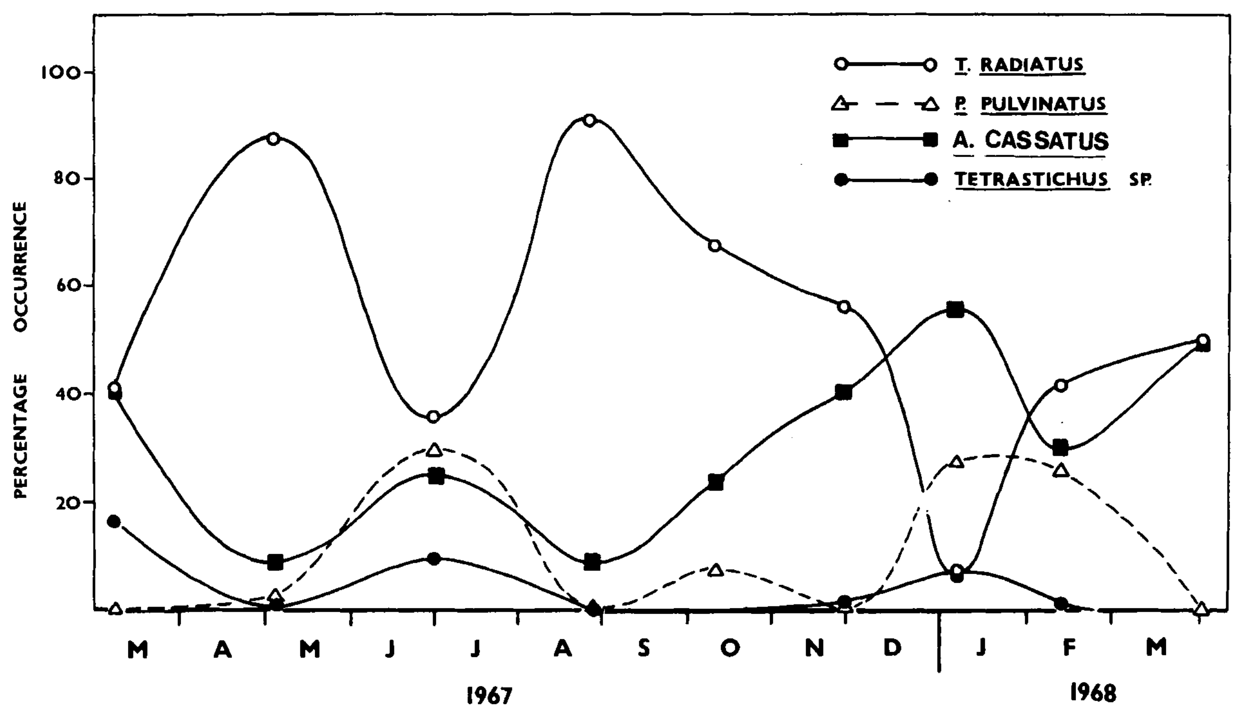
Parasite population fluctuations. The most abundant primary parasite was T. radiatus, P. pulvinatus becoming an important species in April of both years, in June/July and in October, A. cassatus was present continuously and was particularly evident in June/July (when it was attacking both primaries), October and early November, and in December/January. Tetrastichus sp. was more common than at Malkerns Research Station, becoming fairly abundant in winter and showing a small peak in October.

Parasite numbers were very low in September and October, but primaries built up rapidly to high peaks in December and, although they were slightly outnumbered by A. cassatus in January, they later reasserted themselves before dropping to low winter levels.

(iv) Other sites in Swaziland. Small-scale parasitism counts, rearings and observations at five farms in the Malkerns district showed similar trends in the activity and abundance of T. erytreae parasites. T. radiatus was more abundant than P. pulvinatus, large numbers of A. cassatus were evident at times, while Tetrastichus sp. was infrequently recorded in small numbers. The percentage parasitism from six counts involving 2,268 nymphs varied from 9.0 - 63.5%, rearings of adults from this and other material yielding 272 T. radiatus, 21 P. pulvinatus, 187 A. cassatus, and 49 Tetrastichus sp.

All of the four main parasites were found at times in the scattered outbreaks of T. erytreae in the Lowveld region, percentage parasitism varying from 0.0% to approximately 40%.

(v) Discussion. Because T. radiatus is ectoparasitic, and the larval and pupal stages of Tetrastichus sp. and pupal stage of A. cassatus are external when attacking T. radiatus, parasitism counts (and rearing of adults) gave a good reflection of the activity of the four main species attacking T. erytreae. The role of P. pulvinatus was obviously underestimated at certain periods but this was largely compensated for by examining catches from the insect sampling machine.


T. RADIATUS
P. PULVINATUS
A. CASSATUS
TETRASTICHUS SP.
PERCENTAGE OCCURRENCE
100
80
60
40
20
M
A
M
J
J
A
S
O
N
D
J
F
M
1967
1968

The successive nature in the waves of abundance of the four main parasites seen at both experimental sites at Malkerns represented additional evidence of their interrelationships. Fig. 20 shows the fluctuations of these parasites at Malkerns Research Station during the first season of study. Examination of field data indicated the presence of a number of field generations of T. radiatus which corresponded fairly well with generations of the host.

The unnamed Trioza sp. which acts as an alternate host for T. erytreae parasites is believed to provide a natural unsprayed reservoir of parasites in the vicinity of the pest which is of special significance in some of the low-lying areas where T. erytreae is usually at low densities.

Parasites as a limiting Factor. Husain & Nath (1924) contended that parasites were an important limiting factor in populations of D. citri in the Punjab, up to 95% of the nymphs being attacked in October and November. They attributed 50% of this parasitism to T. radiatus and expressed the opinion that the failure of this parasite had resulted in outbreaks of D. citri in some localities. However, Husain (1924) found T. radiatus to be least numerous when the host was most abundant in March/April which immediately suggests that, as with T. erytreae, there may be a considerable time lag between host and parasite numbers at critical times in some seasons. Atwal (1962) reported from West Pakistan that T. radiatus was particularly effective on D. citri in the post-monsoon months. In South Africa, Van der Merwe (1941) stated that on occasions 75% of the more advanced nymphs may become parasitized, while in Kenya, Anderson (1914) reported that citrus psylla was kept in check by parasites.

Letaba district, Transvaal (Catling, 1967; 1969b). Of the two primary parasites, T. radiatus was responsible for most of the parasitism, P. pulvinatus being more active in the winter months. Hyperparasites were rare. Parasites were active in all the groves studied but at lower altitudes their influence was inconsistent and usually low on the rising host population in spring. Parasitism levels were irregular on the scattered T. erytreae populations at Fairview and parasites were totally absent in the very low host populations at the Letaba experimental site in 1965-66.

Parasitism levels were consistently high at Forest Hill, the "effective parasitism" in the first two broods of 1966-67 standing at 40.0% and 68.7% respectively. These high levels of parasitism are explained firstly by the

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EXPLANATION OF FIGURE

Fig. 20 Percentage occurrence of the four main parasite species attacking T. erytreae at Malkerns Research Station from March, 1967, to March, 1968. Data obtained from parasite rearings and catches from the insect sampling machine for each brood of the host moderate host populations which developed at this site (maximum of 0.6 colonies per 10 square feet of tree canopy) and secondly, by the nature of the flushing rhythm. Catling (1969a) showed that the overlapping flush cycles at this site caused less distinct field generations of *T. erytreae*. This meant that there was a more constant supply of susceptible host stages for the main parasite, *T. radiatus*.

Malkerns district, Swaziland. Since fluctuations of *T. erytreae* parasitism levels, and interactions of the main parasite species were essentially similar at Malkerns Research Station and Ross Citrus, both sites are discussed together for the 1967-68 season. Due to the heavier flushing of Navels, higher populations of *T. erytreae* and parasites developed at Ross Citrus in April and May, 1967.

In the first two seasons parasites attacked a fairly constant fraction (30-50%) of *T. erytreae* nymphs during the winter months. In the 1967-68 season the host surged rapidly to high population densities on the spring growth cycle in August and September due to the extreme natality of broods 4 and 5 (Fig. 18). By the middle of September at the Malkerns Research Station, population density stood at 4.3 colonies per 10 square feet of tree canopy. At the start of each brood, 80-90% of the population was present as eggs or instars I and II and as such were not susceptible to *T. radiatus* for 12-14 days. Moreover, from Fig. 18 it appears that there was no appreciable rise in the numbers of primary parasites until late September. Hence towards the end of August and into September parasitism declined sharply to reach levels as low as 1.2%. A similar trend was evident at Ross Citrus where the arrows in Fig. 19 showing parasitism levels of nil at the end of September coincided with high populations of *T. erytreae* and low numbers of parasites.

During brood 5 the primary parasites recovered strongly, 42.2% of the nymphs being attacked when the bulk of the population was in the susceptible stage (Table 10).

In November, with another population rise of *T. erytreae*, the parasites again became out of phase with their host, "effective parasitism" of brood 6 dropping to 9.3% (Table 10). Numbers of primary parasites had declined while *A. cassatus* began to increase. Of more importance still was that unfavourable weather in October caused a high mortality of eggs and young nymphs, the more tolerant adults continually laying new batches of eggs so that the bulk of the population was not susceptible for 3-4 weeks. Fig. 18 shows the long interval before the start of brood 6 and also the high levels of parasitism (60-70%) recorded in the small fraction of instars III-V present at this time. On the return of more favourable weather the population quickly developed into third and fourth instars, thus providing a large number of potential hosts for the primary parasites which were at a low ebb. By the end of December high levels of parasitism were again evident and the numbers of primaries and hyperparasites reached their highest peaks for the season.

Numbers of primaries were considerably higher at Ross Citrus (Fig. 19) than at Malkerns Research Station. A. cassatus became numerically dominant at both sites, especially at Malkerns Research Station, and must have reduced the numbers of primaries though there was a small, dominant spike of primaries at both sites in February, 1968.

T. radiatus was the main primary parasite and at Malkerns Research Station was responsible for approximately 70% of parasitism at all times, and commonly 90-100%. P. pulvinatus was most abundant when the host was at low population densities, as in winter, and on the rapidly declining populations in midsummer. A large fraction of T. radiatus was attacked by A. cassatus at some periods (46% at Malkerns Research Station and 59% at Ross Citrus in December, 1967). It was concluded by Husain & Nath (1924) that the two unnamed hyperparasites of D. citri in the Punjab have little effect on T. radiatus for in one investigation only 2.4% of parasitized nymphs were successfully attacked. The tertiary parasite, Tetrastichus sp., was relatively unimportant at Malkerns Research Station, but during the 1967 winter both hyperparasites were present in large numbers at Ross Citrus.

In the following season population fluctuations of T. erytreae and its parasites were very different at Malkerns Research Station. Fig. 18 shows that spring population densities of the host rose to about one quarter of that recorded in 1967 and "effective parasitism" in the first two broods was 51.1% and 47.7% respectively. The rise in numbers of primary parasites, which reached a sharp peak at the end of September, was well synchronized with brood 6. A. cassatus became dominant in October.

The host/parasite relationship was severely disturbed at Malkerns in 1969 when no parasites were recorded at all for 4 - 5 months. It appears that the two primaries were not able to effectively search out their host at the extremely low densities which prevailed during winter and early summer, though they were clearly able to maintain themselves and are capable of existing in the scattered populations of T. erytreae in the Lowveld region. It is unlikely that the severe summer weather of the 1968-69 season was directly responsible for the negligible numbers of parasites since the activity of Aphytis africanus Quednau, a parasite of red scale, Aonidiella aurantii (Mask.) known to be especially vulnerable to hot, dry conditions (De Bach, 1958), was not disturbed in Malkerns. Despite the negligible affect of parasites in August and September, 1969, there was only a moderate population rise of T. erytreae in early summer.

At most times parasites represent a fairly constant limiting factor to populations of T. erytreae. As is often the case, the effectiveness of parasites depends on their ability to maintain a tenuous synchrony with every fluctuation of their host. Where a favourable host-parasite synchrony was evident (as at Malkerns Research Station in 1968 and probably at Forest Hill in 1965 and 1966) high levels of parasitism were maintained. Where this delicate balance was disturbed, however, (as at Malkerns Research Station in 1967 and 1969, and Ross Citrus in 1967) parasitism plunged to low levels or went undetected.

Influence of Insecticides on the parasite complex of citrus psylla. Annecke & Cilliers (1963) were of the opinion that changes in pest control programmes, which have upset the natural balance of beneficial insects of some citrus pests, were not responsible for serious outbreaks of T. erytreae in the eastern Transvaal during the late nineteen-fifties and early sixties. The present author supports this view. T. erytreae parasites were found in all heavily sprayed groves and the low levels of parasitism on the first spring generation was frequently common to both sprayed and unsprayed groves. At the Ross Citrus site which received four applications of parathion and one of malathion in the year previous to the laying out of the experiment, parasite numbers were higher and parasitism levels as high as the Malkerns Research Station site which had received a single yearly application of parathion.

In a trial where 6 trees were sprayed with DDT at monthly intervals from August to March, 1968, only a moderate reduction in percentage parasitism was evident between sprayed (20.3%) and unsprayed trees (41.8%) in March.

6. INFLUENCE OF PREDATORS

Since predators were believed to play a fairly small part in regulating populations of T. erytreae less time was devoted to the study of this limiting factor. Data was obtained from field observations, collections, modest field experiments, and small-scale observation tests. It was not possible to make use of more sophisticated methods such as those based on radio-active tracers and serology.

Psyllids are attacked by many groups of predators. Psylla pyricola Foerster is preyed on by anthocorids, coccinellids, lacewings, and syrphids (Georgala, 1957; Wilde, 1962; Madsen et al., 1963; Peterson, 1964). The eucalypt psyllid, Cardiaspina albitextura Taylor is attacked by syrphids and even birds, (Clark, 1963b, 1964), while two broom psyllids studied by Watmough (1968a) are attacked by mirids, anthocorids, coccinellids, hemerobiids, a dermapteron, mites and spiders. In the case of Diaphorina citri Kuw., a complex of predators consisting of five species of coccinellids, a syrphid, a chrysopid, and spiders and mites was reported by Husain & Nath (1927) to ....."play a very important part in keeping this pest in check". After detailed studies Watmough (1968a) concluded that predators were an important mortality factor in broom psyllids. However, though predators may take a fair toll of their host they have been found to be relatively unimportant in limiting the numbers of other psyllids. Madsen et al., (1963) found that it was rare for predators to effectively reduce populations of P. pyricola, and Clark

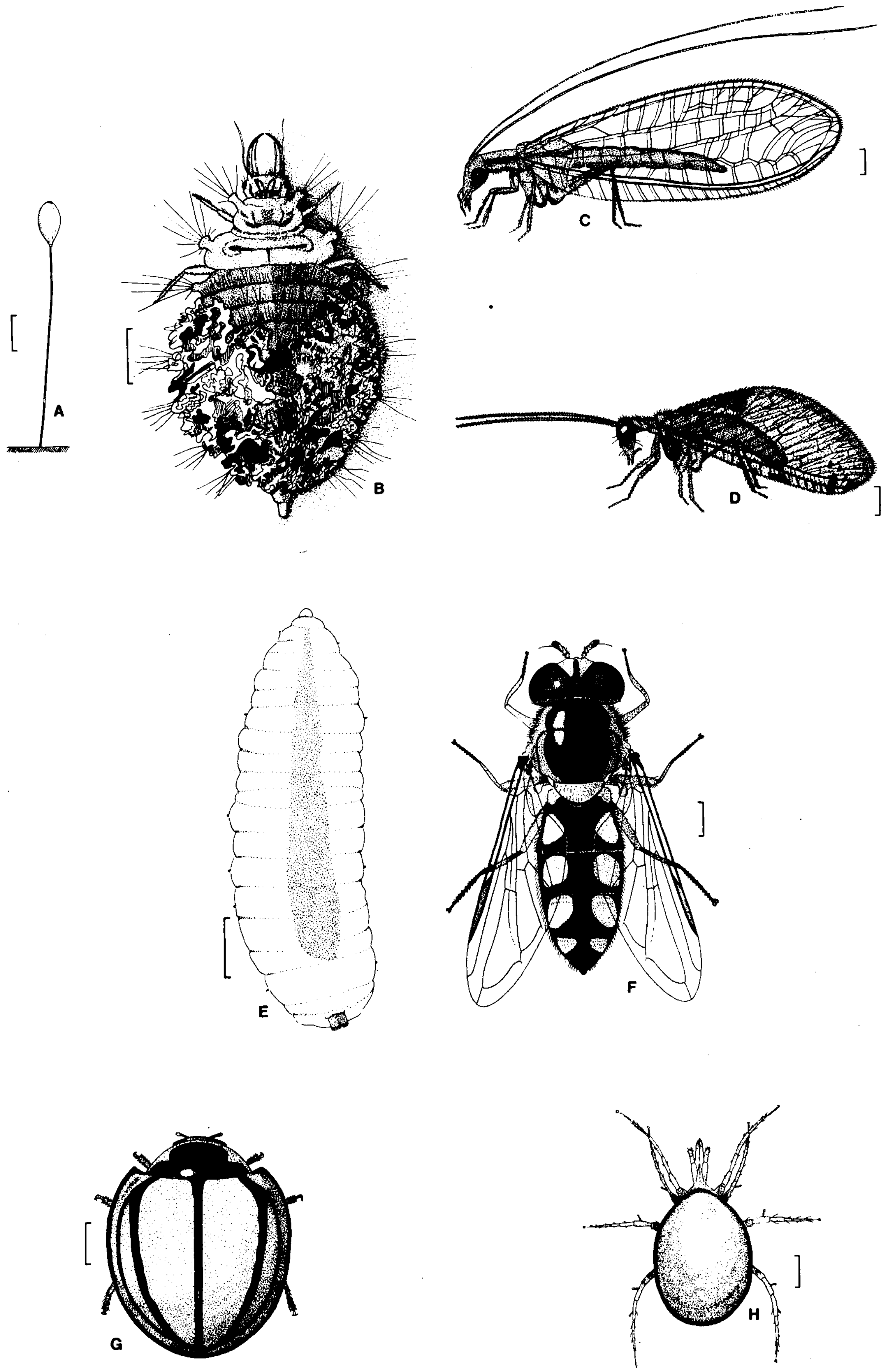
(1963b) concluded that although up to 35% of the third, fourth and fifth nymphal instars of C. albitextura may be killed by Syrphus sp., this predator plays but a minor part in determining the abundance of the host.

(i) Predators of T. erytreae. The species listed below were observed to attack T. erytreae in one or more of the study groves. Because it was soon realized that many were also aphid feeders, small-scale observation tests were carried out to determine feeding preferences. For these tests predators collected in the field were individually confined on citrus seedlings and given a choice between all stages of the citrus aphid, Toxoptera citricidus (Kirk.) and nymphal instars III-IV of T. erytreae. Their subsequent feeding behaviour was then observed for 3-6 hours. Predators are listed in their believed order of importance as predators of T. erytreae.

1. Chrysopa spp. (Neuroptera: Chrysopidae), green lacewings. (Fig. 21 A, B,C), Malkerns and Letaba districts. Specimens from Malkerns were determined by Dr. B. Tjeder as a complex of five species, namely C. pudica Nav., C. burgeonina Nav., C. congrua Walk., C. handschini Nav., and C. squamosa Tjd. C. pudica was also recorded as a predator at Zebediela in the northern Transvaal (Schoeman, O.P. 1969, personal communication). Green lacewings are usually more abundant than the brown species. The larvae are robust, an overall light grey in colour with black markings on the thorax, and are usually partly concealed beneath a bundle of exoskeletons representing the remains of their prey. Green lacewings are mainly considered as aphid feeders in Californian citrus (Ebeling, 1959). In feeding tests at Malkerns one individual was observed to feed preferentially on T. erytreae nymphs on four separate occasions. In one test a single larva consumed 20-25 nymphs in 1½ hours and at one stage an aphid was attacked briefly. A second individual fed on T. erytreae only, sucking dry approximately 20 nymphs in an hour and completely ignoring aphids even when all the nymphs had been consumed. A third individual attacked aphids before feeding on nymphs.

2. Micromus sjoestedti Weele (Neuroptera : Hemerobiidae), brown lacewing. (Fig. 21 D). Determined by Dr B. Tjeder. Malkerns and probably Letaba district. The larva is slender and dark in colour feeding on aphids and the nymphs of T. erytreae. In California hemerobiids feed mainly on citrus mites (Ebeling, 1959). On testing, three individuals showed immediate and persistent preference for aphids, but another individual attacked nymphs after an initial feed on aphids.

3. Allograpta pfeiferi Bigot (Diptera : Syrphidae) (Fig. 21 E, F). Determined by Mr K.G.V. Smith. Malkerns and Letaba districts. This was the most common syrphid species, the adult being a handsome fly with a yellow-striped abdomen. In several feeding tests syrphid larvae showed an immediate preference for aphids and ignored T. erytreae nymphs entirely.


A
B
C
D
E
F
G
H

When fed nymphs only the larvae were induced to feed after 1-2 days.

4. Baccha sp. (Diptera : Syrphidae) Determined by Mr K.G.V. Smith Malkerns and Letaba districts. Adult recognized by its black abdomen and slender petiole.

5. Cydonia propinqua Muls. (Coleopter : Coccinellidae). (Fig. 21G). Determined by Miss H.A.D. Van Schalkwyk. Feeding tests showed an equal appetite for aphids and nymphs of T. erytreae. This species has also been recorded as a predator in the northern Transvaal (Schoeman, O.P. 1969, personal communication).

6. Araneida, spiders. A large number of undetermined species were found to be predators in the Malkerns and Letaba districts. Spiders attack nymphs, adults, and even eggs on some occasions. They were also mentioned as predators by Van der Merwe (1941).

7. Coniopterygidae, "dusty wings". Larvae sent to the British Museum were identified by Mr D.E. Kimmins as Coniventzia sp. This is the first record of the genus in southern Africa, and this species may possibly have been introduced on citrus. The larvae appear to be just occasional feeders on T. erytreae nymphs, for in three feeding tests they showed a total preference for aphids.

8. Acarina, mites. Erythraeidae, determined by Dr M.K.P. Meyer. Bochartia sp. larvae and Abrolophus sp. adults were observed to attack T. erytreae nymphs at the Forest Hill grove only. Abrolophus, a large red mite, also preyed on two other psyllid species. Iphiseius (Iphiseius) degenerens (Berlese), (Fig. 21H), a small dark mite, was found attacking the eggs and nymphs of T. erytreae in the winter of 1967 at Malkerns. The effectiveness of this mite was not investigated and, according to Dr G.G. Van der Merwe (personal communication, 1967), who also determined this species, this group feed mainly on tetranychid mites and pollen. C.P. Van der Merwe (1941) also reported a red mite predator of T. erytreae.

Several other predators of T. erytreae have been reported. Larvae of the syrphid Baccha helva Bez. were recorded by Van der Merwe (1941) and B. sapphirina Wied. by Dr O.P. Schoeman (personal cummunication, 1969). The latter also lists a Scymnus sp. (Coccinellidae) and Xylocoris afer Reuter (Anthocoridae) as possible predators.

EXPLANATION OF FIGURE

Fig. 21 Some predators of T. erytreae. A,B,C - Chrysopa spp. (Chrysopidae), egg, larva and adult; D - Micromus sjoestedti Weele (Hemerobiidae); E, F - Allograpta pfeiferi Bigot (Syrphidae) larva and adult; G - Cydonia propinqua Muls. (Coccinellidae); H - Iphiseius (Iphiseius) degenerens (Berlese) (Phytoseidae). A - G scale line 1 mm; H scale line 0.1 mm. del. H.D. Catling

(ii) Experiments on the effectiveness of predators as limiting factors

Experiments were carried out in or near the experimental trees at Malkerns Research Station using several check methods described by De Bach (1964).

DDT - check method, September to March, 1967-68. Starting in September, six trees adjacent to the unsprayed experiment block of similar size, condition, and flushing rhythm were sprayed with DDT at monthly intervals to check the activity of predators. Initial populations of *T. erytreae* were similar in both lots of trees. In early February the numbers of *T. erytreae* and predators in a four foot band around the canopy of the six sprayed trees were compared with numbers in six of the surrounding unsprayed trees. In the sprayed trees were found 241 colonies of *T. erytreae* (11 - 66 per tree) and only two predators (one spider and one syrphid larva). In the unsprayed trees, however, were only 38 colonies (3 - 14 per tree) but 8 predators (5 lacewings, one spider and two coccinellids). Counts made in early March showed that the level of parasitism had apparently been reduced from 41.8% - 20.3% in the DDT-sprayed trees.

Thus, despite six applications of DDT, each of which may give a 42% control of nymphs (Catling, H.D., unpublished results) and only a moderate reduction in parasitism, the DDT sprays apparently produced a six-fold increase in the nymphs of *T. erytreae* due to the elimination of predators.

Sleeve cage check method, August 8 to September 14, 1967. Fourteen *T. erytreae* colonies were marked in the egg and small nymph stage. Four were caged in organdy sleeves, four given a vaseline barrier to exclude larval insect predators, and five colonies were left untreated as controls. No significant differences were found in survival between the control and either of the two treatments. Predators were observed to be at low densities in the surrounding trees at this time.

February 8-28, 1968. Ten pairs of *T. erytreae* colonies were selected in the egg or instar I-II stage, the members of each pair being situated on the same branch or close together on the same tree. One colony of each pair was then enclosed in an organdy sleeve to eliminate predators. Apart from colony pair 10, where flush condition was poor, and unsleeved colonies 6 and 10 where populations of aphids developed, all nymphs developed normally and those in the sleeves were particularly healthy. Final counts of live, unparasitized insects were made in the late fifth instar or adult stages, the results appearing in Table 11.

Survivals were greater in the sleeved colonies in 8 of the 10 pairs. The reversal in survival in colony pairs 6 and 10 may be explained by poor flush condition and the detrimental effect of honeydew produced by invading aphids. Eventual survivals would possibly have been even more in favour of the sleeved insects for some of the fifth instar nymphs in the final count of the unsleeved colonies could have been attacked by predators before emerging as adults. Predators were active in the unsleeved colonies on February 20.

Table 11 Survivals of sleeved and unsleeved colonies of *T. erytreae* at Malkerns Research Station in February, 1968

Colony pair	SLEEVED			UNSLEEVED		
	Initial no. insects Feb. 8	Final no. insects Feb. 28	Percent Survival	Initial no. insects Feb. 8	Final no. insects Feb. 28	Percent Survival
1	108	49	45	39	4	10
2	57	46	81	84	0	0
3	144	40	28	40	2	5
4	182	139	76	78	44	56
5	56	17	30	75	5	7
6	129	50	39	118	66	56
7	144	144	100	65	22	34
8	23	23	100	84	20	24
9	221	221	100	94	85	90
10	136	3	2	122	9	7
			mean 60.1%			mean 28.9%

Results were treated as 10 paired comparisons and the angular transformation applied to percentage survival. The higher mean survival in the sleeved colonies, 60.1%, as compared to the unsleeved colonies, 28.9%, was found to be significant at the 5% probability level.

(iii) Predator activity in field populations

Letaba district. Predator activity was apparently negligible in six *in situ* counts carried out at Forest Hill between August and early November, 1966. Between mid November and the end of January the fate of 786 instar III nymphs was carefully watched in another series of six counts. At the time of adult emergence 1.5% of the insects were still alive, 9.5% were parasitized, and 89.0% were dead or missing due to other mortality factors. Since the weather was favourable during this period and the advanced instars are in any case more resistant to lethal extremes, it is believed that the high level of nymphal mortality was caused partly by the poor quality flush which prevailed at this time, and partly by the action of predators. Relatively large numbers of neuropteran larvae were observed in the experimental trees during this period. Predators were active in a small outbreak of *T. erytreae* in the winter of 1965 at Letaba Estates, and at a grove in Duiwelskloof in early summer of the same year.

Thus predators only appeared in meaningful numbers when the host was at fairly high population densities. In both seasons at Forest Hill they were absent or at very low densities during the early summer period of steady population rise by *T. erytreae*.

Malkerns Research Station. Apart from regular field observations in the 20 data trees and surrounding groves during the study period from February, 1967, to January, 1970, predator activity was assessed from a series of 15 *in situ* counts during the first year of study, by estimating the proportion of host colonies infested with one or more predator species during the 1968-69 season, and by a fortnightly collection of predator species during 1968 and 1969.

Observations and in situ counts - March, 1967, to March, 1968

Chrysopa spp., spiders and I. degenerens were active on T. erytreae nymphs from March to the end of July but no signs of predators were observed from mid August to the end of September. Irregular syrphid activity and the corpses of sucked out nymphs were seen in October and November. In the middle of December the activity of coccinellids and lacewings increased steadily reaching a peak in January and persisting to March.

An attempt was made to deduce the quantitative effect of predators on their host from 10 in situ counts made during this period. Again, the influence of weather on the more resistant nymphal instars III-V was ignored and it was possible to make a fairly accurate estimate of mortality due to parasitism. Thus the balance of nymphal mortality may be regarded as the combined effect of host condition and predator activity. Unlike the Forest Hill trees, however, the experimental trees at Malkerns Research Station were well-managed and the influence of flush quality was fairly low. Table 12 shows the residual mortalities grouped into three fairly distinct catagories. Even after allowing for a possible seasonal fluctuation in the quality of the host plant and conceding the need for several assumptions in the derivation of the Table, it is indicated that higher predator activity occurred from midsummer to midwinter, than in the June - November period. The three highest levels of mortality occurred in December, March and May.

Table 12 Survivals of T. erytreae in 10 in situ counts made at Malkerns Research Station between March, 1967, and February, 1968

Period	No. of counts	No. instar III nymphs studied	Mean percent mortality presumably due to predation and plant host effect	Range
March - June	3	728	83.7	72.9 - 94.0
June - November	5	1886	40.2	22.9 - 61.2
December-February	2	382	62.6	43.0 - 82.1

Percentage host colonies infested with predators - December, 1967, to March, 1969. Colonies of T. erytreae counted on the 20 data trees in the main population study were examined for predators and the percentage colonies with one or more predators recorded on each sampling date. The following predators were considered: lacewing eggs and larvae, syrphid larvae, all species of coccinellid larvae and adults, and spiders. Fig. 22 shows that predators were active in T. erytreae colonies from January to May but were totally absent from June to the beginning of September. Their relative numbers increased briefly in early October but slumped again in November. A fairly steady increase in activity took plade in December and January reaching a peak in February - by which time host populations were at a low ebb.

FIG. 22

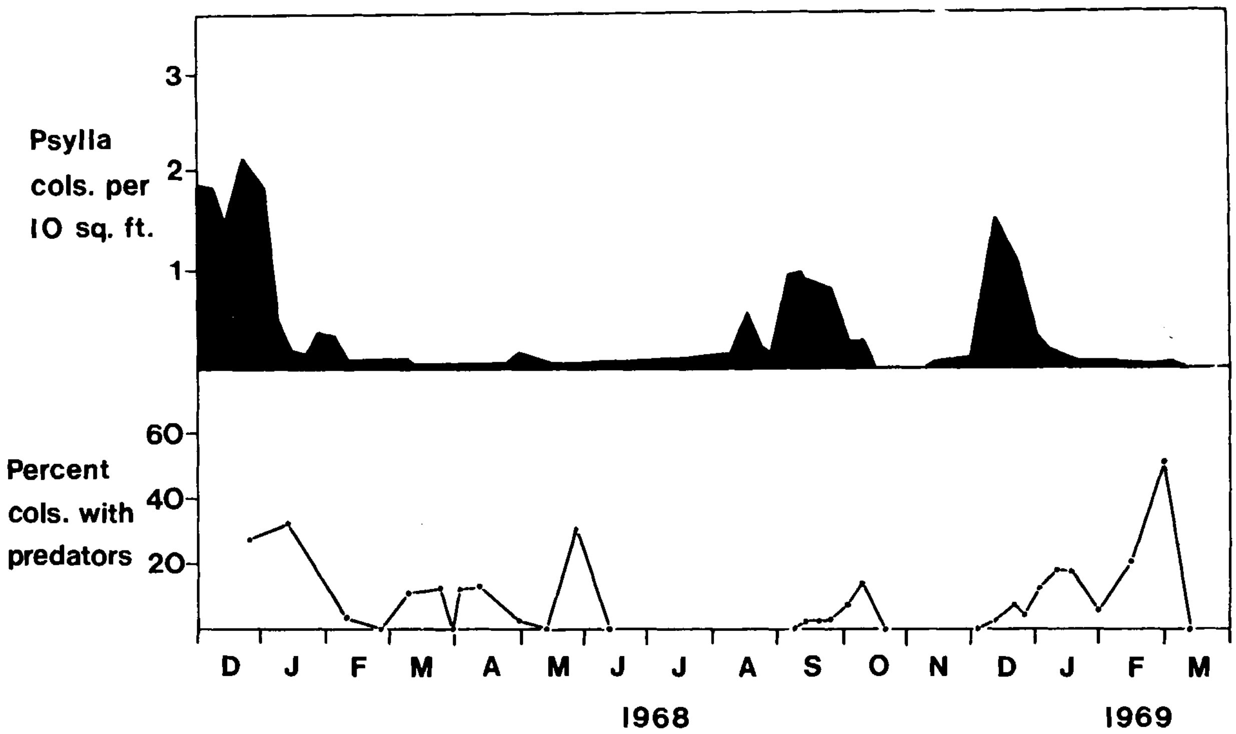
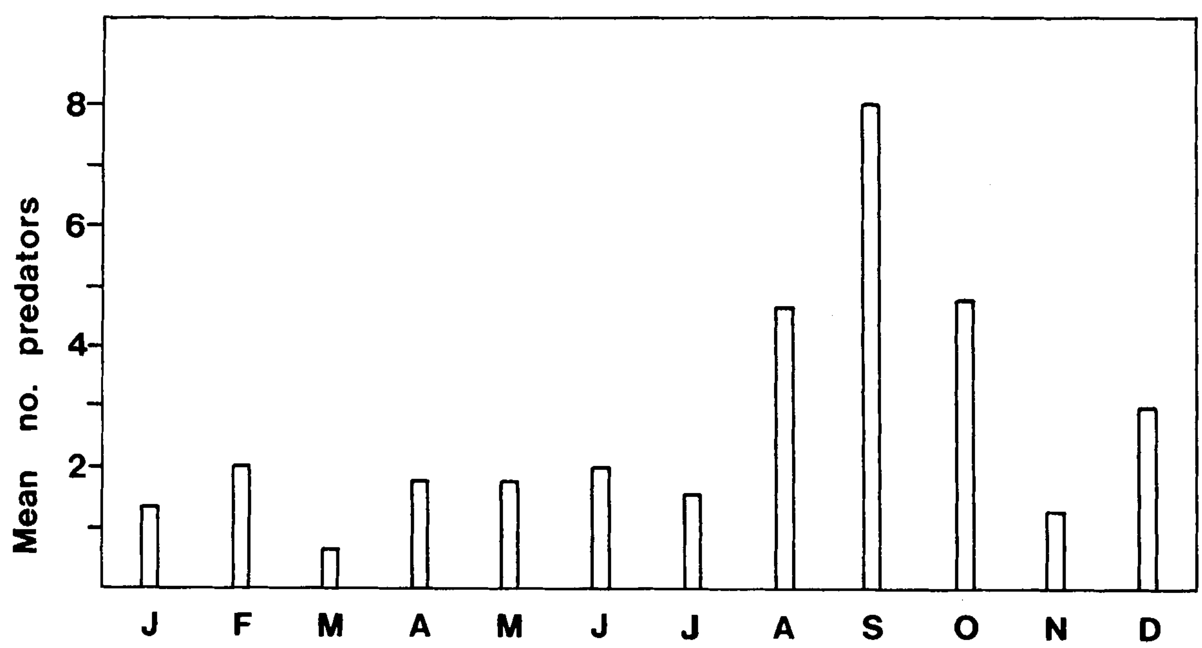

3
Psylla
cols. per
10 sq. ft.
2
1
60
Percent
cols. with
predators
40
20
D J F M A M J J A S O N D J F M
1968
1969

FIG. 23


Mean no. predators
8
6
4
2
J F M A M J J A S O N D

Collection of predators - 1968 and 1969. Fortnightly collections of lacewing adults and larvae, syrphid adults and larvae, coniopterygid larvae, C. propinqua adults, and spiders, were made with the insect sampling machine on each of five haphazardly-selected trees as described previously. Despite the crudeness of this method, certain trends in the abundance of predators were discernible. The numbers of spiders tended to be slightly higher in late summer and winter but were well represented at all times. Results for all other species were grouped into monthlymeans for the two years of collection and appear in Fig. 23. It is seen that there was little difference in numbers for the months of January to July, but a definite rise was indicated in August, September and October when host populations are commonly at high densities.

Observations - June to December, 1969. No predator activity was noticed in June, July and early August, T. erytreae populations being at exceptionally low densities. In the latter half of August lacewings made an appearance and several nymphal colonies were quite heavily attacked. Lacewing eggs were common in early September but these predators were feeding mainly on the large aphid populations present on the young flush. No predators were observed in October and November, small numbers appearing again in December.

(iv) Discussion.

A complex consisting of two lacewings, two syrphids, the coccinellid C. propinqua, and several species of spiders appear to be the main predators of T. erytreae. Yet each of the five insectan predators is also an aphid feeder and at least three species showed a marked feeding preference for aphids. Because T. erytreae and the citrus aphid are virtually sympatric having almost identical habitats and very similar population fluctuations it is difficult on the present evidence to relate predator activity with the abundance of a single host, namely T. erytreae. For the main predators no attempt was made to directly ascertain the proportion of aphid feeding to T. erytreae feeding, and it would appear that for most, if not all species, aphids represent their main source of prey.

De Bach (1958) drew attention to the difficulty of assessing the true significance of predators and warned against the hasty acceptance of incomplete evidence. Because of the rather superficial methods used to assess the role

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EXPLANATION OF FIGURES

Fig. 22 Percentage colonies infested with predators, and population fluctuations of T. erytreae from January, 1968, to March, 1969, at Malkerns Research Station

Fig. 23 Mean monthly numbers of insectan predators of T. erytreae collected with the insect sampling machine in 1968 and 1969 at Malkerns Research Station of predators in this study, only general, qualitative, conclusions will be drawn from the results described. In both study areas over a period of nearly five seasons there was a general tendency for predator numbers to increase during midsummer and remain fairly active into the winter months. During this time of the year they are undoubtedly a significant limiting factor and together with several other ecological factors assist in suppressing populations of T. erytreae. However, there is a conspicuous time lag in their host synchrony in early summer when T. erytreae is building up steadily on the young growth. (It is interesting to note here that both aphids and T. erytreae begin their first population rise of the season on the July/August flush cycle). Similarly, in scattered outbreaks at other times of the year predator numbers only became meaningful some time after the outbreaks had reached fairly high proportions. Their failure as a limiting factor in spring and their increased importance in midsummer was confirmed by the check experiments.

7. INFLUENCE OF EXTREMES OF WEATHER ON SURVIVAL

Many species of Psyllidae are known to be intolerant of high temperatures, for instance, Paratrioza cockerelli (Sulc.) (List, 1939), Psylla pyricola Foerster (Madsen et al., 1963) and Cardiaspina albitextura Taylor (Clark, 1964b) to mention just a few. In the Letaba district of the Transvaal the present author observed high mortalities in the young stages of Diaphorina punctulata Pettey and an unnamed Trioza sp. following extremes of hot, dry weather.

The sensitivity of T. erytreae to high temperatures was first reported by Van der Merwe (1941) and was later shown under laboratory conditions by Moran & Blowers (1967). In 1965 the present author found it extremely difficult to establish a successful culture of T. erytreae at Letaba without the use of cooling machinery. The work described here, which is based entirely on field studies, supports the above findings. Preliminary field evidence was presented by Catling (1967) and Catling & Annecke (1968) from a study in the Letaba district. Additional studies made in Swaziland, and a more detailed analysis of the results from both districts are presented here.

The experimental sites in the Letaba district of the Transvaal, namely Forest Hill, Fairview, Letaba, Letswalo and Riverside, and those in Malkerns and the Swaziland Lowveld were described previously. In the Letaba district there were fairly large differences in the density of leaf canopy at the three main sites, density assessments showing the following ratios: Letaba (most dense) 15, Fairview 14 and Forest Hill 11. At each of the three main sites in the Letaba district a thermohygrograph was operated according to specifications suggested by the South African Weather Bureau. Temperature and relative humidity were checked biweekly against a set of meteorological thermometers and all equipment was housed in standard Stevenson screens. At Malkerns Research Station and the Lowveld Experiment Station at Big Bend, meteorological data were available from a class 2 weather station. Methods for assessing populations of

T. erytreae at the main experimental sites, and in four additional groves in Malkerns, were described previously. In situ counts were made at Forest Hill, Fairview and Letaba in the Transvaal, and at the Malkerns Research Station and Tambankulu Estates in Swaziland. Mortality was shown by collapsed or non-hatching eggs and shrivelled nymphs.

(i) Preliminary evidence of the lethal effect of high temperatures. In the Letaba district a linear relationship was found between altitude and the previous indidence of T. erytreae. Highest populations occurred in the cooler, upland groves while low or negligible populations characterized the hotter lowlands (Catling, 1967; 1969c).

The role of shade in moderating the effect of summer temperatures, first observed by Van der Merwe (1941), was soon confirmed in the Letaba district. The majority of T. erytreae colonies were situated on the lower section of the tree. On many occasions trees partly shaded by high windbreaks were observed to support higher populations than unshaded trees in the same grove. It is likely, however, that interference in the airflow near windbreaks, which tends to accumulate insects (Lewis, 1968), may be an additional factor. Counts of pitted leaves in a mature grove at Malkerns along three rows at right angles to a high windbreak, revealed the following mean number of colonies per tree: windbreak 89.3, 99.7, 72.7, 46.7, 33.0, 57.0, 41.3, 51.3. Surveys on Letaba Estates showed that groves of small trees (which have little internal shade) are rarely infested during the summer months. (Catling, 1967; 1969c).

(ii) Survival of eggs and first instar nymphs from In Situ counts. Of a large number of in situ counts carried out at the main sites in the Letaba district between December, 1965, and January, 1967, 32 were selected for a study of the influence of weather on egg and nymphal survival. Fifteen counts were made at Letaba, four at Fairview, and 13 at Forest Hill. This involved a total of 10,458 eggs in 82 colonies. Twenty-two in situ counts were carried out at the Malkerns Research Station and one at Tambankulu Estates in the Swaziland Lowveld, involving a total of 21,112 insects. Egg to first instar survival was calculated from the total number of eggs in the colony and the maximum number of first instar nymphs to emerge and settle normally. Counts were made over a period of 8-13 days with a mean of 10 days.

Despite the use of means for various aspects of prevailing weather for the duration of the counts, which frequently concealed short but extremely lethal weather conditions, Catling (1967) and Catling & Annecke (1968) were able to come to the following preliminary conclusions: 1. There was a definite trend for a decrease in survival with a rise in temperature or decline in relative humidity (RH); 2. within the range of climate studied, high temperatures and low RH's became lethal only when applied together; 3. combinations of temperature and RH become particularly critical in the region above 30°C and below 25% RH (or at a saturation deficit above 25 mm Hg).

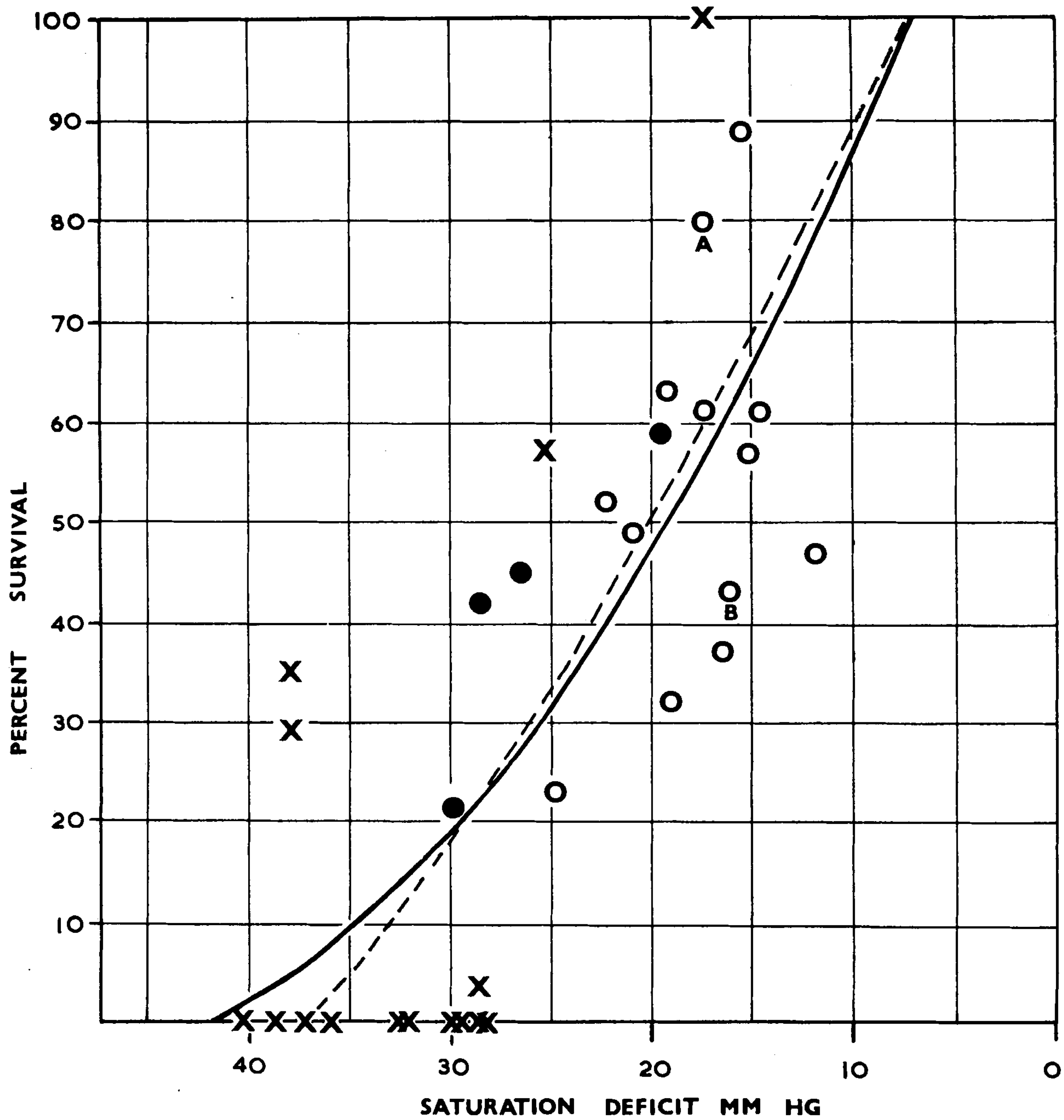
Table 13 Survival of eggs and first instar nymphs of T. erytreae from an in situ count on Tambankulu Estates, Swaziland, against the prevailing daily maximum saturation deficits. Dead first instar nymphs were removed on each day

Date	Number of insects			Saturation deficit mm Hg
	Live eggs	Live I	Dead I	
1967 Oct 19	-	-	-	20.6
20	-	-	-	21.9
21	-	-	-	21.3
22	-	-	-	21.4
23	-	-	-	33.2
24	872	458	0	46.7
25	-	149	361	7.1
26	-	119	54	4.0
27	-	108	9	2.4
28	-	5	103	7.1
29	-	-	-	10.7
30	0	0	0	17.9

Table 13 shows the results of an in situ count at Tambankulu Estates. On October 19 eight egg-infested citrus seedlings were placed in diffuse shade near a thermohygrograph housed in a Stevenson screen. The maximum daily saturation deficit was clearly favourable for 10 of the 12 days over which the count was made. On October 23 and 24, however, just at the onset of hatching, the saturation deficit rose to 33.2 and 46.7 mm Hg respectively. Five days later, despite cool overcast weather, all the insects were dead - many eggs collapsing or remaining unhatched and all first instars shrivelling. Though live nymphs were recorded from October 25 to 28 their general sluggishness indicated that they were succumbing to the effects of the severe conditions on October 23 and 24.

Correlations between survival and various aspects of weather. A correlation analysis was carried out between percentage survival (1) and various aspects of weather (2-20), first singly and then in combination. The following aspects of daily weather were considered:

(2) daily maximum temperature
(3) hour degrees Centigrade per day above 20°
(4) hours per day temperature exceeded 26°C
(5) " " " " " 28°C
(6) " " " " " 30°C
(7) " " " " " 32°C
(8) " " " " " 34°C
(9) " " " " " 36°C
(10) " " " " " 38°C
(11) daily minimum RH
(12) hours per day RH below 40%
(13) " " " " " 35%
(14) " " " " " 30%
(15) " " " " " 25%
(16) " " " " " 20%
(17) " " " " " 15%
(18) maximum saturation deficit, from daily maximum temperature and minimum RH
(19) summation of one hour units of RH above 0%



PERCENT SURVIVAL
SATURATION DEFICIT MM HG
100
90
80
70
60
50
40
30
20
10
40
30
20
10
0
A
B

(20) vapour pressure, from daily maximum temperature and minimum RH

Survival was correlated with means of the severest weather conditions for 1, 3, and 6 days during the 8 to 13 day study period. The best results were obtained with the mean for three days; therefore only the series representing mean weather conditions for the 3 severest days are considered in correlations with egg to first instar nymph survival.

Table 14 shows the coefficients of correlation of the dependent variable (survival) with various aspects of prevailing weather. As single aspects, maximum temperature (2) and vapour pressure (20) are highly correlated with survival. Vapour pressure is a measure of humidity which is largely independent of temperature. Single aspects which are dependent on both temperature and vapour pressure, such as RH (11) and saturation deficit (18), were shown to be even more significantly correlated, the latter having the highest correlation coefficient of - 0.755. It is emphasized here that RH is the percentage ratio between actual vapour pressure and saturated vapour pressure, while saturation deficit is the difference between the two.

Table 14 Coefficients of simple and multiple correlation between the survival of eggs and first instar nymphs of T. erytreae (dependent variable) and numbered aspects of weather (independent variables). Based on the mean of the three severest days during the study period

Single aspects of weather	r	Combined aspects of weather	R
2	-0.684+	2-10	0.811+
3	-0.535*	11-17	0.779+
11	0.705+	4-10	0.684+
18	-0.755+	12-17	0.774+
19	0.664+	2, 11, 18, 19	0.753+
20	0.606+	2, 20	0.802+

* $.001 < P < 0.01$ + $P < .001$

Of the multiple correlations, one of the most significant was a linear combination of maximum temperature and vapour pressure. The only superior predictor of survival appeared to be a combination of nine aspects of temperature. However, the requirement of such detailed meteorological data makes this combination impractical. The acceptable predictors for survival are thus saturation

EXPLANATION OF FIGURE

Fig. 24 Scatter diagram and regression curves for survival of eggs and first instar nymphs of T. erytreae against mean maximum saturation deficit for the three severest days of the count. Solid line curve and points on the figure are based on in situ counts made at the three main experimental sites in the Letaba district; X - Letaba, • - Fairview, O - Forest Hill; $Y = 137.7709 - 5.5766X + 0.0547X^2$; standard error of estimate = 19.99%. Broken line curve is based on in situ counts made in Swaziland, $Y = 134.7968 - 4.9386X + 0.0351X^2$

deficit as a single aspect, and maximum temperature with vapour pressure as a simple combination. Examinations of thermohygrograph traces showed that in general the daily durations of lethal temperature and RH were directly proportional to the maxima reached.

A scatter diagram and regression curves for survival against saturation deficit are shown in Fig. 24. The variation is believed to be due to the operation of other mortality factors such as differences in the density of leaf canopy, foliage condition, and the differential effects of lethal weather on different stages in the development of eggs and first instar nymphs. (Natural enemies appear to play a negligible role in these early stages). For instance, the tendency for the points of each site to be grouped is explained by differences in leaf density. The highest leaf density and highest survival at a constant saturation deficit occurred at Letaba, the lowest leaf density and survival at Forest Hill, with Fairview being intermediate. From points marked A and B in Fig. 24, which represent two counts over the same period at Forest Hill, it is seen that survival varied from 43 - 80% under virtually the same conditions of atmospheric stress. It is probable that differences in foliage condition were responsible for this variation. Other mortality factors are again suggested by the nil survivals between saturation deficits of 27 and 41 mm Hg in spite of two cases of near 30% survival at a saturation deficit of 38 mm Hg.

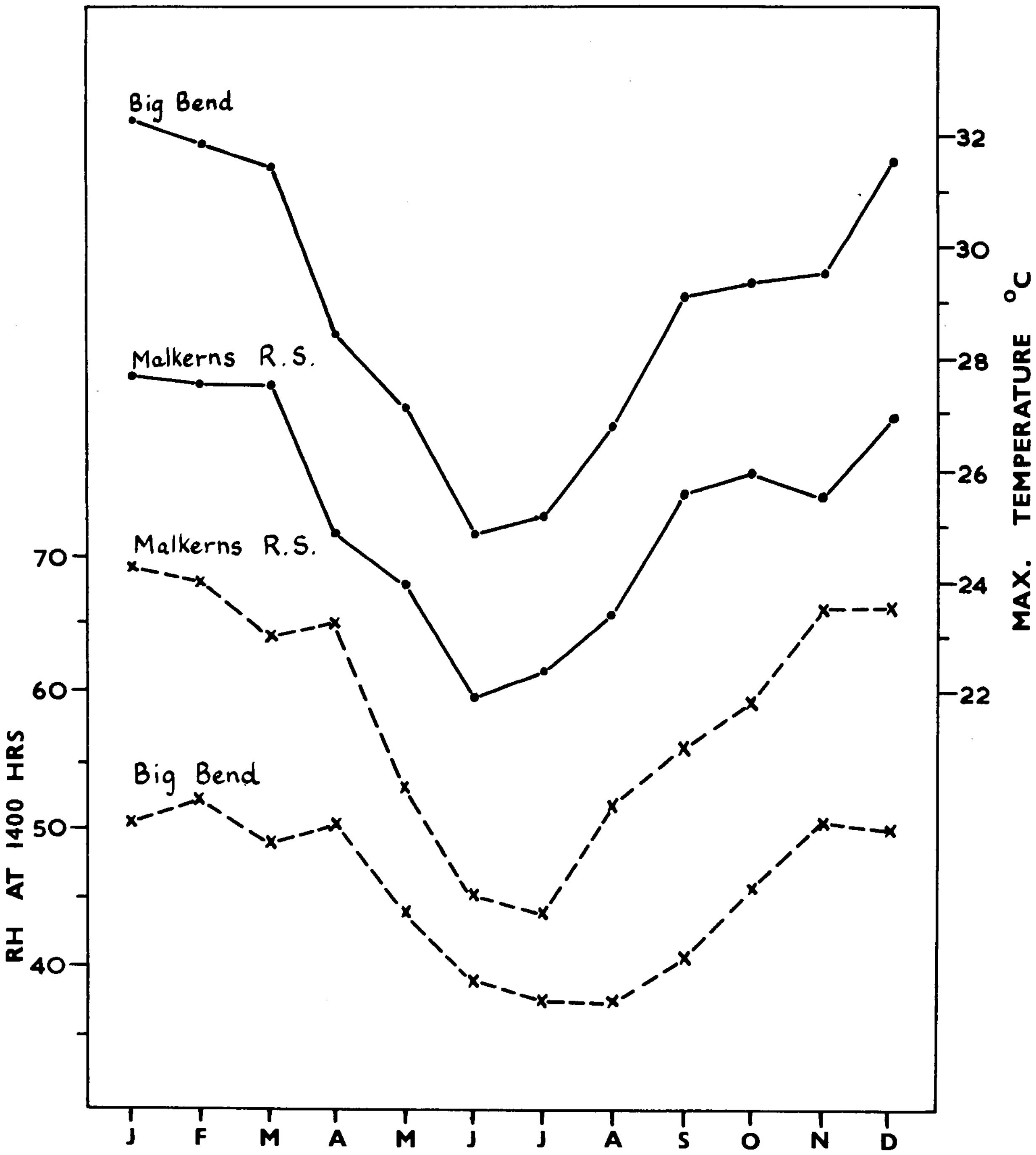
A scatter diagram of observed survival against survival estimated from a multiple regression on maximum temperature and vapour pressure was, to all appearances, very similar to the scatter diagram in Fig. 24. The equation for this second regression, which has a lower standard error of estimate, is $Y = -4.4985\ X_1 + 6.0922\ X_2 + 114.4968$ where X_1 = maximum temperature and X_2 = vapour pressure (standard error of estimate = 18.37%).

A similar analysis of survival against saturation deficit was made from the 22 <u>in situ</u> counts made in Swaziland. Fig. 24 shows excellent agreement between survival curves for the two regions, indicating very similar temperature-moisture tolerances between populations of *T. erytreae* some 200 miles apart.

<u>Survival and age</u>. A number of separate field observations showed that the more advanced nymphal stages of *T. erytreae* are more tolerant of severe weather than eggs and first instar nymphs (Catling, 1967).

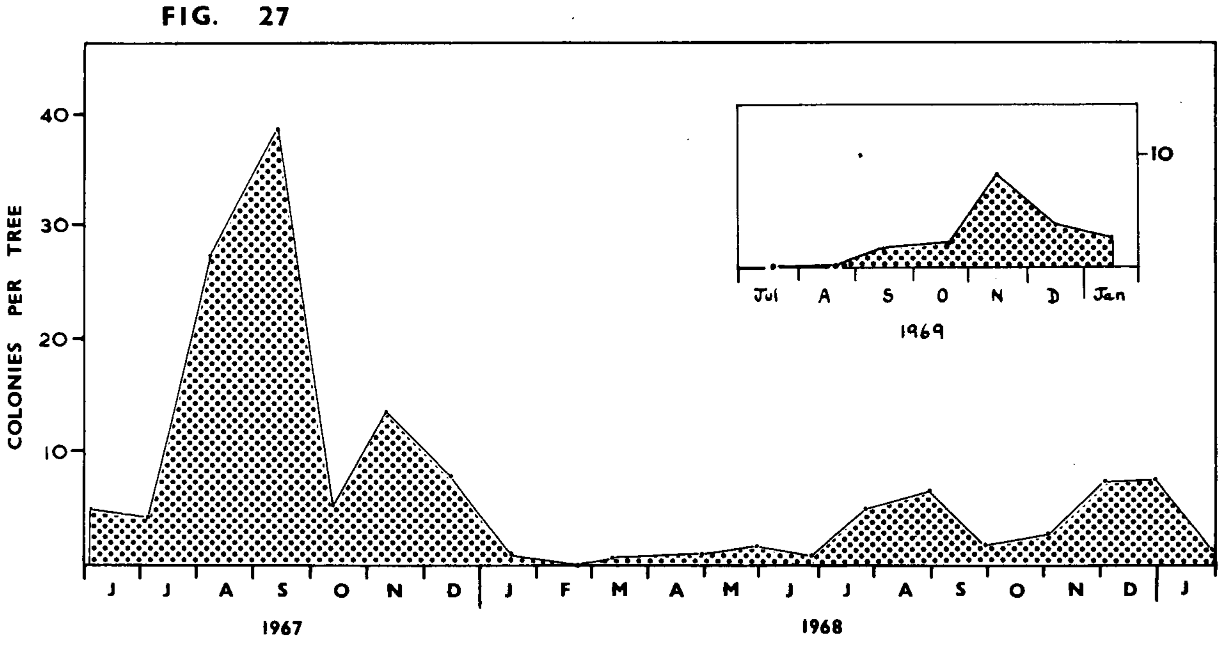
The series of <u>in situ</u> counts described before were continued through the five nymphal stages to the emergence of the adults. Though the influence of additional mortality factors was stronger during this period of survival, there was a similar trend for higher survival under milder conditions of prevailing weather. Table 15 compares the mean weather conditions which prevailed for six <u>in situ</u> counts of egg to first instar nymph survival with four counts of first instar nymph to adult survival. In both cases survivals were greater than 60%.

FIG. 25



Big Bend
Malkerns R.S.
Malkerns R.S.
Big Bend
70
60
50
40
RH AT 1400 HRS
32
30
28
26
24
22
MAX. TEMPERATURE °C
J F M A M J J A S O N D

FIG. 27



40
30
20
10
COLONIES PER TREE
J J A S O N D J F M A M J J A S O N D J
1967
1968
10
Jul A S O N D Jan
1969

Clearly, instars II-V were able to withstand greater extremes of weather than eggs and first instar nymphs.

Table 15 Mean weather conditions permitting survivals of *T. erytreae* above 60%. Data from *in situ* counts made in the Letaba district of the Transvaal

Survival class	No. *in situ* counts	No. insects	Mean daily max. temp °C	% days max. temp > 29.9°C	Mean min. RH	% days RH < 26%	Mean max sat. def. mm Hg
Egg to instar 1 .	6	2024	23.7	9.2	54.5	2.8	10.2
Instar 1 to adult	4	1019	27.3	30.3	40.8	24.8	16.9

(iii) Population fluctuations of *T. erytreae* in relation to prevailing weather. The influence of weather on the population fluctuations of *T. erytreae* in the Letaba district was described in detail by Catling (1967; 1969c) and Catling & Annecke (1968) and will not be repeated here.

Swaziland Lowveld

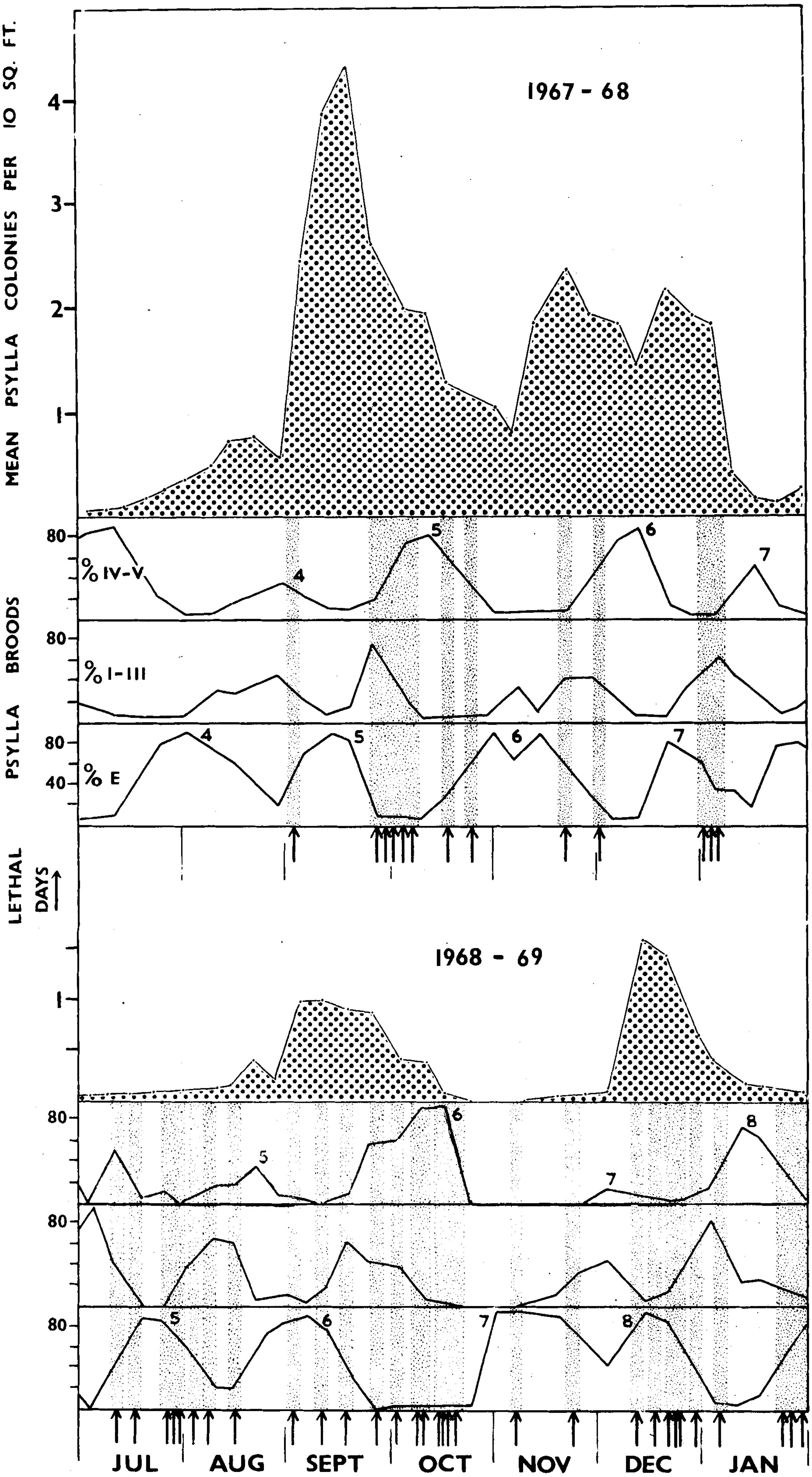
Fig. 25 compares the mean monthly maximum temperatures and mean monthly RH at 1400 hours for Malkerns Research Station, and the Lowveld Experiment Station at Big Bend which is representative of the Swaziland Lowveld. The Malkerns district is considerably cooler with higher relative humidities, and is less windy with an average run of 68.2 miles per day in 1967, as opposed to 93.6 miles per day for Big Bend.

Scattered colonies appear on citrus at Crookes Plantations in the Big Bend area during early summer, especially on mature trees partly shaded by windbreaks. Regular surveys in the 100,000 trees belonging to the Swaziland Irrigation Scheme revealed the presence of isolated colonies in 22 of 51 survey blocks between October, 1968, and January, 1969 (Jackson, D. 1969, personal communication). In general, populations appeared to be lower at Tambankulu Estates since, in the 1965-66 season, twenty trees examined at monthly intervals from September to March, and surveys in 8,000 trees in November showed no trace of the insect (Le Roux, A. 1966, personal communication). No *T. erytreae* adults were taken in fortnightly samples between March, 1968, and March, 1969, with the insect sampling machine. Noteceable populations on this Estate occurred in the autumn of the 1966-67 season following long periods of humid, overcast weather.

EXPLANATION OF FIGURES

Fig. 25 Mean monthly maximum temperatures and RH at 1400 hours for Malkerns Research Station (1959-1968), and Big Bend (1962-1968), Swaziland Lowveld

Fig. 27 Mean population density of *T. erytreae* at four sites in the Malkerns district for the three study seasons



MEAN PSYLLA COLONIES PER 10 SQ. FT.
1967 - 68
PSYLLA BROODS
% IV-V
% I-III
% E
LETHAL DAYS
1968 - 69
JUL
AUG
SEPT
OCT
NOV
DEC
JAN

Following unusually high humidities and mild temperatures in November and December, 1969, a general outbreak of *T. erytreae* occurred on the midsummer flush in several parts of Swaziland. Relatively high populations were observed at Ngonini in the northern Middleveld and at Swaziland Irrigation Scheme in the Lowveld. In a large grove at Tambankulu Estates, counts on December 10 revealed that 92% of the trees were infested with a mean density of .32 colonies per 10 square feet of tree canopy.

Malkerns district

In the Malkerns district fairly high populations of *T. erytreae* were usual during the July to December period. In Fig. 26 population fluctuations, broods, and the occurrence of "lethal days" at Malkerns Research Station are compared for the 1967-68 and 1968-69 seasons. In September, 1967, the population surged to a peak of 4.31 colonies per 10 square feet of canopy and persisted at densities between 0.85 and 2.30 colonies until the crash in the first week of January. From July to January there were 13 "lethal days", only one occurring prior to the September peak population. Five "lethal days" occurred between September 27 and October 7 when the bulk of brood five were in the more tolerant III-V instar stage, but a slight hesitation in the rise of brood six was evident, many young colonies being decimated by these extremes. With the continued laying of new batches of eggs by tolerant adults, the advent of more favourable weather at the end of October permitted the rise of brood six.

In the following season populations were considerably lower and there were 31 "lethal days" between July and January. During the peak density in September the population rose to 0.95 colonies per 10 square feet which is less than one quarter of that for 1967. Five "lethal days" occurred between July 11-28 when the bulk of brood five was present as eggs and young instars. There were three "lethal days" at the start of the following brood and, as in the previous season, a severe spell of hot, dry weather postponed the rise of the October brood. Due to the eight "lethal days" between September 27 and October 19 no definite rise of egg colonies was evident for four weeks and populations were at very low densities until early December. Very favourable weather in November and the first two weeks of December resulted in brood eight momentarily approaching the densities recorded in 1967, but another hot, dry spell in the third week of December contributed to an early population crash for the season.

For the 10 days, December 30 to January 8, the mean daily maximum saturation deficit was 28.6 mm Hg, "lethal days" occurring on January 1, 2, 3 and 4. Population studies showed that on January 4,33.7% of the population were in the egg stage and 65.7% present as nymphal instars I-III. Fig. 24 forecasts a survival of 22% for eggs and first instar nymphs following such extremes of saturation deficit. In order to compare such a prediction with actual field mortality,

EXPLANATION OF FIGURE

Fig. 26 Population fluctuations, broods of *T. erytreae*, and the occurrence of "lethal days" (shown by arrows) at Malkerns Research Station for the 1967-68 and 1968-69 seasons. On each "lethal day" the saturation deficit exceeded 25.9 mm Hg (34.6 mbars) colonies of T. erytreae were removed at random from the experimental trees on January 8 and examined under a stereo-microscope. Of 875 eggs and first instar nymphs examined, 22% were alive, the remainder clearly having succumbed to severe weather.

February, 1969, was also abnormally hot and dry, the mean maximum temperature being 3.4°C above, and the mean RH at 1400 hours 11% below the 10 year average for Malkerns Research Station. There were 5 "lethal days" in this month (Fig. 10) compared with one for 1968 and nil for 1967. During late summer and winter of 1969, populations reached their lowest densities for the entire study period. No colonies were recorded in the data trees from March 14 to May 14, no adults were taken in 12 collections of the insect sampling machine between February 14 and July 29, and no specimens were seen in 23 samples taken with the sticky plates during this period. Mean population density of T. erytreae from mid May to the end of July was .009 colonies per 10 square feet of canopy as opposed to .044 for the previous season.

Despite the favourable weather which prevailed in July and the first half of August when no "lethal days" occurred (Fig. 10), there was only a gradual population rise on the spring growth of 1969. This can only be explained by the unusually small winter nucleus population at the start of the season, and the lower flush density which was heavily populated with citrus aphids. Mean temperatures and "lethal days" for August to November were similar to those for 1968, thus holding populations of T. erytreae at relatively low densities. There were three "lethal days" in early September when the bulk of the population was in a susceptible stage and as in the two previous seasons, there was a slight hesitation in the rise of the October brood due to severe weather. With only one "lethal day" in November, none in December, and a fairly heavy December flush cycle, populations reached their highest peak at the end of December. There was a gradual decline during January.

Populations were considerably lower in the 1969-70 and 1968-69 seasons than in the 1967-68 season at four other sites in the Malkerns district, (Fig. 27). Population densities in these groves were rather variable in the 1969-70 season due mainly to irregular flushing. Population explosions, where every flush point becomes overcrowded with eggs, were observed on two occasions in the 1967-68 season, but did not occur at any time during the following seasons. It was established that differences in chemical control measures were not responsible for these differences in population densities.

(iv) Discussion

Survival of eggs and first instar nymphs. The in situ counts proved the sensitivity of the developmental stages of T. erytreae to extremes of hot, dry weather, the eggs and first instar nymphs being particularly vulnerable. This partly confirms the work of Moran & Blowers (1967) who reared the insect at three regimes of controlled, fluctuating temperature. At a regime of 24 hour degrees Centigrade per day above 20° with a maximum temperature of 25° all stages flourished. But at 54 Hr °C/Day above 20° and a plateau of 32° for several hours eggs failed to hatch and when introduced from outside newly-emerged first instar nymphs died in seven hours, older first instars surviving for just over a day. However, as those authors rightly point out, the "plateaux" of temperature used in their exposures are different to the "peaks" experienced in the field. And the influence of humidity was not considered in their study.

According to Woodbury (1954) temperatures near the limits of toleration are usually resisted more strongly when applied gradually. In the field, especially during September and October, not only do extremes develop rapidly but several days of extreme heat and dryness may often be followed immediately by cool, humid weather (Table 13). Wind will also heighten the lethal effect of hot, dry conditions by increasing the evaporative power of the air.

Despite the operation of a number of additional mortality factors, several aspects of both temperature and humidity, singly and in combination, proved to be closely correlated with survival. The best of these correlations involved either single aspects comprising both air temperature and absolute humidity elements eg. the minimum RH and maximum saturation deficit, or a linear combination of maximum temperature and water vapour pressure. The interaction of temperature and RH is further demonstrated with reference to the regression of survival against maximum saturation deficit shown in Fig. 24 from which predictions of mortality can be made. At 32°C and 10% RH, which represents a saturation deficit of 32.1 mm Hg, there is a 15% survival of eggs and first instar nymphs, while an RH of 40% at the same temperature gives a saturation deficit of 21.4 mm Hg and a survival of 43%. It is thus abundantly clear that both temperature and humidity operate together to produce lethal conditions. The best single predictor of mortality was maximum saturation deficit and the best of the combined factors was maximum temperature with vapour pressure.

Temperatures and RH's used in this study were based on recordings from instruments housed in Stevenson screens. The survival of _T. erytreae_ is also very dependent on microclimate, _in situ_ counts sometimes showing considerable variation in survival according to the position (or shading) of the colony. Keetch, D.P. (personal communication, 1966) found that large temperature differences at the surface of citrus leaves was dependent on the degree of shading and Wellington (1950) showed that leaf temperatures fluctuate rapidly and may rise 10°C above the ambient air. In the present study the moderating effect of shade was indicated by the occurrence of high populations near windbreaks; by the preponderance of breeding sites on the lower section of tree canopy; and by small trees at low altitudes being infested only in the cooler months. Leaf density was also found to influence the microclimate of citrus trees, those with lower leaf densities allowing greater solar radiation penetration and the freer movement of air. The fairly large differences in leaf density between the main experimental sites in the Letaba district is thought to account for much of the scatter in the survival correlations. Nevertheless, the effect of both dense and fairly open trees is well balanced and probably increases the value of the survival regressions for field use.

Survival from second instar to adult. The work of Moran & Blowers (1967), who found that under laboratory conditions the more advanced nymphal stages are more tolerant of extreme temperatures, was supported by in situ counts and field observations in the Letaba district. In both studies, resistance to extremes was found to increase with successive moults, fully mature adults being the most resistant.

Influence of weather on population fluctuations of *T. erytreae*

Regional differences. In both study districts moderate to high populations of *T. erytreae* were found only in the upland or cool, moist regions - at the Forest Hill and Fairview sites in New Agatha; the Letswalo site in the upper Letsitele Valley; groves in the Tzaneen/Duiwelskloof area; and the Malkerns district of Swaziland. Survivals in in situ counts were consistently high at Forest Hill but low and commonly nil during early summer on Letaba Estates. Low, isolated populations occurred in the hot, arid regions such as Letaba and Riverside in the Transvaal Lowveld, and in the Swaziland Lowveld.

Seasonal differences. There was a tendency for higher populations in cool, humid seasons or during spells of milder weather between July and January. The monthly means for critical aspects of weather frequently concealed the occurrence of lethal extremes, especially in early summer when spells of hot, dry weather tend to alternate with cool, overcast conditions. This was particularly evident when comparing population densities at Malkerns Research Station for the 1967-68 and 1968-69 seasons. Although differences in the October flushing rhythm and levels of parasitism contributed to the higher populations recorded in 1967 (Catling, 1969a and b), the most significant factor was the more favourable weather which prevailed during the first season. The 13 "lethal days" recorded in 1967-68 as opposed to 31 "lethal days" in the following season were poorly reflected in the monthly means for the two seasons. Population fluctuations in the 1969-70 season were similarly explained in terms of "lethal days".

There is little doubt that the abnormally severe midsummer weather of the 1968-69 season was the main factor responsible for the extremely low populations of *T. erytreae* in the following winter and early summer.

Timing of lethal extremes of weather

The occurrence of distinct broods or field generations and the extreme sensitivity of eggs and first instar nymphs suggest that the lethal effects of severe weather depend largely on the age distribution of the population. Severe weather when the bulk of the population is in the egg and early nymphal stage will produce higher mortalities than similar stress applied when the population consists mainly of advanced nymphs. For this reason the unfavourable weather during July and August of 1968 was particularly limiting and was probably the main reason for low populations in early summer.

Causes of heat mortality

The physiological changes which take place in insects succumbing to heat exposure are discussed by Woodbury (1954). There is some evidence that on poorly-nourished flush, nymphs of *T. erytreae* may die of protein starvation during midsummer (Catling, 1967). In their laboratory exposures Blowers & Moran (1967) found that in insects succumbing to high temperatures, the mycetome (the microorganisms of which are assumed to be essential for normal metabolism) shifted from its normal position in the egg and underwent colour changes in adults and eggs.

However, there is much evidence to show that the main cause of mortality in eggs and early nymphal stages is desiccation. The presence of collapsed and shrivelled young stages following severe weather conditions; the need for favourable internal water relationships for the normal development of eggs (Blowers & Moran, 1967); and the strong correlation between survival and saturation deficit, are all factors supporting this theory. It is also known that when radiant heat raises the body temperature above certain levels (between 30° - 40°C for most insect species), the waxy cuticle of the egg chorion and the epicuticle itself is rapidly broken down allowing excessive drying out (Wigglesworth, 1965). Furthermore, because heat uptake is proportional to the surface area of the body, and heat loss to the volume of water which can be evaporated, eggs and young instars being small exposed organisms on the tips of flush points with a proportionately large surface area, are extremely vulnerable to desiccation. The larger, more advanced stages on the shaded underside of leaves are less exposed in their protective leaf galls.

8. EFFECT OF WEATHER EXTREMES ON DISTRIBUTION AND OUTBREAKS OF T. ERYTREAE

From extensive surveys conducted in the main citrus growing areas of South Africa, Schwarz (1967) found a convincing correlation between the incidence of greening and the activity of *T. erytreae*. Greening was particularly severe in the cool, moist upland citrus areas of the Transvaal where the vector is commonly abundant. Very little greening and no natural spread of the disease was found in the Transvaal Lowveld and the Eastern and Western Cape where populations of *T. erytreae* are low and isolated. A similar relationship exists in Swaziland (Catling, 1969a).

Previous serious outbreaks of the disease took place during the periods 1932-36 and 1939-46 but were mainly confined to the White River and Plaston areas (Oberholzer *et al.*, 1965). In 1958, after greening had existed at low levels for many years a general outbreak commenced in most of the higher-lying citrus regions of the Transvaal and Swaziland.

TABLE 16

LOCATIONS OF METEOROLOGICAL STATIONS AND QUALITATIVE ESTIMATES OF GREENING AND *T. ERYTREAE*

Station	Region	Altitude	Position	Greening	Psylla
Malelane	Eastern Transvaal	1180 ft.	25°30'S, 31°30'E	None	Very low
Nelspruit	Eastern Transvaal	2165 "	25°27'S, 30°58'E	Low	Low
White River	Eastern Transvaal	2950 "	25°18'S, 31°03'E	High	High
Big Bend	Swaziland	500 "	26°52'S, 31°56'E	None	Very low
Malkerns	Swaziland	2400 "	26°34'S, 31°10'E	High	High
Rustenburg	Western Transvaal	3800 "	25°43'S, 27°18'E	Low	Very low*
Addo	Eastern Cape Province	280 "	33°34'S, 25°42'E	None	Very low
Elsenburg	Western Cape Province	590 "	33°51'S, 18°50'E	None	Very low

*Since 1962/63

TABLE 17

ACCUMULATED S.D.I. VALUES IN EXCESS OF THE 34.6 MBAR (70 PER CENT MORTALITY) BASELINE

Year	Rustenburg	Big Bend	Malelane	Addo	Nelspruit	Elsenburg	Malkerns	White River
1956/57	95.7	-	-	-	-	-	-	-
1957/58	24.3	-	-	-	-	-	-	-
1958/59	94.0	-	-	-	108.3	-	-	-
1959/60	128.9	-	-	-	126.2	-	-	-
1960/61	76.2	-	-	48.3	78.6	-	-	-
1961/62	121.2	-	-	127.7	99.7	-	-	-
1962/63	138.6	154.2	-	155.4	90.6	61.0	31.1	-
1963/64	172.1	118.6	-	130.1	100.3	33.6	22.1	-
1964/65	99.6	204.3	-	85.7	82.5	65.3	11.1	-
1965/66	253.4	126.7	23.8	149.3	155.8	29.6	39.7	53.8
1966/67	142.2	153.5	124.8	77.2	94.9	41.5	10.8	18.9
1967/68	77.3	144.5	49.7	44.9	59.3	84.1	32.3	3.1
Total*	472.9	424.7	411.3	271.4	310.0	155.2	82.8	75.8

*For last 3 years only

Discussions with growers and agriculturists revealed that a serious outbreak of <u>T. erytreae</u> began in the 1959/60 season and continued for several years in Rustenburg, White River, Tzaneen and New Agatha (Transvaal), and in Malkerns (Swaziland). Catling (1967, 1969c) suggested that differences in climate may account for the simultaneous outbreaks of the vector in such widely scattered regions.

Green & Catling (in press) developed a weather index for predicting vector outbreaks. They then applied this index to the known status of greening and <u>T. erytreae</u> in the main citrus areas of southern Africa, and related it to the history of both disease and vector in two districts of the Transvaal.

(i) <u>Derivation of a weather index.</u> The young stages of <u>T. erytreae</u>, which at the beginning of each brood comprise the bulk of the population, are far more susceptible to weather extremes than the more advanced stages and thus the egg and first instar nymphs represent a particularly vulnerable part of the population.

Regressions calculated in the previous chapter reliably predicted the mortality of eggs and first instar nymphs from daily maximum temperature and corresponding vapour pressure values on the one hand, and maximum saturation deficit values on the other. The parabolic regression of mortality against maximum saturation deficit enabled Green & Catling (in press) to define a saturation deficit index (S.D.I.). This index was used to estimate mortality from standard weather records inclusive of daily maximum temperatures and values at 1400 hours of either temperature and RH or dewpoint. The set of values at 1400 hours provided a good approximation of the vapour pressure at the time of the maximum temperature, making possible the calculation of the corresponding value of saturation deficit. Total dosages of extreme conditions were derived for successive ten-day periods, each period overlapping its predecessor by five days. This provided 73 estimates per year of egg to first instar mortality, and thus a near-continuous graph of mortality due to the weather factor.

(ii) <u>Regional mortality assessments.</u> Table 16 lists eight weather stations in southern Africa for which S.D.I. values were computed, together with a broad classification of greening incidence and vector abundance. Table 17 shows striking differences in S.D.I. values accumulated for these eight stations for periods of 3-12 years, with totals for the three years 1965/66 to 1967/68. Extremely low values (75.8 and 82.8) characterize the vector-abundant White River and Malkerns areas at relatively high altitudes, whereas values for Big Bend and Malelane at lower altitudes were considerably greater (424.7 and 411.3). Rustenburg is subject to moderately high temperatures combined with low vapour pressures giving high accumulated S.D.I. values. The stations at Addo, Nelspruit and Elsenburg are intermediate. Large fluctuations in both the S.D.I. values at 5-day intervals and the accumulated annual S.D.I. values limit the usefulness of further comparisons on a 3-year basis.

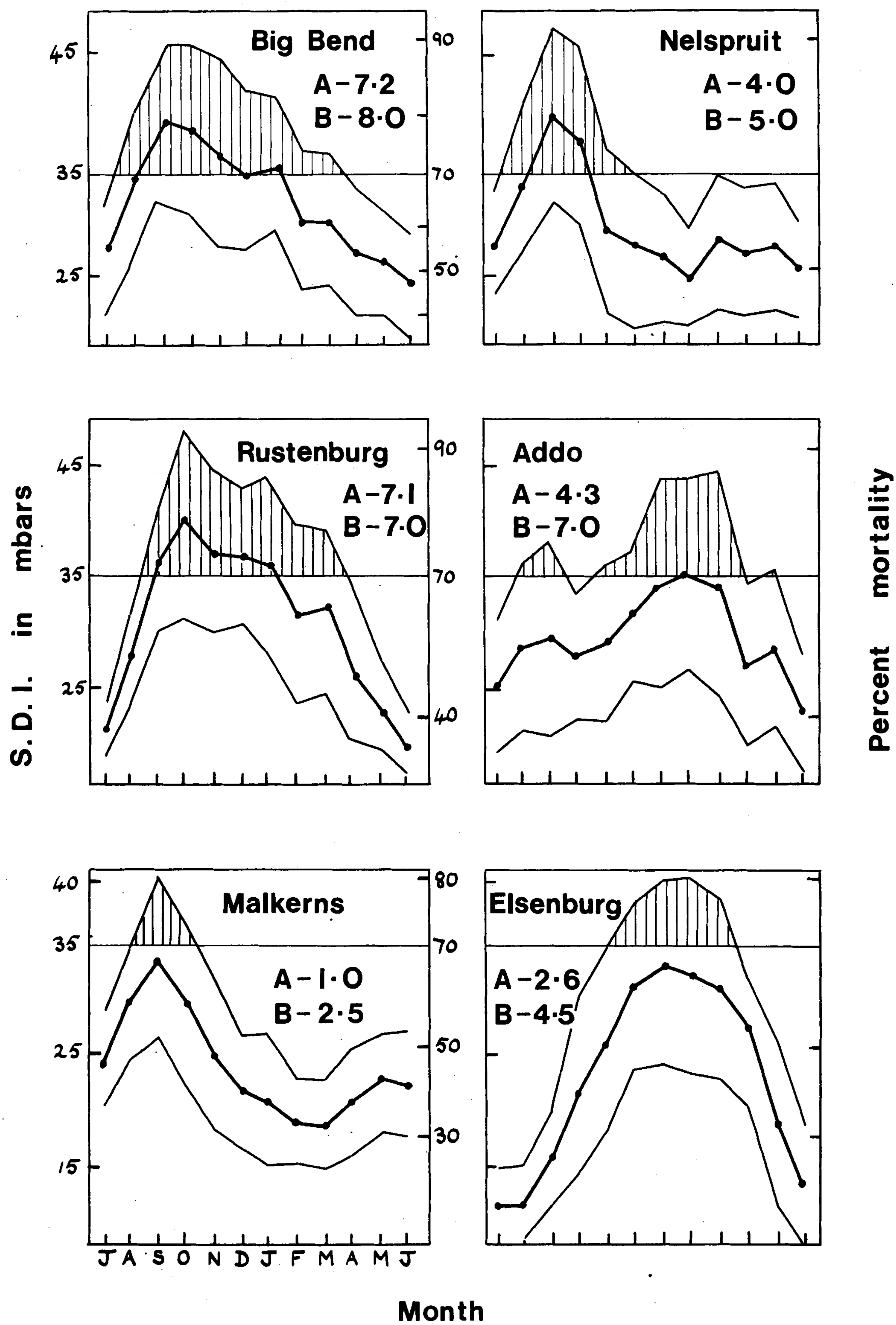

Big Bend
A-7·2
B-8·O
Nelspruit
A-4·O
B-5·O
Rustenburg
A-7·1
B-7·O
Addo
A-4·3
B-7·O
Malkerns
A-1·O
B-2·5
Elsenburg
A-2·6
B-4·5
S.D.I. in mbars
Percent mortality
45
35
25
40
15
90
70
50
40
80
30
J A S O N D J F M A M J
Month

Fig. 28 shows the seasonal trend of lethal weather in different citrus areas. Only those stations which had at least six years of available data (1962/63 to 1967/68) were considered. Each point, representing a monthly mean S.D.I., was derived from at least 36 values, comprising six per month for each month over the six-year period. Curves flanking the mean S.D.I. curve on either side differ point for point by one standard error from the central curve and form a band of probable values. Considering the cross-hatched portion of this band, i.e. the portion projecting into the lethal range, it is possible to discuss in greater detail the weather-induced vector mortality in the different citrus areas.

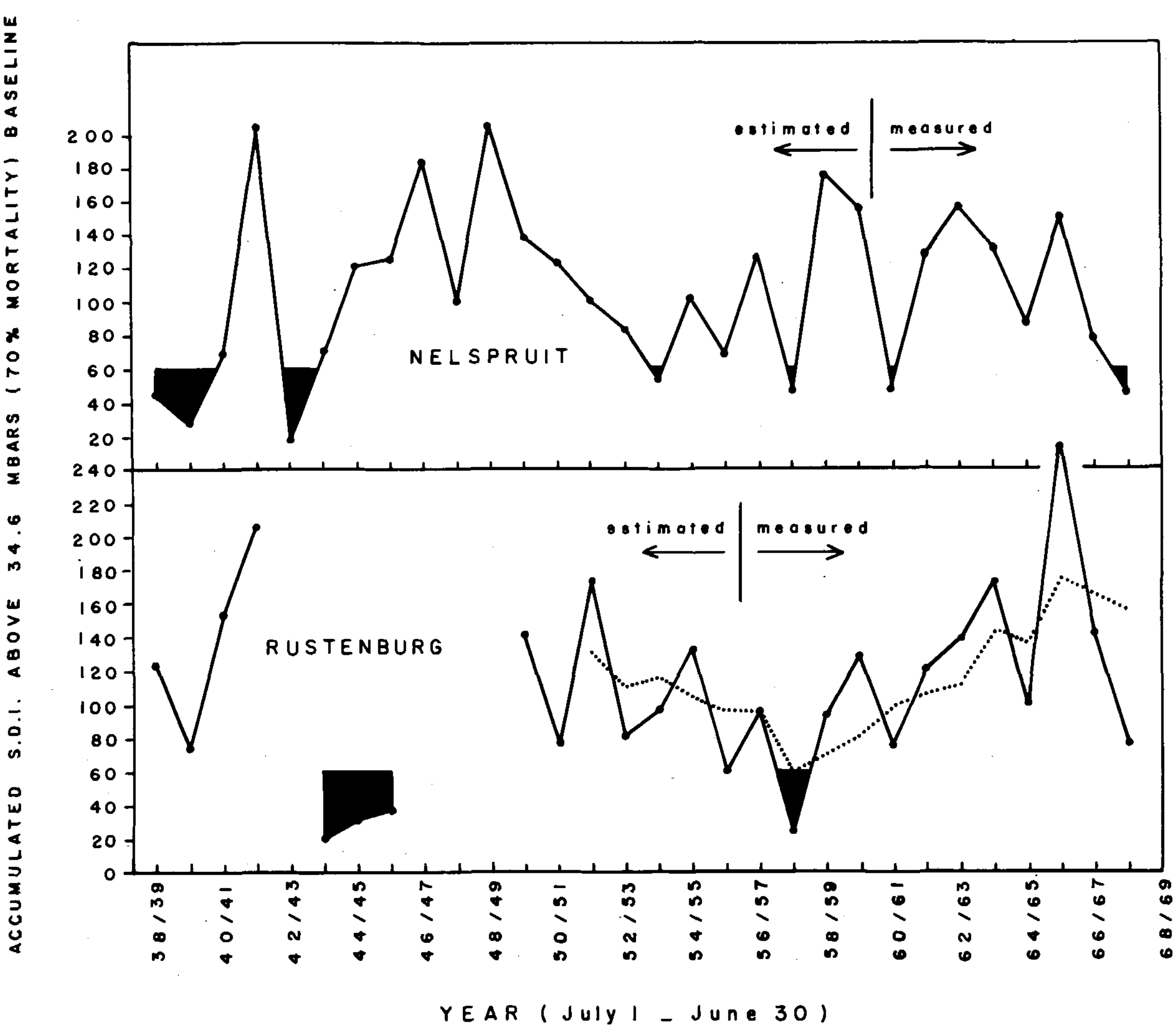
The length of time that a portion of the probability band exceeds the 70 per cent mortality baseline is indicated for each station by the value B in Fig. 28. Thus the Addo (Eastern Cape) climate may be bracketed with those of Big Bend and Rustenburg as the most lethal for T. erytreae. The Elsenburg climate (Western Cape) compares with that of Nelspruit, while at Malkerns lethal conditions are confined to 2.5 months in spring. A second factor which may be considered, value A, is the relative area of the probability band above the same baseline, taking the area for Malkerns as unity. In terms of this factor the weather stations are virtually in the same order of increasing potential for vector mortality as before. Nevertheless, those taken to represent areas in the Cape Province, i.e. Addo and Elsenburg, appear to be rated slightly more favourably for vector survival. However, it must be added that Elsenburg, while typical for the winter rainfall region, experiences far lower levels of temperature and general aridity than most citrus areas in this region. A major difference between the S.D.I. curves for the northern (Transvaal and Swaziland) and southern (Cape) regions, namely the position of the peak S.D.I. values, will be discussed later.

(iii) An explanation for outbreaks of T. erytreae and greening: 1938-1968

At both Nelspruit and Rustenburg, serious outbreaks of greening and, more recently, relatively high populations of T. erytreae have been recorded. The 10-12 years of accumulated S.D.I. values for these stations shown in Table 17 indicate considerable yearly variation and suggest marked differences in vector potentials from year to year. Thus in order to account for these past outbreaks, yearly estimates of the S.D.I. were made from weather records going back to the nineteen-fifties.

EXPLANATION OF FIGURE

Fig. 28 Seasonal trends in the probable saturation deficit index (S.D.I.) bands at six locations in different citrus areas. The control curve depicts the trend in the monthly mean of six S.D.I. values per month over six years. The upper and lower limits of the band are defined by the mean, plus and minus the standard error of an observation respectively. A - relative area with Malkerns as unity, and B - duration in months of region of band above the 34.6 mbar threshold



ACCUMULATED S.D.I. ABOVE 34.6 MBARS (70% MORTALITY) BASELINE
estimated
measured
NELSPRUIT
RUSTENBURG
YEAR (July 1 _ June 30)
38/39
40/41
42/43
44/45
46/47
48/49
50/51
52/53
54/55
56/57
58/59
60/61
62/63
64/65
66/67
68/69

Values of a maximum temperature index were derived from daily maximum temperatures, taking into account 12 mean vapour pressure values, one for each month, which were based on observations over the periods 1960/61 - 1967/68 at Nelspruit and 1956/57 - 1967/68 at Rustenburg. A linear relationship was found to exist between bimonthly and annual values of the maximum temperature index and accumulated S.D.I. totals above the 34.6 mbar baseline for corresponding periods. This enabled accumulated S.D.I. values to be estimated for the complete 1938-1968 period for both areas though, unfortunately, there were serious gaps in the records for Rustenburg for the years 1942/43 and 1946/47 to 1948/49.

Fig. 29 shows significant trends in the accumulated S.D.I. when viewed in relation to greening and T. erytreae outbreaks. The shaded areas indicate periods when the accumulated S.D.I. values dropped into a range characteristic of the more vector-abundant areas such as White River and Malkerns. The graph for Nelspruit suggests that vector outbreaks occurred during the years 1938/39 to 1942/43 (populations in the adjacent, higher-lying White River area were probably considerably higher). Thereafter, ten unfavourable years in succession probably reduced populations to very low levels. This is consistent with the relegation of greening to a consistently low level for approximately twelve years after 1946. From 1953, sporadic seasonal occurrences of favourable weather appear to have contributed to a gradual buildup culminating in large populations in 1960/61 and the reappearance of greening in 1959.

In Rustenburg similar vector outbreaks are indicated in seasons 1943/44 to 1945/46, and in the late nineteen-fifties. A decided upward trend in the accumulated S.D.I. since 1960 apparently accounts for the subsequent suppression of the vector observed by two workers in this area (Bedford, E.G.C. and Milne, D.L., 1969, personal communication). Nevertheless, greening has persisted due to what appears to be a particularly systemic strain of the disease (Schwarz, 1969).

(iv) Discussion

Catling (1969c) established that population densities of T. erytreae in the Letaba district and in Swaziland increase with increasing altitude. This trend is typical of those observed in most citrus areas near the eastern escarpment of southern Africa, i.e., in the N.E. Transvaal, E. Transvaal, Swaziland and Natal. The author observed a similar effect of altitude in Rhodesia, while Bové, J. & Cassin, J. (unpublished report, 1968) reported no signs of T. erytreae below 1,000 to 1,300 feet in Réunion and Madagascar but both symptoms of greening

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EXPLANATION OF FIGURE

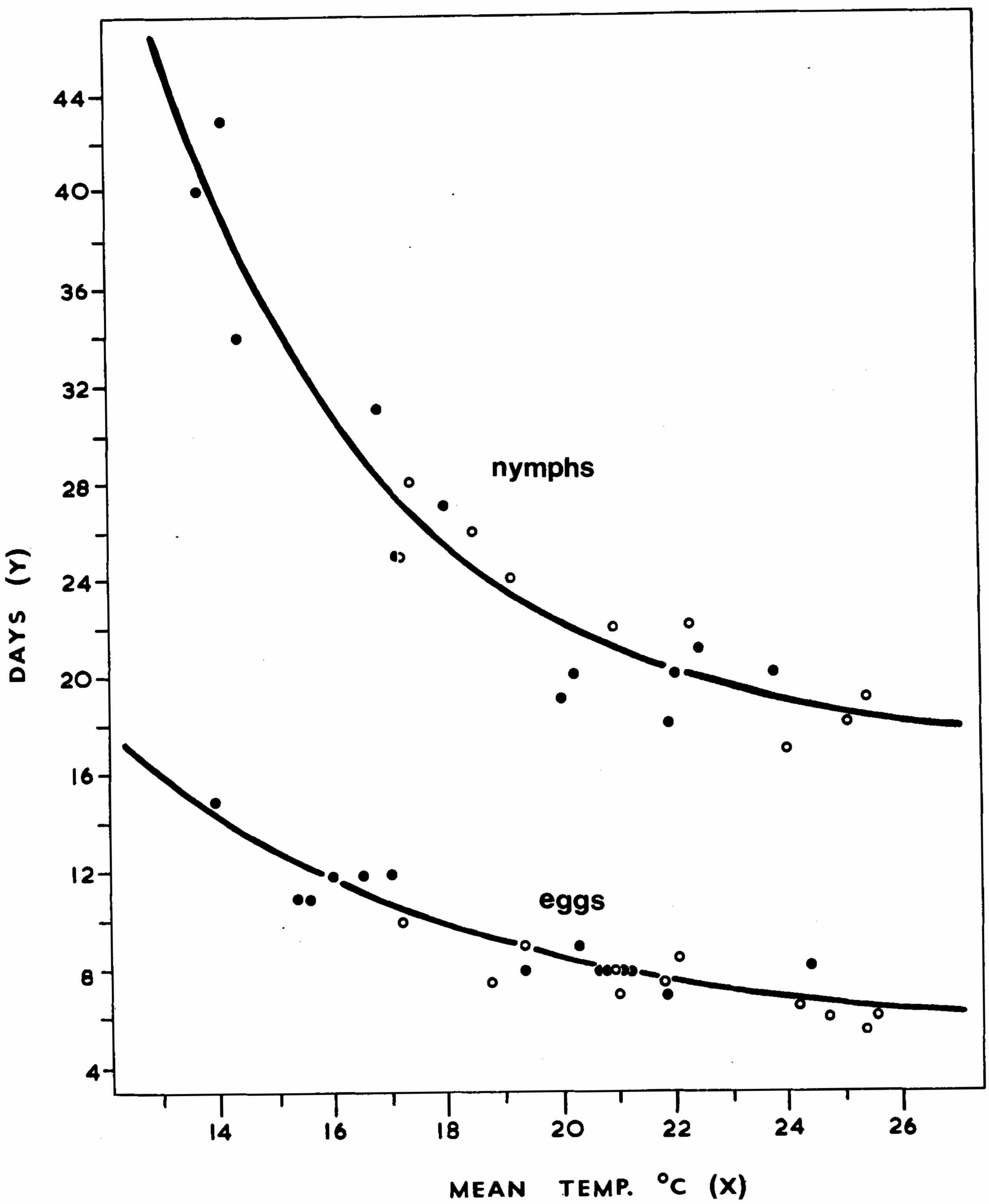
Fig. 29 Long term trends in annual accumulated lethal-range saturation deficit index (S.D.I.) values for Nelspruit and Rustenburg. The shaded areas indicate values typical of those where T. erytreae is more abundant. The broken line represents a running mean S.D.I. value calculated from the year in question plus the two preceeding years and signs of the vector above 3,300 feet. Consideration of lethal S.D.I. values (those in excess of 34.6 mbars) for three locations in E. Transvaal and two in Swaziland, confirm the altitude-related trend. Durations of probable S.D.I. values in the lethal range varies from approximately 8 months at an altitude of 500 feet, to 2.5 months at 2,400 feet. The longer the duration of lethal conditions, the more improbable it becomes for the vulnerable egg to first instar stages, which at regular intervals form the bulk of the population, to escape heavy mortality.

In summer rainfall areas further away from the escarpment e.g., Central and Western Transvaal, altitude alone is no indicator of the normal levels of vector populations. Rustenburg, at the relatively high altitude of 3,800 feet, has in recent years had very low populations. This seemingly low potential was well accounted for by the finding that probable S.D.I. values may be in the lethal range for up to 7 months per year in this district. The negligible vector populations which characterize the Cape citrus areas cannot be fully explained by the magnitude of the accumulated S.D.I. values. It is necessary here to consider the timing of the peak S.D.I. values in relation to the seasonal abundance of the vector. In the summer rainfall areas peak S.D.I. values occur in spring and early summer when populations tend to be fairly well established on vigorously-flushing trees and the more resistant stages thus capable of producing a substantial population recovery following short periods of lethal conditions. In the Cape areas, however, the peaks fall in mid- to late summer when the trees are reported to be relatively devoid of flush and when the other limiting factors are probably more severe. There is thus a low potential for population growth, lethal weather at this time being especially crippling to vector populations. The long-term effect of severe midsummer weather in reducing populations of <u>T. erytreae</u> to very low levels was observed in Malkerns following the 1968-69 season.

The S.D.I. was also found to provide an explanation for past outbreaks of <u>T. erytreae</u> and greening in the Nelspruit and Rustenburg districts. The S.D.I. value in certain years, roughly one in eight, appear sufficiently low at both Nelspruit and Rustenburg for severe outbreaks of the vector even though both are marginal areas for the insect. There is therefore a real danger of renewed transmission activity of the disease unless careful precautions are taken.

9. <u>DURATION OF IMMATURE STAGES</u>

Under field conditions in the Letaba district Catling (1967) found that the duration of the immature stages of <u>T. erytreae</u> was closely related to mean temperature. Highly significant regressions were calculated for incubation period from 11 <u>in situ</u> counts within a temperature range of 17.2 - 25.5°C, and for nymphal development from nine counts within a temperature range of 17.4 - 25.3°C. Extremes of humidity were not found to affect the duration of nymphal development.



DAYS (Y)
44
40
36
32
28
24
20
16
12
8
4
nymphs
eggs
14
16
18
20
22
24
26
MEAN TEMP. °C (X)

Additional data was collected during 1967 and 1968 by making a similar series of 14 in situ counts on citrus seedlings exposed in the field at Malkerns Research Station (Table 18). As in the Letaba series, the limits of duration were usually fixed on the day on which the maximum number of individuals hatched or emerged as adults. In order to reduce the influence of host plant on development, counts on plants which grew poorly were rejected. The Malkerns studies extended the temperature range at the lower extreme by 3-4°C and since the new results corresponded closely with those obtained in the Letaba district, the data for both regions was pooled and new regressions calculated.

Table 18 Incubation period and duration of nymphal development of *T. erytreae* against prevailing mean temperature at Malkerns Research Station

Period	INCUBATION			NYMPHAL DEVELOPMENT		
	No. instar I nymphs	Mean temp °C	Duration in days	No. instar V nymphs	Mean temp °C	Duration in days
1967						
Mar 29 - Apr 5 - Apr 24	614	20.5	8	559	20.0	19
May 3 - May 11 - Jun 10	205	20.3	9	47	16.8	31
May 20 - May 30	307	16.5	12	-	-	-
Jun 20 - Jul 1 - Aug 3	337	17.0	12	111	14.4	34
Aug 10 - Aug 22 - Sept 18	882	16.0	12	156	18.0	27
Sept 25 - Oct 2	278	21.1	8	-	-	-
Oct 11 - Oct 18 - Nov 6	171	20.7	8	29	20.2	20
Nov 17 - Nov 24 - Dec 13	598	19.3	8	101	22.0	20
Dec 15 - Dec 22 - Jan 11	270	21.8	7	182	23.8	20
1968						
Jan 17 - Jan 24 - Feb 13	40	24.4	8	40	22.4	21
Feb 15 - Feb 22 - Mar 10	233	21.2	8	233	21.9	18
May 22 - Jun 2 - Jul 11	13	15.4	11	13	13.7	40
May 22 - Jun 2 - Jul 17	72	15.4	11	72	14.1	43
Jun 21 - Jul 6 - Jul 30	153	13.9	15	153	17.1	25

Several types of curves were fitted to the durations of both incubation period and nymphal development. The curve of best fit, an asymptotic regression of duration in days on mean temperature, accounted for a very high percentage of variance, 86.59% and 91.25% respectively, and took in the new points at the lower temperature extreme where there is clearly a steep rise in duration in the case of nymphal development (Fig. 30).

EXPLANATION OF FIGURE

Fig. 30 Scatter diagram and regressions for incubation period and duration of nymphal development of *T. erytreae* against mean temperature from field studies in the Letaba district (hollow points) and at Malkerns Research Station (solid points).
Incubation : $Y = 4.9763 + 3.3443 \times 0.8452^{x-20}$,
variance accounted for = 86.59%.
Nymphal development : $Y = 16.7974 + 5.2726 \times 0.7843^{x-20}$,
variance accounted for = 91.25%. x-20 was used to reduce computor time

Because the curves were asymtotic it was not possible to extrapolate for developmental zeros and then calculate the thermal constants as described by Wigglesworth (1965). The curve for nymphal development does indicate that the threshold temperature must lie between 10 and 12°C. However, mean temperatures are unlikely to approach the thresholds for the development of T. erytreae in all of the main citrus regions. No diapause has ever been observed in the immature stages.

In a single insectary study where 19 insects were studied individually from egg to adult stage with daily observations, the incubation period and duration of nymphal development was found to be in agreement with the regressions in Fig. 30. At a mean temperature of 18.1°C the mean durations were 9.1 and 28.3 days respectively. Durations of instar III were the shortest (4.3 days) and were the longest for instar V (9.2 days) which confirms the earlier work of Catling (1967).

10. INFLUENCE OF POPULATION DENSITY, LEAF SIZE AND LEAF PLACEMENT ON EGG HATCH AND NYMPHAL SURVIVAL

In two species of *Arytaina* studied by Watmough (1968a) crowding caused intraspecific strife which led to nymphal mortality. Clark (1964b) reported a similar increase in nymphal mortality at high population densities of *Cardiaspina albitextura* Taylor. Catling (1967) found that nymphs of *T. erytreae* .... "have higher survival rates when developing on the smaller terminal leaves, than on larger leaves lower down the same flush point".

The influence of population density, leaf size and leaf position on the survival of the immature stages of *T. erytreae* was investigated by analysing nine *in situ* counts made on citrus seedlings exposed under field conditions. In these counts mortality due to weather, natural enemies and host condition was relatively insignificant. The percentage egg hatch and percentage first to fifth instar survivals were calculated on 93 individual leaves comprising 5,782 insects. Scatter diagrams showed a fairly constant relationship between leaf length and leaf area in Navel and Valencia varieties so that leaf length was a fairly reliable indicator of leaf area. Leaf length was measured only once, at the start of each count when the insects were in the egg stage. All leaves were classed into (a) five catagories of length, i.e. .13, .25-.33, .50, .75 and 1.00 inches and (b) into six catagories of position on the shoot, i.e. a (terminal), b, c, d, e, f. The percentage egg hatch and percentage nymphal survival were then calculated for each leaf. In those comparisons where mean values then indicated meaningful differences, the angular transformation was applied and an analysis of variance made.

(i) Influence of population density. Six to seven classes of population density were considered within the leaf length catagories .25-.33, .50, and .75 inches. The population density varied from less than 10 eggs or nymphs per leaf to more than 100 individuals per leaf. There was no correlation between density and egg hatch or density and nymphal survival. Even with populations of more than one hundred eggs on leaves a quarter inch in length no apparent decrease in survival was observed.

Table 19 Mean percentage egg hatch and nymphal survival according to leaf length, from in situ counts on citrus seedlings

Leaf length inches	Number of leaves	Percent egg hatch	Percent nymphal survival
.13	5	60.8	61.2
.25-.33	38	69.2	61.5
.50	29-30	56.4	52.4
.75	14-15	40.9	32.0
1.00	5	20.8	5.0
		Sign. at P = 1% C.V. 44.5%	Sign. at P =.1% C.V. 45.8%

(ii) Influence of leaf length and position. Table 19 shows a progessive decline in both egg hatch and nymphal survival with an increase in leaf length. On leaves greater than .25 inches in length, egg hatch decreased progressively down the shoot with the highest survivals on the terminal leaves and the lowest survivals on the basal leaves - Table 20. A similar trend in survival and leaf position was indicated in nymphal survivals but this proved to be non-significant.

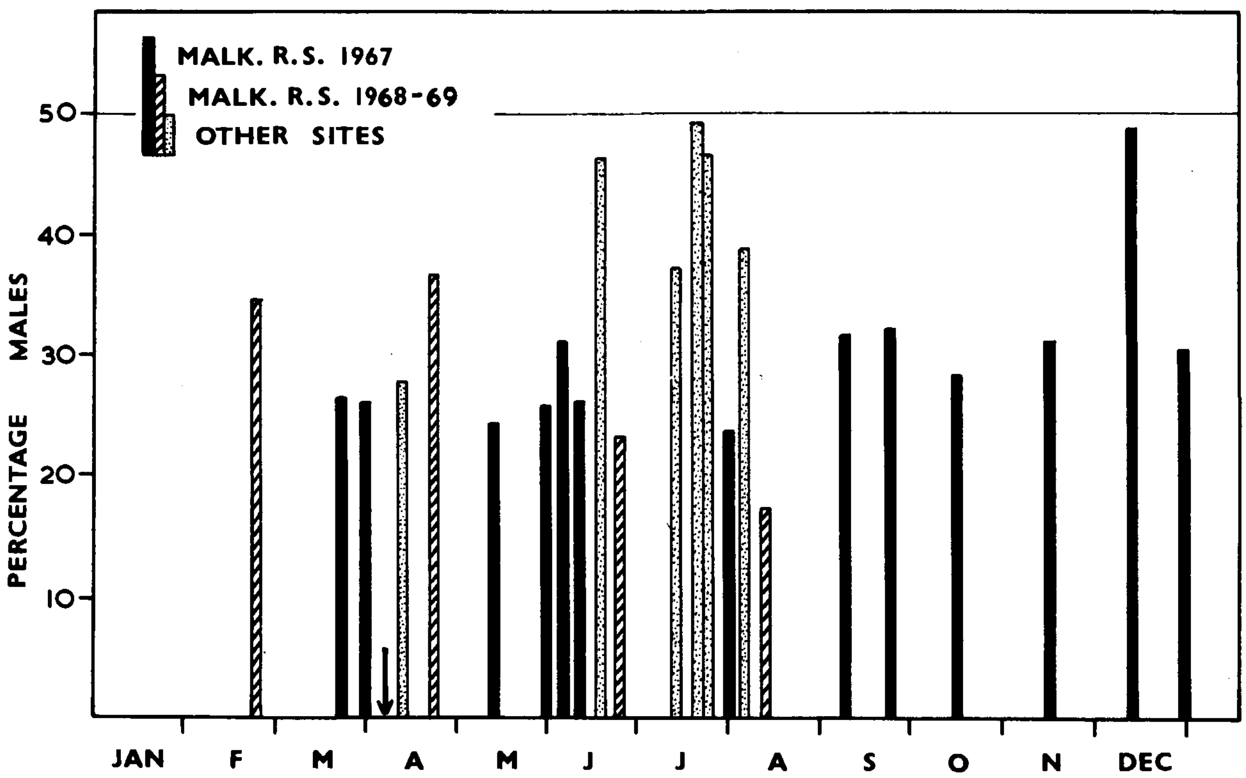
Table 20 Mean percentage egg hatch according to leaf position, from in situ counts on citrus seedlings

Leaf length inches	Number of leaves	Percent survival						
		terminal a	b	c	d	e	basal f	
.25 - .33	38	81.3	70.1	60.0	23.0	-	-	Sign. at P = 1% C.V. 30.4%
.50	30	38.3	78.6	55.4	55.3	33.7	12.0	Sign. at P = 5% C.V. 41.2%

(iii) Discussion

Since for a number of reasons this data was not considered to be of sufficient accuracy for the multiple regression method to be applied to egg hatch and nymphal survival, the results were grouped into a number of catagories and the three factors analysed separately.

There was no indication of a decrease in either egg hatch or nymphal survival due to differences in population density. However, small flush points heavily populated with eggs have been observed to shrivel up and fall from citrus trees. Overcrowding of flush points has been observed in the field on some occasions and was reported at Malkerns Research Station in January, 1968. At such times intraspecific strife and nymphal competition undoubtedly occurs. However, it ap-



MALK. R.S. 1967
MALK. R.S. 1968-69
OTHER SITES
PERCENTAGE MALES
50
40
30
20
10
JAN
F
M
A
M
J
J
A
S
O
N
DEC

pears that in general, citrus flushes are not more crowded than the seedlings used for this investigation so that density-related mortality does not appear to be a regular feature in the dynamics of T. erytreae.

The marked decrease in egg hatch with increase in leaf size is interesting from a biological point of view. The eggs of T. erytreae are supplied with a stalk which is inserted into the leaf tissue and is thought to have a water absorption function (Blowers & Moran, 1967). It is tempting to suggest that physiological changes which take place in maturing leaves may detrimentally affect this mechanism of water absorption in the egg.

There was also a trend for a decrease in the survival of eggs and nymphs the further the leaf is situated from the shoot tip. Though within a flush point there is obviously a distinct relationship between leaf position and leaf length, it did appear that leaf position by itself contributed to this mortality trend.

11. SEX RATIO

Catling (1967) found that females predominated in early summer populations of T. erytreae in the Tzaneen-Duiwelskloof area of the northern Transvaal. Of 577 adults reared from fifth instar nymphs in October, 1966, 38.5% were males, and in the following month 40.6% of 456 adults were males.

It appears that males and females of T. erytreae develop at about the same rate and, from insectary studies at Malkerns, both sexes have a similar longevity. Thus the sex ratio does not change with the age of the brood as is the case in Cardiaspina albitextura Taylor (Clark, 1962) and Psylla pyricola Foerster (Burts & Fischer, 1967).

(i) Sex ratio in field populations at Malkerns. Between March, 1967, and February, 1968, adults were collected haphazardly on citrus at several sites in the Malkerns district. Insects were either collected with a simple aspirator (pooter), or by means of the insect sampling machine with the outer mesh removed as it was found that this sieve trapped many gravid females. In addition, a few counts were made by rearing adults from fifth instar nymphs.

Fig. 31 summarizes the results of 24 separate determinations of sex ratio. It is immediately evident that there was considerable variation in sex ratio. The percentage males varied from 0.0% to 49.2%, females being predominant at

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EXPLANATION OF FIGURE

Fig. 31 Sex ratio, as percentage males, in field populations of T. erytreae in the Malkerns district from 1967 to 1969. Arrow indicates no males present all times. No relationship could be found between sex ratio and flush density, photo-period, season of the year, or mean temperature, though the three lowest values for percentage males occurred in the cool months of April, June and August.

However, there is some evidence that a relationship exists between sex ratio and population density. The 24 determinations shown in Fig. 31 were grouped into two classes according to the population density which prevailed at the time the adults were collected. Of 2202 adults collected at low population densities 24.56% were males (range 0.0 - 36.8%), whereas at medium to high population densities 37.25% of 4722 adults were males (range 28.0 - 49.2%). An analysis of variance using the angular transformation showed these means to be significantly different at the 1% probability level (transformed S.E. ± 2.21). On two occasions at Malkerns Research Station during April, 1969, at very low population densities, small colonies of T. erytreae were without males.

Sex ratios in three in situ counts on citrus seedlings varied from 13.7 - 50.0% males (355 adults examined).

(ii) Sex ratio in laboratory cultures. T. erytreae was reared in a controlled temperature room for a two year period. In June of 1968 after 6-8 weeks of temperatures between 18-22°C the adult population was found to consist of a very low proportion of males. In April of 1969, at fairly low populations, following several months with a photo-period of 12 hours light and 12 hours dark and temperatures of 21-24°C, no males could be found in the adult population. Large numbers of infertile eggs were laid and the culture soon died.

(iii) Discussion

The sex ratios of a number of psyllids have been recorded. In Diaphorina citri Kuw. in the Philippines a ratio of 44.8% males was encountered by Catling (1968a). In C. albitextura (Clark, 1962) and P. pyricola (Burts & Fischer, 1967) the ratio was usually close to 1:1. Swirski (1954) found that summer adults of P. pyricola consisted of 52.3% males, and winter adults 43.3% males.

For the purpose of sex ratio studies Moran (1967) reared T. erytreae in the open and in an environment room both on citrus and on two rutaceous plants. His experiments showed (i) the sex ratio to vary from 0% males to males being predominant, but never 100% males (ii) a seasonal fluctuation, being about 50% males when reared outside in February and dropping to as low as 6% males when reared in April/May (iii) that the proportion of females increased and often reached 100% when T. erytreae was reared under cool conditions of 12 hours light in the environment room. Moran suggested that the lower temperatures of winter cause a change in the sex ratio from the approximate 1:1

ratio of summer to the female predominance in winter. (iv) there was no clear evidence that photoperiod, plant host species or time of fertilization of the female are involved in controlling the fluctuations in sex ratio.

The Malkerns study showed the sex ratio of T. erytreae in field populations to be variable but that females were always predominant. The ratio was not apparently related to photoperiod, season, flush density, or even to temperature as suggested by Moran (1967). The only factor which was found to correlate with sex ratio was population density. As with many Lepidoptera (Andersen, 1961), the percentage of T. erytreae males tended to increase with population density. Clearly the whole question of fluctuation in the sex ratio of psyllids will need careful study before the controlling mechanism is properly understood.

The significance of a low ratio of males to females in the population fluctuations of T. erytreae is obvious. At times of low population density when colonies are widely scattered, the chances are that many females will be without a mate and thus lay batches of infertile eggs. Colonies of infertile eggs were observed at Letaba Estates in 1966 (Catling, 1967).

12. MATING BEHAVIOUR, OVIPOSITION AND LONGEVITY

(i) Mating behaviour

Catling (1967) briefly described the mating behaviour of T. erytreae. Further observations were made during a series of egg-laying tests to be described later and in small-scale mating trials in the insectary at Malkerns. In the mating trials males were placed with single females for an eight hour period of observation during each day and removed at the end of the observation period.

Mating took place as soon as the newly-emerged adult had hardened up and become mature, i.e. in about three days in summer and seven days in winter. All females mated several times during their lives and copulation took place at any time of the day. Table 21 shows that under insectary conditions many females mated three or four times a day; female 1 copulated 12 times in six days with a mean copulation time of four minutes, 18 seconds, while female 2 copulated 13 times in five days with a mean copulation time of four minutes, 12 seconds.

Mating is initiated by the male who sometimes displays an aggressive behaviour. He may butt or beat the female with his wings until her abdomen is lowered sufficiently from a feeding position for the union of the genitalia. Once in the copulatory position the female may move about or take up a feeding stance. Eggs are deposited immediately after the mating act has ceased.

According to Blowers & Moran (1967), the relative size of the spermatheca of the female suggests that T. erytreae requires more than a single mating to

Table 21 Mating behaviour of *T. erytreae* in the insectary at Malkerns

	Female 1		Female 2	
	No. of copulations	Duration of copulations in secs.	No. of copulations	Duration of copulations in secs.
Jan 23	3	195, 355, 295	1	180
24	1	190	2	495, 405
25	2	453, 320	2	200, 190
26	2	260, 210	4	165, 225, 210, 115
29	1	200	4	285, 290, 280, 240
30	3	325, 165, 125	-	

fertilize the full complement of eggs. The above results confirmed that females mate repeatedly. Moreover, it was found in the egg-laying tests that once males are removed, the eggs become infertile within 11-16 days.

(ii) Oviposition

Several aspects of egg-laying behaviour were studied by Van der Merwe (1941) on cut citrus twigs in the laboratory, on seedlings in an environment room at fluctuating temperatures by Moran & Blowers (1967), and on seedlings in the laboratory at constant temperature by Catling (1967). In the present study egg-laying tests and general observations on oviposition and longevity were carried out in the insectary at Malkerns during summer and winter periods.

Shoots with fifth instar nymphs were collected in the field and placed in water in the insectary. On emergence, the teneral females were carefully transferred to young, vigorously-growing grapefruit or sweet orange seedlings. A single female was confined on each plant, males being introduced according to the nature of the specific test. Despite the careful handling of the delicate, saltatorial adults with a fine sable hair brush, many were lost or damaged, some being trapped in the chimneys used to cover the plants. Studies on 136 insects over a two day period revealed that few adults emerged during the hours of complete darkness. Most adults emerge during early morning beginning with the first light of dawn. On the first day 92.5%, and on the second day 74.7% of the adults emerged between 0500 and 1100 hours.

Six series of egg-laying tests were carried out. In series 1-5 it was usual to keep a daily record of the egg production of each female, counts being done with a hand lens between 0800 and 0900 hours. Eggs were counted at weekly intervals in series 6. At weekly intervals, or sooner if all young leaves became densely packed with eggs, the insects were carefully transferred to a new seedling. An accurate check count was then made on the egg-infested seedling and where necessary an adjustment made to the running total of eggs per female.

In series 1, "single early mating", fully mature females were supplied with 2-3 males for three days after which the males were removed. Series 2, "virgin females", tested the egg-laying potential of unfertilized females. In series 3-5, "continuous mating", the females were supplied with 1-2 males throughout their life and this test was repeated in series 6 during the winter. Table 22 summarizes the results of the six series.

Table 22 Results of six egg-laying tests made in the insectary at Malkerns on citrus seedlings between December, 1967, and July, 1968. "Normal females" died a natural death and lived longer than 14 days. Mean daily egg production excluded pre-oviposition period

	Single early mating	Virgin females	Continuous mating	Continuous mating	Continuous mating	Continuous mating
	Series 1	2	3	4	5	6
Period of study ...	Dec 5-Jan 3	Dec 6-Jan 3	Dec 12-30	Dec 29-Jan 24	Jan 16-Mar 4	May 21-Jul 31
Mean temp °C (insectary).	23.7	23.7	23.3	25.3	23.4	15.7
Mean RH (screen)...	69.3	69.3	68.4	68.9	73.3	50.4
No. females studied....	7	7	8	7	7	7
No. "normal" females....	5	4	3	3	3	6
Mean longevity "normal" females in days	26.4 (23-28)	19.5 (15-28)	17.0 (17)	22.3 (15-26)	36.3 (27-45)	52.5 (23-71)
Mean egg production "normal" females....	828.2 (550-1140)	216.8 (101-437)	341.7 (165-517)	359.7 (31-721)	1304.7 (1049-1604)	1303.8 (266-2542)
Mean daily egg production all females....	34.5	10.9	29.8	20.6	37.1	29.8
Max. no. eggs per day........	143, 100, 97	76, 33, 29	73, 53, 50	64, 58, 15	159, 106, 89	-

<u>Egg production - continuous mating</u>. The tests showed the high egg-laying capacity of *T. erytreae*. In the three tests made during the summer months, the mean egg production was 341.7, 359.7 and 1304.7 per female with a mean daily egg production of 29.8, 20.6 and 37.1 respectively. A single female deposited more than one hundred eggs per day on two occasions in series 5. In the winter series, six females laid a mean of 1303.8 eggs, one laying 2542 eggs in 71 days. The daily rate for this series was 29.8 eggs.

In the laboratory, disregarding escaping females and premature deaths, Van der Merwe (1941) found females of *T. erytreae* to deposit a mean of 611 eggs, with a maximum of 815 eggs for one female. He contended that greater fertility occurs under field conditions. At fluctuating temperatures in an environment room seven females produced a mean of 858 eggs (542-1222) for Moran & Blowers (1967).

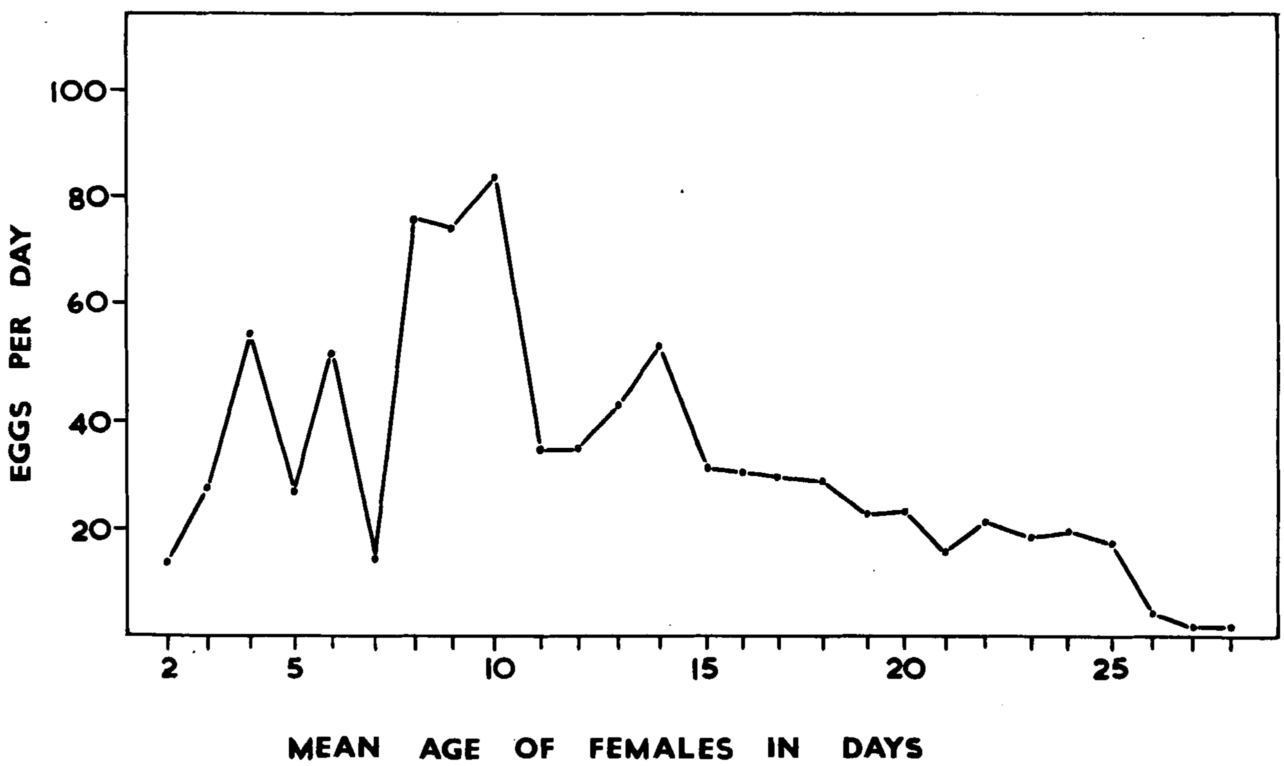
Under favourable conditions of prevailing weather and quality of host plant the fertility of eggs deposited by normally-mated females may exceed 95%. Egg-hatch is discussed more fully in chapter 10.

Egg production - single early mating. Five females in series 1 produced a mean of 828.2 eggs at a daily rate of 34.5 eggs thus showing no reduction in production when compared to females with continuous mating. In P. pyricola, Burts & Fischer (1967) found the oviposition rate to decrease in the absence of males. Within 11-16 days of the removal of males, the eggs of T. erytreae became infertile, thus resembling the pear psylla where, for the full complement of eggs to be produced, the female must be mated once every 10 days (Burts & Fischer, 1967).

Egg production - virgin females. Four unfertilized females laid a mean of 216.8 eggs at a daily rate of 10.9 eggs and thus produced fewer eggs and at a lower rate than fertilized females. The same has been reported for P. pyricola (Swirski, 1954; Burts & Fischer, 1967). All unfertilized eggs were infertile and many were observed to collapse and become compressed.

Influence of temperature and relative humidity. Oviposition proceeded at mean daily temperatures between 14.0 and 29.0°C and RH's between 27 and 94%. In temperate regions it appears that the rate of egg-laying is partly controlled by temperature, e.g. in Arytaina genistae Latreille (Watmough, 1968b). However, there was no evidence of such a relationship for T. erytreae in the mean temperatures prevailing for each series shown in Table 22. Therefore the individual egg records of each female were examined and scatter diagrams drawn for egg production against mean temperature for (a) the day on which the eggs were laid, and (b) the preceeding day. Though there was a slight tendency for more eggs to be deposited with a rise in temperature, the high day to day variation in egg rate rendered this trend of doubtful significance. According to Bursell (1964) egg production may not follow any simple relationship with mean temperature with the fluctuating temperatures experienced in the field. Under conditions of constant temperature Catling (1967) found that egg production was considerably reduced. At 23°C ± 1° eleven females produced a mean of only 188.1 eggs at 9.2 eggs per day.

High temperatures have been reported to depress the egglaying of a number of psyllids. List (1939) reported that at a constant temperature of 32°C oviposition was reduced and that one or two hour periods of 38°C virtually suspended the egg-laying of Paratrioza cockerelli (Sulc.). According to Westigard & Madsen (1963) high summer temperatures retard the oviposition of P. pyricola. In T. erytreae, working with laboratory cultures, Moran & Blowers (1967) found that oocyte development was inhibited at a fluctuating temperature regime of 54 Hour degrees Centigrade per Day above 20°C with a maxi-



EGGS PER DAY
100
80
60
40
20
2
5
10
15
20
25
MEAN AGE OF FEMALES IN DAYS

mum temperature of 32°C for several hours. In the insectary at Malkerns, however, no inhibition of egg-laying was observed during or following maximum daily temperatures of 32°C for 10 days. On each of the five consecutive days December 31 to January 4, 1968, readings in a Stevenson screen near to the insectary showed that the mean daily maximum temperature rose above 33.0°C with 3-7 hours above 32° and the Hr °C/Day above 20°C between 130-178. Yet the mean egg production of six females on January 3 and 4 was 32.0 and 31.0 eggs respectively. It is not unlikely that under the constant though fluctuating daily temperatures of Moran & Blowers' culture the insects became conditioned to the artificial conditions and thus reacted differently to natural populations of T. erytreae.

Differences in RH may also affect the reproductive rate in natural populations, egg-laying generally increasing with a rise in humidity (Bursell, 1964). In the winter series of tests during which low levels of RH prevailed, there was strong evidence of a decline in production below RH's of 50%. The mean production of six females for 8-11 day periods declined through 38.2, 31.1, 27.7 and 24.4 eggs per day with a respective decrease in mean daily RH of 62, 49, 45, and 44%. In series 1-5, however, no simple correlation was found between mean daily RH and the rate of oviposition.

Influence of age of female. Individual graphs were drawn for the daily egg production of 10 females living for 21 days or more. Though daily production was irregular there was a definite trend for a rise in production at the start of the ovipositionperiod, with a peak towards the middle of life span followed by a gradual decline. Egg-laying continued until a few days before death. This trend is illustrated in Fig. 32 which shows the mean daily egg production for 5 females having a similar lifespan. A similar rise and fall in oviposition rate with age has been reported in P. pyricola by Swirski (1954) and Burts & Fischer (1967).

Influence of host plant. Since eggs are laid at all times of the year and both mated and unmated females start to lay at about the same time, it is clear that the overriding stimulus for egg-laying is the presence of young flush for breeding sites.

The egg-laying tests were carried out on well-nourished, freely-flushing seedlings. In chapter 4 itwas shown that the nitrogen content, and thus possibly the nutritive value, of young growth of seedlings is higher than in the young flush of mature trees. Moreover, the females under test had an unlimited supply of young leaves so that very little searching was necessary to locate new breeding sites. There was also no competition for breeding sites from the citrus aphid. For these reasons it is possible that the oviposition rates obtained in the insectary tests were higher than would normally be realized under natural conditions, except possibly during the early summer period.

EXPLANATION OF FIGURE

Fig. 32 Mean daily egg production of five T. erytreae females on citrus seedlings in the insectary at Malkerns

It will be shown later that the influence of the nutritional value of young flush on the egg-laying potential of *T. erytreae* is an important factor still to be investigated.

(iii) Pre-oviposition period. Pre-oviposition periods recorded in the insectary tests (Table 23) and in four other smaller tests during 1967 varied from approximately 3-5 days in summer to 6-7 days in winter. These durations correspond fairly well with the results of Van der Merwe (1941), Catling (1967), and Moran & Blowers (1967). During summer occasional pre-oviposition periods of as short as two days were reported by Annecke & Cilliers (1963) and Catling (1967). Catling (1969a) found that the pre-oviposition period is indefinitely extended in the absence of young flush for breeding sites. Females confined on mature leaves died without laying eggs.

Both mated and unmated females were found to have similar pre-oviposition periods.

Table 23 Pre-oviposition period according to mean temperature from observations on citrus seedlings in the insectary at Malkerns in 1967 and 1968

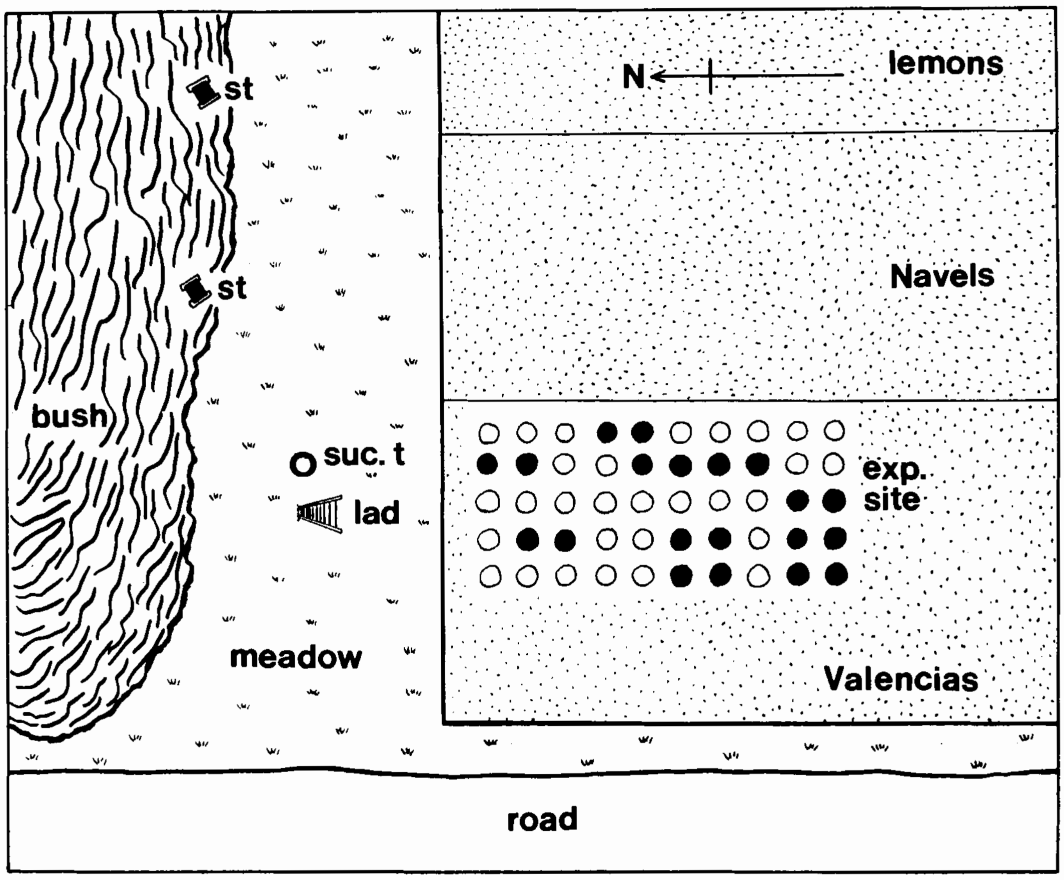
Period	No. of insects	Mean temp. °C	Pre-oviposition period in days	
Jul 3-10	c.10	13.9	minimum	7
Jul 21-27	c.10	14.3	"	7
Jun 30-Jul 5	6	15.5	"	6
May 21-Jun 1	7	15.9	mean	7.3
Aug 3-8	c.20	16.3	minimum	5
Apr 25-30	c.20	20.0	"	3-4
Dec 12-16	8	22.1	mean	3.4
Dec 5-9	7	22.8	"	3.1
Sept 28-Oct 1	12	23.0	minimum	3-4
Dec 6-10	7	24.5	Mean	3.6
Jan 16-23	7	25.6	"	4.0
Dec 29-Jan 2	7	25.7	"	5.3

(iv) Longevity

Under controlled, fluctuating conditions with a mean temperature of 15.5°C Moran & Blowers (1967) found adults to live for a mean of 34 days (28-48), which agrees well with longevities obtained by Van der Merwe (1941). In the present study on flushing seedlings, Table 22 shows that the mean longevity attained by batches of 3-5 females during the five series of tests made during summer at mean temperatures of 23.3 - 25.3°C varied from 17.0 - 36.3 days with a maximum of 45 days. In winter at a mean temperature of 15.7°C six females lived for a mean of 52.5 days (23-71). Winter longevities on mature leaves were 62.3 days for males (44 - 73), and 52.2 days for females (16 - 82) (Catling, 1969a).

Unmated females appear to have a shorter life than mated females.

FIG. 33



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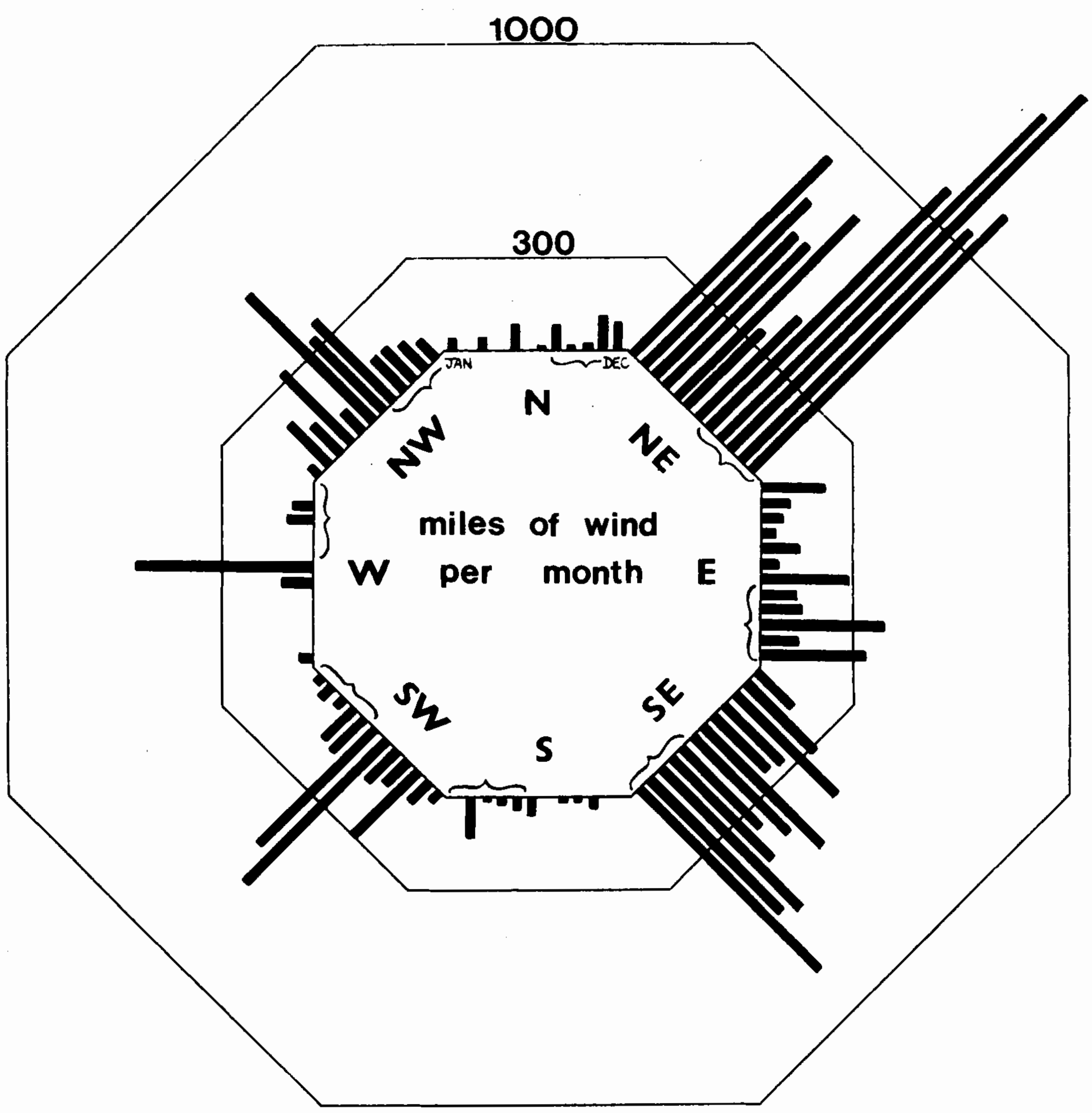
meadow
Valencias
road

FIG. 34



1000
300
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miles of wind
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per
month
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13. DISPERSAL

Catling (1967) concluded that *T. erytreae* disperses weakly under conditions of low population density, plentiful flush, and the absence of appreciable prevailing wind. In that study the progeny developing over a 2.5 month period from two isolated colonies of *T. erytreae* in a large block of citrus on Letaba Estates was plotted. It was found that in the succeeding generations 63% of the colonies appeared on the tree which supported the original population, and 88% appeared within a 24 foot radius of this tree.

In February, 1968, the author visited Mazoe Estates near Salisbury, Rhodesia, to study the incidence of *T. erytreae*. Usually the insect is extremely rare on this large citrus Estate (Searle, C.M. 1968, personal communication). In September and October of 1967, however, an outbreak in a block of mature lemon trees provided a good opportunity to observe dispersal into neighbouring trees. Counts of leaves pitted by *T. erytreae* on foliage 4-6 months of age in the vicinity of the infested lemon grove suggested that the insect had not dispersed further than 50 feet into an adjacent Valencia grove.

(i) Dispersal at Malkerns Research Station. The flight activity of *T. erytreae* was studied by operating several traps on the northern side of the study grove between November, 1968, and December, 1969 (Fig. 33). Three pairs of yellow sticky traps, described previously, were mounted in wooden frames between the rungs of a specially-constructed ladder at heights of 5, 26 and 50 feet above the ground. The ladder was placed in a meadow halfway between the study grove and a large thicket of natural bush which included many trees and shrubs representative of the flora of the Malkerns district. One trap of each pair faced towards the study grove in a southerly direction, while the other faced towards the bush in a northerly direction. Two other traps placed at five feet above the ground were operated in the bush. The traps were usually inspected at fortnightly intervals in summer and three week intervals in winter. In addition, between August and December, 1969, air samples were taken at regular intervals with a Johnson & Taylor enclosed cone suction trap (Vent-Axia propellar trap) mounted near the ladder carrying the sticky traps.

EXPLANATION OF FIGURES

Fig. 33 Plan of the Malkerns Research Station study grove and surrounding area. Data trees are indicated by solid rings. st - sticky traps; suc. t. - suction trap; lad - ladder with three pairs of sticky traps

Fig. 34 Wind rose for Malkerns Research Station for 1967 showing total miles of wind per month. The five months of highest *T. erytreae* populations, August to December, are bracketed. (Method of representation partly after Clark, 1962)

Large numbers of psyllids were trapped on the yellow sticky traps. In the 1968-69 season Diaphorina punctulata Pettey and Diaphorina zebrana (Capener MS) were common from November to January, Pauropsylla trichaeta Pettey was particularly abundant between February and June, 181 individuals being collected in a three week period in April, and Trioza sp. ex Euclea undulata Thunb. was taken regularly. The majority of psyllids were trapped on the central pair of traps, with fewer on the upper pair and negligible numbers on the lower traps. Larger numbers were always present on the traps facing away from the grove.

On the ladder traps only four specimens of T. erytreae were taken in the 1968/69 season. These were collected between December 24 and January 13 when population densities were at their highest and a peak of adults was indicated in the study grove. In the following season six adults were trapped (with fragments of possibly two more adults) between September 25 and December 12. Most individuals were collected on the lower trap facing the study grove.

T. erytreae was not found on sticky traps placed in the bush in the 1968/69 season but five specimens were collected between September 19-26 and four between October 10-16 in 1969. Both sexes were present on the sticky traps but females were predominant.

The suction trap yielded one adult T. erytreae in the first season and five in the second season.

(ii) Discussion

Dispersal of other psyllids. Southwood (1962) analysed the phenominon of migration in many groups of arthropods and proposed the acceptable theory that migration is an inherant behavioural response to an impermanent environment. Southwood found that nearly all strongly dispersing species have temporary habitats. Phytophagous groups which depend on host plants which are either annuals, deciduous with a completely dormant period, short-lived or widely-scattered perrenials, must be able to rediscover their main host or find alternate host plants.

The wide variation in dispersal powers found within the Psyllidae seem to fit this theory. For example, summer generations of P. pyricola existing on abundant pear foliage show very limited flight activity whereas the spring and autumn generations at the close and onset of the winter dormant period, disperse strongly (Swirski, 1954; Wilde, 1962; Westigard & Madsen, 1963). Adults of two Arytaina spp. regularly migrate from broom which is widely scattered in England and lives for only 10-15 years (Watmough, 1968a). P. cockerelli, which attacks potatoes and tomatoes, appears to migrate strongly from winter breeding areas (Jensen, 1954). It was shown earlier that D. punctulata and D. zebrana move into citrus when their normal host is dormant. On the other hand, weak dispersers usually have more permanent plant hosts such as evergreen trees of shrubs, for example, C. albitextura on eucalypts (Clark, 1962),

D. citri on citrus in India (Husain & Nath, 1927). T. erytreae clearly belongs in this catagory, the adults being able to survive on citrus at all times of the year. Few, if any, of the recognized alternate hosts of T. erytreae are completely deciduous (Van Hoepen, E. 1969, personal communication) and probably retain sufficient foliage to support overwintering insects.
Dispersal of T. erytreae. The dispersal powers of T. erytreae appear to be very limited. Though large numbers of several psyllids were collected on traps operated at Malkerns Research Station adjacent to the main study site, very few of these were T. erytreae. No active dispersal phase was ever observed in the field - even at fairly high population densities. There was no indication of adult movement from alternate host plants into citrus groves or vice versa, yet this may occur in some areas where alternate hosts are common and in close proximity to citrus.

According to Compton (1966) there are nine species of Rutaceae in Swaziland. Five of these are known to be alternate hosts of T. erytreae. The most common of these, and the only one ever found to be infested, was Clausena anisata (Willd.). Within several miles of the Malkerns study sites, and in experimental groves in the Letaba district (Catling, 1969a), alternate hosts were rare and were never found to be infested. The nearest infested alternate host plants were observed on C. anisata 4-5 miles due south of Malkerns Research Station in montane forest. Fair densities of this host plant are found along shaded water courses in the Lowveld but repeated examinations revealed evidence of the vector on just two occasions.

Several psyllids with strong migratory powers have been collected at fairly high altitudes above the ground. P. cockerelli was caught in aerial scoops between 100-4000 feet and is clearly dispersed by air currents (Jensen, 1954). According to Nichols et al., (1965), the invasion of the pear psylla, P. pyricola, into Californian orchards from Oregon has definitely been assisted by prevailing winds. Not only does T. erytreae appear to possess, weak dispersal powers and show no behavioural response to reach the upper air levels, but the adults do not survive very long away from suitable foliage. Ten mature adults confined in bottles with no foliage lived for a mean of 35.2 hours, five tenerals surviving for a mean of 55.2 hours. After a few hours away from foliage the adults become noticeably restless and shortly before death their abdomen shrinks and compresses.

Nevertheless, there is a possibility that at times of high population density adults could be blown into the Lowveld citrus groves from the severely greened Middleveld region. In order to investigate this possibility an examination was made of the frequency and direction of prevailing winds. Wind roses were drawn for the year 1967 for meteorological stations at Malkerns Research Station, Big Bend and Mpisi (central Lowveld) (Fig. 1) from tables appearing in the Report on Meteorological Data of the Year 1967 (South African Weather Bureau, 1968). The results showed a fairly consistent pattern of wind frequency and direction for each station, with a relatively small fraction of air movement in an easterly direction (10-32%) for the months in which the highest population densities of T. erytreae occur. Fig. 34, calculated from daily readings of wind run and direction at 0800 hours and 1400 hours, indicates a similar pattern of wind direction at Malkerns Research Station for 1967. In August 12%, and for September to December a mean of 4.5% of recorded wind was in an easterly direction towards the Lowveld. The main prevailing wind direction at ground level is thus from the Lowveld region towards the Middleveld and thus works against the spread of the vector into the Lowveld. However, insects in the small plantings of citrus along the Lembombo mountain range in the east may possibly be carried by winds into Lowveld citrus.

14. POPULATION DYNAMICS OF T. ERYTREAE

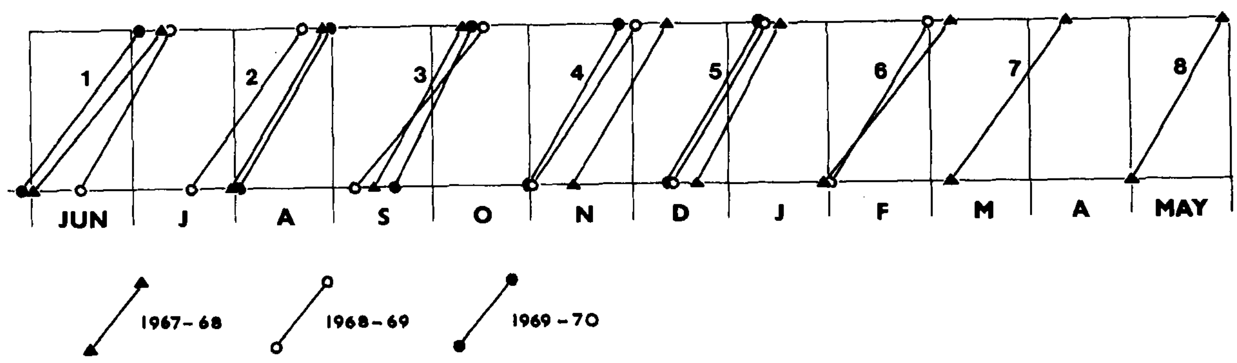
The dispersal powers of T. erytreae are weak and the insect was almost entirely confined to citrus groves during the study period. One aspect which was not considered in this study was the possibility of genetic variation. Though this would not seem to be an important factor in the dynamics of T. erytreae, a variation in the vitality of females, i.e. early deaths (also reported by Van der Merwe, 1941) and differences in the pigmentation of nymphs were observed on several occasions, both of which could be inherited differences.

(i) Numerical fluctuation. In all but the winter months, there was a perpetual fluctuation in the numbers of T. erytreae, with large differences between the peaks and troughs of population density. Table 24 shows that the highest recorded peak occured on September 18, 1967, when more than a million individuals of all stages were estimated at Malkerns Research Station. In a population explosion encountered at Ross Citrus Estate in the same month, 5,385 adults were collected in a five minute collection around the tree canopy with

Table 24 Estimated peak numbers of T. erytreae in the 50 citrus trees at Malkerns Research Station site during the study period. Estimates for adults very approximate

	Eggs	Nymphs	Adults	Total all stages
1967 Sept 18	1,098,728	92,000	6,208	1,196,936
Nov 22	246,225	116,675	2,345	365,245
Dec 20	650,513	36,000	12,450	698,963
1968 Sept 5	266,828	9,635	1,508	277,971
Dec 13	505,780	5,625	3,798	515,203
1969 Sept 26	57,525	39,600	325	97,450
Dec 30	67,925	38,500	510	106,935

the insect sampling machine. By contrast, it will be recalled that in 1969 no colonies were recorded for two winter months. An example of the usual population density prevailing during the winter months is that for April 19, 1968, when 2,850 individuals of all stages were estimated at the study site.



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JUN
J
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S
O
N
D
J
F
M
A
MAY
1967-68
1968-69
1969-70

(ii) Field generations. Because several mortality factors are age-specific, the regular occurrence of distinct field generations or broods is of considerable significance in the dynamics of *T. erytreae*. (Table 25). The broods form convenient time periods for discussion and make for greater understanding of the population fluctuations. (The numbering of the broods in Fig. 35 is different from that used in previous chapters).

Table 25 Age-specificity of three mortality factors of *T. erytreae*

Mortality factor	Nymphal instars						Adult
	Egg	I	II	III	IV	V	
Parasites	Not susceptible			Susc.	Highly favoured	Susc. but frequently not fatal	Not susceptible
Predators	Infrequently attacked	All stages attacked					Infrequently attacked
Weather extremes	Extremely susceptible		Increasing resistance				Highly resistant

The annual cycle of broods is considered from June to May during the study period at Malkerns Research Station. In the first season of study it will be recalled that a very similar cycle of broods was completed at two other groves in this district. Fig. 35 shows that eight broods were completed each year, and that for broods 1-5 (June to January) there was a similar sequence in their timing for the three years. Field generations were more nebulous in the period February to May when the population was low, or recorded as nil as in 1969. The mean durations of broods 1-5 shown below were related with mean temperature:-

Brood 1 .... 33.8 days
2 .... 30.6
3 .... 30.3
4 .... 28.8
5 .... 27.8

The above durations for broods 3, 4 and 5 corresponded closely with those indicated from regressions of incubation and nymphal development periods (Fig. 30). This difference in the rate of development of the immature stages, or completion of a brood, (and in the length of the pre-oviposition period), will obviously influence the potential rate of increase of the population.

EXPLANATION OF FIGURE

Fig. 35 Broods or field generations of *T. erytreae* for the study period at Malkerns Research Station. The two points which set the line for each brood were calculated from the peak of egg colonies and peak of instars III-V

(iii) Fecundity. Having a long reproductive life, a sex ratio in favour of the female, and a high egg-laying capacity, T. erytreae is an extremely fecund species. Several theoretical concepts are useful in examining the fecundity of an organism. The biotic or reproductive potential (r) is defined as the potential rate of a species to increase its numbers in an unlimited environment and is fequently used in population ecology. Laughlin (1965) proposed the use of a new population statistic - capacity for increase (r_c). However, due to the short interval between generations and the extended reproductive life of the female which cause an overlap of generations, and the unstable age distribution, the calculation of r or r_c is difficult and is of limited application in the case of T. erytreae. Nevertheless, the following simple calculation is of interest in illustrating the high reproductive potential of the insect.

The calculation assumes that all eggs hatch normally and that there is no nymphal mortality. Ignoring a few colonies where males were totally absent, sex ratios in the field varied from 60-79% females. Under near optimum conditions in the insectary the natality of batches of 3-5 females varied from 360-1305 eggs per female. Disregarding the possibility of the following generation beginning to reproduce during the lifetime of the generation in question, the biotic potential of T. erytreae is thus:-

$$.60 - .79 \times 360 - 1305 = 216 - 1031$$

In other words, in an unlimited environment T. erytreae is capable of increasing its numbers by 216 to 1031 times in one brood. Under favourable conditions in the field the percentage egg hatch may be as high as 95% and nymphal survivals of 60% have been frequently recorded.

The highest growth rates actually performed in the field take place on the main growth cycles of citrus in spring or early summer. At this time the environment may be particularly favourable and the population structure at its optimum for rapid increase. Graphs of the population fluctuations of T. erytreae at Malkerns Research Station indicated that optimum growth takes place in broods 2 and 3 and in brood 4 or 5. When plotted as logarithms these growth rates were linear for brood 2 in 1967 and brood 5 in 1969, and approached the linear for brood 3 in 1967. The linear relationship of log population density with time indicates an exponential growth form and the slope of this line may be regarded as the "unlimited specific growth rate" of the species (Odum, 1964). The population growths in log colonies per day were as follows:-
1967 brood 2 - .02619, brood 3 - .05789; 1969 brood 5 - .03269.

Table 26 expresses these maximum population growth rates in another way and indicates that the specific growth rate is attained most frequently by brood 3.

Table 26 Time required, in days, for a population of 10 colonies of *T. erytreae* to double itself

	1967	1968	1969
Brood 2	11	4-7	6-11
3	3-5	3	-
4 or 5	6-8	3-4	9

(iv) Survival. The survival of the immature stages of *T. erytreae* was studied in numerous *in situ* counts on citrus seedlings and experimental trees during the elucidation of weather extremes, natural enemies and plant host quality as mortality factors. At any one experimental site, however, there was no continuous record of total survivals from egg to adult stage for more than a few months.

A summary of egg to adult survival in 52 *in situ* counts at various times and places during the study period appears in Table 27. Survivals were extremely irregular and in 22 counts there were no survivors. Interestingly, the Table indicates a tendency for high mean survivals in broods 3 and 5 when rapid population increases do occur. Survivals in excess of 20% were not uncommon during this period. The number of counts in the period February to June were too few to allow any valid conclusions to be drawn.

The relative importance of each mortality factor was discussed separately before and will again be considered below.

Table 27 Summary of egg to adult survivals in 52 *in situ* counts made on study trees in the Letaba and Malkerns districts

		No. of insects	No. *in situ* counts	Mean % survival	Individual survivals >20%
Brood 1	June	677	2	11.82	1
2	August	1574	10	5.97	3
3	Sept/Oct	5239	10	13.00	2
4	November	4098	14	6.27	1
5	Dec/Jan	4789	12	8.12	1
6	February	495	1	9.70	0
7	Mar/Apr	1029	2	0.68	0
8	May	669	1	0.90	0

(v) Significance of the main ecological factors

Flush density and quality. Flush density and quality vary independently of the population density of *T. erytreae* and are thus true density-independent factors. At all times the supply of young foliage is a prerequisite for population increase. Young flush is rarely completely absent but when sparsely distributed and beyond the searching powers of the adult, a relative shortage of favourable breeding and feeding sites develops and the reproductive rate declines sharply. The synchrony between the emergence of waves of adults at the end of a field generation with the supply of young growth is thus of consequence to the population. Hence flushing rhythm imposes a similar rhythm on both the numbers and age distribution of T. erytreae and, especially during spring and summer, produces distinct seasonal broods. Lower levels of nutrition probably contribute to nymphal mortality following midsummer weather extremes, but the main influence of flush quality would appear to lie in its effect on the fertility and vitality of adults.

Since the seasonal rhythm of flush density and flush quality are fairly constant, they are not likely to influence very much the variation in population density from year to year.

The main period of psylla abundance occurs during the three growth cycles of spring, early summer and midsummer. Flush quality, particularly nitrogen content, is at its highest in the first two flushes and probably stimulates maximum natality. Calculations of the percentage infested flush points from flush studies and psylla population counts at Malkerns Research Station revealed a tendency for (a) the proportion of infested flushes to increase progressively in each of the main flush cycles as the foliage hardened and matured, and (b) for this proportion to increase with successive flushes in some seasons. Thus in October, 1968, and January, 1968 and 1970, this proportion rose to between 70-75%, serious overcrowding occurring in January, 1968, (Catling, 1969a).

From autumn to spring citrus is usually semi-dormant and supports low to very low population densities. From February to August, during which time 4-5 broods are completed, T. erytreae never approached the carrying capacity of available growth. In the three seasons at Malkerns the percentage infested flushes rose to 20.0% on one occasion (July, 1968) but on the average only 3.9% were infested during this period. After a careful consideration of the various mortality factors which operate at this time and allowing for an increase in the pre-oviposition and developmental durations of the insect, it is believed that environmental resistance is mainly provided by the relative shortage of breeding and feeding sites and, possibly, by the decline in the nutritive value of the flush. T. erytreae disperses weakly and adults seem to have poor searching powers for breeding sites. Many females are thus obliged to feed on mature leaves for extended periods and many probably die without laying eggs. Due to the trend for a lower proportion of males at low population densities, there is also the hazard of females not acquiring a mate.

It is possible that the vitality and fecundity of winter adults are adversely affected by lower nutrient levels which in turn reduce the power of searching for breeding sites. A reduction in the number of eggs per colony during the winter dormant period was observed by Catling (1969a). This explanation is supported by the fact that where major growth cycles take place during the winter, as in the upper Letsitele Valley of the northern Transvaal, and in young trees, population outbreaks and large vigorous colonies have been observed. Moreover, it will be recalled that there was no decline in egg-laying on vigorously-growing seedlings in the insectary during winter.

Population ecologists who support Nicholson's theory would perhaps argue that this decrease in vitality and fecundity represents a "mutual adaptation" between insect and plant host which has evolved as a density-related mechanism to prevent an absolute shortage of food which could endanger the existence of the species during dormant periods of the plant host.

Weather extremes. Basically the influence of weather was studied as follows:-

(a) By measuring the direct effect of extremes on colonies of *T. erytreae* in the field. Multi-variate analysis was then used to define the lethal conditions for the highly susceptible egg and first instar nymphal stages.

(b) By relating the occurrence and severity of these known lethal extremes to observed changes in population density in the field. A series of study groves were selected in such a way as to include a range of climatic extremes, the so-called "gradient design" discussed by Baltensweiler (1965).

(c) By the derivation of a weather index which reliably explains the regional status of the insect and partly accounts for the history of past outbreaks.

Abundant evidence has been presented to show that weather is a key factor in the population dynamics of *T. erytreae*. Being a strong and variable component of the environment weather is believed to be the chief factor to regulate citrus psylla populations.

Most authorities agree that weather may influence the mean density level and fluctuations of insects. In the case of *T. erytreae* the young stages frequently suffer high mortalities. After a given fraction of the population has been removed a certain time must elapse before the former density is regained. Thus if spells of unfavourable weather are repeated in quick succession the rate of increase is obviously halted. Since the optimum supply of available breeding sites is usually present for relatively short periods and the age structure of the population is continually changing, it may not be possible for the residual population to rise to its former level on the return of more favourable weather.

In discussing the regulatory effect of weather it is necessary to enter a basic controversy among population ecologists. Huffaker & Messenger (1964) have shown that even a high rate of mortality may not be regulatory for .... "the population density at which regulation occurs is not determined by total percent mortality but rather by the rate at which mortality increases with density". In other words, in order to contribute to the regulation of populations a limiting factor must intensify its effect as population numbers increase. But many ecologists believe with Klomp (1964) that ...."(weather) cannot have any regulating influence" .. because its effect is independent of density. Thus the controversy revolves around whether weather is density dependent or density independent.

Papers by De Bach et al., (1955) and De Bach (1958, 1965) indicate that this author is a strong protagonist of the view that weather is a density-dependent factor for many species. He argues that the effect of weather is not uniform and that within the broad habitat of the species there are always some microhabitats where survival from lethal extremes is possible. Therefore, as the severity of weather increases, the number of favourable microhabitats will decrease so that the higher the population density rises, the greater the proportion of mortality during lethal conditions. The presence of sheltered microhabitats in citrus trees for T. erytreae was mentioned earlier. De Bach described in detail the regulatory effect of weather extremes on populations of two Aphytis spp. and Comperiella bifasciata Howard which parasitize the red scale, Aonidiella aurantii (Mask.), in Californian citrus.

Natural enemies. Solomon (1957) has mentioned three essential requisites if parasites are to effectively reduce the numbers of their host. Parasites must be able to disperse and rapidly discover their host; their activity should be well synchronized with that of their host(s); and they should be able to reproduce continuously and rapidly.

The parasites of T. erytreae were clearly related to the population density of the host and apart from a few periods when they were noticeably absent or in undetectable numbers, they attacked a variable fraction of nymphal instars III - V throughout the study period at all sites. Between them the two main species appeared to seek out colonies of nymphs fairly effectively at all but the extreme densities of their host. They were not observed at all for several months in the very low host densities recorded at Malkerns in 1969 but they recovered later the following season. Parasitism levels dropped sharply at the start of several broods in the 1967-68 season when populations of T. erytreae were very high. Hyperparasitism does occur, the rate usually increasing towards midsummer, but this does not seem to seriously impair the synchrony between primary parasites and their host.

Parasites are not regarded as an important regulatory factor. The "effective parasitism" of susceptible stages rarely exceeded 50% and because of the distinct broods of the host and the fact that the eggs, nymphal instars I and II, and adults are not attacked, the parasite complex inevitably fails to prevent large population increases.

The influence of predators was studied rather superficially. While they proved to be a significant mortality factor during some periods, as in late summer and early winter, in general their activity was irregular and poorly synchronized with fluctuations of *T. erytreae*.

Competition. The effect of increasing density on the survival and reproductive rate of *T. erytreae* was not investigated in any great detail. Studies on fairly heavily populated citrus seedlings did not reveal the expected increase in mortality with increase in the number of eggs or nymphs per leaf. However, in January of 1968 at Malkerns Research Station, the dwindling supply of flush points became heavily overcrowded with eggs and nymphal stages resulting in considerable mortality. Overcrowding was not repeated in the following two seasons and unfortunately this intraspecific competition was not properly measured in 1968. Thus it would appear that a stabilizing mechanism working via density-related egg and nymphal mortality could operate only during seasons of severe population outbreak.

T. citricidus, the black citrus aphid, is virtually sympatric with the citrus psylla. Hence a certain amount of interspecific competition is common and this may become fairly intense in some seasons, particularly on the midsummer flush. Competition takes the form of reducing the attractiveness of the foliage rather than direct nymphal disturbance or mortality.

(vi) *A population model*. Fig. 36 and the accompanying text represent a preliminary 'verbal model' or a synthesis of the interacting environmental factors believed to govern the seasonal abundance of *T. erytreae* in a favourable region.

Serious outbreaks in favourable regions, and abnormal populations in some of the hotter, marginal regions are possible at almost any time when favourable weather corresponds with a major growth cycle. Such outbreaks were observed in the Letaba district in late January, 1967, and in Swaziland in January, 1970. Regular population outbreaks occurred in the upper Letsitele Valley area in June/July of the early nineteen sixties.

Though environmental factors are largely interdependent and to a certain extent operate continually, fundamentally the dynamics of *T. erytreae* appear to be governed by (a) the flushing rhythm of citrus, which determines the *potential* population density at any time, and (b) the occurrence and sequence of lethal weather extremes which directly determine the rate of population increase during growth periods. Thus the life system of *T. erytreae* is perhaps best explained by the theory of Andrewartha & Birch (1954) which, simply stated, depends on "weather and a place to live".

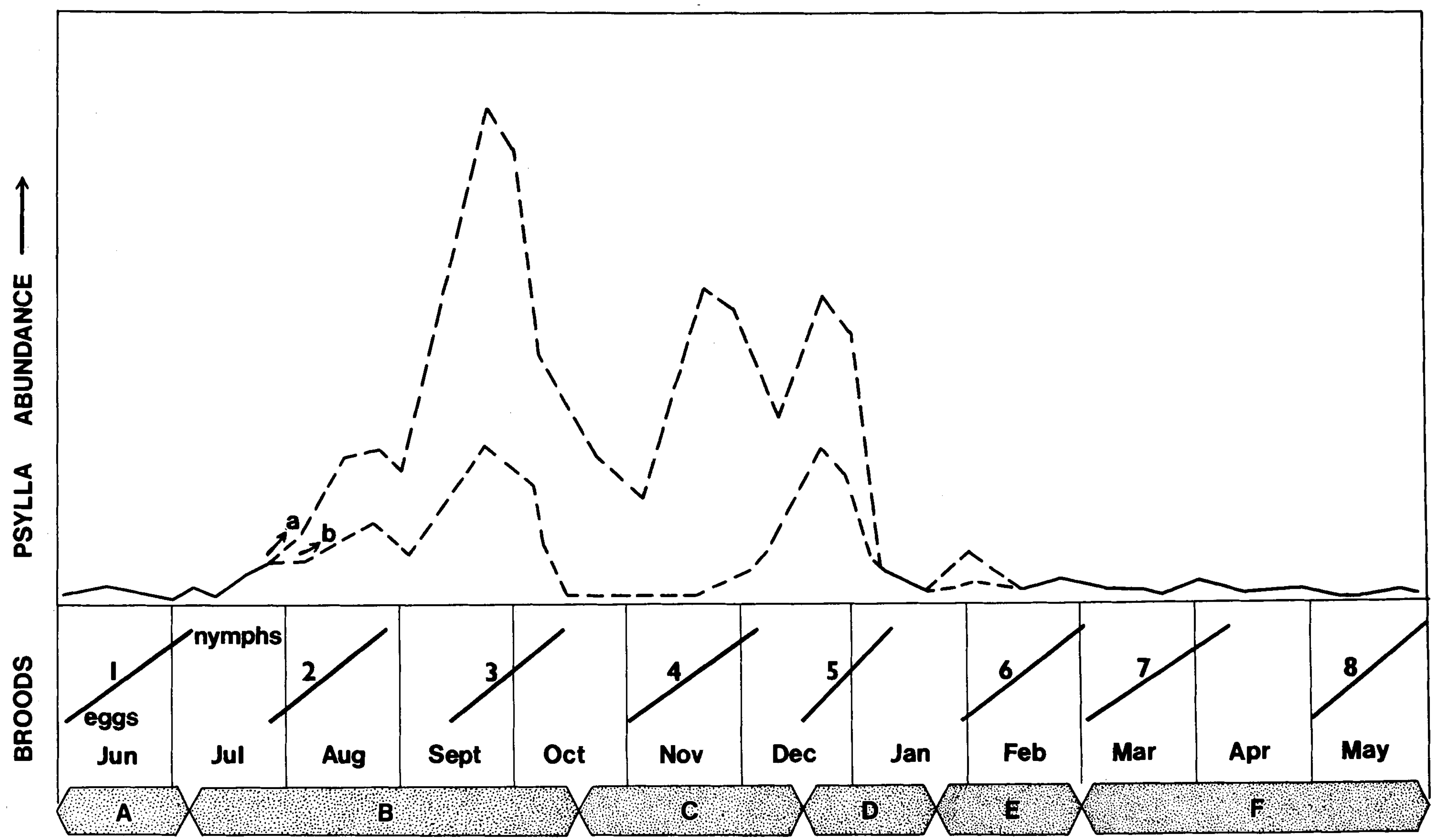

PSYLLA ABUNDANCE
BROODS
a
b
1
eggs
nymphs
2
3
4
5
6
7
8
Jun
Jul
Aug
Sept
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
A
B
C
D
E
F

Fig. 36 Population model of the seasonal abundance of *T. erytreae* in a favourable region

Period	State of *T. erytreae* population	Governing environmental factors
A. June Brood 1	Usually low and stable (numbers at end of this brood determine size of winter nucleus)	Low flush densities with relative shortage of favourable breeding and feeding sites Low flush quality Fairly regular action of parasites and predators Low rate of development of immature stages (Lethal weather extremes infrequent)
B. July - mid October Broods 2 and 3	Rising steadily (optimum growth rate often attained by brood 3)	Dense, nutritious spring growth cycle Number and timing of lethal weather extremes variable and largely determines the population density attained and rate of increase-(a) or (b) Parasite activity variable Predation irregular and poorly synchronized Some interspecific competition from aphids
C. Mid October - mid December Brood 4	Rapid decline to low or medium densities followed by another rise	Spring growth cycle maturing, low flush densities until onset of the second growth cycle of the season from the end of October to the end of November Lethal weather extremes frequent in October, less frequent in November and early December Parasites fairly active Predators increasing in activity
D. Mid December to late January Brood 5	Third rise in some seasons Population crash at end of this brood in every season	Rapid decline in young growth causing severe intraspecific competition in some seasons Fairly frequent lethal weather extremes Parasite and predator activity fairly high Interspecific competition with aphids fairly common Poorer flush quality
E. February Brood 6	Low to very low	Brief growth cycle followed by low flush densities Fairly frequent lethal weather extremes Natural enemies active Flush quality declining further
F. March - May Broods 7 and 8	Low and stable	Environmental factors very similar to period A, brood 1

15. SUMMARY

1. The population fluctuations of T. erytreae are closely correlated with the flushing rhythm of citrus. The synchrony of emergent adults with growth cycles is important to breeding populations. Flushing thus imposes a rhythm on the numbers and age distribution of the insect. The prolonged flushing of trees in the cooler, moister upland areas was found to be more favourable to the insect than the shorter, well-defined flush cycles which characterize the arid, lowland areas. There are 3-4 annual growth cycles in southern Africa, the main population rise taking place on the flushes of early summer. The role of temperature and moisture in regulating flushing rhythm is discussed. On some flushes intraspecific competition occurs. Interspecific competition with the citrus aphid is fairly common on the spring and mid-summer flushes. There are considerable differences in flushing rhythm due to tree age, variety and tree condition. The greening disease tends to induce heavier winter flushes and overlapping growth cycles in summer.

2. On host tissue of poor quality there is prolonged nymphal development and higher rates of mortality, this affect probably being intensified under hot summer conditions. Protein starvation was recorded on leaves with a nitrogen content below 1.5% of dry weight, these levels rarely occurring in well-managed citrus groves. The precise protein requirements of psyllids are unknown but large quantities of amino acids were found in the excreta of T. erytreae. Studies on the nitrogen content of young flush in the field showed that nitrogen declines with age; that nitrogen in the flush of seedlings and young trees is higher than the flush of mature trees; and that there is a marked seasonal fluctuation in the nitrogen content of successive flushes - highest levels occurring in the spring flush and lowest levels in winter flushes.

3. Parasites attack the third, fourth and fifth instars of T. erytreae. The degree of parasitism achieved was variable and depended on the presence of a favourable synchrony between the two main species and the host. During periods of favourable synchrony at least 40-50% of the susceptible stages were parasitized. Under conditions of poor synchrony, however, parasitism frequently dropped below 10% and parasites were not recorded for several months at Malkerns in 1969. The parasite complex was relatively unaffected by regular applications of insecticides. Tetrastichus radiatus Waterston was the main primary parasite which at times was challenged in importance by Psyllaephagus pulvinatus (Waterston). In most seasons at Malkerns, Aphidencyrtus cassatus Annecke attacked a fairly constant and sometimes large fraction of the two primaries, but this secondary parasite did not appear to seriously affect the degree of parasitism of T. erytreae. The four main parasite species were found associated with another Trioza sp.

4. A complex of predators attack mainly the nymphal stages of T. erytreae. These include several green lacewings, Chrysopa spp.; a brown lacewing, Micromus sjoestedti Weele; two syrphids; a coccinellid; and several spiders and mites. Most of these species are also aphid feeders, some showing a marked preference for aphids. Predator activity is irregular in early summer when T. erytreae populations are rising, but assumes greater importance from midsummer to midwinter.

5. Extremes of weather play a predominant role in regulating population fluctuations of T. erytreae. Populations were consistently the highest in the cool, moist upland region of each study district and were nearly always low and isolated in the hot, arid lowlands. There was a trend for higher populations to develop in mild seasons or following spells of cool, overcast weather during the summer months. The insect favoured well-shaded breeding sites in the lower section of tree canopy, was frequently found in large numbers near windbreaks, and rarely colonized small trees in the hot regions during the summer months. A large number of in situ counts revealed that all stages of T. erytreae are sensitive to high temperature combined with low relative humidity. The eggs and first instars were found to be considerably more vulnerable to these extremes than the more advanced stages. A correlation analysis for egg to first instar survival showed that maximum daily saturation deficit, and maximum daily temperature combined with vapour pressure were both highly significant and convenient predictors of mortality. Because of the occurrence of distinct field generations and the extreme sensitivity of the young stages, the degree of mortality depends largely on the age distribution in the population. The frequency and timing of daily saturation deficits exceeding 25.9 mm Hg (34.6 mbars) were found valuable in explaining differences in population densities. It is believed that severe weather kills the developmental stages by desiccation. A saturation deficit index (S.D.I.) was derived for assessing regional weather-induced mortality of T. erytreae. This index explained the known pest status of the insect in southern Africa and also shed light on past outbreaks of the vector and the greening disease in two citrus areas in the Transvaal.

6. The durations of the immature stages of T. erytreae are related with mean temperature. Highly significant regressions of incubation and nymphal development period were calculated from field studies at both study areas. In Malkerns development is completed in about 50 days in winter and 26 days in summer.

7. Studies on citrus seedlings showed that population density does not normally affect the percentage egg hatch or nymphal survival. Percentage egg hatch usually varied from about 60–100%. There was a progressive decrease in the survivals of eggs and nymphs with an increase in leaf length. Survival was also influenced by the position of the leaf on the flush point.

8. Females predominated in field populations at all times of the year, the sex ratio varying from 0-49% males. The sex ratio was apparently correlated with population density, a higher proportion of males occurring at medium to high population densities.

9. Egg-laying studies and observations on mating behaviour were carried out on citrus seedlings in the insectary. T. erytreae was found to be extremely fecund, some batches of females laying a mean of 1,304 eggs during their lifespan. Egg-laying is stimulated by the presence of young flush and females die without laying eggs if breeding sites are not available. There was a fairly short pre-oviposition period (3-7 days) and batches of females lived for a mean of 17-53 days. Males and females appear to have similar longevity. Unmated females lay fewer eggs and these are infertile. For the full complement of fertile eggs females required several matings. High temperatures were not found to decrease egg production.

10. In common with other psyllid species living mainly on evergreen hosts, T. erytreae has weak dispersal powers.

11. The interaction and relative significance of the various limiting factors operating in the population dynamics of T. erytreae is discussed and a population model is given which explains the seasonal abundance of the insect.

SECTION B

Studies on disease transmission and control of *T. erytreae*

1. INTRODUCTION

The symptomology of South African greening has been described in considerable detail by several workers and will not be repeated here (Oberholzer *et al.*, 1965; McClean & Oberholzer, 1965a; Schneider, 1968).

The incidence of greening in the Letaba district was discussed by Catling (1967) who found no visible symptoms of the disease in and around the Riverside study site at 1,650 feet (Fig. 3). With the exception of a single grove where infection had clearly originated in the nursery, greening was scattered and of the sectorial type on Letaba Estates at an average altitude of about 2,000 feet. In the Tzaneen-New Agatha-Letsitele Valley areas above 2,500 - 3,000 feet, however, greening was common and frequently severe.

Similar gradients in the incidence of greening have been reported in the Eastern Transvaal by Schwarz & Green (1969) and will be shown to exist in Swaziland.

2. INCIDENCE OF GREENING IN SWAZILAND

(i) Malkerns, Swaziland Middleveld. In the early 1960's, despite reasonable nutrition, young trees in the Malkerns district were observed to lack vigour and develop what appeared to be severe foliar deficiency symptoms. In 1965, following a visit to the Nelspruit district, Mr P.G.C. Dodson, horticulturist of the Swaziland Department of Agriculture (personal communication, 1967), suspected greening to be the cause of this decline. Accordingly, Dr A.P.D. McClean of the Plant Protection Research Institute, Pretoria, and later, Prof. P.C.J. Oberholzer of Pretoria University, both authorities on the greening disease, visited Swaziland to confirm these suspicions and to assess the general incidence of the disease in the territory.

Both authorities came to the conclusion that greening was the major cause of citrus decline in Malkerns. They noted that the disease was particularly severe in young trees up to 4-5 years of age. Trees planted in the mid fifties had grown well and were found to be only sectorially infected. In an unpublished report, McClean expressed the view that the disease had become epiphytotic during the 1958-60 period, which agrees well with studies made on the population fluctuations of the vector in neighbouring citrus areas by Green & Catling (in press). McClean stated that ..."completely normal trees were difficult to find" and in September of 1965 rapid surveys in 60 representative groves (Dodson, P.G.C. 1967, personal communication) revealed that the disease was present in all groves, trees in the 1-5 year age-group being severely affected. A similar account of the greening position was given by Drs. J. Grobler, F.C. Loest and R.E. Schwarz following a visit to Swaziland in 1967. Legislation now prohibits the movement of citrus propagative material out of the severely infected Malkerns district.

Between 1967 and 1969 many of the severely stunted young trees were removed or abandoned. However, trees of medium age or trees near maturity have shown improved growth and vigour during this period, due probably to higher midsummer temperatures and lower vector populations.

Incidence of greened fruit. The incidence of greening in fruit dropped prior to picking and at picking was studied in four groves of mature or nearly mature trees. In each grove 50 trees were selected for the collection of dropped fruit at weekly intervals from early May to picking time in 1967, and from January to picking time in 1968. At picking, 30-60 representative lugs of fruit were sorted according to the accepted visual symptoms of the disease, doubtfully greened fruit being tested by the albedo-fluorescence method of Schwarz (1968a). In chapter 3 a brief comparison was made between the incidence of greening at Kelly's Hope and Malkerns Research Station.

Table 28 shows that a large proportion of the fruit dropped before picking was greened. In 1967, between May and picking, 35.5 - 81.9% (mean 62.2%) of the fruit was greened in the four study groves. From Janary to picking in the two groves studied the following year, 59.6 and 63.0% of the dropped fruit was greened. In 1968 a large number of fruit, more than half of which were greened, fell between January and picking. It is also very probable that much of the fruit falling before January, i.e. before greening symptoms became recognizable, is caused by greening (Schwarz, R.E. 1967, personal communication). Between November, 1967 and the end of January, 1968, 146 and 150 fruit per tree

Table 28 The incidence of greening in fruit dropped prior to picking and at picking in four groves in the Malkerns district

Site	Variety	Dropped fruit		Picked fruit	
		Fruit per tree	Percent greened	Mean lugs per tree	Percent greened
May-picking, 1967					
Malkerns Res. Stn.	Valencias	16.5	78.8	5.3	19.5
Ross Citrus Estates	Valencias	13.8	81.9	2.3	14.7
Kelly's Hope	Valencias	6.1	52.4	7.7	2.6
Ross Citrus Estates	Navels	14.9	35.5	4.4	1.8
January-picking, 1968					
Malkerns Res. Stn.	Valencias	52.8	63.0	4.1	23.5
Ross Citrus Estates	Navels	106.9	59.6	-	6.1
July, 1969					
Malkerns Res. Stn.	Valencias	-	-	4.8	33.0

of diameter greater than 12 mm was collected at Malkerns Research Station and Ross Citrus Estate respectively. The percentage of greened fruit at picking varied from 1.8 - 33.0% and there was a tendency for more greened fruit to be present on Valencias than on the Navel variety.

Incidence of foliar symptoms. Foliar symptoms are present in every grove in Malkerns during the winter months. In August of 1967 symptoms were counted in the study groves at Kelly's Hope and Malkerns Research Station. Using the frame method described previously, points of vein-yellowing and greening-induced deficiency symptoms (mottling) were sampled in 32 square feet of canopy on each of the 50 trees. At Kelly's Hope there were 1.7 vein-yellowing and 1.9 mottling symptoms per 32 square feet while at Malkerns Research Station the means were 5.4 and 13.3 respectively.

(ii) Swaziland Lowveld. Surveys by McClean (1965, unpublished report) at Sipofaneni, Big Bend and Tshaneni, and by Dodson (1967, personal communication) revealed no clear cases of greening in the Lowveld. However, in 1966 Oberholzer (1967, personal communication) discovered a small pocket of suspicious trees in a grove of midseasons at Swaziland Irrigation Scheme, Tshaneni. Subsequently Dr R.E. Schwarz collected fruit from these declining trees which showed the full syndrome of visual symptoms and which tested positive by the albedo-fluorescence and thin layer chromatographic methods. Identical evidence was found independently by the present author in the same year. This is the only known and fully-substantiated case of greening in the Lowveld and the disease does not appear to be spreading to the surrounding trees. At Tambankulu Estates branches supporting colonies of *T. erytreae* have not been observed to develop foliar symptoms.

McClean (1965, unpublished report) found evidence of the vector and two possibly diseased trees at Mpangelo Ranch near Mliba on the edge of the Swaziland Middleveld. At Ngonini Estates, (Fig. 1), which at 1,500 - 1,800 feet is ecologically intermediate between Middleveld and Lowveld, low but significant sectorial greening is evident. The vector is fairly common during early summer and could reach outbreak proportions in cool wet seasons. McClean obtained evidence of a gradual spread of the disease on this Estate.

Backyard trees at Stegi, situated at 2,150 feet on the Lebombo range to the east of the Lowveld (Fig. 1), are infected with greening and support fairly high populations of the vector.

3. VECTOR TRANSMISSION STUDIES

T. erytreae was first suspected as a vector of the greening disease by Schwarz (1964), conclusive evidence being obtained the following year by McClean & Oberholzer (1965b). Catling (1967) described a correlation between the abundance of *T. erytreae* and the incidence of greening in the Letaba district of the northern Transvaal, and Schwarz (1967) found a similar correlation in the major citrus areas of the Republic of South Africa. Such a relationship also exists in the Swaziland citrus areas.

Unpublished work (McClean, 1967) indicates that the greening organism persists in the vector for at least 2-3 weeks but that the nymphs are not capable of transmission. There is as yet no evidence of transovarial transmission in T. erytreae. McClean & Oberholzer (1965b) also showed that the citrus aphid, Toxoptera citricidus (Kirk), is not a greening vector.

Field observations suggest that fairly high vector populations are needed before appreciable disease transmission occurs. In the Transvaal and Swaziland noticeable spread of the disease has usually followed severe outbreaks of T. erytreae. Similar observations have been made on the spread of greening in the Philippines by Diaphorina citri Kuw. (Catling, 1968a).

(i) Screening of adults and nymphs of T. erytreae and the citrus aphid

Main trial

Transmission studies were made in Malkerns to confirm (1) that T. erytreae is the vector of greening, (2) that nymphs of T. erytreae are not able to transmit the disease, and (3) that T. citricidus is not a vector.

Transmission studies were made during April, May and June of 1967 on Valencia seedlings raised under insect-free conditions in the insectary. The 10 seedlings to be used for each of four treatments were carefully matched for size and condition and placed beneath organdy-covered cages in the greenhouse. All insects used in the trial were collected from greened branches in a severely-diseased grove of young trees on Malkerns Research Station. For treatment one, adults of T. erytreae were first confined in the field for a 1-3 day acquisition period on mature leaves exhibiting definite greening symptoms. After acquisition feeding approximately five males and five females were transferred to each test seedling and allowed to feed for 38 days. For the second treatment, 20-30 young nymphal stages were transfered to each seedling, allowed to feed for 26 days, and removed just prior to the final moult. Six adult aphids were placed on each plant in treatment three, large progenies developing in the 64 day exposure period. The 10 control plants were kept free of insects. At the end of the exposure period the seedlings were sprayed with insecticide and kept under insect-free conditions to await the development of greening symptoms.

No clearly defined foliar symptoms had developed by November, 1968, some 18 months later. Hence bark shavings were taken from each plant, made into two composite samples for each treatment, and screened by the fluorescence test. Both replicates of the plants exposed to T. erytreae nymphs and to T. citricidus were negative for greening, as were the control seedlings. On the other hand, bark samples from seedlings exposed to adults of T. erytreae were strongly positive. In addition, Table 29 shows that there were marked growth differences in the exposed plants, the feeding of T. citricidus and both stages of T. erytreae apparently reducing seedling growth when compared with the control plants.

Table 29 Growth differences in citrus seedlings exposed to T. citricidus and T. erytreae. Mean shoot length per plant

Treatment	Shoot length in inches
T. citricidus	38.6
T. erytreae-adults	36.3
T. erytreae-nymphs	38.6
Control	54.2

Sign. at P = 5%; S.E. of means 4.40

In a repeat experiment, another batch of 10 seedlings were exposed to T. erytreae nymphs from the same source for 16 days. Again, fluorescent tests and foliar symptoms were negative.

Minor trials (No control plants used)

(1) Malkerns - In June of 1967, eight Valencia seedlings were exposed to large numbers of T. erytreae collected from greened trees. Seventeen months after exposure five plants showed clear foliar symptoms of greening.

(2) Malkerns - In order to investigate possible differences in the transmission efficiency of adult T. erytreae according to feeding site, nine Orlando-Tangelo seedlings were exposed during October, 1968. One batch of newly-emerged adults were confined on young flush removed from diseased branches, while another batch of adults were confined on mature leaves showing severe greening symptoms. One year later no greening symptoms were observed in any of the test plants.

(3) Lowveld - Thirty-two seedlings were exposed in a citrus nursery at Tambankulu Estates from July to October, 1968. Though 37.5% of the seedlings became infested with T. erytreae, no greening symptoms developed in these plants. However, when bark samples were taken three plants were found to be positive.

(4) Lowveld - Twenty-five seedlings were used to support a culture of T. erytreae in a controlled temperature room kept at 18-22°C. The culture originated from insects collected at Tambankulu Estates in the Swaziland Lowveld. Though the seedlings became heavily infested in the 4-6 months of their exposure, no greening symptoms were observed under these favourable temperature conditions, nor was any marker substance found in the bark of these plants.

In trial (1) carried out at Malkerns a high percentage of plants became infected showing clear foliar symptoms. In all the other transmission studies, including the series of exposures to investigate a possible seasonal fluctuation in transmission efficiency (see later), definite foliar symptoms developed in only one plant. However, the bark fluorescence test did reveal a number of positives among these plants - three of these in trial (3) whose plants had been exposed at Tambankulu Estates where greening is unknown. Thus either the bark fluorescence test is not reliable when applied to the bark of 1-2 year-old seedlings, or a latent strain of greening exists in the Lowveld which does not manifest itself in foliar symptoms.

(ii) Screening of other psyllid species. During the winter of 1966 the adults of two psyllid species were found overwintering on citrus at Letaba Estates in the northern Transvaal. Both species, *Diaphorina punctulata* Pettey and *Diaphorina zebrana* (Capener MS), were collected in large numbers from their breeding host, the marula, *Sclerocarya caffra* Sond., in November, 1966, and taken to Pretoria for transmission tests to be carried out in collaboration with Dr. A.P.D. McClean. Adults were allowed a 3-4 day period of acquisition feeding on diseased plants and were then confined for a week on test seedlings at a rate of 20 adults per plant. By this method 34 seedlings were exposed to *D. punctulata*, 32 seedlings to *D. zebrana*, and as a standard treatment 24 seedlings were similarly exposed to *T. erytreae* adults. By the following winter none of the 66 plants exposed to the two *Diaphorina* spp. had developed greening symptoms, whereas 15 of the 24 plants exposed to *T. erytreae* showed unmistakable greening symptoms.

Using similar methods, McClean (1967, personal communication) was not able to achieve transmission with *D. punctulata* from Rustenburg ex *Fagara capensis* Thunb. and ex *Carissa bispinosa*, or with the psyllids *Agonoscena* sp. and an unnamed brown *Diaphorina* sp. both ex *Rhus lancea* L.f.

(iii) Seasonal fluctuation in transmission efficiency. It is recognized that the spread of virus-like diseases is dependent on a number of interrelated factors. Besides vector density and the degree of host plant infection, transmission may be influenced by changes in the properties of the pathogen, the physiological status of the host plant, and by variations in the transmission efficiency of the vector. Typically the greening pathogen is irregularly distributed and spreads slowly within the tree (McClean *et al.*, 1968). Studies have also shown that the organism is sensitive to high temperatures and this may explain the apparent seasonal fluctuation in the pathogen content of infected trees found by Schwarz (1968b) where the highest percentage of successful graft transmissions occurred in the cooler months, April to August, and the lowest in the hotter months of September to December and in February and March.

These facts suggest that there may be a corresponding seasonal fluctuation in the transmission efficiency of the vector. Several diseases are known to be heat inactivated in the body of their homopteran vectors, for example aster yellows in *Macrosteles fascifrons* in the hot summer months (Maramorosh, 1953). Moreover, because the nymphs of *T. erytreae* have so far proved to be non-infective and the adults seem to require acquisition feeding to become carriers, the proportion of infective vectors will depend largely on the exact feeding site of the vector. *T. erytreae* breeds exclusively and feeds preferentially on young flush so that it is probable that at normal population densities the proportion of carriers declines when the trees have been flushing profusely for some weeks as in early summer. On the other hand, on the semi-dormant trees of winter adults are forced onto mature leaves and twigs which have presumably higher pathogen concentrations. Thus the first adults to colonize the spring flush cycle in July/August, when mean temperatures are favourable, are probably highly infective and carry the disease to the new shoots.

In order to investigate this hypothesis, eight series of citrus seedlings were exposed to field populations of *T. erytreae* in severely greened groves in Malkerns at various times of the year. Seedlings for this experiment were grown under insect-free conditions and only vigorously-growing plants were selected for exposure. Orlando-Tangelo seedlings were used in series 1 and series 4-9, Valencia seedlings for series 2 and 3. Series 1-3 were exposed in the open at the study grove at Ross Citrus Estates (Fig. 3), and series 4-8 were placed in a partially shaded position near the main study grove at Malkerns Research Station. Studies already described showed that the degree of greening and population trends of the vector were very similar at both sites. After exposure the seedlings were sprayed with insecticide and kept under insect-free conditions in the greenhouse or insectary. Series 1-7 were inspected for greening symptoms in June and November of 1968. Series 6, 7, and 8 were later moved to a cool room at 22-24°C to promote symptom expression. Due to the almost complete lack of symptom development the fluorescence test was applied to bark samples taken from each test plant.

The results are summarized in Table 30. By November, 8-16 months after exposure, only one plant had developed good greening symptoms in series 1-7. In the June inspection symptoms were too nebulous to enable a reliable diagnosis for greening and were confined to stunting and vein-yellowing, the latter of which had disappeared by the following summer. No greening-induced trace element deficiencies (mottling), so typical of foliar symptoms in the Malkerns district, were seen in any of the plants. There was no relationship between the plants showing the indistinct symptoms recorded in June, and plants found positive by the bark fluorescence test. Nor was there any correlation between plants which supported breeding populations of the vector and those found positive by bark fluorescence.

Attempts were made to determine the rate of transmission by searching for a correlation between the percentage of infected plants (as indicated by the fluorescence test) and the activity of the vector. It was assumed that because all exposed plants were flushing vigorously and were thus fairly constant in attractiveness, that the number of plants to support breeding populations of the vector at the end of the exposure period would be some

Table 30 Results of exposing 8 series of greening-free seedlings to field populations of T. erytreae in Malkerns. Series 1-3 exposed at Ross Citrus Estates, series 4-8 at Malkerns Research Station. Presence of greening determined by the bark fluorescence method of Schwarz (1968a)

Series	Exposure period	No. plants exposed	Percent plants infested with eggs or nymphs	Percent plants infected
1	1967 Jun 6 - Jul 20 - 45 days	50	36.0	18.0
2	Jul 20 - Aug 15 - 26	24	0.0	12.5
3	Aug 15 - Sept 26 -42	25	0.0	44.0
4	Oct 18 - Nov 15 - 28	44	13.6	34.1
5	Dec 8 - 29 - 21	45	80.0	13.3
6	Dec 29 - Jan 30 - 32	48	40.8	0.0
7	1968 Feb 26 - Mar 21 - 24	48	50.0	56.3
8	Aug 6 - Sept 12 - 37	49	c. 50.0	10.2

measure of the amount of feeding. Of the various ratios of vector activity and percentage transmission considered, all showed a trend for a low rate of transmission in midsummer but were exceedingly variable at other times of the year.

The results of this experiment should be regarded as preliminary and incomplete for the following reasons; (1) the absence of clear visual symptoms in the exposed seedlings (2) the lack of correlation between infested plants and plants shown positive by the fluorescence test (3) the absence of controls, i.e. unexposed plants, in each series (4) the many variables involved such as different exposure sites, and length of the exposure period. Nevertheless, the following valid conclusions do appear to support the hypothesis that marked fluctuations occur in transmission efficiency. Firstly, in the 1967-68 season, despite high vector populations in the surrounding trees (1.5 - 2.2 colonies per 10 square feet in series 5, and 0.2 - 2.0 colonies per 10 square feet in series 6), which resulted in 80.0% and 40.8% of the exposed plants becoming infested by breeding populations, the percentage transmission in midsummer was low - 13.3% and 0.0% respectively. Secondly, though irregular, fairly high rates of transmission occurred in August/September (series 3), October/November (series 4), and March (series 7).

A similar series of exposures is being carried out at Malkerns Research Station in the 1969-70 season using batches of control plants in each series, and a constant exposure period. A daily count is made of the number of adults on each plant, and all plants are kept in a cool room after exposure.

(iv) Proportion of infective individuals in field populations. This experiment was designed to test the hypothesis that the proportion of infective individuals in field populations is low.

Orlando-Tangelo seedlings were specially grown under insect-free conditions in Pretoria by Dr. A.P.D. McClean, transported to Malkerns for exposure to the vector, and then returned to the greenhouse in Pretoria to await the development of greening symptoms. Adults of T. erytreae were haphazardly collected in the field from greened citrus trees at the Malkerns Research Station and Ross Citrus Estates study sites and immediately confined individually on test seedlings in the insectary. Most plants were flushing at the time of exposure. It must be stressed that no acquisition feeding was given. Between October 8 and December 9, 1968, 127 seedlings were exposed to the feeding of single adults of T. erytreae, 20 unexposed plants acting as controls. In the first 57 seedlings exposed, adults were confined for a maximum of seven days and mean of 4.7 days; thereafter adults were allowed to feed for a maximum of 14 days with a mean of 11.9 days.

By December of 1969, twelve months after the last exposure, 17 plants had developed possible greening symptoms, while all the control plants were completely healthy. From each of the suspect plants two subinoculations were made by Dr. A.P.D. McClean to confirm the presence of greening. Subinoculating onto disease-free seedlings is considered as a reliable method to test for greening. Thirteen plants were found to be negative, two were very doubtful and fresh inoculations from the remaining two plants developed clear greening symptoms. In the first case greening had been transmitted by a male feeding for six days from October 9-15, in the second case by a female feeding for 13 days between November 25 and December 8. Both adults originated from the Malkerns Research Station site. Disregarding the two doubtfully greened plants, it is indicated that the proportion of infective adults in field populations of T. erytreae at Malkerns in the early summer of 1968 was fairly low at 1.6%. This experiment also showed that single adults, both males and females, will transmit the disease.

(v) Rate of spread of greening in the field. To study the rate of spread of greening in the Malkerns district, 50 Valencia nursery trees on Rough Lemon rootstock from Tambankulu Estates were planted out at the Malkerns Research Station in December, 1967. Originating in the Swaziland Lowveld, these trees were regarded as being free of greening though the possibility of latent strains must not be completely overlooked. The trees were well managed and inspected for colonies of T. erytreae at weekly or fortnightly intervals. Insecticidal sprays were applied when populations rose above 0.5 - 2.0 colonies per tree depending on tree size, this being regarded as a practical threshold for growers. The trees were regularly inspected for greening symptoms.

T. erytreae populations exceeded one colony per tree in December, 1968, and in September and November/December in 1969. In the first year after planting out three insecticidal sprays were required, and in 1969 five sprays were applied. Despite fairly effective control of the vector Table 31 shows that nearly half of the trees had become infected to some extent after 20 months in the field. In July, 1969, five trees were unmistakably greened, three showing severe decline and general stunting. Despite the occurrence of sectorial symptoms, the growth of the remaining 45 trees was good.

Table 31 The spread of greening into newly-planted Valencia trees at Malkerns Research Station

Date	Months after planting	Greening symptoms
July 1968	7	2 trees with slight vein-yellowing
November 1968	11	12 trees with sectorial leaf mottling
July 1969	20	21 trees with sectorial leaf mottling or vein-yellowing; 5 trees clearly greened

It is very likely that the close proximity of greened trees on two sides of the experimental planting was a major cause in the rapid spread of greening. It is also true that the heavy and prolonged flushing of young trees makes them very attractive to the vector. It is probably for these reasons that small replantings of healthy trees at Lipa (Philippines) and Pokhara (Nepal) have become heavily infected within 3-4 months (Catling, 1968a).

4. LOCATION OF THE GREENING PATHOGEN IN THE VECTOR

It is highly probable that the greening pathogen multiplies in the body of the vector and is thus present in fairly high concentrations in infected adults. In collaboration with other research workers, two small-scale attempts were made to isolate the pathogen from the excised salivary glands of *T. erytreae* adults by electron microscopy methods. Both attempts proved unsuccessful.

Fixing in Bouin's solution and staining with borax carmine revealed the presence of large, globular salivary glands in the prothorax of the adult on either side of the suboesophagial ganglion. For excision, anaesthetized adults were fixed to a layer of wax in a Syracruse watch glass and the salivary glands, together with the suboesophagial ganglion, dissected out in saline solution with a pair of fine tweezers.

The first attempt was made in November, 1967, in collaboration with Prof. A.H.P. Engelbrecht of the Department of Botany, Pretoria University. Infected and non-infected adults from Malkerns were dissected at Pretoria and the excised tissue fixed and embedded immediately. No positive results were obtained.

A second attempt was made in February, 1969, when 30 pairs of excised salivary glands were sent to Dr. J.M. Bové of the Institut Francais de Recherches Fruitières Outre Mer (I.F.A.C.), Versailles, France. Non-infected adults were taken from the culture room at Malkerns Research Station, and infected adults were obtained by confining insects from the same source on

Table 32 Results of chromatographic studies on extracts of *T. erytreae* adults from various sources. Trial 1, paper chromatography; trials 2-7, thin layer chromatography. I-V - nymphal instars

Trial	Date	Source of vector	Number of insects and stage	Colour and Rf value of fluorescent spots			
				1	2	3	Others
1	Aug 1966	Greened trees N. Tvl	850 adults	.20	.35	.58	-
2	Aug 1967	Non-infected seedlings Malkerns	40 adults	diffuse blue .18	yellow .33	yellow .55	-
3			40 adults	-	.29	.51	diffuse blue .42
4			30 I-III	no definite fluorescent spots			
5			30 IV-V	-	.30	.53	-
6	Nov 1967	Non-infected trees Swaziland Lowveld	30 adults	blue .17	diffuse yellow .33	diffuse yellow .56	diffuse yellow .46
7	Jul 1969	Greened seedlings Malkerns	40 adults	diffuse blue (.04)	yellow .27	-	diffuse yellow .42

diseased seedlings for 16 days in the culture room. The salivary glands plus suboesophagial ganglion were fixed in a glutaraldehyde solution plus phosphate buffer, and postfixed in osmium tetroxide - both steps being carried out in ice. The tissue was then placed in 70% ethanol plus .2M sucrose and sent by air to Versailles for embedding and electron microscopy study. The results were again unsatisfactory, due either to the method of fixation or the unavoidable time which elapsed between fixation and embedding.

5. DETECTION OF GREENING MARKER SUBSTANCES IN THE VECTOR

Schwarz (1965b; 1968a) discovered a specific fluorescent marker substance of diagnostic value in the fruit and bark of greening-infected citrus trees. Small-scale trials using similar methods of extraction and detection were made to determine whether this substance, or a closely-related derivative, is present in the insect vector.

Adults and nymphs of T. erytreae were collected in the field or taken from laboratory cultures, anaesthetized, placed in a suitable solvent, and macerated in an embryological watch glass. Ether appeared to be a superior solvent to distilled water, or 90% ethyl alcohol. After evaporating at 40°C, 0.5 ml distilled water was added to the residue and the new solution either spotted onto Whatman No. 1 filter paper for paper chromatography, or onto thin layer chromatographic plates as described by Schwarz (1968a). The chromatograms were developed for two hours with n-butanol, dried, and examined under an ultra-violet lamp having 95% of the radiation at 365 mμ.

The results of seven trials are shown in Table 32. The marker substance present in citrus tissue at Rf .08 - .09 was not found in extracts of the vector. No consistent differences were found in the chromatographic profiles of infected and non-infected adults of T. erytreae. However, a fairly consistent pattern of three fluorescent spots was present at Rf values of .17 - .20, .27 - .35, .51 - .58.

A rapid and reliable method of screening vector adults for infectivity would clearly be of immense practical value. Therefore, although the above preliminary trials failed to detect a suitable marker substance in the body of the vector, it would be advisable to continue the search using new methods of extraction and detection.

6. CONTROL OF THE VECTOR

It appears unlikely that T. erytreae will be controlled biologically. Being the vector of a virus-like disease, populations must be held at fairly low densities at all times. No micro-organisms appear to be associated with the insect and studies at Malkerns indicated that predator activity is relatively insignificant at the start of a population build-up. Catling (1969b) found that although two primary parasites consistently attack the more advanced nymphal stages, this does not prevent the extremely fecund insect from regularly surging to high population densities on the growth cycles of early summer. Typically at the start of each field generation 70-80% of the population is present in the non-susceptible egg and young nymphal stage. Unfortunately, egg parasites are unknown in the Psyllidae.

Kaloostian (1968) attempted the chemosterilization of males of the pear psylla, Psylla pyricola Forst., with tepa. The treatment caused a high mortality in the males, but in the following generation produced by the survivors there was a marked reduction in egg hatch. Chemosterilization is a new approach in the control of psyllids and more basic work will be required before effective measures are devised.

Hence the control of T. erytreae depends mainly on the effective use of insecticides, (Catling, 1969d) though according to Broadbent (1957) the use of insecticides has often failed to control the incidence of virus diseases even though vector populations were apparently severely reduced. Another disquieting fact is the report that P. pyricola has developed resistance to organophosphorus insecticides in Israel, and to several powerful modern insecticides in the U.S.A., including parathion and dimethoate (Anonymous, 1967).

(i) Preliminary screening of insecticides. The following materials were tested at standard rates against all stages of T. erytreae on seedlings in the insectary - Temik (UC 21149), parathion, malathion (mercaptothion), endosulphan (Thiodan), dimethoate (Rogor), mineral oil (Alboleum), and lime sulphur. All materials gave some degree of control, the most effective being dimethoate, endosulphan and parathion - which corresponds with the official South African recommendations (Pettey et al., 1968). Of these parathion was not considered for further testing because of its general hazards and detrimental effect on beneficial insects, and endosulphan because of its high cost. The preliminary tests showed dimethoate to be extremely effective against eggs and nymphs for as long as 15 days. Lime sulphur was also promising and was included in subsequent field trials.

(ii) Soil-applied systemics vs foliar sprays. During the early summer of 1967 two soil-applied systemic materials were compared with insecticides applied as foliar sprays in a grove of mature Navel oranges (mean canopy area 250 square feet)in the Malkerns district. Treatments consisted of phorate (Thimet 10% granules) at 227 gram and 454 gram per tree; Temik 10 G granules at 227 gram per tree; lime sulphur at .32% a.i. (active ingredient,) and dimethoate W.P. (Rogor 20W) at .02% a.i. The granular materials were lightly worked into the clean tree basin and watered, while foliar sprays were applied as a thorough cover spray with a standard power sprayer at 500 p.s.i. Blocks of three trees were used for each treatment with at least one tree acting as a barrier between treatments.

Table 33 Percent egg hatch and survival of nymphs of *T. erytreae* in 3 series of *in situ* counts following applications of insecticide. *First emergence of adults noted

SERIES 1

Treatment	Initial no. eggs Aug. 22	Percent egg hatch					Initial no. nymphs Aug. 22	Percent survival of nymphs				
		Aug. 29	Sept. 5	Sept.* 12	Sept. 19	Sept. 26		Aug. 29	Sept.* 5	Sept. 12	Sept. 19	Sept. 26
Phorate 227g/tree	333	48	43	32	17	0	459	97	95	7	0	0
Phorate 454g/tree	261	15	73	61	56	1	457	86	84	80	0	0
Temik 227g/tree	611	37	55	45	8	1	173	55	42	13	1	0
Lime Sulphur .32% a.i.	348	37	55	50	30	3	368	29	17	2	1	0
Dimethoate .02% a.i.	397	1	0	0	0	0	418	1	0	0	0	0
Control	638	52	86	52	10	1	502	84	62	13	1	0

SERIES 2 SERIES 3

	Initial no. eggs	Percent egg hatch				Initial no. eggs & nymphs	Percent survival of nymphs	
	Sept. 12	Sept. 26	Oct. 3*	Oct. 9	Oct. 18	Oct. 24	Nov. 6	Nov. 13
Phorate 227g/tree	1510	58	20	13	5	1210	12	1
Phorate 454g/tree	911	13	1	1	0	1230	11	1
Temik 227g/tree	1310	12	0	0	0	930	7	4
Control	840	57	9	7	1	1385	12	1

The effectiveness of the insecticides was mainly assessed by studying mortality in three successive series of *in situ* counts. Beginning in the egg or young nymphal stage, live insects in tagged *T. erytreae* colonies were counted at weekly intervals until the completion of nymphal development. Where densely crowded, eggs and young nymphs were counted in tens. Table 33 summarizes the results of the three series of counts.

After applying the angular transformation, a statistical analysis was made on the survivals recorded in the first two post-application counts in series 1 and 2. Transformed standard errors appear below.

In series 1 dimethoate gave complete control of egg and nymphal stages, mortality of eggs being significant on September 5 at the 1% level (S.E. ± 15.78), and of nymphs on August 29 and September 5 at the .1% level (S.E. ± 7.73 and ± 8.79). Lime sulphur was ineffective against the eggs and though it produced a significant reduction in the nymphal population on August 29 and September 5, it was clearly inferior to dimethoate. With the exception of Temik which on August 29 produced a significant mortality of nymphs at the 1% probability level (S.E. ± 9.69), none of the soil treatments were effective. Series 2 considered the effect of soil treatments only. The steep decline in survival in all treatments between September 26 and October 3 was attributed to the adverse effect of three days when the saturation deficit exceeded 26 mm Hg, such extremes being lethal to eggs and first instars (Catling, 1969c). Nevertheless, there appeared to be some measure of control by phorate at 454 gram and by Temik, both treatments being significant on September 26 at the 1% probability level (S.E. ± 9.85 and ± 10.49). Though unfavourable weather and the activity of natural enemies severely affected the survivals recorded in series 3, it is clear that there was little or no effect from the soil treatments.

Populations of *T. erytreae* were fairly high in this grove during the period of the trial, new egg colonies appearing on flush points in the experimental trees. Counts in a four foot band around the canopy of each experimental tree 21 and 64 days after application of the insecticides showed no obvious differences in the degree of infestation between treatments.

(iii) Foliar sprays of dimethoate. Three separate field trials were carried out between September and December, 1967, at Malkerns Research Station testing lime sulphur (once) and several concentrations of dimethoate W.P. Ten *T. erytreae* colonies were marked in the egg or nymphal stage for each treatment and the insecticides were applied with a power sprayer at 400 p.s.i. Prespray and intermediate postspray counts were made with a hand lens, while final counts were usually made under a stereo-microscope. In one trial spraying water on the control trees did not affect the survival or development of the immature stages.

From Table 34 it is clear that dimethoate gave outstanding control of eggs and nymphs at concentrations between .01% and .02% a.i. and of nymphs at concentrations as low as .0025% a.i. Lime sulphur again gave no significant control of eggs.

In a similar trial with three colonies per treatment comprising 1022 insects, dimethoate was shown to be effective against eggs at .01% and .0025% a.i. (Fig. 37).

Table 34 Combined results of 3 field trials to control eggs and nymphs of T. erytreae by foliar sprays. Abbott's (1925) formula was used as a correction for natural mortality. E - eggs; N - nymphs

Treatment	Prespray count no. insects	Final post-spray count no. live nymphs	Percent control
Dimethoate .020% a.i.	3928 E & N	0	100.0
Dimethoate .015% a.i.	3799 E & N	0	100.0
Dimethoate .010% a.i.	6935 E & N	0	100.0
Dimethoate .005% a.i.	1387 N	0	100.0
Dimethoate .0025% a.i.	2141 N	1	99.9
Lime sulphur .32% a.i. + wetter	1360 E	360	34.8
Control	5266 E & N	3291	-

(iv) Laboratory trials with dimethoate. Dip tests. To investigate the mode of action on the nymphal stages, small scale dip tests were carried out with dimethoate W.P. at .02% a.i. Untreated controls were used in each trial and all counts were made under a stereo-microscope.

The first two trials were essentially tests of the contact action of the insecticide. In the first, using a dip test method described by Coates (1969) in which organisms are affixed to adhesive tape, fifth instar nymphs were dipped for five seconds. Sixty-eight hours after dipping all of the 40 treated nymphs were dead, while 22 of the 40 undipped nymphs were alive. In the second trial, in which nymphs in situ on a leaf were dipped for five seconds, all of the 55 fifth instars were dead after 21 hours, whereas 67% of 21 nymphs on untreated leaves were still alive. In the final trial a comparison was made between emersing the entire leaf and painting the upper surface of the leaf on the opposite side to the nymphs. After 21 hours 86% of 236 dipped nymphs and 78% of 180 nymphs on the painted leaves were dead (most of the survivors were clearly succumbing to the insecticide), while only 22% of 164 untreated nymphs had died. After 45 hours survivals were 0.0, 0.6 and 48.8% respectively.

The three trials show that dimethoate possesses both a contact and systemic action against T. erytreae nymphs, the systemic action being more rapid.

Control of adults. Dimethoate W.P. at .01% a.i. plus ¼% mineral oil was tested against adults confined on citrus seedlings in the insectary. Adults collected in the field were allowed to establish themselves on unsprayed seedlings for 24 hours, and were then either sprayed directly or carefully transferred to a newly-sprayed plant. After 24 hours there was no survival of 76 adults on the sprayed plants and an 88% survival of 60 adults on the unsprayed plants.

(v) Discussion. Choice of insecticide. The soil systemics Temik and phorate gave poor control of the egg and nymphal stages of *T. erytreae* at the application rates tested. Though higher rates of Temik (2 pounds per tree) have been found effective against nymphs (de Villiers, E.A., 1969 personal communication), these materials cannot be recommended. Besides being expensive and extremely toxic to mammals, many soil systemics, including Temik, have been found lethal to predacious coccinellids on citrus (Ortega, 1967).

Dimethoate (Rogor 20 W) was found to be outstanding for *T. erytreae* control. Possessing both systemic and contact action it proved effective against adults at .01% a.i. and against eggs and nymphs at .0025% a.i., such low concentrations being relatively inexpensive. In bioassays at .04% and .075% a.i. Searle (1965) and Rosen (1967) found dimethoate to have an adverse affect on citrus parasites. At the concentrations recommended for *T. erytreae* control, namely .01% and .005%, and with the addition of ¼ - ½% mineral oil which reduces the initial toxicity of dimethoate (Searle, 1965), no disturbance was observed in an integrated control grove where three sprays of dimethoate were applied in the 1968-69 season. Neither was the activity of *T. erytreae* parasites seriously affected in any way, *Tetrastichus radiatus* Waterston and *Aphidencyrtus cassatus* Annecke emerging normally from pupae on leaves sprayed with dimethoate at .01% a.i. Citrus aphids, which frequently occur with *T. erytreae* on young flushes, were effectively controlled with dimethoate at .005% a.i.

Time of application. It is always difficult to assess the economic threshold level of insect vectors. But high populations of *T. erytreae* which are always related to growth cycles of citrus, cannot be tolerated at any time of the year and should be prevented through adequate control measures. Population explosions of the order encountered in one grove in Malkerns in mid September, 1967, where a five minute suction sample around the tree canopy yielded 5,385 adults, are particularly dangerous. In general the most critical periods for control would seem to be just before and during the main growth cycle in spring when the vector is capable of surging to high densities and is presumably at its most efficient as a disease transmitter.

Spray programme. The following spray programme is recommended for the control of *T. erytreae* in the Malkerns district (Catling, 1969e):-

1. A full cover spray of dimethoate at .01% a.i. plus ¼% mineral oil

FIG. 37

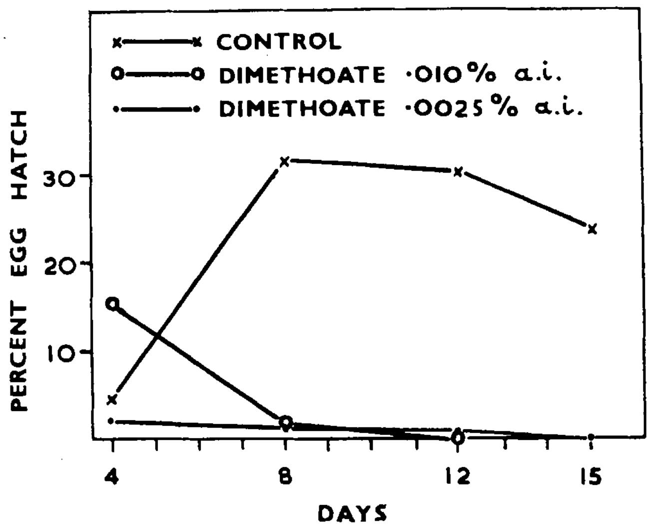
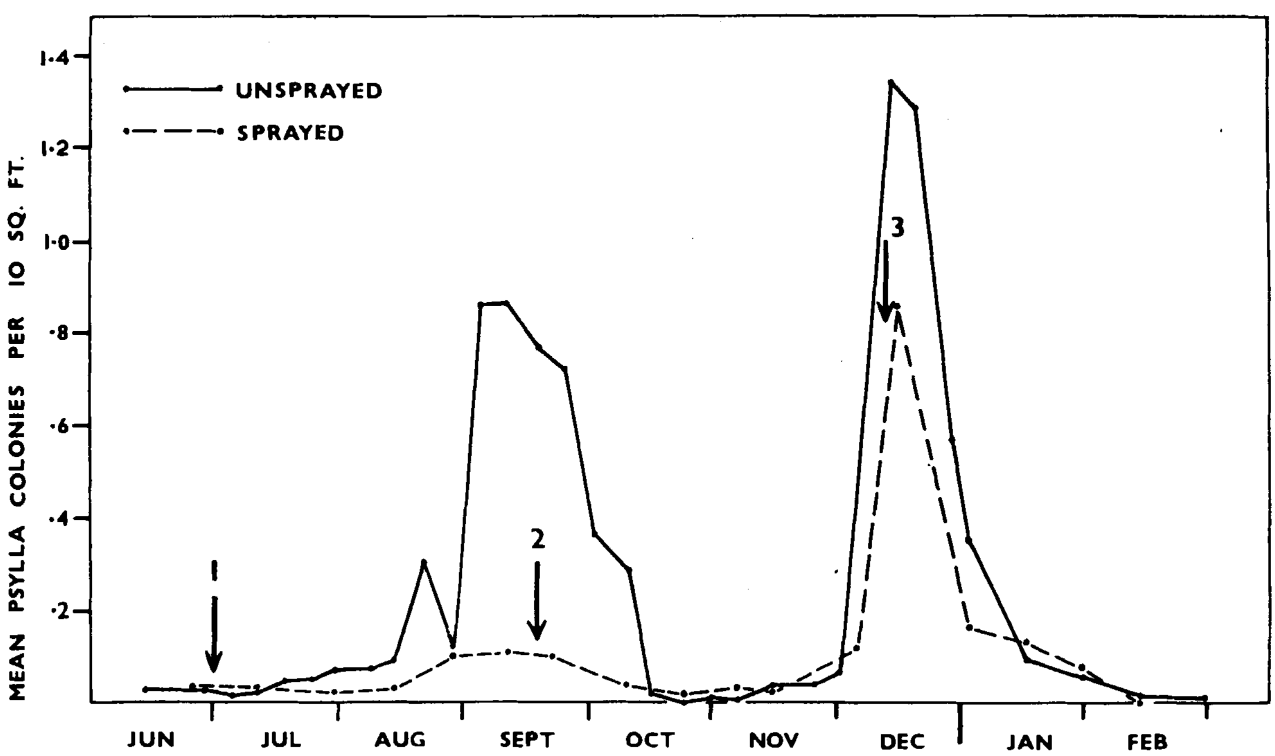

CONTROL
DIMETHOATE ·010% a.i.
DIMETHOATE ·0025% a.i.
PERCENT EGG HATCH
30
20
10
4
8
12
15
DAYS

FIG. 38


UNSPRAYED
SPRAYED
MEAN PSYLLA COLONIES PER 10 SQ. FT.
1·4
1·2
1·0
·8
·6
·4
·2
1
2
3
JUN
JUL
AUG
SEPT
OCT
NOV
DEC
JAN
FEB

in the first week of July to reduce the overwintering population. (Dimethoate requires a 14-day safety period before picking).

2. A second application of dimethoate at .005% a.i. plus ¼% mineral oil in August or September when the bulk of the main generation on the spring growth cycle is in the young nymph stage. The exact time of application will depend on the timing of the flush cycle and level of infestation so that each grove should be judged separately.

3. Further applications of dimethoate at .005% a.i. during the November/December flush cycle (or at other times of the year) will depend on population levels shown by orchard inspections.

During the 1968-69 season the above programme was applied to a block of 50 mature trees near the unsprayed study site at the Malkerns Research Station. In the sprayed block 20 trees were selected at random for fortnightly vector assessments and flush counts. Flushing rhythm was very similar in both sets of trees and there was no indication of any meaningful difference in levels of parasitism. Fig. 38 compares population densities in the sprayed and unsprayed trees. Populations recorded at the start of the build-up in August and during the two main upsurges were analysed as a time sequence using the pooled error derived from an individual analysis of variance of data collected on each date. A log (x + 1) transformation was used.

T. erytreae populations were considerably lower in the sprayed trees from July to October and during the September peak densities were about one seventh of those recorded in the sprayed block. The July spray appeared to be effective in checking the spring upsurge, populations in the sprayed trees being significantly lower on August 14, September 11 and September 25. Following the September spray environmental factors combined to cause a general population decline in October and November. With the advent of more favourable conditions in December a sharp population build-up took place in both sets of trees, the third spray being applied about two weeks too late to prevent the

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EXPLANATION OF FIGURES

Fig. 37 Effect of dimethoate on the eggs of *T. erytreae*. Trial conducted in February, 1968, application with knapsack sprayer

Fig. 38 Populations of *T. erytreae* in sprayed and unsprayed trees at Malkerns Research Station during the 1968-69 season. Arrows indicate the application of sprays. Mineral oil at ¼% added to all sprays. (1) July 1 - dimethoate .01% a.i. (2) Sept 25 - dimethoate .005% a.i. (3) Dec 12 - dimethoate .005% a.i. Populations were significantly different at the 5% probability level on Aug 14, Dec 19, and Jan 2; at the .1% probability level on Sept 11, 25, and Oct 10. Pooled S.E. of means = .0735. L.S.D. P = 5% .16; P = .1% .34

development of fairly dangerous populations. However, densities remained significantly lower in the sprayed trees and by the end of January both populations declined to tolerable levels for the rest of the summer.

It must be emphasized here that although the spring parathion spray adopted by many growers gives a good kill of T. erytreae, it is usually directed primarily against the other members of the spring pest complex and as such is often applied too late to prevent high populations of T. erytreae in August and September. However, if carefully timed the parathion spray could replace the second dimethoate spray in the above programme.

Due to their vigorous and prolonged flushing, young trees or heavily pruned trees frequently support high and persistent populations. Newly planted trees at Malkerns Research Station are sprayed with dimethoate at .01% a.i. plus ¼% mineral oil when inspections show a mean of 0.5 colonies per tree.

The importance of flushing rhythm in regulating vector populations should be borne in mind at all times. Where possible cultural practices, especially irrigation, should encourage winter tree dormancy and well-defined flushes in the summer (Catling, 1969a).

7. SUMMARY

1. Greening became epiphytotic in the Malkerns district of Swaziland in the early nineteen-sixties and has since been a severe limiting factor to citrus production. In Malkerns the disease causes a decline in growth, premature fruit drop, and a large proportion of unmarketable fruit. Apart from one small pocket of infected trees, no cases of clearly-defined visible greening are known in the Lowveld region, though the presence of a latent strain is not unlikely. Intermediate between Middle- and Lowveld is Ngonini where fairly low but potentially dangerous levels of the disease occur.

2. Transmission studies showed T. erytreae to be the principal vector of greening in Malkerns. No transmission was obtained with the nymphal stages of this vector, or with the black citrus aphid, T. citricidus. Four other psyllid species, two of which may feed on citrus for extended periods, were not found to be vectors. Preliminary investigations suggested a seasonal fluctuation in the transmission efficiency of T. erytreae, highest efficiency occurring in spring and early summer and lowest efficiency in midsummer. The percentage of infective individuals in field populations was found to be low (1.6%), but single adults, both male and female, transmitted the disease to citrus seedlings. Greening spread to new plantings within 3-7 months in heavily-infected areas.

3. First attempts to isolate the causal organism from the salivary glands of infected vectors were unsuccessful. Preliminary tests did not reveal the presence of a definite marker substance of diagnostic value in infected individuals.

4. The control of _T. erytreae_ depends on the use of insecticides. Foliar sprays were found to be more effective than soil-applied systemic materials. A low concentration of dimethoate, which is relatively inexpensive and safe to use in an integrated programme, was found to be effective against all stages of the vector. A spray grogramme based on 2-3 sprays of dimethoate was shown to control vector populations provided that applications were carefully timed during the flushing period.

SECTION C

Observations on *Diaphorina citri* Kuw.

1. INTRODUCTION

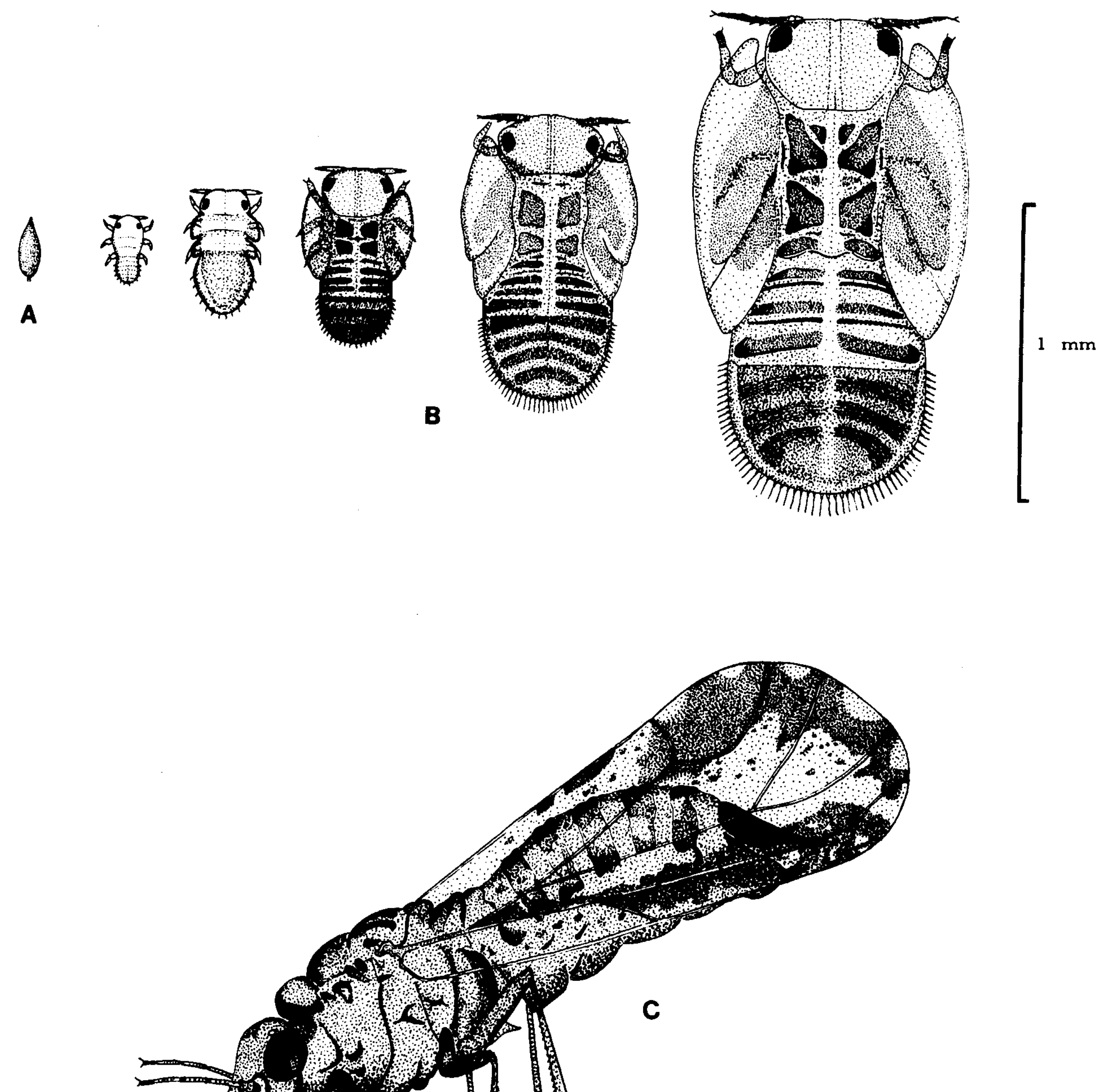
Diaphorina citri Kuw. has been recognized as a serious pest of citrus for the past 50 years. It was recorded as a dangerous pest in Asia by Crawford (1919), in India by Husain & Nath (1927), in southern China by Hoffmann (1936), and according to Dr. Clare R. Baltazar (personal communication, 1968) has been a pest of citrus in the Philippines since 1921.

It appears that toxins are introduced into the plant during the feeding of *D. citri*. Nakadaira *et al.*, (1964) found that the insect produces irregular, yellow feeding spots on leaves. In the Punjab, Husain & Nath (1927) reported that large numbers of *D. citri* cause branches to 'dry up', that two seasons of high populations cause extensive dieback, and that a third successive outbreak may kill entire trees. Ahmad (1961) reported that high populations may reduce citrus yields by as much as 90% in some areas of western Pakistan. Exceptional outbreaks have been observed to cause blossom and fruitlet drop in the Batangas Province of the Philippines (Celino, C.S., 1968, personal communication).

Like *T. erytreae*, however, the present significance of *D. citri* lies mainly in its ability to transmit the causal organism of the greening or leaf mottling disease. In 1965 Tirtawadjaja *et al.*, demonstrated that the vein-phloem degeneration disease of Indonesia is transmitted by *D. citri*. Salibe & Cortez (1966) cited preliminary evidence that this psyllid is the vector of Philippine leaf mottling and this was later confirmed by Celino *et al.*, (unpublished report of 1966), and Martinez & Wallace (1967). In India, Capoor *et al.*, (1967) have shown convincingly that *D. citri* is an efficient vector of greening. It is also believed to transmit the likubin disease of Taiwan (Su & Matsumoto, 1969) and probably greening in Brazil (Rossetti, 1969).

The greening-leaf mottling disease has had a catastrophic effect on citrus in a number of countries in Asia and the Far East. Fraser *et al.*, (1966) concluded that greening is the major cause of the general decline of citrus in many parts of India. According to Thrower (1959) there has been a virtual collapse of the citrus industry in Indonesia due to a disease which strongly resembles greening and which was later named vein-phloem degeneration. It will be shown later that the disease is particularly severe in the Batangas area of the Philippines, and that it occurs in several other countries (Table 36).

Excellent descriptions of the symptomology of Indian greening and Philippine leaf mottling may be found in recent papers (Fraser *et al.*, 1966; Salibe & Cortez, 1966, and Martinez & Wallace, 1967). In Asia and the Far East recog-


A
B
1 mm
C

nition of the disease from symptoms alone is often difficult. Very similar leaf symptoms may be caused by a wide variety of factors varying from nutritional disorders to the presence of other diseases such as root-rots and gummosis, and even other virus diseases such as tristeza and exocortis. Hence tissue grafts and insect transmission studies are often necessary before a reliable diagnosis can be made.

A review of the literature reveals that there has been little significant study on the biology or ecology of D. citri since the work of Husain & Nath in India (1924, 1927). Those authors also included a detailed description of all stages of the insect (1927). The information given in this section is based mainly on the papers of Catling (1968a, 1970).

2. BIOLOGY OF D. CITRI

The following observations on the biology of D. citri in the Philippines are in general agreement with Husain & Nath (1927). Fig. 39 shows all stages of the insect.

The egg is 0.3 mm in length, yellowish-orange in colour, and is firmly anchoured into the plant tissue by means of a short stalk. Eggs are laid on the tips of growing shoots and in leaf axils where they appear to be well placed to resist unfavourable extremes of weather. The nymphs are small, dorso-ventrally compressed, with the general appearance of unarmoured scales, with which they are often confused. They develop deep red compound eyes and dark antennae. Nymphs settle on the stem and leaf petioles of young shoots and when overcrowded move down the shoot but are rarely found on mature foliage. The developmental stages are thus aggregated into distinct colonies. The five instars may be recognized by size differences, the shape of the developing wing buds, and by the arrangement of their dorsal thoracic sclerites.

The newly-emerged adult is approximately 2.4 mm in length, delicate and light in colour. After a few days, in which there is a darkening in colour, adults copulate and the female is then able to lay fertile eggs immediately. Adults are normally active insects which jump at the slightest provocation. They fly strongly for a few seconds before alighting near to their take-off point. Under normal conditions they appear to disperse weakly and are incapable of sustained flight. There is no diapause. Adults may live for several months especially when their host plant is semi-dormant (Husain & Nath, 1927). Feeding produces no malformation of plant tissue. The sex ratio of 518 adults

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EXPLANATION OF FIGURE

Fig. 39. Diaphorina citri Kuw. A-egg; B-five nymphal instars; C-adult female in feeding position. All stages to same scale. Drawn from freshly-preserved specimens in alcohol. del. H.D. Catling

collected at various places in the Philippines was 44.8% males. Faeces is in the form of white threads of honey-dew which according to Husain & Nath (1927) may support a black sooty mould fungus.

Egg-laying is strongly influenced by the availability of flush points for breeding sites and is suspended when trees become dormant. According to Husain & Nath (1927) females of D. citri will lay up to 800 eggs when confined on a continuous supply of young shoots. The rate of egg-laying in the insectary at Lipa during July and August, 1968, was only 8.0 eggs per day; and the mean colony size in the field was 4.5 eggs plus 3.3 nymphs, or 7.8 individuals per colony (60 colonies examined). The mean pre-oviposition period of five females was 12 days. Although larger colonies were observed on some occasions and in Camarines Sur one isolated colony was found with 160 fourth and fifth instar nymphs and 25 adults, in general colony size was small at this time of the year. It is likely that maximum fecundity and colony size occurs on the first flush cycle at the beginning of the rainy season.

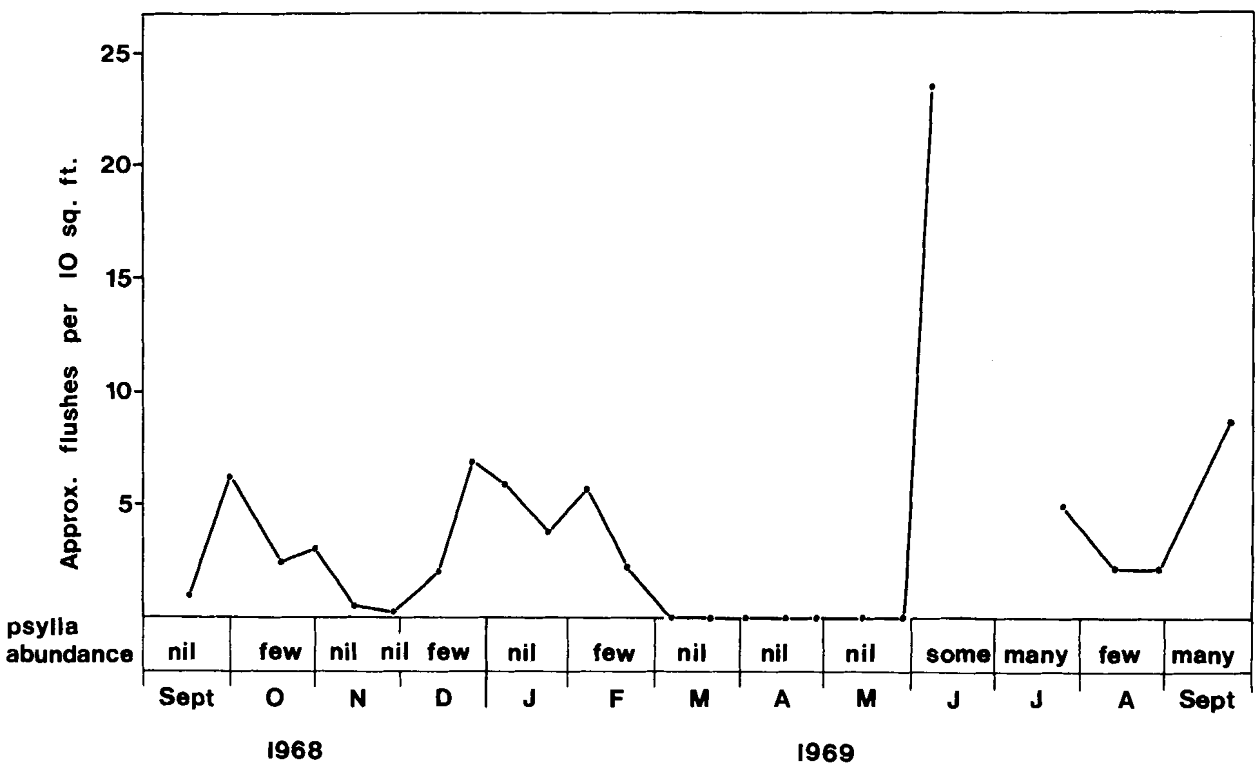
In the insectary at Lipa, at a mean temperature of 25-26°C, the incubation period was three days and nymphal development was completed in 11-15 days (32 adults). Due to the tropical climate of most of the Philippines, durations are probably very similar at other times of the year.

All species of citrus are attacked by D. citri. In the Philippines the insect was collected on oranges, Citrus sinensis (Linn.); mandarins, C. reticulata; pummelos, C. grandis (Linn.); lemons, C. limon (Linn.); limes, C. aurantifolia (Christm.); and calamondin, Citrus x Fortunella hybrid. There is some circumstantial evidence that D. citri has spread to citrus from indigenous host plants in some areas. The Philippine flora is rich in Rutaceae and in India and South East Asia D. citri has been found on five different genera in this family. The author found D. citri breeding on Murraya exotica at Los Baños in the Philippines, and on Murraya sp. in Taiwan. This introduced species is frequently used as a hedge near citrus groves in the Philippines.

3. BIONOMICS OF D. CITRI

(i) Population fluctuations and flushing rhythm of citrus. The population fluctuations of D. citri and the flushing rhythm of the citrus host were studied in an unsprayed grove of mature mandarin trees at the Lipa Experiment Station, Batangas, Philippines, from September, 1968, to September, 1969, by Mr C.S. Celino. The study sitewas laid out and flush counts conducted according to the method described earlier. D. citri was sampled at fortnightly intervals by removing 20-50 flushpoints for examination under a stereo-microscope. No attempt was made to test the reliability of this sampling method.

Fig. 40 shows a clear relationship between insect populations and flushing rhythm. D. citri was not found during the dry period from March to May when the trees were dormant, highest populations were recorded from June to September


Approx. flushes per 10 sq. ft.
25
20
15
10
5
psylla abundance
nil
few
nil
nil
few
nil
few
nil
nil
nil
some
many
few
many
Sept
O
N
D
J
F
M
A
M
J
J
A
Sept
1968
1969

on the main growth cycle of the season which is stimulated by the start of the rainy season, and small numbers were present from October to February on two lighter growth cycles in September/October and January/February. Two yellow sticky traps operated from April to November, 1969, and removed at 2-4 week intervals, indicated corresponding population trends. A similar pattern of seasonal abundance was evident in the previous season at Lipa Experiment Station (Catling, 1968a).

(ii) Natural enemies. Husain & Nath (1924) found *Tetrastichus radiatus* Waterston (Eulophidae) to be the main parasite attacking *D. citri* in the Punjab. This external parasite was not found during field surveys in the Philippines (Catling, 1968a) nor has it been recorded in that country (Baltazar, 1966) and should thus be considered as a candidate for introduction into the Philippines.

Several species of internal parasites, at least two of which are probably hyperparasites, were reared from *D. citri* nymphs collected in the Philippines. The three main species were:-

?*Psyllaephagus* sp. (Encyrtidae) females, from Batangas, Bicol and Mindanao
Marietta nr *exitiosa* Compere (Aphelinidae) from Batangas
Aphidencyrtus sp. (Encyrtidae) from Batangas

Of 147 parasites reared, 51.7% were ?*Psyllaephagus* sp. which appears to be the most common primary parasite in the Philippines and has been recorded by Dr. B.D. Burks of the U.S. National Museum, Washington D.C. in Taiwan (Annecke D.P., 1969, personal communication). *Marietta* nr *exitiosa*, which is probably the main hyperparasite, accounted for 25.2%; and 17.0% were *Aphidencyrtus* sp. Other species recorded in small numbers were *Coccophagus tibialis* Compere (Aphelinidae) males from Balete, Rosario and Lipa; and *Cheiloneurus* sp. (Encyrtidae). In 1969 Mr C.S. Celino (personal communication) reared 536 parasites of which 98.9% were ?*Psyllaephagus* sp. and 0.7% were *Marietta* nr *exitiosa*.

Husain & Nath (1927) observed five species of coccinellids to attack the nymphs, *Coccinella septumpunctulata* Linn. being the most common. Also listed as predators were a syrphid larva, a chrysopid larva and various spiders and mites. Similarly, in the Philippines, larvae of a syrphid, a neuropteran and a coccinellid were found associated with *D. citri* nymphs on several occasions (Catling, 1968a).

EXPLANATION OF FIGURE

Fig. 40 Flushing rhythm and abundance of *D. citri* from September, 1968, to September, 1969, at the Lipa Experiment Station. (From data supplied by Mr C.S. Celino, 1969)

(iii) Extremes of weather. The influence of extremes of weather on the population fluctuations of D. citri is an extremely important factor still to be elucidated before any serious attempt can be made to explain the population dynamics of this vector. It appears from several field observations, however, that D. citri is more resistant to extremes of weather than T. erytreae. In Réunion fairly high populations of D. citri were observed in the hot coastal zone whereas T. erytreae was confined mainly to cooler areas above 1,600-2,000 feet (Bové, J. & J. Cassin, 1968, unpublished report). In their study of D. citri in the arid Indian Punjab, Husain & Nath (1927) did not mention any signs of mortality of eggs and nymphs following extremes of weather. Dr L.C. Knorr, who studied Indian decline during 1969, is of the opinion that the vector must be able to strongly resist high saturation deficits (SD) in order to exist at all in the Punjab. In Multan, western Pakistan, where D. citri is a serious pest (Ahmad, 1961), the mean annual rainfall is 6.6 inches and the mean maximum daily temperature exceeds 38°C for five consecutive months of the year.

In equatorial regions such as the Philippines, high levels of SD rarely occur. Temperature-moisture climographs were drawn for four meteorological stations in or near some of the citrus areas of the Philippines, namely Lipa (Batangas), Lucena (Quezon), Legaspi (Bicol), and General Santos (Cotabato). None of these climographs entered the area of temperature and RH found lethal for T. erytreae in South Africa. In the driest area, the Batangas, Lipa experienced a maximum daily SD in the 1968 dry season (February to July) of 23.1 mm Hg. The six severest days during this period averaged 16.6 mm Hg which is considerably less than the critical level of 25.9 mm Hg (34.6 mbars) for T. erytreae. It is thus unlikely that weather is an important mortality factor in populations of D. citri in these regions.

4. SURVEYS FOR D. CITRI AND GREENING IN ASIA AND THE FAR EAST

(i) Philippines.

The vector was surveyed by two methods depending mainly on the size of the grove selected. On most occasions the same two or three observers examined a number of randomly-selected flush points for eggs and young stages of the insect. In most large groves 50-200 flushes were examined with a hand lens either in situ or after removal from the trees ("surveys"). In small or backyard groves, or where trees were semi-dormant, a rapid search was made for 10-20 minutes or until the vector was recovered ("spot-checks"). The rate of discovery was taken as a measure of prevalence.

Greening was identified mainly by leaf and fruit symptoms. In addition, a small number of fruit and bark samples were taken from diseased trees for indexing by the fluorescence test of Schwarz (1968a).

The results of vector surveys and spot-checks are summarized in Table 35 and the areas surveyed are shown in Fig. 41.

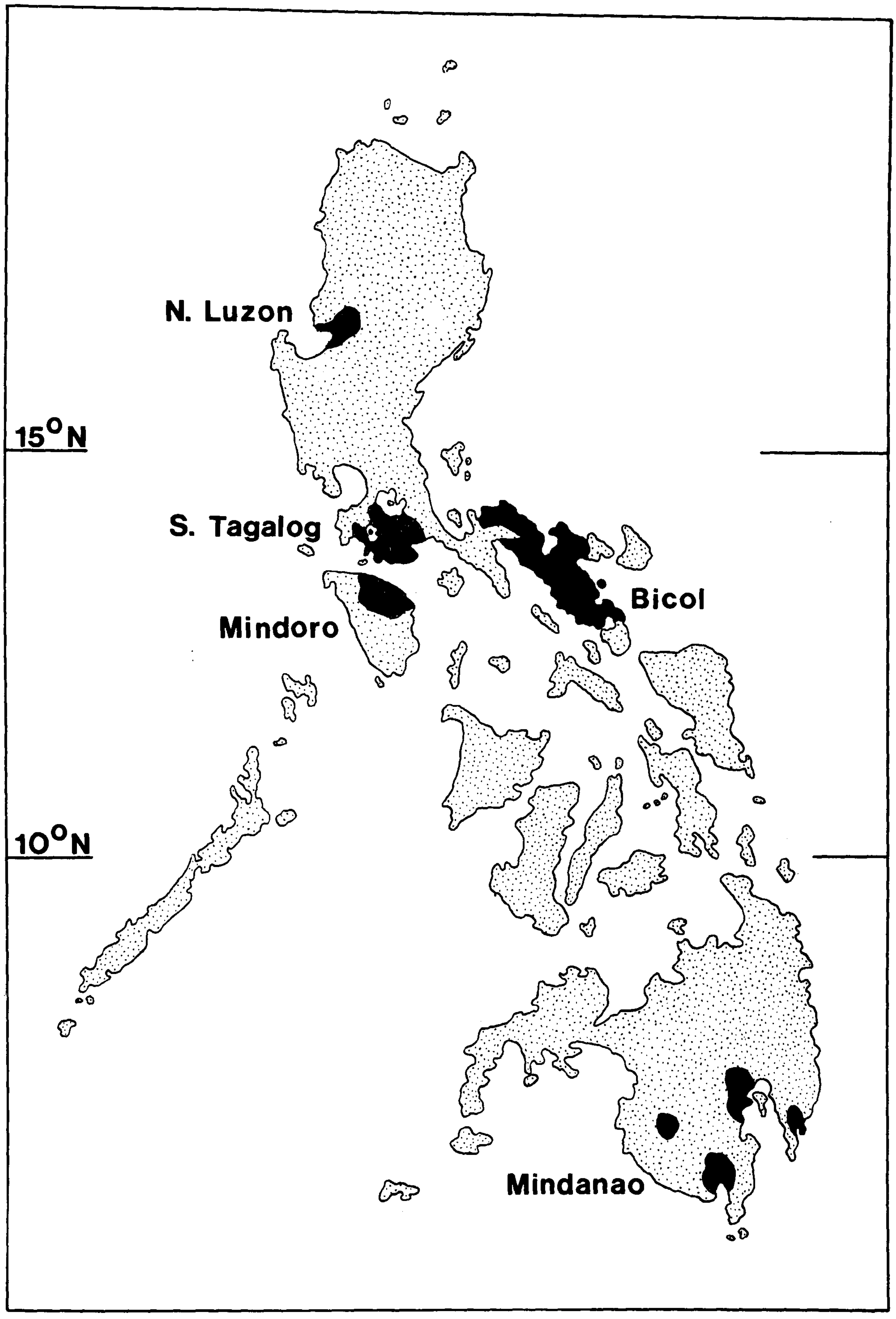

N. Luzon
15°N
S. Tagalog
Bicol
Mindoro
10°N
Mindanao

Table 35 Results of surveys and spot-checks for D. citri in citrus groves in the Philippines during July and August, 1968

Region	Province	SURVEYS				SPOT-CHECKS	
		No. groves surveyed	No. groves infested	No. flushes examined	Percent flushes infested	No. spot-checks	No. infested
Southern Tagalog	Batangas	11	11	1100	35.9	7	6
	Laguna	1	1	80	1.3	-	-
	Cavite	2	2	200	27.5	-	-
	Quezon	-	-	-	-	1	1
Bicol	Albay	5	4	350	42.6	7	7
	Sorsogon	1	1	50	36.0	1	1
	Camarines Sur	4	3	250	8.4	11	8
	Camarines Norte	4	0	230	0.0	5	0
Mindoro	Oriental	4	0	600	0.0	3	0
Mindanao	Davao de Sur	2	1	150	10.0	5	1
	Davao Oriental	3	1	250	27.6	3	1
	Cotabato	4	2	400	20.8	4	2
Northern Luzon	Benguet	1	0	100	0.0	3	0
	La Union	-	-	-	-	2	1

Southern Tagalog. With one exception, D. citri was fairly abundant in all groves searched in this region. Centred in the Batangas province, this is the oldest and formerly the most important citrus growing area in the Philippines. Since the rampant spread of the disease in the late 1950's, however, more than one million trees have been lost and the 1968 crop was estimated at about one tenth of that harvested in 1960. Because much of the propagative material for other citrus areas has originated from the Batangas, it is possible that the disease has been introduced into most of the recognized citrus areas of the Philippines.

Disease symptoms were found in every grove, most trees showing severe decline with the exception of the Rosario/Padre Garcia area where for some unexplained reason trees continue to bear and grow well. Apart from the absence of vein-yellowing, there was a striking resemblance between leaf symptoms and general tree appearance of mandarins in Batangas (mainly Ladu and Szinkom), with greened sweet orange trees in South Africa. It was too early in the season for a valid comparison of fruit symptoms but it would appear that these are not reliable in mandarins. No definite marker substance was

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EXPLANATION OF FIGURE

Fig. 41 Areas surveyed for D. citri and greening disease in the Philippines in 1968 found in two fruit samples from diseased Ladu mandarins, but a bark sample from the same trees was clearly positive for greening. Greening symptoms were also observed in several neglected Valencia trees in Batangas, three fruit samples showing low concentrations of marker substance and a single bark sample again being clearly positive.

Bicol and Mindoro. Table 35 indicates that the vector was common in the Bicol region with the exception of Camarines Norte, but was not found in seven groves in Mindoro Oriental. It is possible, however, that further search will reveal its presence in these areas. Scattered leaf symptoms were observed in both regions but in only three groves could this be associated with greening. In one grove in Mindoro the disease had obviously been introduced with propagative material from Batangas. Cortez (1969) has since observed the vector in Mindoro Occidental and in the Visayas.

Mindanao and Northern Luzon. The vector was present in most groves examined in Mindanao and in one in northern Luzon. Very few symptoms were observed in either region.

The vector is thus widely distributed in the Philippines and the potential exists for greening to spread to most of the citrus growing areas. Fortunately, diseased groves outside of the severely-affected Batangas area appear to be relatively few and are isolated.

(ii) Other countries

Japan. Citrus was examined for *D. citri* and greening symptoms at the Okitsu Horticultural Research Station, in the Miyahara and Arita districts, and in the Ehime Prefecture. No sign of vector or disease was found at any of the five sites surveyed. Greening has not been reported from Japan nor is there any reliable record of *D. citri* occurring in the country.

Taiwan. *D. citri* was collected on citrus at Kwanhsi Citrus Experiment Station outside Taipei and on a hedge of *Murraya* sp. in Taipei. Symptoms of likubin were observed in the field and in test plants in the Phytopathological Laboratory of the National Taiwan University, Taipei. Likubin symptoms were very similar to those of leaf-mottling in the Philippines, particularly in the case of the calamandarin variety which is grown in the Batangas. As yet small-scale transmission tests have failed to implicate *D. citri* as the vector of likubin, but the author considers it very likely that further tests will reveal the necessary evidence.

Hong Kong. *D. citri* was found in one of the three groves visited in 1968 and pinned specimens were examined in the insect collection at Tai Lung (Catling, 1968b). During another visit in 1969 fairly conclusive greening symptoms were observed in sweet orange, mandarins, and pummelos at Tai Po Kau, and in mandarins at Hong Tak Yuen. According to Mr L.Y. Fai, declining trees in

Table 36 Distribution of *D. citri* and the presence of greening-like diseases of citrus

COUNTRY	GREENING-LIKE DISEASES
ASIA	
India (Husain & Nath, 1927; Ebeling, 1959)	greening (Fraser et al., 1966)
Nepal (Eastop, 1969)[1]	greening (Catling, 1968c)
Pakistan (Husain & Nath, 1927; Eastop, 1969[1])	-
Ceylon (Wyniger, 1962)	greening (Moreira, 1967)
Burma (Ebeling, 1959)	-
Thailand (Anonymous, 1965)	decline (Thrower, 1968)
Malaysia (Ebeling, 1959)	possible greening (Chiarappa, 1968)[3]
Southern China (Husain & Nath, 1927; Ebeling, 1959)	yellow shoot (Calavan, 1968)
Hong Kong (So, 1967)	probable greening (Catling, 1968b)
Indonesia (Husain & Nath, 1927; Ebeling, 1959)	decline (Thrower, 1959): vein phloem degeneration (Tirtawadjaja et al., 1965)
Philippines (Husain & Nath, 1927; Ebeling, 1959)	greening (leaf-mottling) Salibe & Cortez, 1966; Martinez & Wallace, 1967)
Taiwan (Husain & Nath, 1927)	likubin (Calavan, 1968; Su & Matsumoto, 1969)
INDIAN OCEAN	
Mauritius (Moreira, 1967; Eastop, 1969[1])	greening (Moreira, 1967)
Réunion (Bové & Cassin, 1968)[2]	greening (Moreira, 1967; Bové & Cassin, 1968[2])
S. AMERICA	
Brazil (Lima, 1942; Eastop, 1969[1])	stubborn (Calavan, 1968) greening (Rossetti et al., 1969)

1 Eastop, V.F. 1969, personal communication, specimens in British Museum

2 Bové, J. & J. Cassin 1968, unpublished reports

3 Chiarappa, L. 1968, personal communication

Hong Kong are identical in appearance to trees infected with yellow shoot or dragon shoot in Canton, southern China. Yellow shoot is believed to be closely akin to greening (Calavan, 1968).

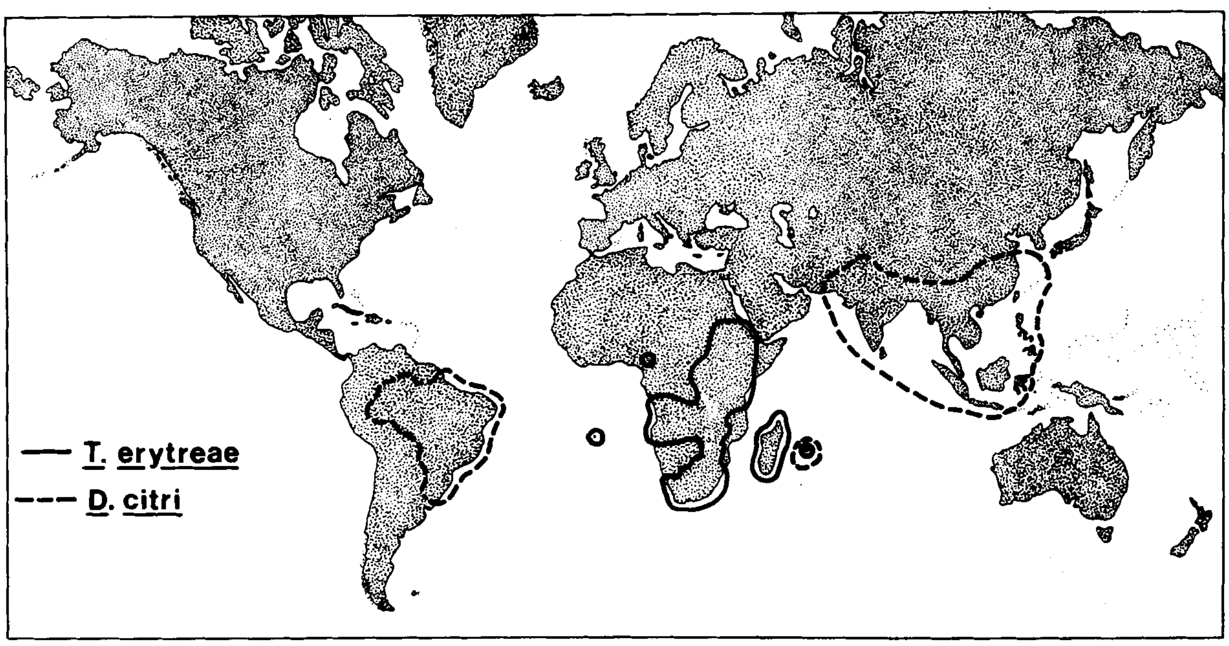
Thailand. Two of six groves in the Chantaburi district were found with low populations of D. citri. Specimens in the insect collection of the Plant Industry Division indicate that the vector is widespread in Thailand. No greening symptoms were evident in the young citrus area of Chantaburi but the disease has been observed in other parts of the Kingdom (Thrower, 1968).

India. D. citri was not found in any of the three groves visited. Greened trees were shown to the author at the Indian Agricultural Research Institute, New Delhi. At Poona Agricultural College and in a nearby grove, severely affected sweet orange trees were observed with the full syndrome of the disease. A single fruit sample was found to be strongly positive with the albedo-fluorescence test.

Nepal. The vector was not observed in the Kathmandu Valley, all trees appearing free of greening (Catling, 1968c). In the Pokhara Valley, where a virulent strain of greening has caused a severe decline of citrus, three out of six sites were infested with D. citri. At the Pokhara Research Substation the complete syndrome of the disease was observed; sweet orange trees showing abundant leaf mottling, vein-yellowing, lop-sided fruit with dark aborted seeds and two fruit samples yielded high concentrations of the greening marker substance; and mandarins showed identical leaf symptoms and general tree appearance to trees examined in the Philippines. As in South Africa and the Philippines, lemons and limes at Pokhara were only slightly affected by the disease and were still growing and bearing well. The vector is also reported to be present in the eastern Terai from where leaf symptoms have been noted. There is evidence that greening-infected material has been introduced into Nepal from Uttar Pradesh, India.

5. WORLD DISTRIBUTION OF GREENING VECTORS

Distribution of T. erytreae (Fig. 42). This vector is restricted to Africa south of the Sahara, i.e. Sudan, Ethiopia, Eritrea, Cameroun, Congo (Kinshasa), Ruanda, Kenya, Uganda, Tanzania, Zambia, Malawi, Rhodesia, South Africa; and is found in Madagascar, Mauritius and St. Helena (Commonwealth Institute of Entomology, 1967). It has also been recorded in Réunion (Bové, J. & J. Cassin, 1968, unpublished report), Swaziland (Catling, 1969a), and is suspected in Angola (Eastop, V.F. 1969, personal communication). Greening is known in South Africa (McClean & Oberholzer, 1965a), Swaziland (Catling, 1969a), Madagascar (Bové, J. & J. Cassin, 1968, unpublished report), Réunion (Bové, J. & J. Cassin, 1968, unpublished report), Mauritius (Moreira, 1967) and has been observed by the author in Rhodesia.



T. erytreae
D. citri

Distribution of D. citri. Fig. 42 and Table 36 show that D. citri is widely distributed in the Orient and is present in Brazil. North of Taiwan the vector occurs in the Ryukyu archipelago (Miyatake, 1965) but as far as can be ascertained has not been recorded in Japan. Greening-like diseases have been reported from 11 of the 15 countries where this vector is known to occur on citrus. Furthermore, the disease is suspected in Malaysia and Hong Kong and there is a strong possibility of it being present in Burma and Pakistan - especially in western Pakistan bordering the Indian Punjab.

D. citri was collected by the author in the Philippines, Taiwan, Hong Kong, Thailand, and Nepal, and he has since received specimens from Brazil, Réunion and India.

Both psyllid vectors thus occur in Réunion and Mauritius.

6. CONTROL OF D. CITRI

At present the application of insecticides is the only practical way of controlling D. citri. Many workers have shown that the immature stages can be effectively controlled with a wide range of modern insecticides. As foliar sprays Ahmad (1961), Sethi (1967) and Atwal & Verma (1968) found parathion and demeton methyl to be effective. Malathion, carbaryl, diazanon and thiometon were tested by Sethi (1967), and malathion and phosphamidon by Atwal & Verma (1968). Ahmad (1961) found endrin, aldrin, dieldrin, chlordane, trichphon and azinphos to give good control. Atwal & Verma (1968) tried soil applications of the systemics dimethoate, demeton methyl, and formothion but absorption and translocation in the tree were disappointingly slow and reinfestation occurred within four weeks of application.

Of the above-mentioned materials only trichlorphon and demeton methyl may be regarded as fairly safe, selective insecticides. Virtually all of the other materials are likely to precipitate severe mite and scale problems on citrus - especially if it becomes necessary to use materials such as endrin three times a year as has been the practice in some parts of India (Fraser, L.R., 1968, unpublished report). Low concentrations of materials such as dimethoate, demeton methyl, and endosulphan as foliar sprays would appear to be the best way of controlling D. citri. In the Philippines dimethoate, which was shown earlier to give excellent control of T. erytreae, gave 79% kill of nymphs at a concentration of .0075% a.i. in a small field trial, despite the occurrence of heavy rain two hours after application (Catling, 1968a). Good control has been obtained with this material at approximately .02% a.i. and many growers in the Batangas are now reported to be using this material, (Celino, C.S. 1969, personal communication).

EXPLANATION OF FIGURE

Fig. 42 The known distribution of Trioza erytreae (Del Guercio) and Diaphorina citri Kuw., psyllid vectors of the citrus greening disease. (Distribution of T. erytreae partly after Map No. 234 of the Commonwealth Institute of Entomology)

There seems to be little hope of eradicating D. citri in most citrus areas of the Orient. The insect is widely distributed and well adapted in the profusion of small plantings and backyard trees which characterize these countries. It has been collected on a wide range of alternate host plants from which it could reinfest sprayed groves. The mounting of a suitable eradication programme would require considerable finance and organization. Fortunately, as mentioned earlier, there is evidence that fairly high vector populations are needed before any large-scale transmission of greening occurs. Therefore, by keeping vector populations at low densities with well-timed foliar sprays of a selective material it is possible that the spread of the disease may be halted or at least drastically reduced.

7. SUMMARY AND CONCLUSIONS

The biologies of D. citri and T. erytreae are very similar. Aspects of biology and appearance which are useful in distinguishing the two vectors are shown in Appendix 1. The world distribution of both species and the occurrence of greening-like diseases of citrus are discussed in this section.

D. citri is an important vector of the disease in Asia and the Far East and is also present in South America. From the results of several transmission experiments it would appear that D. citri is a more efficient vector than the African species. At the present time the only effective method for controlling the vector is the application of selective insecticides.

Very little research has so far been carried out on the ecology of D. citri. That populations vary greatly in size during the season and from year to year, as is the case for T. erytreae, has been recorded in India by Husain & Nath (1927) and in the Philippines (Celino, C.S. 1968 personal communication). The rate of development of the immature stages is fairly constant in equatorial regions such as the Philippines where there is little change in mean temperature throughout the year. And in these regions weather extremes do not appear to be an important limiting factor. In those regions with a continental climate, such as the Indian Punjab, the definite seasonal fluctuation in mean temperature produces a difference in the rate of development during the year (Husain & Nath, 1927). Probably of more importance from an ecological point of view, however, is the extremely hot and arid climate of some of these regions, though there is field evidence that D. citri is more resistant to such extremes than T. erytreae.

Both vectors appear to have a similar complex of natural enemies but this is unlikely to be a key factor in their populations dynamics. Nothing is known of seasonal changes in the quality and nutritive value of citrus flush under tropical conditions. However, studies in the Philippines have shown that there is a strong correlation between flushing rhythm and the numbers of D. citri. The pattern for highest populations to occur on the major flush cycle at the end of the dry season, and lowest numbers to be found during the drier, semi-dormant period, has been observed in Indian citrus by Husain & Nath (1927) and Capoor *et al.*, (1967), and in Brazilian citrus by Rossetti (1969).

It is possible that differences in seasonal flushing rhythm and flushing density play a very important part in regulating numbers. Much Asian citrus is not irrigated and thus totally dependent on rainfall, while still more is subjected to monsoons and violent typhoons which must produce considerable variation in tree growth from year to year. It is conceivable that in some seasons a series of particularly favourable growth cycles could precipitate large outbreaks of the vector.

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APPENDIX

Biological differences of the two psyllid vectors

			Trioza erytreae (Del Guercio)	*Diaphorina citri* Kuw.
Egg	location		mostly along edges of young leaves	on tips of growing shoots, on and between unfurling leaves
	placement on plant tissue		long axis horizontal to surface	long axis vertical to surface
Nymph	location		on lamina of underside of leaves	mainly on young stem and petioles
	appearance:	colour	variable: yellowish orange, light green, grey	yellowish brown
		abdominal spots	advanced nymphs with two dark abdominal spots	no abdominal spots
		sclerites	no definite plates or sclerites	well-defined sclerites on dorsum
		wing pads	small wing pads	massive wing pads
		fringe	complete fringe of fine white filaments	large filaments on abdomen only
	leaf galls		open gall or pit formed, only dorsal surface of nymph exposed	no gall formed, nymphs completely exposed
Adult	appearance:	colour	overall brown-grey, abdomen lighter ventrally	general colour light brown
			head black	head mainly light brown
		wings	clear and transparent	with dark areas (maculate)