

STUDIES ON THE ECOLOGY OF THE
SOUTH AFRICAN CITRUS PSYLLA, TRIOZA ERYTREA
(DEL GUERCIO) (HOMOPTERA : PSYLLIDAE)

BY

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I. INTRODUCTION

1. Economic Importance of *Trioza erytreae* (Del Guercio)

In the past *T.erytreae* was regarded as a citrus pest of minor importance in southern Africa (Van der Merwe, 1941). Though the feeding of large populations may reduce tree vigour by the removal of nutrients and the consequent pitting and malformation of young leaves, Van der Merwe (1941) stated that such leaves appear to function normally and are never shed. In many citrus areas citrus psylla is practically unknown and regarded as a curiosity. Even in the so-called "psylla areas" the author has found that serious outbreaks are commonly sporadic and often isolated.

The work of Schwarz (1964), and McClean & Oberholzer (1965) have completely changed the pest status of citrus psylla. They found that the mysterious citrus greening disease is caused by a transmissible virus and that *T.erytreae* is an important vector. Subsequent work involving successive transmissions of the disease, first by grafting and then by the vector, have confirmed these findings (McClean, personal communication, 1966). The correlation between psylla incidence and greening has been observed by the author on a number of occasions in the field.

2. The Greening Disease of Citrus

In sweet orange, Schneider (1966) found the greening virus to cause a necrosis of sieve tubes in leaves and fruit accompanied by the formation of pathological phloem tissue. The disease attacks all species and varieties of citrus. The whole tree may be stunted and show decline, or only a branch or sector may be affected. A diseased branch is poorly supplied with chlorotic, yellow-veined or mottled leaves and bears small, lop-sided, bitter-tasting fruit. Greened fruit frequently drops prematurely and always colours up poorly - whence the name "greening". Unlike the other well-known virus diseases of citrus, greening produces unmarketable fruit. McClean & Oberholzer (1965) give a detailed description of the disease.

It has become clear that greening is a peculiar and in many respects an atypical virus disease. According to McClean & Oberholzer (1965)

it can be/.....

it can be transmitted by grafting and by the psylla vector but both means are commonly inefficient. The virus spreads slowly in the tree and appears to remain latent for long periods. Greening closely resembles the pear decline disease of California in that both are transmitted by grafting and by a psyllid vector. In the case of pear decline Jensen et al. (1964) found the vector to be a more efficient agent of transmission than the graft. Field observations by the author suggest the same phenomenon in the greening disease.

According to Schwarz (1967), greening was first observed near De Wildt, Western Transvaal and in the White River area in the late twenties. That author states that the disease was severe in the White River and Plaston areas from 1932 to 1946, though the incidence of affected fruit declined in the mid-forties to late fifties. In the other areas the disease apparently decreased after the initial flare-up and within a few years was relegated to the status of a minor citrus malady. Unfortunately, no proper records exist of the exact nature of this first "greening cycle" and facts are based mainly on growers' memories and production figures for various packhouses in the greening areas. Greening again became a serious problem in 1958 and now occurs in most of the citrus growing areas of the Transvaal. It has been reported also from Natal, the eastern Cape, Swaziland and Rhodesia. A number of farms in White River, Tzaneen and Rustenburg have been put out of production and growers forced to seek alternative crops. In 1964 it was estimated that 100,000 trees were affected by the disease (Oberholzer et al., 1965). At the time of writing (January, 1967) this figure would hardly account for the infected trees in the Tzaneen-Letaba area alone.

At a lower level, the disease has followed a similar pattern on Letaba Estates. First noticed in the early 1930's, it persisted at low levels for the next thirty years but has been steadily increasing since 1963. Extremely alarming for Letaba Estates was the rate at which greening increased in the upper Letsitele Valley during 1966. These groves are situated within ten miles of Letaba Estates under similar conditions of climate and altitude.

There is little doubt that greening is but one of a complex of closely related virus diseases distributed widely throughout the major

citrus areas/....

citrus areas of the world. Table 1 shows details of their occurrence and insect vectors. Indian sweet orange decline, whose symptoms are closely allied to those of greening, is particularly virulent and has severely crippled citriculture in India (Fraser, personal communication, 1966). Stubborn has been known in the USA for fifty years and is reported by Chapot (1956) to be similar or identical to the Palestine leaf disease. Schwarz (1967) reported greening from the Mediterranean region.

Table 1. Greening-like diseases of citrus

The first two columns of the table are based on Calavan (196_).

Disease	Occurrence	Insect Vector
Greening	South Africa, Rhodesia, Sicily, Corsica, Morocco	<u>T.erytreae</u> (McClellan & Oberholzer, 1965).
Indian sweet orange decline	India	probably <u>Diaphorina citri</u> Kuwayama (Salibe & Cortez, 1967)
Vein-phloem degeneration (=Oriental leaf mottle)	Java, Philippines	<u>D.citri</u> (Celino et al., 196_)
Likubin	Formosa	possibly <u>Toxoptera citricidus</u> (Kirk) (Matsumoto et al., 1961)
Yellow shoot	China	possibly <u>T.citricidus</u> (Faan & Liu, 1965)
Palestine little leaf	Israel	unknown
Stubborn	All citrus areas of USA; Mediterranean region especially Morocco; Brazil, Argentine, Peru.	unknown

3. Aim of Project

The economic importance of T.erytreae lies in its ability to transmit the greening virus and it was the threat of greening which largely motivated this work.

This project is a study of the ecology of T.erytreae in the Letaba-Agatha district. Though psylla populations on Letaba Estates appear to have been consistently low in the past, this has not been the case in nearby groves in the Letsitele Valley - Agatha areas. The pattern of psylla incidence in these areas, which lie against the Drakensberg escarpment to the east of Letaba, has been one of sporadic population explosions frequently necessitating chemical control measures. Greening is rampant/....

is rampant in many of these groves. It would thus appear that Letaba is usefully placed for a study of the main ecological factors which govern the population fluctuations of citrus psylla.

4. Taxonomic Position

Psyllids belong to the Homoptera and form a single family, the Psyllidae. Van der Merwe (1941) discusses the previous nomenclature of T.erythrae and reports that it was first described in South Africa by Lounsbury in 1896. Synonyms listed by Ebeling (1959) are:-

Spanioza erythrae (Del Guercio)

Trioza erythrae Del Guercio

Trioza merwei Pettey

5. Distribution

T.erythrae appears to be strictly Ethiopian in its distribution (Sweeney, personal communication, 1967). Ebeling (1959) and Van der Merwe (1941) have listed its occurrence as follows: South Africa, Rhodesia, Malawi, the Congo, Kenya, Uganda, and Eritrea. It has been collected in the Sudan and Ethiopia by Sweeney (personal communication, 1967), and in Tanganyika by Harris (1933). It does not appear to be restricted to the eastern side of the continent for Lavabre (1960) has reported citrus psylla from the Camerouns, and Wallace (1960) from St. Helena.

Citrus psylla is common in the summer rainfall areas of the Republic but usually rare in the Eastern Cape and Western Province. Van der Merwe (1941) states that the hot, dry summers of the western Cape are particularly detrimental to T.erythrae. It is often found in gardens of the Cape peninsula (Whitnall, personal communication, 1966).

6. Previous Outbreaks of Citrus Psylla in the Transvaal

There are few reliable records available on the relative abundance of citrus psylla over the years, and the recording of recollected but undocumented observations is commonly of dubious value. Annecke & Cilliers (1963) mention the phenomenal citrus psylla populations reported by Transvaal growers in the years 1959 - 1963, and their own obser-

vations confirmed/.....

vations confirmed this trend in the White River and Tzaneen districts. They were unable to offer an explanation for these outbreaks and did not ascribe it to changes in pest control programmes. It will be remembered that it was during this period that serious outbreaks of greening reappeared.

Farmers and other workers associated with the growing of citrus in the Tzaneen - Agatha - Letsitele areas remember the severe spring outbreaks in the years 1960-1963. In the fifties, though varying in severity from year to year, citrus psylla was always at a comparatively low level in this area. Several farmers have reported that from about 1955 the insect began colonizing the lower-lying areas such as the Letsitele Valley. By 1961 many growers had begun spraying to protect their spring flush. Heavy populations were observed by the author in this district during July-August, 1965, and August, 1966.

The history of citrus psylla outbreaks in the Rustenburg area is almost identical to the pattern described for the White River and Letaba - Tzaneen areas (Engelbrecht, personal communication, 1966).

7. Other Psyllid Pests of Citrus

Diaphorina citri Kuwayama is the only other psyllid species reported in the literature to breed on citrus. Originally described from Japan, Ebeling (1959) lists it as occurring in India, Burma, China, Indonesia, Malaya and the Philippines. It is also reported from Nepal, Pakistan and Mauritius (Sweeney, personal communication, 1967). There is one doubtful record from Brazil (Lavigne, 1957). The eggs of D. citri are laid in the buds and on the young shoots of citrus. Nymphal feeding causes defoliation, die-back, and a reduction in fruit yield and quality (Husain & Nath, 1927). But the work of Salite & Cortez (1967) in the Philippines, and Tirtawidjaja et al. (1965) in Indonesia, has shown that of greater importance is the fact that this psyllid is the probable vector of Indian sweet orange decline and the vein-phloem degeneration disease of the Orient.

In the Letaba district the adults of two species of Diaphorina were collected on citrus in large numbers. One species has been identified as Diaphorina punctulata Petley. These psyllids breed on the

marula, Sclerocarya caffra Sond., during the summer and many appear to overwinter as adults on citrus during those months when marulas are practically leafless. No eggs or nymphs have been found on citrus. These psyllids were not found to be greening vectors in a preliminary test (McClellan & Catling, unpublished results).

Small numbers of Arytaina sp. near mopani Pettey were observed on citrus on Letaba Estates and at Agatha in December, 1965.

II. METHODS AND SAMPLING

1. Psylla Population Assessments

A method for assessing populations of citrus psylla must consider the following factors:-

- i) adults are active insects and are commonly cryptic and solitary. The eggs and nymphs, however, are sessile, aggregated into distinct colonies, and easily found.
- ii) because young foliage is necessary for breeding there are frequently large population variations from branch to branch and from tree to tree.
- iii) the seasonal fluctuation pattern may include long periods when density is so low that destructive sampling would severely damage the population.

Population assessments were therefore based on a direct count of colonies in the field with no removal of material. At weekly or fortnightly intervals all the trees at each experimental site were searched by trained African scouts. Most of the work was undertaken by the same three scouts under the supervision of the author. Allocated a number of trees, the scout was trained to walk slowly around each tree searching for colonies in a band from tree skirt to about six feet above the ground. Since there was little difference in the mean tree size at each of the main experimental sites (see Table 3), the total tree area examined at each site was very similar and comprised about 50% of the tree's total canopy area. The count for each tree was recorded separately, and each colony noted according to its predominant age class, i.e. eggs, small nymphs (instars I-III), or large nymphs (instars IV-V). The time spent searching for colonies varied according to tree size, the volume and stage of flush present, and psylla density.

Table 2 shows the results of a series of tests made to determine the reliability of citrus psylla searching under varied conditions of tree size, and flush and psylla densities. The scouts examined a number of trees in the normal way and the assessment time and number of colonies found, were noted. Then the same trees were scouted again for

Table 2. Reliability tests for citrus psylla searching

No. trees tested	Normal scouting		Double Scouting	General conditions
	Time per tree in secs.	Colonies found	Colonies found	
8	100	0	0	small to medium sized trees
1	80	0	1	
1	80	0	0	
1	210	0	0	
1	240	0	0	moderate amounts of young flush
2	180	0	0	
1	160	1	1	
1	150	0	0	
1	210	2	4	low psylla density
1	210	0	1	
1	230	0	0	
		<u>3</u>	<u>7</u>	
1	300	2	0	medium sized trees
5	300	0	0	
1	300	1	3	
1	300	0	3	
2	300	0	1	heavy flush
1	300	0	2	
1	300	1	2	
		<u>4</u>	<u>11</u>	
1	156	4	4	medium sized trees
2	156	1	0	
1	156	5	2	
1	156	6	7	
1	156	1	1	moderate amounts of young flush
1	156	1	2	
1	156	9	5	
1	156	2	5	
1	156	13	18	moderate psylla density
1	156	5	9	
1	156	4	3	
1	156	9	4	
1	156	8	9	moderate psylla density
1	156	0	1	
1	156	7	13	
1	156	2	3	
2	156	7	11	
1	156	1	6	

twice the time and the total number of colonies recorded. At times the scouts were switched around before the second count was made in order to reduce the human error. The extra time revealed very few additional colonies in trees with moderate flush and psylla densities. At lower densities there were quite appreciable differences but these were probably reduced by scouting all the experimental trees at each site at fairly short intervals.

Letaba Estates has more than 400,000 citrus trees planted along the northern side of the Letaba River for several miles (see Fig. 1). In order to be alerted to possible psylla outbreaks and to assess infestation levels in general, extensive surveys were conducted during 1965 and 1966. These surveys were quite distinct from the population assessments described above. The survey plots were scouted on the same basis as the experimental sites except that extra scouts were recruited and the same degree of supervision was not possible. The sixteen plots comprised 8,614 trees representative of tree age and variety, and included several soil types and cultural practices.

2. In Situ Counts

By marking citrus colonies in the egg or sometimes early nymphal stage, and following up with a detailed count at regular intervals, direct life table data were collected under field conditions. With few exceptions, each in situ count was conducted on an experimental tree or on a tree a short distance away from a weather station so that a complete record of the prevailing climate was available.

Counts were made daily or on alternate days at Letaba. Further afield the colonies were usually counted thrice weekly. Using a hand lens, a small strip of paper marked with the mean lengths of instars III to V, and a few distinctive nymphal characters shown in Table 5, it was possible to recognize each of the five nymphal instars in situ with reasonable accuracy.

Where suitable colonies were not available on trees in the field, a large number of adults from a laboratory culture of citrus psylla were confined on a vigorously growing potted citrus seedling and allowed to lay eggs for 24 hours. The adults were then removed and the

seedling placed in the crotch of an experimental tree. In situ counts on potted seedlings were particularly useful for noting the incubation period of the egg. Also such plants were of course isolated from parasites and predators.

3. Assessment of Parasite Activity

T.erytreae is parasitized in the nymphal stage. The majority of parasitized nymphs cannot be recognized in situ unless the parasite is in the prepupal or pupal stage, which makes it impossible to assess accurately the degree of parasitism from counts made in the field.

Parasite activity was assessed by four methods:-

i) Parasite counts

A representative sample of the population was obtained by removing a single leaf from a number of haphazardly selected citrus psylla colonies. Then the leaves were placed in a plastic bag to await analysis in the laboratory. An effort was made to keep the bag cool for nymphs became active and crawled around when subjected to a sudden rise in temperature. Leaves were taken either from trees immediately adjacent to the experimental site or, at high population densities, were removed from experimental trees. Similarly, counts were made on material collected at various other sites in the Letaba-Tzaneen area.

Nymphs were examined under a dissecting microscope at 16 - 25X. Percentage parasitism was calculated as follows:-

$$\frac{\text{available nymphs parasitized}}{\text{available nymphs parasitized} + \text{available nymphs unparasitized}} \times 100$$

Parasite pupae are visible without dissection. All other instar III, IV and V nymphs were removed from their gall with a fine dissection needle and inverted. The venter of the nymph was then examined for a parasite egg or larva, and the gall for a parasite larva. The instar of each nymph and, if parasitized, the stage of the parasite, was recorded. Empty mummies and host skins left by emerged parasites were included in the count as they are usually firmly attached

to the leaf/....

to the leaf. Final moults showing the emergence of adult citrus psyllas were not counted as they are fragile structures which are soon lost. In older colonies it was sometimes necessary to count freshly-vacated "adult" galls, which represented unparasitized individuals. In most populations, however, such uncounted, non-parasitized adults were partly compensated for by instar III nymphs sampled in the field before being found by the parasite.

In cases where the full nymphal development had been completed an estimate of parasitism was made by comparing the number of vacated, fully-formed pits and final moults, with mummies and other structures associated with the parasite.

Details on the size and position of parasite exit holes, and the incidence of superparasitism and hyperparasitism were recorded.

ii) Emergence boxes

Some of the leaves collected for parasite counts, or leaves collected for this purpose alone, were placed in emergence boxes in the laboratory. Emergent parasites were removed and stored in 70% alcohol for identification.

iii) In situ counts

Many of the colonies used for in situ counts were invaded by parasites. Though such nymphs were not dissected, the total effective parasitism could be directly calculated on completion of the in situ count.

iv) Observation of adult parasites

Adult parasites were observed in the field on numerous occasions.

4. Laboratory Culture of *T. erytreae*

In June, 1966, a culture of citrus psylla was successfully established in the laboratory at Letaba Estates. They were bred on young, freshly-potted citrus seedlings. Natural light was supplemented by

three fluorescent/....

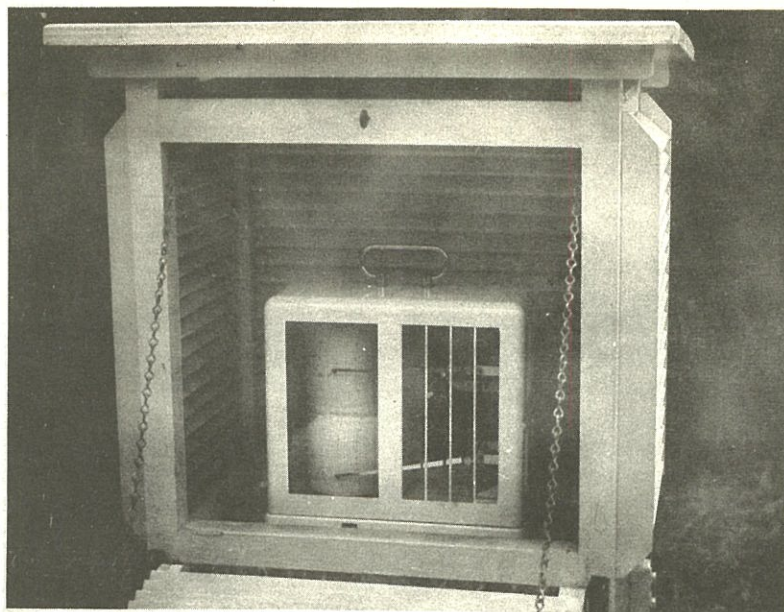


PLATE 1

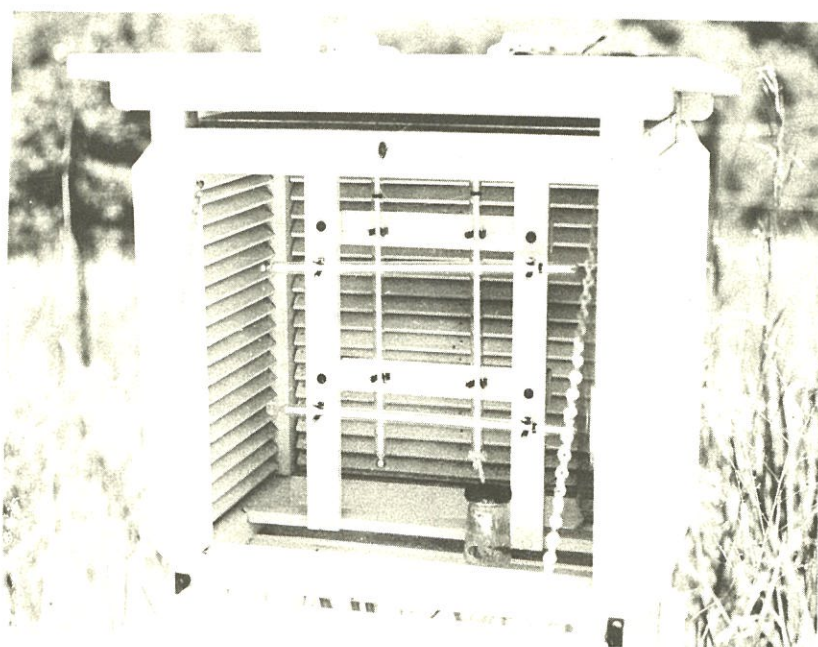


PLATE 2

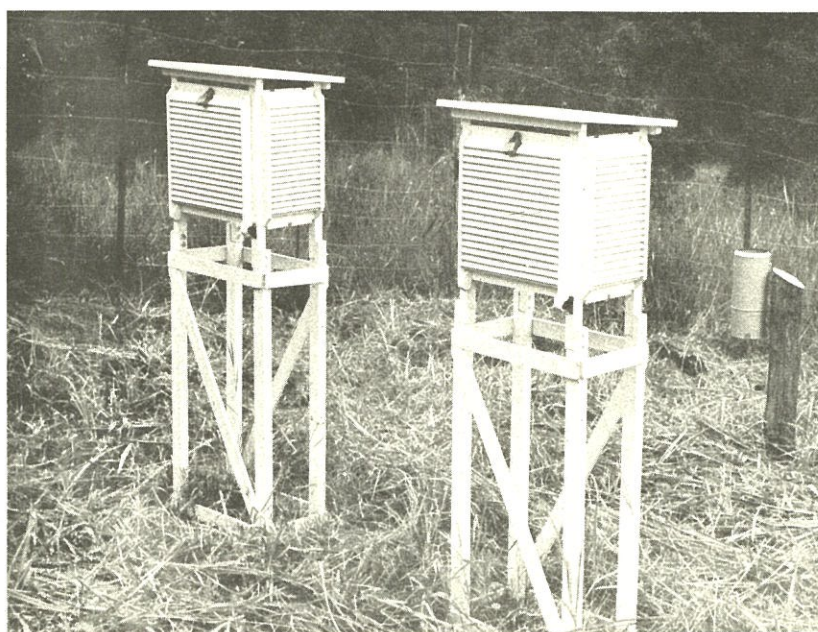


PLATE 3

three fluorescent tubes mounted directly above the plants. Aluminium foil was used along the walls to concentrate the light and a time-switch ensured a 14 hour photo-period. The room was maintained at a temperature of $21^{\circ}\text{C} \pm 2^{\circ}$ by a standard air-conditioning unit fitted with a portable thermostat. The relative humidity fluctuated but was usually in the region of 30% in winter and 60% in summer.

The culture was started with psylla collected in the variety orchard on Letaba Estates. Subsequently, a few batches of teneral adults collected elsewhere on the Estate were added.

5. Recording of Meteorological Data (Plates 1 - 3)

Five weather stations were established in the Letaba district. At each of the three main experimental sites were a Lambrecht thermohygrograph with a weekly recording cycle, a set of four meteorological thermometers, and a Lambrecht rain gauge of 190 mm diameter. The thermohygrograph and set of thermometers were each housed in a single Stevenson screen, and the station enclosed by a wire fence.

The instruments were erected and operated according to the official specifications laid down by the South African Weather Bureau in their Technical Manual (1960). Each set of thermometers comprised a maximum and minimum, and a wet and dry bulb thermometer. Initially the thermohygrographs were calibrated against the meteorological thermometers. Thereafter the latter were read twice weekly and the necessary corrections, if any, applied to the weekly trace. An accuracy of 0.5°C and 5% relative humidity was maintained.

The two minor weather stations consisted of a single Stevenson screen with a set of thermometers as described above. On five or six days each week the maximum and minimum temperatures were recorded at 0800 hours, and the wet and dry bulb temperatures at 1400 hours. Rainfall figures were available for the farm on which the screens were situated.

EXPLANATION OF PLATES

Plate 1. Thermohygrograph in Stevenson screen

Plate 2. Maximum, minimum and wet and dry-bulb thermometers in Stevenson screen

Plate 3. General view of a main weather station with rain gauge and two Stevenson screens

III. DESCRIPTION OF EXPERIMENTAL SITES

1. Main Sites

The main study of the population dynamics of T.erytreae was carried out at three experimental sites at different altitudes in the Letaba district. The sites were established in November, 1965. Each site consisted of a block of fifty sweet orange trees with similar aspect and proximity to natural bush. A weather station was established in each block of trees. There was a reasonable state of biological balance in all trees due to the general lack of insecticidal applications during the preceding years. Tree canopy area was comparable and was calculated from measurements of tree height and diameter from a formula developed by Serfontein and Catling, 1967 (in preparation).

From Figs. 1 and 2 it is seen that the lowest experimental site was on Letaba Estates and the highest was situated in the mist belt of the Drakensberg escarpment at Forest Hill. The intermediate site was at Fairview, 12 miles by road from Letaba and 6 miles from Forest Hill. Table 3 gives details of the three sites.

Table 3. Details of the three main experimental sites in the Letaba district

	LETABA	FAIRVIEW	FOREST HILL
Altitude a.s.l.	1960 ft	2800 ft	4200 ft
Mean canopy area of trees	279 ft ²	225 ft ²	292 ft ²
Tree variety	mid-seasons	24 Navels: 26 Valencia	Valencias
Foliage density	dense	fairly dense	sparse
Water supply	rain and basin irrigation	rain only	rain only
Nutrition	good	fairly good: extra nitrogen applied	poor: extra nitrogen applied
Insecticidal history of trees	ant banded; fruit-fly baited; trees 1-37 not sprayed since 1961; trees 44-50 fungicidal sprays only from 1963	1962-1964 one parathion + oil spray in March, not sprayed since	unsprayed since February, 1963

FIG. 1

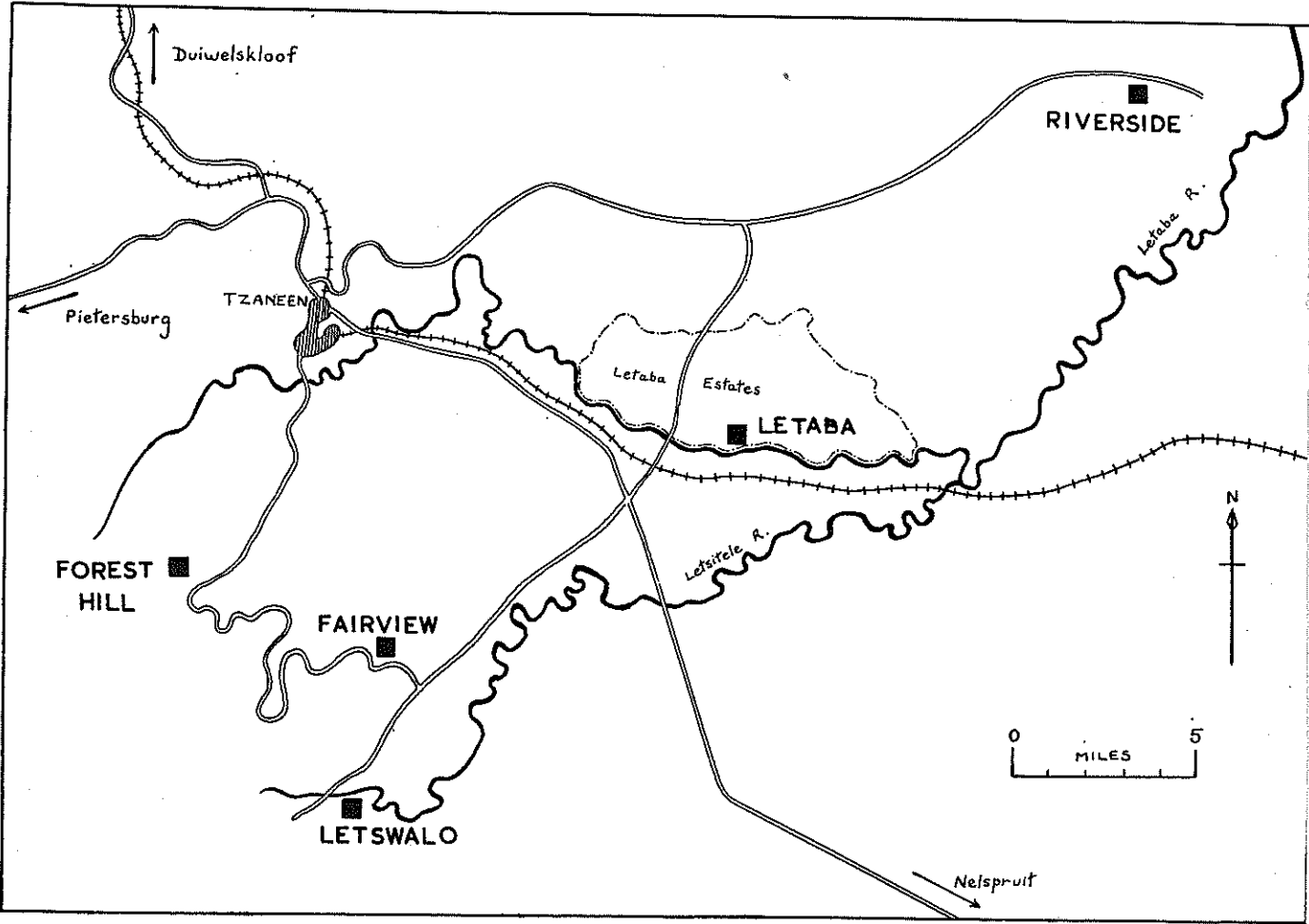
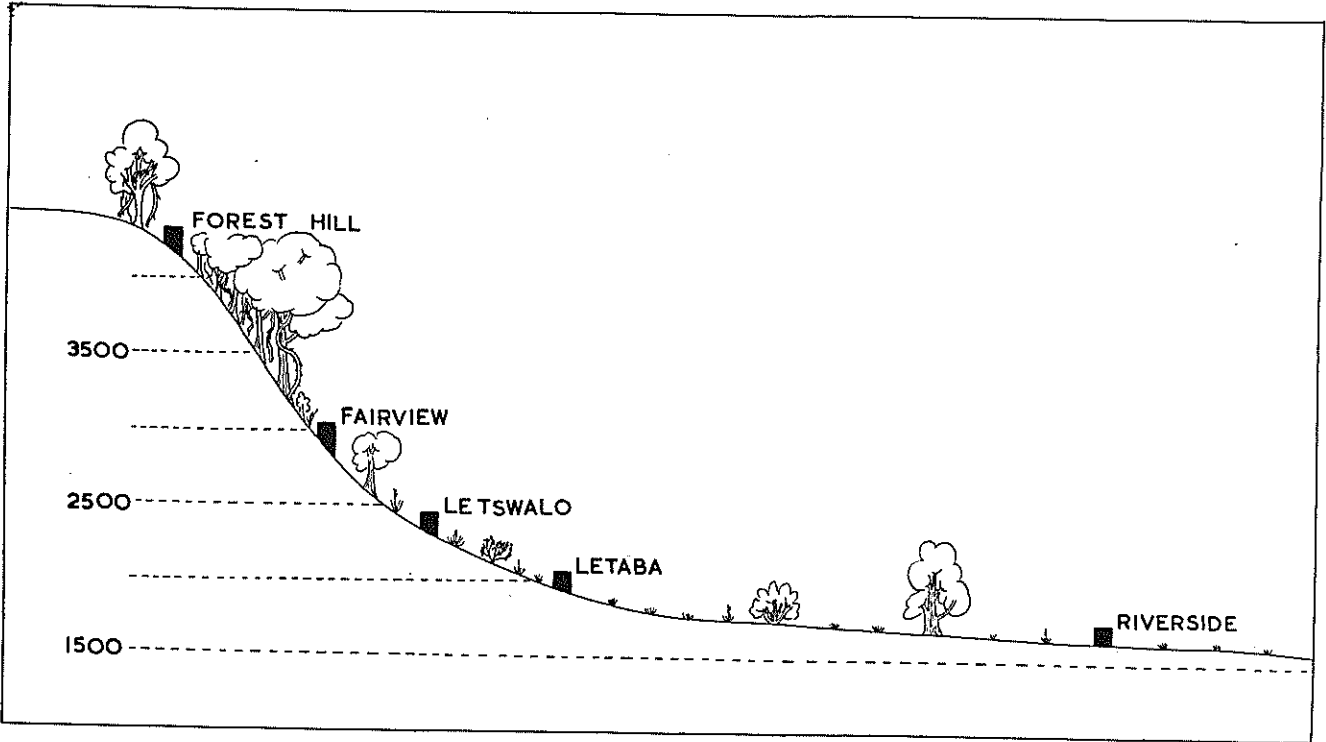


FIG. 2



Vegetation. The predominant trees and shrubs around each site were found to correspond fairly well with those listed by Acocks (1953) who places Letaba between "Lowveld Sour Bushveld" and "Arid Lowveld"; Fairview between "North Eastern Mountain Sourveld" and "Lowveld Sour Bushveld"; and Forest Hill in the "North Eastern Mountain Sourveld". No species of Rutaceae were found.

Greening. The incidence of greening was checked in the experimental trees. In April 1966, eight twigs were cut from each tree and screened for the marker substance found to be indicative of the greening virus (Elphinstone, 1966). In addition, in September 1966, the trees were examined for leaf symptoms. Table 4 shows that with the exception of the results from the fluorescent test on the Letaba trees, there was a tendency for higher levels of greening at higher altitudes.

Table 4. Greening incidence in 50 trees at each experimental site
(Figures in parenthesis represent doubtful cases)

	No. trees with greening	
	Fluorescent test	Leaf symptoms
Forest Hill	42 (+4)	41 (+9)
Fairview	39	32
Letaba	44	6

Elphinstone (1966) has found his technique to consistently show high percentages of greened trees when applied to normal looking mid-seasons on Letaba Estates.

2. Minor Sites

Letswalo. Fourteen miles from Letaba in the foothills of the escarpment at an altitude of 2300 ft, this site was established in February, 1966 (Figs. 1-2). The site consisted of fifty large, well fertilized Valencias irrigated by sprinklers. A standard insecticidal programme was applied during 1966. Surrounding vegetation closely resembles that of

EXPLANATION OF FIGURES

Fig. 1. Map showing experimental sites in the Letaba district

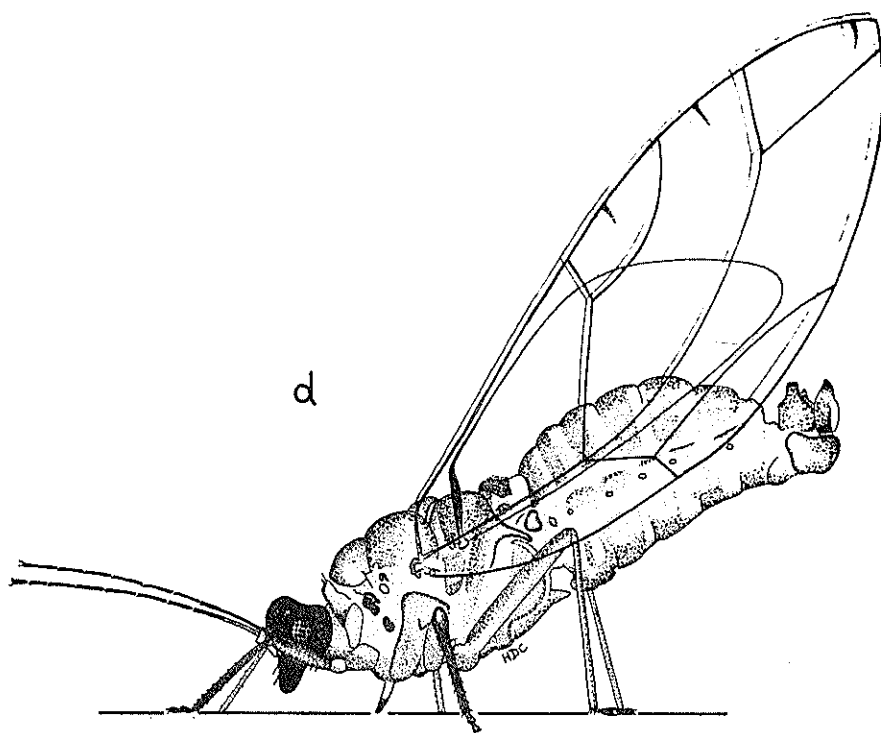
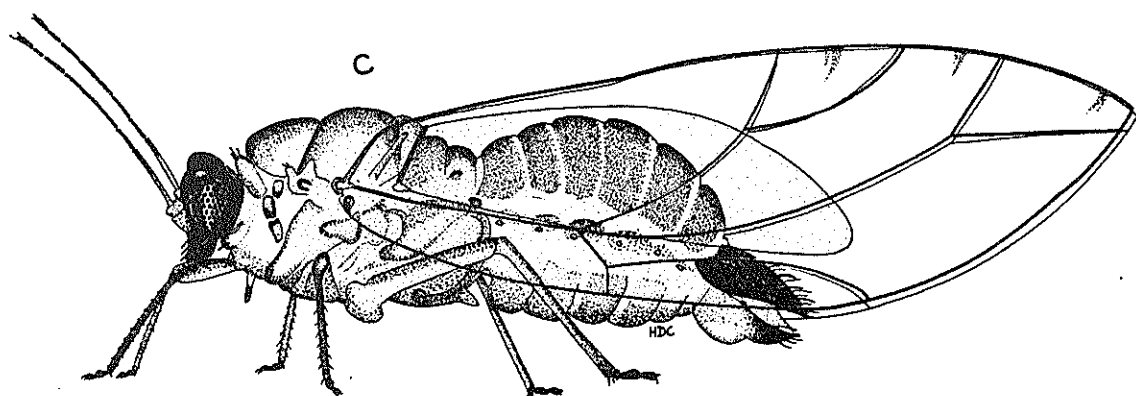
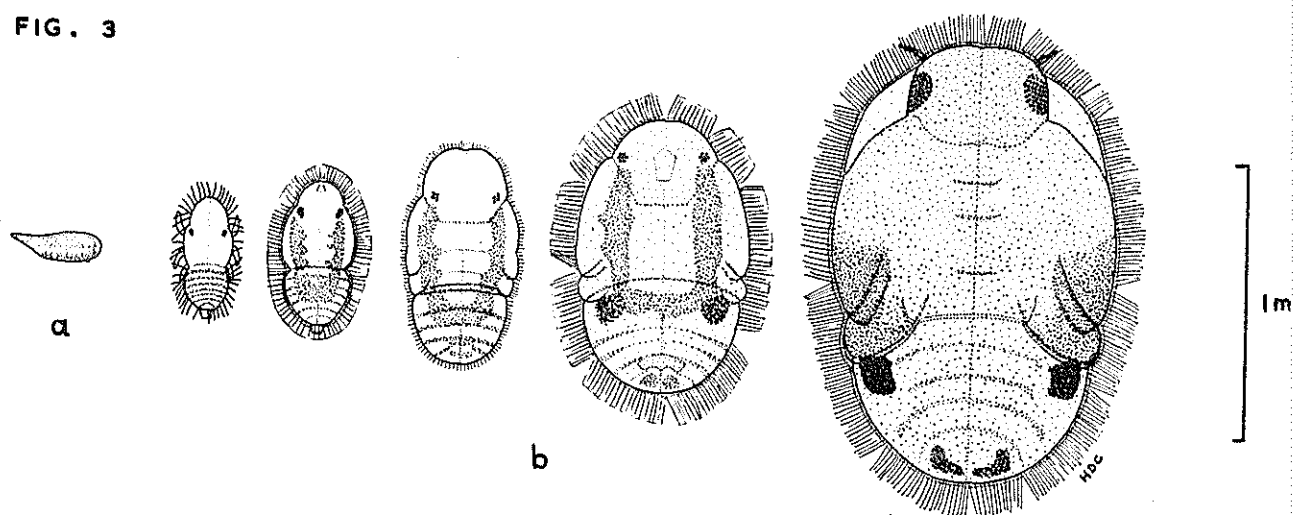
Fig. 2. Diagrammatic representation of Drakensberg escarpment showing experimental sites and their altitudes

Letaba Estates. The experimental trees were badly greened and had supported large populations of citrus psylla during the preceding years.

Riverside. This site was 13 miles east of Letaba at an altitude of 1650 ft and suggests the "Arid Lowveld" of Acocks (1953), (Figs. 1-2).

It was established in July, 1966, using fifty vigorous mid-seasons of medium size. The trees were irrigated by sprinklers and received a standard insecticidal programme.

FIG. 3



IV. THE BIOLOGY OF T.ERYTREAE

Except where otherwise stated the following description is based mainly on field observations and small-scale laboratory studies made by the author. Dimensions given are from Moran & Blowers (1967) and these were confirmed on citrus psylla collected in the field. Details of egg and instar duration are presented in chapter 8.

The development cycle of T.erytreae consists of egg, sessile nymph, and winged adult. There are five nymphal instars and sexes are separate.

1. Egg (Fig. 3a)

Description. The egg has a mean length of 0.28 mm and its surface is smooth and unsculptured. Anteriorly it is produced into a distinct process, while from the posterior end a short stalk arises which enters the leaf cuticle and fastens the egg to the leaf. Secretions from the cement gland further assist in securing the egg stalk to the leaf (Blowers & Moran, 1967). So effectively is the egg fastened that violent rainstorms at Letaba failed to dislodge the eggs. The egg stalk appears to have a similar moisture absorbing function as reported for Psylla mali Schaidberger (Lees, 1916) and for aleurodids (Wigglesworth, 1965), because eggs on the point of hatching shrivel when the leaf is picked unless the leaf is kept on moist wadding. The egg is initially orange but later deepens in colour and develops two eyespots prior to hatching. On hatching it is usual for the crumpled chorion to adhere to the leaf.

Unfertilized eggs are paler in colour and appear to be infertile. Some batches of unfertilized eggs laid by virgin females in laboratory studies were seen to collapse and become distinctly flattened.

Oviposition site. Most eggs are deposited in a row along the margin of juvenile leaves less than $1\frac{1}{2}$ inches in length. Sometimes eggs are laid on leaves up to $2\frac{1}{2}$ inches in length. Some leaves become strikingly outlined in orange by the densely-packed eggs. A few may be laid on the petiole wing, along the midrib, on adjacent juvenile

EXPLANATION OF FIGURE

Fig. 3. Trioza erytreae (Del Guercio). All stages to the same scale.

a - egg	c - gravid female
b - the five nymphal instars	d - male in feeding position

FIG. 4

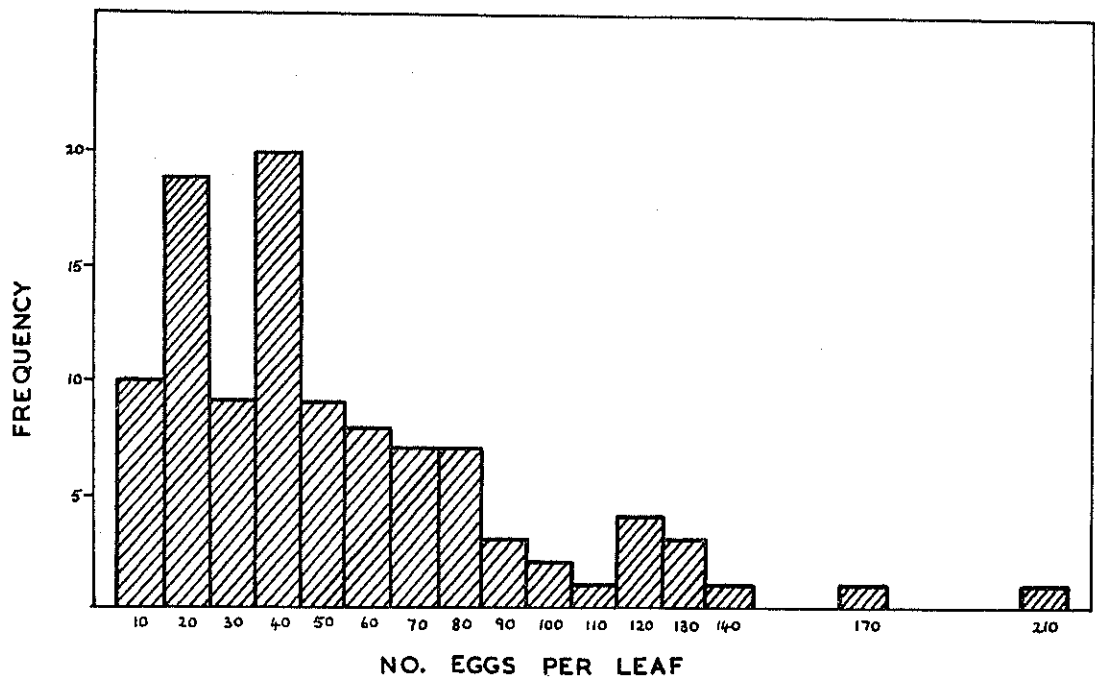
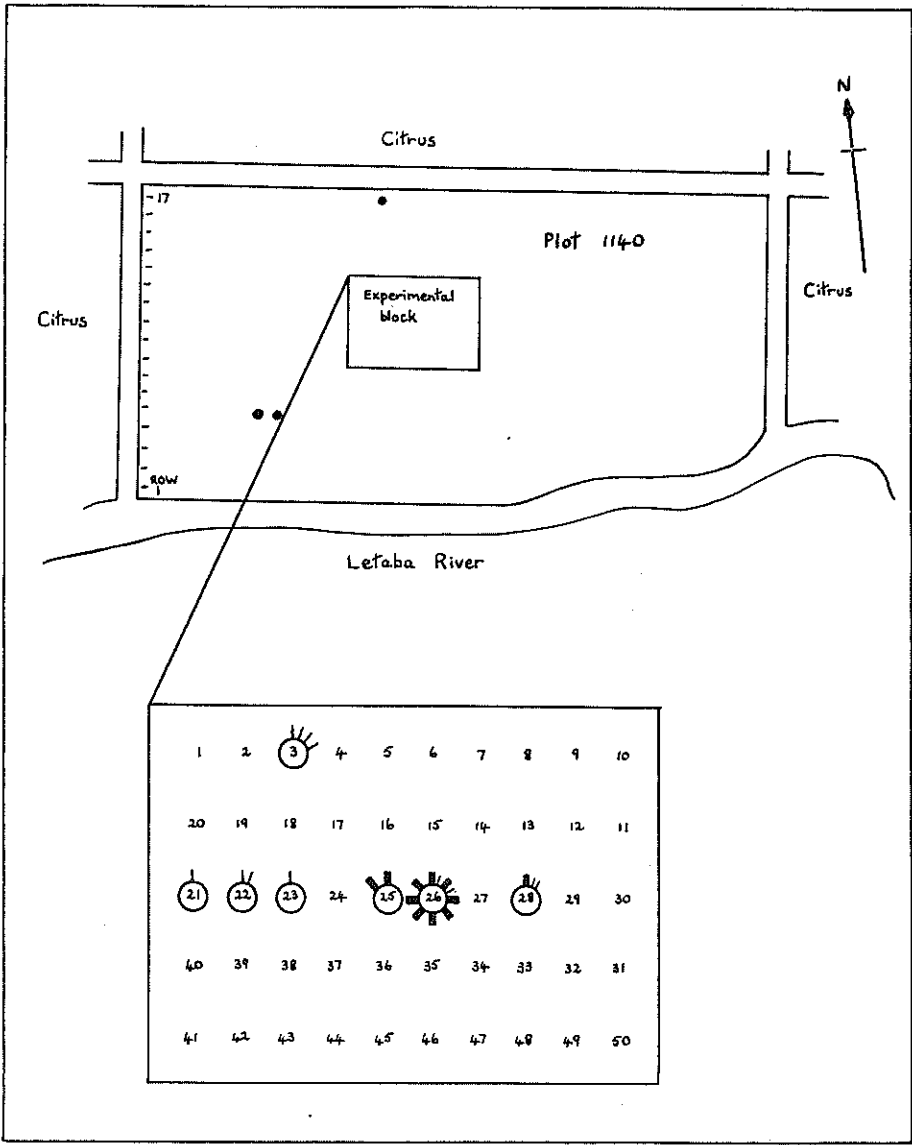


FIG. 5



thorns and stem, or simply scattered on the lamina - especially when the leaf margin is crowded with eggs. Sometimes rudimentary and barely unfurled flush points are so completely covered with eggs that they shrivel and drop from the tree. It is common for citrus psylla and the citrus aphid, Toxoptera citricidus Kirk.) to be found on the same leaf.

Number per leaf. A number of field counts were conducted to determine the number of eggs laid per leaf. All sizes of juvenile leaves were considered. Fig. 4 shows the results of counts made on 105 leaves. The arithmetic mean was 48.13 eggs per leaf. Though the citrus psylla was seen on occasions to lay several hundred eggs on a single leaf, the maximum number counted during this series was 202.

The number of leaves per flush point on which eggs were laid was extremely variable. This is because the flush points themselves vary from two or three leaves, to water shoots with seven or eight succulent leaves. It also depends on how advanced the flush point is when oviposition begins. Most citrus psylla colonies were supported on three or four leaves.

2. Nymph (Fig. 3b)

Settling. On emergence the fragile first instar nymph crawls slowly over the underside of the leaf seeking a suitable site on which to settle and insert its mouth parts. Only very occasionally does the nymph settle on the upper leaf surface, and rarely on the petiole and stem. When overcrowded or poorly nourished nymphs will sometimes migrate to adjacent more favourable leaves.

Leaf distortion. Within two or three days of settling a characteristic cup-shaped open gall or pit begins to form beneath the nymph. The gall takes on the general shape of the developing nymph so that only the nymph's dorsum is visible on the lower surface of the leaf.

EXPLANATION OF FIGURES

Fig. 4. Frequency histogram showing the number of eggs laid on single citrus leaves in the field by T. erytreae N = 105

Fig. 5. Dispersal of citrus psylla from a single infested tree (tree No. 26) in Plot 1140, Letaba Estates. Colonies within the experimental block shown by thin lines (one colony) and heavy lines (5 colonies). Trees outside the experimental block which became infested are shown by dots.

A corresponding/....

A corresponding blister forms on the upper leaf surface. The gall increases in size as the nymph develops. Once settled on a leaf the nymph remains in its gall to complete its development. If the leaf toughens prematurely, however, the gall fails to develop normally and is usually deserted. When this happens to young nymphs their chance of survival is slim. Older nymphs may survive in their shallow pit but do not develop normally and become unusually flattened.

It is common for leaves supporting a large nymphal population to curl and pucker after a few days of nymphal feeding. At a later stage some leaves unfurl and take on their normal shape, but others remain permanently twisted and deformed.

Description. The nymph is dorsoventrally compressed, oval in outline, with a marginal fringe of white, waxy filaments (Fig. 3b). The fringe is secreted by glands situated along the edge of the dorsum and is newly formed after each moult. The number of filaments increases with each moult, there being approximately 50 on instar I and 450 on instar V nymphs (Moran & Blowers, 1967). The legs are usually only visible from above in the first instar before the gall deepens. The dark-tipped antennae are partly obscured by the fringe in later instars. Dark red compound eyes are prominent, the ommatidia increasing in number with successive moults. Pulsations of the cibarial pump are sometimes seen in early instars. Ventrally, the dark, whip-like stylets of the mouth parts are clearly visible and when fully retracted are coiled beneath the head. The mycetome is a conspicuous nymphal structure, especially in instars II and III. In many psyllids this organ harbours allegedly symbiotic bacteria or yeasts of uncertain function (Proffitt, 1937). These organisms are believed to synthesize protein in some aphids (Wigglesworth, 1961). Wing buds gradually become more prominent with age but were not found to be as helpful for instar recognition as in some other psyllids, for example Diaphorina citri Kuwayama (Husain & Nath, 1927).

The nymph moults at night. In newly-moulted nymphs the waxy fringe is short or absent. The new cuticle of fourth and fifth instars is deep yellow in colour.

There is little difference in the essential shape of each instar.

Instars/....

Instars II and III can be distinguished only on size and filament number. Dimensions, and characters which proved useful for instar recognition in the field, are given in Table 5.

The coloration of instars IV and V is extremely variable. The abdominal dorsum may be deep lemon, olive green, or brown to dark grey; head and thorax are usually paler in colour and never green. The venter is also paler in colour and is commonly a yellowish amber, but may be olive green or pale grey in some nymphs. Occasional deeply-pigmented

Table 5. Instar Dimensions and Distinguishing Characters

Instar	Dimensions in mm		Distinguishing characters
	Length	Breadth	
I	0.35	0.17	light red in colour
II	0.50	0.27	pale, transparent yellow; light orange mycetome with well-defined outline
III	0.72	0.40	deeper yellow; mycetome unchanged
IV	1.03	0.62	colour variable; two grey abdominal spots appear
V	1.52	1.00	colour variable; abdominal spots dark

fourth and fifth instars sometimes appear among a population of otherwise pale nymphs.

On the completion of nymphal development, the nymph crawls from its gall and moults for the last time leaving next to the vacated gall the distinctive final exuviae. The empty galls may be visited by thrips, scavengers, such as various mites, or occupied by scale insects such as Aonidiella aurantii (Maskell) and Lepidosaphes beckii (Newman).

Faeces. Small white pellets are voided by both nymph and adult. Heavy populations sprinkle whole branches with these sugary granules. The faeces leaves the anus as a translucent, semi-solid globule and is often not released until it becomes white and completely solid. Jerky movements of the abdomen from side to side appear to assist in dislodging the pellet.

Number per leaf. Nymphal population depends on the number of eggs laid and their subsequent mortality. The number of eggs per leaf was

discussed earlier in this chapter and mortality is described in chapter 7. Some leaves become densely crowded with psylla nymphs. One leaf at Forest Hill was found with 226 instar III-IV nymphs and the five leaves of this colony totalled 640 nymphs. On such heavily populated leaves large nymphs have been seen to overlap and their galls become continuous.

3. Adult (Fig. 3c, d)

Teneral adult. The teneral adult is a delicate insect, yellow to pale green in colour with dark compound eyes. At first, each hyaline wing is rolled up on itself and held next to the thorax before expanding fully two to three hours later. The wings are held roof-like over the abdomen in repose, the anterior pair being about $1\frac{1}{2}$ times the length of the body. The posterior pair is smaller and the venation greatly reduced. The adult usually begins to feed close to its nymphal gall almost immediately and within two to three days is fully mature.

Mature adult (Fig. 3c, d). The cuticle and wing veins have darkened and the integument become fully sclerotized. There are well-developed compound eyes, ocelli, and ten-segmented, filiform antennae. The hind legs are exceptionally stout and provided with powerful muscles. They are folded beneath the body and enable the insect to jump strongly when disturbed.

The female has a mean length of 2.24 mm. The head is dark, the thorax an overall brown-grey colour. The abdominal tergites are grey, while the pleural and sternal regions are a pale green to brown. Externally the genitalia consist chiefly of two pointed valves giving the abdomen an acute apex. A gravid female may be recognized by the swollen abdomen.

The male is smaller with a mean length of 2.17 mm, and the abdomen is darker and narrower than the female. There is a blunt tip to the abdomen formed by a large ventral valve and two prominent parameres.

General behaviour. Adults are positively phototactic. They are quick to find breeding sites of young flush. While resting or walking on plant surfaces they often execute a series of distinctive tail-wags. When disturbed the adult either moves away from the source of stimulation, or more commonly launches itself into the air with a powerful jump. Under warm conditions they are very active and jump at the slightest provocation/....

vocation. Though powerful fliers, their usual flight habit is to circle for a second or two and then resettle near the take-off point, or even on the original leaf. Like aphids, though they appear incapable of sustained flight, once in the air they can probably be carried over long distances by air currents.

Mating. A mating pair align themselves side by side, both facing in the same direction with fused terminalia. They remain in the position for a few minutes. ~~about two hours~~. It is not known how many times a female mates during her egg-laying life but from the size of the spermatheca, Blowers & Moran (1967) surmise that to fertilize the full complement of eggs more than one mating is necessary.

The morphology of the female reproductive system is described by Blowers & Moran (1967).

Sex Ratio. Leaves infested with instar V nymphs were collected during 1966 from trees on two farms in the Tzaneen-Duiwelskloof area, and the emerging adults were counted and sexed. Table 6 shows that females outnumbered males in these samples. Daily emergences reflected about the same sex ratio.

Table 6. Sex ratios of *T.crytreae* collected in Letaba district during 1966

Site	Month	No. insects examined	Percent males
Tzaneen	October	503	37.6
Duiwelskloof	October	74	44.6
Duiwelskloof	November	456	40.6

Pre-oviposition period. Copulation normally takes place as soon as the teneral adult matures. As fertile eggs can be laid almost immediately after copulation, this gives a minimal pre-oviposition period of two to three days. At Letaba, laboratory studies and in situ counts conducted during early summer, 1966, showed the minimal pre-oviposition period to be 2-3 days, the mean 5 days. These findings correspond closely to those of Van der Merwe (1941), Annecke & Cilliers (1963), and Moran & Blowers (1967). The latter authors found that the normal pre-oviposition period was 3-6 days.

Van der Merwe (1941) gives the maximal pre-oviposition period as 14 days but the author suspects this period to be considerably longer when there are no breeding sites available.

Oviposition and longevity. Van der Merwe (1941) studied oviposition by confining newly-emerged adults on cut twigs in the laboratory. Disregarding those which escaped or died prematurely, females laid a mean of 611 eggs, and one was seen to produce 815 eggs. He suggested that females are even more productive under field conditions.

In an experiment using vigorously-growing seedlings at a constant temperature of 23°C, Table 7 shows that the total egg production of single females (some mated and some unmated) was considerably lower than Van der Merwe's mean.

Table 7. Egg Production of single females of *T.erytreae* at 23°C

Eggs laid per female	Time in days	Mean eggs per day
67	5	13.4
74	9	8.2
374	46	8.1
210	17	12.3
148	15	9.9
374	46	8.1
91	16	5.1
64	10	6.4
98	8	12.3
199	46	4.3
370	29	12.8

This may have been the effect of constant temperature for fluctuating temperatures within the normal range generally increase egg production (Woodbury, 1954). It also appeared that females had alternate periods of egg-laying and feeding. However, the daily oviposition rate was remarkably consistent and there was no evidence that the oviposition rate declined with age as contended by Van der Merwe (1941). Under these conditions unmated females did not lay fewer eggs than mated females.

Oviposition is strongly influenced by the availability of suitable foliage. The author has found that poor foliage considerably extends the egg-laying period of *T.erytreae* and thus the longevity of the fe-

males/....

male. Clark (1963) states that the egg-laying of Cardiaspina albitextura Taylor, an Australian eucalypt psyllid, appears to be similarly inhibited. The effect of climate on oviposition will be discussed in chapter 7.

At a fluctuating temperature regime with a daily mean of 15.5°C, Moran & Blowers (1967) found citrus psylla adults to have a mean longevity of 34 days (range 28-48), which agrees fairly well with Van der Merwe (1941). At a constant temperature of 23°C as described previously, and including premature mortalities, adult females had a mean longevity of 16 days.

Diapause and Voltinism. There is no sign of diapause in the egg or nymph of T.erytreae. Provided young flush is available, citrus psylla appears to breed at all times of the year. Between flush cycles, and especially in the winter months when citrus is dormant in some areas, the longevity of the adults is probably considerably prolonged. The effect of poor foliage on the female has already been noted. Many adults survive by feeding mainly on mature leaves at such times. The advent of new flush permits breeding and during semi-dormant periods they exploit any showings of flush which become available.

It would appear that the number of field generations per annum is influenced by the annual flushing rhythm of the host, particularly during the winter period. Though there is considerable overlapping of generations during the summer psylla cycle, a number of broods were distinguished at Forest Hill (See Fig. 8).

4. Feeding

Feeding process. The mouth parts are of the piercing-sucking type. The host tissue is pierced by a set of four, whip-like stylets which are the modified mandibles and maxillae. Plant sap is ingested by the combined action of the capillary and turgor pressure of the plant, and by contractions of the cibarial pump of the insect (Imms, 1960). In the resting position the stylets are withdrawn into the grooved rostrum, the distal extremity of which emerges between coxae I (Fig. 3). In order to insert the stylets the adult takes up a distinctive stance with head held low and body at an angle of about 35° to plant surface (Fig. 3d).

Although/....

Although adults spend some time in a resting position, they require large amounts of plant sap and do not survive for more than a few days without feeding. Females, due to their larger size and prolific egg production, probably have greater food requirements than males. Nymphs remain in a feeding position continuously and do not leave their gall unless disturbed. The mouth parts of T.erytreae probably enter the leaf through stomata to penetrate the phloem tissue and this is consistent with the apparent site of the greening virus. Most aphids and jassids are phloem feeders (Imms, 1960). Clark (1962) states that all stages of the psyllid C.albitextura insert their stylets through stomata, and by following feeding tracks he was able to establish that this species feeds on phloem tissue and the parenchyma cells around vascular bundles. According to Webber & Batchelor (1948), citrus leaves have from 350-600 stomata per square mm on their lower surfaces, density depending on species and climate. Stomata are only occasionally found on the upper leaf surface, and together with the fact that the lower surface is shaded, this probably accounts for the nymphs favouring the underside for their development. However, due to the softness of juvenile citrus tissue, the possibility of the mouth parts reaching the phloem region directly must not be overlooked. The saliva of some Coccidae appears to dissolve cell walls (Wigglesworth, 1961).

Feeding effect. The open gall caused by the nymph has been described earlier in this chapter. Though some plant galls are caused by the mechanical irritation of feeding, Pearse (1939) states that most are formed by the release of a chemical substance through the mouth parts which stimulates cell proliferation.

The feeding of citrus psylla nymphs and adults is not believed to cause any direct discoloration of host tissue, defoliation or die-back as reported in citrus by Husain & Nath (1927) from the feeding of D.citri. Yet according to Imms (1960), an enzyme-rich saliva is injected by all Homoptera which reacts with plant sap to form a tubular sheath around the stylets. Sweeney (1966) states that a toxin or toxins associated with such extra-intestinal digestion possibly contributes towards some of the greening symptoms. He gives convincing examples of other psyllids which cause stunting and yellowing, presumably due to toxins, where no

associated virus has been shown. He cites Paratrioza cockerelli Sulo., P.mali and Trioxa anceps Tuthill which cause stunting and chlorosis similar to the greening syndrome.

5. Adult dispersal

Knowledge of the dispersal and migratory powers of T.erytreae is important for an understanding of the spread of the greening disease. This aspect was not studied directly but the discovery of an isolated population of psylla in a plot on Letaba Estates in the winter of 1966 presented an opportunity to study dispersal on a field scale.

Plot 1140 (Fig. 5) consisted of 587 three-year-old Valencias planted in rows 21-27 feet apart and 12 feet apart in the row. The trees had an average height of 5 feet and diameter of $5\frac{1}{2}$ feet. From June to August there was a plentiful supply of young flush on most trees and the climate was favourable for psylla development. From the middle of September the cessation of new growth and the onset of summer temperatures severely crippled psylla populations so that by October no colonies were found. Apart from a strong westerly duststorm on September 4th there was no significant air movement during this period.

On June 15 two egg colonies were found on a single tree in the centre of this plot and a careful search revealed this to be the only tree infested. Fifty trees were then marked around this tree (which became tree No. 26) to form the main experimental block (Fig. 5). These were carefully searched at about weekly intervals and psylla recorded as total colonies per tree. Every two to three weeks the rest of plot 1140 was thoroughly scouted for psylla colonies. Between July 16-18 105 adults emerged from tree 26.

The whole of the plot, save the main experimental block, was searched for psylla on July 29, August 24, September 7 and 20 and October 12. The five surveys revealed a total of 5 colonies on three trees and their approximate positions in relation to the main experimental block is shown in Fig. 5. Although it is possible that these trees were colonized by adults issuing from tree 26, it appears more likely that these were separate populations in no way associated with the main experimental block. It was found that of the 67 colonies recorded in the experimental block over a $2\frac{1}{2}$ month period, 63% occurred on tree 26 (the original tree to be infested/....

infested), and 95% occurred in the central row of trees on either side of tree 26 where the trees were only 12 feet apart. The remainder (6%) were found on tree 3 in row one. In every case the developmental stage of the psylla colonies found in the experimental block suggested that their origin was tree 26.

These results indicate that with adequate supplies of suitable flush and the absence of strong air currents, adults breed on the nearest available flush points and thus disperse weakly. There appears to be no definite migratory phase. Clark (1962) found that although dispersal is greatly influenced by wind direction and possibly speed, C.albitextura is not able to cross clearings wider than 130 yards with much success, even when assisted by prevailing winds.

Despite the results of the above investigation and the limited survival powers of the adult away from foliage, the potential migratory powers of T.erytreae should not be underestimated. Like aphids, citrus psylla is efficient in seeking out new breeding sites and is probably carried over long distances as aerial plankton. Aphids have been collected at altitudes of 1500 ft (Johnson, 1951). The regular prevailing winds of some citrus areas may be found to disperse citrus psylla adults quite effectively.

6. Host Plants

Apart from doubtful records on Alchornea cordifolia Muell and Erythrina abyssinica Lam. ex DC. (Le Pelley, 1959), the host plants of T.erytreae all belong to the family Rutaceae which includes the genus Citrus.

Citrus psylla breeds and feeds on all species and varieties of citrus. It has been reared by the author on C.sinensis (Linn.) (Sweet Orange), C.aurantifolia (Christm.) (lime), C.limon (Linn.) (lemon), and C.aurantium (Linn.) (Seville) and observed in the field on C.paradisi (Macf.) (grapefruit) and the "naartjie" (C.reticulata Blanco.)

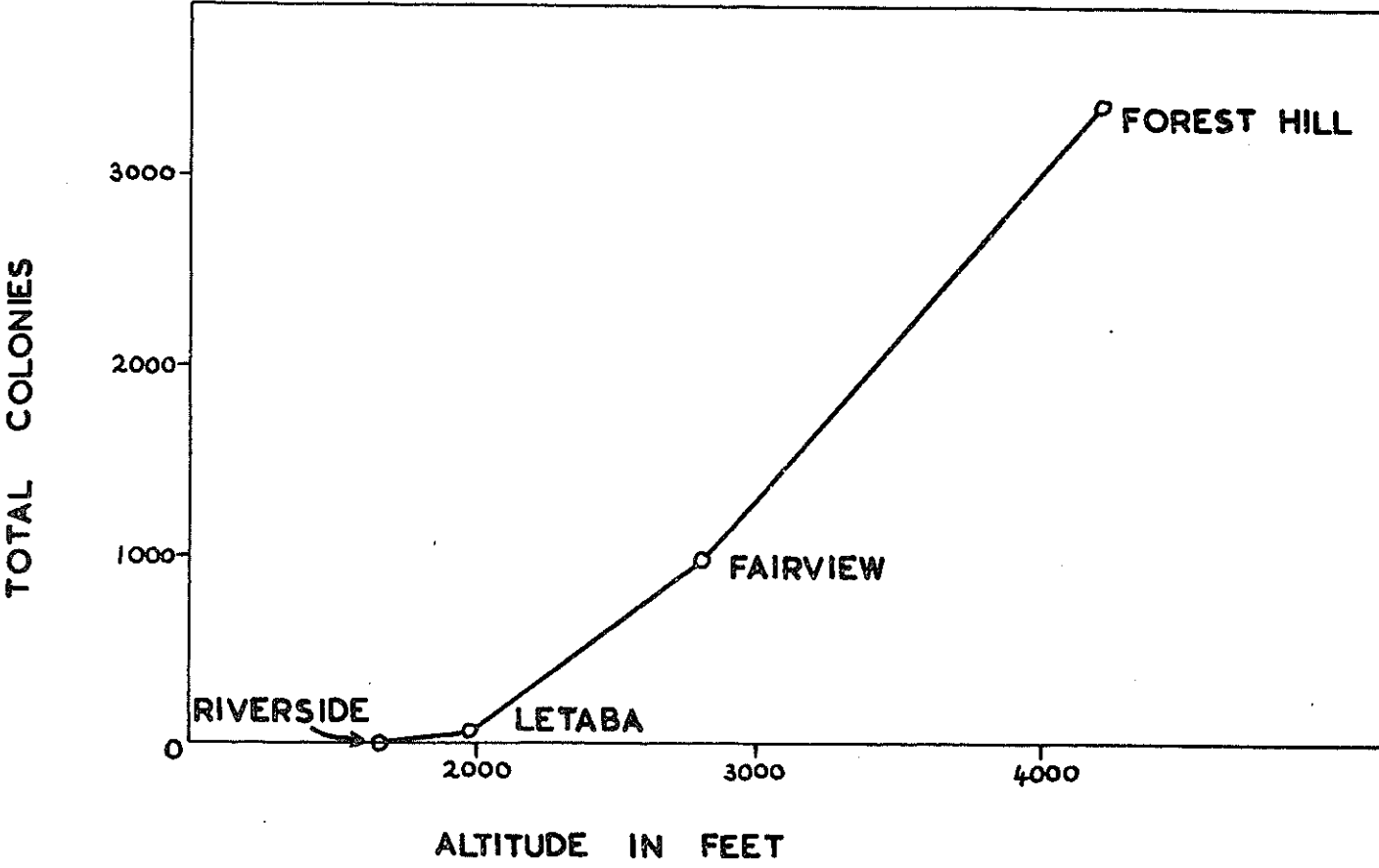
The main natural host plant appears to be Clausena anisata (Willd.) Hook. f. ex Benth. Nymphs were collected on this plant in November, 1966, at Trichardtsdal 30 miles south of Letaba in the montane forests of the Drakensberg escarpment. Typical galls were also seen on old leaves indicating previous attack by T.erytreae. Moran (personal com-

communication, 1966) reared T.erytreae on citrus and several other Rutaceae, including Fagara sp. and Calodendron capense (L.f.) Thumb. under the same temperature conditions. Mortality was very high on C.capense which corresponds to the findings of Van der Merwe (1941). However, Moran found that nymphs were larger and completed their development more rapidly when grown on C.anisata. Van der Merwe also noted this and concluded this plant to be the preferred host.

The Clausena genus is widely distributed throughout the world and contains many species. Swingle (in Webber & Batchelor, 1948) distinguishes three species native to Africa, though it is now usual to group two of these, C.inequalis Benth. and C.anisata, together as C.anisata. This species is found in central, western, and south-east Africa including the Transvaal, Natal, Pondoland, and the Cape. Though it is possible for psylla to have been introduced into new citrus areas on nursery trees, there is also a strong likelihood that on many occasions the insect has spread to citrus from indigenous Clausena species and other Rutaceae.

At Trichardtsdal old psylla breeding sites were occasionally found on Oricia sp. In Pretoria, Vepris undulata (Thumb.) Verdoorn & C.A. Sm. has been observed supporting very heavy populations. Van der Merwe (1941) also records Toddalia sp. and Fagara capensis Thumb. as hosts and mentions several exotic Rutaceae on which he colonized citrus psylla. He was not able to rear psylla on Barosoma lanceolata Sond.

FIG. 6



V. SEASONAL ABUNDANCE AND FLUCTUATION

1. Main Experimental Sites. (see Figs. 1 and 2)

Previous Incidence of Citrus Psylla

A citrus leaf has a long life. According to Webber & Batchelor (1948): "The leaves of oranges--- persist for two seasons or more", and it is generally accepted that most leaves are at least three years old before being shed. Thus an examination of mature leaves for psylla galls and remnants give a useful indication of the total psylla abundance over the previous two to three seasons.

During September, 1965, the experimental trees at each site were thoroughly searched for this evidence. The survey was simplified by the fact that the trees were carrying small amounts of young flush. The same two scouts were used throughout and on average each tree was searched for about three minutes. The previous psylla colonies were found to be evenly distributed on the trees at each site and there was no evidence that some trees were less susceptible to attack than others. Table 8 shows the total number of psylla colonies at each site with a break-down of their position on the tree according to quadrant and height. A height of five feet above the ground was used to demarcate "high" and "low" colonies. It can be seen that colonies were evenly distributed in all quadrants of the tree, but that the majority were

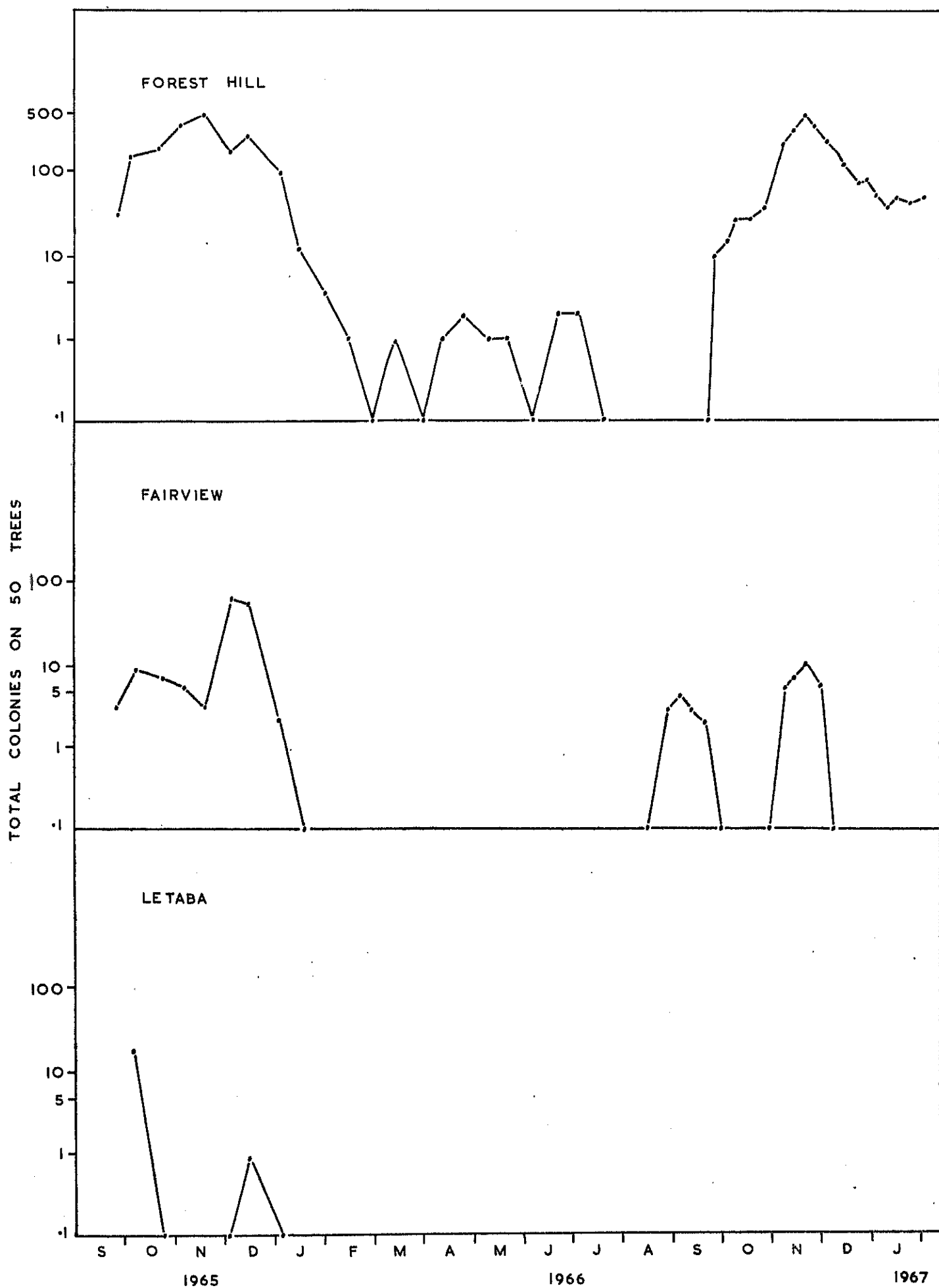
Table 8. Previous psylla incidence - total colonies per site

Site	No. Colonies per quadrant				Height of colonies		Total Colonies
	North	East	South	West	Low	High	
Letaba	7	11	16	5	39	0	39
Fairview	219	297	287	181	965	19	984
Forest Hill	865	835	811	842	2871	482	3353

EXPLANATION OF FIGURE

Fig. 6. The relation between altitude and previous incidence of T.erytreae at four experimental sites in the Letaba district. Previous psylla colonies were shown by pits on mature leaves and are expressed as the total number of colonies found on the 50 trees at each site.

FIG. 7



within five feet of the ground. This indicates that shade is important for the developing nymph. The almost linear correlation between altitude of site and past psylla incidence is illustrated in Fig. 6.

Population Fluctuations 1965-67

In the Letaba district the seasonal fluctuation pattern of T.erytreae was found to consist of a rapid population rise in the spring and early summer, followed by a crash in midsummer leaving small numbers to persist through the winter until the start of the following cycle. Thus the citrus psylla, in common with most insects, shows the so-called J-curve of population growth where environmental resistance is applied suddenly and numbers decline almost as rapidly as they had built up. This pattern of heavy, early summer infestations was noticed by Annecke & Cilliers (1963) in the Eastern Transvaal.

The determination of citrus psylla densities at the main experimental sites was based entirely on field counts. Fig. 7 shows the population fluctuations at the three sites from September, 1965, to January, 1967, which included two almost complete psylla cycles. During the first cycle and the winter of 1966 counts were conducted at fortnightly intervals but from August onwards, every week. The colony count per tree was discontinued on reaching the fifty colony level, this maximal count occurring twice in October and twice in November on a tree at Forest Hill during the first cycle. No tree reached this level during the second psylla cycle. In the 1966-67 cycle, age classes were i) egg, ii) small nymphs (instars I-III), and iii) large nymphs (instars IV-V).

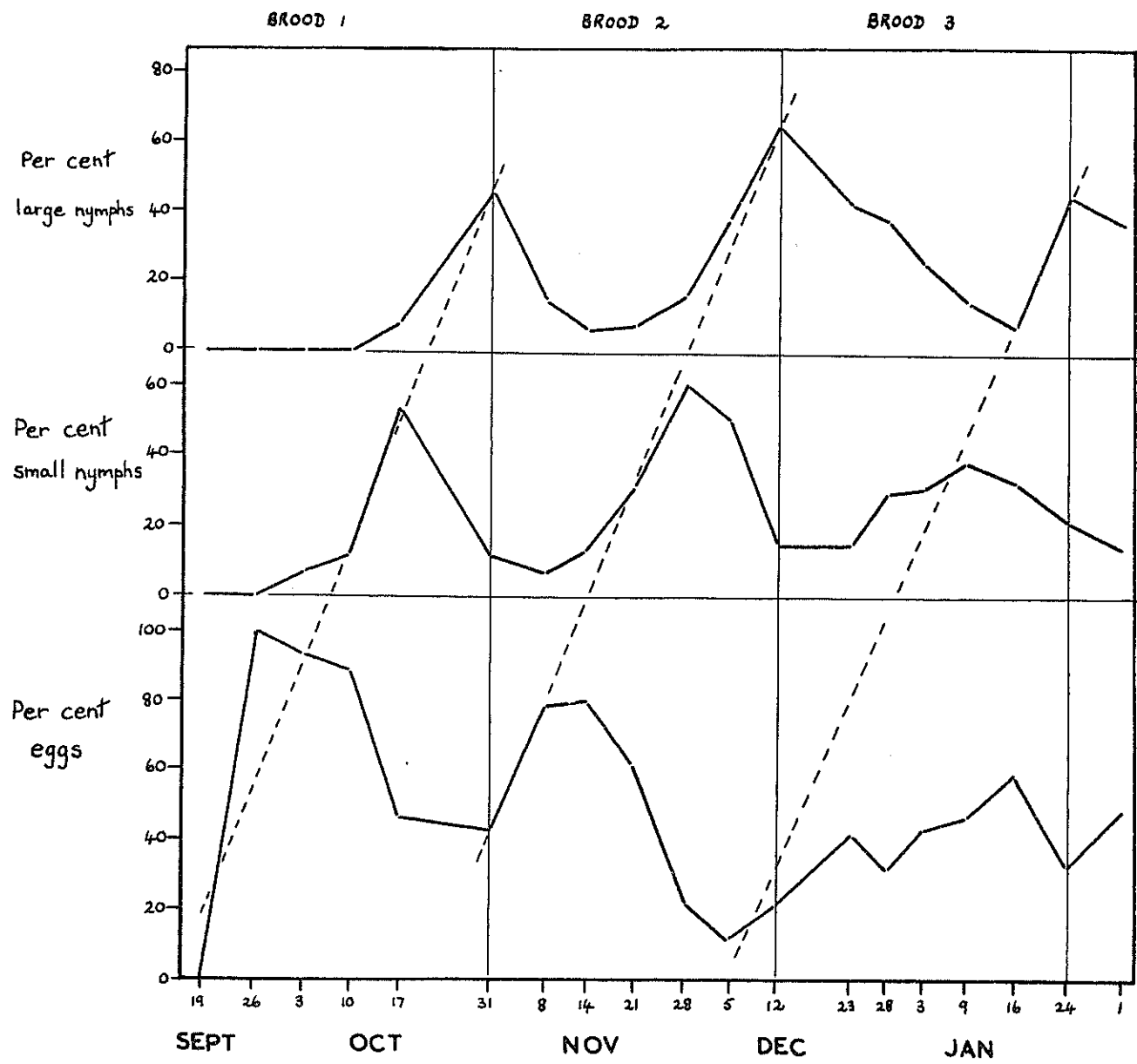
Fig. 7 shows that citrus psylla densities were consistently the highest at Forest Hill; low at Fairview; and almost negligible at Letaba. Previous psylla incidence and actual observed populations thus have the same relationship with altitude.

At Letaba in 1965, final moults and freshly-vacated galls on young flush indicated nineteen psylla colonies in October, and a single nymphal colony was found in December. There were no signs of citrus psylla during the 1966-67 season.

EXPLANATION OF FIGURE

Fig. 7. Population fluctuations of T.erytreae from September, 1965, to January, 1967, at the three main experimental sites in the Letaba district. Populations expressed as the total number of psylla colonies found on 50 trees at each site.

FIG. 8



The Fairview trees were transitional as regards altitude, climate and psylla abundance. When compared with the Forest Hill site there was a similar but smaller spring build-up each season. There was no psylla activity during the winter months, and numbers were lower and more irregular in the 1966-67 season.

Forest Hill is clearly in a favourable environment for citrus psylla. In September there is a rapid population increase on the spring flush; a peak is reached in November, and from late December onwards a number of factors combine to produce a population crash. An analysis of the 1966-67 cycle into age classes (Fig. 8) showed that, though some measure of overlap is present, the bulk of the population passed through two definite broods in early summer, and one less distinct brood in midsummer. Slight differences in the shape of the population curves for the two psylla seasons were mainly due to climate and are discussed in chapter 8. Forest Hill was the only site to support low but significant breeding populations of citrus psylla during the 1966 winter.

2. Other Experimental Sites

Letswalo (Figs. 1 and 2)

The trees at this site were scouted for psylla from February, 1966, to January, 1967. Due to continual light flushes on these trees, substantial populations of psylla were found during the winter. For this reason the results of this experiment are discussed fully in chapter 7 and the population fluctuations shown in Fig. 14.

Riverside (Figs. 1 and 2)

This was the hottest site in the Letaba area and at the lowest altitude. No sign of psylla damage was found on mature leaves and regular inspections from July to December, 1966, revealed no live psylla - despite the vigorous flushing of these trees.

Letaba Estates - Block 8 Valencia and Plot 34

Psylla populations in Block 8 Valencia (B8V) are related to available flush and compared with the Letswalo site in chapter 7. Large populations of citrus psylla were present in this block from August to September, 1965, and parasites and predators were very active.

EXPLANATION OF FIGURE

Fig. 8. Field generations or broods of T.erytreae during the summer of 1966-67 at Forest Hill.

Table 2. Citrus psylla surveys conducted on Letaba Estates during 1965 and 1966. Populations expressed as total colonies per plot. Figures in parentheses represent percentage of trees found to be infested. N-Navels; M-Mid-seasons; V-Valencias.

Plot	Planting date	Variety	Total psylla colonies				
			1965		1966		
			July	September	December	September	December
$\frac{1}{2}$ 33 : $\frac{1}{2}$ 34	1951	N	0	154(22)	8(2)	0	0
143	1942	N	0	38(8)	26(7)	9(3)	10(3)
$\frac{1}{2}$ 114 : $\frac{1}{2}$ 116	1949	V	2(0)	13(2)	28(6)	6(1)	0
$\frac{1}{2}$ 318 : $\frac{1}{2}$ 320	1942	N	0	19(3)	20(5)	3(1)	4(1)
395	1950-1965	M	1(0)	51(6)	2(0)	1(0)	0
625	1947-1964	M	0	1(0)	3(1)	0	0
776	1942-1954	N:V	0	36(4)	4(1)	5(1)	1(0)
Blk 11 Val.	1957-1963	M:V	12(1)	23(2)	0	24(2)	0
1063	1961	V	1(0)	1(0)	0	0	0
1146	1961	V	0	5(0)	0	0	0
1320	1963	V	0	0	0	0	0
1244	1963	V	0	0	0	0	0
1031	1961	V	2(1)	11(3)	0	0	2(1)
1184	1957-1964	M:V	0	0	0	0	0
1309	1962-1964	V	0	2(0)	0	0	0
1303	1959	V	0	0	0	1(0)	4(1)

Plot 34 was a fifty-tree block of Navels similarly inspected for psylla colonies during 1966. The flushing rhythm was similar to B8V, though it was heavier in March and about a month later to begin in spring.

3. Psylla Surveys on Letaba Estates

These psylla surveys are quite distinct from the population assessments made at the main experimental sites on Letaba. A summary of the results of five surveys carried out during 1965 and 1966 is given in Table 9. The extremely low densities of T.erytreae on Letaba during this period is immediately evident. Even in the plot with the highest infestation ($\frac{1}{2}$ 33: $\frac{1}{2}$ 34), only 81 trees (or 22%) were infested - with an average of two colonies per tree.

The 1966 surveys showed that citrus psylla densities were lower than the previous year, results which tend to confirm those obtained from the experimental sites. The extreme midsummer heat of 1965-66 and the long dormant period of the trees the following winter are believed to be the main factors responsible for these low populations.

In 1966 the only plot with a significant psylla population was Block 11 Valencia. Routine Estate blossom surveys conducted prior to the spring parathion application showed this plot to have a very irregular and thus prolonged spring flush. Repeated inspections by the technical staff established that most trees in this block were severely greened.

The surveys also show that psylla activity is far less in young, small trees than in older and larger trees. Most of the first eight plots in Table 9 were planted in the 1940's and fifties and for these trees the five surveys revealed a total of 504 psylla colonies. Most of the trees in the remaining eight plots were planted after 1960 and totalled 29 colonies. Repeated surveys of the nursery for this period showed no signs of citrus psylla.

VI. NATURAL ENEMIES

The nymphs of T.erytreae are attacked by chalcid parasites. The most abundant parasite in the Letaba district has been identified by Dr B.D. Burks of the United States National Museum, Washington D.C., as Tetrastichus radiatus Waterston. Of lesser importance are the encyrtid, Psyllaephagus pulvinatus (Waterston), and a number of others to be briefly mentioned later.

No indication of adult parasitism was seen during these investigations, nor was there any sign of the egg parasite, Psyllechthrus oophagus Ghesquière, said to attack citrus psylla in Central Africa (Annecke & Cilliers, 1963).

1. Notes on Parasite Species

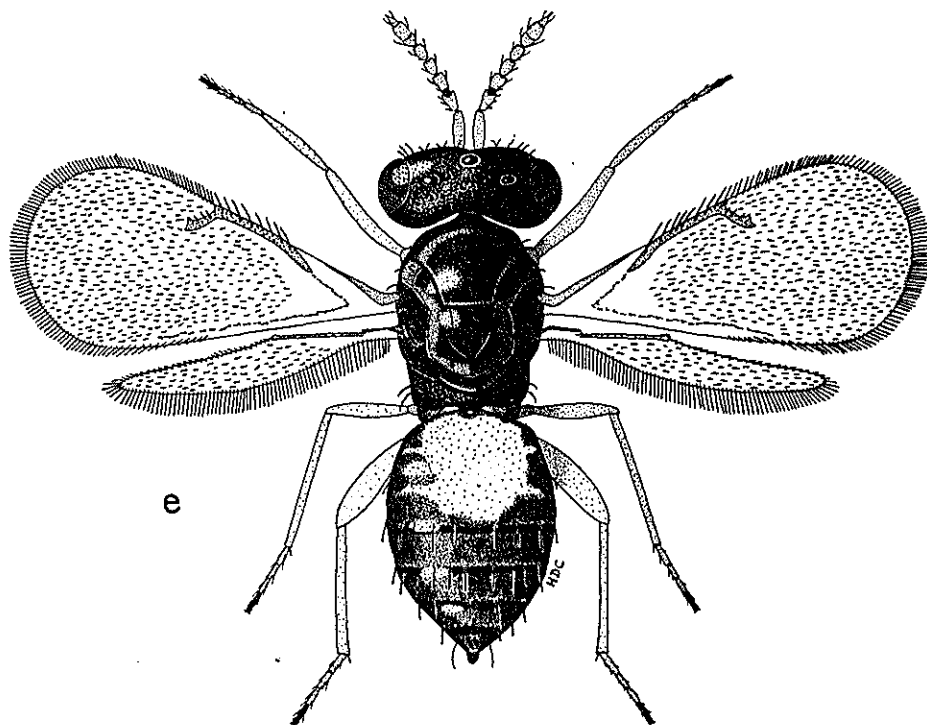
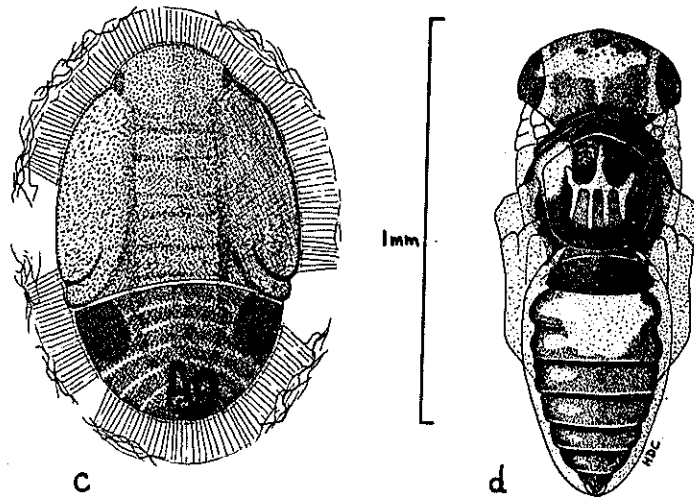
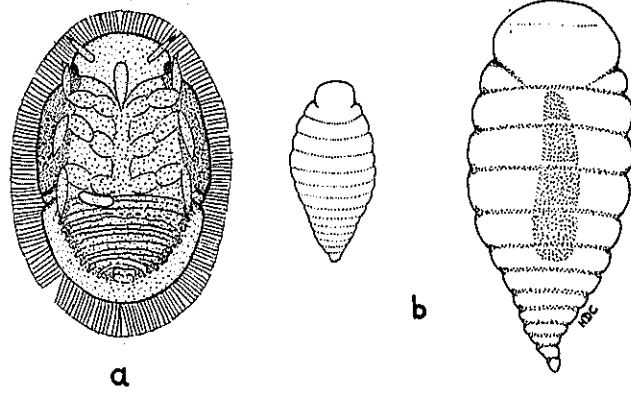
Tetrastichus radiatus (Chalcidoidea: Eulophidae)

T.radiatus was originally described as a parasite of Diaphorina citri Kuwayama, (= Euphalerus citri Kuwayama), the Indian citrus psylla, in the Punjab by Husain & Nath (1924). Annecke & Cilliers (1963) were the first to record this parasite in Africa. These authors also regard the psylla parasite recorded by van der Merwe (1941) as T.radiatus.

T.radiatus is abundant in the Transvaal and has been reared from material collected at Zebediela, Nelspruit and Pretoria (Annecke & Cilliers, 1963). The author has specimens from White River and the Letaba district, and has observed it on citrus psylla at Malkerns (Swaziland). The biology and general description of the parasite in the Letaba district corresponds closely with that described briefly by Husain & Nath (1924).

The egg is pale and in the shape of a slightly curved sausage, 0.20 mm (10 measurements) in length, and 0.08 mm (10) in breadth. It is placed externally on the venter of the nymph in the region of the hind coxae. Usually it rests in the groove between the thorax and first abdominal segment, i.e. almost at right angles to the main axis of the nymph as shown in Fig. 9a. On one occasion, in heavily parasitized nymphs, eggs were observed placed longitudinally between coxae II and III but these may not have been T.radiatus eggs. According to Husain & Nath (1924), the ovipositing female settles beside a nymph, bends her abdomen beneath the insect and at the same time thrusts out her ovipositor which places the egg. This process takes three to four minutes.

FIG. 9



The parasite oviposits beneath instars III, IV and V, the fourth instar appearing the most attractive. Many fifth instars survive the attack of the parasite. On hatching the grublike larva inserts its mouth parts and begins to suck out the body contents of the host. When fully grown it almost completely fills the gall beneath the now shrunken and collapsed nymph. There is a short prepupal stage before the pupa forms. The pupa may face in the same direction as its host, or the two may lie head to tail, but the pupa's ventral surface is always uppermost and thus towards the venter of the host. The pupa darkens in colour and sometimes can be seen quite clearly through the semi-transparent nymphal exoskeleton. Fully-formed antennae and deep red compound eyes differentiate and the pupa takes on the black colour of the adult, relieved only by a white crown design on the thorax, and a distinct white, abdominal spot at the junction of thorax and abdomen (Fig. 9d). Pupal length is 1.13 mm (10 measurements of unsexed pupae). The combined egg, larval, and pupal duration was 14-16 days in November at Fairview.

Apart from occasional nymphs attacked shortly after the second moult which are rendered distinctly pallid, parasitized nymphs usually can be recognized only in the final or penultimate instar - as in most psyllids (Jensen, 1957). The nymph gradually succumbs as its body contents is sucked dry. There appears to be little, if any, mutilation and host feeding by the parasite.

T. radiatus is thus an ectoparasite. The host's flattened and compressed exoskeleton becomes firmly attached to the lip of the leaf gall by fine, white filaments. Husain & Nath (1924) state that these strands are produced by the larval parasite. Similar anchoring processes are seen in T. triozae Burks (Jensen, 1957), and in a Tetrastichus sp. on the South African Chestnut psyllid (Moran, personal communication, 1966).

EXPLANATION OF FIGURE

Fig. 9. Tetrastichus radiatus Waterston. All stages to the same scale.

- a - egg on venter of citrus psylla nymph
- b - larvae
- c - dead nymph with parasite in pupal stage
- d - pupa
- e - adult female

In most Apocrita the stomach first gains connection with the hind gut in the final instar (Imms, 1960). This would seem to be the case in T. radiatus for the conclusion of the larval stage and start of pupation is signalled by the discharge of a reddish - brown meconial curl on to the abdominal surface of the host (Fig. 9c). The adult emerges by chewing a circular hole, of diameter 0.33 - 0.35 mm, through the host's exoskeleton in the thoracic region. Sometimes the exoskeleton is merely pushed aside for the wasp to emerge between it and the mouth of the gall.

The adult is a small black wasp which is sometimes seen running briskly over nymph-infested leaves. It is immediately recognized by the possession of a conspicuous white spot on the abdomen (Fig. 9e). The legs are pale except for darkish coxae and the hind femur which is sometimes light brown dorsally. The female is 1.19 mm in length (10 measurements). Males are smaller, with a length of 1.05 mm (10 measurements) and possess a narrower abdomen with a less prominent abdominal spot. The antennae of the male bear whorls of long setae.

Husain & Nath (1924) found females to live for 20-25 days on psyllid-infested leaves. Confined in sleeves, those authors found that adults lived for 25 days. The maximal winter longevity for females was 31 days and males 36 days.

Superparasitism. Superparasitism was not uncommon at high parasite densities. Usually there were two eggs per host but some nymphs were seen with six eggs. However, only one parasite emerges from a single nymph. Possibly some of the so-called cases of superparasitism cited later were due to the eggs of a secondary parasite.

Hyperparasitism. There is little doubt that T. radiatus has its own parasites. During the period of study, however, their activity was intermittent and of little apparent significance. The species involved are not clear but is presumably one or more of the parasites mentioned below as minor species. They certainly were not observed to restrict the activity of the primary parasites as described by Clark (1964) in a study of the dynamics of C. albitextura. One of the suspected hyperparasites was particularly evident in material from Forest Hill taken at the end of the 1965-66 season. The mature secondary larva was seen to be distinctly segmented and possessed a tapering cephalothoracic region and dark brown-brownish-purple gut/....

ish-purple gut. It was rare for primary and secondary parasite larvae to be observed together beneath a psylla nymph. Most parasite counts on material from the Forest Hill site during the 1966-67 season revealed at least some evidence of hyperparasites.

Husain & Nath (1924) reported two undetermined hyperparasites which attack the larvae and pupae of T.radiatus. Of the three districts in the Punjab selected for their study, the majority of hyperparasites were collected at Lyallpur. This district also seems to have supported heavier and more consistent populations of D.citri and would thus correspond to the Forest Hill site in the Letaba-Agatha district. The occurrence of the hyperparasite may thus be an indication of a more stable 'psylla environment'. Hyperparasites appeared to be of little importance at Lyallpur for of 1424 parasitized nymphs examined only 30 (or 2.1%) were hyperparasitized.

Psyllaephagus pulvinatus (Waterston)

(Chalcidoidea: Encyrtidae)

The taxonomic position and synonymy of this parasite are discussed by Annecke & Cilliers (1963). Those authors state that P.pulvinatus is apparently widespread on the citrus psylla in Africa and probably parasitizes psyllids exclusively. Jack (1916) reported an internal parasite of citrus psylla in Rhodesia, and in 1944 Smee noticed large numbers of an encyrtid parasite in a severe outbreak of T.erytreae in Nyasaland. The parasite was particularly active from June onwards.

Annecke & Cilliers (1963) describe the adult as being "... recognized by its rather dull metallic green body colour, together with the predominantly pallid legs (except the hind femur which is largely brown)". Most encyrtids develop as internal parasites and P.pulvinatus is no exception. The pupa is endoparasitic and a distinctive mummy is formed, emergence taking place through a circular hole (diameter 0.43 - 0.45 mm) in the host's abdominal dorsum.

P.pulvinatus has been collected in the Letaba-Agatha district by the author, especially during the winter months. At all other times it was always eclipsed in abundance by T.radiatus.

Minor Species

Other parasites associated with citrus psylla in the literature or

collected in the field in the Letaba district are shown below. In the latter case their detailed occurrence is shown later in Tables 10-14.

Tetrastichus sicarius Silvestri was reported on citrus psylla in Kenya by Waterston in 1922 (Jensen, 1957). Tetrastichus dryi Waterston was recorded as attacking citrus psylla in Kenya but is not known in South Africa (Annecke & Cilliers, 1963).

Tetrastichus sp. The head, thorax and abdomen are black, as are the femora in this species. It was collected from T.erytreae on citrus and from an unnamed psyllid on two vines to be described later. It was mainly ectoparasitic in psylla in the Letaba district. Blowers (personal communication, 1967) has found this species to be a tertiary parasite, its host being Aphidencyrthus africanus. The parasite was placed in the genus Tetrastichus by Dr B.D. Burks and for convenience is hereafter referred to as Tetrastichus ^{s.p.} ~~_____~~.

Pachyneuron sp. (Pteromalidae) probably attacks T.radiatus in the Letaba district. Jensen (1957) records three species of Pachyneuron as parasites of the Psyllidae.

Coccophagus pulvinariae Compere (Aphelinidae). Males were recorded a few times in the Letaba district. Annecke (1964) states that this is a widely distributed species in Natal and the Transvaal where it parasitizes soft brown scale and Saissetia sp., an unarmoured nigra scale. The male develops as a secondary ectoparasite.

Aphidencyrthus africanus Gahan (Encyrtidae) is a recognized hyperparasite of aphids (Annecke, personal communication, 1966). It was found to be a secondary parasite of T.erytreae, attacking P.pulvinatus. This has subsequently been confirmed by Blowers in the Salisbury district of Rhodesia (personal communication, 1967) and by the author in the Malkerns district (Swaziland).

2. Parasite Activity on T.erytreae

T.erytreae may be severely parasitized, which is unusual for most psyllids (Jensen, 1957). Van der Merwe (1941) states that on occasions 75% of the more advanced nymphs may be parasitized and this agrees with studies in the higher-lying parts of the Letaba district where parasites

FIG. 10

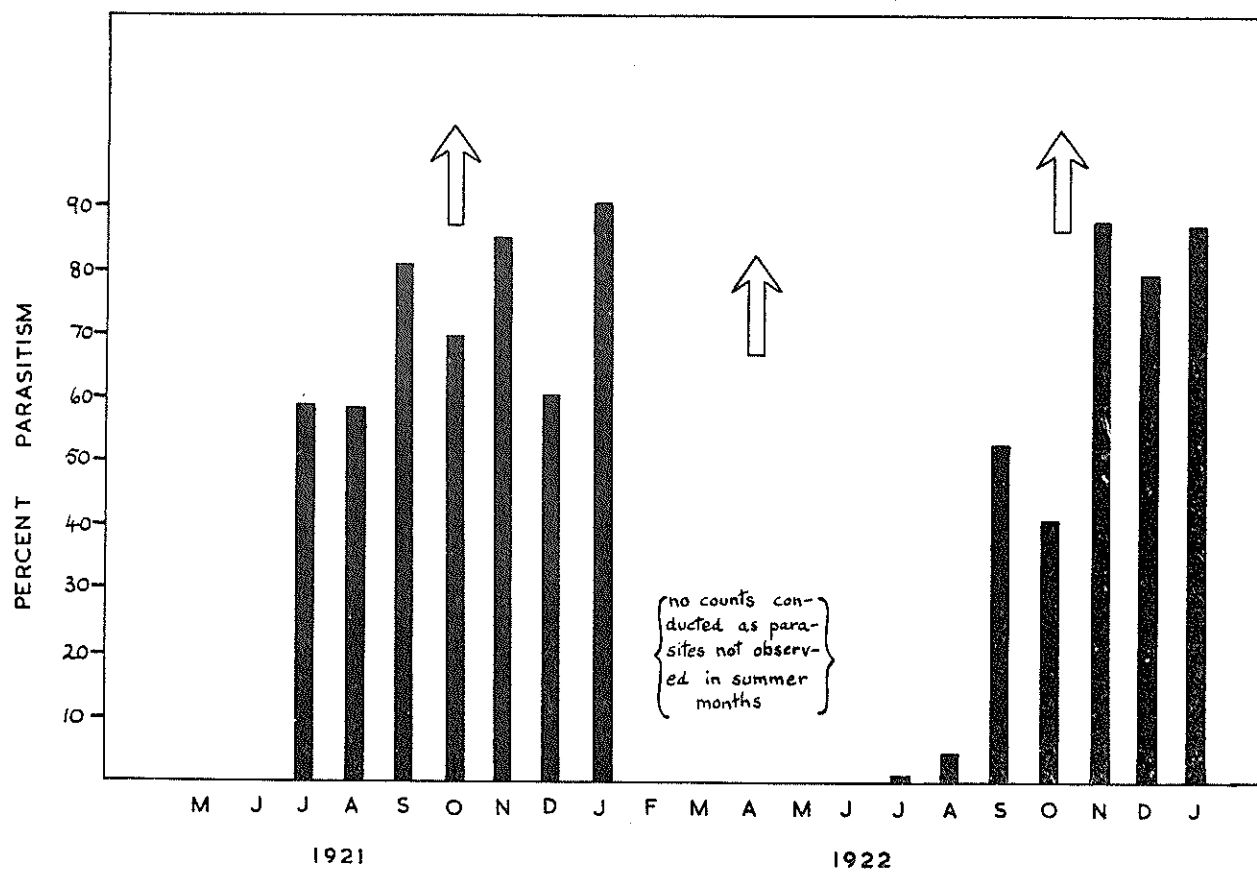
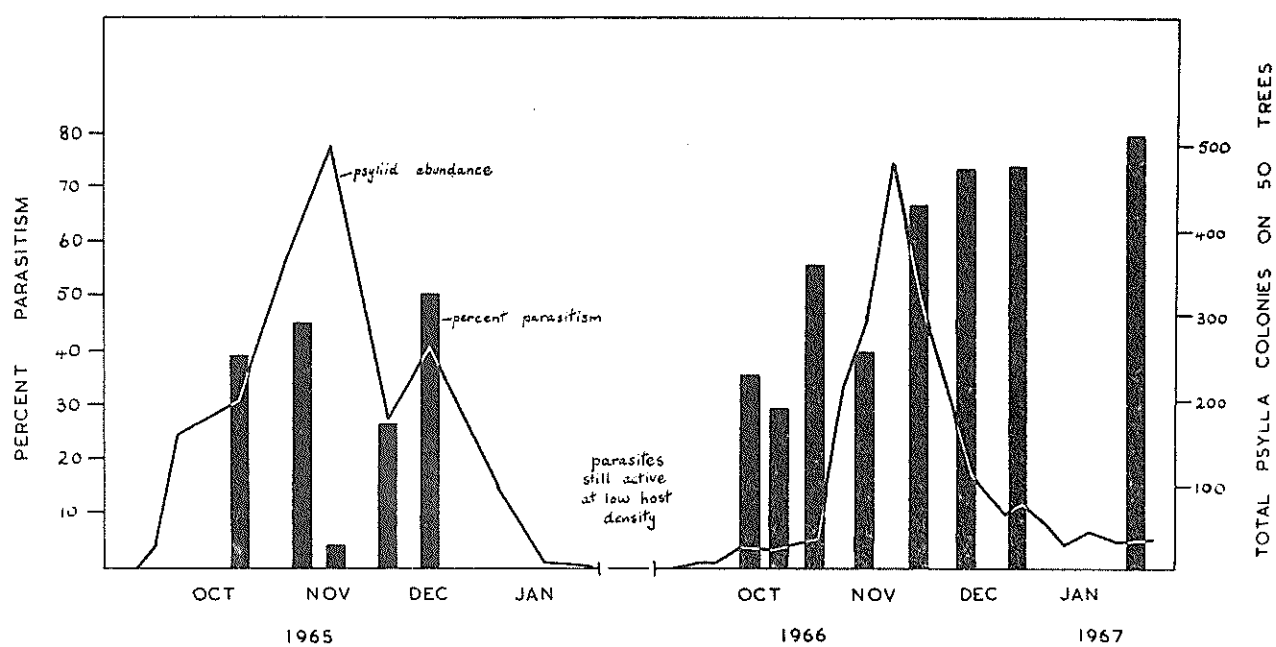


FIG. 11



proved to be an important factor in reducing midsummer psylla populations. Anderson (1914) reported that citrus psylla in British East Africa was kept in check by parasites.

Husain & Nath (1924) show that T.radiatus also attacks the Indian citrus psyllid, D.citri very heavily. There are two annual psyllid cycles in the Punjab and the parasite is particularly active in the autumn outbreak, i.e. in October and November. In 1921 and 1922 counts showed that 80-90% of the nymphs were killed by parasites (Fig. 10) of which about half was attributed to the depredations of T.radiatus.

Main Experimental Sites (Figs. 1 and 2)

Previous Parasite Activity

Prior to the laying out of experimental sites an appraisal of previous parasite activity was made. Where possible, four leaves per tree were removed at random from the sites of former psylla colonies and examined under the microscope. A count was made of (a) dead, unparasitized nymphs (as shown by desiccated exoskeletons - complete or fragmentary); and (b) parasitized nymphs (as shown by mummies, exoskeletons with exit holes, pupal remnants and meconia). 301 clearly parasitized nymphs were found on a total of 447 leaves examined. Furthermore, it was evident that parasites had been active at each site - even at Letaba with a negligible psylla history.

Parasitism: September, 1965, to January, 1967

Tables 10 and 11 show details of parasite counts made during this period. At Forest Hill, and to a lesser extent at Fairview, the action of parasites was clearly an important limiting factor during the two psylla cycles studied. The efficient synchronization between parasite and host at Forest Hill is seen in Fig. 11. There is some lag but according to Huffaker and Messenger (1964) this is always the case with a

EXPLANATION OF FIGURES

Fig. 10. Parasitism of D.citri in the Punjab for 1921-22, 50% attributed to T.radiatus. Peaks of D.citri shown by arrows. (Drawn from tables in Husain & Nath, 1924).

Fig. 11. Percentage parasitism by T.radiatus (bars) and abundance of its host T.erytreae (lines), at Forest Hill for seasons 1965-66 and 1966-67.

rapid change/....

FIG. 12

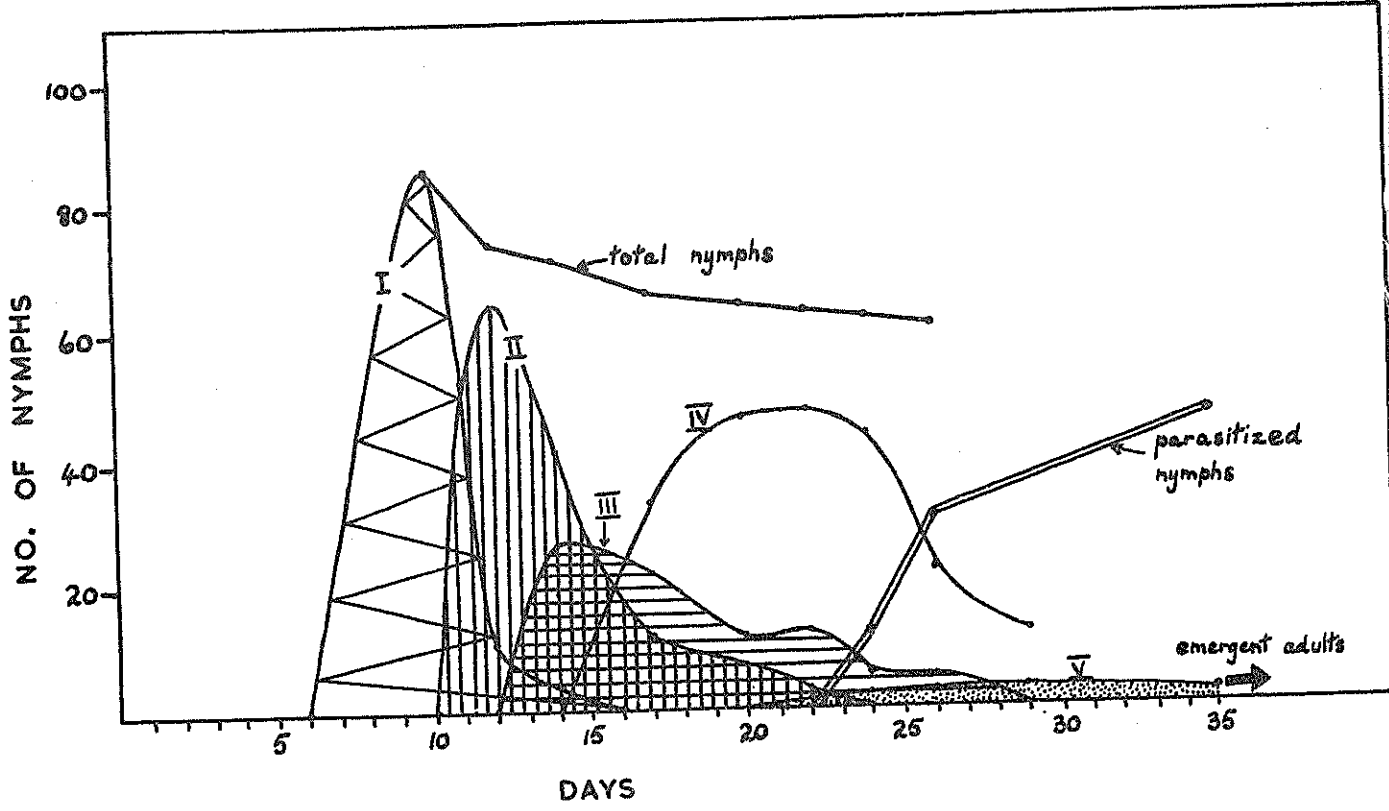
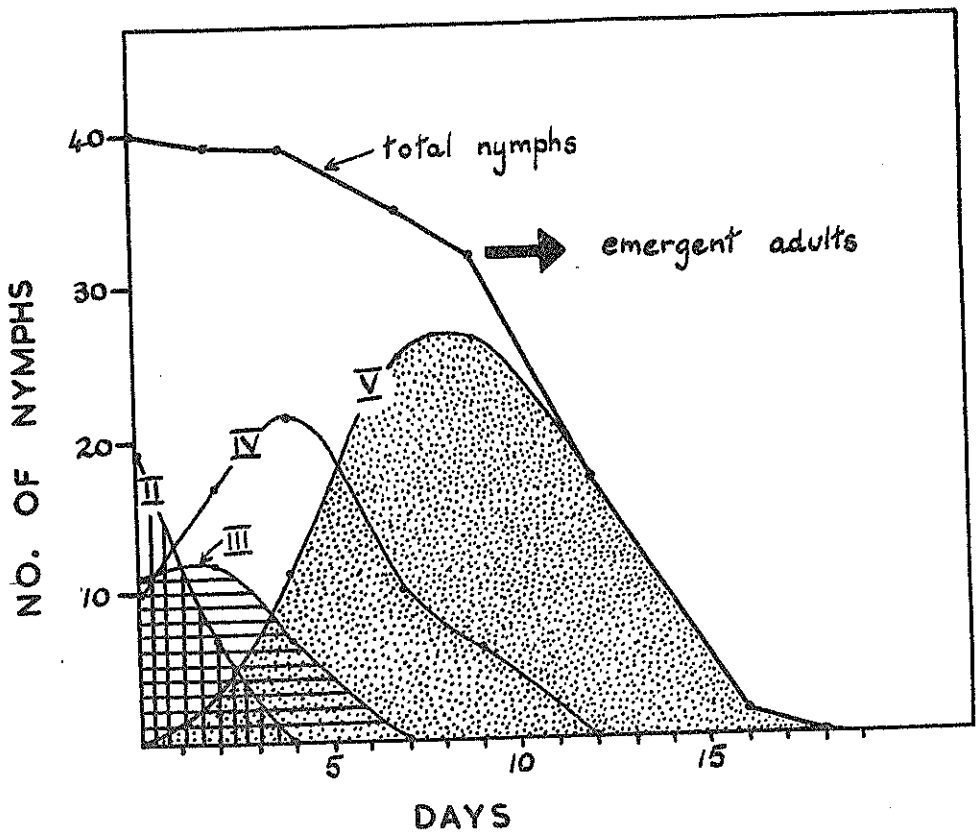


FIG. 13



rapid change in host density. T. radiatus was virtually the sole parasite species involved. No parasites were observed at the Letaba site.

It is probable that the actual degree of parasitism especially in the 1965-66 cycle, was higher than that indicated by the parasite counts. In this first season of study fewer insects were dissected and the recognition of instars II and III was rather uncertain. In the following year counts were more frequent. Sometimes as many as 90% or more of the individuals in some colonies of the in situ counts were parasitized.

In Tables 10 and 11 the class "other mortality factors" undoubtedly contained:-

- a) a few nymphs attacked by endoparasites and secondary parasites but leaving doubtful evidence and thus grouped under this heading, and
- b) Nymphs possibly mutilated by the parasite.

Superparasitism occurred only at Forest Hill. In December, 1965, and November and December, 1966, superparasitized nymphs were provided with two eggs each; in November, 1966, some nymphs had four and a few as many as six parasite eggs each.

The parasites appeared to be remarkably efficient in seeking out their host. They were, for example, observed in the winter of 1966 on May 3 and April 28 at Forest Hill at a time when psylla was at extremely low densities (see Fig. 7). Two in situ counts conducted at Fairview during the 1966-67 season illustrate the invasion and effect of parasites on a psylla population. These counts are shown graphically in Figs. 12 and 13.

During September, 1966, a small psylla population was found to be completely untroubled by parasites. No psylla was encountered at this site in October, and on the 21st of that month a potted seedling with 206 eggs on four leaves was placed in a shady position in an experimental tree. Nymphs were first recorded on October 31 and ten days later the

EXPLANATION OF FIGURES

Fig. 12. Growth of a colony of T. erytreae at Fairview in October, 1966, attacked severely by T. radiatus. The figure shows the rise of successive instars of T. erytreae, the number of parasitized nymphs, and the few nymphs which survived the parasite to become adults.

Fig. 13. Growth of a colony of T. erytreae at Fairview in September, 1966, unmolested by parasites. There was a normal rise of instars IV and V, most of which became adults.

Table 12. Summary of parasite activity at Letswalo for 1966

Date	Source of data	Percent parasitism and no. nymphs examined	Parasite species		
			<u>T. radiatus</u>	<u>P. pulvinatus</u>	Others
March 4	emergence box			5	
March	emergence box		10	4	
March	emergence box			8	
March	emergence box		2		<u>A. africanus</u> 1; <u>C. pulvinariae</u> 6.
July 11	emergence box & parasite count	66.9% : 263	18	1	
July 18	parasite count	40.6% : 286			
July	emergence box				<u>A. africanus</u> 1
Sept. 12	parasite count	1.6% : 305			

colony consisted of 64 nymphs (7 II, 11 III, 46 IV). Parasite activity was first observed on November 12th, and 13 days later the colony had been severely decimated, a microscopic examination revealing 47 nymphs in various stages of parasitization, a single adult psylla and one unparasitized instar V nymph. T.radiatus adults were subsequently reared from this material. Fig. 12 shows the rise and fall of successive psylla instars and their ultimate crash due to parasites.

By contrast, a colony unmolested by parasites developed according to Fig. 13. This data is from a naturally-occurring population first observed on August 29 when comprising instars II-IV. Unlike the parasitized colony, there was a normal rise of the fifth instar. Nearly all nymphs which survived to instar IV attained maturity and emerged as adults. The shape of the curves for instars III and IV in the two populations is also significant. In the parasitized population these curves are skewed to the right, for nymphal development becomes increasingly retarded and thus prolonged as the parasite develops. In the unparasitized colony these curves are almost normal.

Letswalo

Table 12 gives a summary of parasite activity and species involved at this site. Again, parasites were responsible for considerable nymphal mortality - one nymphal count showing 66.9% parasitism. Parasitism was at a low ebb in September, 1966, possibly due to the cover-spraying of all surrounding trees with Rogor in July (see Fig. 14).

T.radiatus was the predominant parasite and there were signs of a secondary parasite - probably Aphidencyrus africanus. Parasites were constantly active in the lower psylla populations during the winter of 1966. Apart from the records shown in Table 12, parasitized nymphs were observed on the experimental trees on March 18 and 31, April 14, and June 16 and 30. T.radiatus adults were seen to be active on June 9. Psyllaephagus pulvinatus was collected fairly regularly during this period.

Letaba Estates

There were no signs of parasite activity at the main experiment for the full duration of the study. Details of activity elsewhere on Letaba for 1965 and 1966 are summarized in Table 13. T.radiatus was dominant

and F.pulvinatus/....

Table 13. Summary of parasite activity on Letaba Estates for 1965 and 1966

Date	Plot	Source of data	Details
<u>1965</u>	?	emergence box	<u>T.radiatus</u> 1; <u>Pachyneuron</u> sp. 1; <u>P.pulvinatus</u> 1; mummies 5
July	Val.BK 11	observation	<u>P.pulvinatus</u> mummies seen in the field
August	Val.BK 8	emergence box	<u>T.radiatus</u> 2; <u>P.pulvinatus</u> 1; mummies
August 1	?	emergence box	<u>T.radiatus</u> 3
August	Val.BK 8	observation	great parasite activity
August 31	Val.BK 11	observation	parasites active
September 2	143	observation	parasites active
early summer	all survey plots	observation	no sign of parasites in field population of psylla except in Val.BK 11 and 143; above
<u>1966</u>			
September 3	1103	parasite count	137 adults emerged from one colony but no sign of parasites
September 6	Val.BK 11	parasite count	no parasitism; 203 unparasitized V; 48 final moults
September 22	316	parasite count	no parasitism; emergence of 200 adults
September 22	1195	parasite count	no parasitism; emergence of 44 adults
September 23	396	parasite count	no parasitism; emergence of 44 adults
September 27	1303	parasite count	no parasitism; 4 unparasitized V; 8 final exuviae; newly-vacated pits
1966	exp. site	all <u>in situ</u> counts	no signs of parasitism
December 27	1303	parasite count	8.2% parasitism from 73 instars 1V and <u>T.radiatus</u> 3

Table 14. Parasite Activity in the Tzaneen-Agatha area for the 1966 season.

Date	Locality	Host density	UNIPARASITIZED						PARASITIZED				Other mortality factors	Total insects available to parasite	Para. nymphs	% age para.	PARASITE SPECIES			
			II	III	IV	V	Adults	Para. egg V	Para. larva			para. pupa					para. emerg.			
									III	IV	V									
August 16	Craighead	high	17	42	40	98			12					192	12	6.3				
August 26	Roumen	low	1	6	6	6								18	0	0.0				
September 2	Monavein	low	13	23	39	160				1				223	1	0.4				
September 7	Duiwelsklf.	mod.	31	14	33	55	295					3		400	3	0.8	4		2	
September 23	Tzaneen	mod.		24	53	111			3	4	4	1		200	12	6.0	49		11	1 Aphidius
September 24	Tricharitaldal	low		12	14	14	29							70	1	1.4				
September 30	Duiwelsklf.	low		9	18	107	11			2		34		181	36	19.9	39	3		
September	Duiwelsklf.	-															3		2	
October 5	Duiwelsklf.	very low															1		1	6 A. afric
November 6	Duiwelsklf.	mod.		13	114	257		3		6	2	18	9	422	38	9.0	32		2	
January 14	Mielieklf.	low															2	20	10	

and P. pulvinatus was recorded in the winter of 1965 at low host densities.

Parasites were active in some plots during the winter and spring of 1965, but were not in evidence for the same period the following year. The first record of T. radiatus in the 1966-67 season was in plot 1303 on December 27.

Tzaneen-Agatha Area

Counts and observations in various citrus groves in the Letaba district present a similar picture of the parasite complex of T. erytreae (Table 14). However, no reasonable explanation can be advanced for the rather lower levels of parasitism in this area.

In October, 1965, there was a citrus psylla explosion in a block of trees belonging to Mrs. A. Morrison of Duiwelskloof. Virtually every flush point of every tree was covered with psylla of all stages. This was the only occasion on which such astronomical numbers were seen during the study period. Parasites and predators were very active.

3. Citrus Psylla Parasites in Other Psyllids

Two vines of the family Menispermaceae are found in the Letaba district which support an unnamed psyllid of the genus Trioza. This insect is remarkably similar in appearance to the citrus psylla and to begin with was thought to be Trioza erytreae. The vines are abundant and frequently grow alongside citrus groves. They continuously produce soft new leaves which makes them ideal host plants for psyllids.

Cissampelos torulosa E. Mey. ex Harv. occurs along rivers and in spruits at all altitudes, and Stephania abyssinica (Dill and Rich) Walp. var. abyssinica is found in dense bush and on open ground above 3000 feet. Both vines are widely distributed in Africa; one herbarium specimen of Stephania from the Congo was seen by the author to have galls identical with those made by this Trioza sp. in the Letaba district.

Further study revealed that the vine psyllid and T. erytreae are biologically distinct and that they do not interbreed. Nymphal coloration and egg placement are quite different, and repeated attempts in both field and laboratory to colonize the vine Trioza on citrus were without success. Citrus psylla adults confined on both vine species died within 2-3 days, a few individuals feeding intermittantly for a few hours. Females did

not oviposit/....

Table 15. Parasites collected from Trioza sp. on vines in the
Letaba district during 1966.

Stephania abyssinica

DATE	LOCALITY	<u>T. radiatus</u>	<u>T. ^{sp.}</u>	Others
July 2	Forest Hill	2	30	
July 2	Westfalia	2	3	<u>Aphidius sp.</u> 3. <u>A. africanus</u> 1.
August 28	Forest Hill	11	10	<u>A. africanus</u> 2.
September 5	Forest Hill	5	1	<u>A. africanus</u> 2.
October 7	Forest Hill	8	12	
November 2	Forest Hill	7	19	27 mummies

Cissampelos torulosa

August 2	Letswalo	101		1 Cynipoid <u>P. pulvinatus</u> 2.
September 1	Letaba	5		
September 2	Letswalo	7	2	
October 13	Letaba [⌘]	4	26	

⌘ parasites were dissected from dead nymphs which made their identification difficult.

not oviposit and nymphs refused to establish themselves on the vines.

Table 15 shows that T.erytreae and the vine psyllid appear to share the same parasite complex. T.radiatus collected from the vine psyllid differ slightly from that from citrus psylla in that the femora are commonly dusky in the former. These parasites were collected from Stephania adjacent to the experimental site at Forest Hill, and from Cissampelos at Letswalo and Letaba. It is thus probable that the vines provide a natural, unsprayed reservoir of citrus psylla parasites in the immediate vicinity of the pest. This source is probably of great significance at the low densities of T.erytreae found on Letaba.

4. Predators

Predators appear to play a minor role in the population dynamics of citrus psylla in the Letaba district. Various predators were present throughout the psylla cycles at Forest Hill, but as limiting factors appeared always to be overshadowed by parasites. They sometimes made a brief appearance in in situ counts. Van der Merwe (1941) listed spiders, a small red mite, and a syrphid larva (identified as Baccha helva Bez.) as predators and was also of the opinion that these were of minor importance in limiting psylla numbers.

The author found various spiders feeding on all stages of T.erytreae, including one which sucked out psylla eggs. Spiders were also a constant scourge of adults in laboratory studies and in the psylla culture. Syrphid larvae were fairly common on psylla-infested leaves but were usually associated with aphids on the same leaf. In a single laboratory trial syrphids could not be induced to attack psylla nymphs. Neuropteran nymphs (probably Chrysopa sp.) were occasionally recorded but again their role as citrus psylla predators was not verified. Two species of erythraeid mites were found attacking psylla nymphs in September and October, 1965, and 1966 at the Forest Hill site. These were identified by Dr M.K.P. Meyer as Bochar-tia sp. larvae and Abrolophus sp. adults. Abrolophus was also collected on the vine psyllid, and on two Diaphorina species on citrus.

VII. THE INFLUENCE OF HOST PLANT

1. Psyllids and Juvenile Foliage

The nymphal stages of most psyllids are found only on the juvenile tissues of their host. This suggests that their life cycle and population fluctuations are closely attuned to the growth cycles of their principal breeding plant. For example, Madsen et al. (1963) shows that most of the eggs of Psylla pyricola Förster are laid on the terminal growth of the pear and that psyllid activity declines as foliage growth ceases in the autumn. The population fluctuations of C. albitextura Taylor, are frequently governed by the supply of juvenile leaves for breeding sites (Clark, 1962), the egg-laying of some females being inhibited by poor foliage condition. The author has observed the eggs and nymphs of several species of Psyllidae on the young growth of various indigenous shrubs and trees in the Letaba district. Large numbers of two Diaphorina species were taken on opening flower buds and young leaves of the marula, Sclerocarya caffra Sond., in the spring of 1966.

The eggs of the Indian citrus psylla, D. citri, are deposited on young flush, never on mature leaves (Husain & Nath, 1927). Lack of oviposition in the winter is commonly due to the absence of suitable growth. The two main flushing periods experienced in the Punjab give rise to two distinct annual psyllid cycles.

The numbers of T. erytreae appear to be similarly regulated. The eggs are deposited on young leaves and the nymphs require succulent, vigorously-growing tissue for normal development. The exact breeding sites are described in chapter 4.

2. The Growth Habit and Flushing Rhythm of Citrus

Citrus is an evergreen aromatic tree which continually sheds senescent leaves and typically produces a yearly quota of new foliage in several growth cycles. According to Webber & Batchelor (1948) each shoot has an apical bud and a series of lateral buds in the leaf axils, each bud consisting of a group of meristematic cells. Leaves develop mainly from buds on shoots of recent growth cycles and thus on the canopy of the tree. On old or debilitated trees, buds on the trunk and older wood often develop into shoots. The developing bud is soft and nearly naked with no definite protective scales.

Each bud forms a small shoot of yellowish green leaves which turn dark green when mature. The leaf is compound, unifoliate and persists for two to three seasons.

Well-managed trees usually make two to four growth cycles each year. In California the spring cycle, which follows the winter dormant period, produces more leaves than subsequent flushes (Webber & Batchelor, 1948). This is followed by a cycle in midsummer and another in autumn. On Letaba Estates the usual pattern is a heavy September growth cycle bearing flush and blossom, and leaf cycles in November-December and February-March. In hotter areas there are additional small winter flushes. The flushing of trees infected with the greening virus is commonly out of phase with healthy trees.

Variation in the flushing cycles of trees (onset, magnitude, duration, and number per season) is chiefly influenced by environmental factors, age and variety.

Moisture. Irrigation and rainfall are very important in controlling flushing rhythm. The sudden, heavy irrigation of semi-dormant trees in early spring is a well-tried citrus practice to induce a uniform and prolific growth cycle. A drought period during the rainy season often delays or indefinitely postpones a recognized growth cycle. In the 1966-67 season the November cycle at Letaba was delayed for about three weeks due to an exceptionally dry November and early December and a shortage of irrigation water. In the Punjab the main vegetative flush in July-August is precipitated by the start of the monsoon rains (Husain & Nath, 1926).

Temperature. Temperature governs growth at all times of the year in areas with a marginal citrus climate, and in most citrus areas during the winter months. Webber & Batchelor (1948) give the threshold temperature for citrus growth as 12.8°C and state that in California the mean daily temperature and the soil temperature of the root zone do not rise significantly above this temperature during the three winter months. This causes a three-month cessation of growth. In the Letaba area, the mean daily temperature for the coldest month of 1966 was 15.2°C (at the Forest Hill site) which represents a temperature regime permitting winter growth. However, as will be shown later, most bearing trees on Letaba Estates produced little young growth during this period, probably due to the overriding effect of minimal irrigation.

Tree age. Young trees tend to flush more profusely and for longer periods than mature trees. Their growth cycles may be irregular and are always less distinct than those of older trees.

Tree Variety and species. Limes, Citrus aurantifolia (Christm.) and lemons C. limon (Linn.) are known to flush more freely than the sweet orange C. sinensis (Linn.). Little is known of the inherent differences in growth habit of the various sweet orange varieties, but the author has observed certain but as yet undetermined differences in the flushing of Navels, Valencias and mid-seasons. In the psylla surveys conducted on Letaba Estates (Table 9) populations were too low to indicate any differences in varietal susceptibility.

An important factor common to the favourable citrus psylla habitats in the Letaba district was the presence of small but significant amounts of flush during the winter months. With the extreme fecundity of T. erytreae, the persistence of even small populations on scattered winter flush can produce outbreak densities in early summer, given plentiful food and a few weeks of favourable climate. Husain & Nath (1926) concluded that one of the main reasons for widespread outbreaks of D. citri in India was the fact that many trees flush perennially. In addition, well-clipped (thus constantly flushing) citrus hedges abound in India, especially in the Punjab.

3. The Relation of Flush to Psylla Populations in the Letaba District

In chapter 5 it was seen that of the three main experimental sites, only Forest Hill supported populations of T. erytreae throughout the winter of 1966. This was the only site to produce small amounts of young foliage at this period. The trees at the other stations were completely dormant and thus devoid of breeding sites.

To investigate more closely the influence of young foliage on psylla numbers, the Letswalo site was compared with Block 8 Valencia (B8V) on Letaba Estates, a fifty-tree block of mid-seasons of comparable size and general tree condition. From February, 1966, to January, 1967, the trees at both sites were searched regularly for psylla colonies and the total quantity of available flush rated. The correlation between available food and psylla density is shown at Letswalo in Fig. 14. Farming operations which influenced flush and psylla density during the investigation are shown in

the legend/....

FIG. 14

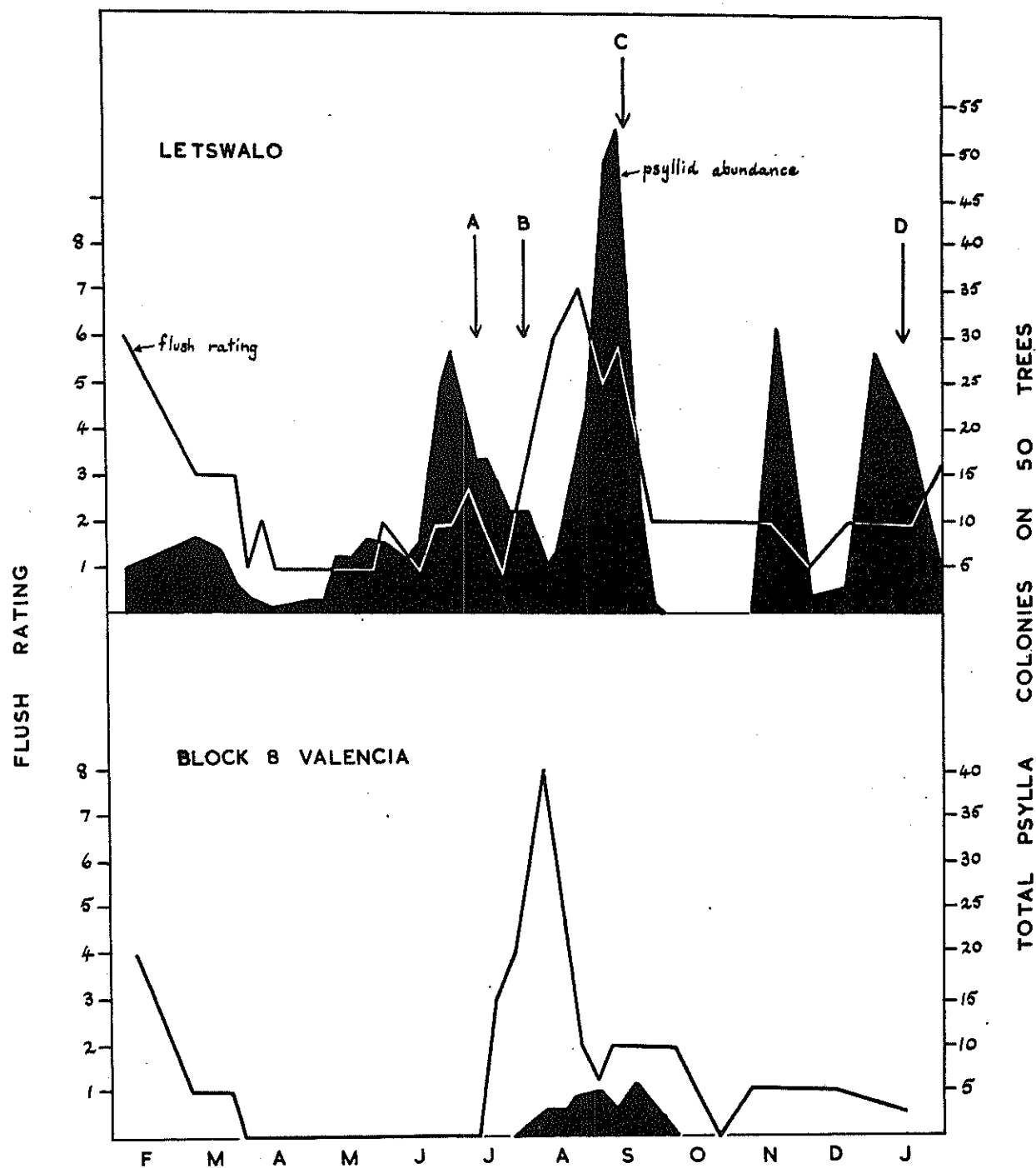
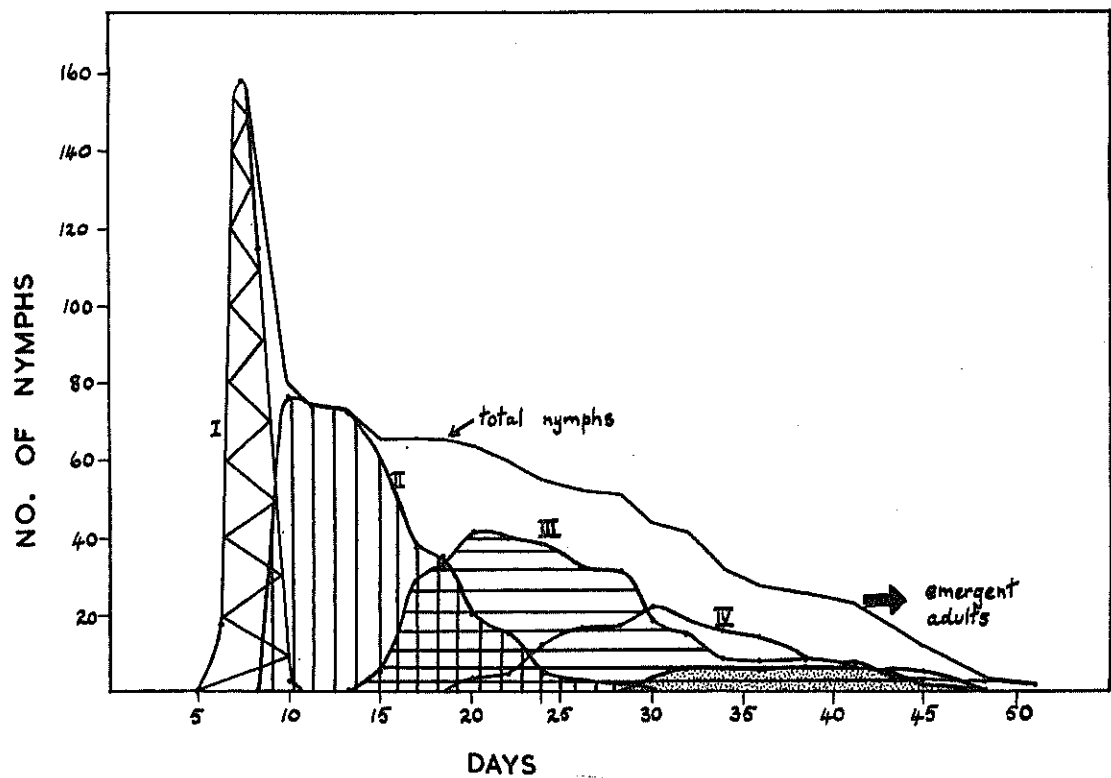


FIG. 15



the legend. The continuous production of small amounts of flush supported significant populations of T.erytreae during the winter, both in the experimental trees and in the surrounding groves of the Letsitele Valley. By late August psylla numbers had increased to such an extent that some farmers in the area were obliged to apply insecticide. These groves have a history of psylla outbreaks, especially in late winter and early summer. The incidence of greening is high and was particularly evident in 1966. One of the main reasons for this position is thought to be the annual occurrence of winter flush, presumably due to the high water table, and excessive sprinkler irrigation. These trees also receive large amounts of nitrogenous fertilizer which produces large succulent leaves. As will be seen in chapter 8, the citrus psylla is virtually unchecked by climate at this time of the year.

Fig. 14 shows similar peaks of foliage production at the B8V site, but there was a winter period of $3\frac{1}{2}$ months when the trees were totally without flush. Thus all psylla breeding activity was suspended. The first colonies were found in July and the subsequent population rise was small. This flush pattern was typical for bearing trees on Letaba Estates during 1966 and was probably partly responsible for the sparse psylla populations in the spring of that year.

The above investigation and other observations by the author indicate that in general the flushing rhythm of citrus on Letaba Estates is not conducive to the development of large populations of citrus psylla. Flush cycles are well-defined and trees remain fairly flush-free between these cycles.

EXPLANATION OF FIGURES

Fig. 14. Population fluctuations of T.erytreae and available juvenile flush at Letswalo and Block 8 Valencia (Letaba Estates) for 1966. Agricultural operations affecting these populations at Letswalo were as follows:-

- A - some flush points removed during harvesting operations;
- B - surrounding trees sprayed with insecticide (Rogor);
- C and D - experimental trees sprayed with insecticide (parathion and Rogor respectively).

Fig. 15. Growth of a colony of T.erytreae on a poorly nourished citrus seedling. For many nymphs the poor quality foliage caused prolonged development and ultimate death.

4. Physiology of Host Tissue

Host tissue must be succulent and nutritious for the normal growth of T.erytreae nymphs. Nymphs on unfavourable leaves often become flattened and reduced in size, and finally cease growing and succumb. First instar nymphs emerging on large, toughened leaves succumb in a few days.

Leaf age and position. In situ counts show that nymphs have higher survival rates when developing on the smaller terminal leaves, than on larger leaves lower down the same flush point. Table 16 is from a count on a single flush point at Forest Hill and is typical of a number of in situ counts made during the 1966-67 psylla cycle. Leaf measurements were from leaf tip to the junction of lamina and petiole. Survivals from egg to instars II to III are shown. There is a progressive decrease in survival down the flush point. Since all the leaves appeared succulent enough for normal development, the differential survival is regarded as being due to differences in available food in leaves of different age or position.

Table 16. Nymphal mortality according to leaf size and position

Leaf	Approximate length in inches	No. eggs Oct 31	No. nymphs (instars II-III) Nov 12	Percentage survival
1	0.50	33	28	85
2	0.50	33	33	100
3	0.50	37	35	95
4	0.50	28	19	68
5	0.75	68	24	35
6	0.75	42	15	36
7	1.00	20	1	5

Young citrus leaves grow rapidly and their composition varies with age. Webber & Batchelor (1948) compared the concentration of the major plant ions in leaves of different ages and found that with the exception of calcium, all ions were present at lower levels in six-week-old citrus leaves than in one-week-old leaves. They also state that young leaves have a greater diastatic activity than mature leaves.

Leaf protein. "Proteins form an important part of the meristematic cells of buds" (Webber & Batchelor, 1948). A few preliminary analyses

by the author/....

by the author have shown that the protein content of young citrus leaves declines steadily with age. Like the leaves on which they develop psylla nymphs grow rapidly and presumably require large amounts of protein. As with most Homoptera, psyllids have a number of adaptations to cope with their sugary diet of plant-sap. The hind gut and oesophagus are wound round each other spirally to form a so-called 'filter chamber' (Wigglesworth, 1961). This arrangement short-circuits excess fluid in the diet and allows only the more concentrated part to enter the main digestive section of the gut. Many Homoptera secrete a honeydew rich in sugar; Trabutina mannipara (Homiptera; Coccidae) produces a secretion of 55% sucrose, 25% invert sugar, and 19.3% dextrin. The faecal pellets of T.erytreae were analysed in the laboratory and were found to be composed of starch, and a disaccharide, probably sucrose. Preliminary tests showed no protein to be present. According to Wigglesworth (1961) it has been generally assumed that the purpose of these adaptations is to balance a surfeit of liquid and sugar with sufficient protein. However, that author rejects this explanation and suggests that these devices are rather for the procurement of some other necessary substance.

There were indications of mortality due to protein starvation in the experimental trees at Forest Hill in December, 1966. Despite a favourable temperature - moisture regime and the negligible affect of parasites in early nymphal stages, there was a high rate of mortality of instars I to III. Table 17 shows that a large part of the mortality of instars III - V was also presumably due to the effect of plant host for predation was low.

Table 17. Survival of instars III - V from in situ counts on trees at Forest Hill, 1966

Count	Total nymphs at rise of instar III.	No. of nymphs which became adults	No. of parasitized nymphs	No. of nymphs presumably starved (a few killed by predators)
40	60	0	12	48
41	179	12	17	150
42	134	0	7	127
43	96	0	3	93
45	175	0	13	162
46	142	3	17	122

On many of the experimental trees the young leaves, though succulent, were abnormally yellow and clearly deficient in nitrogen. Accordingly a leaf sample was removed from a tree at Forest Hill on which in situ counts had shown such high nymphal mortality. Also a composite sample of leaves of the same age and size was taken at random from other experimental trees. Analysis showed a crude protein content of 7.8 and 8.4 per cent respectively. Leaves were then picked from a block of trees on Letaba Estates and matched for size and age. In situ counts had shown that these trees had supported normal nymphal development at the same time as the Forest Hill mortality was being experienced. The leaves were a healthy colour and had a crude protein content of 15.0 per cent.

Differences in Plant Host Quality. Clark (1962, 1963) studied the relationships between C.albitextura and its eucalypt host. He found that adult feeding, though not producing any visible damage to host tissue, markedly lowered the attractiveness of foliage for oviposition. He also found the favourableness of individual trees to differ considerably. On some leaves were found dense clusters of nymphs in discrete zones. These phenomena were all explained in terms of differences in available food supply, the available food being irregularly distributed not only in different trees but also in individual leaves.

Adult feeding does not apparently affect the egg-laying behaviour of T.erytreae females in any way. Teneral adults feed for a few days on the leaf from which they emerged and then seek out young flush for egg-laying. Unlike the plant host of C.albitextura, suitable citrus flush is never older than one to two weeks so that there is little chance for significant amounts of plant food to be removed by adults. Nor have individual citrus trees or flush points been observed to differ in favourability for oviposition. Provided there is young, succulent flush, eggs are laid even on poorly nourished leaves. However, aggregations of nymphs have been observed which seem to indicate an uneven distribution of food in citrus leaves. Sometimes, amongst a normally-growing population of nymphs a few stunted and retarded individuals are seen which presumably placed themselves unfavourably for an adequate food supply.

Cessation of growth and starvation. Besides the effects already described, poorly grown host tissue prevents the formation of the typical gall and results/....

and results in a smaller, excessively flattened nymph, with a prolonged instar duration. This was observed on poorly-nourished plants in the culture room and in two in situ counts. Moran & Blowers (1967) found that instar durations were prolonged when nymphs were reared on single citrus leaves on moist cotton wool.

Fig. 15 shows an in situ count conducted at Letaba in December, 1966, on a poorly nourished seedling. This population was not attacked by parasites. Instar I and the rise of instar II proceeded normally, but thereafter each stage was markedly prolonged until on the 40th day the population consisted of about equal numbers of instars III, IV and V. Many of the nymphs were reduced in size. The duration of nymphal development (from the hatching of the first instar nymphs to the emergence of the first adults) was 35 days. Nymphal development took only 25 days in another in situ count on well-nourished tissue over the same period. The eventual effect of the poor host tissue was an extremely high nymphal mortality, for of the 158 instar I nymphs which emerged only three attained maturity. The effect of poor host tissue is also shown in Fig. 23 in chapter 8.

VIII. THE INFLUENCE OF CLIMATE

T.erytreae is extremely sensitive to high temperatures combined with low humidity. Van der Merwe (1941) was the first to record the sensitivity of the early instars to summer temperatures and concluded that dry summers were probably a limiting factor in many citrus areas of southern Africa.

Many species of Psyllidae are known to be intolerant of high temperatures and the work of Madsen et al. (1963) on P.pyricola, and List (1939) on P.cockerelli are oft-quoted examples. Clark (1964) found C.albitextura to be similarly affected by high temperatures. Sweeney (personal communication, 1967) has observed that, with the exception of a Phytolyma species, most African psyllids are more prevalent in cooler regions above 3000 feet.

In chapter 1 it was mentioned that serious outbreaks of citrus psylla began simultaneously at Rustenburg, White River, Tzaneen-Agatha, and Malkerns (Swaziland) in 1959-60. Heavy populations were evident for the following three seasons in all these areas. It is likely that further study will show climate to be the main factor responsible for the simultaneous occurrence of such widely - scattered outbreaks.

1. Preliminary Evidence of the Lethal Effect of High Temperatures

Population outbreaks and altitude. In most of the citrus areas of the Transvaal, i.e. Rustenburg, Tzaneen-Agatha, Nelspruit-White River, and in Swaziland, psylla numbers have been reported by farmers and agriculturalists, and in many cases observed by the author, to be far higher and more persistent in the cooler, upland groves of each district. In the hot drier lowlands of southern Africa, citrus psylla is found very infrequently and then in small numbers. It is regarded as a curiosity at Hippo Valley (Rhodesia) at 1100 feet above sea level (Fourie, personal communication, 1966); and at Tambankulu Estates (Swaziland) at 750 feet regular inspections in 1965 and 1966 showed psylla to be virtually absent.

Outbreaks and seasonal climate. Serious outbreaks are reputed to occur in cooler seasons. This observation is fairly well supported in this investigation.

Failure of psylla cultures on Letaba Estates. Two psylla cultures were started in the winter of 1965, one in a shaded greenhouse and another in the laboratory, and both were largely destroyed following high temperatures.

The greenhouse/....

Table 18. Monthly mean temperatures in degrees Centigrade at the three main experimental sites in the Letaba district from December, 1965, to January, 1967. Temperatures were taken from hygrothermograph traces. Hr° C/D = number of hour degrees Centigrade per day.

FAIRVIEW																	FOREST HILL																
LETABA																																	
	Max	Min	Mean	Hr° C/Day			Max	Min	Mean	Hr° C/Day			Max	Min	Mean	Hr° C/Day																	
				above 20°	below 20°					above 20°	below 20°					above 20°	below 20°																
1965 D	33.0	18.3	25.7	126	4		30.9	18.1	24.4	89	13		25.9	15.6	20.8	48	31																
1966 J	34.2	20.6	27.4	161	3		32.4	19.6	26.0	118	5		27.1	16.9	22.0	56	21																
F	28.3	19.4	23.9	76	8		27.3	18.2	22.8	54	15		23.3	15.7	19.5	20	49																
M	29.6	16.8	23.2	72	19		27.7	16.4	22.1	46	25		23.5	14.7	19.1	20	50																
A	27.9	14.6	21.3	52	40		26.1	14.3	20.3	39	54		22.2	13.0	17.6	22	86																
M	28.0	9.9	18.9	43	93		26.8	12.1	19.5	33	72		22.8	11.8	17.4	15	84																
J	24.6	10.0	17.3	22	98		23.5	11.8	17.7	16	94		19.5	10.8	15.2	6	128																
J	25.5	8.8	17.2	30	111		24.6	10.9	17.8	22	96		20.7	10.0	15.5	8	124																
A	26.7	9.5	18.2	38	93		25.9	11.3	18.6	31	83		21.5	10.5	16.0	11	114																
S	27.7	12.6	20.1	55	59		26.5	13.2	20.0	47	68		22.4	11.1	16.8	23	106																
O	29.1	13.7	21.4	74	45		28.2	14.2	21.9	64	55		23.0	12.4	17.7	31	92																
N	30.0	17.0	23.5	83	16		27.8	16.5	22.2	61	27		23.1	14.2	18.7	28	70																
D	30.3	19.1	24.7	106	7		28.2	18.0	23.1	71	16		23.5	15.5	19.5	30	48																
1967 J	30.9	20.2	25.6	112	2		28.8	18.7	23.8	68	6		24.1	16.5	20.3	23	35																

Table 19. Monthly mean relative humidities recorded at the three main experimental sites in the Letaba district from December, 1965, to January, 1967. Humidities were taken from hygrothermograph traces.

	LETABA				FAIRVIEW				FOREST HILL			
	Max	Min	Mean	1400 hours	Max	Min	Mean	1400 hours	Max	Min	Mean	1400 hours
1965 D	94	36	65	39	91	39	65	46	93	51	72	61
1966 J	93	33	63	38	95	38	67	43	96	52	74	58
F	95	54	75	58	95	57	76	62	97	72	85	78
M	92	38	65	41	94	42	68	47	94	60	77	66
A	87	34	61	36	88	38	63	42	91	53	72	58
M	86	25	56	26	82	28	55	29	79	38	59	40
J	93	36	65	38	88	37	63	41	84	49	67	54
J	85	27	56	27	81	28	55	29	81	41	61	43
A	86	28	57	29	81	27	54	29	78	39	59	42
S	91	33	62	36	89	36	63	39	85	44	65	48
O	88	34	61	36	88	38	63	40	85	54	70	56
N	90	39	65	43	92	46	69	50	91	58	75	65
D	90	44	67	48	93	51	72	55	95	64	80	70
1967 J	93	44	69	50	95	52	73	57	95	72	84	76

FIG. 16

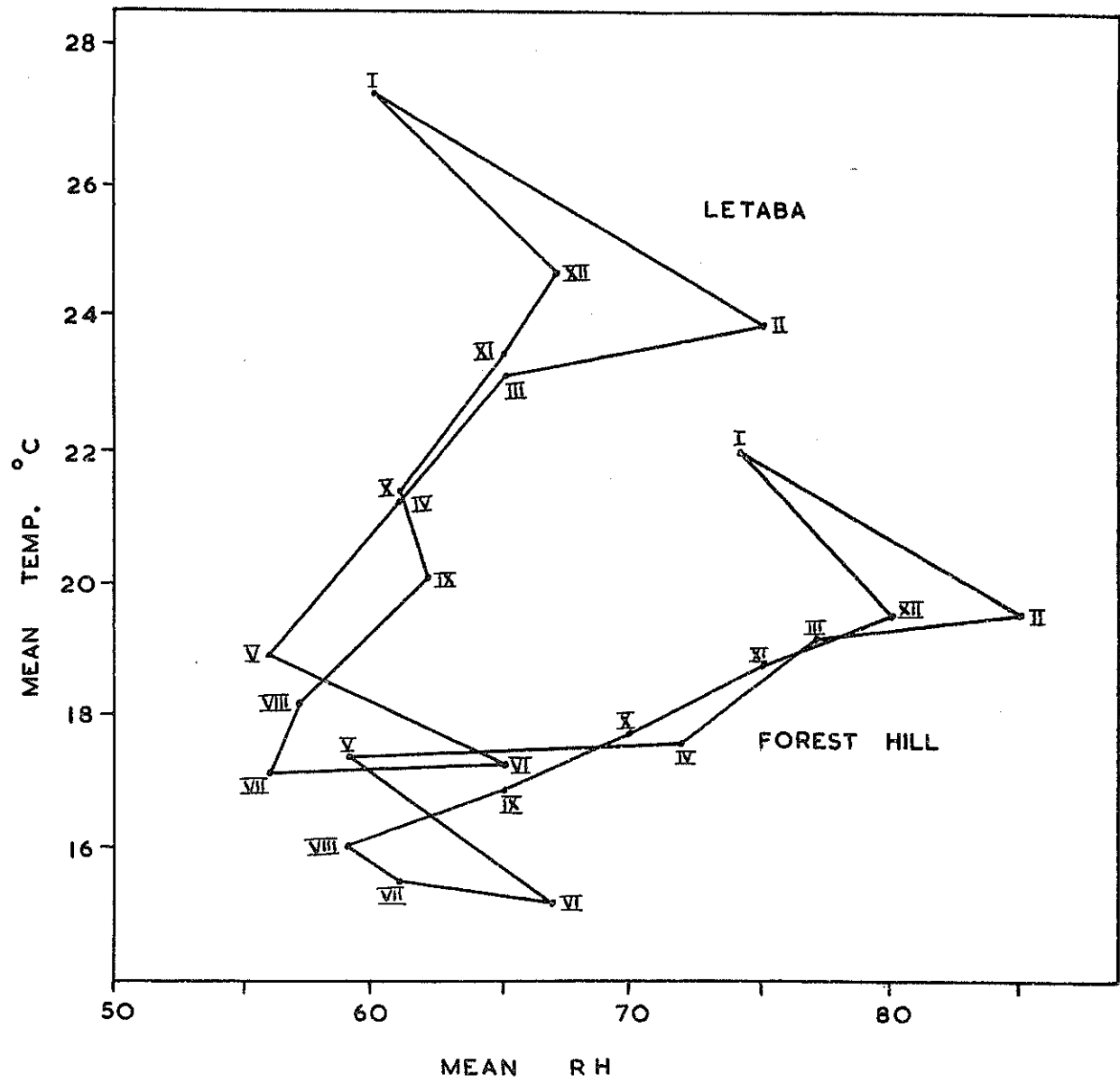
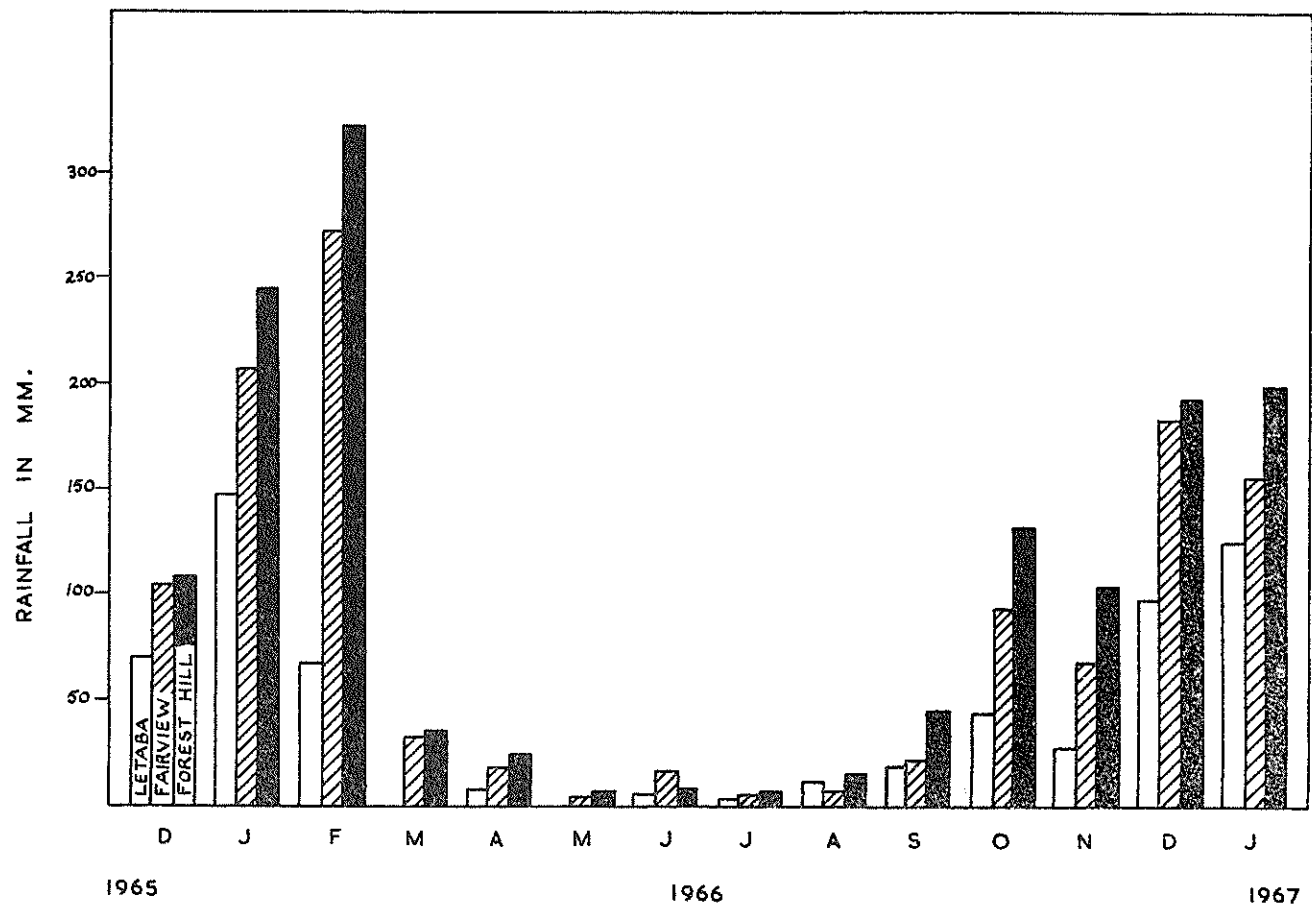


FIG. 17



The greenhouse culture, which at one stage consisted of 40-50 populous nymphal colonies, was decimated after a short spell of hot August weather. In order to maintain a psylla culture on Letaba a thermostatically controlled cool room was necessary.

2. General Climate of the Letaba District

The Letaba-Agatha area is situated between the Drakensberg escarpment to the west and the tropical savannah of the Transvaal lowveld to the east. The climate is subtropical with a warm dry winter and a hot moist summer. Though there is a mean annual rainfall of 760-1520 mm (30-60 inches) within this area, it is extremely variable and the evaporation rate is high. A large part of the rain falls as thunder showers and hail is not uncommon. The climate is exceptional for the lack of significant prevailing winds at ground level, especially on Letaba Estates itself.

3. Climate at the Experimental Sites

Main Sites

Tables 18 and 19 and Figs. 16-18 summarize the climate recorded at the three main weather stations. Letaba was considerably hotter and drier than Forest Hill for all months of the year. Citrus psylla populations were negligible at Letaba but at Forest Hill were high in early summer and persisted at low densities throughout the winter months (see Fig.7). The Fairview site was intermediate for climate and psylla abundance.

The interval and similar shape of the two polygons in Fig. 16 suggest that the difference in climate between Letaba and Forest Hill was due to difference in altitude. It was found that graphs of the daily values of maximum temperature and the number of hour degrees Centigrade per day above 13° for the three stations followed one another closely and never crossed.

Minor Sites

The climate at these sites is compared with that of Letaba Estates, their altitudes being within 300 feet of the latter. At Letswalo (Fig. 19), the monthly mean temperature was slightly below, and the humidity considerably higher than that of Letaba. Citrus psylla was found at this site almost

EXPLANATION OF FIGURES

Fig. 16. Temperature-moisture climograph for Letaba and Forest Hill for 1966. Months shown from I to XII.

Fig. 17. Monthly rainfall at the main experimental sites in the Letaba district from December, 1965. to January, 1967.

FIG. 18

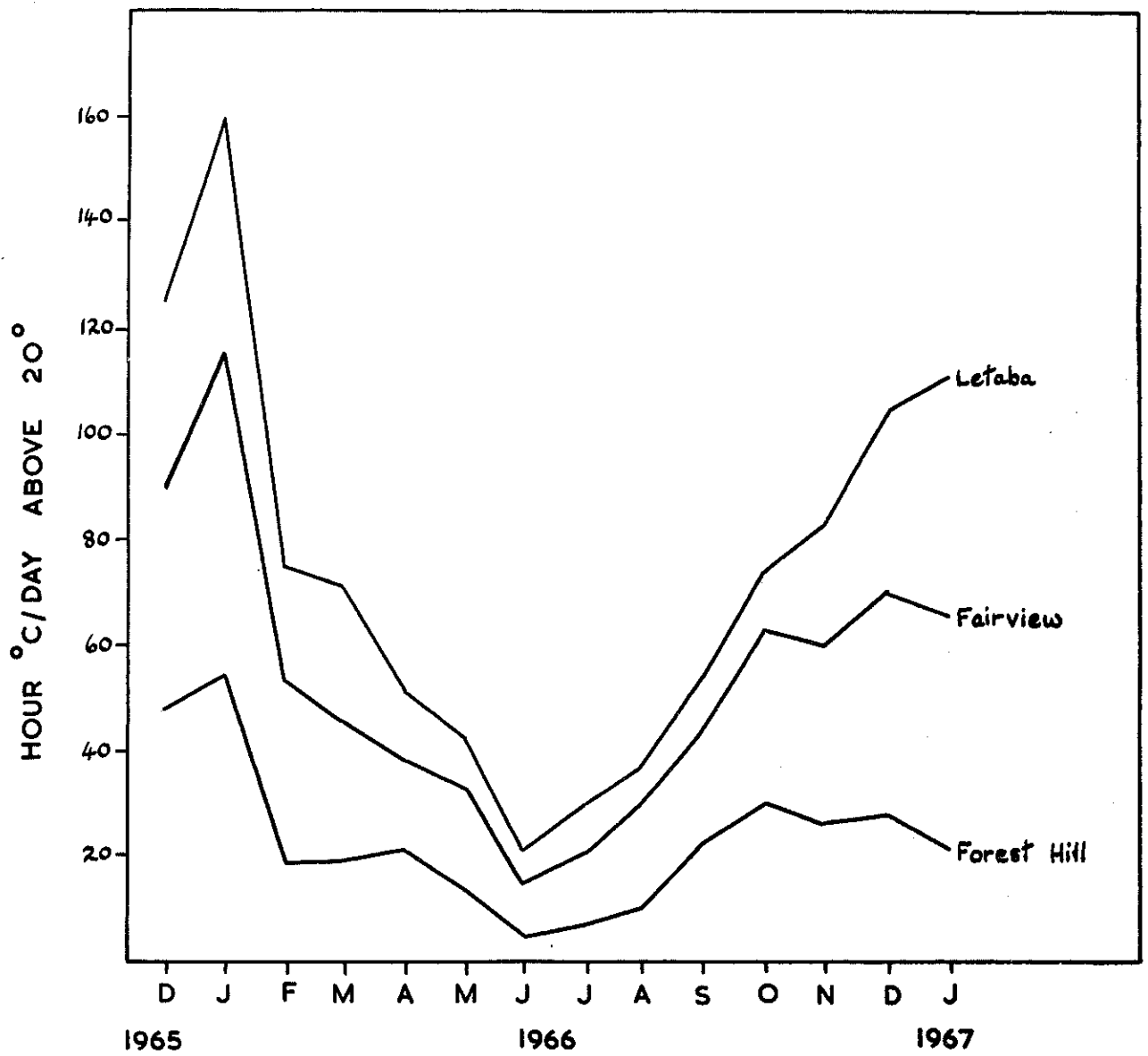


FIG. 19

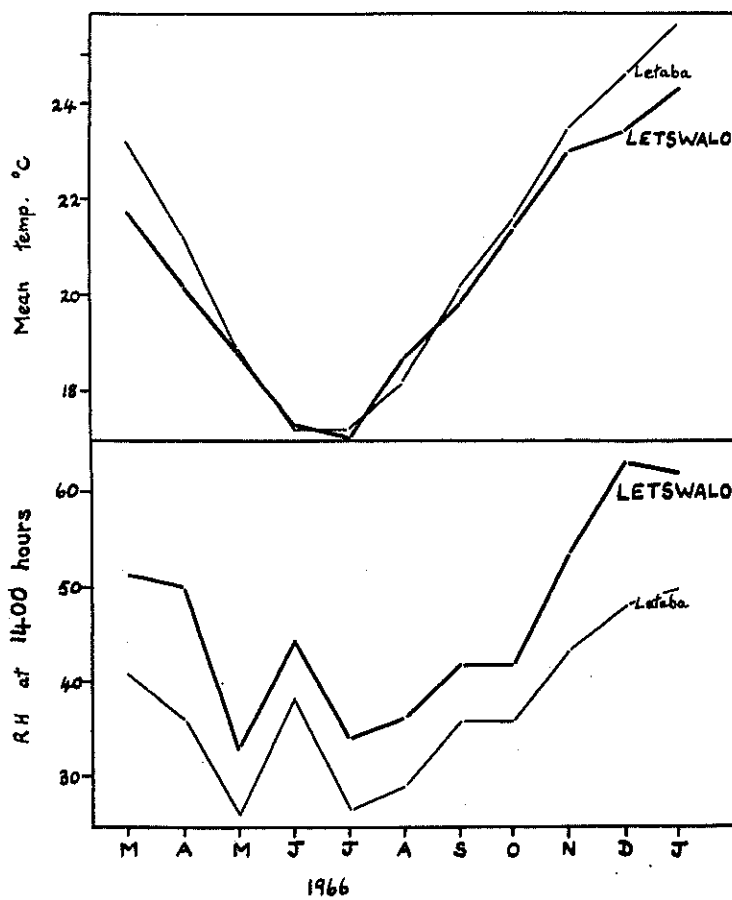
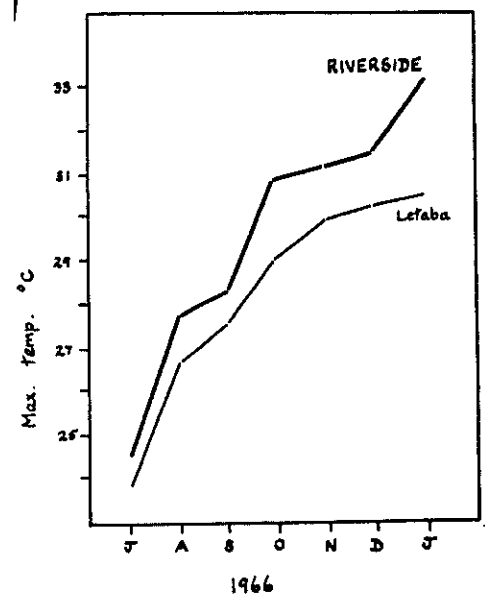


FIG. 20



throughout the study period.

There was little difference in humidity between Letaba and Riverside. However, the monthly maximum temperatures (Fig. 20) ranged from 0.5 (in July, 1966) to 2.5°C (in January, 1967) above those for Letaba. This site would seem to be extremely marginal for no citrus psylla was observed in these trees, nor was there any evidence of previous infestations.

4. Population Fluctuations in the Letaba District in Relation to Prevailing Climate

Spring, 1965, to December, 1966

It was mentioned in chapter 5 that psylla populations at the main experimental sites were found to be slightly higher in the early summer of 1965-66 than in the following season. The same tendency was evident from the psylla surveys conducted on Letaba Estates (see Table 9). Populations were also exceptionally low in the Tzaneen-Duiwelskloof area during the early part of the 1966-67 season.

Fig. 21 compares the monthly maximum temperatures and rainfall for the study period with the 17-year average for Letaba Estates. It is immediately obvious that the midsummer of 1965-66 was unusually hot and dry and thus detrimental to psylla development. Populations were severely reduced by the extreme heat of January leaving small numbers to overwinter rather precariously on semi-dormant winter trees. (A few psylla colonies were discovered on the Estate during the winter after an exhaustive search). In the spring of 1966 mean temperatures approached the 17-year average but rainfall (and thus humidity) was below average and thus again unfavourable for the developmental stages of citrus psylla. Many of the eggs in colonies marked for in situ counts on Letaba either shrivelled and failed to hatch or yielded first instar nymphs which immediately died (Table 24). This effect was observed

EXPLANATION OF FIGURES

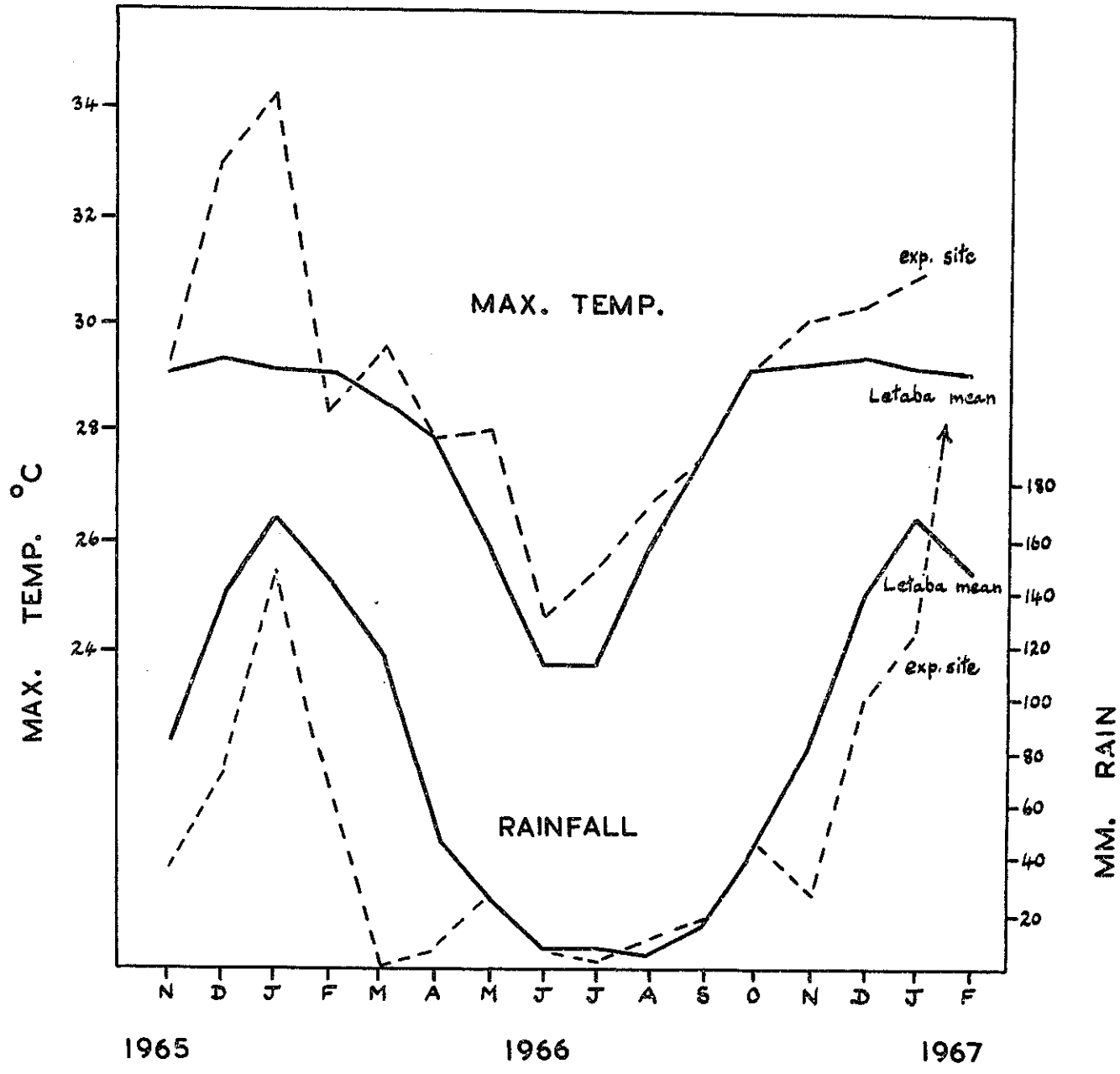
Fig. 18. Monthly means of the number of hour degrees Centigrade per day above 20° (Hr°C/Day above 20°) at the main experimental sites in the Letaba district from December, 1965, to January, 1967.

Fig. 19. Mean monthly temperature and relative humidity at 1400 hours for Letswalo and Letaba from March, 1966, to January, 1967.

Fig. 20. Mean monthly maximum temperature for Riverside and Letaba from July, 1966, to January, 1967.

repeatedly/....

FIG. 21



repeatedly in Block 8 Valencia, and in late September at the Letswalo site where it was partly responsible for the extremely low psylla activity in October and early November (Fig. 14). In the second week of October excessive heat and low humidity were seen to kill off the early stages of *Diaphorina* sp. on the marula, and *Trioza* sp. on *Cissampelos torulosa*.

Some batches of eggs used for in situ counts on Letaba Estates were abnormally pale. None of these eggs was observed to hatch and it is assumed that they were infertile. This is perhaps an indication of small and scattered psylla populations.

The fairly high and persistent populations at Letswalo have been noted. Apart from the profuse flushing of these trees, an important contributory factor was the higher level of humidity (Fig. 19).

January and February, 1967

Despite the low spring populations, there was a widespread build-up of citrus psylla in the Letaba district in the midsummer of 1966-67. Many farmers in the Tzaneen area were faced with a serious outbreak in January and many groves were sprayed with insecticide. This outbreak was preceded by several weeks of humid, overcast weather which coincided with a fairly heavy summer flush. Table 20 shows that at Letaba the midsummer climate of 1966-67 was close to the 17-year average, with a monthly maximum temperature 2.7 - 3.3°C lower than that of the previous season. The temperature was

Table 20. Temperatures and humidities for December and January at Letaba for 1965-66, 1966-67, and the 17-year average.

	December		January	
	Mean max. temp. °C	Mean min. %RH	Mean max. temp. °C	Mean min. %RH
1965-66	33.0	36	34.2	33
1966-67	30.3	44	30.9	44
Letaba average	29.4	-	29.2	-

EXPLANATION OF FIGURE

Fig. 21. Mean monthly maximum temperature and monthly rainfall for the experimental site at Letaba during the study period (broken lines); and the 17-year averages for Letaba Estates (solid lines).

further/....

FIG. 22

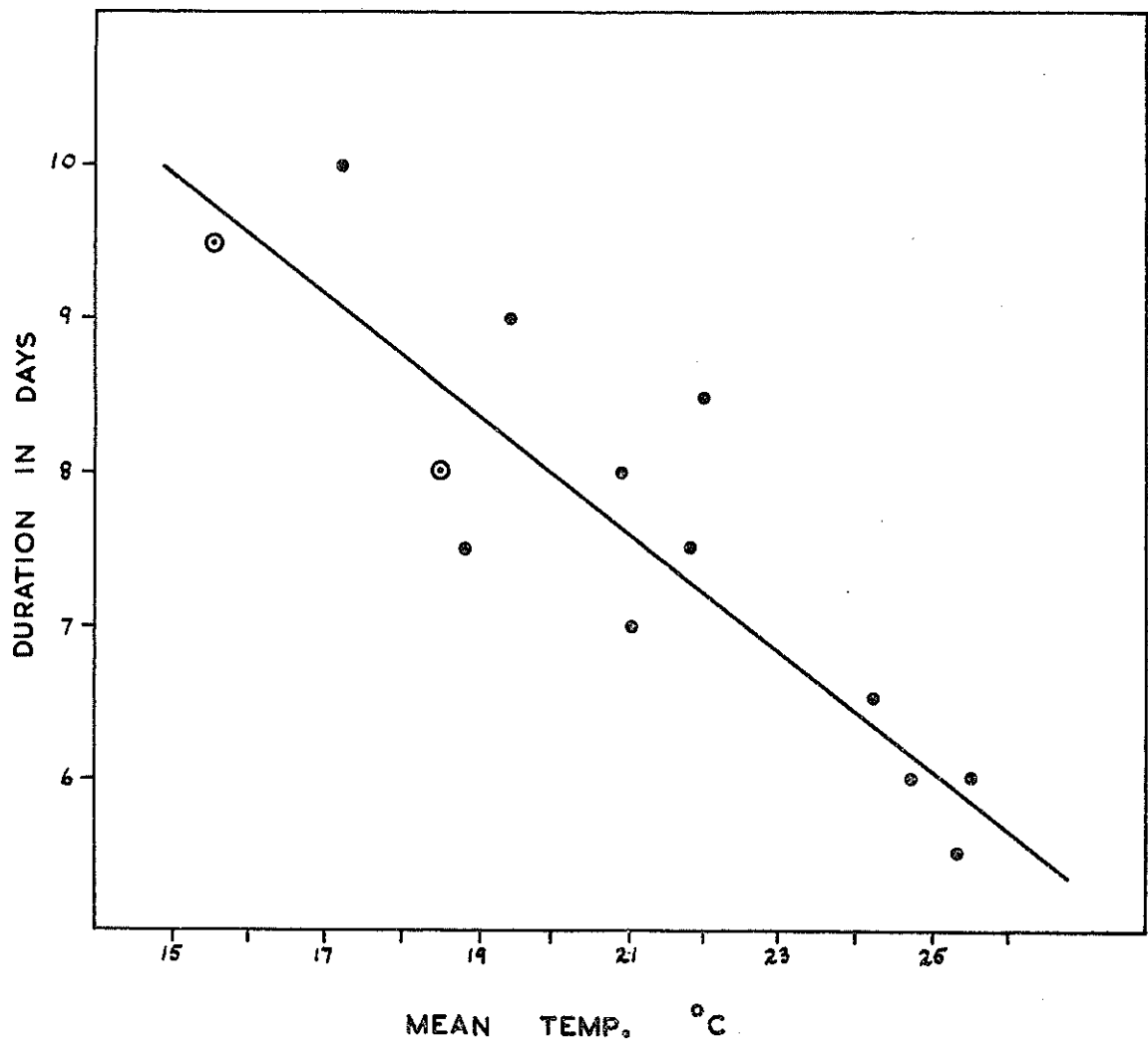
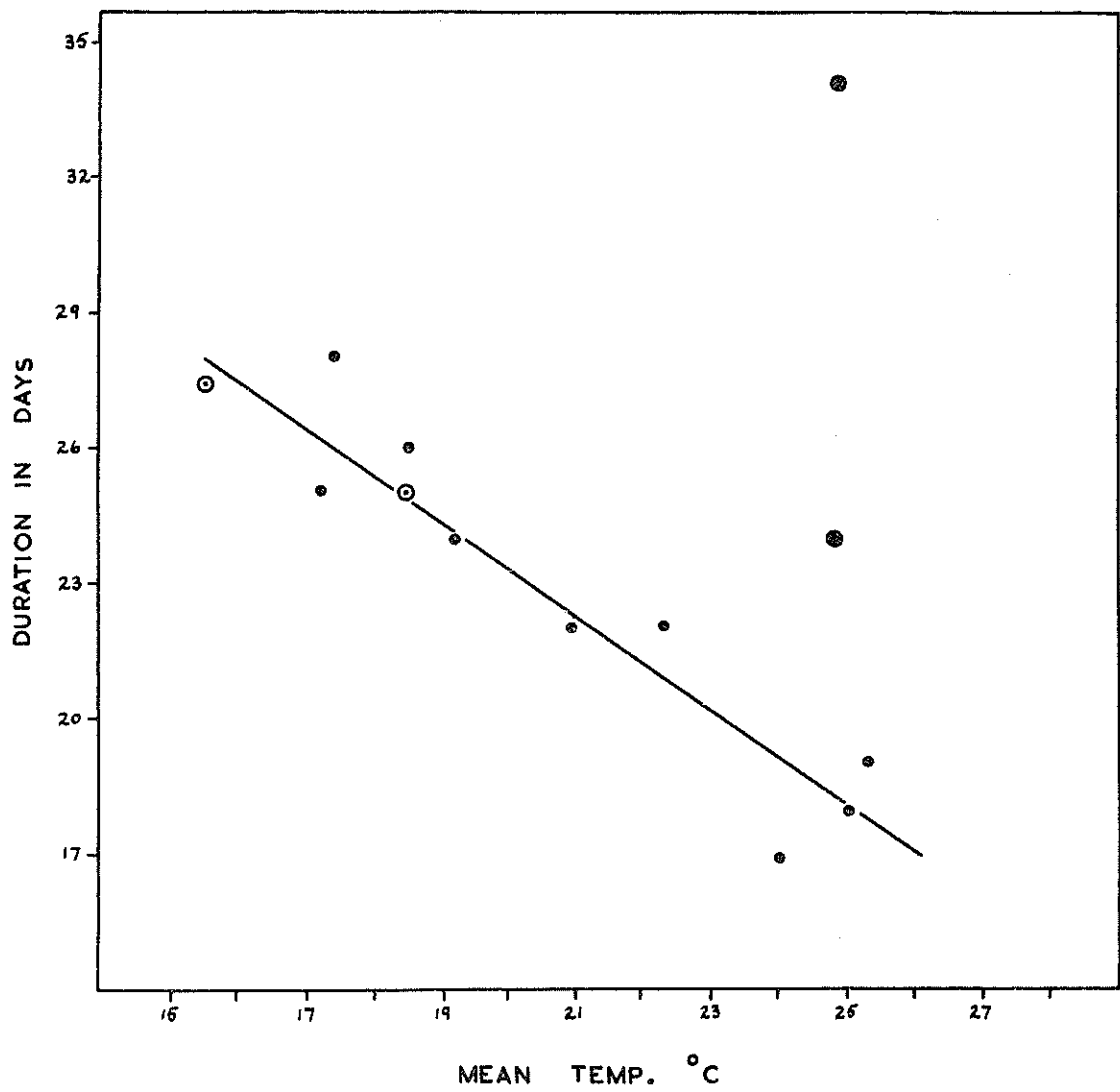


FIG. 23



further ameliorated in 1966-67 by an increase in relative humidity of 8-11% over the previous season. The high survival rates on Letaba Estates at these temperature-moisture regimes are seen in in situ count No. 21 (Tables 24, 25 and Fig. 27).

5. Duration of Developmental Stages

The rate of metabolism of exothermic animals increases with a rise in external temperature and growth is accelerated. Compared with the effect of temperature, Woodbury (1954) states that in general, humidity influences the development of insects very little, though according to Wigglesworth (1961) excessively high and low humidities may retard development. That author states that at low ambient humidities development in the egg of some insects slows down until the return of more favourable conditions. The water-absorbing function of the stalk of the psylla egg has been described previously, and it is probable that a state of wilt in the host plant will prolong the incubation period. Wigglesworth (1961) reports this in aleurodids.

There are several mathematical models for relating temperature to duration of development (Wigglesworth, 1961). A simple and widely-used formula assumes that within the normal tolerance range, velocity of growth is proportional to the prevailing temperature. This principle is supported by Figs. 22 and 23.

Details on the duration of the egg and nymphal stages were selected from a large number of in situ counts conducted on and around experimental trees. Durations were then related with various aspects of climate. For this purpose the daily values of each aspect were averaged for the period over which the duration was calculated.

Incubation periods and the duration of nymphal development from the two temperature regimes studied by Moran & Blowers (1967) were compared with field data from the Letaba district.

EXPLANATION OF FIGURES

- Fig. 22. Scatter diagram and regression for incubation period of T. erytreae with mean temperature. Hollow points are calculated from Moran & Blowers (1967). $Y = 17.07 - 0.44X$ $r = -.881^{***}$
- Fig. 23. Scatter diagram and regression for nymphal development duration of T. erytreae with mean temperature. In situ counts 19 and 20 were not included in the regression but were plotted to show the retarding effect of poor quality foliage. $Y = 45.67 - 1.11X$ $r = -.938^{***}$

Table 21. Incubation period of *T. eryteae* according to prevailing temperatures and humidities

<u>In situ</u> count	Period	No. insects	Mean temp. °C	Mean Hr °C per Day above 20°	Mean Hr °C per Day below 20°	Mean % RH	Duration in days
Ietaba							
10	Sept 2 - Sept 11	c.250	19.4	49	62	59	9.0
11	Sept 27 - Oct 6	c.250	22.0	85	34	54	8.5
12	Sept 30 - Oct 7	c.250	21.8	83	41	53	7.5
18	Nov 6 - Nov 12	265	21.0	40	24	70	7.0
20	Nov 23 - Nov 28	335	25.3	123	9	60	5.5
21	Jan 18 - Jan 23	859	25.5	114	0	71	6.0
Estimate	July, 1966	Many	17.2	30	111	56	10.0
Fairview	Nov 25 - Dec 2	151	24.2	93	15	67	6.5
29	Dec 7 - Dec 13	825	24.7	96	4	64	6.0
Forest Hill	Sept 10 - Sept 16	316	18.8	35	65	59	7.5
35	Dec 5 - Dec 12	879	20.9	38	25	75	8.0
44		127	15.5	4	38	68	9.5
Moran and Blowers		129	18.5	24	33	73	8.0

Table 22. Duration of nymphal development of *T. erytreae* according to prevailing temperatures and humidities

<u>In situ</u> count	Period	No. insects	Mean temp. °C	Mean Hr °C per Day above 20°	Mean Hr °C per Day below 20°	Mean % RH	Duration in days
Letaba	3 Jun 21 - Jul 19	115-80	17.4	31	107	57	28
	8 Aug 9 - Sept 3	44-31	19.2	41	91	58	24
	18 Nov 13 - Dec 1	117-6	25.3	87	15	65	19
	19 Nov 27 - Dec 21	154-26	24.8	109	8	66	24
	20 Nov 28 - Jan 2	158-3	24.9	108	7	66	34
	21 Jan 22 - Feb 6	491-376	25.0	97	0	73	18
Fairview	23 Nov 28 - Dec 15	244-15	24.0	76	13	67	17
	29 Dec 12 - Jan 2	373-265	22.3	55	21	75	22
Forest Hill	32 Nov 29 - Dec 19	135-1	20.9	43	30	79	22
	35 Sept 16 - Oct 9	77-38	17.2	31	101	69	25
	44 Dec 12 - Jan 5	534-2	18.5	20	62	83	26
Moran and		127-67	15.5	4	38	68	27.4
Blowers		129-19	18.5	24	33	73	25.0

Incubation period

The duration of the incubation period at various combinations of temperature and humidity appear in Table 21. The regression for incubation period and mean temperature shown in Fig. 22 was found to be significant at the 0.1% level. It was in general agreement with the work of Moran & Blowers (1967). Much of the scatter was undoubtedly due to the difficulty in determining the exact time of hatching. It is also possible that wilting of the plant host retarded development on some occasions.

Duration of nymphal development

Fig. 23, drawn from data in Table 22, shows the regression for duration of nymphal development on mean temperature. The regression was significant and again supported by the durations obtained at the two temperature regimes studied by Moran & Blowers (1967). Since there was no tendency to form asymptotes it is suggested that the points in Fig. 23 are well inside the range of temperatures favourable for T. erytreae.

There was no evidence that extremes of humidity affect the rate of nymphal development in any way.

The regressions for incubation period and duration of nymphal development with mean temperature agree with the durations of the two psylla broods studied at Forest Hill in the early summer of 1966 as shown in Fig. 8. On working back these broods and calculating the mean daily temperature for the approximate periods during which egg and nymphal development took place, and then reading off the corresponding duration from Figs. 22 and 23, it is evident that there is remarkable agreement between the two methods.

Table 23. Mean temperatures for the development of two psylla broods at Forest Hill in 1966, and the corresponding duration of egg and nymphal stages from Figs. 22 and 23

	Mean temp. °C	Duration in days from Figs. 22 & 23
<u>Brood 1, Sept. 19 - Oct. 31</u>		
Incubation: Sept. 19-27	18.1	8.8
Nymphal dev.: Oct. 1-31	17.7	25.7
<u>Brood 2, Oct. 31 - Dec. 12</u>		
Incubation: Nov. 1-8	19.9	8.1
Nymphal dev.: Nov. 14 - Dec 12	19.8	23.6

Assuming a mean pre-oviposition period of 6 days (see chapter 4) this gives the egg to egg period for the first brood (a complete generation) as

$$8.8 + 25.7 + 6.0 = /....$$

$8.8 + 25.7 + 6.0 = 40.5$ days, which is $1\frac{1}{2}$ days less than that shown in the field counts (42 days). For the second brood this period is $8.1 + 23.6 + 6.0 = 37.7$ days.

Instar duration

An examination of Figs. 12, 13 and 15 shows that some information on the five nymphal instars is provided by most of the available in situ counts. From a large number of scatter diagrams drawn from these counts it appeared that there was a relationship, though rather irregular, between mean temperature and the duration of instars I, II, IV, and V. Instar III was usually the shortest and its duration appeared to be relatively unaffected by prevailing temperature. This appears to conflict somewhat with Moran & Blowers (1967) who found instars II, III and IV to be of almost equal length. However, these counts were not designed for a precise analysis of instar duration and the above results are considered to be tentative.

6. Survival and Microclimate

The macroclimate of an area is made up of innumerable microclimates which frequently differ from each other within the space of a few inches. This is particularly true in the habitat of trees where it is known that leaf temperatures fluctuate rapidly and can rise 10°C above the ambient air (Wellington, 1950). Odum (1964) showed that the temperature of an oak leaf can be varied by $10\text{--}15^{\circ}\text{C}$ within a five minute period by changes in shading and air movement. Similar temperature effects have been found on the surface of citrus leaves (Keetch, personal communication, 1966).

Because of the exposed position of eggs and instars I and II on the upright tips of flush points the exact location of breeding sites is critical in the hot summer months. At a later stage the leaves flatten so that older nymphs are nearly always well shaded. Obvious differences in microclimate between colonies on the same tree were frequently observed during the spring months. For example, on an experimental tree at Forest Hill, in situ counts on the tree canopy showed mortalities of 80-90% in instars I and II in September, 1966. Yet a single leaf in a well-shaded position on the same tree was found with 95 second and third instars with no signs of heat mortality.

Van der Merwe (1941) noted the importance of shade in moderating the effect of high ambient temperatures. It has been mentioned in chapter 5

that the majority/....

that the majority of psylla breeding sites in the Letaba district are situated on the lower half of the tree. Surveys on Letaba Estates (Table 9) showed that populations were always lower on young trees despite their prolonged flushing. At higher elevations citrus psylla was observed to breed on young trees at all times of the year; on Letaba only during the winter and early spring.

7. The Effect of Rain, Hail, Wind and Low Temperatures

Rain. On two occasions in situ counts showed that violent rainstorms have no significant effect on the sessile stages of citrus psylla.

Hail. Hail directly destroys the young stages and removes or damages breeding sites. The temporary reverse in the rising psylla population at Forest Hill in 1966 (see Fig. 7) was due to a hailstorm on October 21 which damaged young growth. The hail appeared to stimulate a small compensatory growth flush.

Wind. Due to the windless climate of the Letaba area this component of climate was only studied on one occasion. In one series of in situ counts using a potted seedling at each main experimental site, an exceptionally hot, dry westerly wind caused considerable mortality to eggs and first instar nymphs. Only the Forest Hill seedling was left with a few survivors.

It is possible that gusty winds disperse adults, especially teneral, so that at low densities many females do not find mates and thus lay infertile eggs. Clark (1962) concluded that long periods of prevailing winds forced the adults of C.albitextura to spend most of their time clinging to trees. Dispersal by prevailing winds is discussed in chapter 4.

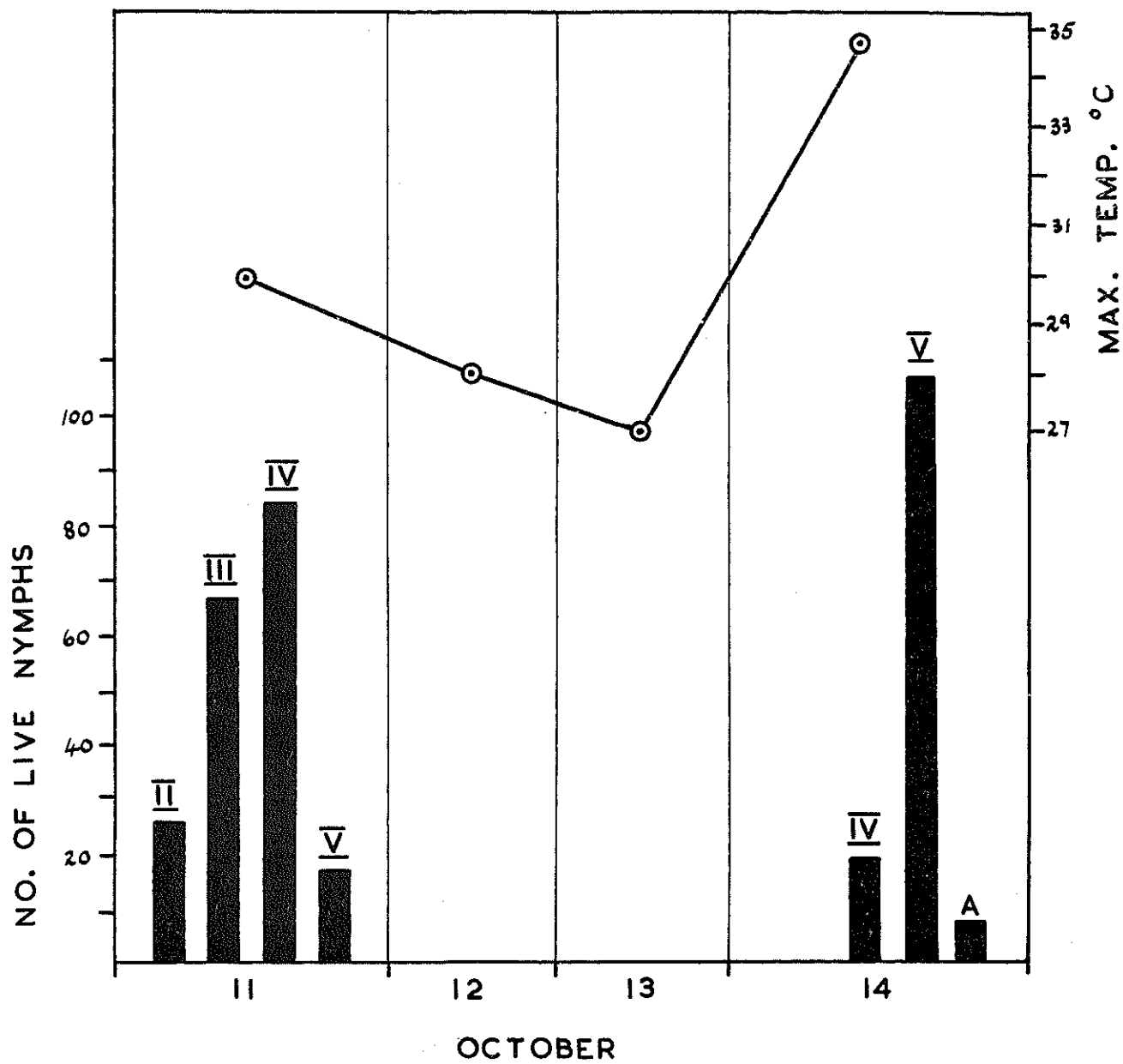
Low temperatures. The minimum temperatures of the winter months do not appear to cause any significant mortality, though the durations of egg and nymphal stages are of course prolonged. All stages of T.erytreae were observed in Pretoria during the midwinter of 1965.

8. The Limiting Effect of High Temperatures

High temperatures cause considerable mortality to the young sessile stages of the citrus psylla and also inhibit egg-laying. The lethal effect is intensified by low humidities.

Many other species of Psyllidae are similarly affected. Clark (1962) states that repeated daily maximum temperatures above 32°C cause a reduction

FIG. 24



in the number of eggs laid by C.albitextura. Madsen et al. (1963) found that the eggs of P.pyricola collapse at high temperatures and that egg laying is inhibited until the return of normal conditions. The optimal temperature for survival for P.cockerelli is 21-27°C (List, 1939). At 32°C nymphs are killed and the female ceases to lay. Many adult psyllids can survive temperatures which are fatal for nymphs and eggs.

Moran & Blowers (1967) reared T.erytreae under controlled, fluctuating conditions of temperature, humidity, and light. When reared at 24 hour degrees Centigrade per day above 20°, with a maximum temperature of 25°C, all stages flourished well. But at 54 Hr°C/Day above 20° and a plateau of maximum temperature of 32°C the eggs failed to hatch and nymphs introduced from outside soon succumbed.

9. Heat tolerance and age

Moran & Blowers (1967) show further that the ability to withstand high temperatures increases with successive moults. When introduced into the temperature regime of 54 Hr°C/Day above 20° with several hours at 32°C, newly-emerged first instars succumbed in about seven hours; older first instars survived for just over a day; instars II and III longer; and some fourth instars survived to moult into fifths though they did not live for very long. Adults survived for several days at this temperature, mature individuals outliving teneral. Oocyte development was inhibited under these conditions.

Similar results were obtained in the field at Letaba. In September, 1966, three consecutive daily maximum temperatures above 34°C were observed to decimate a large number of young psylla colonies, yet populations consisting of instars IV and V were virtually unaffected. Further evidence of the extreme sensitivity of eggs and emergent nymphs and the increased resistance shown by older nymphs is given below (Tables 24 and 25).

Lastly, a field count was designed to demonstrate the differential resistance of instars II to V. Two seedlings infested with 194 nymphs in in-

EXPLANATION OF FIGURE

Fig. 24. Results of an in situ count at Letaba in October, 1966, showing a progressive tolerance to high temperatures with successive instars. The peak of temperature on October 14 was lethal to second instars and many thirds but was resisted by instars IV and V. A = adult.

instars II-V/....

stars II-V were placed in almost total shade in the crotch of a tree near the Letaba weather station on October 11, 1966. Fig. 24 shows the maximum temperatures recorded and the fate of the nymphs. The second count was made in the late afternoon of October 14. A large number of dead second and third instars were found and it appeared that these had been killed by high temperature which reached a peak some three hours earlier that afternoon. Of the live nymphs present few, if any, of the second instars could have become fourths in the 3 days between counts so that it can be assumed that all were killed after 3 days of exposure. Similarly, few of the thirds could have become fifths. Thus the majority of the fifths present on the 14th were recruited from fourths present on the 11th. It is obvious that all the seconds and at least 50% of the thirds were killed after three days of exposure, whereas most or all of the fourth and fifth instars of the 11th survived.

10. Survivals in In Situ Counts

During the course of this investigation 46 in situ counts were carried out in the Letaba district under varying conditions of temperature and moisture. Immediately following periods of unfavourable climatic extremes mortality in populations of T. erytreae was commonly shown by collapsed eggs, shrivelled first and second instars, and the disappearance of larger nymphs from their galls.

By eliminating or considerably reducing other mortality factors it was possible to study the influence of climate in most of these counts. Since parasites attack only in the third and later instars, the effect of climate was usually the chief limiting factor from egg to instar II. In many counts the psyllas were completely unmolested by parasites, and in those colonies which were only slightly parasitized the numbers of instar III-V nymphs were adjusted accordingly. The action of predators was more difficult to assess but in general their effect was slight. The influences of microclimate and plant host were largely balanced by the random selection of colonies on all aspects of the tree, and by the use of all leaf sizes, condition, and degrees of shading. Most of the potted seedlings used were growing vigorously and were exposed in total shade or very diffuse sunlight.

Survivals were expressed as percentages of:

egg to first/....

FIG. 25

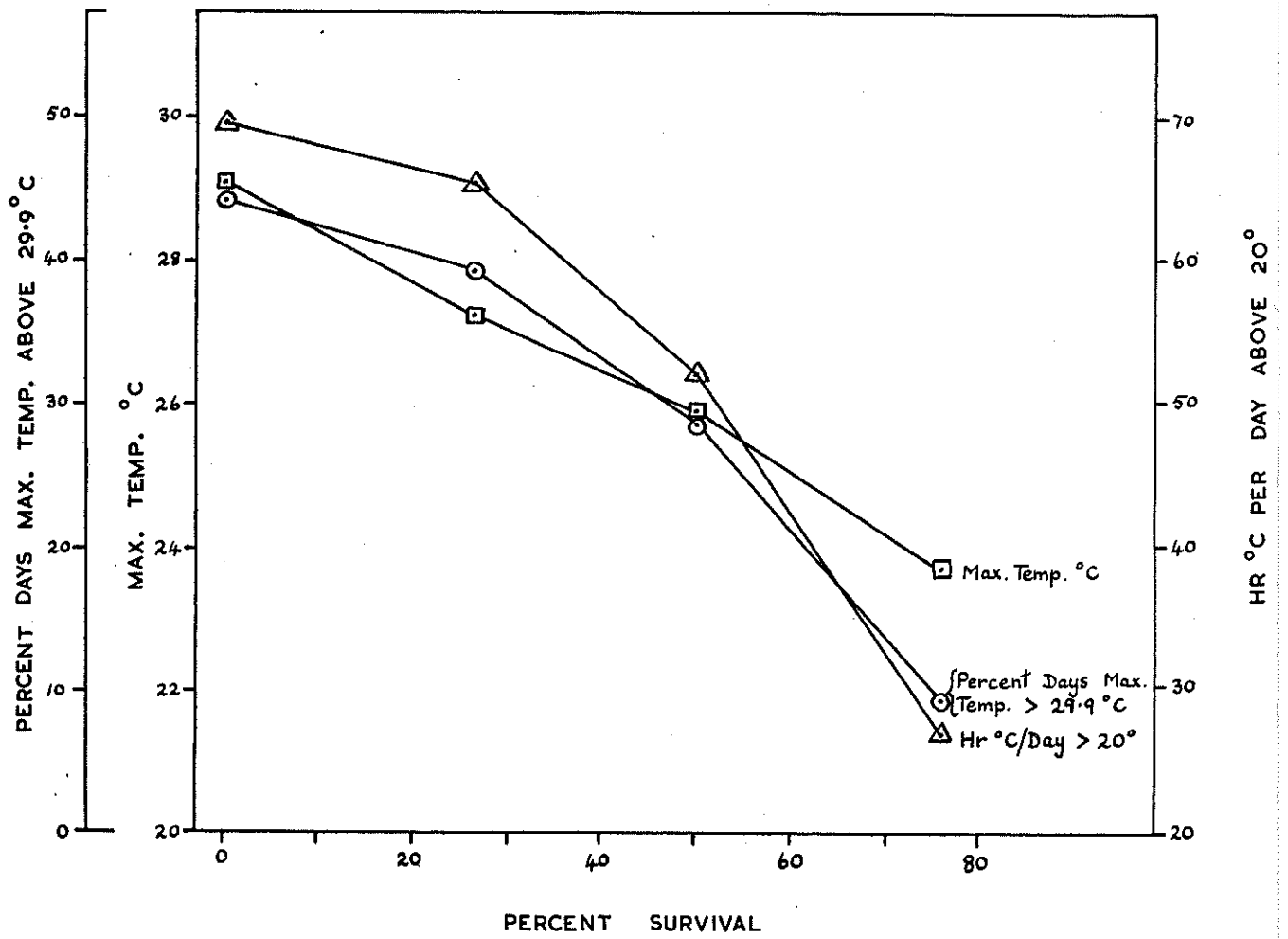
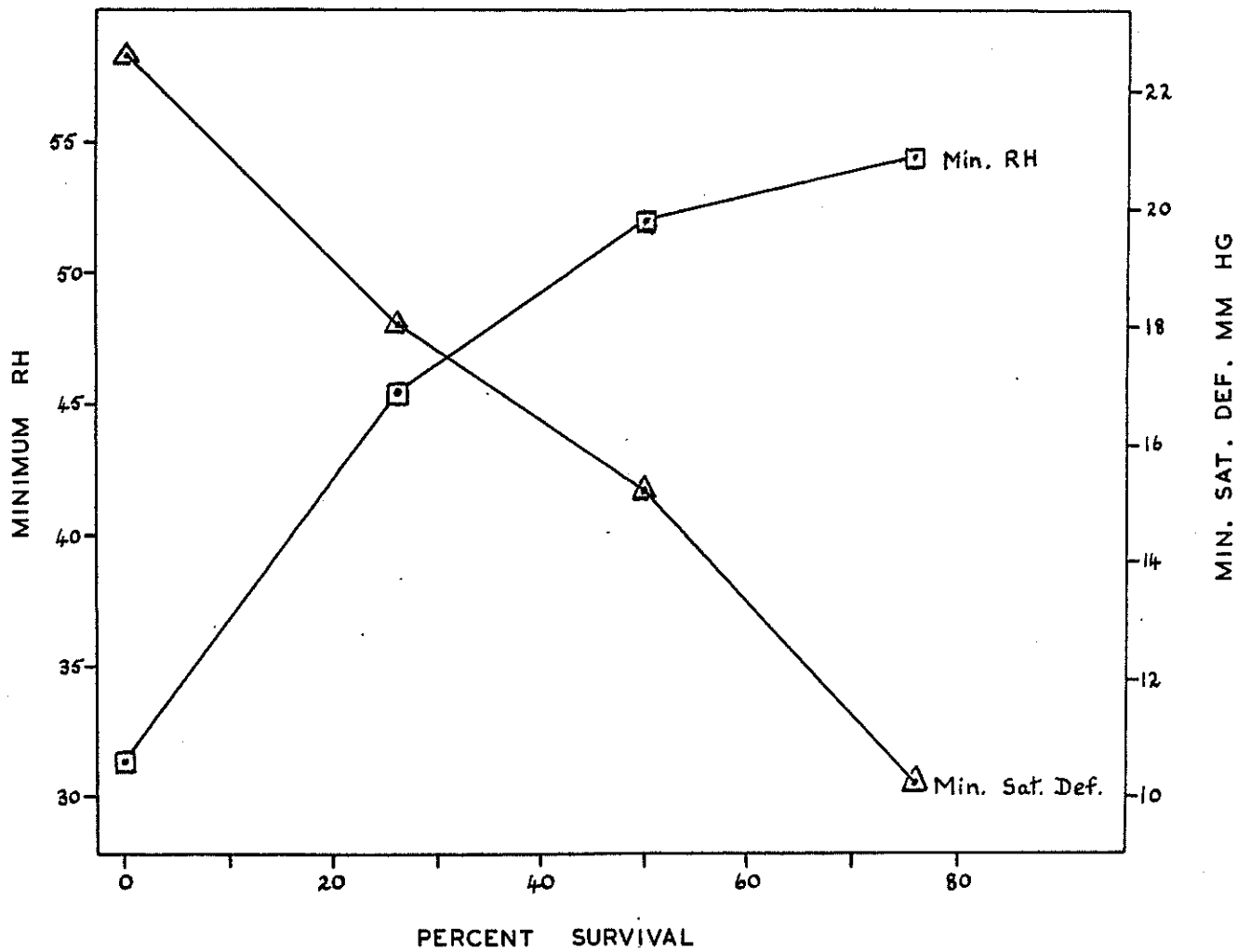


FIG. 26



- a) egg to first instar survival, which was calculated from the total number of eggs, and the maximal number of live first instar nymphs recorded in the field; and
- b) first instar to teneral adult survival, calculated from the maximal number of first instar nymphs to attain maturity.

It soon became apparent in the field that temperatures and humidities became lethal in the region above 30°C and below 26% RH. This corresponds with the tolerances for other psyllids discussed previously. It also agrees with Moran & Blowers (1967) who showed that for the citrus psylla temperature becomes critical somewhere between a daily maximum of about 6 hours at 27°C and 8 hours at 32°C. However, as those authors rightly point out, the "plateaux" of temperature used in their exposures are very different from the "peaks" of extremes experienced in the field. And the effect of humidity was not considered in their studies. Also, high temperatures near the limits of toleration are usually resisted more strongly when applied gradually (Woodbury, 1954). In the field these peaks are usually sharp and sudden.

Survivals were thus related with the following meteorological data which was summed or averaged for the period in question:-

temperature: daily maximum; Hr°C/Day above 20°; percentage days when maximum temperature exceeded 29.9°C.

humidity: daily minimum RH; percentage days when minimum RH was below 26%; daily minimum saturation deficiency calculated from daily maximum temperature and daily minimum RH.

Egg to first instar survival

Table 24 shows the egg to first instar survivals of 32 counts grouped into four classes. For every component of climate considered, there is considerable variation within each survival class. But such variation is to be expected in the short period over which the counts were made. And as a

EXPLANATION OF FIGURES

Fig. 25 The effect of temperature on egg to first instar survival of T. erytreae. Drawn from the means in Table 24.

Fig. 26 The effect of humidity and minimum saturation deficiency on egg to first instar survival of T. erytreae. Drawn from the means in Table 24.

Table 24. Egg to first instar survival from in situ counts made in the Letaba district

	<u>In situ</u> count	Period	No. insects	Mean max. temp °C	Mean °C/Day above 20	Percent days max. temp. above 29.9 °C	Mean min. % RH	Percent days min. RH below 26%	Min. Saturation deficiency mm Hg	Percent survival
Survival 0%	2	December 8-December 18	223	33.5	123	73	34	18	27.2	0
	5	August 25-September 4	48	29.5	59	55	28	45	22.8	0
	6	September 2-September 13	82	27.9	50	33	29	42	20.8	0
	7	September 8-September 19	325	26.2	46	25	41	25	17.6	0
	9	August 22-September 10	333	27.9	47	35	28	50	21.0	0
	13	September 19-September 25	171	28.3	59	29	29	29	21.7	0
	14	September 14-September 27	215	28.0	67	36	35	36	21.6	0
	15	September 27-October 7	321	29.9	82	45	28	55	25.1	0
	16	September 30-October 15	204	30.4	86	56	31	44	24.5	0
	17	October 22-October 31	225	29.4	78	60	30	40	23.2	0
		means		29.1	69.7	44.7	31.3	38.4	22.6	0
		max.		33.5	123	73	41	55	27.2	0
		min.		26.2	46	25	28	18	17.6	0
	18	November 6-November 15	265	27.3	52	30	44	10	17.1	4
	19	November 22-November 30	477	31.9	108	67	35	22	25.4	29
	20	November 23-November 30	335	32.7	117	75	32	25	27.2	35
Survival 1 - 40%	28	November 25-December 2	151	30.9	93	75	41	25	21.9	21
	35	September 10-September 21	316	20.6	21	8	52	17	12.0	23
	39	November 3-November 12	73	21.8	20	0	60	0	9.6	37
	45	November 24-December 2	601	25.7	47	22	55	0	12.6	32
		means		27.3	65.4	39.6	45.6	14.1	18.0	26
		max.		32.7	117	75	60	25	27.2	37
		min.		20.6	21	0	32	0	9.6	4
	21	January 18-January 25	859	30.4	113	75	49	0	17.7	57
	23	November 23-December 1	412	28.0	52	25	50	0	21.2	59
	27	October 22-October 31	206	28.3	70	60	35	30	20.8	42
Survival 41 - 60%	29	December 7-December 14	825	31.1	93	75	38	0	21.7	45
	32	November 24-December 1	288	23.7	23	0	63	0	13.3	47
	36	September 26-October 3	52	24.8	40	13	45	25	14.8	52
	38	October 31-November 7	256	25.2	49	0	47	0	14.1	49
	43	November 14-November 23	900	21.7	14	10	64	0	8.3	43
	46	December 12-December 21	298	19.6	16	0	80	0	5.1	57
		means		25.9	52.2	28.7	52.3	6.1	15.2	50
		max.		31.1	113	75	80	30	21.7	59
		min.		19.6	14	0	35	0	5.1	42

Table 24. Continued

In situ count	Period	No. insects	Mean max. temp °C	Mean Hr °C/Day above 20	Percent days max. temp °C above 29.9 °C	Mean min. % RH	Percent days min. RH below 26%	Min. Saturation deficiency mm Hg	Percent survival
survival 1 - 100%	3 June 12-June 23	115	23.8	18	8	38	17	14.2	100
	33 December 8-December 17	459	27.2	60	20	46	0	9.3	63
	40 November 8-November 16	73	20.7	13	11	66	0	8.3	89
	41 November 14-November 25	319	22.4	17	8	62	0	8.9	61
	42 November 14-November 25	179	22.4	17	8	62	0	8.9	80
	44 December 5-December 12	879	25.5	38	0	53	0	11.7	61
	means		23.7	27.2	9.2	54.5	2.8	10.2	76
	max.		27.2	60	20	66	17	14.2	100
	min.		20.7	13	0	38	0	8.3	61
	First instar to teneral adult survival from in situ counts made in the Letaba district.								
survival 1 - 40%	8 August 9-September 1	103	26.7	40	25	29	50		30
	19 November 30-December 21	137	29.8	101	59	45	14		18
	23 December 1-December 24	220	30.6	89	71	38	13		6
	24 December 13-December 27	255	31.8	109	80	34	13		14
	32 [±] December 1-December 20	120	26.0	47	10	49	0		7
	33 [±] December 14-January 3	237	26.2	53	14	49	5		4
	36 [±] October 3-October 26	27	21.9	26	8	59	8		15
	41 [±] November 25-December 12	179	25.9	48	11	53	0		7
	means		27.4	64	35	45	13		13
	max.		31.8	109	80	59	50		30
survival 1 - 60%	min.		21.9	26	8	29	0		6
	18 November 15-November 30	11	29.8	81	50	41	13		55
	35 September 21-October 17	74	24.2	36	15	52	15		53
	means		27.0	59	33	47	14		54
	max.		29.8	81	50	52	15		55
	min.		24.2	36	15	41	13		53
	3 June 23-July 16	115	25.9	31	4	27	58		70
	21 January 25-February 6	491	29.8	103	54	49	0		77
	25 August 29-September 12	40	26.6	32	27	30	33		75
	29 December 14-January 7	373	26.7	50	36	57	8		71
survival 1 - 100%	means		27.3	54	30	41	25		73
	max.		29.8	103	54	57	58		77
	min.		25.9	31	4	27	0		70

Table 26. The frequency of extremes of high temperature and low relative humidity, and their simultaneous occurrence at the three main experimental sites in the Letaba district for July, 1966, to January, 1967.

LETABA					FAIRVIEW			FOREST HILL		
	No. days max. temp. exceeded 29.9°C	No. days min. RH below 26%	No. days two extr- emes simultaneous	No. days max. temp. exceeded 29.9°C	No. days min. RH below 26%	No. days two extr- emes simultaneous	No. days max. temp. exceeded 29.9°C	No. days min. RH below 26%	No. days two extr- emes simultaneous	
1966 July	3	17	3	0	15	0	0	7	0	
A	8	16	7	4	15	3	0	6	0	
S	9	10	9	9	11	7	3	6	2	
O	17	12	11	16	9	9	3	2	0	
N	16	6	6	14	5	5	3	0	0	
D	20	4	4	15	1	1	0	0	0	
1967 J	22	2	2	11	2	2	2	1	1	

method of showing the effect of critical peaks and troughs of temperatures and humidity, which are probably only lethal for relatively short periods, the averaging of the weather data for the survival period leaves much to be desired. Nevertheless, the influence of the 6 components of climate is apparent in Figs. 25 and 26. There is a constant decrease in survival with a rise in temperature (Fig. 25), and a decrease in survival as the air becomes drier (Fig. 26).

Table 24 shows that in the majority of psylla counts conducted at Letaba from August to December, 1966, the survival rate was very low and commonly nil. For the same period survivals at Forest Hill were usually above 40%. Table 26 compares the frequency of extremes of maximum temperature and minimum R.H. at the main experimental sites during the 1966-67 season. At Letaba, and to a slightly lesser extent Fairview, high temperatures and low humidities were frequent during the early summer of 1966, but were uncommon at Forest Hill. The table also appears to explain the high survival rates during the winter and midsummer of 1966-67 for in July and August the low humidities were accompanied by moderate temperatures, while the effect of high maximum temperatures from November to January was modified by high humidity. But in September and October the weather was hot and dry and almost without exception relative humidities below 26% coincided with maximum temperatures exceeding 30°C.

The interaction of temperature and moisture extremes is further illustrated in Fig. 27 which shows three in situ counts made on Letaba Estates during winter, spring, and midsummer of 1966-67. An examination of the weather records for these counts showed that daily minimum relative humidities below 15% (in June and July), and daily maximum temperatures of 32°C and above (in January and February), became severe limiting factors only when applied together. In Fig. 27 this interaction has been expressed in terms of saturation deficiency.

Saturation deficiency

Saturation deficiency is calculated from relative humidity and the vapour pressure of water at that temperature. It is a measure of the actual evaporation power of the air as opposed to R.H. which is the amount of water vapour present in the air (Odum, 1964). According to Wigglesworth (1961)

in general water loss from the integument of insects is proportional to the saturation deficiency of the air. That author describes a number of factors which may accelerate water loss still further at high temperatures.

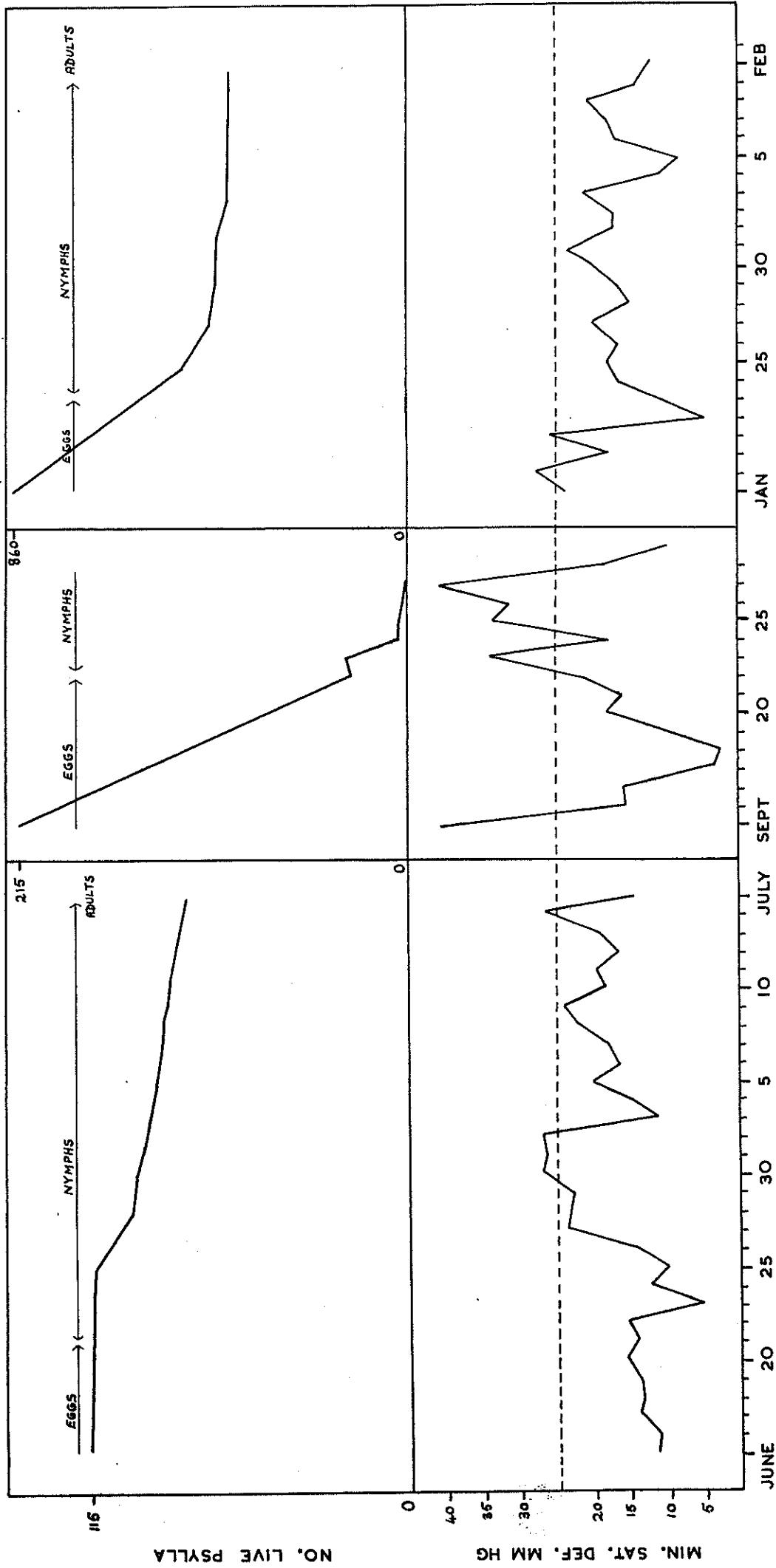
Table 27 shows that the monthly means for the daily minimum saturation deficiency were consistently the highest at the Letaba site, the lowest at Forest Hill, and intermediate at Fairview. Summer and winter means were surprisingly similar at all sites. However, the table shows that the means conceal marked differences in the frequency of extremes of saturation deficiency. From September to November the climate at the two lowest sites included cycles of hot, dry days followed by short periods of cool, overcast weather. Such peaks of high saturation deficiencies, which are lethal to the citrus psylla, are not revealed by the monthly means. The effect of such a cycle, with saturation deficiencies exceeding 25 mm Hg, is evident in Fig. 27.

Table 27. Mean monthly minimum saturation deficiency and the frequency of its extremes above 24.9 mm Hg.

	LETABA		FAIRVIEW		FOREST HILL	
	Monthly mean	No. days min. sat. def. exceeded 24.9 mm Hg	Monthly mean	No. days min. sat. def. exceeded 24.9 mm Hg	Monthly mean	No. days min. sat. def. exceeded 24.9 mm Hg
1966 J	20.0	5	17.5	3	11.7	0
A	20.0	8	18.9	6	12.7	0
S	20.6	9	19.0	8	13.6	1
O	22.3	14	20.5	11	11.9	2
N	21.5	12	17.0	6	10.7	0
D	20.2	12	15.9	5	9.1	0
1967 J	19.9	6	15.3	2	7.1	1

In view of what has been shown of the effect of climate on the survival of the young sessile stages, it would appear that saturation deficiency defines the temperature-moisture tolerance of T.erytreae more closely than any other single component of climate. Because the egg and first instar are so highly sensitive to extremes, a description of the lethal areas of climate for these early stages is important in predicting outbreaks and mapping the likely distribution of the citrus psylla.

FIG. 27



IN SITU COUNT NO. 3

IN SITU COUNT NO. 14

IN SITU COUNT NO. 21

First instar to teneral adult survival

Less field data were available for this analysis. The survival period is longer and the population more liable to the influences of other mortality factors. However, Table 25 does show a tendency for higher survival rates under conditions of cooler, moister weather. It also shows that the more mature stages are far more tolerant of extremes lethal to the egg and first instar.

11. The Causes of Heat Mortality

Excessive heat is believed to kill insects by the coagulation and denaturing of proteins, the deactivation of enzymes, and the melting of fats, all of which bring on paralysis and finally rigor mortis (Woodbury, 1954). Desiccation probably results in a fatal increase in the concentration of body fluids (Woodbury, l.c.).

It appears that extremes of climate are fatal to the citrus psylla in at least two ways, namely by starvation and by desiccation, and that on occasions these may operate together.

Starvation. Odum (1964) has shown that intense sunlight and high temperatures decrease the protein content and general metabolic processes in leaves. The selective nutritional requirements of psylla nymphs, particularly under these conditions, was discussed in chapter 7. Blowers & Moran (1967) state that high temperatures are known to kill the micro-organisms in the mycetome of many insects, organisms assumed to be essential for normal metabolism. They found that on exposure to high temperatures this organ shifted from its normal position in the egg, and changed from yellow to light orange in colour in adults and eggs. Mortality was high in all these individuals.

Body temperature and desiccation. Radiant heat raises the body temperature of many insects. In direct sunlight the body temperature of Locusta hoppers was raised from 28° to 42°C in 10 minutes (Wigglesworth, 1961).

EXPLANATION OF FIGURE

Fig. 27 The effect of the daily minimum saturation deficiency on populations of T.erytreae from 3 in situ counts on Letaba Estates during 1966-67.

At such temperatures/....

At such temperatures the wax layer of the epicuticle breaks down and water is lost rapidly. Wigglesworth shows that for many species there is a critical temperature (usually between 30° and 40°C) above which the transpiration rate increases sharply.

The chorion of the egg also possesses a wax layer to protect the embryo from desiccation (Wigglesworth, 1961). Moreover, excessive drying out may harden the chorion to such an extent that the embryo is unable to escape. Abundant fluid is needed for the hatching process as the chorion of most insects is partly burst open by the swallowing of amniotic fluid. The function of the egg stalk, and the collapsing of eggs under extremes of climate, leave little doubt that favourable internal water relationships are essential for the normal development and hatching of the citrus psylla egg.

Because high humidity modifies the lethal effect of high temperatures and the survival of the young stages is so closely related to the saturation deficiency of the air, it would appear that the major cause of heat mortality in T. erytreae is desiccation. This is supported by Wigglesworth (1961) who argues that heat uptake is proportional to the surface area of the body, heat loss to the volume of water which can be evaporated. With a decrease in size the surface area becomes greater in relation to volume so that more water is needed for evaporation to reduce the temperature than is available in the insect. Eggs and early instars are small organisms in an exposed position and thus very susceptible to desiccation. The larger, more mature stages have been shown to be more resistant. They are contained in a snug gall with only their dorsal surfaces exposed to the atmosphere.

IX. DISCUSSION AND CONCLUSIONS

The biology and ecology of the citrus psylla was studied in the Letaba district for two summers and a winter. Though this is a relatively short period for an ecological study, it was found to be sufficient for a provisional elucidation of the main ecological factors governing the abundance of T.erytreae.

In the higher-lying areas the annual population cycle begins in early summer with a steady rise in numbers in which two broods can be distinguished. Shortly after reaching a peak in midsummer, the abrupt action of a number of limiting factors causes a rapid population crash which may be halted briefly in late summer but which ultimately leaves small numbers to persist over the winter months. Such wide population fluctuations are probably due to the short life cycle, to the high fecundity (maximal natality probably being approached at times during the spring), and to the operation of several limiting factors which become ineffective at the start of each cycle.

Although a typical "psylla explosion" was observed on one occasion in an isolated grove in the Letaba district which presumably corresponds to infestations described in previous "psylla seasons", at no time did populations at the experimental sites approach such proportions.

The citrus psylla is efficient in seeking out breeding sites and exploiting favourable niches. There is no diapause and in the presence of suitable flush they continue to breed at all times of the year. Alternate host plants appear to be of little importance, particularly around Letaba Estates itself, suggesting that psylla must exist on citrus at all times. Due to the windless weather, adult dispersal is probably weak though at times small numbers may be blown from upland groves into the lower, less-favourable regions. At Letaba the egg and nymphal stages are completed in about 38 days in winter, and 25 days in summer. Field observations, population assessments, and numerous in situ counts in which the fate of individual insects was studied in the field, indicate that there are three principle factors which govern psylla fluctuations:-

- 1) extremes of climate
- 2) the flushing rhythm and foliage quality of the host plant
- 3) the action of parasites

Climate. The limiting effect of extremes of climate has been demonstrated in this project. During the study period populations were always considerably higher in the cooler, moister upland groves than in the hot, drier lowlands. Similarly, there was a strong correlation between previous psylla activity and altitude. At Letaba, infestations were usually low for most months of the year. Further east at still lower altitudes there was no indication of the insect during 1966, nor were there any signs of earlier infestations. The distribution of psylla colonies on the tree also appears to indicate the detrimental effect of high temperatures.

Survival rates were consistently low under conditions of high temperature and low relative humidity, the young stages on the tips of growing shoots being particularly sensitive. The sequence and timing of such lethal peaks and troughs of temperature and humidity are critical during the population rise in early summer. The occurrence of such lethal conditions decimates spring populations at Letaba, most of the insects surviving the heat being killed by the annual application of parathion in September. It is suggested that desiccation is the main cause of death at high temperatures, but protein starvation is also indicated. Egg laying is suspended at high temperatures.

It was found that the high temperature regimes of midsummer were considerably modified by high levels of humidity. During long periods of humid, overcast weather, survival rates at Letaba rose sharply during January and February, 1967. If such conditions coincide with a summer flush, a sudden rise in numbers may be expected.

Flush. Population fluctuations are closely correlated with the flushing rhythm of the host plant. The main psylla upsurge takes place on the spring growth cycle and declines as the supply of new flush dwindles in summer. The pattern of winter flushes largely determines the size of psylla populations prior to the spring build up. The exceptional winter dormancy of 1966 was important in limiting this spring nucleus at Letaba. It appears that the quality of flush borne during midsummer is somewhat less nutritious than that of the spring months.

The prolonged flushing of the well-watered trees of the escarpment are favoured by the citrus psylla. The rhythm of Letaba trees consists of shorter,

well-defined/....

well-defined flushes separated by long, virtually flush-free periods and is therefore less conducive to psylla populations.

Parasites. T.radiatus was found to be more active, persistent, and closely attuned to psylla fluctuations in the higher-lying citrus areas. The parasite was fairly well synchronized with its host and in the study grove up to 80% of the available nymphs became parasitized during the mid-summer of 1966-67. T.radiatus is thus regarded as an important limiting factor in these areas though the predominance of this single species is perhaps a little precarious.

Despite the low host densities, psylla parasites were intermittently encountered on Letaba. These parasites were found in association with another species of Trioza on two vines in the Letaba district and there is some evidence that this alternate host acts as a reservoir of citrus psylla parasites.

Table 28. The interaction of ecological factors believed to regulate the abundance of citrus psylla in the Letaba area. Factors which seemed to be of overriding importance are underlined.

Season	Psylla Numbers	Limiting Factors
winter	low	<u>flush volume small or negligible</u> flush nutritious extremes of climate not critical parasites at low density
spring	rising	<u>extremes of climate critical for short periods</u> <u>flush plentiful and nutritious</u> parasite activity gradually increasing (psylla explosions possible)
midsummer	crashing	<u>parasitism high</u> <u>flush volume declining rapidly</u> flush less nutritious extremes of climate less critical due to higher humidities
autumn	low to moderate	all factors operating but net result dependent on seasonal weather and flushing rhythm

The precise relationships between the above limiting factors and their mode of action in the ecosystem of the citrus psylla are complex. On the basis of the present study their operation is discussed in general terms only.

Even in/....

Even in species which have received much study the exact causes of population fluctuations are still hotly debated by many ecologists. Table 28 is an attempt to simplify the operation of the main limiting factors believed to regulate the population fluctuations of psylla in the Letaba area.

It is very probable that psylla explosions are triggered off by an exceptional combination of the above factors. This seems most likely to occur in spring or early summer when an abundant and nutritious flush cycle is accompanied by mild weather and a slightly lagging parasite complex.

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