STUDIES ON THE BIOLOGY OF THE CAPE CHESTNUT PSYLLA PAUROCEPHALA CALODENDRI MORAN (IN PRESS) AND THE SOUTH AFRICAN CITRUS PSYLLA TRIOZA ERYTREAE (DEL GUERCIO) (HOMOPTERA: PSYLLIDAE).

by

V.C. MORAN M.Sc.

A THESIS PRESENTED TO RHODES UNIVERSITY
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Department of Zoology and Entomology,
Rhodes University, Grahamstown.
South Africa.

December, 1967.

TABLE OF CONTENTS

1. INTRODUCTION

Citrus is grown as a commercial crop in several areas surrounding Grahamstown in the Eastern Cape Province of South Africa. Twelve miles South-west of Grahamstown is an orchard of about 6000 trees on the farm "Mosslands". This orchard attracted attention as the insect pests of citrus have been kept at a sub-economic level by natural biological control since 1949. This orchard is completely surrounded by indigenous bush and originally the object of this study was to see, in how far, the insect fauna of the indigenous bush was influencing the biological control which had been achieved in the orchard. As citrus is a member of the family Rutaceae, four indigenous plants in this family, which occured in the indigenous bush, were chosen for a closer study of their associated insect fauna.

This study continued for a year during which time a bewildering number of insects and their parasites were collected and it was realized that only an investigation of a very specific aspect of the problem could possibly yield meaningful results. As a starting point, therefore, Trioza erytreae (Del Guercio) (Homoptera: Psyllidae), the South African citrus psyllid, was singled out. This psyllid was found on citrus at "Mosslands" and was also found on all but one of the indigenous rutaceous plants. It was chosen for study because of its polyphagous habit and because very little is known of the biology of this economically important species in South Africa. Also very little work has been done on the Psyllidae generally.

Associated with the nymphs of T. erytreae is a primary ectoparasite Tetrastichus radiatus Waterston (Hymenoptera : Eulophidae). This parasite is morphologically very similar to the primary parasite of the Cape chestnut psyllid Paurocephala calodendri Moran (in press), which occurs at "Mosslands". The Cape chestnut psyllid, which was found to be a new species, is common on one of the indigenous rutaceous plants and as nothing was known of the biology of this species or its parasites it was decided to include it in this study.

Essentially, therefore, this is a laboratory and field study of two psyllid species, T. erytreae which is polyphagous, and P. calodendri which is monophagous and which are linked by a very similar parasite. In this study special attention is paid to the life history of these two psyllids, to the influence of temperature on their developmental history and to the factors responsible for their control.

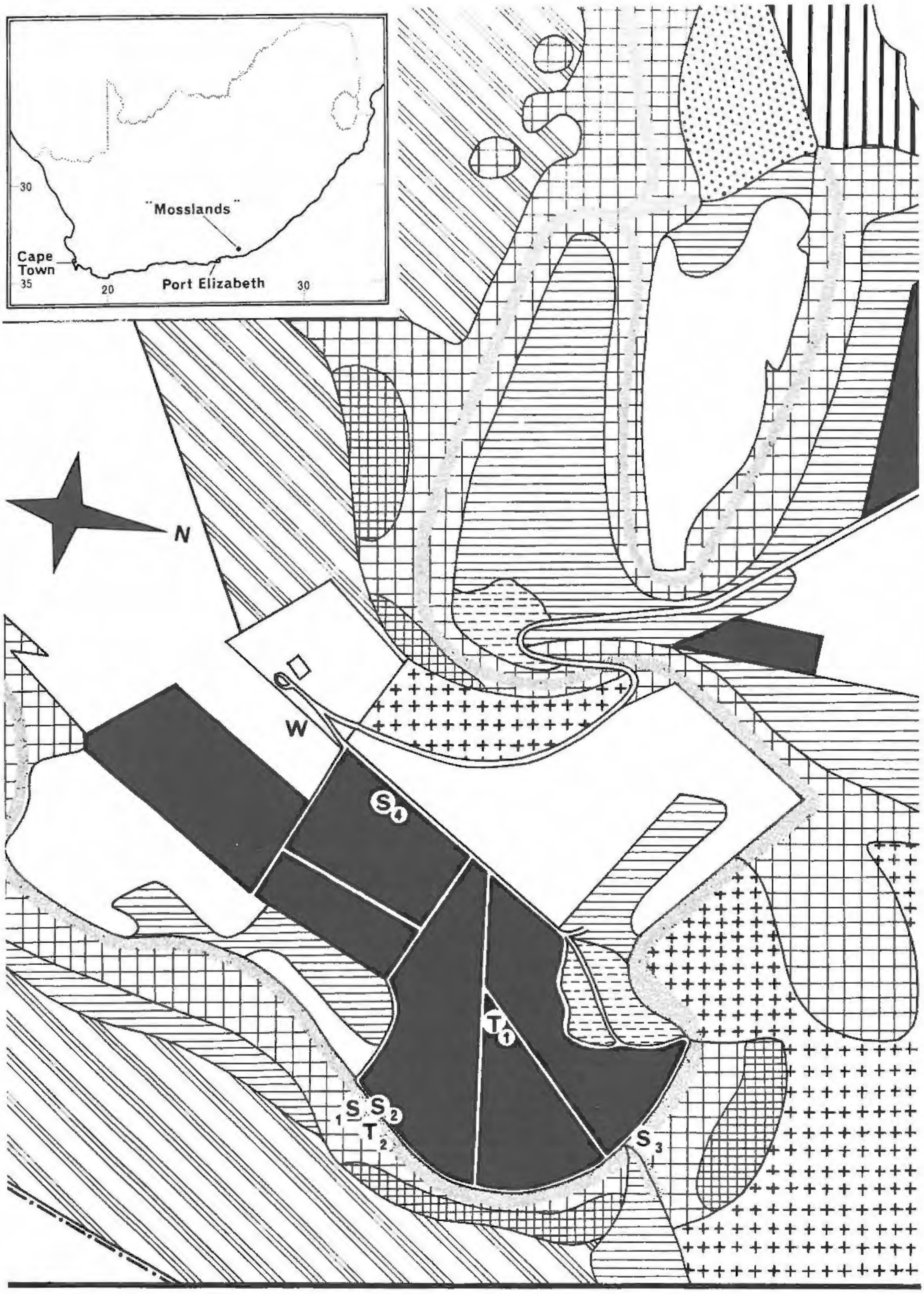


Fig. 1. Vegetation at "Mosslands." 1:9,000

■	Citrus Orchard	▥	Eastern Province Thornveld	▦	Moist Valley Bushveld
□	Cultivated Lands	▧	Open Scrub	▩	M.V. Euphorbia Bushveld
▤	Basic Valley Bushveld	⁘	Water	✚	M.V. Bushveld Cleared
┄	B.V. Bushveld Cleared	⋱	Farm Boundary	░	Streambank Woodland

W - Wind Recorder; S - Sticky Traps; T - Thermohygrographs

2. GENERAL SURVEY

As a start to a general survey of the insect fauna, the indigenous vegetation surrounding the orchard at "Mosslands" was studied to obtain an understanding of the distribution of rutaceous plants. A knowledge of this distribution and a general classification of the vegetation types assisted in the planning and execution of the survey and also to some extent in the interpretation of results. The Eastern Province of South Africa is characterized by a wide variety of vegetation types, from semi-desert to forest, and by the large number of plant species in each type. The vegetation types in the "Mosslands" area may be divided into two major types according to Acocks (1953); (i) Valley Bushveld Southern variety and (ii) Eastern Province thornveld. The latter is to be found mainly on the plateau areas. Subdivision of these two major categories was difficult and the advice of the Government Botanist, Mr. M.J. Wells was sought. After a thorough inspection of the vegetation at "Mosslands" the following vegetation types were recognised and the areas occupied by these types are diagramatically represented in figure 1.

(i) Valley Bushveld Southern Variety.

a. Basic valley bushveld. This type of vegetation is found on the low ridges and drier slopes and is almost completely virgin bush as it is too thick for grazing animals. The area cleared for the orchard was originally of this vegetation type.

b. Cleared basic valley bushveld. Areas of basic valley bushveld which have been cleared of most of the primary woody species fall into this category. *Acacia* sp. thorn trees have subsequently invaded the area but it remains mostly as open grassland.

c. Moist valley bushveld. This veld type includes the same species as the basic valley bushveld community but has more of the larger species of tree as a result of the cooler more shaded conditions.

d. Euphorbia dominated moist valley bushveld. This vegetation type merges with the basic valley bushveld and with the moist valley bushveld but it occurs predominantly on the North facing rocky slopes which receive most sunshine.

e. Cleared moist valley bushveld. These are areas of moist valley bushveld which have been cleared for grazing. The clearing is recent and no secondary invasion of thorn trees has taken place.

f. Stream-bank woodland. This comprises a narrow fringing community of plants along the river bank and includes several large conspicuous species of trees.

(ii) Eastern Province Thornveld.

g, Basic Eastern Province thornveld. This vegetation type is of little relevance in this study as it does not typically include members of the Rutaceae and because this veld type is located a few miles from the orchard. The community is dominated by thorn trees some of which are secondary invaders in areas of partial clearing.

h. Open Scrub Parkland. This vegetation type, which is also of little relevance in this study, is very close to Eastern Province thornveld but is more open and may be thought of as transitional between Eastern Province thornveld and the basic valley bushveld.

Only four rutaceous plant species were found commonly in the vegetation at "Mosslands". Firstly, the Cape Chestnut, Calodendrum capense, which is a typical indicator of the stream-bank woodland vegetation. This species is scattered in the valley along the river bank. Secondly, Clausena anisata, is a moderately sized bush scattered throughout the indigenous vegetation surrounding the orchard. The species extends from the stream-bank woodland up into the higher lying areas where it was a very common species among the basic, cleared and moist valley bushveld communities. It was not usually found in the Euphorbia dominated bushveld. Thirdly, Fagara capensis, which is also known as wild lemon or knobwood, was not a very common species of rutaceous plant in the "Mosslands" area although it was scattered through the basic and moist valley bushveld types. Fourthly, Vepris undulata or white iron wood, which is a large tree associated with stream-bank woodland and with the moist valley bushveld. The nearest grove of white iron wood trees is situated about 400 metres from the North-eastern boundary of the Citrus orchard.

A general survey of the insects associated with these four indigenous plants and with citrus was started in July 1964. Samples were taken from the plants at two weekly intervals until the end of February 1965. By that time the numbers of insects recorded had decreased to such an extent that samples were taken at monthly intervals and the survey was stopped in June 1965. In this connection it should be noted that Calodendrum capense and Fagara capensis are deciduous and that leaves were seldom available from these species after June. Location of the relevant plants in the bush was facilitated by red patches painted on the stems of the plants. Leaf samples were collected separately in plastic bags from all five species. Each sample comprised leaves from several specimens of the same species of plant.

In an attempt to make the sampling more quantitative, a standard size of leaf sample was taken from each of the plants based on the criteria of surface area and time taken to inspect the leaves from the samples. A sample of 100 leaves of Calodendrum capense could be inspected microscopically for insects in about three hours. Taking this as a convenient sample size the surface areas of the leaves from the other plant species were calculated so that the same leaf surface area was examined in each case. The areas were measured using a polar planimeter and the results of these measurements are given in Table 1.

Table 1 Leaf area (cm^2) of Citrus sp. and of indigenous rutaceous plants. The approximate number of leaves required in samples from each plant species to give a standard surface area is also tabulated.

PLANT	NUMBER OF LEAVES MEASURED	TOTAL AREA (cm^2)	MEAN AREA PER LEAF (cm^2)	APPROX. NO. OF LEAVES REQUIRED IN SAMPLES
Calodendrum capense	50	1046.97	20.94	100
Citrus sp.	50	920.77	18.41	114
Clausena anisata	200	292.71	1.47	1430
Fagara capensis	200	282.26	1.41	1483
Vepris undulata	50	480.19	9.60	218

Table 1 shows that 100 leaves of Calodendrum capense have a total surface area of 2094 cm^2. Taking this as the criterion and in order to survey the same surface area of leaf in the other plant species, it was necessary to examine 114 citrus leaves per sample, 1430 leaves of Clausena anisata, 1483 Fagara capensis leaves and

218 leaves from *Vepris undulata*. The insects collected from each of these leaf samples were counted, catalogued, preserved and eventually sent to specialists for identification.

Only certain aspects of this survey are relevant and the results, therefore, need not be considered in any detail. In the first place only a small percentage of the insects collected was positively identified. In some cases this was because the stages collected were unsuitable for identification. In other cases only identification to Genera was possible and even then some identifications were tentative. A number of the animals despatched is still awaiting identification. Secondly the sample sizes were too small and the numbers of insects collected too low to enable meaningful conclusions to be drawn about seasonal variations of the insects.

However the survey was partially successful in that several polyphagous insects were collected and identified. These included a number of sap-sucking Hemiptera and Thysanoptera. The coccids included *Coccus hesperidium* Linn. and *Aonidiella aurantii* (Mask.) which are scales commonly found on citrus, *Calodendrum capense* and *Vepris undulata*. The aphid *Toxoptera citricidus* Kirk. was found on all the host plants except *Clausena anisata*. The psyllid *Trioza erytreae* (Del Guercio) was found on all the rutaceous host plants except for *Calodendrum capense*. Species of Jassidae and Aleyrodidae were found to be polyphagous but were not identified to species. The psocopteran *Ectopsocus briggsi* Mch. was collected from all five plant species but is only of passing interest as it is a scavenger and does not feed directly on the plants. Species of many other orders of insects were collected but only in small numbers. Mites and spiders were extremely abundant and represented by many species but were ignored.

With these data as a background *Trioza erytreae* and *Paurocephala calodendri*, (the latter is associated only with *Calodendrum capense*), were chosen for further study. The reasons for this choice have already been outlined in the introduction.

3. CLIMATE

The climatic conditions prevailing at "Mosslands" were recorded for nearly a year before laboratory observations on T. erytreae and P. calodendri were started. The climatic data were then used in the planning of both laboratory and field experiments and provided a background upon which these experiments were interpreted. The relevant climatic conditions are described below.

Temperature.

Temperature recordings at "Mosslands" were made using two Juchheim thermo-hygrographs which were set up in the positions T_1 and T_2 indicated in figure 1. The thermo-hygrograph T_1 was placed in the citrus orchard and in this position was estimated to be 20 metres higher than thermo-hygrograph T_2 which was set up in the valley adjacent to the citrus orchard. The latter instrument was arranged in the middle of a large Calodendrum capense tree and both instruments were housed in Stevenson screens. Before the instruments were placed in their permanent positions they were matched in one large Stevenson screen. In addition to the thermo-hygrograph a maximum and minimum thermometer was placed in each Stevenson screen and the weekly maximum and minimum temperature recordings were used for monitoring the accuracy of the thermograph. When there was a discrepancy in temperature recordings they were corrected.

Recordings of mean weekly maximum and minimum temperatures, while indicative of the limits to which the insects had been subjected, are seldom of great relevance biologically. In the first place when an insect is living within its normal distribution range it is unlikely that temperature extremes will exceed the upper or lower lethal limits of the animals. If these limits were exceeded regularly the insect in question would clearly not be living in that habitat. In a study of poikilothermic animals it is essential to know how hot or cold it was for how long, rather than having a record of maximum and minimum temperatures. Throughout this account, therefore, reference is made to summations of temperature which give a far better estimate of the temperatures relevant to the psyllids than do maximum and minimum temperatures.

The principal of temperature summations has been widely used in plant growth studies. For example it is known that the lower developmental temperature limit for Citrus sp. is approximately 13.5°C. An estimate of the potential growing period for Citrus sp. may then be calculated by taking 13.5°C as a baseline and summing daily, weekly or hourly, the number of degrees centigrade above this baseline. Hughes (1963) has made extensive use of temperature summations in his studies on the population dynamics of the cabbage aphid Brevicoryne brassicae (L.) and has used this method of temperature analysis in the interpretation of his results.

Throughout the present study 20°C has been chosen as a baseline and the number of hour degrees centigrade per week (Hr°C per week) above and below this baseline have been calculated. It must be emphasised that a baseline of 20°C cannot be interpreted as the lower developmental temperature limit for psyllids because this has not been determined and in any event this limit would vary from species to species. 20°C is in fact an arbitary, convenient baseline and of course, in terms of temperature summations above and below a

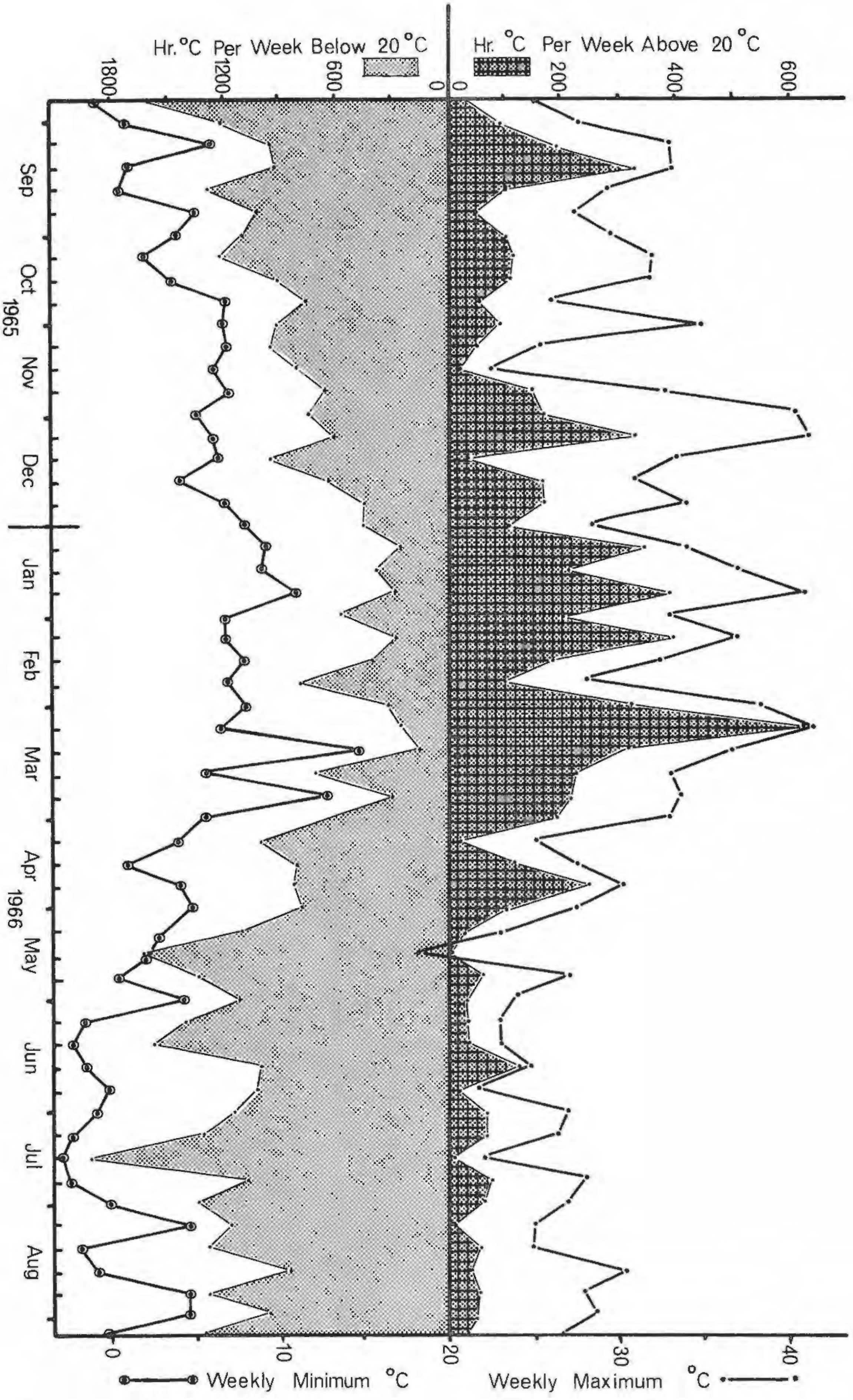


Fig. 2 Temperature summations (Hour degrees centigrade per week above and below 20°C) and maximum and minimum temperatures (°C) recorded at "Mosslands" for the period September 1965 to September 1966 on thermograph T_2 (See Fig. 1).

certain baseline, it would not matter which baseline had been chosen. Clearly if 10°C had been chosen as a baseline there would be very few hour degrees per week below this baseline and a great number above, while the opposite would be true if 40°C had been chosen.

Temperature records, from "Mosslands", were kept for over three years. In figure 2 the temperature summations in Hr°C per week above and below 20°C and the weekly maximum and minimum temperatures are recorded for the period September 1965 to September 1966, (these dates are relevant in terms of a survey of nymphs of P. calodendri and will be refered to later). The data in figure 2 were obtained from thermograph T_2 and give an idea of seasonal fluctuations of temperature at "Mosslands". During the summer period the maximum temperatures recorded often exceeded 40°C and during winter the minimum temperatures often dropped below freezing point. Diurnal fluctuations in temperature were also considerable. During summer the normal diurnal fluctuations of temperature had a range of 20° -30°C - diurnal fluctuations in temperature of more than 30°C were only rarely exceeded. During winter diurnal fluctuations were less, usually ranging between 15° and 25°C. A summary of the data shown in figure 2 is given in table 2 which records mean monthly maximum and minimum temperatures together with mean monthly temperature summations above and below 20°C per week. These data have been used in programming the "environment room" and in a comparison of field and laboratory data.

Table 2. Mean monthly maximum and minimum temperatures (°C) and mean monthly temperature summations (Hr°C per week above and below 20°C) recorded at "Mosslands" between September 1965 and September 1966 on thermograph T_2.

MONTH	MEAN MONTHLY HR°C/WEEK ABOVE 20°C	MEAN MONTHLY MAXIMUM °C	MEAN MONTHLY HR°C/WEEK BELOW 20°C	MEAN MONTHLY MINIMUM °C
SEPTEMBER 1965	155	30.9	1076	2.8
OCTOBER	99	30.1	997	4.2
NOVEMBER	79	28.9	828	6.9
DECEMBER	176	36.3	670	6.0
JANUARY 1966	265	34.2	332	9.4
FEBRUARY	222	31.1	514	7.8
MARCH	432	36.7	436	9.8
APRIL	147	28.9	850	3.9
MAY	51	24.0	1204	2.6
JUNE	54	23.2	1231	0.0
JULY	56	25.8	1452	- 1.9
AUGUST	44	25.7	1198	1.6

The temperatures recorded in the chestnut tree on thermograph T_2 can be compared with those recorded in the citrus orchard on thermograph T_1. The temperature record obtained in both cases is very similar, even the smallest fluctuations in temperature recorded on the one thermograph approximate very closely to those on the other. However, what is significant, is that the temperatures recorded in the citrus orchard were consistently 1° - 2°C higher than those recorded in the chestnut tree. If maximum readings are compared from the two sites the temperatures recorded during winter were very often the same in the orchard as in the chestnut tree. During summer the temperatures recorded in the orchard were higher than those in the chestnut tree. The minimum temperatures recorded from both sites throughout the year showed that the chestnut tree was always 1° - 2°C colder than the orchard. It would seem from these very minor differences in maximum and minimum readings from the two sites that conditions as far as the insects were concerned may be regarded as very similar. However, this is not the case and it can be shown that there are very real differences between the two sites if the average temperature summations in Hr°C per day are compared. Summer temperature summations, above and below 20°C, for the 70 days between 30th November, 1966 and the 1st February, 1967 in the citrus orchard and in the chestnut tree were compared. This revealed that during summer there was a mean daily increase of 40.1% in Hr°C above 20°C in the orchard as compared with the chestnut tree. (Standard errors for the percentages have been calculated but were found to be very small and are ignored). Similarly during the same summer period the chestnut tree was 50.4% cooler than the orchard in terms of the totals of Hr°C per day below 20°C. During the winter period from 1st June 1966 to the 3rd August 1966 there were, on the average, 33.6% more Hr°C per day above 20°C in the orchard than in the chestnut tree. During the same winter period the tree was cooler having an average of 27.9% more Hr°C per day below 20°C than the orchard.

These differences in temperature summations between the two stations are surprisingly high considering the small differences in maximum and minimum temperatures recorded and would obviously be of great significance in a consideration of developmental times in

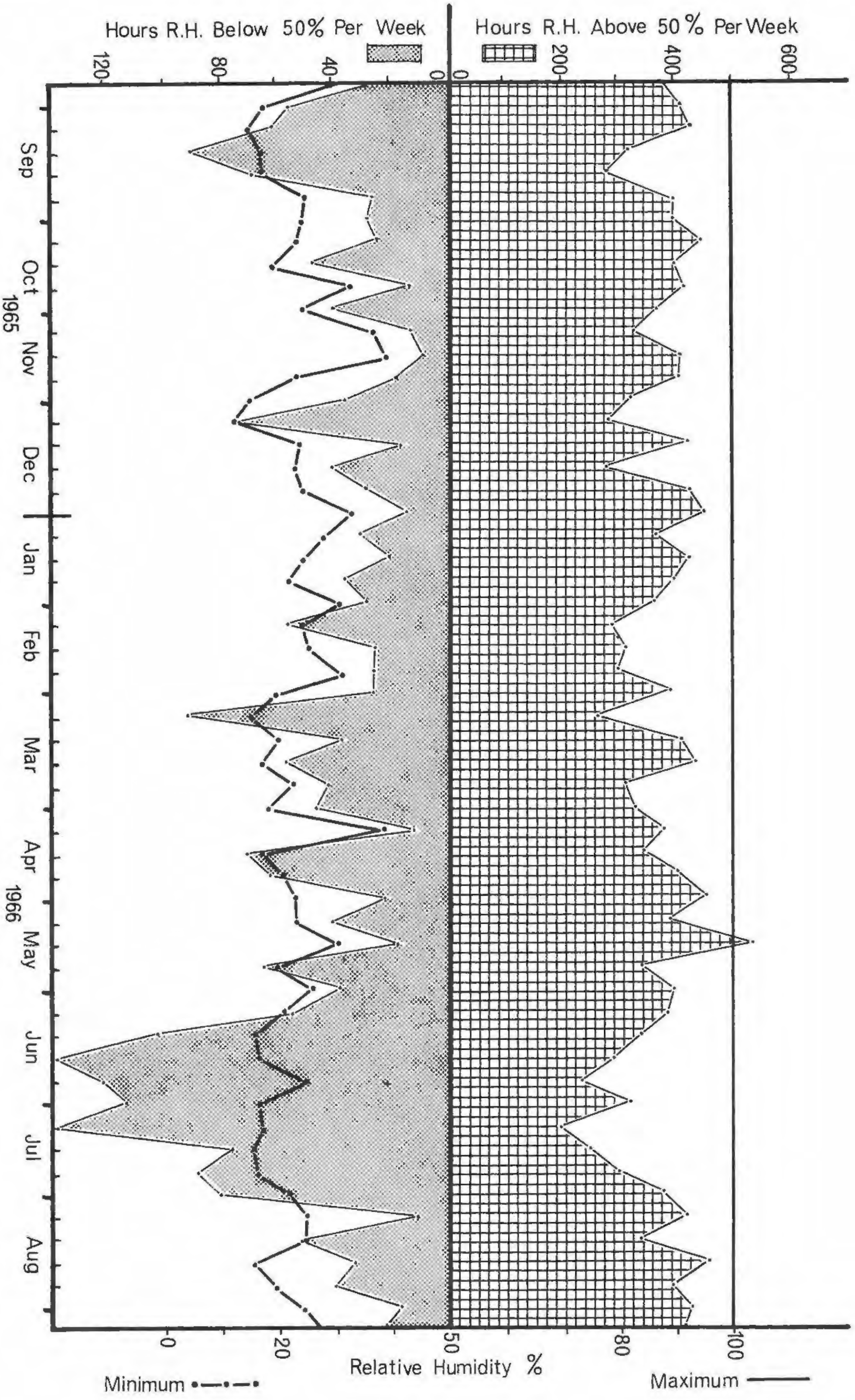


Fig. 3 Relative humidity summations (Hours above and below 50% relative humidity) and maximum and minimum relative humidities (%) recorded at "Mosslands" for the period September 1965 to September 1966 on hygrograph T_2. (See Fig. 1).

psyllids. The significance of these observations are considered later in connection with the distribution of Trioza erytreae.

Humidity.

Humidity records from the hygrographs (in positions T_1 and T_2 - see figure 1) were checked, using a whirling hygrometer, when the Stevenson screens were first erected. Several weeks of checking showed the relative humidity records to be reasonably accurate provided the humidity sensitive hairs in the instruments were saturated with distilled water every week and the hygrograph standardized while the hairs were wet. (This procedure is in accordance with the recommendations of the Weather Bureau in Pretoria).

The humidity conditions prevailing at "Mosslands" are represented in figure 3. Humidity summations are plotted with an arbitary baseline of 50% relative humidity and maximum and minimum relative humidities are recorded for the year from September 1965 to September 1966. The figure shows that there was little evidence of seasonal fluctuations in relative humidities during the year. Dew point was reached almost every night and thus the maximum humidity recorded from week to week was always 100%. During the day, throughout the year, the relative humidity dropped to between 15 and 35%. The humidity summations above and below 50% showed little seasonal fluctuations although an obvious exception to this generalization was seen during the last weeks of June and the beginning of July 1966 (figure 3). During this very dry period the total numbers of hours relative humidity below 50% per week was very high in comparison to that during the rest of the year. This very dry period was caused by the hot dry "berg" wind. The wind blew for three weeks and resulted in a very low

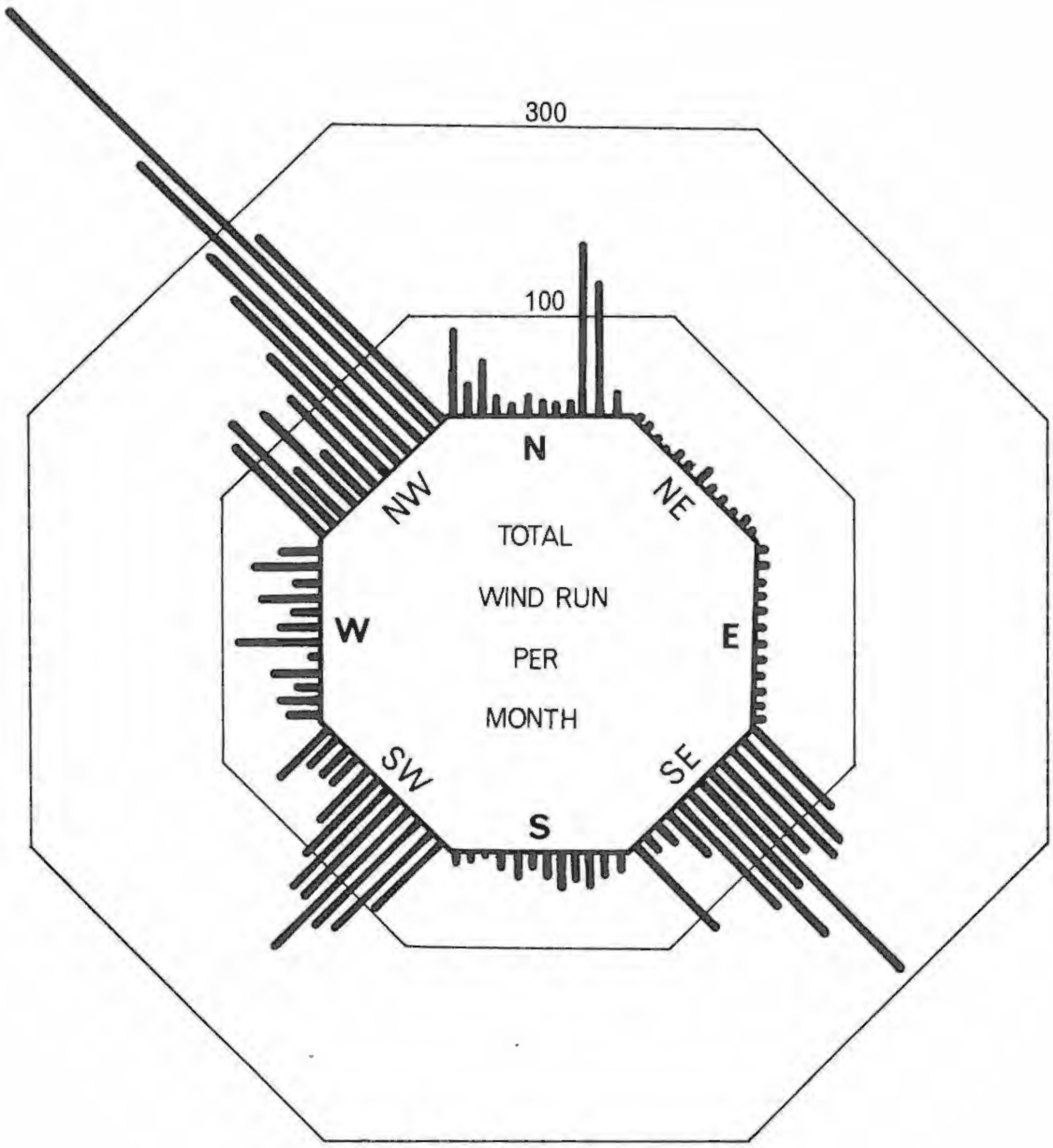


Fig. 4 Total wind run per month recorded at "Mosslands" for the period September 1965 to September 1966. The sides of the octogon represent the cardinal and semi-cardinal points. The 12 histogram columns at each side of the octogon represent wind run (in arbitary units of 10,000 metres) for each month, reading in a clockwise direction. Method of representation after Clark , (1962).

humidity during the day and night which caused considerable damage to citrus orchards throughout the area. The "berg" wind is an annual occurence in this area but the 1966 wind was of unusual severity. These humidity patterns have been taken into account in the programming of the environment room.

Wind.

A Lambrecht wind speed and direction recorder was set up at "Mosslands" in the position indicated in figure 1. The instrument, which runs without attention for over a month, was mounted on a metal pole two metres from the ground and correctly orientated to magnetic North using a prismatic compass. The site chosen for the wind recorder was open and elevated above the orchard; it was not possible to place the instrument in the citrus orchard near the survey sites as the orchard is surrounded by tall trees.

The total wind run per month for the period from September 1965 to September 1966 is diagramatically represented in figure 4. In this figure the sides of the octogon represent the cardinal and semi-cardinal points and the total wind run for each month in any particular direction has been calculated in units of 10,000 metres. These units are approximately equal to the total wind run for a wind of 3 metres per second blowing constantly for one hour. These units were chosen as they are convenient and easy to interpret from the original wind records. Each histogram at each of the compass points represents the total number of 10,000 metre units for one month starting in September 1965 and reading in a clockwise direction until August 1966. The two surrounding octogons represent the levels of 100 and 300 wind units respectively.

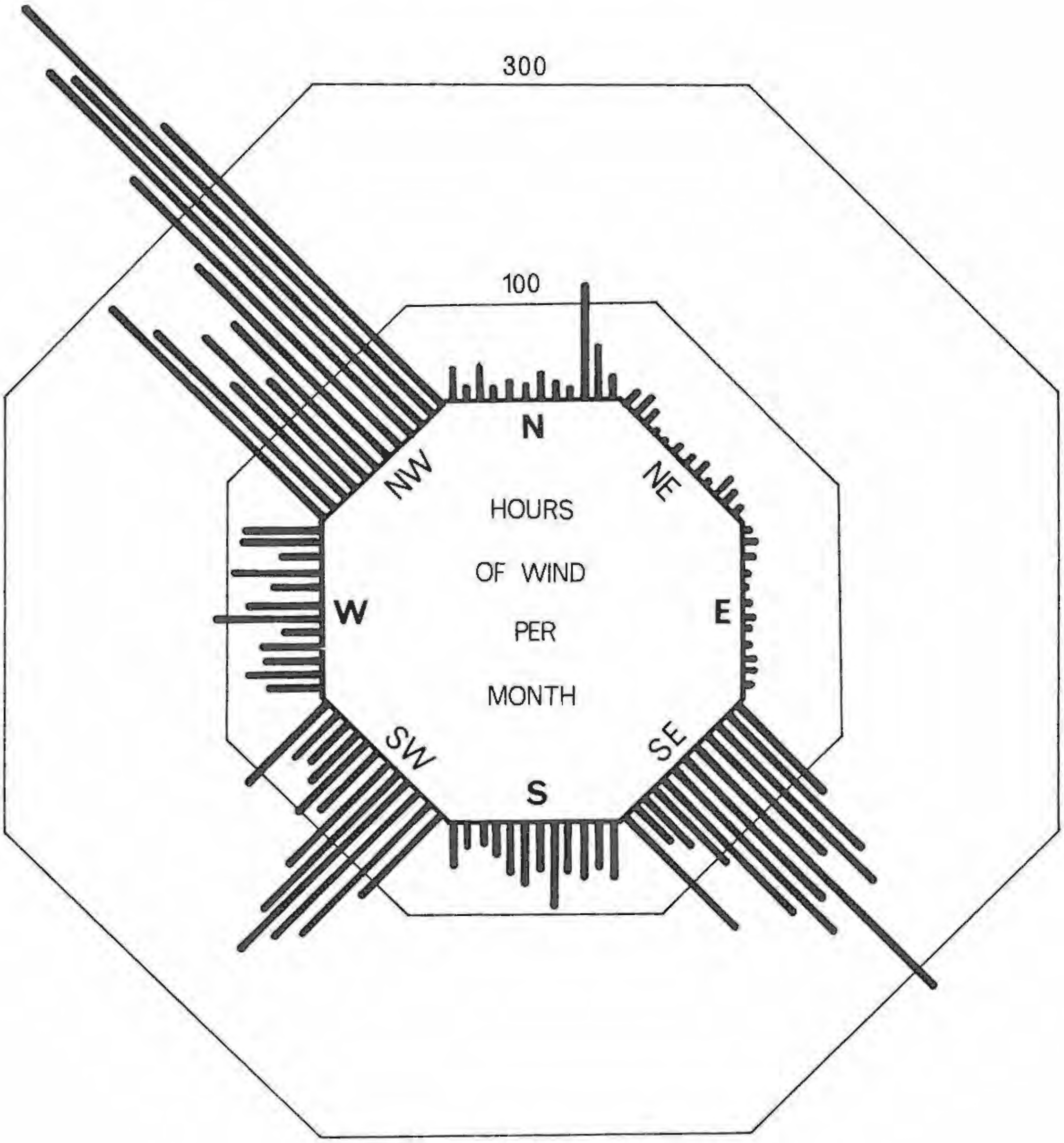


Fig. 5 Total number of hours of wind per month recorded at "Mosslands" for the period September 1965 to September 1966. The sides of the octogon represent the cardinal and semi-cardinal points. The 12 histogram columns at each side of the octogon represent hours of wind for each month reading in a clockwise direction. For further explanation see text and Fig. 4. Method of representation after Clark .,(1962).

From figure 4 it can be seen that the North-westerlies, South-easterlies and South-westerlies are the prevailing winds in the "Mosslands" area. The South-easterlies and South-westerlies dominate during the summer months, with the intensity of the North-westerlies increasing during winter. The high totals of North-westerlies recorded during June and July were brought about by the "berg" winds.

Figure 5 is given to supplement figure 4 and represents the total number of hours of wind per month in any one direction recorded for the period from September 1965 to September 1966. The two octogons surrounding the figure represent the levels of 100 and 300 hours of wind respectively. Figure 5 gives a similar wind picture to figure 4 except that it shows that the Northerly, South-easterly and South-westerly winds tend to be strong winds blowing for a relatively short period of time per wind run unit. The North-westerlies, North-easterlies, Southerlies and Westerlies on the other hand tend to blow steadily and gently for longer periods of time per wind run unit. Figure 4 and 5 show the total wind run and the time a particular wind blew for each month during the year. Wind records have been kept for over three years and are relevant in a consideration of catches of adult psyllids on sticky yellow "impact" traps which are discussed later.

Rainfall.

Rainfall data may be relevant where storms flood the leaves upon which the psyllids live and this may bring about mortality of the nymphs. However, no mortality of this type was observed during the course of the investigation. The following data are included for completeness and to give a better idea of the area in which these studies were conducted.

At "Mosslands" daily rainfall records have been kept since the turn of the century and an analysis of the rainfall records over the last 30 years shows an average of 588.0mm (23.2 inches) per annum with a maximum of 777.2 mm (30.6 inches) and a minimum of 353.1mm (13.9 inches). Rain falls intermittently throughout the year although it tends to rain more frequently and more heavily during the summer months. The maximum monthly rainfall recorded during the survey period was 115.3mm (4.5 inches) during December 1965, 56.4 mm (2.22 inches) of this falling within a 24 hour period.

4. THE "ENVIRONMENT ROOM"

Insects are normally subjected to considerable variations in temperature, humidity and light. If reared under constant conditions, development is often slowed down (Odum, 1961) and under such conditions developmental durations cannot be compared directly with those in the field. There is also evidence that fluctuating temperatures stimulate insect development. Shelford (1927) concluded that the effect of normal daily fluctuations of outdoor temperatures resulted in 7 - 8% more rapid growth in the codling moth than under constant conditions. Hamilton (1950) found that for Schistocerca, fluctuating conditions speed sexual maturity compared to locusts reared under constant temperature conditions. Also Schistocerca and Locusta females deposited more eggs per egg pod when conditions were fluctuating than when they were constant. More recently Clarke (1967) has investigated the growth rates of Locusta migratoria migratorioides (R. & F.) in response to fluctuating temperatures (changes in temperature were brought about every two hours). He found that growth rates of fourth instar and adult locusts were higher when a fluctuating temperature regime of $30 \pm 10^{\circ}C$ was maintained than when kept at a constant temperature of $30 \pm 0.25^{\circ}C$.

An aspect to be considered when insects are reared on potted seedlings is the effect of environmental conditions on the seedlings. Several authors have shown that constant temperature environments are detrimental to the general growth and development of plants (Highkin, 1960). With pea plants, for example, this inhibition of growth under constant environmental conditions becomes more pronounced in successive generations. Clearly the environment in which the food plant is grown will have a direct influence on its physiological state and on the development of the insect which is feeding on it.

With these considerations in mind, the psyllids were studied under controlled fluctuating conditions of temperature, humidity and light. All laboratory data on the biology of Paurocephala calodendri and Trioza erytreae were derived from experiments on insects reared on potted seedlings in an insulated "environment room". P. calodendri was reared throughout on Calodendrum capense seedlings. T. erytreae on the other hand was usually reared on Citrus limonia, the Cape rough lemon, although this insect was often reared on seedlings of the four indigenous Rutaceae which were collected from the field. The controlled, fluctuating environment in the room was provided by two modified air conditioning units and two humidifying units. The one air conditioner provided hot or cold air while the other was used as a de-humidifier and acted antagonistically to the two humidifiers. The room was provided with 14,2.4 metre (eight foot) daylight simulating neon tubes and the conditions switched from "day" to "night" at 6 p.m. and vice versa at 6 a.m. The air conditioning units and the humidifiers were controlled by a thermo-hygrostat which activated time delay circuits and relays. The time delays were necessary to ensure that the contacts were not constantly "chattering" as the units were switched on or off. Initially the environment room was programmed to a temperature regime of 28 - 33 Hr°C per week above 20°C and approximately 266 Hr°C per week below 20°C. The maximum temperature at this regime was 21°C and the minimum about 11°C. These conditions are referred to throughout the text as the "lowest" temperature regime. These temperatures were chosen because it was known that high temperatures affect the psyllids adversely. There were, however, considerable differences between the actual environmental conditions in the room

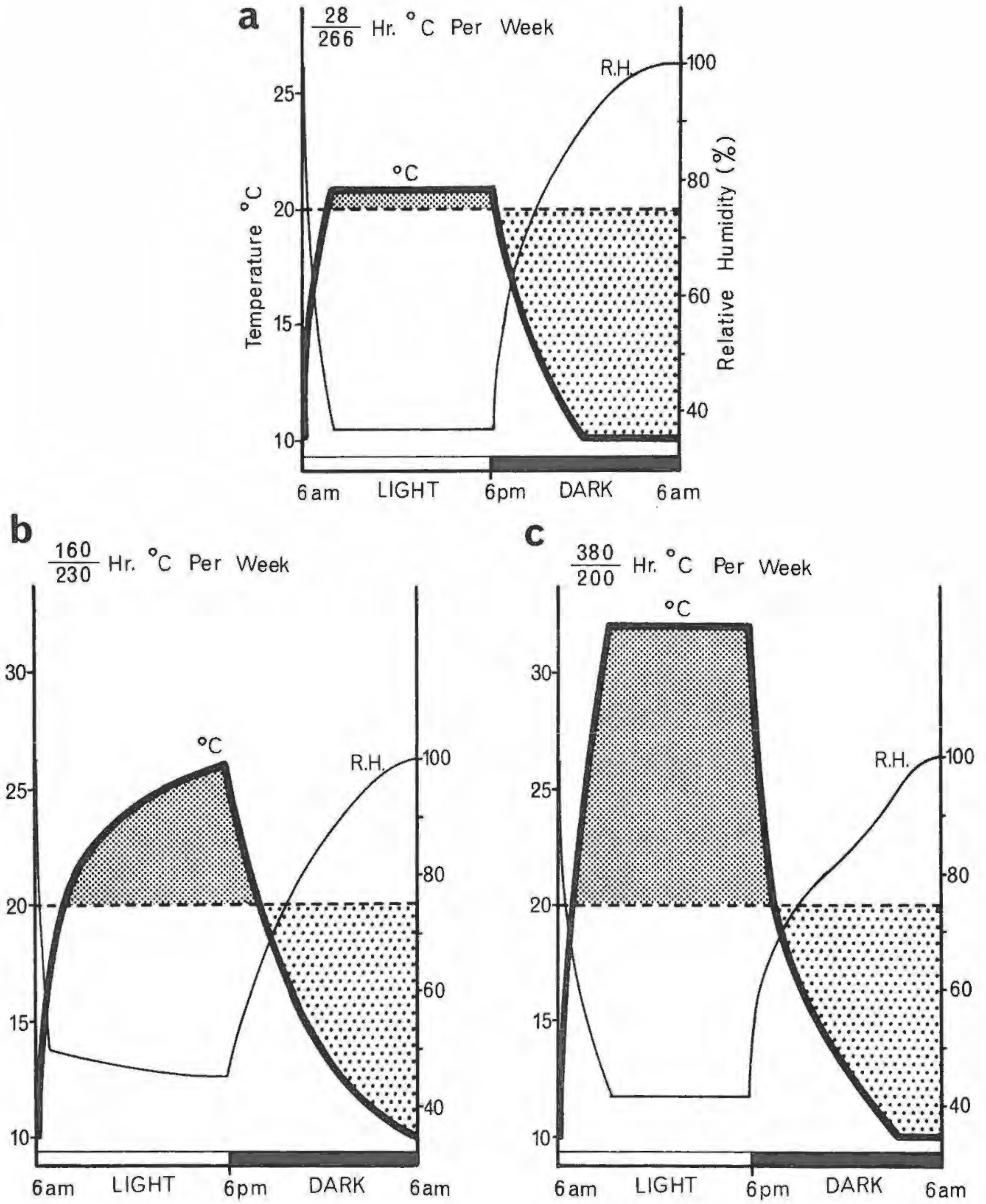


Fig. 6 The fluctuating conditions of temperature, humidity and light prevailing in the "environment room". 6 a - the lowest temperature regime with a total of 28 Hr°C per week above and 266 Hr°C per week below 20°C. 6 b - the median temperature regime with a total of 160 and 230 Hr°C per week respectively above and below 20°C. 6 c - the highest temperature regime with a total of 380 and 200 Hr°C per week respectively above and below 20°C.

and those in the field. Diurnal temperature fluctuations were much greater in the field as compared with the environment room and temperature and humidity "plateaux" were maintained in the room while peaks of temperature and humidity were normal in the field. Rates of change of temperature and humidity varied considerably in the field but remained constant in the environment room. The rates of change of temperature and relative humidity in the environment room were however, rough approximations of those in the field. The actual conditions which prevailed in the environment room at the lowest temperature regime are diagramatically represented in figure 6 a.

In experiments on the effects of temperature on psyllids two hotter temperature regimes were used and the environment room programmed accordingly. Firstly the temperature was raised to a maximum of 27°C with a minimum temperature of about 11°C and at this regime the temperature summations were approximately 160 Hr°C per week above 20°C and 230 Hr°C per week below 20°C. These conditions are referred to as the "median" temperature regime and are diagramatically represented in figure 6 b. Secondly a temperature regime with a maximum of 32°C and a minimum of about 11°C was established which gave a total of approximately 380 Hr°C per week above 20°C and 200 Hr°C per week below 20°C. These conditions are referred to as the "highest" temperature regime and are diagramatically represented in figure 6 c. The humidity fluctuations were approximately constant at all three temperature regimes. Other changes in the environment room were made occasionally and will be explained in the appropriate section.

5. THE BIOLOGY OF *PAUROCEPHALA CALODENDRI*

The general survey has shown that *Paurocephala calodendri* is a monophagous species which is numerous on the leaves of the Cape chestnut tree *Calodendrum capense*. *C. capense* has a wide distribution in Southern Africa. It extends from Knysna in the Eastern Cape Province along the coastal forests to Natal where it is found in coastal and midland areas. It also occurs on the Western mountains of Swaziland and extends as far West as Rustenburg in the Transvaal. It has been reported from the Eastern highlands of Rhodesia and has been found occasionally in Malawi, Tanzania and Kenya. The distribution of *C. capense* in the more temperate regions of the country is of interest because the laboratory studies on the biology of *P. calodendri* and field observations show that this insect can thrive only under temperate conditions.

In this account of the biology of *P. calodendri* a detailed description is given of the adult and immature stages of this new psyllid species. This is followed by an account of the effects of temperature on the developmental stages of the insect in the laboratory and then the effects of temperature and parasites on a field population of immature and adult stages of *P. calodendri* are considered. This leads to a consideration of the biology of *Tetrastichus* sp. the major parasite of *P. calodendri* and finally, in the light of all this information, the control of populations of *P. calodendri* is discussed.

Systematic position.

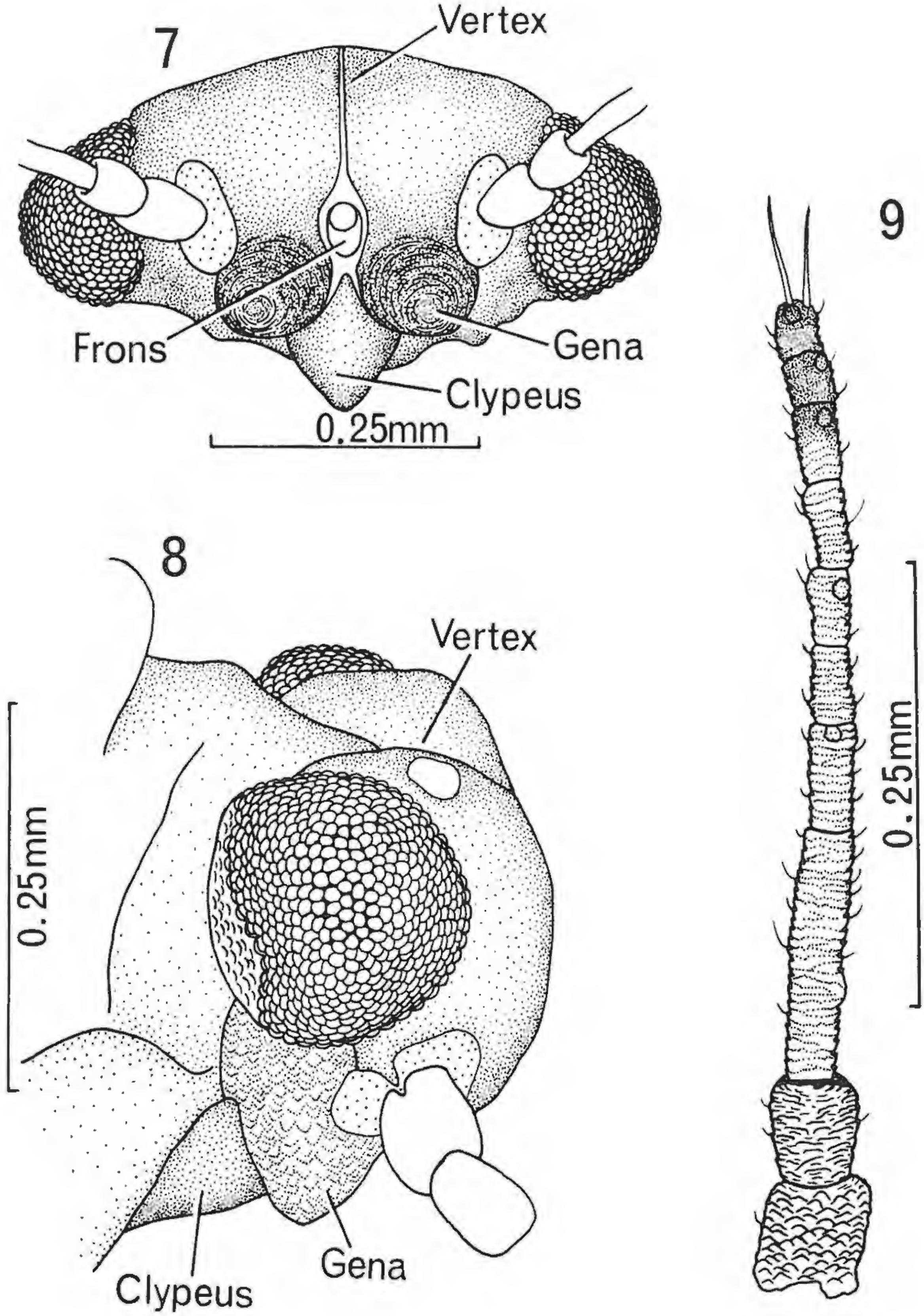
A thorough survey of the literature on the Sub-family

Aphalarinae, and particularly of the so-called rhinocolan Genera (Heslop-Harrison, 1952) in the Sub-family, showed that the Cape chestnut psyllid was to be regarded as a new species. Consequently, the adult and immature stages of this species have been described (Moran, 1968) and the manuscript has been accepted for publication. For purposes of completeness the description is included in this thesis.

Paurocephala calodendri Moran (In Press) - Adult.

(i) Size. Newly emerged females, body length (excluding wing tips and antennae) (see table 3) 1.81 mm - 2.13 mm, mean 1.99 mm standard error ± 0.04 mm; body width (across thorax at level of fore wings) 0.63 mm - 0.75 mm, mean 0.65 ± 0.02 mm. Based on seven measurements. Newly emerged males, body length 1.75 mm - 1.88 mm, mean 1.77 ± 0.03 mm; body width 0.53 mm - 0.75 mm, mean 0.60 ± 0.02 mm. Based on eight measurements. Mature females, body length 1.83 mm - 2.18 mm, mean 2.00 ± 0.02 mm; body width 0.59 mm - 0.66 mm, mean 0.62 ± 0.006 mm. Based on 20 measurements. Mature males, body length 1.40 mm - 1.76 mm, mean 1.63 ± 0.02 mm; body width 0.51 mm - 0.62 mm, mean 0.56 ± 0.007 mm. Based on 25 measurements.

(ii) Coloration. In this account the names and numbers of colours are taken from the Wilson Colour Chart (Wilson, 1939, 1942) and these colour choices are based on the assessment of three independent observers. The colours are included as an aid to identification in other geographical areas where colour in this species might differ. Coloration similar in males and females but in both sexes colour varies considerably with age, newly emerged insects with a background colour predominantly green maturing to

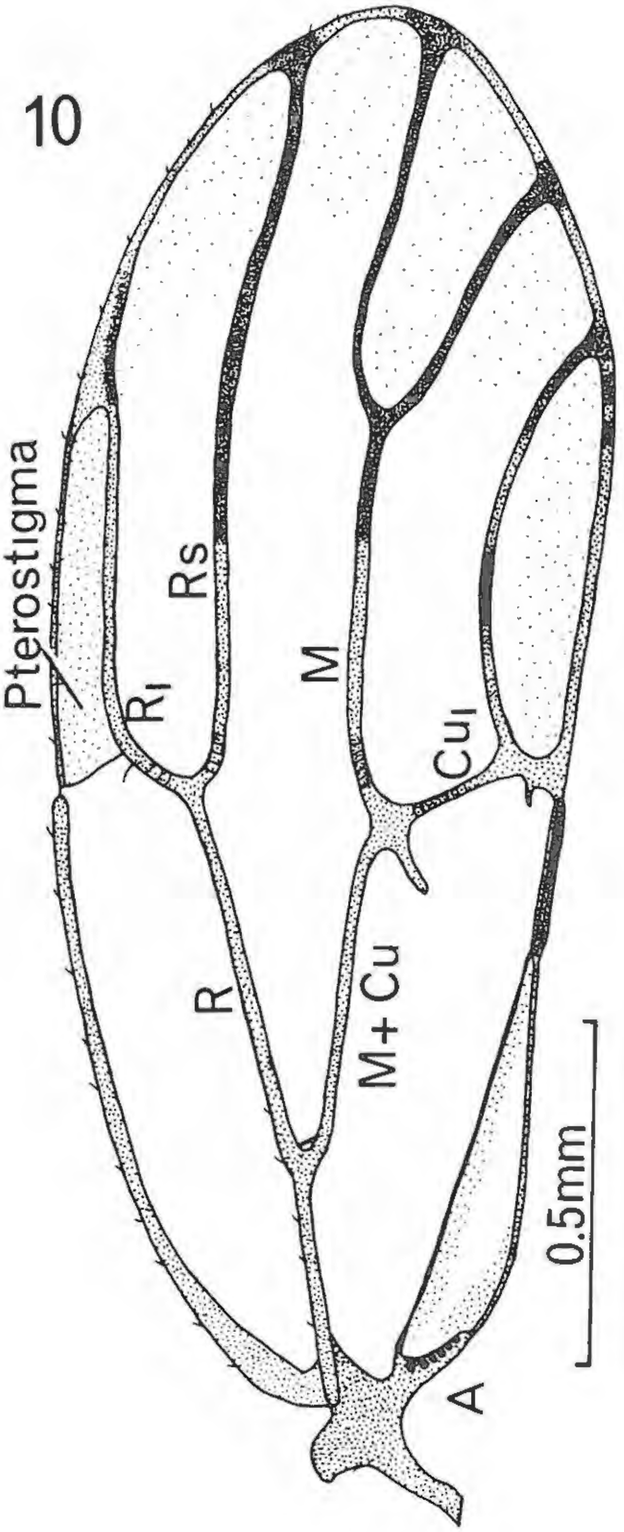


Figs. 7 - 9 Head and antenna of *Paurocephala calodendri*. Fig. 7 - anterior - ventral view of head. Fig. 8 - lateral view of head. Fig. 9 - antenna.

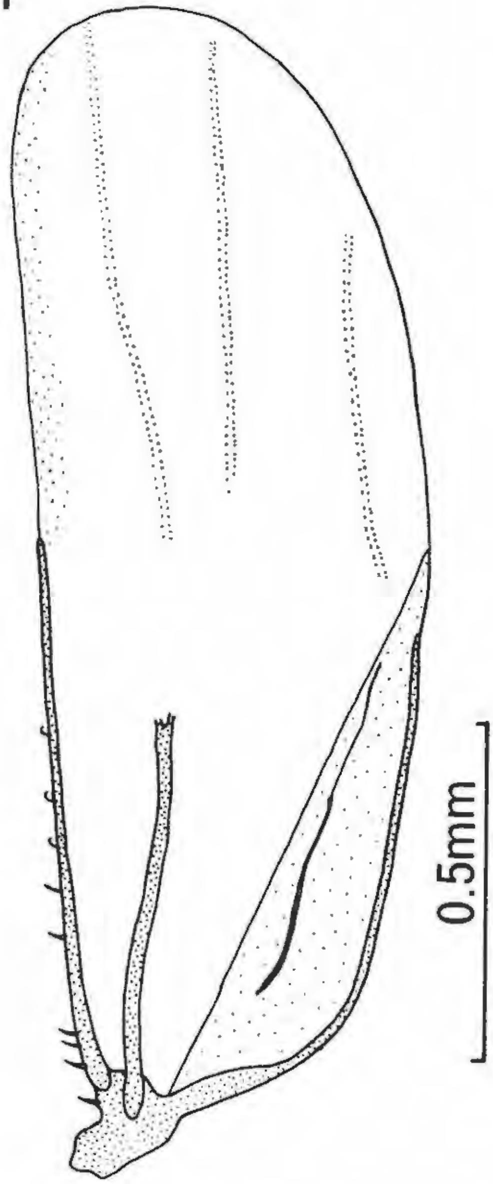
dull orange buff. In mature specimens head overall orange buff (No. 507/1) except for posterior regions of vertex, eyes and most of genae which vary from Cyprus green (No. 59/3) to viridian green (No. 55/2). Compound eye facets black. Antennae usually with distal end of eighth segment and last two segments dark brown to black. Thoracic terga; pronotum orange buff, semi-circular area on anterior part of meso-prescutum also orange buff, remainder varying from Cyprus green to light pea green (No. 61/3); mesoscutum characterized by two conspicuous dark brown or black patches laterally abutting on suture between meso-prescutum and mesoscutum and by two similar dark brown patches posteriorly on the mesoscutum. These four dark brown patches on the thorax are very conspicuous in mature adults but pale at emergence. Rest of mesoscutum orange buff except for lateral margins near axillary sclerites and for broad band on mid-line of mesoscutum which is Cyprus green to light pea green. Mesoscutellum viridian green to chrysocolla green (No. 56/2). Metascutum chrysocolla green to orange buff. Metascutellum generally straw yellow (No. 604), meta-postnotum dark brown in mid line otherwise orange buff. Legs very pale, varying from off white to extremely pale green or orange. Abdominal tergites Cyprus green to light pea green except for posterior margins which are straw yellow. First two abdominal terga sometimes dominated by dark brown or black. Abdominal sterna viridian green to Cyprus green.

(iii) Head. (Figs. 7 and 8). Head almost as wide as thorax and strongly deflexed. Vertex rounded forward and downward, lateral ocelli close to compound eyes. Vertex divided by clear epicranial suture. Frons distinct, located above genae at anterior end of epicranial suture and bearing median ocellus dorsally.

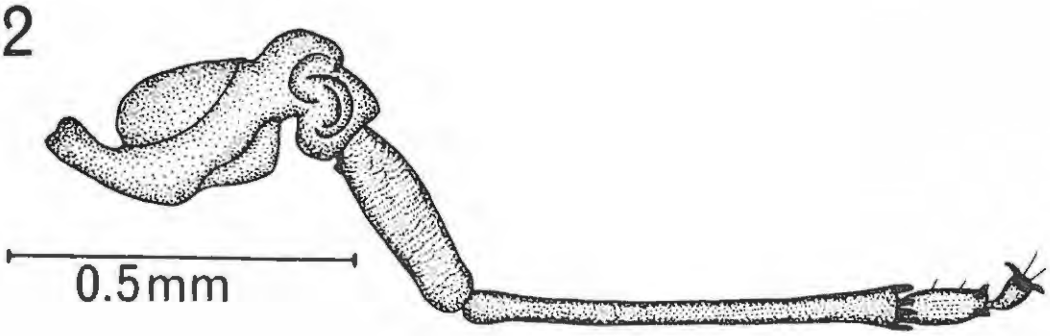
10



11



12



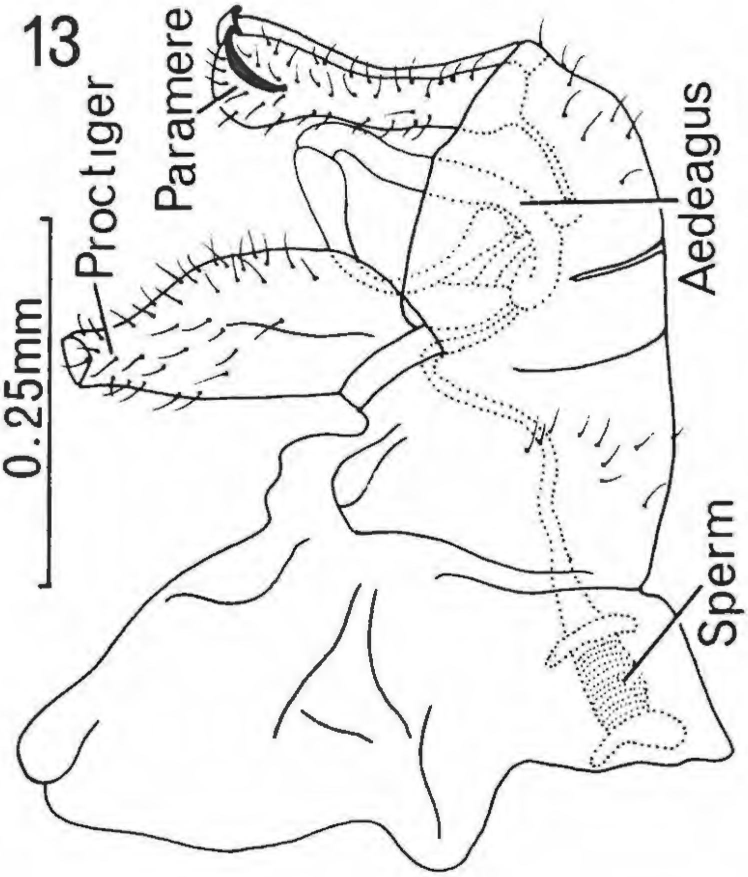
Figs. 10 - 12 Thoracic appendages of Paurocephala calodendri. Fig. 10 - right fore wing. Fig. 11 - right hind wing. Fig. 12 - meta-thoracic leg.

Genae swollen and rounded but not produced into cones and not visible in dorsal view. Clypeus small, triangular and convexly rounded. Antennae (Fig. 9) ten segmented, length 0.605 mm; all segments bearing short irregularly arranged setae, distal segment bearing two large apical setae. Sensoria or rhinaria present on antennal segments four, six, eight and nine with that on segment four indistinct.

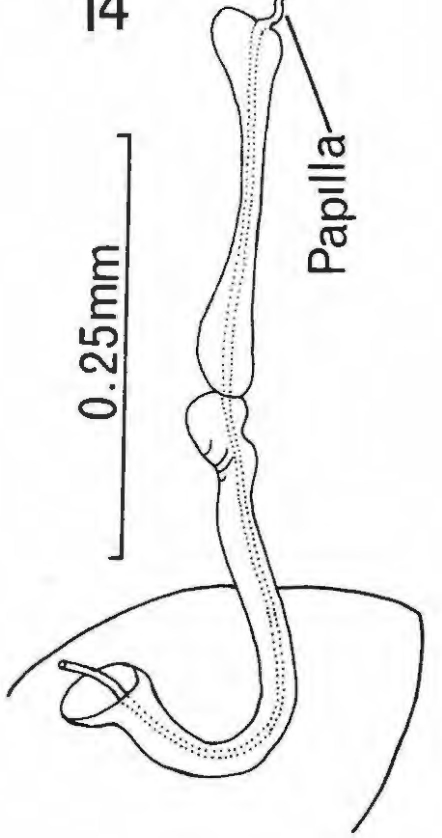
(iv) Thorax. Meso-prescutum and mesoscutum well developed and arched dorsally. Metascutellum not noticeably produced into a median horn-like epiphysis. Fore wings (Fig. 10) transparent but with veins well defined and darkened distally. Base of median plus cubitus (M + Cu), (cubital petiole), almost equal in length to base of radial vein (R); radial sector (Rs) slightly convex and unbranched; nodal line (nodal cross vein) absent; bases of radius 1 (R_1), radial sector (Rs), median (M) and cubitus 1 (Cu_1) with ring-like thickenings, anal vein (A) thickened and bearing a row of square protuberances of doubtful function. Wing veins covered with small setae. Entire surface of wing covered with minute tubercles (spinules - Ossiannilsson, 1963 a and b) which are larger and most evident in the pterostigmatic area. Hind wings (Fig. 11) with only a few veins proximally; distal half of wing transparent. Costal vein with nine wing coupling hooklets. Wing surface completely covered with minute tubercles only easily visible using phase contrast illumination. Pro- and mesothoracic limbs very similar but fore leg (1.39 mm) slightly longer than middle leg (1.35 mm). Hind leg (Fig. 12) with enlarged coxa. Meracanthus on metathoracic coxa not developed. Distal end of trochanter in all legs bears a row of six circular colourless areas of unknown function.

(v) Abdomen. Abdomen without special diagnostic features except for terminalia. Male genitalia (Fig. 13) with proctiger held vertically, anus at apex and bearing numerous setae, parameres

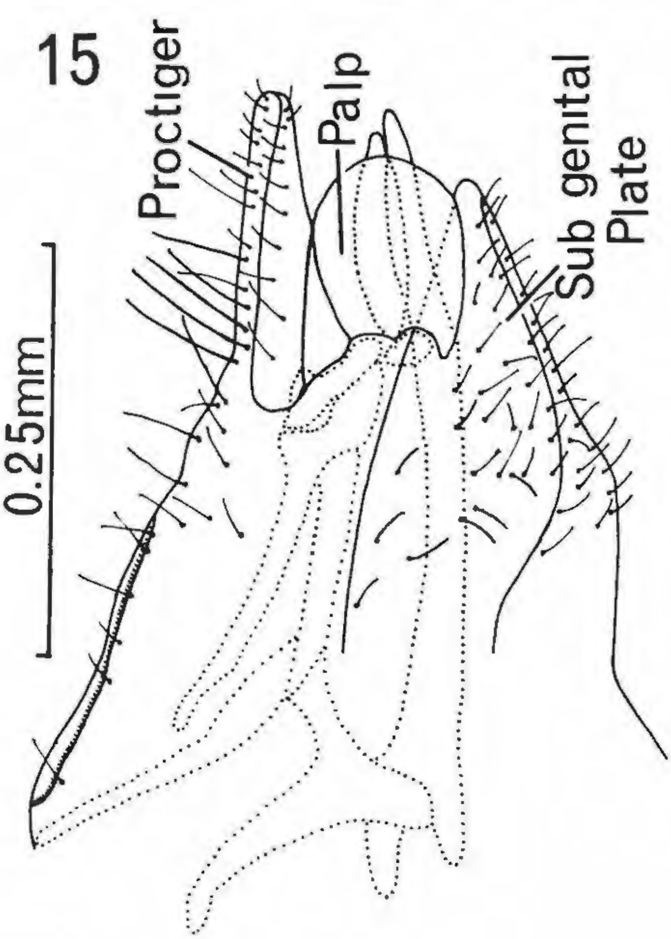
13



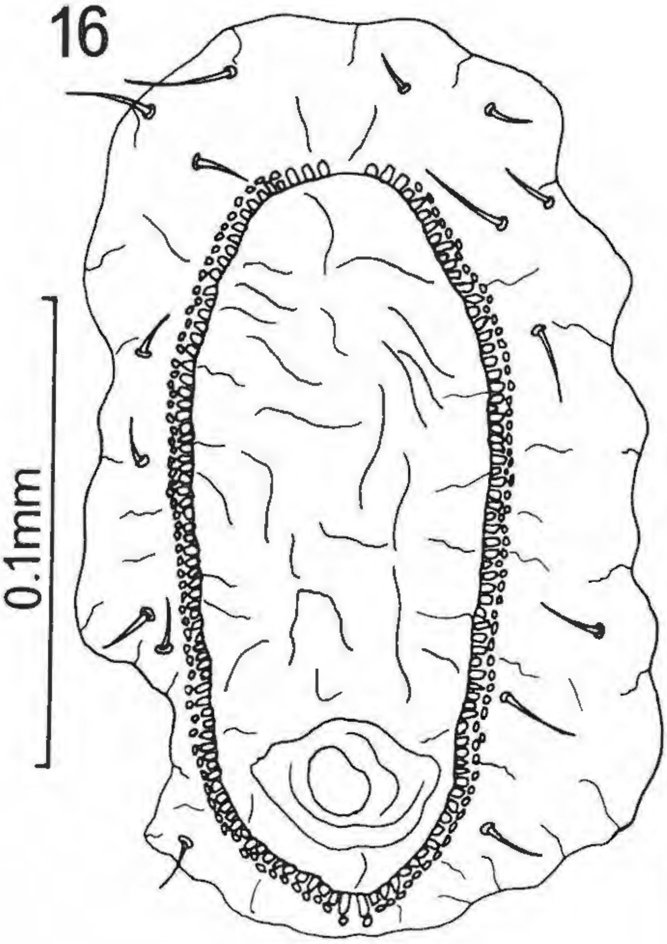
14



15



16



Figs. 13 - 16 Genitalia and associated structures of *Paurocephala calodendri*. Fig. 13 - lateral view of male terminalia. Fig. 14 - extended aedeagus. Fig. 15 - lateral view of female terminalia. Fig. 16 - dorsal view of circum-anal ring in female.

(forceps or claspers) held parallel to proctiger bearing setae and a heavily sclerotized hook distally. Aedeagus (Fig. 14) normally geniculate, two jointed, largely folded within hypandrium bearing papilla at distal end through which ejaculatory duct opens. Female genitalia (Fig. 15) with proctiger and subgenital plate bearing long conspicuous setae, palps (dorsal valvulae- Muir, 1930) scored with lines radiating posteriorly from median anterior region. Circum-anal ring (Fig. 16) on anterior half of proctiger, roughly oval in shape comprising an inner ring of rectangular pores bounded by minute circular pores. Cuticle within circum-anal ring thin and folded, bearing anus anteriorly.

Holotype female, South Africa; Eastern Cape, Grahamstown, on Calodendrum capense. 24.i.1967 (V.C. Moran), deposited in Albany Museum, Grahamstown, South Africa. Slide preparation. Paratypes: same data as holotype. 10 slide preparations plus 10 males and 10 females in alcohol, in Albany Museum, Grahamstown, South Africa. 10 male and 10 female paratypes to be deposited in British Museum (Nat. Hist.) and National Collection of Insects, Plant Protection Research Institute, Pretoria, South Africa.

The assignment of P. calodendri to the genus Paurocephala Crawford, 1913 is problematical as this species has some features which seem alien to Paurocephala and other features which would indicate a close affinity to Camarotoscena Haupt, 1935. Also the situation with regard to these two genera is confused as Dobreanu and Manolache (1962) and Klimaszewski (1963) regard Camarotoscena as a subgenus of Paurocephala while Heslop-Harrison (1952) and Vondrâcek (1963) regard it as a valid genus. Further, most authors consider the genus *Agonoscena* Enderlein, 1914 to be synonymous with *Paurocephala* while Heslop-Harrison (1952) regards *Agonoscena* as a distinct genus which he suggests is "not wholly distinct" from *Camarotoscena*. The distinctions between these closely related genera are not clear and *Paurocephala* itself is not a clearly demarcated genus which makes it necessary to discuss certain features of *P. calodendri* and indicate the relationship of this species to these genera.

Firstly the head of *P. calodendri* has most of the features of the genus *Paurocephala* but mention must be made of the genae. Crawford (1913) in his original description of *Paurocephala* does not mention the genae specifically although he does say "lobes or cones wanting" which presumably refers to the genae. In a later paper by Crawford (1914) however, the genae are used as diagnostic characters in keying out *Paurocephala* and here the genae are mentioned as forming, together with frons and vertex, "a relatively smooth surface" on the head; in the same paper, however, the genae are described as "not conical, though often swollen". The genae in *P. calodendri* seem to fit the latter description in that they are rounded and swollen and it must be concluded therefore, that this character allows inclusion of this species in the genus *Paurocephala*. With regard to the thorax, Heslop-Harrison (1952) has emphasised the importance of the "horn-like metascutellar epiphysis" as a diagnostic character in "true representatives of the genus *Paurocephala*". This feature is also mentioned by Crawford (1913) in his original description of the genus. In *P. calodendri* the metascutellum is well developed but is only slightly swollen dorsally. In *P. gossypii* Russell, 1943 and *P. urenae* Russell, 1946, however, the metascutellar tubercle is apparently similar to that in P. calodendri being small and rounded and it would seem therefore that this is a variable character for the genus in its present sense. The legs are not useful in placing P. calodendri although there are no sub-apical meso-tibial combs of hairs the absence of which, according to Eastop (1961), would indicate an affinity to Paurocephala. The fore wings in P. calodendri have a venation and texture typical of Paurocephala and in this genus R_1 is divided with a distinct cell formed by R_{1a} and R_{1b} (Heslop-Harrison, 1952) which is true for P. calodendri. Haupt (1935) distinguishes between Camarotoscena and Agonoscena (synonymous with Paurocephala according to most later authors) in that the former have the fore wings broadened apically and almost all the veins running parallel to the margin of the wing while in the latter genus the fore wings are not broadened apically and the veins are not parallel to the margin. In P. calodendri the fore wings are broadened apically but the wing veins are not as straight or parallel as in Camarotoscena speciosa (Flor) the wings of which are figured by Dobreanu and Manolache (1962) and Haupt (1935). It is also interesting to compare the venation of the fore wings in P. calodendri with that of Camarotoscena sp. Vondrâcek, 1963 as the two appear very similar except for Rs which is more convex in P. calodendri. This might indicate that the venation in P. calodendri is intermediate between that in Camarotoscena and Paurocephala. This similarity in wing venation however, is probably to be regarded as taxonomically superficial as there are several other clear differences between P. calodendri and Camarotoscena sp.. Heslop-Harrison (1952) regards the nodal line in the fore wings as of doubtful generic significance but points out that this line is best developed in Camarotoscena and less so in Agonoscena while only being present in certain species of *Paurocephala* (listed by Heslop-Harrison, 1951a). The nodal line is absent in *P. calodendri* and this may be regarded as another point of similarity with the latter genus. Lastly the abdomen of *P. calodendri* provides few clues as to the systematic position of this species. The genitalia and aedeagus of the male in *P. calodendri* and the genitalia and circum-anal ring of the female show a superficial similarity to the structures in *Camarotoscena speciosa* as figured by Dobreanu and Manolache, (1962) but the significance of this is uncertain.

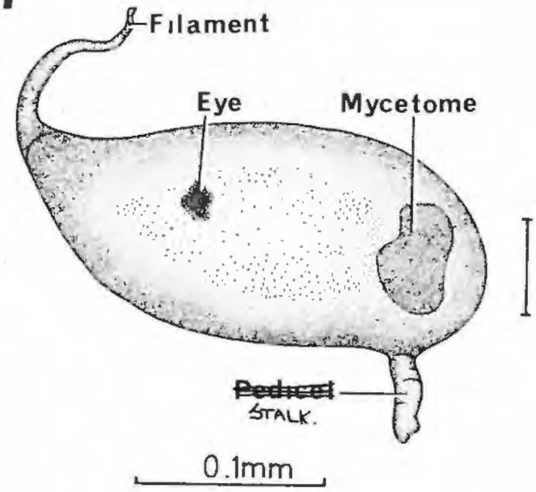
The Cape chestnut psyllid has numerous features in common with *Paurocephala* which allows its inclusion in this genus while it retains strong affinities to the genus *Camarotoscena*. There is little doubt, however, that the genus *Paurocephala* and its closely related genera are in need of revision.

I am very grateful to Professor L.D. Tuthill (University of Hawaii, Honolulu. Hawaii) and to Miss L.M. Russell (Entomological Research Division, United States Department of Agriculture, Washington. D.C.) for their comments on specimens of *P. calodendri* which they have examined. Their conclusions about this species were communicated to me through Mr. A. L. Capener (Plant Protection Research Institute, Pretoria, South Africa) and both these workers are agreed that the specimens of *P. calodendri* in their possession show affinities to both the genus *Paurocephala* and *Camarotoscena*.

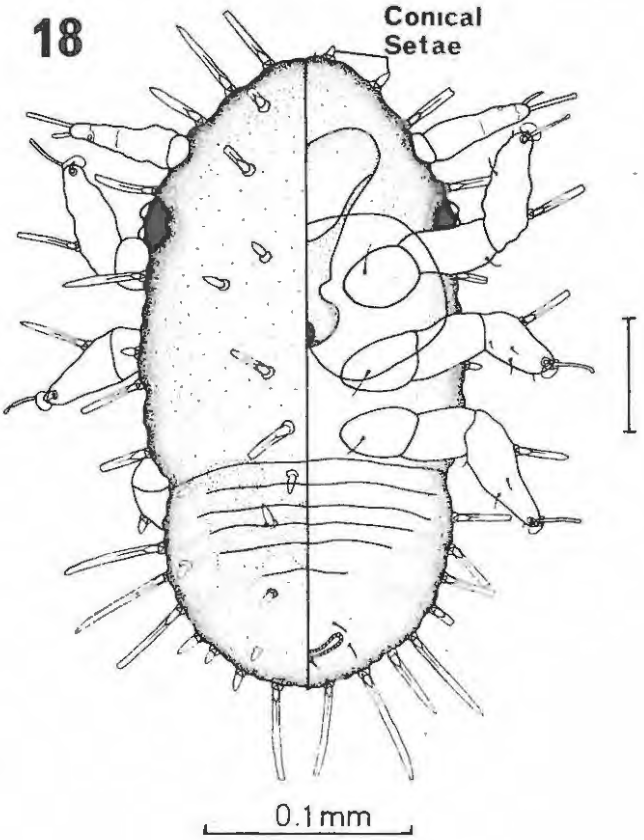
Developmental History of P. calodendri.

Adults of *P. calodendri* were enclosed in perforated plastic bags on *Calodendrum capense* seedlings in the environment room.

17



18

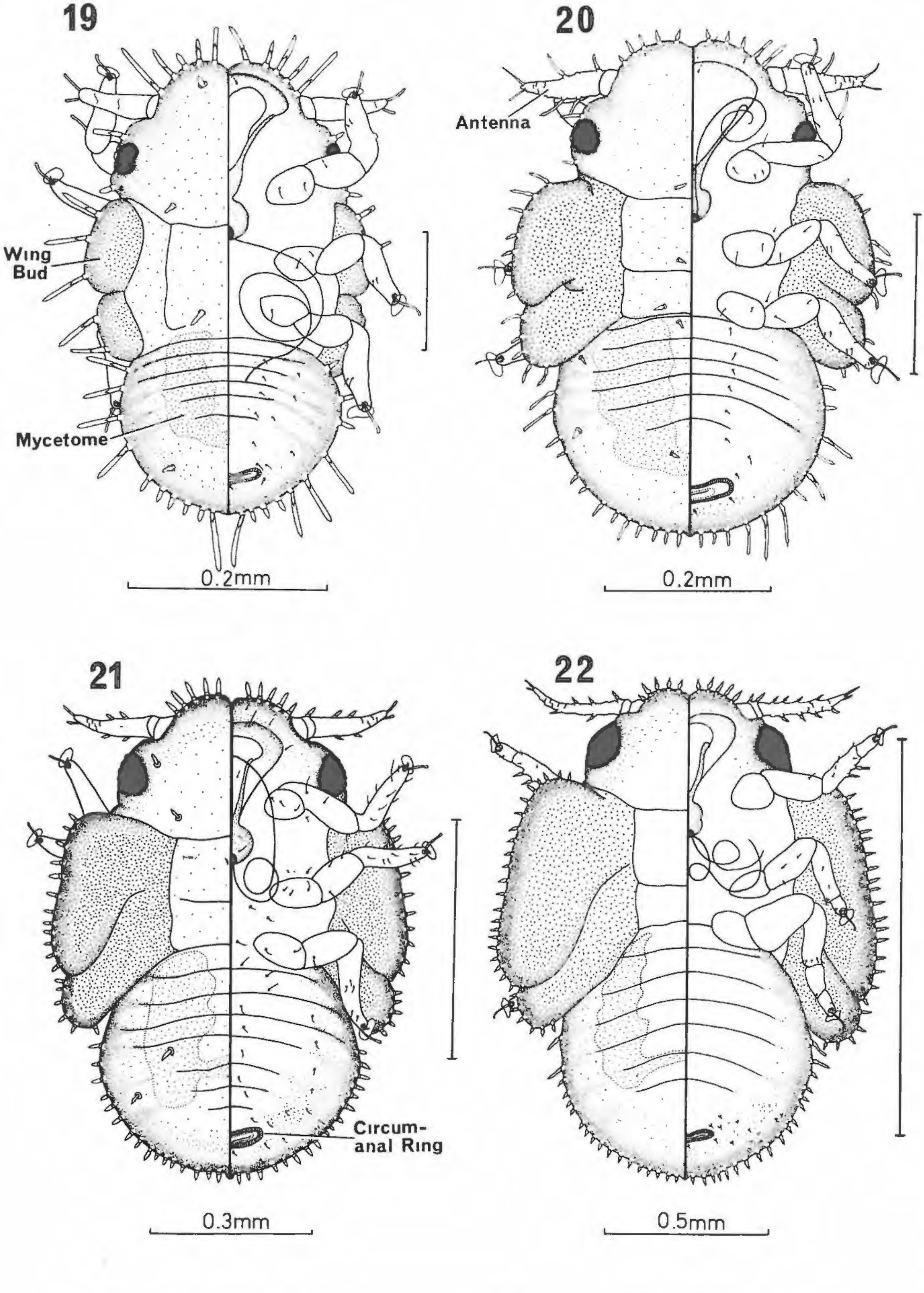


Figs. 17 - 18 Egg and first instar nymph of Paurocephala calodendri. Fig. 17 - lateral view of egg. Fig. 18 - first instar nymph, the left half in dorsal view and the right half in ventral view. These figures may be compared with Figs. 19 - 22 which are drawings of the other immature stages. The scale, vertically and to the right of each figure, is drawn 100X the size of the insect.

The females were allowed to lay eggs for 24 hours after which they were removed. The lowest temperature regime (Fig. 6a) was used first. The hatching times of the eggs were noted and maps drawn to show the positions of the first instar nymphs after they had settled down and started to feed on the leaves. In this way the progress of each individual psyllid was followed from the time of hatching until adult emergence.

Newly emerged females of P. calodendri mated two or three days after emergence and laid eggs within a week. Adult males and females lived for 30 - 45 days although unmated females lived for 60 - 70 days. During their life time, fertilized females laid a mean number of 838 eggs with a minimum of 470 and a maximum of 1228. These data are based on records from ten females. Unmated females became distended with eggs during their life but would lay only a few eggs none of which ever hatched. The egg of P. calodendri (Fig. 17) has a smooth chorion which is almost transparent, through which the eyes and mycetome area of the developing embryo can be seen. (The mycetome is discussed more fully under the biology of Trioza erytreae). The egg has a conspicuous anterior filament of variable length and is attached to the host plant by a posterior stalk or pedicel. The colour of the egg is variable, depending on its maturity. The newly laid egg is off-white to pale yellow becoming a dark lemon yellow as it matured.

Invariably in the Psyllidae there are five nymphal instars all of which are markedly dorso-ventrally flattened. In this account descriptions of the nymphs of P. calodendri were based on animals mounted in lactophenol (Ossiannilsson, 1966) except where



Figs. 19 - 22 Immature stages of *Paurocephala calodendri*. Fig. 19 - second instar nymph. Fig. 20 - third instar nymph. Fig. 21 - fourth instar nymph. Fig. 22 - fifth instar nymph. In each case the left half of the nymph is drawn in dorsal view and the right half in ventral view. These figures may be compared with Figs. 17 - 18. The scale, vertically and to the right of each figure, is drawn 100X the size of the insect.

colouration was noted in which case living insects were used.

On eclosion the first instar nymphs (Fig. 18) wandered about the leaf before settling on the under surface, usually close to one of the leaf veins. After settling they inserted their mouth parts and, if conditions were favourable, remained in the same position for the rest of their nymphal life. The first instar nymphs are very pale straw yellow in colour and have, characteristically, large heads which are not clearly demarcated from the thorax. Wing buds are not developed and the body is fringed with filaments arising from thick conspicuous conical setae. The filaments often became detached leaving the conical setae at their bases. Ossiannilsson (1965) has categorized the different spines in some psyllid nymphs but the spines of P. calodendri do not readily fit his scheme. There are 14 - 16 conical setae spaced around the periphery of the abdomen and this number is constant for all first stage nymphs. The number and arrangement of conical setae on the dorsum, however, is very variable and they are sometimes absent. On the ventral surface there are slender setae which are always in the same position around the circum-anal ring but are variable in other positions. The circum-anal ring of the first stage nymph characteristically has 42 pores in the outer ring.

The second instar nymph (Fig. 19) is usually pale straw yellow. The small colourless wing buds have minute tubercles visible on their surface. Dark sclerotized areas are visible dorsally on the body in the living insect. There is a variable number of conical setae on the dorsal surface but there are always 20 - 22 such setae arranged around the periphery of the abdomen.

The ventral setae are typically in the positions indicated in figure 18 and the circum-anal ring has 56 pores in the outer ring.

The <u>third instar nymph</u> (Fig. 20) varies in colour according to age from pale straw yellow to dark straw yellow. This stage is very similar in appearance to the second instar except for size (Table 3) and for the slightly larger wing buds. There are 24 - 28 conical setae arranged around the periphery of the abdomen with a variable arrangement of ventral setae. Circum-anal ring has 76 - 78 pores in the outer ring, with the inner ring of minute circular pores now easily visible.

The <u>fourth instar nymph</u> (Fig. 21) is usually dark straw yellow overlaid with dark sclerotized areas. This stage is distinguished by size and by the 32 - 36 conical setae around the periphery of the abdomen. The circum-anal ring has 96 - 98 pores in the outer ring with a clear inner ring of minute circular pores.

The <u>fifth instar nymph</u> (Fig. 22) is noticeably larger than the fourth stage nymph and is variable in colour although the dorsal surface is straw yellow to dark yellow. The wing buds and head are a much darker straw yellow. The dorsum is overlaid by dark sclerotized areas of dark grey or green while the ventral surface of the abdomen is green. The mycetome is clearly visible through the integument and the eyes as in other instars are dark red. There are 38 - 40 conical setae around the periphery of the abdomen and 138 - 140 pores in the outer circum-anal ring. Adult structures are visible through the nymphal cuticle at the conclusion of the instar.

The effects of temperature on development.

Nymphs of Paurocephala calodendri were reared on Calodendrum capense seedlings at the lowest, median and highest temperature regimes (Fig. 6). In each experimental series batches of nymphs were reared on at least six, apparently healthy, seedlings. Each nymph, during its development, was measured daily and individual records were obtained of instar durations and size increases at the moult and inter-moult periods. From these data, means and standard errors were calculated using an I.C.T. 1300 computer. Two programs were prepared for this machine. Means and standard errors were calculated with the one program and with the other all data points more than two standard deviations from the mean were rejected and the same calculations performed on the corrected data. In practice only the former program was run because with the large numbers of insects measured and with the very small spread around the mean, the latter program made very little difference to the calculations.

No differences were found in the sizes of P. calodendri nymphs reared at the lowest and median temperature regimes. On the other hand a comparison of sizes of the insects at the highest and lowest temperature regimes (Tables 3 and 4 and Figs. 23(a) and 23(b)) shows that insects reared at the highest temperature were significantly smaller than those at the lowest temperature regime. Both the eggs and the first stage nymphs at these two temperature regimes were the same size but at the highest temperature the psyllids became progressively more stunted during development.

These results suggested that the sizes of individuals of

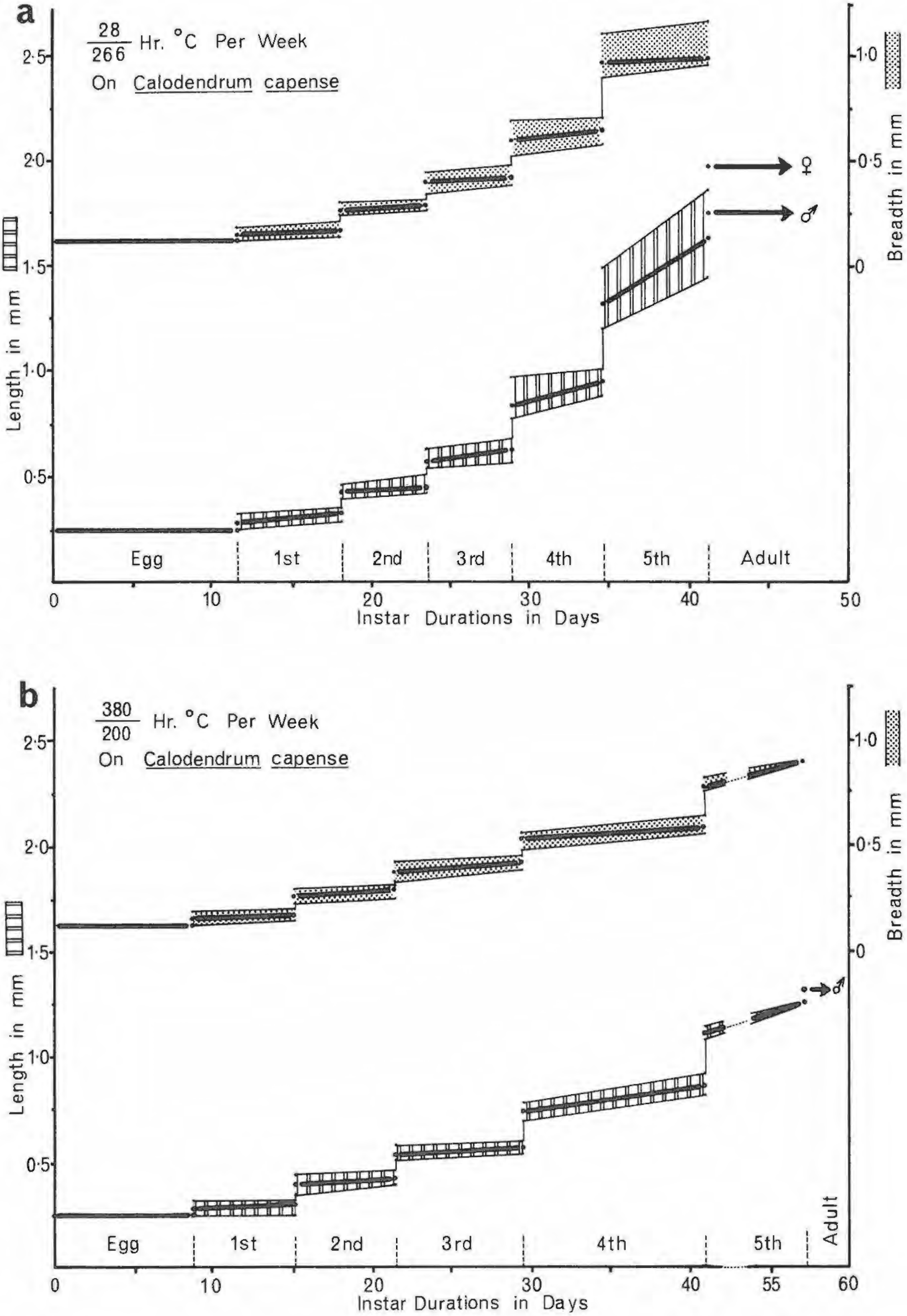


Fig. 23 Lengths and breadths of the developmental stages in Paurocephala calodendri plotted against instar durations. Size limits of the insects in each instar are represented by the thin lines on either side of the thick line which indicates mean size. Fig. 23 a - development at the lowest temperature regime. Fig. 23 b - development at the highest temperature regime.

Table 3 Lengths and breadths (in mm) of the eggs, adults and each of the five nymphal instars of Paurocephala calodendri at the start and end of each stage. The animals were reared at the lowest temperature regime of 28 Hr°C/ week above and 266 Hr°C/week below 20°C.

Length at start of instar.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	ADULT Male	ADULT Female
NUMBER OF READINGS	30	93	54	47	36	31	8	7
MINIMUM	0.25	0.25	0.38	0.53	0.78	1.19	1.75	1.81
MAXIMUM	0.25	0.33	0.46	0.63	0.97	1.50	1.88	2.13
MEAN	0.25	0.29	0.43	0.58	0.85	1.32	1.77	1.99
STANDARD ERROR	-	0.001	0.002	0.004	0.007	0.014	0.029	0.04
Length at end of instar.								
NUMBER OF READINGS	-	57	47	37	32	30	-	-
MINIMUM	-	0.28	0.44	0.56	0.88	1.44	-	-
MAXIMUM	-	0.34	0.51	0.69	1.08	1.88	-	-
MEAN	-	0.32	0.45	0.63	0.95	1.63	-	-
STANDARD ERROR	-	0.002	0.002	0.004	0.010	0.016	-	-
Breadth at start of instar.								
NUMBER OF READINGS	30	93	54	47	36	31	8	7
MINIMUM	0.13	0.13	0.25	0.34	0.54	0.91	0.53	0.63
MAXIMUM	0.13	0.19	0.31	0.46	0.71	1.13	0.75	0.75
MEAN	0.13	0.16	0.29	0.42	0.62	0.99	0.60	0.65
STANDARD ERROR	-	0.001	0.002	0.004	0.007	0.010	0.024	0.017
Breadth at end of instar.								
NUMBER OF READINGS	-	57	47	37	32	30	-	-
MINIMUM	-	0.16	0.28	0.38	0.58	1.00	-	-
MAXIMUM	-	0.21	0.33	0.51	0.72	1.19	-	-
MEAN	-	0.18	0.30	0.44	0.66	1.10	-	-
STANDARD ERROR	-	0.002	0.002	0.004	0.006	0.011	-	-

Table 4 Lengths and breadths (in mm) of the eggs, adults and each of the five nymphal instars of *Paurocephala calodendri* at the start and end of each stage. The animals were reared at the highest temperature regime of 380 Hr°C/week above and 200 Hr°C/week below 20°C.

Length at start of instar.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	ADULT Male	ADULT Female
NUMBER OF READINGS	30	93	85	50	8	3	1	-
MINIMUM	0.25	0.25	0.34	0.51	0.69	1.08	1.31	-
MAXIMUM	0.25	0.33	0.44	0.58	0.78	1.13	1.31	-
MEAN	0.25	0.29	0.40	0.54	0.75	1.11	1.31	-
STANDARD ERROR	-	0.001	0.002	0.003	0.009	0.014	-	-
Length at end of instar.								
NUMBER OF READINGS	-	48	50	19	3	1	-	-
MINIMUM	-	0.25	0.38	0.54	0.81	1.25	-	-
MAXIMUM	-	0.31	0.46	0.59	0.92	1.25	-	-
MEAN	-	0.30	0.42	0.57	0.87	1.25	-	-
STANDARD ERROR	-	0.002	0.002	0.003	0.03	-	-	-
Breadth at start of instar.								
NUMBER OF READINGS	30	93	82	51	7	3	1	-
MINIMUM	0.13	0.13	0.22	0.31	0.47	0.78	0.54	-
MAXIMUM	0.13	0.19	0.29	0.42	0.54	0.81	0.54	-
MEAN	0.13	0.16	0.26	0.38	0.52	0.79	0.54	-
STANDARD ERROR	-	0.001	0.002	0.003	0.01	0.01	-	-
Breadth at end of instar.								
NUMBER OF READINGS	-	47	49	19	3	1	-	-
MINIMUM	-	0.16	0.25	0.38	0.56	0.88	-	-
MAXIMUM	-	0.18	0.29	0.44	0.63	0.88	-	-
MEAN	-	0.17	0.28	0.41	0.59	0.88	-	-
STANDARD ERROR	-	0.002	0.002	0.003	0.018	-	-	-

P. calodendri in a population could be used as an index of thermal stress in these animals at the limits of their geographical ranges. To ascertain whether local field populations of *P. calodendri* differ significantly in size from those reared under artificial conditions in the environment room, field samples were collected and the lengths and breadths of a number of psyllids in each stage were measured. Thirty eggs, 50 of each of the nymphal stages and 67 adults were measured in this analysis and the results are shown in Table 5.

Table 5 Measurements (in mm) of individuals of *P. calodendri* from a field population collected on the 4th February 1967.

Lengths.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	ADULT Male	ADULT Female
NUMBER OF READINGS	30	50	50	50	50	50	34	33
MINIMUM	0.21	0.25	0.39	0.53	0.72	1.13	1.44	1.56
MAXIMUM	0.27	0.33	0.47	0.64	0.98	1.64	1.95	2.28
MEAN	0.24	0.28	0.42	0.59	0.84	1.27	1.68	2.04
STANDARD ERROR	0.003	0.003	0.003	0.004	0.007	0.014	0.023	0.030
Breadths.								
NUMBER OF READINGS	30	50	50	50	50	50	34	33
MINIMUM	0.10	0.14	0.25	0.37	0.51	0.84	0.49	0.55
MAXIMUM	0.12	0.18	0.29	0.47	0.68	1.13	0.66	0.72
MEAN	0.11	0.16	0.28	0.41	0.61	0.96	0.58	0.65
STANDARD ERROR	0.002	0.002	0.002	0.003	0.005	0.009	0.062	0.061

Before comparing the data in Table 5 with those from laboratory populations it must be recalled that with the populations reared in the laboratory, measurements were made at the start and end of each instar.

This was obviously not possible with the field population. Comparisons can be made only on the assumption that insects in all stages of the moult were sampled in the field population and that the measurements obtained fall between those at the start and end of the instar.

The measurements show that the psyllids from the field sample were larger than those reared at the highest temperature regime in the laboratory, but smaller than those reared at the lowest temperature regime. These differences were most marked in the later instars. In fact there was a close agreement between the sizes of psyllids from the field and that of laboratory reared psyllids at the start of the instar at the lowest temperature regime. This information suggests that the animals, collected from the field, were subjected to thermal influence which resulted in smaller psyllids. The extent of thermal stress was however, not as severe as that inflicted on the insects at the highest temperature regime in the environment room. This conclusion is supported by a comparison of the temperature summations in the field and those at the highest temperature regime in the laboratory. The insects in the field samples were collected on the 4th February 1967. The temperature summations for the preceding two months were on the average 348 Hr°C per week above 20°C and 245 Hr°C per week below 20°C as compared with 380 Hr°C per week and 200 Hr°C per week respectively at the highest temperature regime in the environment room. Thus the environment room was effectively hotter and resulted in smaller specimens of P. calodendri than those in the field population. The latter, however, were smaller than the psyllids reared at the lowest temperature regime. An important point to note is that psyllids from the field were of comparable size to those reared in the laboratory. This is a good indication that the individuals reared in the environment room did not comprise an exceptional population.

The influence of the three temperature regimes on instar durations in P. calodendri is compared in Tables 6, 7 and 8. The differences in instar durations shown by populations reared at the lowest and highest temperature regimes are also shown diagramatically in figures 23(a) and (b).

Tables 6, 7 and 8 show clearly that the median temperature regime was more favourable for the development of the immature stages of P. calodendri than either the lowest or highest temperature regimes. At the median temperature regime the rate of development was increased while, by comparison, development rates at the highest and lowest temperature regimes are retarded. The most drastic retarding in development rate was found at the highest temperature regime although egg development times were reduced at this temperature. At the median temperature regime the instar durations in all stages showed very little variation (as expressed by the small standard errors). The variation was greater at the highest and lowest temperature regimes suggesting again that the median temperature regime was more favourable for the development of P. calodendri.

A comparison of instar durations of the psyllids at the lowest temperature regime (table 6) with those at the median temperature regime (table 7) can be made. Firstly there was an 8.6% decrease in development time of the eggs at the median temperature regime. Secondly there was a 34.4% decrease in the duration of the first

Table 6. Instar durations (in days) of Paurocephala calodendri at the "lowest" temperature regime of 28 Hr°C per week above and 266 Hr°C per week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	TOTAL
NUMBER OF READINGS	91	52	43	32	27	23	24
MINIMUM	9	5	3	2	4	5	34
MAXIMUM	12	8	10	9	12	9	47
MEAN	11.6	6.4	5.6	5.3	5.8	6.6	40.04
STANDARD ERROR	0.087	0.092	0.216	0.236	0.343	0.215	0.760

Table 7. Instar durations (in days) of Paurocephala calodendri at the "median" temperature regime of 160 Hr°C per week above and 230 Hr°C per week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	TOTAL
NUMBER OF READINGS	182	80	65	54	31	23	22
MINIMUM	9	3	2	3	2	4	27
MAXIMUM	12	6	5	6	5	7	32
MEAN	10.6	4.2	3.4	3.9	3.3	4.9	29.1
STANDARD ERROR	0.066	0.069	0.071	0.095	0.117	0.160	0.254

Table 8. Instar durations (in days) of Paurocephala calodendri at the "highest" temperature regime of 380 Hr°C per week above and 200 Hr°C per week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	TOTAL
NUMBER OF READINGS	179	97	54	15	3	1	1
MINIMUM	8	4	4	7	9	12	48
MAXIMUM	11	12	13	18	12	12	48
MEAN	8.8	6.3	8.2	11.5	10.3	12.0	48.0
STANDARD ERROR	0.051	0.163	0.291	0.861	0.882	-	-

instar, and a 39.3%, 26.4%, 43.1% and 25.8% decrease in duration in the second ~~and~~ To fifth instars respectively. The decrease in total development time was 27.3%. On the other hand a comparison of the durations at the lowest temperature regime (Table 6) with those for the highest temperature regime (Table 8) shows that development of eggs was 24.1% faster at the highest temperature regime. Development of first stage nymphs was also slightly faster, but development of second to fifth stage was 31.7%, 53.9%, 43.6% and 45.0% slower respectively. The increase in total development time from egg to adult at the highest temperature regime was 16.7%.

An analysis of mortalities during the experimental period at each of the three temperature regimes confirmed that the median temperature regime was the most favourable for development in P. calodendri. This analysis is summarized in Table 9. Total mortalities at any one temperature include deaths and losses. Deaths were recorded when the dried corpse of the insect was found on the plant and a loss recorded when the animal was lost but the corpse not found. When this occured it was assumed that the insect had died, dried up and blown away. It could not simply have moved to another part of the plant because the leaves were always thoroughly searched.

Table 9. Mortalities in the immature stages of Paurocephala calodendri which were reared at three different temperature regimes.

TEMPERATURE REGIME	NUMBERS OF READINGS	"LOSSES"	DEATHS	TOTAL DEATHS AND LOSSES
"LOWEST" $\frac{28}{266}$ Hr°C/Week	123	45%	15%	60%
"MEDIAN" $\frac{160}{230}$ Hr°C/Week	97	49%	6%	55%
"HIGHEST" $\frac{380}{200}$ Hr°C/Week	127	56%	44%	100%

Table 9 shows that the smallest percentage mortality recorded (55%) was at the median temperature regime. Sixty percent mortality was recorded at the lowest temperature regime and 100% at the highest. An analysis of the original data show that 50% of all the mortalities were recorded during the moult period at all temperature regimes. The moult period is very much shorter than the inter-moult period and this fact would indicate that death due to desiccation while the insects were moulting was the major cause of mortality. When the corpses of these insects were found they were always completely shriveled and dry which supports this suggestion.

It is also suggested that the detrimental effects noted at high temperatures could be due mainly to the effects on the host plant and to a lesser extent to some physiological action on the insect itself. At the three temperatures tested, the duration of the egg stage was progressively and proportionately decreased as the temperature rose. Thus the average egg duration at the lowest temperature regime was 11.6 days while at the median and highest temperature regimes it was 10.6 and 8.8 days respectively. This is in contrast to the effect of the highest temperature regime on the nymphal stages where instar durations were prolonged. Although the seedlings, on which the psyllids were reared, at the highest temperature regime were adequately watered they tended to be flacid. It is possible that the condition of the host plant could have affected the instar durations and sizes of the insects.

Wearing and Van Emden (1967) and Wearing (1967) have reported the effects of water stress in host plants on infestation by aphids. Water stress in the host plants produces conflicting effects; in some aphid species the resultant nitrogen concentration increase results in an increase in fecundity, while in other aphids the lack of phloem turgor pressure has an adverse effect on reproduction. It is interesting to speculate whether P. calodendri is also reliant on phloem turgor pressure in the plant for adequate nutrition and Wearings' concluding remarks are relevent in this respect:-

> "It is important to note, however, that lower phloem turgor pressure may be more important in reducing the duration and/or frequency of feeding by the aphids (increasing restlessness) than in directly reducing the rate of ingestion of sap, though the latter may be a causal mechanism of the former; in addition, other host plant factors, such as cell carbohydrates, minerals and pH, may have made an important contribution to the results".

P. calodendri nymphs reared at the highest temperature regime also showed an "increased restlessness" and often wandered about the plant. This wandering obviously decreased feeding frequency and probably prolonged instar durations. It may also have contributed to the over all mortality at this temperature as there was a greater chance of the psyllids being blown off the leaves or dying of desiccation. Further it was observed that at the highest temperature regime the production of lumps of faeces by the nymphs was greatly reduced. This might indicate the nymphs were receiving less nutrients from the host plant. All these considerations suggest that high temperatures were having an indirect effect on P. calodendri nymphs through the host plant.

Field Observations on the Immature Stages of P. calodendri.

Field observations on populations of Paurocephala calodendri and of the major parasite of this psyllid, Tetrastichus sp., were made to verify the conclusions drawn from the laboratory studies. The field work was conducted in two phases. Firstly, leaf samples were collected and records kept of the numbers of immature psyllids and parasites. Secondly sticky impact traps were used to capture adult P. calodendri and parasites. ~~These~~ These aspects are dealt with separately and over all conclusions about population fluctuations in P. calodendri are left until the discussion.

The fluctuations in numbers of nymphs of P. calodendri in a field population were studied to ascertain the response of this population to environmental conditions, particularly temperature. A survey of a natural population of P. calodendri nymphs was started in September 1965, about three weeks after the selected Cape chestnut tree had obtained its first seasonal flush of leaves, and continued until all the leaves had dropped about ten months later. The tree from which leaf samples were taken was the same one in which the thermo-hygrograph (T_2) was positioned (Fig. 1). The climatic data which have already been discussed cover the period of this survey.

(i) Sampling methods.

The initial problem in any survey of this sort is whether to sample from one tree or to sample from several trees and pool the results. The decision will depend on the labour available for the survey and in this case it was found to be impossible to sample adequately from more than one tree. Leaves from one Calodendrum capense tree were therefore sampled and it may be argued that this type of destructive sampling will eventually give a biased result. This may well be, but under the circumstances the greatest number of leaves that could be effectively examined had to be the criterion of sample size even though, as will be pointed out later, this sample

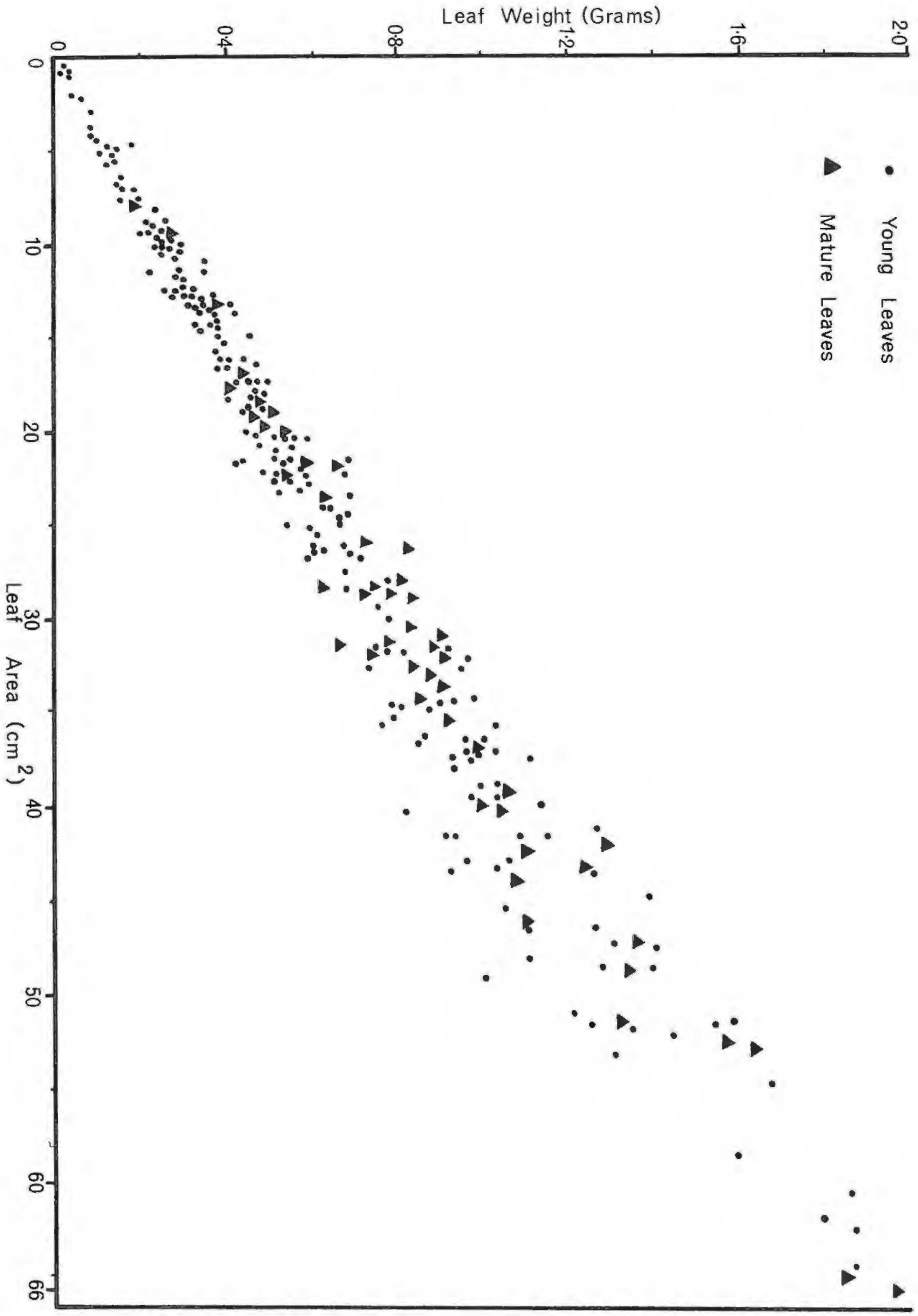


Fig. 24 Weight of mature and young leaves from *Calodendrum capense* plotted against leaf area.

was not large enough to allow the subsequent application of meaningful statistical methods. However, this shortcoming did not obscure several clear trends which emerged from the survey.

Another problem was the need to ensure a consistent sample size throughout the survey period. It was obviously unrealistic to collect a known number of leaves each week because the leaves varied in size as the season progressed. The relationship between leaf surface area and weight was therefore investigated.

Each C. capense leaf from a sample of 250 leaves was weighed and its surface area measured using a polar planimeter. (It was found that area in Cape chestnut leaves was approximately equal to two thirds of the breadth multiplied by length). The sample comprised two groups, one of 200 leaves from a tree that had just come into leaf and another group of 50 leaves from a tree which was about to shed its old leaves. Weights and surface area measurements from these leaves are represented in figure 24. The figure shows that, for the practical purposes of the survey, there was a linear relationship between weight and surface area and that this relationship remained reasonably constant in spite of the age of the leaves. This justified the employment of weight as a criterion of sample size. Using weight of leaves to determine sample size considerably expedited the procedure.

Weekly samples of 100 grams of leaves were taken. Each sampled comprised about 200 leaves with a total average surface area of 3,834 square centimeters (25.66 square centimeters per leaf). This sample could be surveyed by one observer in about eight hours depending on the numbers of psyllids present. In taking a sample of 100 grams of leaves, allowance was made for the weight of the plastic bags in which the leaves were collected and also for the weight of the stalks on the leaves. The former weighed 5 grams and the latter (200 stalks) weighed 4.9 grams, and to compensate for this 110 grams of leaves were collected for each sample. Another complicating factor was the large difference in weight made by moisture on the leaves. Weighed leaves were sprayed with water to simulate dew, shaken to remove water, and reweighed. The reweighed leaves weighed from 50 - 60 grams more per sample. When air dried they returned to approximately their original weight. During this survey the leaves were therefore, allowed to dry off before weighing.

It is also necessary to consider whether the weekly sample of 100 grams of leaves was adequate. In practice the leaves for the survey were collected haphazardly. This must have introduced some bias because it was difficult to collect from the highest outer leaves of the tree but this was not a serious objection to the sampling technique. To determine the statistical validity of the sampling methods, ten samples of 100 grams of leaves were collected from one tree at the same time and the numbers of eggs and individuals of P. calodendri on the upper and lower surfaces of the leaves were recorded. In addition a record was kept of the numbers of P. calodendri which were parasitized, and those which were dead and "dry". Those which were dead but not dry were designated as "other". The ten samples were examined by four observers who took three days to complete the survey. Only one sample was examined at a time while the other samples were kept in a refrigerator which prevented the psyllids from changing instar. The numbers of psyllids and parasites recorded in these ten samples are shown in table 10.

Table 10. The variation in numbers of individuals of P. calodendri recorded from ten samples.

VARIATE SAMPLE NUMBER	1st In-star	2nd In-star	3rd In-star	4th In-star	5th In-star	ADULTS	EGGS	PARA-SITES	DRY	OTHER
1.	198	104	99	107	86	12	455	4	61	15
2.	145	88	115	122	129	11	1309	12	56	14
3.	106	131	119	103	89	14	650	3	54	18
4.	99	86	101	108	114	10	679	8	53	15
5.	112	85	107	115	112	16	888	25	56	28
6.	47	104	92	124	126	7	746	12	35	23
7.	226	74	135	159	159	12	1042	9	54	18
8.	100	113	136	110	70	6	780	14	44	16
9.	93	103	106	114	94	13	600	16	44	19
10.	89	79	86	107	103	5	507	6	37	7

A statistical analysis of the data from table 10 is given in table 11. In table 11 the means of the ten variates are given for the ten samples together with the standard deviations and 95% confidence limits based on a single sample. (The 95% confidence limits were calculated for 9 degrees of freedom where t0.05 = 2.262 x standard deviation.)

Table 11 Means, standard deviations and 95% confidence limits for the variates in the ten samples which are recorded in table 10.

VARIATE	MEAN	STANDARD DEVIATIONS	95% CONFIDENCE LIMITS BASED ON A SINGLE SAMPLE
1st Instar	121.5	51.0	± 115.4
2nd Instar	96.7	16.6	± 37.5
3rd Instar	109.6	15.9	± 36.0
4th Instar	116.9	15.4	± 34.8
5th Instar	108.2	24.3	± 55.0
ADULTS	10.6	3.41	± 7.7
EGGS	765.6	244.7	± 553.0
PARASITES	10.9	6.19	± 14.0
DRY	49.4	8.35	± 18.9
OTHER	17.3	5.29	± 12.0

This analysis shows that in all cases the variation between the samples was large and that the confidence limits were very wide indeed. First instar nymphs, adults, eggs, parasites and "others" showed the greatest variation. The outcome was simply that the sampling method adopted in the survey, while giving an estimate of population trends, was not sensitive enough to allow meaningful statistical analysis of the results. The main reason for this lack of sensitivity is that the sample was not large enough. Not only was a very much larger sample inpracticable in terms of time required for the survey but with a larger sample the tree would have been rapidly denuded.

Another factor aggravating the problem was that psyllid adults laid hundreds of eggs together on a single tender leaf shoot and this eventually led to clumping of the nymphs on the leaves. The variation between samples was exaggerated because the nymphs were not equally distributed over the leaves. There was therefore no point in submitting the nymphal survey data to a multi-variate statistical analysis in which correlations between the numbers of psyllids and various factors in the abiotic environment might be shown. From the data in table 10, however, some interesting correlations did emerge.

Firstly, there was a very significant positive correlation between the numbers of fourth and fifth instar nymphs in all ten samples. A correlation of this sort would be expected and needs no further comment. Secondly there was a significant positive correlation between numbers of first stage nymphs and numbers of "dry" nymphs. This correlation suggested that it was the first stage nymphs which were mainly susceptible to death through desiccation and this was the impression gained when the samples were surveyed. No records were kept of the numbers of "dry" animals in each instar so that it is not possible to be more definite than this. Thirdly there was a significant positive correlation between the numbers of adults and the numbers of "dry" psyllids; this was most likely a chance correlation. Lastly, there was a significant positive correlation between numbers of parasites and numbers of "other" dead psyllids. This correlation is interesting and confirms a point in the biology of the parasites of P. calodendri which will be mentioned in detail later. These parasites often pierce the hosts with their ovipositors and haemolymph oozes from the wound before the animal dies. The majority of "other" dead P. calodendri nymphs were in this condition.

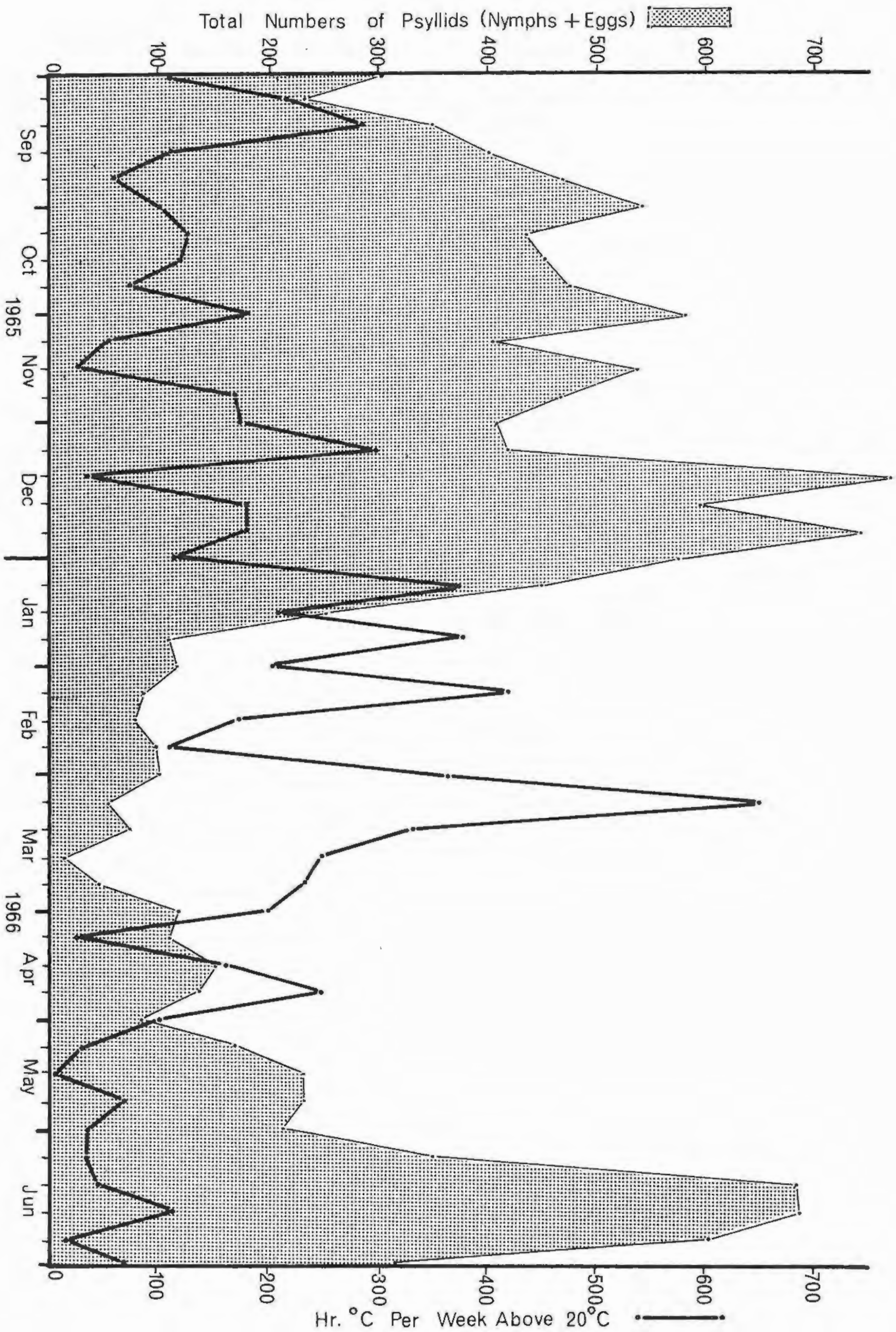


Fig. 25 Weekly totals of *Paurocephala calodendri* collected in a survey of immature stages between 1st September 1965 and 29th June 1966. The temperature summations in Hr °C per week above 20 °C during this period are also plotted.

(ii) Results.

Each leaf in the sample of 100 grams was examined on both surfaces using a dissecting microscope. The stages of P. calodendri present were noted, together with the numbers of animals which were parasitized. Of immediate relevance are the numbers of eggs and nymphs of P. calodendri which were recorded through the ten month survey period. These numbers are shown diagramatically in figure 25, together with the weekly field temperature summations above and below 20°C. Figure 25 shows a clear trend in the population fluctuations of P. calodendri from week to week. The total population was at a low level in September at the start of the survey. There were few psyllids in the later instars and the numbers recorded were made up mostly of eggs and early instar nymphs. There was a steady increase in the population during October and November with a peak at the end of December and the beginning of January. A very sharp decrease in population followed at the end of January and these low numbers were maintained until June when the population increased rapidly. The final sample was collected on the 29th June 1966 after which the last leaves fell from the tree.

If the temperature summations recorded in figure 25 are considered together with these population trends there appears to be an inverse relationship between the numbers of psyllids recorded in the weekly samples and the numbers of hour degrees centigrade per week above 20°C. Low temperature summations were recorded during the period from September to December when the psyllid population was highest, while in January, February and March there was a significant increase in temperature and a corresponding drop in the numbers of psyllids. Another drop in temperature from April onwards may have caused the second peak in psyllid numbers which had a climax in June.

The suggested inverse relationship between psyllid numbers and temperature summations can be seen more clearly if a few specific dates are considered. For example a sudden rise in temperature during the first week of November was followed by a decline in the numbers of psyllids recorded in the sample the next week. The increase in temperature in the second week of January was followed by a sharp fall in psyllid numbers and these numbers were probably kept at a low level while the high temperatures were maintained.. An extremely high average temperature during the second week of March might have caused the very low number of psyllids which were recorded two weeks later. The decrease in temperature during the second week of April was again followed by a rise in psyllid numbers the next week and the temperature rise during the last week of April may have led to a drop in psyllid numbers the following week. There were of course some cases where this simple inverse relationship was not shown. For example the sudden rise in temperature during the second week of December was followed by an increase in psyllid numbers the next week although there was a marked drop in numbers in this case two weeks later which might have been caused by the high temperatures.

It was evident that, when temperature summations recorded in the field were similar to the lowest and median temperature regimes in the environment room, the field population of P. calodendri thrived and increased. This result could have been predicted from the laboratory studies. At the highest temperature regime in the environment room there was a high mortality of psyllids. In the field when the number of hour degrees centigrade above 20°C was more than approximately 200 Hr°C per week the numbers of psyllids per sample decreased. In other words when the temperature summations recorded in the field approached those at the highest temperature regime in the environment room the psyllid population was very severely affected. These fluctuations of psyllid populations in the field may be further explained by reference to some laboratory observations.

It is envisaged that high temperatures in the field result in a decline in the condition of the chestnut tree; this decline is seen in a general "drooping" of the leaves during hot weather. This in turn leads to an increased number of psyllids wandering about on the leaves. Of the wandering nymphs a number will die of desiccation before finding an adequate food supply while others might simply be blown off the leaves in a sudden gust of wind. Also during periods of high temperature, as has been seen from the laboratory studies, mortality is increased, particularly during the moult periods, presumeably from desiccation. It is possible that mortality induced in these ways brought about the almost immediate decrease in psyllid numbers noted during periods of very hot weather. The rapid rise in populations of P. calodendri when the weather becomes cooler may also be explained if the laboratory studies are recalled. Eggs of P. calodendri were not adversely affected by high temperatures and there was no evidence to suggest that these temperatures resulted in mortality among the eggs. Also the adults were not adversely affected by high temperatures. Thus during short exposures of a few days to high temperatures eggs would continue to be laid. If

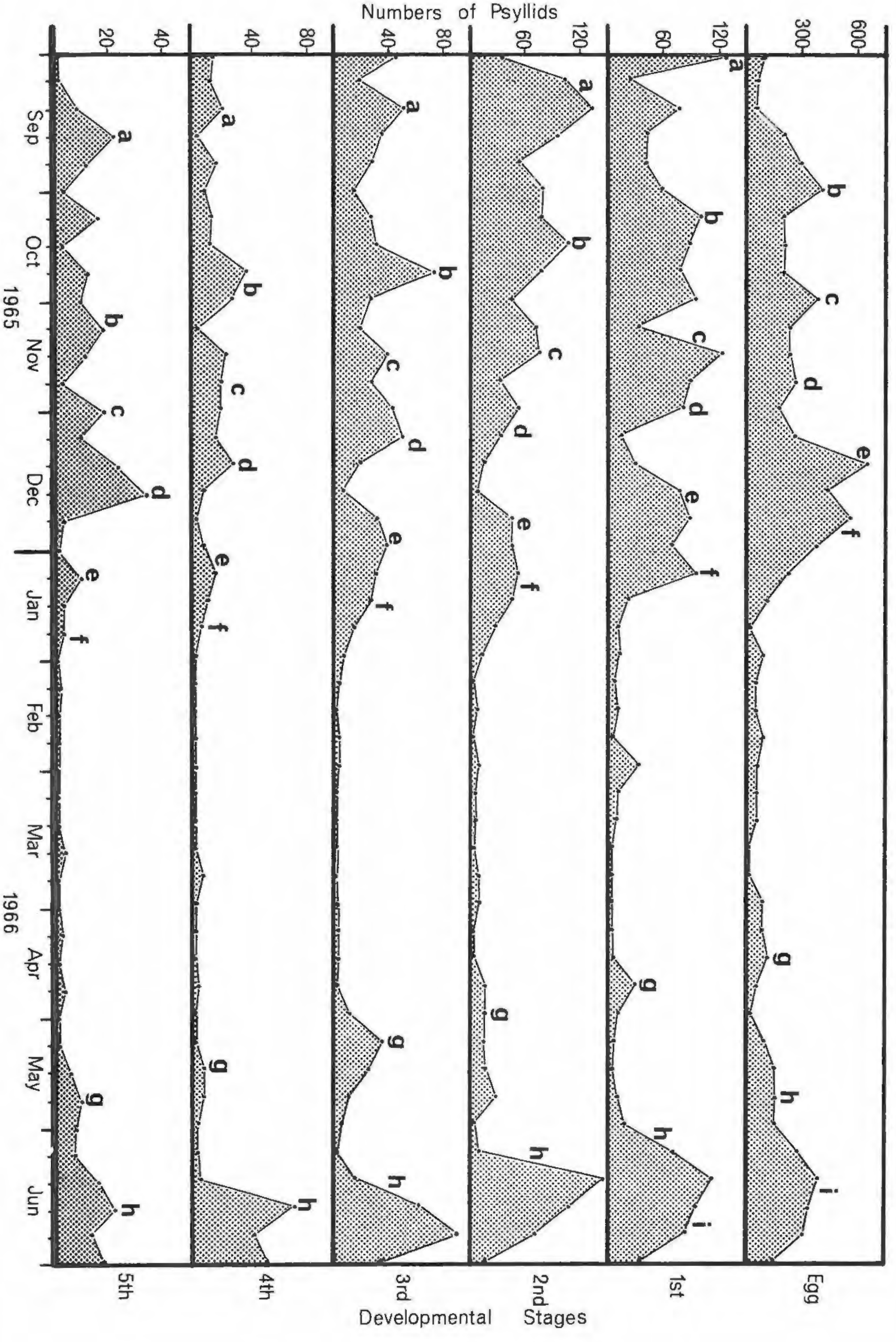


Fig. 26 Weekly fluctuations in numbers of Paurocephala calodendri collected in a survey of immature stages between 1st September 1965 and 29th June 1966. This figure is a more detailed analysis of the information shown in Fig. 25. For explanation of lettering see text.

high temperatures continue the eggs would hatch but a number of the first stage nymphs would be killed resulting in low population numbers. If on the other hand there was cool period most of the hatching first stage nymphs would survive resulting in an almost immediate increase in total psyllid numbers. This was reflected in the survey samples.

In figure 26 the relationship between the results obtained from the laboratory study of P. calodendri and those obtained from a field survey of this species are further emphasised. The data summed in figure 25 as total numbers of psyllids are separated in figure 26 and the numbers of eggs and all five nymphal stages of P. calodendri recorded in the survey are plotted separately against time. Each of these sub-totals (Fig. 26) reflects the same information about seasonal fluctuations as was evident from figure 25. Thus each reflects that there was a high population of psyllids from September until the middle of January, when, with the advent of very hot weather the numbers of animals in all stages decreased. The population recovered only at the end of May when the weather cooled down.

Of interest from figure 26, are the peak numbers of individuals in each stage which were evident throughout the survey period. Theoretically it could be expected that a peak in the number of eggs recorded during one particular week would result in an increase in the number of first stage nymphs in the survey sample collected one or two weeks following. If the laboratory data gained thus far are an approximation of what is likely to affect the population in the field, it should be easy to estimate the hatching times of eggs in the field, or the instar durations of the nymphs from the temperature summations recorded for any particular period. Thus progressive peaks of numbers could be followed from the egg to the fifth stage nymph. An attempt has been made to do this with the peaks of numbers in each stage recorded in figure 26. In each case a peak in the numbers of eggs has been chosen as a starting point and is identified with the letters from a - i.

An example is the peak of eggs "e" during the third week of December. During December there was an average of 176 Hr°C per week above 20°C (see table 2). This approximates with the median temperature regime in the constant environment room where there was a total of 160 Hr°C per week above 20°C. At this temperature in the environment room the egg duration was found to be 10.6 days (see table 7). A point may thus be plotted on the graph for first stage nymphs 10.6 days later than point "e". This point corresponds to a peak in numbers of first stage nymphs during that week and the week following. In a similar way a point was estimated for a peak in numbers of second stage nymphs, which, taking into account the December temperatures, would follow approximately 4.2 days later. This procedure was then repeated for the third fourth and fifth stage nymphs and the progress of the peak of eggs "e" could then be followed through each of the immature stages to the fifth instar. Figure 26 shows that these theoretically estimated points based on laboratory data coincide with the peaks of insects in various stages in the field survey. Thus it can be concluded that at any particular temperature regime, the instar durations of P. calodendri nymphs reared in the laboratory on potted seedlings correspond closely to those of nymphs in the field. An estimate can also be made of the number of generations per year in a natural population of P. calodendri on the assumption that the total development time required in the field (at any particular temperature) corresponds closely to that observed in the laboratory.

During the latter few months of the survey period the numbers of *P. calodendri* nymphs which were found on the upper and lower surfaces of the leaves were recorded. These results are combined with those obtained from the ten test samples (see table 10) where a similar record was kept and the analysis of these results is summarized in Table 12.

Table 12 The numbers of eggs and nymphs of *P. calodendri* recorded from the upper and lower surfaces of *Calodendrum capense* leaves. The numbers of eggs on the upper and lower surfaces of the leaf stalk are also recorded.

VARIATE	NUMBERS OF *P. calodendri*	PERCENTAGE OF TOTAL	TOTAL
Eggs - upper	4186	41.33	
Eggs - lower	5659	55.87	
Eggs - Upper stem	261	2.58	
Eggs - lower stem	22	0.22	10,128
1st instar - upper	51	2.94	
1st instar - lower	1682	97.06	1,733
2nd instar - upper	282	19.41	
2nd instar - lower	1171	80.59	1,453
3rd instar - upper	752	52.77	
3rd instar - lower	673	47.23	1,425
4th instar - upper	653	46.71	
4th instar - lower	745	53.29	1,398
5th instar - upper	580	48.21	
5th instar - lower	623	51.79	1,203

In table 12 four categories have been used for the positions occupied by the first instar nymphs of P. calodendri. These are the upper and lower surfaces of the leaves and the upper and lower surfaces of the stems. Only 2.8% of the 10,128 eggs counted were found on the leaf petioles. The rest were laid on the surface of the leaves, the main concentration being along the mid-rib. 41.3% of the eggs were found on the upper surface of the leaves while 55.9% were found on the lower surface. Most of the eggs were laid on the tender leaves, although occasionally in the field and laboratory they were laid on all sizes of leaves. The greater percentage of eggs laid on the under surface of the leaves does not explain the very high percentage of first stage nymphs which settled there. Less than 3% of the first stage nymphs settled on the upper surface of the leaf. There was a marked behavioural response which led to the majority settling on the under surface. The nature of this response in P. calodendri is not understood but this response is discussed later with respect to Trioza erytreae.

In the second instar 80.6% of the nymphs of P. calodendri were still on the under surface of the leaves although some had moved to the upper surfaces. In the third, fourth and fifth instars practically equal numbers of nymphs were found on the upper and lower surfaces of the leaves. It is suggested that overcrowding on small leaves forces a number of the insects in the third instar to withdraw their mouth parts and move to the upper surface of the leaf although this phenomenon is not understood.

The data presented in table 12 give some indication of relative mortalities in the various instars in a field population of P. calodendri.

These data suggest that, of a potential population of 10,128 eggs, only 1733 eventually "survived" until the first stage. Whether this represented actual mortality in the first stage nymphs or sterility in the eggs, cannot of course be deduced from the figures but it is probable that both factors were involved. Of the five nymphal instars, mortality would seem to be highest among the first instar nymphs, only 1453 "surviving" to the second stage out of the original potential of 1733 first stage nymphs. Mortality among second and third stage nymphs tended to be very low while there was an increase in mortality of fourth stage nymphs before the moult to the final nymphal instar.

The losses shown by these data are comparable with actual mortalities recorded in the laboratory population of P. calodendri. The figures given in tables 6 and 7 under the heading "number of readings" are in fact also an approximate record of the number of mortalities in each instar. These figures show that mortality was highest in the emerging first stage nymphs. All the eggs recorded in tables 6 and 7 must obviously have hatched and of these eggs approximately only 50% reached the end of the first stage. High mortality was also recorded in the field data. There was no evidence, however, from the laboratory data to indicate whether mortalities were higher or lower in any of the other instars.

The seasonal fluctuations of adults of P. calodendri from the field are discussed below.

Field observations on the adults of P. calodendri.

On conclusion of the observations on immature stages of

P. calodendri a field survey was started on the adults of this species. The method used for sampling nymphal populations of *P. calodendri* was very ineffective in gaining an estimate of adult populations. The nymphal survey was stopped at the end of July 1966 when most of the leaves had fallen from the tree and a method was devised to establish the weekly fluctuations of adult *P. calodendri* through one psyllid season. The method, in which sticky yellow impact traps were used proved to be very satisfactory and large numbers of adult psyllids were caught each week.

(i) *Sampling Methods*.

Four hardboard screens painted a bright yellow and measuring 60 x 60 cms were constructed. The screens were designed so that they could be slipped in and out of frames. Strips of wood were fitted to the tops and bottoms of each screen and they were tightened onto the screen by means of wing-nuts. The strips of wood served to secure a square of polythene sheeting to the screens when the wing-nuts were tightened. Each polythene sheet measuring approximately 50 x 50 cms was covered with an extremely sticky substance called "Ostico" which was applied with a roller. "Ostico" does not dry or harden over long periods of exposure and is virtually waterproof. "Ostico" is a propriety product used for banding trees for ant control. Both the "Ostico" and the polythene sheeting were transparent and the yellow colour on the screens was clearly visible through them.

The adult survey was commenced at the beginning of August 1966 and continued for one year. Four frames for the sticky screens

S_1 (see Fig. 1) were positioned in the centre of the sample *Calodendrum capense* tree before any leaves had appeared on the tree. The screens faced outwards towards the four cardinal points. Duplicate sets of screens were constructed and each week they were used to replace those that had been in use in the field. The screens which had been removed from the tree were brought to the laboratory, carefully inspected and insects removed from the "Ostico" using xylene as a solvent. Counts were made of the weekly totals of adult male and female *P. calodendri* caught. Counts were also made of the numbers of both sexes of the main primary parasite of *P. calodendri*, *Tetrastichus* sp., the numbers of other species of psyllids trapped as well as the numbers of small hymenopterous parasites apart from *Tetrastichus* sp.

Three other sets of screens S_2, S_3 and S_4 were set up in other positions at "Mosslands" and the approximate positions of these screens are shown in figure 1. Two screens S_2 were set up approximately two metres from the ground and about 20 metres from the sample *Calodendrum* tree, between the tree and the citrus orchard. They were intended to record the numbers of psyllids migrating from the tree to the orchard and *vice versa.* Two more screens S_3 on a two metre pole were placed in frames in close proximity to a large *Clausena anisata* bush in which the citrus psyllid *Trioza erytreae* had been recorded. On this it was hoped to record the numbers of psyllids flying from the orchard to the indigenous bush. Lastly a pair of frames and screens S_4 were arranged on a pole between two citrus trees in the orchard. These two trees showed evidence of a previous *T. erytreae* infestation.

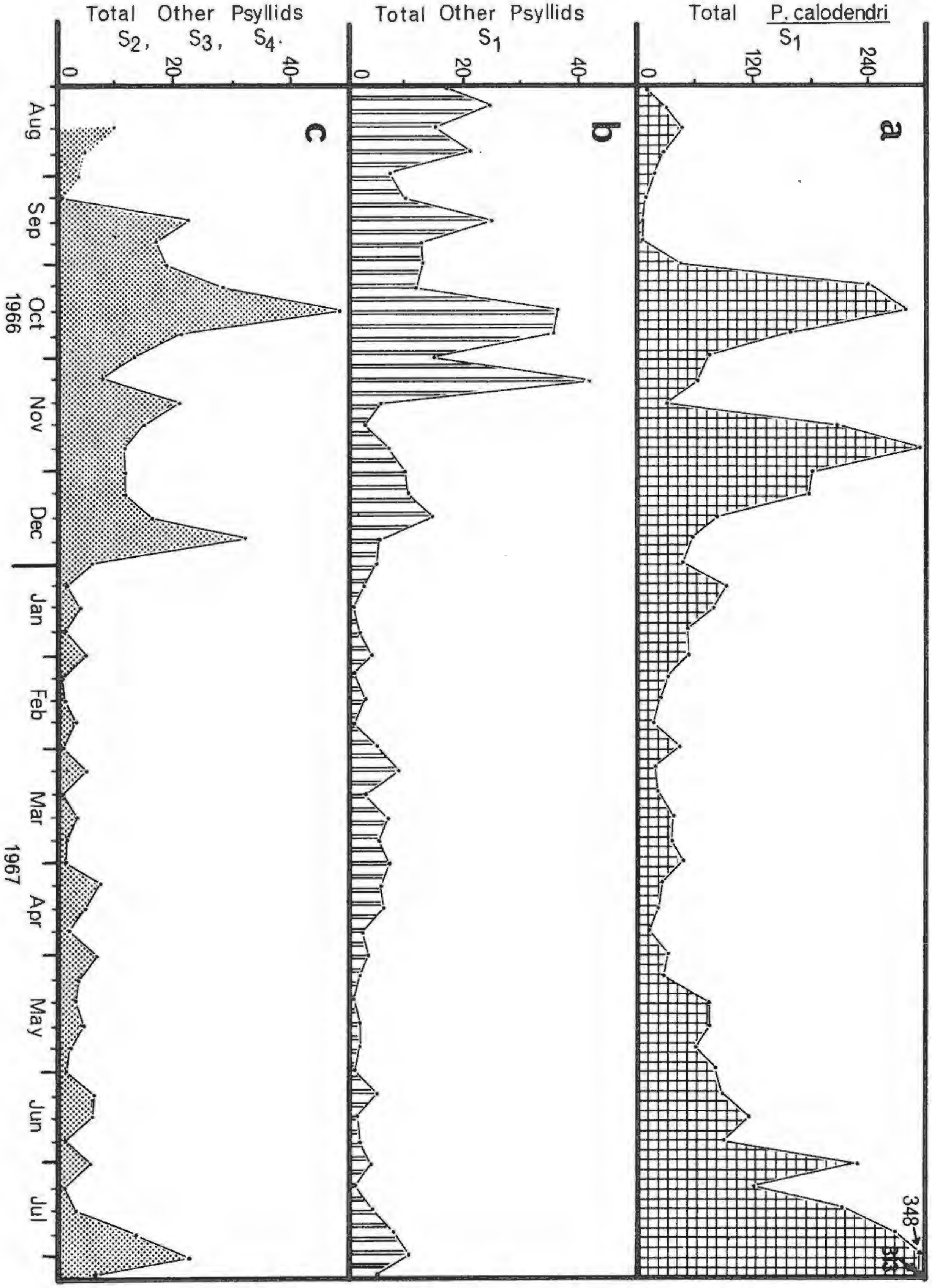


Fig. 27 Total numbers of adult psyllids collected from yellow sticky traps between 10th August 1966 and 9th August 1967. Fig. 27 a - total weekly catches of *Paurocephala calodendri* from traps S_1 (see Fig. 1). Fig. 27 b - total weekly catches of psyllids of species other than *P. calodendri* from traps S_1. Fig. 27 c - total weekly catches of all species of adult psyllids from traps S_2, S_3, and S_4.

(ii) Results.

During the year in which these yellow sticky traps were used at least 20 species of psyllids were caught. Records were kept of the numbers of each species. Firstly, of these 20 species, only P. calodendri occured in sufficient numbers to allow a meaningful analysis of population fluctuations. This species was trapped only on the sticky traps S_1 in the Calodendrum tree, although three individuals were found on the screens S_2. Secondly T. erytreae was never recorded from any of the screens. Significant numbers of Tetrastichus sp. were trapped on the screens in the chestnut tree but very few were found on the adjacent screens S_2 and none on any of the other screens. The catches of Tetrastichus sp. are discussed later.

The fluctuations in numbers of P. calodendri recorded from the four sticky traps S_1 are diagramatically represented in figure 27(a) and can be compared with the fluctuations in numbers of psyllids of other species recorded from traps S_1 (Fig. 27(b)). Figure 27(c) shows the fluctuations of other species of psyllids recorded from screens S_2, S_3 and S_4.

Figure 27(a) shows that there was a marked peak of P. calodendri adults during the months of October, November and December 1966, and that these numbers dropped rapidly from January until about June 1967 when there was another rise in the numbers of psyllids recorded. Of immediate relevance, however, is the similarity between the three graphs in figure 27(a - c). The total numbers of psyllids of other species, apart from P. calodendri , also showed population peaks between September and January with the populations progressively falling to very low levels until the end of June. Thereafter the numbers began to increase. The adult population of P. calodendri showed a marked increase in numbers at the end of July 1967 but this maybe regarded as atypical because 1967 proved to be a year of unusually heavy rains and relatively mild weather. This combination enabled the leaves on the Calodendrum tree to remain succulent throughout the winter period and thus capable of supporting a large P. calodendri population. In more normal seasons the deciduous fall of leaves was complete by the beginning of August and this certainly was the case during the 1966 season when no leaves were left on the tree. This point will be recalled during the discussion of population fluctuations in this species.

Of the catches of P. calodendri adults recorded from the sticky traps S_1 in the Cape chestnut tree, 33.7% were recorded from the South facing screen, 29.1% from the West facing screen, 20.2% from the East facing screen and only 17.0% from the North facing screen. The figures upon which these percentages are based are given in Table 13.

Table 13. Numbers of P. calodendri and other species of psyllids recorded from yellow sticky traps S_1 from August 1966 to August 1967.

STICKY SCREENS S_1	NORTH	SOUTH	EAST	WEST	TOTAL
TOTALS OF P. calodendri	830	1644	985	1417	4876
Percentages	17.02	33.72	20.20	29.06	100.0
TOTALS OF "other" psyllids	91	136	111	130	468
Percentages	19.4	29.1	23.7	27.8	100.0

Also recorded in Table 13 are the numbers of psyllids other than P. calodendri trapped on each of the four sticky screens. The numbers recorded were very low compared to those for P. calodendri but the percentage catch on each of the screens is in remarkable agreement with that of P. calodendri.

An explanation for the unequal psyllid catch on the four screens is not difficult. In the first place, wind direction can be ruled out because the number of psyllids on the screens bears no relation to the prevailing winds. A visual estimate of leaf density on each side faced by the sticky traps showed clearly that the Southern aspect of the tree had a denser mat of foliage than the other aspects and also that this foliage was very close to the South facing screen. The Western aspect of the tree had an almost equal density of foliage, but the majority of the leaves were further from this screen than were the leaves faced by the South screen. The North and East facing screens had little foliage in their immediate vicinity. It seems clear that the percentage catch of psyllids on the four screens was directly related to the density and proximity of the foliage. These visual estimates of foliage density on all four aspects of the tree were confirmed by a sampling method in which a long pole was projected through five different angles from each of the screens; a count was then made of the numbers of leaves and branches actually contacting the projecting pole. Obviously the denser the foliage the greater the number of contacts along the length of the pole. This method is widely used botanically and is known as point quadrat foliage sampling. The highest number of leaf contacts (35) was recorded from the Southern aspect of the tree followed by 20 contacts on the Westerly aspect, 14 on the Northerly aspect and

8 on the Easterly aspect. The number of leaf contacts therefore confirmed the visual impression already gained.

Finally an analysis was made of the numbers of male and female P. calodendri adults recorded from the four screens S_1 between the 10th August 1966 and the 9th August 1967. The results of this analysis are contained in table 14.

Table 14. Numbers of male and female P. calodendri adults recorded from yellow sticky traps S_1 from August 1966 to August 1967. These totals are broken down into sub-totals for the periods 10th August 1966 to 28th June 1967 and 28th June 1967 to 9th August 1967.

STICKY SCREENS S_1	NORTH		SOUTH		EAST		WEST		TOTALS		
P. calodendri	M	F	M	F	M	F	M	F	M	F	TOTAL
10th August 1966 to 28th June 1967	383	269	600	408	470	331	558	373	2011	1381	3392
Percentages	58.7	41.3	59.5	40.5	58.7	41.3	59.9	40.1	59.3	40.7	100
28th June 1967 to 9th August 1967	84	94	270	366	87	97	204	282	645	839	1484
Percentages	47.2	52.8	42.5	57.5	47.3	52.7	42.0	58.0	43.5	56.5	100
10th August 1966 to 9th August 1967	467	363	870	774	557	428	762	655	2656	2220	4876
Percentages	56.3	43.7	52.9	47.1	56.5	43.5	53.8	46.2	54.5	45.5	100

M = Male F = Female

Table 14 shows that during the entire survey period from 10th August 1966 to 9th August 1967, a majority of male P. calodendri were trapped on all four screens. The percentages of males out of the total capture varied from 53.8% from the West facing screen to 56.5% from the North facing screen. There has been no evidence from either spot sampling of adult psyllids from the field or from the data gained in the laboratory to suggest that the sex ratio in P. calodendri is other than 1:1. The preponderance of males on all screens suggested that the males were more active fliers than the females, or that the males were more attracted to yellow. There is no evidence for either of these suggestions in P. calodendri although a comment by Eastop (1961) is relevant:-

> "It seems likely that the wing muscles of some female psyllids autolyse (or that their attraction to yellow changes) only a day or so after the final moult, while males continue to fly for more of their adult life. Catches in yellow traps of Pauropsylla trichaeta consisted largely of rather pale females while most of the males were dark".

This possibility was not investigated in P. calodendri.

A break down of all the data for the survey period suggests that the ratio of male P. calodendri to females varied as the season proceeded. In the early stages of the psyllid season (from 10th August 1966 to 28th June 1967) males of P. calodendri were more often trapped than females. Catches of 59.9% males were recorded for this period from the West facing screen, 59.5% from the South screen and 58.7% from the East and North facing screens. During the latter part of the psyllid season (from 28th June to 9th August 1967) on the other hand, of the psyllids captured on each screen, only 47.3% males were recorded from the East facing screen. 47.2% males were recorded from the North screen, 42.5% from the South screen and 42.0% from the West facing screen. The reason for this clear sex ratio "shift" during the season is obscure and there is no evidence to indicate whether this involved a change in sex ratio or a seasonal behaviour change in males or females of P. calodendri.

The biology of Tetrastichus sp.

At this point a brief recapitualation may be helpful. Laboratory studies on Paurocephala calodendri have revealed the life history of this species and the effects of temperature on development. Two separate field surveys have been conducted, one on the immature stages and the other on the adults of this psyllid in order to verify the laboratory findings. An account of the major parasite of P. calodendri, namely Tetrastichus sp., follows, in which the general biology of this insect is considered. Field studies on Tetrastichus sp. were conducted together with those on P. calodendri and surveys on the immature stages and adults are considered separately. An account of the influence of the parasite on population fluctuations in P. calodendri is given in the discussion.

Tetrastichus sp. (Hymenoptera : Eulophidae) is the primary ecto-parasite of nymphal P. calodendri. The only other parasite of P. calodendri which has been identified is Psyllaephagus sp. Representatives of this genus are very common as parasites of psyllids generally, but in the case of P. calodendri they were found only very occasionally and for this reason have been ignored in the following discussion. Hyper-parasites attacking the larvae and pupae of Tetrastichus sp. were discovered only on three occasions and they also are not considered further.

Observations have shown that predators of P. calodendri were limited to larval chrysopids which were presumed to feed on the nymphs. The dry nymphal cuticles of the psyllids were found among the debris on the backs of these predators. Unidentified chrysopid larvae have also been seen feeding on nymphal psyllids when confined in a petri dish in the laboratory. Chrysopid larvae were rarely found among the leaf samples collected in the field and were therefore probably of little importance in controlling the numbers of P. calodendri. It is likely that other predators of P. calodendri were present in the field but these were not encountered during the period of study.

Tetrastichus sp. is morphologically very similar to Tetrastichus radiatus Waterston (1922). Tetrastichus sp. however, must be distinct from T. radiatus because Tetrastichus sp. did not parasitize T. erytreae under any circumstances even if T. erytreae nymphs were reared on Cape chestnut seedlings. Tetrastichus radiatus was also host specific, indicating a clear biological difference.

Methods.

Adult males and females of Tetrastichus sp. were confined in perforated plastic bags on Cape chestnut seedlings together with at least 100 nymphs of P. calodendri at the lowest temperature regime. The nymphs had been reared on the seedlings and all instars were present on each seedling. In some cases third, fourth and fifth instar nymphs were transfered from other seedlings to make up numbers in any one instar. Only two or three parasite females were allowed access to the psyllids on each seedling. Experience had shown that more than this number resulted in complete extermination of the hosts. Parasitized psyllids were inspected twice daily and the progress of the parasites was recorded. The parasite larvae live externally under the host and care had to be taken to avoid dislodging the parasites when the psyllids were turned over.

Pre-mating and mating behaviour. After emergence from the pupal stage the male and female parasites spent from two to three hours in cleaning activity. There followed a period of apparently haphazard wandering over the surfaces of the leaf during which time both sexes were very strongly attracted to moist areas to which they would immediately apply their mouth parts and start feeding. During this initial phase both sexes fed readily on honey or sugar water and would also eat the sugary faeces excreted by the psyllids themselves. It is likely that in the field the excretion from the psyllids was the initial source of food. Doutt (1964) records that several species of parasitic Hymenoptera feed initially on honey dew or nectar. This initial food source has been shown to contain free amino acids which seem to influence longevity and fecundity in several parasite species.

Doutt (1964) notes that in most hymenopterous parasites a premating period is "not a necessary characteristic" and that mating may take place immediately after emergence from the pupa. Observations on the behaviour of Tetrastichus sp. suggested that feeding was the initial drive and that only following this did mating occur. In any event mating took place within a few hours of emergence and was preceded by a brief courtship display. In the presence of the female the male showed an "excited" behaviour which included vibration of the wings and movements of the antennae. The male eventually mounted the female and mating took place. The male is smaller than the female, has plumose antennae and is completely black in colour. The female on the other hand has a conspicuous yellow patch on the dorsum of the abdomen and has filiform antennae.

Host feeding behaviour and oviposition.

After mating the male and female parasites feed on sugary substances but the females supplemented this diet by feeding on the blood from the host psyllids. Host feeding behaviour in the female began when the parasite wandered over the leaves of the plant "exploring" the surface of the leaf with its antennae. The antennae were used to detect the presence of nymphs and this detection appeared to be chemotactic. The female parasites investigated areas on the leaf where psyllid nymphs had been feeding although the nymphs themselves were no longer present. Once a psyllid nymph of the correct instar was located the female walked over the nymph several times feeling with the antennae and finally on becoming orientated stood on top of the nymph and pierced the side of the abdomen or thorax with its ovipositor. Several stabbing movements were made with its ovipositor before the female parasite climbed off the nymph and applied its mouth parts to the wound. The exuding fluids were then lapped up. The parasite often remounted the psyllid and pierced the insect again with the ovipositor.

The psyllid nymphs responded to the presence of the parasite by raising their bodies and swaying vigorously from side to side. This apparently was an attempt by the psyllid to dislodge the parasite, although the latter seemed completely unaffected by the manoeuvre. The psyllid nymph apart from these swaying movements, does not attempt to escape. The mouth parts of the psyllid were not withdrawn while the female parasite was on its back. It seems likely that the female parasite injected a narcotizing agent into the psyllid while piercing it with the ovipositor. Immediately after being pierced the psyllid ceased all movements and in this condition did not respond to mechanical stimulation for about ten minutes.

Psyllid nymphs killed by host feeding were easy to detect because there was often a bluish patch of haemolymph on the leaf next to the corpse. Normally after the parasite had finished feeding the psyllids were completely dry and shrivelled with their mouth parts still inserted into the leaf. Such nymphs have been referred to previously in this account as "dry". Parasites normally host fed on third or fourth stage psyllid nymphs and less frequently on fifth stage nymphs. A single female was capable of killing many nymphs by host feeding. Doutt (1964) mentions that in a number of hymenopterous parasites ovogenesis can only procede after the parasite has obtained the necessary nutriments from host feeding. It is very likely that this is also the case in *Tetrastichus* sp. and Marchal (1905) has recorded a very similar form of host feeding in *Tetrastichus xanthomelaenae*.

Oviposition in *Tetrastichus* sp. took place two days after the first period of host feeding. Ovipositional behaviour was difficult to distinguish from host feeding behaviour because the female again explored the leaf by wandering rapidly over it until it stopped at a psyllid nymph which it appeared to have detected with its antennae. The nymph was "explored" with the antennae and eventually the female mounted the psyllid, placed its ovipositor underneath the body of the nymph and deposited an egg in the region between the thorax and abdomen. The eggs, which are typically hymenopteriform (Hagen, 1964) are sausage shaped and measure approximately 0.21 mm in length.

The parasite larvae.

The larvae hatched from the eggs after about three days and started feeding externally on the psyllid nymphs. As the parasite started feeding the psyllid nymph responded by excreting copiously. This continued throughout the feeding period of the larval parasite and parasitized psyllids were recognised by cords of the excretion which exuded in coils from the anus. Small pellets are normally excreted in healthy nymphs. The parasite larvae, which were pear shaped, apodous, with a vague body segmentation grew very quickly. The larval feeding period lasted about four or five days at the end of which the psyllid nymph was noticeably shrivelled and was raised from the surface of the leaf by the parasite larva beneath it. The last day of feeding killed the host and the corpse was then used as a cover by the parasite larva. The parasite strapped the psyllid corpse to the leaf using numerous sticky silken threads which were secreted from the anal region of the larva. This region was stretched from underneath the psyllid to the mid-line of the dorsal surface where the silken thread was attached. Threads were then secreted from this point over the surface of the psyllid and attached to the leaf. This was repeated many times and the psyllid was eventually completely covered by a stringy canopy of silken threads.

Pre-pupal and pupal stages.

After exhausting the food supply the larva metamorphosed into the prepupal stage which lasted for three or four days. Pupation occured four or five days after the psyllid had been strapped down and six to seven days after pupation the adult emerged. The pupa was orientated with its ventral surface upwards so that the ventral surfaces of the parasite and host corpse were closely apposed. The adults (male body length - 0.9 mm, female body length 1.1 mm) emerged by biting a neat round hole through its cover in the cervical or thoracic region of the host. The total development time at the lowest temperature regime from the egg to adult emergence was about 19 days.

Individuals of Tetrastichus sp. were also reared at the median temperature regime. At this temperature the duration of the egg stage was reduced to two days, the duration of the larval feeding stage was much reduced taking only two days, while the prepupal stage took three or four days and the pupal stage six or seven days. Thus the total development time at this temperature from the egg to adult emergence was about 14 days. Because of the difficulties experienced in rearing P. calodendri at the highest temperature regime no data have been obtained on the developmental history of Tetrastichus sp. under those conditions.

The efficiency of individual female parasites.

In these experiments single females, together with a male, were placed on a Cape chestnut seedling with a number of psyllid nymphs in known instars. A complete record was however obtained from only one female. The other females escaped or were accidentally killed. This normally happened with the daily transference of the females to fresh seedlings where they were given a fresh supply of psyllid nymphs.

The female parasite for which a complete record was obtained lived for just over three weeks and was supplied with a total of 104 psyllid nymphs. Since it was known that first and second stage nymphs were ignored by the parasites, only third, fourth and fifth stage nymphs of P. calodendri were presented. In all, 55 third instar nymphs were presented, 44 fourth instar and 5 fifth instar nymphs. Of this total, 27 psyllid nymphs were the victims of host feeding and were sucked dry by the parasite.. Fourteen of these were in the third instar and 12 in the fourth instar. Only one fifth instar nymph was killed by parasite host feeding. It is possible that the numbers of psyllids which were killed by host feeding merely reflect the proportion of those originally presented to the female.

Of the 104 psyllid nymphs presented to the single female parasite, 30 eggs were laid on fourth instar nymphs. Three of these fourth stage nymphs were superparasitized with two eggs while one was superparasitized with three eggs. When a psyllid nymph was superparasitized only one parasite larva eventually survived. Eleven eggs were laid on fifth instar nymphs and there were no cases of superparasitism. (Note that the number of fifth stage nymphs stated here is 11 while it was said earlier that five fifth stage nymphs only were presented to the parasite. The reason for this discrepancy is that during the time in which the nymphs were exposed to parasite attack six fourth stage nymphs moulted to the fifth stage.). The preference shown by the parasite for ovipositing on fourth stage nymphs was confirmed by data obtained in the field and this is discussed later. Occasionally during these experiments females of <u>Tetrastichus</u> sp. oviposited on third stage nymphs but the impression gained was that this stage was used for oviposition only when no later instars were available. This impression was supported by the very low numbers of parasitized third stage psyllids recorded in the field. The reason for this is not known but in all probability third instar nymphs do not provide the developing parasite with enough food.

The individual female parasite, during her three week life, killed by parasitization or host feeding about 70% of the total population of 104 psyllids. This seemed to be the upper limit of efficiency in these parasites, because no more than 70% of the hosts available were ever parasitized or killed even when a female was left with only one batch of hosts for several days. Thus a mechanism similar to that found in Trichogramma evanescens by Salt (1936) would seem to be operating in Tetrastichus sp. Salt has found in T. evanescens, which is an egg parasite of Sitotroga cereallela, that once the adult female had walked over eggs even without ovipositing, it virtually immunized those eggs from further parasite attack. Thus with T. evanescens there was never a 100% parasitism. The biological significance of this is clear and it is possible that a similar chemical signal is operative in Tetrastichus sp. although experiments to confirm this remain to be conducted.

Sex determination.

Information about sex determination in Tetrastichus sp. has also emerged from these experiments. As is the case with a number of Hymenoptera, unmated Tetrastichus sp. females gave rise solely to male offspring, while mated females produced progeny of both sexes. Unmated females, however, produced only a few male offspring even if they were provided with numerous host psyllids. The maximum number of males recorded from a single virgin female was 11. The total numbers of progeny recorded from a mated female parasite were 13 males and 42 females. Clark (1962) notes that sex determination in Psyllaephagus is dependent on the stage of the host psyllid. This phenomenon has not been investigated in Tetrastichus sp..

Parasite induced inhibition of moulting.

An important aspect of the biology of Tetrastichus sp. was revealed by an unplanned experiment. During the studies on the life history of P. calodendri, in which individual records of each insect were kept it was noticed that in ten cases the instar durations of the psyllids were excessively prolonged. No explanation could be offered for this until it was discovered that the psyllids had been parasitized. As each of the psyllids were observed individually it was possible to show that in each case parasitization had resulted in an inhibition of moulting in the host. At the median temperature regime, at which these animals were reared, the normal duration of the fourth instar was about four days. The nymphs that had been parasitized, however, did not moult and remained in the fourth instar for ten days. After this time they were strapped down by the parasite and died. In the fifth stage prolongation of the instar was also evident. The normal duration of this stage was five days while parasitized individuals remained in the fifth stage for up to eight days before they were strapped down. Clearly the parasite affected the host in some way which prevented moulting. If the host were to moult the parasite would become dislodged and would never regain the host. When a parasite larva was artificially dislodged in this way, it was unable to reinstate itself even though it was left touching the host psyllid. In these circumstances the parasite larva died of desiccation within an hour or two. The ability of the parasite to inhibit moulting in the host is therefore of paramount importance in its survival.

Field observations on the immature stages of Tetrastichus sp.

Field observations on parasitism of P. calodendri by Tetrastichus sp. lend support and corroborative evidence to a number

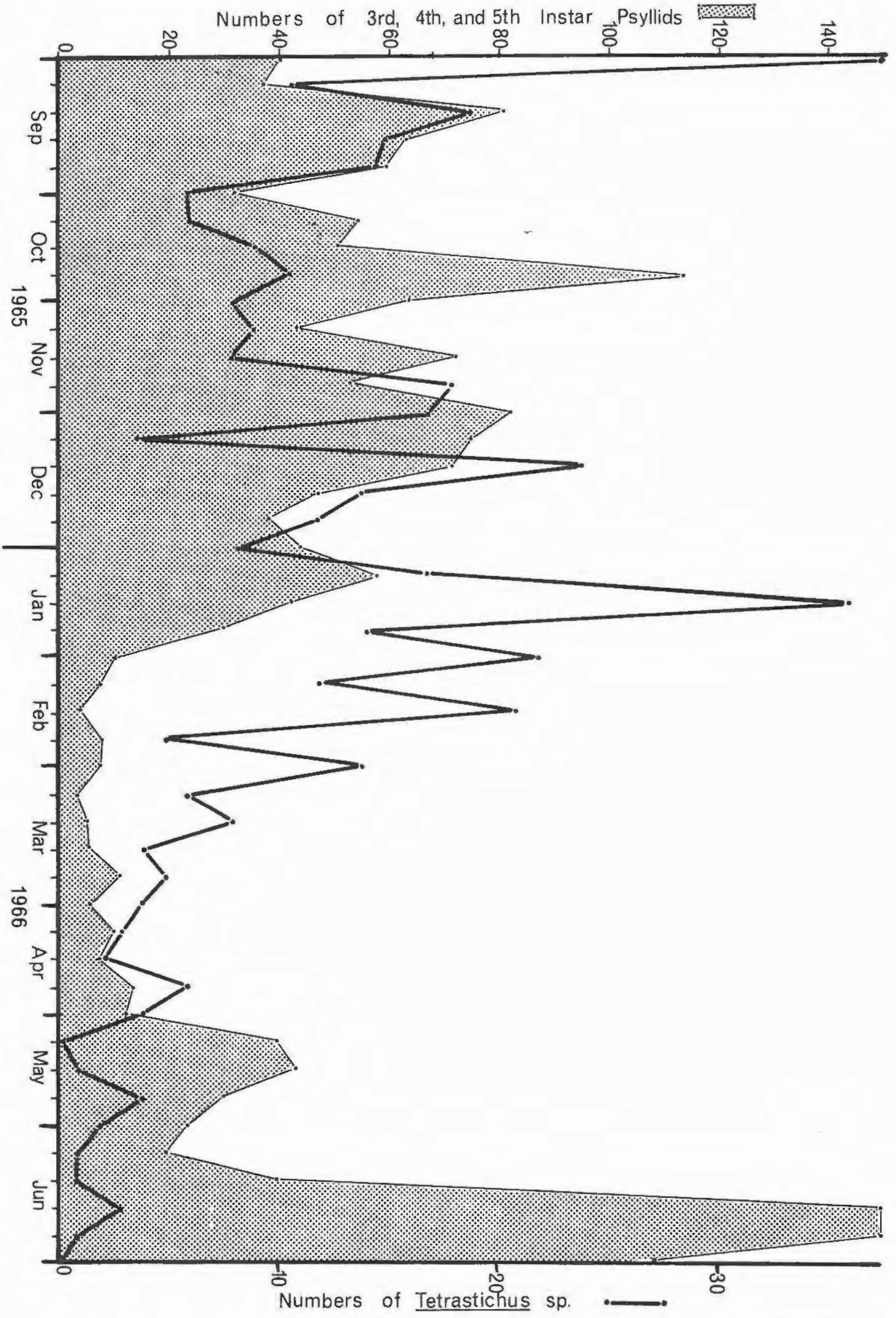


Fig. 28 Total numbers of third, fourth and fifth instar nymphs of Paurocephala calodendri collected weekly from 1st September 1965 to 29th June 1966. The weekly totals of Tetrastichus sp. collected during this period are also plotted.

of the conclusions drawn from laboratory experiments. Concurrent with the survey, which was conducted on the immature stages of P. calodendri from September 1965 to July 1966, a record was kept of the numbers of this species parasitized by Tetrastichus sp. This record included the numbers of P. calodendri in each instar which were parasitized and also the stages of the parasite. The fluctuations in the parasite population are recorded in figure 28 together with a graph showing the weekly fluctuations in total numbers of third, fourth and fifth stage P. calodendri nymphs. Only these psyllid stages were considered in the analysis as they were the only ones parasitized by Tetrastichus sp.

Figure 28 shows that the numbers of parasites recorded throughout the survey period were low and that the maximum number recorded in all stages in any one week was 38. The fluctuations in numbers of parasites from week to week were considerable and can be related in part, to the general inefficiency of the sampling methods which was discussed previously. In spite of this some general trends call for comment. The peak numbers of psyllid parasites recorded occurred some time after the peak abundance of the hosts. A rapid drop in the numbers of psyllids in the third, fourth and fifth stages at the beginning of January 1966 was accompanied by high numbers of parasites. The parasite numbers declined by the end of June 1966 and this was accompanied by a rise in psyllid numbers.

Fluctuations of numbers among the third, fourth and fifth stage nymphs of P. calodendri (Fig. 28) follow those for the total psyllid population as expressed in figure 25 and it was suggested earlier that high temperatures were partly responsible for the observed fluctuations in this case. It is suggested therefore that temperature and parasites were both important components in the control of P. calodendri numbers and this will be discussed fully later.

Of the 90 eggs of Tetrastichus sp. which were found during the survey period, only five were deposited under third stage P. calodendri nymphs, while 60 were deposited on fourth stage nymphs and 25 on fifth stage nymphs. This confirms observations in the laboratory where it was found that the fourth stage nymphs were prefered for oviposition. In the laboratory where all stages of psyllids were always available to the parasites, oviposition never occured on third stage nymphs. The occurence of five eggs on third stage nymphs in the field would suggest that the numbers of psyllids in the fourth and fifth instar was low which would force the parasites to oviposit on third stage nymphs. This is supported by the fact that, during the three week period in which eggs were found on third instar nymphs the numbers of third stage nymphs recorded was far higher than those for fourth or fifth stage nymphs. There was a total of 95 third stage and only 36 and 14 fourth and fifth stage nymphs respectively. Of the total of 90 eggs recorded on psyllid nymphs during the survey period, there were seven cases of superparasitism with two eggs and two cases of superparasitism with three eggs. Thus superparasitism which was recorded in the laboratory also occurs in the field.

Records of the numbers of parasite larvae found during the survey period present a confusing picture. Only four third stage psyllid nymphs were parasitized with larvae while 26 nymphs in the fourth instar and 36 in the fifth instar were parasitized. The low numbers of parasitized third stage nymphs could have been expected

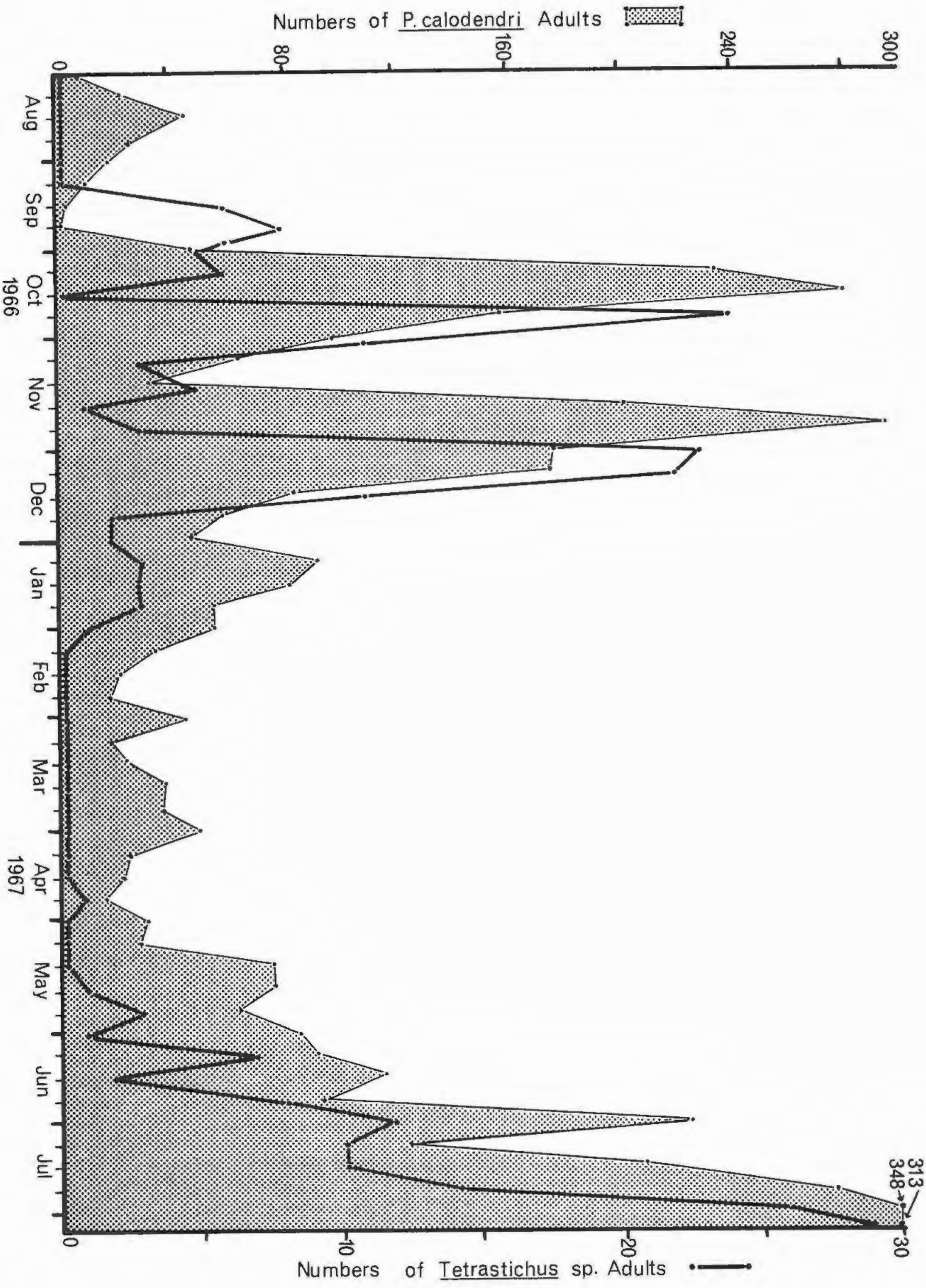


Fig. 29 Total weekly catches of adult *Paurocephala calodendri* and of *Tetrastichus* sp. recorded from yellow sticky traps S_1 (see Fig. 1) during the period 10th August 1966 to 9th August 1967.

both from laboratory and field observations on the numbers of eggs laid on this stage. Why, however, there should have been more parasite larvae found on fifth stage psyllids than fourth stage is obscure and is contradictory to the laboratory results.

Twenty three females and nine male adult parasites were recorded during the survey period. This preponderance of females confirmed the results obtained in the laboratory.

Field Observations on adult Tetrastichus sp.

A second survey was started in August 1966, in which adult psyllids and parasites were trapped on sticky yellow traps. Records from the traps showed that 161 of the captured Tetrastichus sp. were male while only 50 were female. This would seem to contradict previous observations but the data probably indicate that males of Tetrastichus sp. were more active fliers than the females and probably, were attracted more readily to yellow. The numbers recorded from the traps may not necessarily reflect the prevailing sex ratio in this species.

The total weekly catches of adult Tetrastichus sp. on the sticky traps from August 1966 to August 1967 are recorded in figure 29 together with the total weekly catches of adult P. calodendri. Figure 29 shows that low numbers of parasites were caught on the sticky traps compared to the numbers of P. calodendri. However, the way in which the fluctuations in adult parasite numbers followed that of adult psyllid numbers is very striking. Each peak in adult P. calodendri numbers was followed by a peak in parasite numbers. The peak of numbers of psyllid adults in the middle of August 1966 was followed by a peak of parasites in September, while the increase in numbers of hosts in mid October was followed by an increase in the numbers of parasites a few weeks later. The same relationship holds good for the increase in host numbers at the end of November which was followed by an increase in parasite numbers a week later. This pattern was repeated with the minor psyllid population peaks at the beginning of January and May 1967.

The fluctuations in the adult psyllid and parasite populations bring to mind the classical relationship between host and parasite populations which has been advanced on theoretical grounds by Volterra (1926) and later improved and modified by Bailey (1931) and Nicholson (1933). Nicholson and Bailey (1935) visualize host/ parasite populations to be in "dynamic oscillation". The peaks in the oscillation of the parasite population follow peaks in host population and this rise in parasite population leads to a decrease in the numbers of hosts and so on. The observed relationship in the field would suggest very strongly that Tetrastichus sp. was having an important influence on the fluctuations of its host P. calodendri and this relationship is made more impressive by the following considerations. While adults of Tetrastichus sp. were collected from the sticky traps in the Cape chestnut tree, other parasitic Hymenoptera of about the same size as Tetrastichus sp. were also collected because it was thought initially that some of these could be associated with P. calodendri. More than 1,600 of these other parasites were collected in this way, and the fluctuations of their numbers, throughout the survey period, show no obvious relationship to the fluctuations in numbers of P. calodendri or Tetrastichus sp. If such a relationship had existed it would have indicated that the fluctuations of populations as a whole related perhaps, to conditions in the tree or some other abiotic factors and had this been the case the relationships illustrated in figure 29 would have been purely fortuitous. It is evident and important that this was not the case.

Discussion.

It has been postulated that in any animal population, selection, in evolutionary terms, is acting on the population to bring about maximum exploitation of the environment while for obvious reasons preventing over-exploitation. Thus as Wynne-Edwards (1962) puts it: "The whole trend of ecological evolution tends towards stability and stability implies the highest state of productivity of the organism which can be maintained within the limits of the environment." In other words an evolution towards a "population homeostasis".

When certain other conditions were fulfilled, the population of P. calodendri was maintained at a moderate level without overcrowding. Even at peak population levels there was always adequate leaf space available as well as adequate oviposition sites and the feeding of the psyllids did not produce any adverse effects on the tree. Thus in P. calodendri mortality was not caused through over-exploitation of the habitat and other factors were therefore preventing outbreaks in this species. These factors are discussed below and where reference is made to the effects of temperature it should be noted that the inverse relationship between temperature and relative humidity is implied. All thermo-hygrograph records from "Mosslands" showed this ~~direct~~ inverse relationship.

An idealized representation of population fluctuations of Paurocephala calodendri and that of its primary parasite Tetrastichus

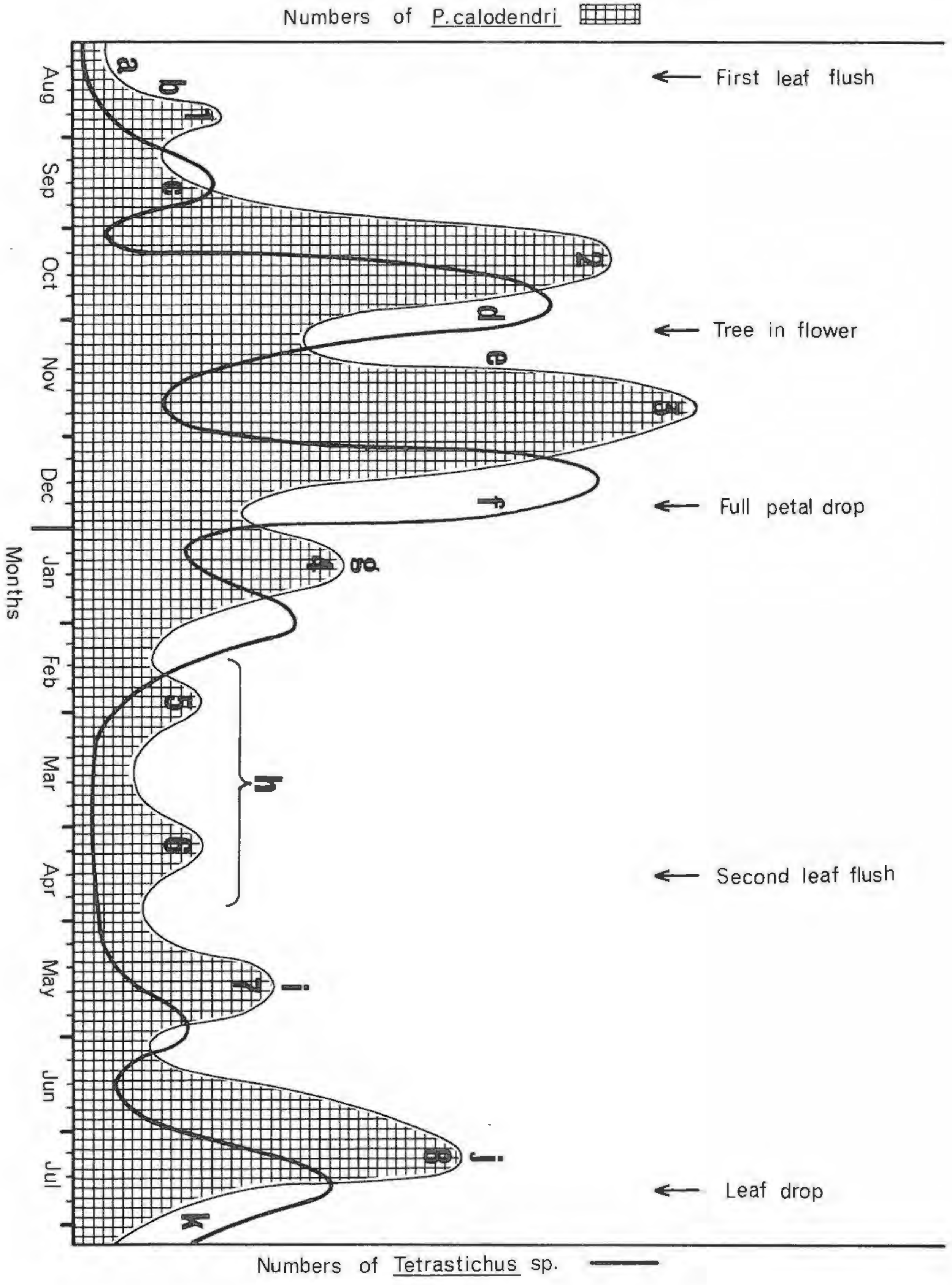


Fig. 30 A representation of the fluctuations of populations of *Paurocephala calodendri* and that of its primary parasite *Tetrastichus* sp. during one "psyllid season". The letters a - k and the numerals 1 - 8 refer to points which are explained in the text.

sp. during one "psyllid season" is presented in figure 30. This figure is derived, mainly, from the fluctuations in adult populations shown in figure 29 but it also stems from the fluctuations in immature stages of P. calodendri shown in figures 25 and 28.

At the beginning of the "psyllid season" in early August (point a, Fig. 30) there are very few leaves which remain and they are yellow and tough and the general level of the psyllid population is very low. The P. calodendri population comprises a few adults, which are very resistant to low temperatures and have survived from the end of July after leaf drop, and a few eggs which are found on the remaining leaves. There is a possibility that some nymphs survive this period by feeding on the shoots which they will do if the leaves are unsuitable and, with this presumeably unsuitable food source and low temperatures, instar durations are prolonged.

Evidence from sticky trap collections showed that it is unlikely that reinfestation of the tree at the beginning of the season takes place by psyllids flying in from other trees. It is also very unlikely that the population of P. calodendri in the tree was significantly depleted by migration. These are important points because it means that the population in this one sample tree can be treated as an entity and that this is virtually an isolated population of psyllids. Interpretation of population fluctuations would have been more difficult if the sample tree had been surrounded by other Cape chestnut trees.

In the middle of August the first flush of leaves appears. This is followed by a rise in the psyllid population (point b) originating from the few psyllids which survived over the leafless period. A first generation peak of psyllids is reached in late August and the numbers decline by early September. (The proposed generations of P. calodendri are numbered from 1 - 8 in figure 30). A decline in the numbers of individuals between generations is often characteristic in multi-voltine insects when a large number of eggs are laid within a short period. The observed times between population peaks in P. calodendri correspond very closely to the generation time recorded in the laboratory. In the case of P. calodendri the distinction between the first and second generations may be accentuated slightly by the rise in numbers of Tetrastichus sp. parasites at the beginning of September.

In mid September (point c) the eggs, produced by the first generation adults, begin to hatch and the numbers rise steeply to a new level in the second generation. This rise in the population is made possible by two factors. Firstly, with the decline in numbers of suitable nymphs for parasitism at the end of the first generation the parasite population declines and remains at a low level during the rise of the second psyllid generation. Secondly, during the early part of the season, the temperature summations are comparatively low and do not rise high enough to have any adverse effects on the insects or the plant. Thus the lack of parasites and the favourable temperatures lead to the increase in the numbers of psyllids to a peak level at the beginning of October.

With the large number of hosts available in early October the number of parasites rises sharply and reaches a peak in the middle of October. The effect of these parasites is to reduce the population level (point, d) by the beginning of November.

The drop in parasite numbers after the second psyllid generation permits a rise in numbers of psyllids in the third generation (point, e). It must be emphasised again that, during this steep rise in numbers of psyllids in the third generation, there are very few psyllids in the correct instar for parasitization and hence the numbers of parasites declines during this period. The third generation peak is reached at the end of November, encouraged by very favourable temperature conditions. These are roughly equivalent to the median temperatures in the environment room which were found to be most suitable for this species.

The decline of the third generation (point, f) starts in early December at which time the parasite population has reached another peak in numbers. Parasite induced mortality is probably mainly responsible for the sharp decline in the numbers of psyllids. When the performance of these parasites in the laboratory is recalled, both in host feeding and in direct parasitism, this explanation for the decline in psyllid numbers seems realistic. Figure 29 shows that approximately 300 psyllid adults were recorded at the peak in population in the last week of November. Following this psyllid peak there was a peak in parasite numbers and 17 male and 6 female parasites were recorded. Laboratory studies on a single Tetrastichus sp. female showed that it could kill over 70 psyllids by host feeding and parasitism during a few weeks. Thus the observed decline in psyllid numbers is well within the capabilities of the parasites (provided the sampling technique is assumed to capture proportionately equal numbers of psyllids and parasites).

It must be emphasized, however, that in the laboratory the parasites were presented with an excess of hosts in the correct instars and that the parasites and psyllids were crowded together on one seedling. The parasites were also given a fresh supply of hosts every day. In the field not all the hosts encountered by the parasites would be suitable for food or parasitism and they would spend considerable periods of time searching for hosts. On the other hand fewer females than males of Tetrastichus sp. were captured on the yellow sticky traps and it was suggested that females were less active or less attracted to yellow. The numbers of female parasites recorded therefore, was probably an underestimate of the proportion actually present. Because of these considerations, a direct comparison of the performance of the parasites in the laboratory and in the field is not possible. At best, the performance of these insects in the laboratory can only give an indication of that in the field. In any event it is clear that parasites are probably mainly responsible for the decline in the third generation of psyllids as they had been with the first and second generations.

The fourth generation of P. calodendri (point, g) builds up and reaches its peak by the middle of January. This peak is far lower than would be expected and it seems that the high temperatures at this time of the year are limiting the numbers of insects in the fourth generation. It has been suggested from laboratory observations that high temperatures in January, February and March cause a high mortality of nymphs of P. calodendri. Circumstantial evidence has been given which suggests that high temperatures are affecting the psyllids indirectly through action on the host plants. Thus it is envisaged that during these months, when the temperatures are particularly high, the leaves on the tree are in poor condition and this leads to inadequate nutrition of the psyllids. As a result the psyllids tend to wander and may either die of desiccation or be blown off the leaves. During this period where there is a decrease in the level of the psyllid population, the parasite population is also very low. However, there is a slight peak in numbers of parasites which follows the increase in hosts during the fourth generation. A decline of the fourth generation of psyllids follows at the end of January and is probably partially accentuated by parasitism.

The fifth generation of psyllids (point, h) reaches a low maximum at the end of February and is followed by a sixth generation with a peak at the beginning of April. During this whole period it seems that high temperatures are responsible for the maintained low levels of the P. calodendri population. Tetrastichus sp. has virtually disappeared and cannot be responsible for controlling the numbers of P. calodendri.

The weather becomes cooler at the end of April and during May. This leads to a build up in the numbers of P. calodendri in the seventh generation (point, i). The relaxation of "temperature control" during this period results in a greater increase of psyllid numbers than was possible during the fifth or sixth generations. The increase in numbers of hosts results again in a slight increase in Tetrastichus sp. which may be partially responsible for the population decline of the seventh generation. A secondary flush of leaves during May also contributes to the build up in population in the seventh generation.

The secondary flush of leaves which encourages oviposition and supplies adequate food for the nymphs, together with the low temperatures in June leads to a build up in numbers in the eighth generation (point, j) which is nearly as impressive as that at the beginning of the season. The decline in the eighth generation (point, k) during the middle of July is brought about by the increasing number of parasites present. The cold weather has caused the tree to drop its leaves and thus for the first time the psyllids are limited by the availability of leaf space. A few leaves from the secondary leaf flush remain on the tree from the end of July to the middle of August and some psyllids are able to live until the first leaf flush of the following psyllid season.

Control of populations in *P. calodendri* therefore, is seen in three phases:-

(i) At the start of the season abiotic factors, namely high temperatures, are not important in the control of *P. calodendri* populations. The main control is effected by *Tetrastichus* sp. During this phase however, the abiotic environment is influencing parasites and hosts and cannot be ignored. No doubt the effect of predators should be taken into account but in the case of *P. calodendri* this influence is slight.

(ii) During the summer period January, February and March the influence of *Tetrastichus* sp. is almost negligible and the population is kept at a low level by high temperatures and low humidities. These have an indirect influence on the psyllids through their action on the host plant and to a lesser extent act directly on the psyllids themselves.

(iii) After a secondary flush of leaves in which the condition of the tree is boosted, temperatures have dropped considerably and the effect of parasites on the population again becomes marked.

The control of population fluctuations in *P. calodendri* can be compared with that in a few other species of psyllids where population fluctuations have been studied in detail.

The control of population fluctuations of the psyllid *Cardiaspina albitextura* Taylor is extremely complex. This psyllid which lives mainly on the leaves of the gum tree *Eucalyptus blakelyi* in Australia has been thoroughly investigated, over a sixteen year period, by Clark (1962; 1963 a, b, c and d; 1964 a, b and c.) In *C. albitextura* there are only two generations annually with a third generation interrupted by an overwintering stage. This species over-winters in the early instars but is also able to survive the winter in the other stages which means that there is an over-lapping of generations at the end of the winter period at the start of the next psyllid season. Further, Clark has found, that there are three primary parasites of *C. albitextura* one of which parasitizes early stage nymphs while the other two attack the later instars. These primary parasites are themselves attacked by three hyper-parasites and the effectiveness of the hyper-parasites depends upon the level of the psyllid population. Predators as well, have a considerable influence on *C. albitextura* populations in both the nymphal and adult stages. As far as abiotic factors are concerned, temperature is of most importance in its influence on *C. albitextura* populations and acts when psyllid population levels are low. This influence is combined with that of parasite and predators to control psyllid numbers.

The population levels in P. calodendri are at a low density when compared with C. albitextura populations. The situation at low population densities has some parallels in the two species. A fundamental difference between the two species, however, is the achievement of very high population levels in C. albitextura which are not reached in P. calodendri. These lead to intra-specific competition in C. albitextura, both for food and space and as an added factor crowding in the adult stage results in a reduction in fecundity. Thus high population levels in C. albitextura have lead to further complexity and difficulty in interpretation. Obviously Clarks' very detailed conclusions are not fully covered here. The interesting point that emerges from the comparison however, is the fact that Clark comes to the same general conclusions about population control in Cardiaspina albitextura that have been reached in the undoubtedly oversimplified case of P. calodendri. Clark shows that both biotic and abiotic factors are important components in the control of C. albitextura populations and his concluding remarks sum up his over all impression:-

> "With some qualifications, each of the "conceptual models" proposed by these workers (Nicholson, 1954, Andrewartha and Birch 1954 and Milne 1962) could be used to explain the population dynamics of C. albitextura. However, in the particular case of the psyllid, and in general, the explanations provided by these models tend to over-emphasise either the role of population processes or that of environmental agencies in the determination of abundance. By doing so, they add to the difficulties inherent in the development of guiding principles for the study of population dynamics and pest management."

The dual role of "population processes" and "environmental agencies" in the control of psyllid populations are borne out quite clearly by other contributions to our knowledge of psyllid ecology. For example Pletsch (1947) has shown from laboratory and field observations that high temperatures on the one hand and predators and parasites on the other are responsible for the natural control of the potato psyllid *Paratrioza cockerelli* (Sulc). He has not dealt specifically with population dynamics in this species but his detailed biological observations clearly indicate this to be the case. Bonnemaison and Missonnier (1956) have worked on the pear psylla *Psylla pyri* L. These authors come to the conclusion that the major controlling factors in this species are the effects of high temperatures and low humidities on the early instar nymphs together with a high mortality due to the action of predators. In pear orchards in the Paris region most predators attacking aphids also attack the psyllids but parasites are very rare at all seasons.

The importance of predators in the control of psyllid populations is also emphasised by Watmough (1963) who worked on two species of broom psyllid in England. Watmough has studied the population dynamics of the psyllids, *Arytaina spartii* Guerin-Meneville and *Arytaina genistae* Latreille, and he states that during the study period from 1960 - 1963 no parasites were found. These two species of psyllids besides being controlled by predators built up to high enough population levels to make intra- and interspecific competition very important in the control of numbers. As far as abiotic factors are concerned Watmough finds that the two species differ in their responses to temperature and he says:-

> "*A. genistae* suffered more from mortality caused by unfavourable weather than *A. spartii*. Frost in Autumn, winter and spring killed many *A. genistae* nymphs and eggs. *A. spartii* is at an advantage in spring should any interspecific competition occur because it can develop at lower temperatures than *A. genistae*. This advantage would be lost in a warmer climate since laboratory studies show that *A. spartii* does not survive as well as *A. genistae* when nymphs of the same age are competing."

All the studies on psyllids dealt with show that, albeit highly complex, populations seem to be controlled by extremes of temperature on the one hand and parasites and/or predators on the other and that the balance between these two factors varies with the seasons. Laboratory studies on *Trioza erytreae* which are reported below indicate that this too is the case in the control of distribution and abundance of this species and the study of population dynamics in *P. calodendri* has assisted considerably in an understanding of the reasons for outbreaks of *T. erytreae* populations in certain areas.

6. THE BIOLOGY OF TRIOZA ERYTREAE (DEL GUERCIO).

Trioza erytreae (Del Guercio), the South African citrus psylla, has in recent years become an increasingly important pest of Citrus in this country. Until the last decade this psyllid was generally accepted as being of minor importance. The adults and immature stages of this species were listed as nursery pests and occasionally as pests of new flush on immature citrus trees. The injurious effects include distortions of the young leaves and as a result of the feeding of the insects an open gall is formed around the feeding site. Immature stages of the insect shelter in this gall, the leaves become distorted and their growth is inhibited.

During the last decade citrus psylla has spread extensively through South African orchards and has recently been found to be the vector of the virus disease known as "greening" (McClean and Oberholzer, 1965 a and b; Scharwz 1964, 1965). The symptoms of this disease are fully described by the former authors (1965b). Aspects of the disease and its relationship to T. erytreae will be discussed later and it is sufficient to say by way of introduction that large numbers of farmers in South Africa have curtailed citrus production as a direct result of "greening".

T. erytreae was not a significant pest of citrus at Mosslands and although leaves were found showing typical psylla damage the adults were found on only two occasions. T. erytreae is polyphagous however and was found occasionally on three indigenous plants at Mosslands namely Clausena anisata, Fagara capensis and Vepris undulata. Because of the low local population density no field observations were made on T. erytreae and this is therefore an account of the biology of this species based on laboratory observations. These results are then compared with published field observations on this species and has enabled definite conclusions to be drawn concerning the relationship between population numbers, distribution and environmental factors.

Systematic position.

Trioza erytreae is placed in the sub-family Triozinae Low, 1876 and the characteristics and status of this sub-family are discussed by Heslop-Harrison 1949, 1951b and 1958. The South African members of the sub-family are dealt with by Heslop-Harrison (1961). Characteristics of the sub-family include the fact that the genae are developed into distinct cones, a very obvious feature of *Trioza erytreae*, and the antennal bases are not obscured by these conical genae. The wing venation is characteristic with the bases of the radial, median and cubital veins all branching together from a single basal vein. The wings are also characterised by the absence of a pterostigma and the antennae are filiform. These are the main distinguishing characters for the sub-family.

Comments about the history and synonomy of *Trioza erytreae* are made by Ghesquiere (1958) and Van der Merwe (1941). Ghesquiere noted that the species was first found and described from citrus in Eritrea in 1918 by Del Guercio who named the insect *Aleyrodes erythreae*. Since the original description the species has been called *Trioza citri* (Laing, 1922), *Trioza merwi* (Pettey, 1923) and *Spanioza erythreae* (Boselli, 1930). The latter genus was later included in the genus *Trioza* by Tuthill (1943) who sank the genus *Spanioza*. It would appear that the correct name for the South African citrus psylla is *Trioza erythreae* (Del Guercio) and yet in a number of recent publications by South African authors on this species it has been referred to as Trioza erytreae (Del Guercio) (Van der Merwe, 1941; McClean and Oberholzer, 1965a; Annecke and Cilliers, 1963; Moran and Blowers, 1967 and Blowers and Moran, 1967). The answer to this anomaly apparently lies in Van der Merwe's paper (1941) in which he states:-

> "According to Boselli, the insect (i.e. the South African citrus psylla) was described in 1918 by Del Guercio in a "Note ed Osservazioni d' Entomologia Agraria" Florence, as Aleurodes erytreae. .... It is not understood why the specific name erythreae was substituted (by Boselli) for erytreae, but it does not appear to be justified."

In the absence of the original description by Del Guercio which could not be obtained it is difficult to decide which of these authors has recorded the facts correctly and consequently in this account Van der Merwe is followed and the specific name erytreae is used.

Developmental History.

Considering the importance of Trioza erytreae it is perhaps surprising that there are few accounts of the developmental history of this species. The first account was that Van der Merwe (1923, republished with addenda 1941) which gives a description of the habits and life history of the psyllid including developmental durations and the approximate sizes of the immature insects in various stages. Van der Merwe's experiments, although giving a basis for the biology of this insect were carried out under field conditions employing admitted imperfect experimental techniques.

The first of Van der Merwe's techniques involved keeping psyllids on cut twigs, confined in glass cylinders. This necessitated frequent replacement of the twigs and hence disturbance of the insects which Van der Merwe states "did not appear to thrive under such conditions". In his second method, insects were enclosed in a muslin sleeve on a growing twig and again disturbance of the animals was involved as the twig had to be cut and withdrawn for examination and the insects subsequently transferred to a new twig. Van der Merwe makes no mention of the numbers of psyllids raised, merely stating that such inefficient methods prevented many insects from being carried through their life cycle and that the numbers carried through might have been insufficient to enable any reliable conclusions to be drawn.

The more recent paper by Annecke and Cilliers (1963) contains only brief life history notes on T. erytreae and has no description of the immature stages stating only "according to Van der Merwe the nymph moults five times". Their studies were made on insects raised on potted seedlings which makes their results more realistic but no attempt to control the environmental conditions was made. Hence it is difficult to make any comparison between the results of these authors. The brief papers of Harris (1936) and Lavabre (1960), which deal with some aspects of the life history of T. erytreae, are the only publications containing any illustrations of this species.

The present account is an extension of our knowledge of the life history of T. erytreae under the same controlled environmental conditions which were used for the rearing of Paurocephala calodendri. Rearing the insects under these conditions enabled subsequent comparison of laboratory data with those from the field. The techniques used and the results obtained in this preliminary study of

T. erytreae have been published by Moran and Blowers (1967) but for completeness are also recorded here.

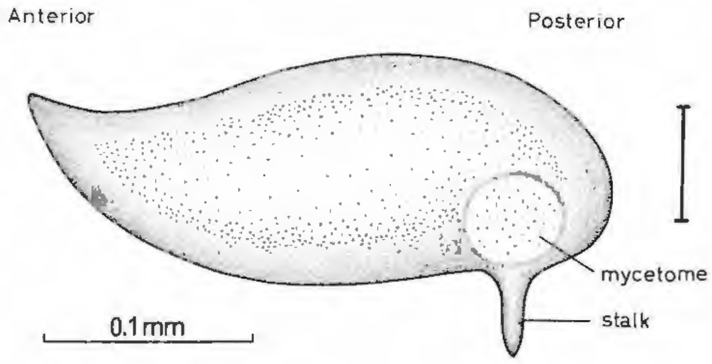
A healthy stock culture of T. erytreae, obtained from Letaba, Northern Transvaal, was maintained on rough lemon seedlings (Citrus limonia) in the laboratory. All insects used in the experiments were taken from this culture. Various methods of raising the psyllids in the environment room were tried, particularly with a view to facilitating measurements of the nymphs which have a marked preference for the under surfaces of leaves. Raising nymphs on single citrus leaves kept fresh on moist cotton wool was not satisfactory and the instar durations were excessively prolonged. Similarly the method of Van der Merwe (1941) using cut twigs was abandoned because of prolongation of the life history. The most satisfactory results were obtained when the psyllids were raised on rough lemon seedlings or in certain experiments on seedlings of other rutaceous plants, using the method of Annecke and Cilliers (1963). Citrus seedlings which were readily available were used extensively as host plants in most experiments although later it was found that Vepris undulata and Clausena anisata were more suitable and these two host plants were used in some cases. In each experiment several seedlings were used to eliminate possible effects of individual plant variation. All the plants appeared vigourous and healthy and were fertilized regularly. This method proved most satisfactory and when the seedlings were clamped upside down, the dimensions of the insects could be measured using a stereomicroscope graticule.

As with P. calodendri, adults of Trioza erytreae were enclosed in plastic bags on seedlings, allowed to lay eggs for 24 hours and then removed. The lowest temperature regime (Fig. 6a) was used initially and the hatching times of the eggs were noted. Maps were drawn of the positions of the nymphs on the leaves and the development of each individual was followed. In some experiments newly hatched nymphs were transferred, before they settled, to the growing tip of another seedling. Provided this transference was done very carefully, it had no apparent effect on the nymphs.

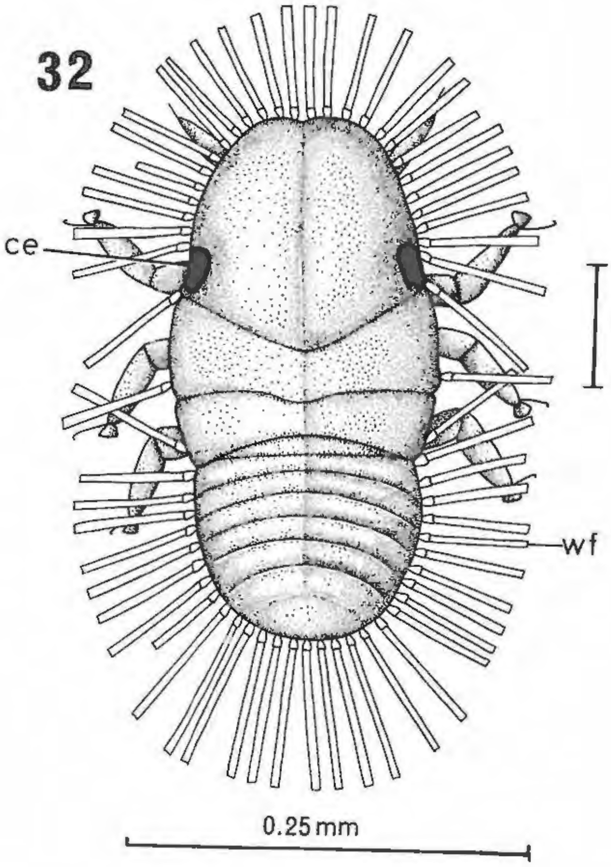
At emergence the adults of T. erytreae were pale green but with maturation a progressive colour change to dark brown followed. The sexes were easily distinguished by the shape of the abdomen and the structure of the genitalia. The females were larger than the males (see table 15 for measurements).

The longevity of the adults and the numbers of eggs laid by the females was determined by enclosing newly emerged females individually on seedlings (together with at least two males) and leaving them to oviposit. All commenced oviposition 3 - 12 days after emergence but the more usual pre-oviposition period was 3 - 6 days (compare Van der Merwe 3 - 14 days, more usually 5 - 7 days). These results correspond with the findings of Blowers and Moran (1967) in which it was found that three days were required for the development of the first mature eggs in the adult female. It was found that a single seedling did not always provide sufficient young foliage for laying purposes, and in this case females were transfered to new plants by means of a small aspirator. Care was necessary to prevent injury to the gravid females. Normally, mated females of T. erytreae lay an average of 858 eggs with a minimum

31



32



Figs. 31 - 32 Egg and first instar nymph of Trioza erytreae. Fig. 31 - lateral view of egg. Fig. 32 - first instar nymph in dorsal view. These figures may be compared with figures 33 - 36 which are drawings of the other immature stages. The scale , vertically and to the right of each figure, is drawn 100X the size of the insect. ce - compound eye; wf - waxy filament.

number of 542 and a maximum number of 1222, based on counts from eight females. At the lowest temperature regime the adult longevity was, an average of 34 days, ranging from 28 - 48 days in different individuals. (Van der Merwe reports an adult logevity of 26 - 36 days for T. erytreae). When the number of young leaves on the seedling was restricted, overcrowding inhibited oviposition,the egg laying period was extended and the females lived for a longer time than normal. Virgin females survived for over 60 days and laid very few eggs,none of which hatched.

The eggs of T. erytreae (Fig. 31) were laid on very young growth; the tips of shoots and tender stems were occasionally thickly covered with eggs but on young leaves the margins were the favoured areas. This was also noted by Van der Merwe (1941) and by Annecke and Cilliers (1963). The latter record that eggs were laid only on leaves 7 - 22 mm in length. In this study females in crowded culture conditions also oviposited on bigger leaves up to 5 cm in length.

The egg has a smooth chorion and is pale yellow in colour. Occasionally some white eggs were laid but the cause of this was not established. The average egg length recorded was 0.28 mm. Both Annecke and Cilliers and Van der Merwe give an approximate measurement of 0.5 mm for the length of the egg. Attachment of the egg to the leaf was by means of a short stalk at the posterior end which was inserted into the leaf tissue as the egg was laid. A similar process was found in the eggs of Psylla mali by Lees (1916) and in members of the closely related family of Homoptera, the Aleyrodidae. Weber (1931) and Poinar (1965) maintain that the stalk has a moisture absorbing function. The function of the egg stalk in T. erytreae, other than as a means of attaching the egg to the leaf, is uncertain, but it is likely also to be used for water absorption from the leaf. Lees (1916) working on P. mali, Van der Merwe (1941) working on T. erytreae and Clark (1962) working on Cardiaspina albitextura', observed that the eggs of all these psyllids collapsed and shrivelled when the leaf on which they were laid was cut off and allowed to dry. This was also the case with the eggs of T. erytreae in this study. In the present investigation experiments were carried out in which dyes were introduced into young leaves upon which eggs of T. erytreae had been laid. Neither analine blue nor eosin were taken up by the eggs although both dyes reached the area of the egg stalk and stained the cement in this area. It is possible of course that the egg stalk was not permeable to the dyes.

A noticeable feature of the egg was the sperical mass of short rod-like, 'symbiotic' organisms which formed the mycetome. This organelle was clearly visible in the intact egg. Most Homoptera, in all stages of the life cycle, harbour these allegedly symbiotic micro-organisms (Imms, 1957; Wigglesworth, 1965). Profft (1937), examined 22 species of psyllid and found 'symbionts' to be present in all. Each mycetome in the eggs of T. erytreae was composed of a central syncytium and a border of mono-nucleate cells, the mycetocytes. The symbionts of the syncytium appear to differ from those of the mycetocytes both in shape and staining properties. Transmission of the micro-organisms in psyllids takes place during oogenesis by invasion of the egg at the posterior pole (De Wilde, 1964). The micro-organisms infect the egg by passing from a depression at the posterior end of the oocyte, either between or through the follicular cells, and are released into the yolk cavity with the nutritive stream.

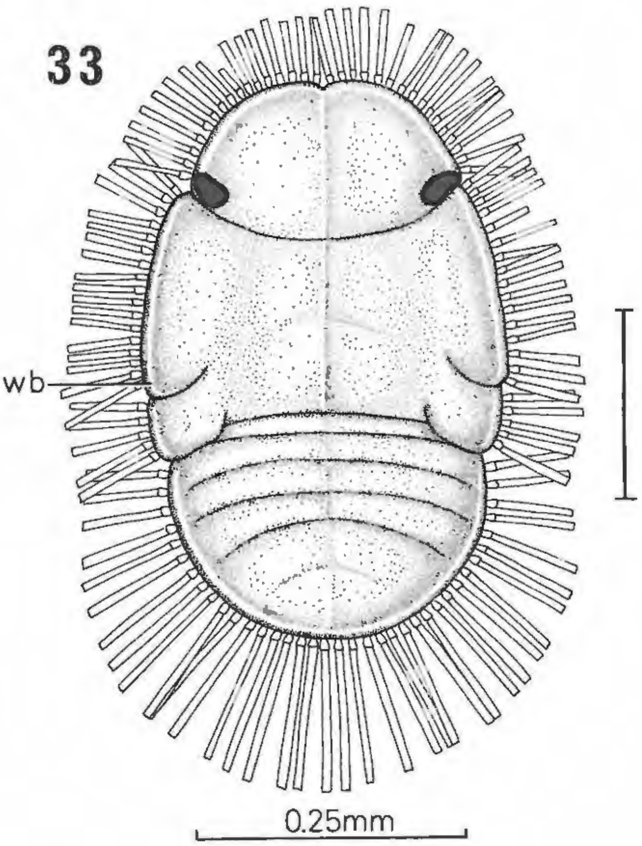
Evidence from histological sections of the developing eggs in the abdomen of the adult female of T. erytreae indicated that a similar method exists in this insect.

High temperatures have been used to kill, selectively, the micro-organisms found in insects and this technique has been used as a tool for establishing the role of these micro-organisms (Cleveland, 1924; Wigglesworth, 1965). It will be shown later that high temperatures have an adverse effect on T. erytreae, preventing eggs from hatching, inducing high mortalities in all stages and inhibiting ovarian development in the adult female. At high temperatures the mycetome shows a clear change in colour from yellow to bright orange in the adults and eggs and in the latter the mycetome moves anteriorly from its normal position at the posterior end of the eggs. These observations suggest that the effects of high temperatures on the micro-organisms in T. erytreae might contribute to the adverse effects noted when individuals of this species were subjected to high temperatures.

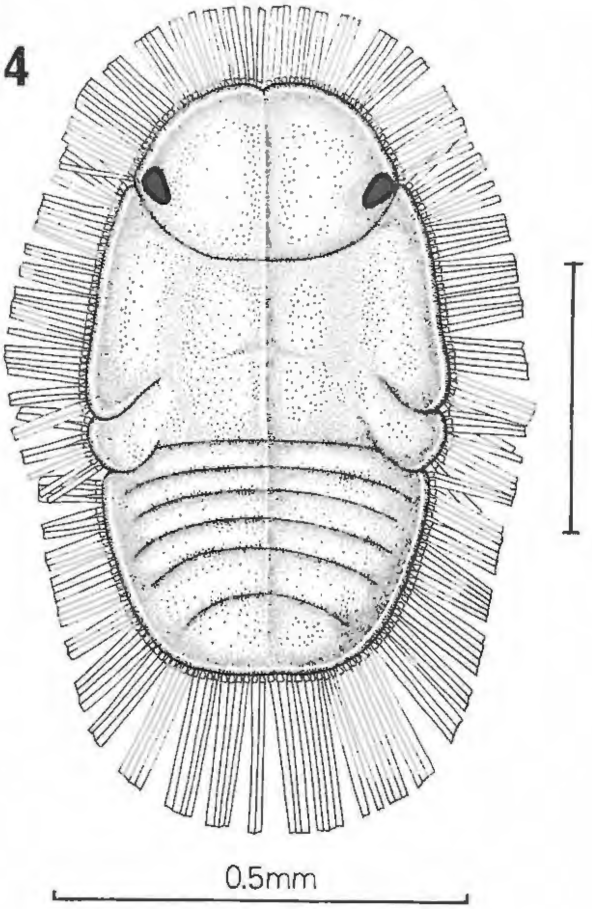
Under suitable temperature conditions the egg turned a darker yellow colour as the embryo within it developed and about one day prior to hatching two red nymphal eye spots became visible towards the anterior end of the egg.

On eclosion the first instar nymph of T. erytreae wandered about for a short time before settling down to insert its mouth parts and begin feeding. The preferredsite was the youngest growth available, including soft stems. On young leaves the nymphs were usually restricted to the undersides. Only under very crowded

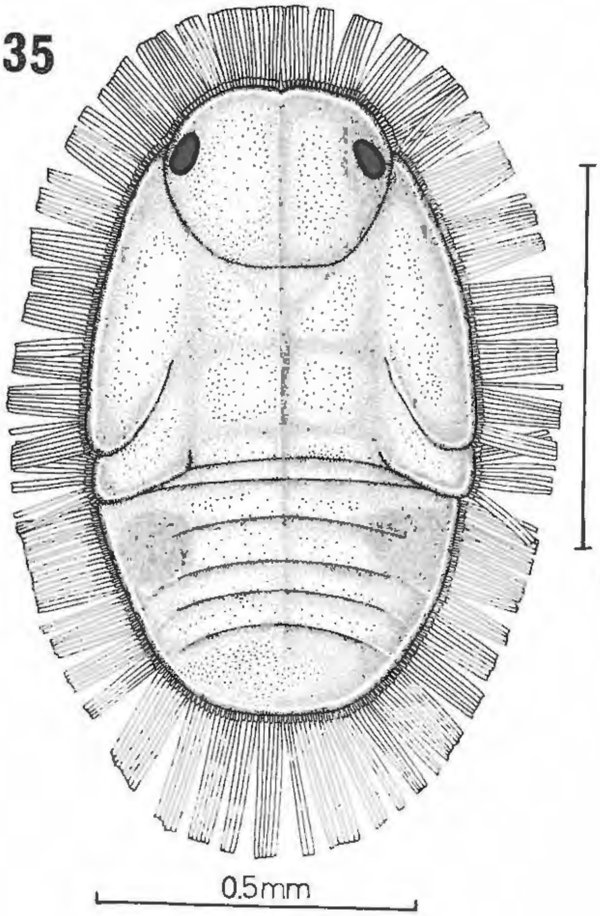
33



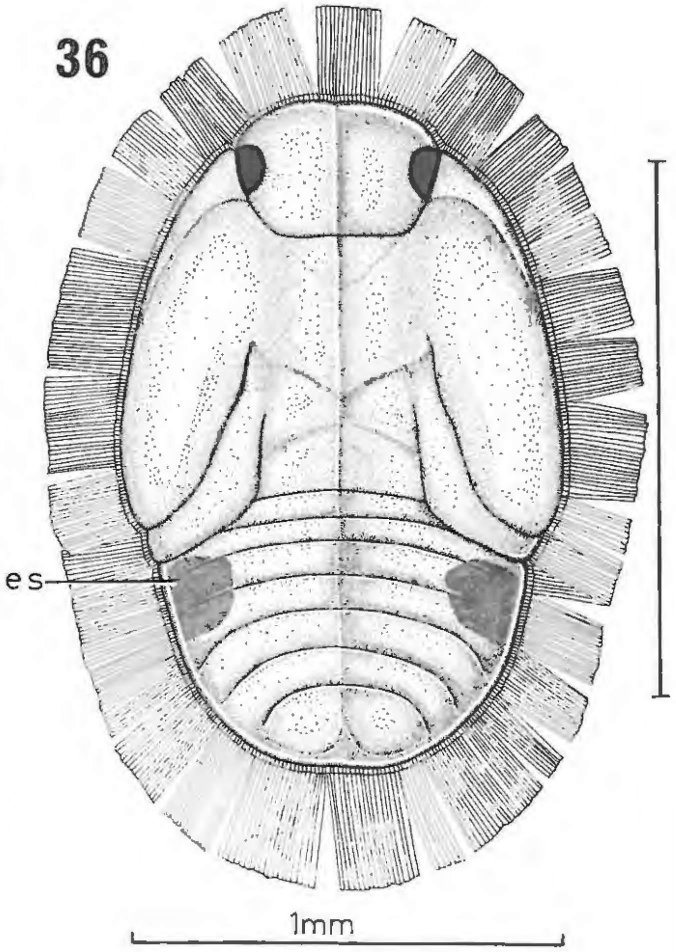
34



35



36



Figs. 33 - 36 Immature stages of *Trioza erytreae*. Fig. 33 - second instar nymph. Fig. 34 - third instar nymph. Fig. 35 - fourth instar nymph. Fig. 36 - fifth instar nymph. All are drawn in dorsal view. These figures may be compared with figures 31 - 32. The scale, vertically and to the right of each figure, is drawn 100X the size of the insect. wb - wing bud; es - "eye" spot.

conditions were they found on the upper surface. Preliminary investigations of this response to the abaxial surface of the leaves in first stage nymphs of T. erytreae were carried out. Briefly, gravity and temperature played no part in the response of the insects to the abaxial surface of leaves but light assisted in their orientation. The over riding factor, however, appeared to be texture of the leaf and as these animals normally fed through the stomata it seems likely that they were responding to the stomata on the lower surfaces of the leaf. In all the rutaceous plants studied i.e. Citrus sp., Fagara capensis, Calodendrum capense, Clausena anisata and Vepris undulata stomata are restricted to the abaxial surface and it seemed possible that T. erytreae nymphs had a positive tactile response to the stomata. On the other hand the adaxial surface has a higher concentration of oil glands and it is possible that the nymphs could have had a negative chemo- or tactile response to these glands. In any event with all five plant species the vast majority of nymphs settled on the lower surface of the leaf although a few seemed to feed adequately through the general adaxial leaf surface. This explanation does not seem to apply to P. calodendri as equal numbers of later instars settle on both leaf surfaces. Clark (1962) has shown that adults and nymphs of Cardiaspina albitextura feed through the stomata on both leaf surfaces of the gum Eucalyptus blakelyi. Stomata are equally distributed on both surfaces, in this species.

There were five nymphal instars in T. erytreae which are shown in dorsal view in figures 32 - 36. A feature common to all the nymphal stages was a margin of white "waxy" filaments fringing the body. At the start of each instar the filaments were very short but during the intermoult period they increased considerably in length and their relative length may be used as a rough estimate of the maturity of the nymphs in any one instar. Further, the number of filaments increased with each moult and there were approximately 50 filaments around the periphery of the body in the first instar nymph, 100 in the second instar, 200 in the third instar, 300 in the fourth instar and 450 in the fifth instar nymphs. The number of filaments was not constant for each instar, but varied with individual nymphs. All the nymphal stages were sedentary and as Van der Merwe (1941) has noted once the nymphs settled, they remained in one place unless disturbed or crowded.

Feeding activity of the nymphs affected the leaf at one point and caused the formation of pit like depressions beneath the bodies of the insects. The leaf surface around the open gall became devoid of chlorophyll. The size of the galls varied with different host plants. The galls were insignificant on Calodendrum capense while they were large and extremely well formed on Vepris undulata. In the latter species gall formation was noticeable during the first day of nymphal feeding. Within the open gall the nymphs were closely applied to the leaf surface and only the dorsal flattened surface of the body and the fringing waxy filaments were exposed. The five nymphal instars were similar in appearance being pale yellow in colour with red eye spots.

The first instar nymph (Fig. 32) has a distinctive head shape, a small number of waxy filaments and has no wing buds. The second and third instar nymphs (Figs. 33 and 34) were very difficult to distinguish from each other. The only reliable criteria for separating these two instars were the size differences and the number of waxy filaments around the periphery of the body. The wing buds were not distinctive enough to allow separation. After the moult to the fourth instar two pale brown spots appeared on the abdomen of the nymph (Fig. 35). These brown spots became darker in the fifth instar nymph (Fig. 36) resembling large "eye" spots. Their significance is obscure but they provided useful distinguishing features. Some of the fifth stage nymphs turned brown in colour with maturation while others were yellow, but all changed to pea green just prior to emergence.

Relative sizes of the egg and nymphs of T. erytreae can be seen from the vertical scale lines drawn with figures 31 - 36. Measurements of the five nymphal stages at the lowest temperature regime on citrus seedlings at the start and end of each instar together with the mean, standard error and number of readings are contained in table 15. These data are also shown diagramatically in figure 37 (a).

Temperature effects.

The durations of the various developmental stages in T. erytreae were determined at the three different temperature regimes already described for P. calodendri (Fig. 6) and the insects were reared on citrus seedlings. The average and maximum and minimum instar durations with respective standard errors at the lowest temperature regime are shown in table 16 and figure 37 (a). These data can be compared with those in table 17 and figure 37 (b) which are similar records at the median temperature regime.

Table 15. Lengths and breadths (in mm) of the eggs, adults and each of the five nymphal instars of *Trioza erytreae* at the start and end of each stage. The animals were reared on *Citrus* sp. at the lowest temperature regime of 28 Hr°C/week above and 266 Hr°C/Week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	ADULT Male	ADULT Female
Length at start of instar								
NUMBER OF READINGS	20	99	86	78	74	73	32	36
MINIMUM	0.22	0.25	0.44	0.63	0.94	1.38	1.88	1.88
MAXIMUM	0.31	0.34	0.50	0.75	1.03	1.63	2.50	2.50
MEAN	0.28	0.32	0.50	0.71	1.01	1.50	2.17	2.24
STANDARD ERROR	0.001	0.002	0.002	0.004	0.004	0.01	0.03	0.03
Length at end of instar								
NUMBER OF READINGS	-	88	78	75	72	68	-	-
MINIMUM	-	0.33	0.46	0.66	1.00	1.38	-	-
MAXIMUM	-	0.41	0.56	0.75	1.13	1.66	-	-
MEAN	-	0.37	0.50	0.73	1.04	1.54	-	-
STANDARD ERROR	-	0.001	0.001	0.003	0.004	0.01	-	-
Breadth at start of instar								
NUMBER OF READINGS	20	99	93	78	72	70	29	32
MINIMUM	0.13	0.13	0.25	0.33	0.47	0.88	0.44	0.44
MAXIMUM	0.13	0.19	0.31	0.44	0.69	1.06	0.56	0.56
MEAN	0.13	0.16	0.26	0.40	0.61	0.99	0.51	0.48
STANDARD ERROR	-	0.001	0.002	0.003	0.005	0.006	0.008	0.007
Breadth at end of instar								
NUMBER OF READINGS	-	93	78	72	70	69	-	-
MINIMUM	-	0.16	0.25	0.38	0.50	0.88	-	-
MAXIMUM	-	0.19	0.31	0.44	0.69	1.03	-	-
MEAN	-	0.17	0.27	0.40	0.62	1.00	-	-
STANDARD ERROR	-	0.001	0.002	0.003	0.005	0.006	-	-

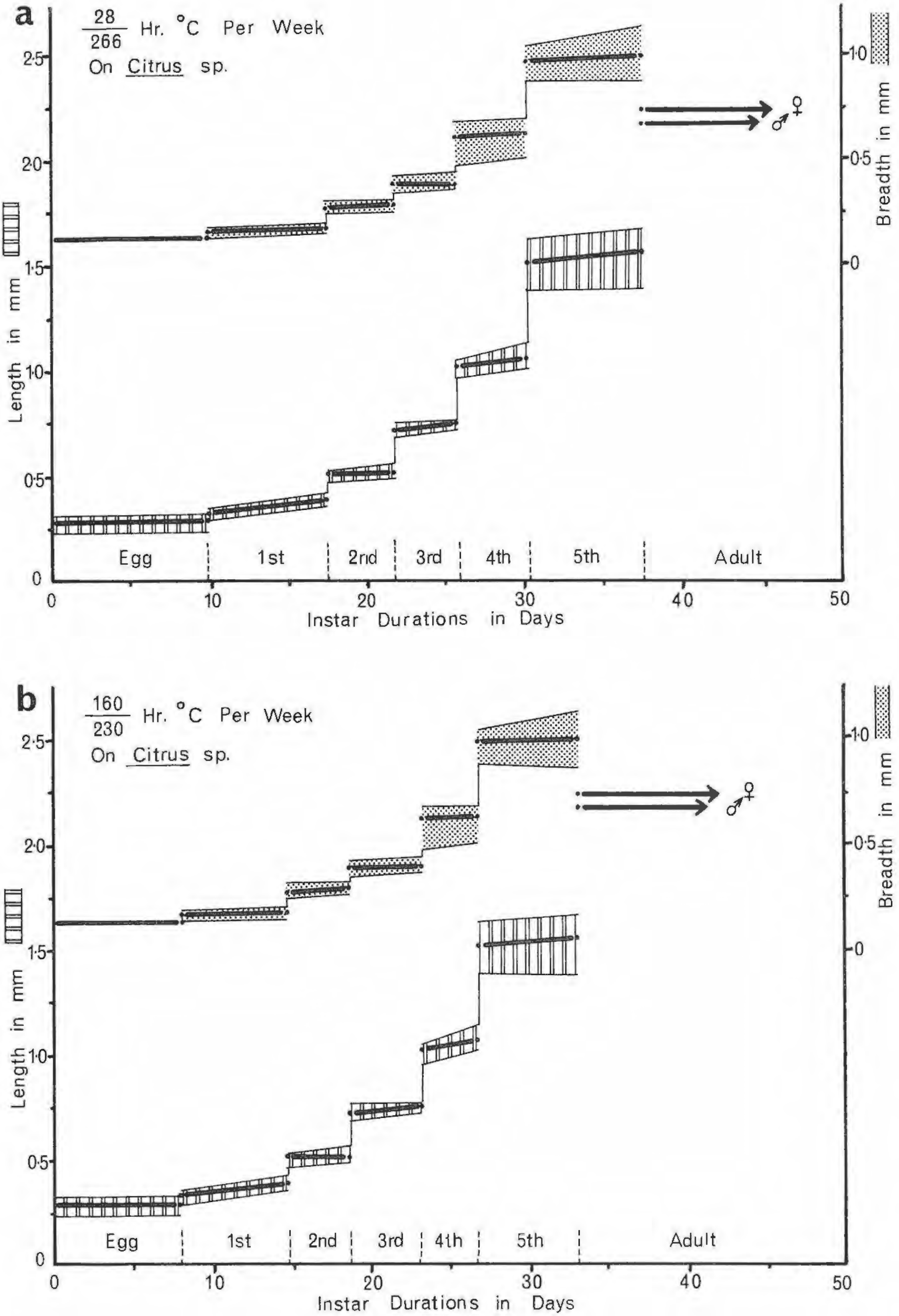


Fig. 37 Lengths and breadths of the developmental stages in *Trioza erytreae* reared on *Citrus* sp. plotted against instar durations. Size limits of the insects in each instar are represented by the thin lines on either side of the thick line which indicates mean size. Fig. 37 a - development at the lowest temperature regime. Fig. 37 b - development at the median temperature regime.

Table 16 Instar durations (in days) of Trioza erytreae at the "lowest" temperature regime of 28 Hr°C per week above and 266 Hr°C per week below 20°C. The insects were reared on citrus.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	TOTAL
NUMBER OF READINGS	127	97	78	73	71	68	67
MINIMUM	8	4	2	3	2	5	31
MAXIMUM	13	15	11	7	7	13	48
MEAN	9.54	7.56	4.37	4.07	4.39	7.32	37
STANDARD ERROR	0.094	0.186	0.179	0.121	0.111	0.176	0.515

Table 17 Instar durations (in days) of Trioza erytreae at the "median" temperature regime of 160 Hr°C per week above and 230 Hr°C per week below 20°C. The insects were reared on citrus.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	TOTAL
NUMBER OF READINGS	129	46	34	28	25	19	19
MINIMUM	7	4	2	2	3	4	28
MAXIMUM	10	11	8	8	5	9	35
MEAN	8.06	6.83	3.91	4.21	3.80	6.32	31.5
STANDARD ERROR	0.036	0.251	0.233	0.293	0.129	0.297	0.509

Two main points emerge from an examination of Tables 16 and 17. Firstly the instar durations were significantly decreased at the median temperature regime. There was a 15.5% decrease in the duration of the egg stage, a 9.7% decrease in the first stage, a 10.5% decrease in the second instar, a 13.4% decrease in the fourth stage, a 13.7% decrease in the fifth stage and a total instar duration decrease of 14.7%. In the third stage there was no significant difference between the durations at both temperature regimes. In fact the instar duration at the median temperature in this instar was slightly longer than that at the lower temperature regime. No explanation can be put forward for this observed effect. Secondly the standard errors for the durations were greater at the median temperature regime which shows that there was considerably more spread around the mean. However, when the insects were reared at the median temperature regime this effect was not noticed in the egg stage. This was an indication that the lower temperature regime was more suitable to these animals in spite of the fact that instar durations were slightly prolonged at this temperature. There is evidence to support this in a comparison of mortality data. Table 18 shows the total number of psyllid losses and deaths. Deaths were recorded when a corpse was found, otherwise a loss was recorded and the animal was presumed to be dead.

Table 18 Total mortalities, deaths and losses recorded for *T. erytreae* at the lowest, median and highest temperature regimes. The insects were all reared on citrus.

TEMPERATURE REGIME	NUMBER OF READINGS	"LOSSES"	DEATHS	TOTAL DEATHS AND LOSSES
"LOWEST" $\frac{28}{266}$Hr°C/Week	90	6.9%	3.6%	10.5%
"MEDIAN" $\frac{160}{230}$Hr°C/Week	70	34.2%	17.8%	52.0%
"HIGHEST" $\frac{380}{200}$Hr°C/Week	Eggs and other stages do not survive.			

Table 18 shows that, at the lowest temperature regime, the total number of deaths and losses was 10.5% while the percentage mortality rose steeply to 52% at the median temperature regime.

At the median temperature regime the nymphs showed "increased restlessness". They often moved from their original positions on the leaf whereas at the lowest temperature regime the nymphs usually remained in their original positions.

At the highest temperature regime eggs of T. erytreae did not hatch although development proceeded until the compound eyes of the first stage nymph became visible beneath the chorion. This suggested that if the eggs were then moved to a lower temperature they might hatch. This was tried but the eggs did not hatch and it would appear that high temperatures after a certain stage of embryonic development killed the developing psyllids.

First instar nymphs, if introduced into the room at the highest temperature regime were very susceptible and, if newly emerged, died within about seven hours. Older first instar nymphs survived for just over a day. Second and third stage nymphs survived for a few days longer under these conditions while a very low percentage of fourth stage nymphs survived and moulted to the fifth instar. There was also a very high mortality among the fifth stage nymphs. One individual began to moult to the adult stage but died in the process. Adults on the other hand survived for several days at this temperature, the more mature adults being most resistant, but in all cases oocyte development was inhibited and very few eggs were laid. From this evidence it is suggested that the lowest temperature regime or a temperature a little higher than this was most favourable for development and survival in T. erytreae.

The effects of temperature on the development of T. erytreae are of interest because of the widely accepted supposition among biologists and citrus producers that the distribution of the South African citrus psylla is limited by temperature. The psyllids have been observed to thrive only in the high lying cooler areas and to becoming more prevalent during cooler seasons. The reason for this distribution is supported by the evidence presented in this investigation and also explain the results of Van der Merwe (1941) who noted high mortalities among nymphs of T. erytreae during the "hot summer days" in Durban while in cooler weather the insects thrived. Van der Merwe also noted a great difference in the number of psyllids infesting two citrus trees which grew about six yards apart. In the one case the tree was in a shady position and supported a large psyllid population while the other which was subjected to higher temperatures as it stood in the open, did not support psyllids during the hot weather. During cooler weather, however, both trees supported psyllids equally.

The adverse effects of high temperatures on T. erytreae reported here are not unusual among psyllids generally and several workers have noted similar effects on other species. For example Bonnemaison and Missonnier (1956) working on the pear psylla, Psylla pyri, in the Paris region have shown that young nymphs are more susceptible to high temperatures than the older nymphs and high mortalities in this species can be attributed to the heat and dryness during the summer period. Conversely they have observed that periods of rapid psyllid build up or periods which are characterised by psyllid outbreaks are always associated with moderate temperatures between 14° and 16°C. The relationship between temperature and the potato psyllid Paratrioza cockerelli is also well known. Hill(1947) has studied the weather conditions in Nebraska for the period 1921 to 1946 and has associated an outbreak of potato psyllid in 1938 with a mild wet July followed by two months of warm weather. Normally, high temperatures in July resulted in high mortalities in this species and this was confirmed by several authors whose work is reviewed by Hill. The suppression of numbers of P. cockerelli in the field due to high temperatures has also been noted in detail by Pletsch (1947) and Wallis (1955). Clark (1962) has shown in field observations on Cardiaspina albitextura that population increases to outbreak proportions in this species followed periods of cool weather although he has shown that other factors also play a role thus complicating the temperature effect.

The conclusions of these authors about the effects of temperature on psyllids have been based upon field observations. It is surprising that so few laboratory studies have been made on temperature effects in these animals. Apart from the results in the present investigation it would seem that the only other laboratory study on the effects of temperature on psyllids is that of List (1939) who worked on the effects of temperature upon egg deposition, egg hatch and nymphal development in Paratrioza cockerelli. List conducted an extensive series of experiments on this insect using incubators to vary temperatures. He found that oviposition, hatching and survival were drastically reduced at 32°C and one or two hour periods of 38°C almost stopped egg laying and was lethal to eggs and nymphs. Further P. cockerelli survived best at temperatures from 21°C to 27°C and List suggested that these results explain the build up of populations in the high altitude, cool areas of Colorado and the great reduction in numbers of psyllids in mid summer.

However, it should be noted that apparently not all psyllids are adversely affected by high temperatures. Husain and Nath (1927) and Atwal (1962) in their accounts of the Indian citrus psylla Diaphorina citri do not mention any suppression of numbers in this species by high temperatures and it would appear that it has acquired some measure of temperature tolerance. Also in brief reports on several species of psyllid by Mathur (1935) in which he deals specifically with seasonal history there is no mention of high temperature induced mortalities.

Development on and the selection of Host plants by Trioza erytreae.

An important aspect of the biology of Trioza erytreae is that this species is polyphagous. The polyphagous habit has been noted by Van der Merwe (1941) and by Harris (1936), both of whom state that the indigenous hosts of T. erytreae are members of the family Rutaceae. Van der Merwe states also that all varieties of Citrus sp. are attacked and that among indigenous hosts Vepris undulata, Fagara capensis and Clausena anisata have been found to be infested and "are probably among the original food plants". Van der Merwe suggests that Clausena inequalis (= anisata) is probably the preferred host and that eggs laid on this species develop more rapidly than those on other host plants. It is of obvious importance to establish the most probable indigenous host of T. erytreae especially as this species is one of economic importance. Citrus cannot be the original host because it was introduced comparatively recently into South Africa. This does not preclude the possibility that citrus psylla may have been introduced at the same time as

Citrus and subsequently spread to closely related plants.

Several aspects of the biology of Trioza erytreae suggest that it has moved from the indigenous Rutaceae to citrus and has infested citrus secondarily. The evidence supporting this assumption includes data on the instar durations and sizes realized by the nymphs on different hosts and evidence from the behaviour of adult insects in their choice of hosts for feeding and oviposition.

Effects of host on sizes of T. erytreae

Trioza erytreae was reared on five host plants, namely Citrus limonia (Rough lemon), Calodendrum capense, Fagara capensis, Clausena anisata and Vepris undulata. These plants were maintained in the environment room at the lowest temperature regime. As before, individual insects were measured and a daily record was kept. The sizes of the nymphs on each of the host plants at the start and end of the instars together with the standard error and the number of readings on which the calculations were based are contained in tables 19 - 23.

Table 19 and figure 38 (a) give the sizes of the nymphs when reared on Calodendrum capense, table 20 and figure 37 (a) those when reared on citrus, table 21 and figure 38 (b) for those on Fagara capensis, table 22 and figure 39 (a) for Clausena anisata and table 23 and figure 39 (b) give the sizes for animals reared on Vepris undulata. Table 20 contains the same data as table 15 but is included in this position to facilitate comparison. Table 24 summarizes all these data.

Table 19 Lengths and breadths (in mm) of the eggs, adults and each of the five nymphal instars of Trioza erytreae at the start and end of each stage. The animals were reared on Calodendrum capense at the lowest temperature regime of 28 Hr°C/week above and 266 Hr°C/week below 20°C.

Length at start of instar.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	ADULT Male	ADULT Female
NUMBER OF READINGS	20	80	7	4	2	1	-	-
MINIMUM	0.22	0.28	0.44	0.66	0.97	1.44	-	-
MAXIMUM	0.31	0.34	0.51	0.69	1.00	1.44	-	-
MEAN	0.28	0.31	0.47	0.68	0.99	1.44	-	-
STANDARD ERROR	0.001	0.002	0.011	0.008	0.016	-	-	-
Length at end of instar.								
NUMBER OF READINGS	-	9	4	3	1	1	-	-
MINIMUM	-	0.34	0.50	0.66	1.04	1.58	-	-
MAXIMUM	-	0.41	0.50	0.71	1.04	1.58	-	-
MEAN	-	0.38	0.50	0.69	1.04	1.58	-	-
STANDARD ERROR	-	0.006	-	0.012	-	-	-	-
Breadth at start of instar.								
NUMBER OF READINGS	20	80	7	4	2	1	-	-
MINIMUM	0.13	0.16	0.28	0.38	0.56	1.00	-	-
MAXIMUM	0.13	0.21	0.31	0.41	0.56	1.00	-	-
MEAN	0.13	0.17	0.29	0.40	0.56	1.00	-	-
STANDARD ERROR	-	0.002	0.005	0.008	-	-	-	-
Breadth at end of instar.								
NUMBER OF READINGS	-	9	4	3	1	1	-	-
MINIMUM	-	0.19	0.29	0.38	0.63	1.04	-	-
MAXIMUM	-	0.21	0.31	0.44	0.63	1.04	-	-
MEAN	-	0.20	0.31	0.42	0.63	1.04	-	-
STANDARD ERROR	-	0.004	0.005	0.021	-	-	-	-

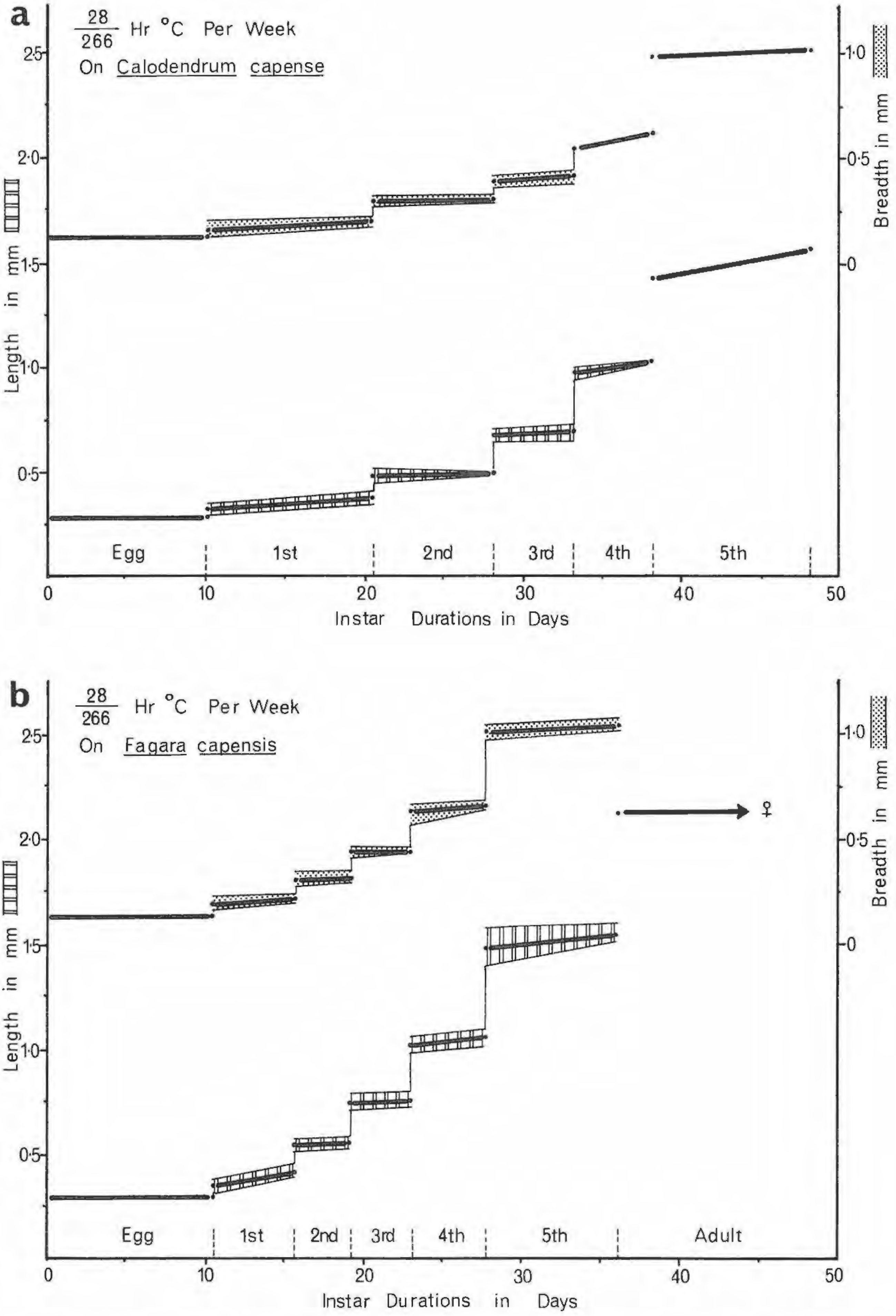


Fig. 38 Lengths and breadths of the developmental stages in Trioza erytreae plotted against instar durations. Size limits of the insects in each instar are represented by the thin lines on either side of the thick line which indicates mean size. Fig. 38 a - development on Calodendrum capense at the lowest temperature regime. Fig. 38 b - development on Fagara capensis at the lowest temperature regime.

Table 20 Lengths and breadths (in mm) of the eggs, adults and each of the five nymphal instars of Trioza erytreae at the start and end of each stage. The animals were reared on Citrus sp. at the lowest temperature regime of 28 Hr°C/week above and 266 Hr°C/week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	ADULT Male	ADULT Female
Length at start of instar								
NUMBER OF READINGS	20	99	86	78	74	73	32	36
MINIMUM	0.22	0.25	0.44	0.63	0.94	1.38	1.88	1.88
MAXIMUM	0.31	0.34	0.50	0.75	1.13	1.63	2.50	2.50
MEAN	0.28	0.32	0.50	0.71	1.01	1.50	2.17	2.24
STANDARD ERROR	0.0001	0.002	0.002	0.004	0.004	0.010	0.026	0.032
Length at end of instar								
NUMBER OF READINGS	-	88	78	75	72	68	-	-
MINIMUM	-	0.33	0.46	0.66	1.00	1.38	-	-
MAXIMUM	-	0.41	0.56	0.75	1.13	1.66	-	-
MEAN	-	0.37	0.50	0.73	1.04	1.54	-	-
STANDARD ERROR	-	0.001	0.001	0.003	0.004	0.010	-	-
Breadth at start of instar								
NUMBER OF READINGS	20	99	93	78	72	70	29	32
MINIMUM	0.13	0.13	0.25	0.33	0.47	0.88	0.44	0.44
MAXIMUM	0.13	0.19	0.31	0.44	0.69	1.06	0.56	0.56
MEAN	0.13	0.16	0.26	0.40	0.61	0.99	0.51	0.48
STANDARD ERROR	-	0.001	0.002	0.003	0.005	0.006	0.008	0.007
Breadth at end of instar								
NUMBER OF READINGS	-	93	78	72	70	69	-	-
MINIMUM	-	0.16	0.25	0.38	0.50	0.88	-	-
MAXIMUM	-	0.19	0.31	0.44	0.69	1.13	-	-
MEAN	-	0.17	0.27	0.40	0.62	1.00	-	-
STANDARD ERROR	-	0.001	0.002	0.003	0.005	0.006	-	-

Table 21 Lengths and breadths (in mm) of the eggs, adults and each of the five nymphal instars of *Trioza erytreae* at the start and end of each stage. The animals were reared on *Fagara capensis* at the lowest temperature regime of 28 Hr°C/week above and 266 Hr°C/week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	ADULT Male	ADULT Female
Length at start of instar								
NUMBER OF READINGS	-	14	13	14	10	9	-	8
MINIMUM	-	0.29	0.50	0.71	0.97	1.38	-	1.88
MAXIMUM	-	0.34	0.56	0.78	1.04	1.56	-	2.25
MEAN	-	0.33	0.53	0.73	1.01	1.47	-	2.13
STANDARD ERROR	-	0.004	0.006	0.006	0.009	0.018	-	0.043
Length at end of instar								
NUMBER OF READINGS	-	11	12	11	9	8	-	-
MINIMUM	-	0.38	0.53	0.71	1.03	1.50	-	-
MAXIMUM	-	0.41	0.56	0.78	1.09	1.59	-	-
MEAN	-	0.40	0.54	0.74	1.05	1.55	-	-
STANDARD ERROR	-	0.005	0.003	0.006	0.009	0.012	-	-
Breadth at start of instar								
NUMBER OF READINGS	-	16	11	13	10	8	-	8
MINIMUM	-	0.17	0.28	0.42	0.56	0.97	-	0.50
MAXIMUM	-	0.21	0.33	0.46	0.67	1.04	-	0.54
MEAN	-	0.19	0.30	0.44	0.63	1.01	-	0.52
STANDARD ERROR	-	0.004	0.005	0.002	0.011	0.011	-	0.009
Breadth at end of instar								
NUMBER OF READINGS	-	11	11	11	9	8	-	-
MINIMUM	-	0.19	0.29	0.44	0.63	1.00	-	-
MAXIMUM	-	0.22	0.33	0.46	0.67	1.06	-	-
MEAN	-	0.20	0.31	0.44	0.65	1.04	-	-
STANDARD ERROR	-	0.004	0.005	0.003	0.005	0.007	-	-

Table 22 Lengths and breadths (in mm) of the eggs, adults and each of the five nymphal instars of *Trioza erytreae* at the start and end of each stage. The animals were reared on *Clausena anisata* at the lowest temperature regime of 28 Hr°C/week above and 266 Hr°C/week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	ADULT Male	ADULT Female
Length at start of instar								
NUMBER OF READINGS	20	37	30	29	27	26	9	17
MINIMUM	0.22	0.29	0.46	0.66	0.94	1.42	1.88	2.06
MAXIMUM	0.31	0.38	0.54	0.78	1.16	1.66	2.56	2.63
MEAN	0.28	0.32	0.50	0.72	1.06	1.53	2.26	2.36
STANDARD ERROR	0.0001	0.004	0.003	0.006	0.010	0.012	0.074	0.043
Length at end of instar								
NUMBER OF READINGS	-	30	29	27	26	26	-	-
MINIMUM	-	0.34	0.51	0.71	1.00	1.53	-	-
MAXIMUM	-	0.44	0.56	0.79	1.17	1.75	-	-
MEAN	-	0.39	0.53	0.76	1.08	1.62	-	-
STANDARD ERROR	-	0.004	0.004	0.004	0.008	0.010	-	-
Breadth at start of instar								
NUMBER OF READINGS	20	37	30	29	27	26	9	17
MINIMUM	0.13	0.17	0.28	0.38	0.63	0.88	0.56	0.54
MAXIMUM	0.13	0.19	0.33	0.47	0.71	1.13	0.69	0.69
MEAN	0.13	0.18	0.30	0.44	0.66	1.03	0.60	0.61
STANDARD ERROR	-	0.002	0.002	0.004	0.005	0.012	0.015	0.010
Breadth at end of instar								
NUMBER OF READINGS	-	30	29	27	26	26	-	-
MINIMUM	-	0.17	0.29	0.42	0.63	1.00	-	-
MAXIMUM	-	0.25	0.33	0.47	0.71	1.16	-	-
MEAN	-	0.19	0.31	0.45	0.66	1.08	-	-
STANDARD ERROR	-	0.003	0.003	0.003	0.005	0.010	-	-

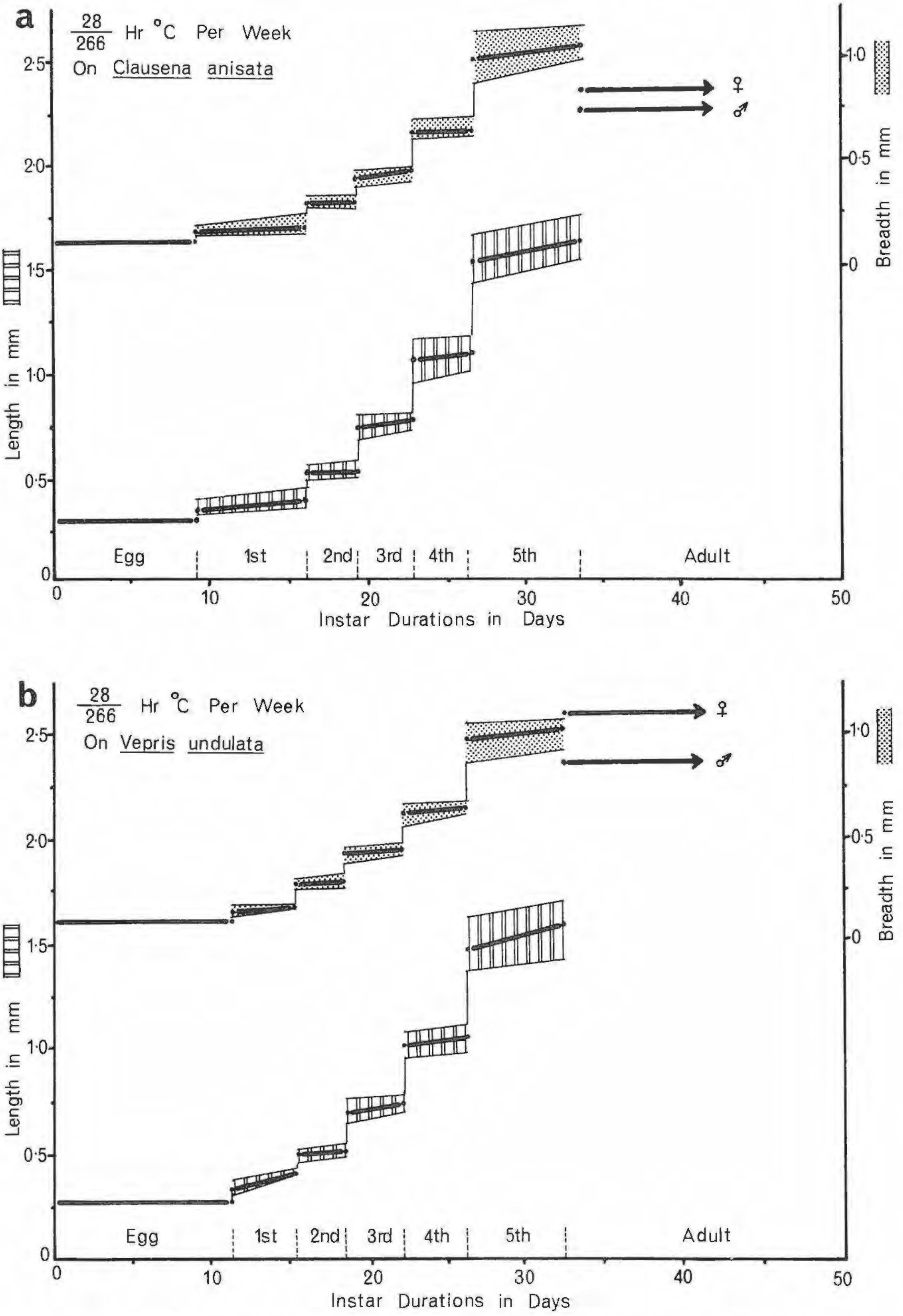


Fig. 39 Lengths and breadths of the developmental stages in Trioza erytreae plotted against instar durations. Size limits of the insects in each instar are represented by the thin lines on either side of the thick line which indicates mean size. Fig. 39 a - development on Clausena anisata at the lowest temperature regime. Fig. 39 b - development on Vepris undulata at the lowest temperature regime.

Table 23 Lengths and breadths (in mm) of the eggs, adults and each of the five nymphal instars of Trioza erytreae at the start and end of each stage. The animals were reared on Vepris undulata at the lowest temperature of 28 Hr°C/week above and 266 Hr°C/week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	ADULT Male	ADULT Female
				Length at start of instar				
NUMBER OF READINGS	-	29	22	26	24	25	10	13
MINIMUM	-	0.31	0.47	0.67	0.96	1.38	2.19	2.56
MAXIMUM	-	0.38	0.53	0.78	1.09	1.63	2.50	2.88
MEAN	-	0.35	0.51	0.70	1.03	1.49	2.39	2.66
STANDARD ERROR	-	0.004	0.004	0.006	0.007	0.015	0.035	0.027
				Length at end of instar				
NUMBER OF READINGS	-	3	27	14	24	25	-	-
MINIMUM	-	0.41	0.50	0.71	1.00	1.44	-	-
MAXIMUM	-	0.42	0.56	0.78	1.13	1.71	-	-
MEAN	-	0.41	0.52	0.75	1.07	1.60	-	-
STANDARD ERROR	-	0.003	0.004	0.008	0.007	0.012	-	-
				Breadth at start of instar				
NUMBER OF READINGS	-	28	24	26	25	24	10	13
MINIMUM	-	0.17	0.28	0.42	0.58	0.92	0.56	0.63
MAXIMUM	-	0.21	0.31	0.46	0.69	1.08	0.63	0.75
MEAN	-	0.18	0.30	0.44	0.63	1.00	0.58	0.66
STANDARD ERROR	-	0.002	0.002	0.003	0.006	0.011	0.008	0.011
				Breadth at end of instar				
NUMBER OF READINGS	-	3	27	14	25	26	-	-
MINIMUM	-	0.19	0.29	0.44	0.63	0.94	-	-
MAXIMUM	-	0.19	0.33	0.46	0.69	1.09	-	-
MEAN	-	0.19	0.31	0.45	0.66	1.04	-	-
STANDARD ERROR	-	0.000	0.003	0.003	0.004	0.008	-	-

Table 24 Means, lengths and standard errors for measurements of T. erytreae nymphs reared on five rutaceous plants at the lowest temperature regime. This summarizes the data in tables 19 - 23.

HOST PLANT		1st	2nd	3rd	4th	5th	ADULT Male	ADULT Female
Calodendrum capense	MEAN LENGTH	0.38	0.50	0.69	1.04	1.58	-	-
	STANDARD ERROR	0.006	-	0.012	-	-	-	-
Citrus Rough Lemon	MEAN LENGTH	0.37	0.50	0.73	1.04	1.54	2.17	2.24
	STANDARD ERROR	0.001	0.001	0.003	0.004	0.010	0.026	0.032
Clausena anisata	MEAN LENGTH	0.39	0.53	0.76	1.09	1.62	2.26	2.36
	STANDARD ERROR	0.004	0.004	0.004	0.008	0.010	0.074	0.043
Fagara capensis	MEAN LENGTH	0.40	0.54	0.74	1.05	1.55	-	2.13
	STANDARD ERROR	0.005	0.003	0.006	0.009	0.012	-	0.043
Vepris undulata	MEAN LENGTH	0.41	0.52	0.75	1.07	1.60	2.39	2.66
	STANDARD ERROR	0.003	0.004	0.008	0.007	0.012	0.035	0.027

Some general conclusions may be drawn from tables 19 - 24 about the suitability of these host plants to T. erytreae. The first point of interest is that the size of insects on emergence from the eggs was not the same. Although the differences were very small, there was a statistically significant difference between the sizes of the insects on emergence when the eggs were laid on citrus, Calodendrum, or Fagara as compared with those laid on Vepris and Clausena. (The standard errors given with each set of data in the tables were used to determine whether or not size differences were significantly different. In any particular case an average was obtained of the two means in question and the null hypothesis made that the two means were not significantly different. Three standard errors were then added or subtracted from the means in each case and if these figures overlapped the average of the means, then the means were not significantly different.)

This suggested that the developing embryo in the egg was gaining nutriments from the plant and that the size of the insect on emergence would depend on the suitability of the host plant. Although clearly requiring further evidence this is not improbable in the light of what has been said about the possible absorptive function of the egg stalk. The indication that Citrus, Calodendrum and Fagara were less suitable as host plants for total development of T. erytreae than either Vepris or Clausena was further borne out by a comparison of sizes in later development of nymphs on each of these plants. The sizes attained by T. erytreae reared on citrus and Calodendrum were very similar and in all cases were smaller than the sizes attained on the other three host plants. Nymphs of T. erytreae, reared on Fagara, were as large at the end of the first, second and third instars as their counterparts on *Clausena* and *Vepris*, but those on the latter two plants grew significantly larger in the last two instars.

A comparison of the sizes of the adult females produced on *Fagara*, *Clausena* and *Vepris* shows that those on *Fagara* were much smaller than those on either *Vepris* or *Clausena* and in fact they were even smaller than those from citrus. *T. erytreae* did not survive to the adult stage on *Calodendrum*. On this evidence it would appear that *Vepris* and *Clausena* were the two most suitable hosts for *T. erytreae*. The sizes of the immature stages on either host were not significantly different. Adults reared from *Vepris* however, were slightly larger than those reared from *Clausena*.

Effects of host on nymphal instar durations.

Differences in instar durations of the various stages of *T. erytreae* on all five host plants provides additional evidence supporting the contention that *Vepris* or *Clausena* are the original hosts. Mean instar durations of the immature stages of *Trioza erytreae* on the five rutaceous host plants are recorded in tables 25 to 29, together with maximum and minimum durations of the instars, the standard error in each case and the number of readings on which the calculations were based. As before all these data were derived from animals reared at the lowest temperature regime. Table 26 contains the same data as table 16 but is included to facilitate comparison. Also to aid the comparison, the mean durations and standard errors of the durations for each stage on each of the five host plants are extracted from tables 25 to 29 and included together in table 30.

Table 25 Instar durations (in days) of *T. erytreae* reared on *Calodendrum capense* at the lowest temperature regime of 28 Hr°C per week above and 266 Hr°C per week below 20°C.

VARIATE \ STAGE	EGG	1st	2nd	3rd	4th	5th	TOTAL
NUMBER OF READINGS	84	8	4	3	1	1	1
MINIMUM	8	7	6	3	5	9	45
MAXIMUM	14	17	10	7	5	9	45
MEAN	10.10	10.38	7.75	5.00	5.00	9.00	45,00
STANDARD ERROR	0.15	1.28	0.85	1.15	-	-	-

Table 26 Instar durations (in days) of *T. erytreae* reared on citrus at the lowest temperature regime of 28 Hr°C per week above and 266 Hr°C per week below 20°C.

VARIATE \ STAGE	EGG	1st	2nd	3rd	4th	5th	TOTAL
NUMBER OF READINGS	127	97	78	73	71	68	67
MINIMUM	8	4	2	3	2	5	31
MAXIMUM	13	15	11	7	7	13	48
MEAN	9.54	7.56	4.37	4.07	4.39	7.32	36.95
STANDARD ERROR	0.094	0.186	0.179	0.121	0.111	0.176	0.515

Table 27 Instar durations (in days) of *T. erytreae* reared on *Fagara capensis* at the lowest temperature regime of 28 Hr°C per week above and 266 Hr°C per week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	TOTAL
NUMBER OF READINGS	24	15	15	13	9	9	9
MINIMUM	10	4	2	3	4	7	33
MAXIMUM	11	6	5	5	6	11	40
MEAN	10.58	5.07	3.40	4.00	4.89	8.22	36.00
STANDARD ERROR	0.10	0.12	0.19	0.16	0.26	0.47	0.71

Table 28 Instar durations (in days) of *T. erytreae* reared on *Clausena anisata* at the lowest temperature regime of 28 Hr°C per week above and 266 Hr°C per week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	TOTAL
NUMBER OF READINGS	39	30	29	28	26	26	26
MINIMUM	9	6	3	3	3	6	31
MAXIMUM	9	9	5	5	5	9	37
MEAN	9.00	7.00	3.31	3.64	3.58	6.88	33.23
STANDARD ERROR	-	0.136	0.100	0.106	0.110	0.140	0.270

Table 29 Instar durations (in days) of *T. erytreae* reared on *Vepris undulata* at the lowest temperature regime of 28 Hr°C per week above and 266 Hr°C per week below 20°C.

STAGE VARIATE	EGG	1st	2nd	3rd	4th	5th	TOTAL
NUMBER OF READINGS	31	27	27	26	25	25	25
MINIMUM	11	4	3	3	3	6	31
MAXIMUM	12	5	4	4	4	7	34
MEAN	11.03	4.07	3.22	3.94	3.88	6.16	31.52
STANDARD ERROR	0.03	0.05	0.08	0.07	0.07	0.08	0.14

Table 30 Mean durations and standard errors for the instars of *T. erytreae* nymphs reared on five rutaceous plants at the lowest temperature regime. This summarizes the data in tables 25 - 29.

HOST PLANT		EGG	1st	2nd	3rd	4th	5th	TOTAL
Calodendrum capense	MEAN DURATION	10.10	10.38	7.75	5.00	5.00	9.00	45.00
	STANDARD ERROR	0.15	1.28	0.85	1.15	-	-	-
Citrus Rough Lemon	MEAN DURATION	9.54	7.56	4.37	4.07	4.39	7.32	36.95
	STANDARD ERROR	0.094	0.186	0.179	0.121	0.111	0.176	0.515
Clausena anisata	MEAN DURATION	9.00	7.00	3.31	3.64	3.58	6.88	33.23
	STANDARD ERROR	-	0.136	0.100	0.106	0.110	0.140	0.270
Fagara capensis	MEAN DURATION	10.58	5.07	3.40	4.00	4.89	8.22	36.00
	STANDARD ERROR	0.103	0.12	0.19	0.16	0.26	0.47	0.707
Vepris undulata	MEAN DURATION	11.03	4.07	3.22	3.94	3.88	6.16	31.52
	STANDARD ERROR	0.03	0.05	0.08	0.07	0.07	0.08	0.14

These data show that the duration of the egg stage differs significantly from one host plant to the other. Thus the shortest duration for the egg stage was recorded for eggs laid on Clausena anisata where all the eggs hatched after nine days and the longest incubation period was recorded from eggs laid on Vepris undulata where the mean egg duration was 11.03 days. These data show that a short duration in the egg stage resulted in a small nymph on emergence. A long duration of the egg stage resulted in larger first instar nymphs. The duration of the egg stage when the eggs were laid on Clausena, citrus and Calodendrum were respectively 9.00, 9.54 and 10.10 days and the mean size of the first instar nymph on emergence were 0.28 mm in each case. On the other hand the duration of the egg stage when the eggs were laid on Fagara and Vepris were respectively 10.58 and 11.03 days and the mean sizes of the first instar nymphs on emergence 0.33 mm and 0.35 mm. Thus the nymphs from these two hosts were significantly larger than those which emerged from eggs on the other three host plants.

This suggested that the nymphs from eggs on Fagara and Vepris were emerging in a more mature state than those on the other three host plants and this was supported by reference to the durations of the first stage nymphs on the five different host plants. The comparison showed that the mean duration of the first stage in nymphs reared on Vepris and Fagara were respectively 4.07 and 5.07 days while that of nymphs reared on Clausena, citrus and Calodendrum were respectively 7.00, 7.56 and 10.38 days. (The very long duration of the first stage for nymphs reared on Calodendrum was partly due to the unsuitable nature of the host plant.) The differences in the first instar duration in these two groups are statistically very significant and support the hypothesis that nymphs reared from eggs laid on *Vepris* and *Fagara* were emerging in a more mature state.

The physiological explanation for this phenomenon is obscure but these data add support to the supposition that substances of great importance to the development of the embryonic insect are entering the egg through the egg stalk and that the nature of these substances differs with different host plants. This whole problem of absorption through the egg stalk in *T. erytreae* would repay further investigation.

The instar durations recorded in table 30 show that they were always prolonged with psyllids on *Calodendrum capense* and the total instar duration was very much longer. Clearly this host plant was unsuitable for *T. erytreae*. Insects reared on citrus seedlings also show significant prolongation of the instars as compared to those on *Clausena*, *Fagara* and *Vepris*. This together with the evidence presented on the sizes of immature stages of *T. erytreae* when reared on citrus makes it clear that while citrus is an adequate host plant it is certainly not as suitable as some of the indigenous hosts. *Fagara*, in terms of instar durations of *T. erytreae*, was a host only slightly more suitable than citrus. In fact the durations of the fifth instar nymphs reared on *Fagara* were longer than those for insects on citrus. The total instar durations of insects reared on *Clausena anisata* and *Vepris undulata* were found to be 33.23 days and 31.52 days respectively and both these mean totals were shorter than those for insects reared on the other three host plants. The performances of these insects in all instars on *Clausena* and *Vepris* were very similar although *Vepris* may be thought of as slightly more suitable than *Clausena* and both more suitable than citrus or *Fagara*.

Relative mortalities on different host plants.

Additional evidence in support of the conclusions on suitability of hosts to T. erytreae comes from a comparison of mortalities and losses of nymphs on the five different host plants. These data are presented in table 31.

Table 31 Total mortalities, deaths and losses, recorded for T. erytreae nymphs reared on five different rutaceous plants at the lowest temperature regime.

HOST PLANT	NUMBER OF READINGS	"LOSSES"	DEATHS	TOTAL
Calodendrum capense	76	45%	55%	100%
Citrus (Rough Lemon)	90	6.9%	3.6%	10.5%
Fagara capensis	20	45%	15%	60%
Clausena anisata	39	36%	0%	36%
Vepris undulata	29	6.6%	3.3%	10%

The data indicate that Calodendrum was an entirely unsuitable host for development of T. erytreae while Fagara, although being adequate was not as good as either Clausena, Vepris or citrus. Vepris was probably the most suitable. This was further borne out by observations on wandering activities in the immature stages. (The term wandering activities means simply changes in position of the nymphs on the leaves when they withdrew their mouth parts and moved to new feeding sites.) Such wandering activity was very common among immature stages on citrus especially in the first and second instars whereas it seldom took place when the nymphs were reared on Clausena and Vepris. It was evident that the nymphs on the latter two hosts were sedentary once they had settled down whereas positional shifts were common among nymphs on citrus. On the balance of evidence it is suggested that *Vepris undulata* is probably the indigenous host of *T. erytreae* with *Clausena anisata* remaining a very likely alternate host.

It is of interest to note the taxonomic affinities of these plant genera within the family Rutaceae. It is generally accepted among botanists (Phillips, 1951; Willis, 1951) that citrus is probably most closely related to *Clausena* among the indigenous Rutaceae which were considered in this investigation. *Fagara* and *Calodendrum* are botanically closely related but neither these two genera nor *Vepris* are closely related to citrus. The psyllids themselves however, are probably responding to some substance in the leaves of these plants and an obvious possibility is that the psyllids may be responding to the essential oil content of the leaves. This leads to a consideration of the responses of the adult psyllids to the five different host plants.

Adult responses to different host plants.

Experiments were designed to test the responses of adult *T. erytreae* to citrus and to the four indigenous host plants. Initially simple choice chambers were constructed comprising a rectangular trough in which stood five small water filled bottles. The mouths of the bottles were covered with thin polythene and the stem of a test leaf was pushed through the polythene into the water beneath. Leaves treated in this manner kept fresh for about five days. The top of the trough containing the test leaves was covered with thin polythene which was pierced with numerous holes. This sucessfully prevented the escape of the psyllids and prevented water condensation on the sides of the vessel and on the leaves. Psyllids were introduced into the test chamber in which there was a choice between five leaves. Readings of the numbers of animals feeding on the leaves were taken at intervals. Usually the experiment was started in the late afternoon because the psyllids were strongly positively phototactic and their first response was to settle on the polythene roof of the trough. Settling on the leaves began during the night. Once the insects had settled on a leaf and begun feeding they remained in one position for several hours. The experimental troughs were rotated through 180° at intervals during the light hours. This counteracted any affects of unequal lighting from the lights in the environment room, in which all experiments were conducted. Besides a record of the numbers of insects feeding on each of the five leaves, the numbers of eggs laid on each leaf were counted at the conclusion of each experiment.

The first experiment in the series was intended as a control in which 37 female and 3 male T. erytreae were given a choice between five citrus leaves. In fact it served as an indicator of the pitfalls inherent in this experimental design. The average numbers of psyllids attracted to each of the five leaves together with other relevant data are contained in table 32.

Table 32. Average numbers of *T. erytreae* adults feeding on each of five citrus leaves and the numbers of eggs laid on each leaf.

	LEAF CHOICE					NUMBERS OF PSYLLIDS USED				
	Citrus 1	Citrus 2	Citrus 3	Citrus 4	Citrus 5	Male	Female	Total	No. Obs.	Time Hrs.
AVERAGE NUMBERS FEEDING	5.4	5.6	8.3	3.3	6.9	3	37	40	8	17
X^2 AVERAGE NUMBERS FEEDING	0.04	0.02	0.98	1.15	0.17	Total $X^2 = 2.36$ $p > 0.5$ Not significant				
NUMBERS OF EGGS	0	83	0	0	184	3	37	40	-	17

In table 32 and in all the following tables in this series the numbers of observations which were made are tabulated together with the total duration of the experiment in hours. The average numbers of psyllids feeding over the duration of the whole experiment is derived by a division of the total numbers of the insects recorded on the leaves by the number of observations. Chi square values are given for the number of animals feeding in each case. Additive Chi values are also given. The comments on the significance of the data are derived from these values.

Table 32 shows that the average number of insects feeding on the five citrus leaves varied from 8.3 in the one case to 3.3 in another. Eggs were laid on only two leaves, predominantly on citrus leaf 5. These differences in the numbers of individuals feeding are not significant although they are unsatisfactory in a control experiment. The reasons for these discrepancies became apparent after the start of the experiment. Firstly the numbers of psyllids on the leaves was in direct proportion to the area of each leaf, thus the largest leaf,

leaf 3, had the most psyllids on it and leaf 4, which was the smallest, the least. Secondly leaf 3 was just large enough to touch the polythene of the container and in their wanderings on the roof the insects came into chance contact with the tip of the leaf and proceeded to feed. It is also interesting that leaf 3 which had the largest number of psyllids feeding upon it was not used as an oviposition site and eggs were laid solely on the two tenderest leaves namely leaves 2 and 5. In the latter case most of the eggs were laid on an extremely small leaf at the base of leaf 5 which measured only a few millimeters in length.

Further experiments were conducted in which leaves of approximately equal sizes were chosen and of approximately equal age and tenderness. Care was also taken to ensure that none of the leaves touched the roof or sides of the experimental vessel. As a result of these precautions a second control experiment gave more satisfactory results which are contained in table 33. In this control experiment psyllids that had been reared on citrus were given a choice between five citrus leaves.

Table 33 Average numbers of *T. erytreae* adults feeding on each of five citrus leaves and the numbers of eggs laid on each leaf.

	LEAF CHOICE					NUMBERS OF PSYLLIDS USED				
	Citrus 1	Citrus 2	Citrus 3	Citrus 4	Citrus 5	Male	Female	Total	No. obs.	Time Hrs.
AVERAGE NUMBERS FEEDING	6.0	6.6	4.0	4.7	4.0	2	35	37	16	47
X^2 AVERAGE NUMBERS FEEDING	0.16	0.44	0.24	0.31	0.24	Total $X^2 = 1.39$ $P > 0.5$ Not significant.				
NUMBERS OF EGGS	19	7	18	40	4	2	35	37	-	47

The control experiments showed that given a choice of five leaves from the same host plant almost equal numbers of adults of T. erytreae fed on each of the leaves and that each was used as an oviposition site.

In four subsequent experiments adults were given a choice between leaves of all five genera namely Citrus, Vepris, Clausena, Fagara and Calodendrum. In the first of these choice experiments adults, which had been reared on Citrus sp. for at least one generation, were given a choice between leaves from the five plant genera. The results are presented in table 34.

Table 34 Average numbers of T. erytreae adults feeding on leaves of citrus and four indigenous hosts, and the numbers of eggs laid on each leaf. The insects were reared on citrus.

	LEAF CHOICE					NUMBERS OF PSYLLIDS USED				
	Citrus 1	Vepris 2	Claus-ena 3	Fagara 4	Calo. 5	Male	Female	Total	No. Obs.	Time Hrs.
AVERAGE NUMBERS FEEDING	8.4	3.9	0.6	2.6	3.1	-	-	36	14	65
X^2 AVERAGE NUMBERS FEEDING	5.97*	0.01	2.60	0.33	0.01	Total $X^2 = 9.01$ $p<0.05$ *				
NUMBERS OF EGGS	118	41	0	14	0	-	-	36	-	65

Calo. = Calodendrum

The data in table 34 show that adults of T. erytreae reared on citrus had a significant preference for citrus leaves both as a feeding and oviposition site. Greater numbers of psyllids and eggs were present on the citrus leaf than on any of the other leaves. Vepris was chosen less frequently for feeding and oviposition but was more attractive than either of the other three hosts. This attraction to citrus was also shown in subsequent experiments even though the psyllids had been reared for at least one generation on either *Clausena* or *Vepris*.

Adult psyllids which had been reared on *Clausena anisata* were given a choice between leaves from the five host plants. The average numbers of psyllids feeding on each leaf are contained in table 35 (a) and the results of a replicate experiment in table 35 (b).

Table 35 (a) Average numbers of *T. erytreae* adults feeding on leaves of citrus and four indigenous hosts and the numbers of eggs laid on each leaf. The insects were reared on *Clausena anisata*.

	LEAF CHOICE					NUMBERS OF PSYLLIDS USED				
	Citrus 1	Vepris 2	Clausena 3	Fagara 4	Calo. 5	Male	Female	Total	No. Obs.	Time Hrs.
AVERAGE NUMBERS FEEDING	11.6	7.4	1.7	0.6	4.7	3	40	43	7	23
X^2 AVERAGE NUMBERS FEEDING	** 7.88	0.93	2.36	* 4.07	0.05	Total $X^2 = 15.29$ $p<0.01$**				
NUMBERS OF EGGS	241	191	0	21	34	3	40	43	-	23

Calo. = Calodendrum

Table 35 (b) Results of a replicate experiment to those shown in table 35 (a).

	LEAF CHOICE					NUMBERS OF PSYLLIDS USED				
	Citrus 1	Vepris 2	Clausena 3	Fagara 4	Calo. 5	Male	Female	Total	No. Obs.	Time Hrs.
AVERAGE NUMBERS FEEDING	13.3	10.2	3.7	0.5	5.2	3	37	40	6	25
X^2 AVERAGE NUMBERS FEEDING	** 6.80	1.96	1.27	* 5.64	0.30	Total $X^2 = 15.97$ $p<0.01$**				
NUMBERS OF EGGS	232	254	2	0	10	3	37	40	-	25

Calo. = Calodendrum

The data in tables 35 (a) and 35 (b) should be compared with those in tables 36 (a) and 36 (b) in which replicated results are given for the choice of hosts exhibited by T. erytreae adults which have been reared for at least one generation on Vepris undulata plants.

Table 36 (a) Average numbers of T. erytreae adults feeding on leaves of citrus and four indigenous hosts and the number of eggs laid on each leaf. The insects were reared on Vepris undulata.

	LEAF CHOICE					NUMBERS OF PSYLLIDS USED				
	Citrus 1	Vepris 2	Clausena 3	Fagara 4	Calo. 5	Male	Female	Total	No. Obs.	Time Hrs.
AVERAGE NUMBERS FEEDING	3.1	1.5	0.2	0.3	1.2	-	-	13	10	50
X^2 AVERAGE NUMBERS FEEDING	2.49	0.31	0.93	0.78	0.07	Total $X^2 = 4.58$ $p<0.50$ Not significant				
NUMBERS OF EGGS	193	29	0	0	0	-	-	13	-	50

Calo. = Calodendrum

Table 36 (b) Results of a replicate experiment to those shown in table 36 (a).

	LEAF CHOICE					NUMBERS OF PSYLLIDS USED				
	Citrus 1	Vepris 2	Clausena 3	Fagara 4	Calo. 5	Male	Female	Total	No. Obs.	Time Hrs.
AVERAGE NUMBERS FEEDING	10.4	3.0	0.5	0.5	1.1	0	20	20	14	65
X^2 AVERAGE NUMBERS FEEDING	** 17.19	0.03	2.18	2.18	1.29	Total $X^2 = 22.87$ $p < 0.001$**				
NUMBERS OF EGGS *	4	0	0	1	0	0	20	20	-	65

Calo. = Calodendrum

* Newly emerged virgin females used hence low numbers of eggs.

The data contained in tables 34, 35 and 36 show that significant numbers of adults of T. erytreae chose citrus as a host for feeding and oviposition in preference to the indigenous hosts tested. This response to citrus was consistent irrespective of the host on which the insects were reared. It was clear that in all cases Vepris was the next most attractive host for feeding and oviposition while the other three host plants were only slightly attractive and were rarely used as oviposition sites. It is interesting that Clausena proved to be least attractive to these psyllids as previous studies had shown it to be an ideal host for the development of the immature stages.

On this information it is suggested that Vepris undulata may be the indigenous host of T. erytreae. It is further suggested that the substance which acts as an attractant to T. erytreae in Vepris undulata is present in citrus and the introduction of citrus into this country has had the effect of attracting T. erytreae from the indigenous vegetation onto citrus. In other words the evidence points to Vepris undulata as the indigenous host of T. erytreae and although Vepris is more favourable for development of the psyllid, citrus has become an important secondary host as a result of some substance in the leaves which is very highly attractive to the psyllid.

Several unsuccessful attempts were made to isolate a fraction from citrus leaves which was attractive to the citrus psylla. These attempts although not successful are of some interest. The first problem in an investigation of this sort was to determine a suitable solvent or extraction method which would isolate the phagostimulant material. This was largely a matter of trial and error and in the experiments the suggestions of Thorsteinson (1955) were found to be most useful.

Steam distillation from citrus leaves was tried first and several different choice chambers were designed in which the extract was tested against distilled water. These choice chambers, which included among others Y tubes, with and without air currents, and double ended tubes with the ends covered in cellophane abutting onto the test solutions were all unsatisfactory and further attempts were abandoned. In two subsequent siting experiments the psyllids were given a choice between a Calodendrum leaf dipped in steam distilled extract and another dipped in distilled water; also artificial leaves were constructed from different materials and the artificial leaves were dipped in either steam extract or distilled water. In both cases the psyllids showed no preferential response to either of the extract covered leaves.

As a result two other extraction procedures were tried. In one, citrus leaves were homogenised in methanol and in the other citrus leaves were homogenised in water. *T. erytreae* adults when given a choice between two leaves of *Calodendrum*, used as a control, fed equally frequently from both leaves although the majority of the 20 animals used in the experiment settled for long periods elsewhere in the apparatus and only for short periods on the leaves. Given a choice between a *Calodendrum* leaf dipped in distilled water and another sprayed with a concentrated citrus/methanol extract an average of eight out of 20 psyllids fed on the untreated *Calodendrum* leaf and an average of two on the leaf which had been treated with extract. In a similar siting experiment the psyllids were given a choice between two *Calodendrum* leaves one of which had been treated with an aqueous extract of citrus leaves and ten of the 20 psyllids in the experiment were attracted to the treated leaf while only one of the 20 was found on the untreated leaf. These two trials suggested that, if anything, the methanol concentrate was acting as a repellant or antifeedant, at least in the concentrations used, while the aqueous concentrate showed promise of containing the attractant.

Further experiments were conducted in an attempt to assess the attractant properties of aqueous extract of citrus leaves on adults of *T. erytreae*. These experiments did show that in all cases citrus proved very highly attractive to the adults both as a host for feeding and oviposition when tested against *Calodendrum* leaves dipped in aqueous extract of citrus leaves. There was also no significant reaction of the psyllids to citrus extract, dipped *Calodendrum* leaves compared with undipped Calodendrum leaves.

Clearly the problem of host selection in T. erytreae would repay more detailed investigation along the lines already outlined by many workers for host selection in the Aphididae. Studies on the chemo-tactic basis of host selection in this closely related family have progressed far (Kennedy, 1961; Thorsteinson, 1960; Dethier, 1951; Alikhan, 1960; Fraenkel, 1958; Fraenkel et al. 1960; and many others) and recently an artificial method of feeding aphids has been devised (Mittler and Dadd, 1963). Following this a series of papers has appeared on improved synthetic diets for these insects, one of the latest in the series being that of Dadd (1967). Comparison between the mechanisms of host selection found in aphids and that in T. erytreae remains a possibility for future investigation.

A comment in the literature which attracted attention in this regard was the opinion of Kennedy (1961),

> "The implication of all this work (work by numerous authors on the relation between nutritional requirements and host selection in phytophagous insects) is that insects are equipped with means of sensory discrimination serving their host-specificity requirements, but with none directly serving their nutritional requirements ......"

This certainly seems to be the case with T. erytreae where citrus was chosen as a host for feeding and oviposition by the adults although the nutritional value of this host, as gauged by development in the immature stages, was far less than that of either Vepris or Clausena. Another point that is very clear in host selection by aphids is that leaf textures, physiological state of the leaves etc. have a considerable influence on host choice and this again is true for T. erytreae where the youngest flush of growth was always preferred to older leaves.

Lastly, Clark's paper (1963a) on factors affecting the attractiveness for oviposition by Cardiaspina albitextura is of particular relevance to this study on T. erytreae. Clark records that in C. albitextura the choice of gum leaves as oviposition sites depends on certain properties of the leaf and the attractiveness of the leaves is increased by the presence of psyllid eggs while it is decreased by the presence of feeding adults or nymphs on the leaves. It is possible that besides the attraction shown by T. erytreae to young leaves, a similar situation may exist in this species and this possibility is being investigated.

The economic implications of host choice experiments conducted on T. erytreae are discussed later.

Moulting times in Trioza erytreae.

During the experiments on host choice in T. erytreae numerous insects were reared on Clausena, Vepris and citrus seedlings in the environment room at the lowest temperature regime. Records were kept on the numbers of insects in each instar which had moulted during the period from 6 p.m. to 8 a.m. and from the period 8 a.m. to 6 p.m. The first of these periods was a "dark" period except for two hours from 6 a.m. to 8 a.m. These data gave an estimate of the numbers of psyllids in all stages moulting during the "dark" and the "light" periods. Clearly the "dark" and the "light" periods were associated with temperature and humidity changes (see figure 6) and the psyllids might have been responding to one or a combination of these environmental signals. However, for convenience, these periods are referred to as "dark" and "light" periods and the numbers of psyllids moulting during these times are recorded in table 37.

Table 37 The numbers of T. erytreae in each stage moulting during the "dark" and "light" periods in the environment room. For further explanation see text.

MOULT	1st - 2nd		2nd - 3rd		3rd - 4th		4th - 5th		5th - Adult	
TIME OF MOULT	D	L	D	L	D	L	D	L	D	L
NUMBER OF PSYLLIDS	72	71	58	52	51	53	47	54	2492	577
PERCENTAGE	50.3	49.7	52.7	47.3	49.0	51.0	46.5	53.5	81.2	18.8
TOTAL	143		110		104		101		3069	

D = Dark hours 6 p.m. to 8 a.m. L = Light hours 8 a.m. to 6 p.m.

Table 37 shows that all the nymphal moults took place with almost equal frequency during the light and dark periods. The final moult, however, from fifth instar to adult took place mostly during the dark period and 81.2% of all the individual moults recorded occurred during this period. This percentage was consistent for both sexes and of 1143 moults recorded for female insects 81% moulted during the dark period and 19% during the light period. Of 348 recorded moults of male insects 81.3% moulted during the dark period and 18.7% during the light period.

The fact that approximately 80% of the moults to the adult stage in T. erytreae occurred during the dark period is probably of adaptive significance. It would allow the adult to sclerotize fully before the onset of daylight when the threat from predators is probably increased. The dark period is also associated with high humidities which would decrease the risk of desiccation during the critical and prolonged moult period from fifth instar nymph to adult.

The nymphal stages on the other hand are sedentary and moult relatively quickly and there appears to be no obvious advantage to be gained by moulting at any particular time of the day.

Sex Determination.

An aspect of importance in the biology of Trioza erytreae is that the ratio of males to females was seldom 1:1; more usually there was a preponderance of females. This fact was first observed when sex ratio counts were made of the laboratory population of T. erytreae and it was decided to investigate the matter further. Only one environment room was available allowing only preliminary observations on this aspect and this excluded the possibility of replicating experiments.

The first conclusive data about sex ratios in T. erytreae came from experiments in the constant environment room in which individual females were reared on separate citrus seedlings at the lowest temperature regime and records were kept of the sexes of the progeny. The parents of the generation of females used in these experiments were also reared at the lowest temperature regime and the numbers and sexes of the progeny are recorded in table 38. (Complete records of progeny were only obtained for the females listed in table 38.)

Table 38 Sexes of the progeny of T. erytreae females reared in the environment room. For further explanation see text.

NUMBER OF INDIVIDUAL PARENT	NUMBER OF HOST PLANTS USED	PROGENY		APPROXIMATE SEX RATIO		
		MALE	FEMALE	MALE		FEMALE
37	1	9	1	9	:	1
44	3	25	12	2	:	1
47	1	46	31	1.5	:	1
45	2	23	24	1	:	1
1	1	0	26	ALL FEMALE		
2	1	0	47		"	
3	2	0	87		"	
4	2	0	29		"	
16	3	0	139		"	
17	2	0	61		"	
18	1	0	3		"	
19	3	0	134		"	
20	2	0	94		"	
40	3	0	83		"	
54	3	0	57		"	

Table 38 shows that, in a number of cases, a particular female was transferred from the original host plant to one or two other plants. This transference became necessary when the demale had covered the small tender leaves with eggs and required fresh oviposition sites. From these experiments it was learned that, in the majority of cases, the female reared under the lowest temperature regime and subjected to 12 hours dark and 12 hours light gave rise to 100% female progeny. Female number 45 however gave rise to equal numbers of males and females while females 37, 44 and 47 produced a larger percentage of males. These results although scanty do indicate that females of T. erytreae may produce 100% female progeny, equal numbers of males and females or a predominance of males. There was no instance of production of 100% males.

Spot samples of psyllids from the laboratory population gave an indication that the sex ratio may alter from season to season. To check this, batches of T. erytreae were reared on Vepris outside the laboratory buildings and just prior to emergence of the adults the plants were placed in the environment room to record the sex ratio of the emerging insects. The first of these stock cultures was started with eggs laid on 26/1/1967 when temperatures were high and day lengths long. The culture was brought into the environment room one month later and the F_1 generation comprised 10 males and 15 females. High outside temperatures prevented a number of the nymphs from reaching maturity. The F_1 adults were then equally divided and placed on two more Vepris seedlings in the environment room. The resulting F_2 generation of adults was very nearly 50% females and 50% males; Vepris plant 1 yielded 77 males and 76 females while Vepris plant 2 yielded 141 males and 130 females. The adult F_2 generations were then allowed to lay eggs on plants maintained in the environment room and the total F_3 generation comprised 230 females to 61 males. This represented a change from a 1:1 female: male ratio in the F_2 to nearly 4 : 1 in the F_3.

A second batch of stock cultures of T. erytreae on Vepris were kept outside until April 1967 and just prior to emergence of the psyllids was brought into the environment room for a count of males and females. One of this batch of stock culture plants was brought into the environment room on the 15th March 1967 and adult emergence continued until 1st April with a resultant total of 98 females and 11 males, a ratio of approximately 9 : 1. Two other *Vepris* plants from the outside began to yield adult *T. erytreae* from 28/3/67 for about two weeks, producing 85 females and 10 males in the one case and 60 females to no males in the other. Finally a *Vepris* seedling infested with *T. erytreae* brought from the outside even later in the season began to produce adult psyllids on the 6th April 1967 and continued until 19/5/1967. This plant yielded a total of 315 females and 22 males a ratio of approximately 14 : 1. This predominance of females was maintained during the next generation which was reared in the environment room and a total of 292 females and 36 males (a ratio of approximately 8 : 1) was recorded. In a fourth generation 479 females and 15 males were produced, a ratio of approximately 32 : 1.

These data, though admittedly lacking adequate replication and control, do indicate that there can be radical changes in sex ratios in *T. erytreae* and there was a suggestion that during summer with long day lengths and high temperatures equal numbers of males and females are produced while with the progression of the seasons and a change to shorter days and lower temperatures more females than males are produced. In view of these findings it is necessary to mention briefly some studies on sex determinations in aphids which are relevant and may assist in an understanding of the data recorded with *T. erytreae*.

There is an extensive literature on the control of polymorphism in aphids which has assisted considerably in the understanding of this very complex problem. On the other hand the problem of sex determination in aphids is poorly understood and the literature on this aspect is sparse. Kenten (1955) in her paper on the effect of photoperiod and temperature on reproduction in the aphid Acyrthosiphon pisum (Harris) reports that while photoperiod has an influence on the production of other polymorphs in this aphid it has no influence on the proportions of sexual offspring produced. On the other hand temperature is most important in determining whether or not sexual forms are produced. Production of sexual forms only started below 20°C while of these sexual forms males were only produced at temperatures between 19 - 20°C and between 11 - 13°C. Females were produced at all temperatures below 20°C but most were produced at a temperature between 11 and 13°C. Lees (1959) points out that in Megoura viciae Buckton (and in other aphids) sex is genetically determined but physiological control in the parent itself and the influence of the environment has an overriding effect. The control exhibited by the parent is expressed by the fact that males are produced in "the middle of the sequence of offspring". In other words the parent gives rise to females during the beginning of the offspring production period while males predominantly are produced during the middle of the sequence followed at the end of the production period by females only. Male production in this species is further influenced by environmental temperature to the extent that no males are produced at high temperatures and few are produced at very low temperatures. Photoperiod appears to have no effect on sex ratio. The production of females on the other hand is influenced by both temperature and photoperiod. Lees' review (1966) however, indicates clearly that sex determination in aphids differs in different species. In some, photoperiod is extremely important in male production while high temperatures inhibit male production. In other species, high and low temperatures inhibit males and in one species male production is enhanced by fluctuating temperature conditions. The precise influences of these environmental conditions on genetic determination of sexes remains obscure although Lees' experiments (1964) using microilluminators is a start to an understanding of this problem.

Following these lines, several Citrus seedlings were isolated in the laboratory and females of T. erytreae from the stock culture were allowed to lay on the plants. During the laying period and for the entire developmental period the plants were subjected to continuous light and eventually a total of 81 females and 16 males were produced. The progeny were then allowed to lay eggs under continuous light and of the small number of progeny produced in the F_2 generation the majority were females. It does not seem therefore, that photoperiod in T. erytreae is having an overriding effect on sex determination. These experiments were run during April/May 1967 and it seems probable that the sex ratio was influenced by the low temperatures during these months in the laboratory. Following this the temperature regime in the environment room was changed to provide a plateau of 27°C, minimum temperature 11°C with temperature summations of 277 Hr°C per week above and 116 Hr°C per week below 20°C; the hot, light period was changed to 16 hours and the dark period to 8 hours. The total temperature summations were between those of the highest and median temperature regimes. Psyllids were introduced into the environment room shortly before emergence as adults and one generation was reared. A total of 83 females and 5 males were produced which showed no change from that which would have been expected at lower temperatures and shorter day lengths.

Rearing of these psyllids through a second and third generation was prevented by a deterioration of the plants due to the high temperatures, to an infestation of mites and also because at the increased temperatures the psyllid mortality became extremely high. In any event rearing of *T. erytreae* for one generation at high temperatures and long day lengths does not appear to influence the numbers of males and females produced.

It should be noted that populations of *T. erytreae* reared on either *Citrus* or *Clausena* gave similar results with regard to sex ratios as obtained from *Vepris* seedlings and there does not appear to be a simple nutritional explanation of the problem. Another possibility that was investigated was that sex ratio determination in *T. erytreae* is dependant on the time of fertilization of the female. Thus in one experiment two groups of virgin females were maintained in the environment room at the lowest temperature regime. One group included several males while the other group was deprived of males for two weeks after which period males were introduced. The group which mated immediately produced a predominance of females and a few males while the latter group produced almost equal numbers of males and females. This suggested that with immediate mating a predominance of females were produced while a delay in mating produced a higher proportion of males, (a system which has obvious functional advantages) but replicates of this experiment failed to produce consistent or confirmatory results.

An interesting sequel to these experiments on sex determination in *T. erytreae* comes from experiments conducted by Catling (1967) on the South African Citrus psylla at Letaba, Northern

Transvaal and in Swaziland. Fifth instar nymphs from the field at Letaba were collected in October and November 1966 and the sex of the emerging adults was recorded. The investigation revealed that about 40% of over 1000 animals examined were males and these data may be compared with records from Malkerns, Swaziland for the months March to June 1967. During this period about 27% of the total population of 2000 were males. One in situ count of psyllids on a potted grapefruit at Malkerns gave a mean percentage of males of about 13% out of approximately 250 animals examined. These data also suggest that more females are produced during the winter months and the whole problem is worthy of further investigation.

Parasites of Trioza erytreae.

The major parasite of T. erytreae is the primary ectoparasite Tetrastichus radiatus (Hymenoptera: Eulophidae) which parasitizes the nymphal psyllids. This parasite was originally described by Waterston (1922) and the specimens used in this description were bred from nymphs of the Indian Citrus psylla Eulphalerus citri (=Diaphorina citri). Husain and Nath (1927) have described T. radiatus as the most important of the chalcid parasites of the Indian citrus psylla and state:-

> "The percentage of parasitization is often very high and as many as 95 per cent. of the nymphs may be attacked. From the observations made by us it seems likely that in all those localities where D. citri, although present, does not increase in numbers sufficiently to cause any serious damage, the credit of keeping the pest in control is mainly due to this parasite."

This has been confirmed by Atwal (1962) writing on Diaphorina citri and who states:-

> "A hymenopterous parasite, Tetriastichus (sic.) radiatus Waterston, is a very effective enemy against nymphs, particularly during the post monsoon months."

The first positive record of Tetrastichus radiatus from Trioza erytreae was that of Annecke and Cilliers (1963) whose specimens were identified by Dr. B.D. Burks of the United States National Museum in Washington, D.C. Since then morphologically similar species from all over Southern Africa have been identified as Tetrastichus radiatus. The situation however, appears to be more complicated. Examination of the specimens sent by Annecke and Cilliers to Burks reveal several minor differences between these and the original description of T. radiatus by Waterston. Also the specimens are morphologically slightly different from those parasites recorded from T. erytreae in the Salisbury and Letaba areas. Although the importance of these differences cannot be assessed at the present time the evidence would suggest that a number of the parasites recorded from the South African Citrus psylla and which have been named Tetrastichus radiatus may in fact comprise a complex of several morphologically similar species. This immediately brings to mind the very well documented case of cryptic species in the genus Aphytis, the ecological and economic implications of which are discussed extensively by DeBach (1959, 1965, 1966) and DeBach and Sundby (1963).

There are also records of other parasites attacking Trioza erytreae. Jensen (1957) in a list of parasites of the Psyllidae, records Waterstons (1922) observations that Trioza citri (= T. erytreae) is parasitized by Tetrastichus dryi and Tetrastichus sicarius in Kenya. Burks (1943) has commented on Tetrastichus dryi as follows:-

> "This species (Tetrastichus triozae) and T. dryrus evidently are closely related to Tetrastichus dryi Waterston, which parasitizes "Trioza citri" in Kenya Colony, Africa, and Tetrastichus radiatus Waterston, parasitic on Euphalerus citri (Kuwayama) in the Punjab, British India. All four species apparently possess the same general kind of remarkable male genitalia."

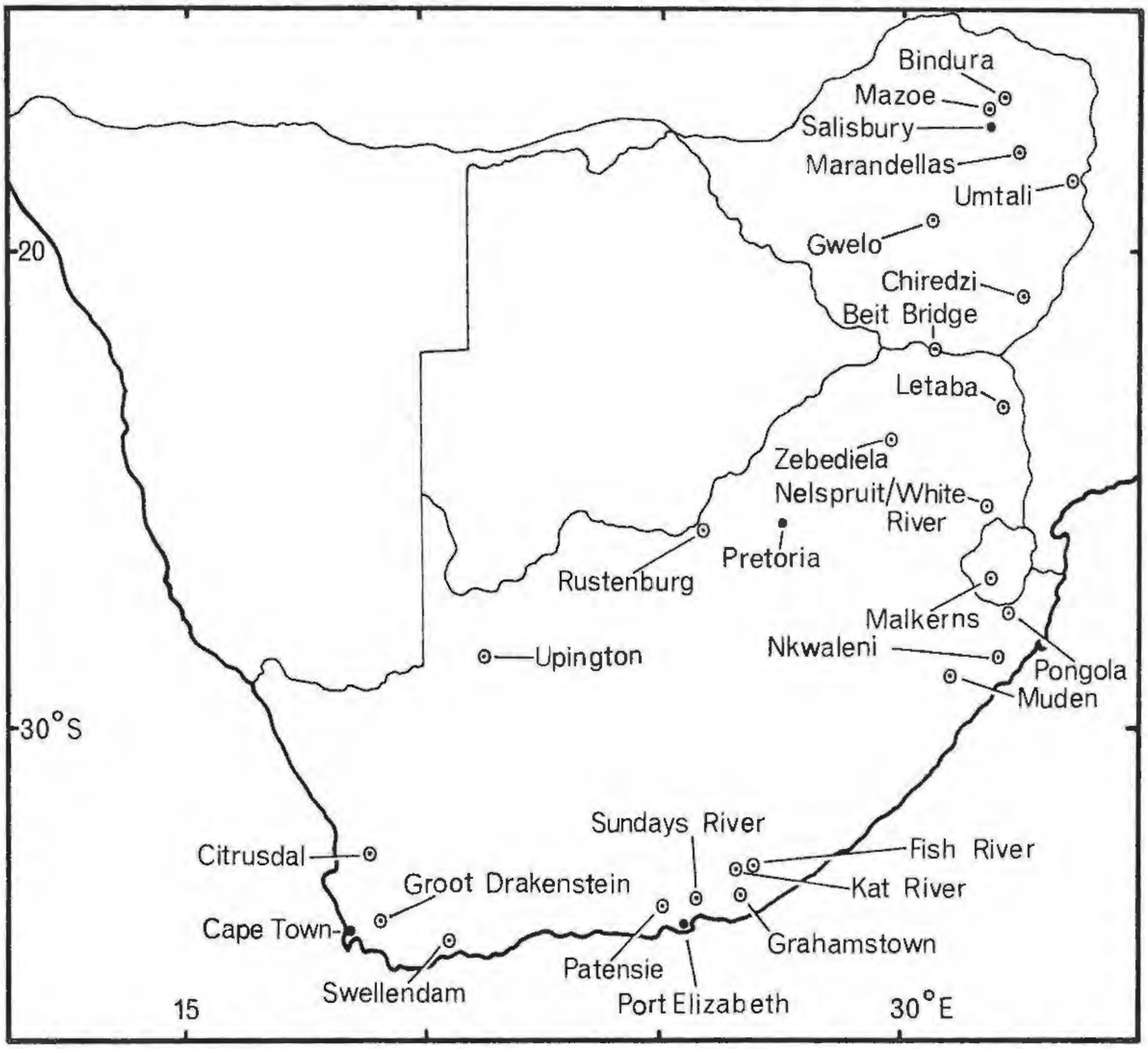


Fig. 40 Citrus growing areas in the Republic of South Africa and in Rhodesia. Open circles represent areas where citrus is produced commercially. Solid dots represent isolated citrus plantings of no commercial importance.

Also the collection of psyllid parasites at the Zebediela Citrus Research Station (northern Transvaal) indicates that *Tetrastichus ovulorum* is the major parasite of *T. erytreae* in that area. Clearly the whole problem of the "*Tetrastichus* complex" on *Trioza erytreae* in Southern Africa needs investigation.

Apart from *Tetrastichus* species *T. erytreae* is attacked by a primary endoparsite *Psyllaephagus pulvinatus* (Waterston) which has been recorded widely from citrus psylla in South Africa (Robinson, 1960; Annecke and Cilliers, 1963).. Finally Ghesquiere (1958) has described a new species of parasite *Psyllechthrus oophagus* which parasitizes the eggs of *Trioza erytreae* and he has commented on the biology of this parasite. These observations were made in the Congo and as yet there are no records of this parasite from South Africa.

Parasites of adult *T. erytreae* have so far never been recorded.

Economic implications and distribution of *Trioza erytreae*.

Citrus is an important commercial crop in Southern Africa and figure 40 is included to show the approximate positions of the main citrus growing areas in the Republic of South Africa and in Rhodesia. *Trioza erytreae* has had a widespread and long association with citrus in some of these areas where the insect was known to be of minor importance and then only in nursery stock. The rise of this insect to pest status in orchards generally and its importance as a vector of the citrus virus disease "greening" has only recently become apparent (McClean and Oberholzer 1965 a and b) and the insect and the disease are increasing in importance. It has been argued that this upsurge in the importance of T. erytreae is correlated with the increasing use of wide spectrum insecticides. Oberholzer (1967) states that an increase in psyllid numbers in the Rustenburg area can be correlated with the use of parathion in the orchards and nurseries which was started in 1950.

The virus disease "greening" is discussed by McClean and Oberholzer (1965 a and b) and further information on the greening virus is given by Schwarz (1964, 1965 and 1967a). In their paper McClean and Oberholzer (1965a) introduce their subject as follows:-

> "Greening disease of sweet orange has been known in the Transvaal for more than 30 years. It has an unusual distribution and up to the present has been of real economic importance only in three comparatively small areas: White River (Eastern Transvaal), along the slopes of the West of Tzaneen (near Letaba) and Politsi (Northern Transvaal), and in a narrow strip of orchards running along the foot-hills on the Northern slope of the Magaliesberg mountains, near Rustenburg (Western Transvaal). Another small "pocket" of greening occurs at some farms at Donkerhoek, North of Rustenburg." They continue: "Orchard surveys in recent years indicate that greening is now appearing in many widely separated citrus regions hitherto regarded as free of the disease. It has been found near Potgietersrust, at Marble Hall, in Swaziland and in many orchards scattered through the Rustenburg district."

McClean and Oberholzer (1965 a) present evidence to show that the disease is caused by a transmissible virus and that normally transmission is achieved by an insect vector which they show later (McClean and Oberholzer 1965 b) to be, in all probability, Trioza erytreae.

There are practical problems in controlling populations of T. erytreae. Insecticidal applications in the orchards are not very effective because of the reservoir of psyllids which is maintained on the surrounding indigenous rutaceous plants. Once a new flush of growth appears on the citrus trees there is an immediate reinfestation

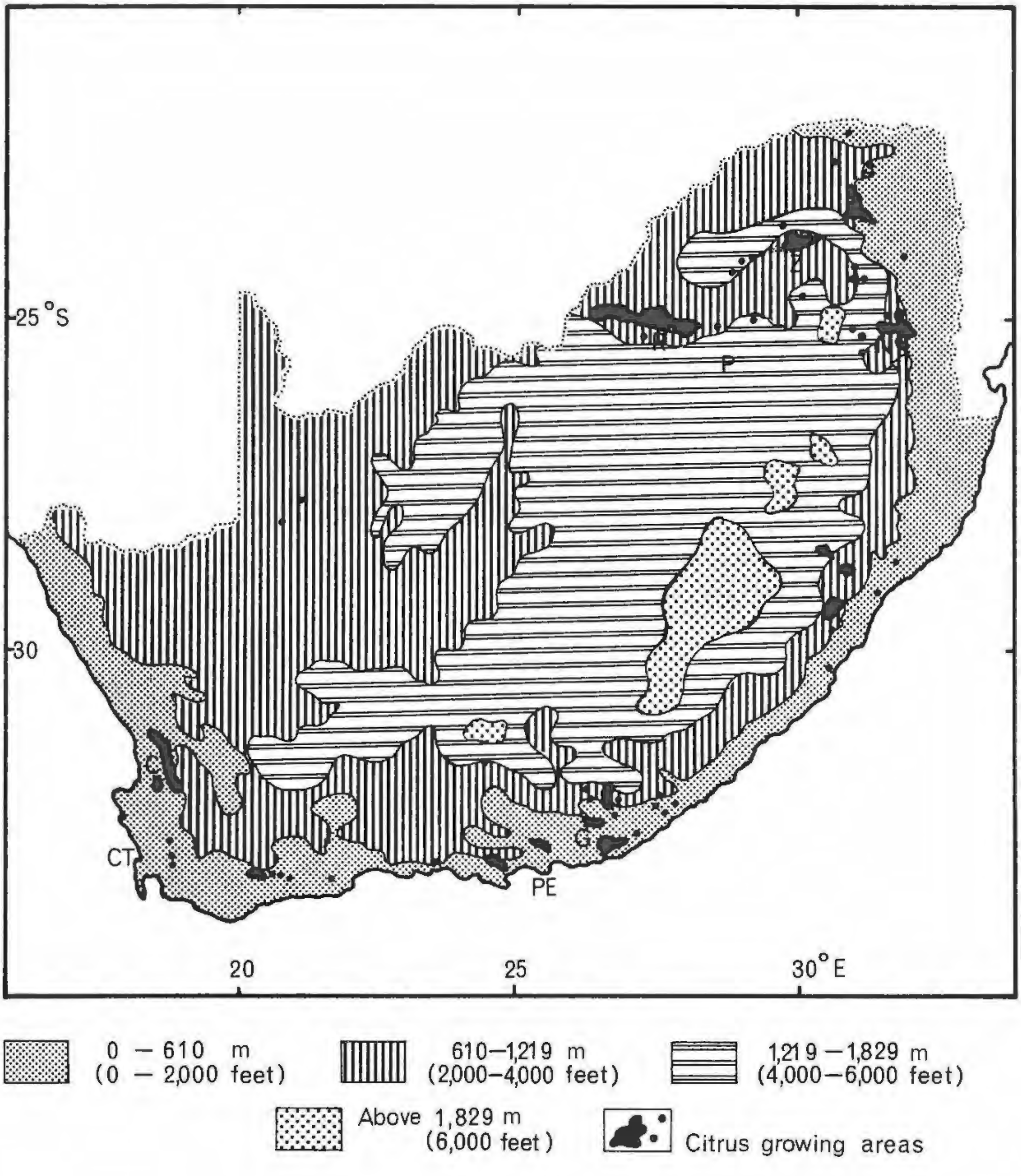


Fig. 41 Contour levels (simplified) in the Republic of South Africa. The major citrus growing areas are also shown.

of psyllids from the surrounding bush. During the warmer periods sufficient flush to support psyllids can appear a few days after insecticidal application and these flush points offer an ideal substrate for feeding and oviposition. Thus it is reported (Schwarz, 1967 b) that even weekly insecticidal applications, which would be economically impossible, would not be effective in controlling populations of T. erytreae. Clearly cultural control or biological control methods offer the only solution and in this respect some suggestions are made later in this discussion.

T. erytreae, greening and temperature effects.

The relationship between T. erytreae and greening and the important effect of temperature on both have been suspected for some time and as a result of the present laboratory investigation on the biology of T. erytreae it is possible to elaborate on this relationship and draw conclusions from information gained in the field.

Considerable information has been gained on two trips to citrus growing areas in the Republic of South Africa and in Rhodesia during December 1965 and 1966; during these periods workers in the field of citrus greening and Trioza erytreae were interviewed. As a result of these discussions it has been possible to construct table 39 which is a summary of the occurence of T. erytreae and greening in the main citrus growing areas in Rhodesia and South Africa together with approximate altitudes of the areas. This table should be considered in conjunction with figures 41 and 42. Figure 41 is a diagramatic representation of the contour levels of South Africa

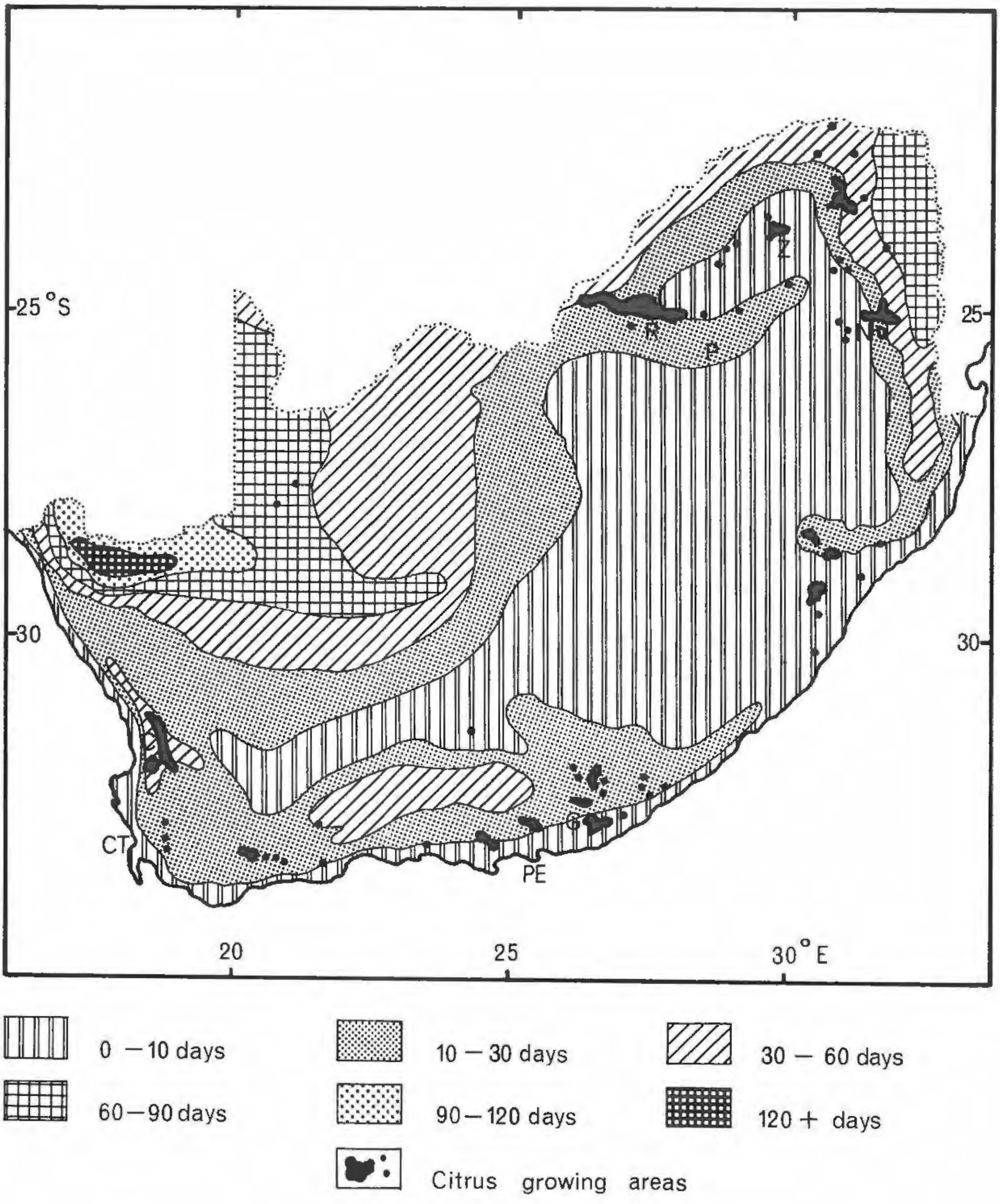


Fig. 42 Average annual frequency of days with a maximum temperature above 35°C in the Republic of South Africa. (After Schulze, 1965). The major citrus growing areas are also shown.

superimposed upon outlines of the major citrus growing areas, while figure 42 shows areas in South Africa in which temperatures exceed 35°C for a specified number of days during the year.

Table 39 shows the clear relationship between the extent of infestation of T. erytreae and the severity of greening. Very recently Schwarz (1967 a) has conducted a survey of the distribution of citrus greening in South Africa and on the basis of this has divided the citrus growing areas in South Africa into three "greening zones". Zone A (see table 39) includes those areas where citrus psylla is common and there is a high incidence of greening infection. In these areas crop losses as a result of greening vary from 30 - 100%. Zone B where citrus psylla populations are relatively low and crop losses vary from 5 - 30% as a result of medium to light infections of greening. Zone C, areas in which greening has not been detected or where there is no natural spread of greening. Where the disease is present it results from the introduction of nursery stock from Zones A or B. In Zone C T. erytreae is of sporadic occurence and crop losses due to greening are negligible. It is evident from table 39 that the classification of greening and T. erytreae infestations used in the present discussion correspond very closely to that of Schwarz. Zone A corresponds with the three plus areas, Zone B with two plus areas and Zone C with one plus areas. It is important that two independant assessments should yield such very similar results.

Table 39 shows that there are no cases where an abundance of psyllids is associated with an absence of greening neither are there cases of serious greening in the absence of large numbers of

Table 39 A list of the major citrus growing areas in Southern Africa. The altitude and the extent of infestation of T. erytreae and "greening" are given for each station.

CITRUS AREA (see Fig. 40)	APPROX. HEIGHT (metres) Above sea level	TRIOZA ERYTREAE	"GREENING"	REMARKS
Bindura Citrus Estates	1128	+ (?)	+ (?)	
Mazoe Citrus Estates	1189	+	+	Psyllid galls have been found but T. erytreae has not.
Salisbury *	1493	+++	+++	Over 50% of all trees with greening.
Marandellas, Citrus Estates	1524	+ (?)	+ (?)	
Premier Citrus Estates, Umtali	1128	+	+	Only few trees found with greening.
Cashel valley, 40 miles South of Umtali	914	+	+	Less than 1% of trees with greening.
Christmas Gift Estates, Gwelo	1219	+	+	
Hippo Valley Estates, Chiredzi	610	+	+	The few trees with greening are suspect nursery imports.
Beit Bridge Plantings	488	+	+	Psyllids very rarely found.
Letaba	762	++	++	Psyllids and greening only important in high lying areas. Zone B.
Zebediela	1219	+	+	Psyllids uncommon and very heavily parasitized.
Nelspruit	701	++	++	Becoming most important in high lying areas. Zone B.
White River	975	+++	+++	Psyllids and greening of great importance. Zone A.
Pretoria *	1402	+++	+++	Very heavily infected area. Zone A.
Rustenburg	1250	++	++	Of intermittent occurrence-important in some orchards but not in others. Zone A or B.

Table 39 continued.

CITRUS AREA (see Fig. 40)	APPROX. HEIGHT (metres) Above sea level	TRIOZA ERYTREAE	"GREENING"	REMARKS
Malkerns, Swaziland	914	+++	+++	Severe psyllid and greening problem.
Muden, Natal	1036	++	++	Decreasing in importance as a Citrus area. Zone B.
Nkwaleni	177	+	+	Zone C.
Pongola	274	+	+	Zone C.
Fish River	152	+	-	Zone C.
Kat River	457	+	+	Zone C.
Grahamstown	518	+	+	Zone C.
Sundays River	61	+	-	Zone C.
Port Elizabeth*	Sea Level	++	+ (?)	-
Patensie	213	+	-	Zone C.
Swellendam	122	+	+	-
Groot Drakenstein	146	+	-	Zone C.
Cape Town*	Sea Level	++	+ (?)	-
Citrusdal	152	+	-	Zone C.
Upington	762	+	-	Zone C.

Symbols used in table

+	- Trioza erytreae and greening present but of no importance.
++	- T. erytreae and greening commonly found and of some importance.
+++	- T. erytreae very common, often in outbreak proportions and greening very common. Both the insect and the disease of considerable economic importance.
+ (?)	- T. erytreae and greening known to be present but status or importance of insect or disease in the area unknown to me.
-	- Greening not detected, Schwarz (1967a).
*	- Areas in which Citrus is grown as a garden plant but is not grown commercially.

For explanation of zones see text and Schwarz (1967a).

psyllids. Citrus in Rhodesia and South Africa is seldom grown above an altitude of 1219 metres (4000 feet) and it is significant that in Pretoria and Salisbury where citrus is grown at 1402 metres (4600 feet) and 1493 metres (4900 feet) respectively, psylla and greening are most severe. The obvious inference from this is that psylla and greening thrive in the cooler citrus growing areas while being scarce in hotter, low lying, areas. This relationship could have been forecast on the basis of the experimental results on the effects of temperature on T. erytreae. This study has shown that temperatures above about 30°C are detrimental to T. erytreae. A period of seven hours at the highest temperature regime (figure 6 c) where the temperature plateau was 32°C was a direct cause of mortality in early instars of T. erytreae while exposure to these conditions for two or three days inhibited development in the later instars and in the adults. It was also established from several lines of evidence that development and survival were enhanced by low temperatures reaching a maximum of 21°C (the lowest temperature regime figure 6 a). Consideration of some specific examples from the field emphasize the importance of temperature in determining the distribution of T. erytreae.

Citrus grown in Salisbury and that grown at Mazoe (approximately 20 miles North of Salisbury) is strikingly different in the degree of infestation by T. erytreae. At Salisbury T. erytreae infestations are very heavy and greening has been detected in at least 50% of all the trees in the area. On the other hand the citrus at Mazoe is virtually psyllid free. A detailed inspection by the staff at Mazoe estates revealed that galls typical of those formed by T. erytreae were found on only a few of more than 300,000 trees on the estate and that living T. erytreae was never found. Also of the trees on the estate only 12 had symptoms similar to those of greening. The suspect trees were uprooted as a precaution.

The difference in T. erytreae infestation on citrus in Salisbury and Mazoe is impressive as the two areas are only about 20 miles apart. Salisbury, however, has an altitude of 1493 metres (4900 feet) with a mean January temperature of 20°C with average maximum temperatures of about 26°C during the month while Mazoe is situated at 1189 metres (3900 feet) and has temperatures on the average of 3 - 4°C hotter than those at Salisbury. While this difference in temperature between the two stations does not seem sufficient to inhibit psyllid growth at Mazoe it will be recalled that at Mosslands the thermograph readings from the stations T_1 and T_2 (see figure 1) were very similar in their fluctuations but that a difference of about 1 - 2°C was noted between the two stations; temperature summations from these two thermograph records showed a difference of approximately 40% in spite of the very small differences in absolute temperature. The differences in temperature summations between Salisbury and Mazoe would be even greater and it seems likely on the basis of laboratory experiments on T. erytreae that the temperature summation differences account for the lack of psyllids at Mazoe and their abundance in Salisbury.

Obviously this interpretation is not complete; temperatures are also having an influence on the parasites of T. erytreae. It may be, that besides the detrimental effects of high temperatures on the psyllids, the temperatures are providing an advantage for the parasites at Mazoe. Also it could be that the differences between the psyllid populations at Salisbury and Mazoe reflect more rigourous control measures at Mazoe. This however is not the case as the pests of citrus at Mazoe are largely under biological control and in all probability citrus in Salisbury is receiving heavier applications of insecticide.

A similar relationship between the abundance of T. erytreae and temperatures has been illustrated at Letaba by Catling (1967). Populations of T. erytreae from three different altitudes in close proximity to Letaba were sampled. At the highest altitude where the lowest temperatures were experienced psyllids and greening were very common and became progressively less common as the temperatures increased at the lower altitudes.

The relationship between T. erytreae and temperature is further emphasised by a consideration of the data contained in table 40. These data should not be interpreted as providing a simple correlation between absolute temperature and distribution of Trioza erytreae. As has been emphasised the important factor is how hot it is for how long and even with temperature summations the responses of the psyllids in different stages varies. These temperature data however are obviously correlated with total temperature summations and could therefore be expected to give an indication of the relation between temperature and T. erytreae. The data contained in table 40 should be considered in conjunction with table 39 and with figures 41 and 42.

Table 40 Temperatures (°C) for January for some citrus growing areas in South Africa. The information is derived from "The Climate of South Africa", Part 1 (1954) and Part 8 (1965), published by the Weather Bureau, Pretoria.

CITRUS AREA	MEAN MONTHLY TEMP.	MEAN DAILY MAXIMUM	MEAN MONTHLY MAXIMUM	EXTREME MAXIMUM
Zebediela	24.4	30.9	36.6	39.0
Nelspruit	23.7	28.8	35.5	37.8
White River	22.5	27.7	32.2	36.7
Nkwaleni	23.8	29.0	38.0	43.3
Pongola	25.1	30.0	37.4	40.3
Pretoria	20.7	26.9	32.2	35.7
Rustenburg	23.7	30.6	35.7	39.4
Grahamstown	21.7	27.6	37.7	41.3
Sundays River (Hermitage)	22.8	29.6	39.9	46.3
Port Elizabeth	20.9	25.4	32.3	34.6
Groot Drakenstein	22.9	30.0	37.9	41.4
Cape Town	21.5	26.5	33.9	39.4
Clanwilliam (near Citrusdal)	25.9	35.4	44.1	46.1
Upington	27.5	35.2	40.1	41.7

The White River and Pretoria citrus growing areas and the citrus grown in private gardens in Port Elizabeth and Cape Town are all subjected to serious attacks by T. erytreae. All four areas have an equable climate. The mean monthly temperatures are lower than those experienced in other citrus growing areas and the maximum temperatures remain relatively low. Table 40 shows that Zebediela and Nelspruit are hot. In the Nelspruit area psyllids are of some importance while they are of little importance in the Zebediela area. Although Zebediela has an altitude of approximately 1219 metres (4000 feet) it experiences high temperatures and this would explain the lack of psyllids in this area. The percentage parasitism of psyllids at Zebediela is very high and it might be that the higher temperatures are offering a suitable environment for the parasites while having a detrimental influence on the psyllids. Also table 40 shows that the temperatures recorded from the Sundays River Valley, Groot Drakenstein, Nkwaleni, Pongola, Citrusdal and Upington regions are high enough to limit populations of T. erytreae.

An explanation of the situation at Grahamstown has so far been omitted. The mean monthly temperatures recorded for Grahamstown seem low enough to allow a build up of psyllid numbers. However, T. erytreae is rare in Grahamstown and surrounding areas and it is evident that the mean daily maximum temperatures during summer together with mean monthly maximum and extreme temperatures are effectively controlling numbers of T. erytreae. The diurnal temperature variation in Grahamstown is high and this accounts for the low mean monthly temperatures recorded.

The distribution of the greening virus of citrus is closely correlated with the distribution of T. erytreae and there is good evidence to suggest that the virus is also adversely affected by high temperatures. McClean (1967) has shown that in any particular area there is an inverse correlation between the temperature and the severity of greening. It has been suggested that four different strains of greening occur in South African citrus. McClean (1967) states that the differences noted are due to temperature effects on the virus and are also correlated with the physiological condition of the plant and that greening is caused by a single virus strain which produces different symptoms under different conditions. McClean comments that in some areas greening symptoms are very clear at the beginning of the season when temperatures are low but at the end of the season when it is hot greening symptoms completely disappear. McClean has conducted experiments with citrus seedlings which showed severe greening symptoms. The experimental batch of seedlings was placed in a "hot-box" at 36 - 40°C for a month and the seedlings subsequently lost all greening symptoms and were apparently free from the disease. It did not recur in these plants provided they were kept psyllid free. The control seedlings which were not subjected to high temperatures retained severe greening symptoms. A similar technique was employed by Elphinstone (1966) at Letaba where citrus seedlings are rendered greening free by being left in an oven at 48 - 55°C for two hours.

Considering the laboratory data on T. erytreae together with the information that has been presented on its distribution and the distribution of greening in the field it can be stated that citrus areas in South Africa which exceed 380 Hr°C per week above 20°C (the highest temperature regime) will be free from T. erytreae. In all probability the critical total temperature summation for T. erytreae will be found to be lower than this. In more general terms it can be stated that citrus in South Africa should only be grown in areas where the mean daily maximum temperature during summer exceeds about 30°C. These areas in South Africa are limited to those below 1219 metres (4000 feet) and those areas away from the temperature

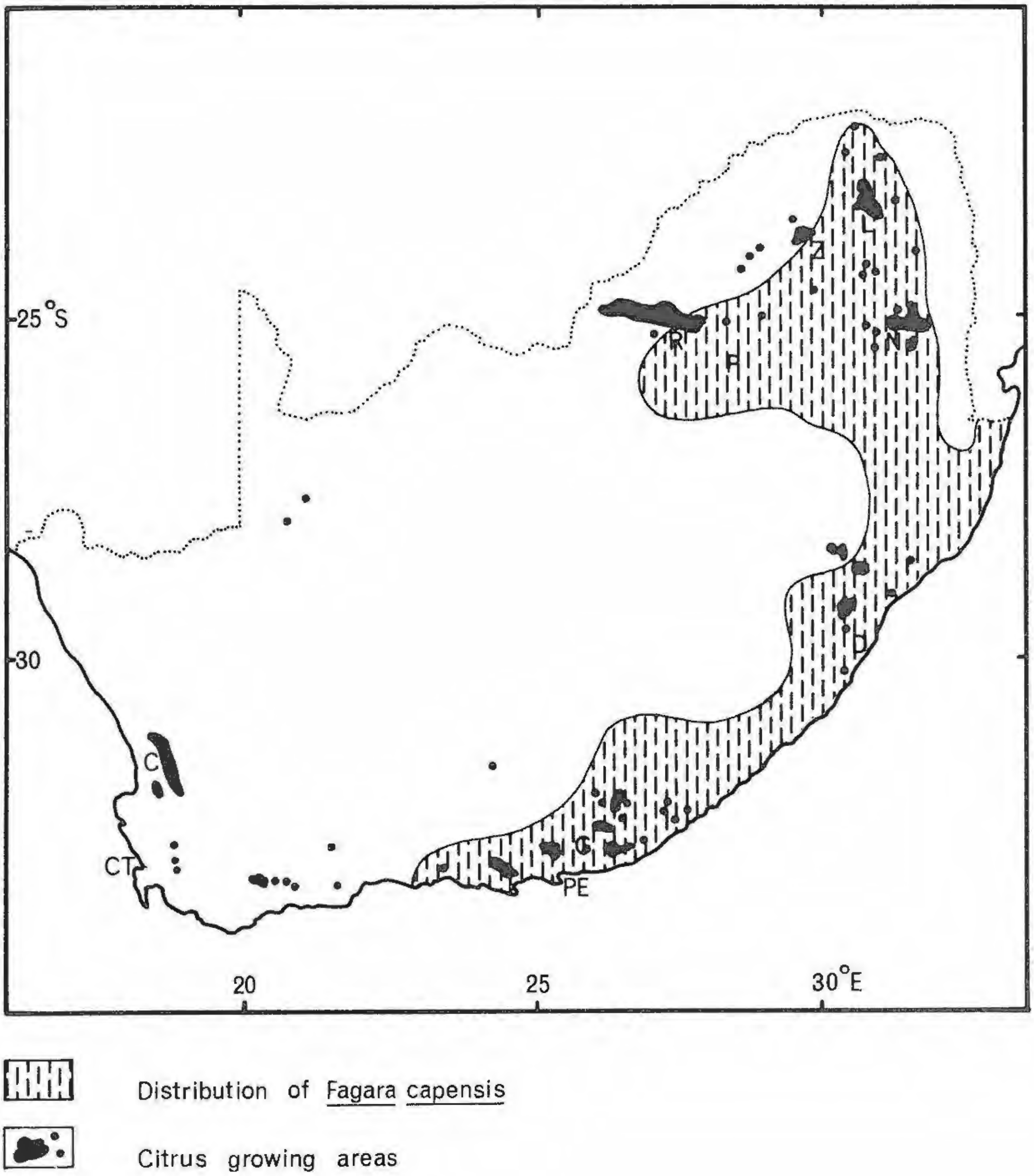


Fig. 43 Distribution of *Fagara capensis* and the major citrus growing areas in the Republic of South Africa.

stabilizing influence of the sea. Areas of citrus cultivation in South Africa which meet these requirements are economically free from T. erytreae and greening.

Distribution of indigenous host plants.

The laboratory data reported in this study have shown that T. erytreae develops well on Vepris undulata, Clausena anisata, Fagara capensis and citrus and there is evidence to suggest that the former two indigenous hosts are more suitable than citrus for the development of the insects and probably are the original host plants of this insect. Figures 43 and 44 show the distribution of Fagara capensis, Vepris undulata and Clausena anisata in South Africa. These figures were drawn using data supplied by the Botanical Research Institute, Pretoria who have kindly supplied the locality labels of the plant specimens housed in the National Herbarium. Figures 43 and 44 should be considered in conjunction with figure 41 which shows the contour levels in South Africa.

Fagara capensis (figure 43) is distributed from Knysna eastwards and has been recorded from the high lying regions of Mozambique and Rhodesia.

Vepris undulata (figure 44) occurs from Port Elizabeth eastwards along the coast. In the more inland areas this plant is restricted to the high lying cooler regions. Clausena anisata (figure 44) has a similar distribution to Vepris undulata in South Africa but it extends further inland. Clausena anisata is also more widespread outside South Africa having been recorded from Rhodesia, Mazambique, Malawi, all the East African countries, Angola, Congo,

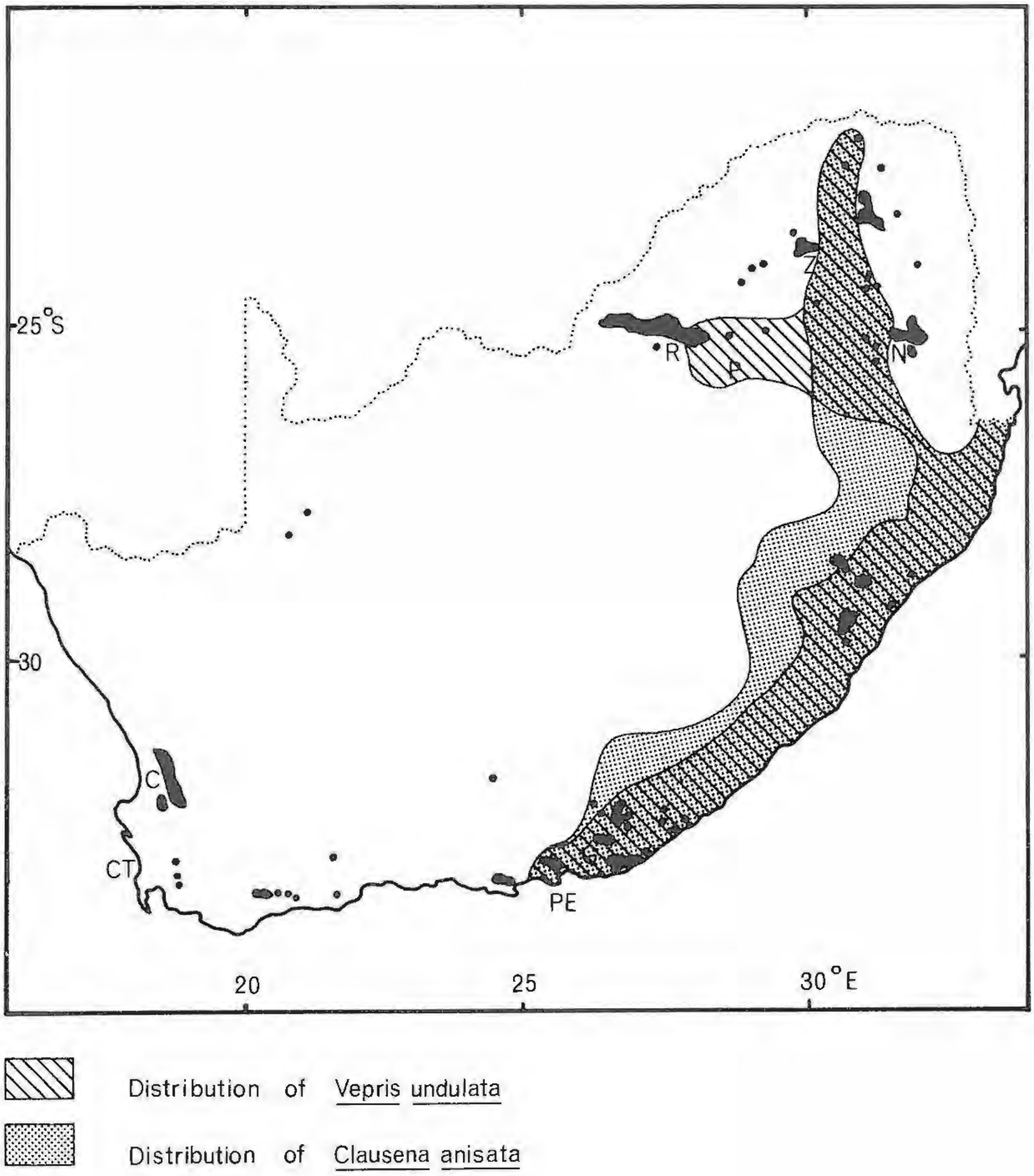


Fig. 44 Distribution of Vepris undulata, Clausena anisata and the major citrus growing areas in the Republic of South Africa.

Camerouns, Gold Coast and Ghana. The distribution of these plants can be compared with the known distribution range of Trioza erytreae which is contained in the distribution maps of pests of the Commonwealth Institute of Entomology Series A (Agricultural) Map No. 234, 1967. T. erytreae is found on the islands of Madagascar, St. Helena and Maritius and otherwise is confined to the following countries in Africa:- Cameroun, Congo, Eritrea, Ethiopia, Kenya, Malawi, Rhodesia, Rwanda, Sudan, Republic of South Africa, Tanzania, Uganda and Zambia.

An obvious deduction from these distribution patterns, and that of citrus, is that a greater abundance of T. erytreae and greening may be expected in areas with the greater number of indigenous host plants. In these areas the indigenous host plants would certainly seem to be an important reservoir for T. erytreae and perhaps for the greening virus, although no attempts have been made to isolate the virus from indigenous rutaceous plants.

In terms of practical control measures against T. erytreae it might be judicious to remove the indigenous host plants from certain citrus growing areas. These areas would exclude those in which high temperatures control T. erytreae. This might bring about a reduction in psyllid numbers and prevent constant reinfestation of the citrus. On the other hand this step might also reduce the reservoir of parasites which would aggravate the situation, also there is no evidence available to suggest that the three indigenous hosts mentioned are the only hosts of T. erytreae. It seems very likely that other Rutaceae may also harbour T. erytreae.

At present control of T. erytreae rests on the application of insecticides and some of the results of the present study might enable insecticides to be applied more effectively. For example, it has been shown that the moult to the adult stage in T. erytreae occurs most frequently during the hours of darkness and in the early morning sclerotization is still incomplete. In this condition the adults are very reluctant to fly or jump and insecticidal sprays applied during the early morning would certainly be most effective against the adults of T. erytreae. Also sprays applied underneath the leaves would obviously be more effective than general top sprays as the nymphs have been shown to be confined to the under surfaces of leaves.

The results of the present study, besides pointing to the importance of the reservoir of psyllids on the indigenous Rutaceae and to the more effective use of insecticides, suggests that a study of attractants, repellants and antifeedants might pay dividends.

These suggestions although highly speculative may offer a chance for a more permanent solution to the control of T. erytreae than can be achieved with conventional insecticides. Ultimately, however, it seems that adequate control of the citrus psylla in South Africa will rely on cultural methods in which citrus is only planted in low lying hot areas. In these areas isolated outbreaks of T. erytreae should be adequately controlled by parasites and high temperatures and the latter will also control greening.

7. DISCUSSION

The difference in status between Paurocephala calodendri and Trioza erytreae is important, not only as an economic problem but also from a wider ecological point of view. T. erytreae is an insect which has achieved pest status in certain areas while P. calodendri populations on the other hand, although widespread, are effectively stabilized by biotic and abiotic factors. The study on P. calodendri populations which has been conducted over a relatively short period of four years has nevertheless led to a partial understanding of population dynamics in this species and it seems that this study might give some useful pointers to a study on population fluctuations in T. erytreae. Before elaborating this point further it is necessary to discuss some opinions expressed on population dynamics by other authors.

Until very recently it was traditional in a study of this sort to argue at length whether population regulation was brought about by density dependent and / or density independent factors. The opinions of Bakker (1964) are very relevant in this respect. Bakker has considered the meaning of ecology and population dynamics and has discussed how terminological arguments have confused the science generally. He has stressed the futility of trying to formulate a general theory of population dynamics. He states:-

> "It is meaningless to combat a conclusion derived from work on territorial insectivorous birds in the tropics with arguments derived from work on phytophagous insects in the temperate regions, to give an extreme example. Animals are so different in their life histories, their requirements and their adaptations, etc., that any attempt to give a useful "general theory" of population-dynamics must necessarily fail, or it becomes so vague that it largely looses (sic.) its meaning."

Bakker has emphasised the extreme complexity associated with population control in any species and has attempted to present a generalized model of the "web of interactions" in a natural population. It might seem that a model of this sort is precisely what Bakker has defined as a "general theory which must necessarily fail" but in fact his model is a summary of all the factors to be considered in an appraisal of the population dynamics of any species. This model embodies nothing new and incorporates no new concepts, rather it is a clarification of ideas in ecology generally and it provides an acceptable compromise between the conflicting theories that have been advanced in population dynamics.

Recently Clark et al. (1967) have expressed their ideas on population ecology in terms of a so called "life system" concept. The concept of a life system as envisaged by these authors has its origins in the writings of Solomon (1949) and Bakker (1964) among many others, and is an attempt to combine the "complex web of interactions" inherent in any population study into a comprehensible whole. Clark et al. (1967) write :-

> "Thus a life system is composed of a subject population and its effective environment which includes the totality of external agencies influencing the population, including man (in practice, those biotic and abiotic agencies whose influence can be observed and, preferably, measured)."

They continue:- "The inherited properties of the subject species, in the form of an array of genotypes, mould matter and energy supplied by environmental resources into phenotypes - the individuals of the species. The inherited ability of individuals to survive and multiply and the conditions for existence provided by the effective environment, namely 'supplies' of all kinds and limited repressive action by inimical agencies, enable them to form a population with group (statistical) characteristics which result from their collective existence. Basically, the persistence and abundance of a population are the outcome of interactions between the inherited properties of individuals and the intrinsic attributes of the effective environment. In other words, the intrinsic qualities of the subject species and those of its environment are the co-determinants of population numbers. These co-determinants define the actual reproduction ability of individuals, and the extent to which immigration adds to the population; they also define the extent to which individuals are removed prematurely by mortality and emigration.

The idea of life system has none of the apparent exclusiveness or bias of some other concepts of population and environment. It imposes no restrictions a priori on thought about how population numbers are held within observed limits, and, by associating the study of single species with the study of communities, it draws attention to the essential unity of ecology. It is as flexible in application as the idea of ecosystem. The spatial delimitation of a life system depends simply on spatial delimitation of the population to be studied- a matter mainly of purpose and convenience. For example, the idea can be used to include all local populations of a species that are linked to some degree by dispersal or by migration, or for a single local population. When a species exists in the form of isolated population, it has as many life systems as it has populations."

Another recent paper which seems to embody a similarly comprehensive view of population dynamics is that of Ehrlich and Birch (1967). They deal with concepts of the "balance of nature" and "population control". They point out that:-

"A realistic basis for building models dealing with the changes of numbers in populations would include the following propositions: a. All populations are constantly changing in size. b. The environments of all organisms are constantly changing. c. Local populations must be recognized and investigated if changes in population size are to be understood. d. The influence on population size of various components of environment varies with population density, among species, among local populations, and through time."

In many ways the writings of Bakker (1964), Clark et al. (1967), Ehrlich and Birch (1967) and others represent the culmination of ecological thought which started with Elton (1953 and 1966) who published his first account of animal ecology in 1927. Elton has dealt with ecology at the community level and has attempted in his writings to express the factors influencing the community. His attempts have been variously criticized and his "natural history" approach to the subject has stimulated numerous investigations to put population ecology on a more quantitative footing. These include the well known accounts of Nicholson (1958), Andrewartha and Birch (1954), Milne (1957, 1962), Solomon (1949, 1957), Slobodkin (1960) and many others. To quote Clark et al. :-

> "It is a truism to say that the theories presented (i.e. those of the authors mentioned among others,) are simply different ways of regarding and evaluating the same things, conditioned by personal experience, preference, and aptitude; but mention of the fact is necessary because of the uncompromising way in which some leading theorists have adhered to their particular viewpoints."

Bakker (1964), Huffaker and Messenger (1964 a and b) Clark et al. (1967) and others have attempted a compromise between the viewpoints of other population ecologists and in so doing have completed a circle in ecological thought and they again come to regard or visualize species and their environments in an all embracing manner. It seems that the future of population ecology rests on the overall unbiased view epitomized in the life system approach and that this approach offers an opportunity for the understanding of population fluctuations at a species level and carries with it promise for the eventual prediction of these fluctuations.

A preliminary discussion of the "life system" in Paurocephala calodendri has been given and some suggestions may be put forward for an approach to the problem in T. erytreae. Clearly an understanding of the "life system" of T. erytreae remains to be done and is of great relevance economically. In the first place it is suggested that an initial survey of population fluctuations in T. erytreae be confined to a naturally occuring population of this insect on one of the indigenous host plants. It is very likely that moderate populations of T. erytreae will be found on a number of the indigenous hosts and an understanding of population regulation at this level will assist in an understanding of why this regulation has broken down when the insect lives on citrus in certain areas. Clark et al. (1967) make some relevant comments in this connection:-

> "It is suggested, however, that more attention should be given to innocuous species because, in confining so much of our work to pests, we are dealing mainly with atypical species and this introduces a bias in attempts to derive general population principles."

Clark et al. (1967) quote examples of where the study of innocuous species have enabled models to be constructed which were later found to be useful in the prediction of population fluctuations in pest species. It is likely that the studies on P. calodendri will assist in an understanding of the life system of T. erytreae. It certainly seems from laboratory studies on T. erytreae that the "key influences" (Clark et al. 1967) of parasites and temperature which were found to be important in population control in P. calodendri will also be important in the control of T. erytreae populations.

The writings of Ehrlich and Birch (1967) and Clark et al. (1967) and the work on P. calodendri have emphasized the importance of studying population fluctuations in local populations of insects. In the case of P. calodendri the population could easily be delimited as it was confined to an isolated chestnut tree and the evidence suggested that there was very little modification of the population either by emigration or immigration. It is suggested therefore that a start to an understanding of the life system of T. erytreae would be to study population fluctuations in this species on an isolated tree. This could either be a naturally isolated indigenous tree or a purposely isolated citrus tree. It seems obvious that the tree should be regarded as the ecological unit and that there would be little gained from a more conventional study of many trees within a citrus orchard. The interaction between trees in a citrus orchard is very likely to cause confusion in interpretation although of course it would be desirable even with isolated trees to replicate the observations on as many trees as possible. It would also be desirable to pick sample trees from widely different areas where the key influences on the population might be expected to vary.

The studies on *P. calodendri* suggest that this approach to an understanding of the life system of *T. erytreae* might be successful and that as a second step attention could be turned to population fluctuations of *T. erytreae* in an orchard where the situation would be expected to be far more complicated. Even at this level it is suggested that a comparative study be made on population fluctuations in orchards with a low population level of *T. erytreae* (for example those at Zebediela) and those where *T. erytreae* is a serious pest of citrus (for example the White River area).

It should be emphasised that effective control of populations of *T. erytreae* will eventually depend on an understanding of the life system of this insect and that this understanding will be gained most easily by a study of local, and preferably natural populations.

8. ACKNOWLEDGEMENTS

I wish to express my appreciation to my supervisors Professor B.R. Allanson and Dr. G.B. Whitehead for their guidance and constructive suggestions throughout the period of this work.

Grateful acknowledgement for financial assistance is made to the Departmental of Agricultural Technical Services, Republic of South Africa; to the South African Council for Scientific and Industrial Research; to the Council of Rhodes University, Grahamstown and to the Koonap River Citrus Co-operative Co. Ltd.

I am very grateful to Mr. H.C. Moss of the farm "Mosslands" for his kindness and help over the last four years.

I am indebted to the following persons with whom I have discussed various aspects of this project:- Dr. D.P. Annecke, Pretoria; Mr. H.D. Catling, Malkerns; Mr. A.L. Capener, Pretoria; Mr. M.J. Wells, Grahamstown; Dr. A.P.D. McClean, Pretoria; Professor P.C.J. Oberholzer, Pretoria; Dr. R.E. Schwarz, Nelspruit; Mr. G.J. Strydom, African Explosives and Chemical Industries Ltd., Johannesburg; Mr. C.M. Searle, White River; Mr. A.F. Heberden, Mazoe; Dr. G.J.O. Whiteside, Salisbury; and to my colleagues in the Department of Zoology and Botany, Rhodes University. My thanks are due to Miss J.R. Blowers, Salisbury whose work on T. erytreae is quoted from our combined papers on this insect. The drawings on the developmental stages of T. erytreae were done by Miss Blowers.

I have been fortunate in having the competent assistance of Mr. J.J. Case who has helped considerably in this work and in the preparation of the figures. The assistance of Mr. J.L. Minshull is also gratefully acknowledged. I am grateful to Miss U. Koch for translating several German publications for me and to Mrs. J.I. Minshull for French translations. I also wish to thank Mrs. Y. Riddin for typing this thesis for me.

Lastly I wish to express my gratitude to my wife for her assistance in the preparation of this thesis.

9. REFERENCES

ACOCKS, J.P.H. (1953) Veld types of South Africa. Pretoria: Government Printer.

ALIKHAN, M.A. (1960) The experimental study of the chemotactic basis of host specificity in a phytophagous insect *Aphis fabae* Scop. Annls Univ. Mariae Curie-Sklodowska **15**: 117.

ANDREWARTHA, H.G., and BIRTH, L.C. (1954) The distribution and abundance of animals. Chicago: University of Chicago Press.

ANNECKE, D.P., and CILLIERS, C.J. (1963) The citrus psylla, *Trioza erytreae* (Del Guercio) and its parasites in South Africa. S. Afr. J. agric. Sci. **6**: 187 - 192.

ATWAL, A.S. (1962) Biology and control of citrus psylla *Diaphorina citri* Kuwayana (Hemi: Psyllidae). Punjab hort. J. **11**: 104 - 108.

BAKKER, K. (1964) Backgrounds of controversies about population theories and their terminologies. Z. angew. Ent. **53**: 187 - 208.

BAILEY, V.A. (1931) The interaction between hosts and parasites. Q. Jl. Math. **2**: 68 - 77. (Not seen in the original.)

BLOWERS, J.R., and MORAN, V.C. (1967) Notes on the female reproductive system of the South African citrus Psylla, Trioza erytreae (Del Guercio) (Homoptera: Psyllidae). J. ent. Soc. sth. Afr. 30: 75 - 82.

BONNEMAISON, L., and MISSONNIER, J. (1956) Le Psylle du poirier (Psylla pyri L.) Morphologie et biologie méthodes de lutte. Annls Épiphyt. 2: 263 - 331.

BOSELLI, F.B. (1930) Studii sugli Psyllidi. Boll. Lab. Zool. Portici 24: 228.

BURKS, B.D. (1943) The North American parasitic wasps of the genus Tetrastichus - a contribution to biological control of insect pests. Proc. U.S. natn. Mus. 93: 505 - 608.

CATLING, H.D. (1967) Personal communication.

CLARK, L.R. (1962) The general biology of Cardiaspina albitextura (Psyllidae) and its abundance in relation to weather and parasitism. Aust. J. Zool. 10: 537 - 586.

CLARK, L.R. (1963 a) Factors affecting the attractiveness of foliage for oviposition by Cardiaspina albitextura (Psyllidae). Aust. J. Zool. 11: 20 - 34.

CLARK, L.R. (1963 b) The influence of population density on the number of eggs laid by females of Cardiaspina albitextura (Psyllidae). Aust. J. Zool. 11: 190 - 201.

CLARK, L.R. (1963 c) On the density and distribution of newly-established nymphs of Cardiaspina albitextura (Psyllidae) at times of high abundance. Proc. Linn. Soc. N.S.W. 88: 67 - 73.

CLARK, L.R. (1963 d) The influence of predation by Syrphus sp. on the numbers of Cardiaspina albitextura (Psyllidae). Aust. J. Zool. 11: 470 - 487.

CLARK, L.R. (1964 a) The intensity of parasite attack in relation to the abundance of Cardiaspina albitextura (Psyllidae). Aust. J. Zool. 12: 150 - 173.

CLARK, L.R. (1964 b) Predation by birds in relation to the population density of Cardiaspina albitextura (Psyllidae). Aust. J. Zool. 12: 349 - 361.

CLARK, L.R. (1964 c) The population dynamics of Cardiaspina albitextura (Psyllidae). Aust. J. Zool. 12: 362 - 380.

CLARK, L.R., GEIER, P.W., HUGHES, R.D. and MORRIS, R.F. (1967) The ecology of insect populations in theory and practice. London: Methuen.

CLARKE, K.U. (1967) The growth responses of *Locusta migratoria migratorioides* (R. & F.) to fluctuating temperature regimes. Bull. ent. Res. *57*: 259 - 270.

CLEVELAND, L.R. (1924) The physiological and symbiotic relationship between the intestinal protozoa of termites and their host, with special reference to *Reticulitermes flavipes* Kollar. Biol. Bull. mar. biol. Lab., Woods Hole *46*: 203 - 227.

CRAWFORD, D.L. (1913) New Genera and species of Psyllidae from the Philippine Islands. Philipp. J. Sci. (D). *8*: 293 - 302.

CRAWFORD, D.L. (1914) A monograph of the jumping plant-lice or Psyllidae of the New World. Bull. U.S. natn. Mus. *85*: 1 - 182.

DADD, R.H. (1967) Improvement of synthetic diet for the aphid *Myzus persicae* using plant juices, nucleic acids, or trace metals. J. Insect Physiol. *13*: 763 - 778.

De BACH, P. (1959) New species and strains of *Aphytis* (Hymenoptera, Eulophidae) parasitic on the Californian red scale, *Aonidiella aurantii* (Mask.), in the Orient. Ann. ent. Soc. Am. *52*: 354 - 362.

De BACH, P. (1965) Some biological and ecological phenomena associated with colonizing entomophagous insects. pp. 287 - 306.
In - The genetics of colonizing species.
Eds. H.G. Baker and G. Ledyard Stebbins.
New York, Academic Press.

De BACH, P. (1966) The competitive displacement and coexistence principles. A. Rev. Ent. 11: 183 - 212.

De BACH, P., and SUNDBY, R.A. (1963) Competitive displacement between ecological homologues. Hilgardia 34: 105 - 166.

DETHIER, V.G. (1951) Host plant perception in phytophagous insects. Trans. IX. int. Congr. ent. 2: 81 - 89.

De WILDE, J. (1964) Reproduction. In - The physiology of Insecta. I. pp. 9 - 58. Ed. M. Rockstein. New York: Academic Press.

DOBREANU, E., and MANOLACHE, C. (1962) Insecta Homoptera Psylloidea. Fauna Repub. pop. rom. 8: 1 - 376.

DOUTT, R.L. (1964) Biological characteristics of entomophagous adults. pp. 145 - 167. In - Biological control of insect pests and weeds. Ed. P. De Bach. London: Chapman and Hall.

EASTOP, V.F. (1961) Some aspects of psyllid taxonomy. Ann. Mag. nat. Hist. 4(13): 165 - 169.

EHRLICH, P.R., and BIRCH, L.C. (1967) The "balance of nature" and "population control". Am. Nat. 101: 97 - 107.

ELPHINSTONE, N.D. (1966) Personal communication.

ELTON, C.S. (1953) Animal ecology. Sixth Edition. London: Sidgwick and Jackson.

ELTON, C.S. (1966) The pattern of animal communities. London: Methuen.

ENDERLEIN, G. (1914) H. Sauter's Formosa - Ausbeute: Psyllidae (Homopt.) Psyllidologica II. Ent. Mitt. 3: 230 - 235.

FRAENKEL, G. (1958) The chemistry of host specificity of phytophagous insects. Proc. IX int. Congr. Biochem. 1 - 14.

FRAENKEL, G., NAYAR, J., NALBANDOV, O., and YAMAMOTO, R.T. (1960) Further investigations into the chemical basis of the insect-host-plant relationships. Proc. XI int. Congr. ent. *3*: 122 - 127.

GHESQUIERE, J. (1958) Le premier Oviparasite de Psylle et son Hôte *Trioza erythreae* (Del Guercio) au Congo Belge. (Hymenoptera : Chalcidoidea, Encyrtidae; Hemiptera: Psyllidae). Proc. X int. Congr. ent. *1*: 275 - 280.

HAGEN, K.S. (1964) Developmental stages of parasites. pp. 168 - 246. In - Biological control of insect pests and weeds. Ed. P. De Bach. London: Chapman and Hall.

HAMILTON, A.G. (1950) Further studies on the relation of humidity and temperature to the development of two species of African locusts - *Locusta migratoria migratorioides* (R. & F.) and *Schistocerca gregaria* (Forsk.). Trans. R. ent. Soc. Lond. *101*: 1 - 58.

HARRIS, W.V. (1936) Notes on two injurious psyllids and their control. E. Afr. agric. J. 1936: 489 - 91.

HAUPT, H. (1935) Unterordnung: Gleichflugler, Homoptera. 2 Uberfamilie Pflanzlause, Hymenelytra (Phytophtires). 1. Familienreihe: Psylloidea (Westw.) C.B. Tierwelt Mitteleur. 4: 221 - 252.

HESLOP-HARRISON, G. (1949) Subfamily separation in the homopterous Psyllidae I. Ann. Mag. nat. Hist. 2 (12): 802 - 810.

HESLOP-HARRISON, G. (1951 a) Subfamily separation in the homopterous Psyllidae - II. Ann. Mag. nat. Hist. 4 (12): 1 - 35.

HESLOP-HARRISON, G. (1951 b) Preliminary notes on the ancestry, family relations, evolution and speciation of the homopterous Psyllidae. - I. Ann. Mag. nat. Hist. 4 (12): 1057 - 1072.

HESLOP-HARRISON, G. (1952) C. - The Genus Rhinocola Forster and associated Genera of the Aphalarinae - I. Ann. Mag. nat. Hist. 5(12): 957 - 974.

HESLOP-HARRISON, G. (1958) Subfamily separation in the homopterous Psyllidae - III (a - c). Ann. Mag. nat. Hist. 1(13): 561 - 579.

HESLOP-HARRISON, G. (1961) Hemiptera (Homoptera): Psyllidae. pp. 487 - 532. In - South African Animal Life 8. Eds. B. Hanstrom, P. Brinck, and G. Rudebeck. Uppsala: Almqvist and Wiksells.

HIGHKIN, H.R. (1960) The effects of constant temperature environments and of continuous light on the growth and development of pea plants. Cold Spring Harb. Symp. quant. Biol. 25: 231 - 238.

HILL, R.E. (1947) An unusual weather sequence accompanying the severe potato psyllid outbreak of 1938 in Nebraska. J. Kans. ent. Soc. 20: 88 - 92.

HUFFAKER, C.B., and MESSENGER, P.S. (1964 a) Population ecology - histroical development. pp. 45 - 73. In - Biological control of insect pests and weeds. Ed. P. De Bach. London: Chapman and Hall.

HUFFAKER, C.B., and MESSENGER, P.S. (1964 b) The concept and significance of natural control. pp. 74 - 117. In - Biological control of insect pests and weeds. Ed. P. De Bach. London: Chapman and Hall.

HUGHES, R.D. (1963) Population dynamics of the cabbage aphid, Brevicoryne brassicae (L.). J. Anim. Ecol. 32: 393 - 424.

HUSAIN, M.A. and NATH, L.D. (1927) The citrus psylla (Diaphorina citri, Kuw.) Psyllidae: Homoptera. Mem. Dep. Agric. India ent. Ser. 10: 5 - 27.

IMMS, A.D. (1957) A general textbook of entomology. Ninth Edition. Revised by O.W. Richards and R.G. Davies. London: Methuen.

JENSEN, D.D. (1957) Parasites of the Psyllidae. Hilgardia 27: 71 - 99.

KENNEDY, J.S. (1951) Host plant selection in Aphididae. Trans. IX int. Congr. ent. 2: 106 - 113.

KENTEN, J. (1955) The effect of photoperiod and temperature on reproduction in Acyrthosiphon pisum (Harris) and on the forms produced. Bull. ent. Res. 46: 599 - 624.

KLIMASZEWSKI, S.M. (1963) Ubersicht der polnischen Arten aus der Unterfamilien Liviinae und Aphalarinae (Homoptera, Psyllidae). Fragm. faun. 10: 257 - 270.

LAING, F. (1922) *Trioza citri.* (nom. nud.) Cited by J. Waterston. (1922).

LAVABRE, M.E. (1960) Presence au Cameroun du Psylle des Citrus, *Trioza* (*Spanioza*) *erythreae* del G. J. Agric. trop. Bot. appl. 7: 132 - 134.

LEES, A.D. (1959) The role of photoperiod and temperature in the determination of parthenogenetic and sexual forms in the aphid *Megoura viciae* Buckton - 1 the influence of these factors on apterous virginoparae and their progeny. J. Insect Physiol. 3: 92 - 117.

LEES, A.D. (1964) The location of the photoperiodic receptors in the aphid *Megoura viciae* Buckton. J. exp. Biol. 41: 119 - 133.

LEES, A.D. (1966) The control of polymorphism in aphids. pp. 207 - 277. In - Advances in Insect Physiology 3. Eds. J.W.L. Beament, J.E. Treherne and V.B. Wigglesworth. London: Academic Press.

LEES, A.H. (1916) Some observations on the egg of *Psylla mali.* Ann. appl. Biol. 2: 251 - 257.

LIST, G.M. (1939) The effect of temperature upon egg deposition, egg hatch and nymphal development of Paratrioza cockerelli (Sulc). J. econ. Ent. 32: 30 - 36.

MARCHAL, P. (1905) Observations biologiques sur un parasite de la galerugue de Lórme, le Tetrastichus xanthomelaenae (Rond.). Bull. ent. Soc. Fr. (1905): 64 - 68. (Not seen in the original.)

MATHUR, R.N. (1935) Notes on the biology of the Psyllidae (Homopt.). Indian Forest Rec. 1: 35 - 71.

McCLEAN, A.P.D. (1967) Personal communication.

McCLEAN, A.P.D., and OBERHOLZER, P.C.J. (1965 a). Greening disease of the sweet orange: evidence that it is caused by a transmissible virus. S. Afr. J. agric. Sci. 8: 253 - 275.

McCLEAN, A.P.D., and OBERHOLZER, P.C.J. (1965 b) Citrus psylla, a vector of the greening disease of sweet orange. S. Afr. J. agric. Sci. 8: 297 - 298.

MILNE, A. (1957) Theories of natural control of insect populations. Cold Spring Harb. Symp. quant. Biol. 22: 253 - 267.

MILNE, A. (1962) On a theory of natural control of insect populations. J. theor. Biol. 3: 19 - 50. (Not seen in the original.)

MITTLER, T.E., and DADD, R.H. (1963) Studies on the artificial feeding of the aphid *Myzus persicae* (Sulzer) - I. Relative uptake of water and sucrose solutions. J. Insect Physiol. 9: 623 - 645.

MORAN, V.C. (1968) The adult and immature stages of a new species in the genus *Paurocephala* (Homoptera: Psyllidae) from South Africa. Proc. R. ent. Soc. Lond. (B). In press.

MORAN, V.C., and BLOWERS, J.R. (1967) On the biology of the South African citrus psylla, *Trioza erytreae* (Del Guercio) (Homoptera: Psyllidae). J. ent. Soc. sth. Afr. 30: 96 - 107.

MUIR, F. (1930) Notes on certain controversial points of morphology of the abdomen and genitalia of Psyllidae. Ann. Mag. nat. Hist. 5(10): 545 - 552.

NICHOLSON, A.J. (1933) The balance of animal populations. J. Anim. Ecol. 2: 132 - 178.

NICHOLSON, A.J. (1954) An outline of the dynamics of animal populations. Aust. J. Zool. 2: 9 - 65.

NICHOLSON, A.J. (1958) Dynamics of insect populations. A. Rev. Ent. 3: 107 - 136.

NICHOLSON, A.J., and BAILEY, V.A. (1935) The balance of animal populations. Proc. zool. Soc. Lond. Part 3: 551 - 598.

OBERHOLZER, P.C.J. (1967) Personal communication.

ODUM, E.P. (1961) Fundementals of Ecology. Philadelphia: Saunders.

OSSIANNILSSON, F. (1963 a) Notes on British psyllids (Hem.- Hom.). Entomologist 96: 249 - 257.

OSSIANNILSSON, F. (1963 b) A replica technique for the study of psyllid wing microstructure. Ent. Tidskr. 84: 9 - 11.

OSSIANNILSSON, F. (1965) Über die Larvenstadien von *Psylla myrtilli* W. Wagner 1947 (Homoptera, Psylloidea). Zool. Beitr. 11: 209 - 219.

OSSIANNILSSON, F. (1966) Making permanent fluid mounts of minute arthropods. Ent. Tidskr. 87: I - 4.

PETTEY, F.W. (1923) A new species of psyllid. S. Afr. J. nat. Hist. 4: 30.

PLETSCH, D.J. (1947) The potato psyllid Paratrioza cockerelli (Sulc) its biology and control. Bull. Mont. agric. Exp. Stn. 446: 1 - 95.

PHILLIPS, E.P. (1951) The Genera of South African flowering plants. Second edition. Botanical survey of South Africa.
Memoir No. 25. Pretoria: Government printer.

POINAR, G.O. (1965) Observations on the biology and ovipositional habits of Aleurocybotus occiduus (Homoptera: Aleyrodidae) attacking grasses and sedges. Ann. ent. Soc. Am. 58: 618 - 620.

PROFFT, J. (1937) Beiträge zur symbiose der Aphiden und Psylliden. Z. Morph. Ökol. Tiere 32: 289 - 326.

ROBINSON, D.M. (1960) Synonymic notes on *Aphidencyrtus pulvinatus* (Waterston) (Hymenoptera: Encyrtinae). Ann. Mag. nat. Hist. *3* (13): 491 - 492.

RUSSELL, L.M. (1943) An apparently new species of *Paurocephala* Crawford (Homoptera, Psyllidae, Pauropsyllinae). Proc. ent. Soc. Wash. *45*: 115 - 120.

RUSSELL, L.M. (1946) A new African species of *Paurocephala* Crawford (Homoptera: Psyllidae: Pauropsyllinae). J. Wash. Acad. Sci. *36*: 94 - 97.

SALT, G. (1936) Experimental studies in insect parasitism. IV. The effect of super-parasitism on populations of *Trichogramma evanescens*. J. exp. Biol. *13*: 363 - 375.

SCHULZE, B.R. (1965) Climate of South Africa. Part 8 General Survey. Pretoria: Government printer.

SCHWARZ, R.E. (1964) An insect-transmissible virus, trapped on sweet orange seedlings in orchards where greening disease is common. S. Afr. J. agric. Sci. *7*: 885 - 890.

SCHWARZ, R.E. (1965) A fluorescent substance present in tissues of greening-affected sweet orange. S. Afr. J. agric. Sci. 8: 1177 - 1179.

SCHWARZ, R.E. (1967 a) Results of a greening survey on sweet orange in the major citrus-growing areas of the Republic of South Africa. S. Afr. J. agric. Sci. 10: 471 - 476.

SCHWARZ, R.E. (1967 b) Personal communication.

SHELFORD, V.E. (1927) An experimental investigation of the relation of the codling moth to weather and climate. Bull. Ill. St. nat. Hist. Surv. 16: 307 - 440.

SLOBODKIN, L.B. (1960) Ecological energy relationships at the population level. Am. Nat. 94: 213 - 236.

SOLOMON, M.E. (1949) The natural control of animal populations. J. Anim. Ecol. 18: 1 - 35.

SOLOMON, M.E. (1957) Dynamics of insect populations. A. Rev. Ent. 2: 121 - 142.

THORSTEINSON, A.J. (1955) The experimental study of the chemotactic basis of host specificity in phytophagous insects. Can. Ent. 87: 49 - 57.

THORSTEINSON, A.J. (1960) Host selection in phytophagous insects. A. Rev. Ent. 5: 193 - 218.

TUTHILL, L.D. (1943) The psyllids of America North of Mexico (Psyllidae: Homoptera) (Subfamilies Psyllinae and Triozinae). Iowa St. Coll. J. Sci. 17: 443 - 667.

VAN DER MERWE, C.P. (1941) The citrus psylla (*Spanioza erytreae*, del G.). Sci. Bull. Dep. Agric. For. Un. S. Afr. 233: 1 - 12.

VOLTERRA, V. (1926) Variazioni e fluttuazioni del numero d' individui in speci animali conviventi. Mem. acad. Lincei 2: 31 - 113. (Not seen in the original.)

VONDRACEK, K. (1963) Jumping plant-lice (Psylloidea - Homoptera) of Central Africa. Part I (Congo). Sb. ent. Odd. nar. Mus. Praze 35: 263 - 290.

WALLIS, R.L. (1955) Ecological studies on the potato psyllid as as a pest of potatoes. Tech. Bull. U.S. Dep. Agric. 1107: 1 - 25.

WATERSTON, J. (1922) On the chalcidoid parasites of psyllids (Hemiptera, Homoptera). Bull. ent. Res. 13: 41 - 58.

WATMOUGH, R.H. (1963) Population studies of two species of Psyllidae on broom. Thesis submitted for the degree of Doctor of Philosophy in the University of London.

WEARING, C.H. (1967) Studies on the relations of insect and host plant. II. Effects of water stress in host plants on the fecundity of Myzus persicae (Sulz.) and Brevicoryne brassicae (L.). Nature, Lond. 213: 1051 - 1052.

WEARING, C.H., and VAN EMDEN, H.F. (1967) Studies on the relations of insect and host plant. I. Effects of water stress in host plants on infestation by Aphis fabae Scop., Myzus persicae (Sulz.) and Brevicoryne brassicae (L.). Nature, Lond. 213: 1052 - 1053.

WEATHER BUREAU, (1954) Climate of South Africa. Part I. Climate Statistics. Pretoria: Government printer.

WEBER, H. (1931) Lebenweise und Umweltbeziehungen von Trialeurodes vaporariorum (Westwood) (Homoptera - Aleurodina). Erster Beitrag zu einer Monographie dieser Art. Z. Morph. Ökol. Tiere 23: 575 - 753.

WIGGLESWORTH, V.B. (1965) The principles of insect physiology. Sixth Edition, Revised. London: Methuen.

WILLIS, J.C. (1951) A dictionary of the flowering plants and ferns. Sixth edition. Cambridge: University Press.

WILSON, R.F. (1939) The Wilson colour chart. I. London: British colour council.

WILSON, R.F. (1942) The Wilson colour chart. II. London: British colour council.

WYNNE-EDWARDS, V.C. (1962) Animal dispersion in relation to social behaviour. London: Oliver and Boyd.