12.5.67

FOOD AND OUTBREAKS OF PHYTOPHAGOUS INSECTS
with special reference to *Cardiaspina densitexta* Taylor,
(Psyllidae, Homoptera) on *Eucalyptus fasciculosa* (Myrtaceae)
in South Australia.

by

T. C. R. WHITE

B.Sc. (N.Z.) : B.Sc. (For.) Edinb.

Department of Zoology

The University of Adelaide

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FRONTISPIECE

Heavily attacked E. fasciculosa trees on deep sand range north of Padthaway.

Most of the "foliage" in these crowns is mistletoe.

CONTENTS

SUMMARY

Major outbreaks of C. densitexta on E. fasciculosa occurred in 1914-20 and 1956-62. Nymphs kill the leaf-tissue on which they feed so high numbers defoliate and sometimes kill trees. Adults disperse widely in the spring but not in the summer and autumn. Aerial dispersal of first-instar nymphs is unimportant. There is a well defined mating "dance" and the males stridulate. Females lay their eggs on recently mature leaves, rejecting young and old leaves. They lay more eggs on north than south facing leaves; they strongly prefer the base of the leaf; but because of a tactile response to irregularities on leaf surfaces, they lay some eggs near other irregularities on other parts of the leaf.

The eggs replace water lost by transpiration by taking up water from the leaf. The rate of water movement varies with the age of the eggs, and in older eggs there is an "inner compartment" - presumably the embryo - which has a slower rate of flow than the rest of the egg. Eggs develop and hatch normally when removed from the leaf to distilled water. Time of hatching is determined by the periodicity of light and darkness, the frequency of the peak depending on the stimulus of "light on", and its amplitude on the duration of the preceding dark period. The time taken to respond to the "light on" stimulus increases with decreasing temperature.

Newly hatched nymphs become more active as their density increases. The proportion settling is inversely proportional to the number already established. Survival and growth rate increase with increasing density, increased light on leaf discs, and

on northern aspects of tree crowns - i.e. in response to improved nutrition.

Field samples were collected at random with the aid of a special six-sided die. In the laboratory psyllids were reared on discs of leaf floated on distilled water under fluorescent lights. Later refinement enabled isolation of the psyllids on one side of the discs from the water on the other.

Outbreaks of C. densitexta and of many other psyllids on Eucalyptus in Australia are associated with periods when wet winters are followed by dry summers. In an experiment in which C. densitexta were raised on E. fasciculosa that received different amounts of water more nymphs survived on the moderately watered trees than on those receiving too little or too much. This relationship between soil-moisture and outbreaks of psyllids is due to water-stress in the plants increasing the soluble nitrogenous food available to the nymphs. This same correlation of outbreaks with rainfall was found to hold for a number of different phytophagous insects in different parts of the world. As a result a general theory is proposed: that the abundance of many phytophagous insects is determined by a shortage of food - absolute when the plant is rare relative to the insect - relative when the insect is rare relative to the plant; and that those of the latter which erupt to outbreaks do so in response to the seasonal rainfall pattern stressing the plant and increasing the amount of nitrogenous food, and thus alleviating the relative shortage of food for the insects.

There is no competition for food when it is scarce, and predators have negligible influence on the prey's abundance when food

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Declaration

The work presented in this thesis is, unless otherwise acknowledged in the appropriate place, my own, and has not previously been published or submitted to this or any other University for the award of any degree.

(T.C.R. White)

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1. INTRODUCTION

1.1 The Problem

When this study was commenced in November 1962, widespread and sustained defoliation of pink gum (Eucalyptus fasciculosa F. v. M.) during a period of some five to eight years, and the eventual death of some trees, had given increasing concern to many farmers in the mid-southeast of South Australia. Numerous species of foliage-eating insects were present in unusual abundance on these trees, but the lerp-forming psyllid Cardiaspina densitexta Taylor was the main cause of the defoliation.

Pink gum is of no great economic importance. In the past it was used extensively as the only durable fencing timber that was available; also it was sought after by beekeepers as a subsidiary source of honey. Today it has largely been superseded by treated pine and lucerne respectively. It still serves on some farms as shelter for stock, but the chief concern for the species has been a matter of aesthetics. The badly defoliated, stag-headed and dead trees look very unsightly, especially around homesteads where a great many pink gums have been retained in favour of other species.

Outbreaks of psyllids on eucalypts are by no means a new phenomenon, but they have been unusually common in many parts of Australia during the last ten to fifteen years. In contrast to the situation on pink gum in South Australia, many outbreaks of lerp-insects in Victoria and New South Wales have been of considerable economic importance occurring in forests of high value and causing considerable loss of increment.

In other parts of the world the Psyllidae contains a number of important pest species. The pear and apple psyllids of Europe and America, the potato psylla of America and the citrus psylla of Africa are probably the best known. These, as well as many other species that are of less or no economic importance would seem like their lerp-forming Australian relatives to be apt to spasmodically and violently increase in abundance.

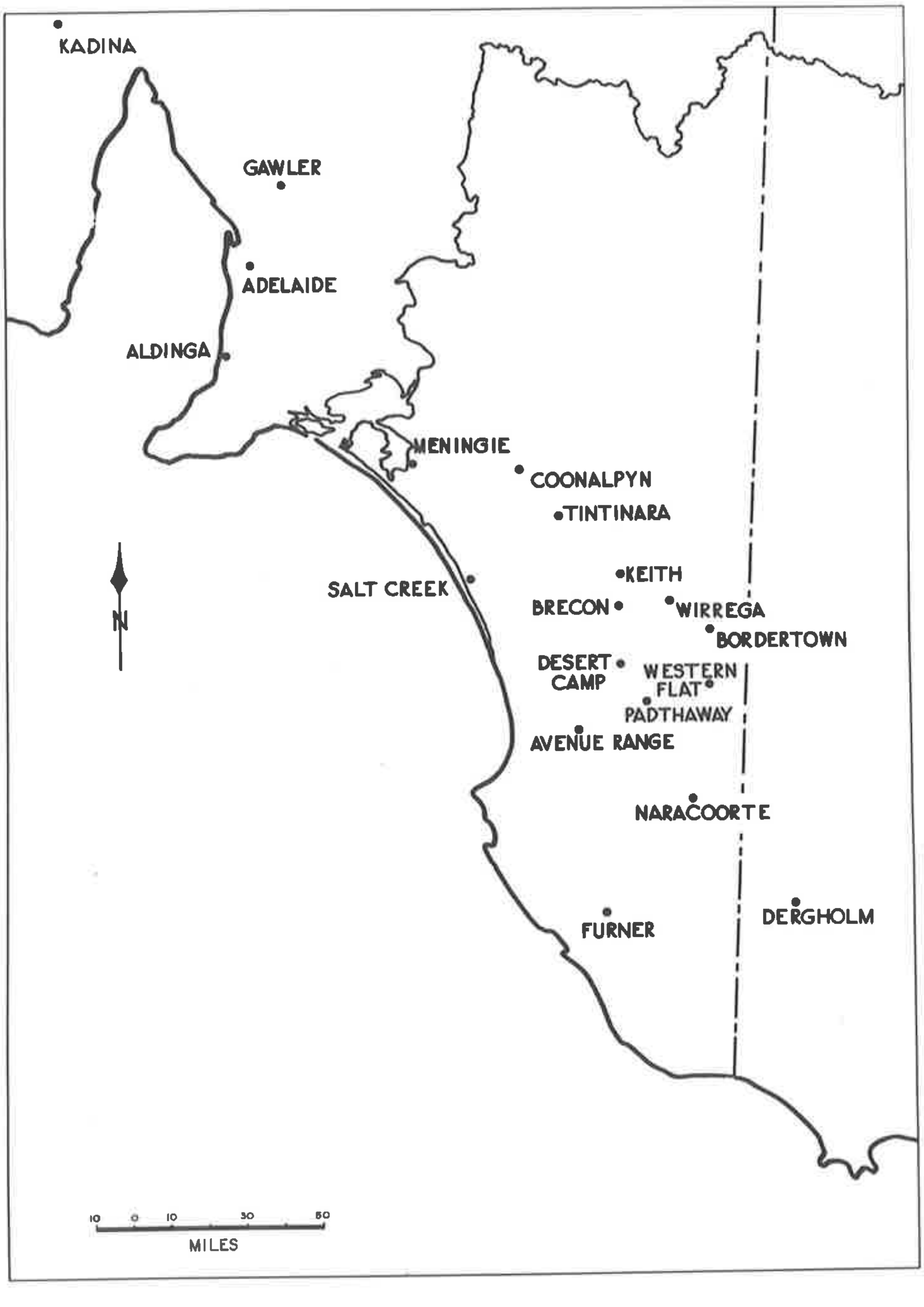
Cardiaspina densitexta had for many years been included, along with other closely related species, in Froggatt's original species *Cardiaspis vittaformis*. As such it was recorded on a wide range of *Eucalyptus* species, and was known to occasionally increase tremendously in abundance causing extensive "scorching" of the trees by killing most of their leaves.

Tuthill & Taylor (1955) and Taylor's (1960; 1962) work on the taxonomy of the Australian Psyllidae has revealed the diversity of species within the old *C. vittaformis* and the often quite rigid host specificity of many of them. It is now clear that few if any of the early reports of outbreaks of *C. vittaformis* refer to *C. densitexta*, but rather to *C. albitextura* and red gum (*Eucalyptus camaldulensis* Dehn.).

Most of the field work for this study was done in the Keith-Brecon-Desert Camp areas, but extensive and repeated travelling throughout the whole southeast of the State and much of the Mt. Lofty Ranges was necessary to assess the situation fully. Figure 1.01 is a map of

Figure 1.01

Map of part of South Australia and Victoria showing the location of places mentioned in the text.


KADINA
GAWLER
ADELAIDE
ALDINGA
MENINGIE
COONALPYN
TINTINARA
SALT CREEK
KEITH
BRECON
WIRREGA
BORDERTOWN
DESERT CAMP
WESTERN FLAT
PADTHAWAY
AVENUE RANGE
NARACOORTE
FURNER
DERGHOLM
N
10 0 10 30 50
MILES

the southern parts of South Australia and the western part of Victoria illustrating the location of the principal place-names referred to in this thesis.

1.2 The Host Tree

(*Eucalyptus fasciculosa* F. Muell. - Pink Gum, Hill Gum, Scrub Gum, Mountain Gum, Sand Gum, White Gum.)

The species was first described by Dr. Ferdinand von Mueller in 1855. According to Blakely (1955) it falls in the series Heterophloiae (Section Terminales) which includes six species of red boxes. All but pink gum are eastern species extending from Victoria to Queensland.

Pink gum is a small to medium sized tree, largely of poor form but varying considerably throughout its range. In the southeast of the state most trees are multi-stemmed and twisted, having originated as suckers from roots, stumps and lignotubers. This poor form is as much due to the long history of repeated burning and more recent land clearing and grazing as to any genetic factor, or inherent harshness of the environment.

As many farmers clearing land in the southeast will testify, there is a big difference in the nature and depth of the root system of pink gum when compared with those of other species of *Eucalyptus* in the area. The mallees, stringy barks and blue gums are all deep rooting species with strong tap roots. Pink gums on the other hand are exceptionally shallow-rooted even on deep sand, having numerous and far flung lateral roots and no tap root. On the shallower sands overlying clay on limestone these laterals occupy the clay, but few if any roots penetrate the limestone.

This difference is reflected in the ease with which pink gums can be uprooted by the heavy machinery employed for land clearing, and contrasts sharply with the difficulty of removing the deep-rooted species, especially the larger blue gums (E. leucoxylon). I have confirmed these differences by inspecting several areas where land clearing was being carried out, and freshly uprooted trees were available. Uprooted trees give the best indication of the true extent and depth of their root system short of digging and washing them out (Jacobs, 1955). Figures 1.02 and 1.03 illustrate the differences found in these root systems.

Pink gum does not differ from other eucalypts in the production, disposition and longevity of its leaves (Jacobs, 1955). Most foliage is produced each year in late spring and early summer (Burbidge, 1960) although some growth will continue into the late summer months, and new foliage will develop after defoliation at any time other than the depth of winter.

A few leaves are being discarded at all times, and if growth is exceptionally fast relatively young leaves may be shed, but major leaf-fall occurs with the late spring flush and there is often a less extensive shedding of leaves in the autumn. Badly damaged leaves will be shed without prior stimulus from new growth and for this reason heavy attack by C. densitexta will tend to accentuate the normal pattern of growth and replacement of foliage.

There is little or no difference between the "inner" and

Figure 1.02

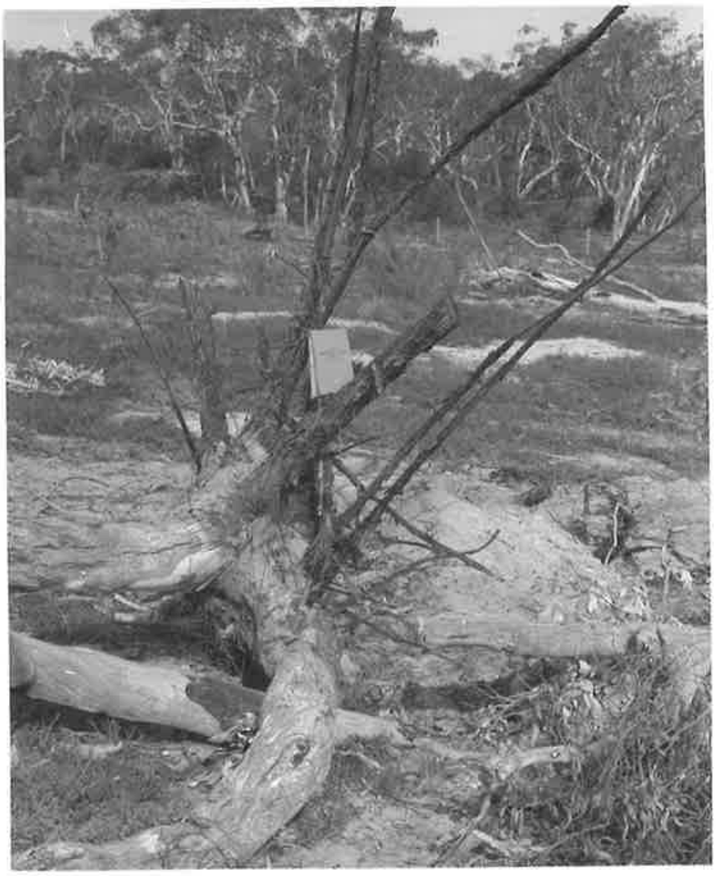
E. fasciculosa - typical root system showing the absence of a tap root and the widespread lateral roots.

Figure 1.03

E. leucoxylon - typical root system

Note the strong deeply penetrating tap root. The original soil surface level is clearly visible on the trunk at the right of this photograph.

Size of field book approx. 5" x 8".



"outer" leaf surfaces (Jacobs, 1955), the species being amphi-isostomatous with a stomatal frequency of 440 square mm. (Millett, 1945).

Early records of the distribution of E. fasciculosa are patchy and incomplete. The original description records it "on barren ridges along St. Vincent's Gulf, on the Gawler River, the Mount Lofty Ranges and Bugle Ranges, and on Encounter Bay". Black (1926) records the distribution as " ......Mt. Lofty Ranges to Encounter Bay, Monarto South, Murray Bridge, Coorong, Kangaroo Island ....", and Blakely (1955) repeats this.

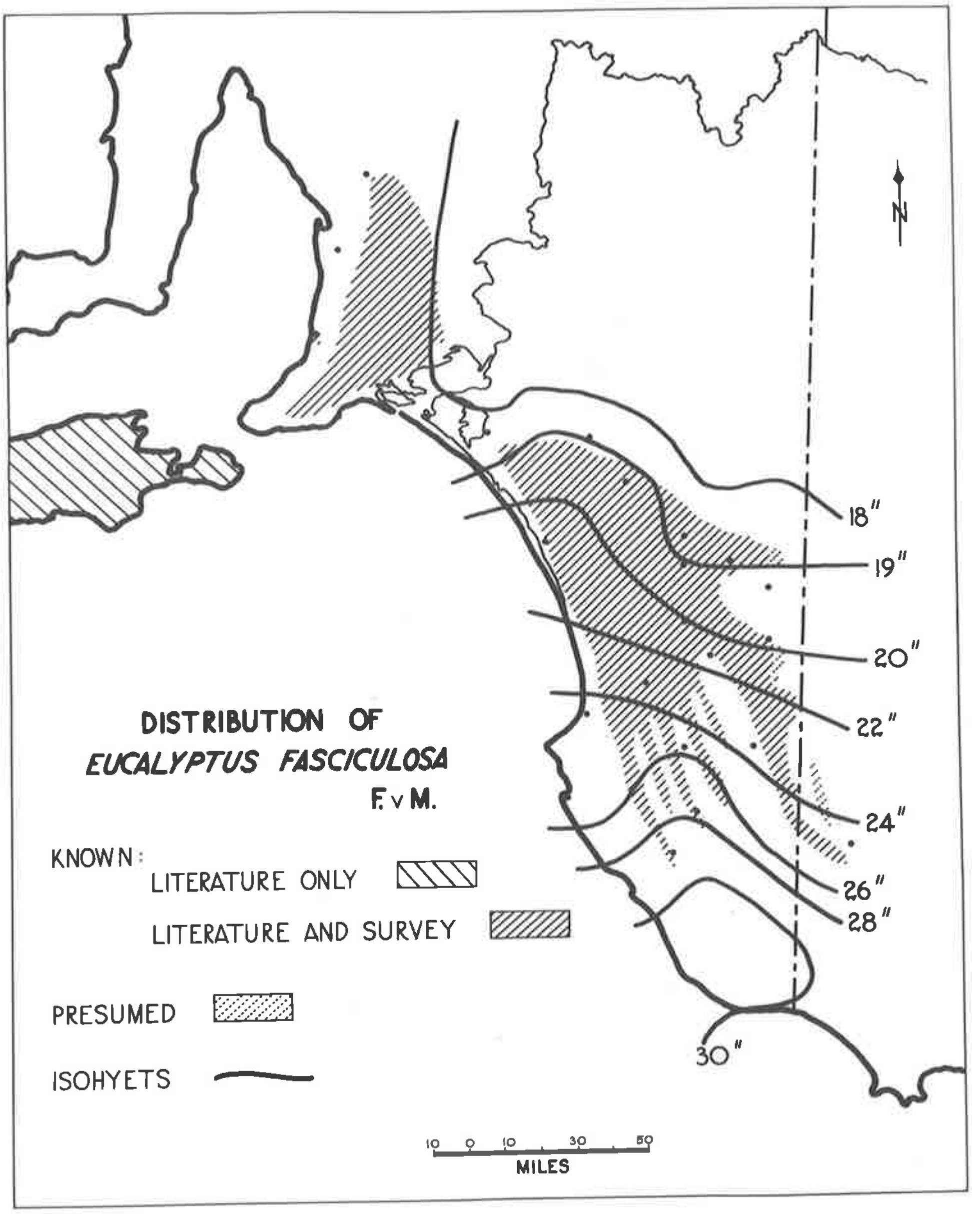
The present day picture is much distorted by land development and clearing, the native flora over large areas having been totally destroyed - so much so that a true delineation of the original distribution is no longer possible. The sketch map (fig. 1.04) of distribution has been compiled from extensive field observations and a thorough search of the literature.

Pink gum extends from a little north of Gawler down through the Mt. Lofty Ranges and on Kangaroo Island. It occurs discontinuously, being restricted to the poorer soils and harder sites (Specht & Perry, 1948; Northcote & Tucker, 1949), A remnant population persists near sea level at Aldinga and odd patches are still to be found west and north of Lake Alexandrina (Jessup, 1946).

Along the eastern shores of the lakes, between Wellington and Meningie and inland at the same latitude, there is no pink gum, so that

Figure 1.04

E. fasciculosa - known distribution



DISTRIBUTION OF *EUCALYPTUS FASCICULOSA* F.v M.

a distinct discontinuity exists between the Mt. Lofty Ranges and southeast portions of its distribution.

The northern limit of the southeastern portion approximates to the 18 to 19 inch isohyets, until the inlier of Wimmera soils just east of Cannawigara (Specht, 1951). Here the eastern limit to distribution is the junction of these soils with the "desert" sands. In the south the species becomes restricted to the tops of the sand ranges where it is replaced by the stringy bark _E. baxteri_ just south of Furner, in the west, and Dergholm (Victoria) in the east.

The distribution and abundance of _E. fasciculosa_ in the southeast is determined by the "water-sensitivity" of the species. This sensitivity takes the form of a low tolerance to seasonal differences in soil moisture, and is largely the result of its shallow rooting habit, accentuated by the prevailing soil types and the marked seasonal distribution of the rainfall in this Mediterranean-type climate.

It cannot tolerate soil that is too wet or too dry. Thus, in habitats where the moisture-holding capacity of the soil, drainage, watertable depth, salinity and topography all change considerably and repeatedly within any given zone of rainfall, the species will colonize only sites which meet its exacting and narrow requirements (Coaldrake, 1951; Litchfield, 1956; Specht & Perry, 1948). It is not surprising, therefore, that pink gum occurs on a wide variety of soils throughout the southeast, although these are all "desert" soils of broadly the same basic form - wind blown sands overlying clays or clay loams on limestones (Taylor, 1933; Crocker, 1944; Jessup, 1946; Specht, 1951;

Jackson & Litchfield, 1954; Coaldrake, 1951; Blackburn, 1952; 1959, a, b; 1964; and Blackburn et al., 1953).

In the area near the northern and northeastern boundary of the southeast part of the distribution (fig. 1.04) the rainfall is lower than elsewhere in the distribution, and the species is limited to the wetter sites - sandplains with shallow watertables, soils with little depth to the subsoil, the base and lower slopes of limestone hills and lee sides or wet hollows between sand-dunes (Jackson & Litchfield, 1954; Coaldrake, 1951). Here the rainfall is such that summer drought reaches intolerable proportions too frequently for the species to maintain a hold on any but these wetter sites.

Further south in areas receiving somewhat higher rainfall (e.g. Brecon) pink gum succeeds best on freely drained sand plains over travertine (especially the Laffer group of soils) but is not able to survive on the shallower calcareous soils or on the higher ridges of deeper aeolian sands. It also shows a low tolerance for the waterlogged and saline type of sand plain (Litchfield, 1956).

Further south again, in the Desert Camp district, this species shows an even more marked preference for free draining, non waterlogging and drier sites. The clayloam subsoils of the Laffer Sands support pink gum while neighbouring Willalooka Sands with their heavier clay subsoils do not. At this point the importance of too much soil water is becoming apparent. These sites with heavy clay subsoils become untenable because a perched watertable will form during most winters causing waterlogging or flooding for long periods.

At Padthaway the species is found at or near the top of the sand ranges, being altogether absent from the plains where E. camaldulensis now occurs, although further towards the coast it is sometimes found on slight rises and on the fringes of the sand ranges (Blackburn, 1952). At the southerly extremes of the distribution with further increase in rainfall, pink gum is confined to the tops of these sand ranges, finally being replaced by stringy bark (Specht & Perry, 1948).

Thus in the north the distribution is limited by summer drought at a point where rainfall in dry years is not sufficient on these desert soils to provide enough stored water to maintain the species through the hot summer (Specht & Rayson, 1957). In the south the distribution is again limited by summer drought because here winter rainfall makes all but the high, dry, sandy sites too wet for pink gum; but on these ridges in dry summers the soil dries out to the extent that only the deep-rooting E. baxteri can survive.

Between these two extremes pink gum colonizes soils which are not liable to overlong periods of waterlogging and yet have the capacity to store sufficient water to enable this shallow rooted species to survive the summer. With such extreme sensitivity quite small differences in the depth and texture of the soil, and small and local variations in topography may be critical.

A similar situation would seem to hold in the Mt. Lofty Ranges / Kangaroo Island portion of the distribution. Here rainfall is higher than that experienced in the Southeast, but pink gum occurs only on the drier north-facing or well drained sites, usually with only skeletal soils on the shattered bedrock (Specht & Perry, 1948; Northcote & Tucker, 1948).

A pink gum tree growing on any particular site becomes adjusted to the conditions prevailing there over a period of years. If a sudden or very pronounced deviation from these prevailing conditions occurs, the tree will be placed under stress. If the site happens to be a marginal one, colonized during a period of favourable years, the tree may be killed. The more violent and/or prolonged this deviation, the greater the number of trees (initially seedlings and over-mature specimens) that will die, and if the deviation is permanent (e.g. a change in climate) many trees may be killed and the boundary of the specie's distribution permanently altered. This is the same type of mechanism as in the model proposed by Andrewartha & Birch (1954) for their hypothetical grasshopper akin to _A. cruciata_.

I believe rainfall to be the predominant factor controlling the distribution and abundance of pink gum, its effect far exceeding that from any other component of environment. Temperature will tend to "complement" the effects of rainfall or rather to increase the severity of its action through its effect on evaporation, but if rainfall is "normal", marked deviations in temperature will have little or no effect on the trees.

1.3 History of Outbreaks

There are sufficient reliable reports available to confirm that there was a major and widespread outbreak of lerp-insects on pink gum in the southeast of South Australia during the period 1914 to 1920-22.

Since that time small, brief and widely separated local increases occurred during the 1930's and 1940's. Before 1930 the area in which the most recent outbreak occurred was sparsely inhabited, and most present day land owners have no memory of these insects before the most recent outbreak.

The first areas to experience this recent outbreak were those located at or near the dry northern boundary of the distribution of pink gum. Farmers on land to the north and east of Tintinara reported intermittent outbreaks since the early 1940's, these becoming more frequent and severe in the early 1950's.

By 1956 very large numbers of C. densitexta were present in and around Tintinara and Coonalpyn but areas to the east and south remained relatively unaffected. In 1958 the outbreak had "spread" west to the coast and south to Brecon, Desert Camp, and beyond. In 1959 the psyllids were prominent near Naracoorte, and it appears that this was the year in which the outbreak was most widespread throughout the Southeast.

The numbers of psyllids decreased and the trees recovered quite generally throughout the area during 1960, but numbers soon built up again and by the spring of 1962 populations were widespread and high, although showing a decreasing trend to the south (fig. 1.05). In 1963 numbers remained high, all pink gum trees in the mid-Southeast being completely "burnt-off". A general "crash" in the population of psyllids occurred in the spring of 1963, and although a few local "pockets" persisted in the north and increased during the summer, numbers continued to decline until the spring of 1964 when they fell to very low levels. In the summer of 1964/65 a few <u>C. densitexta</u> could still be found, numbers tending to increase from the south to the north, where odd isolated patches of greater density still persisted. Table 1.01 shows this trend of increasing numbers from south to north.

<u>Table 1.01</u>

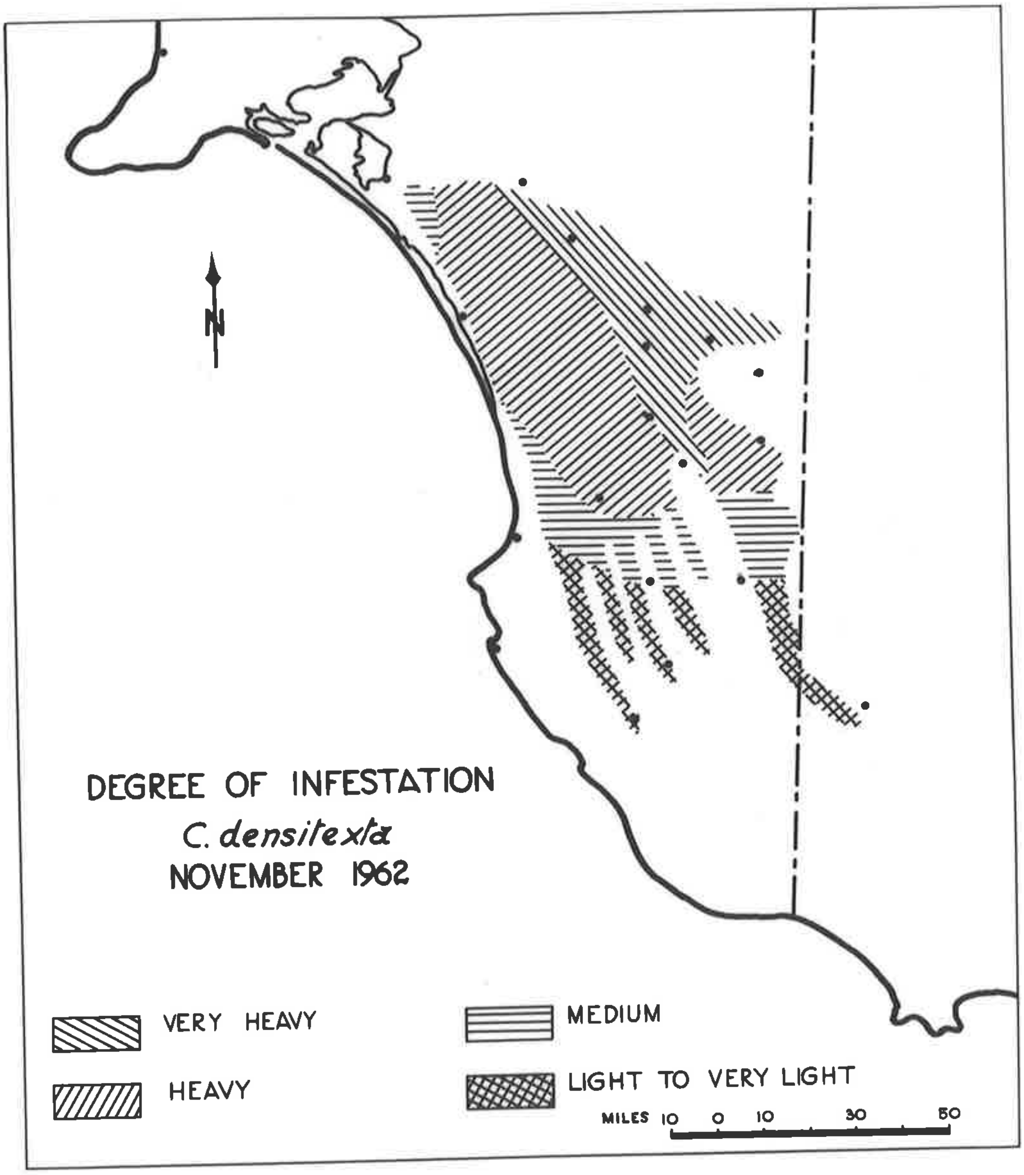
<u>The numbers of <u>C. densitexta</u> on leaves of pink gum trees in the Spring and Summer of 1964/65</u>

(Numbers in brackets are the numbers of twigs in each sample)

Locality (from North to South)	Mean Number of Psyllids per Sample	
	Nov. 1964	Jan/Feb 1965
Coonalpyn	1154 (3)	3.65 (20)
Tintinara	-	2.40 (20)
Keith	-	2.45 (20)
Brecon	738 (3)	1.15 (20)
Western Flat	321 (5)	-
Desert Camp	916 (10)	1.45 (20)
Padthaway	262 (11)	-
12 miles south of Padthaway	98 (11)	0.95 (20)
Avenue Range	-	0.60 (20)
10 miles north of Naracoorte	-	0.45 (20)
10 miles south of Naracoorte	-	0.05 (20)

Figure 1.05

C. densitexta - Degree of Infestation - November, 1962.



DEGREE OF INFESTATION

C. densitexta

NOVEMBER 1962

The November 1964 figures in this table are from twigs chosen subjectively for assessment of predation by birds (sect. 2.722) the Jan/Feb 1965 figures are from random samples made according to the standard procedure described in section 2.1.

In the Mt. Lofty Range-Kangaroo Island part of the pink gum distribution outbreaks of C. densitexta are unknown, or rather, unrecorded. As a result of a radio talk in which an appeal was made for information about high numbers of lerp-insects, I was able to see the aftermath of what had been a quite severe outbreak of C. densitexta on pink gum in 1962-63. This was confined to a small pure stand of pink gum growing on a steep, north-facing slope near Lenswood in the Adelaide Hills. The trees are growing in very thin and patchy soil on a bedrock of shale which frequently outcrops among the trees. Rooting is shallow and widespread, many roots being visible at or just below the surface. Sufficient evidence remained (extensive recent defoliation, dead leaves on the ground bearing lerps, and relatively high numbers of live psyllids still present on the trees) to confirm that this had been a severe outbreak, and that C. densitexta was the psyllid concerned.

1.4 Discussion of the Approach to the Problem: an Outline of the Main Working Hypothesis formed during the Study, and Proposed Theory Arising from this Study.

The conclusions reached in this thesis represent not so much the fruits of two and a half years studying a lerp-insect defoliating a eucalypt, as the culmination of some fifteen years experience with trees and their diseases and pests. This experience has taught me that whenever a tree is heavily attacked by a predator or parasite (insect or fungal) which is normally present at innocuous levels of abundance, there is usually something more deepseated the matter with the tree- some imbalance with the "abiotic" environment - and that the root system is nearly always involved. This "forester's approach" (for such it is) has largely influenced my approach to the particular problem of explaining the distribution and abundance of C. densitexta. In addition I have long felt that the early stage in each generation of a phytophagous insect is the most vulnerable - the weak link in the chain. The fact that, for most of the time, only a very small proportion of the total progeny of such insects survive through the first instar is well known to entomologists, but is nevertheless often forgotten or overlooked by those investigating the ecology of pest species. The number living long enough to be killed by parasites and predators is only a very small fraction of the number that begins each generation. On those occasions when the pressure is lifted allowing a larger proportion to survive beyond this stage for several successive generations, the insects quickly multiply until they have exhausted some resource - usually food - whereupon most individuals die. This ultimate dependence on food, and the apparent inability of parasites and predators to stop an insect from utilizing food at such times, would suggest that more often than not, it may also be a lack of food which is limiting the numbers at times of low levels of abundance - that the apparently wasteful production of offspring is, in fact, vitally necessary if a species is going to be able to find limited and widely scattered food, and avoid extinction.

From the outset of this study it was clear that here was an indigenous insect attacking an indigenous tree. Attack was as severe in "virgin" scrub as on developed farmland. The intensity of attack decreased from the dry north to the wetter south. Other psyllids in different parts of Australia had increased in abundance at about the same time. There was evidence that this sort of widespread outbreak had occurred in the past. All these facts suggested that some widespread and general but reversible change of the environment was responsible for these outbreaks. A change in the weather pattern was the obvious cause to suspect in the face of this sort of evidence, and as discussed in section 1.2, rainfall (interacting with topography and type of soil) seems to be the most likely feature of the weather that might cause such outbreaks.

This, then, very generally, is the broad foundation upon which the thinking which gave rise to the initial hypothesis was based - an amalgam of observation, past experience, and trying to imagine all the things which could have caused such large numbers of animals to be living where so few lived before. It was, however, the observation that first instar nymphs on the much less heavily attacked southern faces of trees, were dying while still feeding beneath their newly formed lerps, while the nymphs on the northern face survived, which crystallized all this into an instand realization that starvation was at the heart of the whole problem - that the weather was altering the plant to make it a better source of food for these young nymphs which, in most generations must try to establish themselves in an environment that is not so much actively hostile, as passively and indifferently inadequate. All the rest followed from this point.

The original hypothesis is as follows:-

An outbreak of C. densitexta develops when, over several consecutive generations, there is a large increase in the proportion of nymphs surviving the first instar; this increased survival being a direct result of an increase in the soluble nitrogenous food available to these nymphs. This increased supply of food results from water-stress of the E. fasciculosa trees upon which the psyllids are feeding. The trees respond to the stimulus of dehydration of their tissues by decreasing the synthesis of protein and increasing the hydrolysis of stored protein, thereby increasing the proportion of soluble nitrogen in their tissues. The trees are subject to water-stress whenever they are unable to get sufficient water from the soil, either because there is not enough available water in the soil - drought - or because a large proportion of the feeding roots have been killed - physiological drought. Drought is usually caused by too little rain in summer and physiological drought by too much rain in winter. If a dry summer follows a wet winter the effect is intensified. Consequently outbreaks of C. densitexta would be expected to be correlated with periods when a dry summer succeeds a wet winter.

This correlation was found to exist not only for C. densitexta, but also for outbreaks of a number of other species of psyllids on eucalypts in different parts of Australia, and for a variety of different phytophagous insects in different parts of the world. I have collected examples of sap-sucking and leaf-, cambium- and wood-chewing species for which outbreaks seem to have the same cause. Consequently this hypothesis has been expanded to a general theory, which can be stated as follows:-

The abundance of many phytophagous insects, especially sap-sucking species living on trees and other perennial plants, is determined by food; an absolute shortage when the food plant is rare relative to the insect; a relative shortage when the insect is rare relative to the plant. An absolute shortage, by its very nature, can only be temporary; relative shortages - of one sort or another - are much more important in the ecology of phytophagous insects. There are many species which are usually rare relative to their food plant but which occasionally increase to outbreak proportions (when they become immensely abundant relative to their food) without any change in the distribution and abundance of the food plant. Usually such species are responding to an increase in food brought about by stressing of the food plant by weather-induced changes of soil-moisture.

On the basis of this theory most phytophagous insects can be placed into one of two broad classes:-

A: Those whose abundance is determined by an absolute shortage of food - created by their own activities in the way described by Andrewartha & Browning (1961) - e.g. *Cactoblastis* larvae when they have destroyed a local patch of *Opuntia*, and any phytophagous insect at the stage where, during an outbreak, it destroys all its available food.

B: Those whose abundance is determined by a relative shortage of food - e.g. any phytophagous insect which occasionally increases to outbreak levels of abundance, during its periods of rarity.

There is a third group of phytophagous insects, however, which does not fit into either of these two classes. Those which are rare in the midst of apparent plenty, and have never been recorded becoming numerous relative to their food plant. These may be held in check by some factor other than food (as for example *Nezara* would seem to be held in check by *Trissolcus* (= *Microphanurus*) or as *Schizoneura* is apparently held in check by *Aphelinus*), or they may represent intermediate situations where the supply of available food never increases sufficiently or for long enough to allow of large increases in abundance. Detailed study of the abundance of such insects in relation to their *available* food may well reveal that many of them are, in fact, regulated in their abundance by the supply of food.

Perhaps the most important point arising from this study is that the explanation of variations in the distribution and abundance of many phytophagous insects should be sought in *changes of* *the environment of the plant upon which these insects feed*. This is, admittedly, merely a shift in emphasis, the plant being a major factor in the environment of the insect. It is, however, an important one requiring, in many instances, that the investigator think about the problem in a new way.

2. SOME ASPECTS OF THE BIOLOGY AND ECOLOGY OF CARDIASPINA DENSITEXTA (TAYLOR) (HOMOPTERA : PSYLLIDAE : SPONDYLIASPINAE)

2.0 Introduction

C. densitexta is a lerp-building psyllid described with a number of other species of the same genus by Taylor (1962).

Its basic life history follows the typical psyllid pattern, and in all but minor details is identical to that of *C. albitextura* (Clark, 1962).

The adults feed through the stomata of the leaves of the host tree, *E. fasciculosa*. Reproduction is bisexual. The females lay eggs which are attached to the leaf by a stalk driven through the cuticle and epidermis. The young nymphs hatching from the eggs settle, insert their stylets through a stomata, and build lerps under which they will normally remain throughout the nymphal period. There are five nymphal instars, the fifth moulting to the winged adult; the adults jump and fly. The sex ratio is approximately unity with males tending to start emerging earlier than females.

There are three generations a year, adults emerging and laying eggs in the spring (mid-October to early December), summer (late January to early February) and autumn (mid-April to early May). As indicated, there is considerable difference from year to year in any one locality in the time of completion of each generation, particularly the spring one; and the rate of development is measurably slower in the southern part of the distribution. It is unlikely, however, with the present climate, that more or less than three generations would be completed in any one year. (A fourth generation has been obtained in the milder climate of Adelaide, very dark adults emerging in the winter).

There is no true hibernation, but first instar nymphs, after hatching and settling early in the winter, grow scarcely at all until the following spring. This has the effect of "phasing" nymphs which have hatched over a period of six to eight weeks to mature within as little as one week of each other. Autumn females confined in organdie bags have lived for up to five months through the winter, becoming active and even laying a few eggs during warm sunny days.

With the exception of Kangaroo Island (for which there are no known records of this insect) I have found _C. densitexta_ associated with pink gum wherever this tree occurs in quantity.

The optimum locality for this psyllid would appear to be approximately within the triangle formed by Tintinara - Wirrega - Brecon, where it has always been more plentiful than elsewhere. It becomes much less plentiful further south, although being more plentiful at the southern limit of its distribution than throughout the Mt. Lofty Ranges, where it is a rare insect- even when elsewhere in great abundance - with exceptions such as the outbreak at Lenswood in 1962-63.

2.1 Field Sampling

2.11 Preliminary Experiment

Anyone who has taken a sample of leaves or twigs from a tree will know how difficult it is to avoid bias, yet it is essential to have a method that will give a random sample. As a preliminary step towards devising a method for taking random samples of natural populations of psyllids the following experiment was done.

Materials and Methods

One pink gum tree was selected. This tree had a single trunk, a symmetrical crown which, with the aid of a stepladder, was fully accessible. The crown was visually divided into four sectors (NE, SE, SW, and NW) and two halves (upper and lower). A sample of one hundred twigs was collected from this tree, as follows:

To choose any twig a start was made from the base of the tree's trunk. At each bifurcation (with the exception of any old dead stubs) a penny was tossed to decide whether to proceed to the left (heads) or the right (tails). This process was repeated at each bifurcation encountered until either the ultimate leaf-bearing twig or a dead twig was obtained.

All live twigs were labelled according to sector and half, collected in individual bags, and taken to the laboratory where all psyllids were counted, and the total leaf area per twig estimated with an air-flow planimeter (a previous study had shown a highly significant correlation ($R = 0.86$; Standard Deviation = 3.04) between the areas of leaves obtained with an air-flow planimeter and with conventional planimeter measurement of their sun prints).

Results

A. Distribution of samples

(i) The distribution of samples between the four sectors was not random, being 40, 14, 15 and 31 respectively; giving a count of 71 on the north face and 29 on the south face, a highly significant (χ^2 = 11.91***) deviation from randomness. This is due to the fact that the major branches arising from the trunk carry unequal proportions of the foliage that make up the crown. Thus, should the first (i.e. lowest) main branch carry (say) 10% of the foliage, 50% of the samples would be expected to be located in this 10% of the foliage, and the other 50% in the remaining 90% of the foliage. This is because the first decision that leads to a particular twig is made at this first bifurcation. Unequal bifurcation higher up the tree would also be expected to contribute to this bias.

(ii) The distribution of the twigs between the upper and lower halves did not differ significantly from that expected by chance (Table 2.01).

Table 2.01

Distribution of twigs between the upper and lower portions of the crown of a pink gum tree.

	Lower Half	Upper Half	Total
Dead	20	24	44
Live	30	26	56
Total	50	50	100

B. Distribution of Dead and Live Twigs

(i) There was no significant difference between the proportion of dead to live twigs in the upper and the lower halves of the crown ($\chi^2 = 0.18$) (Table 2.01).

(ii) There was a significantly greater proportion of dead twigs on the north face than on the south face ($\chi^2 = 5.45$*) (Table 2.02).

Table 2.02

Distribution of twigs between the north and south faces of the crown of a pink gum tree.

	North face	South face	Total
Dead	37	7	44
Live	34	22	56
Total	71	29	100

C. Leaf Area Distribution

Analysis revealed that there was no significant difference between the total area of the leaves on twigs from different parts of the tree. Leaf area was abandoned from this stage onward, however, as, although the regression was significant, only 12% of the variation of the number of lerps per twig was accounted for by variation in leaf area per twig. Having regard to the time and effort involved in obtaining leaf-areas, and the fact that differences between leaf-areas per twigs are not significant, it was considered more profitable to increase the number of replicates in the sampling and simply use total number of animals per twig as the basic sample unit.

Analysis of Variance
(log (x + 1) psyllids/twig = y : Air Flow Planimeter area/twig = x)

Variation due to	d.f.	S.S.			d.f.			
		(x^2)	(xy)	(y^2)		S.S.	M.S.	V.R.
Between strata†	7	6057.61	-94.7184	25.6012	7	26.7051	3.8150	11.45***
Error	48	55510.61	339.6770	17.7296	47	15.6511	0.3330	
Total	55	61568.22	244.9586	43.3308	54	42.3562		

Regression S.S. = 2.0785 F^{1}_{47} = 6.24* $R^2 = 0.12$

†8 strata : upper and lower NE, SE, SW, and NW.

D. Distribution of Psyllids in Different Parts of the Crown

As the accompanying table of means illustrates, there was no significant difference between the numbers per twig in the upper or lower sections of the crown. The distribution of number of psyllids per twig on the north and south faces was, however, quite distinct, there being many more animals in the northern sectors.

Table of Means
Mean log (x + 1) psyllid/twig ± S.E.

	Height		
Orientation	lower half	upper half	Mean
N.E.	2.35 ± 0.24	2.20 ± 0.16	2.25 ± 0.13
S.E.	2.02 ± 0.26	0.71 ± 0.26	1.37 ± 0.18
S.W.	0.55 ± 0.22	0.70 ± 0.26	0.61 ± 0.17
N.W.	1.89 ± 0.17	2.32 ± 0.33	1.98 ± 0.15
Mean	1.71	1.62	

The number of psyllids per twig gave essentially the same results as those obtained for dead and live twig distribution (assuming that increased numbers of dead twigs is associated with increased numbers of psyllids).

2.12 Design of a Sampling Method

As a result of this preliminary experiment, plus some further sampling, the following system of sampling was devised. In order to avoid the bias caused by the unequal contribution of the major branches to different parts of the crown, and because it was desired to make a comparison between north and south faces of the tree, the crown was arbitrarily divided into north and south halves and equal numbers of twigs collected from each half, no cognizance being taken of the height of the sample within the crown. Low-growing and sucker shoots were ignored.

Because of the uneven number of branches and distribution of foliage among them, all large structural limbs were ignored and only the foliage-bearing units (Jacobs, 1955) used. These are quite distinct, and can either be deliberately selected so as to spread the sampling evenly over the whole north or south face, and a sample made within each in turn; or they can be visually divided into right and left groups, and a decision taken by chance, repeating this until only one unit is left, and then proceeding normally within this down to the ultimate twig. The whole process is repeated for each twig collected. Where any difference between foliage units can be observed this latter method of selecting units <u>must</u> be used, in order to avoid personal bias even though it may be unconscious.

Ten or fifteen decisions are usually required to obtain each twig in a heavily foliaged tree, and as few as three to five where there has been much defoliation and death. When sampling was being done to collect live psyllids all dead twigs were ignored.

Instead of the slow and tedious process of tossing a coin or consulting a table of random numbers while trying to keep track of the appropriate position within the crown of the tree, a six-sided die was used. This is a 12 x 12 x 12 mm cube of "Perspex" with three "L"s and three "R"s engraved on its six faces. It was placed in a small screw-topped jar which fits confortably into the palm of the hand. A quick twist of the wrist violently rattles the die in the jar, but it settles almost immediately, allowing a quick reading of "L" or "R". The other hand is free to grasp each bifurcation in turn, where necessary twisting it to make a definite left and right arm <u>before</u> taking a decision from the die. When sampling twigs that are out of reach the jar is held in front of the face so that it can be glanced at without losing sight of the position reached in the canopy. Eleven hundred test throws of this die to check for bias gave the result 546 "L" and 554 "R".

Where individual trees are to be selected at random, this is done by taking a decision "left" or "right" from the die, marching x paces, (depending on the density of the stand) taking another decision from the die, and selecting the nearest tree on the side indicated.

This sounds a tedious and protracted business but in practice is quite fast; the speed with which the die can be rolled and read setting the pace, and all samples are truly random.

In an area with moderately infested trees one man can collect sufficient samples in an hour to keep him occupied counting the psyllids on them for the next two or three days.

This method is only applicable to smallish trees which, with the aid of a short ladder, have the bulk of their foliage readily accessible from the ground. Most of the pink gum in the mid south-east come into this category.

2.13 Investigation of Between-tree Variance

In the light of the information obtained from the initial random sampling, and using the system of sampling outlined above, further sampling was carried out to investigate between-tree variation.

Five north-facing samples were taken in the autumn of 1964 from each of twenty trees in a uniform stand of pink gums. This was one of the few areas that had developed a moderate to light population of psyllids following the "crash" in the spring of 1963.

In the spring of 1964 - by which time numbers were low - a sample of ten twigs from each of five trees was taken in this stand, and a third sample of five twigs from each of five trees in the summer of 1965, by which time numbers were very low. (see sect. 2.15).

Results

Counts of eggs and nymphs were analysed separately.

Analysis of Variance

Eggs - 4.6.64

Variation due to	d.f.	S.S.	M.S.	V.R.
Between trees (T)	19	13.86232	0.72960	1.55^{NS}
Between twigs within trees (W)	80	37.53734	0.46922	
Total	99	51.39966		

Variance components $\sigma^2_W = 0.4692$

$\sigma^2_T = 0.0521$

Analysis of Variance

Eggs - 9.12.64

Variation due to	d.f.	S.S.	M.S.	V.R.
Between trees (T)	4	1.86856	0.46714	1.95^{NS}
Between twigs within trees (W)	45	10.76900	0.23931	
Total	49	12.63756		

Variance components $\sigma^2_W = 0.2393$

$\sigma^2_T = 0.0228$

Analysis of Variance

Nymphs 9.12.64

Variation due to	d.f.	S.S.	M.S.	V.R.
Between trees (T)	4	0.40598	0.101495	2.42^{NS}
Between twigs within trees (W)	45	1.88463	0.041881	
Total	49	2.29061		

Variance components $\sigma^2_W = 0.0419$

$\sigma^2_T = 0.0060$

Analysis of Variance

Nymphs 5.2.65

Variation due to	d.f.	S.S.	M.S.	V.R.
Between trees (T)	4	1.05829	0.26457	2.00^{NS}
Between twigs within trees (W)	20	2.65035	0.13252	
Total	24	3.70864		

Variance components $\sigma^2_W = 0.1325$

σ^2_T 0.0264

The ratios of the variance components for egg samples are very similar, and those for the nymphal samples are reasonably close, but different from those for egg samples i.e.

	Eggs		Nymphs	
	σ^2_W	σ^2_T	σ^2_W	σ^2_T
	0.47	0.05	0.04	0.01
	0.24	0.02	0.13	0.03
$\bar{x}$	0.35	0.035	0.085	0.02

The means of these show a 10 to 1 ratio for egg samples and a 4 to 1 ratio for nymph samples, and this difference is seen to be due to a large reduction in the between twig variance, presumably as a result of the nymphs spreading more evenly from the sites of oviposition before settling.

2.14 "Cost Structure" Analysis

Considering the "cost structure" of the sampling, it was found that each twig took between 30 seconds and two minutes to collect, depending on the number of decisions and accessibility of the foliage. A mean figure of one minute per twig would be reasonable. The time to select each tree on a random basis (including time to divide north from south, and to sort out foliage units ready for sampling) will take from one to five minutes, with a mean time of about three minutes. These are only rough estimates, no accurate timing of sampling having been done, but on this basis a sample of 20 twigs from each of five trees would take one hour 55 minutes, and one of ten twigs from each of 10 trees, two hours 10 minutes. This is about correct.

On this basis we can then calculate the optimum number of twigs per tree from the formula

$$n_1 = \sqrt{\frac{C_T \times \sigma_W^2}{C_W \times \sigma_T^2}}$$

where C_T = "cost" per tree, C_W = "cost" per twig and n_1 = optimum number of twigs per tree.

Using the mean figures for the two variances, and the mean times for trees and twigs, and solving this separately for samples of eggs and nymphs gives:-

Eggs : n_1 = 5.48 (say 6) twigs per tree.

Nymphs: n_1 = 3.56 (say 4) twigs per tree.

It is now possible to select the number of trees which must be sampled in each case to obtain any desired approximate standard error of the mean of the sample.

$$\text{From V (mean)} = \left(\frac{\sigma_W^2}{n_1 n_2}\right) + \left(\frac{\sigma_T^2}{n_2}\right)$$

where n_1 and n_2 are the number of twigs and number of trees respectively per sample.

For samples with a required standard error of 0.1 (in terms of logarithms to the base 10), n_2 = 5.5 trees for samples of eggs and 2.1 trees for samples of nymphs. For samples with a standard error of 0.05 the requirements would be 21.4 trees for eggs and 8.4 trees for nymphs.

From these figures the average time needed to collect samples of this degree of accuracy can be estimated for any selected standard error e.g.

	Samples of	
S.E. (mean)	Eggs	Nymphs
0.1	6 trees x 6 twigs 1 hour 24 mins	2 trees x 4 twigs 14 mins
0.05	22 trees x 6 twigs 3 hours 18 mins	9 trees x 4 twigs 1 hour 3 mins

This then would seem to provide an adequate method of randomly sampling natural populations of C. densitexta when these insects are common, but may not be adequate when they are rare without taking an unduly great number of samples.

2.15 Comparison of a High and a Low Population of C. densitexta on Two Adjacent Trees

Using the same technique of sampling with the die in the bottle, eight samples were made between February 1964 and February 1965, on two trees approximately 125 yards apart. Ten north-face and ten south-face samples were taken from each tree on each occasion.

This sampling was a "salvage operation ". A much more ambitious programme of sampling over a wide area had been planned but was abandoned following the spectacular "crash" of psyllid numbers in the spring of 1963.

Tree A had been sprayed with insecticide in the summer and autumn of 1963. This enabled it to grow new undamaged foliage in the late summer and autumn. In the spring of 1963 this tree provided the only suitable oviposition sites in the locality and received large numbers of eggs.

Tree B had not been sprayed and was, along with all other pink gums in the district, heavily defoliated in the spring of 1963. It received very few eggs on the small amount of remaining foliage.

Sampling of these trees was started after the females of the summer generation of 1964 had laid their eggs. At this stage the leaves of tree A were already extensively damaged by the spring generation's feeding, but it had also grown some more leaves since these nymphs had settled. Tree B, on the other hand, had put on only a little new growth, but had very low numbers of psyllids on its foliage.

Results

Separate analyses of variance (of log. (x + 1)) were carried out for counts of eggs and nymphs. A significant interaction of Tree x Time x Aspect was obtained for both eggs and nymphs; of Tree x Aspect for eggs, of Tree x Time for nymphs, and a significant difference between aspects of nymphs.

Tables of means showing the Time x Tree x Aspect interactions are shown below, and plotted in figure 2.01.

Eggs - Table of Means

(Time x Tree x Aspect)

		Time			
Tree	Aspect	6.2.64	4.6.64	1.7.64	8.12.64
A	N	2.73	1.22	0.51	0.12
	S	2.38	2.36	1.10	0.67
B	N	1.36	2.07	1.80	0.49
	S	0.66	0.00	0.17	0.12

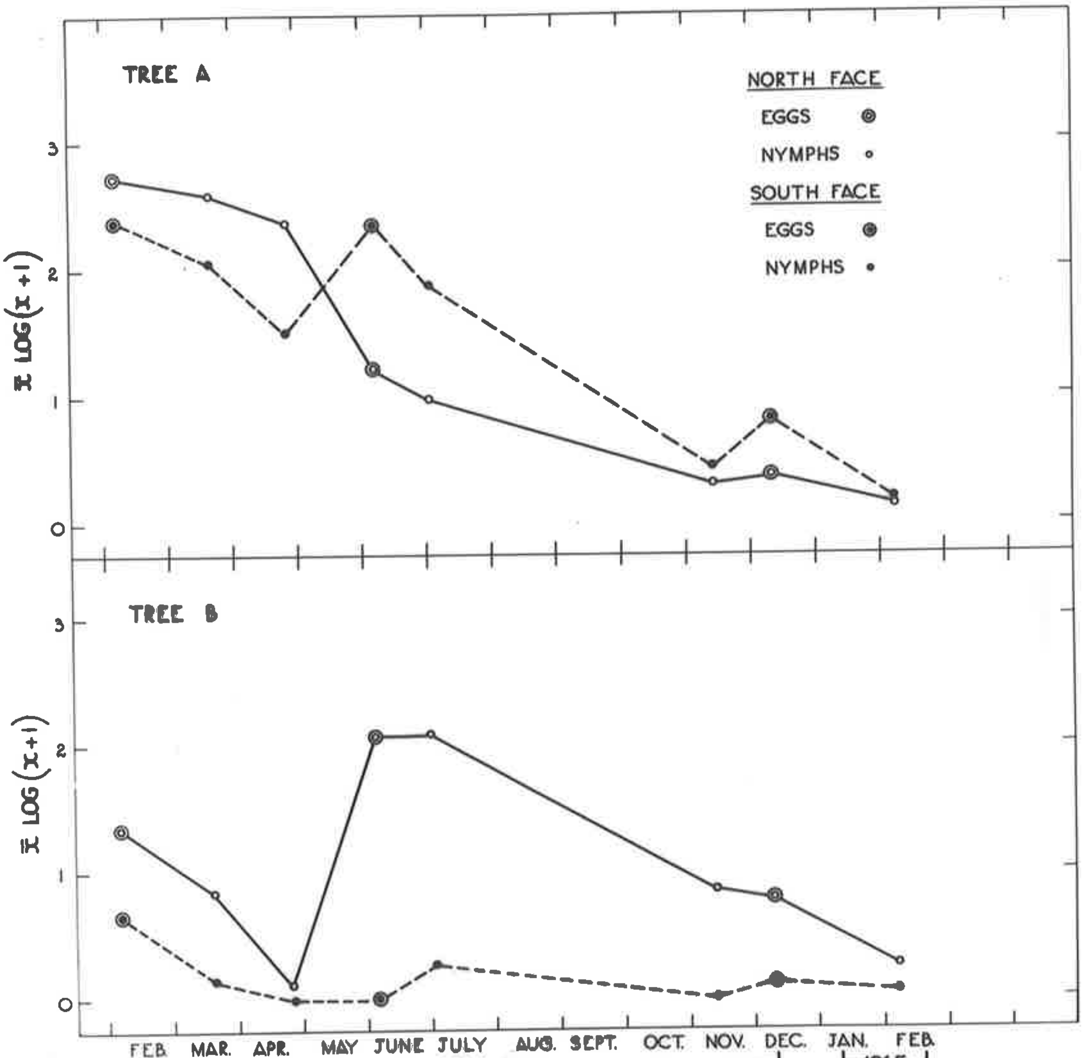
S.E. (mean) = ± 0.26 LSD = 0.78

Figure 2.01

Comparison of population changes on two adjacent pink gum trees; Tree A with an initially high population and tree B with an initially low population.

Solid line with open circles = north face

Broken line with closed circles = south face


TREE A
NORTH FACE
EGGS ◎
NYMPHS ○
SOUTH FACE
EGGS ◉
NYMPHS •
x̄ LOG (x + 1)
0
1
2
3
TREE B
x̄ LOG (x + 1)
0
1
2
3
FEB.
MAR.
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
1964
1965

2.15

Nymphs - Table of Means
(Time x tree x Aspect)

		Time					
Tree	Aspect	19.3.64	25.4.64	1.7.64	13.11.64	8.12.64	6.2.65
A	N	2.61	2.39	0.47	0.32	0.16	0.16
	S	2.07	1.52	0.78	0.45	0.17	0.19
B	N	0.85	0.12	0.31	0.87	0.33	0.26
	S	0.16	0.00	0.09	0.00	0.00	0.06

S.E. (mean) = ± 0.14   LSD = 0.42

In this figure the small number of nymphs present on 8.12.64 have been counted as eggs, and on 1.7.64 the combined egg and nymph totals are shown as nymphs. This has the effect of making the spring 1964 population of eggs a fraction smaller than it should be, and the winter nymphal population in July 1964 a little larger than it should be.

In February 1964 all "mature" leaves on tree A, damaged or undamaged, received large numbers of eggs (a mean of 930 per twig). This contrasted with tree B which, although only 150 yards away, had a mean of only 62 eggs per twig.

More eggs were laid on the north face of both trees, although this difference was not nearly so marked on tree A.

There was a much greater decrease in numbers on tree B than tree A in the ensuing summer and early autumn, indicating that tree A was a more favourable place for the psyllids than tree B. This was the result of stress on tree A from excessive numbers of nymphs feeding on its foliage. On both trees the population on the north face remained higher than that on the south face.

At the time of completion of the summer generation tree A had very little green foliage left, and shed large numbers of dead or badly damaged leaves, especially on the north face, during and after oviposition by the autumn adults. Tree B, apart from the still sparse north face, showed little sign of psyllid attack, and did not shed any appreciable number of leaves.

As a result of the (by then) prolonged period of dry weather, both trees were coming under some degree of stress, especially tree A which had also lost two thirds of its foliage. This stressing is reflected in the high rate of survival of psyllids; many more adults being produced in the autumn than in the summer. The great loss of leaves - many of them bearing large numbers of eggs - on tree A masked this increase in abundance, and also resulted in a reversal of the north/south populations. There were still more eggs *per leaf* on the north face, but so few leaves remained on this side that the counts *per twig* were greater on the south side.

On tree B the difference between the north and south faces became more pronounced than before, indicating that the sun leaves, but not the shade leaves, were being stressed by lack of soil-moisture.

During the ensuing winter of 1964 - which was not unduly wet - the mortality of nymphs was heavy, numbers on both trees declining rapidly. By the spring numbers were low and few eggs were laid on either tree. The cool moist spring with luxurious growth of foliage on both trees caused a further drop in psyllid abundance, so that by February 1965 there was no appreciable difference in the population of psyllids on the two trees where a year (3 generations) earlier tree A had 15.5 times as many insects per twig as did tree B.

2.2 Laboratory Rearing Techniques

In the past the laboratory culturing of lerp-insects on detached Eucalyptus foliage was not considered to be possible. Not only are these insects unable to live for long away from fresh and turgid leaf tissue (except as adults, and then only in cool temperatures and high humidities) but Eucalyptus foliage, once severed from the tree, is notoriously difficult to maintain in a turgid and healthy condition. Consequently the first method tried was to keep potted pink gum seedlings in a controlled temperature room to see if C. densitexta could be cultured on them. They proved to be bulky and space consuming; it is extremely difficult to manipulate their leaves under a microscope, and confining first instar nymphs to one leaf has so far proved impossible. In addition they bear only juvenile foliage, all new growth remains soft, flaccid, and unacceptable to nymphs or adults; and the plants soon become root-bound. So this method was abandoned.

Some of the earlier taxonomist-collectors often kept final instar nymphs for a few days on foliage in closed containers in order to obtain adult insects, and Clark (1963c) maintained nymphs on cut twigs of E. blakelyi "for two or three days". Apparently nothing more venturesome than this has been attempted.

Both twigs of foliage and single leaves of pink gum can be maintained alive and turgid for many weeks if placed in a tightly closed polythene bag and held at 3°C to 5°C. Psyllid nymphs on such foliage remain alive for five to six weeks, providing a useful method of "holding" field material in good condition, but both leaves and insects eventually die.

Several unsuccessful methods of collecting and maintaining cut branches of pink gum were tried. The most successful was a modification of the cage described by George (1961) in which the polythene bag was kept inflated by compressed air bubbled through water, thus maintaining a high humidity around the foliage. At the end of a week, however, all leaves had dried out. Without the bag similar branches had withered in a matter of hours.

A whole leaf or part of a leaf could be kept alive for a little over a week on wet filter paper in a petri dish with the lid on, but the humidity was so high that condensation and mould growth soon killed the leaf. Without a lid on the dish the leaf quickly dried out and died. But whole leaves or parts of leaves floated on water in open dishes at 20°C remained turgid and bright green for several weeks, even with the cut end of the petiole above the surface of the water, and without any form of lid or covering to maintain a high humidity. Furthermore, there was virtually no growth of microorganisms either on the leaf or in the water until a leaf or part of a leaf died. A certain amount of mould grew on any such dead tissue, but did not encroach on to remaining living tissue. At temperatures much above 25°C the exposed surfaces of the leaves showed signs of drying out after a day or two.

Discs of leaf-tissue, 21 mm in diameter, were cut with a sharpened cork borer, and floated on distilled water in individual 2 x 1 inch "clearsite" plastic vials. Provided the light intensity of the photoperiod is kept at a level well above the compensation point of the leaf tissue such discs, while supplied with only distilled water, have been found to stay alive and capable of supporting living psyllids for three to five months at 20°C, and from six to eight months at 15°C - well in excess of the time needed for any psyllid so far encountered to grow from egg to adult. I have subsequently used this technique to raise a number of different psyllid species from field collected eggs. Very detailed and continuous observations of the behaviour and development of these insects are possible with this technique, and fairly precise rearing experiments can be conducted.

There are three methods of establishing first instar psyllid nymphs on such discs.

(1) A disc is cut to include eggs already on the leaf before they hatch. This is the best method for attempting to rear a few unknown eggs collected in the field.

(2) Nymphs are allowed to hatch and settle while the leaf is still on the plant, and a disc is then cut to include them. This enables the number of established nymphs per disc to be controlled, and for them to be kept away from the water. It is fairly wasteful of material, and does not allow quite such precise control of the physiological age

of the experimental animals as does the third method (± one to two hours instead of ± five to ten minutes).

(3) Newly hatched nymphs are transferred to the disc from the leaf bearing the eggs from which they have hatched. The method is tedious, requiring a steady hand and much patience. It is also very wasteful of material as only the bright yellow freshly hatched nymphs which are actively running on the leaf are used. This is done to obtain animals of virtually identical physiological age, and which have not yet started to probe for food. It is also the only time when they can be safely lifted off the leaf. A day or two before nymphs are required, leaves bearing large numbers of eggs which are almost ready to hatch are floated in open dishes in the temperature and light regime to be used for the experiment. Large numbers of nymphs will then be available each morning for several days.

The actual transfer of nymphs is carried out under a binocular microscope using a sable hair brush with all but six to twelve of the hairs removed. The brush is moistened with water and quickly "dabbed" across the back of a running nymph. If this is done quickly enough to take the insect by surprise it will adhere to the wet brush and can be carried to the disc where it is carefully lowered until its legs touch the surface. It will quickly grip the leaf and pull itself away from the surface tension of the water on the brush and run freely on the disc.

If the brush is too wet the nymph is swamped, and if too dry it will not pick it up. Should the operator fumble, the nymph will grip the surface of the leaf and cannot then be removed without injury. This gripping of the leaf surface makes it difficult to remove a stationery nymph, and there is the additional risk of injury if the mouthparts are even partially inserted into the leaf. The dab must be gentle as with rough handling it is very easy to dislodge the tips of the stylets from the labium, and once this has happened, the insect is unable to feed.

The use of detached leaves, and portions of leaves, as a means of culturing sap feeding insects in the laboratory is not new, and leaf discs have been employed for many years in plant physiology, particularly in studies of plant-water relations. (Yarwood, 1946; Barr and Weatherley, 1962).

Leaf discs on moist sand in petri dishes have been used for laboratory rearing of mites (Rodriguez, 1953, 1958) and were used more than 30 years ago for rearing psyllid eggs (Richards, 1931). Johnson and Birks (Johnson, 1965) and Hughes and Woolcock (1965) have used discs floating on water or nutrient solution for rearing aphids, and current work by Willard at the Waite Institute has shown that scale insects can be cultured in this way on discs of lemon leaves.

Although detached leaves have been recorded remaining alive for months or years (Yarwood, 1946), all these leaf discs apart from my own and Willard's, have remained alive for little more than a week. With animals like mites and aphids which can complete a generation in a matter of days this does not matter. At 20°C C. densitexta required four weeks or longer to complete one generation. It is therefore fortunate that Eucalyptus leaves can be kept for so long and without the need for nutrient solutions, thus avoiding trouble from growth of microorganisms.

That these discs of tissue provide an adequate supply of food is demonstrated by survival and growth of the animals feeding on them; and females reared in the laboratory from eggs hatched on such discs have laid viable eggs.

Nitrogen is made available from hydrolysis of proteins in the injured cells around the periphery and from the nymph's own feeding activities. In addition the leaf tissue, if kept well above its compensation point, will maintain photosynthesis in excess of respiration, and so provide surplus photosynthates as food for the nymphs. That this latter source of food is critical was clearly demonstrated by the experiment described in section 2.632 where the mortality on leaf discs at low light intensity was greatly in excess of that on the discs kept well-saturated with light.

Leaf discs are not, of course, the same thing as are attached leaves, but this is not considered to be of any consequence. In fact it is an advantage in ensuring greater uniformity of experimental material than could be obtained by leaving leaves attached to the plant.

It is well known that leaf discs floated on water take up water through their uninjured surfaces, as well as through the cut ends of veins, and by water injection into the cut surface; and that they rapidly gain weight (Yarwood, 1946). Yarwood concluded from this observation that leaves in nature can be considered to be in a regular state of water deficit.

The water content of leaves during the day is less than at night, and less in the sun leaves than in the shade leaves. These and other physiological differences are quickly lost when the leaves are removed and discs cut and floated on water. This loss of initial differences is indicated in the experiment (sect. 2.632) where newly hatched nymphs were placed on discs cut from freshly collected sun, shade, and old overmature leaves. Whereas the discs from the old tough leaves remained a less satisfactory source of food for the psyllids those cut from the sun and shade leaves, although initially different, soon became indistinguishable with respect to the growth and survival rate of psyllids.

Disadvantages of this method of rearing psyllids are (1) that water very readily invades the upper surface of a disc if the container is bumped, if any manipulation of the insects on the disc is necessary, or when the container is being replenished with water (at least twice a week at 20° C). Swamped discs can be dried with paper tissues and refloated without any harm being done to the nymphs on the disc, but this is a very tedious and time consuming process. All handling of insects on the discs (e.g. removal of dead animals and caste skins, placing first instar nymphs onto new discs) requires that each disc be first lifted from the water with a pair of forceps and placed on moist filter paper. It must then be returned to the water in the same manner. This is also very time consuming. (2) First instar nymphs, whether hatched from eggs on a disc or placed there artifically, tend to concentrate most of their activity and eventual settling to the edge of the disc (where protein hydrolysis in cut cells is high). Many of them are thus trapped by the surface tension of the water and die, while others settle so close to the edge that as they grow and build their lerp, this reaches the edge of the disc, and water will then invade onto the disc at this point when the nymph or its lerp touches the water.

Numerous substances were tested to try and form a barrier to prevent nymphs walking and settling too close to the edge of a disc but these either killed the leaf tissue, allowed water to invade the disc, or acted as a trap on to which the young nymphs walked and became stuck. Small cages similar to those employed by Johnson (1965) were of no use, as the dorso-ventrally flattened nymphs can pass through the smallest gap between these and the leaf surface. Very fine rubber bands were made from dental rubber sheet (0.01 of an inch thick) and stuck to the leaf disc surface with a paste of kaolin, water and glycerine. This overcame the problem of gaps as the paste dried holding the 1 mm. high rubber "fence" against the leaf surface. However, the nymphs merely walked up one side of these "fences" and down the other. Painting fluron on to the inner walls might have prevented this escape, but they were very delicate structures which broke away from the leaf at the slightest touch, and were not tested any further.

In spite of these disadvantages it was a workable method for rearing these insects under controlled conditions, and was used for most of thie type of work reported here.

A further problem arose when attempts were made to keep adults on these discs. They are very active animals which jump, and when confined with a lid over the top of a tube they soon became caught in the surface of the water around the disc, and died.

Apart from the difficulty of placing such an active insect under a small cage on a leaf disc, most were able to find large enough spaces to escape between the bottom of the cage and the uneven leaf surface. All these disadvantages, plus the need to develop a method of completely isolating one leaf surface bearing eggs, from the other surface in contact with the water (see sect. 2.51) led to the development of the tube-cage illustrated in figure 2.02.

The method of constructing these cages is as follows:

With an old cork borer heated over a flame, the bottom of a 2 x 1 inch "clearsite" vial was cut out so as to leave a small flange standing away from the sides of the tube by about one millimeter.

A disc of leaf with a diameter approximately 2 mm. less than the inside of the tube was then cut. This, when dropped into the top of the tube, rested on the flange.

Molten low melting point (45°C) paraffin wax was then painted with a fine brush between the leaf disc and the flange, the disc being held firmly in place with the forefinger of the left hand thrust into the tube and pressing the disc gently against the flange. This served to seal the disc to the flange while leaving the cut edge exposed inside the tube where it would be bathed in water.

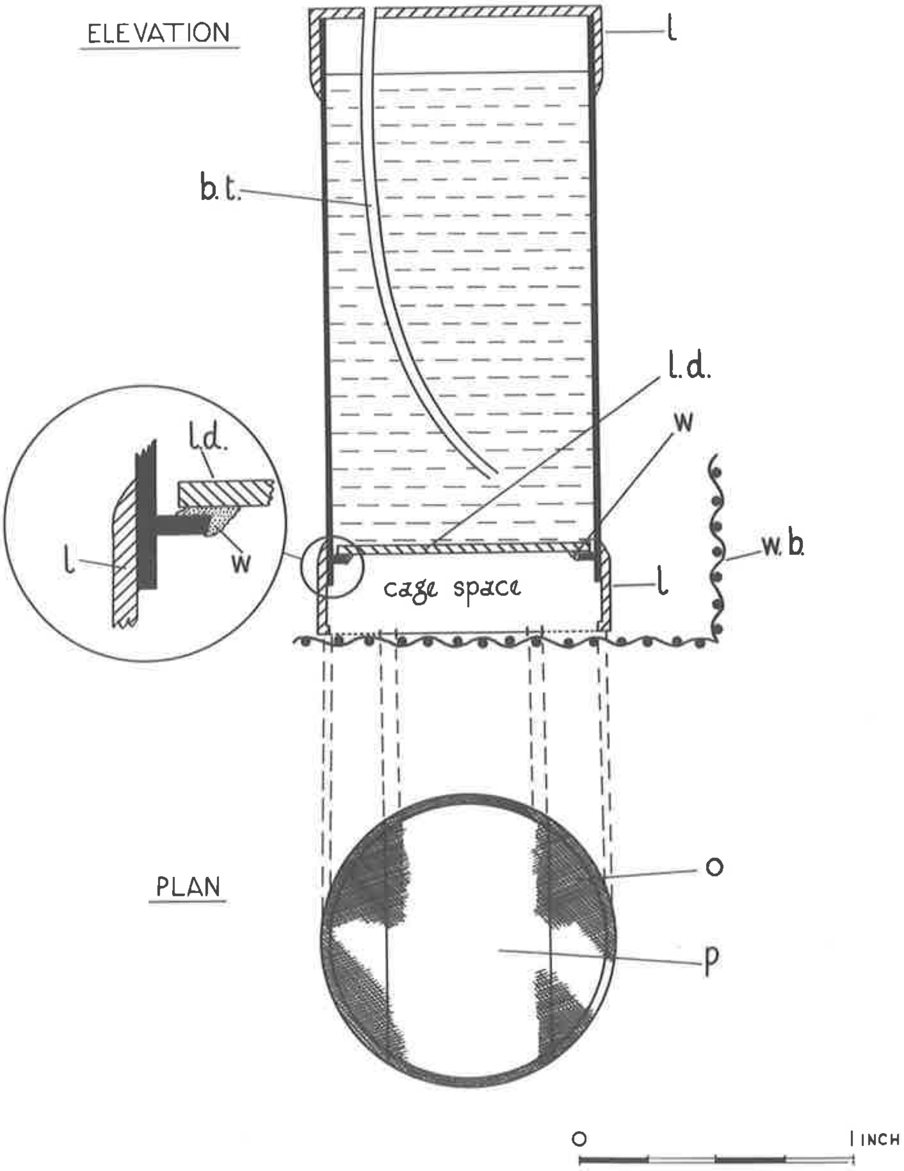
The tube (which now effectively had a "leaf bottom") was

Figure 2.02

Tube-cage for rearing *C. densitexta*

bt = "breather tube"
l = lid
ld = leaf disc
o = organdie

p = perspex sheet
w = wax
wb = wire basket


ELEVATION
l
b.t.
l.d.
w
w.b.
l
cage space
l.d.
l
w
PLAN
o
p
0
1 INCH

three quarters filled with distilled water and stood for a few minutes to check for leaks in the wax seal. A lid which had had a 1 mm. internal diameter plastic tube fitted into it was then very carefully pressed on to the top of the tube (rough handling at this stage will result in leaks in the wax seal). The purpose of the tube is to allow pressures to equalize and thus prevent rupture of the wax seal during this operation, during changes in atmospheric pressure and during changes in temperature. This "breather tube" rather than a simple hole in the lid is needed so that the whole cage can be inverted without water running out of it. This allows inspection and manipulation under a microscope of insects on the disc.

The actual cage to contain the insects was constructed from a second lid. The top was punched out of this and replaced by a piece of organdie cloth. This was done by "ironing" the cloth into the plastic of the lid with a piece of heated steel. A central panel was then cut from this organdie and a sheet of thin "perspex" glued onto it with ethyl acetate. This provides a window for inspection of the surface of the leaf disc without any possibility of insects escaping and the organdie side pieces provide sufficient ventillation to prevent condensation within the cage.

With a little practice these cages can be constructed and assembled quite quickly.

A few will develop leaks in the wax seal after being placed in racks in the controlled temperature room, and the discs from these are best discarded as experience has shown that, even after repeated resealing, they are still liable to leak.

The great advantage of this cage is that at all stages of the life cycle the lerp-insects are isolated from the free water surface, while the leaf tissue has full access to the water. The insects are in a more "natural" position in that they normally keep to the under side of a leaf away from direct radiation. Two or more adults can quite readily be introduced into these cages by employing their natural tendency to walk upwards, and this will also ensure that they find the leaf tissue and do not die sitting in a corner of the cage. The leaf tissue appears to last just as long in these cages as when floating on water. (at the time of writing, discs nine months old are still alive in both 15 °C and 20 °C constant temperature rooms). The tubes need only be filled with water once in 6 months.

Main disadvantages are that much more light is necessary to maintain the discs as a suitable food supply (light must now pass through the tube full of water to reach the disc) and the newly hatched nymphs **readily** run off the disc and many become desiccated and die before they can regain the leaf surface.

2.3 The Adult

2.30 Introduction

The fully grown fifth instar nymph moves out from beneath its lerp, walks a short distance, and usually commences to feed while awaiting transformation to the adult stage. Ecdysis is unremarkable, the animal splitting down the median dorsal line and the callow adult emerging from the nymphal skin. The body is pale pink and the wings but white stumps. At summer temperatures at the time of emergence (mid 60°F) the wings are fully expanded within 20 minutes but remain soft and opaque for up to an hour, and some two or three hours elapse before the body pigments have darkened. During this period the adult runs actively if disturbed, but normally seeks out the lower side of shaded leaves, where it sits quietly.

A definite surge or "flush" of emergence occurs in the early morning hours. I have not investigated this experimentally to see if it is a rhythmic response (as is the case with egg-hatching - see sect. 2.52) but collecting teneral adults in the field for oviposition trials soon reveals that although a few new emergents can be found at almost any time of the day, only in the early hours of the morning can appreciable numbers be taken at one time. As this "flush" occurs equally on warm November and February mornings and on cool to cold April and May mornings, I would suspect that there is some light controlled rhythm present, rather than a simple response to temperature.

General observation supports Clark's (1962) statement that the sex ratio is close to unity. These observations plus laboratory rearings also confirm that males start to emerge a few days before the females, and do not live as long.

Both males and females tend to congregate on the lower sides and towards the petiole end of leaves, where most activity including mating and oviposition occurs. When numbers are high, aggregations of a dozen or more adults are common.

2.31 Mating Behaviour and Stridulation

A well-defined mating behaviour has been observed. Females tend to sit quietly feeding, while males move about more in the foliage. When a female is encountered the male approaches rapidly, running on the surface of the leaf, and takes up a position behind or slightly to one side of the female. He then makes a series of darting movements; forward to touch the female's wings with his antennae, and sideways in a swift arc around her (fig. 2.03) at the same time keeping up a constant "flicking" motion of the wings. He will then remain stationary for some minutes with one antenna just touching the wing of the female. During these periods of immobility the male's genitalia are flexed continuously and rhythmically and spasmodic "flicking" or "twitching" of his wings can be seen. The only movement of the female is an occasional flexing of the tip of the abdomen. The "dance" will be renewed as abruptly as it stopped, and without any sign or stimulus that I could observe. During one of these dances the male will suddenly and very quickly turn and dart backwards and sideways at the female, at the same time thrusting upwards with wide open claspers at the tip of her abdomen.

Figure 2.03

Mating dance of *C. densitexta*

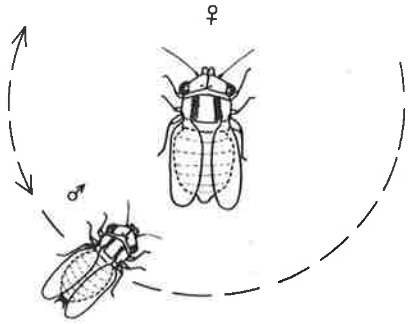
Figure 2.04

Stridulating Mechanism of *C. densitexta*

Diagrams of *A*: the left side and *B*: the right side of the thorax with wings displaced to show the file and scraper mechanism.

L.F.W. - left forewing
L.H.W. = left hindwing
F.W. = forewing
H.W. = hindwing

f = file
s = scraper
msc = mesoscutellum
mtc = metascutellum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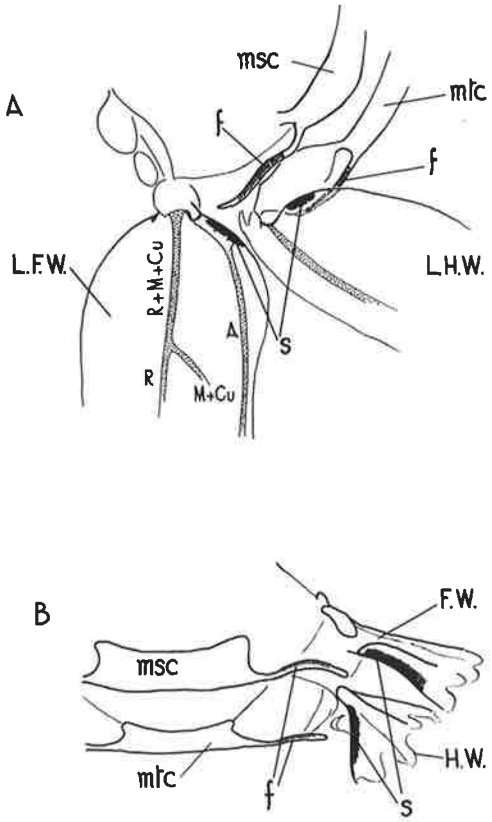

A
msc
mtc
f
f
L.F.W.
R+M+Cu
R
M+Cu
A
S
L.H.W.
B
F.W.
msc
mtc
f
H.W.
S

Very frequently at this moment the female will quickly sidestep, and then remain motionless again. The force and speed of the male's thrust is such that I have seen one spin around three times after missing the side-stepping female. After an unsuccessful thrust the dance is renewed with increased speed and agitation, the whole process often being repeated many times before he is successful in clasping the female. Once this is achieved the pair sit quietly facing in opposite directions, the only movement being occasional "flicking" of wings by both parties and a fairly rhythmic opening and closing of the male's claspers. Pairs remain *in copula* for periods inexcess of 15 minutes, and considerable agitation is required to separate them.

With large numbers of adults present a female with only one male in attendance is an exception. Three males per female is common, but up to six have been observed, and all take up a position in the male "dancing arc". There is a lot of aggressive "shouldering" and jostling between competing males as they move around the arc, and from time to time one male will rush another, "butting" the rival with his head in an attempt (sometimes successful) to drive him away before returning to the dance. New males also dash in at great speed to join a group around a female, so there is a constant movement of males in and out of any one group. Males will commonly attempt copulation with mating pairs and with other males in crowds.

Copulation has been described for *Psylla pyricola* by Cook (1963) and numerous other authors have made brief mention of the act, but there is no previous record of any "courtship" behaviour. The "flicking" of the wings is, in fact, the insect stridulating by rubbing the thickened hind margins of both fore and hind wings back and forth over a series of pegs along ridges on the meso and metathoracic epiphyses (fig. 2.04). Although these structures are present on both sexes, I have heard only males stridulating. A male will stand alone "calling" at a rate of seven to eight "pulses" every five seconds. When a female is approached, and the dancing commences, the speed of pulsing increases to ten to twelve every five seconds, and the sound becomes louder. A stridulating male, whether alone or in attendance on a female, attracts other males which leap in alongside him stridulating vigorously as they do so. The noise produced by this stridulation is very faint and until the ear is attuned to it, will not be detected even when many adults are present. I can only describe it as a faint "whirring" sound, not unlike that of a cicada. It can be amplified by liberating adults into a plastic bag which is inflated and sealed by knotting the open end. (It was in this way that the sound was first detected). When a psyllid stands on the wall of the bag and stridulates, the sound is magnified and becomes audible several yards away. The action can readily be observed through the clear plastic of the bag. The wings vibrate with each pulse, the anal margins being rapidly rubbed back and forth over the thoracic pegs in a typical file and scraper mechanism (Haskell 1961). The movement is so rapid that the edges of the wings appear blurred, but their posterior edges, held roofwise over the body, never quite touch each other. The abdomen is flexed slightly backwards and downwards in time with each pulse, and the antennae also twitch more or less in time with the pulsing. When several males are sitting quietly on the wall of a bag, one of them commencing to stridulate will stimulate the others to do the same.

Having learnt to recognise the sound of a lerp-insect, I find it is possible, providing there is little wind or extraneous noise, to hear and track down a singing male among quite dense foliage.

Stridulation in the Psyllidae was first reported by Ossiannilsson (1950) in Trioza nigricornis Först. He also recorded that Heslop-Harrison stated during a discussion in 1948 that he believed another species, Livia juncorum (Latr.) might be capable of producing sound because of the enlargement of the second antennal joint - the seat of Johnston's organ. He confirms this belief with listening trials. Heslop-Harrison (1960a, b) extended the list of species which stridulate and figured, for Mesohomotoma, the file and scraper and the internal skeletal structure of the metathorax modified to act as a sounding box.

Taylor (1962) described and figured a similar file and scraper in all species of Hyalinaspis, assuming these to have a stridulatory function, and Campbell (1964) reported two species of Cardiaspina stridulating and described the file and scraper mechanism. He recorded these sounds on magnetic tape and in musical notation, by first amplifying the sound with a plastic bag in the same way as I had done. He did not, however, take his investigation any further, assuming the noise was made with the wings and that it has a sexual function.

At the low population densities normally experienced by these insects, this stridulation behaviour would have a definite value in increasing the probability of any one individual finding a mate. Although I have not as yet witnessed this, it would seem probable that the females stridulate to attract males, as the file and scraper is equally well developed in both sexes.

2.32 Dispersal

Clark (1962) said that most females of C. albitextura remain within 150 yards of where they had emerged, and that the majority of eggs are laid within 50-60 yards of where the female originated. He further stated that this species is not very successful at crossing clearings wider than 130 yards, even when aided by the prevailing winds. He concluded that "Clearly, C. albitextura is not a strongly dispersing insect".

This conclusion is based on three main points:-

(a) Two experiments in which psyllids were concentrated on a few trees "within areas of uniformly low psyllid abundance" and the resultant adults allowed to "disperse and oviposit normally". After the oviposition period of these females had ended, foliage from the trees on which the original concentrations had been produced, and from trees at increasing distances from them, was sampled for numbers of eggs laid. (It should be noted that both these experiments were conducted with autumn-emerging adults).

(b) Trapping with 2' x 2' sticky boards sst around several trees at 18 ft. from the edge of the crowns and 8 ft. above the ground.

(c) Observations of high populations in trees separated by only 100 yards or so from trees with low numbers of psyllids; and the record that showed a "creeping" increase in the number of psyllids from tree to tree, and across small gaps, over a period of years.

My own observations of the behaviour of summer and autumn-emerging adults would support the hypothesis that **emigration of** female psyllids from their point of origin is almost nil. Where there are high numbers, each tree has a small "cloud" billowing out on the leeside and swinging like a weather vane with the veering of the wind. This "cloud" is comprised of adults constantly being blown away from the tree and flying back again into the foliage. When a strong gust blows the cloud further out from the tree some individuals do not return, but by and large there is little movement away from the "home tree". (Clark (1962) noted similar behaviour for C. albitextura). As a result of this behaviour, trees with foliage already heavily damaged by the feeding of nymphs receive large numbers of eggs, while nearby trees with many more uninfested leaves, receive relatively few eggs. When numbers are low this would be advantageous to the species, but at high levels it is not so (see sect. 2.15).

Adults emerging in spring exhibit a very different behaviour pattern. Each day a morning flush of emergence occurs but by mid-afternoon very few adults can be found. As soon as the cuticle has hardened and darkened (one to two hours on a sunny morning) adults are observed to fly strongly up and away from the foliage. This behaviour was strikingly demonstrated in the spring of 1963. Dry warm weather prevailed from late August onwards and the large population then extant in the South-East matured a good month earlier than usual, and before any significant amount of new growth had been produced by the pink gums. At this time all the gums showed the typical burnt appearance of heavily damaged foliage. A spectacular disappearance of the vast numbers of emerging adults ensued, and only very few eggs could be found. (See also under "oviposition").

A few trees sprayed with insecticide the previous summer and consequently bearing lush green crowns, and the lopped trees discussed below, all contained large numbers of adults and subsequently received high numbers of eggs. This behaviour and the resultant distribution of adults is quite different from that witnessed in the autumn.

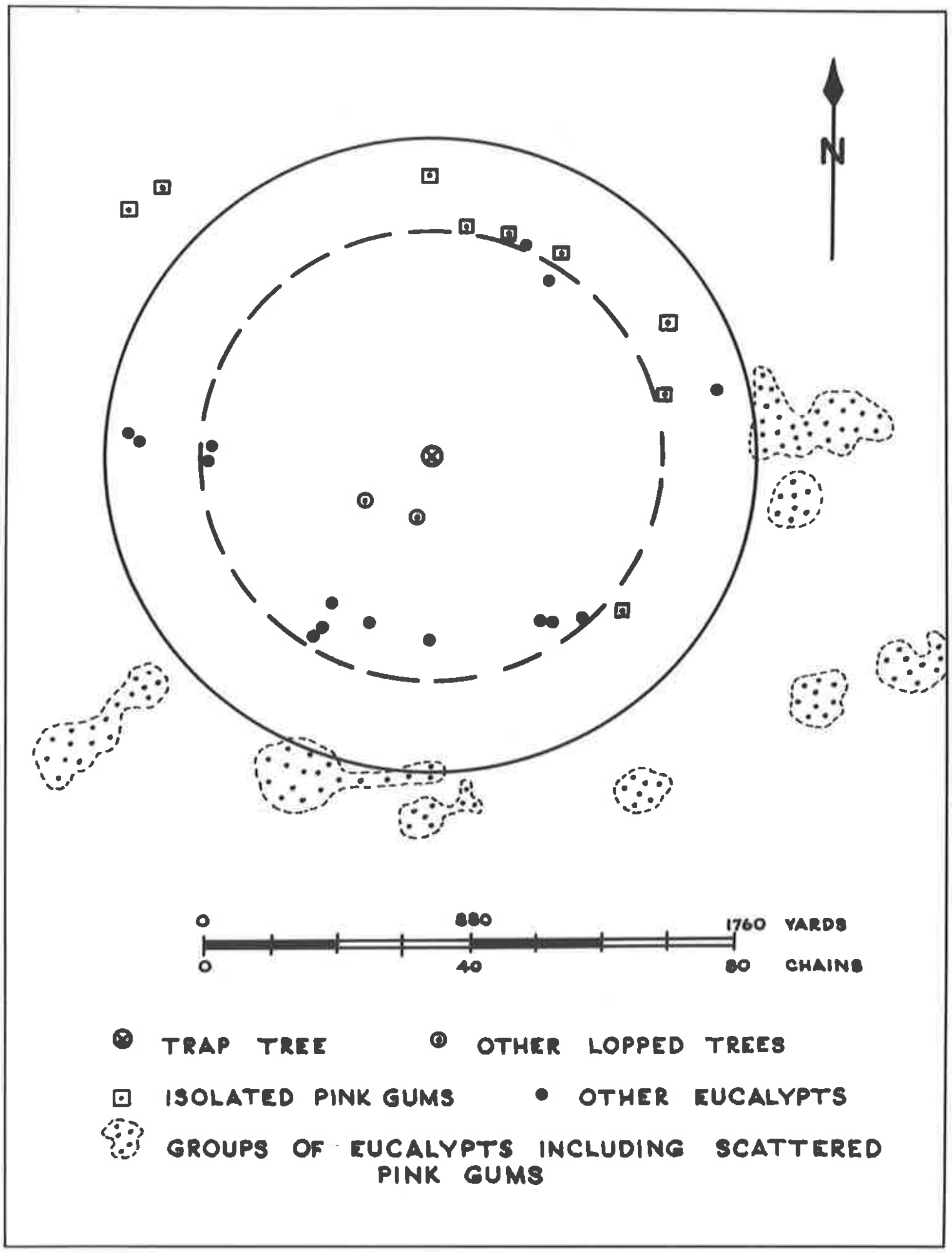
Clark's sticky board collections merely demonstrated the expected - that at a distance of 6 yards away from a tree most insects are caught to leeward of the prevailing wind.

The observations under (c) above would, at first sight, appear to support the theory of limited adult dispersive powers. Closer inspection of Clark's figure 3 and table 4, however, suggests otherwise. Population increases moved right around area A5c almost completely encircling it, by first moving down-wind, then across-wind, and back up-wind, while its (A5c) population remained low - and it is little more than 100 yards away from the original area (A5) of

Figure 2.05

Dispersal of adult *C. densitexta*

Plan of the location of trees lopped and allowed to grow clean foliage which would act as a "trap" for any adults landing on them.


N
0
880
1760 YARDS
0
40
80 CHAINS
⊗ TRAP TREE
⊙ OTHER LOPPED TREES
⊡ ISOLATED PINK GUMS
● OTHER EUCALYPTS
GROUPS OF EUCALYPTS INCLUDING SCATTERED PINK GUMS

persistent high populations. It is hard to credit that this could occur merely because sufficient numbers of adults were unable to migrate to A5c from A5.

The hypothesis of limited dispersive powers of adult psyllids would appear to be an attempt to explain the otherwise anomalous fact of neighbouring trees apparently experiencing identical environments, and yet supporting vastly different populations of psyllids. My hypothesis will allow an explanation of this apparent anomaly without requiring such drastic curtailment of the psyllid's dispersive powers.

To test the ability of these insects to disperse as indicated by these observations three pink gums were selected in an area which had one other pink gum 770 yards away, and no substantial number within a radius of 1100 yards. (See figs. 2.05 & 2.06). In March 1963 these three trees were lopped to remove all foliage. This allowed new growth to start before the onset of winter, but not to reach a stage where any autumn adults could lay eggs on it. When adults emerged in October, the central tree carried two main epicormic "balls" of foliage each about 18 inches in diameter, and with approximately 10% of the leaves sufficiently mature to provide acceptable oviposition sites for C. densitexta. By early November many eggs had been deposited, and adults were still numerous throughout both "balls" of foliage. Far more so than in surrounding groups of heavily attacked trees. Also of significance here is the fact that many of these adults were copulating pairs, indicating that only

Figure 2.06

Dispersal of adult *C. densitexta*
The central lopped tree (x in figure
2.05) looking west.

after the completion of migratory movements is the threshold for trivial or appetitive behaviour lowered (Southw~~ar~~ood, 1962). These 18 inch diameter clumps of foliage represent a remarkably small target in the middle of a five acre circle of open pasture, and they were found not only by *C. densitexta*, but by two other species of psyllids, and numerous other forms of winged insects.

During the winter of 1963 I inspected several land development burns (of known dates) where all growth had been killed, but gums had subsequently put forth new foliage. Areas - the largest of these some 2½ miles across at its narrowest point - burnt in the previous (1962) autumn or winter were already as heavily infested as surrounding unburnt areas, having had the three (spring, summer and autumn) generations to infest and build up the population. In many instances small (12 to 18 inches high) single shoots had sprung up from old lignotuber tissue. To come upon one of these wisps of foliage bearing a dozen or so lerps on each leaf, and surrounded by acres of ploughed land, creates a strong impression of efficient dispersal and host finding powers.

In the spring of 1964 a further attempt was made to demonstrate the dispersive powers of *C. densitexta* by sampling for adult psyllids in the air. This was done by towing a specially designed net from an aeroplane at predetermined heights at a constant speed, and for known time-intervals (figs. 2.07 & 2.08) 7¾ hours were spent in actual sampling, but much of this time was spent learning to use the net effectively, and discovering whether it would in fact capture insects. It has proved to be very effective

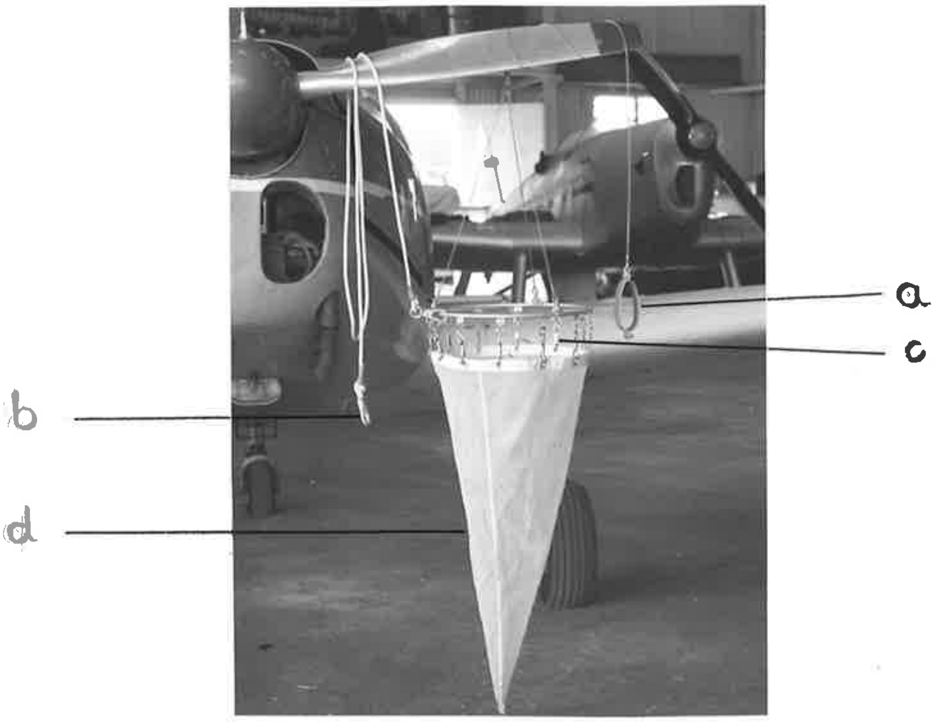
Figure 2.07

Dispersal of adult *C. densitexta*

The Drogue-net used for aerial sampling for adult insects. *a*: clamp fitted to wing strut. *b*: clip fastened to seat in cabin and attached to the rope used to haul the net in at the end of each run. *c*: "dog collar" clips to allow rapid changing of nets between runs. *d*: fine-mesh nylon net.

Figure 2.08

The Drogue-net in operation


a
c
b
d

and simple to use, insects being captured in surprising abundance, diversity and good condition. Unfortunately by this spring the population of C. densitexta had fallen to very low levels. Scarcity of adults was further accentuated by heavy bird predation of remnant pockets (see sect. 2.722) and by the protracted emergence resulting from the cool moist weather experienced this spring. No adult of C. densitexta was captured, but three others of three different psyllid species were, during two "runs" totalling 50 minutes. As Collins and Baker (1934) pointed out, the proportion of the available air space sampled in this way is minute, and the probability of catching an individual of a species is remote unless there are very many of them in the air at the time. In spite of this failure to demonstrate a hypothesis, records of psyllids caught in the air at heights of up to 5,000 feet and more (Glick, 1939, 1957, 1960, 1961; Freeman, 1945; Hardy and Milne, 1938) and as far as 186.5 miles from the nearest land (Yoshimoto et al., 1962a, 1962b; Yoshimoto and Gressitt, 1963; Harrell and Yoshimoto, 1964) are sufficiently common to indicate that more than a few chance individuals are dispersed in this way Lewis and Taylor (1965) have analysed the results of these earlier aerial collections, along with their own data, to demonstrate that with many small insects (including psyllids) "high altitude and long distance migration is very highly correlated with flight by day and small size". That psyllid adults generally function as the effective dispersive stage in the life cycle is also illustrated by autumn flights to hibernacular and spring flights to feeding and breeding sites by several northern hemisphere species (Heslop - Harrison, 1951; Jensen, 1954; Wallis, 1955) and by numerous other casual comments through the literature (e.g. Grove and Ghosh, 1914).

From the available evidence I would propose the hypothesis that psyllids generally are strongly dispersing as winged adults; and that at least C. densitexta (and probably other related Australian species) exhibits two distinct types of seasonal dispersal behaviour.

(a) Non-dispersive or "concentrative" in which the tendency is to reduce the distance between individuals. This occurs with autumn and summer adults and serves to concentrate the population on favourable foliage.

(b) Dispersive in which the tendency is to increase the distance between individuals (subsequent appetitive behaviour will tend to again reduce the distance between individuals, but concentrating them on the available favourable sites). This behaviour is confined to the spring adults.

An explanation of this alternating behaviour may be found in a mechanism similar to that postulated by Johnson (1963). Thus the summer and autumn adults of C. densitexta are derived from larvae which have experienced long day length, optimum temperatures, and abundant food. Their gonads will mature quickly, there will be a very short pre-oviposition period, and they will fly only a few inches or feet before settling and ovipositing. Spring adults on the other hand are produced from larvae subjected to short day length, cold temperatures and often densely crowded. These adults could be expected to have a long pre-oviposition period, and exhibit strong migratory behaviour.

In short, as C.G. Johnson and his associates have demonstrated with alate aphids, there can be little doubt that psyllids are contrary to Clark's hypothesis, strongly dispersing insects.

2.33 Oviposition

2.330 Introduction: The eggs are fixed to the surface of the leaves by means of a posterior stalk or pedicel which is driven through the epidermis into the mesophyll. (All psyllids for which egglaying is recorded either insert an egg stalk into the plant tissue or bury the egg partially or completely in it).

The ovipositing female stands quietly with the tip of the abdomen firmly pressed to the leaf surface. When the stalk has been embedded she walks forward and the tip of the abdomen slips easily over the egg. Actual insertion of the stalk into the leaf was not observed because the tip of the abdomen is held closely against the leaf. After one or two tentative probes the tip of the abdomen is again applied to the leaf surface and the process is repeated. The time occupied in laying an egg varies from 30 seconds to several minutes. The female may feed while laying an egg, but usually does not. (Some species do feed actively while ovipositing, even to the extent of depositing eggs in an arc around the feeding site (Moore, 1961)). The depositing of eggs on foliage by C. densitexta is, however, far from haphazard or random. Strong preferences are exhibited for certain sites.

2.331 Sites of Oviposition: The following two experiments were conducted to gain more precise information about these preferences.

Experiment 1. Free-living psyllids choosing between different aspects of the tree crown, different ages of the leaves, and different positions on the leaf.

After the summer generation had finished laying eggs twenty twigs were collected from the north face and twenty from the south face of the same tree; the twigs were collected by the method described in section 2.12.

On each twig leaves were numbered consecutively from the base to the tip (in order of decreasing age) and subdivided to three classes.

(A) "Old" - Leaves more than one year old and situated at the base of twigs - thick, dark green, rigid, and frequently with necrotic and discoloured patches (other than those caused by the feeding of *C. densitexta*).

(B) "Mature" - Leaves of the current season's growth which have fully expanded - bright green, flexible, and free of blemishes other than occasional early gall formation (again excluding attack by *C. densitexta*).

(C) "Young" - Soft, flaccid and pale green, or incompletely expanded new leaves. Very small newly expanding leaves were ignored.

The line of division between (B) and (C) is more subjective than that between (A) and (B) as there is a continual gradation between "mature" and "young" as long as growth is proceeding, but the presence of an axillary ring usually serves to divide "old" from "mature" foliage.

All eggs on all leaves were counted, each leaf being arbitrarily divided by length into three parts, and the eggs on each third recorded separately.

Finally, using an airflow planimeter, the total area per twig of each class of leaf was measured.

Results

Table 2.03 shows the distribution of eggs according to the age class of the leaf. On an area basis more than 60 times as many eggs are deposited on "mature" leaves than on "young" ones, and 120 times more than on "old" leaves.

Table 2.03

Distribution of *C. densitexta* eggs according to age class of leaf

Leaf type	No. of leaves	No. of eggs (E)	%	Area of leaves (A) cm^2	Eggs per cm^2 (E/2A)
"Old"	70	78	0.4	617.5	0.05
"Mature"	210	19,526	98.8	1,564.0	6.24
"Young"	100	155	0.8	760.0	0.10
Totals	380	19,759	100.0	2,941.5	3.36

Table 2.04 illustrates a pronounced preference for the base of the leaf as a site for egglaying, with a marked tapering off towards the tip of the leaves,

Table 2.04

Distribution of C. densitexta eggs according to position on the leaf

Position on leaf	No. of eggs	Percent of total
Petiole third	17,058	86.33
Middle third	2,153	10.90
Tip third	548	2.77
Totals	19,759	100.00

and table 2.05 shows that more eggs are laid on the north side of the tree crown than the south side.

Table 2.05

Distribution of C. densitexta eggs on the north and south faces of the tree crown

Side of tree	Area of "mature" leaves x 2 (cm^2)	No. of eggs	% Total eggs	Eggs/cm^2
North	1,629 (52%)	11,630	59.6	7.14
South	1,499 (48%)	7,896	40.4	5.26
Total	3,128	19,526	100.0	6.24

$\chi^2 = 4.03$ ($P < 0.05$)

Experiment II: Psyllids confined in cages without choice on "old", "mature", or "young" leaves.

Material and Methods

In the autumn before the adults had started to emerge, four trees of uniform size and crown density were selected. On the south face of each of three of these trees organdie bags were placed over nine twigs, three with only "young" leaves left on them, three with only "mature" leaves, and three with only "old" leaves - 27 bags in all. On the fourth tree only three lots of "mature" leaves were enclosed in organdie bags.

All bags were of the same size and pattern, all were made from the same bolt of material, and all were used for the first time in this experiment. These bags were designed:-

(a) to allow the operator access to the foliage after the bag had been placed in position;

(b) to reduce to a minimum the crevices into which adult psyllids could crawl and die.

Making the outer end open allows access to and inspection of a branch without removing the bag, while tapering the ends reduced the number of folds, and this, combined with the stiffness of the new material, and the spreading of the twigs inside the bag, resulted in the "roof" of the cage being relatively smooth and free from crevices. Most folds tapered downwards so that adult psyllids jumping from the foliage to the side of the bag would walk up onto the "roof" where they would encounter foliage touching the bag.

The leaves in each bag were not matched for size, or number per bag, but there was approximately the same amount of foliage in all bags of each leaf type, and in all there was more than adequate leaf surface upon which the adults could rest, feed and oviposit.

Callow adult *C. densitexta* were collected in the early morning while they were still soft and pale, to ensure that all females still had their full complement of eggs, and placed in the organdie bags as follows:-

For each of three trees -

	Leaves		
Psyllids/bag	"Old"	"Mature"	"Young"
1 female & 5 males	1 bag	1 bag	1 bag
10 females & 15 males	1 bag	1 bag	1 bag
20 females & 30 males	1 bag	1 bag	1 bag

On the fourth tree only the 3 lots of "mature" leaves were covered.

The twigs were left undisturbed in the cages until all adults were dead, when the branches were taken to the laboratory and all eggs counted.

Results

The results of this experiment (table 2.06) confirmed the findings of the first one, that ovipositing females of

C. densitexta show a strong preference for the "mature" type of leaf. More than this, however, it demonstrated that, when wholly confined to unsuitable foliage, these females will die without laying more than one or two eggs.

Table 2.06

C. densitexta - Number of eggs laid when females are confined to one of three age-classes of leaves

Total for three trees

Leaf type	No. females	No. eggs	% Total eggs	Mean No. of Eggs/Female
"Old"	93	121	3.0	1.3
"Mature"	93	3,773	93.0	40.6
"Young"	93	163	4.0	1.75
Totals	279	4,057	100.0	14.5

Analysis of the number of eggs laid per female showed no significant differences at different densities of adult psyllids per bag.

2.332 Preferences Exhibited: In the first place preference is for the lower shaded side of any leaf. Contrary to popular belief regarding eucalypts, very few leaves of this species hang in a truly vertical manner with their edges towards the sun. In most cases the lower surface of a leaf is the original "outer" surface (Jacobs, 1955) and differs very little from the "inner" surface apart from a slightly more prominent mid rib. This preference would seem to be the result of the insects exhibiting the usual response of moving from high to low light intensity. If a leaf is turned over, all adults on it will rapidly walk on to the shaded side.

It is impossible to decide with any certainty which are the lower sides of the leaves on a twig once it has been picked. This preference is, however, very obvious in the field. As an example, on 180 leaves examined in situ for another experiment, 81% of the 8,341 eggs were laid on 153 lower surfaces, and the remaining 19% on 85 upper surfaces.

Secondly, the age of leaves is of great importance, and the behavioural response of gravid females to this variable is apparent at two levels.

(a) An immediate response to the age of the succession of leaves on a single twig.

On any one twig females may be confronted with leaves varying in age from a few days to 24 months. In normal circumstances only a very few old tough leaves will persist at the base of shoots, and a varying number of new leaves may be expanding at the tips. Between these two extremes is the bulk of the current season's foliage, which I have classed as "mature" leaves. As can be seen from tables 2.03 and 2.06, there is an overwhelmingly strong preference for these "mature" leaves. In the absence of this age of leaf, most females will die without laying any eggs, while the few eggs laid when the insects are confined to "young" or "old" foliage are less than enough to replace the parents (table 2.06).

(b) A more general response to the seasonal age of the foliage as a whole.

The above experiments were conducted with the summer and autumn generations. At these seasons females will lay eggs on any turgid "mature" leaves, even when these have been extensively damaged by previous nymphal feeding. Many of these damaged leaves are shed within days of the eggs being laid, or turgid but reddened areas of leaf will dry up and die, killing all eggs on them (fig. 2.09). Females emerging in the spring, on the other hand, avoided even undamaged leaves grown the previous spring and summer.

This change in the behaviour of the psyllids with the seasons is considered to be merely a finer gradation of the insects' response to the age of the leaf as seen between "old", "mature" and "young" leaves on individual twigs. When the "mature" leaves on the twigs collected after summer egglaying was completed were arranged in order of decreasing age, and the eggs on each age-group counted, it became apparent that the psyllids had laid scarcely any eggs on the newly expanded "young" leaves, while on the "mature" leaves there was a continuous gradient with relatively few eggs on the youngest "mature" leaves and most eggs on the oldest "mature" leaves.

Similar counts made on similar twigs from the same trees after autumn egglaying was complete some three months later, revealed a marked "shift" of preference away from the oldest "mature" leaves to younger ones further down the twig (fig. 2.10). These younger "mature" leaves would have been of approximately the same <u>physiological</u>

Figure 2.09

C. densitexta on *E. fasciculosa* leaf.

Eggs and first instar nymphs under their lerps. Note the eggs laid on the patch of dead tissue (white). This would have been red but turgid at the time of oviposition (autumn) but has since died killing all eggs on it which did not hatch prior to its death.

Scale : 1 division = 1 mm.

age in the autumn as the basal ones were when the summer generation were laying their eggs. In the spring of 1963 many leaves died and there were few psyllids present so no count could be made for the spring oviposition. Apparently what happens, however, is that the "preference peak" "moves down the twig" as the leaves age until, by spring, all, or nearly all the leaves are but reluctantly accepted as egglaying sites.

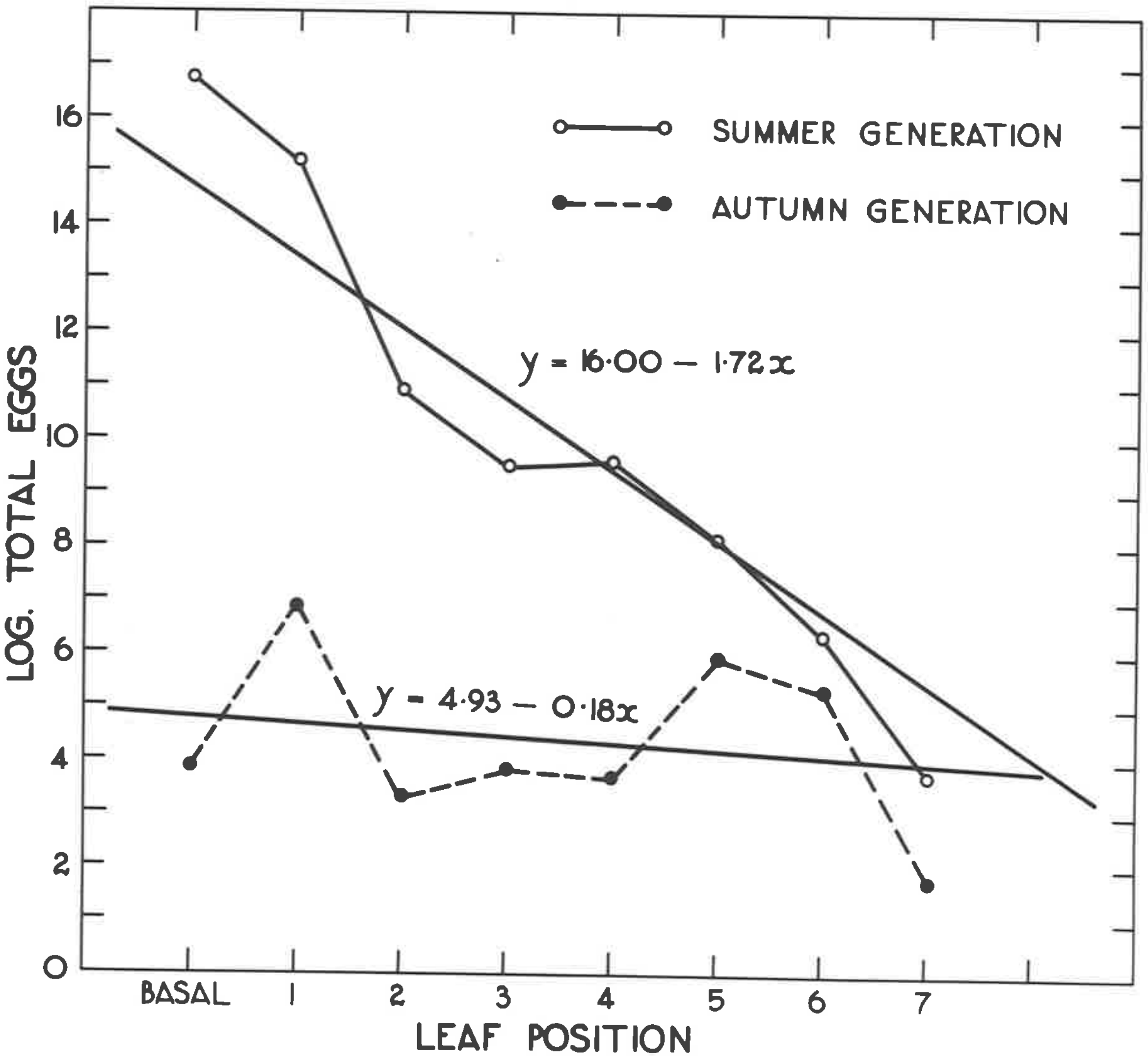
Figure 2.10 illustrates the means of the counts from the summer and autumn lots of eight twigs each, all twigs bearing eight "mature" leaves. Due to great between leaf and twig variability the Time x Position difference of these two lots is only significant at $p = 0.10 - 0.05$.

Clark (1963a) observed a similar preference for the basal leaves of twigs, but attributed this to "extrinsic causes". He argued that the disappearance of this strong preference when the psyllids laid eggs inside organdie bags supported his hypothesis because the bags sheltered the ovipositing females from these "extrinsic causes" (his tables 5 and 6). I would suspect that leaves in table 6 were at least three months older than those in table 5, and that the distribution of eggs would have been much the same in the absence of the bags.

Most leaves present in the autumn would normally remain on the tree until the growth of new foliage next spring, and thus a psyllid settling on them would have a good chance to compete its

Figure 2.10

The distribution of eggs of *C. densitexta* laid in the summer and autumn on eight leaves of each of eight separate twigs. All 128 leaves sampled had grown before eggs were laid in the summer, so the 64 collected in the autumn were three months older when eggs were laid on them than were the 64 collected in the summer.



SUMMER GENERATION
AUTUMN GENERATION
y = 16·00 − 1·72x
y = 4·93 − 0·18x
LOG. TOTAL EGGS
16
14
12
10
8
6
4
2
0
BASAL
1
2
3
4
5
6
7
LEAF POSITION

development. In the spring, however, the chance of any one of these same leaves, (even if developed in the summer months) being shed before the completion of the next generation is great, irrespective of whether or not it had been damaged. Both spring and autumn behaviour (coupled with that described under "Dispersal") therefore ensure that eggs are laid on foliage which will give the psyllid the maximum chance to complete its life cycle (Southwood, 1962).

When psyllid numbers are high, however, this may not be so, as many leaves may be heavily damaged in the summer, autumn and winter, and consequently are shed prematurely, with fatal results for the psyllids on them. When numbers are very high, a widespread and catastrophic reduction of the population may occur. As discussed under "Dispersal", the spring of 1963 produced just such a situation in the Southeast of South Australia. Only old and extensively damaged, or soft new leaves were present on the trees. As was demonstrated in the second experiment, few if any eggs are laid on such leaves.

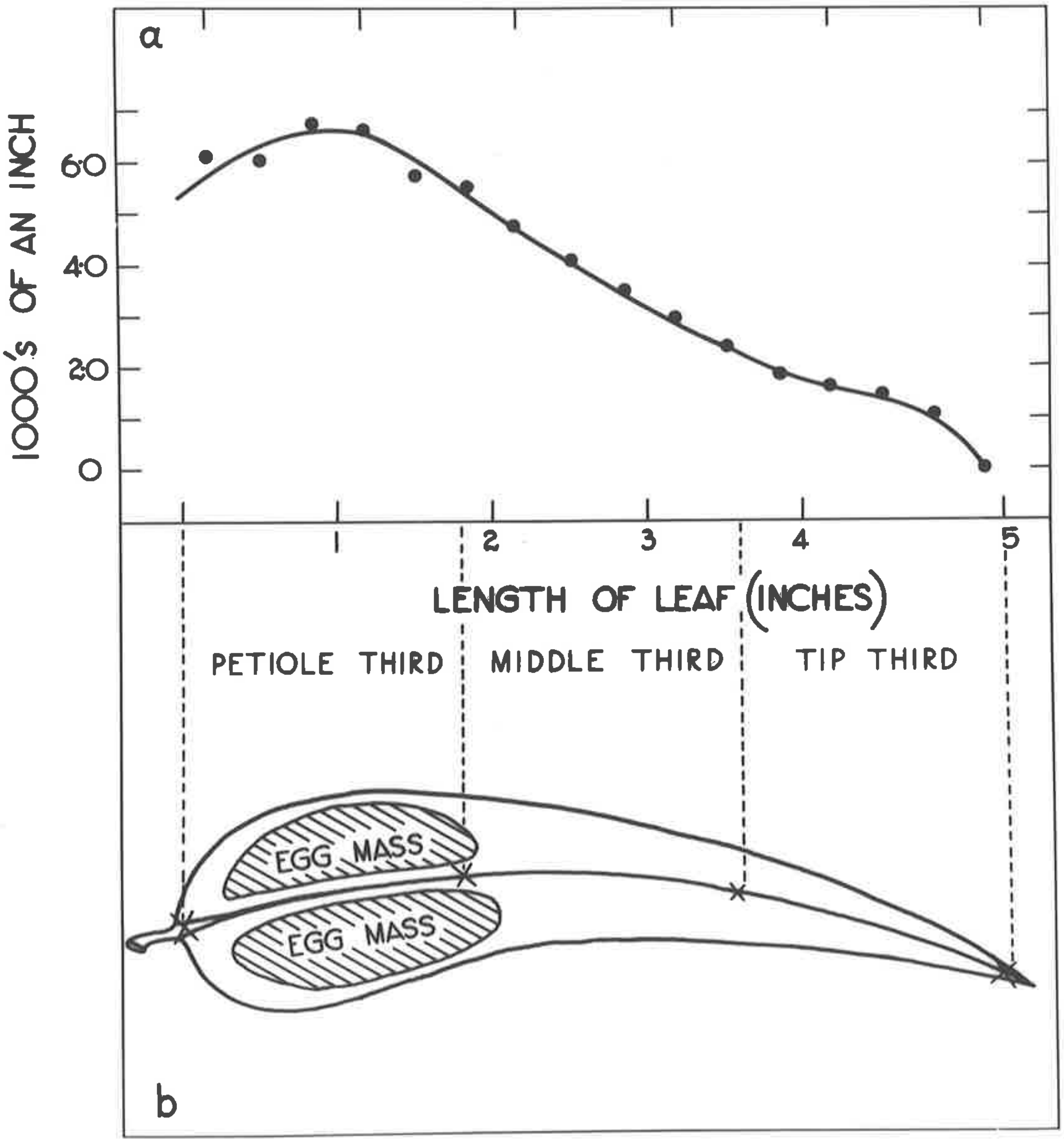
A third type of strong preference was illustrated in the above experiments; virtually all eggs were laid in dense groups on the basal thirds of the leaves (table 2.04; fig. 2.11). This pattern is occasionally destroyed when a leaf has a pit, or gall, or a few eggs of another species of psyllid on the middle or tip thirds. Any such irregularity on the surface of a leaf will provide a nucleus around which large groups of eggs will be laid. The specimen twig-sample extracted from figures for the first experiment and given

Figure 2.11

Relation of Placement of C. densitexta eggs to the thickness of the leaf's Mid-rib

a. The distance (in thousandths of an inch) that the midrib stands up from the leaf blade (mean of 30 "mature" type sun leaves).

b. Generalized "mature" pink gum leaf showing the most common positions of egg masses on these leaves.


a
1000's OF AN INCH
60
40
20
0
1
2
3
4
5
LENGTH OF LEAF (INCHES)
PETIOLE THIRD
MIDDLE THIRD
TIP THIRD
EGG MASS
EGG MASS
b

here illustrates this point.

Specimen twig sample

Tree B : North Side : Twig 1

Leaf No.	Type	No. of Eggs				Remarks
		Petiole Third	Mid Third	Tip Third	Total	
1	Old	-	-	-	0	
2	"	-	-	-	0	
3	"	-	-	-	0	
4	Mature	450	11	-	461	
5	"	379	-	-	379	
6	"	180	1	-	181	
7	"	57	109	-	166	Pit in centre area
8	"	167	1	-	168	
9	"	2	-	-	2	
10	"	4	-	-	4	
11 to 14	Young	-	-	-	0	Mass of soft new growth
		1239	122	0	1361	

For the most part leaves favoured for oviposition are free of surface irregularities other than the midrib, and it would appear that this midrib is one of the factors resulting in concentration of eggs at the base of the leaves (table 2.04). Females encountering this midrib with the tip of the abdomen are stimulated to lay, and the more the rib protrudes above the blade, the stronger the stimulus will be (fig. 2.11). Once some eggs have been laid, the effect is compounded as these are encountered by further females.

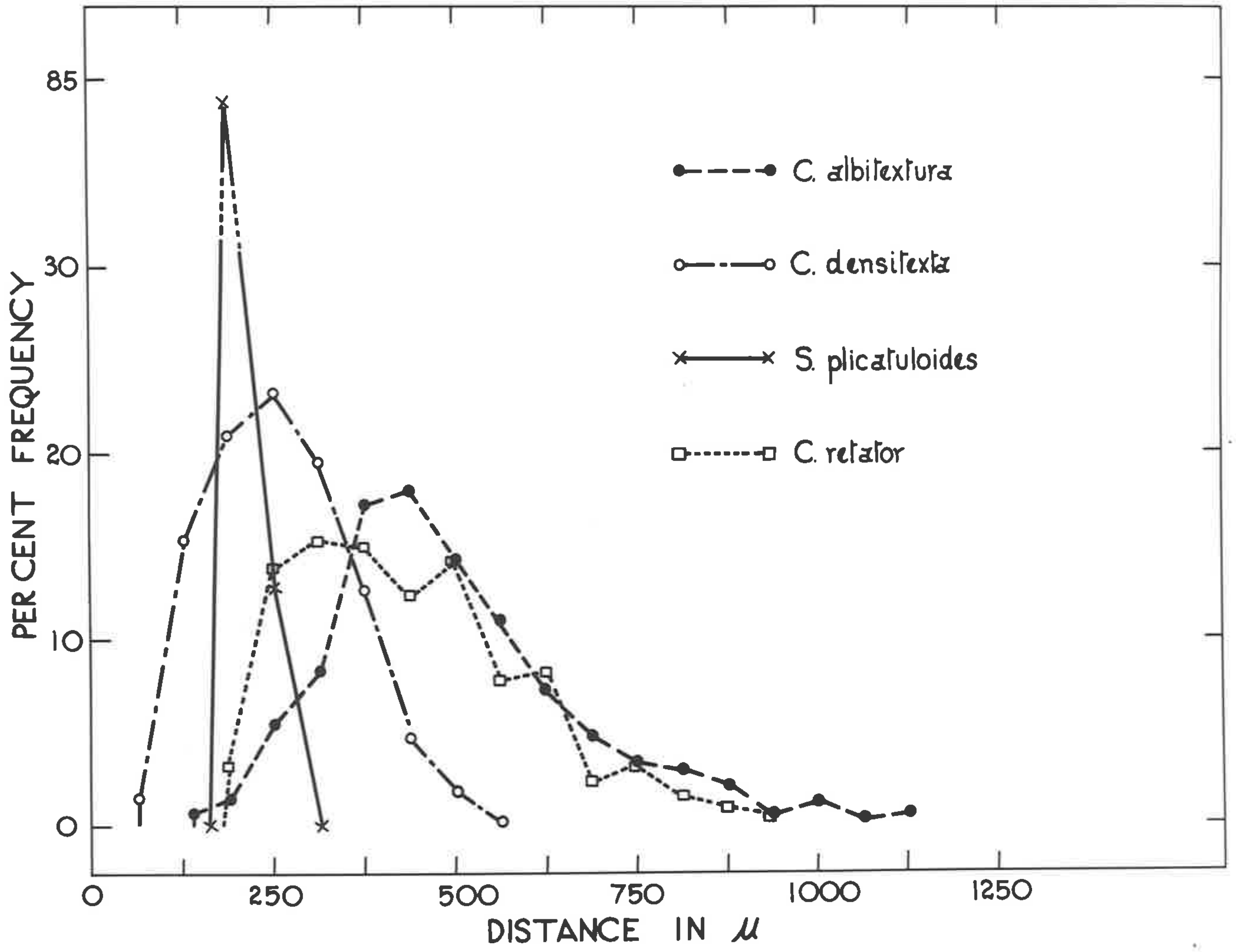
Most if not all psyllids show this tactile response resulting in eggs being laid against a protuberance or in a depression. Clark (1963a) demonstrated that the presence of existing eggs attracted the egg-laying females of C. albitextura and numerous other authors record eggs being laid in crevices, against midribs, etc. (e.g. Grove and Ghosh, 1914; van der Merwe, 1923; Annecke & Cilliers, 1963). Although this behaviour is characteristic of the family particular differences serve to distinguish genera and species (see fig. 2.12). These data were obtained as follows:-

A leaf with a group of C. densitexta eggs on it was taken and one egg selected at random (the nearest one to the zero on the eye piece micrometer of the microscope). The distance from the point of insertion of the stalk of this egg to the point of insertion of its nearest neighbour was measured. This was repeated for the next egg "touching" the scale, or an imagined extension of it, and so on. This was done with a number of leaves.

Similar measurements were made in the egg masses of C. albitextura and C. retator on E. camaldulensis leaves, and with Spondyliaspis plicatuloides eggs on pink gum leaves. Results for each species are from between 300 and 400 measurements. These differences in spacing of eggs are readily apparent in the field. S. plicatuloides always lays a tight bundle of eggs with each one almost touching its neighbour. This allows only very small variation in the distance between stalks at their points of insertion

Figure 2,12

The spacing of *C. densitexta* eggs within major egg-clusters compared with that for two other species of *Cardiaspina* and and one of *Spondyliaspis*.


PER CENT FREQUENCY
85
30
20
10
0
0
250
500
750
1000
1250
DISTANCE IN μ
C. albitextura
C. densitexta
S. plicatuloides
C. retator

(fig. 2.13). Groups of C. densitexta eggs (fig. 2.14) have a more compact and denser appearance than those of C. albitextura (fig. 2.15) and C. retator (fig. 2.16) tends to lay eggs in lots of three to five within the main group, giving an almost "mottled" appearance to the egg groups. In all four species measured a certain "looseness" is apparent around the periphery of egg groups, and this increases with wider mean spacing of eggs in different species.

The above measurements for the three Cardiaspina species were all made on leaves taken from areas where large numbers of the species concerned were present. (It is worth noting that C. retator and C. albitextura also concentrated their eggs on the petiole ends of the leaves in the same manner as C. densitexta).

Clark (1962) says that the eggs of C. albitextura are "... usually laid singly or in small scatters or groups ..." and that only when numbers of females are high, are the eggs laid in close proximity to each other.

This is not the case with C. densitexta. Individual females (isolated in organdie bags or on leaf discs in the laboratory) will lay most of their eggs in groups of this characteristic density. This means that, even at very low levels of population, eggs will tend not to occur in isolation.

One situation has been found where the generally observed pattern of laying eggs at the base of "mature" leaves is not seen. This is on the broad juvenile form of leaf (Jacobs, 1955) produced on epicormic and sucker growth. Eggs are frequently found singly

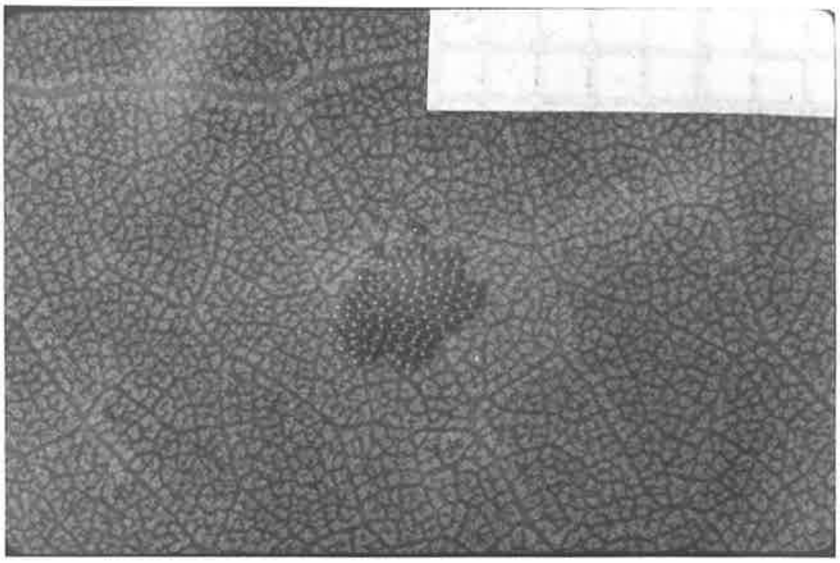
Figure 2.13

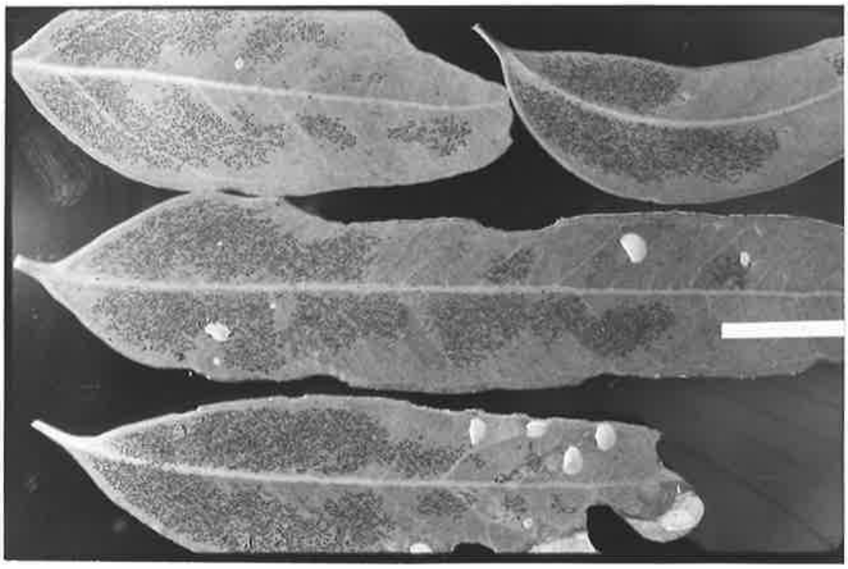
Eggs of *S. plicatuloides* on *E. fasciculosa* leaf. Note the characteristic tight packed grouping of the eggs compared to that for the three species of *Cardiaspina* (figs. 2.14, 2.15, 2.16).

Figure 2.14

C. densitexta eggs on *E. fasciculosa* leaves. These leaves were collected in the autumn of 1963 when numbers were very high. Note the strong preference for the petiole end of the leaves and the much closer spacing of the eggs compared to *C. retator* (fig. 2.16) and *C. albitextura* (fig. 2.15)

Scale : 1 division = 1 mm.





and widely scattered over the entire surface of such leaves. The difference between midrib and blade thickness is just as great on these leaves as on the adult form of leaf; but due principally to the "cupping" of these leaves (with the "outer" surface becoming concave) there is not a sharp angle between the blade and midrib as there is with the adult leaf form. This could, in part, account for the failure to group eggs at the petiole end of these leaves, but if only the tactile response were involved, a series of groups of eggs should be deposited at random over the entire surface rather than widely scattered single eggs. This then strengthens the view that it is the physiological condition of the leaf - or rather part of the leaf - which is providing the primary stimulus for selection of the oviposition site, the tactile response being secondary.

Finally there are preferences for different positions within the crown of a tree.

More eggs are laid on the north than the south faces (table 2.05) but this preference becomes much less marked at high levels of abundance (table 2.07).

Where there is a persistent prevailing wind I would expect higher densities of eggs on the lee side of crowns during summer and autumn. I have no evidence to support this supposition other than the observation of adult behaviour referred to in my discussion of dispersal.

Figure 2.15

C. albitextura eggs on E. camaldulensis leaves. Note the more scattered nature of the group compared to C. densitexta (fig. 2.14) and the preference for the petiole end of the leaf.

Figure 2.16

Eggs of C. retator on leaves of E. camaldulensis. Note the greater distance between eggs within the groups compared to C. densitexta (fig. 2.14) and the preference for the petiole end of the leaves.

Scale : 1 division = 1 mm

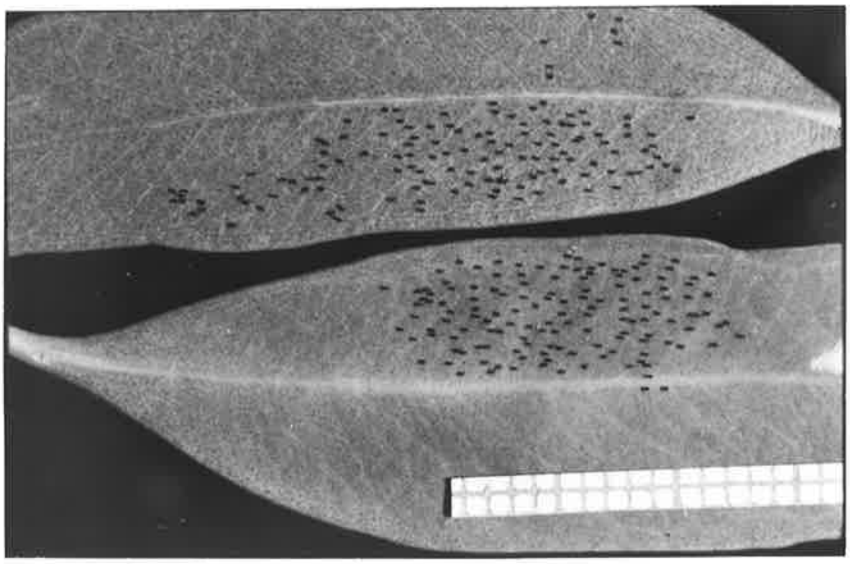


Table 2.07

Numbers of eggs laid on the north and south faces of pink gum crowns

Each of the 5 lots is comprised of 20 samples (10 north face and 10 south face) from individual trees.

Population Level	North		South		Total
	No.	%	No.	%	No.
Moderate	526	90.3	57	9.7	583
	1,119	91.1	109	8.9	1,228
	2,387	100.0	0	0.0	2,387
	4,032	96.0	166	4.0	4,198
High	10,281	56.9	7,797	43.1	18,078
	10,451	61.0	6,770	39.0	17,221
	20,732	59.0	14,567	41.0	35,299

2.333 <u>Discussion of Preferences</u>: One of the first things that becomes apparent from this investigation of oviposition is the comparatively short time in the life of a leaf that it provides optimum stimulus for the females to lay their eggs. Only the current season's leaves during the first few weeks after they have fully expanded and hardened provide this optimum stimulus. Prior to this they are unacceptable, and after this short period they gradually lose their attractiveness, until by the following season they are again unacceptable.

Within this restricted age of leaf oviposition is further concentrated - with certain exceptions - on to a relatively small proportion of the available surface area.

Finally some leaves are selected ahead of other apparently identical ones because of their position on the tree.

Although the total stimuli leading to egglaying are undoubtedly complex, it would seem that there are two principal stimuli responsible for the observed selection of egglaying sites.

(1) Physiological condition of the host tissue.

Nutritional, olfactory and gustatory stimuli will play a large part in the selection by the active female of a suitable site for oviposition. Adults presumably will not remain on a leaf which is "unpalatable", but move on until suitable leaves (or parts of leaves) are located. At such suitable sites adults could be expected to accumulate for feeding, mating and oviposition.

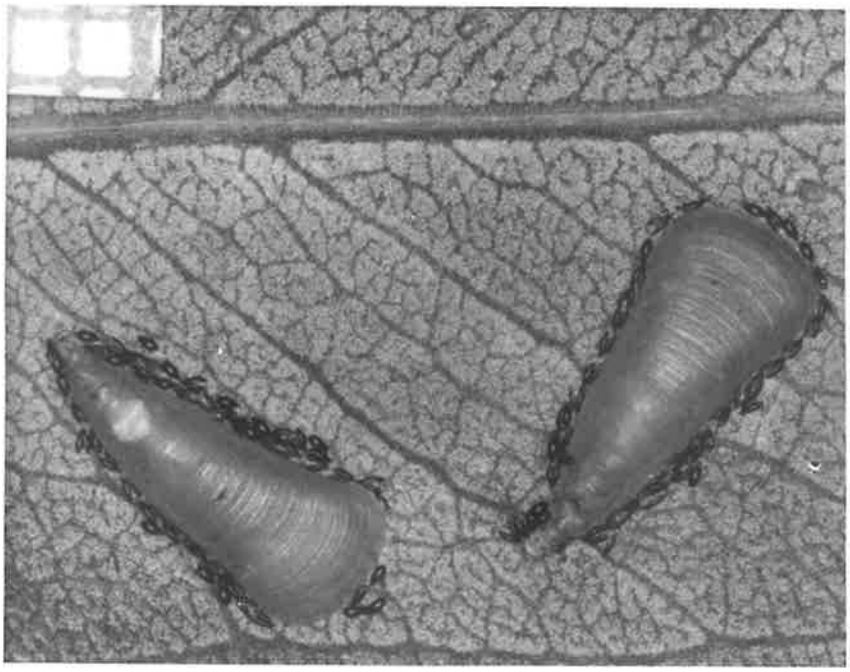
On the hypothesis that the overriding stimulus here is provided by the quantity and proportion of soluble nitrogenous elements available in the sap, the most favoured places on a plant would be at sites where these are most readily available.

The recently fully expanded leaves represent the site of major activity on a tree. Recent work with Eucalyptus (R.J. Cameron, personal communication, and unpublished Ph.D. thesis, 1965, A.N.U.) has demonstrated that photosynthesis reaches a maximum as the leaf becomes fully expanded, remains at this level for several weeks, and then falls slowly as senility sets in. Fennah (1954) has shown with Cacao that this period of maximum photosynthetic activity following full expansion is also a period of great increase

Figure 2.17

Creiis sp. on *E. cladocalyx*. Eggs laid around empty lerps illustrating the strong tactile response to lay against a protruberance on the leaf.

Scale : 1 division = 1 mm.



in the proportion of soluble nitrogen in the leaf. Herein lies an adequate explanation for the choice of the "mature" type of leaf and the preference for individual leaves moving along the twig as the leaves age. Furthermore, the site of greatest concentration of soluble nitrogenous nutrients being translocated away from the actively photosynthesising leaf will be the base of the leaf - hence the preference for the petiole end of the leaf. The observed preference for the north facing side of the crown is similarly explained; the sun-leaves having a greater rate of photosynthesis and higher soluble nitrogen content than the shade-leaves (Fennah, 1954). The addition of water-stress to the leaf tissues will accentuate these preferences (see also sections 2.63 and (especially) 2.65, and chapter 3 for further discussion of the nutrient status of the leaves).

(2) Tactile stimuli.

The gross initial acceptance or rejection of a leaf surface may be determined by a response to tactile stimuli, but if the foregoing hypothesis is correct, such stimuli apparently play a relatively minor part after acceptance. There is, however, unequivocal evidence that a tactile response plays a definite part in the disposition of psyllid eggs. The result of this behaviour is seen in isolated groups of eggs laid around galls, old lerps, pits and calloused wounds (figs. 2.17 and 2.18).

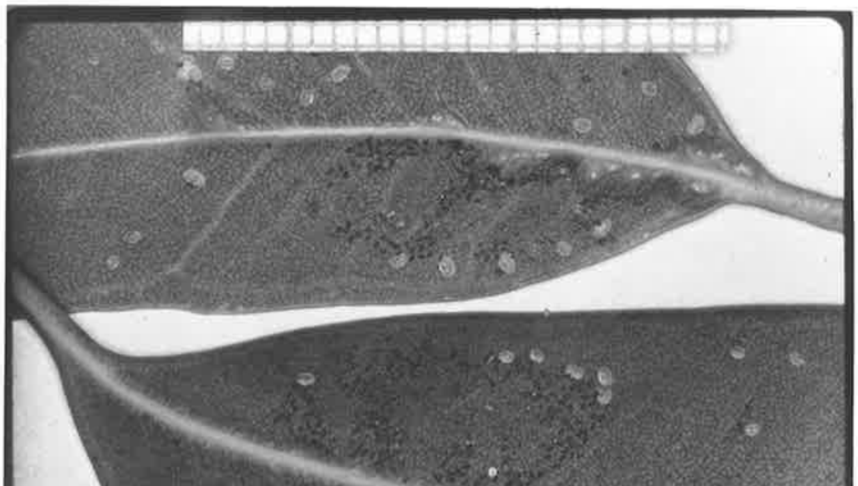
Figure 2.18

C. densitexta eggs on E. fasciculosa leaves, showing the response to the presence of protruberances on the leaves.

Figure 2.19

C. densitexta eggs on E. fasciculosa leaf. Note that only a few eggs are left around the margins of the original groups of eggs. The central ones which were laid earlier have hatched and the shells disintegrated.

Scale : 1 division = 1 mm



C. densitexta eggs are frequently grouped around small lots of eggs of other species, and the large aggregation of its own eggs result in this way, as is illustrated by the central eggs of such groups hatching first (fig. 2.19).

Thus it is seen to complement the response to nutritional stimuli by aiding in the aggregation at various sites which are especially favourable for the nymph to feed when it hatches. Furthermore, the aggregation of early instar nymphs is in itself advantageous (see sect. 2.633).

2.4 Selection of a Host-plant

2.41 Other Species of Eucalyptus on which C. densitexta has been recorded

Although pink gum is the usual host for C. densitexta it has been found on five other indigenous species and three introduced species of Eucalyptus; always during times when the psyllids were unusually abundant.

Indigenous species

(1) E. diversifolia is confined to stony ridges, and thus frequently occurs in isolated patches in developed farm land. Eggs have at times been laid in great profusion on the leaves of this species (fig. 2.20) and frequently some hundreds of yards away from the nearest pink gum. Groups of eggs are laid towards the petiole end in the same way as on pink gum. These eggs hatch and the first instar nymphs settle and build lerps. They will remain alive at

this stage throughout the winter, but die in early spring. I have never seen an adult produced on this species, but once found two live third instar nymphs among many thousands of dead first instar nymphs. I have never observed any discolouration of the leaf tissue from nymphal feeding.

After pink gum this is the species most commonly accepted for oviposition.

(2) E. leucoxylon. This species commonly occurs mixed with pink gum and, in the absence of fruit or flowers, is frequently difficult to distinguish from it. A few scattered groups of eggs have occasionally been found on the foliage of this species, and sometimes a few very small lerps. The few first instar nymphs which manage to establish themselves do not appear to live more than one or two days.

(3) E. leucoxylon var. pauperita. I once found a few fifth instar nymphs and recently vacated lerps (indicating adult emergence) on a tree of this variety near Tintinara. Patches of leaf tissue were discoloured and killed around each lerp.

(4) E. odorata var. angustifolia. This dwarf variety of peppermint gum occurs on granite outcrops. Eggs are laid quite freely on its foliage and a large percentage of the hatching nymphs survive to adulthood. Foliage may be extensively discoloured and many leaves may die on an occasional tree (fig. 2.21).

(5) E. incrassata. This species occurs quite commonly in association with pink gum. The leaves are thick, dark and

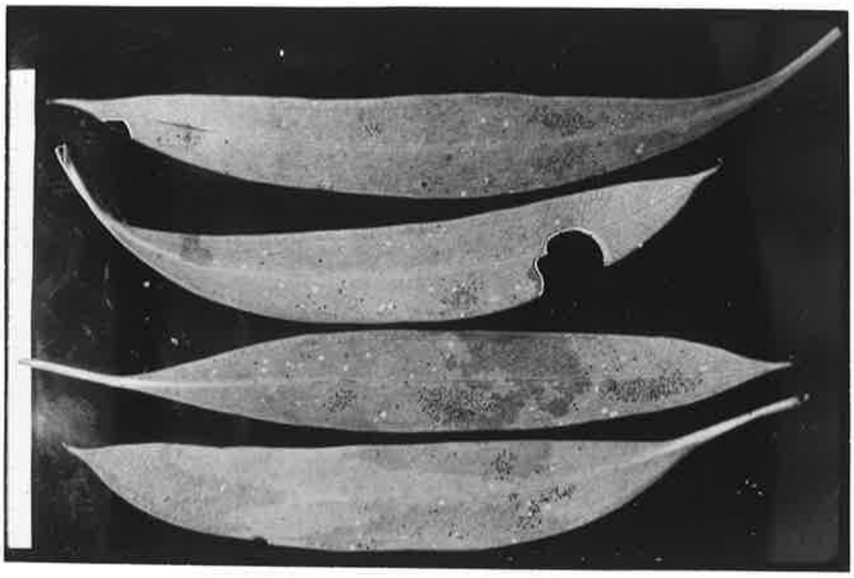
Figure 2.20

C. densitexta eggs and first instar nymphs on leaves of E. diversifolia.

Scale : 1 division = 1 mm.

Figure 2.21

C. densitexta on E. odorata var. angustifolia leaves. White areas are dead tissue.

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leathery and quite unlike those of pink gum. I have never seen eggs laid on this species but once found two fairly large (4th or 5th instar, and possibly adult) lerps on two leaves of one branch. They were unquestionably C. densitexta lerps and around each there was a small area of reddened leaf tissue.

Introduced Species

(1) E. ficifolia (W.A. flowering gum). On a young specimen of this species planted in a farmer's garden at Brecon. There were a few eggs and one or two first instar lerps. None of these progressed beyond the first instar.

(2) E. melliodora (Victorian Yellow Box). Another small tree planted in a garden near Padthaway. This tree was heavily attacked by three different lerp-insects including C. densitexta, and all had advanced to the third and fourth instar before being destroyed with insecticide.

(3) E. cornuta (West Australian Yate Gum). (fig. 2.22) A row of these trees planted near Keith was repeatedly and heavily attacked by C. densitexta as is described elsewhere (sect. 4.212).

In all the above examples except E. cornuta, eggs were commonly seen only in the autumn and summer generations, and much less frequently in the spring generation.

2.42 Field and Laboratory trials with other Species of Eucalyptus

In the arboretum at the Waite Institute, female C. densitexta were confined in organdie bags on the other available species of red boxes (E. polyanthemos, E. dawsoni, E. baueriana and E. conica). A

Figure 2.22

C. densitexta on *E. cornuta* leaf. White patches of leaf are dead tissue.


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1

few scattered eggs were laid on the former two species, and 9.0% of the nymphs from eggs laid on E. polyanthemos survived to produce adults. None survived on E. dawsoni.

In the laboratory newly emerged nymphs were placed on discs of these four species and of E. camaldulensis and E. blakelyi (the usual hosts of C. albitextura) - forty nymphs to each species. One adult was obtained on E. dawsoni but most other nymphs were dead within a week.

2.43 Discussion

Gravid females select the host plant on which to lay eggs; the nymphs select the tissue on which they feed. The range of plants on which C. densitexta can establish and succeed will therefore depend upon acceptance or rejection of the plants by both adults and nymphs.

Assuming that in the spring females become dispersed at random over any given area of land, many will land on foliage other than that of pink gum. If initial olfactory and tactile stimuli are favourable (or at least not repellent) these females will presumably commence probing for food, and if consequent gustatory stimuli are satisfactory, they will remain to feed, mate and lay eggs. If, on the other hand, any repugnant or discouraging stimuli are received, they will again take off to land at random at some new site. This process will be repeated until either a satisfactory substrate is located, or the animal dies. As has been demonstrated, females will nearly always die without laying eggs if confined to foliage which is not suitable. It must be presumed then, that the leaves of other species of Eucalyptus on which eggs were laid in quantity satisfied all the chemical and tactile stimuli necessary for a female to deposit her eggs, and were not laid upon simply because the female chanced to land there and was ready to lay eggs.

The fact that eggs were laid in abundance on E. diversifolia, but that virtually none of the subsequent nymphs survived past the first instar, indicates that something had "gone wrong" with the normal pattern of behaviour leading to selection of a host. Yet in other cases oviposition on foreign hosts was followed by the development to maturity of the majority of the hatching nymphs.

If oviposition by adults, and settling and feeding by nymphs are responses to nutritional stimuli and not to "token" stimuli, then these apparently contradictory happenings can be explained in terms of the greater nutritional value of the sap in leaves growing on trees that had been stressed by an unfavourable regime of soil-moisture. As the trees are stressed by unfavourable moisture in the soil the concentration of nitgrogenous food in the sap will increase in the different species to the point where leaves previously rejected as oviposition sites become acceptable - not because of the removal or diminution of any "token" repellent, but simply because they had previously been "nutritionally negative" and had now become "desirable" to the probing females. Whether or not the nymphs hatching from these eggs are able to establish and survive even for a limited period of time will depend on only two factors (death from predation and misadventure aside).

(a) Whether or not satisfactory stimuli to probe and to feed are received, and if received,

(b) Whether or not the ingested sap is sufficiently nutritious for survival and growth.

A nymph cannot build a lerp until it has ingested sap from the plant, so the presence on a plant of living nymphs under lerps would provide reasonable grounds for supposing that condition (a) above had been fulfilled by that plant.

If at a later date these same nymphs are found dead beneath their lerps, with their stylets still inserted into the leaf and showing no signs of injury or disease, there is a strong probability that the reason for death was starvation - or poisoning by a substance which is not discernable to the insects as such.

With the laboratory trials of nymphs on discs of leaf tissue of species of _Eucalyptus_ other pink gum, several relevant facts were noted. The few nymphs which did settle on the other boxes (particularly _E. dawsoni_) made but one lerp each and died under this; and with their mouthparts fully inserted; but those on red gum and Blakely's gum did not behave in this manner. They made repeated efforts to settle and start lerp construction only to abandon it (often before completing more than the primary arch) and search for another feeding site. They all died exposed on the surface of the leaf disc, and with their mouthparts withdrawn. Before death many of them developed a form of dysentery, discahrging a dark brown liquid from the anus, and no longer constructing lerp material.

I would interpret these facts as demonstrating that on all species of *Eucalyptus* in this trial the nymphs were stimulated to probe and feed. On the Boxes feeding continued, but the sap was seriously lacking in the correct nutrients. Several nymphs survived to the third and fourth instar and one developed to an adult on *E. dawsoni*, indicating that some were able to obtain more nutrients than others, and that there was no general poison present in these tissues. The restless and dysentery-ridden nymphs on the *E. camaldulensis* and *E. blakelyi* on the other hand showed that although the stimulus to probe and feed was there, sap was not only "distasteful" but harmful to them, with the result that they died wandering and sick, rather than quietly feeding on a "palatable" but lethally inadequate food.

In the field the first instar nymphs died on *E. diversifolia* and *E. leucoxylon* in this manner, but continued to thrive on *E. odorata* var. *angustifolia* and *E. cornuta*.

That they survive on one and die on another of two apparently equally suitable hosts indicates that the quantity and/or proportion of amino acids differed in the different species, being adequate in some and not in others. This could be due to different susceptibility to the same degree of soil-moisture stress, or to different amino acid production with equal response to stress, in each species.

The Egg

2.50 Introduction

The eggs are dark golden brown, smooth, shining, of characteristic shape, and 0.34 (± 0.001 S.E.) long by 0.17 (± 0.0002 S.E.) mm wide at the widest point. The pedicel is 0.10 (± 0.0006 S.E.) mm long. They do not alter in colour, shape or size after being laid.

The gross structure of the egg is essentially similar to that of other insects. There is a thick, doubly pigmented exochorion, pitted over most of its surface, and covering all but the pedicel which is inserted into the leaf. The pedicel appears to be a prolongation of the endocuticle and it seems probable that it could be analogous to, if not homologous with, the hydropyle of other insect eggs (Slifer, 1937).

Most of the surface of the egg appears to be finely pitted when viewed under low power magnification (fig. 2.23 B & C). Closer inspection reveals it to be essentially similar to the chorion of Psylla mali (Hartley, personal communication; Wigglesworth and Beament, 1950). As the latter authors note "... the bulk of the substance of the shell is porous ..."

Micropyles, varying in number from one to four, are situated posteriorly just above the base of the stalk in a non-porous area of chorion (fig. 2.23 A & B).

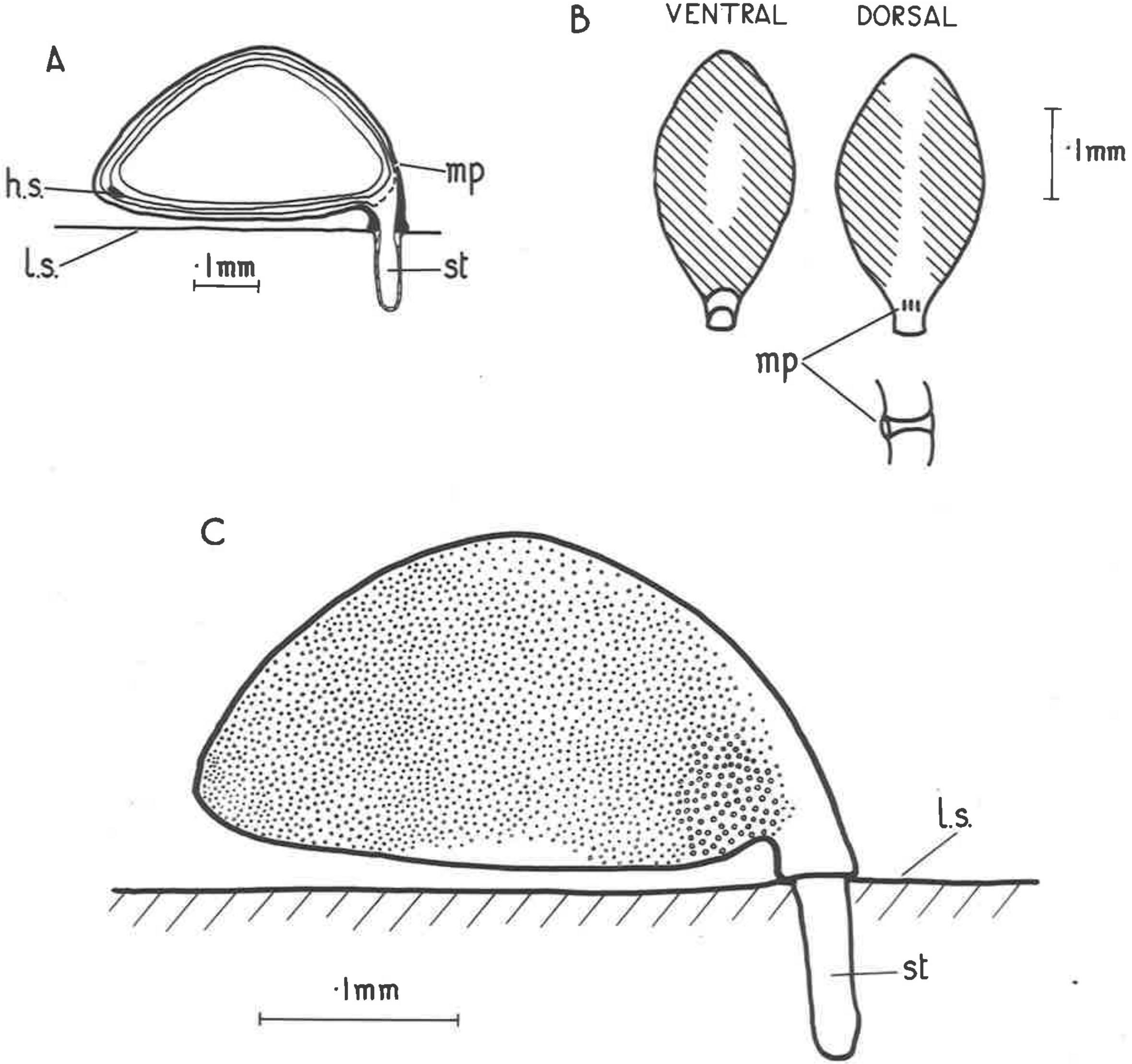
Embryonic development has not been studied, but whole mounts of eggs show a membrane between the chorion and the embryonic cuticle "which is almost certainly the epembryonic membrane of Beament"

Figure 2.23 : C. *densitexta* - Egg

A: Diagrammatic section of egg to show from the outside inwards, the chorion with micropyle (mp), the epembryonic membrane, the embryonic cuticle bearing the hatching spine (h.s.), and the cuticle of the embryonic first instar nymph. l.s. = leaf surface st. = stalk or pedicel.

B: Areas of porosity of the chorion (shaded) the location of the micropyles (mp).

C: Sketch of egg attached to leaf surface (l.s.) by the stalk (st.) driven through the cuticle and epidermis.


A
h.s.
mp
l.s.
·1mm
st
B
VENTRAL
DORSAL
·1mm
mp
C
l.s.
st
·1mm

(Hartley, personal communication) (fig. 2.23A). Speyer (1929) speaks of two more membranes inside the chorion in *Psylla mali* and Wilcke (1941) reports a yolk membrane between the chorion and the embryonic cuticle for *Psylla buxi*.

Incubation-time is related to temperature in the usual way, decreasing the temperature increases the time of incubation (fig. 2.24).

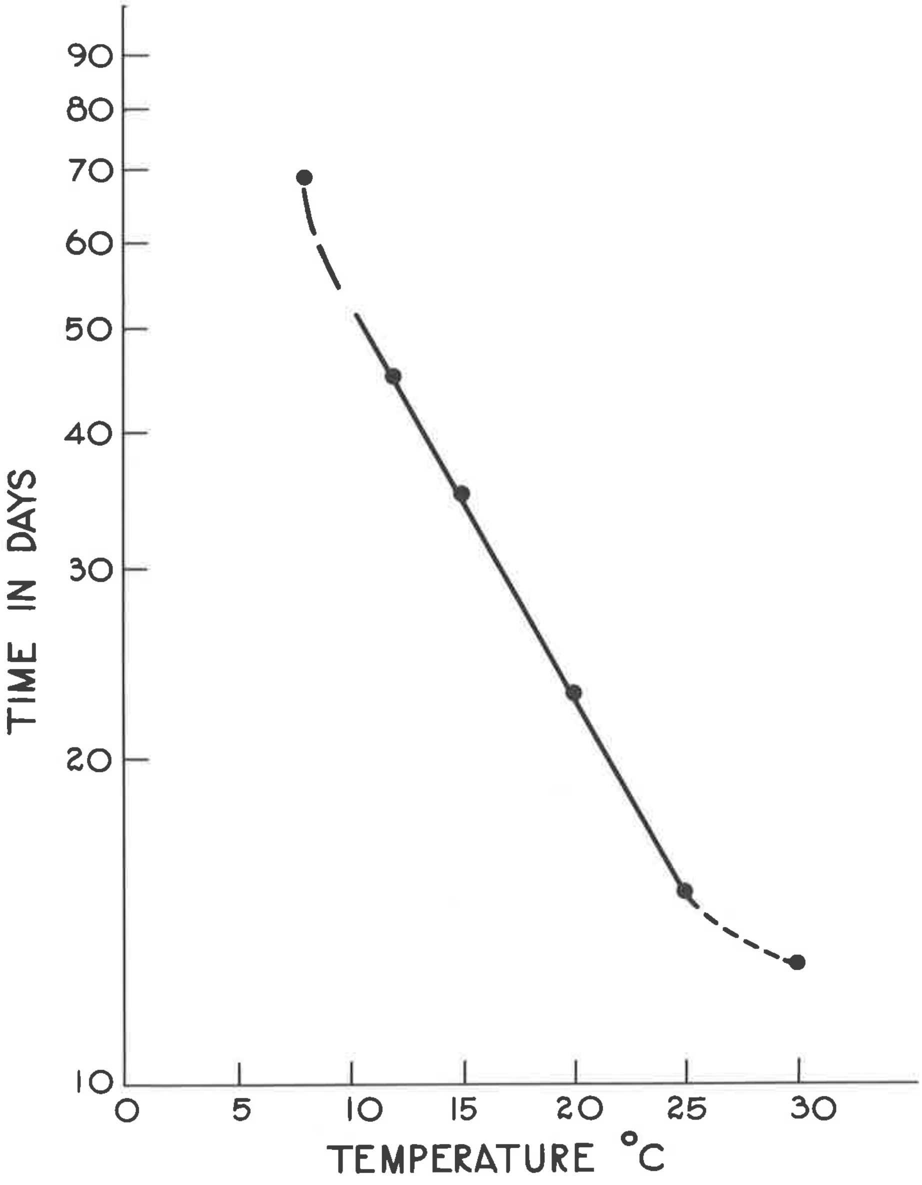
When the egg is ready to hatch the shell is split along a median dorsal line from anterior to posterior as a result of the embryo pressing a hatching spine or eggtooth against the shell until it ruptures. A similar eggtooth has been described for *P. mali* (Lees, 1916; Speyer, 1929) and Wilcke (1941) described paired lateral eggteeth for *P. buxi*. The nymph immediately bulges anteriorly through this slit in the shell, and a ring of fine hair-like processes appears. These form a halo around the protruding head of the nymph, and curve out and fit tightly back over the edges of the slit in the shell as the embryonic membrane splits and the nymph moves forward out of the egg (fig. 2.25).

Awati (1915) briefly discusses and figures "minute teeth which ... form a dovetailing device" in *P. mali* but it is not at all clear just what it is he is describing or whether it is in any way similar to this "ring of bristles".

The last part of the nymph to be freed from the egg is the stylets and their long "embryonic bristle sheath" (Speyer, 1929). The eggtooth, and the "ring of bristles" can all be seen attached to the crumpled embryonic cuticle within the vacated eggshell (fig. 2.25D).

Figure 2.24

Incubation-times for eggs of _C_. _densitexta_


TIME IN DAYS
90
80
70
60
50
40
30
20
10
0
5
10
15
20
25
30
TEMPERATURE °C

2.51 Water Relations

2.510 Introduction. There is an extensive literature on the water relations of insect eggs (Edney 1957; Hartley 1965) but relatively little attention has been paid to those eggs which are inserted into plant tissues and less still to psyllid eggs.

That insects' eggs are frequently attached to their host plant in such a way as to be drawing water (and possibly dissolved nutrients) from the host's tissues, has long been recognized (Reaumur, 1740). Numerous authors have recorded that psyllid eggs are attached to the host plant by means of a "stalk", "pedicel", or "process", actually inserted through the epidermis into the plant tissues. Some have noted the similarity to Aleurodid eggs and commented on the probable water absorbing function of this stalk (Weber, 1931; Speyer, 1929; Wilcke, 1941). Van der Merwe (1923) and Clark (1962) record that eggs collapse and do not hatch if the host tissue on which they have been laid dries out. Some authors (Wille, 1950; Wilcke, 1941) maintain that psyllid eggs possibly derive nutrients as well as water from the host tissues. Wilcke, although not advancing any evidence to support this hypothesis, goes to considerable lengths to show that the work done on water absorption by insect eggs does not eliminate the possibility that dissolved materials may also be taken up. Hartley (personal communication), using acid fuchsin, has demonstrated uptake of this dye from the host by eggs of Aleyrodes, but was not able to do so with Psylla.

As far as can be ascertained the work described here is

Figure 2.25

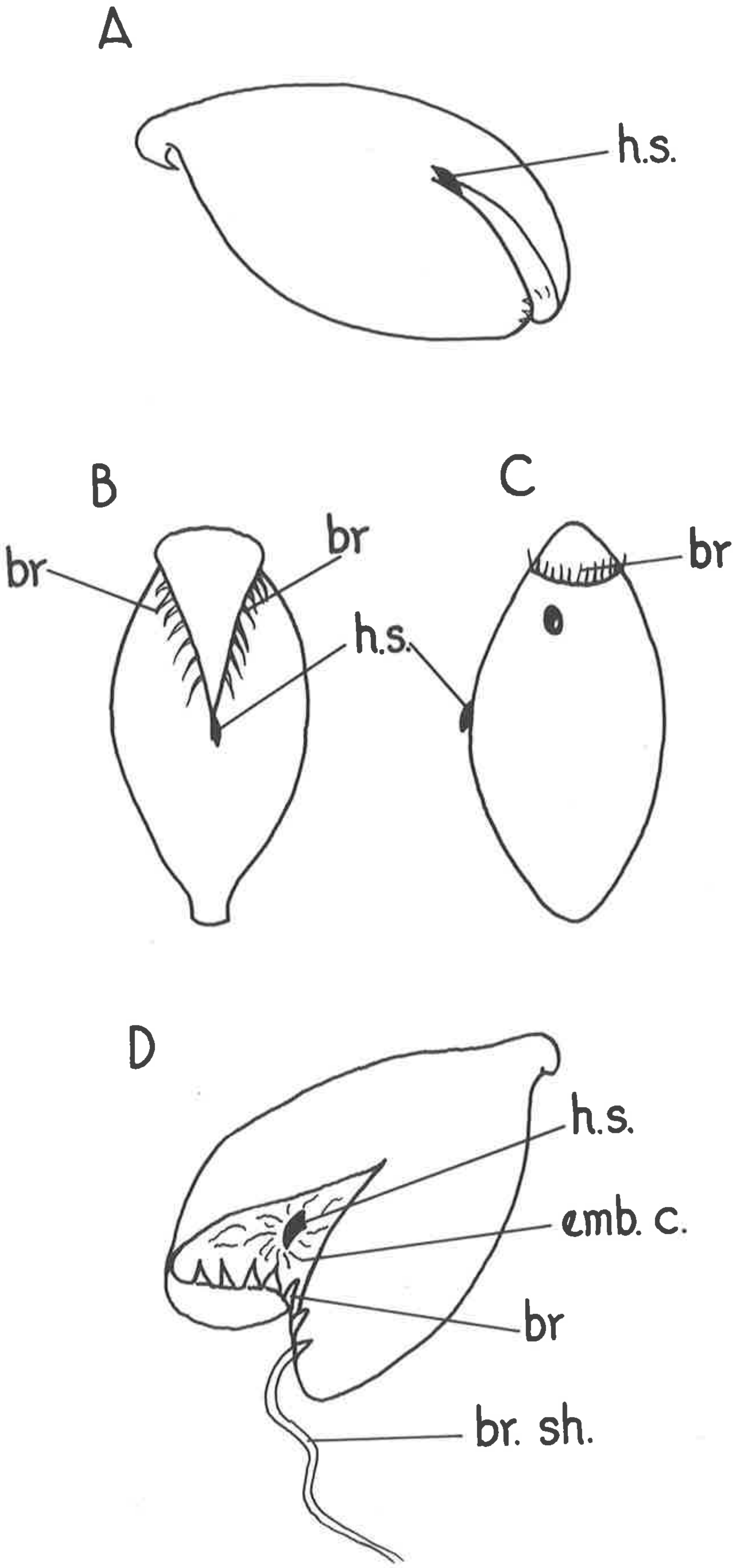
The nymph of C. densitexta hatching from the egg.

A: Beginning of hatching with the chorion split dorsally by the hatching spine (h.s.)

B: The embryo bulges through the anterior end of the split and the ring of bristles (br) curves back over the edges of the chorion.

C: Embryo removed from egg just before hatching

D: Empty eggshell showing the ring of bristles (br) the "bristle sheath" (br. sh.) and the hatching spine (h.s.) all attached to the embryonic cuticle (emb. c.) still within the chorion.


A
h.s.
B
br
br
h.s.
C
br
D
h.s.
emb. c.
br
br. sh.

the first successful attempt to demonstrate that psyllid eggs do take up water from the leaf tissue and that they can develop fully with the addition of nothing other than water and oxygen from their environment.

2.511 Experimental Demonstration of Uptake of Water by the Eggs:

i. Materials and Methods

Eggs for this work were obtained by confining a number of females on leaves in small organdie bags for 24 hours so that all eggs in any one experiment were of the same age ± 12 hours.

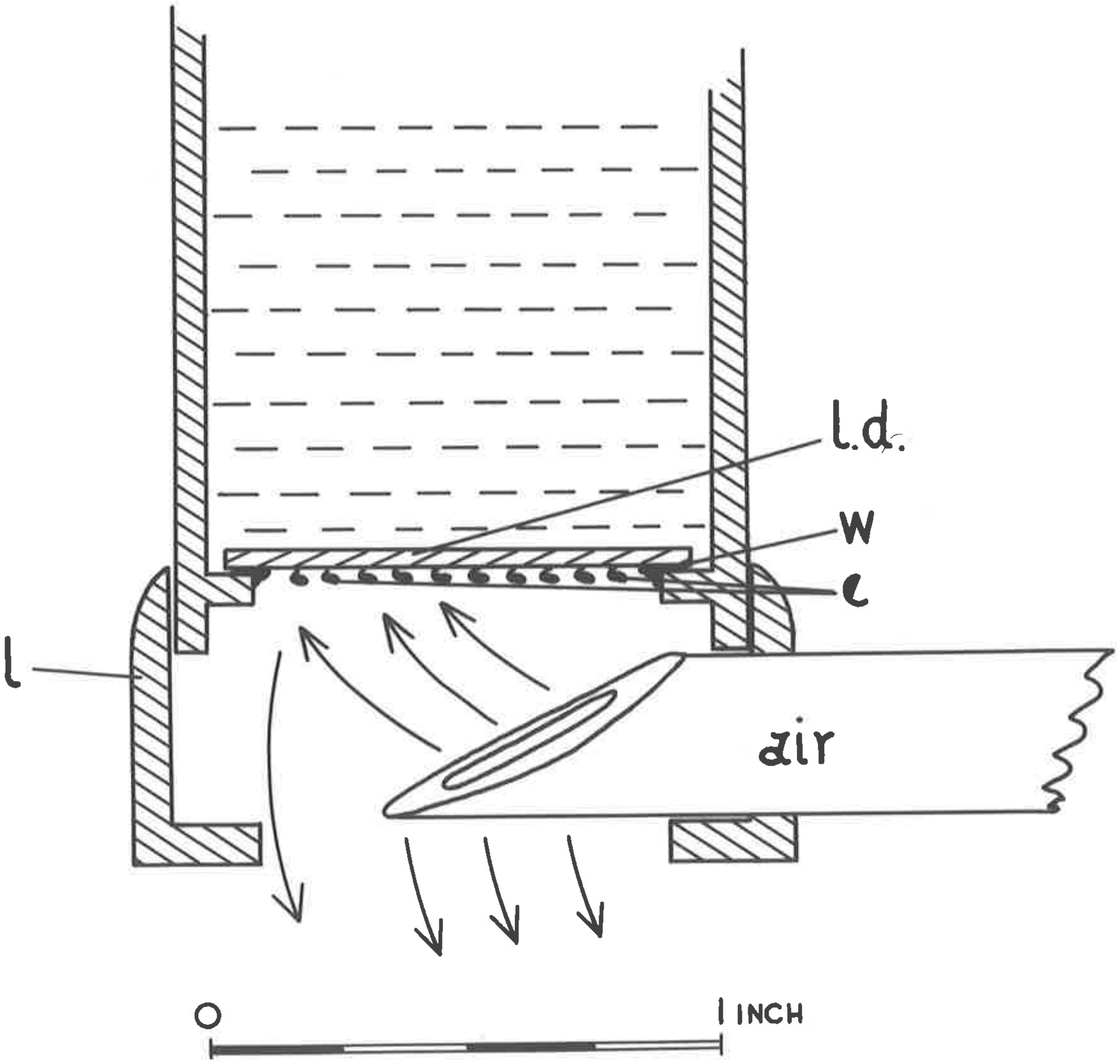
For all experiments involving tritiated water, discs bearing as many eggs as possible were cut from these leaves, sealed into tube-cages (fig. 2.02) and tested for leaks with distilled water before tritiated water was placed in the tubes, and sampling began. Where older eggs were needed, discs were held until required on distilled water and at 20°C and a 10 hour photoperiod; the same temperature and photoperiod that were used for the experiment.

The cage part of the tube-cages was modified to enable a constant gentle flow of air to pass across the surface of the leaf-discs (fig. 2.26). This ensured that any tritiated water transpired by the leaf was quickly removed from the system, thus reducing the chance that it might be absorbed through the chorion of the eggs. The only time when this flow of air was absent was while the eggs were being removed from the leaf tissue. This operation was done under a binocular microscope using a small tool developed for the work (fig. 2.27). With this tool most eggs could be removed without

Figure 2.26

C. densitexta - Egg/Water Relations

Tube cage (see fig. 2.02) modified to allow a constant flow of air to be passed over the leaf surface and eggs while the tube contains tritiated water. e = eggs. l = lid. l.d. = leaf disc. w = wax.


l.d.
w
e
l
air
0
1 INCH

rupturing or crushing them or breaking the stalk, by gently levering the stalk out of the leaf with a side to side rocking action. Most eggs remained cradled between the prongs and could be flicked into the scintillation fluid. The shield caught the few which were catapulted away when being withdrawn. Any damaged eggs were discarded, and whenever egg contents spilled out, the tool was carefully cleaned and dried before removing the next egg.

Before tritiated water was introduced into a system, the inside of the tube and the "water surface" of the disc were touch-dried with clean paper tissue to reduce dilution as much as possible. When tritiated water was being removed from the system, the inside of the tube was washed repeatedly with distilled water, touch-dried, rewashed, and dried again before refilling with distilled water, in order to remove all tritiated water not actually in the leaf and eggs.

Samples were taken variously at one-hourly, two-hourly and 24-hourly intervals following the introduction of tritiated water of known concentration, and again after removal of tritiated water once all of the water in the eggs was tritiated.

Each sample consisted of five eggs removed individually and placed in separate 5 ml. aliquots of scintillation fluid*.

---

*Scintillation fluid used was:-

Dioxane	1.0 litre
P P O (2,5, Diphenyloxazole)	10.0 grams
Dimethyl PO P O P (1,4-bis-2-[4-Methyl-5-phenyloxazolyl]-benzene)	0.25 gram
Naphthalene	100.0 grams

Figure 2.27

Diagram of the special tool used for removing eggs from the leaf.

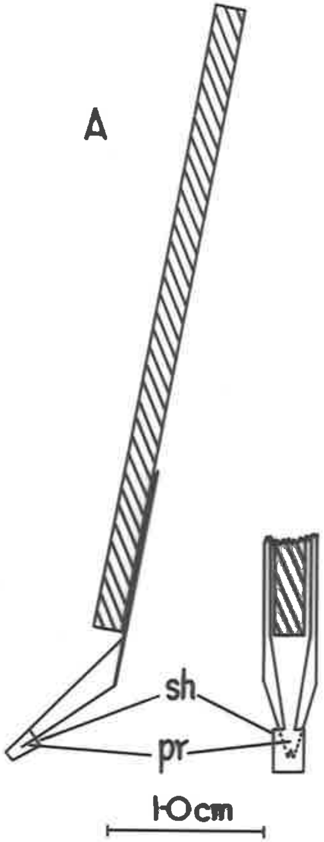
This tool is made from thin "Perspex" sheet glued to a match stick.

A: The tool showing the relative positions of the prongs (pr) and the shield (sh).

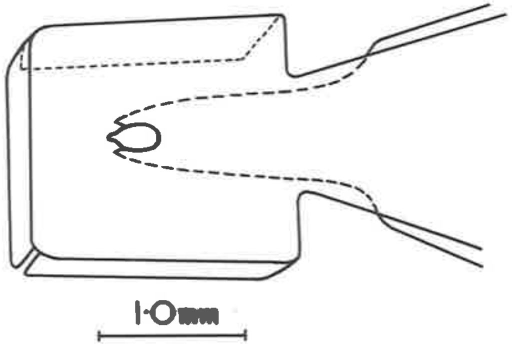
B: Illustrating how the prongs fit around an egg so that it can be gently levered from the leaf.

C: Illustrating the shield covering the prongs and egg to catch any eggs which flick out too violently.

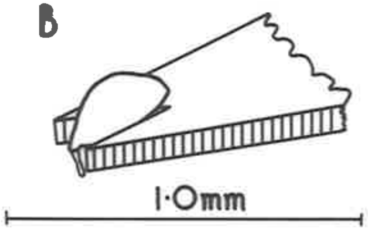
A



C



B



(Average time from withdrawal from leaf tissue to submersion in the fluid was 2-5 seconds). Each egg was then crushed in the fluid as preliminary trials had shown that an undamaged egg could retain water for up to 24 hours while immersed in the scintillation fluid.

The amount of tritiated water in each egg was measured in a Packard Tricarb Liquid Scintillation Spectrometer, multiple counts over five or ten minute periods with a minimum of 10,000 counts for each egg, being made. These counts were converted to micrograms of water per egg, and the mean of five eggs used for all subsequent calculations.

In order to test that the tritium being measured did in fact represent the water in these organisms, the following experiment was done.

Nymphs were collected (as they emerged from the eggs and before they had climbed down on to the leaf surface) from a group of eggs which had been exposed to tritiated water for the whole period of incubation. Some of these nymphs were immediately placed in individual 5 ml. aliquots of scintillation fluid for counting, and others were placed five to a small pyrex tube loosely stoppered with cotton wool, and oven-dried for 24 to 48 hours at 102°C. The lots of five dried bodies were then finely macerated in small amounts of scintillation fluid in a micro mortar and pestle, and made up to 5 mls. for counting. The results (table 2.08) show that 97.5% of the tritium is present in the form of water, or water soluble substances, in nymphs that had completed their embryonic development in the presence of tritiated water.

Table 2.08

Amount of tritium counted in freshly killed and oven-dried nymphs of *C. densitexta*

Treatment	No. of Animals	Mean milli micro curies per animal
Fresh into scint. fluid	21	3.741
Oven-dried 24 - 48 hours	40	0.096

That these results from newly hatched nymphs are representative of unhatched eggs was shown by taking five newly hatched nymphs and five eggs from a leaf-disc bearing eggs of the same age as those used in the previous experiment, and counting the tritium in these individually. The nymphs gave a mean count of 3.886 mμC (2.932, ± 0.140, micrograms of H_2O) and the eggs 3.8640 mμC (2.912, ± 0.480, micrograms of H_2O).

Tritiated water was applied to leaf-discs bearing eggs aged two, five, nine and fifteen days, and removed from those with eggs seven, eleven, fifteen and twenty-three days old after the water in these latter had been replaced with tritiated water, thus:-

Leaf Disc	Tritiated Water added when eggs	Tritiated water removed when eggs
1	2 days old	13 days old
2	5 " "	7 " "
3	9 " "	11 " "
4	15 " "	
5	23 " " (and hatching nymphs)	

For the first eight hours after adding or removing tritiated water, samples were taken hourly or two-hourly and thereafter every twenty four hours.

All results from "runs" when tritiated water was being taken up from the leaf were converted to their deficits (final mean maximum quantity of tritiated water per egg minus amount of tritiated water in eggs at each time of sampling). All results from "runs" when distilled water was being taken up from the leaf were left as the amounts of tritiated water recorded. This meant that all results were in the form of exponential curves of the proportion of water remaining in the egg against time after starting the experiment. These were plotted as the log of the amount of water against time, to give straight line graphs for each age of egg tested. From each of these graphs the time to half concentration ($t\frac{1}{2}$) was obtained and the percentage water turnover per egg per unit time for eggs of different ages calculated thus:-

if 100λ = per cent of the total water-content of an egg that is exchanged in unit time, then since

$$C_t = C_o e^{-\lambda t}$$

$$100\lambda = 100 \times \frac{0.693}{t\frac{1}{2}}$$

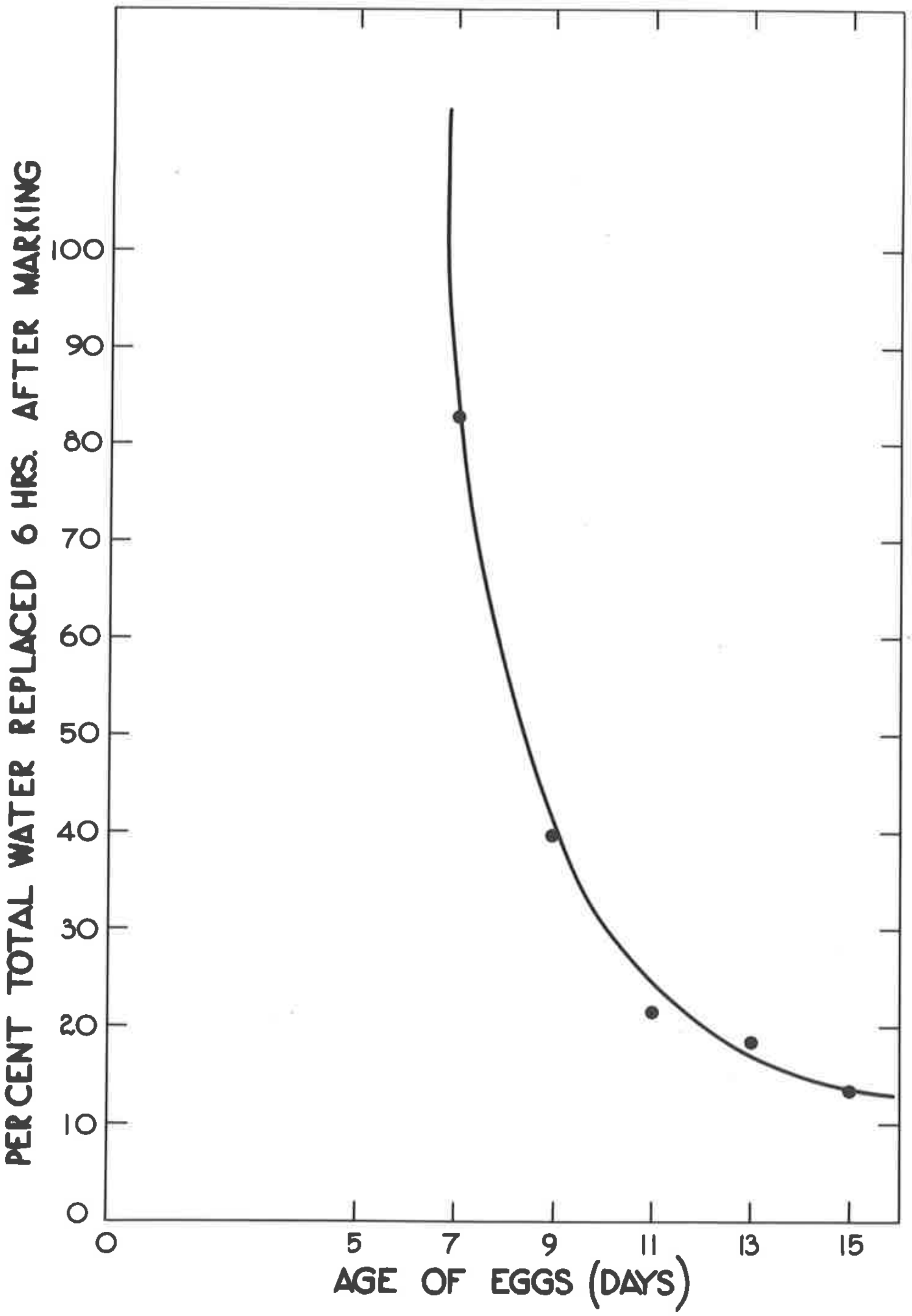
Mean flow rates (d/t) at different times after commencement of each experiment for eggs of various ages were also plotted (fig. 2.29) after d/t had been calculated as shown in table 2.09.

ii. Results

At all stages of development, from two days after oviposition until hatching, within one hour of tritiated water having been applied to or removed from a leaf disc, a measurable change had occurred in the quantity of tritiated water in the eggs. Subsequent sampling in all cases showed that the water in the eggs continued to be replaced by water from the leaf, but the rate at which this took place differed markedly with the age of the eggs. The mean rate of replacement for the first twenty four hours increased from 4% of the total body water per hour in eggs two days old, to 16% in eggs seven days old, and then fell again rapidly to 2% in eggs eleven days old. From this age until hatching only a very slight decrease in the rate was observed. There were also considerable changes in the replacement rate within the first twenty four hours of measurement, and again these differed with the age of the egg. In eggs up to five days old replacement continued unabated until the total water content of each egg had been replaced. In eggs that were older than five days the rate of exchange of water became slower about six hours after the treatment began i.e., after either tritiated or non-tritiated water was supplied to the leaf-disc bearing the eggs. But with eggs that were seven days old or older the proportion of the egg's water that was replaced during the first six hours of rapid exchange depended on the age of the egg because the rate of exchange during this rapid phase was more rapid for younger eggs. Consequently the older the egg at the beginning of the treatment the smaller the proportion of water that had been

Figure 2.28

Percent total water replaced by eggs of different ages in the first six hours after marking.


PERCENT TOTAL WATER REPLACED 6 HRS. AFTER MARKING
100
90
80
70
60
50
40
30
20
10
0
0
5
7
9
11
13
15
AGE OF EGGS (DAYS)

exchanged at the end of the first six hours of the experiment (fig. 2.28).

Finally, if the mean rates are calculated for various times, as shown in table 2.09, and plotted against the age of the eggs as in figure 2.29, the following points emerge:

(1) The rate at which water was exchanged during the initial four hours of the experiment, plotted against the age of the egg when the experiment began, gave a smooth curve which increased to a sharp maximum for eggs seven days old and declined almost to zero for eggs that were about to hatch.

(2) For eggs five days old (and probably for all ages younger than seven days) water was exchanged at the same or at an increasing rate for at least the first 24 hours after the experiment began.

(3) For eggs seven days old or older water was exchanged quickly for the first four hours of the experiment and then more slowly for at least the next 44 hours. For eggs seven or nine days old, the decline in the rate at which water was exchanged continued steeply for at least 48 hours; for older eggs the decline was arrested after six hours and the rate of exchange remained steady and close to zero for the next 42 hours. (Although not illustrated here this low rate of exchange was recorded for seven days with eggs eleven days old at the start of the experiment, and for ten days with eggs thirteen days old at the start).

(4) For eggs that were seven or more days old the steep decline in the rate at which water was exchanged which set in about the sixth

Figure 2.29

Mean flow rates for eggs of different ages at different times after addition or removal of tritiated water.

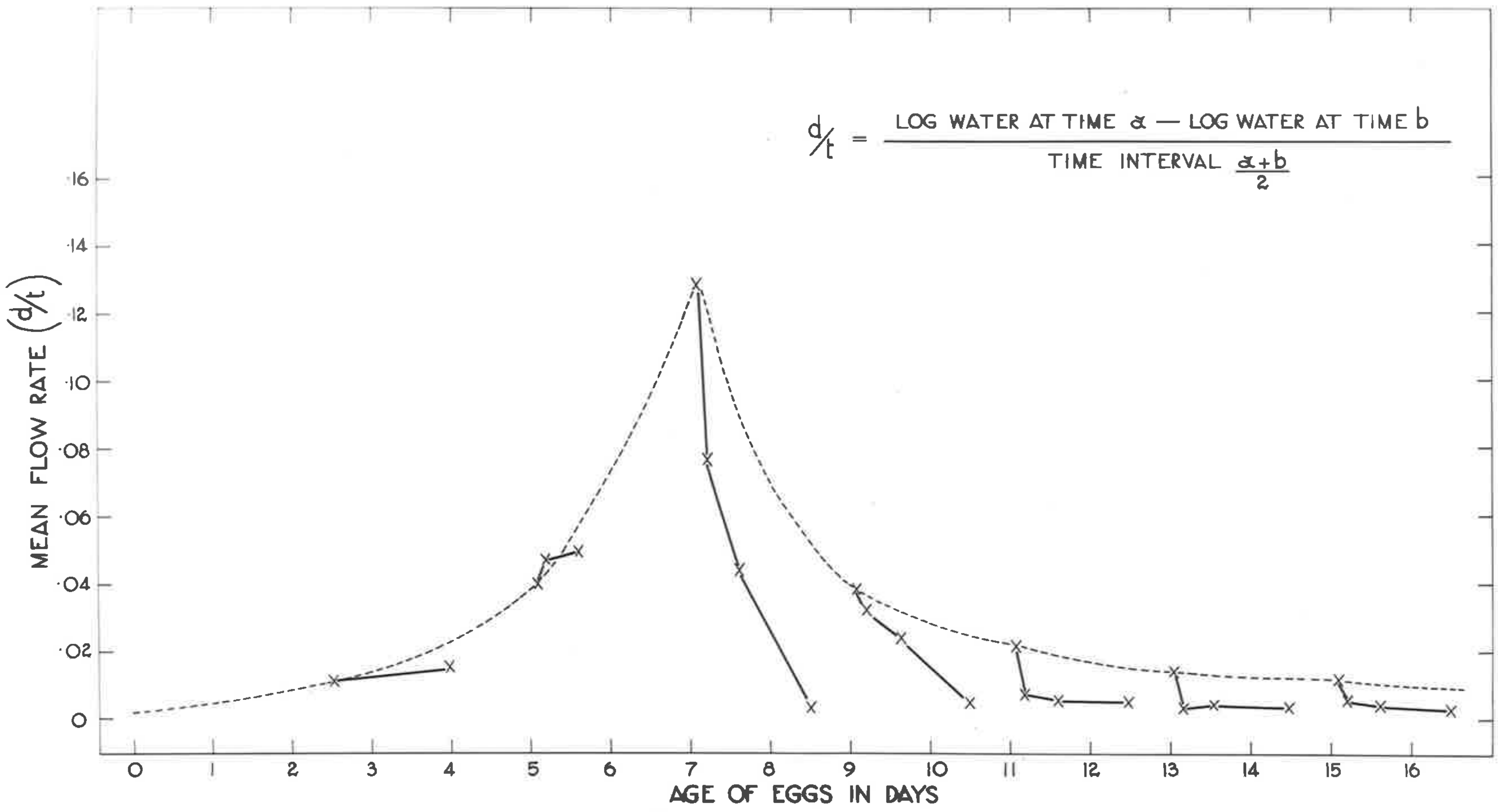

d/t = LOG WATER AT TIME α — LOG WATER AT TIME b / TIME INTERVAL (α+b)/2
MEAN FLOW RATE (d/t)
·16
·14
·12
·10
·08
·06
·04
·02
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
AGE OF EGGS IN DAYS

Table 2.09 - MEAN FLOW RATES

Age (Days)	Time of sample (hrs)	Micrograms of unexchanged water per egg (a)	log a	Difference (d)	Time Interval (t)	d/t
2	0	2.350	0.37107	-	-	-
	24	1.155	0.06255	0.30852	24	0.01285
	72	0.230	$\bar{1}.36173$	0.70082	48	0.01460
5	0	2.450	0.38917	-	-	-
	4	1.695	0.22919	0.15998	4	0.03995
	6	1.365	0.13512	0.09407	2	0.04703
	24	0.169	$\bar{1}.22789$	0.90723	18	0.05040
7	0	2.464	0.39165	-	-	-
	4	0.754	$\bar{1}.87737$	0.51428	4	0.12857
	6	0.421	$\bar{1}.62428$	0.15309	2	0.07654
	24	0.067	$\bar{2}.82607$	0.79821	18	0.04434
	48	0.054	$\bar{2}.73239$	0.09368	24	0.00390
9	0	2.450	0.38917	-	-	-
	4	1.721	0.23579	0.15338	4	0.03834
	6	1.480	0.17026	0.06553	2	0.03276
	24	0.539	$\bar{1}.73159$	0.43867	18	0.02437
	48	0.408	$\bar{1}.61066$	0.12093	24	0.00504
11	0	2.042	0.31006	-	-	-
	4	1.670	0.22272	0.08734	4	0.02183
	6	1.610	0.20683	0.01589	2	0.00794
	24	1.250	0.09691	0.10992	18	0.00610
	48	0.899	1.95376	0.14315	24	0.00596
13	0	2.444	0.38810	-	-	-
	3	2.210	0.34439	0.04371	3	0.01457
	5	2.190	0.34044	0.00395	2	0.00195
	24	1.765	0.24673	0.09371	19	0.00490
	48	1.385	0.14146	0.10527	24	0.00438
15	0	2.450	0.38917	-	-	-
	4	2.187	0.33986	0.04931	4	0.01233
	6	2.126	0.32754	0.01232	2	0.00616
	24	1.758	0.24500	0.08254	18	0.00458
	48	1.417	0.15135	0.09365	24	0.00391

hour continued until this rate had fallen close to zero independent of the age of the egg. This result suggests that during the first six hours all the water in the egg that was readily exchangeable had been exchanged. The fact that the asymptote was reached more quickly in the older eggs suggests that the amount of readily exchangeable water decreased as the eggs grew older.

iii. Discussion and Conclusions

The use of tritiated water merely enables a biologically inert "marker" to be introduced into an assumed flow of water from the leaf tissue into the egg through the stalk, and out as water vapour through the porous exochorion. Any increase with time of the amount of tritium found in the eggs then measures the rate at which the marker is being carried along by this hypothetical flow. Similarly, decreases in the amount of tritium in eggs following removal of tritiated water from the system, merely measures the rate at which the flow of water is carrying themarker out of the egg. The explanation may be more complicated if other than a simple "through movement" of water is involved, as is discussed later.

The results obtained here would seem to be unequivocal evidence of a continuous and rapid flow of water through the egg, the stalk taking up water from the leaf tissue to replace that lost by transpiration from the surface of the egg. It is also apparent that the rate of flow is slow in young eggs, but rapidly increases until they are seven days old, when there is an equally rapid fall in this rate to a low level, followed by a very slight and continuing decline with age for the remainder of the period of incubation.

A possible explanation of what is happening is as follows: When the first eggs are laid the chorion is coated or impregnated with a water-proofing substance. This fairly quickly deteriorates allowing the rate of transpiration, and thus the rate of water turnover, to increase. As the embryo develops the serosa lays down the yellow and white cuticles (Slifer, 1937); later the developing embryo will lay down first an embryonic membrane and then a cuticle. These developing membranes will presumably interfere with the free movement of water through and out of the egg.

The sudden changes in the older eggs from fast rates of water turnover to slower ones can be explained in terms of a two compartment system. Once the embryo is formed it can be thought of as a water-filled sac floating within a larger water-filled container, the egg. The outer container has a hollow "process" or tube inserted into a continuous supply of water (the leaf tissue). Water will pass in through the walls of this tube very readily, and will pass out rather less readily through the walls of the outer container to the air. Water will pass even more slowly through the wall of the inner container once its membranes have been laid down. Thus when the water in the leaf is marked with tritium the marked water will be taken up rapidly and steadily (at constant temperature, air flow, and humidity) until all the water in the outer chamber is marked water. After this stage has been reached the amount of marked water in the egg continues to increase but more slowly because now it can accumulate only in the inner chamber (embryo) after passing through its membranes. The slow rate will persist until all the water in the embryo is also marked. If, once this stage has been reached, the marker is then removed from the continuous supply of water, the reverse process will occur. Outflow to the air from the outer chamber being faster than outflow from the inner one, the outer chamber will rapidly be filled with unmarked water drawn in from the leaf tissue. Once this is completed the much slower rate of outflow from the embryo will show up and continue until all marked water has been exhausted from the system.

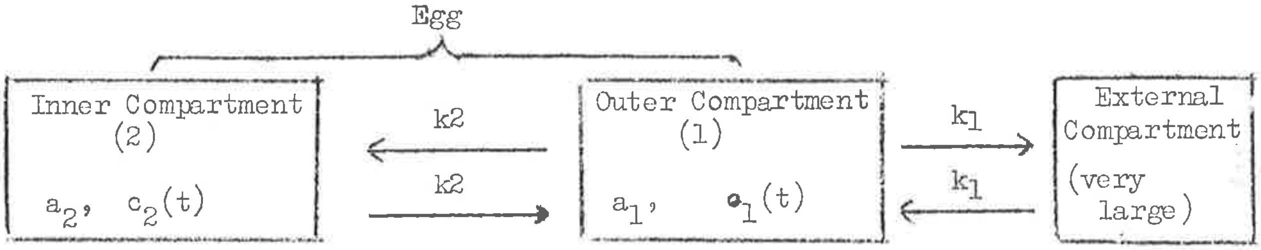
The results in fig. 2.29 can best be explained by assuming that after seven days development the egg is a two-compartment system, the mean flow rates decaying from that of the first compartment (the yolk) to that of the second (the embryo). Prior to this age there is only <u>one</u> compartment - i.e. the embryo has not laid down any membrane that restricts the movement of water.

As the embryo grows, it will take up more and more of the space within the egg until eventually, just before hatching, it is surrounded by only a thin film of moisture between the embryonic cuticle and the egg membranes. In other words, the percentage of the egg's total volume of water contained in the outer chamber will steadily decrease with increasing age of the egg. That this is happening is suggested by the decreasing percentage of total water exchanged with increasing age of eggs before the change from a fast to a slow rate of flow occurs (fig. 2.28). Again in fig. 2.29 it can be seen that as the eggs become older the initial rapid decay of mean flow-rate with time decreases until it virtually disappears as hatching time approaches and the volume of the inner compartment almost equals that of the outer one.

This hypothesis is based purely on the results of my experiments with tritiated water. I have not examined the egg histologically to observe development of the embryonic membranes. Neither have I examined the possibility that the increasing rate of exchange of water in eggs up to the seventh day of embryonic development might be caused by a metabolic change in the egg rather than by changes in the waterproofing of its membranes, nor that the "inner compartment" may be a metabolic one rather than a physical one. Obviously these are points that would be worth investigating.

iv. Kinetic Analysis*

In order to test the hypothesis of two compartments more rigorously, a two-compartment model as described below was fitted to the data by the method of least squares, using a computer programme for non-linear least squares fitting developed by Mr. J. A. Nelder :



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*Footnote: I am indebted to Mr. G.N. Wilkinson and Mrs. Margaret J. Atkinson for this analysis.

Definitions: k_1, k_2; Rates of water turnover between compartments.

a_1, a_2; Compartment size (water content).

$c_1(t)$, $c_2(t)$; Concentration of tritium label at time t (expressed in water equivalents).

$a = a_1 + a_2$ (Total size).

$y(t) = a_1 c_1(t) + a_2 c_2(t)$ = Total content of label (in water equivalents) at time (t).

Assumptions: Equilibrium system, with a_1, a_2, k_1, k_2 constant in time. External compartment very large so that concentration of label in the external compartment remains constant in time (either 0 or 1).

Initial Conditions:

(i) $c_1(o) = c_2(o) = 0$; external concentration of label unity (uptake of label situation).

or (ii) $c_1(o) = c_2(o) = 1$; external concentration of label zero (loss of label situation).

Rate Equations:

(i) $$\frac{a_1 dc_1}{dt} = k_2(c_2 - c_1) - k_1 c_1; \quad \frac{a_2 dc_2}{dt} = k_2(c_1 - c_2)$$

or (ii) $$\frac{a_1 dc_1}{dt} = k_2(c_2 - c_1) + k_1(1 - c_1); \quad \frac{a_2 dc_2}{dt} = k_2(c_1 - c_2)$$

Solutions:

(i) $y(t) = a - f(t)$ (Uptake)

or (ii) $y(t) = f(t)$ (Loss)

where $$f(t) = \underset{(A1)}{\frac{am_1 - k_1}{m_1 - m_2}\, e^{-m_2 t}} + \underset{(A2)}{\frac{k_1 - am_2}{m_1 - m_2}\, e^{-m_1 t}}$$

$$m_1, m_2 = b \pm \sqrt{b^2 - \frac{k_1 \; k_2}{a_1 \; a_2}} \; ; \quad b = \frac{1}{2} \left\{ \frac{k_1 + k_2}{a_1} + \frac{k_2}{a_2} \right\}$$

$$(m_1 > m_2 > 0)$$

[Note that $A_1 + A_2 = a$ (but $A_1 \# a_1 \quad A_2 \# a_2$)]

Results

The results obtained are tabulated in table 2.10.

In the five day series the two compartment and one compartment fits produce exactly the same values for total size $a_1 + a_2$ and the rate k_1 from the external compartment, with the same residual sum of squares. The estimates of $^{a_2}/a_1 + a_2$ and k_2 are small and unreliable, hence there is no evidence of the existence of the inner compartment.

In both the seven and nine day series the data are too variable to allow any definite conclusions to be drawn, and are of no predictive value.

The goodness of fit F - ratios indicate that in the eleven, thirteen and fifteen day series the two compartment model gives an appreciably better fit than a single compartment model [$y(t) = ae^{-kt}$ or $a(1-e^{-kt})$], and that in none of these is there any significant deviation of the observed points from the two compartment model. However, the data are not sufficient in extent or accuracy to give precise information on all the four parameters of the model.

Table 2.10 Results of Kinetic Analysis of the Flow of Water Through Eggs

Treatment	$a_1 + a_2$ (total size)	$a_2/a_1 + a_2$ (inner compt. as fraction of outer)	k_1	k_2	Residual M.S. (& d.f.)	Replicate M.S. (mean of 4) (& d.f.)	M.S. for diff. between 2 compt. & 1 compt. fit (2 d.f.)	F. ratio & signif. level
5 days (Uptake)								
1 compt. fit								
Parameters	2,626	-	5.374	-	0.012173	0.006629	0	0
Std. Errors	0.1808		0.2447		(6)		(identical resid. sums of squares for 1 & 2 compt.)	
2 compt. fit								
Parameters	2.626	0.00003	5.374	0.07575	0.0182595	-		
Std. Errors	0.1233	0.0254	0.2525	0.0556				
11 days (Loss)								
2 compt. fit								
Parameters	1.98	0.694	2.110	0.4736	0.0007615	0.00249	0.01188	4.771*
Std. Errors	0.0346	0.0265	0.3635	0.0247	(4)	(26)		
13 days (Loss)								
2 compt. fit								
Parameters	2.370	0.4529	0.9618	0.3434	0.012166	0.0034	0.02759	8.1 ***
Std. Errors	0.1096	0.36056	0.51962	0.3240	(15)	(69)		
15 days (uptake)								
2 compt. fit								
Parameters	3.090	0.9175	4.269	0.6025	0.00318	0.00919	0.20979	22.82****
Std. Errors	0.74162	0.0162	0.7071	0.6164	(4)	(32)		

2.512 The Survival and Development of Eggs when Removed from the Leaf Tissue: Following these experiments a further experiment was devised to test the ability of eggs to survive and develop independently of the leaf tissue.

Eggs were removed with the special tool (fig. 2.27) within 24 hours of having been laid, and immediately placed on wet filter paper. From there they were manipulated into the arrangements illustrated in figure 2.30. These, and the remainder of the eggs left on the leaf as controls, were kept on distilled water at a constant temperature of 25°C and a 10 hour photoperiod.

Of the eggs which were removed from the leaf and placed with their stalks immersed in distilled water, 76% (16 of 21) completed their development and hatched. The nymphs produced were vigorous and active. Incubation time was 8 to 10 days longer than the controls held at the same temperature and photoperiod. A few eggs removed from the control leaf and placed in the dish the day before hatching, hatched at the same time as those left on the leaf.

Most of the eggs which did not hatch showed no signs of development and some of them were probably injured when being removed from the leaf. One or two eggs were observed to leak their contents through the wall of the intact pedicel onto the filter paper some days after removal from the leaf. This presumably occurred when the egg died.

The 19 eggs placed with the pedicel uppermost and out of the film of water, remained apparently unchanged for four days. On

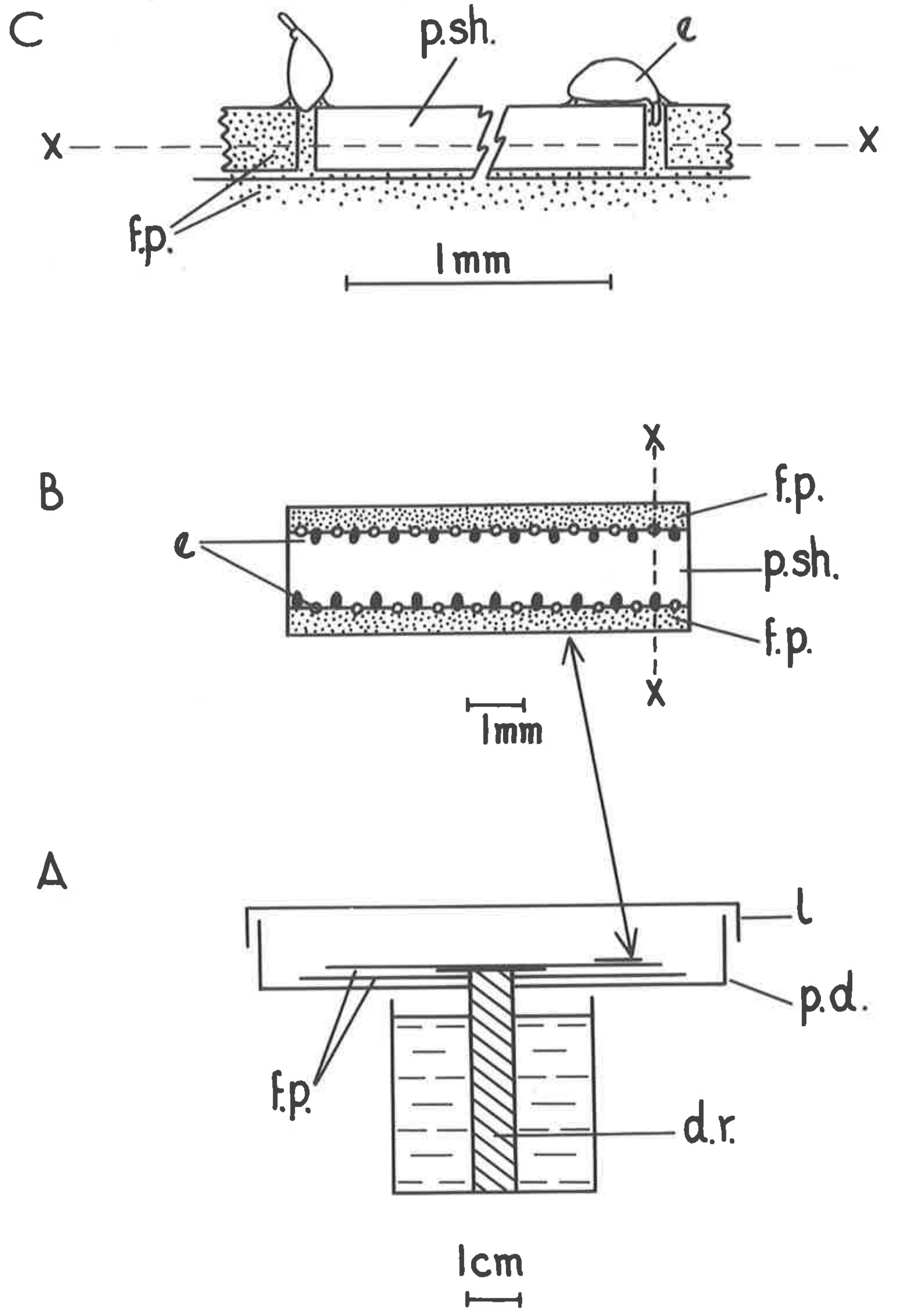
Figure 2,30

Incubation of eggs on distilled water.

A. Plastic petri dish (p,d,) with a lid (l.) containing filter paper (f.p.) and with a wick made from a length of dental roll (d,r,) going through a hole in the bottom of the dish into a reservoir of distilled water.

B. & C. A strip of thin "perspex" sheet (p.sh.) laid on the top layer of filter paper and with a strip of filter paper (f.p.) each side of it. Eggs (e.) placed along the edge of this strip alternatively with the stalk into the water and with the stalk in the air,

C, is a cross section of B at x ....x.


C
p.sh.
e
x
x
f.p.
1mm
B
x
f.p.
e
p.sh.
f.p.
x
1mm
A
l
p.d.
f.p.
d.r.
1cm

the morning of the fifth day the lid was taken off the dish, as it was apparent that the atmosphere within it was saturated with water vapour. One hour after the lid was removed the ventral surfaces on 89.5% (17 of 19) of these eggs had completely collapsed, and the remaining two had collapsed by the afternnon. The lid was replaced and left on for the remainder of the experiment, but none of these eggs regained their shape, nor did any of them hatch. The 21 eggs with their stalks in water seemed not to be damaged, and sixteen later hatched. (At the time of removing the eggs from the leaf it was noticed that on many of them the small unpitted area on the ventral surface (fig. 2.23B) was concave, but by the next day this had assumed full convexity on all eggs in the dish).

Discussion

From these results it is clear that:-

1) Eggs of C. densitexta, removed from the host leaf the day after laying, can develop satisfactorily and produce normal, active, first instar nymphs providing they have access to water through their pedicels. From this it can also reasonably be inferred that their only requirement from the leaf tissue is water. The fact that they took 10 days longer than normal to develop is possibly due to a shortage of oxygen slowing up the metabolic rate rather than lack of any nutrients from the leaf (Hinton 1962a).*

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* I have often observed that eggs placed on the "water side" of discs in the laboratory hatch normally, although the nymphs drown very quickly thereafter. They are not any later in hatching than those on the "air side" of the discs, even after weeks of total immersion, but oxygenation of the water by the actively photosynthesizing leaf tissue would account for this, compared to the enclosed and deoxygenated distilled water in the dish. Again, in the field during winter the eggs are often covered by a film of moisture for weeks at a time without coming to any harm.

It would be unlikely that any of these excised eggs would have developed fully if some nutrient normally obtained from the leaf were lacking.

2) Water can move more rapidly through the wall of the pedicel than it can through that of the remainder of the egg which is covered by the thick exochorion. This would ensure that, so long as the plant tissues remained turgid, the eggs would not go short of water, no matter how fast transpiration from the egg became. In addition, increasing transpiration would have a marked cooling effect on the eggs.

Thus it would seem that C. densitexta eggs are especially well adapted to withstand prolonged exposure to severely high temperatures and low humidities, and sudden big changes in both temperature and humidity.

Just such conditions are commonly experienced by the summer eggs in the southeast of the State. Prolonged periods of submersion in a film of water at low temperatures, which the winter eggs frequently experience, would not seem to affect them adversely. Presumably oxygenation of this film of water would be good, and the porous exochorion of the eggs would provide a large surface area for absorption of oxygen from this water.

2.52 Hatching in Relation to Light and Temperature

2.520 Introduction. It was noted in the field during the early winter that hatching of eggs is concentrated into a peak at about

9.30 each morning. No hatching was observed before this sudden "flush", and within half an hour of it only an occasional egg was seen to hatch. None have been observed to hatch after about midday.

The fact that eggs did not hatch when stored at a temperature of 3°C suggested that hatching may have been inhibited during the night by low temperatures and that the flush which occurs each morning is a result of the increase in temperature. Later, however, when eggs were incubated at a constant temperature of 20°C, and in a 10 hour photoperiod starting at 8.45 a.m., a 9.30 burst of hatching was again apparent. Removing eggs from cool storage at different times of the day produced a minor peak of hatching at the same time the next day, but most hatching still occurred at 9.30 a.m.. By the following day all hatching was at 9.30 a.m. irrespective of when the eggs had been removed from cool storage.

Later it was observed that in late November and early December hatching occurs in the field at about 5 a.m.

These observations strongly suggest that, rather than a temperature effect, one of two things is happening.

(a) A daily rhythm of hatching, deeply imprinted either before or soon after oviposition, is persisting no matter how the environment subsequently varies, or

(b) A diurnal light-entrained rhythm is responsible for this observed periodicity of hatching of eggs of *C. densitexta*.

The experiments discussed here were undertaken to test these hypotheses.

2.521 Materials and Methods. Leaves of *E. fasciculosa* bearing groups of eggs were collected in the field, sealed in plastic bags, and stored at 3°C until required.

These eggs had been laid over a period of some four to six weeks, by a large number of different females. Their behaviour of ovipositing against existing eggs, thus building these large groups, ensures a representative sample of eggs, varying only in age, providing that only leaves with large numbers of eggs on them are collected.

Using a 21 mm. diameter cork borer, discs were cut from these leaves so as to include as many unhatched eggs as possible on each disc, and a different leaf was used for each disc. Discs were floated on distilled water in individual 2" x 1" 'Clearsite' plastic vials. Groups of eight such discs were used for each day-length investigated. The discs were cut and prepared in the cool room.

The morning before an experiment was to begin all discs to be used after preparation as described were removed from the cool store and placed in a constant temperature room at 20°C where all experiments were conducted. Immediately before the start of the first dark period all hatched nymphs were removed from the discs. At the completion of this and each subsequent dark period all nymphs which had hatched in the dark were counted and removed. Throughout each photoperiod (or as much of it as was possible or necessary) hatchings were counted at least every half hour, and every quarter hour during peak periods. The nymphs were removed from the discs as they were counted.

For each day-length tested a minimum of three full days' hatchings were recorded. The photoperiod following the first dark period was, in each case, considered as a "buffer day" to allow the unhatched eggs to adjust to the imposed rhythm. Counts from this day did not appear to differ from that on subsequent days, apart from minor variations found between any two days, but they have not been included in any of the results presented. Unless otherwise indicated, all results are the mean, for each day-length, of two complete 24 hour periods, namely the second and third "days" of each experiment.

All results are presented as percentages of a total number hatching in a given time (mostly a full 24 hours from "light on" to "light on", but in some cases for a shorter period). The mean number hatching per treatment was 195, with a range of 70 to 510 per treatment.

2.522 Results. To test the second of the two hypotheses suggested by the initial observations - that the periodicity of egg hatching is a light-induced rhythm - separate lots of eggs were submitted to 10, 8, 6 and 4 hour photoperiods; all at a constant temperature of 20°C. With a 10 hour photoperiod (starting at 8.45 a.m.) the typical morning peak was obtained at 9.30 a.m., with all hatchings for the 24 hour period taking place within a few hours of the light coming on. In each of the other three lots (which were not exposed to the light until respectively 2, 4 and 6 hours after the 10-hour-day group) the bulk of the 24 hours' hatch occurred <u>before</u> the light came on. Newly hatched nymphs are bright yellow, but over the first few hours the cuticle becomes progressively darker. In view of this it was possible to group the nymphs which had hatched in the dark into broad age classes according to the degree of darkening of the cuticle following hatching. Doing this for the 8, 6 and 4 hour photoperiods indicated that the majority of the hatching in all three had probably taken place at approximately the same time as the peak hatching in the 10-hour photoperiod.

This result suggested the presence of a rhythm independent of both temperature <u>and</u> light. However, there still remained the evidence from the 5 a.m. summer hatching suggesting a response to light. In addition, as the light period in the controlled temperature room had, for convenience, been synchronized with the natural day, the possibility remained that some other external factor such as barometric pressure (e.g. Brown <u>et al</u>., 1955, 1958) could be entraining the periodicity.

A second series of eggs was therefore set up, but with the beginnings of the photoperiods out of phase with each other and also out of phase with the solar day. Again, for eggs in a 10 hour photoperiod, there was a peak of hatching 45 minutes after the light came on, irrespective of the time of the solar day the lights were switched on. With photoperiods of less than 10 hours, hatching again commenced before the light came on. "Aging" of the nymphs indicated that this hatching in the dark was also no longer associated with the solar day but tended to occur, in each case, at approximately the same time after the onset of the dark period as did the peak in the 10 hour photoperiod. In view of this it seemed more profitable to think in terms of the effect of "periods of darkness" rather than "day length".

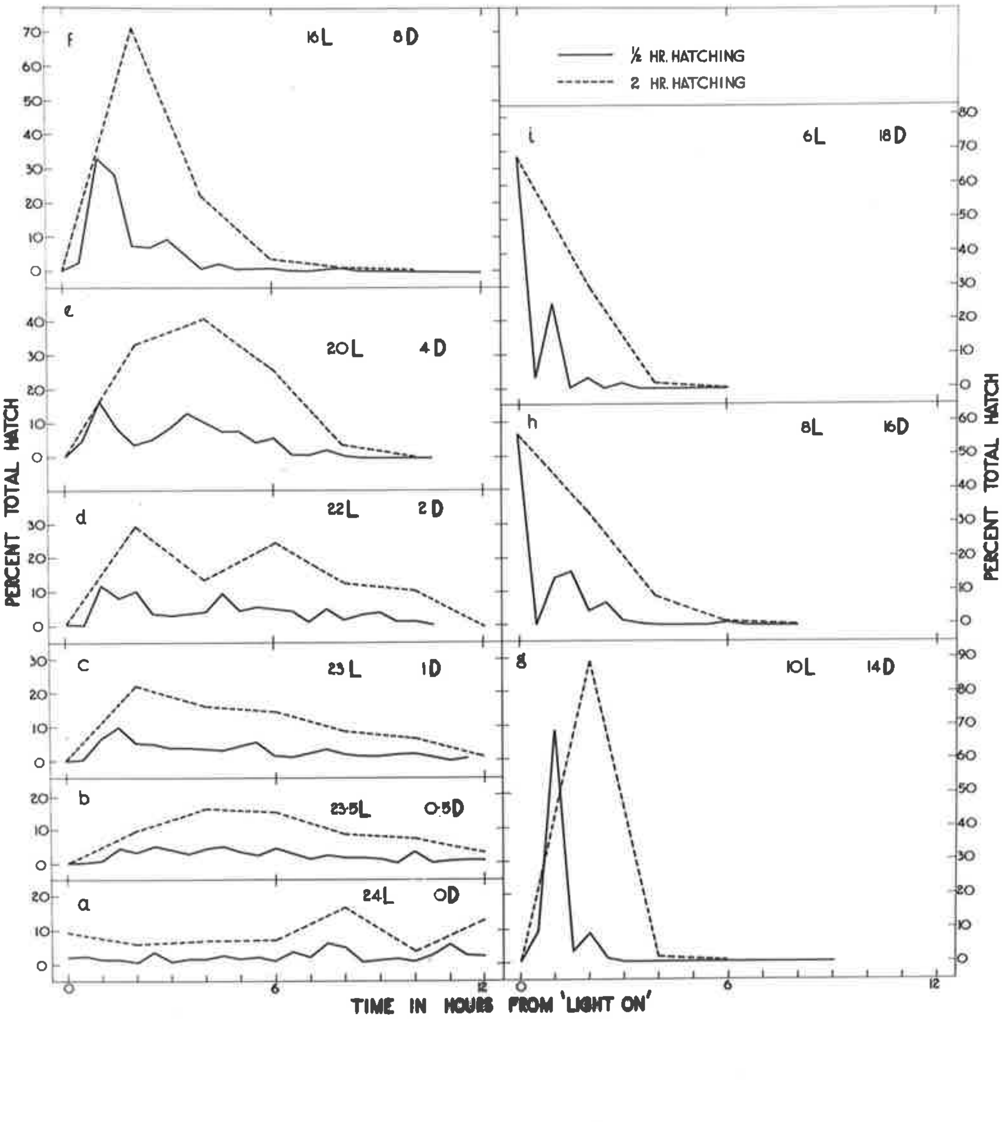
Accordingly further lots of eggs were prepared to test the effect on the periodicity of hatching of shorter periods of darkness than in the previous experiments, and of continuous light. At the completion of these experiments the relationship of hatching to light appeared to be as follows:-

1. Effect of varying the dration of darkness in a 24-hour period.

Under conditions of continuous light (fig. 2.31a) hatching occurred at random throughout the 24-hour period. The application of half an hour of darkness in every 24 hours (fig. 2.31b) produced a significant trend away from this random distribution, and towards a concentration of the total hatch into the first 12 hours of the light period. Further increases in the length of the dark period (fig. 2.31c, d, e and f) intensified this peaking or clumping until with 14 hours of darkness in every 24 (fig. 2.31g) almost 90% of the eggs for the "day" had hatched within one hour of the cessation of darkness, and all had hatched within four hours. Prolonging the dark period beyond 14 hours (fig. 2.31h and i) resulted in the bulk of the hatchings for the 24 hour period occurring before the light was turned on.

Figure 2.31

The effect of different times spent in darkness on the subsequent distribution of hatching of C. densitexta eggs during the first 12 hours of the photoperiod. xL, yD = x hours light and y hours darkness in each 24 hour period.

f
16L
8D
e
20L
4D
d
22L
2D
c
23L
1D
b
23·5L
0·5D
a
24L
0D
½ HR. HATCHING
2 HR. HATCHING
i
6L
18D
h
8L
16D
g
10L
14D
PERCENT TOTAL HATCH
PERCENT TOTAL HATCH
TIME IN HOURS FROM 'LIGHT ON'
0
6
12
0
6
12
0
10
20
30
40
50
60
70
80
90

These data are presented as cumulative hatchings in figures 2.32 and 2.33 which clearly illustrate this trend in response to increasing dark periods.

2. Response to the stimulus of "light on".

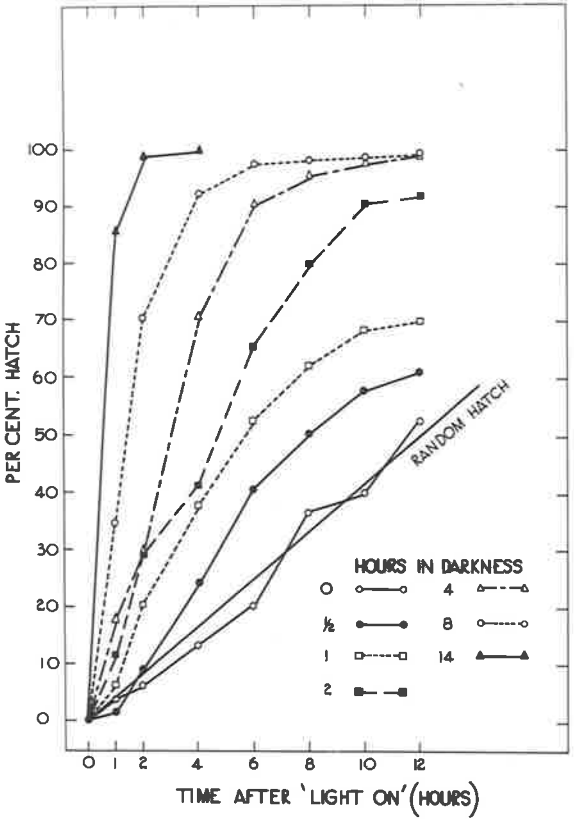
At a temperature of 20°C there was a marked pattern of hatching following the onset of light after darkness. In the first half hour - even in very short photoperiods when most hatching has occurred before the light comes on - little or no hatching takes place (fig. 2.31h and i). Between 40 and 50 minutes after "light on" a definite burst of hatching occurs. After 14 hours of darkness this is at a maximum, involving most of the day's hatch; but it decreases in both intensity and magnitude as the dark period is shortened (fig. 2.34). As the size of this initial peak decreases with shortening of the dark period, another small peak - or tendency to peak - appears later in the day but still within the first 12 hours after the dark period. Furthermore, with the shorter dark periods - and increasing with decreasing time in the dark - there is evidence on successive days of a reduction in size of the first peak and an increase in the second peak (fig. 2.35).

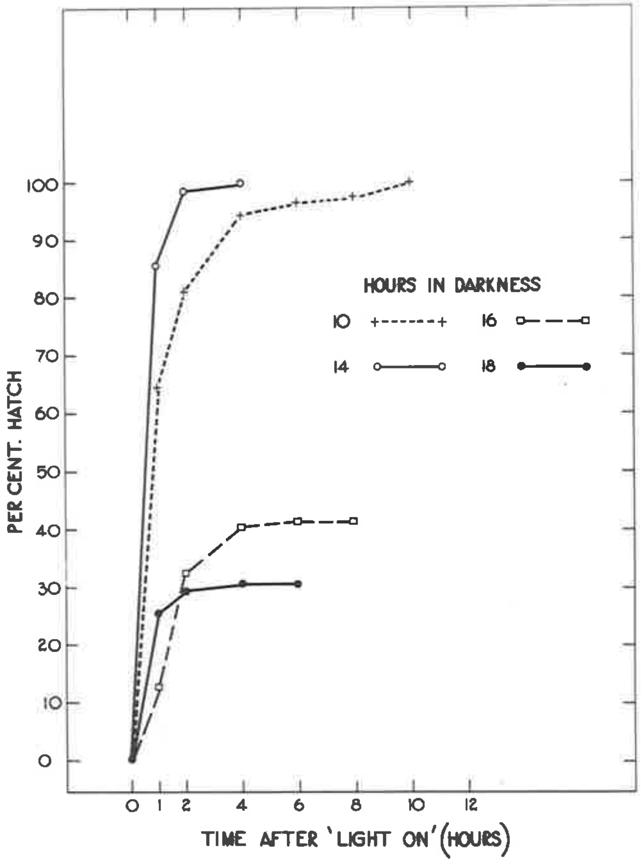
3. Persistence of the rhythm.

Figure 2.36 illustrates the result of placing under continuous light eggs which had been subjected to varying periods of darkness for 3 complete 24 hour periods. The rhythm persists, the time of onset of hatching coinciding very closely with that of previous days, but with the loss of the sharp response to the

Figure 2.32 Figure 2.33

Effect of time spent in darkness on the distribution of time of hatching of _C. densitexta_ eggs in the first 12 hours of the photoperiod. The same data as in figure 2.31 (plus data for 10 hours darkness) expressed as cumulative percentages.


PER CENT. HATCH
100
90
80
70
60
50
40
30
20
10
0
0 1 2 4 6 8 10 12
TIME AFTER 'LIGHT ON' (HOURS)
RANDOM HATCH
HOURS IN DARKNESS
0
½
1
2
4
8
14


PER CENT. HATCH
100
90
80
70
60
50
40
30
20
10
0
0 1 2 4 6 8 10 12
TIME AFTER 'LIGHT ON' (HOURS)
HOURS IN DARKNESS
10
16
14
18

"light on" signal. There is a general spreading of the occurrence of hatching, indicating a fairly rapid return to random hatching as occurs under constant light.

4. Effect of temperature.

When observed times of hatching in the field are compared with the beginning of day light (civil twilight) for 35° south latitude (fig. 2.37), the time of 45 minutes after "light on" to a hatching peak agrees well with the summer observations, but not with those for the winter months. Different lots of eggs were therefore observed under a standard 10L14D period at a range of constant temperature. The effect of temperature on the speed of the response to the "light on" stimulus is shown in figure 2.38. The response is simply delayed by lower temperatures, until at approximately 6°C to 7°C hatching is permanently inhibited.

5. Effect of coloured and dim light.

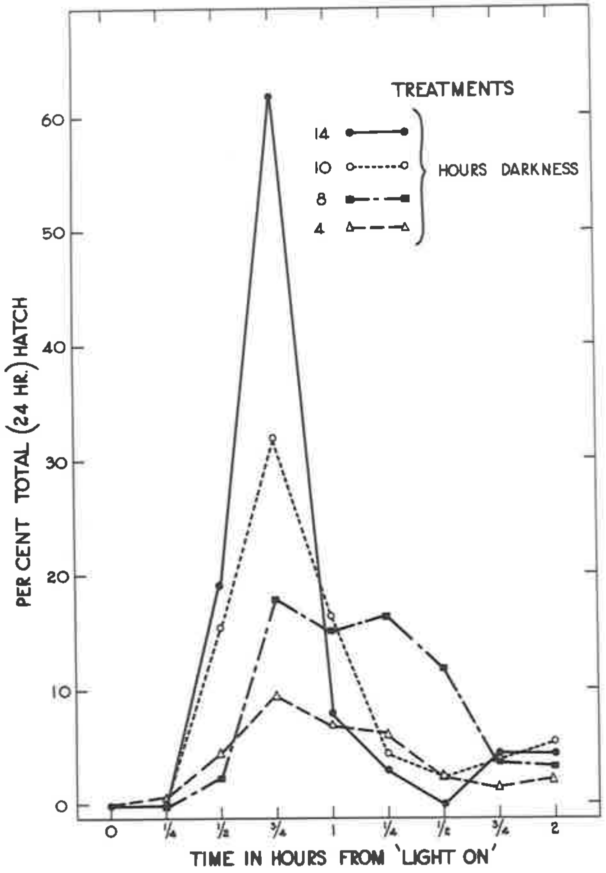
Replacing white fluorescent light during the photoperiod with red light (Philips TL 40W/15 Red tubes), or blue light ("Cinemoid" No. 19 dark blue filter over white fluorescent tubes) had no observable effect at 20°C and 10L 14D, hatching occurring when red or blue light followed darkness, just as it did when white light followed darkness. Similarly, decreasing the white light of the photoperiod down to 10 foot candles (measured two to three inches above the leaf discs with an Eel Broad Spectrum photocell) at the same regime of 10L 14D and 20°C, did not lessen or stop the response to the "light on" stimulus.

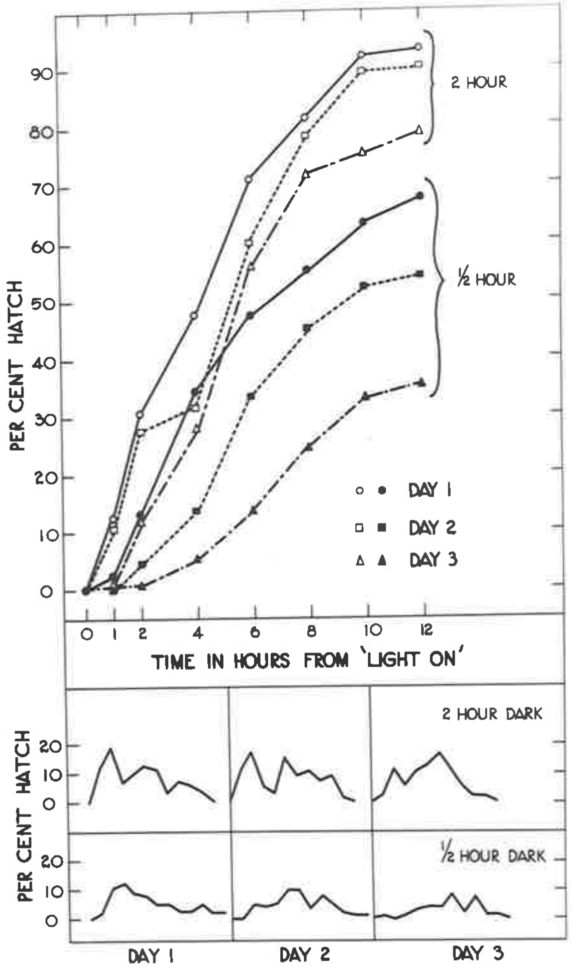
Figure 2.34

Response to the "light on" stimulus showing how this peak persists although with decreasing intensity and magnitude as the time spent in darkness prior to receipt of the stimulus decreases.

Figure 2.35

Hourly actual (below) and cumulative (above) percentage of the total 24 hour hatch occurring in the first 12 hours of the photoperiod with ½ hour and 2 hour dark periods over three consecutive days. This illustrates the marked "drift" away from the predominance of the "primary" peak.


TREATMENTS
14
10
8
4
HOURS DARKNESS
PER CENT TOTAL (24 HR.) HATCH
0
10
20
30
40
50
60
O
¼
½
¾
1
¼
½
¾
2
TIME IN HOURS FROM 'LIGHT ON'


2 HOUR
½ HOUR
PER CENT HATCH
0
10
20
30
40
50
60
70
80
90
○ ● DAY 1
□ ■ DAY 2
△ ▲ DAY 3
O
1
2
4
6
8
10
12
TIME IN HOURS FROM 'LIGHT ON'
PER CENT HATCH
2 HOUR DARK
½ HOUR DARK
20
10
0
20
10
0
DAY 1
DAY 2
DAY 3

2.523 Discussion. These results strongly support the hypothesis of a light-entrained rhythm being responsible for the observed periodicity of hatching of *C. densitexta* eggs.

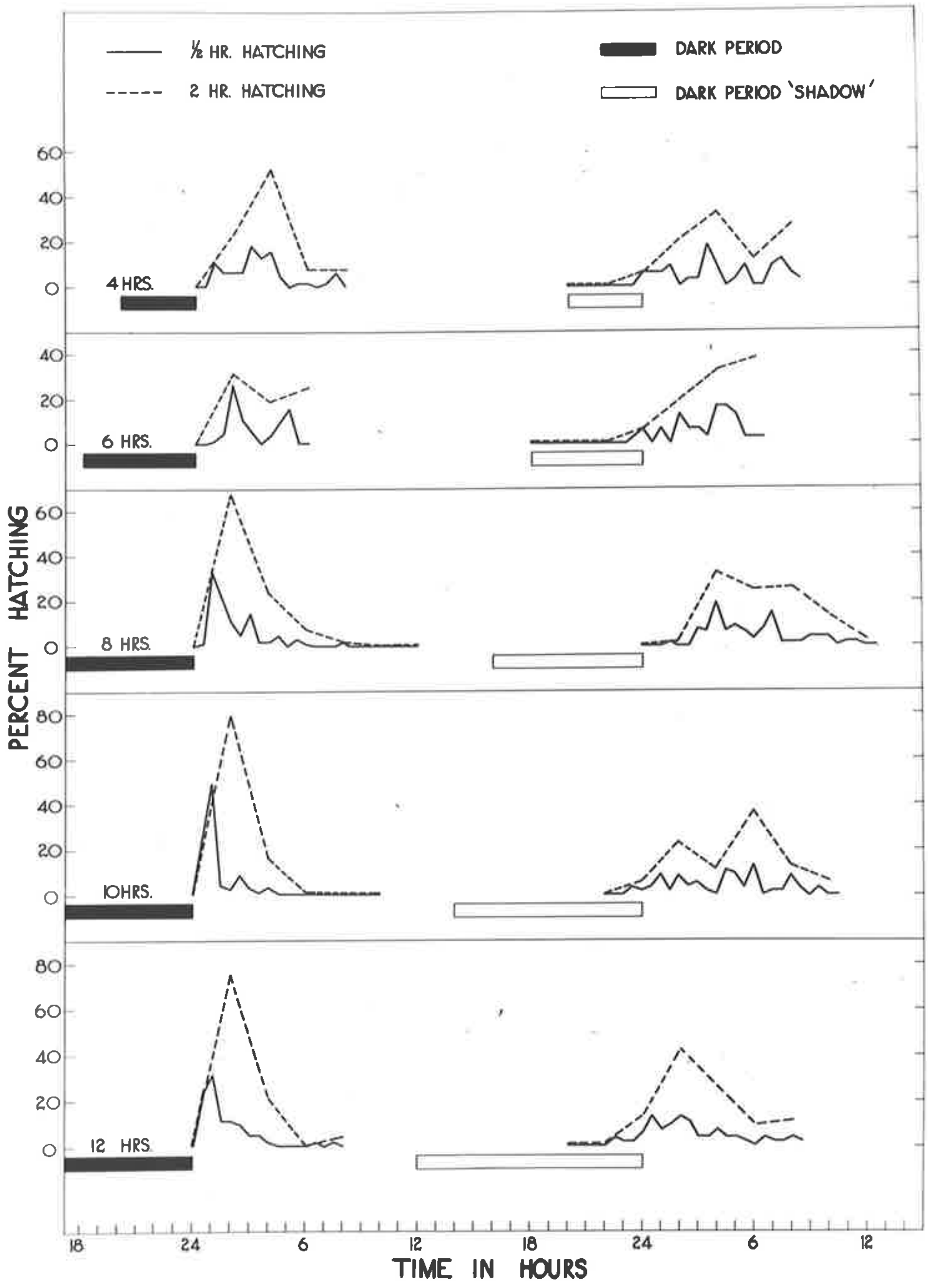
The phasing of this periodicity of hatching is determined by the alternation of light and dark during each 24 hour period, the stimulus of the change from dark to light providing a sharp, clear-cut response. The amplitude of this hatching rhythm, on the other hand, is controlled by the duration of the dark period which the eggs have experienced immediately prior to hatching. In constant light there is no rhythm, hatching occurring at random throughout each 24 hour period, although after several days in a fixed L:D cycle a peak of hatching is seen to persist in constant light for at least one day.

Ambient temperature will determine the time taken for the response to the "light on" stimulus to proceed to culmination each day, but will not alter the frequency, i.e. will not impair the ability to find the appropriate time on following days. This is a common feature of biological clocks (Bunning, 1964).

There would appear to be two peaks of hatching consequent upon the introduction of a period of darkness into a 24 hour day. One of these - the "secondary peak" - will (in the absence of a return to light) occur between 12 and 14 hours after the onset of darkness (fig. 2.31h, i; fig. 2.33). The other or "primary peak" will only occur in response to the stimulus to light after darkness. Without this stimulus (fig. 2.36) it is completely absent.

Figure 2.36

Persistence of the hatching rhythm of *C. densitexta* eggs when dark periods are discontinued leaving all treatments in continuous light. The peaks all occur in the following 24 hour period at the same time that they would have done with the dark period still imposed, but there is a marked loss of sharpness of the response indicating a fairly rapid "degeneration" to a state of non-periodic random hatching throughout the 24 hours.


½ HR. HATCHING
2 HR. HATCHING
DARK PERIOD
DARK PERIOD 'SHADOW'
4 HRS.
6 HRS.
8 HRS.
10HRS.
12 HRS.
0
20
40
60
80
PERCENT HATCHING
18
24
6
12
18
24
6
12
TIME IN HOURS

Where these two peaks are synchronized (or nearly so) there will be a steep and "simple" peak of hatching (fig. 2.31g, [half hour figures]), but as they are separated (by shortening the dark period) the occurrence of hatching will be spread out. Initially the "primary peak" will predominate but with progressive shortening of the dark period (fig. 2.31f, e, d, c, b, [half hour figures]) or with continued subjection to an abnormally short dark period (fig. 2.35) this dominance diminishes and a drift towards the secondary peak occurs.

Although temperature will considerably affect the time of occurrence of the primary peak relative to time of receipt of the "light on" stimulus (fig. 2.38) it does not appear to have any influence on the secondary peak (i.e. after 14 hours in darkness at 25°C and 30°C hatching still does not occur before the light comes on).

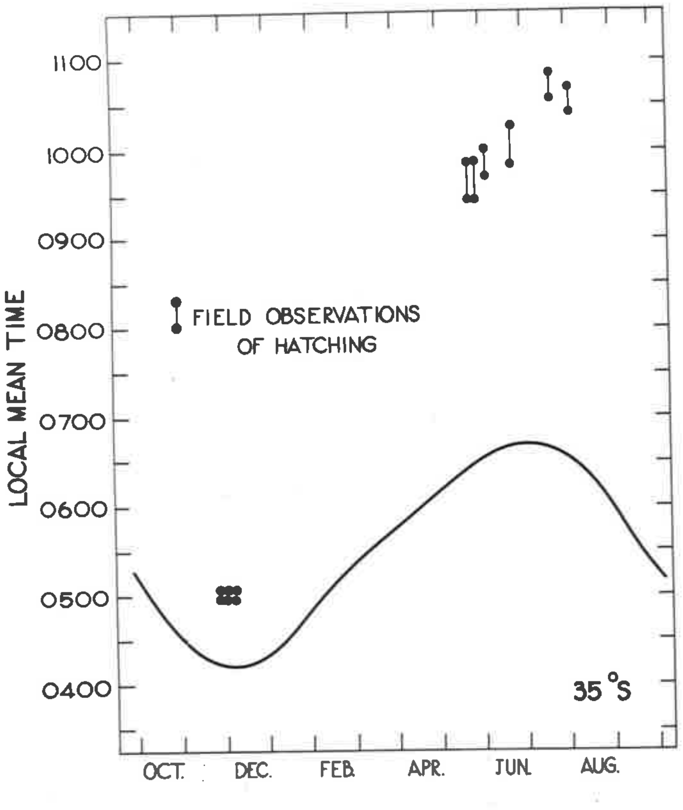
In the extensive literature on circadian rhythms I have found only two which discuss a rhythm in the hatching of insect eggs. Remmert (1955) has shown, with eggs of a chironomid, that periodicity of hatching is lost under continuous light as it is with <u>C. densitexta</u>. He also demonstrated that it is lost in continuous darkness, and that a hatching rhythm can be entrained to equal cycles of light and dark from 12L:12D to 48L;48D . Hulley (1962) found that eggs of the citrus mussell scale exhibit a hatching rhythm which is influenced by both temperature and light. A peak of hatching was recorded in constant temperature following light after

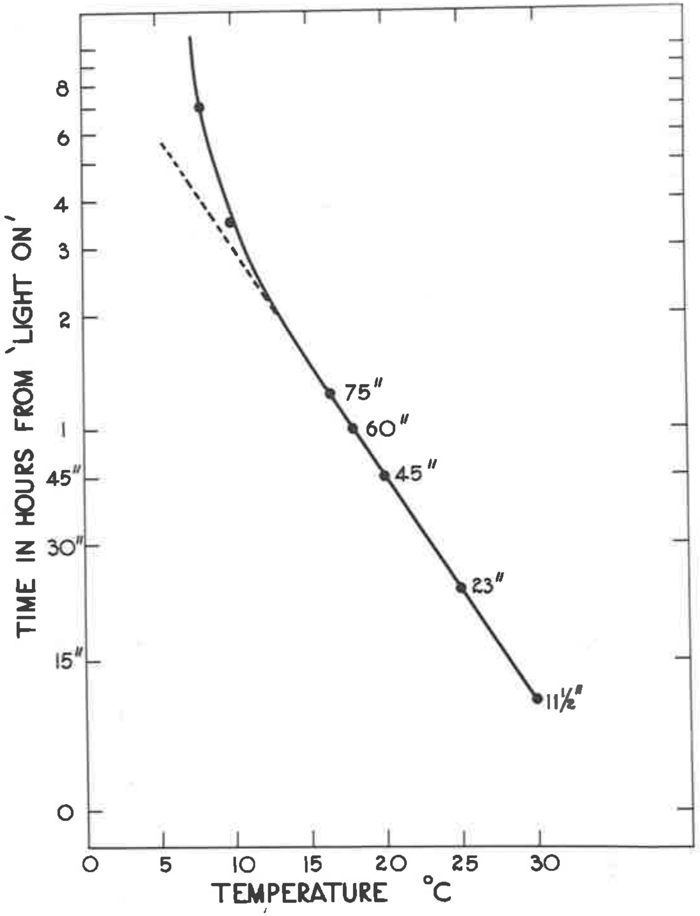
Figure 2.37

Observed times of peak egg-hatching in the field at Keith compared with the beginning of daylight at 35° south latitude. Note the long delay in the winter months compared with the summer months.

Figure 2.38

Effect of temperature on the time from receipt of the "light on" stimulus to peak hatching in a standard 10 hour photoperiod.


LOCAL MEAN TIME
1100
1000
0900
0800
0700
0600
0500
0400
FIELD OBSERVATIONS
OF HATCHING
35 °S
OCT.
DEC.
FEB.
APR.
JUN.
AUG.


TIME IN HOURS FROM 'LIGHT ON'
8
6
4
3
2
1
45"
30"
15"
0
75"
60"
45"
23"
11½"
0
5
10
15
20
25
30
TEMPERATURE °C

darkness, and in constant light following an increase in temperature. Under conditions of constant light and temperature hatching occurred at random.

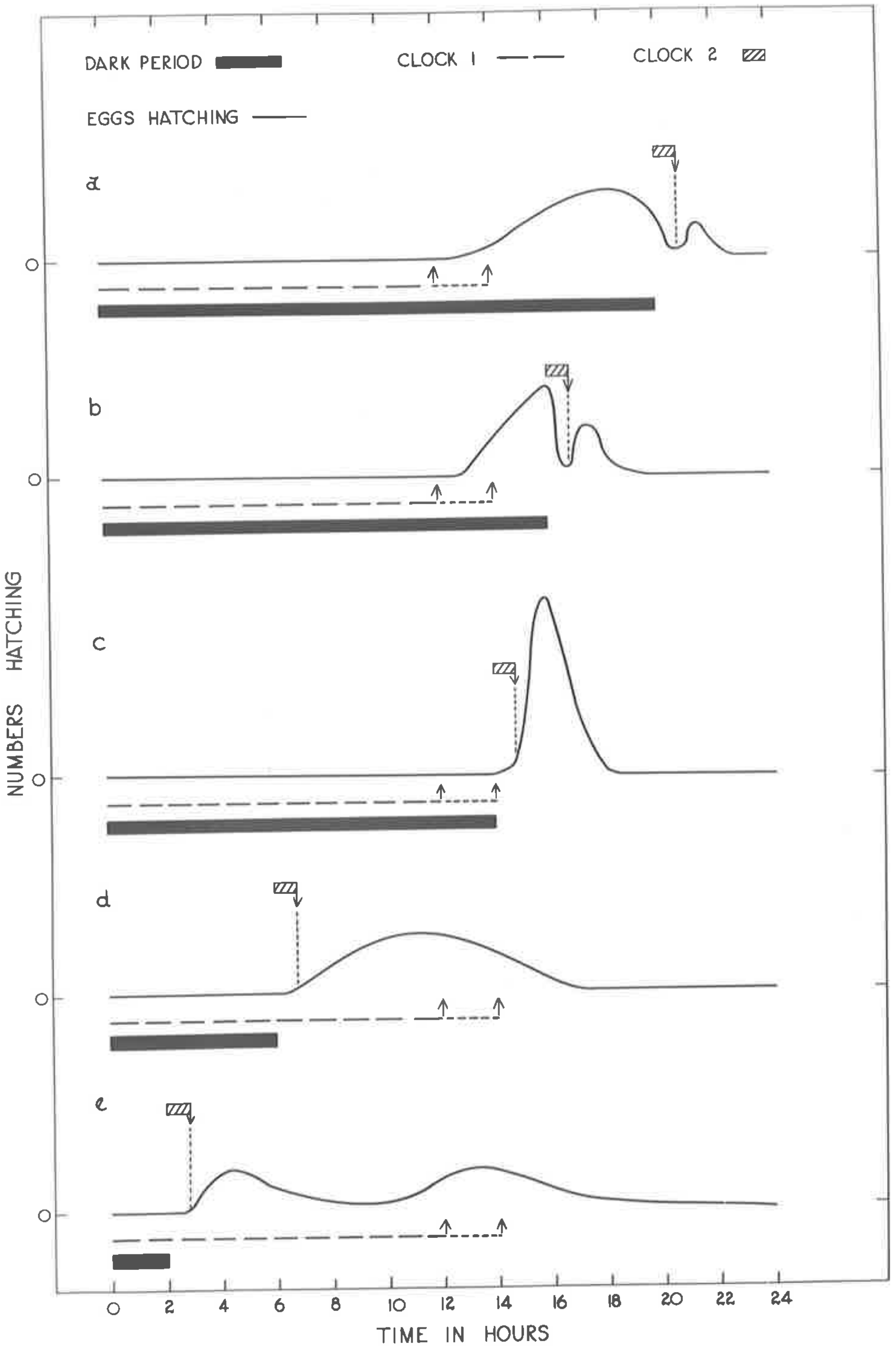
There is considerable similarity between the rhythm of hatching of eggs of C. densitexta and the eclosion of pupae of Drosophila. Both exhibit a marked morning peak shortly after the onset of light, both show a loss of rhythm in constant light, and in both eclosion will occur towards the end of the dark period where this is longer than would be encountered in nature (Pittendrigh, 1954; Brett, 1955).

A further similarity is that the process controlled by the L:D cycle is, for any individual insect, a "once only" event. This situation is quite different to that of most circadian rhythms studied, where a stimulus is entraining a rhythm into a continuous or periodic process within one organism (e.g. leaf movements of plants and running activity of cockroaches).

Harker (1965) has convincingly shown that "this eclosion rhythm [of Drosophila]is a population effect and does not reflect the phasing of individuals to a dawn eclosion; the majority of adults emerge at dawn because of the summation effect of circadian rhythms of development at earlier stages". This could also be the case with hatching of C. densitexta eggs, but at this stage there is not sufficient knowledge of either the rhythm or the steps in embryonic development leading to hatching, to speculate very far on this idea. However, there is clearly an entrainment of individuals to a rhythmic periodicity by the imposition of a L:D

Figure 2.39

Hypothetical model of the time of hatching of C. densitexta eggs in response to artifically separating the two postulated "clocks" by shortening or lengthening the dark period beyond the range of 10 to 14 hours experienced in nature.


DARK PERIOD
CLOCK 1
CLOCK 2
EGGS HATCHING
a
b
c
d
e
0
0
0
0
0
NUMBERS HATCHING
0
2
4
6
8
10
12
14
16
18
20
22
24
TIME IN HOURS

cycle. From general experience - no specific experiments to investigate phase shifting have yet been done - eggs will quickly (within 24 hours) adjust to hatching in a series of quite different L:D cycles and times relative to their previous common experience of the solar day.

Interpretation of this periodicity in terms of a simple inhibition of hatching by darkness can be ruled out. Quite apart from the fact that eggs will hatch in the dark, the concentration of hatchings following a period of darkness is far in excess of the accumulated hatchings which would result from inhibition over the period of darkness experienced (figs. 2.31 and 2.32). There is, however, an obvious need for a minimum of approximately 12 hours of darkness - or time from the change from light to dark - for the full expression of this hatching rhythm, so it is not a straightforward phasing to the "light on" signal.

A possible hypothesis is that there are two independent "clocks" operating; one being set by the change from light to dark, and the other by the change from dark to light.

The first clock, set by the "light off" stimulus, will result in eggs being ready to hatch 10 to 12 hours later. In the event of darkness persisting these eggs will start to hatch approximately 14 hours after the onset of darkness.

The second clock is set by the "light on" signal and will entrain the eggs to hatch 45 minutes (at 20°C) after receipt of the signal.

Within the range of day length experienced in nature from winter to summer these two clocks will remain in phase with each other and produce a strong morning peak of hatching (fig. 2.39c).

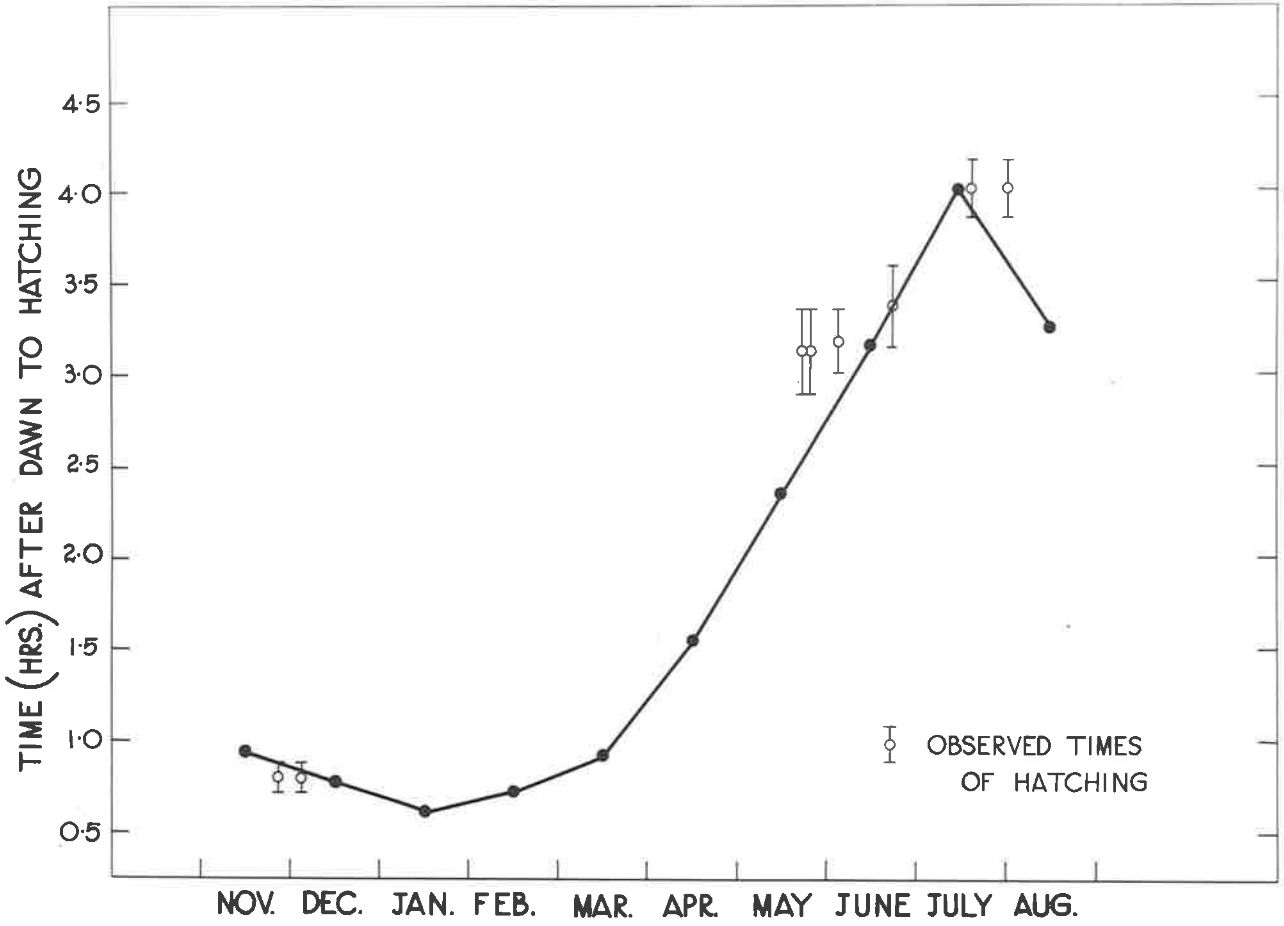
Subjecting eggs to artificially long dark periods will result in eggs hatching in the dark (fig. 2.39b), and the longer the dark period, the more will have hatched by the time the light comes on (fig. 2.39a). Unnatural shortening of the dark period will have the reverse effect, in that the eggs will be receiving the "light on" signal before they have had sufficient time since receiving the "light off" signal. This could be expected to spread the occurrence of hatching more widely over the light period, and "damp" the normally strong peak following "light on" (fig. 2.39d). Repeated subjection to a very short dark period should, in theory, produce two distinct but small and "spread out" peaks (fig. 2.39e).

The tendency with short dark periods for two peaks to develop, and the apparent drift of hatching towards the secondary peak when a short dark period is maintained, would give some support to this hypothesis.

The mean monthly temperature $\left(\frac{\text{max.} + \text{min.}}{2}\right)$ for any locality approximates very closely its mean monthly 9 .am. temperatures. These means for 1963 at Keith were calculated, and from figure 2.38 the time from "light on" to hatching was read off for the mean temperature of each month. These values were then plotted to give the curve in figure 2.40. The recorded field hatching times were

Figure 2.40

Observed times from the beginning of daylight to hatching of *C. densitexta* eggs in the field at Keith (from fig. 2.37) plotted on the calculated curve of time from "light on" (dawn) to hatching for the monthly mean $\left(\frac{\text{max.} + \text{min.}}{2}\right)$ temperatures for Keith (from fig. 2.38)


TIME (HRS.) AFTER DAWN TO HATCHING
4·5
4·0
3·5
3·0
2·5
2·0
1·5
1·0
0·5
NOV.
DEC.
JAN.
FEB.
MAR.
APR.
MAY
JUNE
JULY
AUG.
OBSERVED TIMES
OF HATCHING

then converted to times after daylight from figure 2.37 and plotted onto figure 2.40. This results in a reasonably good agreement between the observed and the expected times of hatching.

The ecological significance of these findings are simple enough. Within the natural range of C. densitexta the length of the dark period varies from a little under 10 hours in midsummer to a little over 14 hours in midwinter. Within this range of dark period, both in the field and under experimental conditions, effectively all hatching occurs one and a half to two hours after the onset of light. Thus, in summer, hatching is completed and the young nymphs have started construction of their lerps before desiccating temperatures and humidites prevail. In the winter, when desiccation is unlikely, hatching is delayed until the temperature is high enough for nymphs to be able to free themselves from the eggshell, settle, and commence feeding.

The only other reference to time of hatching of psyllids that I have found is in Speyer's (1929) paper on P. mali, where he states than "in most cases the hatching occurs in the morning hours" This statement, plus the evidence presented here, is hardly sufficient upon which to postulate that hatching of psyllid eggs is generally controlled by the diurnal L:D cycle, but I would expect a similar mechanism to that found in C. densitexta to be operating at least with related Australian species, and possibly much more widely throughout the family, and in related families of Homoptera.

2.6 The Nymphs

2.60 Introduction

There are five nymphal instars as in all Psyllidae so far described. Ecdysis in the first four instars occurs beneath the lerp - the cast skin being "kicked" from under the lerp by the nymph. (In many other genera of lerp-insects [e.g. Glycaspis] these four exuviae are incorporated in the lerp after each moult). These skins are soon blown away in the field, but remain lying on the leaf surface in the laboratory, providing a ready means of recording instars (fig. 2.43). Before the final moult to the adult stage the 5th instar nymph vacates its lerp and sits quietly nearby (usually feeding) until the skin ruptures along the mid-dorsal line and the callow adult emerges.

2.61 First Instar Nymphs

2.611 Dispersal: The newly hatched nymphs run freely on the leaf, and can pass with ease from one surface to the other. Even when a blustering wind is blowing they move about actively without appearing to be knocked or blown from the leaf.

To gain some idea of the extent to which wind-blown first instar nymphs might contribute to local dispersal, two small pink gum trees were selected; one (A) standing 15 feet away from its nearest neighbours (which were also small trees of about the same height as tree A) and the other (B) growing directly under the canopy of a large pink gum. At this time (May 1963) all the trees concerned were carrying very large numbers of eggs.

Both trees were stripped of most of their foliage; tree A being left with 108 leaves and tree B with 110. All the remaining leaves were very carefully examined and all eggs and lerps removed from them. This was done after all adults were apparently dead, but it is possible that a few eggs could have been laid on this foliage after the initial cleaning. I did not, however, find any eggs during subsequent inspections, although looking very carefully for them. By August tree A had 17 C. densitexta nymphs on its leaves, and tree B had 97. None of those on tree A survived beyond the second instar, but 30 (on 21 leaves) of those on tree B grew to adults in the spring.

It can reasonably be assumed that few if any of these nymphs were established on the two trees as eggs, but were presumably dislodged as nymphs from other trees and carried by the wind to the two trap trees. This is not altogether unexpected in the case of tree B which was directly beneath a large volume of foliage carrying vast numbers of eggs. On tree A, however, even these very few insects establishing (relative to the surrounding population)indicate that considerable numbers of newly emerged nymphs become disloged from the foliage and are carried along by the wind. That this represents a significant mode of dispersal for the species seems most improbable, especially in the summer, when the nymphs would desiccate and die within minutes of leaving the leaf. Any effect of such dispersal would, in any case, be trivial compared with the dispersal of gravid females.

Newly hatched nymphs do disperse freely from leaf to leaf by active running, but this appears to be largely confined to the immediate twig on which the eggs were laid. The first nymphs hatching from an egg group tend to settle close to the edge of this group and on the petiole end of the leaf. Many of those which hatch later, and do not settle after the first few preliminary probes and "walks", have been observed to run about actively with but brief pauses, for up to an hour. During this time they showed a strong tendency to move upwards and outwards towards the periphery of the crown. Nymphs were frequently observed after some minutes of apparently aimless wandering on a leaf blade, to run in a very "purposeful" manner up onto the petiole and so on up the twig. Most moved out along the next petiole they encountered on to a leaf blade, where they settled; but some were seen to return and move further up the twig, past the last leaf, and eventually out on to another twig.

At a temperature of approximately 15°C these nymphs travelled at about an inch a minute (measured along twigs) but a great deal of their running time is spent criss-crossing over leaf blades rather than running along twigs. (On very cold mornings (approx. 5°C) the only nymphs seen to move at all were those in direct sunlight. It is rarely, however, that temperature remains as low as this for more than an hour or two after daylight.)

2.612 Effects of Crowding: When a leaf with many eggs on it was floated on water so that the petiole protruded above the surface, the hatching nymphs soon accumulated in a dense mass on this petiole.

When numbers are high on leaf discs, many nymphs walk off on to the surface of the water. In an attempt to test more precisely the suggestion that the number of nymphs present may influence the settling behaviour of these nymphs, the following experiment was carried out.

Experiment 1. The effect of crowding on settling and survival of newly hatched *C. densitexta* nymphs.

Materials and Methods

Discs were cut from freshly picked north facing "mature type *E. fasciculosa* leaves. Only one disc was taken from the petiole third of each leaf and this was cut so that the section of the midrib of the leaf was running more or less through its centre.

As they were cut these discs were floated on distilled water in 2 x 1 inch "Clearsite" plastic vials, and placed in a constant temperature of 20°C and a 10 hour photoperiod of low light intensity (approx. 20 ft. candles). Such a low light intensity was known (sect. 2.632) to produce within a few days, leaf tissue which is inadequate as a source of food for nymphs of *C. densitexta*. It can be assumed that during the first 24 hours these leaf discs would become only marginal as sites for settling of first instar nymphs.

Newly hatched nymphs were transferred to discs as follows:

Treatment	No. of discs	Nymphs per disc	Nymphs per cm^2 of leaf tissue	Total nymphs
1	10	20	5.78	200
2	10	15	4.33	150
3	10	10	2.90	100
4	10	5	1.44	50
5	50	1	0.29	50
	90	-	-	550

After 24 hours the number of live nymphs and the number of lerps formed were counted, and after four days the number of both dead and living nymphs remaining on the discs were counted.

Results

Fitting a regression to proportions, and testing for significance of deviation about the regression (see Cochran & Cox : Second Edition 1957) showed that there was a highly significant negative correlation of both nymphs alive after 24 hours (fig. 2.41a), and nymphs remaining on the disc (fig. 2.41c). The proportion of lerps formed was not significantly different between treatments, but followed the same trend (fig. 2.41b).

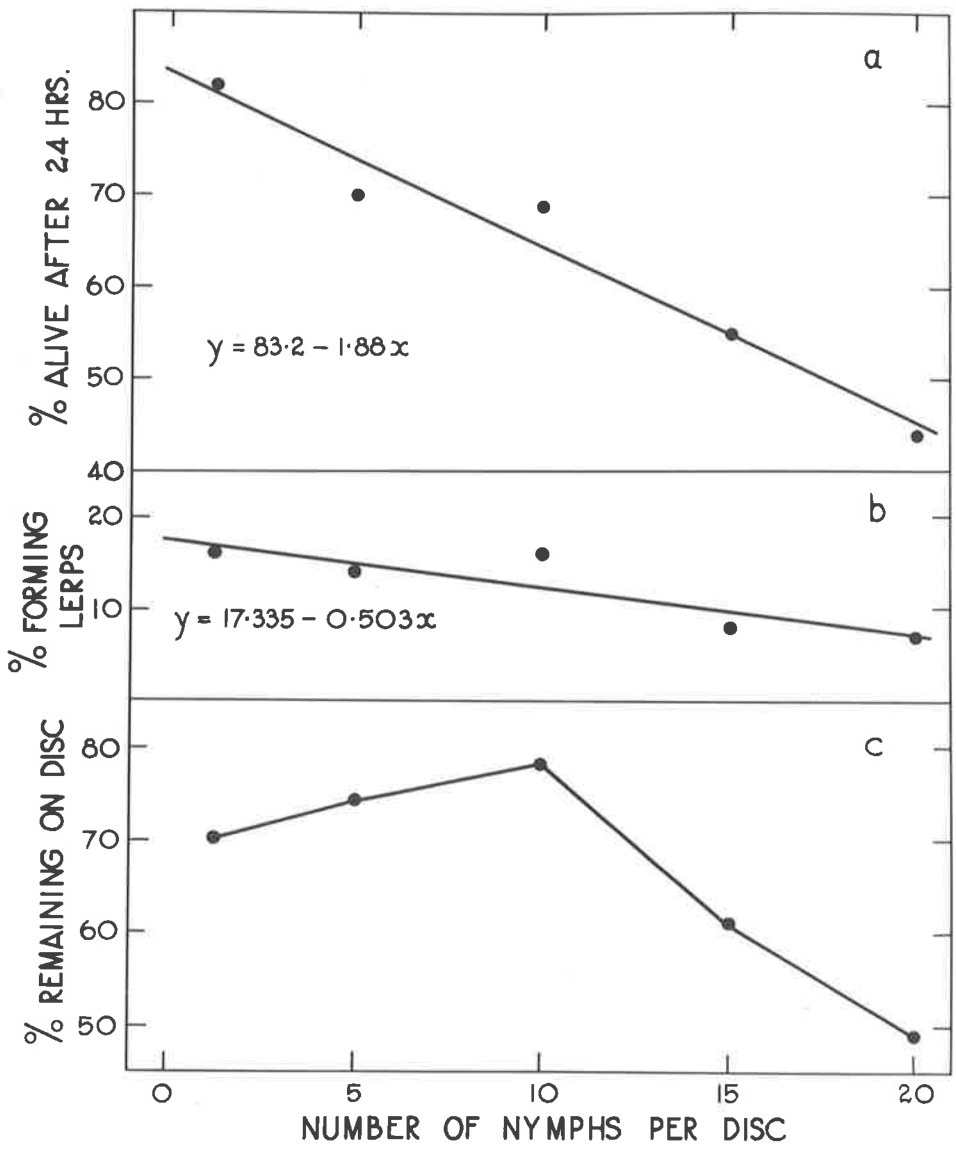
In the case of the proportion finally remaining on the discs (fig. 2.41c) there was a significant deviation of the results about the regression, indicating that something other than a straight line relationship may exist. Deviations were not significant in the other two cases, although showing a similar tendency.

Figure 2.41

Effect of crowding on the settling and survival of newly hatched nymphs of *C. densitexta*.

a. Live nymphs on the discs 24 hours after hatching.
b. Lerps formed 24 hours after hatching.
c. Nymphs (dead and alive) remaining on the discs four days after hatching (i.e. by the time all nymphs which were going to settle had done so).

All results are expressed as a percentage of the total nymphs per treatment.



a
% ALIVE AFTER 24 HRS.
80
70
60
50
40
y = 83·2 − 1·88 x
b
% FORMING LERPS
20
10
y = 17·335 − 0·503 x
c
% REMAINING ON DISC
80
70
60
50
0
5
10
15
20
NUMBER OF NYMPHS PER DISC

Variation due to	d.f.	χ^2	Significance level
A) Nymphs alive after 24 hours			
Regression	1	34.039	$P < .001$
Dev. from regression	3	0.699	N.S.
Total	4	34.74	$P < .001$
B) Lerps formed after 24 hours			
Regression	1	7.10	N.S.
Dev. from regression	3	1.831	N.S.
Total	4	8.93	N.S.
C) Nymphs remaining on discs			
Regression	1	21.37	$P < .001$
Dev. from regression	3	8.87	$P < .05$
Total	4	30.24	$P < .001$

Discussion

These results support the hypothesis that the number of nymphs present will influence the behaviour and survival of other nymphs, and that, as the density increases, nymphs tend to become more active, with the result that (under the artificial conditions of the leaf disc) a bigger proportion leave the disc and become trapped in the water. Under natural conditions in the field this behaviour would result in nymphs dispersing away from overcrowded leaves.

The proportion of nymphs finally remaining on the discs **shows** a significant deviation from the regression, indicating that, until the numbers reach a density of 10 per disc (three nymphs per square centimeter of leaf tissue), density has no influence on dispersal. (There may be, in fact, a reverse effect - that at very low densities a nymph will tend to search out others of its own kind. The differences are not significant, however, so this must remain but a suggestion).

At densities in excess of three per square cm. there is a marked increase in the proportion of nymphs leaving the discs, indicating that when crowding is intense there is a strong stimulus to disperse (fig. 2.41c). The "tolerated" density of nymphs will be a function of the suitability of leaf tissue as food, as much as a function of leaf area - thus the apparent optimum of three per square cm. may be much greater on more nutritious leaf tissue, and much lower on poor quality leaves.

A further experiment was set up in an attempt to discover whether or not the same effects would apply where other nymphs had already settled and built their lerps on the leaf surface.

Experiment 2. The effect of different densities of established nymphs of *C. densitexta* on the settling and survival of newly-hatched nymphs.

Four treatments were set up as follows:-

Treatment	No. of discs	Settled nymphs per disc	Nymphs added per disc	Total new nymphs added
1	20	20	5	100
2	20	10	5	100
3	20	5	5	100
4	20	1	5	100
-	80	-	-	400

Thus five newly hatched nymphs were added to each of 20 discs in each treatment. These discs had the indicated number of newly established first instar nymphs on them. The same methods and techniques used in the previous experiment were employed here except that the discs were kept in high light (approx. 750 ft. candles).

Counts were made of the numbers of added nymphs building lerps in the first 24 hours, the number of added nymphs alive after 48 hours, and the number of added nymphs alive after 7 days.

Results

A significant negative correlation of numbers settling with increased numbers already present ($\chi^2_3 = 16.55$ ($P < .001$) was obtained (fig. 2.42a). A similar, but non significant ($\chi^2_3 = 7.41$) correlation holds for the numbers alive after 48 hours (fig. 2.42b) and after 7 days a positive (although non significant) correlation of survival rate with numbers already present was obtained (fig. 2.42c).

Discussion

These results show that a smaller proportion of nymphs settled where the density of already established nymphs was higher.

Figure 2.42

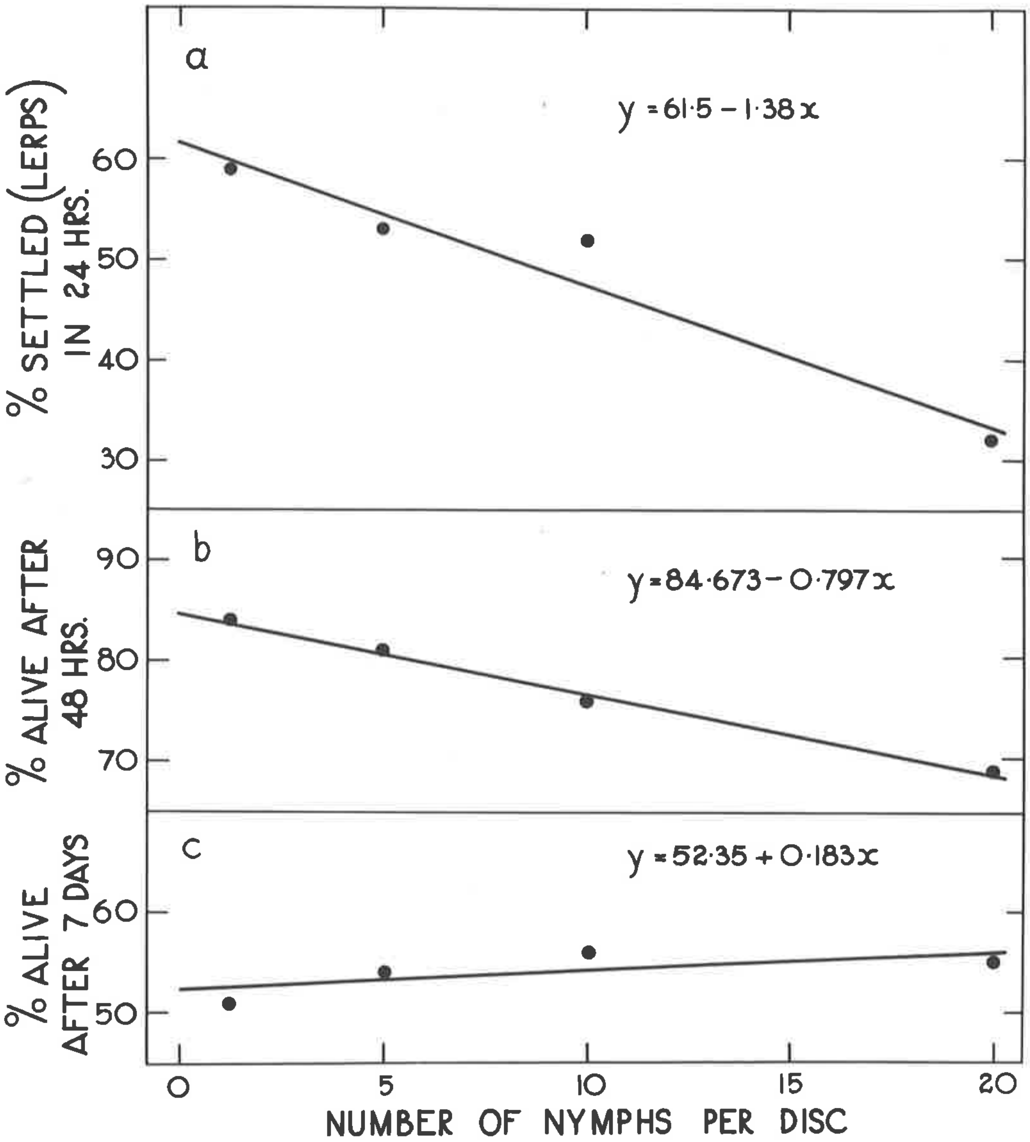
The effect of different densities of established *C. densitexta* nymphs on the settling and survival of newly hatched nymphs.

a. Nymphs settling and building lerps 24 hours after hatching.

b. Nymphs alive 2 days after hatching.

c. Nymphs alive 7 days after hatching.

abscissa = Number of already established first instar nymphs per 21 mm. leaf disc.


a
y = 61·5 − 1·38 x
% SETTLED (LERPS) IN 24 HRS.
60
50
40
30
b
y = 84·673 − 0·797 x
% ALIVE AFTER 48 HRS.
90
80
70
c
y = 52·35 + 0·183 x
% ALIVE AFTER 7 DAYS
60
50
0
5
10
15
20
NUMBER OF NYMPHS PER DISC

But conversely, there was a non-significant tendency for a larger proportion of newly settled nymphs to survive on discs where the density of already established nymphs was higher.

The initial settling response agrees with the findings of the first experiment that increasing density results in an increasing tendency to disperse.

An explanation of the higher mortality on the more sparsely inhabited discs will be found in section 2.633.

2.613 Selection of a Site to Settle: Sites selected for settling by first instar nymphs were similar to those selected by females for egglaying. Thus "old" and "young" type leaves were rarely occupied although as the leaves were maturing all the time, nymphal settling extended further down the twig than did egglaying. Also, the dispersal behaviour of the nymphs resulted in their being more evenly distributed through the foliage than were the eggs (see sect. 2.13).

On individual leaves the tendency was to favour the basal end, but this became less apparent as numbers increased, either because shortage of space forced colonization of more of the leaf surface; or, more probably, because more of the leaf tissue became attractive to probing nymphs, and so more of it was colonized.

The lower side of a leaf was preferred to the upper side, and it is suggested that this is the reason for Clark's (1963b) finding that, on picked foliage, "there was a tendency for numbers to be relatively low on one side of a leaf where they were high on the other side".

Once settled nymphs will remain at the same site until attaining the adult condition, unless forced to move by the death of the leaf.

2.62 The Lerp

Once having settled and started to feed the nymph commences to construct a covering over itself - the lerp. This term is generally used today as a common name for any psyllid where the nymphal stage builds a covering over itself. All workers from Dobson (1850) onwards have, however, used the term more precisely to refer only to this covering. Clark in his recent series of papers on C. albitextura rejects it in favour of "test". "Lerp" would seem to be a perfectly good and well established term for this peculiarly Australian specialization within the Psyllidae, and has the added advantage of avoiding confusion with "scales" and "tests" of coccids. Accordingly, I am following the earlier writers and retaining "lerp" to mean the covering built by the nymphs of many psyllids, and use the more general "lerp-insect(s)" as a common name for this characteristic group of psyllids.

The word apparently derives from the aboriginal name for the sweet encrustations sometimes found on twigs and branches of mallees, and is variously spelt "laarp", "laap", "larp" and "lerp" in the early literature. Early observers did not recognise the animal origin of this "manna", assuming it to be a form of exudate from the plants. It is, however, built entirely from the excrement of the nymph in all species so far investigated; although in some species not all of the excrement is formed into lerp, sweet, liquid, honeydew being produced as well. (Hence, I presume, Froggatt's (1900) statement that the lerp is formed from "excess sap ... ejected from the anus, but is quite different from the excrement").

In C. densitexta the excrement is extruded from the anus as a slightly opaque liquid of honey-like consistency, which rapidly hardens on contact with the air. The young nymph first fixes a small amount of this material to the leaf surface and then builds - "paints" is a better description of the operation - with the tip of the abdomen, a narrow arch over its body. From this beginning the "juvenile" lerp is formed, differing from the true lerp in being quite amorphous, more transparent, and almost circular. On this foundation the remainder of the lerp is built in a series of radiating ribs, to form a structure characteristic of the species (Taylor, 1962).

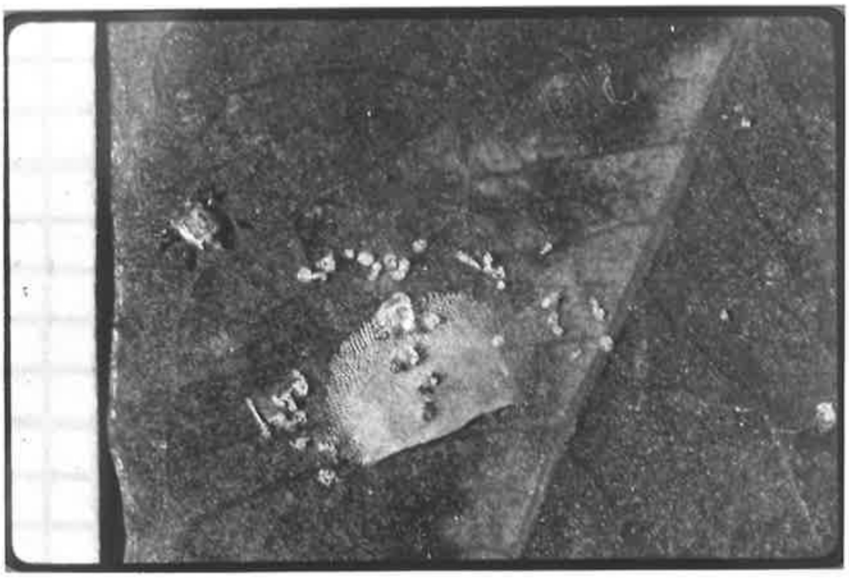
The fully grown fifth instar nymph does not build on to the lerp once it is large enough to cover the body, but deposits the excrement outside the perimeter in the form of "pellets". In the field these fall off the leaf almost immediately but in the laboratory remain on the leaf disc in a semi circle around the lerp (fig. 2.43).

Practically nothing is known of the chemical composition of lerp. Anderson (1849) analysed what was probably the lerp of a

Figure 2.43

The fully formed lerp of C. densitexta with the five cast nymphal skins and the "pellets" of excrement voided away from the lerp once this is large enough to cover the fully grown fifth instar nymph.

Scale : 1 division = 1 mm.



species of Glycaspis, but this was obviously contaminated. C. densitexta lerps are insoluble in water, tasteless, and contain 75% carbohydrate in the form of an insoluble polymer of glucose, and about 2% of ether-soluble substances*. As mentioned previously, some lerp-insects also produce honey-dew, as do some free-living psyllids. In both cases the nymphs are attended by ants in the same way as are many aphids and coccids. (The production of flocculent masses of wax, and the encasing of the excrement in tubes of wax is found in some free-living psyllids, and these are not attended by ants). Cardiaspina does not produce honey-dew.

Pletsch (1947) records that the honey dew of Paratrioza cockerelli has only a trace of protein-like matter, and is essentially carbohydrate. There would seem to be a general similarity in the composition between lerp and honey-dew from psyllids and aphids (Ewart & Metcalf, 1956; Auclair, 1963). A possible hypothesis as to the origin of lerp-building is suggested by this similarity and a statement of Auclair's (1964) "this peculiar property of invertase of building up in the digestive tract of aphids larger molecules of carbohydrates from sucrose and its breakdown products may well be an expedient way of 'packaging' excess sucrose, thus reducing osmotic pressure in the gut and speeding up elimination of surplus sugar" (see also Kennedy & Stroyan, 1959). A similar development in psyllids could well have resulted in the production of larger and larger

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*I am grateful to Dr. J.M. Oades for the carbohydrate analysis, and to Dr. D.J. Lewis for the ether extraction.

molecules, until polymers were formed which solidify on contact with the air and thenceforth remain insoluble in water, (as are the lerps made by _C. densitexta_). From here the evolution of lerp-building is not a big step to contemplate.

The function of the lerp is protective (Heslop-Harrison, 1949) providing a barrier (albeit not a very good one) against predator and parasite attack, acting as a reflective shield against radiation, and aiding in maintaining a high humidity. This last would seem to be its chief function. In the absence of a satisfactory method of measuring humidity beneath this structure, the following experiment was carried out to test this hypothesis.

A leaf bearing several third and fourth instar nymphs under their lerps was placed on wet filter paper in a petri dish, and the lerps removed. The soft-bodied nymphs immediately started moving "nervously" about, feeling above them for the lerp with their antennae and the tip of the abdomen, but not removing their stylets from the leaf. This behaviour ceased in one or two minutes, and construction of new lerps commenced. Once sufficient material had been deposited to provide the nymphs with a concave surface to press their heads against building activity could be interrupted merely by replacing the lid on the petri dish. Removing the lid (and thus lowering the humidity) resulted in vigorous renewed building; this could be repeated indefinitely until the bodies of the nymphs were again completely covered by new lerps, when the insects no longer responded to removal of the lid. The psyllids were probably responding to changes in humidity. The nymphs are soft bodied and soon desiccate and die if removed from the leaf and placed in anything but a near-saturated atmosphere. In the field relative humidity frequently drops to the 10% - 15% level in the summer, especially when hot dry northerly winds are blowing. Exposed to such weather few nymphs could survive for long, but under the lerp air movement would be virtually nil, resulting in a marked increase in the humidity from water vapour transpired by the leaf beneath this structure. This increased humidity would, in turn, result in the stomata beneath the lerp remaining open when elsewhere on the leaf they would be closed to reduce transpiration, thus increasing the humidity still further.

2.63 Development and Survival after Settling

2.631 Orientation on the Leaf: It was noted that on any one leaf most nymphs settled as though orientated by some common stimulus, the "hinge" or head edges of the lerps pointing in the general direction of the petiole. On closer inspection this appeared to be a response to gravity as lerps on both sides of a leaf tended to be "pointed" in the same direction which is upwards on an undisturbed leaf hanging on the tree. This was confirmed by tying leaves upside down before the eggs on them had hatched. Subsequently settling nymphs all built their lerps with the hinge uppermost and pointing towards the tip of the leaf, while those on undisturbed and pendent leaves on the same twig also built in relation to gravity but with the "hinge" ends towards the petioles. Nymphs settling on discs floating horizontally on water in the laboratory were not orientated to a common direction.

2.632 Effect of Aspect: As discussed in the section on oviposition, more eggs were laid on the north faces of the tree crowns. A number of leaves on the north and south faces of two trees were tagged after all the eggs had been laid, and all eggs on them were counted. On each subsequent visit all unhatched eggs and established nymphs were counted.

Table 2.11 shows the results of counts made at approximately fortnightly intervals through the winter of 1963.

The results show that eggs hatch about 2 weeks earlier on the north face of a tree, that many more nymphs on the south side than on the north side die without ever forming a lerp, and that there is a much greater total mortality of those that do establish themselves on the south side. Moreover, most of the established nymphs which died did so in July and August as early first instar nymphs. Although it was suspected at the time that many of them were dead, it was not until rapid growth started in September-October that these early deaths showed up. When this happened, the ratio of surviving nymphs was seen to be not 2 to 1, but 5 to 1, north to south.

Table 2.12 shows two of a series of counts of all nymphs present on leaves collected at random from the north and south faces of six or more trees. A minimum of 500 nymphs was counted from each aspect on each occasion.

Table 2.11

Rate of hatching of eggs and establishment and survival of nymphs on north and south faces of pink gum crowns.

Date	North				South			
	No. Eggs	% Hatched	No. Nymphs alive	% Survival (of those hatched)	No. Eggs	% Hatched	No. Nymphs alive	% Survival (of those hatched)
24.5.63	1581	0	0		1132	0	0	
5.6.63	-	-	43	-	-	-	1	-
20.6.63	-	-	373	-	-	-	12	-
4.7.63	624	60.5	635	66.4	891	21.2	55	22.8
18.7.63	183	88.4	790	56.5	437	61.4	157	22.6
1.8.63	79	95.0	796	53.0	193	83.0	236	25.2
14.8.63	39	97.5	830	53.8	58	95.0	264	24.6
26.8.63	7	99.6	668	42.5	4	99.6	243	21.6
19.9.63	0	100.0	599	37.9	0	100.0	135	11.9
3.10.63	-	-	516	32.6	-	-	122	10.8
17.10.63	-	-	339	21.4	-	-	46	4.1
6.11.63	-	-	All emerged	-	-	-	All emerged	-

Table 2.12

Rate of growth of nymphs on north and south sides of crowns of pink gums - percentages in each instar on the same date.

Instar	Summer Generation		Winter Generation	
	North	South	North	South
1	7.0	8.4	4.2	26.2
2	16.0	30.3	37.8	68.2
3	54.0	61.0	55.9	5.6
4	23.0	0.3	2.1	0.0
5	0.0	0.0	0.0	0.0
Total	100.0	100.0	100.0	100.0

These counts showed that the nymphs on northern aspects grow faster than those on southern aspects both in the winter and the summer. Being destructive counts they enabled confirmation of the fact mentioned above, that many first instar nymphs on the south leaves had died beneath their lerps, while few such deaths were found on north facing leaves. (All such dead nymphs were excluded from counts for comparison of speed of development.)

The end result of this initial favouring of the north faces as egg laying sites, followed by the higher survival and faster rate of growth of the subsequent nymphs, is a definite "scorching" of these north faces; much more leaf tissue being killed by the greater numbers feeding thereon. This scorching of the north faces is apparent at the end of all three generations.

In the spring, at the end of the winter generation, the burnt face is towards the northeast, but at the end of the summer and autumn generations it is more nearly towards the north. At very high population levels this "north-south effect" is not so readily apparent as nearly all foliage on both faces is attacked and discoloured. Trees which have been very badly attacked no longer have a crown, but merely the main branch system bearing a few epicormic sheets. Moderate to heavy infestation persisting over several generations will result in the characteristic "cutting back" of the northern faces of pink gum crowns (fig. 2.44 : table 2.13).

Table 2.13

Numbers of dead and live twigs on the north and south faces of pink gum crowns

Collected according to the method described in section 2.1

A. Five north side and five south side samples from ten trees.

B. 100 samples from one tree.

χ^2 of means = 32.5***

		North	South	Total
Live Branches	A	10	41	51
	B	8	35	43
	$\bar{x}$	9	38	47
Dead Branches	A	40	9	49
	B	40	17	57
	$\bar{x}$	40	13	53
Totals	A	50	50	100
	B	48	52	100
	$\bar{x}$	49	51	100

Figure 2.44

C. densitexta on E. fasciculosa

Photograph of a pink gum taken from the west to show the typical "cutting back" of the northern face of the crown by repeated heavier attack of C. densitexta on that face.

Clearly then, a higher death-rate of leaves on the northern faces of pink gum crowns is associated with a greater number of *C. densitexta* nymphs feeding on these leaves.

The temperature of both the air and the leaves will undoubtedly play a part in this uneven survival, especially in the winter. Earlier egg hatching in winter on the northern faces (Table 2.11) can fairly certainly be attributed to greater radiant heating of north-facing leaves (there is no evidence to suggest that they were laid before those on southern aspects), and possibly the faster rate of development in both winter and summer on north leaves is due to this earlier hatching, plus more radiant heat. The higher death-rate among first instar nymphs on the south side could also be attributed to cold temperatures in the winter (although this is very doubtful) but *not* in the summer months. As this early mortality is the major part of the observed differences between populations on the two aspects, a cause other than temperature was sought.

The distinction between sun and shade leaves of plants has long been recognised, and those of *Eucalyptus* are no exception. Their shade leaves show lower rates of photosynthesis and respiration, less chlorophyll, fewer layers of palisade tissue, fewer stomata per unit area, thinner cuticle, larger inter-cellular spaces, and much more open spongy palisade than do equivalent sun leaves (R.J. Cameron personal communication, 1964).

The morphological differences are unlikely to be of any significance in determining the number of nymphs which can survive on a leaf, whereas any physiological differences could be of considerable importance. There are more than enough stomata, mesophyll and phloem cells available in shade leaves to accommodate all the nymphs which could crowd on to them; but differences in the quality of the sap might be very different in the two leaf types. Apart from their greater rates of photosynthesis and respiration, sun leaves are much more subject to water stress than are the shade leaves (D. Aspinall, personal communication, 1964).

Thus, even when the trees are not stressed by changes in soil-moisture the amount of food available to the settling nymphs is going to be greater in the sun leaves by virtue of their greater chlorophyll and soluble nitrogen content, and higher rate of photosynthesis. When the trees are stressed by a shortage of water (caused as explained in chapter 3.0, by an excess of rain in the winter and a shortage of rain in the summer) the physiological differences between sun and shade leaves will be accentuated, resulting in even greater survival of early instar nymphs on the north faces.

These physiological differences would also explain the death on shade leaves of the young nymphs still beneath their lerps and with their stylets inserted - they have starved to death while feeding on a "palatable" but impoverished food.

An attempt to investigate in the laboratory the differences between north and south leaves are outlined in the following three experiments.

Experiment I: The Photosynthetic Ability of Sun and Shade Leaves at high and low Light Intensities.

Five "mature" sun leaves and five "mature" shade leaves of *E. fasciculosa* were collected. From each of these leaves two discs were cut and floated on distilled water in 2 x 1 inch vials. One member of each pair was placed in direct light (730 ft. candles) and the other in shade (12 ft. candles). All were maintained in a 10 hour photoperiod and at a constant temperature of 20°C.

Results

After 79 days all discs in the shade, except one from a shade leaf, were dead and black, while all ten discs in bright light were still alive. The sun leaves in the shade had started to deteriorate after 25-30 days and were all dead by 46 days, but the shade leaves in the shade did not start to die until the 55th day, and one was still alive when the experiment was terminated on the 79th day.

Discussion

This simple experiment clearly demonstrated the different photosynthetic ability of sun and shade leaves. Under low light intensity the shade leaves were able to maintain themselves for almost 2 months while the sun leaves were all dead in half this time.

In high light intensity both sun and shade leaves were not only able to maintain themselves, but had become quite discoloured with accumulated photosynthates.

This apparent absence, at high light intensities, of the marked physiological differences between north and south leaves so strongly exhibited at low intensities, may still be apparent to psyllid nymphs feeding on this tissue. To investigate this possibility, the next experiment was carried out.

Experiment II: The Effect of Leaf Age and Aspect on the Success of Settling and Survival of First Instar Nymphs on Discs cut from Leaves of Different Ages and Aspects.

Twenty discs were cut from each of three lots of leaves - "mature" sun leaves, "mature" shade leaves and "old" leaves - and floated on distilled water in 2 x 1 inch vials under 750 ft. candles of light at 20°C.

One hundred newly hatched nymphs (five per disc) were placed on each type of leaf, and the number of nymphs building lerps and subsequently surviving was recorded as a measure of the suitability of each leaf type as a site for settling and feeding by these nymphs.

Results (fig. 2.45)

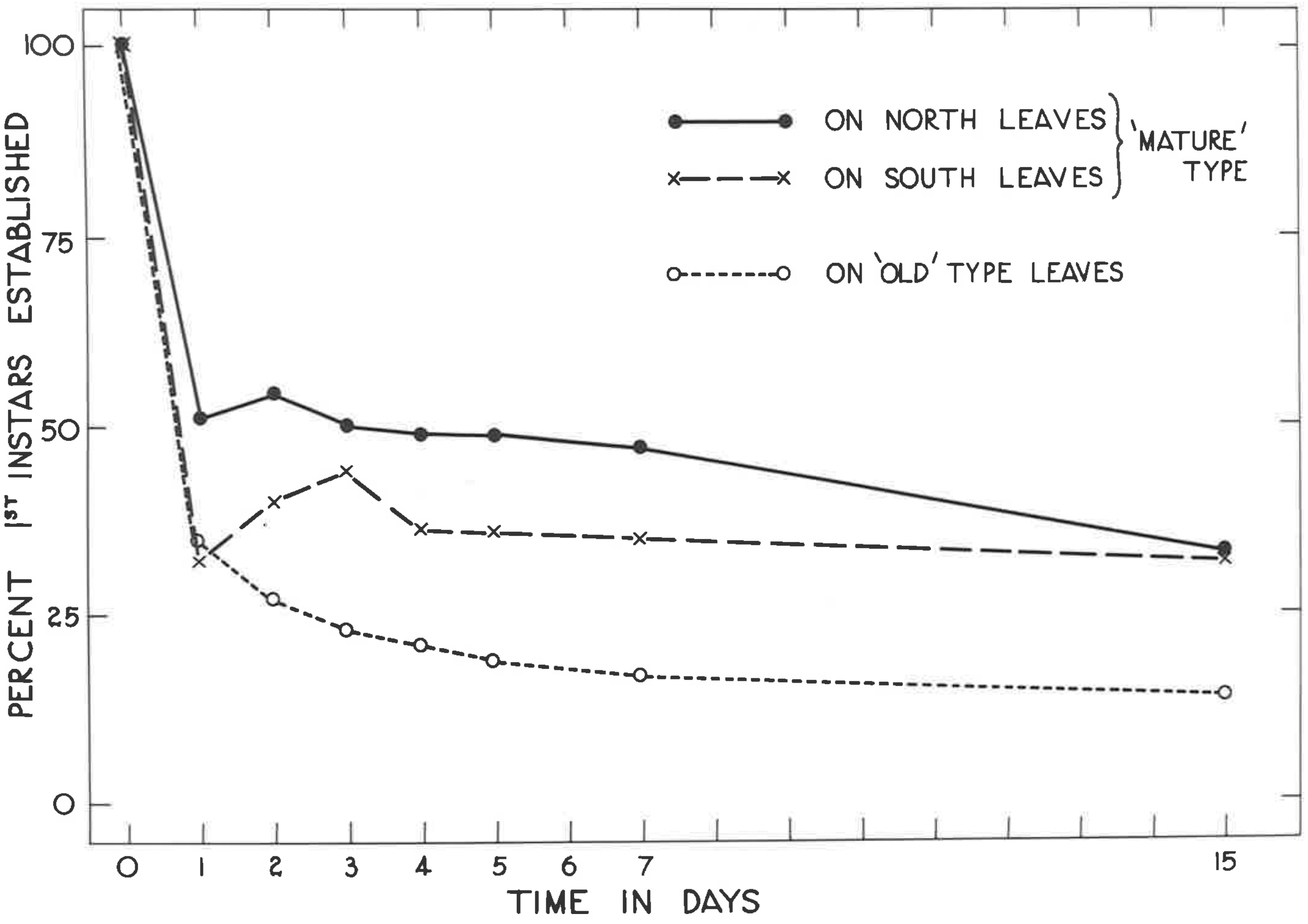
Initially the sun leaves were much more favourable as a settling and feeding site than either the shade leaves or the old leaves (χ^2 (of the number of nymphs established after one day) between sun and shade = 6.67** and between sun and old = 4.81*)

Figure 2.45

Effect of leaf age and aspect on the settling and survival of first instar *C. densitexta* nymphs.

An "established" nymph is one which has built a lerp and is alive beneath this lerp On day one more nymphs were wandering on the shade leaves than on the sun leaves, indicating that more nymphs on the shade leaves were still searching for a suitable feeding site. By the third day most of these had settled and built lerps.

The subsequent higher mortality on the shade leaves probably resulted from this longer time spent wandering, but was still not sufficient to make a significant difference between the two lots of "mature" leaves. The "old" leaves remained a poorer site throughout.



100
75
50
25
0
PERCENT 1ST INSTARS ESTABLISHED
0
1
2
3
4
5
6
7
15
TIME IN DAYS
ON NORTH LEAVES
ON SOUTH LEAVES
'MATURE' TYPE
ON 'OLD' TYPE LEAVES

but this margin was soon lost. By the third day all of the living but unsettled nymphs on the shade leaves had settled and built lerps, there then being virtually no difference between the number of living nymphs settled and under lerps on these two lots of leaves. Subsequent mortality was higher on the shade leaves (probably as a result of the longer period the nymphs on them spent wandering) but the difference between the two aspects remained non-significant. The "old" leaves continued to be a poorer site than the "mature" leaves.

Discussion

The main point of interest arising from this experiment is not the initial greater favourability of the sun leaves - I had expected this - but the rapidity with which it was lost.

I would interpret this as indicating that, in addition to the morphological differences between sun and shade leaves, there are physiological ones, but these are quickly lost when excised tissue from both is subjected in the laboratory to identical (and adequate) temperature and light. Furthermore it is these physiological differences and not the morphological ones which are important to the survival of the young nymphs.

From the results of this and the previous experiment, it would seem that there was no physiological difference between discs of sun and shade leaves after a few days in full light, but this may not be so at low light intensities where sun leaves die much sooner than the shade leaves.

The next experiment was carried out to investigate the effects of both high and low light intensity on settling and survival of nymphs.

Experiment III: The effect of high and low light intensity on the success of settling and survival of first instar nymphs on leaf discs.

Materials and Methods

"Mature" sun and shade leaves were collected from one tree and stored for six days at 3°C. Discs were then prepared from these as described below, and kept for 48 hours under continuous and direct light and at a temperature of 20°C, before placing newly hatched nymphs on them.

Six replicates of the following were set up.

Five pairs of discs (one pair from one leaf) were taken from 5 sun leaves and five pairs from 5 shade leaves and segregated in trays of ten 2" x 1" vials, as follows:-

(Sun Leaves (N)	Shade Leaves (S)
A_1	V_1
B_1	W_1
C_1	X_1
D_1	Y_1
E_1	Z_1

Lot I (High Light)

Sun Leaves (N)	Shade Leaves (S)
A_2	V_2
B_2	W_2
C_2	X_2
D_2	Y_2
E_2	Z_2

Lot II (Low Light)

- thus one disc of each pair (e.g. A_1 & A_2; V_1 & V_2) went into each lot. Whether sun leaves or shade leaves went on the right hand side of the tray was decided by the toss of a coin. Five newly hatched C. densitexta nymphs were placed on each disc.

Lot I was placed under direct radiation from a bank of fluorescent tubes providing a mean of 700 ft. candles (580 to 785 foot candles) illumination.

Lot II was placed in the shade of the shelf carrying Lot I and immediately below Lot I. Here it received 20 ft. candles of indirect light.

Lots I and II of the second replicate were placed alongside these and so on along the two shelves with the six replicates.

The number of nymphs establishing and building lerps, and the numbers of these successful ones subsequently dying were recorded over a period of 28 days.

Results

Analysis of variance of the numbers of nymphs established after 5 days (using percentages transformed to angles) revealed that significantly fewer nymphs became established on discs from sun leaves in the shade than in the light; but that on discs from shade leaves there was no significant difference between the numbers settling in light or shade. The difference between sun leaves in the light and in the shade although significant was small (table 2.14).

Table 2.14

Treatment	Interaction Table (angle)		Equivalent Percent	
	North	South	North	South
Light	62.9	62.2	79.2	78.2
Shade	57.8	61.7	71.6	77.5

Least significant difference for comparison of light and shade within aspects (angles)

= 4.70 (P = 0.05)
= 6.70 (P = 0.01)

From the ninth day onwards many nymphs on discs in the shade started to die. (By the 12th day 50% of those established on day seven were dead) while in direct light mortality remained very low throughout the experiment (fig. 2.46a).

There was no significant difference between the total numbers dying on sun and shade leaves in either high or low light intensity.

Looking more closely at the discs in the shade revealed that a great many of the nymphs were dying while still beneath their lerp, and with their stylets still fully inserted into the leaf tissue.

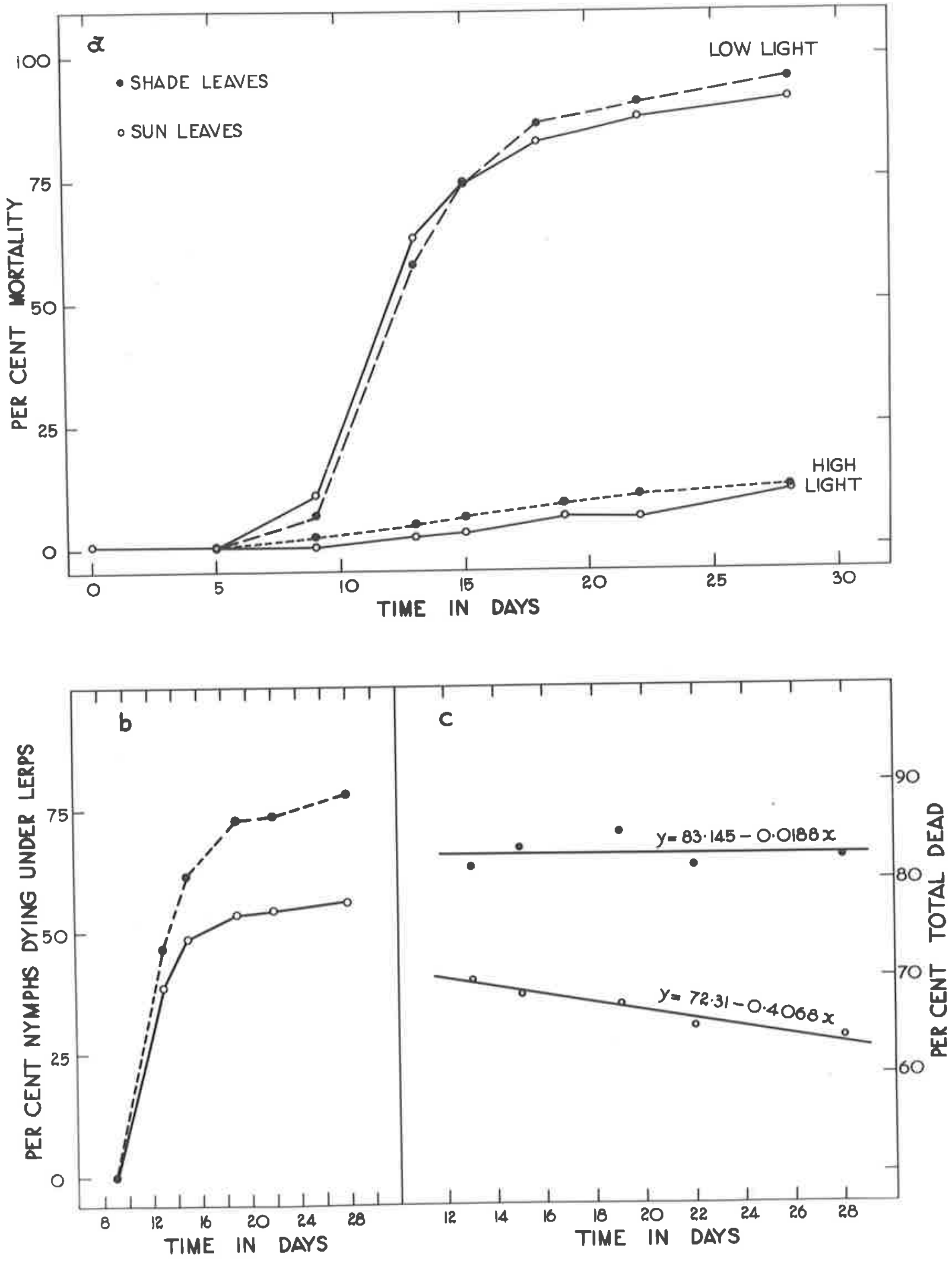
Furthermore, as time passed, an increasingly greater number of the nymphs on shade leaves than on sun leaves had died while still beneath their lerps. (Significantly more [χ^2 = 16.00***] from day 19 onwards) (fig. 2.46b).

Expressing the number of nymphs dying beneath their lerps as a proportion of the total number of nymphs dying (fig. 2.46c)

Figure 2.46

The effects of high and low light intensity on the success of settling and survival of early instar nymphs on leaf discs.

a. Mortality of established nymphs on leaf discs from sun and shade leaves in both light and shade.
b. Nymphs dying while still beneath their lerps, on both sun and shade leaf discs in the shade. Symbols as in a.
c. Nymphs dying beneath their lerps, expressed as a percentage of the total nymphs dying, on sun and shade leaf disc in the shade. Symbols as in a.


a
LOW LIGHT
● SHADE LEAVES
○ SUN LEAVES
HIGH LIGHT
PER CENT MORTALITY
0
25
50
75
100
0
5
10
15
20
25
30
TIME IN DAYS
b
PER CENT NYMPHS DYING UNDER LERPS
0
25
50
75
8
12
16
20
24
28
TIME IN DAYS
c
y= 83·145 − 0·0188 x
y= 72·31 − 0·4068 x
PER CENT TOTAL DEAD
60
70
80
90
12
14
16
18
20
22
24
26
28
TIME IN DAYS

reveals that, on both types of leaf tissue, there is an increasing tendency for nymphs to move out from beneath the lerp and wander about before they die. This tendency was increasing more rapidly on sun leaves than on shade leaves, the slope of the two lines being significantly different ($t_6 = 2.57 : P < 0.05$)

Discussion

Several things are indicated by the results of this experiment.

(1) Under inadequate light the sun leaves cannot photosynthesise as well as the shade leaves and they therefore provide less food and so are less favourable as settling sites for nymphs. As a result fewer nymphs settled on the discs from sun leaves kept in the shade.

When they are kept in adequate light, however, both sun and shade leaves can produce sufficient photosynthates and there is no significant difference in the numbers of nymphs settling (table 2.14).

(2) Once settled the nymphs' demand for food will increase rapidly. At this point leaf tissue of either sun or shade leaves under inadequate light cannot meet this demand, with the result that the nymphs starve to death, while in full light little or no mortality occurs (fig. 2.46a).

(Throughout the duration of this experiment (28 days) all discs in both light and shade - apart from one or two which rapidly and completely died - remained green, turgid, and to all outward appearances perfectly healthy and suitable tissue for nymphal feeding).

(3) The fact that on discs kept in the shade most of the nymphs died while still feeding, demonstrates that the food was quite "palatable" although lethally deficient in nutrients. The production of normal lerps by these nymphs indicates that adequate supplies of carbohydrates were present.

Before a nymph will vacate its lerp and search elsewhere for a new feeding site it seems probable that the actual flow of sap must be decreased below a certain point (Kennedy et al., 1958). Thus nymphs will quickly become restless and then move out from under their lerps if a leaf is detached and allowed to dry out in the air. Similarly, if the tissues of the leaf were becoming moribund the flow of sap would slow down once deterioration had gone a certain way.

The fact that, prior to death, more nymphs left their lerps on the sun leaves than the shade leaves, and that the proportion of these "wanderers" increased at a faster rate on sun leaves than on shade leaves (fig. 2.46b & c) demonstrates the extreme sensitivity of the feeding nymphs to physiological changes in the leaf tissue. They were, in fact, responding to the faster rate of deterioration of the sun leaves under low light intensity. At this point there were no visible signs of this faster decline of the sun leaves, but previous experiments have clearly demonstrated that this is in fact occurring. There is also abundant evidence in the literature to support the contention that shade leaves can make more efficient use of weak illumination than can sun leaves (J. Clark, 1961).

In summary then, it would seem that the marked physiological differences between sun and shade leaves undergo changes once these leaves are detached from the plant.

At high light intensity the sun leaf tissue, although initially a more favourable site for nymphal feeding, soon becomes indistinguishable from shade leaf tissue - at least in the experiments so far conducted.

At low light intensity below the compensation point of the tissue, both sun and shade leaf tissue becomes inadequate as a source of food for nymphs, but sun leaf tissue with its lesser photosynthetic ability in low light, deteriorates at a faster rate than does shade leaf tissue.

The manner of death of those nymphs which die while feeding under the lerp on detached leaf tissue in inadequate light, on the south leaves of pink gum in the field, and on the leaves of "unnatural" hosts (e.g. E. diversifolia) in the field, is strikingly similar. The explanation that in all three cases these insects are starving to death while feeding on an abundance of "palatable" but inadequate food seems reasonable.

The hairline margin between such acceptable food and non-acceptable food is indicated by the different rates of rejection of feeding sites on the sun and shade tissue deteriorating at different rates at low light intensity.

2.633 <u>Effect of Crowding</u>: Although the newly established nymphs tend, for the most part, to settle fairly uniformly over the leaf surface (fig. 2.47), later instars are almost invariably unevenly clumped into groups of crowded, overlapping lerps, interspersed with quite large areas of unoccupied leaf surface (fig. 2.49 and 2.50).

At high densities per leaf often the only contact that fourth and fifth instar nymphs retain with the leaf is the stylets inserted between the "floor" of lerps of other nymphs on which they are standing. This contagious distribution is apparent, however, at both high and low densities per leaf, and should not be confused with the preference for settling at the base of a leaf. Rather does this clumping occur within the colonized area. This suggested that there might be some benefit to any individual nymph in having others of its kind settling nearby on the leaf, or that there are patches of leaf tissue which are more favourable than others for survival of the nymphs. To test the former hypothesis the following experiment was carried out.

Experiment I: The effect of crowding on the survival and rate of growth of nymphs of *C. densitexta*.

Materials and Methods

Nymphs were allowed to hatch, settle, and build juvenile lerps on "mature" leaves still on the trees. Leaves were then collected

Figure 2.47

Late first instar nymphs of *C. densitexta* on *E. fasciculosa* leaf showing how the initially even distribution over the leaf surface begins to change to a "clumped" distribution.


2
INCHES
1
2

and discs cut from them to include these newly established nymphs. Where necessary individuals were removed to give the required number per disc. All this was done before the nymphs had been established more than 24 hours. These discs were floated on distilled water in 2" x 1" plastic vials and placed in a 10 hour photoperiod of relatively high light intensity (750-1000 ft. candles) and a constant temperature of 20°C - conditions known to be satisfactory for _C. densitexta_ to develop to maturity on discs of pink gum leaf.

The following treatments were set up:-

Treatment	No. of discs	No. Nymphs per disc	Nymphs per cm^2 of leaf surface	Total Nymphs
1	10	20	5.78	200
2	9*	15	4.33	135
3	10	10	2.90	100
4	20	5	1.44	100
5	100	1	0.29	100
Totals	149	-	-	635

*Error in setting up the experiment

Over a period of 90 days the deaths on each disc were recorded and all cast skins counted by instars and removed. At each of these counts the positions of the discs beneath the bank of fluorescent lights were changed to counteract any possible influence of slight differences in light intensity.

Results

(a) Survival

The percentage surviving to the fifth instar and to adults in each of the five treatments are illustrated in figure 2.48. A 2 x n chi square analysis of the total number reaching each stage in each treatment showed significant differences ($\chi^2_{(4)} = 15.94$, $P < 0.01$; at the fifth instar stage; $\chi^2_{(4)} = 27.99$, $P < 0.001$; at the adult stage).

(b) Rate of Growth

An analysis of variance of the mean time taken to reach each instar in all five treatments showed significant differences in the speed of development to each instar (table 2.15).

Discussion

This experiment demonstrates very clearly that the number of nymphs feeding on a given area of leaf will have a definite influence on both the numbers of these nymphs which survive, and the speed with which they develop.

It would seem that up to a density of approximately three nymphs per square centimeter of leaf surface increasing density is beneficial in that significantly faster rates of growth are achieved, and significantly more of the nymphs survive to maturity as density increases.

Beyond this density the trend is not quite so clear. The number of animals maturing decreases, although there would seem to be a continuing increase in the speed of development with increasing

Figure 2.48

Effects of crowding on the survival of *C. densitexta* nymphs to the fifth instar and to adult insects.

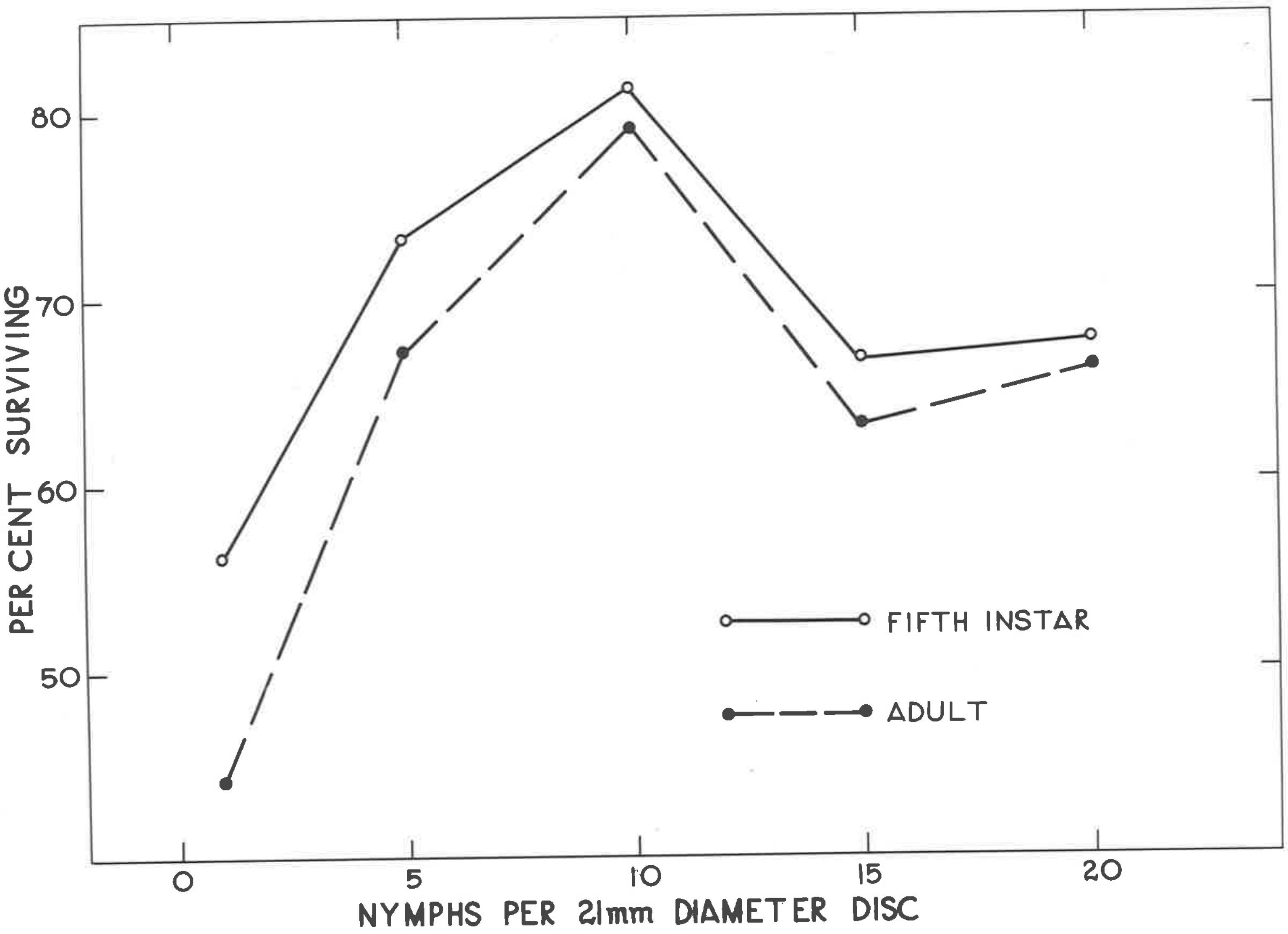

80
70
60
50
PER CENT SURVIVING
0
5
10
15
20
NYMPHS PER 21mm DIAMETER DISC
FIFTH INSTAR
ADULT

Table 2.15

Rate of growth in days to reach each instar of *C. densitexta* nymphs at different densities per square centimeter of leaf under a constant photoperiod of 10 hours, and temperatures of 20°C.

Treatment Nymphs/ Disc	1st Instar	S.E.	2nd Instar	S.E.	3rd Instar	S.E.	4th Instar	S.E.	5th Instar	S.E.
1	14.65	± 0.30	26.27	± 0.75	33.93	± 1.10	40.13	± 1.20	48.91	± 1.20
5	14.35	± 0.30	25.87	± 0.76	34.14	± 1.10	40.85	± 1.00	50.40	± 1.00
10	13.14	± 0.30	22.51	± 0.75	28.20	± 1.00	36.37	± 1.00	44.84	± 0.90
15	13.43	± 0.27	23.75	± 0.65	33.01	± 0.90	38.56	± 0.90	46.21	± 0.90
20	12.97	± 0.21	24.22	± 0.52	30.03	± 0.80	36.12	± 0.70	44.24	± 0.80
$\bar{x}$	13.71	± 0.28	24.52	± 0.69	31.86	± 0.98	38.41	± 0.96	46.92	± 0.96

density. On balance it would seem that crowding beyond the density of 3 nymphs per square cm. becomes unfavourable.

These results can be interpreted in terms of amelioration of the plant tissue by salivary secretions as is discussed a little later in this section.

2.64 Feeding

2.641 Mechanism and Site of Feeding: The stylets of nymphs are naked and when not inserted into the leaf are carried in a loop in front of the body, only the tip being held in the labium. (A frequent cause of death of newly emerged nymphs - at the time of hatching and with handling in the laboratory - is the displacement of these stylets from the labium, making it impossible for the animal to feed). Insertion, withdrawal and probing are all reflected in movements of this loop and of the dorsal surface of the head where muscles are attached.

It is assumed that the mechanism of penetration is similar to that proposed by Weber (1930) and Pesson (1944) with the exception that the mouthparts are always inserted through stoma. This is an interesting habit which, from my own and Clark's (1962) observations, would appear to be common to many if not all Australian leaf-feeding psyllids, both nymphs and adults. It is recorded for a few aphids (Auclair, 1963) and some Aleyrodids (K.M. Smith, 1926) but not, as far as I can ascertain, for any psyllid outside Australia. In one paper (Eyer, 1937) there is an illustration of a leaf section with stylets apparently entering through a stomata, but no mention of this is made in the text. (Jensen (personal communication, 1965) knows of no record for North American species of this mode of insertion of stylets).

A feeding "track" which is formed by the closely related C. albitextura usually ends in phloem tissue or sheathing parenchyma (Clark, 1962). Although I have not investigated this point, it would seem reasonable to assume that C. densitexta feeds in the same manner.

It is often stated that aphids which produce copious amounts of honey-dew are obligate phloem feeders, while those producing little or none are not, or at most facultative, phloem feeders (Bodenheimer & Swirski, 1957; Klomp, 1957; Kennedy & Stroyan, 1959). Some psyllids, as well as building lerps, produce considerable quantities of honey dew. These species show marked tendencies to settle over veins and do not produce any discolouration of the host tissue. A species of Glycaspis on E. baxteri is an extreme example of this (fig. 2,51). Nymphs of Cardiaspina and similar species do not produce honey dew, and do not show any tendency to settle on or near veins*. There is no evidence in the form of collapsed or punctured cells to indicate that Cardiaspina species are mesophyl feeders rather than phloem feeders, in spite of the absence of honey-dew. Clark maintains (personal communication, 1965) that the psyllids which produce honey-dew are probably xylem feeders. It seems more likely, however, that these are tapping the larger phloem vessels of the main and

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* I have once observed first instar nymphs of C. densitexta settling above the main lateral veins at the base of a very young pink gum leaf which, although almost fully expanded, was not yet hardened and darkened.

lateral veins of the leaf, while those which do not produce honeydew are feeding from the fine vessels in the lamina (see also section 2.65).

2.642 Effect of Feeding on the Tissues of the Plant: The nymphs cause death of leaf tissue in the immediate vicinity of their feeding. This actual killing of leaf tissue at the site of larval feeding is the most obvious and probably the principal damage inflicted upon pink gum by C. densitexta (figs. 2.49 & 2.50). There is little or no visible sign of this injury until the nymph is in the late third to early fourth instar. At this stage a light yellow discolouration is visible immediately beneath the lerp. This rapidly spreads, turns pink and then deep red. Shortly after the adult insect has emerged, the discoloured tissue dies, becoming a brown dry patch in an otherwise healthy leaf. This dead patch will usually be several times the area of the vacated lerp, and sharply limited by the mid, lateral or sub-marginal veins. If two or more nymphs have settled near each other the dead areas will coalesce, and when there are many individuals, the whole leaf is killed. During outbreaks nearly all leaves in the crowns of trees growing over a large area may be killed (particularly in the spring) appearing as if a hot ground fire had swept through the area. (The local name for these attacks is "fireblight").

That this destruction of the leaf tissue is the cumulative result of continuous nymphal feeding is demonstrated by the two

Figure 2.49 and 2.50

Damage to leaves of E. fasciculosa from feeding by C. densitexta nymphs. White areas are dead tissue, dark areas are red tissue, and the remainder of the leaf is green. Note the uneven "clumping" of lerps into groups.

Scale: 1 division = 1 mm.

2.49 = moderate damage   2.50 = heavy damage.

following experiments.

At various times between May and October 1963 ten leaves, selected at random from previously chosen heavily infected ones, had both sides of one half (also selected at random) of each carefully cleaned of all lerps. In the spring, after adult emergence had finished, the numbers of dead and living half-leaves were counted. Table 2.16 and figure 2.52 illustrate the results.

Table 2.16

Effect of removing C. densitexta nymphs from foliage at different times after settling.

Number of weeks from settling of nymphs to cleaning of half leaves	0-4	15	17	19	22
Number of cleaned half leaves dead after completion of adult emergence.	0	2.5	5	6	10
Number of infested half leaves dead after completion of adult emergence.	10	10	10	10	10

Half leaves were not cleaned during June and July as the first instar nymphs "sit" through the winter months and do not grow appreciably until August. A peculiar feature noted was that discolouration started to show up on the cleaned halves before any sign of necrosis could be detected beneath the living nymphs on the opposite sides of the leaves.

A second more precise laboratory investigation was made with insects of known age, on discs of leaf floated on water, and

Figure 2.51

A species of <u>Glycaspis</u> on <u>E. baxteri</u> leaves. Note the strong preference for feeding along the main veins of the leaves. The glistening of the leaf surface is caused by light reflecting off the sticky coating of honey-dew spread over the surface.

Figure 2.52

The result of removing first instar <u>C. densitexta</u> nymphs from one side of <u>E. fasciculosa</u> leaves. The white areas under the lerps are dead leaf tissue and the dark parts are green and turgid.

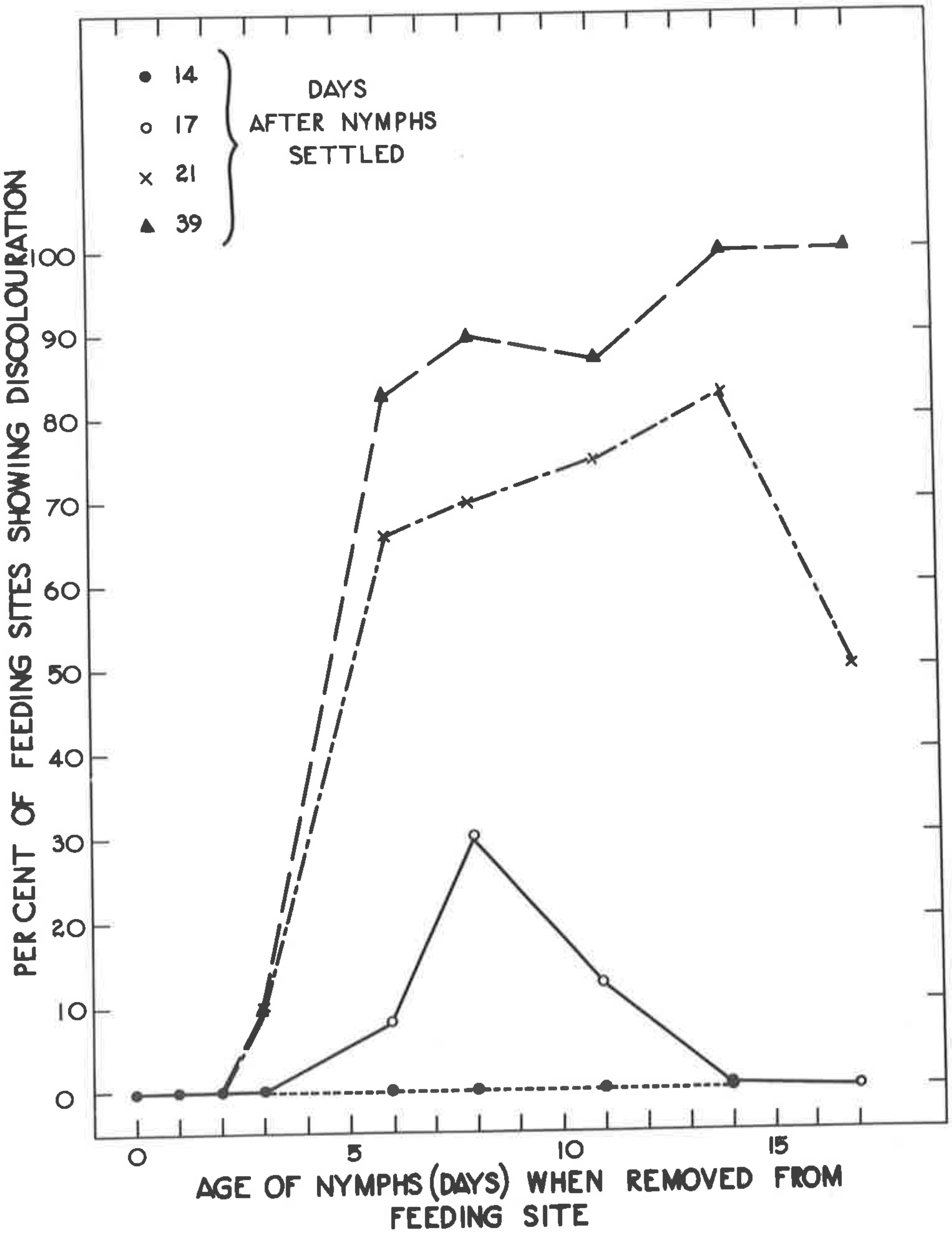
Scale: 1 division = 1 mm.

maintained at 20°C and at 10 hour daylength. This experiment consisted of allowing a number of newly hatched nymphs to settle and then removing some of them on succeeding days. Removal was accomplished by irritating each nymph with a fine brush until it withdrew its mouthparts from the leaf, and walked out from under the lerp. This ensured that broken stylets were not left in the leaf as would often happen when scraping off the insects in the field. (This could have contributed to the premature discolouration observed). Each vacated lerp was marked with a number, and all sites were inspected at intervals until the completion of the experiment.

The results (fig. 2.53) indicate that nymphs must feed for about aweek under constantly favourable conditions before any discolouration of the host tissue will occur. The amount of tissue discoloured and killed remains very small until the nymph is well into the third instar when removed. Even then it is very little compared with the intense reddening and necrosis occurring after completion of nymphal feeding. Discolouration is quite definite, however, and clearly visible where nymphs of more than a week old have fed. Clark (1962) says that any nymph (of C. albitextura) which survives beyond the second instar discolours the leaf tissue. This early discolouration is of importance in studying the ecology of these insects as it provides a ready means of observing sites where nymphs have fed and subsequently died or been destroyed, and approximately when death occurred (the eventual size of the discoloured patch of leaf tends to increase with age of the nymph

Figure 2.53

C. *densitexta*: Effect of time after settling of removal of the nymph from the feeding site on the rate and extent of discolouration of the leaf tissue at the feeding site. Note the "lag" effect, discolouration appearing at vacated feeding sites while there is no sign of discolouration where nymphs are still feeding.


● 14
○ 17
× 21
▲ 39
DAYS AFTER NYMPHS SETTLED
PER CENT OF FEEDING SITES SHOWING DISCOLOURATION
0
10
20
30
40
50
60
70
80
90
100
0
5
10
15
AGE OF NYMPHS (DAYS) WHEN REMOVED FROM FEEDING SITE

at death or departure, and when late second to early third instar nymphs die, the tissue goes yellow rather than pink or red).

More important, however, is that the absence of any discolouration under small dead nymphs, or where lerps were built and have subsequently disappeared, provides sure evidence that these nymphs only lived for a few days. (see sect. 5.2).

The other point of interest arising from this experiment is the quite definite delay of discolouration under living nymphs compared to vacated feeding sites. This confirms the previous field observation (fig. 2.53 illustrates this "lag" effect). I am unable at the moment, to offer any adequate explanation for this difference.

2.643 Possible Causes of Damage to the Host's Tissues: All species of the genus Cardiaspina investigated, as well as some members of other lerp-forming genera, have this effect of discolouring and killing the tissues of their host. Others cause various forms of pitting, galling, twisting, rolling or callousing of leaves. Many cause no visible damage. (Most of the Australian free-living forms and Glycaspis-like lerp-builders fall into this latter category). Others cause stunting or reduced yields indicating translocation of the causative agent from the feeding site (Wallis, 1955; Harris, 1936) and some cause the complete death of the host (Lindner et al., 1962).

That psyllid nymphs damage host tissue when feeding has been known for many years (Scott, 1881) but the cause of this damage is still not fully understood. The present weight of evidence would tend to indicate a toxic salivary secretion. Clark (1962) presumes this to be the case with C. albitextura, but makes no further comment. Other workers (e.g. von Bollow, 1960; Taylor 1962) have made similar assumptions.

Pear Decline, a disease associated in America with the pear psylla, Psylla pyricola Foerst., is reported on the one hand to be a virus disease transmitted by the psyllid (Jensen et al., 1964) although the toxin/virus relationship is still not fully explained (Jensen, personal communication, 1965) and on the other hand to be purely a toxic condition (Williams and Lindner, 1965), the actual toxins probably originating in the mycetome (Lindner, personal communication, 1964).

Another important disease in America, Psyllid Yellows of tomato and potato, is associated with the feeding of Paratrioza cockerelli (Sulc.). D. Carter (unpublished Ph.D. thesis, quoted by Jensen in personal communication, 1965) "confirmed in a more detailed and quantitative way earlier conclusions that this virus-like disease is due to a toxin produced by the nymphs".

Lewis and Walton (1964) have demonstrated that galls produced on Hackberry (Celtis sp.) leaves by several species of Pachypsylla result from the injection with the saliva of a cecidogen which they consider to be a virus. It is produced in the X cells, mycetome and fat body of the insects, and passes from one generation to the next through the reproductive cells. The effect on the plant is to cause the cells to return to the meristematic condition.

Two observations on C. densitexta, although not in any way conclusive, would tend to support the toxin hypothesis.

A cold water extract of fifth instar nymphs was prepared by grinding the insects to a fine paste in distilled water. Five pairs of discs were cut from five healthy "mature" type pink gum leaves. One disc from each pair was floated on distilled water and the other on the "lerp extract" (in 2 x 1 inch vials). Each of the five "lerp extract" vials contained half the concentration of extract in the preceding vial. All were kept at 20°C in a 10 hour photoperiod of approximately 750 foot-candles. All vials were kept "topped up" to the same level with distilled water.

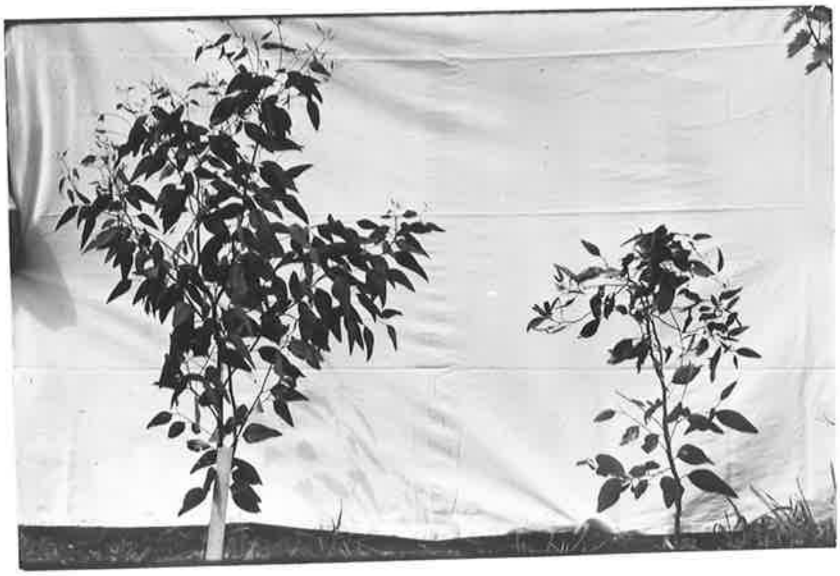
After five days all discs on "lerp extract" showed signs of ill-health. At six days two had extensive dead patches on them, and by thirteen days all five had dead areas. The amount of dead tissue showed a strong gradient, decreasing with decreasing concentration of "lerp extract". Three and a half weeks after commencing this trial all discs on the extract were black and decaying while the five on distilled water were without any sign of necrosis or discolouration.

One of a group of four pink gum seedlings of the same age and size (planted in Adelaide) was artificially infested with large numbers of C. densitexta in December 1963. These numbers were kept high for two generations (i.e. until March 1964) when all were removed. By this time its growth was markedly less than the other three uninfested trees, most of its foliage having been killed. Throughout the remainder of the Autumn and in the following Spring and Summer of 1964/65, although remaining free of psyllids, it put on little new growth, remaining stunted and in marked contrast to the others, which put on large amounts of new foliage (fig. 2.54). This would suggest that there may be a secondary systemic toxic effect which would normally be difficult to distinguish in the field.

It would seem reasonable, in the light of the available evidence, to postulate - as Kennedy (1953, 1958) has done for Aphids - that all these forms of modification of the original host tissue (from discolouration of tissue through pitting and curling to gall formation - all different forms of plant tissue response to feeding by toxinogenic insects (Carter, 1962)) represent a physiological amelioration of the available food supply - specifically, an induced breakdown of tissue - a "premature senescence" resulting in the liberation at the site of feeding of greater amounts of soluble nitrogen (Kennedy and Stroyan, 1959; Fennah, 1953, 1954a, 1955, 1959, 1963). In the case of C. densitexta the area of leaf around the feeding site does in fact senesce at a much faster rate than the remainder of the leaf, but does not die until the insect has completed its growth and departed. Kloft (1957) proposes a similar hypothesis in regard to the feeding of aphids on Abies bark, recording increased concentration of protein around feeding sites to form "physiological galls" under the bark. He has demonstrated

Figure 2.54

Effect of nymphal feeding by *C. densitexta* on seedling *E. fasciculosa*. The tree on the right had been heavily infested for two generations, while the tree on the left had not been attacked. Both trees were the same height and had approximately the same amount of foliage before the right-hand one was infested.



that this increase of soluble nitrogenous constituents results from the feeding of aphids increasing respiration and phosphatase activity in the cells at the feeding sites. He also observed that this "increase in tissue metabolism is more pronounced in such hemipterons which are sucking in the parenchymatic tissue than those forms which feed on the phloem".

Feeding by adults does not cause any visible damage to the host, and it would seem that this is so for many if not all species of psyllids whose nymphs cause some form of damage at the site of feeding, (e.g. Annecke and Cilliers, 1963; Grove and Ghosh, 1914; Eyer, 1937), and for some other homopterous insects (Carter, 1962). Clark (1963a) reports the same thing for C. albitextura, suggesting it may be due to the very short time any one adult feeds at one site. In America D. Carter (loc. cit.) found an occasional adult of P. cockerelli to be toxic, although these were always teneral, and toxicity disappeared in a few days. Richards and Brooks (1958) suggested that this absence of damage from the feeding of adults could be due to degeneration of the mycetome in the adults. R.D Carter (1961) has shown a change in form of the mycetome from nymph to adult, so this could well be true.*

Adult psyllids do not have as high a requirement for nitrogenous food as the immature stages. Being much more active they

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* I have one record of C. densitexta nymphs developing to maturity without causing any discolouration of the leaf tissue. This was on a potted E. fasciculosa seedling in the laboratory, and has never been repeated.

will require a higher proportion of carbohydrates. Increasing the proportion of nitrogenous matter in the food will not therefore be of such great importance as it is for survival and growth of the young nymphs.

Whether this effect on the host tissue is caused by a toxin or a virus (W. Carter (personal communication, 1965) says that the spread of discolouration from the feeding site is _prima facia_ evidence of secretion of a toxic agent with the saliva) or whether the causative agent comes from the feeding sheath or from the saliva, the ecological implications of the end effect are clear. Each nymph apparently has the ability to increase the amount of available food in its immediate vicinity by stimulating the release of soluble amino acids from the plant tissues. To what extent this is successful in enabling any one nymph to survive will depend on the condition of the plant, the age of the leaf, and on the number of other nymphs nearby (see sect. 2.633).

2.65 Food and its Influence on Abundance.

From the evidence presented in chapter 3, it would seem legitimate to make the following conclusions about the food which is available to psyllids.

(1) The most important, although by no means the only necessary nutrients are the soluble nitrogenous compounds, and particularly the amino acids, which become available directly from photosynthesis (e.g. Osipova & Nikolaeva, 1964; Zak & Nichiporovich, 1964) from

hydrolysis of stored root protein (e.g. Bolland, 1957; Gordon, 1964) or from sites of senescence and death (e.g. Kennedy, 1958, *et ante*; Fennah, 1953).

(2) It is the first instar nymphs especially when they are first settling and feeding which are most dependent for their survival upon an abundant supply of these nitrogenous nutrients.

(3) These substances are *not* generally or continually available at all possible feeding sites on the plant. They are, in fact, only rarely, and usually very locally available *in concentrations sufficient to provide adequate sustenance to the young insect*.

(4) These soluble nitrogenous nutrients are continually in transit from their sites of origin or release, but become concentrated to a greater or lesser degree at certain sites.

(i) *Actively growing tissue*: These are the sites of maximum protein synthesis, and high concentrations of amino acids will result both from photosynthesis and translocation. The main veins leading to these sites will be carrying high concentrations of nutrients which will be readily available to an insect tapping the veins. The small ultimate veins of the leaf lamina will also carry high concentrations of amino acids, but anabolic pressure will make it difficult for an insect probing at this site to gain sufficient of them (see Fennah, 1955).

(ii) *Senescing tissue*: Hydrolysis of protein will be occurring in all senescing tissue, releasing soluble nitrogen at a fairly steady rate for translocation to regions of growth or storage. This rate will increase with the age of the tissue, but never equal the initial inward rate of flow to meristematic tissues. These solutes will, however, be much more readily available to an insect probing the fine veins or the surrounding tissue in the lamina.

(iii) <u>Wound tissue</u>, including sites where feeding insects chew or otherwise rupture cells or attack them with salivary proteases. Protein breakdown in dead and damaged cells will provide a locally high concentration of soluble nitrogen.

(iv) <u>Feeding sites of certain sap-sucking insects</u>. Where an insect introduces a salivary substance or substances which cause hypertrophy and/or a speeding up of the metabolism of the tissue around the feeding site - ("a condition of chronic juvenescence-senescence", Kennedy, 1953), soluble nitrogen will be locally more abundant. Galls are the most obvious of these sites, but all forms of disruption of the normal metabolism, including the damage from <u>C. densitexta</u> and similar psyllids, belong to this category.

(v) <u>Water-stressed tissue</u>. Poor physical condition of the soil, lack of nutrients or trace elements, poor drainage, excessive crowding or shading, wounding, flooding, droughting; all these things will result in water-stress in the tissues of the plant, and a concomitant and proportional increase of soluble amino acids in these tissues.

Such stress will increase the percentage of soluble nitrogen throughout the whole plant thereby intensifying the concentrations of these nutrients at the sites listed above.

Although C. densitexta is a phloem feeder, it feeds in the small ultimate veinlets in the lamina of the leaf. In this it is distinct from many other psyllids which tap larger veins (e.g. Glycaspis sp., see Moore, 1961, and fig. 2.51). It is also distinct from these species in that it will not colonize young soft new growth, and that it causes discolouration and death around the feeding site.* There is no puncturing, collapse, or distortion of cells at the feeding site, merely a diffusion of a presumed substance or substances which cause cells around the feeding site to senesce more rapidly than those further away on the same leaf.

I have already postulated in the previous section that this feeding damage is a method of increasing the supply of soluble nitrogen in the immediate vicinity of the site of feeding, thus supplementing that already available from photosynthesis plus hydrolysis.

If this is, in fact, what happens when a nymph of C. densitexta settles and starts to feed, and assuming that the physiology of pink gum leaves is similar to that of other leaves, then a number of things demonstrated in the preceding sections become explicable in terms of availability of nutrients.

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* Species of Glycaspis (Moore, 1961; and Clark, pers. comm.) will cause discolouration of leaves when their numbers are very high, but this is quite distinct from the killing around individual insects seen in Cardiaspina.

A: The preference for "mature" type leaves and the rejections of "young" and "old" leaves for oviposition and nymphal settling.

Anabolic processes in the young expanding leaf are at their maximum, the "pressure" in the direction of protein synthesis being very great, and probably offering strong resistance to any protein hydrolysing activity from the nymphs' salivary secretions. The newly mature leaf on the other hand, having just past its apogee of protein synthesis, and starting on the slow decline of senescence, will have a greatly increased proportion of soluble nitrogen which is readily available. The "pressure" of protein synthesis is now replaced by the start of hydrolysis of protein, and at the same time photosynthesis is still at a maximum, producing nutrients for translocation away to areas of storage or growth (e.g. Fennah, 1954, Fig. 6; and Fennah, 1963).

The old leaves will have exhausted most of their protein and will have very low rates of photosynthesis.

B: The movement of preference down the twig with increasing age of the leaves is similarly explained in terms of the amount of soluble nitrogen available to the probing insect.

C: The increased rate of growth and percentage surviving with increasing numbers of nymphs settling per unit area of leaf. The combined action of the salivary "irritants" of the nymphs feeding in one spot will make a greater amount of soluble nitrogen available at that spot, materially improving the chances of any one individual getting enough to eat.

D: The greater rate of growth and percentage surviving on the north sides of tree crowns. The metabolic rate of sun leaves is faster than the equivalent shade leaves, and they have a higher proportion of soluble nitrogen available than the shade leaves throughout their life (e.g. Fennah, 1954, fig. 5 & 6).

E: The greatly increased numbers of psyllids surviving during times of drought. The application of water-stress to the plant decreases anabolic activity and increases the proportion of soluble nitrogen throughout the plant. The effect of this will be particularly marked at the site where first instar nymphs are settling and probing for food. If this stress supplements the action of the nymph's salivary secretions sufficiently to give these young animals enough nutriment to survive and grow on tissue which would not have supported them in the absence of stress, many more will survive.

F: The absence of honeydew. By concentrating the soluble nitrogen content at the feeding site a lesser quantity of sap need be ingested to obtain adequate nutrients, all surplus being incorporated into the construction of the lerp (cf. Mittler, 1958c).

These features contrast sharply with those of many free living psyllids and aphids, and some lerp-forming psyllids which do not kill or deform the host tissues. Presumably none of these animals have the "ability" to induce the host tissue to increase the quantity of soluble nitrogen in the sap (cf. Kloft, 1957 and Mittler 1958d). This means they are dependent on what is already present in the plant, and must therefore seek out the sites of greatest concentration of amino acids. This would explain why these sorts of insects feed only on rapidly growing or rapidly senescing tissue (Kennedy, Ibbotson & Booth, 1950; Moore, 1961) why they feed in major vessels (Moore, 1961) and why they produce large quantities of excrement in the form of honeydew.

2.7 Parasites and Predators

2.71 Parasites

Three species of encyrtid parasites which, although they have not been specifically identified, would appear from their general appearance, stage of host attacked and killed, and type of "mummy" produced, to be the same or very similar to the three *Psyllaephagus* species recorded by Clark (1962) as attacking *C. albitextura*.

General observations and counts support Clark's finding that the numbers of parasites tend to be low in the spring generation, and to increase to a maximum each autumn.

At no time, however, have I counted more than 10% total parasitism of *C. densitexta* by all three species combined, and it was very soon obvious that these parasites play little if any part in reducing the abundance of this psyllid.

The role of these encyrtids in the population ecology of psyllids is discussed in section 5.2.

2.72 Predators

2.721 Invertebrate Predators: A number of different invertebrates prey upon *C. densitexta* at all stages of its life history, but of these the only ones observed to be at all plentiful were several species of ants and the larvae of a syrphid fly (near *Syrphus viridiceps* - see Clark 1963c).

Of the ants, the ubiquitous "meat ant", *Iridomyrmex* detectus Sm. is the most commonly observed predator. The workers take fifth and occasionally fourth instar nymphs from beneath the lerp.

Clark (1964a) states that this ant removes the lerp in the same way as do predatious birds. I have many times witnessed these ants collecting nymphs, but have never seen more than a slight tear made in the edge of the lerp. Usually the edge of the lerp is grasped in the mandibles and twisted so that the ant can reach under, grasp the nymph, and pull it out. This twisting leaves a "kink" (occasionally a tear) which soon disappears, so that later there is no way of distinguishing the vacated lerps from ones from which the adults have emerged. Syrphus larvae when encountered, were taken just as readily as the C. densitexta nymphs.

Several other smaller ants have been observed to take nymphs in the same manner, and adult psyllids are sometimes taken.

In general the relationship of ants to lerp-insects would appear to be that of the casual predator/scavenger taking anything edible encountered on the foliage. The great majority of ants on eucalypt foliage are there primarily to search for insects producing honey-dew.

The syrphid was only once observed to be at all plentiful, and that was in the spring of 1963, the last occasion that its prey - the fourth and fifth instars - have been in high numbers. At this time I estimated that 5% - perhaps 10% - of the late instar nymphs were killed by this predator. However, had it been 50% of the total population, this would have made little impression on the next generation, merely serving to "cream off" some of the surplus from the vast numbers then present.

Clark (1963c) came to much the same conclusion about syrphid predation of C. albitextura, stating that "... mortality caused by Syrphus played only a minor part in the determination of psyllid abundance".

Other invertebrate predators observed - none in numbers high enough to make any measurable impression on the numbers of psyllids present, but all common when the numbers of psyllids were high, were briefly as follows:-

Arachnida - Several species of hunting or "wolf" spiders were observed taking adults, and many adults became trapped in spiders' webs.

Neuroptera - Larvae of a hemerobiid and a chrysopid have been observed taking late instar nymphs. Adult lacewings and their eggs were quite common in areas of high population.

Coleoptera - A small coccinellid larva was found attacking and eating newly hatched nymphs often before they were free of the eggshell. Several of these larvae were kept alive for some weeks on leaf discs bearing eggs, but no adults were obtained.

Diptera - A small black biting midge (Ceratopogonidae) attacks callow adults as they are emerging from the nymphal skin, piercing them with its proboscis and sucking the body contents.

A small asilid-like empidid fly hovers on the lee side of trees in which adult psyllids are active, and pounces upon those adults which fly out from the foliage.

Quite frequently late instar lerps are found empty with a small ragged hole in them. There is never any sign of the remains of a nymph beneath these lerps, or dried body fluids on the lerp (a punctured nymph will usually leave brown stains on the lerp), and yet the holes are too small for a fourth or fifth instar nymph to have been dragged through them. Furthermore the edges of the holes are always bent inwards as if a sharp point had been driven through the lerp from above. I have also found several lerps with active nymphs still under them and with one of these holes patched over from beneath. In spite of many hours of searching and watching, I have never seen these holes being made, and cannot imagine what is making them.

Moore (1961) records a similar array of predators on *Glycaspis baileyi* Moore, and various northern hemisphere authors commonly report spiders, syrphids, coccinellids, neuropterons and anthocorids as predators of psyllids. The general opinion throughout, is that in the regulations of numbers of psyllids "apparently none of these are of any importance" (van der Merwe, 1923).

2.722 Predation by Birds: In the summer and winter of 1963, when numbers of *C. densitexta* in the mid-Southeast were high, several species of small birds which frequent the crowns of trees were occasionally observed picking in a desultory manner at the great aggregations of lerp-insects on the foliage around them. Sustained and concentrated feeding was never seen, and all attempts to approach closer to these birds caused them to move away. (Observations were made through binoculars). Foliage collected from where birds had been seen searching through the crown rarely revealed signs of more than one or two psyllids having been removed from among the many hundreds on the leaves. (The "hinge" of the lerp left on the leaf when a lerp-insect has been taken by a bird is quite characteristic - see Clark 1964a, fig. 2).

During the autumn of 1964, when some of the remnant populations of C. densitexta had moderate numbers present, small groups of birds were several times observed moving through infested foliage and feeding on the late instar nymphs. They still kept high up in the tops of the trees, however, moving continually from one place to another, and merely pecking at a leaf in passing.

By the spring of 1964 numbers of C. densitexta had fallen to the point where only small isolated groups remained. These often consisted of no more than a few dozen insects on one isolated twig, although occasional trees with a number of infested shoots could still be found.

As these insects developed to the fourth and fifth instar, they became readily apparent as the leaves on which they were feeding discoloured and showed up red among the green foliage.

At this time birds began to feed on these insects, and in a very deliberate and systematic manner. Each patch of infested foliage was thoroughly searched leaf by leaf, and for the first time I was able to approach to within two or three yards of these birds, and without binoculars, watch them feeding.

The birds take the insects with the side of the bill, each peck producing a click audible from several yards away. Both the nymphs and their lerps are consumed. A series of quick sweeping pecks moving from the base of the leaf towards the tip, usually served to remove most nymphs and their lerps from its surface.

In every case the birds seen feeding at this time were diamond-backed sparrows (Pardalotus sp.) but I have seen waxeyes (Zosterops sp.), tits (Acanthiza sp.) and a wren-like species taking nymphs of C. densitexta. James (1964) also records Pardalotes feeding on C. densitexta nymphs in the autumn of 1964.

To gain some measure of the extent of this predation by birds on the remnant population, several twigs were collected and counts made of the number of nymphs eaten.

The twigs to be sampled were selected by their red colour, and from a distance where it was not possible to see whether or not the insects had been removed. (The fact that nearly all nymphs were on the lower sides of leaves helped to reduce the bias. Not until a discoloured leaf was turned over could any idea be gained of the numbers removed).

As Clark (1964a, fig. 2) has shown, the number of nymphs removed can be determined by the small pieces of lerp "hinge" left adhering to the leaf. Sometimes even this is removed so counts tend to underestimate the numbers that were eaten.

Table 2.17 gives the result of a series of these counts from the northern limit of pink gum in the south east (Culburra) to a point 16 miles north of Naracoorte.

Table 2.17

Bird predation of C. densitexta at seven sites in the southeast of South Australia in November, 1964.

Locality	No. of twigs sampled	Total psyllids counted	$\bar{x}$ lerps per twig	% total eaten per twig and range	
Culburra	3	1154	385	79.2	-
Brecon	3	738	246	86.7	83.5 - 91.0
Desert Camp (a)	9	902	100	98.2	95.8 - 100.0
Desert Camp (b)	12	931	78	61.0	5.1 - 97.0
Western Flat	5	321	64	97.4	75.0 - 100.0
Padthaway	11	262	24	82.6	28.6 - 100.0
The Gap	11	98	9	96.4	82.4 - 100.0
Total	54	4406	-	-	-
$\bar{x}$	7.7	-	81.6	85.9	

These figures would indicate that throughout the southeast, something in excess of 80.0% of the remaining C. densitexta population was being destroyed by birds. This is probably an over-estimate as the feeding birds do not discriminate between lerps from which adults have emerged, and those still containing nymphs. However, it seems clear that, at this level of population, bird predation is playing a significant part in reducing the numbers of nymphs surviving in this generation. It is doubtful, however, whether it would have made any difference to the numbers of nymphs establishing in the next generation.

Cleland _et al._, (1918) reported 15 species of birds "feeding on psyllids" but did not distinguish between adults and nymphs. Lea & Gray (1935) did make this distinction and reported 25 species actually having "lerp-scale material" in their stomachs. Campbell & Moore (1957) record the bell bird feeding on _Glycaspis_ nymphs and P.G. Martin (personal communication) records Musk lorikeets feeding on _Glycaspis_ nymphs.

Clark (1964a) records three species of birds feeding on _C. albitextura_ nymphs, with a Pardalote being predominant. He also confirms that their feeding is confined to the late nymphal instars.

His conclusions agree with my observations that at high psyllid population levels bird predation is negligible, but becomes significant when numbers are lower, _patches_ of high density being discovered and eaten.

Tinbergen (1960) working with species of _Parus_ preying on various lepidopterous and hymenopterous larvae in Scots pine forests in Holland, found a similar relationship (see fig. 8, Tinbergen & Klomp, 1960) and proposed the hypothesis that these birds develop "specific searching images" for different prey species.

This hypothesis would satisfactorily explain the observed levels of predation by birds on lerp-insects.

At very low levels of *C. densitexta* abundance, such as is usually found on pink gum in the Mt. Lofty Ranges, encounters would be too few for the birds to develop a specific searching image. If numbers increased to a level where clusters of lerps and red patches of foliage are produced, the birds' behavioural responses are such that by developing a searching image for this insect they can quickly take advantage of an increased food supply. Should this increase continue, the searching image for this particular species is lost or masked, thus preventing the diet of these birds from becoming "unbalanced" (Tinbergen, 1960). A similar mechanism could be expected with decreasing abundance of *C. densitexta*, the specific searching image only becoming operative over a fairly narrow range of density.

Whether or not this is a correct interpretation of the observed feeding behaviour of small insectivorous birds, it is apparent that they are not able to prevent increases to outbreak level, nor, I would contend, will the *decrease* of a population be significantly hastened by this predation. The birds are merely responding to behavioural stimuli which prevent them from spending long periods hunting for a rare food species, or gorging themselves on an excess of one type of food. These stimuli are "switched on and off" as changes take place in the abundance of the various organisms which constitute the food of these birds. Buckner & Turnock (1965) would seem to have observed a similar type of attack at intermediate level of abundance, and Readshaw (1965) shows that birds have no measurable effect at high density of the prey, but at low densities "birds were largely responsible for the almost complete elimination of ... the small pockets of relatively high prey density ..." (my emphasis).

3. THE VIGOUR OF THE PLANT AND INSECT ABUNDANCE

3.0 Introduction

It has long been recognised by foresters that the intrinsic vigour or health of a tree is in large part responsible for the success or otherwise of some insects and diseases attacking it, and that this vigour is determined by the complex of climatic, edaphic and physiographic factors, collectively termed the "site-conditions", under which the tree is growing. Accordingly, insects attacking trees are commonly placed in one of two categories, primary or secondary, according to whether they are independent of or dependent upon, some debility within the tree (Rawlings, 1953).

Bark beetles, woodborers and wood attacking fungal pathogens usually occur at a time when the tree is already visibly debilitated, and are secondary; foliage eating and sap sucking insects are classed as primary. Most primary insects persist at low levels of abundance, but some species multiply occasionally to outbreak proportions. Even those that seem never to have outbreaks are known to have enormous powers of increase.

The usual explanation for the prevailing low numbers is given in terms of heavy pressure from parasites and predators and the occasional outbreak is explained by the temporary release of this pressure. Even when the importance of fluctuations in the weather has been recognised the explanation has usually been sought in terms of the direct influence of the weather either on the phytophagous insect or, more usually, on its parasites and predators.

It has been tacitly assumed (with a few exceptions - see Huffaker, 1957, 1964) that the plant remains uniformly favourable as a source of food and that while the insects are few they are surrounded by an abundance of good food. This is a misleading assumption because the plant does not remain consistently a source of good food for phytophagous insects independent of fluctuations in its own environment. Fluctuations in weather can alter quite profoundly the condition of the plant, especially the nutritive value of its tissues as food for phytophagous insects.

3.1 The Relationship of Soil-moisture to Vigour of the Plant

It is obvious that excessive wetness or excessive dryness of the soil may kill trees and other perennial plants. What is more important for the purposes of this discussion is that plants that are exposed to sub-lethal levels of wetness or drought may have their condition changed so that their tissues become higher quality food for the insects that may feed on them.

In a waterlogged soil the fine feeding roots are drowned. In a dry soil the roots cannot absorb the water and dissolved nutrients that the plant needs. If drought follows close on the heels of flood the plant may react more strongly to the drought simply because it has lost a proportion - perhaps a large proportion - of its feeding roots during the recent flood. This is a circumstance likely to occur in a mediterranean climate where the winter is wet and the summer is dry, and any departure from the mean in the direction of abnormal rain during winter and subnormal rain during summer may stress the plant in this way. Of course flood and drought are relative terms depending for their effectiveness on the soil, topography, aspect, temperature and other components of the plant's environment.

3.2 The Relationship of Soil-moisture to Insect Abundance

There are many records in the literature of the correlation of increased abundance of many different phytophagous insects with drought. These are discussed in more detail in chapter 4. There also are numerous references to similar responses to waterlogging (e.g. Withycombe, 1926; Smee & Leach, 1932; Smith & Harris, 1952; Fennah, 1959; Kostik, 1965) including one of a psyllid (Howard, 1921; and see also Batjer & Schneider, 1960), and of soil conditions combined with summer drought being associated with increased abundance of insects (e.g. Szontagh, 1962; Heikkenen, 1964).

3.3 The Relationship of Soil-moisture to the Nitrogen content of the Plant.

Although there is still some difference of opinion (e.g. Stocker, 1961; Specht, 1965) it is now generally accepted that the soluble nitrogen increases in drought-stressed plants, including those physiologically drought-stressed by waterlogging (e.g. Richards & Wadleigh, 1952; Fennah, 1955, 1959, 1963; Vozhenko & Shkol'nik, 1963; Gordon, 1964; Chen *et al.*, 1964).

A general decrease in protein synthesis and conversion of existing protein into water soluble forms takes place, increasing the water retaining forces of the plant tissues. There is an increase in total nitrogen in aerial parts of plants and a decrease in the roots, as stored root protein is mobilized in response to dehydration. Although there is an overall rise in soluble nitrogen, the individual amino acids within the common pool <u>increase and decrease at different times and rates without exhibiting any common pattern</u>. A phytophagous insect could therefore be expected to respond differently to different degrees and duration of stress of the plant, according to its amino-acid requirements. Two closely related species could each respond quite differently to the same degree of stress of the plant if their amino-acid requirements differed. but do they?

3.4 <u>The Relationship of Nitrogen Changes in the Plant to Insect Abundance</u>

Earlier workers (e.g. Lee, 1926; Mumford & Hey, 1930) had suggested that the nitrogen content of the plant may be important to the success of insects feeding on it. There are now many records of the greater success of phytophagous insects (e.g. Evans, 1938; West, 1945; Smith & Northcott, 1951; Bottger, 1951; McGinnis & Kastings, 1961; Ting, 1963; Knapp <u>et al</u>., 1965, Metcalfe, 1965), and mites (Hamstead, 1957; Breukel & Post, 1959; Rodriguez, 1960; Cannon & Connell, 1965) being positively correlated with increased nitrogen in the food plant.

In recent years several workers in different fields have demonstrated that the response is to increases in the soluble nitrogen - and especially to amino acids - in the host plant (e.g. Auclair et al., 1957; Maltais & Auclair, 1957, 1962; Mittler, 1958; Marble et al., 1959; Kennedy et al., 1958; Fennah, 1953, 1955, 1959, 1963; Hirano, 1964).

Experiments with artificial diets have shown that amino acids are essential for larval growth, and that comparatively minor changes in their absolute and relative amounts can have major effects on the growth and survival of larvae of a variety of insects (e.g. Vanderzant, 1958; House, 1959; Dadd & Mittler, 1965). Quite small quantities may have large effects. Simple imbalance of the relative amounts of different amino acids can be sufficient to retard or prevent development (House, 1965) and may even reach toxic concentrations (Friend et al., 1957).

It is these recently hatched first instar insects which are so dependent on the availability of amino acids in the food plant. As Auclair (1953) states "Young growing animals, rapidly increasing in size and weight, are in constant need for more and more amino acids for the building of new tissue proteins. Many amino acids can be synthesised by the growing animal. Other amino acids cannot be synthesised by the growing animal and finally some can be synthesised but not at a rate rapid enough to satisfy the needs of the growing animal. The animal must receive from an external source the amino acids that it cannot synthesise and this external source is the food".

From the evidence it would seem that it is in fact the first instar (or at most the very young) larvae which die as a result of amino acid deficiency or imbalance in their diet, (e.g. Parson & Marshall, 1941; Fennah, 1953; House, 1954; Beck, 1956; Mittler, 1958a,b; Friend et al., 1957; Pant & Kapoor, 1964) and it would also seem that in nature most mortality occurs in the early larval instars (e.g. Pletsch, 1947; Morris et al., 1963).

3.5 The Relationship of Nutrition of the Plant to Insect Abundance

That the nutritive value of a plant is important to the phytophage is well recognised (Friend, 1958; Morris et al., 1963) as is the fact that nutrition of the plant is of importance to the success of insects and mites feeding on it. There are, however, many conflicting reports about the response of insect and mite numbers to the application of fertilizers to the soil or nutrient solution in which the food plant is growing (Rodriguez, 1960; Megalov, 1963; Eidmann, 1963; Henneberry & Shriver, 1964; Hirano, 1964; Scott, et al., 1965; Stark, 1965).

Work in Europe on the application of fertilizers to forest soils has demonstrated that on impoverished sites, this treatment results in a marked improvement in the vigour of the trees and a decrease in the abundance and vigour of the insects on them (Stark, 1965). These results are at variance with the concept of "primary insects", and led to attempts to locate poisonous or repellent substances in the foliage of trees after treatment with fertilizers (Eidmann, 1963).

An alternative explanation, which has been supported by Eidmann (1963), Rudnew (1963), and Schimitschek (1963, 1964), is that the insects are favoured by a physiological condition of the tree which develops when the tree is stressed from any cause whatever. This explanation makes the concept of "primary" and "secondary" insects redundant. Schwenke (1963) went further than this, stating that the limiting element in the diet of phytophagous insects is the sugar content of the sap, and that this drops below a critical minimum level when the "water management" of the tree is improved by application of fertilizer, or rain following drought.

I agree with Schwenke (and the others) that it is indeed the changes in the physiology of the tree in response to conditions of water stress which are primarily responsible for increases in abundance of insects feeding on any <u>living</u> part of the tree, and think they are right in rejecting the distinction between primary and secondary insects. The changes of the sugar concentration, however, are not important (although they may help with later instar larvae (e.g. Beck, 1956)). It is the changes in the soluble nitrogen content of the sap so vital to the first instar insects, which are critical.

The response of amino-acid content of plants to the application of fertilizer is complex (Parish, 1965; Carter & Larsen, 1965). If a plant is suffering from mineral deficiency it will have a higher amino-acid content (Steinberg, 1951; Baxter, 1965) and the application of fertilizer will decrease this and thus the abundance of insects feeding on the plant. Application of excessive amounts of fertilizer will cause root injury, again stressing the plant (Schwenke, 1963; Eidmann, 1964). Between these two extremes there are a range of conditions where the effect of fertilizer application would vary.

3.6 Previous Work relating Water-stress, Nitrogen changes in the plant, and Insect Abundance

Several workers in different branches of entomology have been arriving at similar conclusions. Markkula (1953) working in Finland with aphids on cabbage, and Fennah (1953, 1954a,b, 1955, 1959, 1963) working in Trinidad on several insects on cacao and cashew, have both come to a similar conclusion about stressing of the plant increasing the available nitrogen for the insects, and Kennedy and his associates (Kennedy *et al.*, 1959; Kennedy & Booth, 1959) discuss the same idea with aphids on sugar beet and Spindle. Ting's (1963, 1964), and Kostik's (1965) work reveal a similar relationship between stress, nitrogen and the outbreak of insects. Markkula demonstrated experimentally the positive correlation of insect numbers with drought-stress of the host plant (see his fig. 29). Similar attempts by Kennedy with the beet aphids gave the opposite result, due to too much drought too quickly applied. As

Kennedy (personal communication, 1964) states it is the "appropriate rate" at which "premature senescence" is induced by the "water strain" which is important in deciding whether or not a particular insect will succeed. Fennah, however, is the one person (whose work I have found) who has fully and convincingly demonstrated that stressing the plant increases the soluble nitrogen content of the tissues, thus determining not only the abundance of the insects, but their feeding sites on the plant.

Other than Markkula's work, the only experimental demonstration of a correlation between soil-water and success of phytophagous insects that I have found, are Withycombe's (1926) demonstration of equal amounts of froghopper feeding causing greater damage to droughted than well-watered sugar cane plants in pots, and Wardle's (1927) demonstration of increased abundance of thrips on cotton plants kept under soil-water stress in the field.

The similarity between the leaf-age preferences, feeding sites, and response to moisture-stress in the host plant, of cacao thrips on cashew and C. densitexta on pink gum are impressive (Fennah, 1963).

My own preliminary attempts at demonstrating that either too little or too much soil moisture will favour psyllids feeding on the foliage of pink gum are given in the following section.

3.7 Watering Experiment

3.71 Materials and Methods

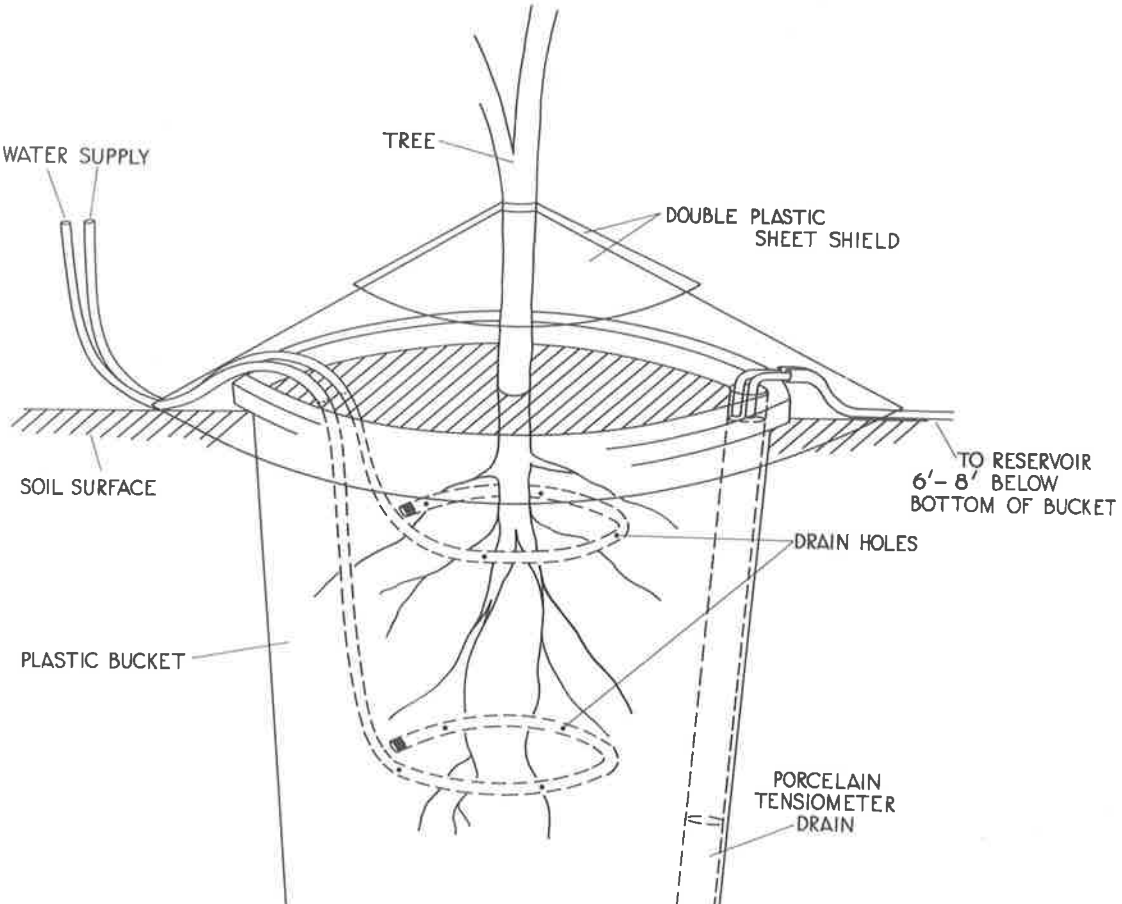
Twenty-five potted E. fasciculosa seedlings were selected from a number grown from seed sown in January, 1963. As far as possible trees of similar size, branching habit and general vigour were selected.

In June, 1964 these trees were transplanted from twelve inch earthenware pots into two gallon plastic buckets prepared as in figure 3.01. Instead of drainage holes, ceramic cup drainage tubes were placed in each bucket as illustrated. Standard Waite Institute "second soil" potting mix was used in all buckets. As each tree was transplanted into a bucket two 1/8 inch bore plastic tubes were introduced with it. As illustrated these were placed in a circle approximately equidistant from the centre and sides of the bucket, and at two heights; approximately four inches and eight inches above the bottom of the bucket. The end of each tube was sealed off, and at approximately every four inches around the circle a 1 mm. hole was drilled. A tightly fitting calico sleeve was fitted over each tube to cover these holes.

The purpose of these tubes was to enable small amounts of water to be distributed as evenly as possible throughout the total volume of soil in the bucket. This avoided the problem arising with conventional top-watering of a wetting face only penetrating a couple of inches below the surface. Tests using glass containers filled

Figure 3.01

C. densitexta - Watering experiment. Method of potting each of the 25 trees in plastic buckets.


WATER SUPPLY
TREE
DOUBLE PLASTIC SHEET SHIELD
SOIL SURFACE
TO RESERVOIR 6'– 8' BELOW BOTTOM OF BUCKET
DRAIN HOLES
PLASTIC BUCKET
PORCELAIN TENSIOMETER DRAIN

with the same potting mix had shown that 100 cc. of water introduced through a small hole in a plastic tube would wet a more or less pear-shaped body of soil about four inches deep and three to four inches in diameter. The calico sheath was to prevent the water "jetting" through the small aperture and making a cavity in the soil, and to prevent the holes becoming blocked by small particles of soil.

After holding these twenty five trees in an open-sided glasshouse for some weeks to allow them to recover from transplanting, the buckets were buried up to the rim in the ground behind a retaining wall. They were buried to aid in keeping the root systems cool, and they were placed behind the retaining wall so that a fall of some six to eight feet was available to enable the drainage cups to function by gravity. These trees were then left for some months so that they could grow and extend their root systems throughout the soil in the buckets. During this time they were watered two or three times a week with distilled water through the plastic tubes, all receiving luxury amounts of water.

In February, 1965 they were all sprayed with Phosdrin to kill all scale and other insects living on them.

Late in March one twig on each tree was selected and covered with a small organdie bag. As far as was possible these twigs were selected to provide "mature" type leaves of as even an age as possible, and free of blemishes.

On the 8th April five female and five male C. densitexta were placed in each bag.

On the 10th May, when all adults were dead, and the trees had been randomly assigned to five lots of five trees, all eggs laid on the enclosed leaves were counted (Table 3.01). Double plastic shields were then fitted around each tree to prevent rain from wetting the soil in the buckets (fig. 3.01), and each of the five lots was randomly assigned to one of the following treatments:-

1. (lot E): Surplus water - kept waterlogged throughout the experiment - drain reservoirs placed above the level of the soil surface.
2. (lot D): Wet - kept soil wet - approximately 500 cc. water per week - drains open.
3. (lot A): Moist - maintained as nearly as possible just below field capacity - soil surface almost dry - approx. 250 cc. per week - drains open.
4. (lot C): Dry - soil surface dry throughout - approx. 125 cc. water per week - drains removed to prevent water being sucked back from the reservoirs.
5. (lot B): Very dry - approx. 65 cc. of water per week - drains removed.

These watering regimes were maintained from the 10th May until the 30th August, 1965, when all twigs (still in their organdie bags) were removed to the laboratory for counting.

The total number of psyllids establishing (as represented by all the lerps on the leaves), and the number of early instar nymphs subsequently dying (as represented by the number of empty lerps and lerps with dead insects beneath them) were counted (Table 3.01).

Table 3.01

C. densitexta on *E. fasciculosa*. Establishment and subsequent survival of nymphs at different levels of soil moisture.

Treatment & Degree of Wetness	No. of Trees	A No. of Eggs Laid	B No. of Nymphs Established	C No. of 1st Instars Dying	Per cent Establishing $\frac{B}{A}$ x 100	Per cent Mortality $\frac{C}{B}$ x 100
A(3) Moist	5	1926	1217	155	68.2	16.2
B(1) Very Dry	5	1512	1059	50	71.5	4.8
C(2) Dry	5	1819	1546	76	84.1	5.0
D(4) Wet	5	1181	953	53	77.5	6.9
E(5) Very Wet	5	1338	1039	86	81.0	7.2

3.72 Results

The success of establishment is measured by considering the total nymphs as a percentage of the original number of eggs laid.

The subsequent mortality of the successful nymphs is measured by expressing the number dying after establishment as a percentage of the successful nymphs.

Counts of numbers establishing showed so much variability between trees that, although the means trended in the predicted direction of greatest mortality on the least stressed trees, no analysis was made of these figures.

Counts of numbers of early instar nymphs dying after settling and feeding also showed great between-tree variability, but this was not as great as with the first counts, and there was a much stronger trend in the predicted direction (fig. 3.02). A quadratic analysis of percentages transformed to angles was therefore carried out on this data. The result shows a significance at the 7% level of probability.

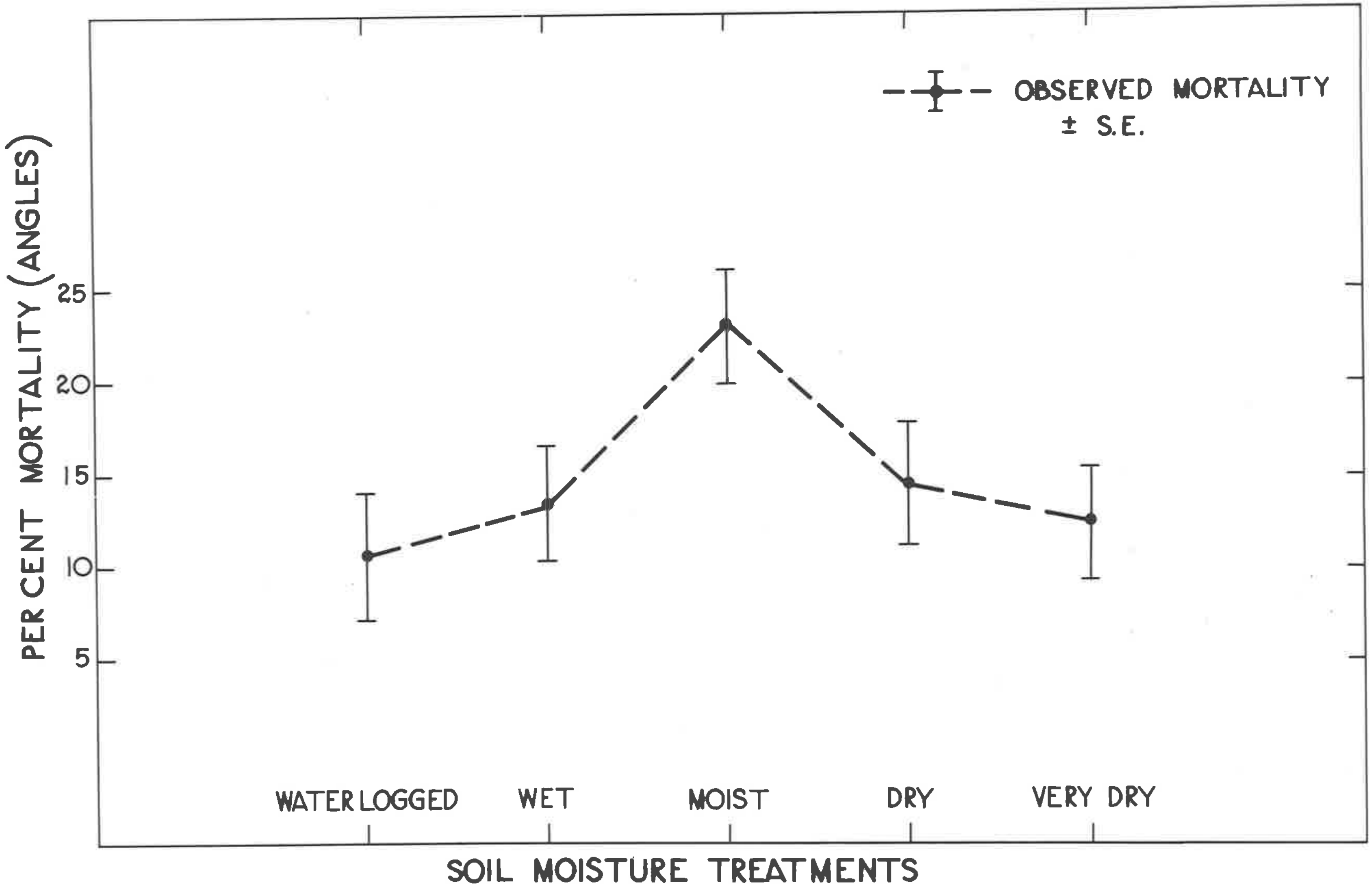
	d.f.	S.S.	M.S.	V.R.
Linear Component	1	0.4802	0.4802	-
Quadratic Component	1	180.8035	180.8035	3.77
Remainder	2	202.2665	101.1333	
The quadratic is significant at p = 0.07				

3.73 Discussion

The first count should provide a measure of the response to a fairly early stage of soil water stress, while the second count should reflect the response to well-pronounced stress, the buckets at the dry end of the range having had time to lose all surplus water and be dependent on the weekly ration, and the waterlogged trees having had their roots submerged for 6 weeks or more. This second count is doubly important in that it represents those nymphs which have died while feeding. Presumably these can be equated with those which die in a similar manner on leaves on the south sides of trees in the field, and on detached leaf tissue maintained under

Figure 3.02

C. densitexta - Watering experiment. The mortality of those first instar nymphs which had succeeded in settling and building lerps.


OBSERVED MORTALITY
± S.E.
PERCENT MORTALITY (ANGLES)
25
20
15
10
5
WATERLOGGED
WET
MOIST
DRY
VERY DRY
SOIL MOISTURE TREATMENTS

inadequate illumination in the laboratory. Furthermore, as genetical weaklings have presumably been eliminated at the time of hatching and settling, leaving only their more robust fellows to face the rigours of possible starvation, it can be assumed that these deaths do indeed represent those dying from starvation and not from any inherent weakness.

The technique in this experiment was inadequate. The quickly growing trees rapidly became root-bound so they were stressed in this way in addition to the stress caused by the deficiency or excess of water. As a result there was no control group of unstressed trees and there was little contrast in the condition of the least and the most stressed groups.

Some unevenness of irrigation undoubtedly developed, as blockages occurred in some of the watering tubes. This can only be overcome with a more elaborate system of individual point-watering tubes. Finally, the natural variability between trees, twigs, and leaves is such that much larger numbers of insects spread over many more twigs per tree will be necessary to reduce variance.

Chief among the improvements needed in future experiments are very much larger containers for the plants, a better system of watering, and much larger samples per treatment.

In view of all this it is encouraging that fewer nymphs established on the least stressed trees, even although the results are so variable as to lack any statistical significance.

That the subsequent survival of early instar nymphs followed the predicted trend with a probability of one in 14.5 of having done so by chance is a far more definite result than I expected once the deficiencies in the experiment began to show up. There is little or no difference between the survival on the trees with too much or too little water, but the mortality on the trees not subjected to additional stress by extremes of soil-moisture is clearly in excess of that on the other four treatments. It is, in fact, more than double that on any of the heavily stressed trees. The significance of this result also becomes more apparent when it is realized that each end of the range of treatments represents only half the story in the field when a dry summer follows a wet winter.

It is an admittedly low probability upon which to base any very strong arguments, but I consider it lends considerable strength to the other evidence supporting the theory of stress-induced survival, and certainly encourages more precise experimental testing of the hypothesis.

3.8 Summarized Hypothesis erected on the Evidence presented in this Section

In view of the evidence presented here, it seems reasonable to postulate that C. densitexta and many other phytophagous insects usually remain at low levels of abundance relative to their reproductive potential because very few individuals in any generation living on normal healthy plants manage to get enough to eat to survive for more than a few hours or days. The situation changes when the plant is stressed; the concentration of soluble nitrogen (perhaps only one or a few critically scarce amino-acids) in the plant increases; the high death-rate among the newly emerged insects is ameliorated, and an outbreak occurs.

To quote Fennah (1953) discussing outbreaks of homopterous insects, "If an attempt is made to analyse the data [of outbreaks] simply in terms of the insect itself, in relation to the ecoclimates in which it is found and the history of its parasitic or predatorial complex, then the timing, distributional area, and duration of outbreaks appear to be largely fortuitous. If, however, the available data include even a broad outline of the past physiological history of the individual host plants which are attacked, then the facts do conform to a broad general principle".

It is further postulated that the major factor contributing to this general stressing of the plant is the changing pattern of rainfall that it experiences from season to season, year to year, and decade to decade; and finally, that the susceptibility of the plant to this stress will vary with such things as the type of soil, the level of nutrients in the soil, the topography and the aspect of the place where the tree is growing.

How far this hypothesis agrees with what is observed to happen in nature is the subject of chapter 4 which follows.

4. CORRELATION OF OUTBREAKS OF PHYTOPHAGOUS INSECTS WITH STRESS CAUSED BY WATER-LOGGING OR DROUGHT

4.1 The Stress Index

The "Stress Index" measures the fluctuations of rainfall which are considered to be primarily responsible for soil-water stress of trees.

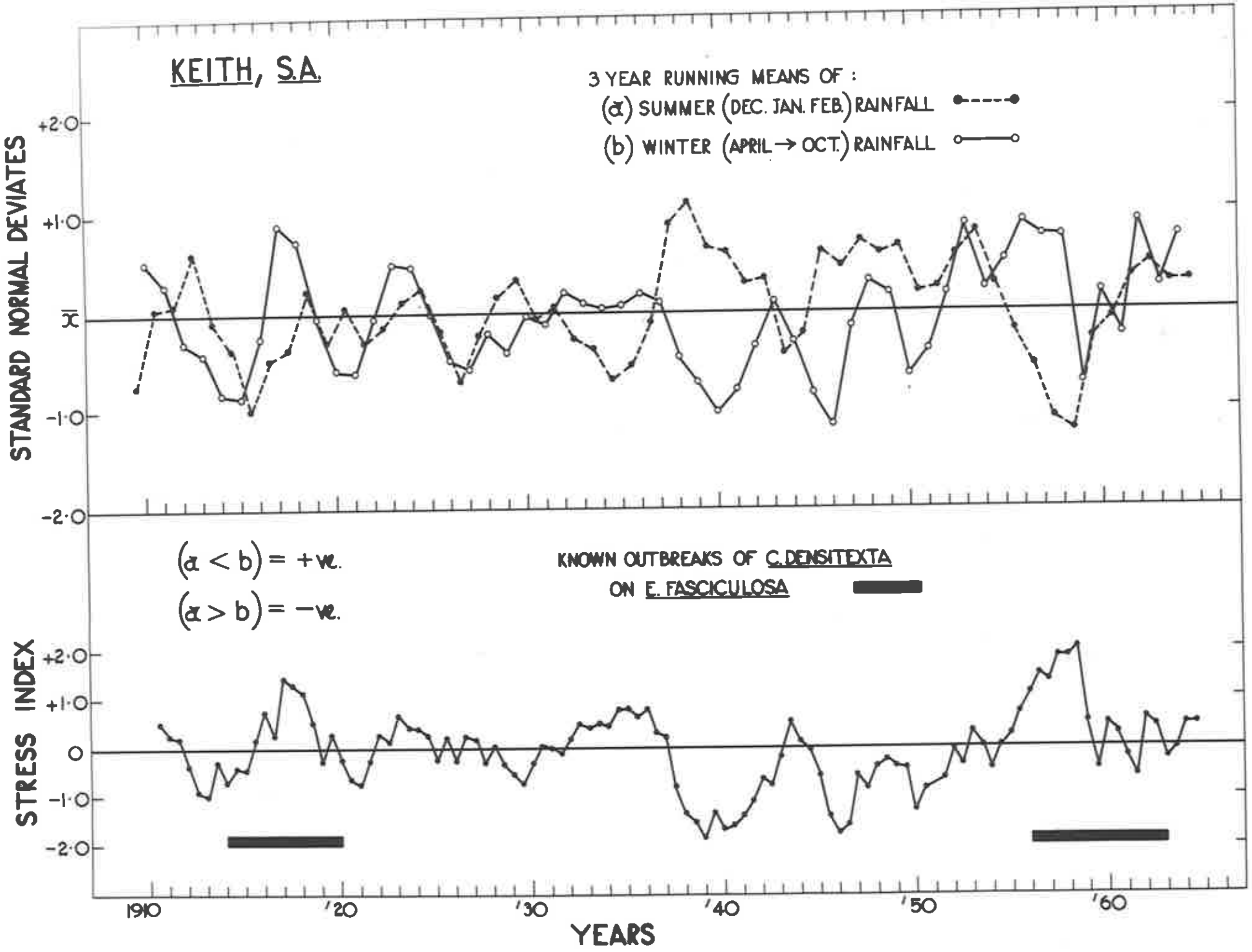
For each year the total summer and winter rainfalls were expressed as standard normal deviates from their respective means. For the southern hemisphere the summer rainfall was taken as the total for December, January and February and the winter rainfall was the total for the period April to October. For the northern hemisphere the summer was taken as June, July, August and the winter as the period from October to April. The means were calculated from 30 years' records except that for Keith 57 years' (fig. 4.01), Texas 54 years', and for Wyoming 30 and 24 years' (fig. 4.07) records were used.

Three year running means of these deviates were then calculated for each season and plotted around a common mean line (e.g. fig. 4.01). From this point no further consideration was given to the relationship of these rainfalls to their means. The important factor is the magnitude of the difference between the rainfall during each winter and its succeeding summer.

When the line for the summer rainfalls is below that for the winter (i.e. the summers were dry relative to the winters) the

Figure 4.01

Method of Calculating the Stress Index from Standard Meteorological Data. In the upper half of the figure curve "a" shows the summer rainfall plotted in units of the normal deviate about its mean and curve "b" shows the winter rainfall similarly plotted in units of the normal deviate about its mean. Both curves are three-year running means. The curve in the lower part of the figure shows the "stress index" which is simply the algebraic sum of $b - a$. The stress index is positive when $a < b$, i.e., when the summer is dry relative to the preceding winter.


KEITH, S.A.
3 YEAR RUNNING MEANS OF :
(a) SUMMER (DEC. JAN. FEB.) RAINFALL
(b) WINTER (APRIL → OCT.) RAINFALL
STANDARD NORMAL DEVIATES
+2·0
+1·0
x̄
-1·0
-2·0
(a < b) = +ve.
(a > b) = −ve.
KNOWN OUTBREAKS OF C. DENSITEXTA
ON E. FASCICULOSA
STRESS INDEX
+2·0
+1·0
0
-1·0
-2·0
1910
'20
'30
'40
'50
'60
YEARS

stress index is positive. The stress index is greatest when a series of very wet winters followed by very dry summers occurs. Conversely when the summers are wet relative to the corresponding winters, the stress index becomes negative (fig. 4.01).

In figure 4.01 the scale for the stress index is such that a stress index of 1 represents a difference between the two running means equivalent to one standard normal deviate of rainfall.

A positive value for the stress index implies that the tree is under stress and is consequently providing more food for the insects feeding on it. Conversely a negative value for the stress index implies that the tree is growing rapidly and is consequently unfavourable for the insects seeking to feed upon it.

The intensity with which stress is applied to the tree is indicated by the magnitude of the stress index, the duration of a stressful soil-moisture state by the time the index remains positive, and the rate at which stress is applied by the steepness of the slope of the index.

The tree's reaction to these changes of stress will vary, and the way in which the stress index comes to represent the favourableness of the tree as a source of food for the insect can best be illustrated by describing two hypothetical situations; always remembering that in nature a large number or gradations are likely to occur between these two extremes. In the first situation a tree is growing in an area where the winter is wet and the summer dry. The soil becomes waterlogged or flooded in the winter for varying lengths of time, depending on the amount of rain, and it has a low capacity to store water during the summer. In the second situation a tree is growing in an area where the rainfall is much more evenly distributed, and on a deep well-drained soil which rarely if ever becomes flooded in winter, and yet never dries out in summer.

Clearly the second situation is more favourable to the tree than the first. But plants tend to be adapted to their environments, so however favourable the norm may be, abrupt or large changes may place the tree under stress. Trees in the first situation will, however, be more sensitive to small departures from the norm than those in the second situation. Similarly, although up to a point a tree has the capacity to respond to changes in the level of soil-moisture by growing more feeding roots, a tree in the first situation with much less latitude for such adjustment, may be under more or less continuous stress so long as the stress index remains positive while a tree on better soil with the identical stress index might only be stressed when the index first increases, or at very high values of the index.

In the following sections a series of "case histories" are presented to illustrate the association of outbreaks of psyllids and of a variety of other phytophagous insects, with periods when the stress index is positive.

4.2 Outbreaks of Psyllids

4.21 In South Australia

4.211 C. densitexta on E. fasciculosa: The stress index for Keith (fig. 4.01) shows that the two major outbreaks of C. densitexta recorded this century (sect. 1.3) occurred during the only two periods when there was a sudden and steep rise from a period of no stress to a period of extreme and prolonged stress.

The greater frequency of outbreaks in the extreme north east of the range during the late 1940's and 1950's, the southward "spread" of the second major epidemic, and the observed distribution of intensity of attack (fig. 1.05) can all be explained by the fact that trees on the marginally dry sites are likely to be more severely and more frequently stressed than those in the higher rainfall areas. In addition the stress indices for Tintinara and Keith show that not only was a greater maximum stress attained in Tintinara (+ 2.4 as against + 1.9 for Keith - both in 1958) but the stress index for Tintinara became positive for the first time two years earlier than did that for Keith. This lead was maintained; massive outbreaks in which pink gums were extensively defoliated began two years earlier at Tintinara than at Keith; in both localities the massive outbreaks began after the stress index had been positive for about six years, and when the index first reached + 1.9. The one recorded outbreak of this species in the Mt. Lofty Ranges occurred on an extremely stressful site during a very dry summer (sect. 1.3).

Influence of Irrigation

A further piece of evidence supporting the general hypothesis that soil-water stress is the most important cause of outbreaks of C. densitexta is provided by the results from summer irrigation.

About 15-20 acres of an area of flat pasture land at Desert Camp have been flood-irrigated with the equivalent of approximately two to four inches of rainfall each summer since 1958-59, while the remaining 40 acres have remained unwatered.

The soil type of this flat is Normal phase Laffer Sand (Taylor, 1933) and there are scattered individuals and groups of pink and blue gum growing on it. Two such groups are growing on the watered portion, and the pink gums in them contrast strikingly with others on the non-watered portions (figs. 4.02 and 4.03).

Two important differences between the irrigated and non-irrigated trees can be expressed quantitatively:-

(1) the mean log (n + 1) of psyllids per north-facing twig was 0.8333 (± 0.09 SE) on the irrigated and 1.97 (± 0.09 SE) on the non-irrigated trees.

(2) The amount of death of foliage in the crown as a whole, and on the north face in particular, is greater on the non-irrigated trees (Table 4.01).

Figure 4.02

Irrigated trees. Note that the second tree from the left is a blue gum, (*E. leucoxylon*).

Figure 4.03

Non-irrigated trees. Note the two white markers on the fence in the middle distance to the right of this group of trees. These can be seen in figure 4.02 and give some indication of the relative position of these two groups of trees.

Table 4.01

Extent of killing of foliage by C. densitexta in crowns of irrigated and non-irrigated pink gums - 100 random samples (20 from each of 5 trees) in each group.

	Irrigated trees			Non-irrigated trees		
	North faces	South faces	Total	North faces	South faces	Total
Dead Twigs	19	13	32	59	21	80
Live Twigs	32	36	68	8	12	20
Total	51	49	100	67	33	100

The difference between north and south samples on the irrigated trees is not significant ($\chi^2_1 = 0.88$) but significant ($\chi^2_1 = 6.88^{**}$) on the non-irrigated trees, and there is a highly significant difference ($\chi^2_1 = 44.82^{***}$) between the total live and dead twigs on the two groups, the non-irrigated trees having far more dead twigs.

There was also a marked difference in the length of branches and twigs of the foliage units, those on the irrigated trees being much longer and more pendant than those on the non-irrigated trees (fig. 4.04).

The lower population of psyllids over several years - presumably as a result of the extra water each summer reducing or eliminating soil-water stress - has resulted in the irrigated trees having denser, more luxurious crowns, with a complete absence of the cut away north face so characteristic of pink gums throughout the Southeast (fig. 2.44).

Repeated defoliation and killing of new growth on the non-irrigated trees, apart from making the crowns more open, with many more dead twigs and branches, has resulted in regrowth continually arising from accessory buds which produce much shorter internodes than do the naked buds (Jacobs, 1955).

4.212 *C. densitexta* on *E. cornuta*: In 1948 a farmer at Keith planted a row of *E. cornuta*. Initially these thrived, but by 1958-59 were starting to look sickly. When I first saw them in 1963, many were very thin-crowned and had branches and twigs heavily encrusted with *Eriococcus coriaceous* (Maskell) (fig. 4.05). Towards one end of the row, however, the trees had more foliage and were little affected by the scale insect. In the summer and autumn of 1963-64 *C. densitexta* laid many eggs on the foliage of the trees that were in better condition; the nymphs matured to adults and caused quite extensive "burning" of foliage (fig. 2.22).

By the following summer the poorest looking trees, *which at no stage had been attacked by C. densitexta*, were dead or dying and the ones which had been attacked by *C. densitexta* were still alive and free from psyllid attack.

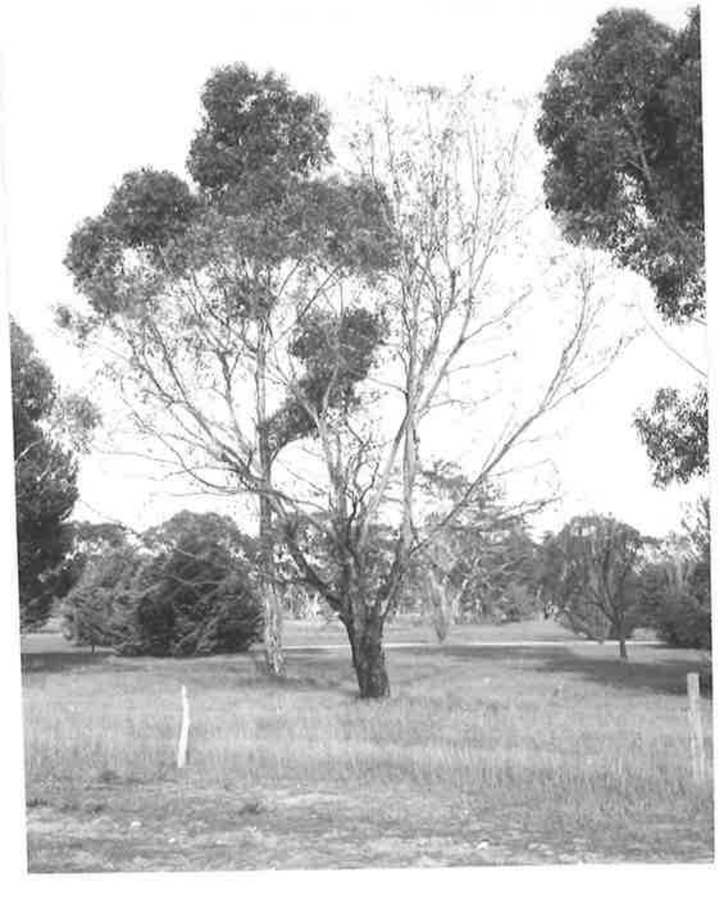
E. cornuta is a West Australian species growing on well-drained soil in a 40 to 60 inch rainfall (Anon, 1957). It was

Figure 4.04

Irrigated (left) and non-irrigated (right) foliage. Note the greater length of twigs on the irrigated trees. This foliage was taken from the trees illustrated in figures 4.02 and 4.03 respectively.

Figure 4.05

E. cornuta at D. Moseley's property, Keith - April 1964. This tree died and was never infested by *C. densitexta* - note the healthy sugar gums behind the tree in the foreground.



planted at Keith on a shallow and poorly drained soil in an 18 inch rainfall. It happened that the weather was favourable for a number of years after the trees were planted and the young trees did well at first (fig. 4.01). But during the latter part of the decade 1950-1960 the stress index was great, and the trees with their large crowns making heavy demands on the greatly restricted root systems, began to deteriorate. The trees which were the first to show signs of stress and were the most severely stressed supported an outbreak of the scale insect E. coriaceous. The more gradually stressed trees reached a stage in 1963 where they became an acceptable and adequate source of food for C. densitexta, which promptly and successfully colonized their foliage. With the easing of stress in the spring of 1964 the psyllid no longer succeeded on these trees.

This sudden outbreak on a completely "foreign" host by C. densitexta again illustrates the association between the condition of the plant and the success of the psyllids that seek to feed on it. The fact that the most severely stressed trees which were killed by drought were never attacked by this psyllid, although heavily attacked by the scale insect, emphasises the importance of the rate and degree of stress in determining whether or not, and to what extent, an insect species can succeed on a plant.

4.213 C. albitextura on E. camaldulensis: In the Adelaide foothills E. camaldulensis is subject to occasional attack by

C. albitextura (or a sibling species - see Taylor, 1962). Old records at the Waite Institute show that there have been five widespread and heavy outbreaks on red gum in the period 1934-60. All five have occurred during a period when the stress index remained positive (fig. 4.06, Adelaide). Furthermore, on a graph showing the detailed rainfall patterns (not here illustrated), all five outbreaks are seen to follow after one especially wet winter interpolated between periods of summer drought.

Apparently this species, growing on good deep soil, responds only to sudden and extreme changes in soil moisture. Values of the stress index that might indicate a persistent outbreak on pink gum growing on the shallow soils of the southeast of South Australia, might indicate only a short-lived outbreak during the worst of the weather on red gum.

4.214 C. retator on E. camaldulensis: During the especially long dry spring and summer of 1963/64 a moderately severe outbreak of Cardiaspina retator occurred on red gum (E. camaldulensis) trees growing along the banks of the River Torrens immediately above the Gumeracha Weir. This was sufficient to cause noticeable "burning" of the crowns, and counts of 850 eggs/twig in the autumn of 1964. The spring 1964 generation only produced 72 eggs/twig and the summer 1965 generation 1.5 eggs/twig - a decline of 99.8% in two generations.

An extensive search of the remainder of the course of the Torrens, and numerous other water-courses in the surrounding hills, failed to reveal any other sign of lerp-insects increasing in abundance, except for a smaller increase of C. albitextura on red gum above the second and lower weir on the Torrens.

The Gumeracha Weir is usually allowed to "scour through" in the winter to clear accumulated silt, but in the winter of 1963 the daily records of the Engineering and Water Supply Department of South Australia show that the weir was full or overflowing for 44 days during June, July and August. (The 20-year mean for this period is 15 days, and the longest in the previous 6 years was 7 days). It remained full until the 30th September, when it was emptied, and remained empty throughout the ensuing summer. In the winter of 1964 it was full for only eight days during June, July and August. When the weir is full most of the affected trees are flooded, or nearly so, but once the weir is emptied the river level is some 20 feet lower, leaving the trees literally "high and dry".

This very localised outbreak would appear, then, to have arisen as a result of a sudden and extreme increase in stress caused by the artifically prolonged winter flooding followed by the prolonged summer drought of 1963/64. This is very similar to the natural rainfall pattern associated with general outbreaks of psyllids on red gum.

4.215 Creiis sp. on E. cladocalyx: In Kadina, 100 miles north of Adelaide, during the summer of 1963/64, a number of sugar gums (E. cladocalyx) in the town square were heavily infested by a variety of foliage inhabiting insects, especially a species of Creiis which caused considerable "burning" and defoliation. This outbreak was confined to these few trees; other sugar gums in the town, although carrying a few psyllids, had not been badly attacked. The trees attacked were approximately 80 years old, and 60 to 70 feet tall, while all other specimens located were young, or had been kept pollarded.

These trees originated from parents growing in a 25 to 30 inch rainfall in the Flinders Ranges and will only succeed in the lower rainfall areas (Kadina approximately 15 inches p.a.) if they are kept pollarded. If allowed to grow unchecked they will deteriorate, start dying back from the top, and become stag-headed. Even repeated pollarding will not preserve them indefinitely and the trees will gradually deteriorate and die.

The attacked trees had been pollarded, but not for the last 10 to 15 years. They were obviously becoming considerably stressed and the long dry summer added sufficient stress to enable this large build-up of the psyllids to occur.

4.216 Other Psyllids in South Australia: The only period of great abundance of C. densitexta that I witnessed - the autumn and winter of 1963 - was also a time of abundance of many other species of psyllids, both lerp-forming and free-living, which have since been rare : many I have not found again. *E. diversifolia* in particular carried a large and diverse psyllid fauna which has virtually disappeared since 1963.

4.217 Response to "frilling" of trees: Another example of the way in which psyllids (and other foliage-eating species) respond to stress in the tree (although induced by man and not weather in this case) is the large increase in abundance reported to occur on "frilled" trees just before they die. Frilling, by leaving the sapwood intact, effectively cuts off the supply of food to the roots while still allowing water to be taken up by the plant. As the roots starve and die, their ability to maintain the necessary flow of water decreases, their stored protein is translocated to the aerial parts, the plant becomes increasingly more stressed, and eventually dies from drought. This may take several years, and during this time a tree will continue to put on increment above the frilling, but not below it, and there is a general accumulation of photosynthates above the frill.

4.22 In other States of Australia

4.221 *C. albitextura* on *E. blakelyi* in A.C.T. and N.S.W.: Clark's series of eight papers on the ecology of *C. albitextura* on *E. blakeyli* in the Australian Capital Territory and parts of New South Wales over the past twelve years, reveals a complex pattern of rising and falling levels of abundance, both in time and in space. Running through this confusing patchwork, however, there is a more general pattern of population fluctuation over the whole area.

In the first place, even although localized outbreaks of brief duration were known to occur for many years before 1950, lerp-insects have been much more plentiful in all localities than they had been for some years before this date. (Even Clark's low population levels represent considerably greater abundance than the degree of rarity usually encountered).

Early in this period of general abundance several species, including C. albitextura, increased rapidly, reaching outbreak proportions in many widely separated areas by 1952-53. There followed a general decline in abundance in 1955, and most species have since remained at relatively low levels. On the other hand, C. albitextura and E. blakelyi, followed somewhat spasmodically by one or two other species of Cardiaspina on different host species, increased again in 1956, declined in 1958-59, and returned to another peak in 1960-61. From there it declined to a relatively low level in 1962 which has been more or less maintained until the present. (See for example Clark, 1962, fig. 6, and Clark, 1963c, fig. 1).

The stress index compiled from the Canberra Forestry School rainfall data, shows very good agreement between the changes in the overall abundance of lerp-insects and the changing weather pattern (fig. 4.06, Canberra). The graph shows that the time when the greatest number of species reached outbreak levels coincided with the first, most suddenly imposed and most severe stress as measured by the stress index. The fact that all but one or two species declined after this period indicates the differing degree of stress necessary for insects on different species of tree on different sites, before outbreaks can develop.

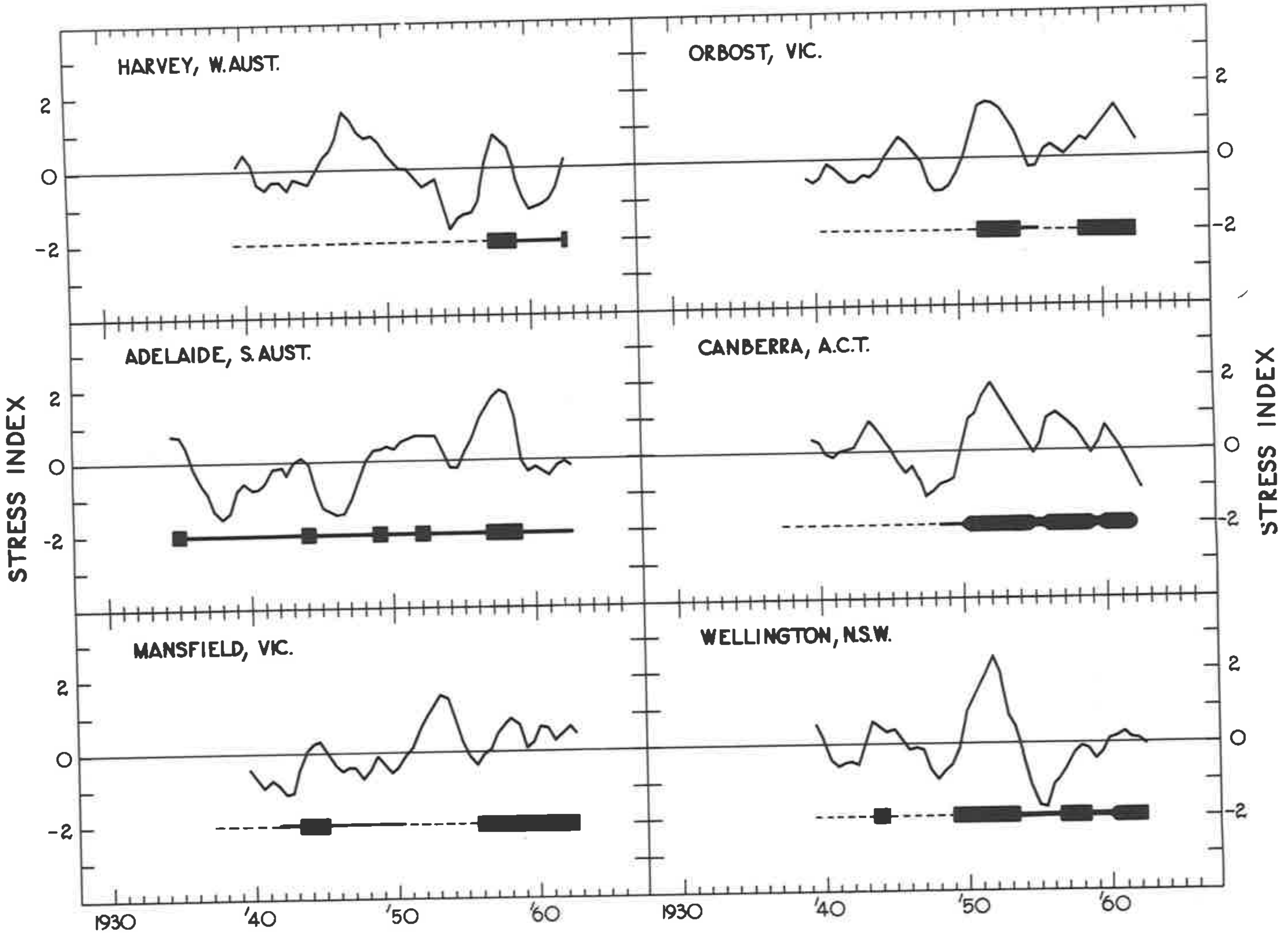
4.222 Glycaspis spp. in N.S.W.: In addition to Clark's work, Moore (1961) has published information on the psyllid genus Glycaspis which indicates that many species of this genus were present in outbreak proportions throughout New South Wales during the same period (fig. 4.06, Wellington).

4.223 Cardiaspina spp. in Victoria: Reliable reports of outbreaks of lerp-insects in Victoria are few, but there are sufficient of them to reveal that outbreaks were widespread during the decade 1950-60 (fig. 4.06, Mansfield, Orbost). Before this they appear to have been rare or unknown apart from the years 1943-45, when one authentic report from Mansfield, Victoria (fig. 4.06, Mansfield) and another record in Moore (1961) (fig. 4.06, Wellington) show that these outbreaks also coincide with positive values of the stress index. These reports also indicate that a number of different species of Eucalyptus and psyllids have been involved, and that the predominant psyllid species have been of the leaf killing sort, principally species of Cardiaspina.

4.224 Creiis periculosa on E. rudis: Creiis periculosa (Ollif), a lerp-insect which discolours and kills leaf tissue, periodically

Figure 4.06

Psyllid outbreaks in Australia - stress indices for various representative localities. A dotted line indicates no known records, a heavy black line indicates records but no outbreaks, and a black blocking indicates a recorded period of outbreak of one or more species of lerp-insects. See text for details.


HARVEY, W. AUST.
ORBOST, VIC.
ADELAIDE, S. AUST.
CANBERRA, A.C.T.
MANSFIELD, VIC.
WELLINGTON, N.S.W.
STRESS INDEX
STRESS INDEX
2
0
-2
1930
'40
'50
'60

reaches outbreak proportions on Eucalyptus rudis growing in wet habitats and particularly on the plains which are prone to winter flooding in the southeast of Western Australia. Little appears to have been recorded about past outbreaks other than that they usually tend to be of short duration, and to vary from district to district. Reports obtained from the Forestry and Agricultural Departments of Western Australia and the C.S.I.R.O. Division of Entomology in Perth, indicate that a widespread and severe outbreak occurred between 1957 and 1959, especially in the Harvey-Waroona irrigation areas.

From the stress index for Harvey (fig. 4.06, Harvey) it seems likely that the condition of the trees may have become highly favourable for the multiplication of psyllids in 1956-57. The graph also suggests that the last general widespread outbreak before this was probably in 1947-48.

4.23 In America - Paratrioza cockerelli on Potatoes

The potato psyllid, Paratrioza cockerelli breeds on a number of native perennial Solanaceae in Texas and Wyoming and it may also infest potatoes in Wyoming. Wallis (1955) showed that the psyllids which infested the potatoes in Wyoming usually came from Texas where the insects had been breeding in the winter. There were not likely to be many psyllids in Wyoming unless there were many in Texas but large populations in Texas did not invariably give rise to outbreaks in Wyoming. Vagaries of wind currents and temperatures may inhibit the northward movement of these insects in some years, and a large invasion may not necessarily be followed by an outbreak, as these insects are very susceptible to high temperatures. It would seem then, that a complex of cool summers in Wyoming, north-moving spring air currents, and an environment conducive to big increases in numbers in Texas are necessary for large sudden outbreaks of this psyllid in the potato-growing states.

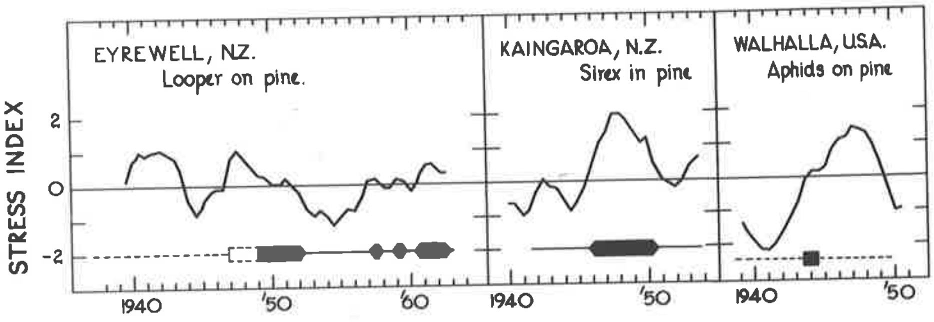
Comparing the stress indices for both Texas and Wyoming with records of outbreaks of P. cockerelli on potatoes in Wyoming (fig. 4.07) would suggest that outbreaks tend to occur at times when the stress index for Texas is high. There is not such a close correlation with the Wyoming weather.

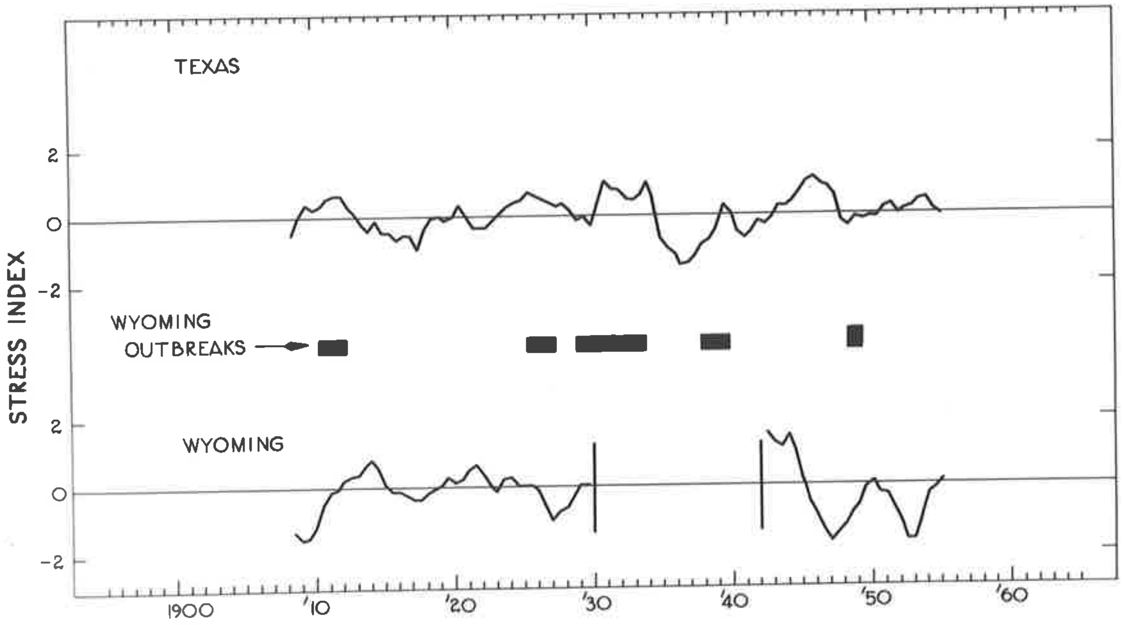
These observations suggest that the first link in the chain of events leading to an outbreak of P. cockerelli on potatoes in Wyoming is a sequence of weather in Texas that causes stress in the plants, chiefly native Solanaceae, which provide the chief food of the psyllids in Texas.

It is perhaps of interest to record here Jensen's (1951) statement that "the semi-desert and mountainous regions of the west, which have relatively low precipitation during the summer months, have proved to be rich in psyllid species compared to other parts of the country". In other words, those areas most likely to produce stress in perennial plants, during summer.

Figure 4.07

Outbreaks of Insects and Rainfall - stress indices for various representative localities. A dotted line indicates no known records, a heavy black line indicates records but no outbreak, and a black blocking indicates a recorded period of outbreak of the insect concerned. See text for details.


EYREWELL, N.Z.
Looper on pine.
KAINGAROA, N.Z.
Sirex in pine
WALHALLA, U.S.A.
Aphids on pine
STRESS INDEX
2
0
-2
1940
'50
'60
1940
'50
1940
'50


TEXAS
2
0
-2
STRESS INDEX
WYOMING
OUTBREAKS
2
WYOMING
0
-2
1900
'10
'20
'30
'40
'50
'60

4.24 Discussion

Over the whole of southeastern Australia the weather during the decade 1950-60 was characterized by winters that were wetter than usual and summers that were drier than usual. The stress indices that are plotted in figures 4.01 and 4.06 confirm this observation. Although the broad pattern is the same over the whole region there are local differences. For example in Victoria and New South Wales the stress index was maximal between 1950 and 1954, but in South Australia it was greatest during the years 1956-59. Even within the smaller region of South Australia local differences occur - compare Keith (fig. 4.01) with Adelaide (fig. 4.06). Similarly compare Canberra with Wellington and Mansfield with Orbost (fig. 4.06). This diversity within similarity will be found at all levels down to that of the individual tree where; although no measurable difference in rainfall occurs, differences in the nature of the soil may markedly effect the reaction of two trees to the same rainfall pattern. The influence of the weather may be modified over quite large areas by the type of soil. For example during the period under review the most severe and prolonged outbreaks of psyllids have been recorded from trees growing on shallow soils that are liable to be flooded e.g. C. densitexta on E. fasciculosa, C. albitextura on E. blakelyi, Creiis periculosa on E. rudis, and various Glycaspis species on several species of Eucalyptus. On the other hand, trees that are growing on better soil may remain unstressed through all but the most extreme variations in the weather, and consequent variations in soil moisture. Outbreaks would not be expected on such trees except when the stress index is extremely high; and when they do occur they would be expected to be short-lived. This was the situation described for outbreaks of Cardiaspina species on E. camaldulensis growing near Adelaide.

All this diversity helps to explain the different severity, duration and extent of observed psyllid outbreaks, and the way in which the abundance of each species changes independently of each other while all still conforming to a broad pattern of increase and decrease in response to the local stress index.

A further source of variability is that on very favourable host trees some species (e.g. Cardiaspina) will quickly destroy all available foliage and "crash" to low levels of abundance. Once new foliage appears numbers will again increase if the host trees are still stressed, and at a rate determined by the degree of this stress.

Thus the level of stress that may develop in a tree will depend not only on the relative departures of the winter and summer rainfalls from their norms (i.e. the stress index) but also on the topography, the type of soil, the age of the tree and the density of the stand. In addition the response of the insects to the stressed tree will depend on the timing of these changes in the condition of the tree relative to the life-cycle of the insect.

It is not surprising, therefore, that a complex pattern of population-change may develop during a decade when the weather is more or less continuously favourable to the multiplication of psyllids.

4.3 Outbreaks of other Phytophagous Insects

4.31 Other Australian Insects

Throughout the southern and eastern parts of Australia over approximately the last decade, there has been a general increase in trouble from insects attacking trees. In addition to psyllids, the sawflies (*Perga*) leafbeetles (*Paropsis*) stick-insects (*Podocanthus* and *Didymuria*) and defoliating caterpillars (*Roeselia*) have all caused defoliation of eucalypts, and species of the native geometrid genus *Chlenias* were sufficiently numerous in pine plantations in Victoria and South Australia between 1959 and 1961 for spraying with insecticide to be necessary to prevent excessive defoliation. Also *Sirex noctilio* became established in Victoria during this period.

Investigations of *Roeselia lugens* (Walk.) attacking *E. camaldulensis* in New South Wales (Campbell, 1962) show that an outbreak of this insect in 1957-58 occurred during a dry period following a record winter flood, and that the epidemic ended (from heavy and unaccountable larval mortality) following another flood during the spring of 1958. This same species, or one very closely related to it, was the most prominent of the many other foliage-eating insects which increased in abundance on pink gum in South Australia at the times of peak abundance of *C. densitexta*.

A recent paper by Readshaw (1965) records three species of normally rare stick insects reaching outbreak levels and causing extensive defoliation of *Eucalyptus* forests in New South Wales and

Victoria during the period when these areas were experiencing a period of stress-producing weather (compare his fig. 3 with the graphs in my fig. 4.06).

The poor powers of dispersal of these insects, the widely separated epicentres of outbreaks, and the absence of any evidence of parasites or invertebrate predators containing their increase, led Readshaw to explain the outbreaks in terms of predation by birds.

On the other hand, he described how the outbreaks at the beginning are extremely spotty and for the most part the spots where they begin are on ridge tops and western slopes. This is just what would be expected if the initial cause was stress in the trees caused by the sort of weather that is reflected in a large value for the stress index. The outbreaks would appear first on trees growing in exposed places on shallow soils.

4.32 Two examples from New Zealand

4.321 Selidosema suavis on Pinus radiata: Eyrewell Forest is a pine plantation situated on the shingle soils of the Canterbury Plains of the South Island of New Zealand. These gravels have a consolidated layer at 12 to 18 inches which impedes drainage so that soils become waterlogged in winter, and yet have little or no capacity to store water in the summer. The mean rainfall of 37 inches is fairly evenly distributed throughout the year, but evaporation is high during summer, especially in the early summer when it may exceed precipitation. A major feature of the climate is the warm dry föhn-type north west winds. These winds may reach gale force at any time of the year, frequently reaching velocities between 45 and 55 m.p.h..

The principal tree species in Eyrewell is Pinus radiata D. Don., planted between 1926 and 1931. Its roots are incapable of penetrating the compacted subsoils with the result that trees are very shallow rooted (Wendelken, 1955). Since about 1945, P. radiata has suffered periodic and increasing windthrow (Prior, 1959). This wind-throw was usually first experienced after the trees attained a mean height in excess of 50 feet. It became more frequent and severe as, with continued growth, the ratio of top to root became increasingly unbalanced, culminating in some two thirds of the forest being blown down in 1964.

A native species of looper caterpillar, the bivoltine Selidosema suavis (Butler), has become adapted to life on a wide range of exotic pines throughout New Zealand. This species was first reported in high numbers on P. radiata in Eyrewell Forest late in 1951, by which time it had already caused a considerable amount of defoliation. By the end of 1952 some 6,000 acres of Eyrewell were carrying epidemic numbers of this insect, and the forest was sprayed with D.D.T. from the air to prevent further damage. A week or so after the completion of spraying a polyhedral virus disease reduced the numbers of S. suavis to low levels in a similarly infected forest of P. radiata some miles away (Rawlings, 1953).

Although this species had been known to be present in Eyrewell - as in all other plantations of P. radiata - for many years before this outbreak, it had never before attained high enough numbers to warrant any record being made of such an event. That an outbreak of this insect could have occurred in Eyrewell without being noticed is most improbable, as men were working in some part of the forest all the year round. However, considerable changes in abundance short of an actual epidemic could well have passed unnoticed. In 1956 with the inception throughout New Zealand of sampling of lepidepterous defoliators by the newly formed Forest Biology Survey, an accurate record of the changes in abundance of S. suavis in Eyrewell Forest commenced.

As can be seen from figures 4.07 and 4.08 a close correlation exists between the stress index compiled from Eyrewell Forest Headquarters rainfall figures and the peak number of first instar larvae in each generation (White, unpublished F.B.S. data).

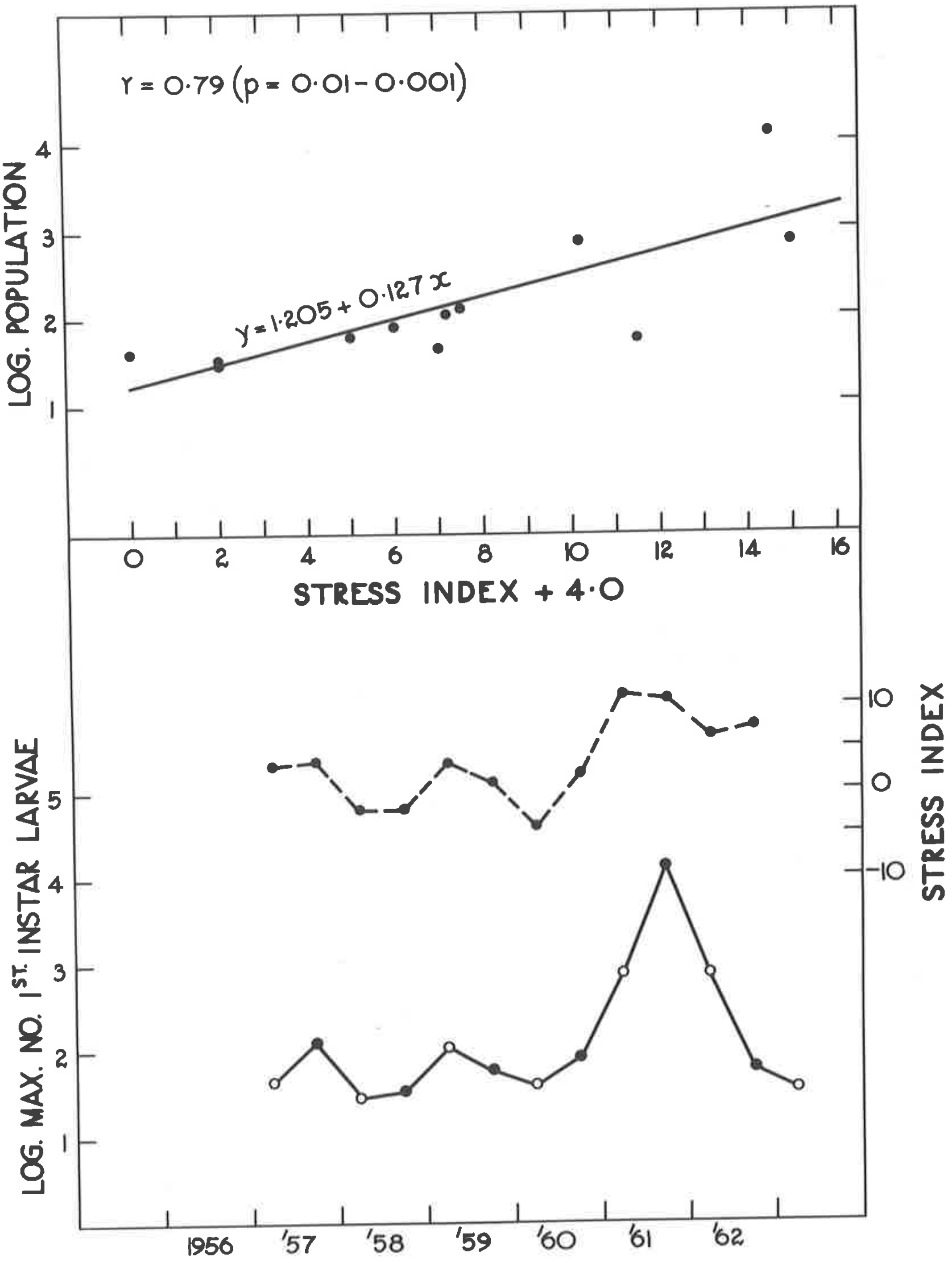
The two small peaks in 1957 and 1959 were not sufficient to cause any readily observable defoliation, and, in the absence of specific sampling, would never have been detected.

During 1960-62 an outbreak reached sufficient density to defoliate the trees noticeably before the numbers were reduced to a low level by a polyhedral virus; but the damage was much less than from the outbreak of 1950-52.

On each of the four occasions when an outbreak or an

Figure 4.08

Selidosema suavis population fluctations at Eyrewell Forest, New Zealand. See text for details.


r = 0·79 (p = 0·01 – 0·001)
y = 1·205 + 0·127 x
LOG. POPULATION
1
2
3
4
0
2
4
6
8
10
12
14
16
STRESS INDEX + 4·0
LOG. MAX. NO. 1ST. INSTAR LARVAE
1
2
3
4
5
STRESS INDEX
10
0
-10
1956
'57
'58
'59
'60
'61
'62

incipient outbreak has been observed, it has begun in a particular area of the forest where, presumably, the imbalance between root and crown was greatest because this was the area that was first destroyed by the "big blow" of 1964. On any particular tree the numbers begin to increase and the caterpillars grow faster on older semi-suppressed foliage of the lower parts of the crowns, and also on the north faces of the crowns. These are the parts of the tree that would first show signs of stress and where the stress would be greatest.

The evidence that outbreaks of S. suavis in Eyrewell Forest occur when the trees are stressed seems quite clear. Trees were planted on a site which had never previously supported trees, and where the nature of the soil and the weather combine to produce the classical cause for stress - winter flooding followed by summer drought. As the trees grew, the demands on the root system for water would increasingly exceed its ability to supply these requirements, with the result that the trees would become increasingly sensitive to changes in soil moisture. The fact that, apparently no major outbreak occurred between 1939 and 1944 when the stress index was positive (fig. 4.07, Eyrewell) can be interpreted as indicating that at that time the trees were still small enough to avoid excessive stress.

The large epidemic of 1951-52, discovered when it had already caused considerable defoliation, must have originated about

1947, soon after the stress index again became positive. It was at about this time that the first substantial amounts of windthrow occurred (Prior, 1959) indicating that the ratio of root to top was becoming unbalanced. Such trees would doubtless be highly sensitive to and easily stressed by an unfavourable water regime in the soil.

From 1952 onwards the trees were becoming increasingly unstable, liable to be windthrown, and sensitive to changes in the water content of the soil. By the time the stress index again became positive in 1957, there occurred an immediate and positive response in the abundance of S. suavis. From that time until 1963 the numbers have risen and fallen in very close correspondence with the changing weather pattern (fig. 4.08).

The general parallel development of susceptibility to windthrow and to attack by S. suavis is to be expected as a result of the growing crowns making increasing physical and physiological demands on their restricted root systems. Similarly it could be expected that areas of the forest where soil depth and moisture extremes were harshest would be the areas where these two weaknesses would be most pronounced. This expectation is borne out by the fact that the epicentres of epidemics were the areas with trees most susceptible to windthrow.

4.322 Sirex noctilio in P. radiata: Small local outbreaks of the introduced wood-boring siricid Sirex noctilio Fabr., had been known to occur in various parts of New Zealand since early in the century. In 1946 numbers increased in pine forests of the Bay of Plenty and of the central pumice plateau of the North Island. The insects continued to multiply and by 1948-49 a massive outbreak had developed which killed 25-30% of the trees over many thousands of acres. Numbers subsided to low levels in 1950 (Rawlings and Wilson, 1949).

Figure 4.07, Kaingaroa, shows that this great outbreak coincided with a period when the stress index was extremely great (+ 2 S.D. - equivalent*) in an area of moderately high rainfall (59 inches p.a.) on very deep, free draining pumice soils in which tree roots are deep and widely ramifying. The different circumstances associated with this outbreak at Kaingaroa and the one of S. suavis in Eyrewell Forest emphasise the important influence that soil-type may have on the susceptibility of the trees to fluctiations in weather. Between them these two outbreaks represent the two extremes that were discussed as hypothetical situations in section 4.1.

These two outbreaks also serve to again draw attention to the differing requirements of different species of insects. The general pattern of weather in the two places was similar (see fig. 4.07) although of differing magnitude, and the two outbreaks occurred at much the same time. Both insects live in both forests. The looper caterpillar did increase in the Rotorua forests at this time but did not reach outbreak levels (Rawlings, 1955) and Sirex increased in

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* The actual summer rainfalls varied from + 1.93 S.N.D. in 1943-44 to - 2.1 S.N.D. in 1945-46, a decrease of 4.03 S.N.D. of rainfall in two seasons!

Canterbury at the same time but not to outbreak proportions (Prior et al., 1959). A third insect common to the two areas, the scale Lecanium hesperidium var. pini reached outbreak numbers in Canterbury and high but not outbreak levels in the Rotorua district between 1949 and 1951 (Rawlings, 1955).

4.33 Spruce Budworm in Canada

A recent major publication (Morris, et al., 1963) summarizes present knowledge of the spruce budworm in Canada. For some years the association of outbreaks of spruce budworm with periods of warm dry summer weather has been recognised, but the emphasis has, as usual, been upon the direct effects of weather on the insect and its predators and parasites. Dispersal and migration of small larvae and adults resulting in "invasions" into new areas has received much attention, as has the investigation of influence of temperature, humidity, sunshine, etc., on survival, fecundity, parasitism and so on. "Climatic release" is a term often used, and reflects an appreciation of the major influence of changing weather on the level of abundance of the budworm, without any really adequate explanation of how this happens. Recent thinking is turning more and more towards a reappraisal of the effect of weather, especially as recent work is revealing that the movement of outbreaks across the country is matched by the west to east movement of the weather pattern thought to be favourable to increased abundance of the budworm.

Stands of over-mature trees are susceptible to outbreaks, while young vigorously growing stands are relatively immune. This fact has been well documented. One explanation for this is that older trees modify the "ecoclimate" so that the later instars of the budworm survive better and grow more quickly. The increased survival of second instar larvae feeding on staminate flowers of Balsam Fir and the correlation of increased populations with years of heavy male flowering is also well known. The generally accepted view has been that this is the chief cause of the increases in population that lead to outbreaks. These facts have led to investigation of the influence of weather - largely temperature - on synchronization of the insect's life history with time of production of male flowers and "bud-flush". Recently, however, doubts have been cast on this explanation (Morris, et al. 1963, sect. 31). But, so far as I know, no one has suggested that changing rainfall patterns may, by altering the soil-moisture regime, alter the physiology of the tree, and thus its value as food for the foliage-eating larvae.

If, however, the whole picture of population abundance of spruce budworm is considered from this point of view - of stress on the tree increasing survival of early instar larvae - many things become explicable. For example, overmature stands are more susceptible simply because they are more readily stressed by the changing weather pattern than are younger stands. Sudden (and in the face of present ideas on migration of larvae) puzzling increases of numbers in isolated stands of trees result from stress caused by weather increasing survival of young larvae already present in sufficient abundance. The correlation with staminate flowering is seen to be only part of the story of a general increase in the availability of soluble amino acid in the plants - the whole tree, not just the male flowers, becomes more favourable. In fact, I would suggest that male flowering and spruce budworm increase are correlated because they have the same or a very similar basic cause (e.g. MacAloney, 1944). The ancient practice of whipping the walnut tree is not just superstition!

As with most other insects, even though the number of females in an area is small, a slight increase in survival of the huge numbers of young produced per female will quickly result in a population which will "swamp" its predator complex, and rapidly approach the limits of its food supply.

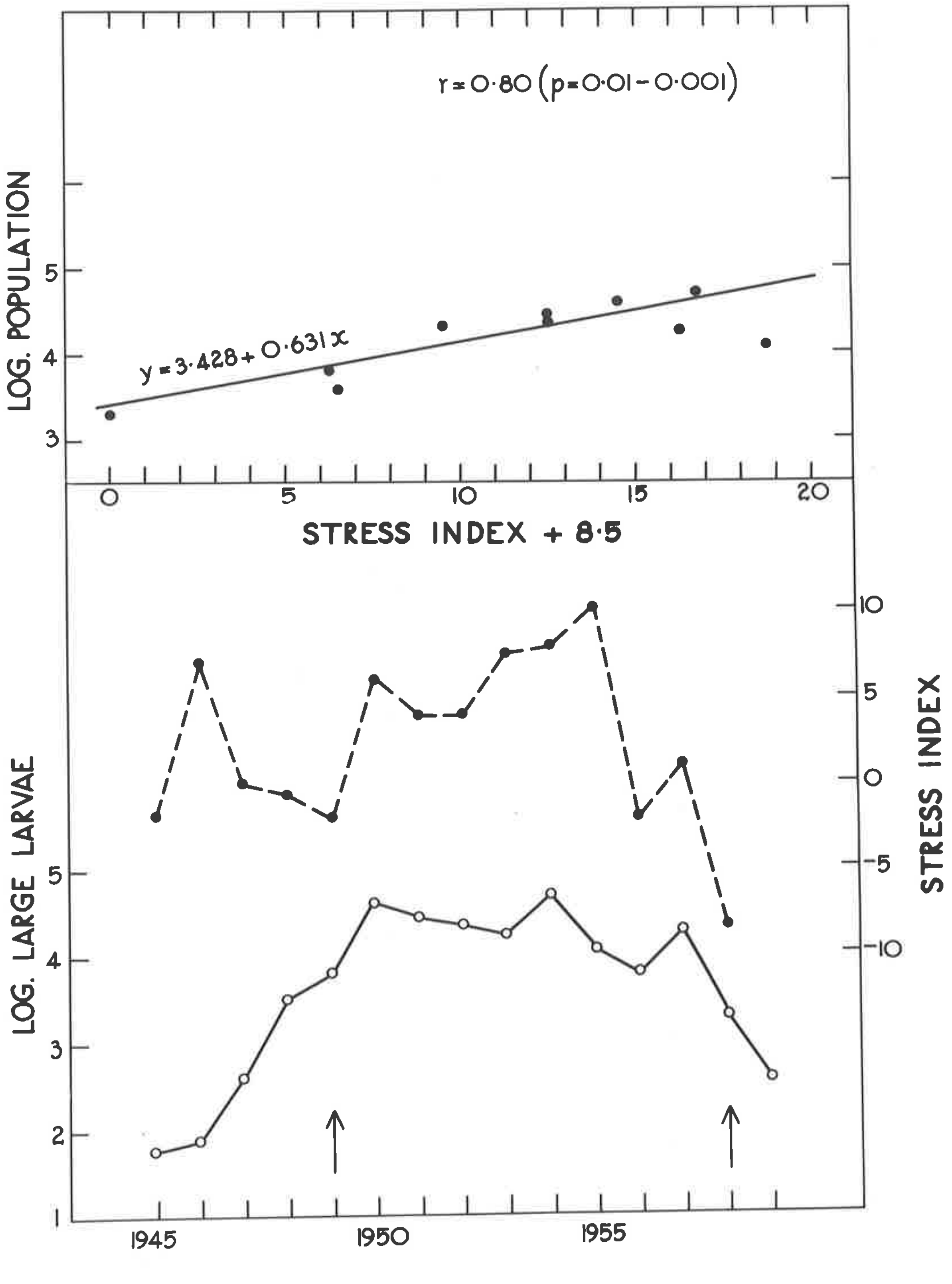
If a change in the rainfall pattern does stress the trees to the point where a significant increase in the survival of early instar larvae - which, in the absence of such stress, would have starved to death - does occur, then just such a population explosion would follow.

In figure 4.09 the stress index calculated from the rainfall records for Green River New Brunswick is compared with the records of fluctuations in the numbers of budworm given by Morris et al. (1963); the data are taken from his figure 18.1A, log N_n. Close agreement, with a significant correlation coefficient ($P < 0.01$) is obtained between these two measures for the outbreak years. The first significant increase in numbers was recorded in 1947 (following

Figure 4.09

Spruce budworm outbreak, Green River, Canada.

See text for details.


r = 0·80 (p = 0·01 – 0·001)
y = 3·428 + 0·631 x
LOG. POPULATION
3
4
5
0
5
10
15
20
STRESS INDEX + 8·5
LOG. LARGE LARVAE
1
2
3
4
5
STRESS INDEX
10
5
0
-5
-10
1945
1950
1955

the 1946 increase in the stress index) and by 1949 defoliation was becoming severe. Populations began declining in 1956-57 (after the steep drop in the stress index in 1955-56) and had reached very low levels by 1960 (Greenbank, in Morris et al., 1963: p. 20). In other words the outbreak of spruce budworm in the Green River area between 1949 and 1958 was associated with a period of unusually wet winters and unusually dry summers; weather that is known to produce stress in trees, through an unfavourable regime of soil-moisture.

4.34 Bark Beetles

Outbreaks of bark beetles have often been associated with drought (Beal, 1943; Thatcher, 1961), and there have also been observations of wet weather suddenly bringing an outbreak to an end (Heering, 1957). Many theories have been proposed to explain how lack of rain may allow these insects to build up to high levels of abundance; most of them attribute the outbreak to the decrease in resin which occurs in dry weather (e.g. Stark, 1965).

What is usually overlooked is that these insects are phloem feeders, living on essentially the same tissue as do psyllids, or any other foliage-eating insects. The composition and nutrient value of the phloem in the bark will vary in the same way as the phloem in other parts of the plant (see Kloft's (1957) work with bark feeding *Adelges*) and thus bark beetles can be expected to respond in a similar way as do other consumers of living plant tissue. This interpretation is supported by a recent report (Thomas, 1965) of various species of bark beetles attacking girdled pines just before they died, while ungirdled trees intermingled with these trees were not attacked. Similarly West's (1947) report of obtaining adult buprestids from above but not below the girdle in Ponderosa pine (see also sect. 4.217).

4.35 Aphids, Mites, Thrips, Miscellaneous Species and Forest Defoliators in Europe

The correlation of outbreaks of aphids with dry summer weather has frequently been recorded (e.g. Cottier, 1935; Petherbridge and Wright, 1938; Walker, 1954; Cumber and Todd, 1959). One worker (Markkula, 1953) has demonstrated that this is related to changes in the nutrition of the insect feeding on water-stressed plants (see sect. 3.6).

Hoffman (1945) reported a widespread and sudden outbreak of aphids belonging to the genus Cinara on different species of pine in North Carolina, South Carolina and Virginia, U.S.A.; during the winter of 1943 and the spring and summer of 1944. Figure 4.07, Walhalla, shows that this outbreak coincided with a very large and sudden increase in the stress index for Walhalla, South Carolina. The maximum numbers apparently occurred at the time that the index became positive. I can find no further reference to this outbreak and assume that it had subsided by the following season. In the absence of any information about soils and topography, I would suggest that the trees were quickly able to adjust to the continued stress indicated by the weather pattern, to the point where they were once again no longer providing adequate nutrition for more than a minute proportion of the total offspring being produced.

A similar picture of association of outbreaks with periods of drought is found with phytophagous mites (Rodriguez, 1960), and considerable evidence exists to show that the success of many species of thrips depends on drought (physical or physiological) experienced by the host plant (Wardle, 1927; Mumford & Hey, 1930; Fennah, 1955, 1963).

There are records of mealey bugs (Fennah, 1959) Chinch bugs (Haseman, 1946) mirids (Ting, 1964) armyworms (Marcovitch, 1957) and miscellaneous forest defoliators (MacAloney, 1944; Albertson & Weaver, 1945) all increasing to outbreak proportions when drought imposes stress on the food plant.

Finally there is, in Europe, a long and voluminous recorded history of outbreaks of various defoliating forest insects which are associated with periods of dry summer weather (e.g. Gasow, 1925; Thalenhorst, 1953; Voûte, 1957; Schwenke, 1963; Baltensweiler, 1964). Cramer (1961) has shown that five of the more important of these European defoliators are not only associated with periods of drought, but that outbreaks of each species are associated with different degrees of intensity, magnitude and duration of stress of the host plant.

4.36 An Example of the Recorded Effects of a Drought in British Columbia.

On Vancouver Island, British Columbia, the longest period of drought recorded for 50 years occurred during the summer of 1951, and this had a pronounced effect on the abundance of plant-eating insects (Downes,1956). Downes emphasized that numbers of grass and herb feeding species decreased markedly, but at the same time there was an inexplicable increase in abundance of some tree and shrub feeding species. He records large populations of two different species of *Empoasca* on alder and willow, heavy infestation of oak by an aphid and a moth, increased abundance of "many other species of aphids", and increased numbers of *Psylla alni* on alder.

Table 4.02 which has been compiled from Downes' paper, demonstrated that there is a significant difference ($\chi^2_1 = 8.63^{**}$) between the numbers of grass and herb feeders and tree and shrub feeders benefiting from the drought. The contrast was probably much greater than this as the emphasis in this paper was on grass and herb feeding insects (72.0% of the species mentioned) and was aimed at recording the tremendous *decrease* in numbers resulting from the drought. As a result it is probable that many inconspicuous arboreal species which had increased or remained at "normal" levels of abundance were overlooked by the author.

Table 4.02

Influence of drought on abundance of insects in Vancouver Island during the summer of 1951.

(from Downes, 1956)

Type of Insect	No. spp. recorded	No. species decreasing in abundance by		Total decreasing	No. spp. maintaining "normal" abundance	No. spp. increasing in abundance	Total of "normal" & increasing
		70-90%	30-50%				
Grass and Herb Feeders	43	31	8	39	4	-	4
%	100.00	72.2	18.6	90.8	9.2	0.0	9.2
Tree and Shrub Feeders	17	6	3	9	5	3	8
%	100.00	35.2	17.6	52.8	29.4	17.7	47.1
Total spp.	60	37	11	48	9	3	12

5. AN INTERPRETATION OF THE CHANGES OF ABUNDANCE OF PHYTOPHAGOUS INSECTS;

5.0 Introduction

C. densitexta is an insect which, for most of the time and over most of its geographic distribution, is rare relative to the quantity of foliage apparently available as food. Occasionally local outbreaks occur, and less frequently an intense widespread outbreak may develop. When the psyllids continue to increase for several successive generations they become *very* common relative to the amount of foliage, and may eventually destroy most of it. If this happens, the psyllid again becomes rare (on a "per acre" basis, but not on a "per leaf" basis).

When the trees grow new leaves the psyllids may begin to increase again and may again become extremely abundant repeating the cycle; or they may fail to multiply on the new foliage, remaining rare relative to the amount of foliage, as they were before the outbreak began. Also the progress of an outbreak may be reversed at any stage, with the psyllids reverting to their characteristic of rareness relative to the amount of foliage. While the psyllids are increasing towards an outbreak "parasites" and predators* fail to make any effective impression on the numbers of the psyllid, not even after they have been continuously abundant for several years. A similar situation obtains for other lerp-forming psyllids in various

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* In future "parasitic" insects are included with other predators under the term "predator".

parts of Australia, and for a great many other species of insects feeding on the living tissue of plants (particularly perennials) in all parts of the world.

I have postulated that these observed major fluctuations of abundance are the result of changes in the amount of food available to the young stages of these insects, and that changes in abundance of food are in turn the result of changes in the pattern of rainfall, the application of stress to the plant from changes of moisture in the soil greatly increasing the amount of food available to the young insects.

5.1 The Role of Food in Changes of Abundance of Phytophagous Insects

Whether an animal eats the wood, leaves or sap of plants, or whether it eats part or all of other animals, it actually ingests only a "carrier" from which it must extract the nutrients it needs, and then discard the exhausted carrier. There is a physical limit to the total bulk of carrier that any animal can "process" in a given time and therefore both the proportion and concentration of the nutrients in the carrier will determine whether or not an animal can survive, and if so, the rate at which it can grow, and its general fitness for living and reproducing. The greater the concentration of nutrients in the carrier, the less of the latter need be processed by the animal, providing always that there is a "balanced diet" - that one or more essential nutrients are not scarce relative to the other constituents of the diet.

At one extreme of this "concentration gradient" are the internal hymenopterous "parasitic" larvae which defaecate only once at the end of the larval life. At the other extreme are the insects eating plant tissue - leaf eaters, sapsuckers, cambium-feeders - and all manner of filter-feeders all of which must pass large amounts of carrier through their bodies in order to obtain sufficient nutriment to survive and grow. It is these insects at the "starvation" end of the scale which are so susceptible to small changes in the concentration of the nutrients in the carrier. And this is why, for any young phytophagous insect which is processing the maximum amount of carrier per unit time that it is able, a small increase in the concentration of free amino acids in the plant tissue can change a scarcity of food to an abundance of food. In most cases sufficient amino acids will be available only locally, or seasonally, or at specific sites on the plant (see sect. 2.65). In the case of some species the plant on which they feed may always provide enough nitrogenous nutrients for most of the young to establish and survive through the first instar. But in the case of many other species the amount or distribution of these nutrients is such as to allow only a small fraction of the offspring to survive in each generation.

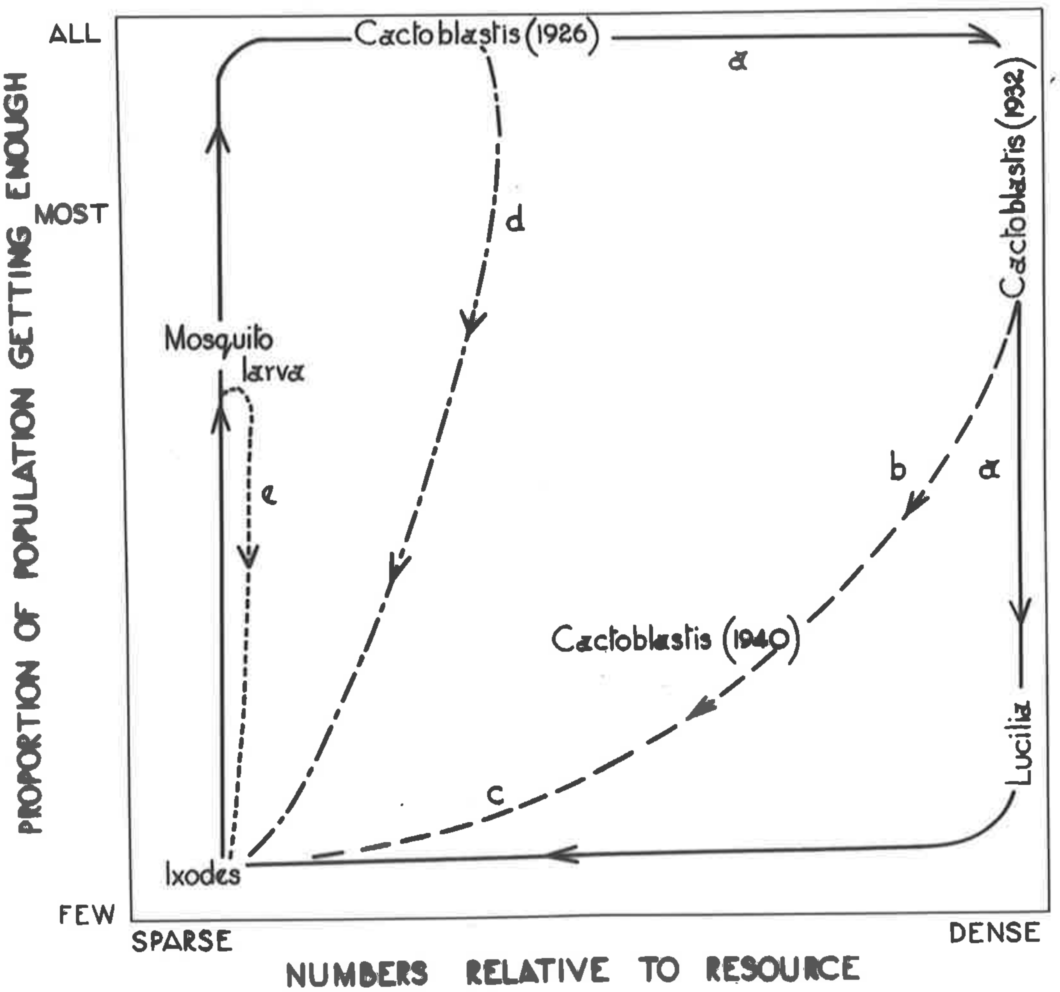
When, for any reason, the plant is stressed, the availability of these nutrients is increased and a greater proportion of young insects survive. When changes in the pattern of the weather cause soil-moisture to stress plants many plants over wide areas may simultaneously become sources of abundant nitrogenous food enabling the insect to increase to outbreak proportions. Insects which respond in this way are, like the mosquito larvae and Ixodes quoted by Andrewartha and Browning (1961) experiencing for most of the time, a relative shortage of food. It is not, as many authors have assumed, the common lot of these sorts of phytophagous insects to be surrounded by plenty of food that is entirely accessible to all of them; for many species this condition may pertain only during times when the plant is stressed. When a plant is stressed insects which benefit from the resulting increase of soluble amino acids will respond by moving from a position near the bottom left-hand corner of Andrewartha & Browning's "map" to near the top left-hand corner, i.e. they still remain sparse relative to the resource, but nearly all are now getting enough to eat (fig. 5.01). From here several things may happen depending on the duration and intensity of stress.

A. If this stress is maintained for longer than one generation, they will quickly move to the "Cactoblastis (1926)" position, and the longer that stress is maintained, the further they will move to the right, all getting enough to eat and becoming more and more dense relative to their food, until this is exhausted ("Cactoblastis (1932)" position). When this happens, the position changes rapidly in one of two ways:-

1. Where such a phytophagous insect is living (as in C. densitexta) on an "instantly" renewable resource, the position will move quickly

Figure 5.01

Interpretation of changes in abundance of phytophagous insects which respond to increased food supplies in stressed plants in terms of Andrewartha and Browning's (1961) "map". See text for explanation.


ALL
MOST
FEW
PROPORTION OF POPULATION GETTING ENOUGH
Cactoblastis (1926)
a
Cactoblastis (1932)
d
Mosquito larva
e
b
a
Cactoblastis (1940)
Lucilia
c
Ixodes
SPARSE
DENSE
NUMBERS RELATIVE TO RESOURCE

through the "Lucilia" position (most of the resource is destroyed and the animals become dense relative to the little food that remains) and back to the lower left-hand corner of the map as most of the animals die before new food grows (fig. 5.01a).

2. In the case of a phytophagous insect where exhaustion of the food also results in death of the whole plant (as happens with Cactoblastis), a position akin to "Cactoblastis (1940)" will be the end-point as long as stressful weather continues (fig. 5.01b), but will move back to the "Ixodes" position once stress is removed (fig. 5.01c).

B. When stress does not last long enough for such an insect to reach the stage of destroying all of its resources, the position returns rapidly (at the beginning of the next generation after the removal of stress) to the original position (fig. 5.01d).

C. In the event of stress being short-lived and insufficient to affect all parts of the plant, or because of the vagaries of the weather only some trees in a locality are stressed, more, but not all of the insects will get enough to eat for a short time (fig. 5.01e). There are an indefinite number of situations which may exist between e, d and a in figure 5.01, and vertical "movement" on this map is usually many times faster than horizontal "movement".

The relationship of C. densitexta to its food supply during times of stress of the foodplant is thus, in essence, identical to that of Cactoblastis cactorum to the Opuntia cacti when this moth was first introduced into Australia (Dodd, 1936). In both cases when a tremendous amount of food was suddenly made available to a species of insect with high powers of dispersal and rapid rate of increase, the insect increased in abundance until most of its source of food was destroyed, whereupon both insect and food became relatively scarce.

From this point the two cases differ only in the ability of the prey* to reproduce and disperse relative to the "predators" ability to do so. Opuntia must disperse and establish new colonies with seed, while Eucalyptus trees can replace their foliage in less time than it takes the psyllid to complete one generation - the Eucalypt's "power of increase"† is virtually instantaneous, whereas Opuntia only just keeps ahead of Cactoblastis.

Both insects are, in other words, pressing hard against the limits of their primary resource, food. Both are engaged in the intense struggle for existence against the passive resistance of a shortage of a resource. Any increase in this resource is immediately utilized and the insect increases in abundance quite independently of the activities of its predators.

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* For the purpose of the present ecological argument it is convenient to ignore the verbal distinction usually made between the food of a herbivore and that of a carnivore.

† "Power of increase" may be defined as the combination of all the intrinsic attributes of an organism which determine how effectively it can utilize the resources which are available to it.

It is food, therefore, which controls the upper limits of abundance of most (although not necessarily all) phytophagous insects. A relative shortage when the food plant is <u>not</u> subject to stress - an absolute shortage during times of persistent stress, or when, in cases where stress of the plant is not necessary for it to provide abundant food, the insect's power of increase is greater than that of the plant, when the insect destroys all, or virtually all of the available food.

At times when plants are not stressed by soil-moisture, certain parts of the plants will continue to provide an adequate source of food for some of the young insects settling on these parts (sect. 2.65).

There is, however, <u>no</u> competition for this limited supply of food. The only insects surviving will be those which, by chance, settle on tissue which is more nutritious than the surrounding tissue. The remainder will seek food in places where there is sufficient nutriment to stimulate them to continue feeding - but not enough for survival and growth - and will die.

This is the "common" or "usual" condition to which a great many such phytophagous insects would seem to be adapted. They must produce a super-abundance of offspring, and disperse them as widely as possible, in order to maintain a tenuous foothold on life - to find the few sites which will support them in a great sea of palatable inadequacy.

Thus the lower limits of abundance are also, in the final analysis, decided by these "refuges" of food during times of lack of stress on the host plant. The abundance and distribution of these refuges will fluctuate in a random manner, but there will always be some suppressed or damaged branches, and some overmature or injured trees providing these local refuges of stressed tissue no matter how long the stress index remains below zero.

5.2 The Role of Predators in Changes of Abundance of Phytophagous Insects

To ignore the part played by predators in the life cycle of a phytophagous insect, or to deny that they can and do influence the abundance of their prey - sometimes very strongly - would be foolish. I consider, however, that predators of those phytophagous insects which occasionally reach outbreak proportions but mostly remain rare in the midst of apparent plenty, do not control the increases and decreases in abundance of their prey. They merely "damp" the moderate increases in abundance, ceasing to have any but a negligible effect once the prey's food supply is no longer limiting. This is because they do not have a power of increase equal to or better than their prey when the latter's potential power of increase is given full expression. Their success depends upon the efficiency with which they can find and utilize the available food (prey). When their prey's power of increase is limited by shortage of its "prey" (the food in the plant) they are able to utilize nearly all of the available prey individuals because their power of increase is greater than the restricted power of increase of their food (prey). But once the prey has enough food to realize its full potential, the predators can no longer keep pace with it.

In other words a density-dependent relationship of predator and prey _may_ exist so long as the prey's _effective_ power of increase is less than the predator's _absolute_ power of increase. Beyond this point no such relationship exists (see Holling, 1959; and Solomon, 1964). This is why, so often, predators are observed not to have any measurable influence on a developing outbreak of a phytophagous insect. Later these same predators may be found to be "controlling" the outbreak, suddenly appearing in great numbers relative to their prey, and causing high mortality. What I believe happens at such times is that the prey's abundance is decreasing as a result of a reimposed lack of food, and the predator's numbers are simply "overriding" those of the declining population of the prey.

Clark (1964b) has formulated a general hypothesis - based essentially on the activities of predators - to explain the observed fluctuations in abundance of _C. albitextura_, a psyllid whose ecology is very similar in most respects to that of _C. densitexta_. He says there are two types of "agencies" operating in the environment of the psyllid: "conditioning" or "deciding" agencies, and "density governing" or "stabilising" agencies, and that "unless a sufficiently high number of psyllids died prematurely as a result of the influence of these [conditioning] agencies, stabilization could not occur".

Essentially his argument is that "probably the whole complex of species predacious upon the psyllid nymphs and eggs" keep the abundance of C. albitextura at a low level. "Unusually low temperatures reduce percentage parasitism" thus decreasing the premature mortality, causing the "stabilizing processes" to fail, and an outbreak to develop (see Clark, 1962 and 1964b, fig. 4, and discussion p. 378).

He is quite right in asserting that "stabilization" will not occur unless there is a large number of psyllids dying prematurely in each generation. But the only "conditioning agency" involved is a relative shortage of food - most of the newly hatched nymphs starve to death and leave little or no trace of their former presence (see sect. 2.642). If they normally fell prey to encyrtids their presence would be very obvious as they are almost fully grown when killed by these predators. By then they have built a full-sized lerp and killed a patch of leaf.

When species of Cardiaspina are at low levels of abundance in the field only single widely scattered nymphs are found, not the majority of each female's progeny established but parasitised by encyrtids, as would be expected if Clark's explanation was correct.

If in Clark's (1964b) figure 4 the line "density above which E. psyllae and Syrphus sp. attack" is relabelled "zero stress index", then this figure can be used as a fairly true diagram of what happens at one specific and uniform site just before and during a period of weather-induced stress on the host plant. Below the zero line the psyllid's abundance is determined by the availability of sites of adequate food and the effioiency of its predators. At such times there will not necessarily be any correspondence of these fluctuations in abundance with the stress index, because factors other than weather may be playing a dominant role in determining this abundance. Only when the stress index becomes positive can there be close agreement between these two varieties. If the index remains positive for long enough, the foliage is exhausted and the number of psyllids "crashes", so that the correspondence between population level and stress index is lost. With the growth of new foliage numbers of psyllids will again increase (Clark's fig. 4"b") if the index is still positive, or they may return to the original condition of scarcity if stress has been removed (Clark's fig. 4"a").

This figure does not illustrate the effects of a shorter period of positive stress, when the abundance of the psyllids would increase part of the way towards the upper limit of abundance (but not reaching the level of abundance that saturates the foliage and destroys most or perhaps all of it), and then fall back again once stress is removed, the predators meantime increasing "behind" it and then "overriding" it, and appearing to be behaving in terms of a "negative feedback mechanism" of density-dependent reduction of numbers to a predetermined mean.

Diseases - particularly virus diseases - are frequently recorded as terminating outbreaks of phytophagous insects. The concept of a latent virus being "activated" in insects which have been stressed by crowding and jostling is fairly generally accepted today; the usual interpretation being that disease is essentially "a density-dependent mortality factor" (Steinhaus, 1954).

But are such diseases the true cause of declining abundance, or are they merely symptoms of a decline already under way? Are disease organisms, like their host and its other predators, increasing in response to a change from a relative or absolute shortage to an abundance of food, and is this the result of a physiological change in the host insect caused by a change in its diet? Is the host insect stressed not by crowding, but by imbalance in its diet? Or is it actually starving and doomed to die anyhow, the disease merely hastening the process?

The fact that two outbreaks of a virus disease of S. suavis in New Zealand (sect. 4.321) appeared after the stress index declined, and at levels of abundance of the host which, although high, were not such as to result in any great amount of physical contact between larvae, suggests that something like this may indeed be true (Rawlings, 1963 & White, unpublished F.B.S. data).

The removal of stress and the consequent decline of food value could be making these insects restless and irritable in the same way as does crowding, thus causing an upset in their metabolism. Or it may be that dietetic imbalance or actual starvation is causing metabolic changes which favour multiplication of disease organisms.

The effect of dietary deficiencies or imbalance and of starvation on the metabolism of insects are known to be pronounced. There is a certain amount of contradictory evidence, but the general picture would seem to be that, along with the general loss of nutrient reserves, breakdown of protein takes place, considerably increasing the free amino acid content of the body (House, 1965; Sobetskii & Derzhavina, 1964).

It may be, on the other hand, that improved nutrition alone is sufficient to change the bodies of the insect host from a marginal to an optimal site for the proliferation of microorganisms. Hirano (1964) has shown that larvae of the rice stem borer fed on a synthetic diet high in protein have a much higher nitrogen content (particularly amino acids) than do those reared on a synthetic diet rich in carbohydrate, and that they are much more susceptible to infection by bacterial disease when removed to a diet of rice stems than are the ones from the carbohydrate diet. The induction of virus diseases is also known to be influenced by the nutrition and physiological condition of the insect host (Aruga, 1963). But it does seem that in nearly all cases some sort of "shock" - some stress of the insects - is necessary before any general outbreak of disease will occur.

It would then, seem reasonable to postulate that changes in stress of the plant may first provide an insect with better food, thus making it a better medium for the multiplication of microorganisms, and then administer the necessary "shock" to induce the actual proliferation of these microorganisms.

This is, of course, largely speculation, but the thought that the fluctuation of abundance of phytophagous insects and their predators (including microorganisms) might all be directly influenced by the action of weather upon the primary source of food, the plant, is an attractive one with its unifying implications not only in ecology, but in biology generally.

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